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1 **Canopy interactions and physical stress gradients in subtidal communities**

2

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36 design. All authors help with data collection and logistics. S.B wrote the manuscript with  
37 contributions from all authors.

38

39 **Abstract:**

40 Species interactions are integral drivers of community structure and change from negative to  
41 positive with increasing environmental stress in many ecosystems. In subtidal marine  
42 ecosystems, however, interactions along physical stress gradients have seldom been tested.  
43 We observed seaweed canopy interactions across depth and latitudinal gradients to test  
44 whether light and temperature stress structured interaction patterns. We also quantified inter-  
45 specific and intra-specific interactions among nine subtidal canopy seaweed species across  
46 three continents to examine the general nature of interactions in subtidal systems under low  
47 consumer pressure. We reveal that positive and neutral interactions are widespread  
48 throughout global seaweed communities and the nature of interactions can change from  
49 competitive to facilitative with increasing light stress in shallow marine systems. These  
50 findings provide support for the stress gradient hypothesis within subtidal seaweed  
51 communities and highlight the importance of canopy interactions for the maintenance of  
52 subtidal marine habitats experiencing environmental stress.

53

54 **Introduction:**

55 Species interactions can be important drivers of community structure and function (Kikvidze  
56 *et al.* 2005) from local and global scales (Cavieres *et al.* 2014) and have the capacity to buffer  
57 ecosystems against stressful environmental conditions that could otherwise lead to habitat  
58 loss or fragmentation (Bruno *et al.* 2003). Species interactions can change along physical and  
59 biotic stress gradients from competitive in benign conditions to become increasingly  
60 facilitative under stressful conditions, as the benefits of stress amelioration from neighbours  
61 begins to outweigh the costs of living together (SGH: Stress Gradient Hypothesis, Bertness &  
62 Callaway 1994). For terrestrial plants, the SGH has received strong empirical support across

63 a diverse range of communities from alpine plants to coastal salt marshes (e.g. Bertness &  
64 Ewanchuk 2002; Callaway *et al.* 2002) and across a range of physical, resource and biotic  
65 stress gradients (He *et al.* 2013). For subtidal marine plants (i.e. seaweeds and seagrasses),  
66 however, the nature of species interactions in response to changes to the physical  
67 environment are less well resolved (Bulleri 2009).

68 The physical environment has long been recognised as a strong driver of species interactions  
69 underwater (Kitching 1941; Reed & Foster 1984; Witman 1987; Dayton *et al.* 1999),  
70 however, few studies have examined whether the nature of species interactions change  
71 predictably in response physical stress gradients (Bulleri 2009). Among the few studies that  
72 have examined physical gradients, changes to abiotic conditions appear to have strong  
73 influence on the nature of interactions (Wernberg *et al.* 2010; Bulleri *et al.* 2011; Bennett &  
74 Wernberg 2014). Bulleri *et al.* (2011), for example demonstrated that the nature of  
75 interactions between tube building gastropods and seaweed was influenced by both physical  
76 (sediment deposition) and biotic (grazer density) gradients. Bennett and Wernberg (2014),  
77 while not examining stress gradients per se, demonstrated that canopy-recruit interactions  
78 became increasingly positive or remained positive along a latitudinal gradient.

79 To date, positive species interactions in subtidal communities have been primarily reported in  
80 response to high consumer pressure (Bulleri 2009) whereby chemical defences (Hay 1986;  
81 Stachowicz & Hay 1999), mechanical defences (Anderson *et al.* 1997) and physical barriers  
82 (Bennett *et al.* 2010) reduce the incidence of predation on beneficiary species. Other  
83 important drivers of positive interactions in subtidal communities include demographic  
84 constraints, (i.e. Allee effects), whereby population fitness displays positive density  
85 dependence (Berec *et al.* 2007) and resource availability, whereby benefactors can increase  
86 the nutrient availability for beneficiary species (Peterson & Heck 2001).

87

88 Physical gradients are prevalent in the subtidal, most notably from sunlight attenuation with  
89 depth (Duarte 1991), water velocity which decreases with depth and increases with wave  
90 exposure (Siddon & Witman 2003), and temperature which decreases with increasing depth  
91 and latitude (Smale & Wernberg 2009). While light is often considered to be a limiting  
92 resource underwater, excessive light can become stressful for organisms (Demmig-Adams &  
93 Adams Iii 1992), and therefore any modification of these conditions could promote  
94 facilitation. Within the photic zone, seaweed canopies are dominant habitat formers of  
95 benthic marine ecosystems globally and dramatically alter the physical environment for  
96 organisms living within them. Light levels are altered by all canopy types ranging from the  
97 surface canopies of the giant kelp, *Macrocystis pyrifera* (Reed & Foster 1984) to subsurface  
98 canopies of species such as *Ecklonia radiata* (Toohey *et al.* 2004). Water velocities are also  
99 modified by seaweed canopies, reducing the amount of drag an organism experiences by over  
100 80% in dense canopies (Johnson 2001). Under low flow velocities, individuals can grow  
101 larger, than in high flow areas (de Bettignies *et al.* 2013a) thereby providing a mechanism for  
102 subtidal canopies to promote facilitation in high-flow environments. Temperature conditions  
103 in contrast, while critical to the distribution and abundance of seaweeds(Lüning 1984) are  
104 assumed to be largely unaffected by subtidal canopy conditions due to the high mixing of  
105 seawater (Kordas *et al.* 2011). Nevertheless, dense shallow water canopies have been  
106 observed to reduce ambient temperatures, suggesting that temperature stress amelioration  
107 could occur in high density canopies (Critchley *et al.* 1990).

108 Here we test the nature of seaweed canopy interactions in subtidal marine ecosystems in  
109 response to depth and latitudinal gradients in light and temperature stress respectively. We  
110 also examine general patterns in the nature of canopy interactions under low consumer

111 pressure in the subtidal by observing inter-specific and intra-specific interactions among nine  
112 dominant canopy formers across three continents. This study advances our understanding of  
113 how subtidal canopies function under low consumer pressure and in response to increasing  
114 abiotic stress. In doing so, we broaden the generality of the stress gradient hypothesis to  
115 incorporate subtidal light climates and reveal widespread importance of positive canopy  
116 interactions in subtidal communities.

117

## 118 **Methods:**

### 119 *Depth experiment:*

120 Intra-specific interactions within kelp, *Ecklonia radiata*, canopies were measured along a  
121 depth gradient in Hamelin Bay, south-western Australia (34°S, 115°E), during Austral  
122 summer, December 2013 to February 2014. Nine reefs (sites) each separated by at least 1.8  
123 km, were chosen along a depth gradient (3, 5, 6, 9, 11, 12, 16, 18 and 19 m depth). Reefs in  
124 the region are exposed to relatively small tidal fluctuations (<0.5 m), meaning canopies can  
125 grow up to the surface and experience almost full sunlight conditions while remaining  
126 constantly submerged. At the other end of the spectrum, kelps in south-western Australia live  
127 down to 60-70 m depth where they grow as solitary individuals, but no longer form canopies  
128 due the limiting light availability (GAK, unpublished data). Reefs used in our study were in  
129 the upper third of kelp depth distribution where light is not a limiting resource, but could  
130 form a 'non-resource' stress gradient from benign deeper reefs (16-20 m) to stressful high-  
131 light shallow reefs (2-5 m). All reefs were dominated by dense, closed *Ecklonia radiata*  
132 canopies (7-11 sporophytes m<sup>-2</sup>, following Bennett & Wernberg 2014) and had relatively flat,  
133 'simple' topography (sensu Toohey *et al.* 2007). Within each site, 30 adult kelps were  
134 haphazardly selected and tagged around the stipe. Of those, 15 individuals were left to grow

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135 inside the unaltered canopy and 15 had all surrounding neighbours removed within a 1 m  
136 radius of the tagged kelp. Experimental setup was conducted by divers on SCUBA.  
137 Kelp productivity was measured over two months using the hole-punch method (Kirkman  
138 1984; de Bettignies *et al.* 2013b). Two holes were punched in the centre of the primary  
139 lamina, 5 cm and 10 cm above the junction between the stipe and the primary lamina. Thallus  
140 extension after the two months was quantified in the laboratory by measuring the distance  
141 between the two holes and the stipe-lamina-junction and subtracting the initial 10 cm  
142 distance. The kelp was then sliced into segments at 5 cm intervals along the length of the  
143 primary lamina, with each segment incorporating both primary lamina and lateral (secondary  
144 blades coming off the primary lamina) tissue. The segment with the greatest biomass in the  
145 first 30 cm above the meristem was used to calculate biomass accumulation (BA, or kelp  
146 productivity) as  $BA = L_{\text{ext}} \cdot W_F / 5T$  where  $L_{\text{ext}}$  is lamina extension (cm),  $W_F$  = fresh weight (g)  
147 of the heaviest segment and T is the number of growth days between punching the holes and  
148 collecting the kelp (de Bettignies *et al.* 2013b).

149 Differences in biomass accumulation patterns between plants with and without neighbours  
150 were converted to a Relative Interaction Index (RII, Armas *et al.* 2004) to compare the nature  
151 and intensity of interactions among sites of different depths. RII was calculated as  $RII =$   
152  $(BA_w - BA_o) / (BA_w + BA_o)$ , where  $BA_o$  = biomass accumulation ( $\text{g.FW.d}^{-1}$ ) without neighbours  
153 and  $BA_w$  = biomass accumulation with neighbours. The RII ranges between -1 and 1 and  
154 presents a continuous scale for competitive ( $-1 \leq x < 0$ ) and facilitative ( $0 \leq x < 1$ ) interactions  
155 that is symmetrical around zero. Patterns in RII along the depth gradient were analysed by  
156 comparing a set of polynomial models of degree = 1, 2, 3 using Akaike's Information  
157 Criterion (AIC). Linear regression (AIC = 55.5) and second order polynomial (AIC = 54.8)  
158 displayed the best relationship to the data and therefore linear results are presented as AIC  
159 values differ by less than 2 units between the models (Anderson 2008).



160 Kelp tissue ‘health’ was measured by quantifying the cover of epiphytic algal growth on the  
161 lower and upper laterals of each kelp. Epiphyte cover was quantified by haphazardly  
162 selecting four lower and four upper laterals from each replicate kelp and photographing them.  
163 Each image was then analysed by randomly allocating points to the image and counting the  
164 presence/absence of epiphytes under 15 random points on each lateral ( $n = 120$  points per  
165 kelp) using CPCe V4.1 software (Kohler & Gill 2006). Epiphyte counts on each lateral were  
166 then used to calculate the mean percent epiphyte cover per kelp.

167 At the end of the two month experimental period the physiological acclimation of the depth  
168 and canopy treatments to experimental conditions were measured by quantifying oxygen  
169 evolution of kelps using photorespirometry chambers *in situ* under their respective  
170 experimental settings. Photosynthetic rates were measured at ambient light levels *in situ*, and  
171 respiration rates were measured in the dark. A detailed description of the methods can be  
172 found in Appendix S1(a).

173 Temperature ( $^{\circ}\text{C}$ ) and illuminance (Lux) was measured *in situ* at 15 minute intervals in each  
174 site throughout the course of the experiment using data loggers (onset HOBO<sup>®</sup> data  
175 loggers Pendant Temp-Light, Onset Computer Corporation). Hobo pendant loggers provide  
176 light intensity measurements that accurately reflect photosynthetically active radiation (PAR)  
177 measurements taken in underwater marine environments, and enable cost effective  
178 deployment across multiple (18) experimental treatments (Long *et al.* 2012). At each site, one  
179 logger was attached to a dive weight and placed within the kelp canopy to record canopy  
180 conditions. A second logger was placed in the open adjacent to the canopy-free treatments.  
181 Daily minimum, maximum and mean temperatures for each site were extracted and averaged  
182 among days for the duration of the experiment to compare between depth and canopy  
183 treatments. For light, mean, maximum, and the standard deviation of light levels between the  
184 hours of 0800 – 1600 were extracted for the first 14 days of the experiment. Fouling on the

185 logger meant that recordings taken after this time were not representative of ambient  
186 conditions. Daily values were averaged among the first 14 days to compare among depth and  
187 canopy treatments. Variation in water velocities among sites was measured using  
188 gravitational data loggers (HOBO Pendant G, Onset Computer Corporation, Bourne, MA,  
189 USA) mounted on a hemispherical float (110 mm diameter) and attached to a 750 mm length  
190 of nylon rope (12 mm thickness) which was anchored to the bottom (Evans & Abdo 2010).  
191 The accelerometer was laid flat on the float such that only 2 channels were used (x,y) to  
192 account for horizontal acceleration (*cf.* H2O motion V2 design; Evans & Abdo 2010). The  
193 logger was set to record the acceleration ( $\text{ms}^{-2}$ ) at 2 minute intervals over the duration of the  
194 experiment. At each site the relative water movement (WM) was expressed as the mean of  
195 the 95th percentile WM over the duration of the experiment.

196 Kelp productivity, mean epiphyte cover, temperature and light conditions were compared  
197 between canopy treatments along the depth gradient using an Analysis of Covariance  
198 (ANCOVA) with ‘canopy-treatment’ as a categorical grouping factor (two levels: with and  
199 without canopy) and depth as a continuous covariate. Epiphyte cover data was arcsine-square  
200 root transformed to address the non-normality and heteroscedasticity of the data, after  
201 examining the residual vs fitted value plot and the Q-Q plot. Productivity, temperature and  
202 light all met assumptions of normality and homoscedasticity and no transformations took  
203 place.

204

205 *Latitudinal experiment:*

206 Latitudinal comparisons of intra-specific interactions took place along a  $\sim 2^\circ\text{C}$  temperature  
207 gradient in south-western Australia, on two occasions during Austral spring (August –  
208 October 2012) and summer (January - March 2013), representing the periods of highest kelp  
209 growth rates and temperature stress respectively (de Bettignies *et al.* 2013b). Interaction

210 experiments were conducted at nine sites (9-12m depth) across three locations, Hamelin Bay  
211 (34°S), Marmion (32°S) and Jurien Bay (30°S), spanning the warmest third of *E. radiata*'s  
212 latitudinal distribution in Australia (~43°S - 29°S). This north-south trending coastline is  
213 characterised by the warm poleward flowing Leeuwin current, consistent limestone habitat,  
214 low nutrient conditions and a stable ocean climate gradient (Smale & Wernberg 2009).  
215 Within each site, kelp productivity, RII and environmental measurements in canopy and  
216 canopy-free treatments were recorded as described for the depth experiment. Tissue health  
217 was quantified for the summer sampling period only, by estimating the percentage cover on 4  
218 replicate laterals from each of the lower, middle and upper sections of each kelp. Patterns in  
219 RII between spring and summer, across the latitudinal gradient were examined with an  
220 ANCOVA, using time as a fixed factor (two levels: spring and summer) and latitude as a  
221 continuous covariate. ANCOVA assumptions were checked as described for the depth  
222 experiment and no transformation took place. Mean epiphyte cover on kelps was compared  
223 between canopy treatments along the latitudinal gradient using an ANCOVA with 'canopy-  
224 treatment' as a categorical grouping factor (two levels: with and without canopy) and latitude  
225 as a continuous covariate. Epiphyte cover data was arcsine-square root transformed to  
226 address the non-normality and heteroscedasticity of the data.

227

#### 228 *Nature of interactions among different canopy types*

229 The nature of inter-specific and intra-specific interactions among different subtidal canopy  
230 species experiencing low consumer pressure were tested for nine dominant canopy species (4  
231 kelps and 5 fucoids) from Australia, South Africa, Norway and France (Table S1). Sites  
232 varied dramatically between regions ranging from shallow (3 – 4 m) tropical *Sargassum* beds  
233 in Australia, to deeper (10 – 12 m) cool temperate kelp forests in Norway (Table S1). Sites

234 were selected that had dense closed seaweed canopies and low herbivore consumer pressure  
235 (Appendix S1b, Fig. S1, Table S2). Intra-specific interaction strength was tested by  
236 haphazardly selecting and tagging 30 plants, of which 15 individuals were left to grow inside  
237 the canopy and 15 had the surrounding canopy removed, by clearing a circular area around  
238 the tagged seaweed as described for the depth experiment. Clearing sizes varied in  
239 accordance with the size of the seaweed, ensuring that no contact or shading by the canopy  
240 occurred. Inter-specific interactions using *Laminaria pallida* and *Sargassum decurrens* as  
241 beneficiary species were tested using the same methodology described for intra-specific  
242 interactions. Inter-specific interactions using *Ecklonia radiata*, *Scytothalia dorycarpa*,  
243 *Arthrophyucus* and temperate *Sargassum* sp. as beneficiaries were conducted by translocating  
244 individuals into the desired canopy and canopy-free treatments due to low natural densities in  
245 the study sites. All translocations occurred within the same site and depth contour from which  
246 they were collected, without removing the seaweed from the water (Appendix S1c). For both  
247 inter-specific and intra-specific interactions kelp (*Ecklonia radiata*, *E maxima*, *Laminaria*  
248 *pallida* and *L. hyperborea*), productivity rates were measured using the hole-punch method  
249 and converted to RII as described for the depth experiment. For the five furoid species  
250 (temperate *Scytothalia dorycarpa*, *Arthrophyucus* sp and *Sargassum* sp, tropical *S. illicifolium*  
251 and *S. decurrens*) net growth rates were determined by measuring the length (L) and  
252 circumference (C) of tagged individuals at the beginning and end of the experiment, and  
253 converting the measurement to fresh weight ( $W_F$ ) using the equation  $W_F = LC^2$  (following  
254 Aberg 1990). Each individual was also collected at the end of the experiment and weighed in  
255 the laboratory to the nearest 0.1 g to calibrate the biomass conversion model for each species  
256 (Fig. S2). A detailed description of the site and species specific methods can be found in  
257 Appendix S1(c).

258

259 **Results:**

260 *Depth comparison of intra-specific interactions*

261 Intra-specific interactions between *Ecklonia radiata* and the canopy changed from net  
262 competitive to facilitative from deep to shallow along a 20 m depth gradient ( $F_{1,7} = 7.32$ ,  $p =$   
263  $0.030$ , adjusted  $R^2 = 0.442$ ; Fig. 1A). In sites deeper than 8 m, kelp biomass production was  
264 generally higher in canopy-free treatments, whereas shallower than 8 m biomass production  
265 was consistently higher within the canopy (Fig. S3). This transition in productivity was  
266 coupled with a dramatic increase in epiphyte loading in shallow canopy-free treatments ( $73.2$   
267  $\pm 9$  % of total thallus area) compared to shallow canopy treatments ( $2.1 \pm 0.6$  % of total  
268 thallus area) and all deep treatments (Fig. 1B; Table 1). Interestingly, after the two month  
269 experimental period, short term photosynthesis and respiration rates measured in the  
270 photorespirometry chambers resulted in positive RII in five out of seven sites tested, with  
271 deep sites recording the highest RII values (Fig. S4A). Large differences in interaction  
272 strength (RII) in deep sites were driven by high photosynthetic rates and low respiration in  
273 canopies compared to canopy-free treatments (Fig. S4B,C). In shallow sites, photosynthetic  
274 rates were higher than expected for canopy-free treatments, which may be attributable to the  
275 dense epiphytic cover growing on the thallus of canopy-free kelps.

276 Both light and temperature significantly increased with decreasing depth, however only light  
277 was consistently modified by the canopy and represented a stress gradient per se (He &  
278 Bertness 2014, Fig. 1C - D, Table 1). Shallow canopy-free treatments had ten-fold higher  
279 mean light levels ( $14,408 \pm 780$  Lux) than shallow canopy treatments ( $1352 \pm 329$  Lux), and  
280 four-fold higher levels than deep canopy-free treatments ( $3673 \pm 164$  Lux). This pattern was  
281 also consistent for maximum daily illuminance and standard deviation in daily illuminance  
282 (Fig. S5). Temperature conditions by contrast changed more uniformly with depth in both

283 canopy and canopy-free treatments. Canopy treatments had significantly lower temperatures  
284 than canopy-free treatments, but the difference was not uniform among sites, and small  
285 (maximum difference between canopy and canopy-free treatments = 0.29°C, mean difference  
286 = 0.07°C ± 0.04°C) in comparison to temperature differences along the depth gradient  
287 (maximum difference between depths = 0.73°C, Fig. 1D, Table 1). Furthermore the  
288 temperature gradient was relatively benign compared to the seasonal temperature range  
289 experienced by kelps in the area (16-23°C) and is therefore not considered to represent a  
290 stress gradient per se. No clear depth pattern in relative WM was observed among the nine  
291 sites. Mean 95th percentile relative WM in both shallow and deep sites was between 4 – 6  
292 ms<sup>-2</sup>, whereas the intermediate depths recorded between 6 – 9 ms<sup>-2</sup> (Fig. S6).

293

#### 294 *Latitudinal comparison*

295 Intra-specific interactions along the latitudinal gradient revealed predominantly positive  
296 interactions across all latitudes and did not display a significant difference in interaction  
297 strength among latitudes during either spring (p = 0.168, adjusted R<sup>2</sup> = 0.145) or summer (p =  
298 0.269 adjusted R<sup>2</sup> = 0.052, Fig. 2A, Fig. S6). Epiphyte cover varied among latitudes, but not  
299 in accordance with the latitudinal differences in temperature (Fig. 2B - C, Table 2).  
300 Consistent with long term profiles, summer temperatures were warmer at 32°S and 30°S than  
301 34°S, but did not consistently vary between canopy and canopy-free treatments (Fig. 2C,  
302 Table 2). Despite differences in temperature among latitudes, nutrient levels remained  
303 relatively constant (NO<sub>3</sub> concentrations = 0.8 – 1.5 μmol L<sup>-1</sup>) across all nine sites (Fig. S8).  
304 Light levels did not vary among latitudes but as in the depth experiment, mean illuminance  
305 under the canopy was significantly lower than in canopy-free treatments (Fig. 2D, Table 2).

306 Patterns in light and temperature were consistent among mean, maximum, minimum  
307 (temperature only) and standard deviation (light only) measurements (Fig. S9 and S10).

308

### 309 *Generalities in intra-specific and inter-specific interactions*

310 Examining the nature of subtidal canopy interactions under low consumer pressure, across  
311 dominant species from around the world, revealed that positive and neutral interactions were  
312 widespread. Growth rates of seaweeds within the canopy were higher than canopy-free  
313 growth rates, resulting in net positive intra-specific interactions for five of the six species  
314 tested including three temperate kelp species from Australia (*E. radiata*) and South Africa (*E.*  
315 *maxima* and *L. pallida*), and temperate and tropical furoids (subgen. *Sargassum* sp. and  
316 *Sargassum illicifolium*, respectively; Fig. 3). *Laminaria hyperborea*, in populations from both  
317 France and Norway, was the only species to show net competitive intra-specific interactions.

318 Facilitation was less pronounced among inter-specific interactions in seaweed canopies.  
319 Productivity rates of kelp (*L. pallida*) and temperate furoids (*Scytothalia dorycarpa*,  
320 *Arthrophyucus* sp. and *Sargassum* sp.) species growing within kelp canopies displayed neutral  
321 interactions. In contrast, kelp, *E. radiata*, displayed positive interactions within temperate  
322 *Sargassum* sp. canopies while *Sargassum decurrens*, displayed net competitive interactions in  
323 tropical *Sargassum illicifolium* canopies (Fig. 3).

324

### 325 **Discussion**

326 Our results revealed that positive and neutral canopy interactions are common within global  
327 seaweed communities and that the nature of interactions can change in response to physical  
328 stress gradients in subtidal marine ecosystems where consumer pressure is low. Under benign

329 light conditions below 8 m depth, canopy interactions were primarily competitive or neutral,  
330 whereas under shallow, high-light conditions seaweeds became increasingly facilitated by the  
331 canopy. These findings provide support for the SGH and the first example along a light-stress  
332 depth gradient as far as we are aware. In contrast, interaction strength stayed predominantly  
333 positive and did not change along a latitudinal temperature gradient. While these findings do  
334 not support the SGH, they do not contradict it either, as canopy treatments were unable to  
335 consistently lower temperature conditions and alleviate temperature stress. These results  
336 were, however, consistent with interactions among nine dominant subtidal canopy species  
337 from around the world, where facilitation was the most common outcome of intra-specific  
338 interactions.

**Commentaire [sb3]:** Discuss importance of Allee effects in driving these patterns?

339

340 Light is a fundamental resource for plants and attenuates with depth in the ocean, limiting the  
341 vertical distribution of seaweeds. In the upper depths of the ocean however, light is not a  
342 limiting resource, and high-light levels can act like a non-resource stress gradient (*cf* resource  
343 gradient; Maestre *et al.* 2009) whereby photosynthetically active radiation exceeds saturating  
344 levels and ultra violet radiation can penetrate the water column and potentially damage kelp  
345 tissue (Wood 1987). The reduction of high-light conditions within the canopy at shallow  
346 depths appears to be fundamentally important to the health and productivity of seaweed  
347 canopies. As light attenuates toward deeper depths, the dependence on neighbours reduces  
348 and interactions were observed to become neutral to competitive. Given canopies can only  
349 reduce light levels, not increase them, it would be expected that below the depths observed  
350 here, interactions would continue to become increasingly competitive as light becomes  
351 limiting toward a species vertical distribution limit. Our findings are consistent with previous  
352 studies that examined recruitment patterns in response to canopy shading and observed



353 primarily competitive interactions in depths between 10-18 m where canopy shading effects  
354 were similar to those observed here (Dayton *et al.* 1984; Reed & Foster 1984).

355 While light conditions appear to be the dominant driver of interaction patterns, other non-  
356 stressful environmental gradients (*sensu* He & Bertness 2014) were present and may have  
357 partially contributed to the nature of interactions. All depths experienced relatively high wave  
358 exposure, and no clear pattern between depth and water velocities were observed, suggesting  
359 that water velocity cannot explain the observed change in interactions with depth.

360 Nevertheless, the presence of a canopy can reduce drag on a thallus by over 80 %, compared  
361 to a solitary individual (Johnson 2001) enabling canopy kelps to attain greater size than  
362 solitary individuals in wave exposed areas (de Bettignies *et al.* 2013a), potentially promoting  
363 facilitation. Water movement also influences physical scour from the canopy and is likely to  
364 reduce the settlement and growth of epiphytes on kelp in the canopy. Interestingly, despite  
365 high wave exposure, temperatures changed both across the depth gradient and between  
366 canopy treatments, with slightly cooler temperatures recorded inside the canopy at some sites.  
367 Temperature differences among canopy treatments were, however, small in comparison to  
368 differences among depths and very small relative to the temperature range of *E. radiata*. In  
369 isolation, therefore, temperature cannot explain the interaction patterns observed along the  
370 depth gradient.

371 Temperature also did not modify interaction patterns along the latitudinal temperature stress  
372 gradient, with positive interactions prevailing at five out of the six latitudinal trials. These  
373 observations are consistent with canopy-recruit interactions observed for *Scytothalia*  
374 *dorycarpa* in the same region, however differ from canopy-recruit interactions for *Sargassum*  
375 sp. and *Ecklonia radiata* which have been observed to change from competitive to facilitative  
376 in response to latitudinal temperature gradients (Wernberg *et al.* 2010; Bennett & Wernberg  
377 2014). It remains unclear why some recruits change the nature of their interaction with the

378 canopy along temperature gradients while adults do not, particularly given we observed that  
379 canopies did not modify temperatures sufficiently to reduce thermal stress. These results  
380 suggest that a combination of processes (i.e. light and temperature stress) can interact to  
381 determine interaction patterns in subtidal canopies (Wernberg *et al.* 2010), and that there may  
382 be ontogenetic changes in the nature of interactions within canopy species (He & Bertness  
383 2014).

384 In subtidal systems elsewhere, combined effects of warm temperatures and low nutrients  
385 have been shown to influence kelp interactions. The recovery of the competitively dominant  
386 giant kelp, *Macrocystis pyrifera* following storm events depends on low-frequency cycles in  
387 nutrient and temperature conditions in response to the El Niño Southern Oscillation, which in  
388 turn influences the recruitment and abundance patterns of subordinate kelp species (Dayton *et*  
389 *al.* 1999). *M. pyrifera* canopies have also been adversely affected by warm temperatures and  
390 low nutrient conditions in south-eastern Australia (Johnson *et al.* 2011), but *E. radiata*  
391 canopies have not, suggesting that *E. radiata* canopies may be more tolerant of low nutrient  
392 conditions than *M. pyrifera*. High rates of canopy erosion (*c.f.* dislodgement in *M. pyrifera*)  
393 could increase nutrient supply within canopies, thereby supplementing local nutrient  
394 conditions within the canopy and promote facilitation (de Bettignies *et al.* 2013b). It is  
395 unclear whether the small-scale clearings used in our experiment, were large enough to  
396 modify local nutrient availability, nevertheless the North American example illustrates that  
397 multiple stressors can influence the nature of interactions and may help explain the variable  
398 responses observed along the temperature gradient.

399 The consistent pattern of neutral to positive interactions of *Ecklonia radiata* among latitudes  
400 agrees with observed global interaction patterns, where positive and neutral interactions were  
401 found to be widespread among multiple subtidal canopy types that experience low consumer  
402 pressure. Among the kelp species observed, *Laminaria hyperborea* in the North Atlantic was

403 the only species to display negative interactions with the canopy, whereas Australian and  
404 South African kelps displayed primarily positive interactions. Light availability may have  
405 contributed to these patterns as French reefs in particular were generally deeper and had  
406 lower light (due to turbidity) than canopies observed in Australia and South Africa. Life  
407 history traits may also help to explain the observed interaction patterns, particularly for  
408 *Sargassum* which displayed competitive inter-specific interactions within the kelp canopy.  
409 *Sargassum* has a buoyant thallus that has adapted to fragment easily as a means of propagule  
410 dispersal (Schiel & Foster 2006). Fragmentation of *Sargassum* by the abrasive canopy might  
411 have contributed to the lower net biomass production of *Sargassum* within the canopy, yet  
412 may assist its dispersal and reproductive success.

413 In addition to contemporary environmental processes influencing interactions, the stability of  
414 canopies over evolutionary time scales may contribute to the prevalence of positive  
415 interactions, particularly in southern Australia. Modern canopy seaweeds (orders  
416 Laminariales and Fucales) evolved during the Miocene (Silberfeld *et al.* 2010), since which  
417 time the marine climate of southern Australia has been remarkably stable (McGowran *et al.*  
418 1997). While the diversification of Australia's marine flora was likely to have begun prior to  
419 the arrival of canopy species (Hommersand 1986), the long climatically stable history of  
420 seaweed canopies in Australia and their dense cover on reefs is likely to have favoured  
421 adaptations among canopy and understory seaweeds to thrive within canopy conditions.

422 Collectively, our findings highlight that canopy interactions may have an important influence  
423 on the response of subtidal habitats to physical stress. Kelp forests are often thought to be  
424 resilient to disturbance due to their fast growth rates and rapid colonisation of space (Dayton  
425 *et al.* 1984; Steneck *et al.* 2002). Our results suggest that many seaweed communities may in  
426 fact be dependent on the surrounding canopy to ameliorate stressful abiotic conditions. On  
427 shallow reefs canopy loss could result in high-light conditions that inhibit kelp recovery,

428 providing a positive feedback mechanism that reinforces a canopy-free state. Such scenarios  
429 may become increasingly common under climate change and may help to explain subtidal  
430 community changes, as were observed following a decline in seaweed canopy cover in  
431 Western Australia in response to an extreme marine heatwave (Wernberg *et al.* 2013).  
432 Understanding the role of other abiotic stress gradients (i.e. wave exposure) and the additive  
433 or synergistic effects of multiple stressors on interactions in the subtidal will help to improve  
434 our understanding and management of subtidal communities in the face of such global  
435 changes. The stress gradient hypothesis provides a useful concept to address these questions  
436 and has been underutilised in subtidal ecology to date (Bulleri 2009). Our results reveal that  
437 neutral to positive canopy interactions are widespread throughout subtidal ecosystems  
438 globally and may be critical to reduce high-light stress in shallow subtidal marine systems.  
439 Positive canopy interactions may represent an important process, sustaining the health and  
440 function of seaweed communities in the face of rapid changes to the physical environment in  
441 coastal marine ecosystems

**Commentaire [sb4]:** Suggestions  
welcome for better concluding sentence

442

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639

640 **Figure captions**

641 **Figure 1:** Nature of intra-specific interactions of *Ecklonia radiata* along a subtidal depth  
642 gradient from 3 – 19m. A) Relative Interaction Index (RII) of *E. radiata* based on mean  
643 productivity rates with and without canopy. Positive values from 0 to 1 indicate increasingly  
644 facilitative net interactions and negative values from 0 to -1 indicate increasingly competitive  
645 net interactions. B) Comparison of kelp health based on mean epiphytic cover of secondary  
646 laterals after the two month experimental period with (dark grey) and without (open) canopy  
647 (n = 10 kelps per treatment). C) Mean light illuminance recorded with and without canopy  
648 between the hours 0800 – 1600 for 14 days among the different depths. D) Mean, maximum  
649 and minimum temperatures recorded with and without canopy over the 2 month experimental  
650 period among the different depths

651

652 **Figure 2:** Nature of intra-specific interactions of *Ecklonia radiata* among nine sites along a  
653 subtidal latitudinal gradient from 34°S – 30°S. A) Relative Interaction Index (RII) of *E.*  
654 *radiata* based on mean productivity rates with and without canopy. Positive values from 0 to  
655 1 indicate increasingly facilitative net interactions and negative values from 0 to -1 indicate

656 increasingly competitive net interactions. B) Comparison of kelp health based on mean  
657 epiphyte cover of secondary laterals after the two month experimental period with (dark grey)  
658 and without (open) canopy (n = 10 kelps per treatment). C) Mean temperatures recorded with  
659 and without canopy over the 2 month experimental period among the different latitudes D)  
660 Mean light illuminance recorded with and without canopy between the hours 0800 – 1600 for  
661 14 days among the different latitudes.

662

663 **Figure 3:** Patterns in intra-specific and inter-specific interactions between dominant subtidal  
664 benthic habitat forming species from around the world. Positive values from 0 to 1 indicate  
665 increasingly facilitative net interactions and negative values from 0 to -1 indicate increasingly  
666 competitive net interactions. Numbers underneath the species name indicate the number of  
667 replicate sites where each interaction type was measured. Sites range between 6-12 m depth  
668 except tropical *Sargassum* sites which were recorded in 3-4 m depth (Table S1).

669

670

671

672 **Table 1:** Results of ANCOVA models comparing A) Productivity, B) Epiphyte cover, C)  
 673 Illuminance and D) Temperature, between canopy treatments along the depth gradient.  
 674 Epiphyte cover was arcsin-square root transformed and illuminance was log10 transformed.

675

<b>Productivity</b>	<b>Estimate</b>	<b>Std. Error</b>	<b>t value</b>	<b>Pr(&gt; t )</b>
(Intercept)	3.14928	0.361	8.722	<b>0.000</b>
Canopy treatment (CT)	-0.816	0.515	-1.583	0.115
Depth	-0.030	0.029	-1.028	0.305
CT:Depth	0.089	0.042	2.133	<b>0.034</b>
<b>Epiphyte cover</b>	<b>Estimate</b>	<b>Std. Error</b>	<b>t value</b>	<b>Pr(&gt; t )</b>
(Intercept)	0.156	0.062	2.530	<b>0.013</b>
Canopy treatment (CT)	0.784	0.091	8.589	<b>0.000</b>
Depth	-0.006	0.005	-1.170	0.244
CT:Depth	-0.051	0.008	-6.506	<b>0.000</b>
<b>Illuminance (Lux)</b>	<b>Estimate</b>	<b>Std. Error</b>	<b>t value</b>	<b>Pr(&gt; t )</b>
(Intercept)	2.888	0.061	47.429	<b>0.000</b>
Canopy treatment (CT)	1.446	0.083	17.443	<b>0.000</b>
Depth	-0.036	0.005	-7.024	<b>0.000</b>
CT:Depth	-0.005	0.007	-0.737	0.462
<b>Temperature (°C)</b>	<b>Estimate</b>	<b>Std. Error</b>	<b>t value</b>	<b>Pr(&gt; t )</b>
(Intercept)	21.394	0.074	290.516	<b>0.000</b>
Canopy treatment (CT)	0.222	0.100	2.219	<b>0.027</b>
Depth	-0.032	0.006	-5.193	<b>0.000</b>
CT:Depth	-0.015	0.008	-1.908	0.057

676

677

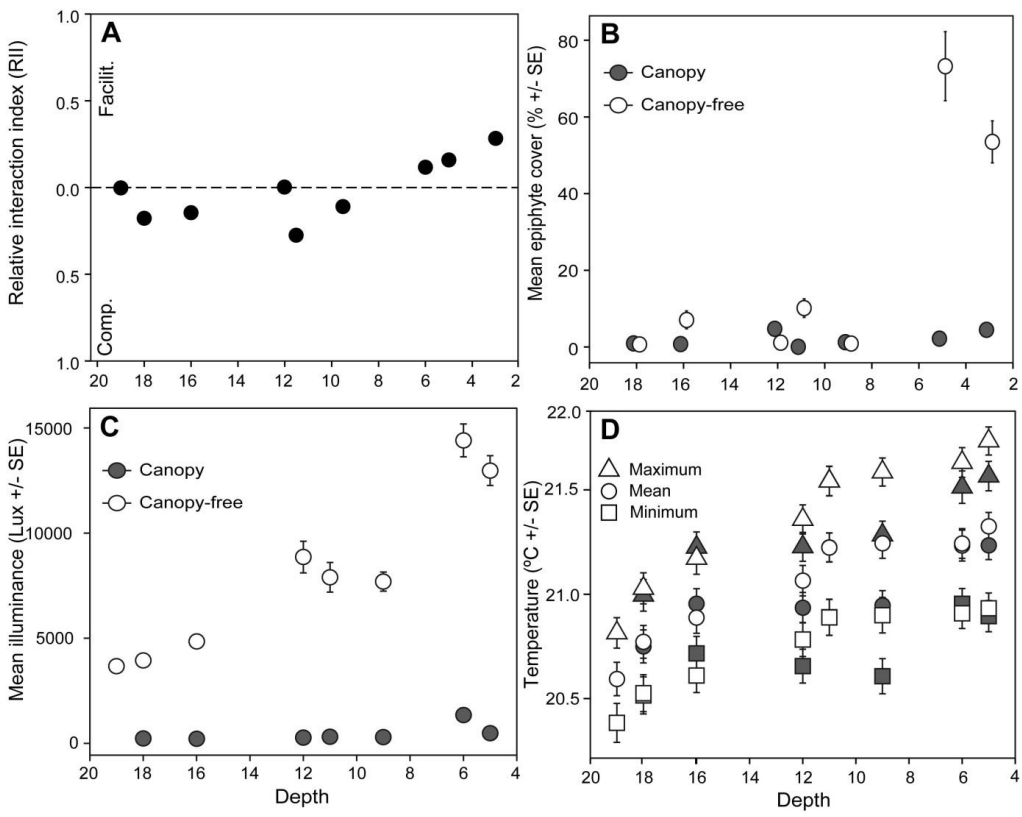
678 **Table 2:** Results of ANCOVA models comparing A) Relative interaction index between  
679 seasons along a latitudinal gradient, B) Epiphyte cover, C) Illuminance and D) Temperature,  
680 between canopy treatments along a latitudinal gradient. Epiphyte cover was arcsin-square  
681 root transformed and illuminance was square root transformed.

<b>RII</b>	<b>Estimate</b>	<b>Std. Error</b>	<b>t value</b>	<b>Pr(&gt; t )</b>
(Intercept)	0.956	0.935	1.022	0.325
Season	-0.026	1.322	-0.020	0.985
Latitude	-0.026	0.029	-0.876	0.397
Season:Latitude	-0.003	0.041	-0.085	0.934
<b>Epiphyte cover</b>	<b>Estimate</b>	<b>Std. Error</b>	<b>t value</b>	<b>Pr(&gt; t )</b>
(Intercept)	1.018	0.262	3.892	<b>0.000</b>
Canopy treatment (CT)	-0.523	0.374	-1.400	0.163
Latitude	-0.024	0.008	-2.918	<b>0.004</b>
CT:Latitude	0.018	0.012	1.553	0.122
<b>Illuminance (Lux)</b>	<b>Estimate</b>	<b>Std. Error</b>	<b>t value</b>	<b>Pr(&gt; t )</b>
(Intercept)	52.198	25.324	2.061	<b>0.040</b>
Canopy treatment (CT)	103.286	35.813	2.884	<b>0.004</b>
Latitude	1.177	0.790	1.490	0.138
CT:Latitude	1.600	1.118	1.431	0.154
<b>Temperature (°C)</b>	<b>Estimate</b>	<b>Std. Error</b>	<b>t value</b>	<b>Pr(&gt; t )</b>
(Intercept)	37.012	0.658	56.289	<b>0.000</b>
Canopy treatment (CT)	-0.761	0.930	-0.819	0.413
Latitude	0.425	0.021	20.565	<b>0.000</b>
CT:Latitude	-0.026	0.029	-0.888	0.375

682

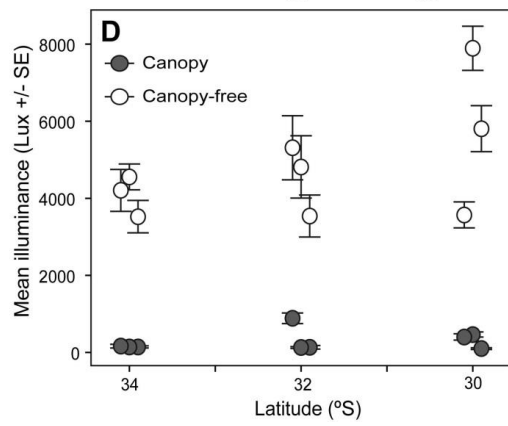
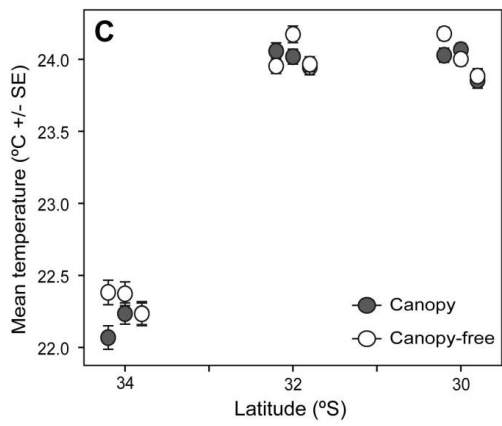
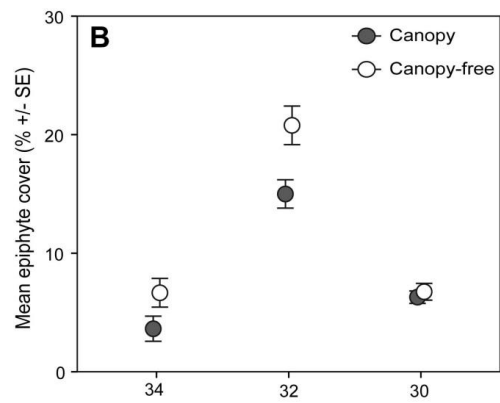
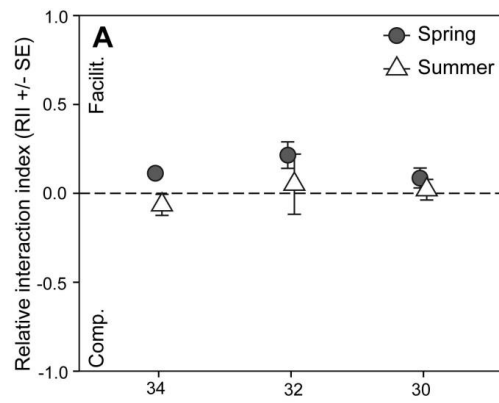
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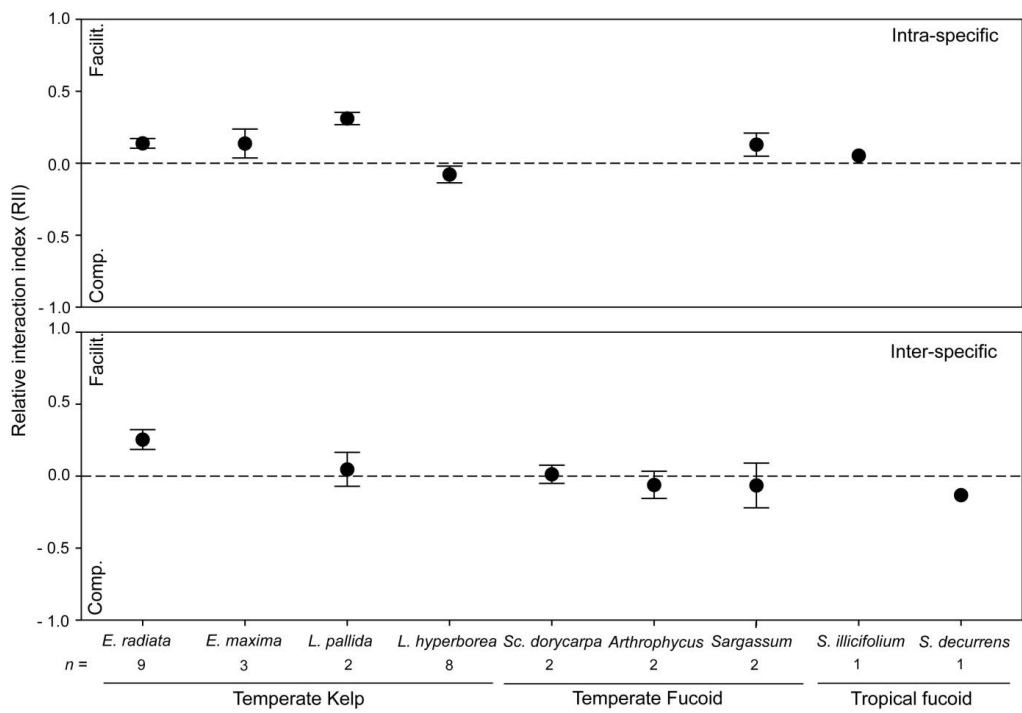
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