

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

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Summary

1. Theoretical and empirical ecology has transitioned from a focus on the role of negative interactions in species coexistence to a more pluralistic view that acknowledges that coexistence in natural communities is more complex, and depends on species interactions that vary in strength, sign, and reciprocity, and such contexts as the environment and life-history stage.

2. We used a whole-community approach to examine how species interactions contribute to the maintenance of a rocky intertidal macroalgal canopy–understorey assemblage. We determined both the types of interactions in this network, and whether interactions were sensitive to environmental gradients.

3. Focusing on a structurally dominant canopy kelp *Saccharina sessilis*, and its diverse co-occurring understorey assemblage, we evaluated the role of the understorey in controlling *S. sessilis* recruitment and quantified the reciprocal effect of the *S. sessilis* canopy and understorey on one another using a removal experiment replicated across 600 km of coastline. We determined the sensitivity of interactions to natural variation in light and nutrient availability (replicated among four regions on the N.E. Pacific coast), and under different wave conditions (three wave regimes).

4. Surprisingly, species interactions were similar across sites and thus not context-dependent. Unexpectedly, the understorey community had a strong positive effect on the *S. sessilis* canopy, whereby the adult canopy decreased dramatically following understorey removal. Additionally, *S. sessilis* recruitment depended on the presence of understorey coralline algal turf. In turn, the canopy had a neutral effect on the coralline understorey, but a negative effect on non-calcifying algal turfs, likely eventually generating positive indirect canopy effects on the coralline understorey. Density-dependent intraspecific competition between *S. sessilis* adults and recruits may moderate this positive feedback between the *S. sessilis* canopy and coralline understorey.

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

Key-words: aquatic plant ecology, benthic, environmental gradients, macroalgae, marine, plant-plant interactions, positive interactions

Introduction

A longstanding goal of community ecologists has been to reconcile the patterns of species diversity within communities with the mechanisms that promote coexistence. At local

scales, competition has the potential to decrease species diversity in favour of a competitive dominant (Chesson 2000), but decades of research on other species interactions have illuminated the role of consumers (Caswell 1978), positive interactions (Hacker & Gaines 1997; Bruno, Stachowicz & Bertness 2003; Thomsen *et al.* 2010) and indirect effects (Paine 1966; Wootton 1994) in promoting coexistence. Positive interactions, specifically, have gained attention with the recognition

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that they can promote coexistence in diverse communities, both empirically (Verdú & Valiente-Banuet 2008; Cerfonteyn *et al.* 2011) and theoretically (Gross 2008; Kéfi *et al.* 2012). In practice, however, positive and negative interactions may not be easily disentangled, and feedbacks between different types of interactions within a diverse network complicate our understanding of species coexistence.

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

In the rocky intertidal of the north-east Pacific, the low zone is occupied primarily by macrophyte communities, with the kelp *Saccharina sessilis* (C. Agardh) Kuntze (henceforth *S. sessilis* or 'kelp canopy') often forming a dense, monospecific canopy that overlies a diverse mosaic of understory algae and invertebrates (Dayton 1975). Despite the presence of several other kelp species in the low intertidal, *S. sessilis* is often the 'ecological dominant' (Dayton 1975), both in terms of its abundance and its deterministic return to dominance after disturbance (Paine 1984). Despite consistent co-occurrence of these canopy and understory species across environmental conditions, we know little about the biotic factors (recruitment, species interactions) that allow these species to co-occur, given their seeming overlap in use of essential resources (Menge *et al.* 2015). In this study we examined the reciprocal interactions between *S. sessilis* and the understory community to understand how these interactions could promote observed diversity in this system, and ultimately species coexistence.

The effect of plant canopy species on their understory community has been variably characterized, from positive recruitment facilitation by canopy nurse plants (Valiente-Banuet & Verdú 2007) to negative light limitation by the canopy (Holmgren, Scheffer & Huston 1997). Studies of kelp canopy-understorey systems have largely focused on the unidirectional effect of the canopy on the understory, given consistently strong effects of canopies (Irving & Connell 2006). Competitive release of understory algae following kelp removal has been demonstrated many times in intertidal and subtidal systems, with competition for light strongly

structuring these communities (Dayton 1975; Ojeda & Santelices 1984; Kennelly 1987; Benedetti-Cecchi & Cinelli 1992; Lilley & Schiel 2006; Arkema, Reed & Schroeter 2009). However, in a few studies kelp canopies have been shown to facilitate the understory via amelioration of thermal or desiccation stress (Dayton 1975; Paine 1984; Bennett & Wernberg 2014) or modification of the light environment (Benes & Carpenter 2015).

The reciprocal effect of the understory on kelp canopies is less well understood, and few studies have attempted to fully characterize reciprocal interactions in vertically-structured communities given the often obvious importance of the canopy for community structure. Strong negative interactions characterize some subtidal kelp canopy systems, with canopy recruitment inhibition by algal turfs (Graham 1997; Okamoto, Stekoll & Eckert 2013). However, in terrestrial plant communities, understories can facilitate the recruitment of other plant species by ameliorating stressful conditions (Arroyo *et al.* 2003; McIntire & Fajardo 2014; Holmgren *et al.* 2015). Similarly, some intertidal understory turf algae have been found to facilitate the recruitment of canopy species (Johnson & Brawley 1998). For example, *S. sessilis* recruits have been found on articulated coralline algae, a functional subgroup of the understory consisting of calcified algal turfs (Milligan & DeWreede 2000), suggesting that recruitment facilitation is a potential mechanism of coexistence in this system (e.g. Gouhier, Menge & Hacker 2011).

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

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

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

Materials and methods

STUDY SYSTEM

Our study system was the low zone of the rocky intertidal of the north-east Pacific, which is dominated by the perennial canopy kelp, *S. sessilis* (Dayton 1975). Sites in the N.E. Pacific vary in environmental conditions (temperature, light and nutrients) as the result of regional upwelling and coastal geomorphology (Menge *et al.* 2015; Fig. 1, Appendix S1, Table A1 in Supporting Information). Varying abiotic conditions along the coast drive differences in community structure among regions, though sites within each region have consistent community structure (Menge *et al.* 2015). Our study focused on the association between *S. sessilis* and a diverse understory that varied in species composition among regions but was always comprised of a macroalgal turf and invertebrate mosaic. Given the species turnover across regions, we followed a commonly used functional group approach (Steneck & Dethier 1994) to balance our interest in how species groups interact (group = similar functional morphology) with the difficulty of factorial determination of interactions in a diverse system. The functional groups included the abundance of non-calcified ('fleshy') algal turf, coralline turf, algal crusts, macrophyte blades and sessile invertebrates (Appendix S1, Table A2).

EXPERIMENTAL DESIGN

We measured the reciprocal interaction between the kelp canopy and the understory using two separate pulse removal experiments. In each, we established 15×15 cm plots around the centre of a single adult *S. sessilis*, marked with stainless steel lag screws at each corner. Unlike massive subtidal kelps, *S. sessilis* is relatively small (mean *S. sessilis* length during wave exposure experiment = $20.73 \text{ cm} \pm 0.87$), thus a 15×15 plot captures the area directly around the kelp holdfast and under the kelp blades to isolate the interaction between a single kelp and the understory community. Three treatments were applied to the plots: kelp (*S. sessilis*) removal (-K), understory removal (-U), and a no-removal control (C) (Fig. 2). In the removal plots, the focal removal functional group (either *S. sessilis* or the understory) was carefully scraped away down to bare rock at the start of the experiment. After the original removal, the plots were allowed to recover for 2 years. Each treatment was repli-

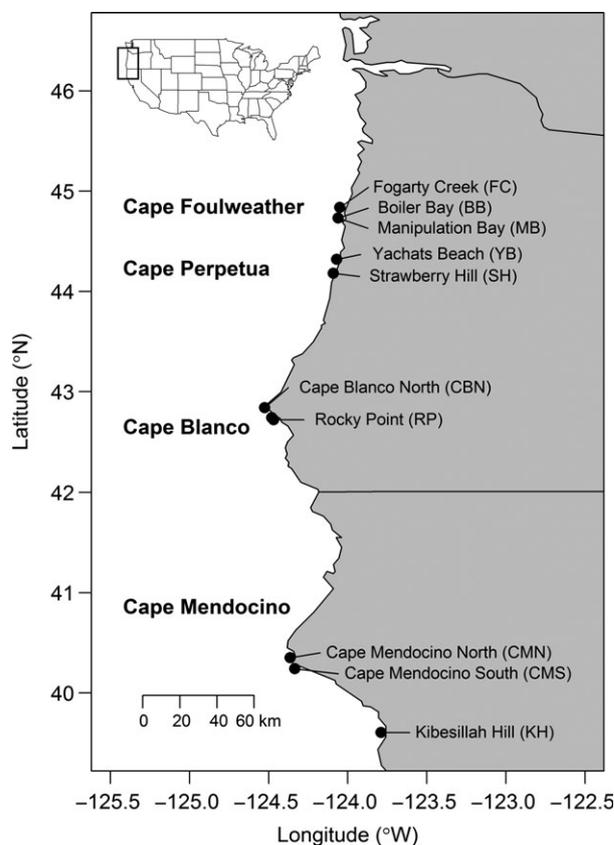


Fig. 1. Map of study sites within the four regions (capes). The regional interaction experiment occurred at all 10 sites, while the wave exposure experiment took place at Fogarty Creek (FC) only.

cated five times in a complete block design, with each of the three treatment plots established in five blocks. Canopy intact and removal plots within each block were close enough to encompass the same environmental conditions (block size = ~ 1.5 m), but far enough apart that the canopy intact plots did not shade the canopy removal plots (~ 0.5 m apart). Overall, due to the necessary functional group approach of these experiments, and the pulse (rather than press) nature of the species removals (Bender, Case & Gilpin 1984), these experiments more closely reflect functional group responses rather than species interaction estimates (Novak & Wootton 2010), though we continue to refer to species interactions to facilitate interpretation.

Experiment 1: species interactions across regions

To first test whether species interactions varied among four regions in Oregon and California on the U.S. west coast, we conducted the removal experiment described above in a spatially nested design, at multiple sites per region for a total of 10 sites and 150 experimental plots (Appendix S1, Table A1, Fig. 1). This experiment ran from April–May 2008 to August 2009, at which time all species were identified, recording per cent cover for the sessile organisms and number of *S. sessilis* recruits.

Experiment 2: species interactions and wave exposure

We tested for the effects of wave exposure on the interaction between *S. sessilis* and the understory at Fogarty Creek (FC), Oregon (Fig. 1). In May 2012, we established the same treatment plots as

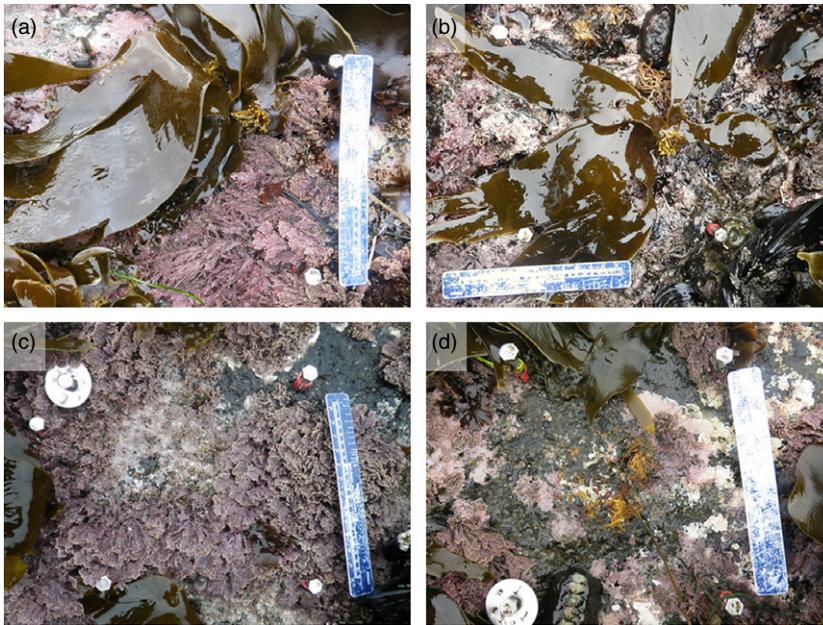


Fig. 2. (a–c) The three experimental manipulations used for both experiments: (a) control, (b) understorey removal and (c) canopy removal. (d) An example of an understorey removal plot where the *Saccharina sessilis* canopy has fallen off the substrate. In each photograph, the square plot is marked by lag screws in each corner, with a 15 cm ruler for scale.

described above in three locations at the site that differed in wave exposure (protected, intermediate and exposed). The wave-intermediate location was the same area of FC where we conducted the regional interaction experiment. The wave-exposed area was chosen because of its known high wave activity (Blanchette 1997), and it is the area before the wave-adapted kelp *Lessoniopsis littoralis* begins to dominate, suggesting it is the wave exposure distributional limit of *S. sessilis* (Dayton 1975; Menge *et al.* 2005). The wave-protected area was selected for its protection by rocky outcrops that shelter the intertidal from breaking waves, with overall lower relative wave acceleration than the wave-intermediate and exposed areas (Appendix S2). The three areas have similar slope (slope_{exposed} = $4.08 \pm 2.12^\circ$, slope_{intermediate} = $7.14 \pm 2.11^\circ$, slope_{protected} = $7.20 \pm 1.51^\circ$) and aspect (aspect_{exposed} = $234 \pm 7.5^\circ$, aspect_{intermediate} = $292 \pm 8.6^\circ$, aspect_{protected} = $340 \pm 6.3^\circ$), measured at the block level. We conducted a monthly survey in May–August of 2012 and 2013, collecting the same data as in the regional interaction experiment.

OBSERVATIONAL RECRUITMENT SURVEYS

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

STATISTICAL ANALYSES

Focal response variables in the experiments

To characterize the effect of the understorey on kelp, we used total adult *S. sessilis* per cent cover (blades + holdfast) to compare understorey removal treatments (-U) with controls (C). We also eval-

uated the effect of both kelp and the understorey community on the number of *S. sessilis* recruits, using the last time point (August 2008) in the regional interaction experiment, and the end-of-summer time points (August 2012, 2013) in the wave exposure experiment. To characterize the effect of kelp on the understorey community, we first compared the response of overall understorey community structure in the kelp canopy removal treatment (-K) with the control (C), then individually analysed this response by understorey functional group.

Statistical models

We analysed the reciprocal effects of the understorey on *S. sessilis* adults and recruits, and *S. sessilis* on the understorey community, using a linear framework. For the regional interaction experiment, we used general linear or generalized linear mixed effects models (general, Gaussian response = GLMMs; generalized, Poisson response = GLIMMs) to account for the nested structure of the data and to assess the fixed effects of treatment and region on the response variables. A random intercept model accounted for the spatial nesting of sites within regions. For the wave exposure experiment, we used general linear models (GLMs) on the last time point only to facilitate comparison between the two experiments (see Appendix S3 for full repeated measures methods and results for the wave exposure experiment). To construct the fixed effects for both experiments, we used Akaike's information criterion corrected for small sample sizes (AICc) to compare the fit of a treatment-only model to a model that included a treatment by region interaction or a treatment by wave exposure interaction, depending on the experiment. When analysis indicated that region should be included in a model, we used AICc to test whether a model including site as a predictor was a better fit. For models with interaction terms, we used Tukey *post hoc* contrasts to compare the treatment of interest to the control within region or wave exposure.

To examine the effect of kelp removal on overall understorey community structure, we conducted a blocked two-way permutational multivariate analysis of variance (PERMANOVA) based on Sørensen (i.e. Bray–Curtis coefficient) dissimilarities (n permutations = 999; Anderson 2001). PERMANOVA considers all species abundances as a

response, rather than simplifying to a single diversity metric. Thus, for this analysis, we analysed the whole-community matrix instead of functional groups. This matrix was relativized as per cent of the maximum for either per cent cover or counts (column totals) in order to standardize the units of species abundance (McCune & Grace 2002). We first tested if there was an interaction between canopy removal and either region or wave exposure, depending on the experiment. Neither showed an interaction (regional interaction experiment: $P = 0.239$, wave exposure experiment: $P = 0.856$), so we conducted a second analysis without the interaction. We tested whether certain species were consistently associated with kelp removals, as found by Dayton (1975), using a blocked indicator species analysis with permutations randomized within blocks, using the indicator value metric of Duf re & Legendre (1997). Indicator species analysis measures the strength of association between each species in the community and different habitats, or in this study, different treatments, to determine the degree of habitat/treatment fidelity of each species (see De C ceres & Legendre 2009 for more information).

We conducted two more analyses to further examine the relationship between adult *S. sessilis*, *S. sessilis* recruitment and the understorey. To examine the potential relationship between adult *S. sessilis* and *S. sessilis* recruitment, we regressed the per cent cover of adult canopy on recruitment for the regional interaction experiment (the wave exposure experiment did not have enough samples) using GLIMM to account for differences in *S. sessilis* abundance among regions. We tested whether a linear model fit the data better than a nonlinear model using AICc. Finally, the relationship between *S. sessilis* recruitment and various understorey functional groups in our observational surveys was examined using a Poisson GLIMM to assess the effects of site and understorey substrate (bare rock and five algal functional groups) on the number of *S. sessilis* recruits. We accounted for differences in sampling years and amount of available understorey substrate among sites by allowing intercepts and slopes to vary randomly with year and sites, respectively. For all response variables, per cent cover was transformed *a priori* with an arcsine square root transformation to meet the assumptions of normality. All counts (number of kelp recruits) were analysed using a Poisson distribution in a generalized linear model (GLM or GLIMM). All analyses were conducted in R 2.3.03 (R Core Team 2014), with main analyses using the packages ‘LME4’ (Bates *et al.* 2013), ‘LMERTEST’ (Kuznetsova, Brockhoff & Christensen 2014), ‘VEGAN’ (Oksanen *et al.* 2013) and ‘INDICESPECIES’ (De C ceres & Legendre 2009).

Results

EFFECTS OF THE UNDERSTOREY COMMUNITY ON KELP ADULTS

The understorey community had a strong, positive effect on the *S. sessilis* canopy (Figs 3 and 4, Appendix S1, Fig. A1). Understorey removal decreased the abundance of the kelp canopy in all experiments (regional interaction experiment GLM, $\beta_U = -0.25 \pm 0.071$, $P = 0.00070$; wave exposure experiment GLM, $\beta_U = -0.37 \pm 0.16$, $P = 0.028$; Appendix S1, Table A3) and had a consistent effect across region and wave exposure regime. We observed that adult *S. sessilis* was frequently removed from the rock in the absence of the understorey community (Fig. 2d).

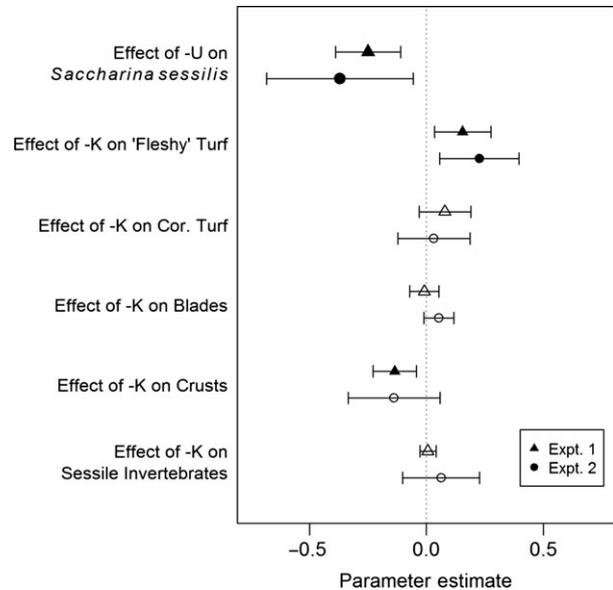


Fig. 3. Regression coefficients for the effect of a removal treatment (-K, kelp removal, or -U, understorey removal) compared with the control reference group, with 95% confidence intervals, for the main functional groups in Experiment 1 (regional interaction experiment) and Experiment 2 (wave exposure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

EFFECTS OF KELP ADULTS ON UNDERSTOREY COMMUNITY

Saccharina sessilis canopy removal had mixed effects on the structure of the understorey community. In the regional interaction experiment, understorey community structure changed with the removal of kelp (PERMANOVA, $P = 0.017$, Appendix S1, Table A4), though treatment explained little of the variation relative to region ($R^2_{\text{treat}} = 0.022$, $R^2_{\text{region}} = 0.17$), and unexplained variance in community structure was high. Across a broad spatial scale, three species were associated with the removal of the kelp canopy (regional interaction experiment): two red algal turf groups (the *Cryptopleural Hymenena* complex and *Osmundea spectabilis*), and the surfgrass *Phyllospadix* spp. (indicator species analysis: $\text{indval}_{\text{crypto}} = 0.601$, $P = 0.001$; $\text{indval}_{\text{osmund}} = 0.345$, $P = 0.008$; $\text{indval}_{\text{phylo}} = 0.320$, $P = 0.042$). Across wave exposure, canopy removal had no effect on overall understorey community structure (wave exposure experiment PERMANOVA, $P = 0.71$, Appendix S1, Table A5). However, as in the regional experiment, *S. sessilis* removal plots were associated with the *Cryptopleural Hymenena* complex (indicator species analysis: $\text{indval} = 0.663$, $P = 0.015$).

Saccharina sessilis had some negative, but mostly neutral, effects on understorey functional groups (Fig. 3, Appendix S1, Fig. A1). Overall, the effect of *S. sessilis* was consistent across region and wave exposure regime (no interaction). Similar to the indicator species analysis, in both

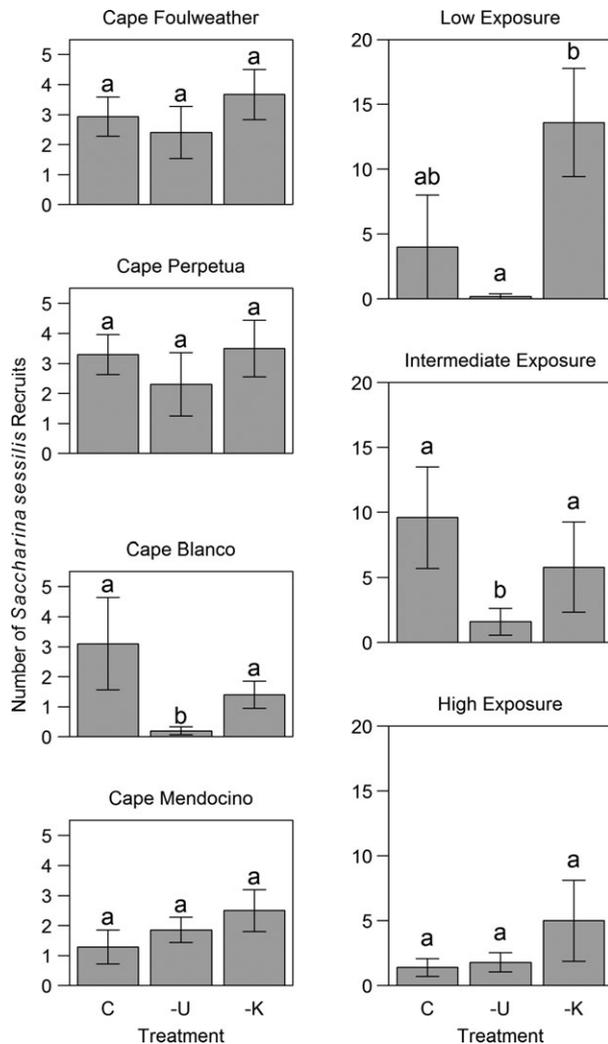


Fig. 4. Effect of canopy (-K) and understory (-U) removal on the number of *Saccharina sessilis* recruits at (a) different regions and (b) different wave exposures (2012 only, see Appendix S1, Fig. A2 for 2013 results). Lowercase letters represent *post hoc* contrasts (differences for $P < 0.05$) among treatments within a level (region or exposure).

experiments *S. sessilis* had a negative effect on non-calcified algal turf abundance (regional interaction experiment GLMM, $P = 0.014$; wave exposure experiment GLM, $P = 0.014$; Appendix S1, Table A6). However, *S. sessilis* had no effect on coralline turfs (regional experiment GLMM, $P = 0.16$; wave exposure experiment GLM, $P = 0.69$; Appendix S1, Table A7) or macrophyte blades (regional experiment GLMM, $P = 0.76$; wave exposure experiment GLM, $P = 0.11$; Appendix S1, Table A8) relative to the controls. The effect of *S. sessilis* on understory algal crusts was inconsistent across experiments (Fig. 3), with a positive effect in the regional experiment (GLM, $P = 0.0051$; Appendix S1, Table A9) and no effect in the wave exposure experiment (GLM, $P = 0.18$; Appendix S1, Table A9). The *S. sessilis* canopy did not affect sessile invertebrate abundance in either experiment (regional experiment GLMM, $P = 0.72$; wave

exposure experiment RM-GLMM, $P = 0.45$; Expt. 2 GLM, $P = 0.46$; Fig. 3; Appendix S1, Table A10).

EXPERIMENTAL EFFECT OF KELP ADULTS AND UNDERSTOREY COMMUNITY ON KELP RECRUITMENT

Removals of both adult kelp and understory algae had context-dependent effects on the number of *S. sessilis* recruits (Fig. 4). In the regional interaction experiment, the effect of treatment on recruitment depended on region (GLIM treatment \times region interaction, $P = 0.0014$; Fig. 4a; Appendix S1, Tables A11, A12) with a negative effect of understory removal relative to the control in the Cape Blanco region (contrasts, $P < 0.01$; Fig. 4a, Appendix S1, Table A12) and no effect in other regions. Similarly, in the wave exposure experiment, the effect of treatment on *S. sessilis* recruitment depended on wave exposure and year (GLIM treatment \times exposure interaction, $P < 0.0001$; year, $P < 0.0001$; Fig. 4b, Appendix S1, Tables A11, A13) with recruitment higher after the first summer (2012) than the second ($\beta_{2013} = -1.27 \pm 0.15$, $P < 0.0001$; Appendix S1, Table A15). In 2012, recruitment was lower in understory removal plots than the control (*post hoc*, intermediate exposures $P < 0.01$, Appendix S1, Table A13) but in 2013 recruitment did not differ among treatments (all *post hoc* contrasts $P > 0.05$, Appendix S1, Table A15, Appendix S1, Fig. A2). Kelp removal plots at wave-protected exposures tended to have higher recruitment than the control plots (2012 only, *post hoc* $P = 0.067$, Fig. 4, Appendix S1 Table A13). Moreover, in the regional experiment, *S. sessilis* recruitment was highest at intermediate cover of *S. sessilis* adults (polynomial vs. linear model, $\Delta\text{AICc} = 10.13$), indicating recruitment inhibition at low and high cover of kelp adults ($\beta = -2.23$, $P = 0.0015$, Appendix S1, Table A14, Appendix S1, Fig. A3).

OBSERVATIONAL EFFECT OF UNDERSTOREY COMMUNITY ON KELP RECRUITMENT

Saccharina sessilis recruitment differed among understory substrate types (GLIM substrate term, $P < 0.0001$; Appendix S1, Table A15). After accounting for differences in understory substrate abundance among sites, recruitment to coralline turf was orders of magnitude greater than recruitment to bare rock or other algal functional groups (Fig. 5, Appendix S1, Table A16). Kelp recruits rarely were observed on alternative recruitment surfaces including on the base of *S. sessilis* holdfasts, coralline crust, non-coralline turfs and bare rock (Fig. 5, Appendix S1, Table A16).

Discussion

We used experimental and observational tests to disentangle species interactions in a diverse rocky intertidal community and found a complex array of positive and negative interactions (Fig. 6). Importantly, although the kelp canopy had a negative or neutral effect on the understory community as a

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

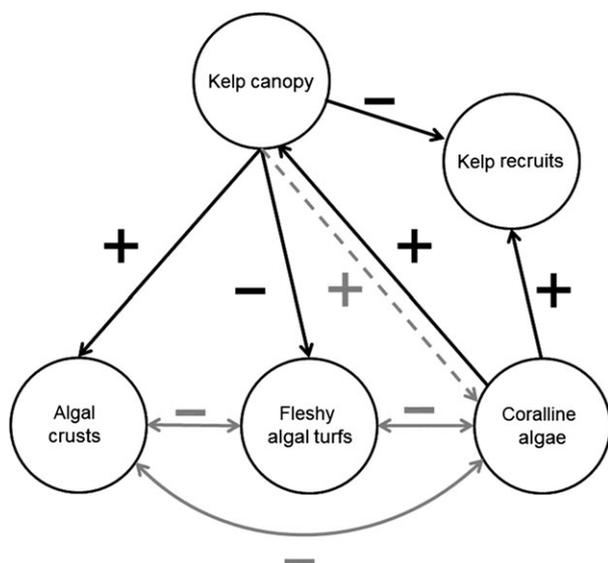
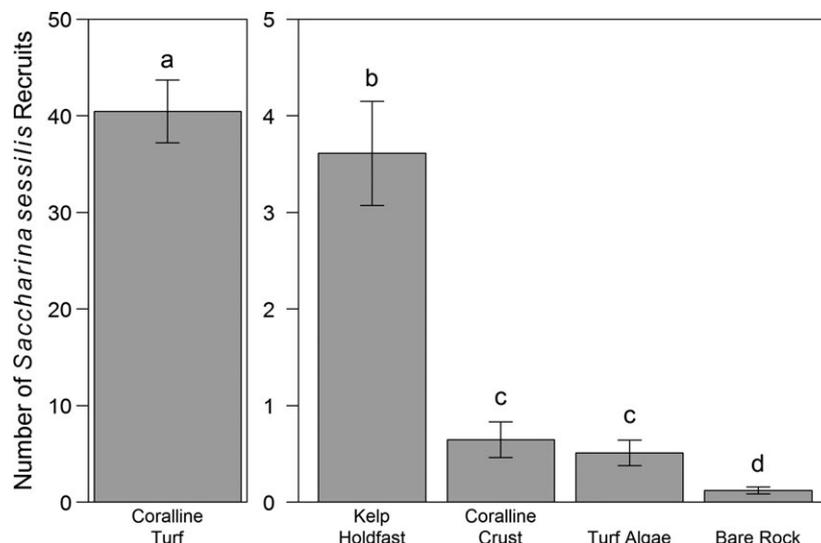


Fig. 6. Emergent species interaction network for the *Saccharina sessilis* canopy–understorey community. Black, solid arrows represent direct effects found in our experimental and observational study. Grey, solid arrows represent hypothesized direct effects with empirical support in the literature, though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

whole, kelp removal had no negative effects on the coralline turfs that facilitate kelp recruitment (similar to Duggins & Dethier 1985). The canopy had a negative effect on non-calcifying algal turfs, as has been found in other studies in intertidal systems (Dayton 1975; Paine 1984; Schiel 1988) and subtidal kelp forests (Dayton *et al.* 1984). Because articulated coralline algae and non-calcifying algae have been shown to compete in north-east Pacific rocky intertidal systems (Dayton 1975; Van Tamelen 1996), we infer that by suppressing the abundance of competing non-calcifying algae, kelp canopy likely indirectly promotes the persistence of the

corallines (Fig. 6). In turn, coralline turfs facilitate the recruitment of the kelp canopy, and the understory as a whole promotes the persistence of the adult canopy (Fig. 6). Thus, coexistence of macroalgal species in this system may depend on the positive feedback between the subdominant coralline understory and the dominant kelp, *S. sessilis*.

Despite previous research suggesting that strong negative canopy–understorey interactions are ubiquitous, our study reinforces empirical and theoretical work that suggests that facilitation is both common and important for coexistence in plant canopy–understorey communities (Holmgren, Scheffer & Huston 1997; McIntire & Fajardo 2014). Countering the general finding that kelp canopies have a negative effect on all understory recruitment, recent studies have found that subtidal kelp canopies can facilitate the recruitment of some understory algal species (Connell 2003; Bennett & Wernberg 2014; Benes & Carpenter 2015). In this study, we found that certain understory species directly facilitate the recruitment and persistence of the kelp canopy. The strong facilitation of the dominant kelp canopy by coralline turf was unanticipated, given that in subtidal and some intertidal systems, algal turfs have been widely found to inhibit kelp recruitment even in the absence of canopy shade (Dayton *et al.* 1984; Graham 1997), with strong negative effects of both crustose coralline algae (Okamoto, Stekoll & Eckert 2013) and articulated coralline algae (Reed & Foster 1984; Schiel & Lilley 2011) on canopy recruitment. Recruitment facilitation, in theory, has the potential to promote coexistence when a subdominant competitor facilitates either a competitive dominant in a meta-community (Gouhier, Menge & Hacker 2011) or the consumer of a competitive dominant, through indirect effects (Baskett & Salomon 2010). Indirect facilitation by the canopy has also been found to be key for species coexistence. For example, a dominant competitor for light in the north-east Pacific subtidal, the kelp *Macrocystis pyrifera* indirectly facilitates sessile invertebrates through suppression of their competitors, understory macroalgae (Arkema, Reed & Schroeter 2009). Similarly, in this study, if the canopy kelp suppresses

competition from non-calcifying algae, a positive indirect effect of the canopy on coralline algae results, which could counter any direct negative effect of the canopy, for a neutral net effect, as observed here. More nuanced experiments are needed to tease apart the generally strong net effects observed in this study to fully understand the bidirectional nature of canopy–understorey interactions in this system.

Unlike the widespread evidence that many species interactions are highly context-dependent (Chamberlain, Bronstein & Rudgers 2014), and contrary to our expectation, we found a general lack of environmental contingency in this system through repeated local interaction experiments. In fact, there was only one context-dependent interaction: the interactions among *S. sessilis* recruits, adults and the understorey. However, some context dependency in the interactions might be masked either by context dependency in the recruitment process (Wernberg *et al.* 2010) or by the use of functional group abundance as a response, especially in the regional interaction experiment, given species turnover among regions (both discussed below). Nevertheless, the effect of canopy removal was not context-dependent in either experiment when we analysed whole-community structure despite known regional differences in community composition (Menge *et al.* 2015). Overall, though, unlike other studies of kelp canopy–understorey systems (Wernberg & Connell 2008; Smale, Wernberg & Vance 2011) and what we expected, interactions varied little in space, along either a wave exposure gradient or among regions exhibiting variation in light and nutrient availability. Instead, a few strong interactions were spatially consistent, suggesting that the mechanism of these interactions is not strongly affected by the environment.

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

be an artefact of our functional group approach. In particular, the articulated coralline algae of Oregon and California are comprised of ~5 common species, and if species turnover among sites in this region is high and if *S. sessilis* recruits differentially to these different coralline species, then shifts in the abundance of the coralline species across latitude may explain variation in *S. sessilis* recruitment.

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

Kelp recruitment, though generally unaffected by the presence of the adult *S. sessilis*, experienced context-dependent intraspecific competition with the adult canopy, which may provide a negative control on the positive feedbacks in this system. Density-dependent mortality, or ‘self-thinning’, is common in terrestrial plant communities (Antonovics & Levin 1980) and subtidal kelp forests (Schiel & Foster 2006), and two lines of evidence in this study support our hypothesis of intraspecific competition among life-history stages. First, the number of *S. sessilis* recruits increased when the canopy was removed in wave-protected plots in the wave exposure experiment. Conditions in this wave-sheltered location may be optimal for *S. sessilis*, as measurements of *S. sessilis* growth show that adult growth was higher there than in more wave-exposed locations (A. K. Barner unpubl. data, measured as meristematic growth every 2 weeks). If *S. sessilis* performance is enhanced and abiotic conditions are benign, intraspecific competition is likely to be strong, and the reduced number of *S. sessilis* recruits in this area may be due to increased competition for resources, such as light. Recruitment inhibition by kelp canopy shading is common in subtidal kelp communities (Reed & Foster 1984). Secondly, we found that recruitment is inhibited under higher cover of *S. sessilis* adults across all treatments in the regional interaction experiment. Future work should explicitly incorporate density estimates of both adults and juveniles. Overall, a positive effect of coralline algae on *S. sessilis* may result in large, dense canopies that shade recruits, thus creating a density-dependent indirect control to May’s (1982) ‘orgy of reciprocal benefaction’ in networks dominated by positive interactions.

The understory had a positive effect on adult *S. sessilis*, though as with recruitment facilitation, the mechanism was unclear. If the understory retains enough water at low tide, water retention may benefit *S. sessilis* adults as the blades lie atop the turf mosaic. Understories have also been hypothesized to cushion the canopy against tattering due to strong waves (Milligan & DeWreede 2000). However, since we did not see a differential effect of the understory on the canopy across wave exposures, vulnerability to waves alone is unlikely to drive the positive effect of the understory. Another alternative is that understory removal may provide access for herbivores whose movement is inhibited by turf. Trophic interactions were not considered in this experiment, given the weak effect in earlier studies of grazing on algal succession and adult kelp in the *S. sessilis* zone (Dayton 1975; Burnaford 2004; Menge *et al.* 2005). However, in regions north of our study, the herbivore chiton *Katharina tunicata* has been found to weaken the holdfasts of young *S. sessilis*, increasing mortality (Markel & DeWreede 1998). The positive effect of the understory on the canopy is likely to be complex, with possible synergisms that deserve more detailed treatment.

That the canopy kelp affected understory community structure in a multitude of ways was an anticipated result, given previous rocky intertidal removal experiments (Dayton 1975; Paine 1984). Dayton (1975) hypothesized that the canopy has both positive and negative effects on the understory and showed that when the canopy was removed, obligate understory algae disappeared and weedy 'fugitive' species increased in abundance. We found that overall, fleshy turfs as a whole benefited by *S. sessilis* removal (mostly 'fugitives'), with few obligate understory species. Interesting exceptions include a positive effect of the canopy on crustose algae (dominated by encrusting corallines: mean proportion of total crusts that are coralline = 0.830 ± 0.128 [standard error] in the regional experiment, 0.877 ± 0.0452 in the wave exposure experiment), and no direct effect of the canopy on articulated coralline algae. Previous research has found that per cent cover of encrusting corallines can be higher under subtidal kelp than under less dense canopies or no kelp (Melville & Connell 2001), and experimental subtidal kelp removal decreased encrusting corallines (Kennelly & Underwood 1993). Kelp canopies have been hypothesized to promote coralline crust persistence by inhibiting the growth of epiphytes, either by reducing light or attracting mobile invertebrates that graze on epiphytes (Duggins & Dethier 1985; Melville & Connell 2001). Few studies have examined the effect of kelp canopies on articulated coralline algae, but the absence of an effect of the *S. sessilis* canopy on these coralline turfs is tantalizing and more explicit work is needed to understand the specific mechanism of a potential positive feedback. Ultimately, examination of species coexistence in this community will require further characterization of the mechanisms driving both fitness and stabilizing niche differences, likely involving significant empirical and theoretical work (Siepielski & McPeck 2010).

Conclusions

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

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Data accessibility

Data associated with this paper are deposited in the Dryad repository (doi: 10.5061/dryad.7950f) (Barner *et al.* 2015).

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Supplementary tables (Tables A1–A16) and figures (Figures A1–A3).

Appendix S2. Supplementary methods and results for wave exposure measurement.

Appendix S3. Supplementary material for wave exposure experiment (repeated measures).