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Coexistence despite recruitment inhibition of kelps by subtidal algal crusts

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ABSTRACT: In temperate subtidal reefs, kelp species often dominate light, while encrusting algae often dominate the substrate and are well adapted to low light conditions. Yet whether changes in algal crust cover impact recruitment dynamics of kelp species remains largely unexplored. To address this gap, we combined field surveys with laboratory and field experiments to investigate (1) the impact of algal crusts on kelp settlement and recruitment and (2) the potential effect such inhibition may have on density of subtidal kelps in a southeast Alaskan fjord. Experimental removal of algal crusts in the field resulted in dense kelp recruitment, whereas in plots where algal crusts dominated space, kelp recruitment was sparse. Kelp zoospores settled in the laboratory with no apparent selectivity for bare rock over crust surfaces, yet kelp sporophyte densities were reduced by 97 to 99% on non-coralline algal crust patches compared to bare rock, suggesting post-settlement recruitment inhibition. Despite such strong inhibition, we show that very low kelp recruit density, such as that observed in the algal crust dominated patches of our experiment, can yield high adult densities. Such observations are supported by positive correlations between kelp density and crust percent cover in field surveys of 1 m^2 plots across 6 reefs, suggesting broad-scale coexistence. Thus, the strong ability of kelps to colonize bare substrata in this region appears to facilitate persistence of kelps despite strong dominance of space by certain algal crusts.

KEY WORDS: Kelp · Space competition · Macroalgae · Alaska · Algal crusts · Recruitment

INTRODUCTION

Kelp forest ecosystems are among the most productive on the planet (Reed & Brzezinski 2009). The algal functional diversity therein (e.g. canopy, understory, and space-occupying forms) can enhance invertebrate larval recruitment (Rogers-Bennett et al. 2011), reduce temporal variability in primary productivity (Miller et al. 2011), and buffer against exotic species invasions (Britton-Simmons 2006). Yet strong competition frequently occurs among coexisting functional groups. While established adults of canopy-forming kelp species hold a competitive advantage with respect to light (Reed & Foster 1984), their recruiting stages lack such advantage and must compete with space-occupying species on the benthos for space. Algal crusts represent one such suite of competitors that can form an epithelium over the rock, transforming abiotic surface into living substrate, and include crustose corraline and fleshy red and brown crustose forms.

Algal crusts are well adapted to overgrowth and/or shading (Airoldi 2000, Dethier & Steneck 2001, Underwood 2006) and can depend on the canopy for

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establishment and/or persistence (Connell 2003, Irving et al. 2004, Irving & Connell 2006a,b, Smale et al. 2011). Yet it remains uncertain how algal crusts impact recruitment of kelp and thereby densities of adult kelp. Kelps release millions of vulnerable reproductive propagules, which settle on the benthos, where germination, fertilization, and sporophyte development occur (Schiel & Foster 2006). Algal crusts may inhibit recruitment of some algae, as suggested with the invasive fucoid *Sargassum muticum* (Britton-Simmons 2006), turf algae (Johnson & Mann 1986, Bulleri et al. 2002), and encrusting cyanobacteria (Benedetti-Cecchi et al. 1999), while some evidence of facilitation exists (Reed & Foster 1984). Proposed antifouling mechanisms employed by crusts include epithelial sloughing (Johnson & Mann 1986, Littler & Littler 1999), allelopathy (Suzuki et al. 1998), increased herbivore abundance (Day & Branch 2002), or microclimate modification (Amsler et al. 1992). The considerable challenge of kelp propagules to settle on suitable substrata by chance provides an opportunity for local competitive exclusion through preemptive recruitment inhibition by algal crusts.

Crust-dominated communities that lack upright macroalgae completely are common in nature (Steneck et al. 2002), and crustose corralline algae can facilitate increased herbivore densities to maintain such a state (Pearce & Scheibling 1990, Baskett & Salomon 2010). In most cases, they form either as a result of grazing by herbivores or changes in water quality (Matsunaga et al. 1999, Steneck et al. 2002). In the former case, removal of herbivores can prove insufficient for recovery of macroalgae and can require removal of algal crusts before communities can recover to resemble ungrazed areas (Bulleri et al. 2002). However, in many cases, kelp can recover rapidly once herbivore densities are depressed despite the dominance of primary space by algal crusts (e.g. Watanabe & Harrold 1991, Hagen 1995). Algal crusts are highly diverse in growth rate and performance when overgrown. The fleshy red alga *Hildenbrandia occidentalis*, for example, is a slow-growing taxon that performed well when covered experimentally, whereas 2 species of the fleshy brown algae *Ralfsia* that differ in growth rate (fast: *R. confusa*; slow: *R. pacifica*) both performed poorly when covered (Dethier & Steneck 2001). Encrusting coralline taxa show similar diversity in growth and performance (Dethier & Steneck 2001). Understanding what properties determine the outcome between crusts and kelp recruitment can provide insight into how important foundation kelp species persist and recover in the face of disturbance.

Several hypothetical circumstances allow canopy-forming species to recruit successfully despite space monopolization by algal crusts that are well adapted to life under the canopy; among them are (1) canopy species are not inferior competitors for space, and recruitment is not inhibited by space occupiers; (2) canopy species require large-scale disturbance that exposes bare rock to facilitate recolonization in the face of recruitment inhibition by space occupiers; or (3) recolonization by the canopy requires only minute unoccupied spaces and is thus resilient to inhibitory effects. In cases 2 or 3, crust-driven recruitment inhibition can occur by (1) prevention of spore settlement or germination or (2) post-germination mortality.

In this study, we used multiple approaches to test whether low-dwelling algal crusts preempt establishment of understory kelp species on local scales and if such interactions result in competitive exclusion of kelps or coexistence. We performed field manipulations to assess the nature of the interaction between crusts and kelp recruits. To test the direct influence of algal crust taxa on settlement and germination of spores and eventual recruitment of kelp sporophytes, we conducted laboratory assays using *Saccharina bongardiana*. To document correlation between kelps and crusts in nature, we conducted field surveys of kelp habitats. Finally, to determine how inhibition of kelp recruitment by crusts may influence kelp population dynamics, we examined how variation in kelp recruitment translated to subsequent adult densities in the field.

MATERIALS AND METHODS

Study system

Near Juneau, Alaska (Fig. 1), study reefs along shallow shorelines host mixed stands of 2 to 3 perennial understory kelp species (*Saccharina bongardiana*, *Laminaria yezoensis,* and *Agarum clathratum*), as well as algal crusts, other benthic algae includingless common kelp species (*Cymathere triplicata*, *Alaria marginata*, and *Costaria costata*), and encrusting invertebrates. Horizontal surfaces are dominated by fleshy algal crusts (including *Ralfsia* spp. and *Hildenbrandia* spp.) and encrusting corallines (unidentified spp.) (pictured in Fig. S1 in the Supplement, available at www.int-res.com/articles/suppl/m493p103_supp.pdf). In late March and April, recruits of *S. bongardiana* and *L. yezoensis* appear en masse and colonize sparsely available bare substrata within several months (Okamoto 2009).

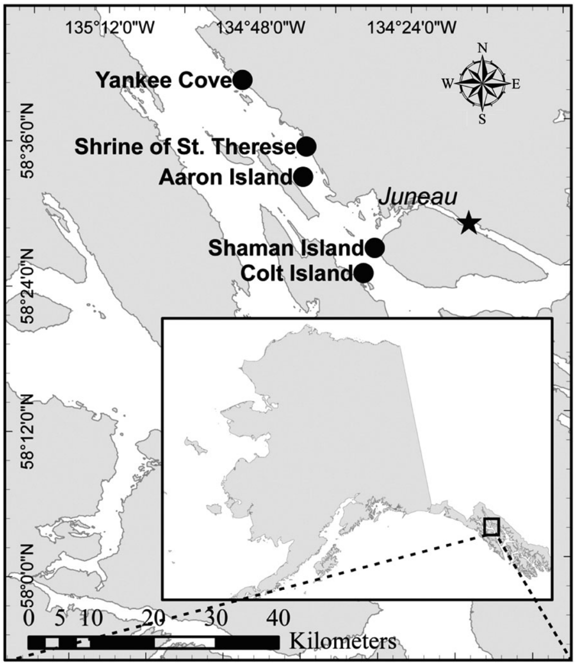

Fig. 1. Survey locations and experimental site (Yankee Cove) near Juneau, Alaska

Field experimental manipulations

To evaluate the effect of crusts on recruitment of kelps, we manipulated crust abundance at Yankee Cove near Juneau, Alaska (Fig. 1). We marked 23 horizontal, 0.09 m^2 plots along 6 m isobaths and surveyed them prior to manipulation in November 2007 by counting kelps and estimating percent cover of erect algae and percent primary cover of encrusting algal taxa, other encrusting taxa, and bare rock. Visual estimation of percent cover was performed using a quadrat strung with 5 monofilament lines on each axis that formed a 6 × 6 square grid to facilitate accurate visual estimation of cover. Brown crusts (primarily *Ralfsia* spp.) and fleshy red algal crusts (*Hildenbrandia* spp.) occupied an average of 51.1% (SD = 24.1) and 36.0% (SD = 24.3) of exposed rock, respectively, while encrusting coralline algae (unidentified spp.) occupied 6.9% (SD = 5.5), encrusting invertebrates occupied <1% (0.8%, SD = 1.6), and bare rock occupied 5.2% (SD = 9.3). On December 5, 2007, we randomly assigned and applied one of the following 3 treatments to each plot: (1) 9 plots scraped clean of all non-algal and algal crusts and sessile animals, hereafter referred to as 'scraped' plots; (2) 5 plots (a reduced sample size because of logistical constraints) cleared of any upright algae and non-encrusting organisms, with crusts wiped clean using a neoprene pad, hereafter referred to as 'cleared and crust intact' plots; and (3) 9 unmanipulated plots, hereafter referred to as 'control' plots. We did not apply a fully factorial design (lacking a crust-absent, kelp-present treatment) because we were primarily interested in the independent effect of crusts on kelp recruitment. On April 30, 2008, we counted kelp recruits in all plots and recorded whether kelp recruits occurred on crusts or other substrata (bare rock or deceased sessile invertebrate remnants). To be conservative, for a recruit to be recorded as having recruited to a non-crust surface, no part of the holdfast could be touching algal crusts. If a recruit was touching a crust, we recorded the crust group (brown, red, or coralline) the recruit was touching but, because of the diversity of other substrata and number of recruits, did not record the identity of non-crust substrata for other recruits. For each plot, we recorded percent primary cover of algal crust taxa (red crust, brown crust, and encrusting coralline) and bare rock.

We used 1-way ANOVA to test the hypothesis of no difference in mean kelp recruit density (square root transformed) among treatments. We then used planned contrasts in testing our *a priori* hypotheses of (1) no difference in means between cleared and control plots and (2) no difference in means between the latter groups (combined) and scraped plots. In plots with algal crusts intact, we compared densities of recruits on algal crusts and on non-crust substrata using a paired *t*-test. The relationship between kelp recruitment and algal crust percent cover in these plots was examined using a Poisson generalized linear model with overdispersion. We performed all analyses using R (R Development Core Team 2011).

Laboratory assessment of recruitment on algal crust and bare substrata

We tested for direct preemptive effects of crusts on kelps in a laboratory assay that isolated the effects of 3 major crust taxa on development of microscopic *Saccharina bongardiana* sporophytes. We exposed *S. bongardiana* spores to paired bare rock and crust treatments within small aquaria, allowed settled spores to germinate, and enumerated juvenile sporophytes 33 to 35 d after settlement. Rocks (20 cm diameter maximum) used in the assay were collected from Yankee Cove. Each rock had a horizontal surface ubiquitously covered by at least 15 × 15 cm of one of 3 taxa: a brown crust (*Ralfsia confusa*), a fleshy red crust (*Hildenbrandia* spp., tentatively identified as a *Hildenbrandia occidentalis*), or an unidentifiable encrusting coralline alga. We protected an 8 × 15 cm flat crust section on each rock using paper towels wetted with sterile seawater and quickly cleaned the remainder of the rock by sterilizing it with a butane torch 3 cm outside of the protected region. Epiphytes were removed from all rock surfaces by gently brushing each crust surface with paper towels moistened with sterile seawater. We then divided the protected 8 × 15 cm crust surface and cleared half of it using a fine wire brush, leaving the other half unmanipulated. Therefore, each rock served as a replicate with a clearing and crust treatment. Although we began with 8 replicates for each taxon, introducing live crusts to our mesocosms led to contamination by filamentous brown algae in several replicates. Thus, we used only those replicates with no sign of contamination (n = 4, 5, and 7 for *Ralfsia*, *Hildenbrandia*, and the encrusting coralline, respectively). We created an individual mesocosm around the isolated 8 × 15 cm experimental surface on each rock by attaching a square 1 l plastic container with an 8 × 15 cm section removed. Containers were sealed to the rock using a combination of HoldFast™ non-toxic aquarium epoxy (Aquarium Systems) and hot glue, such that the rock-container seams did not leak. During all preparations, we kept crust surfaces wet with enriched seawater produced as in Stekoll & Else (1990). These rock-container aquaria served as mesocosms for our experiment (Fig. S2 in the Supplement). We provided fresh air through a submerged air stone and a portable aquarium pump. Coverslips were attached to the horizontal surfaces of the 1 l plastic container to monitor microscopic development before kelps could be seen under a dissecting scope. Coverslips from each container were periodically removed, viewed under an inverted compound scope and discarded throughout the course of the experiment.

To obtain kelp spores, we collected reproductive *Saccharina bongardiana* from Yankee Cove in October 2007. We prepared fertile sori and released spores as detailed by Stekoll & Else (1990). The final spore solution consisted of a dilution to 10 000 spores ml^{-1} in modified Provasoli's enriched seawater (PES) treated with 0.66 mg l^{-1} germanium dioxide to reduce diatom contamination as well as 0.02 g l^{-1} penicillin G to reduce bacterial contamination (Stekoll & Else 1992).

We provided each rock container with 1 l of spore solution and left them incubating in the dark for 48 h at 10 to 13°C, after which we changed to a photoperiod of 16:8 h (light:dark) and exchanged PES medium weekly. Monitoring of coverslips took place weekly until all visible female gametophytes under multiple fields of view produced sporophytes large enough to be seen under a dissecting scope. At this point (35 to 37 d after spore settlement), we used a dissecting scope to photograph six 3 mm^2 sections (haphazardly chosen) of each crust and bare rock patch. In photographs where sporophytes clearly exceeded several hundred, we randomly subsampled 8 rectangular areas each consisting of 1/64 of the photograph and scaled up (8×) to an estimate of the total abundance in the photograph (Fig. S3 in the Supplement).

Hypotheses of no effect of taxon, treatment, or taxon–treatment interaction were tested in a repeated measures analysis. We used the square root of sporophyte densities (mm^{-2}) for each photograph as a subsample nested within each replicate patch and patch nested within each replicate aquarium, both serving as random factors within a linear mixed-effects model (R package nlme; Pinheiro et al. 2011). We tested *a priori* hypotheses of no difference between crust and bare rock treatments for each taxon using planned contrasts (R package multcomp; Hothorn et al. 2008).

Laboratory assessment of settlement and germination inhibition

We tested whether inhibition of kelp recruitment occurs prior to or following settlement and germination of kelp spores. We collected rocks containing crusts as described above and chipped off small sections (approximately 5 mm in diameter) of the rock that contained a single algal crust or bare rock. We placed each chipped rock section, after being stored for 24 h in sterilized seawater, into well plates (24 wells) with 3 ml modified PES medium in each well into which we could then settle kelp spores. We also placed glass coverslips into some wells to track spore development and to serve as procedural controls.

To determine the stage at which inhibition of kelp recruitment occurred, we used epifluorescence and fluorescent stains to track cell presence and fate on non-transparent or irregular surfaces. We used this tool to determine whether pre-stained spores settle and germinate on brown algal crusts at the same densities as on bare rock. Other crust taxa produced excessive background autofluorescence that prevented visualization of microscopic epiphytes with fluorescent microscopy. We exposed a 255 000 spores ml^{-1} spore solution for 3 h to different concentrations (0, 5, and 22.5 µM in filtered seawater) of CellTracker™ green 5-chloromethylfluorescein diacetate (provided from a stock solution at 10 mM in anhydrous DMSO, Invitrogen) in independent glass vials kept on ice (to keep spores from settling during the staining process). We then injected each well in the well plates with 60 µl of the appropriate spore solution and placed the well plates into an incubator at 10°C for 24 h in the dark. We used 3 stain concentrations to test the effect of the stain on settlement and germination of spores. Spore settlement was evaluated on the substrata with light and/or epifluorescence microscopy after the 24 h incubation period (Fig. S4 in the Supplement). We compared mean abundance of settled and germinated spores on substrata placed in wells (coverslips, bare rock, and crust chips) and tested for differences between stain concentrations (0, 5, and 22.5 µM).

Kelp recruitment and subsequent adult densities on artificial substrata

To understand whether the reduction of kelp recruit densities by the crusts influences adult kelp densities, we followed a cohort of recruits on a large area of bare substrate and then modeled how recruit density translates to adult density. Within a few meters of our field experiment (offshore) at Yankee Cove, a 30 × 10 m area of quarry rock was installed in December 2007 (2 wk after the field experiment was initiated). We surveyed densities of recruit and adult kelps in July 2008 and July 2009 on fixed transects using the survey methods described above for reef surveys using 1 m^2 plots. From these data, we can infer the potential impact of algal crust recruitment inhibition.

We examined how kelp recruit density translates to subsequent adult kelps by a reparameterization of Shepherd's (1982) 3-parameter model given by Quinn & Deriso (1999):

$$A = R/(\alpha + [R]^{\gamma}\beta) \qquad \text{(Shepherd model)}$$

where A is the density of adults in July 2009, R is the density of recruits in July 2008, $1/\alpha$ is the density-independent survivorship, and β and γ are estimated parameters controlling density-dependent survivorship. When $\gamma = 0$, there is only density-independent survival; $\gamma > 1$ indicates overcompensation; $0 < \gamma < 1$ indicates weak density-dependent survival and no asymptotic adult density; $\gamma = 1$ indicates both density-dependent survivorship and an asymptotic adult density at $1/\beta$ (also known as the Beverton-Holt model). Because the initial density-independent survival rate ($1/\alpha$) cannot exceed 1 (more adults than recruits), we constrained α to a minimum of 1. This framework allowed us to estimate whether reductions in recruit densities because of encrusting algae would impact adult densities. For model descriptions, see Quinn & Deriso (1999). We used nonlinear least squares to estimate model parameters.

Reef surveys evaluating correlation of crusts and kelps

We investigated correlations between algal crusts and both recruit and adult kelps using subtidal field surveys conducted with SCUBA. To document patterns of community structure, we surveyed 6 subtidal rocky reefs (Fig. 1). At each reef, we surveyed two 30 m transects at 5 m depth below mean lower low water, which represents the approximate median depth range of *Saccharina bongardiana*, the most abundant local understory kelp (D. K. Okamoto pers. obs.). Along each transect, all adult kelps were first counted within 6 systematically placed 1 m^2 quadrats, and then kelp recruits (approximately 2 to 6 cm in total length) were enumerated in a haphazardly placed 0.25 m^2 quadrat within each larger quadrat. Percent primary cover (using point-contact with 20 pre-determined points on a 10 × 10 grid) of the benthos occupied by encrusting algal species as well as sand and bare rock was estimated. We examined the relationship between kelps and algal crusts from reef surveys by estimating the correlation of adult kelps (square root transformed) with algal crusts and its consistency at each site using a linear mixed-effects model (R package nlme; Pinheiro et al. 2011).

RESULTS

Field experimental manipulations

In our field experiment, recruitment occurred in nearly all plots (23 of 24). However, densities of kelp recruits in scraped plots far exceeded those in control plots and crust-only plots ($F_{1,20} = 7.15$, p = 0.015, Fig. 2a), whereas densities in control plots and crust-only plots did not differ ($F_{1,20} = 0.09$, p = 0.77, Fig. 2a). Kelps were able to recruit to plots where crusts dominated the substratum because they used cracks and other spaces uninhabited by algal crusts or areas where invertebrates (primarily spirorbid and serpulid worms as well as encrusting bryozoans) had colonized on top of crusts. In general, kelps recruited in the field almost exclusively

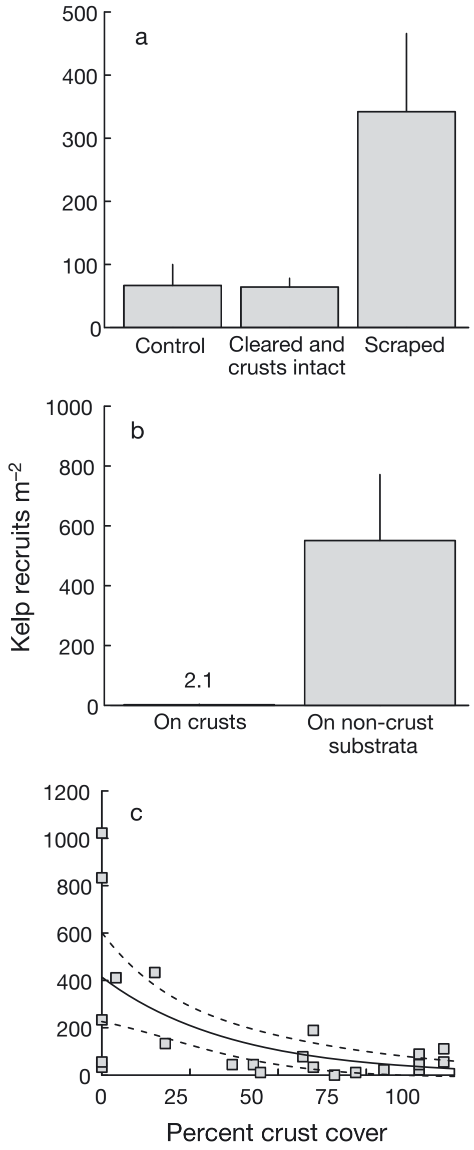

Fig. 2. Field experimental results. (a) Mean density of kelp recruits (m^{-2}) in experimental plots of 3 treatments: unmanipulated control, cleared of all but algal crusts, and removal of all organisms by scraping. Error bars represent 1 SE with n = 5, 9, and 9, respectively. (b) Mean density of kelp recruits on crust versus non-crust substrata in each plot that contained algal crusts. Error bars represent 1 SE. All but 2 total recruits were found on non-crust substrata. (c) Kelp recruit density (m^{-2}) in each plot against percent cover by algal crusts. The solid line represents the fitted relationship between kelp recruits and algal crust cover, with dashed lines representing 95 % CI of the fitted values

on non-crust substrata rather than on crusts, and only 2 recruits occurred on crusts in all plots. Recruit densities were significantly higher on non-crust substrata versus on crusts in plots where crusts were present (1-sided, paired *t*-test, t_{17} = 8.83, p < 0.001, Fig. 2b). The density of recruits in experimental plots was negatively correlated with percent cover of crusts (deviance explained = 48 %, $F_{1,21}$ = 20.16, p < 0.001, ϕ (dispersion parameter) = 13.39; Fig. 2c).

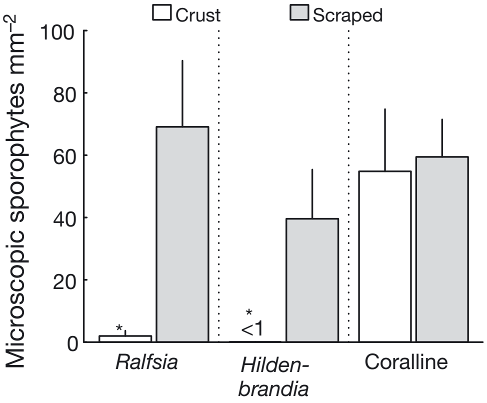

Fig. 3. *Saccharina bongardiana*. Laboratory results showing mean number of cultured, microscopic sporophytes on crusts and treatments where algal crusts were scraped away (bare rock). Plots are segregated by crust taxon. Error bars represent 1 SE, with n = 5, 4, and 6, respectively, by taxon. Asterisks represent crust treatments that differed significantly from associated scraped treatments

Laboratory assessment of recruitment on algal crust and bare substrata

In laboratory mesocosms, the effect of scraping differed with taxon, as indicated by a significant treatment–taxon interaction (χ^2 = 12.05, df = 2, p = 0.002). Microscopic *Saccharina bongardiana* sporophyte densities on *Ralfsia* and on *Hildenbrandia* patches were reduced by 97 and 99 % compared to bare rock (p < 0.001 for both; Fig. 3), respectively. However, there was no significant difference in sporophyte densities on encrusting coralline patches versus bare rock treatments (p = 0.55, Fig. 3).

Laboratory assessment of settlement and germination on algal crust and bare substrata

Kelp spores settled and germinated in equal densities (mean ± SE) on brown crusts (230 ± 38 mm^{-1}), bare rock (237 ± 41 mm^{-1}), and coverslips (231 ± 25 mm^{-1}) (ANOVA, $F_{2,24}$ = 0.01, p = 0.98). Settlement and germination of *Saccharina bongardiana* spores

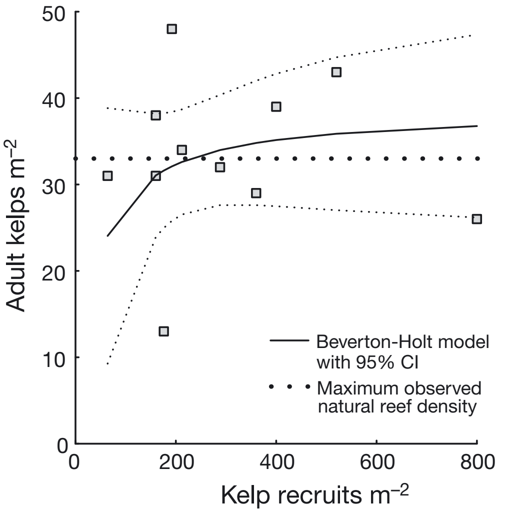

Fig. 4. Density of adult kelps in 2009 from estimated kelp recruit densities in 2008 on an artificial reef at Yankee Cove several meters from the site of the field experiment. The heavy dashed line represents the maximum density of understory kelps observed in surveys at locations shown in Fig. 1. The solid line represents the estimated Beverton-Holt model. Dotted lines represent 95% CIs for the fitted values

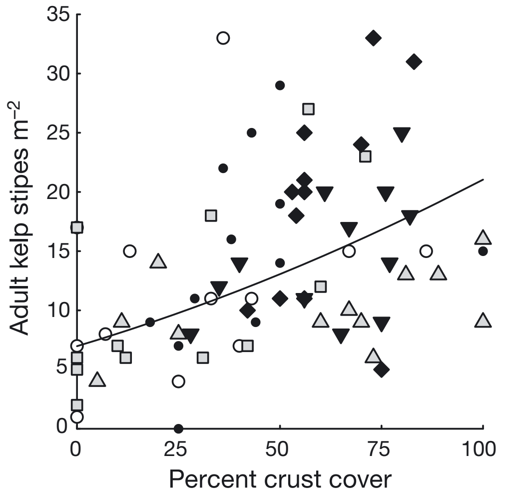

Fig. 5. *Saccharina bongardiana*, *Agarum clathratum*, and *Laminaria yezoensis*. Density of adult kelp stipes (m^{-2}) as a function of algal crust cover in survey quadrats from the 6 surveyed sites shown in Fig. 1. Each unique symbol and color combination represents a single site. The line represents the fitted relationship of the fixed effects of the linear mixed-effects model

was not affected by the concentration (0, 5, or 22.5 µM) of the CellTracker™ green stain (ANOVA, $F_{2,11} = 0.13$, $p = 0.88$). These results suggest that recruitment inhibition occurs not by prevention of settlement or germination but by influencing later growth, development, and/or survivorship of microscopic sporophytes.

Kelp recruitment and subsequent adult densities on artificial substrata

Kelp recruitment on the introduced substrata during summer 2008 was high but variable. The 2009 adult data suggest strong asymptotic density dependence, as indicated by the Shepherd model estimate of $\gamma = 1.14$ (95% CI = 0.24 to 1.61) and its similar fit to the Beverton-Holt model ($F_{1,8} = 0.65$, $p = 0.44$). Meanwhile, the Beverton-Holt model fit the data significantly better than the density-independent model ($F_{1,9} = 35.59$, $p = 0.0002$). CIs of the estimated asymptotic density ($1/\beta = k = 38.5$ m^{-2}, 95% CI = 29.5 to 55.7) include the maximum density observed in our regional reef surveys (33 m^{-2}). These data show that very low recruit densities can yield adult densities around the observed maximum (Fig. 4).

Reef surveys evaluating correlation of crusts and kelps

In contrast to the patterns for kelp recruits in our field experiment, reef surveys revealed that density of adult kelps was positively correlated with percent cover of crusts ($\chi^2 = 14.78$, $p < 0.0001$, Fig. 5), with no significant variation in the slope among sites ($\chi^2 = 2.32$, df = 2, $p = 0.31$). All 3 major algal crust groups (brown, fleshy red, and encrusting coralline) inhabited each site (data not shown), with crust taxa cumulatively occupying between 0 and 100% of sampled points. Kelp recruits occurred in 45 of the 72 plots, and their densities were highly variable (mean ± SD: 56 ± 110 m^{-2}), while adult kelps were more consistent (13.7 ± 7.6 m^{-2}, max. = 33 m^{-2}).

DISCUSSION

Although strong resource competition can often give rise to competitive exclusion, a wide variety of mechanisms can facilitate coexistence in the face of such antagonistic interactions (Chesson 2000). Our results show that algal crusts can directly and severely impede recruitment of kelp species; yet despite this impact, the small amount of bare space left unoccupied can be sufficient to yield high adult densities observed in the field. Such a phenomenon demonstrates that kelps are able to thrive in spite of such inhibition because of their intrinsic abilities to take advantage of space left unoccupied by antagonistic crusts and produce high densities of adults with relatively few recruits.

In our field experiment, only 2 individual recruits emerged on crusts, providing a powerful indication of the extent of this interaction between non-calcified crusts and kelps in nature. Such inhibitory effects may be widespread in many different types of kelp forests. In the San Juan Islands, removal of algal crust communities increased recruitment of the invasive brown alga *Sargassum muticum* (Britton-Simmons 2006, Britton-Simmons & Abbott 2008). Our field study took place in a location where non-calcified crusts were dominant and have large effects on recruitment. In contrast, encrusting corallines did not inhibit recruitment in the lab and were rare in the field; thus, we could not evaluate their effects in the field. Our results, in combination with previous work, suggest that different crust taxa may employ disparate antifouling capabilities or mechanisms. In Nova Scotia, encrusting corallines reduced fleshy algal cover (Johnson & Mann 1986); in Japan, coralline extracts produced inhibitory chemical effects on cultured kelp spores (Denboh et al. 1997, Suzuki et al. 1998); moreover, several authors propose that encrusting coralline epithelial instability (Johnson & Mann 1986, Keats et al. 1997, Littler & Littler 1999) can impact macroalgal establishment (but see Reed & Foster 1984).

Despite inhibition of kelp recruitment by some crusts, kelps thrive in their presence as demonstrated by the positive correlation of the two in field surveys. Although some systems require large-scale disturbance of preemptive species to enable establishment of inferior space competitors, such a phenomenon is unlikely to yield the observed patterns of high crust cover and dense kelp stands (Fig. 3) given the slow recovery rates of algal crusts (Dethier 1994, Dethier & Steneck 2001) and the short life span of kelps (Duggins 1980). Instead, we propose that inundation of the habitat by propagules compensates for strong preemptive effects, provided a small amount of suitable non-crust surface space is made or left available. This is evident by the fact that relatively few kelp recruits are capable of yielding high densities of adults (Fig. 4). Like many systems, space occupiers in this study seldom monopolized the entirety of available habitat, leaving minute space for kelp recruitment. The provisioning of such space may result from small grazing events, cracks, and crevices impeding the lateral expansion of crusts or from competitive apices formed between algal crusts. Moreover, some kelp recruits in our field experiment occurred on sparsely distributed encrusting invertebrates, which often hold competitive advantage over algal crusts (Sebens 1986, Konar & Iken 2005). Despite their rarity, invertebrates growing on crusts may provide small amounts of substrate suitable for settling kelp zoospores or even facilitate increased recruitment by altering laminar flow. In this manner, non-transitive (cyclical) networks (sensu Durrett & Levin 1997, Kerr et al. 2002) of competition may exist and facilitate coexistence. Whichever forces restrict algal-crust dominance, crust-free patches may be the 'toe-hold' by which kelps frequently establish dominant stands amidst algal crusts that are abundant but that lack a complete monopoly on space. Thus, the positive correlation observed between kelps and crusts may be facilitated by the positive effect of kelps on crusts and is not impeded by the negative effect of crusts on kelp recruitment.

The ability of species to take advantage of such minute spaces requires the ability of microscopic stages to recruit and have high enough survival that sufficient numbers of recruits become adults. In our experiments, kelp zoospores settled indiscriminately and thus may partially colonize bare substrata by chance (although zoospores show some capability for nutrient-induced settlement preference (Amsler & Neushul 1990). Therefore, a decrease in propagule availability (perhaps by a reduction in adult densities) or recruit survival, through environmental changes (Matsunaga et al. 1999) or increased grazing of recruits (Duggins et al. 2001), may disproportionately influence dynamics in habitats with such inhibitory space occupiers. Thus, while quantitative documentation of macroalgal population dynamics remains scarce because of the challenges posed by their unique multiphasic life history (Schiel & Foster 2006), the effects shown here highlight a potentially strong bottleneck to recruitment in circumstances where propagule pressure of an individual species is unusually low or mortality of successful recruits is unusually high (i.e. much more recruitment is required to maintain adult densities). Thus, the presence of strong and negative interactions may not always lead to competitive exclusion but may change the resilience or resistance of one or more groups to additional stressors.

Here, we demonstrate that a group of dominant space occupiers has the potential to exclude recruiting stages of light-monopolizing species to unoccupied space. Despite such exclusion, local coexistence appears widespread. We contend that this coexistence results, in part, from a kelp life history strategy geared toward colonization and the slight, but prevalent, restriction of preemptive crust species from complete dominance of space. Our results indicate that despite dominance of the benthos by space occupiers that inhibit recruitment, the canopy can persist in this circumstance because it requires very little space for establishment. Thus, strong preemptive interactions in this case do not scale to competitive exclusion but instead give way to coexistence because of robust recruitment dynamics of kelps.

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