# COMPETITION AND RECRUITMENT IN SOUTHEAST ALASKAN SUBTIDAL KELP COMMUNITIES

By

Daniel Kenji Okamoto

RECOMMENDED

Advisory Committee Chair

S Atkinson

Chair, Fisheries Department

APPROVED

Dean, School of Fisheries and Ocean Sciences

Lawrence K Duffy

Dean of the Graduate School

Aug 13, 2009

Date

# COMPETITION AND RECRUITMENT IN SOUTHEAST ALASKAN SUBTIDAL KELP COMMUNITIES

A

THESIS

Presented to the faculty of

The University of Alaska Fairbanks

In Partial Fulfillment of the Degree of

MASTER OF SCIENCE

By

Daniel Kenji Okamoto

Fairbanks, Alaska

August 2009

## ABSTRACT

Shallow subtidal rocky reefs in the Northeast Pacific host frequent physical and biological disturbances as well as multiple competing algal species, including kelps and algal crusts. Kelps serve a critical role in local ecosystems by generating primary productivity and essential fish habitat. While kelp forests rank among the best understood ecosystems in the marine environment, protected and subarctic systems remain largely ignored. Because of the importance of kelp habitat in Southeast Alaska, and the susceptibility of kelps to both disturbance and competition, I estimated the variability in kelp community structure of subtidal, kelp dominated reefs in the Lynn Canal and quantified kelp recruitment in response to both competing algae and bare space which included clearings, artificial reefs, and settlement tiles installed at different periods. Surveyed communities varied most within rather than among reefs. Kelps exhibited strong, rapid, variable and apparent taxa specific colonization potential to clearings, artificial reefs and settlement tiles installed from summer to late fall. Algal crusts imposed a near 100% inhibition of kelp recruits in the field and lab; however the strong colonization potential of kelps facilitated recruitment in the face of strong inhibition by algal crusts.

## TABLE OF CONTENTS

Page

Page

## LIST OF FIGURES

**Chapter 1** Page

**Chapter 2** Page

# LIST OF TABLES

**Chapter 1** Page

## ACKNOWLEDGMENTS

The completion of this endeavor came with the unrelenting support of many through challenges of both labor and illness. I am grateful to all those who graciously supported my academic pursuits and provided the opportunities which facilitated my success. I particularly thank Ginny Eckert, who not only afforded me this opportunity, but also relinquished to me enormous freedom to pursue my own curiosities of ecology and natural history and provided me thorough guidance and support. She and the other faculty at the Juneau Center of the School of Fisheries and Ocean Sciences generate a truly collegial and cooperative atmosphere dedicated to student learning and aspiration which deserves both praise and gratitude. Many thanks to those who provided funding for my graduate studies, including the Alaska Department of Transportation & Public Facilities, Alaska Sea Grant, the Dr. H. Richard Carlson Scholarship and the School of Fisheries and Ocean Sciences. Many thanks also to my friend and comrade in underwater science Jodi Pirtle, and to Jeff Douglas, Bill Bechtol and all others who assisted in field work. Thanks to Reuben Yost and Sue Walker who strove for the installation of the Yankee Cove Artificial Reefs. Mike Stekoll provided unique guidance, advice and conversation concerning algae and their cultivation; Chris Siddon offered generous advice and insight into subtidal research. Finally, my parents, as well as Angus Taylor and Iwao Okamoto all made enormous sacrifices which provided me the capacity and inspiration for the dedicated pursuit of this work.

## GENERAL INTRODUCTION

Kelp forests rank among the most productive ecosystems on the planet (Dayton 2003) and provide critical habitat for fish, invertebrates, and other species of economic, ecological, and intrinsic value (Dayton 1985; Steneck *et al.* 2002). Beyond their productivity and genesis of structural habitat, they provide a model system for ecological research. Their rapid dynamics (Steneck *et al.* 2002), diversity with approximately 30 genera of kelps (Lane *et al.* 2006), accessibility, and their important functional role in nearshore ecosystems (Duggins *et al.* 1989; Britton-Simmons *et al.* 2009) makes them well-suited to serve as model ecosystems. Although kelp forest ecosystems rank among the most extensively studied systems in the marine environment, many fundamental questions concerning which factors regulate their productivity remain unanswered or debatable (e.g. Foster *et al.* 2006; Halpern *et al.* 2006).

Kelp forests provide enormous productivity and experience immense competition and disturbance. Though canopy and sub-canopy kelp species can preempt light as adults, they also undergo ontogenetic shifts in their dominance as recruiting life stages in which they may succumb to various perturbations and competition. This susceptibility to both disturbance and competition as recruiting life stages provides challenges to kelp forest productivity and leads to fundamental questions regarding how kelp populations regenerate following deforestation, how they propagate following the introduction of bare space, and how they replace senescing adult individuals.

Because a large variety of factors influence kelp recruitment dynamics (Dayton 1985; Steneck *et al.* 2002), understanding which processes regulate recruitment can provide a daunting challenge. Gradients of water motion (Hurd 2000), UV and light availability (Lüning *et al.* 1990), temperature (Dieck 1993), nutrient availability (Dayton 1985), salinity (Buschmann *et al.* 2004), and other chemical properties of the microclimate composition can all have dramatic impacts on recruitment success. Beyond physical influences, herbivory by mesograzers (Sala & Graham 2002) or urchins (Simenstad *et al.* 1978; Estes & Duggins 1995) can influence microscopic kelps or kelp recruits. Lastly, competition resulting from high settlement densities or the influence of pre-existing competitors can strongly influence recruitment success (Reed 1990). Efforts of investigation, conservation or restoration of kelp forest habitats can have very different results in different places, times and conditions because of the sensitivity to biotic and abiotic factors that can vary over space and time.

Artificial reefs have been utilized to restore kelp forests in subtidal habitats around the world (Buckley & Hueckel 1985; Carter *et al.* 1985; Reimers & Branden 1994; Svane & Petersen 2001; Steimle *et al.* 2002; Rule & Smith 2005; Wyllie-Echeverria *et al.* 2005; Bortone 2006; Perkol-Finkel *et al.* 2006; Reed *et al.* 2006). Artificial reefs have successfully been used to generate large scale kelp communities with dense recruitment occurring within one year (Reed *et al.* 2004; Wyllie-Echeverria *et al.* 2005). Yet recruitment of many benthic species on artificial reefs is often non-linear (Reed *et al.* 2000; Reed *et al.* 2005; Wyllie-Echeverria *et al.* 2005), spatially variable (Reed *et al.* 2005), dependent upon variable processes of succession and biological interactions (Buckley & Hueckel 1985) and some models predict that full benthic community maturation on reefs may take as long as a decade or more (Aseltine-Neilson *et al.* 1999).

The establishment of biological communities on artificial reefs has received considerable attention in temperate kelp forests; subarctic kelp habitats and colonization of artificial reefs remain understudied, especially in the protected waters of Southeast Alaska (Lindstrom 2009). Kelp forests in this region host spawning herring, salmonids (Murphy *et al.* 2000; Johnson *et al.* 2003), gadids (Murphy *et al.* 2000; Johnson *et al.* 2003), juvenile shellfish, sea otters (Estes & Duggins 1995), sea lions (pers. obs.) and other marine mammals. Kelp forests in this region, in particular, may serve as a unique system for investigation not only because of the species which they support but also the changing subarctic environment in which they inhabit. Kelps lie at the apex of marine, terrestrial and freshwater ecosystems, influenced by processes of all three as well as anthropogenic influences to the coastline.

This collection of studies aims to understand two fundamental processes in subarctic kelp forests. In the first chapter I address the capability of kelps to recruit to bare space and associated variability depending on the location and timing of space availability. In the second chapter I investigate the role of algal crusts in inhibiting recruitment of coexisting kelp species. Collectively, these studies provide novel, basic information concerning the dynamics of kelp forests in this subarctic climate, and reveals new insights regarding fundamental interactions in productive, functionally diverse plant ecosystems.

## REFERENCES

Aseltine-Neilson D.A., Bernstein B.B., Palmer-Zwahlen M.L., Riege L.E. & Smith R.W. (1999) Comparisons of turf communities from Pendleton Artificial Reef, Torrey Pines Artificial Reef, and a natural reef using multivariate techniques. *Bull. Mar. Sci.*, 65, 37-57

Bortone S.A. (2006) A perspective of artificial reef research: The past, present, and future. *Bull. Mar. Sci.*, 78, 1-8

Britton-Simmons K.H., Foley G. & Okamoto D. (2009) Spatial subsidy in the subtidal zone: utilization of drift algae by a deep subtidal sea urchin. *Aquat. Biol.*, 5, 233-243

Buckley R.M. & Hueckel G.J. (1985) Biological Processes and Ecological Development on an Artificial Reef in Puget-Sound, Washington. *Bull. Mar. Sci.*, 37, 50-69

Buschmann A.H., Vásquez J.A., Osorio P., Reyes E., Filun L., Hernández-González M.C. & Vega A. (2004) The effect of water movement, temperature and salinity on abundance and reproductive patterns of *Macrocystis* spp.(Phaeophyta) at different latitudes in Chile. *Mar. Biol.*, 145, 849-862

Carter J.W., Carpenter A.L., Foster M.S. & Jessee W.N. (1985) Benthic succession on an artificial reef designed to support a kelp-reef community. *Bull. Mar. Sci.*, 37, 86-113

Dayton P.K. (1985) Ecology of kelp communities. *Annu. Rev. Ecol. Syst.*, 16, 215-245

Dayton P.K. (2003) The importance of the natural sciences to conservation. *Am. Nat.*, 162, 1-13

Dieck T. (1993) Temperature tolerance and survival in darkness of kelp gametophytes (Laminariales, Phaeophyta): ecological and biogeographical implications. *Mar. Ecol. Prog. Ser.*, 100, 253-253

Duggins D.O., Simenstad C.A. & Estes J.A. (1989) Magnification of secondary production by kelp detritus in coastal marine ecosystems. *Science*, 245, 170-173

Estes J.A. & Duggins D.O. (1995) Sea otters and kelp forests in Alaska: generality and variation in a community ecological paradigm. *Ecol. Monogr.*, 65, 75-100

Foster M.S., Edwards M.S., Reed D.C., Schiel D.R., Zimmerman R.C., Steele M.A., Schroeter S.C., Carpenter R.C., Kushner D.J. & Halpern B.S. (2006) Top-down vs. bottom-up effects in kelp forests. *Science*, 313, 1737-1739

Halpern B.S., Cottenie K. & Broitman B.R. (2006) Strong top-down control in Southern California kelp forest ecosystems. *Science*, 312, 1230-1232

Hurd C.L. (2000) Water motion, marine macroalgal physiology, and production. *J. Phycol.*, 36, 453-472

Johnson S.W., Murphy M.L., Csepp D.J., Harris P.M. & Thedinga J.F. (2003) A survey of fish assemblages in eelgrass and kelp habitats of southeastern Alaska. National Marine Fisheries Service, NOAA Technical Report NMFS-AFSC-139

Lane C.E., Mayes C., Druehl L.D. & Saunders G.W. (2006) A multi-gene molecular investigation of the kelp (Laminariales, Phaeophyceae) supports substantial taxonomic re-organization. *J. Phycol.*, 42, 493-512

Lindstrom S.C. (2009) The biogeography of seaweeds in Southeast Alaska. *J. Biogeogr.*, 36, 401-409

Lüning K., Yarish C. & Kirkman H. (1990) *Seaweeds: their environment, biogeography, and ecophysiology*. Wiley-Interscience, New York.

Murphy M.L., Johnson S.W. & Csepp D.J. (2000) A comparison of fish assemblages in eelgrass and adjacent subtidal habitats near Craig, Alaska. *Alaska Fish. Res. Bull.*, 7, 11-21

Perkol-Finkel S., Shashar N. & Benayahu Y. (2006) Can artificial reefs mimic natural reef communities? The roles of structural features and age. *Mar. Environ. Res.*, 61, 121-135

Reed D.C. (1990) The effects of variable settlement and early competition on patterns of kelp recruitment. *Ecology*, 71, 776-787

Reed D.C., Raimondi P.T. & Washburn L. (2000) Patterns and consequences of spore dispersal in the giant kelp, *Macrocystis pyrifera. J. Phycol.*, 36, 56-56

Reed D.C., Schroeter S.C. & Raimondi P.T. (2004) Spore supply and habitat availability as sources of recruitment limitation in the giant kelp *Macrocystis pyrifera* (Phaeophyceae). *J. Phycol.*, 40, 275-284

Reed D.C., Schroeter S.C. & Huang D. (2005) Final Report on the Findings and Recommendations of the Experimental Phase of the SONGS Artificial Reef Mitigation Project. California Coastal Commission, San Francisco, CA 136 pp

Reed D.C., Schroeter S.C., Huang D., Anderson T.W. & Ambrose R.F. (2006) Quantitative assessment of different artificial reef designs in mitigating losses to kelp forest fishes. *Bull. Mar. Sci.*, 78, 133-150

Reimers H. & Branden K. (1994) Algal colonization of a tire reef - influence of placement date. *Bull. Mar. Sci.*, 55, 460-469

Rule M.J. & Smith S.D.A. (2005) Spatial variation in the recruitment of benthic assemblages to artificial substrata. *Mar. Ecol. Prog. Ser.*, 290, 67-78

Sala E. & Graham M.H. (2002) Community-wide distribution of predator–prey interaction strength in kelp forests. *Proc. Nat. Acad. Sci.*, 99, 3678–3683

Simenstad C.A., Estes J.A. & Kenyon K.W. (1978) Aleuts, sea otters, and alternate stable-state communities. *Science*, 200, 403-411

Steimle F., Foster K., Kropp R. & Conlin B. (2002) Benthic macrofauna productivity enhancement by an artificial reef in Delaware Bay, USA. *ICES J. Mar. Sci.*, 59, S100-S105

Steneck R.S., Graham M.H., Bourque B.J., Corbett D., Erlandson J.M., Estes J.A. & Tegner M.J. (2002) Kelp forest ecosystems: biodiversity, stability, resilience and future. *Environ. Conserv.*, 29, 436-459

Svane I. & Petersen J.K. (2001) On the problems of epibioses, fouling and artificial reefs, a review. *Mar. Ecol.*, 22, 169-188

Wyllie-Echeverria T., Wyllie-Echeverria S., Duggins D. & Young C. (2005) Curtis Wharf and Dock Kelp Mitigation Efforts--Final Report (2001-2005): Establishment of Kelp Habitat. Port of Anacortes, Anacortes, WA, 47 pp

# Chapter 1

# COLONIZATION POTENTIAL OF UNDERSTORY KELPS IN A SOUTHEAST ALASKAN GLACIAL FJORD[1]

---

[1] Okamoto, D.K. & G.L. Eckert. 2009. Colonization potential of understory kelps in a Southeast Alaskan glacial fjord. Prepared for Marine Ecology Progress Series.

## ABSTRACT

The capability for colonizing newly available substrata represents a critical component of population persistence in competitive and disturbance prone environments. Knowledge of such potential, its timing, and its local constraints remain limited for many kelp species. In a Southeast Alaskan fjord, we 1) surveyed several subtidal understory kelp reefs to determine patterns of variability, 2) empirically determined colonization potential of kelps to newly available substrata, including small clearings and artificial reefs in comparison to undisturbed habitats and 3) determined how timing of space availability influenced kelp recruitment. In this fjord, kelps and algal crusts (kelp competitors) existed at all six surveyed sites and varied most within transects rather than among transects or reefs, with some exceptions. At two study locations on either side of a single cove, kelp recruits (< 6 cm tall) appeared within several months to both small clearings and small plots on artificial reefs in greater densities than in undisturbed, control plots with established kelp canopies and algal crusts. However, these differences were not consistent at each location, and highly variable. Moreover, treatment effects differed by size class. Laminariaceae (*Saccharina bongardiana* f. *subsimplex* and *Laminaria yezoensis*) juvenile kelps (< 20 cm tall) occurred in consistently greater densities at one location. Juvenile density also differed by species. Our results show *A. clathratum* juveniles occurred in only 4% of plots in contrast to Laminariaceae juveniles which occurred in 52% of plots, despite the fact that dense adult stands of *A. clathratum* and Laminariaceae kelps rested within several meters of cleared plots and artificial reef plots (averaging 4.1 $m^{-2}$ & 9.5 $m^{-2}$ respectively). While sediment covered an average of

35% of plots, sediment did correlate significantly with kelp recruit or juvenile densities which suggests a robustness of kelp recruitment to sedimentation. Larger plots showed artificial reefs consistently hosted far more kelp recruits than natural reefs. Lastly, kelps recruited in consistent densities to settlement tiles placed in the water between July and mid-December, but none recruited to tiles introduced the following March, indicating settlement ends sometime beforehand. Our results demonstrate that understory kelps in this region have immense capacity to rapidly colonize clearings and artificial reefs, and bare space introduced from summer to late fall, with large variability and potentially dramatic differences among species.

## INTRODUCTION

The magnitude of species' colonization potential can dramatically influence how populations respond to both competition (Tilman 1994, Amarasekare 2003) and disturbance (Sousa 1980, Tilman 1988). In temperate through polar seas, intense disturbance regimes and competition often characterize shallow-subtidal environments with high potential for productivity. For kelp forests in particular, a variety of small and large scale disturbances such as storm events (Dayton et al. 1992), urchin grazing (Steneck et al. 2002) or shifts in oceanographic conditions (Dayton et al. 1999, Matsunaga et al. 1999) can destroy adult kelp stands. Kelps thrive in disturbance-prone environments, exemplified by their production of massive amounts of organic carbon (Duggins et al. 1989, Simenstad et al. 1993, Bustamante & Branch 1996), amplification of secondary productivity (Duggins et al. 1989, Bustamante & Branch 1996, Duggins & Eckman 1997) and subsidization of external consumers (Britton-Simmons et al. 2009). Yet such productivity results in competition for light (Reed & Foster 1984) and primary space (Reed 1990). Because of their susceptibility to disturbance and intense competition, colonization potential for kelp forests represents a critical feature of their dynamics and productivity.

Much of the literature concerning kelp forest recruitment in response to competition and disturbance comes from open coast, temperate regions (see Steneck et al. 2002 for review, but see Dayton 1975, Duggins 1980, Leinaas & Christie 1996); thier productivity regimes differ substantially from those in protected, subarctic waters. In the fjords of Southeast Alaska, seasonality in water column stratification and temperature regulate productivity (Bruce et al. 1977, Weingartner et al. 2009), in contrast to California or other areas where seasonal upwelling is primarily responsible (Bakun 1990). Southeast Alaska hosts high nutrient concentrations during fall and winter until spring runoff and warming-induced stratification trigger phytoplankton blooms. Blooms in turn deplete nutrients throughout the summer to depths of 90 m until fall mixing events reintroduce water column homogeneity (Iverson et al. 1974, Bruce et al. 1977, Weingartner et al. 2009). Such oceanographic differences, in combination with strong seasonal variation in daylength, the presence of (receding) glaciers, and precipitation ranging from 116 to 215 cm per year near Juneau, Alaska (Wing et al. 2006) indicate Southeast Alaskan benthic macroalgae inhabit a physical environment which abides by different dynamics than those in temperate regions, and thus may invest in different strategies of colonization with respect to rate and timing. Documenting colonization and recruitment dynamics can serve as a first step in understanding the adaptation of these ecologically valuable, habitat-generating, primary producers to this environment.

In Southeast Alaska, forecasted climatic changes include large increases in precipitation along Alaska's coastline (Meehl et al. 2005) and the disappearance of glaciers (Larsen et al. 2007) which serve as major community drivers in nearby benthic, marine environments (Carney et al. 1999, Wlodarska-Kowalczuk et al. 2005). Southeast Alaska's glaciers discharge exceptionally high sediment loads (Hallet et al. 1996), which may induce significant mortality of kelp recruits (Dayton 1985) or invertebrates and other algae which compete with kelps for space, but may facilitate increased diversity or individual algal abundances (Airoldi & Cinelli 1997). Silt laden glacial discharge can dramatically decrease transmittance of UV radiation (Hanelt et al. 2001) which may impact *Laminaria saccharina* spore release (Makarov & Voskoboinikov 2001) and decrease its primary productivity (Apprill & Lesser 2003). Yet subtidal phycology in this region remains a wholly unstudied realm (Lindstrom 2009) despite such impending changes in Southeast Alaska's protected waters, the importance of subtidal kelp forests in this region and the discrepancies between subarctic and temperate waters.

In Southeast Alaska, the productivity of understory kelp forests provides the foundation for many rocky, nearshore ecosystems, generating nursery, spawning, and foraging environments for fish (Murphy et al. 2000, Johnson et al. 2003) invertebrates, and marine mammals (Estes & Duggins 1995). Because of such productivity, biological interactions often control kelp recruitment densities or survival. Biological constraints to kelp recruitment and survival include recruitment inhibition by algal crusts (Okamoto et al. 2009), grazing by benthic mesograzers (Duggins et al. 2001, Sala & Graham 2002), light reduction from surface and subtidal canopies (Reed & Foster 1984) and algal whiplash by prostrate kelps and other benthic macroalgae (Kennelly 1987, Britton-Simmons 2004). Because of the diversity of negative impacts from the biological community on young kelps, recruitment to bare space provides the best index of colonization potential. Yet many benthic species often require not only bare space for successful recruitment, but require that its availability is adequately timed for seasonal reproduction and growth (Levin 1984).

Many high latitude, perennial, subtidal canopy species exhibit seasonal life histories and reproductive cycles. In Southeast Alaska in Laminariaceae kelps, including

*Saccharina bongardiana* f. *subsimplex* (Setchell & N.L. Gardner) and *Laminaria yezoensis* (Miyabe) exhibit pseudoperennial life histories (Okamoto, pers. obs, but see Druehl et al. 1987) in which the adult meristem and stipe persist, and thalli begin regrowth in the winter, persist through summer and senesce in the fall (Lüning 1969). Other kelps including the perennial kelp *Agarum clathratum* (Dumort) retain their thallus through the winter (Dayton 1975). On *S. bongardiana* and *L. yezoensis* a single reproductive sorus appears at the base of the thallus above the meristem in the fall (Figure 1.1). In contrast, *A. clathratum* displays fertile sori from mid-summer through winter (Okamoto, pers. obs.). These different life histories suggest that seasonal variation in competition, sporulation, timing of settlement and recruitment occur. Thus, the time in which space becomes available (either through disturbance or artificial introduction) likely influences recruit abundance. In subtidal habitats, timing of space availability may alter the order in which species settle (Levin 1984, Reimers & Branden 1994) or upon growth conditions when space becomes available (Airoldi 2000). While Stekoll & Else (1992) document when kelp recruits appear throughout the year in Southeast Alaska, appearance of kelp recruits does not indicate when settlement timing occurs. In fact, some subtidal macroalgal microscopic life-stages can overwinter when the adult thallus is gone (Edwards 2000). Moreover kelp gametophytes may grow slowly in light limited conditions but when stimulated with light they can produce viable sporophytes. Therefore appearance of recruits does not necessarily indicate the timing of settlement. Understanding how timing of space availability influences recruitment can provide basic information regarding when species recruit and a qualitative evaluation of how certain experimental results may change if experiments were performed at different times.

Objectives for this study included documenting kelp colonization potential on newly available substrata, revealing the influence of timing of space availability on kelp recruitment and documenting general patterns of kelp community composition and variability for contextual purposes. Surveys of natural reefs provide context by demonstrating average species densities, as well as how species and communities vary among and within reefs. By surveying newly installed artificial reefs and clearings in paired natural reefs, we estimated recruitment densities to those large bare areas, to small gaps in understory kelp communities and within undisturbed kelp communities. Lastly, we investigated the timing of kelp settlement and the influence of timing of space availability by evaluating recruitment on substrate deployed at different times. These experiments and observations provide novel, basic information regarding the colonization potential and variability of understory kelps in this glaciated, subarctic fjord.

## METHODS

### Lynn Canal Reef Surveys

We evaluated understory kelp community structure and variability in Lynn Canal, Southeast Alaska by surveying six shallow subtidal, exposed, rocky reefs supporting productive understory kelp communities (Figure 1.2). At each site, divers laid two 30 m transects parallel to shore at 6 m below mean low low water (MLLW) in series and separated by 10 m. We placed 1 $m^2$ quadrats systematically every 5 m along each transect line. In each 1 $m^2$ quadrat we enumerated the density of each kelp species by counting stipes, and then percent understory canopy cover by *Agarum clathratum* and Laminariacaean kelps (*Saccharina bongardiana* and *Laminaria yezoensis*) from above the quadrat. We could count the two Laminariacaean kelp species individually for stipe densities; however because the two Laminaraiceaen kelps are only differentiable by the holdfast we lumped these species as Laminariaceae for estimates of percent cover by blades. Within each 1 $m^2$ quadrat, we placed a 50 x 50 cm quadrat strung with a 10 x 10 grid and estimated percent of cover by red algae and other upright algal species as well as enumerated kelp recruits and juveniles. We then estimated percent cover of the benthos by encrusting algal species and other sessile species, as well as sand, silt, and rock using point-contact with 20 systematically determined points on the 9 x 9 grid.

### *Statistical Analyses*

We evaluated variability of the kelp community in two ways: first by addressing kelp species collectively in a multivariate setting and then by addressing each kelp species, kelp recruits, and kelp competitors individually using analysis of variance (ANOVA). For multivariate analyses and univariate ANOVAs we treated site and transect as random effects. We nested transect within site because each transect belongs only to the reef in which it rests. We natural log transformed ( + 1 ) all response variables to meet assumptions of normality and heterogeneity of variance in these and all subsequent analyses unless otherwise noted. For these and subsequent ANOVA models we tested model assumptions using Shapiro Wilk's W test and Levene's test.

We evaluated variability of the kelp assemblages as a whole with two multivariate analyses with variables including log ( +1 ) density of each of the kelps *Laminaria* *yezoensis*, *Saccharina bongardiana*, and *Agarum clathratum* as well as kelp recruits. Prior to these analyses, we standardized variables by the maximum observed value for each, and then calculated a matrix of Bray-Curtis similarities. Using this matrix, we performed an ordination via non-metric multidimensional scaling (nMDS) and plotted the first two axes. With the same matrix, we generated components of variation for the different scales (among site, between transect within site, and residual (among replicate plots within transects)) using PERMANOVA (permutational analysis of variance) (Anderson 2001). PERMANOVA estimates components of variation analogous to variance components from univariate ANOVA (Anderson et al. 2008), and allowed us to test whether variability among sites and between transects within site differed significantly from zero. Because PERMANOVA assumes homogeneity of multivariate dispersion (Anderson 2001), we tested for violations using PERMDISP. We performed these analyses using PRIMER (Clarke & Gorley 2006).

For univariate analyses, we estimated variance components using ANOVA output as in Sahai and Ageel (2000) for reef, transect within reef, and residual to determine how communities vary with regards to these factors. Individual response variables included density of each kelp species, percent cover by Laminariaceae canopy, percent cover by *Agarum clathratum* canopy, density of kelp recruits, and percent cover of the rock by brown algal crusts, non-calcified red algal crusts, and calcified algal crusts. We performed these and all subsequent analyses in R (R Development Core Team 2009) unless otherwise noted.

## Kelp Recruitment on Natural Reefs, Disturbed Habitat and Artificial Reefs

We quantified kelp recruitment in 30 x 30 cm flat, horizontal plots at approximately 5 m below MLLW which included three treatments: 1) undisturbed natural reef plots (controls), 2) cleared natural reef plots and 3) artificial reef plots at the East and West Yankee Cove locations. Artificial reef plots included newly installed artificial reefs at Yankee Cove in the southern Lynn Canal near Juneau, Alaska (Figure 1.2). On either side of the peninsula bordering Yankee Cove (Figure 1.2, Figure 1.3), natural rocky habitats descend to flat, sandy substrate at approximately 6 - 8 m below MLLW. In December, 2007 two artificial reefs were introduced on these East and West sandy habitats (Figure 1.2), with a gap of 1 -5 m separating each artificial reef from the nearby natural reef. Artificial reefs are composed of granite quarry rock 0.5-1.0 m in diameter stacked one to three rock layers thick (Figure 1.4 A) with dimensions of 30 m x 10 m. We surveyed all natural reef plots in September 2007. In December, 2007 we cleared natural reef plots by removing non-encrusting algae, encrusting algae, and sessile animals using chisels, hammers, and scraping implements. We surveyed all plots in June, 2008 for density of kelp recruits (defined as kelps < 6 cm total length), kelp juveniles (defined as < 20 cm total length) as well as percent cover of other macroalgae, sessile invertebrates and sediment.

While these small plots (0.09 $m^2$) provided a manageable size for removal of encrusting algae, they may overestimate variability in the event of patchy recruitment and their isolation to flat, horizontal substrata may not accurately represent general recruitment patterns to the heterogeneous habitat. For this reason we also surveyed larger quadrats (0.25 m$^2$) on each artificial and natural reef by systematically placing six 50 x 50 cm quadrats every 5 m along each of two 30 m transects per reef in July, 2008. Use of larger quadrats allowed for better estimates of true recruitment densities, as recruits often occur patchily rather than uniformly. These systematic surveys allowed for illustrating overall recruitment densities on artificial versus natural reefs which included more than just horizontal, flat substrata portrayed in the 30 x 30 cm fixed plot experiment. We laid transects on natural reefs in series, separated by approximately 20 m while we laid artificial reef transects in parallel, separated by approximately 5 m.

### *Statistical Analyses*

In evaluating kelp recruit and juvenile densities in our 30 x 30 cm experimental plots, we tested for effects of location (East versus West), treatment (undisturbed, cleared and artificial reef), and location-treatment interaction on recruit density and juvenile density with two-way crossed ANOVAs. In the case of a significant interaction, we utilized Tukey's HSD for comparisons of cell means to describe the interaction. We then estimated relationships between 1) kelp recruits and 2) juveniles with other species and sediment percent cover in these plots using linear regression. In analyzing our systematic transect surveys of Yankee Cove natural and artificial reefs, we tested for effects of location (East versus West), reef type (natural vs. artificial), location-reef type interaction and transect nested in reef type at each location on recruit density using a two-way, partially nested ANOVA.

## Kelp Recruitment Timing Experiment

We measured the timing of kelp recruitment by deploying 6 x 6 cm ceramic tiles in July, August, September, October, and December, 2007 and March, 2008 to stations at 5, 6, 7, 8, 9 and 10 m below MLLW along the East and West Yankee Cove locations. We placed all stations at the edge where the rocky reefs meet sand. Each station consisted of a large cinder block that anchored two plastic, perforated pipes stretched horizontally. We suspended tiles 0.5 m above these pipes with monofilament and floats to minimize the effect of consumers, local variation in water motion and adult kelp canopies (Figure 1.5). We deployed two tiles per station in July 2007 and December 2007 because July represents the earliest period where reproductive kelps were observed and December corresponded to artificial reef installation. In other periods we deployed only one tile per station due to effort limitations and the difficulty of tile deployment. Winter storms destroyed the shallowest station at the West location and some individual tiles on other stations resulting in a slightly unbalanced design. Because kelp recruits emerged over a period of several months in the spring and early summer, we surveyed tiles in September, 2008 to allow kelp recruit emergence and facilitate comparison between tiles. Because of the high density of kelp recruits on tiles, divers counted only larger recruits (3 – 6 cm) and then photographed tiles *in situ* for quantifying smaller recruits (0 – 3 cm) in from photos. We analyzed photos by counting all identifiable kelps smaller than 3 cm without magnifying the photograph to ensure consistency in enumeration. We then combined counts of both size classes for total number of kelp recruits.

### *Statistical Analyses*

Because of a high abundance of zeros, we tested the effect of tile deployment time on recruit abundance using two analyses. We first tested the effect of timing of deployment (as a continuous variable) on the presence or absence of kelp recruits using logistic regression. With this model we generated predicted probabilities of observing one or more recruits following deployment with 95% confidence intervals. We then eliminated periods where recruitment probability approached zero, and tested for differences in density between sites and among months of deployment (nominal) using a repeated measures analysis with the functoin *lme* (linear mixed effects model) in R (R Development Core Team 2009), including station as the random factor. This method, while similar to repeated measures ANOVA, uses restricted maximum likelihood estimation and allows use of our unbalanced design.

## RESULTS

### Lynn Canal Reef Surveys

We found the kelps *Saccharina bongardiana* and *Agarum clathratum* as well as recruits at all reefs, while *Laminaria yezoensis* was absent from two reef (Figure 1.6 A-D). PERMANOVA results show that collectively, the kelp community varied significantly between transects within reefs (Figure 1.7 B, Table 1.1), varied least among reefs, and exhibited the greatest degree of variability among replicate plots within each transect, hereafter referred to as residual variation (Figure 1.7 B, Table 1.1). Graphical depiction of the dispersion of the kelp community via ordination (nMDS) illustrates separation of reef point clouds (Figure 1.7 A), but it remains minor in comparison to overall dispersion. Thus, despite *L. yezoensis'* absence from two reefs, the kelp assemblage (all kelp species plus recruits) variation between replicate plots and transects within reefs was greater than reef variation.

On a univariate scale, *Saccharina bongardiana, Agarum clathratum*, and kelp recruits exhibited mostly residual variation rather than variation among transects within reef or among reefs as indicated by the magnitude of estimated variance components (Figure 1.6 E-G). For these variables, we could not reject that variance among reef or transect within reef differed from zero at $\alpha = 0.05$ (Table 1.2). In contrast, the fact that we found the kelp *Laminaria yezoensis* (Figure 1.6 D) at only four of the six sites made estimates of variance components through ANOVA unreliable (because of a high abundance of zeros). Kelp canopies and algal crusts covered a large percentage of surveyed plots on average ($\bar{x}_{kelps} = 59\% \pm 35$ SD and $\bar{x}_{crusts} = 46\% \pm 27$ SD when combining taxa; n = 72, Figure 1.8 A-E). Most of the variance for algal crusts and canopies of *Agarum clathratum* and Laminariaceae rested in the residual, with some variation for brown and red crusts among reefs, albeit not statistically different than zero (Figure 1.8 G-K, Table 1.2). The other major space occupier at some reefs, the barnacle *Balanus crenatus* existed only at the two reefs without *L. yezoensis* (Figure 1.8 F, Figure 1.6 D).

## Kelp Recruitment on Natural Reefs, Disturbed Habitat and Artificial Reefs

Artificial reef plots and cleared natural reef plots hosted greater kelp recruit density at both locations when compared to control plots (non-cleared plots on natural reefs) ($\bar{x}_{clear}$ = 231 m$^{-2}$ ± 303 SD and $\bar{x}_{AR}$ = 116 m$^{-2}$ ± 112 SD versus $\bar{x}_{control}$ = 13 m$^{-2}$ ± 26 SD, with n = 20, 20, and 14, respectively, Figure 1.9 A, Table 1.3). The West locations had fewer recruits ($\bar{x}$ = 89 m$^{-2}$ ± 110 SD) than Eastern locations ($\bar{x}$ = 171 m$^{-2}$ ± 274 SD, and 28, Table 1.3), yet a significant interaction between treatment and location (Table 1.3) shows an inconsistency where far more kelps recruited to East cleared plots than West cleared plots, but fewer kelps recruited to East artificial reef plots than West artificial reef plots (Figure 1.9 A).

We found a distinct species specificity in juvenile kelp density in our control, cleared, and artificial reef plots (Figure 1.9 B, C). While adults of *Agaum clathraum*, *Saccharina bongardiana* and *Laminaria yezoensis* were present at both natural reef locations (Figure 1.6 A-D), we found only 4% of plots hosted *A. clathratum* juveniles (on one East and one West natural reef scraped plots, n = 4 and 3, respectively, Figure 1.9 C) and 54% of plots hosting Laminariaceae (lumping *S. bongardiana* and *L. yezoensis*) juveniles. When examining Laminariaceae juvenile density among plot types and location, a very different pattern emerged than we saw for the recruits. We observed significantly more Laminariaceae juveniles on the West plots ($\bar{x}$ = 111 m$^{-2}$ ± 60 SD) than on the East plots ($\bar{x}$ = 11 m$^{-2}$ ± 28 SD; Figure 1.9 B, Table 1.3), but no effect of treatment or interaction between the two.

Sediment covered all treatments at all locations (Figure 1.9 F), with average percent cover of 36 % ( ± 27 SD) of cleared and artificial reef plots with a range of 0 to 95 % cover. Neither kelp recruits nor juveniles showed significant linear correlation with percent sediment cover ($F_{1,52} = 0.22$ and 0.09, $p = 0.64$ and 0.75, respectively, Figure 1.10 A, B). Green algae (Ulvaceae, Figure 1.9 D) recruited in large quantities at the West artificial reef; barnacles (*Balanus crenatus*, Figure 1.9 E) recruited in all treatment type and location combinations except at the West artificial reef; and red algal recruitment was negligible (1.5 % ± 3.5 SD for *Odonthalia setaceae*, the red algal species with the greatest average percent cover). Neither kelp recruit nor juvenile density correlated with percent cover of any of these taxa.

In systematically surveying larger 50 x 50 cm quadrats that were not restricted to flat, horizontal plots, we observed significantly more recruitment to the new artificial reefs ($\bar{x} = 66$ $m^{-2}$ ± 48 SD) versus natural reefs ($\bar{x} = 4$ $m^{-2}$ ± 7 SD, Figure 1.11, Table 1.4). Recruits occurred in slightly higher densities in the West locations ($\bar{x} = 40$ $m^{-2}$ ± 50 SD) versus those along East locations ($\bar{x} = 30$ $m^{-2}$ ± 42 SD, Figure 1.11, Table 1.4). We observed no significant interaction between location and reef type, but found significant differences between transects within each reef (Figure 1.11, Table 1.4).

### Kelp Recruitment Timing Experiment

Kelps settled on tiles deployed in July through December, 2007 but not on those installed in March, 2008 (Figure 1.12, Figure 1.13) which remained bare throughout the summer of 2008. The probability of recruitment (1 or more recruits) remains consistent from July through December when we prepared our experimental plots and deployed artificial reefs, but drops to zero by March (deviance = 43.27, df = 2, $p < 0.001$, Figure 1.12). When excluding March, 2008 tiles, recruitment abundance on tiles showed no difference with regards to period ($F_{4,53} = 0.98$, $p = 0.43$, Figure 1.12), or location (East vs. West, $F_{1,9} = 2.88$ $p = 0.124$). Surprisingly recruitment on tiles far exceeded that in artificial reef and cleared natural reef plots by several orders of magnitude, averaging 82 recruits per tile which translates to 7000 recruits $m^{-2}$ ± 8400 SD with 93% of non-March tiles with recruits. In contrast we saw an average of 0.8 juveniles per tile, with only 17% of non-March tiles with kelp juveniles.

## DISCUSSION

This study focused on documenting patterns of kelp recruitment in neighboring locations on bare versus occupied space, and on bare space introduced in different periods in time. Our results show that while understory kelps colonize small clearings and artificial reefs within several months, colonization occurred with dramatic variability and apparent differences among kelp taxa. Although a plethora of literature exists concerning the recruitment dynamics of benthic, subtidal species in temperate regions and open coast systems, this study provides a novel quantitative description of the variable colonization potential of kelps in this high latitude fjord.

Providing context for our experiments, Lynn Canal reef survey results demonstrate that kelps and algal crusts maintain consistent presence across reefs and that reefs provide accurate (although not necessarily precise) representations of one another with regards to the algal community. No significant variation in the kelp assemblage as a whole occurred among reefs, but rather occurred among transects within reef and in the form or residual variation. These results support the use of Yankee Cove reef habitats as generally representative of the structure of understory kelp dominated reef in the region in terms of the algal assemblage. An interesting exception to the overall pattern, one kelp and one space occupier existed patchily among reefs; *Laminaria yezoensis* existed at only four of six reefs with the barnacle *Balanus crenatus* at two of six. These two species only appeared in reefs lacking the other, suggesting a possible interaction or perhaps opposite population responses to external factors such as current or exposure differences.

At Yankee Cove, kelps recruited to bare areas in densities exceeding that in undisturbed communities indicating a dramatic influence of established biological communities. This rapid colonization of large bare areas agrees with previous temperate studies in California and Washington, where native kelps colonized newly available artificial reef habitats within one year (Reed et al. 2004, Wyllie-Echeverria et al. 2005). Similar phenomena occur following the disappearance of urchins from barren habitats in Nova Scotia (Johnson & Mann 1993) open coast areas of Alaska (Estes & Duggins 1995), California (Ebeling et al. 1985) and other regions (Steneck et al. 2002). It was surprising in our study that patterns of kelp recruitment varied at the East and West locations. Kelps recruited in the highest densities at the artificial reef at the West location but at the highest densities on the cleared plots at the East location. The combination of patchy recruitment densities and small plot sizes combined to provide large variability. Although we minimized the distance spores must travel in reaching artificial reefs and selected for homogeneous plots, zoospores can settle in highly variable densities within or near an adult stand (Reed 1990, Reed et al. 1997). Our systematic, larger 50 x 50 cm quadrats better accounted for this variability and show artificial reefs consistently hosted significantly more recruits than natural reefs at both locations. Collectively, these results illustrate the strong potential of kelps to colonize bare space in this region.

Our results show large differences both in Laminariaceae juvenile densities by location, despite only 100-200 meters of separation. Laminariaceae juveniles occurred in consistently greater densities on the West natural and artificial reef plots than on East natural and artificial reef plots. We suspect increased growth rates at the West locations resulting from environmental differences facilitated faster transition to the larger size class. West reefs lie approximately 100 m from the East reefs, yet because East reefs lie protected from the northern exposure, they may occupy slightly different physical habitats. West and East sites showed no difference in temperature profiles and only slight differences in salinity profiles through the photic zone (Figure 1.14). However, other water column properties such as turbidity or current velocity may cause such site differentiation. Water motion in particular can significantly alter growth and nutrient uptake (see Hurd 2000 for review) and development of microscopic or macroscopic sporophytes (Gordon & Brawley 2004). We speculate that the greater density of kelp juveniles and percent cover of Ulvaceae on the West artificial and natural reefs results in part from increased water motion and less turbidity around the West reefs. Moreover, because the East location lies on the protected side of the cove and the West location on the exposed side, we expect inconsistencies in the physical environment between the two locations may contribute to differences in propagule distribution as well as reproduction and development. Such differences were not isolated to kelps; both green algae and *Balanus crenatus* exhibited spatially explicit patterns. Thus, highly variable patterns of recruitment may arise from a combination of differential settlement, growth parameters, and rates of mortality induced from grazing or physical stress and other biological interactions. Such stochastic, location specific differences underscore not only strong variability in recruit densities, but also in size distributions associated with location.

Such different size distributions can result from factors such as grazing or density dependent effects (Dean et al. 1989). Greater density may increase competition among kelp recruits and depress transition rates to juvenile stages. Cleared plots on the East natural reef hosted more recruits but fewer juveniles that on the artificial reef 30 x 30 cm plots. Similarly, we saw high densities of recruits but few juveniles on settlement tiles. We show a vast discrepancy between the densities of recruitment on settlement tiles and in experimental plots. Because we minimized the influence of grazers on tiles, their increased densities may result from decreased grazer abundance in comparison to the benthos. Reduced recruitment from grazing may alleviate interspecific competition. Thus, the magnitude of colonization on tiles may provide an index of propagule supply, but does not represent true magnitudes of recruitment on the benthos.

While we could not differentiate kelp recruits of the three primary kelp species, an apparent taxa specificity in juvenile kelp abundance occurred in our experimental plots. *Agarum clathratum* juveniles ( < 20 cm) occurred in only 4 % of plots in comparison to the 52% of plots where we found Laminariaceae juveniles (including *Saccharina bongardiana* and *Laminaria yezoensis*). Such a difference may originate from differences in recruitment timing, growth rates, and/or reproductive output. Considering that *L. yezoensis, S. bongardiana* and *A. clathratum* adults existed consistently at both of our Yankee Cove natural reefs, we infer that propagule availability and environmental conditions are sufficient for sustaining populations of all three species. Marine benthic species frequently employ alternative strategies for competitively colonizing and retaining space (Levin 1984, Airoldi 2000). In northern Norway following removal of urchins, the annual kelp *Saccharina latissima* colonized quickly  followed by a slow subsequent colonization by the dominant perennial *Laminaria hyperborea* (Leinaas & Christie 1996).  Considering the different perennial life histories of *Agarum clathratum* and our Laminariaceae kelps, observed differences in juvenile abundance may result from different reproductive output in terms of timing of recruitment or overall quantity of propagules produced, a common occurance in sympatric kelps.  For example, in California, *Pterygophora californica* only produces spores from November through April (Reed et al. 1996) but sympatric *Macrocystis pyrifera* produces spores year round (Reed et al. 1996).  But unlike *M. pyrifera* and *P. californica*, the coexistence of *Agarum* spp. and Laminariaceae kelps in both the north Atlantic and north Pacific provides a uniquely provocative dynamic as these persist perennially, coexist and compete for the same location in the water column. Previous studies qualitatively support our observations of quick colonization by Laminariaceae kelps and slower recruitment of *Agarum* spp. in the San Juan Islands, Washington (Vadas 1968) and Nova Scotia (Johnson & Mann 1988). However, such regional comparisons of genera should be made carefully as species within individual genera may exhibit different patterns of reproduction in different areas, as shown by California *M. pyrifera* reproducing year round but not *Macrocystis integrifolia* in Alaska (Stekoll & Else 1992).  Considering that Laminariaceae often dominate *Agarum* spp. in competition (Dayton 1975, Duggins 1980), the difference in juvenile density between *A. clathratum* and Laminariaceae is intriguing and worthy of further study.

While sediments can decrease attachment capabilities of spores and induce gametophyte mortality by burial (Devinny & Volse 1978), in our experiment we saw no meaningful impact of sediment on kelp recruits or juveniles. Glacially fed riverine discharge in Southeast Alaska, which can serves as a proxy for glacial sedimentation, runs high in spring and summer months, but drops to near zero when kelps settle in late fall (Figure 1.15) near Juneau Alaska (Figure 1.2). Recruiting kelp stages may avoid the negative influence of sedimentation with early settlement, reproduction, and development of susceptible stages during the season of low freshwater discharge and sedimentation. We were not able to quantitatively assess sedimentation over time. It is possible that sedimentation could be important in later stages of kelp colonization and is a topic worthy of further study.

While our field experiment included the introduction of bare space in December, our settlement tile experiment demonstrates that space made available between summer and late fall holds a consistently high probability of hosting recruits the following spring (Figure 1.12), assuming adequate growth conditions exist. The density of recruitment remained homogeneous so long as the timing of space availability took place in that window, with settlement finishing before spring (although when settlement commences remains unknown). This pattern of late-fall settlement is similar to that found by Reed et al. (1988), who demonstrate a distinct spike in *Macrocystis pyrifera* and *Pterygophora californica* wintertime settlement. Several seasonal factors make late fall or early winter settlement advantageous in this cold marine environment. Storm intensity often increases in late fall and winter, which may significantly increase the availability of suitable habitat for colonization, particularly by displacing boulders covered with inhibitory algal crusts. Wintertime reduction in kelp canopies may free light to the benthos which becomes scarce at these latitudes in winter. Additionally, kelp gametophytes' capability to withstand extremely low temperatures and low light (Dieck 1993) allows them to survive when temperatures drop to lows of around 3° C (Figure 1.15). While some benthic taxa require disturbances which coincide precisely with abundance of their recruiting life stages for successful colonization (Levin 1984), we demonstrated that kelps can take advantage of space made available through half of the year.

The recruitment capabilities of species in disturbance prone, competitive environments can represent a critical component of population persistence. In this study, kelps rapidly colonized both artificial reefs as well as small clearings liberated from established competitors, and may do so as long as space becomes available during a large window from the summer through late fall. Moreover, differences between kelp taxa in patterns of recruitment exist. Such differences raise questions concerning what different strategies of reproduction or growth different kelp species employ and how these contribute to the interaction of these coexisting of kelp competitors Lynn Canal. Although we demonstrated a large colonization potential for kelps in this region, overall recruitment depends upon stochastic factors that can vary considerably by location and from plot to plot. These results illustrate that kelps are highly adapted to take advantage of bare space in many forms, albeit with dramatic variability in space with large differences among kelp species in this high latitude Alaskan fjord.

## ACKNOWLEDGEMENTS

We thank Jodi Pirtle, Bill Becthol, Jeff Douglas, Mike Stekoll, and the 2007 Research Experience for Undergraduates (NSF grant no. 0553000) and others who assisted with fieldwork for this project. We thank Chris Siddon who reviewed this manuscript, and Franz Mueter for statistical advice. This research was supported by the Alaska Department of Transportation and Public Facilities, Alaska Sea Grant and the Dr. H. Richard Carlson Scholarship.

## REFERENCES

Airoldi L, Cinelli F (1997) Effects of sedimentation on subtidal macroalgal assemblages: an experimental study from a Mediterranean rocky shore. J Exp Mar Biol Ecol 215:269-288

Airoldi L (2000) Responses of algae with different life histories to temporal and spatial variability of disturbance in subtidal reefs. Mar Ecol Prog Ser 195:1-92

Amarasekare P (2003) Competitive coexistence in spatially structured environments: a synthesis. Ecol Lett 6:1109-1122

Anderson MJ (2001) A new method for non-parametric multivariate analysis of variance. Austral Ecol 26:32-46

Anderson MJ, Gorley RN, Clarke KR (2008) PERMANOVA+ for PRIMER: guide to software and statistical methods. PRIMER-E, Plymoth, UK

Apprill AM, Lesser MP (2003) Effects of ultraviolet radiation on *Laminaria saccharina* in relation to depth and tidal height in the Gulf of Maine. Mar Ecol Prog Ser 256:75-85

Bakun A (1990) Global climate change and intensification of coastal ocean upwelling. Science 247:198-201

Britton-Simmons KH (2004) Direct and indirect effects of the introduced alga *Sargassum muticum* on benthic, subtidal communities of Washington State, USA. Mar Ecol Prog Ser 277:61-78

Britton-Simmons KH, Foley G, Okamoto D (2009) Spatial subsidy in the subtidal zone: utilization of drift algae by a deep subtidal sea urchin. Aquat Biol 5:233-243

Bruce HE, McLain DR, Wing BL (1977) Annual physical and chemical oceanographic cycles of Auke Bay, southeastern Alaska. NOAA Technical Report NMFS SSRF-712, National Marine Fisheries Service

Bustamante RH, Branch GM (1996) The dependence of intertidal consumers on kelp-derived organic matter on the west coast of South Africa. J Exp Mar Biol Ecol 196:1-28

Carney D, Oliver JS, Armstrong C (1999) Sedimentation and composition of wall communities in Alaskan fjords. Polar Biol 22:38-49

Clarke K, Gorley R (2006) PRIMER V6: User Manual/Tutorial. PRIMER-E, Plymouth, UK

Dayton PK (1975) Experimental studies of algal canopy interactions in a sea otter-dominated kelp community at Amchitka Island, Alaska. Fishery Bulletin 73:230-237

Dayton PK (1985) Ecology of kelp communities. Annu Rev Ecol Syst 16:215-245

Dayton PK, Tegner MJ, Edwards PB, Riser KL (1999) Temporal and spatial scales of kelp demography: The role of oceanographic climate. Ecol Monogr 69:219-250

Dayton PK, Tegner MJ, Parnell PE, Edwards PB (1992) Temporal and spatial patterns of disturbance and recovery in a kelp forest community. Ecol Monogr 62:421-445

Dean TA, Thies K, Lagos SL (1989) Survival of juvenile giant kelp: the effects of demographic factors, competitors, and grazers. Ecology 70:483-495

Devinny JS, Volse LA (1978) Effects of sediments on the development of *Macrocystis pyrifera* gametophytes. Mar Biol 48:343-348

Dieck T (1993) Temperature tolerance and survival in darkness of kelp gametophytes (Laminariales, Phaeophyta): ecological and biogeographical implications. Mar Ecol Prog Ser 100:253-253

Druehl LD, Cabot EL, Lloyd KE (1987) Seasonal growth of *Laminaria groenlandica* as a function of plant age. Can J Bot 65:1599-1604

Duggins DO (1980) Kelp beds and sea otters: an experimental approach. Ecology 61:447-453

Duggins DO, Simenstad CA, Estes JA (1989) Magnification of secondary production by kelp detritus in coastal marine ecosystems. Science 245:170-173

Duggins DO, Eckman JE (1997) Is kelp detritus a good food for suspension feeders? Effects of kelp species, age and secondary metabolites. Mar Biol 128:489-495

Duggins DO, Eckman JE, Siddon CE, Klinger T (2001) Interactive roles of mesograzers and current flow in survival of kelps. Mar Ecol Prog Ser 223:143-155

Ebeling AW, Laur DR, Rowley RJ (1985) Severe storm disturbances and reversal of community structure in a southern California kelp forest. Mar Biol 84:287-294

Edwards MS (2000) The role of alternate life-history stages of a marine macroalga: a seed bank analogue? Ecology 81:2404-2415

Estes JA, Duggins DO (1995) Sea otters and kelp forests in Alaska: generality and variation in a community ecological paradigm. Ecol Monogr 65:75-100

Gordon R, Brawley SH (2004) Effects of water motion on propagule release from algae with complex life histories. Mar Biol 145:21-29

Hallet B, Hunter L, Bogen J (1996) Rates of erosion and sediment evacuation by glaciers: A review of field data and their implications. Global Planet Change 12:213-235

Hanelt D, Tüg H, Bischof K, Gross C, Lippert H, Sawall T, Wiencke C (2001) Light regime in an Arctic fjord: a study related to stratospheric ozone depletion as a basis for determination of UV effects on algal growth. Mar Biol 138:649-658

Hurd CL (2000) Water motion, marine macroalgal physiology, and production. J Phycol 36:453-472

Iverson RL, Curl Jr HC, O'Connors Jr HB, Kirk D, Zakar K (1974) Summer phytoplankton blooms in Auke Bay, Alaska, driven by wind mixing of the water column. Limnol Oceanogr 19:271-278

Johnson CR, Mann KH (1988) Diversity, patterns of adaptation, and stability of Nova Scotian kelp beds. Ecol Monogr 58:129-154

Johnson CR, Mann KH (1993) Rapid succession in subtidal understorey seaweeds during recovery from overgrazing by sea urchins in eastern Canada. Bot Mar 36:63-77

Johnson SW, Murphy ML, Csepp DJ, Harris PM, Thedinga JF (2003) A survey of fish assemblages in eelgrass and kelp habitats of southeastern Alaska. NOAA Technical Report NMFS-AFSC-139, National Marine Fisheries Service

Kennelly SJ (1987) Inhibition of kelp recruitment by turfing algae and consequences for an Australian kelp community. J Exp Mar Biol Ecol 112:49-60

Larsen CF, Motyka RJ, Arendt AA, Echelmeyer KA, Geissler PE (2007) Glacier changes in southeast Alaska and northwest British Columbia and contribution to sea level rise. J Geophys Res 112:F01007

Leinaas HP, Christie H (1996) Effects of removing sea urchins (*Strongylocentrotus droebachiensis*): stability of the barren state and succession of kelp forest recovery in the east Atlantic. Oecologia 105:524-536

Levin LA (1984) Life history and dispersal patterns in a dense infaunal polychaete assemblage: community structure and response to disturbance. Ecology 65:1185-1200

Lindstrom SC (2009) The biogeography of seaweeds in Southeast Alaska. J Biogeogr 36:401-409

Lüning K (1969) Growth of amputated and dark-exposed individuals of the brown alga *Laminaria hyperborea*. Mar Biol 2:218-223

Makarov MV, Voskoboinikov GM (2001) The influence of ultraviolet-B radiation on spore release and growth of the kelp *Laminaria saccharina*. Bot Mar 44:89-94

Matsunaga K, Kawaguchi T, Suzuki Y, Nigi G (1999) The role of terrestrial humic substances on the shift of kelp community to crustose coralline algae community of the southern Hokkaido Island in the Japan Sea. J Exp Mar Biol Ecol 241:193-205

Meehl GA, Arblaster JM, Tebaldi C (2005) Understanding future patterns of increased precipitation intensity in climate model simulations. Geophys Res Lett 32: L18719.18711-L18719.18714

Murphy ML, Johnson SW, Csepp DJ (2000) A comparison of fish assemblages in eelgrass and adjacent subtidal habitats near Craig, Alaska. Alaska Fish Res Bull 7:11-21

Okamoto DK, Eckert GL, Stekoll MS (2009) Recruitment inhibition, reproductive inundation and coexistence between subtidal algal crusts and kelps. In: Okamoto DK. Competition and recruitment in Southeast Alaskan subtidal kelp communitiies. Masters Thesis, University of Alaska Fairbanks, Fairbanks, Alaska

R Development Core Team (2009) R: A language and environment for statistical computing. R. Foundation for Statistical Computing, Vienna, Austria

Reed DC (1990) The effects of variable settlement and early competition on patterns of kelp recruitment. Ecology 71:776-787

Reed DC, Anderson TW, Ebeling AW, Anghera M (1997) The role of reproductive synchrony in the colonization potential of kelp. Ecology 78:2443-2457

Reed DC, Ebeling AW, Anderson TW, Anghera M (1996) Differential reproductive responses to fluctuating resources in two seaweeds with different reproductive strategies. Ecology 77:300-316

Reed DC, Foster MS (1984) The effects of canopy shadings on algal recruitment and growth in a giant kelp forest. Ecology 65:937-948

Reed DC, Laur DR, Ebeling AW (1988) Variation in algal dispersal and recruitment: the importance of episodic events. Ecol Monogr 58:321-335

Reed DC, Schroeter SC, Raimondi PT (2004) Spore supply and habitat availability as sources of recruitment limitation in the giant kelp *Macrocystis pyrifera* (Phaeophyceae). J Phycol 40:275-284

Reimers H, Branden K (1994) Algal colonization of a tire reef - influence of placement date. Bull Mar Sci 55:460-469

Sahai H, Ageel MI (2000) The analysis of variance: fixed, random and mixed models. Birkhauser, Boston

Sala E, Graham MH (2002) Community-wide distribution of predator–prey interaction strength in kelp forests. Proc Nat Acad Sci 99:3678–3683

Simenstad CA, Duggins DO, Quay PD (1993) High turnover of inorganic carbon in kelp habitats as a cause of d 13 C variability in marine food webs. Mar Biol 116:147-160

Sousa WP (1980) The responses of a community to disturbance: the importance of successional age and species' life histories. Oecologia 45:72-81

Stekoll MS, Else PV (1992) The feasibility of *Macrocystis* mariculture in Southeast Alaska. The State of Alaska and the Japan Overseas Fisheries Cooperation Foundation, Tokyo

Steneck RS, Graham MH, Bourque BJ, Corbett D, Erlandson JM, Estes JA, Tegner MJ (2002) Kelp forest ecosystems: biodiversity, stability, resilience and future. Environ Conserv 29:436-459

Tilman D (1988) Plant strategies and the dynamics and structure of plant communities. Princeton University Press, Princeton, NJ

Tilman D (1994) Competition and biodiversity in spatially structured habitats. Ecology 54:2-16

Vadas RL (1968) The ecology of *Agarum* and the kelp bed community. PhD Dissertation, University of Washington, Seattle, WA

Weingartner T, Eisner L, Eckert GL, Danielson S (2009) Southeast Alaska: oceanographic habitats and linkages. J Biogeogr 36:387-400

Wing BL, Masuda MM, Taylor SG (2006) Time Series Analyses of Physical Environmental Data Records from Auke Bay, Alaska. NOAA Technical Memorandum NMFS-AFSC-166 National Marine Fisheries Service

Wlodarska-Kowalczuk M, Pearson TH, Kendall MA (2005) Benthic response to chronic natural physical disturbance by glacial sedimentation in an Arctic fjord. Mar Ecol Prog Ser 303:31-41

Wyllie-Echeverria T, Wyllie-Echeverria S, Duggins D, Young C (2005) Curtis Wharf and Dock Kelp Mitigation Efforts--Final Report (2001-2005): Establishment of Kelp Habitat. Port of Anacortes, Anacortes, WA, 47 pp

Figure 1.1: *Saccharina bongardiana* sloughing sorus tissue.

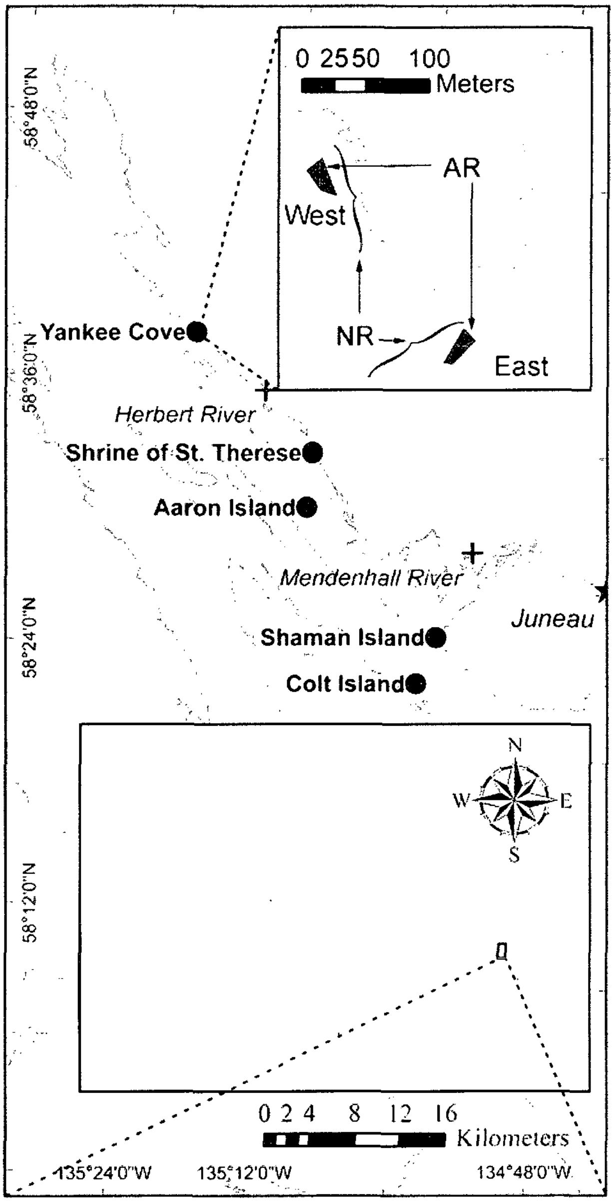

Figure 1.2: Map of the location of Lynn Canal, reef survey sites and Yankee Cove artificial reefs offshore of the low water shoreline at Yankee Cove. Black circles represent survey sites, and crosses represent river drainages. Artificial reef (AR) sites are indicated by black rectangles, natural reef (NR) sites are approximated by brackets, and East and West locations are denoted.

Figure 1.3: Yankee Cove.

Figure 1.4: The West Yankee Cove artificial reef in January, 2008.

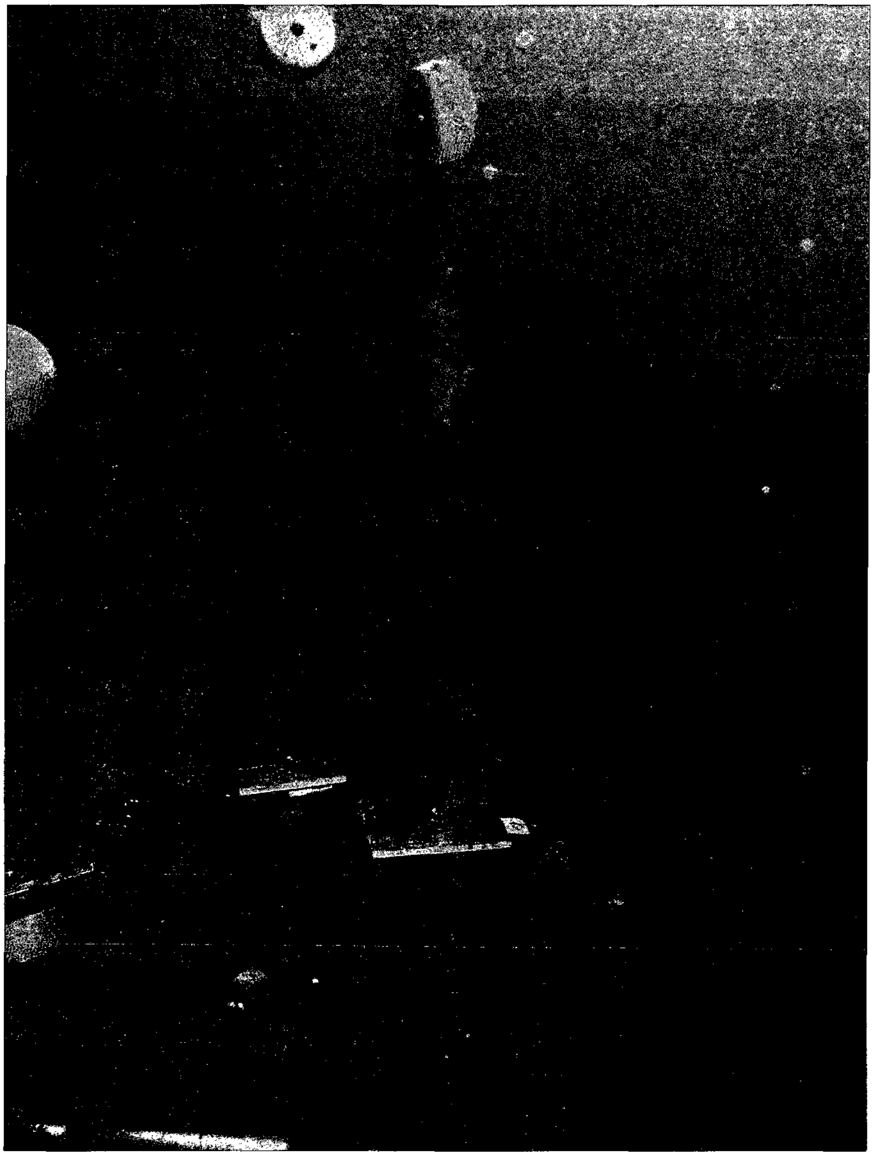

Figure 1.5: Settlement tiles installed in March, 2008 before kelp recruits appeared.

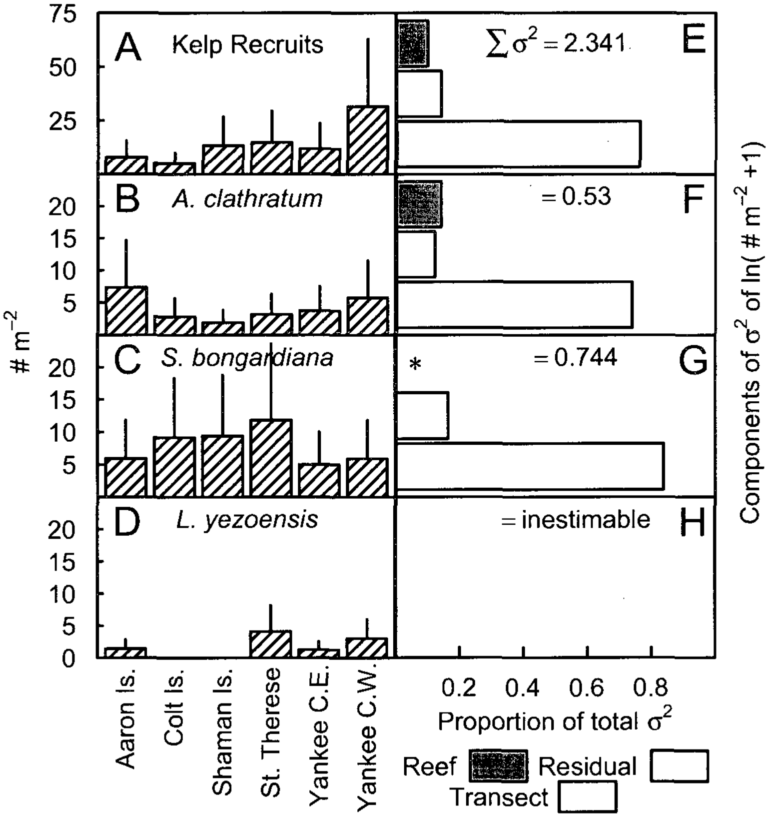

Figure 1.6: Density of Lynn Canal kelps, kelp recruits, and associated variance components. (A-D) Mean density of kelp recruits and adult kelps in the Lynn Canal by reef from surveys. Error bars represent 1 SD. (E-H) Proportion of variance from individual ANOVAs for recruit and adult kelp density (ln ( +1 ) transformed) from each spatial scale (reef, transect and residual). The sum of all variance components for each response variable is displayed in each figure. Inestimable indicates that we could not estimate variance components due to serious violations of homogeneity of variance and normality. Statistical tests for variance components are reported in table 1.2. *variance components rounded to zero because of negative estimates.

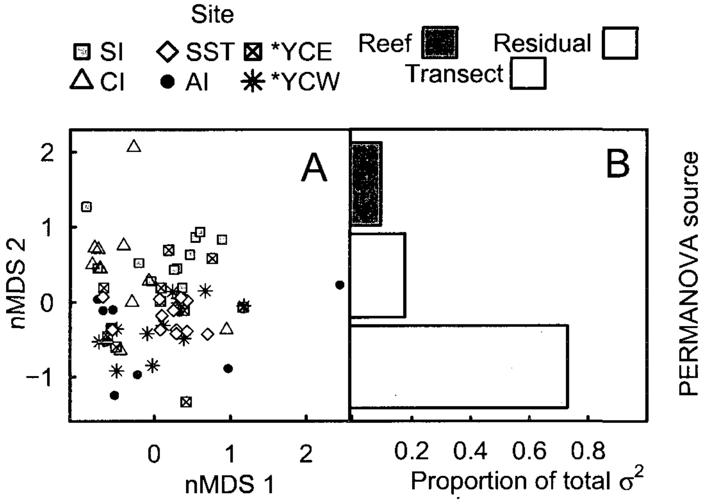

Figure 1.7: nMDS and PERMANOVA results showing (A) Non-metric multidimensional scaling (nMDS) plot based upon densities ($m^{-2}$) of three kelp species and kelp recruits from Lynn Canal reef surveys at six sites, calculated from a Bray-Curtis matrix of similarities using ln ( +1 ) transformed and standardized (by maximum) variables. Shown are the first two of three nMDS axes, stress = 0.12. Site abbreviations represent the following: SI = Shaman Island, CI = Colt Island, SST = Shrine of St. Therese, AI = Aaron Island, YCE = Yankee Cove East, YCW = Yankee Cove West. (B) Proportions of sum of components of variation from different spatial scales (reef, transect within reef and residual) estimated using PERMANOVA.

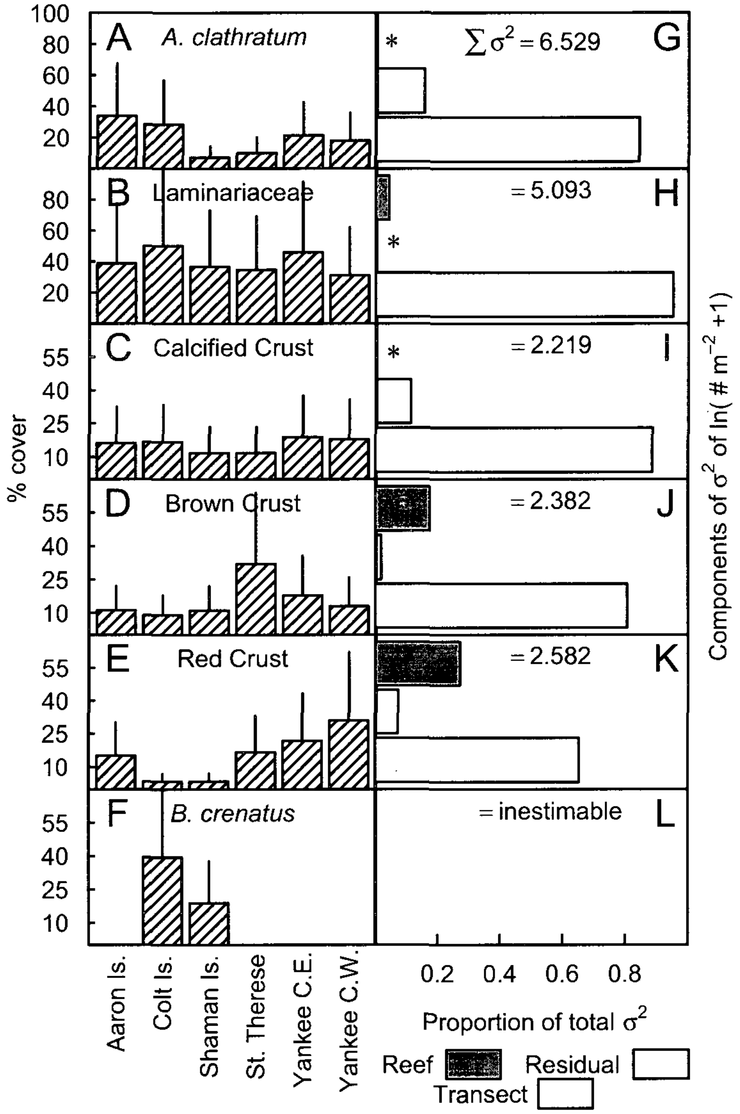

Figure 1.8: Percent cover and variance components of Lynn Canal benthic taxa. (A-F) Mean percent cover of kelp blades and competitors for by reef from surveys. Error bars represent 1 SD. (G-L) Proportion of variance from ANOVAs for recruit and adult kelp density (ln ( +1 ) transformed) representing reef, transect in reef, and residual. The sum of all variance components for each response variable is displayed in each figure. Inestimable indicates that we could not estimate variance components due to serious violations of homogeneity of variance and normality. Statistical tests for variance components are reported in Table 1.2. *variance components rounded to zero because of negative estimates.

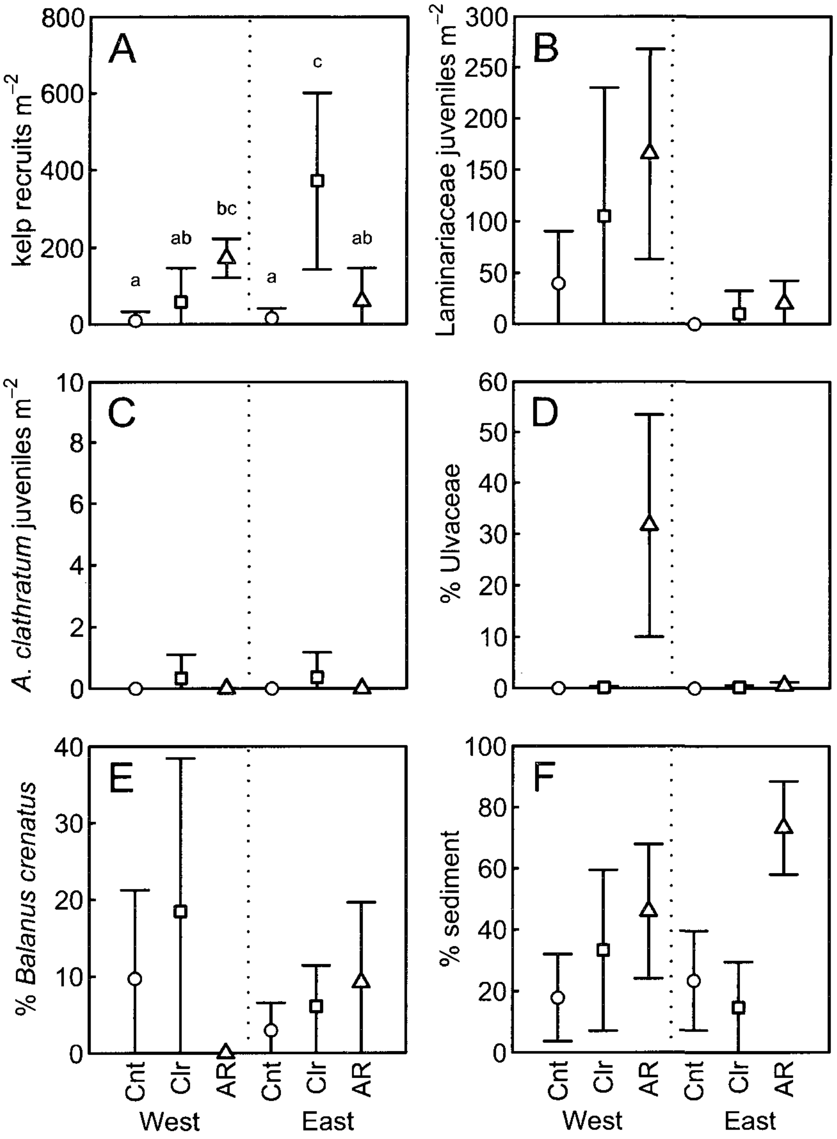

Figure 1.9: Density and percent cover of flat, horizontal 30 x 30 cm plots. Mean density of (A) kelp recruits (< 6 cm tall) with common letters indicating no statistical difference from Tukey pairwise comparisons, (B) Laminariaceae juveniles (< 20 cm tall), and (C) *Agarum clathratum* juveniles; percent cover by (D) Ulvaceae, (E) *Balanus crenatus* and (F) sediment in undisturbed control plots, cleared plots and artificial reef plots Error bars represent 95% CI.

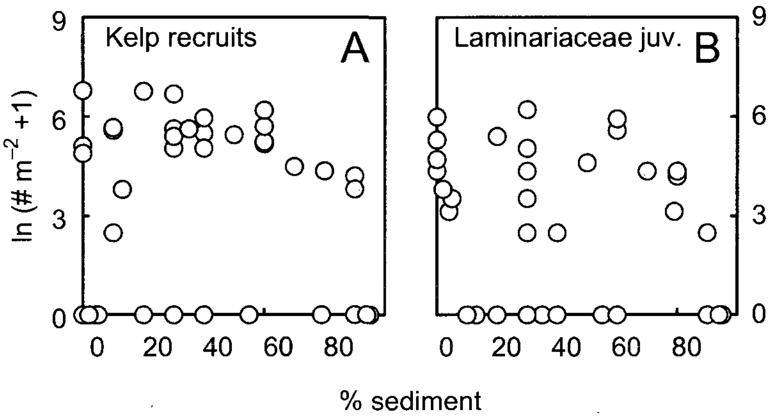

Figure 1.10: Kelp recruits and juveniles versus sediment. Kelp recruit (A) and Laminariaceae juvenile (B) densities (m-2, ln ( + 1 ) transformed) versus percent cover sediment in flat, horizontal 30 x 30 cm control, cleared, and artificial reef plots.

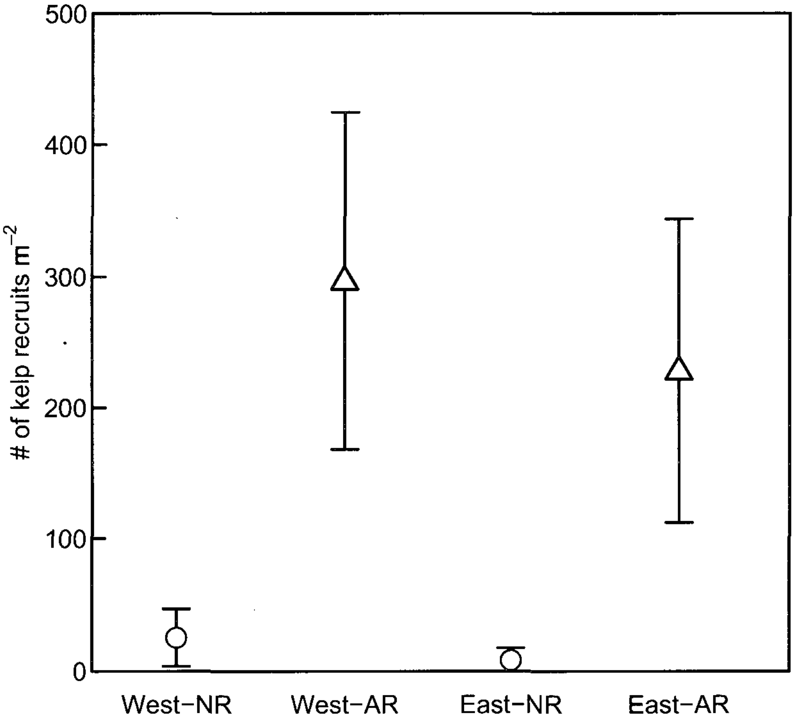

Figure 1.11: Kelp recruitment on artificial and natural reefs. Mean density of kelp recruits (< 6 cm length) in systematically surveyed 50 x 50 cm quadrats along natural and artificial reef transects. Grey circles represent natural reefs and grey triangles represent artificial reefs. Error bars represent 95% CI.

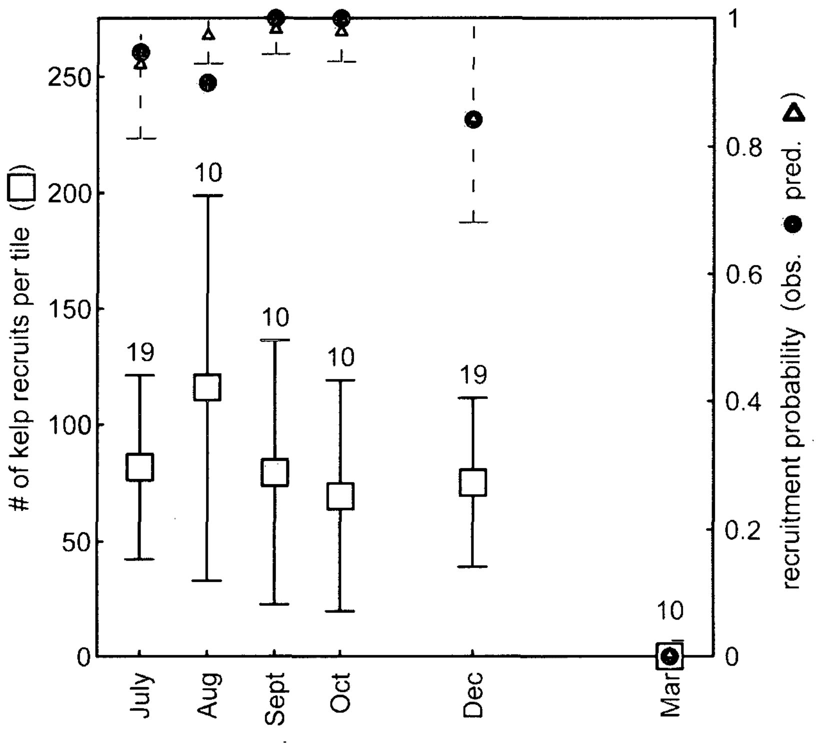

Figure 1.12: Kelp recruitment on settlement tiles. Mean number of kelp recruits (grey squares, left axis) on settlement tiles in September, 2008 versus the month in which they were deployed with the sample size denoted above with black error bars representing 95% CI. Proportion of tiles with recruits (dark circles, right axis) in September, 2008. Predicted probability of a tile hosting one or more recruits (grey triangles, right axis) from logistic regression with dashed error bars representing 95% CI of the model estimate.

Figure 1.13: Kelp recruits on a settlement tile along with the barnacle *Balanus crenatus* and *Margarites pupillus* in June, 2008.

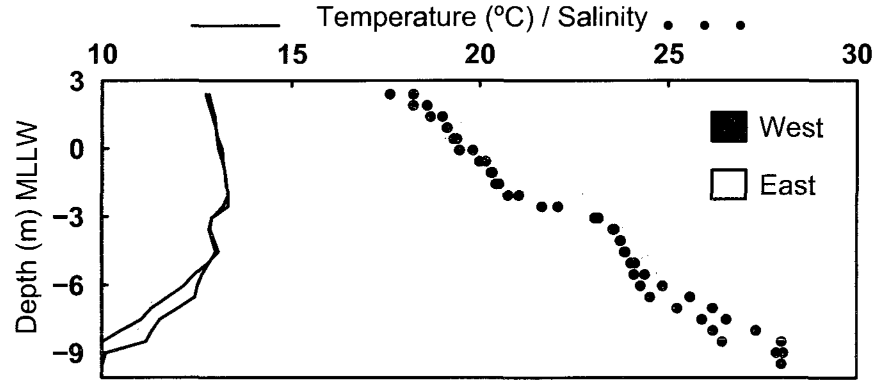

Figure 1.14: Temperature and salinity profiles at Yankee Cove East (grey) and West (black) locations by depth taken from a single CTD cast at a tidal height of 3 m, recording both on descent and ascent at each location .

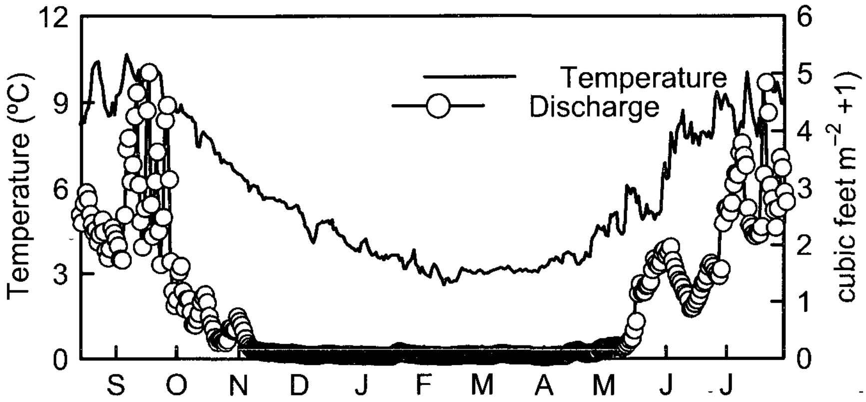

Figure 1.15: Daily minima in temperature and mean Mendenhall River discharge. Temperature data comes from a logger at 6 m below MLLW at Yankee Cove; discharge data provided by the United States Geological Survey (USGS 2009).

Table 1.1: Results of PERMANOVA testing for variation in structure of kelp assemblages among reef and transect within reef. Analyses based on Bray-Curtis dissimilarities from log (+1) transformed and standardized (by the maxiumum x 100). Each term was tested using 999 random permutations. Estimates of components of variation are provided for reef, transect, and residual. ** $p < 0.01$, ns: not significant.

| Source | df | MS | F | Component of variation |
|---|---|---|---|---|
| Reef | 5 | 2619.1 | $1.7^{ns}$ | 86.3 |
| Transect in Reef | 6 | 1583.4 | 2.2 ** | 145.7 |
| Residual | 60 | 709.2 | | 709.2 |
| Total | 71 | | | |

Table 1.2: Individual ANOVAs from survey data testing whether variance from spatial scales differs from zero for kelp species, kelp recruits, and encrusting algae, segregated by density ( m$^{-2}$ ) and percent cover data. $^{+}$p <0.1, ns: not significant.

| | # per m$^{2}$ | | | | |
|---|---|---|---|---|---|
| Response | MS | | | F | |
| Source | Location | Transect | Residual | Location | Transect |
| *S. subsimplex* | 1.05 | 1.35 | 0.62 | 0.78 $^{ns}$ | 2.17 $^{ns\ +}$ |
| *A. clathratum* | 1.67 | 0.78 | 0.39 | 2.16 $^{ns}$ | 1.98 $^{ns\ +}$ |
| Kelp Recruits | 6.50 | 3.75 | 1.79 | 1.73 $^{ns}$ | 2.10 $^{ns\ +}$ |
| df | 5 | 6 | 60 | | |

| | % Cover | | | | |
|---|---|---|---|---|---|
| Response | MS | | | F | |
| Source | Location | Transect | Residual | Location | Transect |
| Laminariaceae | 7.66 | 4.98 | 4.85 | 1.54 $^{ns}$ | 1.03 $^{ns}$ |
| *A. clathratum* | 8.32 | 11.64 | 5.51 | 0.72 $^{ns}$ | 2.11 $^{ns\ +}$ |
| Red Crust | 11.27 | 2.84 | 1.69 | 3.97 $^{ns\ +}$ | 1.68 $^{ns}$ |
| Brown Crust | 7.18 | 2.19 | 1.92 | 3.28 $^{ns\ +}$ | 1.14 $^{ns}$ |
| Encrusting Coralline | 1.84 | 3.48 | 1.97 | 0.53 $^{ns}$ | 1.77 $^{ns}$ |
| df | 5 | 6 | 60 | | |

Table 1.3: Yankee Cove experiment ANOVA table. Tests of hypotheses of no difference in density ( $m^{-2}$ ) of kelp recruits and Laminariaceae juveniles (ln ( + 1 ) transformed) among treatments (artificial reef plots, cleared natural reef plots, and undisturbed control plots) or location (East and West Yankee Cove locations) or location and treatment interaction. * $p < 0.05$, *** $p < 0.001$, ns: not significant.

| Source | Recruits | | | Laminariaceae Juveniles | | |
|---|---|---|---|---|---|---|
| | Df | MS | F | Df | MS | F |
| Location | 1 | 15.83 | 12.20 ** | 1 | 13.47 | 5.16 *** |
| Treatment | 2 | 14.64 | 11.28 *** | 2 | 1.01 | 1.18 $^{ns}$ |
| Location x Treatment | 2 | 19.39 | 14.94 *** | 1 | 0.31 | 0.36 $^{ns}$ |
| Residual | 48 | 1.30 | | 48 | 0.86 | |

Table 1.4: Yankee Cove transect survey ANOVA table. Tests of hypotheses of no difference in density ( m-2 ) of kelp recruit (log +1 transformed) on 50 x 50 cm quadrats along transects on artificial and natural reefs, with factors including reef location, reef type, reef location and type interaction, and transect within location and reef.

| Source | Df | MS | F |
|---|---|---|---|
| Location | 1 | 6.96 | 6.72 * |
| Reef Type | 1 | 86.94 | 83.98 *** |
| Location x Reef Type | 1 | 0.00 | 0.00 $^{ns}$ |
| Transect in (Location x Reef Type) | 4 | 4.58 | 4.42 ** |
| Residuals | 40 | 1.04 | |

## Chapter 2

# RECRUITMENT INHIBITION, REPRODUCTIVE INUNDATION AND COEXISTENCE BETWEEN SUBTIDAL ALGAL CRUSTS AND KELPS[1]

[1] Okamoto, D.K., M.S. Stekoll & G.L. Eckert. 2009. Recruitment inhibition, reproductive inundation and coexistence between subtidal algal crusts and kelps. Prepared for submission in Ecology Letters.

## ABSTRACT

Understanding coexistence among dominant plant groups requires identifying the mechanisms of interactions between coexisting competitors. Southeast Alaskan kelp forest host abundant canopy species and encrusting algae which dominate the rock beneath. We combined field surveys with laboratory and field experiments to investigate the role of subtidal encrusting algae in preempting recruitment of coexisting kelp species. *Saccharina bongardiana* f. *subsimplex* failed to recruit on brown and red non-calcified crusts, although brown crusts hosted both settlement and germination. In field plots, clearing space by scraping algal crusts drastically increased kelp recruitment success. In unscraped plots only non-crust surfaces hosted kelp recruitment. Preemption of kelp recruitment by crusts may explain the reduction of kelps in crust-dominated habitats. The ability of kelps to take advantage of small amounts of bare space likely compensates for the competitive space-occupancy advantage of crusts, and possibly explains why this interaction did not translate to competitive exclusion in nature.

## INTRODUCTION

The presence of multiple species functional groups (e.g. canopy, understory, or space occupying species) in plant communities can substantially increase productivity in terrestrial (Tilman 1999) and marine environments (Griffin *et al.* 2009), amplify ecosystem services (Díaz *et al.* 2007) and generate invasion resistance (Britton-Simmons 2006). While common anatomical and morphological characteristics define functional groups, competition for resources frequently occurs among coexisting functional groups. Much controversy exists concerning how species coexist when species compete for identical resources (Silvertown 2004). In the event of functional differences between competitors, models which incorporate ontogenetic shifts in competitive capability among species (Loreau & Ebenhoh 1994) or relax assumptions of preemption (Calcagno *et al.* 2006) can allow for coexistence. Interactions between canopy species and space monopolizers provide a provocative case where contrasting functional groups may co-dominate despite strong competitive relationships.

Established adults of canopy forming species hold competitive advantage with respect to light, yet their recruiting stages lack such advantage and must compete with other space-occupying species. In several cases interactions between canopies and space occupiers may range from facilitation to competitive exclusion depending upon circumstance. Examples include trees and grasses in Savannas (Scholes & Archer 1997), bryophyte mats and conifers in temperate forests (Nakamura 1992), coral reefs and macroalgae (McCook *et al.* 2001), and understory and canopy corals (Connolly & Muko 2003). Most research concerning these functional groups, especially in the marine environment, focuses on how space occupiers persist beneath the canopy, rather than how space occupiers influence canopies and how the canopy can persist in the face of space preemption.

Temperate, nearshore marine habitats often host several dominant, coexisting functional groups of macroalgae (Steneck & Dethier 1994). Kelps (order Laminariales) which form surface and subtidal canopies can dominate light (Reed & Foster 1984), alter water flow & increase particulate deposition (Eckman *et al.* 1989), and erode and suppress benthic species via physical abrasion (Irving & Connell 2006b). Yet lying beneath the canopy, an epithelium of calcified and non-calcified algal crusts often forms a skin over the benthos, transforming an abiotic surface into living substrate (Figure 2.1).

Algal crust-dominated, kelp free communities establish frequently in nature (Steneck *et al.* 2002) and may persist for decades without regenerating formerly dense kelp stands (Matsunaga *et al.* 1999; Martínez *et al.* 2003). Such barren areas may result from grazing (Bulleri *et al.* 2002), runoff from coastal anthropogenic activity (Matsunaga *et al.* 1999), as well as oceanographic changes which can cause deforestation (Martínez *et al.* 2003) and cyclical fluctuations in kelp abundance (Dayton *et al.* 1992). Morevoer, algal crusts can withstand partial overgrowth by understory canopies and algal turfs (Airoldi 2000; Dethier & Steneck 2001; Bulleri 2006; Underwood 2006) and thrive despite high rates of sedimentation (Connell 2003, 2005). In some cases canopies can facilitate the presence of crusts (Irving *et al.* 2004; Irving & Connell 2006b).

While kelps' canopy forming life-stage often monopolizes light, they also release millions of vulnerable, microscopic, reproductive stages which settle on the benthos, where germination, fertilization and sporophyte development occur (Steneck *et al.* 2002). Kelps' high reproductive potential can lead to rapid colonization (within one year) up to several km from a source of propagules, (Reed *et al.* 2004; Wyllie-Echeverria *et al.* 2005). While subtidal canopies can affect survival of successful recruits (Reed & Foster 1984), algal crusts may inhibit recruitment altogether, as shown with the invasive fucoid *Sargassum muticum* (Britton-Simmons 2006). Some algal crusts exhibit antifouling of turfs (Johnson & Mann 1986; Bulleri *et al.* 2002) and invasive macroalgae (Britton-Simmons 2006; Britton-Simmons & Abbott 2008). Proposed antifouling mechanisms include epithelial sloughing (Johnson & Mann 1986, Littler & Littler 1999) or allelopathy as exemplified by inhibition of cultured sporophyte production by extracts from the calcified crust *Lithophyllum* (Suzuki *et al.* 1998). Moreover, various characteristics of the benthic boundary layer can influence settlement of zoospores, including chemical microclimate and surface properties (Amsler *et al.* 1992). Thus crusts may pose a considerable threat to the vulnerable recruiting stages of kelps through preemption.

Despite these facts and the potential ecosystem impact of algal crust preemption on kelps, a gap remains in the literature detailing the direct influence of encrusting species on native canopy species in nature and impacts on their coexistence. Potential negative impacts of crusts may include direct inhibition of recruitment or crusts facilitating increased abundances of herbivores (Day & Branch 2002). If crusts can reduce recruitment of coexisting kelps, they will increase the thresholds of recruit survivorship required for population maintenance. Moreover, in the event that kelps cannot recruit upon algal crusts dominating the substrata, and kelp zoospores rely upon chance in locating the remaining suitable substrata, then threshold levels of zoospore abundance required of populations will also increase. Therefore demonstrating the effect of crusts on kelp settlement and recruitment can provide insight into inter-guild competition and coexistence and provides a step towards quantitative predictions of sensitivity and resiliency in this ecosystem.

In this study we utilized multiple approaches to understand the effect of algal crusts on kelps and kelps' recruitment response in the face of algal crust dominance. We documented how the benthic community of crusts influenced densities of adult kelps and kelp recruits using field surveys. We assessed the nature of the interaction between crusts and kelp recruits using manipulations in the field. Lastly, we conducted laboratory assays to determine the direct influence of algal crust taxa on recruitment of sporophytes and settlement and germination of zoospores.

## METHODS

### Field Surveys and Field Plot Experiment

#### *Reef Surveys*

We investigated the relationship between algal crusts, kelp recruits and adult kelps using field surveys. All subtidal surveys, collections and experiments were conducted using SCUBA. In southern Lynn Canal near Juneau, Alaska, USA, exposed rocky reefs host mixed stands of kelps (Laminariales), algal crusts (Figure 2.1), other benthic algae, and encrusting invertebrates. Reef composition includes bedrock, boulders, as well as large cobble.

To document patterns of community structure, we surveyed six subtidal rocky reefs (Figure 2.2). We selected reefs that were similar to our field experiment site (see *Experimental Manipulations* below) with respect to exposure, gentle slope and mixed bedrock, boulder habitat. At each reef, we surveyed two 30 m transects at 5 m below mean lower low water (MLLW). This depth represents the approximate median depth range of *Saccharina bongardiana* f. *subsimplex*, the most abundant understory kelp (Okamoto, pers. obs.). Along each transect we first quantified all adult kelps within six 1 $m^2$ quadrats and then within 0.25 $m^2$ of the larger quadrat enumerated kelp recruits and percent primary cover (using point-contact methods) of the benthos occupied by encrusting algal species as well as sand and bare rock.

*Experimental Manipulations*

To evaluate the interaction between crusts and recruiting kelps in the field, we manipulated crust abundance at one of the survey reefs, the west reef at Yankee Cove (58.58970 N, 134.90556 W; NAD 83, Figure 2.2) near Juneau, Alaska. In May 2007 we selected 23 flat, horizontal, 30 x 30 cm plots along the two surveyed 30 m transects at this site (the same transects but different plots than in surveys detailed above). Outside each plot we fixed two evenly spaced, labeled PVC markers to the rock with marine epoxy (Z-Spar™ Splash Zone Compound A-788, Z-Spar, Los Angeles, CA). These markers also served as anchor points for a square PVC quadrat which snapped into place over the plot markers for consistent repeated measurements. We surveyed plots prior to plot manipulation in November, 2007 for erect algae, kelp recruits, and percent primary cover by encrusting algal taxa and other encrusting taxa. On December 5th, 2007, we randomly assigned and applied one of three treatments to each plot, including 1) 9 plots cleared of all non-encrusting algae, encrusting algae, and sessile animals using chisels, hammers, and scraping implements, hereafter referred to as “scraped” plots; 2) 5 plots (a reduced sample size due to logistical constraints) cleared of upright algae and non-encrusting organisms with crusts wiped clean using a neoprene pad, hereafter referred to as “cleared” plots; and 3) 9 unmanipulated plots, hereafter referred to as “control” plots. In April, 2008 we quantified kelp recruitment in all plots and recorded whether kelp recruits occurred on crusts or on other substrata, and recorded primary percent cover of algal crust taxa (red crust, brown crust, and calcified red crust).

### *Statistical Analyses*

We examined the relationship between abundance of kelps, kelp recruits, crust cover and bare rock from reef survey data using a linear regression of the square root of adult kelp density ($m^{-2}$) with respect to percent crust cover, and linear regressions of the square root of kelp recruit density ($m^{-2}$) with respect to percent crust cover, percent bare rock, and number of adult kelps. For the field plot experiment we utilized a one-way analysis of variance (ANOVA) testing the hypothesis of no difference in mean kelp recruit density 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 (adjusting $\alpha$ using the sequential Bonferroni method for our two hypotheses). In the experimental plots we examined the relationship between algal crusts and kelp recruitment with linear regression of the square root of recruit density with respect to percent crust cover.

Lastly, we compared kelp recruitment density on crust and non-crust substrata within each experimental plot using one-sided, paired t-test. We performed all analyses using R (R Development Core Team 2009).

## Laboratory Assessment of Recruitment on Algal Crust and Bare Substrata

We investigated recruitment of microscopic *Saccharina bongardiana* sporophytes on three major crust taxa or bare rock in a laboratory assay in which we exposed spores to paired bare rock and crust treatments within small aquaria, allowed settled spores to germinate, and enumerated juvenile sporophytes 35 days after settlement. We collected rocks (20 cm diameter maximum) from Yankee Cove near Juneau, Alaska at approximately 5 m below MLLW. Each rock had a horizontal surface ubiquitously covered by at least 15 x 15 cm of either a single brown crust, a non-calcified red crust, or a calcified crust. We transported the rocks in seawater and placed them in flowing seawater at our lab. We protected an 8 x 15 cm flat crust section on each rock using sponges and paper towels wetted with sterile seawater and 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 moist with sterile seawater. We then divided the protected 8 x 15 cm crust surface and cleared one half using a fine wire brush leaving the other half unmanipulated. Therefore, each rock served as a replicate with a cleared and crust treatment (n = 4, 5 & 7 for brown, non-calcified red, and calcified crusts respectively). Though we began with eight replicates for each taxa, introducing live crusts to our mesocosms lead to contamination by filamentous brown algae of several replicates. Thus we utilized only those replicates with no sign of contamination. We created an individual mesocosm around the isolated 8 x 15 cm experimental surface on each rock by attaching a square 1 l plastic food storage container with an 8 x 15 cm section removed. Containers were sealed to the rock using a combination of HoldFast™ non-toxic aquarium epoxy (Aquarium Systems, Sarrebourg, France) and hot glue such that mesocosms did not leak. During all preparations we kept crust surfaces wet with sterile paper toweling saturated with enriched seawater (see *Experimental Application and Analysis of Laboratory Assay* below). These rock-container aquaria then served as mesocosms for our experiment. We provided fresh air through a submerged air stone and a portable aquarium pump. Coverslips were attached to the horizontal surfaces of the food container to monitor microscopic settlement before kelps could be seen under a dissecting scope.

### *Experimental Application and Analysis of Laboratory Assay*

To obtain kelp spores, we collected reproductive *S. bongardiana* from Yankee Cove in October, 2007. We prepared fertile sori by scrubbing *S. bongardiana* with paper towels, rinsing with sterile seawater several times, wrapping them with moist, sterile paper towels and then placing them in the dark at 4 °C for 12-24 h (Stekoll & Else 1992). Thereafter we provided light, temperature, and osmotic shock by immersing them in 10 °C sterile, modified Provasoli Enriched Seawater (PES) created with filtered seawater (Millipore, 0.45 μm pore size) as detailed in Stekoll & Else (1992). After 1-2 h sori released a dense cloud of spores. We quantified spore densities using a hemocytometer and standardized spore solutions to 10,000 spores $ml^{-1}$. Typical spore densities released were 200,000 to 1,000,000 spores $ml^{-1}$. Final spore solution consisted of modified PES treated with 0.66 mg l $^{-1}$ $GeO_2$ 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 10-13 °C; after which we changed to a photoperiod of 16:8 (light:dark) and exchanged PES medium weekly. We randomized the orientation (to the right or left in the incubator) of treatments within the incubator in order to avoid a confounding influence of orientation with treatment effects. Monitoring of coverslips took place weekly until all visible female gametophytes (excluding those which produced extensive vegetative growth rather than eggs) under multiple fields of view produced sporophytes large enough for visualization under a dissecting scope. At this point (35-37 d after spore settlement), we photographed five 3 $mm^2$ sections of each crust and bare rock patch, selected haphazardly, through a dissection scope, as well as photographing sections from the horizontal sides of each container adjacent to each treatment surface, and three sections from each of two coverslips. Where feasible all sporophytes were counted in each photograph. In photographs where sporophytes clearly exceeded several hundred, we subsampled using a frame with 8 rectangular subsamples each consisting of 1/64th of the photograph placed over each photo and scaled up (8x) to an estimate of the total abundance in the photograph.

### *Statistical Analyses*

We tested the hypotheses of no effect of taxa, treatment, or taxa*treatment interaction with the individual aquaria and patch nested within each aquaria serving as random factors in a repeated measures analysis with a linear mixed effects model with the function *lme* in R (R Development Core Team 2009). We used the square root of sporophyte densities (mm$^{-2}$) for each photograph as a subsample within each replicate patch.

### Laboratory Assessment of Settlement and Germination on Algal Crust and Bare Substrata

We collected rocks containing crusts as described above, and chipped off small sections (approximately 5 mm in diameter) of the rock which contained a single algal crust or bare rock using a hammer and chisel. These chips served as replicates within an experiment testing the hypothesis that kelps settle and germinate upon algal crusts. We placed each chipped rock section, after being stored for 24 h in sterilized sea water, into well plates (24 wells) with 3 ml modified PES medium in each well. We also placed glass coverslips into some wells as controls for any staining effect.

In order to determine the stage at which inhibition of kelp recruitment occurred, we used epi-fluorescence and fluorescent stains as a unique method to track cell presence and fate upon non-transparent or irregular surfaces. We employed this tool to determine whether pre-stained spores settle and germinate upon brown algal crusts at the same densities as upon 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 CMFDA (provided from a stock solution at 10mM in anhydrous DMSO, Invitrogen, USA) in independent glass vials kept on ice which kept spores from settling during staining. 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 three 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. We compared mean abundance of settled and germinated spores on substrata placed in wells (coverslips, bare rock, and crust chips), and we tested for differences between stain concentrations (0, 5 and 22.5 μM).

### *Statistical Analyses*

For the evaluation of CellTracker™ Green CMFDA on spore settlement and germination, we used a one-way ANOVA with our three concentrations as treatments. We used a one-way ANOVA to test the hypothesis of no mean difference in spore abundance on crust, bare rock, and coverslip treatments.

## RESULTS

### Field Surveys and Field Plot Experiment

#### *Reef Surveys*

In systematic reef surveys, understory adult kelp density correlated positively with algal crust percent cover of the benthos ($r^2 = 0.19$, $F_{1,70} = 16.72$, $p < 0.001$, Figure 2.3 A). All three major algal crust taxa inhabited each site, with crusts taxa cumulatively occupying between 0 and 100% of points (Figure 2.3 A). Kelp recruit density was highly variable (56 $m^{-2}$, SD = 110) and not significantly related to adult kelp abundance, adult kelp canopy cover, or crust cover (Figure 2.3 B), but correlated positively with availability of bare rock ($r^2 = 0.12$, $F_{1,70} = 9.26$, $p = 0.003$). Okamoto & Eckert (2009) describe fully individual densities and percent cover by kelp species and other taxa at these locations.

*Experimental Manipulations*

Kelp recruit densities in scraped plots exceeded that in control plots and cleared plots (removal of everything but crustose algae) by more than 500% ($F_{1,20} = 7.15$, $p = 0.015$, Figure 2.4 A), whereas densities in control plots and cleared plots did not differ ($F_{1,20} = 0.09$, $p = 0.77$, Figure 2.4 A). Despite this pattern kelps managed to recruit to the small amount of non-crust spaces in plots with nearly 100% crust cover (Figure 2.4 B). Strikingly, kelps recruited almost exclusively on non-crust substrata rather than upon crusts in the field (Figure 2.4 B, $t_{17} = 8.83$, $p < 0.001$). Despite this inhibition, kelps exhibited a strong, though variable, capability to recruit to even minute spaces uncolonized by algal crusts or where invertebrates (primarily spirorbid and serpulid worms as well as encrusting bryozoans) had colonized on top of crusts. Within plot variation correlated with percent of the substrate covered by crusts, with density of recruits decreasing with crust abundance (Figure 2.4 B, $r^2 = 0.33$, $F_{1,70} = 10.25$, $p = 0.0043$). Prior to clearings, non-calcified red and brown crusts occupied a high percentage of the exposed rock, while calcified crusts, invertebrates, and bare rock occupied less than 14% on average (Figure 2.5). When we conducted surveys, we observed recruits in nearly all plots.

## Laboratory Assessment of Recruitment on Algal Crust and Bare Substrata

In laboratory mesocosms we observed a 97% reduction in cultured microscopic *S. bongardiana* sporophyte densities upon brown crust patches in comparison to bare rock and a 99% reduction upon non-calcified red crust patches in comparison bare rock (Figure 2.6). However, we saw no difference in sporophyte densities upon calcified crust patches versus bare rock treatments. Despite significant effects of treatment (scraping) ($F_{1,12} = 29.63$, $p < 0.001$), and crust taxa ($F_{2,9} = 6.22$, $p = 0.02$), the effect of scraping differed with taxa as indicated by a significant treatment-taxa interaction ($F_{2,12} = 6.92$, $p = 0.01$).

## Laboratory Assessment of Settlement and Germination on Algal Crust and Bare Substrata

Kelp spores settled and germinated in equal densities on brown crusts ($\bar{x} = 230$ mm $^{-2}$ ± 38 SE, Figure 2.7), bare rock ($\bar{x} = 237$ mm $^{-2}$ ± 41 SE, Figure 2.7) and coverslips ($\bar{x} = 231$ mm $^{-2}$ ± 25 SE, $F_{2,24} = 0.01$, $p = 0.98$). There was no effect of the stain Cell-Tracker Green among concentrations (0, 5, or 22.5 μM) on the settlement and germination of *S. bongardiana* spores ($F_{2,11} = 0.13$, $p = 0.88$).

## DISCUSSION

Our results demonstrate that algal crusts can inhibit recruitment of the sub-canopy; yet despite strong preemption, the small amounts of bare space left unoccupied proves sufficient for sub-canopy recruitment. These experimental and observational results show that algal crusts can directly inhibit kelp recruitment where the two groups coexist in the field. Our laboratory mesocosm revealed that recruitment inhibition occurs on the microscopic scale as a direct preemption by algal crusts, and our staining experiment suggests that settlement upon brown crusts is indiscriminant and thus inhibition occurs post-settlement. In experimental field plots this influence of crusts scaled up to dramatically reduce recruit densities in the field. Despite this fact, adult kelp densities correlated positively with algal crusts suggesting that immense preemption by crusts has little effect on adult kelp abundances.

We observed near complete exclusion of kelps from crust substrata in the field, and almost 100% microscopic sporophyte inhibition by brown and non-calcified red crusts in the laboratory; however, our laboratory results for calcified crusts (the least abundant in the field) show no immediate inhibitory effect. This preemption by algal crusts resonates with suggestions from previous studies. In the San Juan Islands, removal of algal crust communities of mixed taxa increased recruitment of the invasive brown alga *Sargassum muticum* (Britton-Simmons 2006; Britton-Simmons & Abbott 2008). However algal crust antifouling literature focuses mainly on calcified crusts. In Nova Scotia boulders covered in the calcified crust *Phymatolithon* hosted less than 50% of the biomass of recruited fleshy algae than bare granite, regardless of species (Johnson & Mann 1986). Moreover, testing of the influence of calcified crust extracts on kelp recruitment (Denboh *et al.* 1997; Suzuki *et al.* 1998) demonstrates inhibitory chemical effects on kelp gametophytes and sporophyte production. In addition to chemical defenses, proposed mechanical antifouling by calcified crusts include epithelial sloughing (Keats *et al.* 1997; Littler & Littler 1999) and epithelial instability (Johnson and Mann 1986). The latter may require a mechanical stimulus such as wave action, a factor which we did not apply in the laboratory but may exist in nature. Moreover, because our experiment only took place over 37 days, calcified crusts may not have been given enough time for a mechanically based defense against kelp recruits. While one should consider such evidence when making conclusions from our calcified crust treatments, crusts can also affect species differentially. Near Livorno, Italy, calcified crusts reduced the abundance of the green alga *Acetabularia acetabulum*, but not filamentous algae or the small brown alga *Padina pavonica* (Bulleri *et al.* 2002). Because the habitat in our field manipulations hosted mostly non-calcified crusts, our focus lies principally with the most abundant groups, which our lab and field experiments indicate reduce the suitable habitat available for kelp recruits through preemption.

While algal crusts covered a large majority of our experimental plots and showed strong preemption of kelp recruits, they never completely monopolized the surface. In addition, Okamoto & Eckert (2009) show that complete monopolization never occurs but rather abundance varies highly within reefs. Algal crusts can recruit quickly (Buckley 1985), yet substratum monopolization may take far longer given their slow growth rates, ranging from 2-16 mm per year for some taxa in the northeast Pacific (Dethier 1994; Dethier & Steneck 2001). Moreover, grazers may influence not only growth rates of crusts (Dethier & Steneck 2001) but also facilitate overgrowth by invasive macroaglae (Britton-Simmons & Abbott 2008). Additionally, other organisms can easily overgrow crusts, such as neighboring macroalgae or settling encrusting invertebrates. Thus, while space occupancy by algal crusts provided limited opportunity for kelp recruitment in our studies, such preemption proved insufficient for total exclusion of kelp recruits in the field.

In addition to utilizing bare space, some of the kelp recruits we observed in our experimental field plots recruited on top of the sparsely distributed encrusting invertebrates, such as encrusting bryozoans, Serpulid and Spirorbid worms, and basal plates of the barnacle *Balanus crenatus*. These encrusting organisms, in some cases, had settled on algal crusts. Invertebrates often hold competitive advantage over encrusting algae (Sebens 1986; Konar & Iken 2005), although the invertebrates can quickly disappear because of predation. Despite their rarity, even minute recruitment of encrusting invertebrates upon crusts may alleviate preemption by crusts by providing small amounts of substrate suitable for settling kelp zoospores. In this manner, nontransitive (cyclical) networks of competition may exist and facilitate coexistence in this system. Moreover, the presence of kelps can positively benefit algal crust communities (Irving *et al.* 2004; Irving & Connell 2006a), indicating that, perhaps, algal crusts inhibit direct overgrowth but depend upon kelp canopies for persistence. We suggest that future studies explore this possibility. Yet such a scenario remains contingent upon kelps' large colonization potential and capability to take advantage of minute amounts of bare space.

Modified competition-colonization trade-off models indicate that, despite strong preemption and strong competitive asymmetry, coexistence of competitors can occur so long as colonization potential by one player remains considerably high (Calcagno *et al.* 2006). In our field experiment (as well as in Okamoto & Eckert 2009) kelps demonstrate such colonization potential, taking advantage of even minute amounts of bare space and demonstrating successful recruitment in the midst of algal crusts competitive advantage for space. Thus, despite the presence of strong preemption, recruitment of the sub-canopy can occur in densities observed in healthy sub-canopy populations, but depends upon a combination of high colonization potential and the availability of small amounts of bare space.

In our experiment we observed similar rates of kelp colonization in the presence of preemptive crusts as we observed in our reef surveys (Figure 2.3 B, Figure 2.4 B). Yet in light of these data, we suggest sub-canopy kelps may not always overcome the competitive advantage held by primary space occupiers, especially with shifts in availability of reproductive propagules or survival of recruits. We showed that *S. bongardiana* zoospores settle indiscriminately on bare space and on at least one algal crust group in our fluorescence experiment. We thus assume that zoospores settle indiscriminately at least between brown crust substrata and bare rock, if not others, and thus colonize bare substrata in part by chance (although zoospores show some capability for nutrient chemotaxis (Amsler & Neushul 1989) and nutrient induced settlement preference (Amsler & Neushul 1990). In the scenario of indiscriminant settlement, decreases in reproductive propagule availability (for example as a result of local deforestation by urchins), which might prove inconsequential in the absence of algal crusts, and may instead, in the face of such preemption, decrease the probability of settlers locating bare space and decrease the probability of reconolization. Moreover, experimental plots with algal crusts hosted some kelp recruits, but such recruitment may not always prove sufficient. Shifts which slightly decrease survivorship, such as unfavorable hydrological properties (Matsunaga *et al.* 1999), increased grazing of recruits (Duggins *et al.* 2001) or increased consumption of microscopic sporophytes (Sala & Graham 2002) may require greater recruit densities for persistence. Thus, the algal-crust preemptive influence we demonstrated likely decreases the threshold levels of recruit mortality kelp populations can tolerate and increases threshold levels of reproductive output required for recruitment, thereby reducing their overall resilience.

## ACKNOWLEDGEMENTS

Many thanks to those who assisted with and shared in the challenge of conducting field research and collections, especially to Jodi Pirtle, Bill Bechtol, Jeff Douglas, and 2007 and 2008 University of Alaska Southeast Research Experience for Undergraduate students. Funding for this work was provided by NSF Grant # 0553000, the Alaska Department of Transportation and Public Facilities, Alaska Sea Grant, and the Dr. H. Richard Carlson Fellowship awarded to Daniel Okamoto. Thanks to Jim Taggart and USGS for SCUBA equipment, Sue Walker for administrative assistance, Marion and Naomi Hobbs for providing access to the experimental field site, and to Kevin Britton-Simmons, Chris Siddon, Megan Dethier, and David Duggins for providing advice, insight, and suggestions concerning the experimental system.

## REFERENCES

Airoldi L. (2000) Effects of disturbance, life histories, and overgrowth on coexistence of algal crusts and turfs. *Ecology*, 81, 798-814

Amsler C.D. & Neushul M. (1989) Chemotactic effects of nutrients on spores of the kelps *Macrocytis pyrifera* and *Pterygophora california*. *Mar. Biol.*, 102, 557-564

Amsler C.D. & Neushul M. (1990) Nutrient stimulation of spore settlement in the kelps *Pterygophora californica* and *Macrocystis pyrifera*. *Mar. Biol.*, 107, 297-304

Amsler C.D., Reed D.C. & Neushul M. (1992) The microclimate inhabited by macroalgal propagules. *Eur. J. Phycol.*, 27, 253-270

Britton-Simmons K.H. (2006) Functional group diversity, resource preemption and the genesis of invasion resistance in a community of marine algae. *Oikos*, 113, 395-401

Britton-Simmons K.H. & Abbott K.C. (2008) Short-and long-term effects of disturbance and propagule pressure on a biological invasion. *J. Ecol.*, 96, 68-77

Buckley R.M.G.J.H. (1985) Biological processes and ecological development on an artificial reef in Puget Sound Washington. *Bull. Mar. Sci.*, 37, 50-69

Bulleri F., Bertocci I. & Micheli F. (2002) Interplay of encrusting coralline algae and sea urchins in maintaining alternative habitats. *Mar. Ecol. Prog. Ser.*, 243, 101-109

Bulleri F. (2006) Duration of overgrowth affects survival of encrusting coralline algae. *Mar. Ecol. Prog. Ser.*, 321, 79-85

Calcagno V., Mouquet N., Jarne P. & David P. (2006) Coexistence in a metacommunity: the competition-colonization trade-off is not dead. *Ecol. Lett.*, 9, 897-907

Connell S.D. (2003) The monopolization of understorey habitat by subtidal encrusting coralline algae: a test of the combined effects of canopy-mediated light and sedimentation. *Mar. Biol.*, 142, 1065-1071

Connell S.D. (2005) Assembly and maintenance of subtidal habitat heterogeneity: synergistic effects of light penetration and sedimentation. *Mar. Ecol. Prog. Ser.*, 289, 53-61

Connolly S.R. & Muko S. (2003) Space preemption, size-dependent competition, and the coexistence of clonal growth forms. *Ecology*, 84, 2979-2988

Day E. & Branch G.M. (2002) Effects of benthic grazers on microalgal communities of morphologically different encrusting corallines: implications for abalone recruits. *Mar. Ecol. Prog. Ser.*, 244, 95-103

Dayton P.K., Tegner M.J., Parnell P.E. & Edwards P.B. (1992) Temporal and spatial patterns of disturbance and recovery in a kelp forest community. *Ecol. Monogr.*, 62, 421-445

Denboh T., Suzuki M., Mizuno Y. & Ichimura T. (1997) Suppression of *Laminaria* sporelings by allelochemicals from coralline red algae. *Bot. Mar.*, 40, 249-256

Dethier M.N. (1994) The ecology of intertidal algal crusts: variation within a functional group. *J. Exp. Mar. Biol. Ecol.*, 177, 37-71

Dethier M.N. & Steneck R.S. (2001) Growth and persistence of diverse intertidal crusts: survival of the slow in a fast-paced world. *Mar. Ecol. Prog. Ser.*, 223, 89-100

Díaz S., Lavorel S., de Bello F., Quétier F., Grigulis K. & Robson T.M. (2007) Incorporating plant functional diversity effects in ecosystem service assessments. *Proc. Nat. Acad. Sci.*, 104, 20684-20689

Duggins D.O., Eckman J.E., Siddon C.E. & Klinger T. (2001) Interactive roles of mesograzers and current flow in survival of kelps. *Mar. Ecol. Prog. Ser.*, 223, 143-155

Eckman J.E., Duggins D.O. & Sewell A.T. (1989) Ecology of understory kelp environments. 1. Effects of kelps on flow and particle transport near the bottom. *J. Exp. Mar. Biol. Ecol.*, 129, 173-187

Griffin J.N., Mendez V., Johnson A.F., Jenkins S.R. & Foggo A. (2009) Functional diversity predicts overyielding effect of species combination on primary productivity. *Oikos*, 118, 37-44

Irving A.D., Connell S.D. & Elsdon T.S. (2004) Effects of kelp canopies on bleaching and photosynthetic activity of encrusting coralline algae. *J. Exp. Mar. Biol. Ecol.*, 310, 1-12

Irving A.D. & Connell S.D. (2006a) Predicting understorey structure from the presence and composition of canopies: an assembly rule for marine algae. *Oecologia*, 148, 491-502

Irving A.D. & Connell S.D. (2006b) Physical disturbance by kelp abrades erect algae from the understorey. *Mar. Ecol. Prog. Ser.*, 324, 127-137

Johnson C.R. & Mann K.H. (1986) The crustose coralline alga, Phymatolithon Foslie, inhibits the overgrowth of seaweeds without relying on herbivores. *J. Exp. Mar. Biol. Ecol.*, 96, 127-146

Keats D.W., Knight M.A. & Pueschel C.M. (1997) Antifouling effects of epithallial shedding in three crustose coralline algae (Rhodophyta, Coralinales) on a coral reef. *J. Exp. Mar. Biol. Ecol.*, 213, 281-293

Konar B. & Iken K. (2005) Competitive dominance among sessile marine organisms in a high Arctic boulder community. *Polar Biol.*, 29, 61-64

Littler M. & Littler D. (1999) Epithallus sloughing: a self-cleaning mechanism for coralline algae. *Coral Reefs*, 18, 204

Loreau M. & Ebenhoh W. (1994) Competitive exclusion and coexistence of species with complex life cycles. *Theor. Popul. Biol.*, 46, 58-77

Martínez E.A., Cárdenas L. & Pinto R. (2003) Recovery and genetic diversity of the intertidal kelp *Lessonia nigrescens* (Phaeophyceae) 20 years after El Nino 1982/83. *J. Phycol*, 39, 504-508

Matsunaga K., Kawaguchi T., Suzuki Y. & Nigi G. (1999) The role of terrestrial humic substances on the shift of kelp community to crustose coralline algae community of the southern Hokkaido Island in the Japan Sea. *J. Exp. Mar. Biol. Ecol.*, 241, 193-205

McCook L., Jompa J. & Diaz-Pulido G. (2001) Competition between corals and algae on coral reefs: a review of evidence and mechanisms. *Coral Reefs*, 19, 400-417

Nakamura T. (1992) Effect of bryophytes on survival of conifer seedlings in subalpine forests of central Japan. *Ecol. Res.*, 7, 155-162

Okamoto D.O. & Eckert G.L. (2009) Colonization potential of understory kelps in a Southeast Alaskan glacial fjord. In: Okamoto DO. *Competition and recruitment in Southeast Alaskan subtidal kelp communities*. Masters Thesis, University of Alaska Fairbanks, Fairbanks, AK

R Development Core Team (2009) R: A language and environment for statistical computing. In:Masters Thesis, R. Foundation for Statistical Computing, Vienna, Austria

Reed D.C. & Foster M.S. (1984) The effects of canopy shadings on algal recruitment and growth in a giant kelp forest. *Ecology*, 65, 937-948

Reed D.C., Schroeter S.C. & Raimondi P.T. (2004) Spore supply and habitat availability as sources of recruitment limitation in the giant kelp *Macrocystis pyrifera* (Phaeophyceae). *J. Phycol.*, 40, 275-284

Sala E. & Graham M.H. (2002) Community-wide distribution of predator–prey interaction strength in kelp forests. *Proc. Nat. Acad. Sci.*, 99, 3678–3683

Scholes R.J. & Archer S.R. (1997) Tree-grass interactions in savannas. *Annu. Rev. Ecol. Syst.*, 28, 517-544

Sebens K.P. (1986) Spatial relationships among encrusting marine organisms in the New England subtidal zone. *Ecol. Monogr.*, 56, 73-96

Silvertown J. (2004) Plant coexistence and the niche. *Trends Ecol. Evol.*, 19, 605-611

Stekoll M.S. & Else P.V. (1992) *The feasibility of Macrocystis mariculture in Southeast Alaska*. The State of Alaska and the Japan Overseas Fisheries Cooperation Foundation, Tokyo

Steneck R.S. & Dethier M.N. (1994) A functional group approach to the structure of algal-dominated communities. *Oikos*, 69, 476-498

Steneck R.S., Graham M.H., Bourque B.J., Corbett D., Erlandson J.M., Estes J.A. & Tegner M.J. (2002) Kelp forest ecosystems: biodiversity, stability, resilience and future. *Environ. Conserv.*, 29, 436-459

Suzuki Y., Takabayashi T., Kawaguchi T. & Matsunaga K. (1998) Isolation of an allelopathic substance from the crustose coralline algae, *Lithophyllum* spp., and its effect on the brown alga, *Laminaria religiosa* Miyabe (Phaeophyta). *J. Exp. Mar. Biol. Ecol.*, 225, 69-77

Tilman D. (1999) The ecological consequences of changes in biodiversity: a search for general principles. *Ecology*, 80, 1455-1474

Underwood A.J. (2006) Why overgrowth of intertidal encrusting algae does not always cause competitive exclusion. *J. Exp. Mar. Biol. Ecol.*, 330, 448-454

Wyllie-Echeverria T., Wyllie-Echeverria S., Duggins D. & Young C. (2005) Curtis Wharf and Dock Kelp Mitigation Efforts--Final Report (2001-2005): Establishment of Kelp Habitat. Port of Anacortes, Anacortes, WA, 47 pp

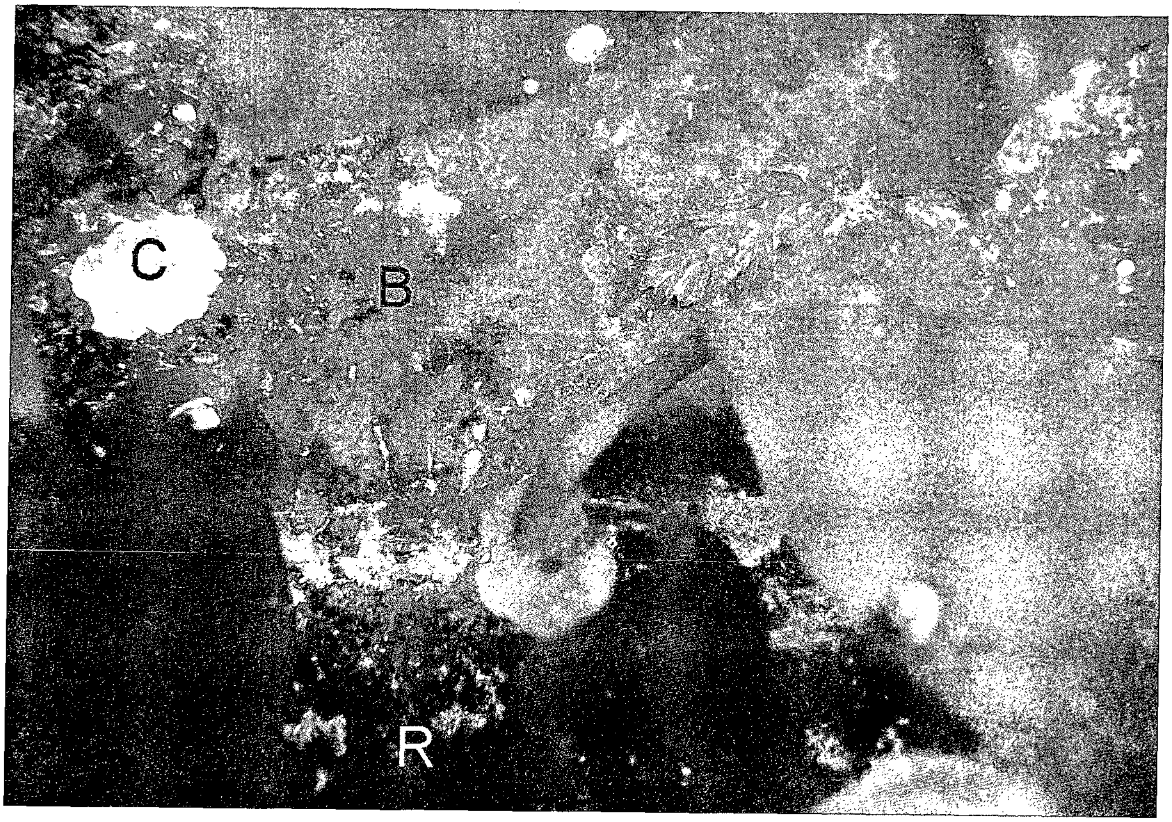

Figure 2.1: Algal crusts underneath *Laminaria yezoensis*. Letters indicate brown (B), non-calcified red (R) and calcified (C) algal crusts.

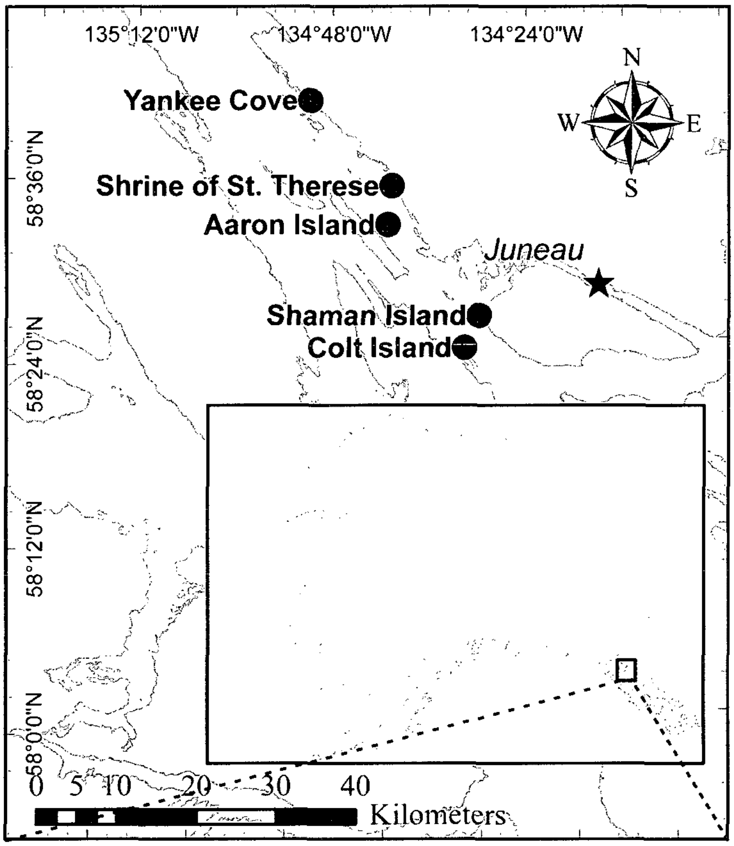

Figure 2.2: Map of survey locations and the experimental site (Yankee Cove West) in the Lynn Canal near Juneau, Alaska

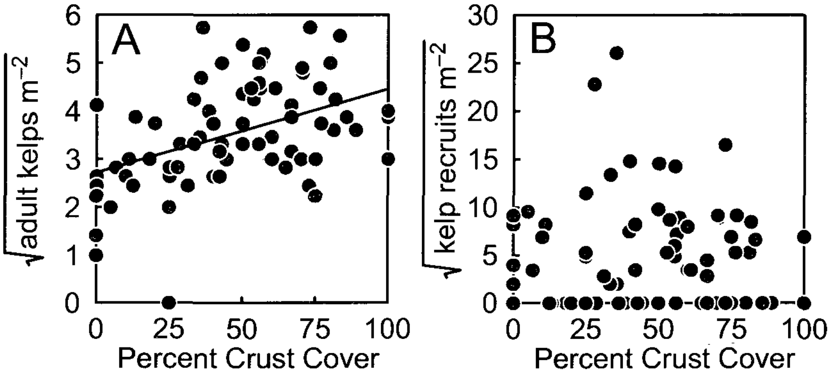

Figure 2.3: Kelps and kelp recruits versus algal crust cover; A) Square root of adult kelp density ($m^{-2}$; *S. bongardiana*, *A. clathratum* and *L. yezoensis*) as a function of algal crust cover in survey quadrats from six surveyed sites in Southeast Alaska. The regression line represents the relationship between kelps and algal crust cover ($r^2 = 0.19$, $p < 0.001$); B) kelp recruit density ($m^{-2}$) as a function of algal crust cover from the same sites. No significant correlation existed between kelp recruits and algal crust cover.

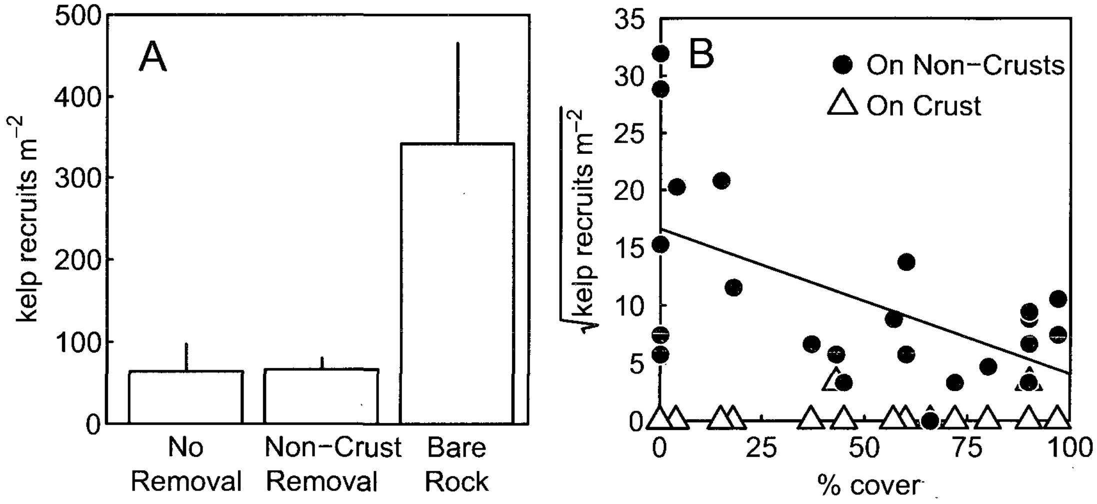

Figure 2.4: Barplot and scatterplot of field experimental results; A) Mean density of kelp recruits (m$^{-2}$) in experimental plots of three treatments: unmanipulated control, removal of non-algal crusts, and removal of all organisms. Error bars represent 1 SE with n = 5, 9, and 9, respectively. B) Square root of the kelp recruit density (m$^{-2}$) in each plot against percent cover by algal crusts, segregated by those growing on non-algal substrate (bare rock, encrusting invertebrates, etc.; dark circles) and on algal crusts (grey triangles). The regression line represents the relationship between kelp recruits on hard substrate and algal crust cover ($r^2$= 0.33, p = 0.0041).

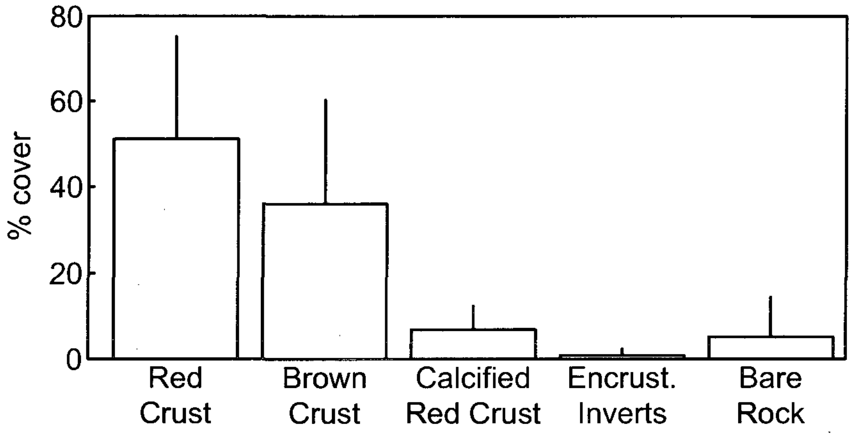

Figure 2.5: Mean percent cover of experimental plots by algal crusts, invertebrates, or bare rock. Surveyed area included all visible rock surfaces left unoccupied by holdfasts or buried by silt. Error bars represent 1 SD.

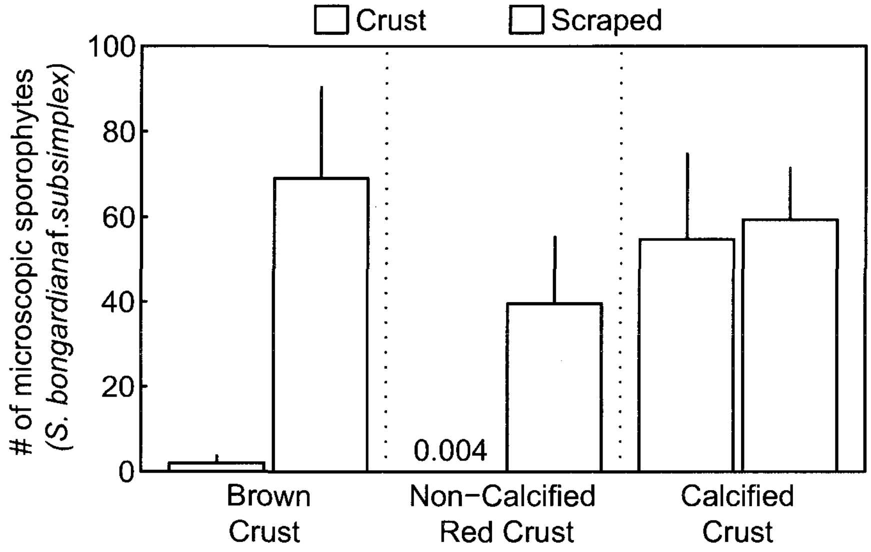

Figure 2.6: Barplot of laboratory results showing mean of cultured, microscopic *S. bongardiana* sporophytes on crusts and treatments where algal crusts were removed (bare rock) segregated by crust taxa. Error bars represent SE, with n = 5, 4 and 6, respectively for taxa.

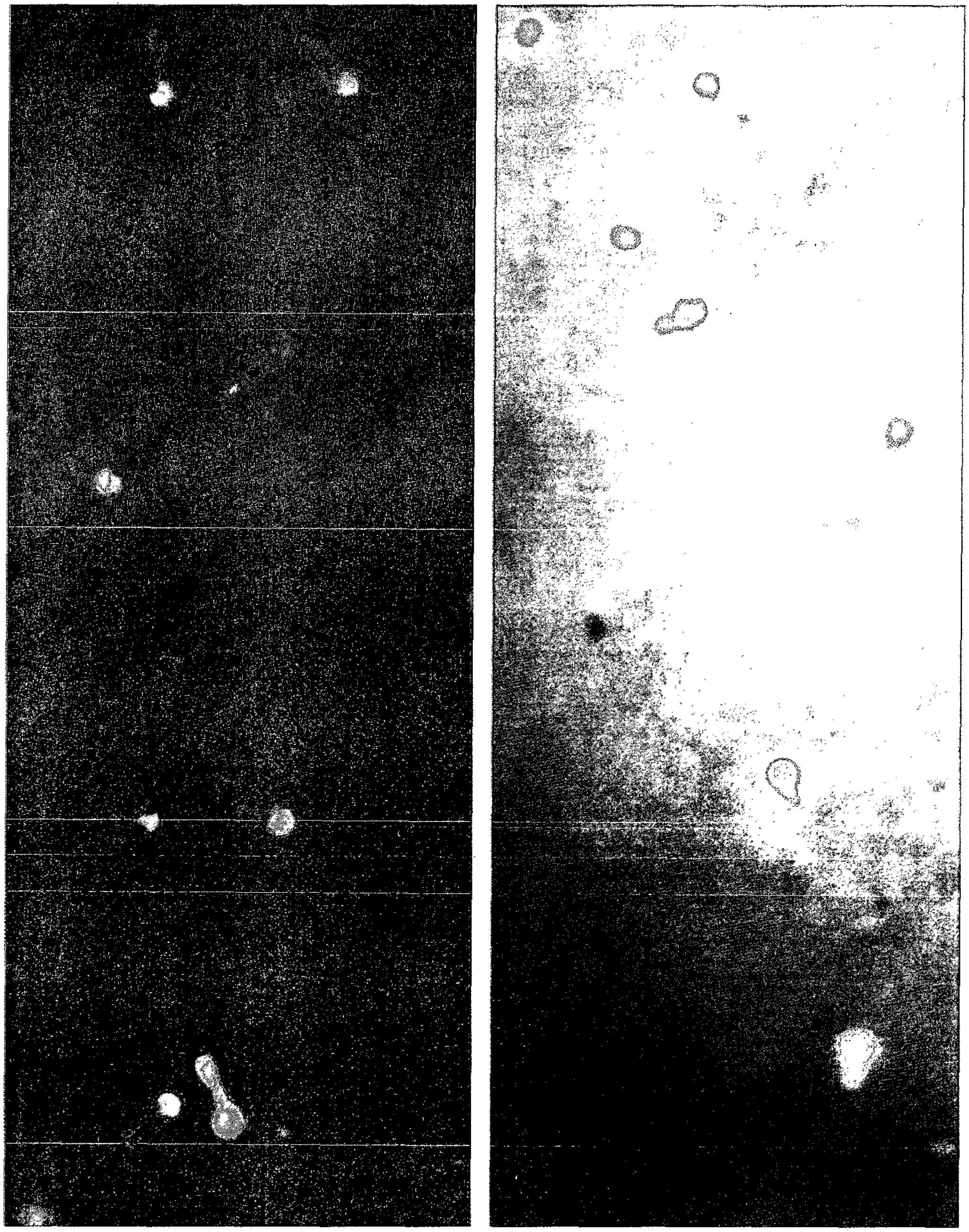

Figure 2.7: Germinated *Saccharina bongardiana* gametophytes stained with CellTracker™ green CMFDA and settled onto a brown crust chip (red fluorescing cells) and a bare rock chip (black background) as viewed under epi-fluorescence.

# CONCLUSIONS

This field and lab research documents the resilience of a group of Southeast Alaskan kelps by demonstrating their strong recruitment capability when presented with bare substrata as well as the inhibitory effect of algal crust taxa. Kelps rapidly and densely colonized unoccupied substrata, ranging in size from small cracks and crevices to large artificial reefs. Although we initiated these field experiments at one point in time, kelps also settled onto tiles which we installed at different periods throughout the summer and late fall. Studies in Chapter 1 show that such colonization potential can rapidly benefit restoration or mitigation efforts such as the Yankee Cove artificial reefs. In contrast, studies in Chapter 2 illustrate such colonization potential facilitates kelp recruitment into remaining bare cracks and crevices in plots where inhibitory algal crusts covered up to 95% of the rock.

Kelps worldwide inhabit the apex of terrestrial and marine ecosystems and thus succumb to biological, physical and anthropogenic disturbance. In many habitats kelps recover from such disturbances rapidly (Johnson & Mann 1988; Dayton *et al.* 1992; Estes & Duggins 1995). Often they may recover from storm events (e.g. Dayton *et al.* 1992) or urchin deforestation (e.g. Johnson & Mann 1988) within one to several years. Studies in Chapter 1 show similar results, but with the caveats that such recovery appears species specific and highly variable in space. Recolonization of disturbed areas or colonization of newly installed artificial reefs such as those at Yankee Cove may occur in this region within one year. However as we demonstrate, the small scale spatial variability exhibited between artificial reefs and clearings in natural reefs demonstrates that even comparisons among reefs separated by a few meters can yield large unexplained differences.

Experiments in Chapter 2 reveal that algal crusts, which occur in kelp forests worldwide, may dramatically reduce the magnitude of recruitment by the light monopolizing kelps; such a result occurs, in part, because of post-settlement and post-germination mortality. Foundation species such as kelps generate both the biomass and structure in an ecosystem and thus control much of the productivity of species dwelling around them (Barrales & Lobban 1975; Power *et al.* 1996). However, in addition to studying the single species dynamics of these organisms, it is in part the quest of ecologists to reveal those taxa whose influence comes not as a result of massive biomass or productivity, but through interactions which impact the dynamics of foundation species (Power *et al.* 1996). In this case, algal crusts, which may benefit substantially from kelp canopies (Melville & Connell 2001; Irving *et al.* 2004), can also strongly influence kelp recruitment dynamics despite their typical subordinate position in the water column. While many suspect algal crusts inhibit recruitment dynamics of kelps (Suzuki *et al.* 1998), this study provides empirical data linking algal crusts directly to inhibition of kelps.

This stable coexistence of competitors for the same resources provides a conundrum (Silvertown 2004). Yet our results show that slight limitations in substratum monopoly can provide avenues for recruitment given the enormous colonization potential of kelps demonstrated herein. These studies thus emphasize that this colonization potential facilitates resilience of kelp species to both disturbances and to an inconspicuous group of algal competitors that covers the substratum beneath the kelp canopy. However, our results show dramatic spatial differences in recruitment and apparent species specific patterns of recruitment, raising questions concerning whether these patterns hold true over space, time and among different kelp species in this subarctic fjord.

## REFERENCES

Barrales H.L. & Lobban C.S. (1975) The comparative ecology of *Macrocystis pyrifera*, with emphasis on the forests of Chubut, Argentina. *J. Ecol.*, 63, 657-677

Dayton P.K., Tegner M.J., Parnell P.E. & Edwards P.B. (1992) Temporal and spatial patterns of disturbance and recovery in a kelp forest community. *Ecol. Monogr.*, 62, 421-445

Estes J.A. & Duggins D.O. (1995) Sea otters and kelp forests in Alaska: generality and variation in a community ecological paradigm. *Ecol. Monogr.*, 65, 75-100

Irving A.D., Connell S.D. & Elsdon T.S. (2004) Effects of kelp canopies on bleaching and photosynthetic activity of encrusting coralline algae. *J. Exp. Mar. Biol. Ecol.*, 310, 1-12

Johnson C.R. & Mann K.H. (1988) Diversity, patterns of adaptation, and stability of Nova Scotian kelp beds. *Ecol. Monogr.*, 58, 129-154

Melville A.J. & Connell S.D. (2001) Experimental effects of kelp canopies on subtidal coralline algae. *Austral. Ecol.*, 26, 102-108

Power M.E., Tilman D., Estes J.A., Menge B.A., Bond W.J., Mills L.S., Daily G., Castilla J.C., Lubchenco J. & Paine R.T. (1996) Challenges in the quest for keystones. *Bioscience*, 46, 609-620

Silvertown J. (2004) Plant coexistence and the niche. *Trends Ecol. Evol.*, 19, 605-611

Suzuki Y., Takabayashi T., Kawaguchi T. & Matsunaga K. (1998) Isolation of an allelopathic substance from the crustose coralline algae, *Lithophyllum* spp., and its effect on the brown alga, *Laminaria religiosa* Miyabe (Phaeophyta). *J. Exp. Mar. Biol. Ecol.*, 225, 69-77

# APPENDIX

The following details methods and results from an independent experiment not included in the previous chapters which serves as part of an attempt to understand the mechanisms of algal crust inhibition of microscopic *Saccharina bongardiana* f. *subsimplex* sporophytes.

## METHODS

I tested whether algal crusts inhibited development of *Saccharina bongardiana* f. *subsimplex* oogonia and early developing sporophytes (less than 200 µm in length) through indirect (chemical) means. I covered algal crusts and bare rock with porous dialysis tubing, settled *Saccharina bongardiana* spores into the individual containers hosting each rock, and enumerated oogonia density and microscopic sporophyte density upon the dialysis tubing after 21 days.

In August and September of 2008 I collected cobble sized rocks covered in various algal crust taxa from Yankee Cove between 6 and 10 m below mean low low water and transported them to flow through seawater systems at the Juneau Center of the School of Fisheries and Ocean Sciences. I selected rocks covered in a single algal crust (either calficied crust, non-calcified red crust, or brown crust) and broke off one 6-8 cm wide section of each rock using a rock chisel while keeping the rock and crust submerged. I selected 10 rock pieces with each algal crust taxa in addition to 10 bare rock pieces of the same size with flat surfaces.

I covered each rock surface with a single thin film of 1 cm dialysis tubing using zip ties and electrical tape such that dialysis tubing contained no wrinkles and lay flush with each algal crust or rock surfaces with no bubbles. Before use, I prepared dialysis tubing by rinsing it in running distilled water for 24 h, then soaked it in a 0.3% (w/v) solution of sodium sulfide at 80 °C for 1 minute, following by a rinse in hot distilled water (60 °C) for 2 minutes, then by soaked it in a 0.2% (v/v) solution of sulfuric acid. I then rinsed the tubing with hot water for 10 minutes to remove the acid and soaked it for another 48 hours in cold, distilled running water. I placed each dialysis tubing covered rock in a single 118 ml container filled with sterile PES medium as detailed in Chapter 2 of this work, covered them with a transparent lid and bubbled in air continuously to each container. I placed containers on a slow gyrating table for 24 h on-24 h off cycles within an incubator with a 16:8 h light dark cycle. I then I collected, released and cultured *Saccharina bongardiana* spores within these containers with identical culture methodologies as detailed in Chapter 2, with settlement initiated on September 15, 2008.

After 21 days I removed the dialysis tubing from rocks, placed them upon microscope slides and immediately photographed a 2.25 - 3 mm area of the upward facing tubing under light microscopy for later enumeration of oogonia and sporophytes. I analyzed for differences in oogonia and sporophyte densities among treatments using analysis of variance (ANOVA).

## RESULTS

Brown crusts yielded 6.5 ± 7.8 SD oogonia mm $^{-2}$ (n = 8); red crusts 3.8 ± 3.1 (n = 9); calcified crusts 11.2 ± 3.8 (n = 10); and controls 9.8 ± 5.0 (n = 10). Brown crusts yielded 1.6 ± 2.1 SD sporophytes mm $^{-2}$; red crusts 0.2 ± 0.4; calcified crusts 3.6 ± 2.8; and controls 2.3 ± 3.4. Significant differences existed in both the density of developing eggs and microscopic sporophytes among treatment means ($F_{3,29} = 3.55$, $p = 0.026$, ln ( +1 ) transformed), but after analysis with Tukey pairwise comparisons, no crust treatments differed from the controls in either egg or sporophyte density. The only differences in treatment means occurred between red crusts and calcified crusts ($p = 0.035$ for eggs and $p = 0.014$ for sporophytes).