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Biotic and Abiotic Influences on Bull Kelp (*Nereocystis luetkeana*) Abundance
and Distribution in the Salish Sea

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Abstract

Biotic and Abiotic Influences on Bull Kelp (*Nereocystis luetkeana*) Abundance and Distribution in the Salish Sea

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Bull kelp, *Nereocystis luetkeana*, is an annual species of subtidal marine macroalgae that serves as major biogenic habitat in the Salish Sea of Washington State. Kelp forests are ecologically important because they provide structure for a variety of other organisms and contribute substantial primary production to food webs within and below the photic zone. Like all kelp, *N. luetkeana* has a complex life history with alternating macroscopic sporophyte and microscopic gametophyte life stages. The mature sporophyte reaches up to 30 meters in length and is the most recognizable life stage, but the surface of a bull kelp bed only hints at the complexity below. Juvenile bull kelp need light and space and must compete with perennial understory kelp as soon as they begin to grow. Additionally, survivorship is low for those recruits that do begin to grow; the narrow stipes and single blades of bull kelp recruits are likely far more vulnerable to damage by herbivores than mature bull kelp with thicker stipes and many blades. Conversely, adult bull

kelp have ample access to light, but are far more susceptible to the effects of current flow and the accompanying drag than juveniles. Because juvenile bull kelp sporophytes (stipe length < 40 cm) face very different biotic and abiotic pressures than adult bull kelp that have reached the surface, it is crucial to improve our understanding of this canopy-forming kelp across multiple life stages. The four major goals of this dissertation are: 1) track the appearance and survivorship of *N. luetkeana* recruits across seasons 2) examine how propagule availability and removal of competitors influence *N. luetkeana* recruitment at two sites within and across seasons; 3) quantify how morphology and material properties of *N. luetkeana* change across ontogeny, investigating morphological scaling of both juvenile and mature bull kelp and testing how juvenile stipes fail; and 4) determine feeding patterns of the Northern Kelp Crabs (*Pugettia producta*) in laboratory experiments and assess how protecting juvenile *N. luetkeana* from large consumers in the field influences growth.

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DEDICATION

For Coach Mac

Chapter 1. THE INFLUENCE OF COMPETITION AND SEASONALITY ON RECRUITMENT OF BULL KELP, *NEREOCYSTIS LUETKEANA*

Keywords: Clearing, Kelp Forest, Propagule Enhancement

1.1 INTRODUCTION

The population dynamics of annual species are strongly tied to their capacity for recruitment each year. Many annual species have ruderal life history types, characterized by high reproductive rates and long dispersal distances, with persistence at the species-level enabled due to the short-term use of different, recently-disturbed areas (Grime 1977). Some annual or semelparous species may actually generate their own disturbances that provide suitable free space or resources for the next generation (Foster 1977, Paine 1977).

In the temperate nearshore subtidal zone, kelp forests are ecologically important because they provide structure for a variety of other organisms and contribute a source of primary production to food webs within and below the photic zone (Dayton 1985, Duggins et al. 1989, Siddon et al. 2008). Kelps (order Laminariales) have a heteromorphic life history consisting of a macroscopic sporophyte that makes patches of fertile tissue. These sori release swimming zoospores, which settle and grow into the microscopic gametophyte stage (John 1994). The giant kelp, *Macrocystis pyrifera*, is a perennial species that forms expansive beds that persist for multiple years (Dayton 1985). Conversely, an annual species such as the bull kelp, *Nereocystis luetkeana*, must complete its lifecycle within a single growing season and deposit propagules locally to appear in the same location from year to year. In Alaska, experimental removal of a key consumer (sea urchins) led to colonization by *N. luetkeana* initially, but this annual kelp was

replaced by the perennial kelp *Laminaria groenlandica* in the second growing season; in this system, *N. luetkeana* is considered a ruderal species that will eventually be replaced by another more competitively dominant species (Duggins 1980).

Two factors typically govern plant recruitment – propagule (seed) availability and safe sites suitable for seeding recruitment (Harper et al. 1961, Harper et al. 1965, Grubb 1977). Populations may be establishment-limited, with abundant propagules or seed-limited, with unoccupied safe sites (Duncan et al. 2009). In macroalgae, propagule availability can be difficult to track because this life stage is microscopic and frequently found on the benthos. Also, many macroalgae undergo alternation of heteromorphic generations in which the development and gamete production by a microscopic gametophyte stage intervenes between successive generations of macroscopic sporophytes. However, algal propagule availability has been studied in relation to the spread and persistence of invasive species. Increasing propagules in disturbed (cleared) plots greatly increased recruitment of the invasive brown alga *Sargassum muticum*, indicating that propagule-supply drives appearance of this alga when space is available (Britton-Simmons and Abbot 2008). The presence of the subtidal canopy kelp, *Eisenia arborea* influences which macroalgal propagules can settle and form a macroalgal understory (Benes et al. 2015).

Another important factor that determines where macroalgae recruit each year is competition for space and/or light. There may be competition among different kelps even at microscopic life stages, as *Pterygophora californica* spores have been shown to inhibit the recruitment of *M. pyrifera* (Reed 1990). At larger life stages, competition via light availability influence macroalgal community structure. Perennial canopy-forming kelp species, such as *M. pyrifera*, can reduce available bottom light by 60%, while *P. californica* can reduce bottom light

by 75% as compared to levels at the surface. After removal of these canopy species, the bottom-cover of an annual brown alga (genus *Desmarestia*) increased significantly and lowered the bottom light levels even further to ~1% of ambient light (Clark et al. 2004). Adult sporophytes of *Ecklonia radiata*, a habitat-forming kelp in southern Australia, grow up to 2 meters in height and effectively block light for understory macroalgal species. However, out-planted microscopic *E. radiata* sporophytes cannot grow in the presence of high understory algal cover, highlighting the importance of light availability across different life stages (Tatsumi and Wright 2016).

In many instances, plant and macroalgal recruitment are likely influenced by a combination of both propagule availability and availability of space. In a terrestrial forested area, experimentally increasing seed supply and availability of safe sites increased recruitment in numerous species (Eriksson and Ehrlén 1992). In southern California kelp forests, disturbance from storms may help clear substrate for settlement, recruitment, and growth as well as disperse propagules of *M. pyrifera* and *P. californica* (Reed 1988). Additionally, seasons are likely to differ in propagule and space availability. In laboratory experiments, the filamentous kelp gametophytes of numerous kelp species, including *Saccharina latissima*, *Laminaria setchellii*, and *Laminaria digitata*, survived an 18 month period of darkness at low temperatures between 0°C and 8°C (tom Dieck 1993). This suggests that propagules that are dispersed in one season may not begin to produce gametes immediately, waiting for enhanced light or space availability.

Here we use field observations and experiments to examine the factors influencing the recruitment of an annual species of marine macroalgae serving as major biogenic habitat. How does bull kelp, *Nereocystis luetkeana*, maintain persistent kelp beds despite its annual life history? We investigated recruitment dynamics of *N. luetkeana* by tracking the natural appearance of juveniles and manipulating both propagule and space availability. We

hypothesized that 1) juvenile *N. luetkeana* would exhibit a seasonal appearance as a cohort in the spring when there is low biomass of macroalgal competitors 2) a delay of at least six weeks would occur between spore release and appearance of visible *N. luetkeana* sporophytes, based on laboratory evidence of time needed for progression through microscopic stages; and 3) space would be more limiting than propagules (spores) to recruitment at sites adjacent to established *N. luetkeana* beds.

1.2 METHODS

1.2.1 *Study Species*

Bull kelp, *N. luetkeana*, is an annual kelp that exhibits alternation of heteromorphic generations. Gametophytes germinate from swimming zoospores, which are the primary dispersive stage as they are carried in sori on detached blades and/or swim as single-celled spores. Following settlement and germination, male gametophytes produce swimming gametes that fertilize females, from which the juvenile sporophyte grows (reviewed in Springer 2010). In lab-grown *N. luetkeana* under ideal conditions (10°C, white light between 80-100 $\mu\text{E}\cdot\text{m}^2\cdot\text{s}^{-1}$), zoospore settlement and germination occurs within 24 hours, and germ tubes begin to grow, branching to form filamentous gametophytes that can become reproductively mature within 10-14 days. After 21 days, microscopic sporophytes (~1 mm length) are visible (Merrill and Gillingham 1991).

A demographic study of *N. luetkeana* sporophytes in the field gives an indication of the timing of major life history events at a subtidal site in southern Salish Sea, approximately 100 miles south of our study sites (Maxell and Miller 1996). At this site, recognizable juvenile *N. luetkeana* first appeared in March, stipe growth reached a maximum in late June, followed by an increase in blade growth, and the first reproductive individuals were observed in early May. This

timing is consistent with reproduction occurring in summer of one year that results in appearance of juveniles the following spring. In between these events, *N. luetkeana* goes through its microscopic benthic gametophyte stage.

1.2.2 *Study Sites*

To track seasonal appearance and survivorship of juvenile *N. luetkeana* (stipe <30 cm), we established a 15 m x 25 m subtidal site in February 2014 near south Shaw Island in the San Juan Islands of Washington State (N 48.54706°, W 122.95091°; 8 m max depth; hereafter, South Shaw 1), marking the boundaries with sub-surface floats attached to half-size concrete blocks. We chose the site based on our observations of a robust kelp bed during summer 2013 in the same approximate location, although only a few mature individuals remained during the winter when we established the site.

One site for subtidal experimental manipulation of competition and propagule abundance was located approximately 25 meters from South Shaw 1, further offshore toward the San Juan Channel (N 48.54710°, W 122.95130°; 7-9 m max depth; hereafter, South Shaw 2; Fig. 1A). We established a second site for clearing and seeding near Point Caution on San Juan Island (N 48.56323°, W 123.02555°; 8-10 m max depth; hereafter, Point Caution; Fig. 1B)

All three sites were accessed via SCUBA. Dive length was consistent (~50 minutes), providing a means of standardizing the seasonal appearance of new recruits (catch per unit effort as number of recruits detected per dive).

1.2.3 *Tagging and Tracking Recruits*

Using numbered plastic flagging tape (as in Maxell and Miller 1996), we tagged all of the juvenile bull kelp that we encountered (stipe length < 30 cm) between June 2014 and January

2015 at South Shaw 1. We monitored survivorship of these recruits every two weeks and surveyed for appearance of new *N. luetkeana* recruits during each month of the year (2014-2015).

1.2.4 *Experimental Manipulation of Competition and Propagule Abundance*

A two-factor crossed design was used to assess the effects of competition (hereafter clearing) and propagule availability (hereafter seeding) on appearance of new *N. luetkeana* sporophytes. Subtidal plots were marked at the corners with bricks and flagging tape while the edges of each plot were delineated with yellow polypropylene ropes connecting the bricks. Plot size was 2x2 m and five replicate plots were established for each of the four treatments: cleared and seeded, cleared and unseeded, uncleared and seeded, and uncleared and unseeded. We established the experiment across four seasons at South Shaw 2: spring (April), summer (August), fall (October) 2015, and winter (February) 2016. The same experimental setup was employed three times at Point Caution in two seasons: July and August 2016 (summer) and April 2017 (spring). For statistical analysis, we combined the July and August experimental setups into one group (“summer”) because of the close proximity of plots, the similarity in cleared biomass, and short (6-week) interval between setups.

Treatments were assigned to plots at random. In cleared plots, we reduced competition by clearing attached macroalgae taller than 5 cm. In seeded plots, we enhanced propagule availability by anchoring fertile sori of *N. luetkeana* (five per plot, collected at the surface prior to the dive) to the substrate in the center of the plot using small rocks already in the subtidal environment. We collected the cleared macrophytes from 0.3 m² subsamples within each cleared 4 m² plot and dried them in a drying oven for 24 hours at 60°C to allow comparison of biomass between seasons at each site. We monitored experimental plots for one year following each

initiation, counting the number of kelp in each plot on each survey, except for the spring experimental initiation at Point Caution, which was monitored for three months.

1.2.5 *Data Analysis*

We tested for normality of residuals using a Shapiro-Wilk test and used a Bartlett test to test for homogeneity of variances.

The two-factor experiment was analyzed separately for each site and each season. The response variable was the maximum count of *N. luetkeana* per plot. The main effects were clearing and seeding and their interaction. These counts did not meet the assumptions of normality, even after various transformations, and also were overdispersed relative to Poisson distribution, so we used a resampling approach to determine statistical significance of the main effects and interactions ($\alpha=0.05$): PERMANOVA with Euclidean distances and 9,999 permutations.

Across seasons at each site we compared the cleared biomass of macroalgae and the magnitude of juvenile *N. luetkeana* recruitment, using counts of new recruits, and the time to appearance of the first *N. luetkeana* in each plot. The time to appearance used only plots in which juvenile recruits appeared. Because of the lack of normality and heteroskedastic variances, we analyzed these data using PERMANOVA (as described above). When a factor was significant, we used pairwise PERMANOVA to compare all possible combinations and Bonferroni-corrected p-values as the threshold for significance.

We measured the macroalgal biomass only in cleared treatment plots. The dried biomass data for South Shaw 2 met the assumptions of normality and we tested for seasonal differences using a one-way ANOVA followed by a Tukey HSD test. Because Point Caution biomass data

did not meet the assumptions of normality, we used PERMANOVA (as described above) to compare the biomass between spring and summer experiment initiations at Point Caution.

All data analyses were performed using R (R Core Team 2016). For PERMANOVA, we used the “vegan” package (Oksanen et al. 2017).

1.3 RESULTS

1.3.1 *Tagging and Tracking Recruits*

We tagged and tracked 41 *N. luetkeana* recruits in the spring/summer and 10 in the fall/winter at South Shaw 1. Survivorship of juvenile bull kelp recruits was low for individuals tagged in both seasons, as less than half of tagged individuals survived the initial two-week observation period (Fig. 2A). On survey dives, we observed at least one new juvenile *N. luetkeana* recruit (stipe length < 30 cm) appearing in every month except February (Fig. 2B).

1.3.2 *Experimental Manipulation of Competition and Propagule Abundance*

Test statistics and p-values for experimental manipulation of competition and propagule abundance are summarized in Table 1 for South Shaw and Table 2 for Point Caution.

Following the spring initiation at South Shaw, clearing increased the number of new *N. luetkeana* that began to grow (Fig. 3A); the cleared plots grew more individuals (mean \pm SE = 23.5 ± 7.2) than the uncleared plots (mean = 0.4). Seeding did not influence the appearance of new *N. luetkeana* and the interaction between clearing and seeding was also not significant. Clearing made no difference in the number of new individuals that grew in plots within one year following the summer (Fig. 3B), fall (Fig. 3C), and winter (Fig. 3D) experiment at South Shaw. Seeding also did not significantly impact appearance of new *N. luetkeana* in plots established in summer, fall, or winter. The interaction between clearing and seeding was also not significant in

summer, fall, or winter. At Point Caution, cleared plots had more *N. luetkeana* recruits in the spring (Fig. 4A) but seeding did not change the number of recruits and the interaction between clearing and seeding was also not significant. In the summer, the number of new *N. luetkeana* that began to grow was greater in cleared plots (Fig. 4B) but did not differ between plots with propagule enhancement. The interaction was also not significant.

Among plots in which new kelp grew at any point in the year following the experimental initiation, the time in months to appearance at South Shaw varied by season ($F_{3,30}=25.4$, $p<0.001$; Fig 5; Table 3). New *N. luetkeana* appeared the soonest following the spring experiment (mean \pm SE = 1.6 ± 0.16 months) as compared to the summer (7.3 ± 2.27), fall (8.5 ± 0.52), and winter (4.5 ± 0.47) experiments. New kelp took longer to appear following the fall setup as compared to the winter setup, while the time to appearance of new kelp was statistically indistinguishable for summer and fall as well as summer and winter.

The number of new individuals also varied by season at South Shaw ($F_{3,76}=6.09$, $p<0.001$; Fig. 6A; Table 4). The number of juveniles that appeared following the spring initiation (mean \pm SE = 23.9 ± 7.1) was greater than in the summer (1 ± 0.32) or fall (1.4 ± 0.26). The number that grew in plots following the winter initiation was greater than in the summer (3.75 ± 1.1). The number that appeared in spring was not statistically different than in winter initiations nor between summer and fall or fall and winter. At Point Caution, the number of new *N. luetkeana* recruits did not vary by season ($F_{1,57}=1.2$, $p=0.65$; Fig 6B).

Understory macroalgal (potential competitor) biomass varied seasonally at both sites in keeping with an increase during the growing season (South Shaw 2: $F_{3,35}=3.24$, $p=0.03$; Fig. 7A and Point Caution: $F_{1,28}=8.4$, $p=0.005$; Fig. 7B). At South Shaw 2, the cleared biomass of plots established in the fall was greater than those in the winter ($p=0.02$), while the pair-wise

comparisons of cleared biomass from the plots established in spring, summer, and fall were all statistically similar. At Point Caution, the cleared biomass was lower in the spring initiation than the summer initiation.

1.4 DISCUSSION

Juvenile *N. luetkeana* represent a life stage whose success is crucial to the persistence of beds of this annual species from year to year. This kelp's alternation of heteromorphic generations means that there is always an interval between sporophyte generations, in which the microscopic life stages occur. Our experimental removal of competitors and enhancement of propagule availability across multiple seasons suggests that *N. luetkeana* shows strong seasonality in regeneration, decoupled from seasonal availability of space or propagule availability. Successful regeneration may be inhibited by competition from other macroalgae, which allows some recruits to appear in multiple seasons following a disturbance event. Additionally, although disturbances may generate sites for recruitment in a propagule-rich system, high juvenile mortality plays a role in determining where recruits persist and mature.

The effect of clearing, creating gaps in the canopy and increasing the availability of light and/or space, may vary between subtidal and intertidal kelp species because of different environmental pressures for each. In our subtidal experiment, more *N. luetkeana* recruits appeared in cleared plots in the spring at South Shaw and in both spring and summer at Point Caution, when conditions are expected to be otherwise favorable for kelp growth. Similarly, the perennial giant kelp (*M. pyrifera*) did not start growing in undisturbed patches of low-growing understory kelp until experimental clearing took place, suggesting that this canopy-former also requires gaps in existing understory to initiate growth (Dayton et al. 1984). However, when larger canopy-forming individuals of the annual kelp *Alaria marginata* were cleared from

intertidal plots, the smaller understory individuals did not begin to grow rapidly or become fertile as might be expected following the removal of intraspecific competitors (McConnico and Foster 2005). This may have been because the clearing happened in the summer, after the optimal season for vegetative growth had passed, or because the abrupt removal of the over-story individuals exposed the remaining *A. marginata* to deleterious levels of light and heat during midday low tides (McConnico and Foster 2005).

The lack of influence of seeding indicates that propagule limitation is not a major factor influencing where *N. luetkeana* recruit and begin to grow in our experimental plots. Our plots at both sites were established adjacent (<5 m) to a known *N. luetkeana* beds and this close proximity likely contributes to a high natural availability of propagules in both seeded and unseeded plots. Working at a site more distant from adult *N. luetkeana* might have produced different results; in a clearing study, new *M. pyrifera* individuals did not begin to grow in cleared patches 10 or more meters from an existing *M. pyrifera* bed (Dayton et al. 1984). However, there is also evidence that *M. pyrifera* propagules can be transported longer distances (<1000 m) to potentially maintain or restore populations even when an individual kelp bed disappears (Gaylord et al. 2002, 2006).

We set up clearing and seeding experiments across multiple seasons to examine whether these main effects would differ due to seasonal variation in competitor biomass, seasonal sori availability, or environmental factors. The winter experiment at South Shaw resulted in higher densities of juveniles than in summer or fall, but showed no effect of clearing. In February, the cleared biomass of understory species was also the lowest, suggesting that competition might not be as limiting for kelp beginning to grow in the late winter and early spring as it would be later in the year after a seasonal increase in understory biomass. Even perennial kelp species do not

increase in biomass as quickly in the winter (vs. summer) due to lower light levels and continued loss of biomass through tissue sloughing (Mann 1973). The long interval before the appearance of macroscopic juvenile sporophytes in plots established in the summer and fall suggests that microscopic stages of *N. luetkeana* can persist for an extended period of time and resume growth when conditions are favorable. In laboratory experiments with low nutrient levels, *M. pyrifera* gametophytes remained vegetative, delaying reproduction for at least seven months with low nutrient levels before rapidly producing sporophytes after nutrients were added (Carney 2011). Gametophytes of the subtidal, annual brown alga *Desmarestia ligulata* var. *ligulata* can persist for up to 15 months in the field (Edwards 2000). New recruits appeared the soonest following our spring experimental initiation, possibly due to environmental conditions such as increased light, that may facilitate life stage transitions. Laboratory evidence shows that growing *N. luetkeana* gametophytes at reduced light intensity and duration slowed both growth and attainment of reproductive maturity (Vadas 1972). However, it is also possible that some of the recruits that appeared after a long delay came from zoospores that settled after our propagule enhancements, as we observed reproductively mature individuals throughout the year and plots were located adjacent to existing *N. luetkeana* beds. The fact that clearing yielded more recruits following the summer experimental setup at Point Caution but not at South Shaw may indicate some subtle effect of site or temporal variation that may be acting on any one of the life stages.

Although overall appearance of new *N. luetkeana* was low following the summer and fall experimental setups, a few new individuals did begin to grow in each time period, which matches our monitoring of natural *N. luetkeana* recruits. This likely contributes to the presence of *N. luetkeana* of different life stages observed throughout the year, and suggests that not all *N. luetkeana* begin to grow as a cohort in the spring as Maxell and Miller (1996) observed. In

laboratory experiments, gametophytes of another kelp (*Laminaria hyperborea*) persisted under dark conditions for up to five months and resumed development after exposure to white and/or blue light (Luning 1980). Gaps in the understory can form during any time of year, increasing light availability and stimulating development of waiting gametophytes or sporophytes already present in the environment.

This improved understanding of competition as an important factor governing the seasonal appearance of new *N. luetkeana* sporophytes in a propagule-rich system furthers our understanding of bull kelp bed regeneration from year to year. However, observed low survivorship of *N. luetkeana* recruits indicates that appearance of new individuals does not necessarily lead to generation of a kelp bed due to post-recruitment effects such as herbivory and post-recruitment competition. Experimentally caged juvenile bull kelp (stipe length < 30 cm) protected from large local consumers such as kelp crabs (genus *Pugettia*) and urchins (*Strongylocentrotus* sp.) increased in blade length and mass, while uncaged individuals decreased in both (Dobkowski 2017). In one study of *M. pyrifera*, only about 2% of tagged recruits survived into a second year due to herbivory by white urchins (*Lytechinus anamesus*) and/or competition from conspecifics (Dean et al. 1989). Grazing by urchins (*Echinus esculentus*) and shading from canopy kelps both contribute to mortality of small *Laminaria hyperborea* individuals (stipe length <10 cm) in the eastern North Atlantic (Sjotun et al. 2006). These intertwined factors contributing to kelp bed appearance and maintenance highlight the importance of studying organisms with complex life histories across multiple life stages.

1.5 TABLES AND FIGURES

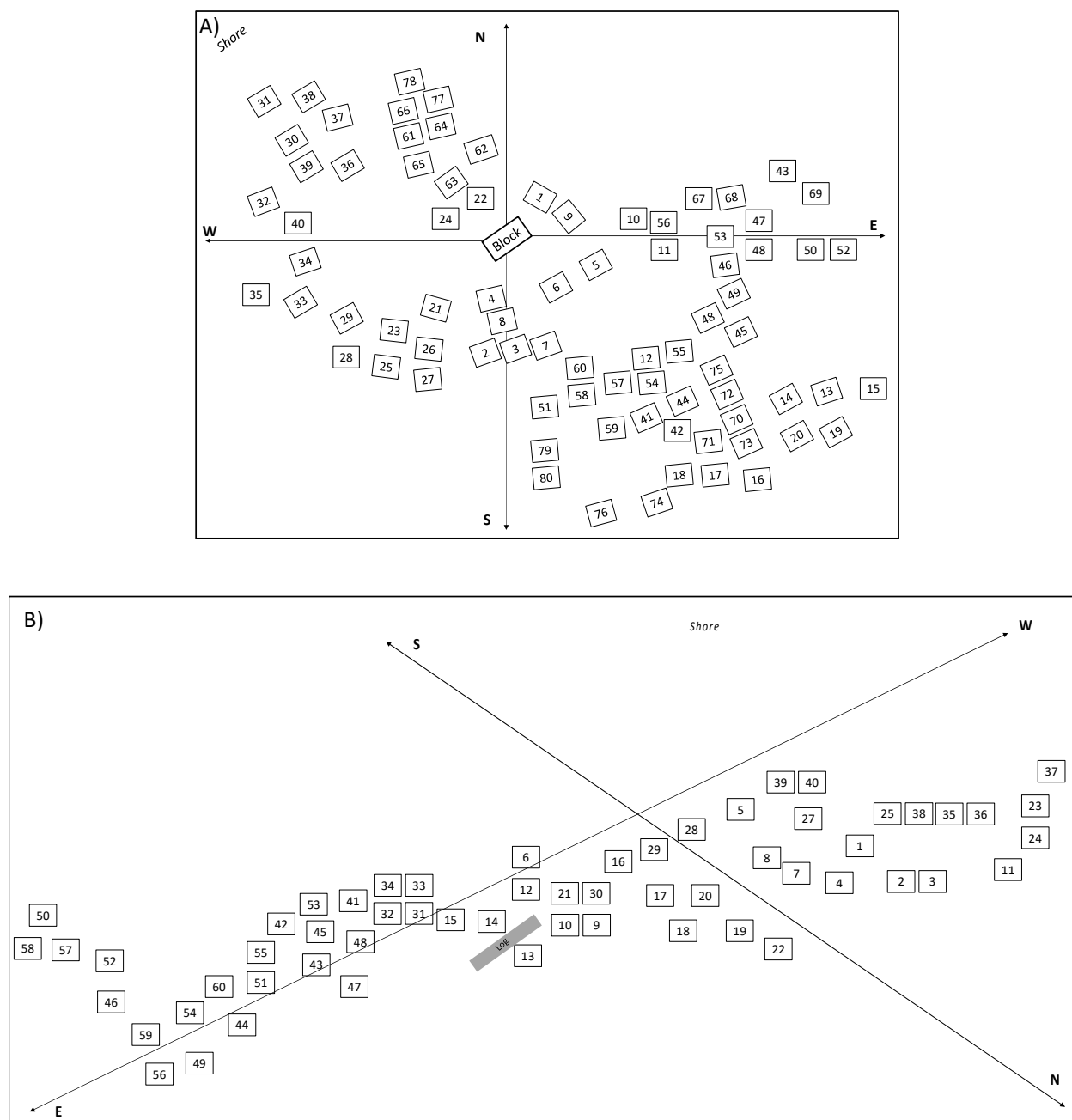


Figure 1.1 Site maps of A) South Shaw and B) Point Caution

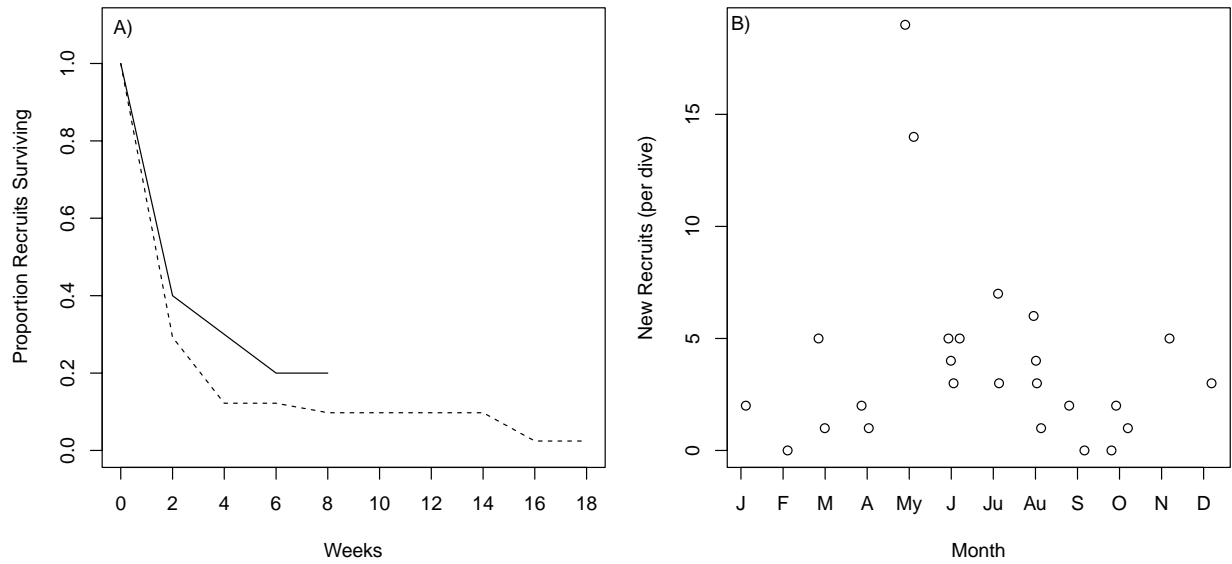


Figure 1.2 A) Survivorship and B) Appearance of new bull kelp, *N. luetkeana* recruits at South Shaw Island, USA in 2014-2015; A) dashed line indicates recruits tagged in the spring/summer and tracked for 18 weeks; solid line indicates recruits tagged in the fall/winter and tracked for 8 weeks B) new recruits were surveyed in every month except February

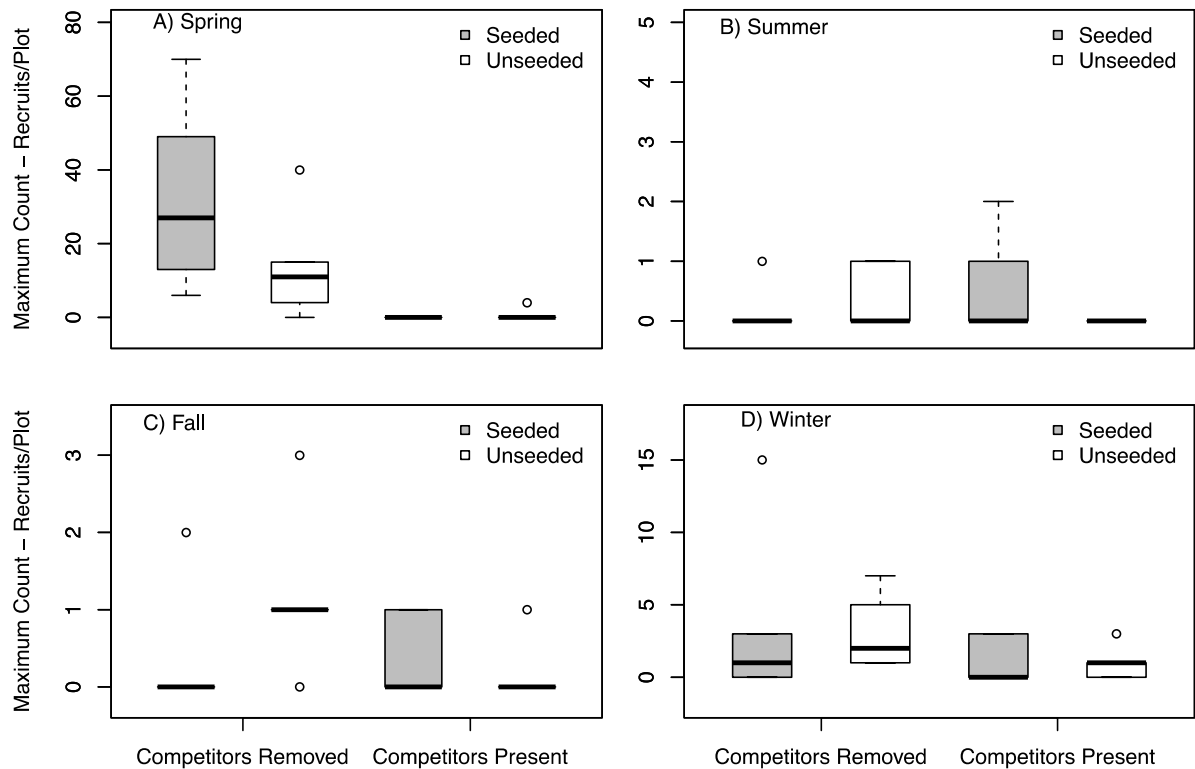


Figure 1.3 Appearance of bull kelp (*N. luetkeana*) recruits, South Shaw

Island, USA in A) Spring B) Summer, C) Fall, and D) Winter at A) Spring - the number of new kelp that began to grow differed between cleared and uncleared plots ($p=0.0018$) but not between seeded and unseeded plots ($p=0.21$); the clearing * seeding interaction was also not significant B) Summer, C) Fall, D) Winter – neither clearing nor seeding significantly increased the appearance of new bull kelp and the interaction was not significant

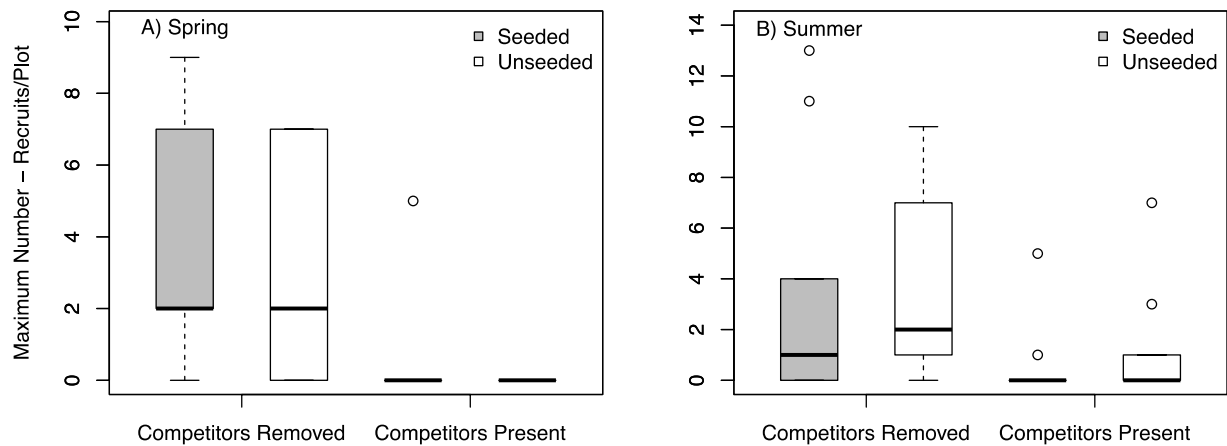


Figure 1.4 Appearance of bull kelp (*N. luetkeana*) recruits, Point Caution

in A) Spring and B) Summer, A) The number of recruits that appeared differed between cleared and uncleared plots ($p=0.01$) but not between seeded and unseeded plots ($p=0.57$); the interaction was also not significant ($p=0.85$) B) The number of recruits that appeared differed between cleared and uncleared plots established ($p=0.04$) but not between seeded and unseeded plots ($p=0.37$); the interaction was also not significant ($p=0.36$)

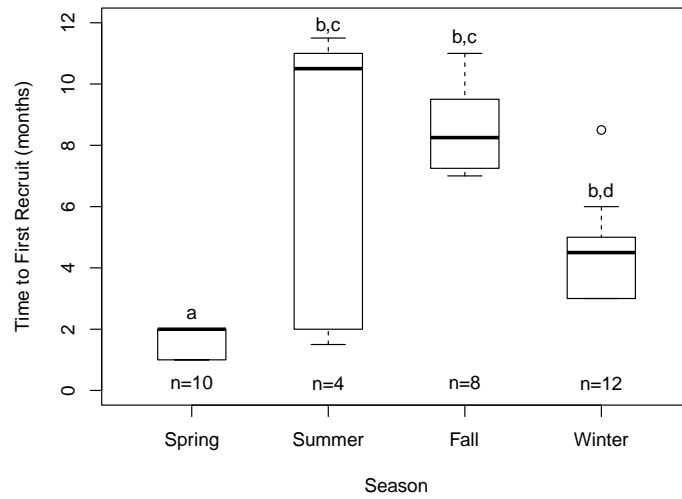


Figure 1.5 Time to appearance of bull kelp, *N. luetkeana*, recruits following experimental setup in four seasons at South Shaw Island. The time for new kelp at South Shaw to appear was the shortest in the spring ($p < 0.001$), while the amount of time to first kelp was not distinguishable between summer and fall and summer and winter; fall and winter were also different ($p = 0.02$). Letters indicate statistically significant differences.

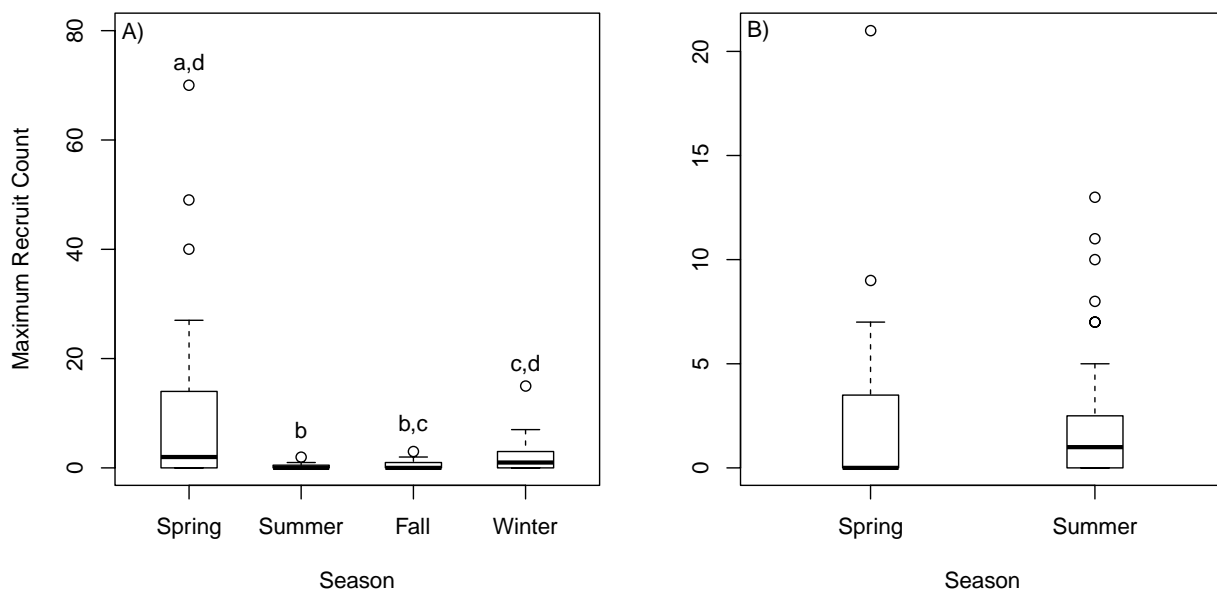


Figure 1.6 Appearance of new bull kelp recruits at South Shaw and Point Caution

A) At South Shaw, the most new recruits grew following the spring setup ($p < 0.001$), while the number of new kelp that appear following the summer and fall setup and the winter and fall setup did not differ. Letters indicate statistically significant differences. B) At Point Caution, there was no statistical difference in kelp that grew between seasons ($p = 0.65$)

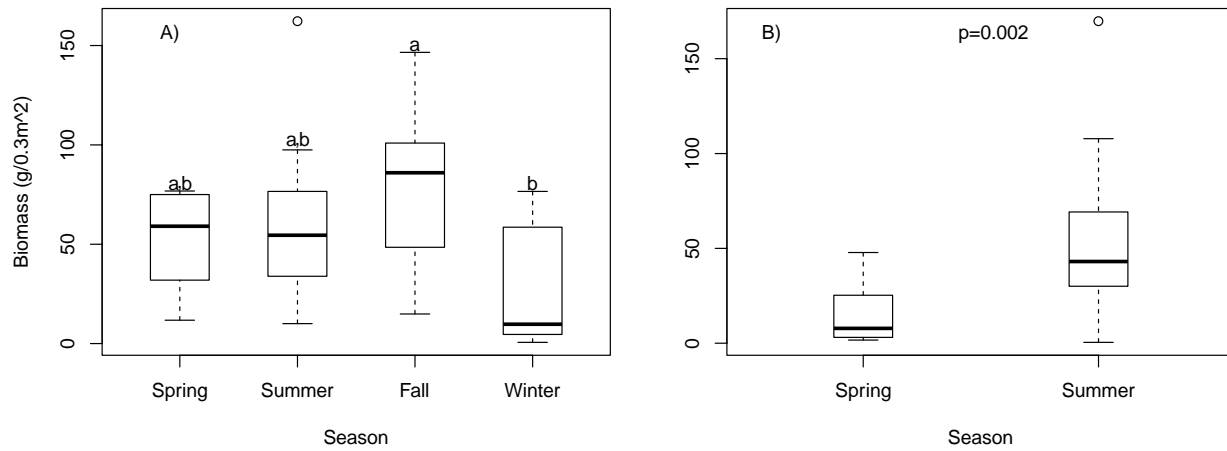


Figure 1.7 Understory macroalgal biomass across seasons at both sites

A) South Shaw, where the cleared, dried biomass was the same between spring, summer, and fall but different between fall and winter ($p=0.02$) and B) Point Caution, where cleared, dried biomass differed between spring and summer ($p=0.005$)

Factor	Season							
	Spring		Summer		Fall		Winter	
	F_{1,16}	p	F_{1,16}	p	F_{1,16}	p	F_{1,16}	p
Clearing	11.3	0.002	0	0.99	2	0.17	2.2	0.15
Propagule Enhancement	1.7	0.21	0.62	0.44	0.72	0.39	0.06	0.86
Interaction	2.1	0.17	2.5	0.24	0.20	0.18	0.02	0.92

Table 1.1 South Shaw two-factor experiment: Main effects and interactions

($\alpha=0.05$); $F_{\text{numerator df, denominator df}}$ and p-values from PERMANOVA (Euclidean distances; 9,999 permutations); statistically significant effects are shaded.

Factor	Season			
	Spring		Summer	
	F_{1,16}	p	F_{1,35}	p
Clearing	4.1	0.03	5.3	0.03
Propagule Enhancement	0.05	0.84	0.12	0.75
Interaction	0.45	0.59	0.02	0.88

Table 1.2 Point Caution two-factor experiment: Main effects and interactions

($\alpha=0.05$); F_{numerator df, denominator df} and p-values from PERMANOVA (Euclidean distances; 9,999 permutations); statistically significant effects are shaded

	Spring (n=10)		Summer (n=4)		Fall (n=8)	
Summer (n=4)	F _{1,12} =27.5	p=0.007	-	-	-	-
Fall (n=8)	F _{1,16} =194.6	p<0.001	F _{1,10} =0.02	p=0.93	-	-
Winter (n=12)	F _{1,20} =28.6	p<0.001	F _{1,14} =8.6	p=0.02	F _{1,18} =32.3	p<0.001

Table 1.3 Test statistics and p-values for time to appearance of new recruits in plots that grew kelp within one year at South Shaw; F and p-values from PERMANOVA (Euclidean distances; 9,999 permutations); statistically significant effects are shaded (p<0.008 with Bonferroni correction)

	Spring		Summer		Fall	
	<u>F_{1,38}</u>	<u>p</u>	<u>F_{1,38}</u>	<u>p</u>	<u>F_{1,38}</u>	<u>p</u>
Summer	7.0	<0.001	-	-	-	-
Fall	6.7	0.002	1.2	0.39	-	-
Winter	4.7	0.03	6.2	0.003	4.6	0.02

Table 1.4 Test statistics and p-values for number of new recruits that appeared following each seasonal setup within one year at South Shaw; $F_{\text{numerator df, denominator df}}$ and p-values from PERMANOVA (Euclidean distances; 9,999 permutations); statistically significant effects are shaded ($p < 0.008$ with Bonferroni correction)

Chapter 2. SCALING AND MATERIAL PROPERTIES OF JUVENILE BULL KELP (*NEREOCYSTIS LUETKEANA*)

Keywords: Kelp Forest, Ontogenetic change, Allometric Scaling

2.1 INTRODUCTION

Bull kelp (*Nereocystis luetkeana*) is an important foundation species in the nearshore subtidal zone of the Salish Sea (Dayton 1985). It is a primary producer in shallow water, and also subsidizes food webs below the photic zone, as stipes and blades are transported to the benthos (Duggins et al. 1989, Britton-Simmons et al. 2009). Like all kelp (Laminariales), bull kelp exhibits a heteromorphic life history with alternating macroscopic sporophyte and microscopic gametophyte stages (John 1994). The kelp canopy is formed by the large sporophyte, comprised of a holdfast attached to the benthos, a long and slender stipe up to 30 meters in length, and a floating bulb supporting up to one hundred long, straplike blades (Foreman 1976). Bull kelp is an annual species, thus each individual must successfully complete all life stages within a single growing season for a kelp bed to persist from year to year (Scagel 1947).

Young bull kelp sporophytes must quickly grow toward the surface to maximize light availability to their blades. Other canopy-forming seaweeds, such as the giant kelp (*Macrocystis pyrifera*), can reduce available bottom light by 60% as compared to levels at the surface (Clark et al. 2004). Young bull kelp with short stipes face much lower flow than adult bull kelp that have reached the surface. The young sporophyte may face fewer hydrodynamic challenges, but they are certainly subject to attack by diverse herbivores. Small snails (*Lacuna vincta*) remove tissue by radula scraping, which weakens the kelp thallus; field observations show greater snail density and damage on juvenile bull kelp (Chenelot and Konar 2007). Juveniles grow more when they

are caged to exclude large consumers such as the Northern kelp crab (*Pugettia producta*) or sea urchins (*Strongylocentrotus* sp.) indicating some level of top-down control of this life stage by herbivores (Dobkowski 2017).

In contrast, adult canopy-forming kelp must cope with increased drag, tangling with conspecifics, holdfast detachment, as well as damage from consumers. Environments with variable current flow especially increase the risk of adult bull kelp mortality and even a small amount of damage from a consumer such as *L. vincta* can greatly reduce the force required to break the stipe (Duggins et al. 2001). Stipes of many drift bull kelp washed up on beaches exhibit stipe damage, which changes the cross-sectional area and concentrates stress on that point (Koehl and Wainwright 1977). Undamaged bull kelp stipes may fail if detached individuals become tangled with them, increasing the force exerted on the intact holdfast; similar effects result from tangling of two attached individuals when some of the entangled stipes and/or holdfasts are pulled unequally, causing failure (Koehl and Wainwright 1977). Tangling has also been implicated in contributing to stipe and holdfast failure in giant kelp, *Macrocystis pyrifera* (Seymour et al. 1988). Consumers such as isopods (genus *Idotea*), red sea urchins (*Mesocentrotus franciscanus*), and kelp crabs (genus *Pugettia*) readily consume fresh and/or detrital bull kelp (Dethier et al. 2014, Dobkowski 2017)

The material properties of macroalgae are affected by growth and have an impact on stipe failure. For non-canopy forming kelp, as well as red and green algae, material properties change relative to distance from the meristem, the center of growth. Newer, younger tissues tend to be less stiff and more extensible than older tissues (Krumhansl et al. 2015). Some kelp, such as *Agarum* and *Saccharina*, exhibit conveyor-belt like growth; in these species, the youngest tissue near the holdfast is also the most extensible, while the older, stiffer tissue sloughs off at the distal

end of the blade (Mann 1973, Krumhansl et al. 2015). Mature bull kelp exhibit high extensibility under tension at the narrow region a few decimeters from the holdfast, indicating that they avoid breakage by being tough, not brittle (Koehl and Wainwright 1977). In young individuals, this is the region of the stipe where rapid growth takes place (Fig. 1D), and so in the adults is likely the youngest region. In contrast, the hollow region of the bull kelp stipe closest to the surface is much less flexible (Koehl and Wainwright 1977); this is also the oldest region of the stipe (Fig. 1B).

Exposure to different flows may affect ontogenetic scaling; currents and waves acting on larger individuals increase the tensile stress applied to the stipe by increasing drag. It has been suggested, for example, that small (< 2m) kelp grow quickly and isometrically, to contend with large stresses generated by drag on the blades, but grow allometrically at larger sizes because their size allows them to mediate wave forces by “going with the flow” (Denny et al. 1997). The goals of this study are to a) determine how juvenile bull kelp scale, particularly the relationship between bulb size and stipe length (as a proxy for age); b) identify differences in how juvenile macrophyte stipes fail over an ontogenetic series, including differences in material properties and location of stipe failure, again using stipe length as a proxy for age; and c) compare the morphology and material properties of juvenile bull kelp to adult kelp, with focus on very young sporophytes from a week (2 cm) to several weeks old (36 cm).

2.2 METHODS

2.2.1 *Field Collection*

Twenty-eight juvenile bull kelp (stipe lengths 2.1 cm to 36.1 cm) were collected at three subtidal sites in the San Juan Channel near Friday Harbor Laboratories (Fig. 2): South Shaw (48°33'12.33"N, 123°0'26.00"W), Paradise (48°31'42.47"N, 122°58'15.71"W), and Bell Island

(48°35'42.38"N, 122°58'45.75"W). While all of these sites are more protected from most direct wave activity, they do experience similar effects of strong tidal currents. Individuals were collected by scuba divers using dive knives to remove intact holdfasts from the substrate without applying force to the stipe or the junction between the stipe and the holdfast. Collected individuals were held in flow-through seawater tables until materials testing occurred. To minimize specimen degradation, we tested individuals within 48 hours of collection and measured and photographed them prior to testing. We recorded stipe length (mm), bulb width (mm), stipe width below the bulb and above the holdfast (mm), as well as the region of the stipe and stipe width where the stipe was visually estimated to be narrowest (mm; Fig. 1).

Additionally, we collected 27 intact, mature drift bull kelp at three sites on San Juan Island: the FHL dock (48°43'42.14"N, 123°00'44.02"W), Eagle Cove (48°27'41.45"N, 123°01'55.18"W), and Cattle Point (48°27'00.06"N, 122°57'45.94"W). For these larger, mature individuals, we measured the stipe length and bulb diameter to allow for comparison of morphological scaling relationships to the juvenile kelp. However, because we had no control over the state of degradation in these individuals, we did not include them in the material properties tests.

2.2.2 *Lab Testing*

To measure the material properties of juvenile kelp, individuals were loaded in tension using a materials testing system (MTS; Synergie 100, MTS Systems Corp.) fitted with a 500N load cell recording at 100 Hz. We custom built four 3D printed cradles to hold kelp bulbs while minimizing stress concentrations (Crofts and Dobkowski 2017; Fig 3A). Based on diameter, the bulb was fitted into the appropriately sized 3D printed cradles, which was attached to the moving load cell. If a kelp bulb was too small to fit in one of our cradles, we freeze-clamped the bulb in

place instead. Freeze-clamping was achieved by loosely clamping the tissue with metal clamps attached to the load cell and applying dry ice to the metal clamps, effectively freezing the tissue to the clamp. Holdfasts were also held stationary by a 3D printed platform with a hole in the middle; or, if they were too small, freeze-clamped to a stationary metal clamp using dry ice (Fig. 3B). In some cases, the stipe length exceeded the working height of the MTS, so a pulley system with aramid fiber (Kevlar) lines was added to test longer specimens. This ensured kelp were still subjected to a purely vertical tensile load. For each test, the stipe was put under tension by raising the bulb at a loading rate of 50.8 mm/min until the kelp failed. Specimens that failed at the clamp or within the cradle were excluded from analysis.

We recorded the continuous load and extension for each test, and took photographs of the fractured stipe surface, which were analyzed in ImageJ (NIH) to determine the cross-sectional area of the break. With this information, we were able to generate stress-strain curves and, for each test, recorded the maximum force (F_{Max} ; N), the force at failure (F_{fail} ; N) which was determined by a drop in force equal to 50%, the strain at failure (ϵ_{fail}), and calculated Young's Modulus (E , Pa) and energy absorbed by the stipe prior to failure (toughness; Pa). We calculated maximum stress (δ_{max} , Pa) by dividing F_{Max} by surface area of the break (mm^2).

2.2.3 *Data Analysis*

Data were analyzed with R (R Core Team 2016) using the 'lmodel2' package to perform Model II regressions using the standard major axis (SMA) method when both variables were random and subject to measurement error that needed to be minimized (Legendre 2015). Regression using the ordinary least squares (OLS) method was used for the nominal strain failure percentage because this represents a unit-less calculated value. We used the R package

“segmented” to predict where the “breakpoint” is for juvenile vs. adult morphological scaling (Muggeo 2008).

Because scaling is a question of structure and not material properties, we begin with the assumption that there will be no change in material properties over ontogeny. Thus, the isometric slopes for Young’s modulus, maximum stress (δ_{\max} , Pa), strain (ϵ), and toughness (the measured amount of stress for a given amount of strain, Pa) will all be zero ($b=0$; Table 1). When comparing morphologies of adult or juvenile kelp we did a comparison of stipe length and bulb width (length-length) and have a predicted isometric slope of 1. Since force acts on cross-sectional surface area, comparisons of force to stipe length will have a predicted isometric slope of 2. Work, the force multiplied by deformation, scaled against the stipe length should have an isometric slope of 3. Allometry (positive or negative) meant the isometric slope fell significantly outside the calculated 95% confidence intervals of the experimental slope.

2.3 RESULTS

All slope, intercept, R^2 , and confidence interval values for adult and juvenile scaling, and materials properties ~stipe length comparisons are summarized in Table 1.

2.3.1 *Morphology*

The mature bull kelp (stipe length > 200 cm) displayed negative allometry, indicating that the stipe length increases more rapidly than the bulb width (slope=0.71; Fig 4A). For juvenile bull kelp (length <40 cm), we found that bulb diameter scales isometrically with stipe length (slope=1.19; Fig 4B). There is an abrupt breakpoint where the relationship changes (Fig. 4C); we estimated this change from juvenile and adult morphology to be at a stipe length (cm) of 33.2 ± 14.8 SE.

2.3.2 Mechanical Testing

For small bull kelp, stipe break surface area shows negative allometry, increasing more slowly than stipe length ($b=0.66$, Fig. 5). All stipes broke close to the bulb, but there was no relationship between the distance of the break from the holdfast and the stipe length ($R^2=0.05$, $p=0.30$). A comparison of force at failure (N) versus stipe length displays negative allometry, with F_{fail} increasing much less rapidly than stipe length (slope= 0.70 , Fig. 6A). Work, the tensile force integrated over the extension to failure (calculated as the area under the force/extension curve), also shows negative allometry (slope= 1.8 , Fig. 6B) when compared to stipe length. The slope of the regression line for maximum extensibility versus stipe length does not differ from 0 (slope= 0.02) and the R-squared value is nearly zero, indicating that nominal strain at failure is independent of stipe length (Fig. 7A). The maximum stress (slope= 0.55 ; Fig. 7B), Toughness (slope= 1.31 , Fig. 7C), and Young's modulus (slope = -1.23 , Fig. 8) do change over the course of ontogeny.

2.4 DISCUSSION

Contrary to our initial assumptions, kelp material properties change as juvenile *N. luetkeana* grow, with very young kelp becoming tough and strong more rapidly than would be expected if material properties scaled isometrically with stipe length. The sporophyte grows isometrically (bulb diameter vs. stipe length; Fig. 4b) as the stipe grows from 2 cm to nearly 40 cm over the course of one or two weeks. Since size changes in this regular fashion, the positive allometry of both strength (Fig. 7b) and toughness (Fig. 7c) must be due to ontogenetic changes in the material properties of the stipe. In mature kelp tissues, the youngest areas are less stiff than the older regions of the stipe (Krumhansl et al. 2015). However, in the early stage of bull kelp studied here, the youngest stipes are stiffer (Fig. 8).

In the full-grown bull kelp, sporophyte negative allometry leads to relatively small bulbs compared with stipe length (Fig. 4A; Denny et al. 1997). This breakpoint between isometry and allometry occurs when kelp stipes reach about 33 cm, after approximately one week of growth at a maximum growth rate of 6 cm per day (Scagel 1947). This shift in scaling likely occurs because the early stages of bull kelp growth focus on increasing stipe length. Later, when the bulb and blades are nearer the surface, resources are allocated towards increasing blade surface area to maximize photosynthesis (Duncan and Foreman 1980).

Comparing our measurements to predictions under the null hypothesis, force to failure increases less quickly than would be expected for a given stipe length ($b=0.7$), as does work ($b=1.8$). However, this may be due to changes in morphology rather than material properties. Previous studies have suggested that kelp morphology scales similarly to land plants, especially changes in morphology associated with taper, which will affect failure (McMahon and Kronauer 1976, Starko and Martone 2016). In this light, we proposed two alternative hypotheses pruned from terrestrial plant literature explaining the scaling of tree height and branch length: H_1 – stress similarity, and H_2 – elastic similarity (Table 1; McMahon and Kronauer 1976). The main assumption behind the stress similarity hypothesis is that the cross-sectional diameter will scale at a different rate ($b=2$) than total length, to assure that δ_{\max} will be constant across all sizes. Under this hypothesis, we would expect force to scale with area with a slope of 4 and work would scale with a slope of 5. Both of these predictions are much greater than our measured slopes, are well outside of the confidence intervals, and can be rejected. Our second alternate hypothesis, elastic similarity, also incorporates taper and is based on Euler's Buckling equation. For our purposes, it assumes that the free end of the kelp will have the same amount of deflection relative to the stipe length when the cross-sectional diameter scales with a slope of $3/2$. Under

this assumption, force to failure should scale with a slope of 3, and work should scale with a slope of 4. Both of these values are well beyond their respective 95% confidence intervals and the hypothesis can be rejected.

There are a number of reasons why neither of these scaling hypotheses explain our data. The mode of taper seen in trees and branches is likely a poor analogue for the changes in bull kelp profile over the length of the stipe. In addition, these models assume compressive forces acting on the trunk/branch to be primarily generated by the trunk's/branch's own weight. This is fundamentally not the case for bull kelp, which are buoyed by their own gas-filled bulb, and for which dominant forces are flow-induced drag.

Extensibility for juvenile kelp showed a degree of consistency across the size range (Fig. 7A) and there was no measurable change in location of failure along the length of the stipe. This means that, contrary to what one might expect based on the material properties of new versus old kelp tissue, a very small bull kelp with a stipe 2 centimeters in length is no more or less likely to fail than one with a stipe 36 cm in length when stretched to a similar extent. However, when the juvenile kelp in our study failed, they all failed close to the bulb in areas of older tissues as would be expected (Krumhansl et al. 2015).

This similarity in extensibility between sizes tested also means that differences in environmental drag may have an impact on stipe failure. Peak tidal currents at Turn Rock, the site of a robust bull kelp bed that reliably reappears from year to year, have been measured at $0.7\text{-}1.5\text{ m s}^{-1}$ at bulb-level for mature bull kelp (Koehl and Wainwright 1977). This value is high for the tidally driven currents of the Salish Sea, but low compared to the flow experienced by seaweeds in wave-exposed intertidal areas, where water velocity during winter storms can reach up to 20 m s^{-1} (Denny 1988). However, if tidal current-induced drag were the only factor

influencing the morphology of bull kelp, individuals should become much stronger as they grow larger (indicated by δ_{\max} ; Fig 7B), as the effects of drag are more pronounced in mature individuals that have reached the surface and have increased blade surface area. Mature bull kelp at the surface also change orientation in response to high current, using their flexible stipe to bend closer to the substrate (without breaking) and bundling all of their blades into a streamlined stack (Koehl and Wainwright 1977, Koehl and Alberte 1988). Our results show that blade reconfiguration may not as useful in juvenile kelp, which have only one or two blades and do not come near the surface of the water, and therefore experience a different suite of evolutionary pressures than adults that have reached the surface.

Changes in morphology and material properties may be related to different rates and regions of growth exhibited by the stipe and the blades (Fig. 9), leading to differences in biomass allocation. On average, adult kelp across a range of taxa have nearly 80% of their biomass in their blades as compared to ~11% in their stipes; however, blade mass in mature subtidal and intertidal kelp scales with negative allometry when compared with stipe mass (Starko and Martone 2016). Similarly, frond area in the intertidal kelp, *Egregia menziesii*, shows negative allometry when compared with the mass (Friedland and Denny 1995). More work needs to be done comparing relative growth rates of holdfasts, stipes, and blades in juvenile kelp, however, as this life stage is subject to a very different host of selective pressures.

Variation in material properties will have ramifications for structural scaling, and may allow the kelp greater morphological flexibility. For example, it is known that seaweeds can vary in morphology to cope with changes in water movement. Mature bull kelp growing in more exposed locations tend to have smooth, streamlined blades, reducing drag per blade, while individuals growing in more sheltered locations have ruffled blades (Koehl and Alberte 1988,

Koehl et al. 2008). This ruffled morphology likely employs the increased drag to help the blade flap, increasing nutrient acquisition via diffusion across the blade (Stevens and Hurd 1997).

Future work needs to be done quantifying and comparing blade morphology to see if/how this varies in juvenile kelp, and if this has an effect on stipe strength, as increased drag on the blades means greater forces pulling on the stipe.

Factors other than drag may also be influencing juvenile bull kelp morphology and material properties, such as grazing pressure from gastropod, echinoderm, or crustacean consumers. Even mesograzers, such as a tiny snail (*Lacuna vincta*), can have population level impacts on bull kelp by causing seemingly minor radula damage, which makes bull kelp more vulnerable to breakage due to waves and currents. (Chenelot and Konar 2007, Duggins et al. 2001). In one survey of drift bull kelp washed up on beaches, stipes of solitary individuals appeared to have failed at locations of abrasion or damage from urchin feeding, likely due to a reduction in cross-sectional area (Koehl and Wainwright 1977). Such effects have not yet been studied in juvenile sporophytes, which may be expected to be even more vulnerable to the effects of grazing due to their small overall size and cross-sectional stipe area and proximity to benthic grazers.

Based on our findings, it is clear that mature *Nereocystis* sporophytes experience a vastly different environment than juvenile sporophytes. This can be seen in the differences in morphological scaling of juveniles and adults, as well as in the scaling patterns of material properties across ontogeny. This research serves to highlight the importance of studying all stages of an organism's life cycle in order to account for differences in evolutionary pressures.

2.5 TABLES AND FIGURES

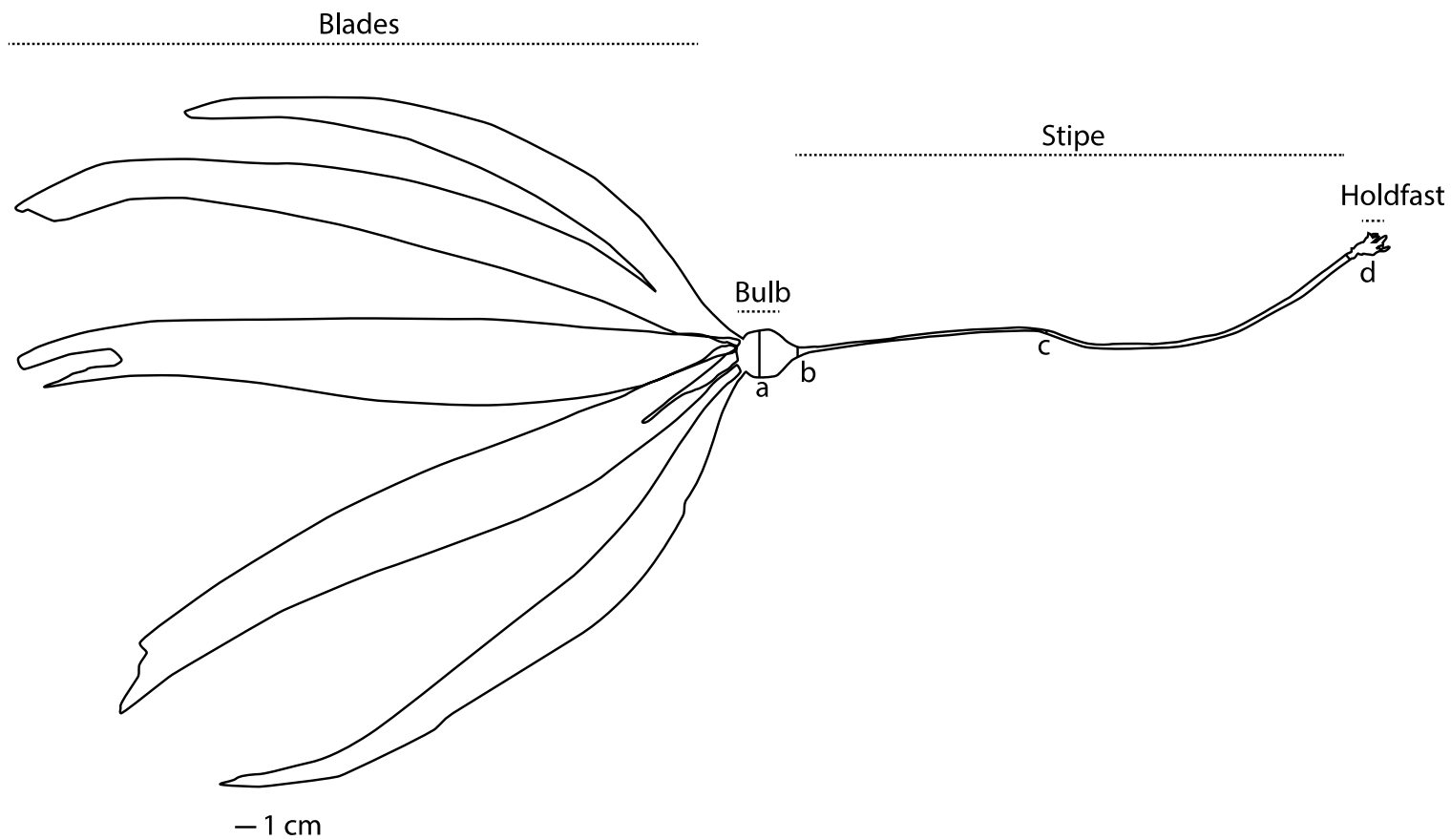


Figure 2.1 Morphological characteristics of bull kelp

Bull kelp morphology (dotted lines) and morphological measurements (solid lines; a=bulb width, b=stipe width underneath the bulb, c=narrowest stipe width, d=stipe width above holdfast)

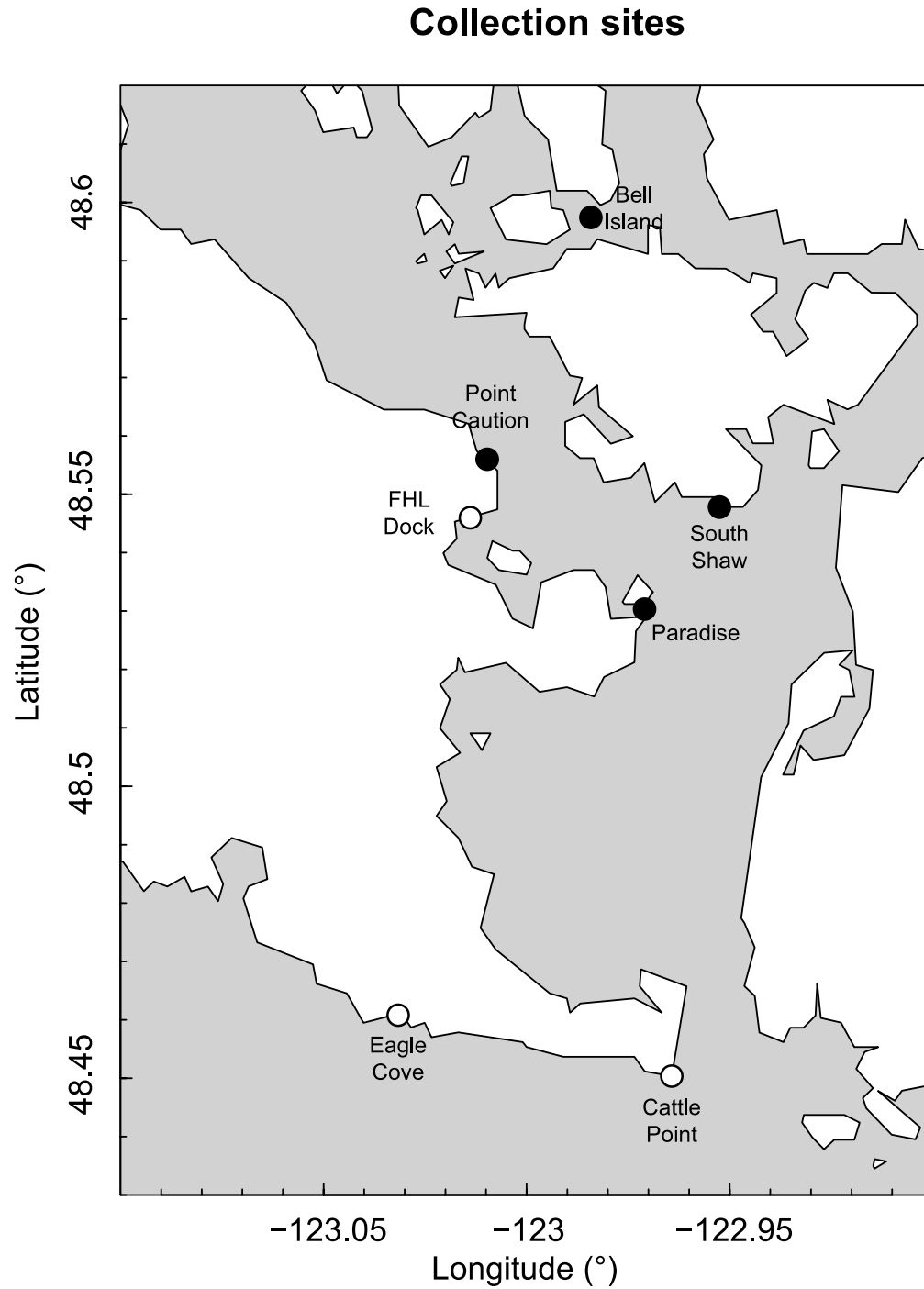


Figure 2.2 Map of kelp collection sites along the San Juan Channel near Friday Harbor, WA. Empty dots represent sites where adult drift kelp were collected. Solid dots indicate sites where subtidal juvenile kelp were collected.



Figure 2.3 Experimental setup

a) 3D printed kelp cradle, b) clamp with freeze-clamped holdfast

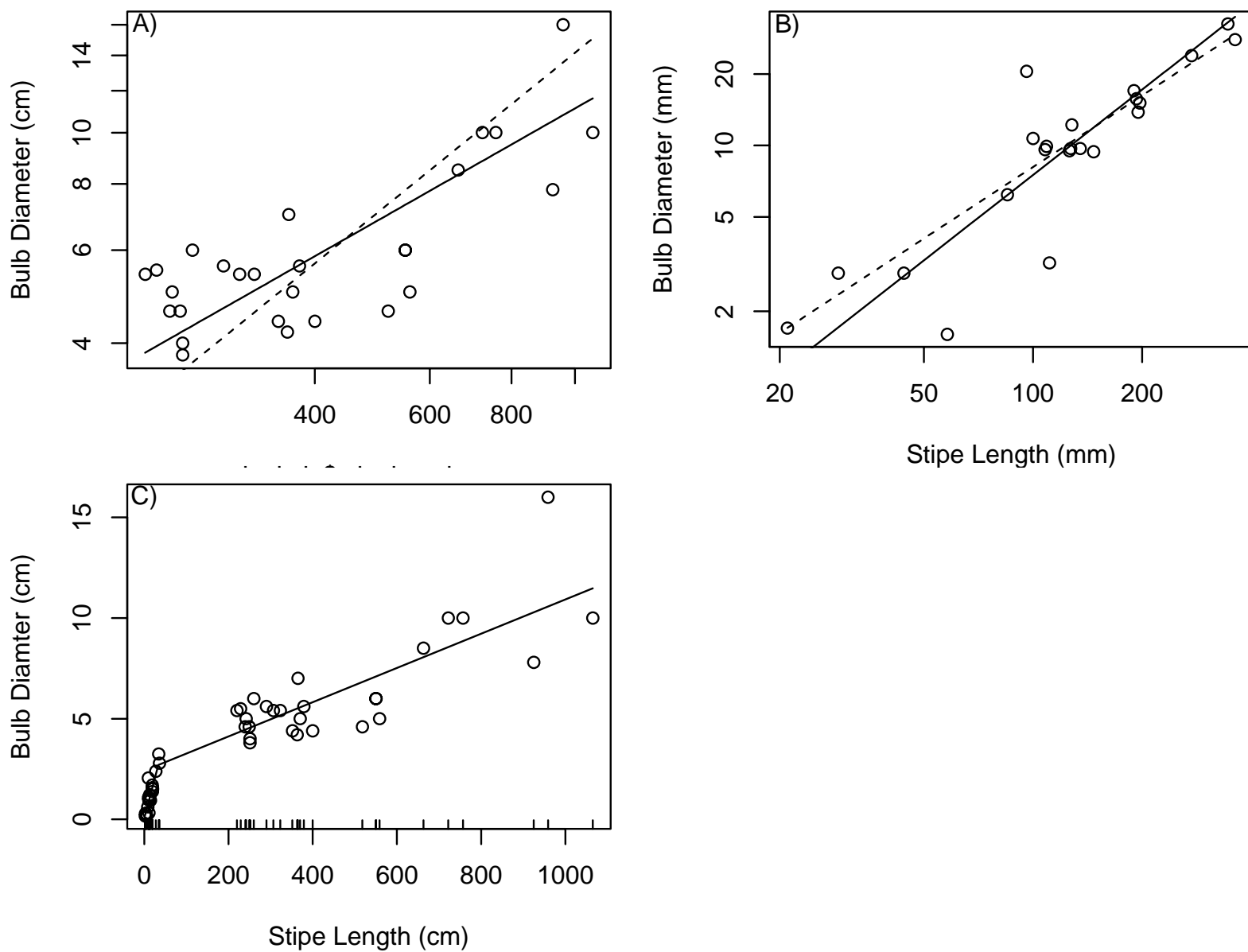


Figure 2.4 Bull kelp scaling changes across life stages

Mature bull kelp (n=27) bulbs show negative allometry with stipe length as they grow; b)

Juvenile bull kelp (n=22) bulbs scale isometrically with stipe length. Solid lines show SMA regression lines, dotted lines show predicted isometry (predicted slope = $H_0=1$). c) Growth switches from isometry to allometry at a predicted stipe length of 33.2 cm (± 14.8 SE)

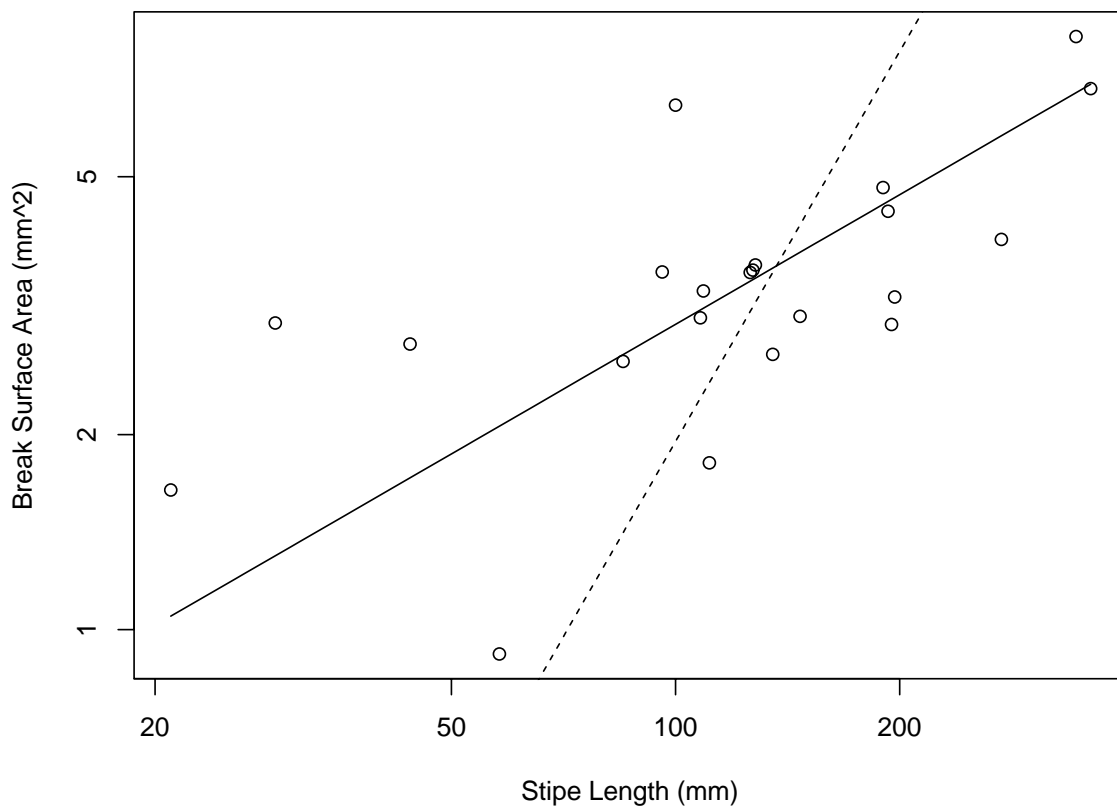


Figure 2.5 Surface area of stipe breaks increases hypoallometrically with stipe length. Solid lines show SMA regression lines, dotted lines show predicted isometry (predicted slope = $H_0=2$).

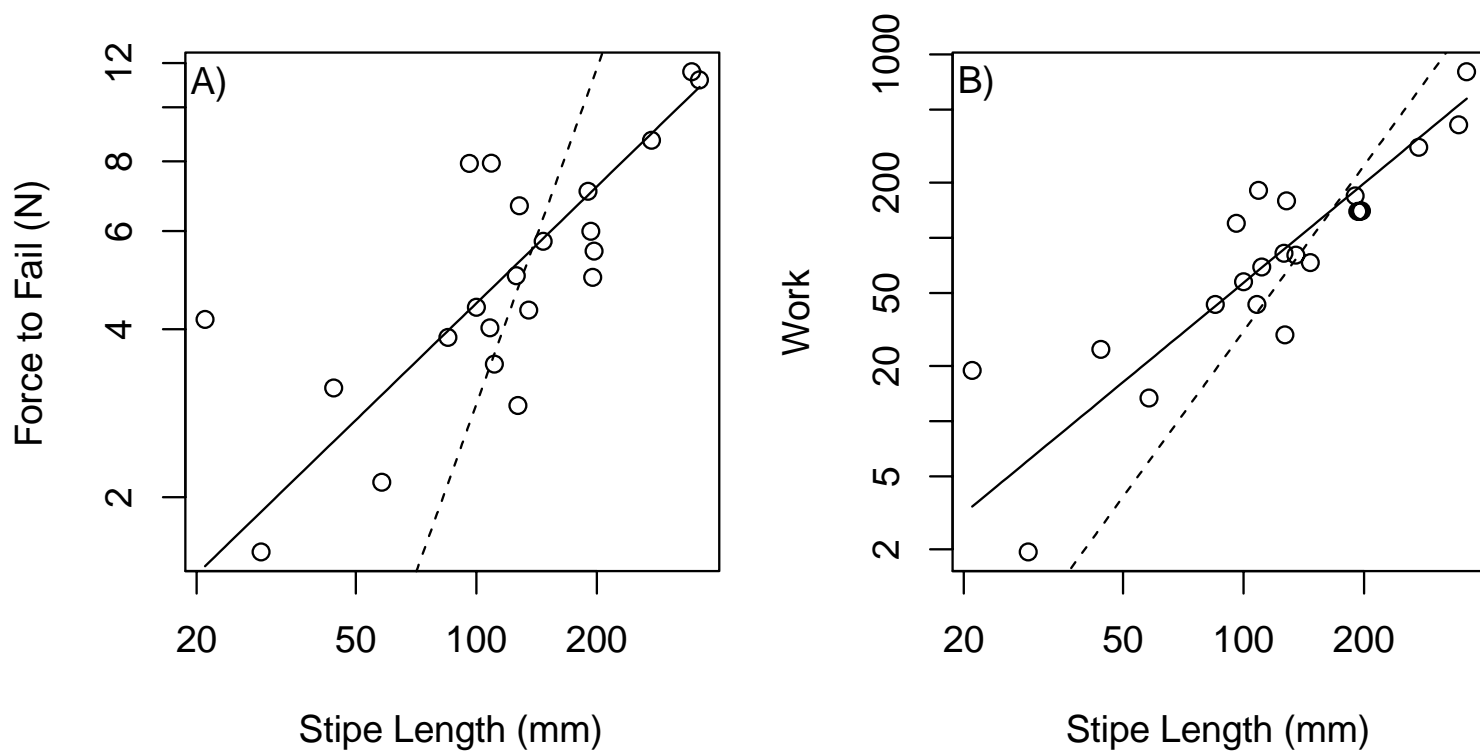


Figure 2.6 Force to fail and work to fracture both increase less rapidly than stipe length.

a) F_{fail} scales with negative allometry (predicted slope = $H_0=2$). b) Work to fracture scales with negative allometry ($H_0=3$); solid line shows SMA regression line, dotted line shows predicted isometry

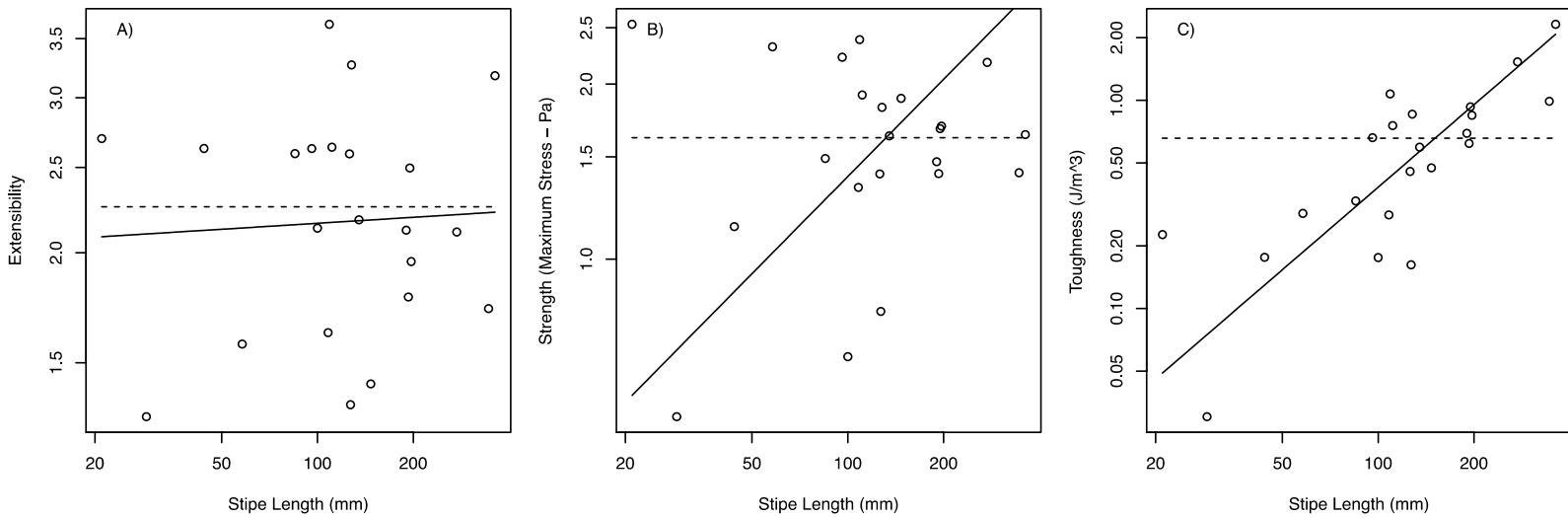


Figure 2.7 Extensibility is independent of stipe length, while strength ($\text{stress}_{\text{max}}$) and toughness scale with positive allometry

a) Extensibility (nominal strain failure %) does not change with stipe length (predicted slope = $H_0=0$); solid line shows OLS regression line; dashed line shows predicted slope = $H_0=0$ b) $\text{Stress}_{\text{max}}$ scales with positive allometry (predicted slope = $H_0=0$); c) toughness (J/m^3), predicted slope = $H_0=0$, scales with positive allometry; on panels B-C, solid line shows SMA regression line, dotted line shows predicted isometry

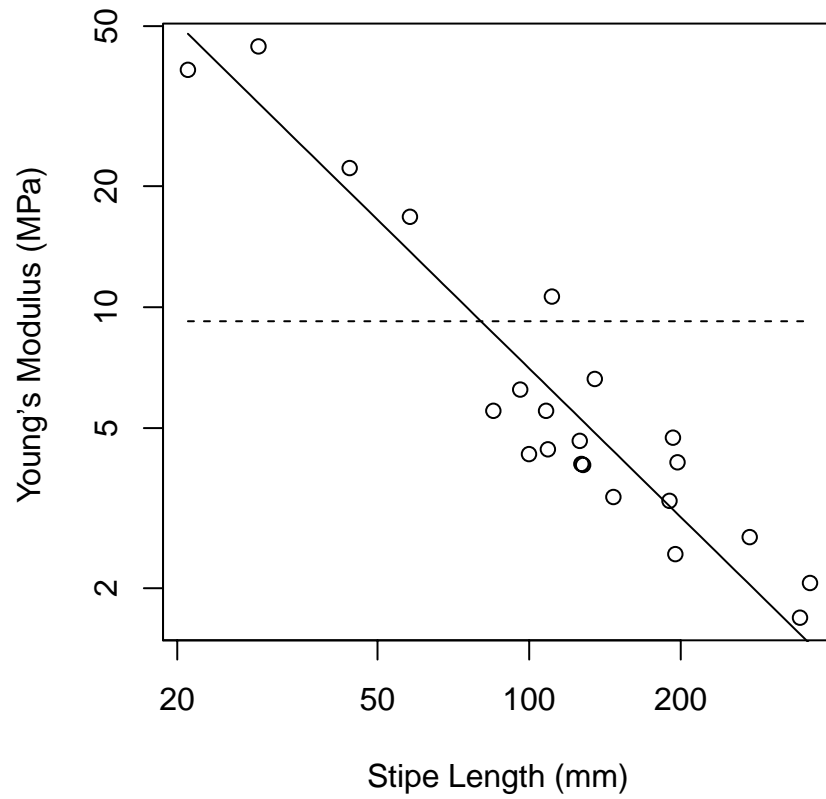


Figure 2.8 Young's Modulus scales with negative allometry (predicted slope= $H_0=0$).



Figure 2.9 A comparison of juvenile and mature bull kelp to demonstrate differences in scale and morphological scaling. Juvenile and mature bull kelp are shown to scale, with the shadow of a juvenile kelp scaled to the same stipe length as the mature bull kelp.

Regression	H₀	H₁*	H₂**	Slope	± 95% CI	Type of Scaling[†]	y-intercept	r²
<i>Adult Kelp</i>								
Bulb~Stipe	b=1	-	-	0.70	0.54-0.91	Negative Allometry	-2.44	0.59
<i>Juvenile Kelp</i>								
Bulb~Stipe	b=1	-	-	1.19	0.96-1.49	Isometric	-3.49	0.78
BreakSurfaceArea~Stipe	b=2	b=4	b=3	0.66	0.49-0.94	Negative Allometry	-1.98	0.41
Young's Modulus	b=0	b=0	b=0	-1.23	-1.44- -1.05	Negative Allometry	7.61	0.88
Stress~Stipe	b=0	b=0	b=0	0.55	0.36-0.87	Positive Allometry	-2.23	0.03
NominalStrainFail~Stipe	b=0	b=0	b=0	0.02	-0.17-0.21	Independent	0.67	0.00 3
Toughness~Stipe	b=0	b=0	b=0	1.31	0.98-1.75	Positive Allometry	-7.03	0.61
F _{fail} ~Stipe	b=2	b=4	b=3	0.69	0.51-0.95	Negative Allometry	-1.71	0.55
Work~Stipe	b=3	b=5	b=4	1.80	1.44-2.26	Negative Allometry	-4.25	0.76

Table 2.1 Scaling analyses of morphological (adult, juvenile) and biomechanical properties (juvenile) of bull kelp; “stipe” refers to stipe length (proxy for kelp age)

*H₁ – Stress similarity model takes into account change in diameter due to taper along stipe length, and assumes that kelp of different sizes maintain same δ_{\max} ; **H₂ – Elasticity similarity model also takes taper into account, and assumes that the free end of the kelp will deflect similarly relative to the kelp “height”; [†] Scaling relative to the null hypothesis

Chapter 3. THE ROLE OF KELP CRABS AS CONSUMERS IN BULL KELP FORESTS – EVIDENCE FROM LABORATORY FEEDING TRIALS AND FIELD ENCLOSURES

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Keywords: *Nereocystis luetkeana*, Bull kelp, *Pugettia gracilis*, Choice feeding experiments, *Pugettia producta*, Herbivory

3.1 INTRODUCTION

Kelp forests provide habitat for many organisms (Steneck et al. 2002) and consumers of kelp, including various mollusks, sea urchins, and vertebrates such as odacid fishes, can strongly influence kelp distribution and abundance (Paine and Vadas 1969, Andrew and Jones 1990, Paine 1992). While snails consume less biomass directly than sea urchins, damage from their grazing on blades indirectly increases tissue loss, especially during storms (Krumhansl and Scheibling 2011). In Alaska, California, and Nova Scotia, grazing by sea urchins is a dominant top down control when urchins are present in high densities (Pearse and Hines 1979, Duggins, 1980, Estes and Duggins 1995, Scheibling et al. 1999). In extreme cases, sea urchins may lead to the collapse of kelp-dominated ecosystems and establishment of urchin barrens as an alternative stable state (Filbee-Dexter and Scheibling 2014).

While sea urchins are known to destructively graze kelp beds (Leighton 1966; Foreman 1977), gastropods have subtler, but still important effects on kelp forests. For example, the snail *Lacuna vincta* lives and feeds on bull kelp, *Nereocystis luetkeana* (Phaeophyceae, Laminariales) in the eastern Pacific Ocean including the Salish Sea. Grazers with scraping radulae, like *L.*

vincta, can influence population distribution of bull kelp by weakening the thallus (Chenelot and Konar 2007, Duggins 2001), which may be especially detrimental to juvenile bull kelp because of their small size, suggesting a need for further investigation into the role of non-echinoid grazers across bull kelp life history stages.

In addition to urchins and snails, other consumers that may affect the distribution and abundance of kelp include amphipods and herbivorous fish. High numbers of grazing amphipods after an El Nino event decimated algal biomass in the Point Loma area of southern California, decreasing drift macroalgal availability, which further resulted in destructive grazing of standing giant kelp (*Macrocystis pyrifera*) beds by sea urchins (Tegner and Dayton 1991). In the Mediterranean Sea, the herbivorous fish *Sarpa salpa* can consume large amounts of the dominant genus of macroalga, *Cystoseira* in shallow rocky subtidal areas. Herbivorous fish drive seaweeds in this genus into deeper or more wave exposed environments or may lead to the evolution of chemical defenses, as in *C. balearica* (Vergés et al. 2009).

Decapod crustacean grazers live in kelp beds, but their effect on kelp species in different geographical regions is not entirely clear. In California, where there is no *N. luetkeana*, kelp crabs eat several of the dominant kelps: *M. pyrifera*, *Egregia menziesii* and *Pterygophora californica* (Knudsen 1964, Leighton 1966). In this system, the Northern Kelp crab, *Pugettia producta*, influences biomass and nutrient uptake of the feather boa kelp, *Egregia menziesii* (Bracken and Stachowicz 2007). In central California, the preferred habitat of *P. producta* (and also primary food source) changes ontogenetically, with the red juveniles living among and feeding on red intertidal macroalgae, while adult kelp crabs dwell within kelp beds, and consume kelp (Hultgren and Stachowicz 2010). Field observations as well as gut content analysis from crabs collected in central California suggests that *P. producta* lives on and specializes in feeding

on *M. pyrifera* (Hines 1982). These diverse feeding choices suggest variability in the dietary composition of kelp crabs.

Bull kelp (*N. luetkeana*) and giant kelp (*M. pyrifera*) both range from Alaska to California. However, it is *N. luetkeana*, not *M. pyrifera*, that dominates the kelp forests of the Salish Sea, including the waters surrounding the San Juan Islands of Washington state, providing food and habitat for a variety of marine species (Dayton 1985, Steneck et al. 2002, Carney et al. 2005, Springer et al. 2006). This large kelp provides abundant food, including detrital material, to food webs within and below the photic zone (Duggins and Eckman 1994), as well as habitat and nursery space for a variety of fish species (Carr 1991). Red urchins play a smaller role in structuring these bull kelp forests than in many other habitats because of the high availability of drift kelp that limits their need to search for food (Britton-Simmons et al. 2009, Lowe et al. 2014).

The Northern kelp crab (*Pugettia producta*) and the graceful kelp crab (*Pugettia gracilis*) are both common in kelp beds in the Pacific Northwest, but to what degree they feed on the dominant canopy-forming kelp (*N. luetkeana*), as compared to other macroalgal, invertebrate, or detrital food choices, remains less well-studied. Kelp crab feeding patterns have not been thoroughly quantified in the lab or in the field. In this study, I combine laboratory feeding experiments with a field experiment to quantify kelp crab feeding patterns and evaluate their role as consumers. Specifically, I: 1) determine feeding choices of *P. producta* among different macroalgal species; 2) evaluate whether *P. producta* are herbivorous, detritivorous, or omnivorous; 3) quantify how food consumption scales with body size in two common species of kelp crabs (*P. producta*, *P. gracilis*); 4) determine the effect, in the field, of exposure to and exclusion of kelp crabs (and other large consumers) on juvenile bull kelp net tissue gain.

3.2 METHODS

3.2.1 *Laboratory feeding experiments*

To evaluate kelp crab feeding patterns, I used four types of laboratory feeding experiments: 1) feeding electivity between *N. luetkeana* and seven species of co-occurring macroalgae in four separate choice experiments; 2) feeding electivity on aged vs. fresh *N. luetkeana*; 3) feeding preference between *N. luetkeana* and a local snail (*Lacuna* sp.); and 4) scaling of crab body size with feeding rates on *N. luetkeana*. Studies of feeding preferences require experiments in which potential diet items are offered both separately and together to determine whether feeding rates are similar on alternative food items in both cases. Determining feeding rate involves enclosing consumers with a single food source; feeding electivity, as defined by Singer (2000), emerges from buffet-style experiments in which consumers have a choice of what to eat (Grason and Miner 2012). I employed electivity experiments to distinguish among macroalgae common in the local environment, including the invasive brown alga, *Sargassum muticum*, addressed the possibility of a detritivore role by offering both fresh and aged *N. luetkeana*, and offered snails as a test of omnivory.

I conducted feeding experiments in 43 cm x 30 cm x 18 cm (15.1 L) plastic aquaria in a seawater table with flow-through seawater at Friday Harbor Laboratories (FHL), Washington, USA. Aquaria were covered with plastic egg crate material to prevent crabs from escaping while allowing air and water flow (~3 L/min). I collected the organisms shortly preceding laboratory experiments by snorkeling or using SCUBA at sites near FHL and in the San Juan Channel (48°43'42.14"N, 123°00'44.02"W). Crabs and snails were maintained in flow-through aquaria and fed *ad libitum* on a mixed diet of macroalgae prior to use in experiments. A new cohort of

crabs was used for each of the different feeding experiments. I starved kelp crabs for 12 hours prior to experiments to reduce variability in consumption due to recent feeding history.

All data analyses were conducted with R v. 3.3.2 (R Core Team, 2016). A Shapiro-Wilk test was used to assess the normality of all residuals prior to analysis and a Levene's test was used to test for homogeneity of variance. Due to the high levels of variability inherent to feeding experiments, the data did not meet these assumptions, and I used non-parametric statistical tests as presented in the following methods for each separate type of experiment.

Feeding electivity on N. luetkeana vs. co-occurring macroalgae.

To determine electivity of kelp crabs for co-occurring macroalgae, I conducted four separate feeding experiments, each time offering the kelp crabs a choice of *N. luetkeana* and two other locally abundant macroalgae with varied morphology and ecological roles. Species offered in addition to *N. luetkeana* included three subtidal kelps (*Costaria costata*, *Saccharina latissima*, *Agarum fimbriatum*), an intertidal kelp (*Alaria marginata*), one invasive brown alga (*S. muticum*), as well as one red alga (*Mazzaella splendens*) and one green macroalga (*Ulva* sp.). These subtidal species tested represent two different functional groups of native seaweeds and one invasive seaweed that occurs in the San Juan Islands; the subtidal kelps form the canopy structure below *N. luetkeana*, while the smaller red and green seaweeds offered belong to the understory (Britton-Simmons 2006). I included the intertidal kelp *A. marginata* because kelp crabs sometimes reside in intertidal zones and would likely encounter this species. I included *N. luetkeana* in each of the experiments because crabs consistently chose to eat it in pilot studies. I offered macroalgae in groups of three to suit the size of the experimental arenas that I used.

Before each experiment, I wiped the macroalgal thalli clean with a paper towel to reduce associated bacteria and epiphytes. Pieces were approximately 10 cm x 30 cm, with some

variation due to algal morphology. This standardized size ensured that some macroalgae remained at the end of the feeding experiment for measurement (eliminating food limitation bias) and to prevent crabs from feeding only on the largest or most visible food item, as Knudsen (1964) suggested that kelp crabs often respond to movement and use visual cues to locate food. Based on pilot studies, the amount of food provided was enough to avoid food limitation during the feeding experiment. I recorded the blotted wet mass (g) of each macroalgal sample before and after the feeding period. To account for autogenic changes in macroalgal mass over time, control tanks contained macroalgal tissue but no crabs and were run simultaneously to the experiments.

Control and experimental treatments were randomly allocated among the individual tanks. While these controls do not account for the possible influence of fertilization by crab urine, the 12 h feeding period is likely too short for this to strongly influence the results. The feeding experiments took place during both day and night; due to ambient light from outside fixtures, the laboratory was never completely dark. Although it is often suggested that crabs are nocturnal, a careful examination of many natural history and behavioral studies does not provide a clear answer for kelp crabs. Hines (1982) reported little behavioral change in spider crabs during nighttime SCUBA surveys and Zimmer-Faust & Case (1982) reported the kelp crabs endogenous feeding rhythm as unknown. Mesocosm experiments by Hultgren and Stachowicz (2010) indicate that *P. producta* may increase use of kelp habitat at night, but do not provide details on whether this habitat use includes increased feeding on the kelp.

For each experiment, I set up replicate aquaria containing one crab and one blade piece from each macroalgal species ($n = 7 - 10$; Table 1). Crabs were allowed to feed for 12 hours. I analyzed the wet mass consumed (g) for each piece of macroalgae (calculated by subtracting the

final mass from the initial mass), and adjusted for the autogenic change in mass by subtracting a randomly-assigned paired control value that contained the same species of macroalgae (Roa 1992; Duarte et al. 2015). I then used these adjusted values to calculate the Quade's test statistic (T_1), a non-parametric rank-based test, to test the null hypothesis of no preference, as in Roa (1992). I then used a pairwise post-hoc Quade multiple comparison test with a Bonferroni correction to determine which food types were preferentially consumed.

Feeding electivity on aged vs. fresh N. luetkeana

To determine if kelp crabs might be detritivores that choose to eat detached drift kelp, I conducted a choice experiment ($n = 12$ crabs; Table 1; mean crab mass \pm SE = 182.1 g \pm 23.0 g) using the same methods described above with respect to experiment setup, autogenic controls, time of day and duration, and laboratory conditions on aged and fresh *N. luetkeana*. I collected fresh *N. luetkeana* from kelp beds in the San Juan Channel on the day of the experiment. To simulate detached drift bull kelp, I aged non-reproductive blades in a black-plastic covered outdoor tank with flowing seawater for one week prior to the feeding experiment (Raymond et al. 2014). As in the other electivity experiments, each crab was offered an approximately 10 x 30 cm piece of fresh (mean mass \pm SE = 17.6 \pm 1.4 g) and aged bull kelp (mean mass \pm SE = 21.3 g \pm 1.6 g) in a choice experiment. I analyzed the changes in mass in the experimental tanks, adjusted by randomly paired control tank changes in mass, using a Wilcoxon signed rank test.

Feeding preference on N. luetkeana vs. Lacuna sp.

To determine the trophic tendency of kelp crabs ($n = 10$), I tested the preference of *P. producta* for *N. luetkeana* versus *Lacuna* sp. (< 1 cm) in choice and no-choice experiments in the same manner as those described above based on previous laboratory observations of *P. producta* devouring these small snails as well as natural history information suggesting omnivory

(Knudsen 1964). The no-choice experiment represents a block design experiment with crabs as blocks, as each crab was fed kelp and snails separately. I randomly assigned the order of feeding replicates (kelp, snail, or kelp and snail) to each of the 10 crabs. In the choice experiments, I offered crabs an approximately 10 cm x 30 cm piece of kelp (mean mass \pm SE = 18.6 g \pm 0.9 g) and 20 snails (mean mass \pm SE = 0.45 g \pm 0.06 g); based on pilot data, these amounts of each food resource represented enough material to ensure that food limitation did not influence the results of the feeding experiment and autogenic changes in these quantities of kelp and snails were minimal during the short time period of the experiment. I analyzed the proportional change in blotted wet mass of kelp and snails (whole, not including shell fragments present at the end of feeding trials) using the Wilcoxon signed rank test for the choice experiments and the Friedman test for the no-choice experiments, treating crabs as blocks (random effect).

Crab feeding rates

To examine how feeding rates scale with body size, I used 11 *P. producta* (mass ranging from 80-265 g) and 11 *P. gracilis* (mass ranging from 5-39 g). The crabs were held in flowing seawater tables with unlimited access to fresh *N. luetkeana* to acclimate to laboratory conditions. I starved each crab for 12 hours before offering a 10 cm x 30 cm piece of fresh *N. luetkeana* for 12 hours (starting mass ranging from 13-21 g). Bull kelp was blotted and weighed before and after the experiment. Crab mass in grams was measured after completion of all feeding experiments. The relationship between kelp mass loss and crab body size was analyzed in R for each crab species using the package `lmodel2` to run standardized major axes (SMA) linear regressions, since both kelp mass loss and crab body mass exhibit variability (Legendre, 2014).

3.2.2 Subtidal caging experiment

To assess the influence of consumers on net tissue gain of juvenile bull kelp (stipe length <30 cm), I designed a subtidal caging field experiment with four treatments. The completely open treatment (n = 4) consisted of a small *N. luetkeana* collected from the FHL floating dock with intact holdfast glued directly to a half-size concrete block (15 cm x 20 cm x 20 cm). This treatment left the juvenile bull kelp exposed to any and all consumers (possibly including snails, urchins, and kelp crabs) present in the subtidal environment. The fully enclosed treatment (n = 4) consisted of the concrete block, attached kelp, and a wire frame with plastic mesh (with 1 cm x 1 cm openings) on all sides. The partially enclosed treatment (n = 4) was a procedural control for the effects of caging. It included the same kind of concrete block with kelp as the open treatment, but had a wire frame covered in plastic mesh on the top and two sides, with the other sides left open. The fully enclosed treatment with a crab (n = 4) was identical to the fully enclosed treatment but included one adult *P. producta* (carapace diameter at widest point > 10 cm) inside the cage and was supplemented with additional kelp to ensure that the crab survived the entire study period (15 days). Blotted wet mass (mean mass \pm SE = 4.31 g \pm 0.57 g) and blade length (mean length \pm SE = 13.8 cm \pm 0.93 cm) of each juvenile kelp was recorded prior to the start of the experiment.

I assembled the concrete blocks in all treatments on land and deployed them from a small boat into a shallow subtidal kelp bed (max depth = 7.6 m) near Point Caution on San Juan Island, Washington, United States (48°33'43.26"N, 123°01'02.33"W). Scuba divers followed the blocks into the water, made sure that all had settled on appropriate horizontal, rocky substrate, and installed the crabs in the appropriate cages. Divers visited the blocks after one week to remove any fouling organisms. Blocks were collected after 15 days. I analyzed the effect of the caging

treatment (4 levels) on the change in blotted wet mass and blade length of the juvenile kelp using one-way ANOVA followed by Tukey's HSD test for pairwise comparisons.

3.3 RESULTS

3.3.1 Laboratory feeding experiments

In choice feeding experiments, *P. producta* consumed more mass of *N. luetkeana* than of six of the seven other macroalgal species offered (Fig. 1). Among the three kelps tested in the first feeding experiment, crabs showed a statistically significant feeding pattern ($T_1 = 8.45 > F_{0.05;2,12} = 5.46$; $p=0.004$; Fig. 1A), consuming a much greater mass of *N. luetkeana* (mean mass \pm SE = 6.74 g \pm 2.36 g) than of the kelps *Alaria marginata* (mean mass \pm SE = 0.58 g \pm 0.51 g; $p=0.01$) or *Saccharina latissima* (mean mass \pm SE = 0.30 g \pm 0.57 g; $p=0.01$). Crab feeding on *A. marginata* and *S. latissima* was not statistically distinguishable ($p=0.99$). In the second feeding experiment, crabs also showed a significant pattern ($T_1 = 7.62 > F_{0.05;2,16} = 4.69$; $p=0.005$; Fig. 1B), consuming a greater mass of *N. luetkeana* (mean mass \pm SE = 4.33 g \pm 0.88 g) than of the kelp *Costaria costata* (mean mass \pm SE = 0.42 g \pm 0.36 g; $p=0.005$) and the green alga *Ulva* sp. (mean mass \pm SE = 1.40 g \pm 0.30 g; $p=0.05$). The consumption by *P. producta* of *Ulva* and *Costaria* was statistically similar ($p=0.79$). When offered *N. luetkeana*, *Ulva* sp. and *Mazzaella splendens* (a red seaweed), consumption by *P. producta* differed ($T_1 = 6.26 > F_{0.05;2,18} = 4.56$; $p=0.009$; Fig. 1C). The crabs chose to eat very little *M. splendens* (mean mass \pm SE = 0.12 g \pm 0.07 g; $p=0.008$) compared to *N. luetkeana* while consuming statistically indistinguishable amounts of *N. luetkeana* (mean mass \pm SE = 3.39 g \pm 1.53 g) and *Ulva* sp. (mean mass \pm SE = 1.84 g \pm 0.30 g; $p=0.51$) as well as *M. splendens* and *Ulva* sp. ($p=0.15$). When offered a choice between two native kelps (*N. luetkeana*, *Agarum fibriatum*) and the invasive brown alga *S. muticum*, *P. producta* showed significant differences in feeding ($T_1 = 14.56 > F_{0.05;2,18} = 4.56$;

$p < 0.001$; Fig. 1D), consuming more *N. luetkeana* (mean mass \pm SE = 6.43 g \pm 1.03 g) than *A. fimbriatum* (mean mass \pm SE = 0.17 g \pm 0.05 g; $p = 0.003$) or *S. muticum* (mean mass \pm SE = 0.48 g \pm 0.15 g); $p < 0.001$). There was no difference in consumption between *S. muticum* and *A. fimbriatum* ($p = 0.78$).

When offered a choice of fresh and aged *N. luetkeana*, *P. producta* consumed both food items, but ate, on average, nearly six times as much fresh *N. luetkeana* ($V = 50$, $p = 0.02$; Fig. 2). I also compared *N. luetkeana* and *Lacuna* sp. as food for *P. producta* in both choice and no-choice feeding experiments. There was no difference between the percentage of mass consumed for kelp and snails in the choice feeding experiments ($V = 15$, $p = 0.23$; Fig. 3A) or in the no-choice feeding experiments ($X^2_1 = 0.4$, $p = 0.53$; Fig. 3B).

When offered only bull kelp, the slope of the relationship between feeding rate (g/h) and body size (g) for *P. producta* differed significantly from the expected $3/4$ scaling rule of metabolic rates (Kiorboe and Hirst, 2014). This indicates that the feeding rate of *P. producta* increases more quickly than crab mass (slope = 1.37; Table 2; Fig. 4A). The feeding rate for *P. gracilis* did not differ from the predicted slope of 0.75 (slope = 0.77; Table 2; Fig. 4B).

3.3.2 Subtidal caging experiment

Juvenile bull kelp mass varied significantly among treatments (ANOVA, $F_{3,12} = 6.711$, $p = 0.007$). *Nereocystis luetkeana* (< 30 cm stipe length) increased in mass by 77% over 15 days in the fully enclosed (caged) treatment but suffered extreme loss of tissue in the treatments that were open (-95%), partially enclosed (-55%), and fully enclosed with a crab (-98%) treatments (Fig. 5A). Mass of *N. luetkeana* in the fully enclosed treatment differed statistically from the mass in the treatments that were open and fully enclosed with a crab (Tukey's HSD, $p < 0.01$); the

difference between the fully caged and partially caged treatment approached statistical significance (Tukey's HSD, $p=0.09$).

Similarly, juvenile bull kelp length varied among treatments (ANOVA, $F_{3,12}=10.4$, $p=0.002$). Only the juvenile bull kelp in the fully enclosed (caged) treatment showed a positive change in blade length (33.15%). Blade tissue was completely lost (-100%) in the open and fully enclosed with a crab treatments and was greatly decreased in the partially enclosed (-70%) treatment (Fig. 5b). Blade length of *N. luetkeana* in the fully enclosed treatment was statistically different from the other treatments (Tukey's HSD, $p<0.02$).

3.4 DISCUSSION

Herbivory by Northern kelp crabs (*P. producta*) may play a larger role in structuring bull kelp forests than previously suspected, as kelp crabs elect to eat fresh bull kelp over other macroalgae and also consume a greater quantity of bull kelp in relation to body mass than the $\frac{3}{4}$ metabolic scaling rule would suggest. However, kelp crabs also readily consume snails, indicating some tendency toward omnivory. In the field, protecting juvenile bull kelp from large consumers led to net tissue increases, further suggesting some level of top-down pressure from large consumers.

I found that kelp crabs elected to feed on bull kelp over other co-occurring macroalgae in the laboratory. The attributes that reduce kelp crab feeding on other kelps may include morphology or chemistry; however, no clear role for either factor emerges from comparisons across the kelp species tested in this study. Both *S. latissima* and *C. costata* are thick bladed with bullations, but *A. marginata* "wings" (blade) on either side of the midrib have a thinner morphology similar to bull kelp but were nevertheless consumed less than *N. luetkeana*. *A. marginata*, *C. costata*, and *N. luetkeana* share low levels of phlorotannins (less than 1% dry

mass for each) in their blades, with some environmental variability in concentration (Van Alstyne et al. 1999b, 2001). Urchins do not prefer *C. costata*, although other invertebrates will consume it (Van Alstyne et al. 1999a). Some species of the green seaweed *Ulva* have activated chemical defenses but also favorable nutritional characteristics (high nitrogen), which might account for reduced, but not absent, consumption by kelp crabs (Van Alstyne et al. 2009). *Mazzaella splendens* was also not preferentially consumed by generalist herbivore snails (Van Alstyne et al. 2009) This red seaweed appears iridescent due to its cuticle structure, which might function as a visual or mechanical deterrent to feeding (Gerwick and Lang 1977). Unlike *L. vincta*, which has been shown to live on and consume invasive *S. muticum* (Britton-Simmons et al. 2010), Northern Kelp crabs did not choose to consume *S. muticum* in laboratory feeding experiments, indicating that this invasive seaweed is not a food substitute for native bull kelp for all local consumers. The mechanisms underlying diet choice by kelp crabs require additional investigation.

Kelp crab electivity for bull kelp aligns with diets of other marine macroalgae consumers. Previous laboratory and field experiments showed that *N. luetkeana* was frequently the preferred brown algal food of a snail, *Tegula funebris* (Steinberg 1985). Sea urchins have also been shown to prefer bull kelp over other macroalgae and displayed high absorption efficiencies and growth rates in laboratory feeding experiments (Vadas 1977). For herbivorous amphipods, kelp is most palatable as a food source when the carbon to nitrogen ratio is neither too high nor too low (Norderhaug 2006).

However, the feeding rates by kelp crabs that I measured are large, both in absolute and body size specific terms compared with other kelp grazers present in the kelp beds of the Salish Sea. Northern and graceful kelp crabs can consume large quantities of kelp; on average, *P.*

producta consumed *N. luetkeana* at 0.65 g/h, while *P. gracilis* consumed at 0.14 g/h, consistent with generally smaller body size. These rates correspond to 8% and 20% of body mass per day, respectively. In contrast, green urchins (*S. droebachiensis*) can consume kelp at a rate of 0.052 g/h and red sea urchins (*S. franciscanus*) consume 0.17 g/h (Vadas 1977), rates that correspond to about 2% of their respective body masses per day. Additionally, the feeding rate of *P. producta* on bull kelp that exceeds the $\frac{3}{4}$ rule of metabolic scaling indicates that in this species larger individuals can be disproportionately more voracious consumers of bull kelp. Bull kelp would be particularly vulnerable to herbivory as a juvenile (stipe length < 30 cm), which could be entirely consumed by a kelp crab within one to a few days.

Although these results suggest kelp crabs exert underappreciated control of the dynamics of this annual kelp species through direct grazing, Northern kelp crabs, *P. producta*, may not be as exclusively herbivorous as previously reported (e.g. Knudsen 1964, Kozloff 1983). While they consumed fresh macroalgae (herbivory), they also ate small snails (omnivory), and aged bull kelp (detritivory) in laboratory feeding trials. It was unexpected that crabs would maintain their feeding rate on both snails and bull kelp, regardless of whether these species were offered singly or in combination with the other resource. However, it is worth noting that the total mass of snails eaten was small even if the proportional consumption was similar. This may result from the long handling times observed in pilot studies. Crabs in choice treatments were offered ~10 g of kelp and ~0.1 g of snails. Nevertheless, kelp crabs that consume small snails in the field might indirectly facilitate bull kelp, in addition to direct negative effects, by removing another grazer that feeds on kelp and causes damage that weakens the thallus. *P. producta* disproportionately uses fresh over aged kelp, consuming an average of five times more fresh bull kelp, indicating that they are unlikely to be detritivores when live kelp is available. This

differs from red urchin feeding in the San Juan Channel (Britton-Simmons et al. 2009}. This difference in electivity indicates that kelp crabs are likely to actively consume the kelp on which they live instead of passively consuming detached drift kelp present in the subtidal environment with potentially greater implications for kelp population dynamics.

The result that juvenile bull kelp completely protected from large consumers increased net mass and blade length more than those exposed to herbivory in the subtidal experiment indicates that some level of top-down control of bull kelp populations exists in this system. While the change in mass of kelp in the partially open cages was not statistically significant from the other treatments, the median change was similar to the other treatments with some level of consumer access. The high variability present in the partially open treatment may be due to consumers having more difficulty accessing and consuming the kelp in this treatment. The magnitude of damage experienced by kelp in completely open treatments was similar to the level of damage to kelp enclosed in a cage with a crab, which suggests that kelp crabs could be a particularly influential cause of failed kelp recruitment, although other herbivores (including red and green urchins and herbivorous snails) may also have contributed. The mesh on the cages had holes large enough (1 cm x 1 cm) to allow small snails to enter, potentially to consume the kelp or be consumed by the enclosed crab. However, it seems unlikely that snails alone could cause the level of damage exhibited by the exposed juvenile kelp, and the increase in net mass as well as blade length of the fully enclosed individuals indicates that kelp in open treatments experienced herbivory from some larger consumer than a snail. Because bull kelp is an annual species and must complete its entire life cycle each year, the effect of destructive grazing by herbivores could be especially dangerous during the small, vulnerable period; laboratory feeding studies have suggested that *L. vincta* prefers juvenile *N. luetkeana* to adult tissue

(Chenelot and Konar 2007), and this may hold true for other kelp consumers as well, including kelp crabs. Herbivore-inflicted damage to the stipes of small bull kelp could also make them more vulnerable to breakage from abiotic forces, increasing indirect losses on top of direct consumption.

Kelp crab feeding in the Salish Sea near the San Juan Islands has not produced barrens like those created by high densities of sea urchins in other geographical regions (Scheibling et al. 1999, Steneck et al. 2002), possibly due to the high levels of diversity in terms of potential food resources (both macroalgal and invertebrate) as well as rich nutrient and detrital inputs in this system that limit strong top-down control. However, the combined results of these laboratory feeding and subtidal field experiments suggest that kelp crabs may be one of a number of kelp consumers that negatively impact the growth of bull kelp. While urchins and snails likely cause some of the observed damage to bull kelp in the nearshore subtidal, my laboratory and field experiments clearly show that Northern Kelp crabs elect to eat *N. luetkeana* over most other macroalgae, can eat even larger quantities than might be expected for a given crab's mass, and cause damage of great enough magnitude to decimate small bull kelp. For these reasons, Northern Kelp crab (*P. producta*) may play a previously unrecognized role as an important consumer influencing the dynamics of the annual bull kelp. Future work to quantify kelp crab abundance in subtidal kelp forest habitats in the Salish Sea will help to further illuminate the level of top-down control that kelp crabs might exert on bull kelp populations during different life stages.

3.5 FIGURES AND TABLES

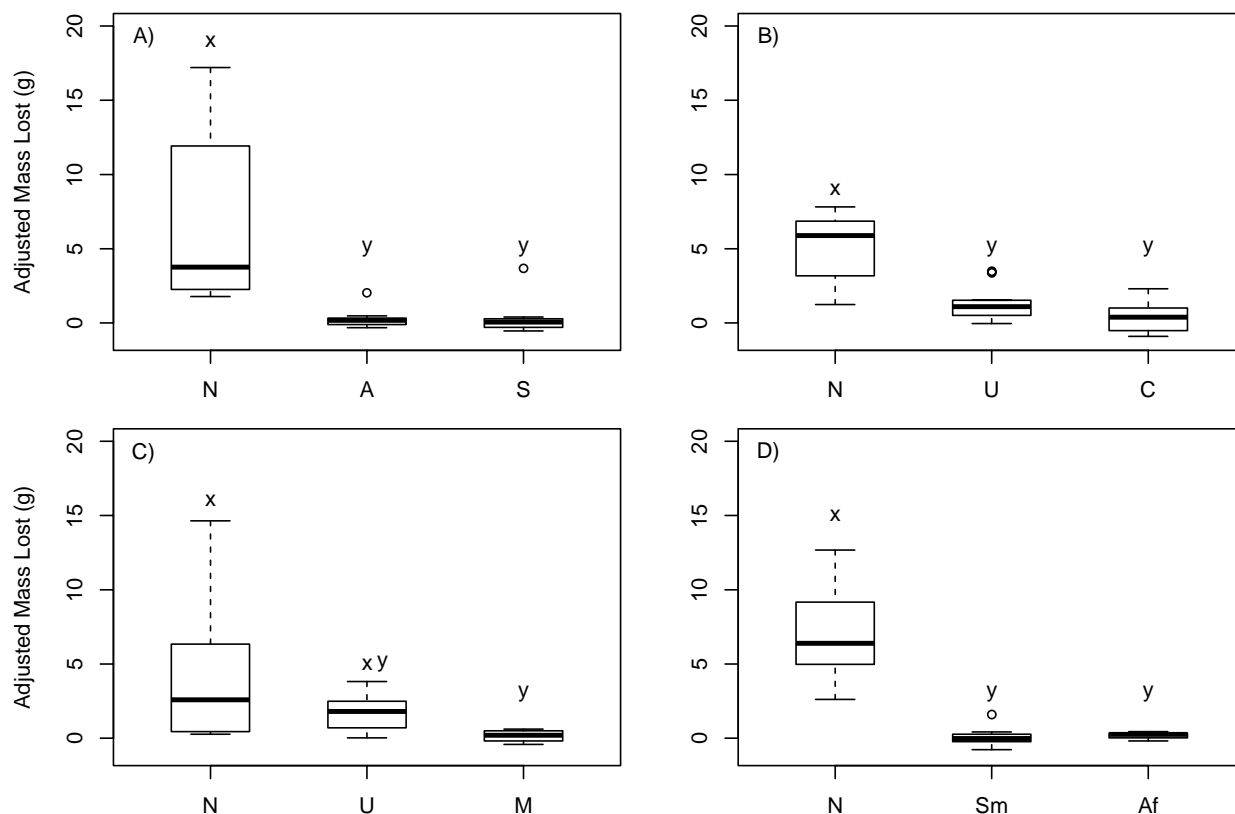


Figure 3.1 Kelp crab feeding in choice experiments

Change in mass of macroalgae adjusted by change in randomly paired autogenic controls in choice feeding experiments with *P. producta*. Letters correspond to macroalgal species offered: N, *Nereocystis luetkeana*; A, *Alaria marginata*; S, *Saccharina latissima*; C, *Costaria costata*; M, *Mazzaella splendens*; U, *Ulva* sp.; Sm, *Sargassum muticum*; Af, *Agarum fimbriatum*. Box plots show median (dark horizontal line), interquartile range (box), minimum and maximum values (bottom and top “whiskers”), 1st and 3rd quartile (bottom and top of box, respectively), and suspected outliers (dots). Letters indicated statistically significant differences.

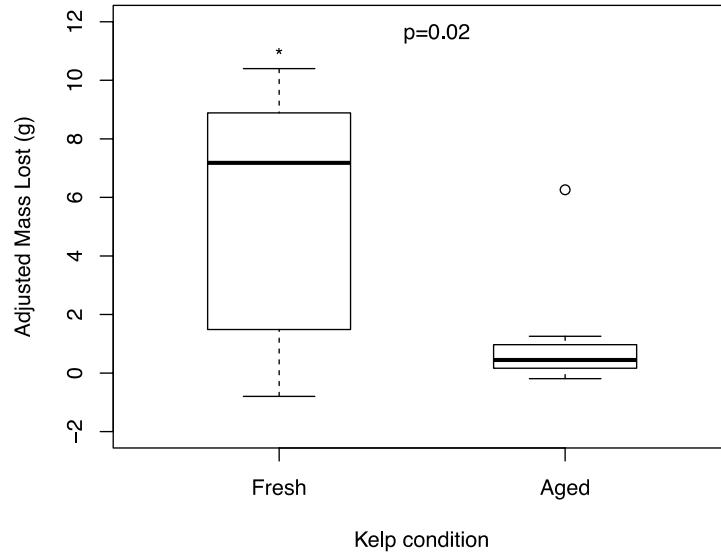


Figure 3.2 Feeding on fresh and aged bull kelp

Consumption of fresh and aged *Nereocystis luetkeana* by kelp crabs (*Pugettia producta*) in a choice feeding trial (including adjustment from randomly paired auto-genic controls). * indicates statistically significant difference in consumption of fresh *N. luetkeana* vs. aged.

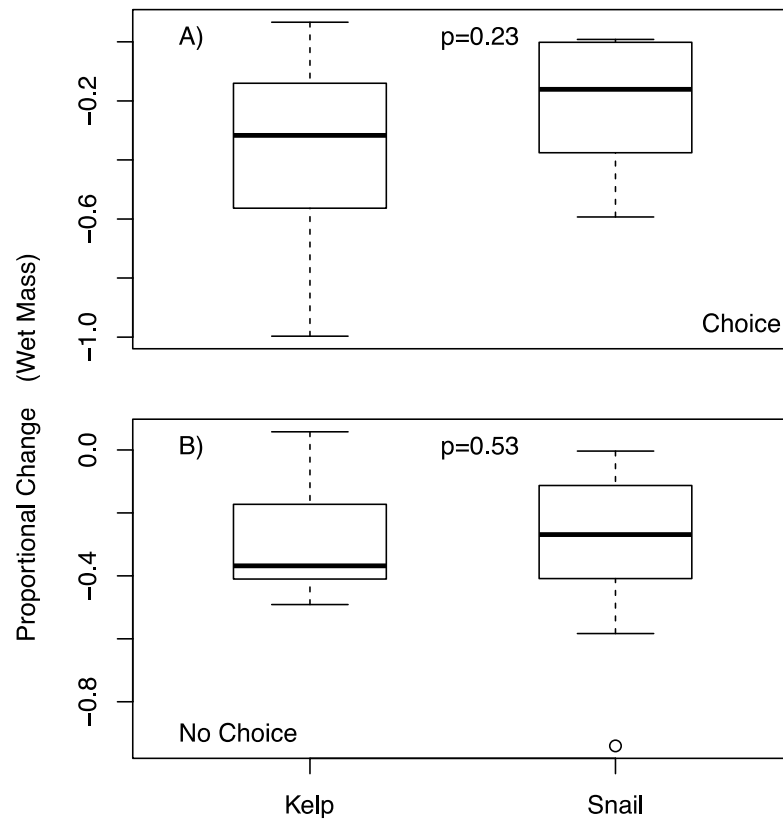


Figure 3.3 Choice and no choice feeding experiments with kelp and snails
 Proportional change (in wet mass) of bull kelp (*N. luetkeana*) and snails (*Lacuna* sp.) in (A) choice and (B) no choice feeding trials; p-values from choice and no-choice indicate no significant difference between proportional food consumption in either experiment.

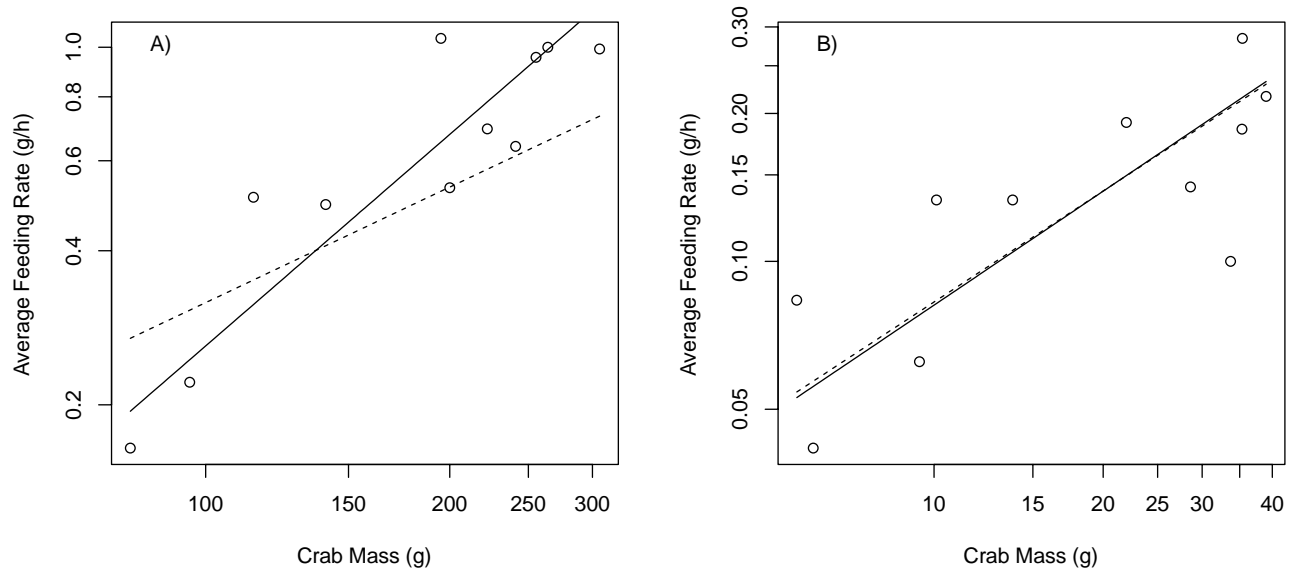


Figure 3.4 Scaling relationships between feeding rates (g/h) and crab mass (g)

Log–log plots showing scaling relationships (SMA regression) between feeding rate (g/h) and crab mass (g) for two species of kelp crabs; (A) *P. producta* shows a noticeable departure from 3/4 scaling rule; (B) *P. gracilis* shows negative allometry close to the expected 3/4 rule. Circles and solid line show observed relationship. Dashed line shows the expected slope of 0.75.

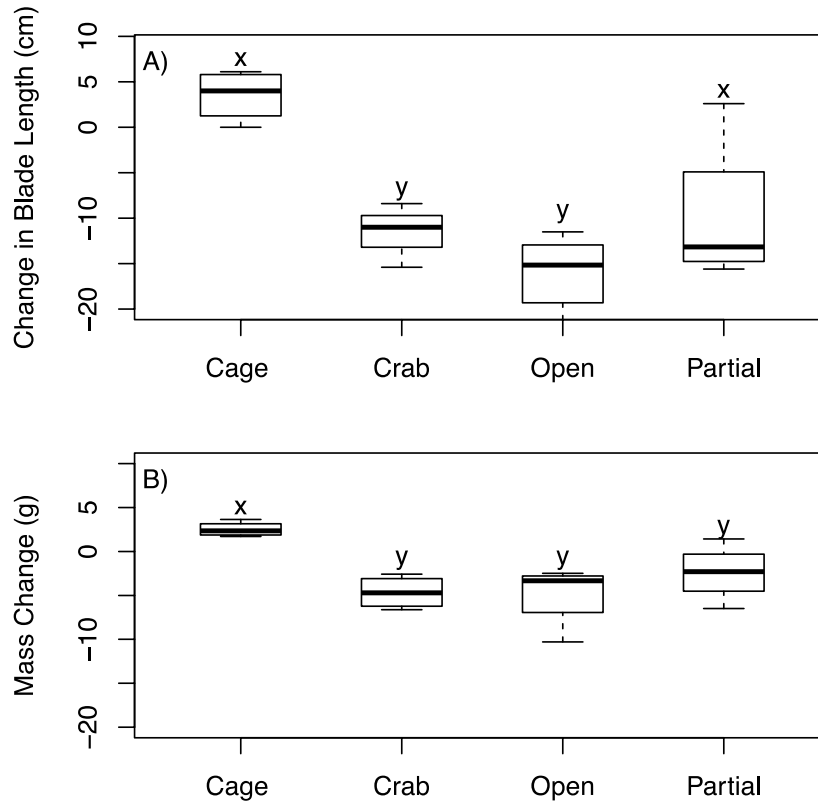


Figure 3.5 Field exclusion cage experiment

The effect of four experimental treatments on the change in (A) mass and (B) blade length of juvenile *N. luetkeana* in a subtidal field experiment. The “cage” treatment was fully enclosed to protect the individual kelp from all large grazers; the “crab” treatment was fully enclosed with one adult *P. producta* included inside; the “open” treatment offered no protection to attached kelp; the “partial” treatment was a procedural control that included caging material over the top and two sides but left the other two sides open. Letters indicated statistically significant differences.

Experiment	n	Macroalgal Species		
		Species 1	Species 2	Species 3
1	7	<i>Nereocystis luetkeana</i> (22.8 ± 1.4)	<i>Alaria marginata</i> (11.3 ± 0.6)	<i>Saccharina latissima</i> (21.8 ± 2.0)
2	9	<i>N. luetkeana</i> (24.6 ± 0.9)	<i>Costaria costata</i> (31.3 ± 2.4)	<i>Ulva</i> sp. (3.0 ± 0.2)
3	10	<i>N. luetkeana</i> (17.0 ± 1.7)	<i>Mazzaella splendens</i> (8.7 ± 0.7)	<i>Ulva</i> sp. (4.0 ± 0.4)
4	10	<i>N. luetkeana</i> (17.4 ± 0.8)	<i>Sargassum muticum</i> (10.0 ± 0.7)	<i>Agarum fimbriatum</i> (11.9 ± 0.4)
5	12	Fresh <i>N. luetkeana</i> (17.6 ± 1.4)	Aged <i>N. luetkeana</i> (21.3 ± 1.6)	n/a

Table 3.1 Choice feeding experiments on different macroalgal species

Details of macroalgal species comparisons in five separate choice feeding experiments.

Parentheses under each algal species report the average starting mass in grams ± the standard error. Sample size, n, is equal to the number of crabs used in each ‘‘buffet-style’’ feeding experiment.

Crab Species	Predicted Slope	Observed Slope	95% CI	y-intercept	R²
<i>P. producta</i>	0.75	1.37	0.99-1.88	-7.66	0.81
<i>P. gracilis</i>	0.75	0.77	0.48-1.21	-4.28	0.61

Table 3.2 Feeding rate regression analysis in two species of kelp crabs

Relationship between kelp crab feeding rates (g/h) and body mass (g) using standardized major axes (SMA) regression. Observed slopes with confidence intervals that do not overlap 0.75 indicate a significant departure from expected 3/4 scaling rule.

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2. Dobkowski, K.A., Kobelt, J., Brentin S., Van Alstyne, K.L., Dethier, M.N. Picky *Pugettia*: a tale of two kelps – *submitted Marine Biology*
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