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FACTORS INFLUENCING RECRUITMENT AND APPEARANCE OF BULL KELP, *NEREOCYSTIS LUETKEANA* (PHYLUM OCHROPHYTA)[1]

Running Title: Influences on *N. luetkeana* recruitment

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Abstract

The dynamics of annual species are strongly tied to their capacity for recruitment each year. We examined how competition and propagule availability influence recruitment and appearance and tracked survivorship of an annual species of marine macroalgae, the bull kelp (*Nereocystis luetkeana*), which serves as major biogenic habitat in the Salish Sea of Washington State. We hypothesized that 1) juvenile *N. luetkeana* would exhibit a seasonal appearance as a cohort in the spring and 2) competition for space would be more limiting than propagules (spores) to recruitment at sites adjacent to established *N. luetkeana* beds. We tagged *N. luetkeana* recruits in the field to track appearance and survivorship across seasons (spring, summer, fall, and winter), using a two-factor crossed design to assess effects of competition and propagule availability on appearance of new *N. luetkeana* sporophytes. Survivorship of *N. luetkeana* recruits was low and, while most new individuals arose in the spring, some appeared in every season. New *N. luetkeana* recruits also appeared the earliest (median 8 weeks vs. >20 weeks) after experimental "seeding" in the spring as compared to other seasons. Eliminating macroalgal competitors ("clearing") influenced the appearance of recruits more than enhancement of propagules in the spring. An improved understanding of factors regulating the seasonal appearance of new *N. luetkeana* sporophytes furthers our understanding of this crucial foundation species' appearance and persistence across seasons, which is increasingly important as global ocean conditions change, and highlights the importance of studying organisms with complex life histories across multiple stages and geographical regions.

Key index words: clearing; kelp forest; propagule enhancement; nearshore subtidal; Salish Sea

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; instead of competing with other species, ruderals persist by exploiting different, recently-disturbed areas, each for a limited period of time (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 1979).

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, Krumhansl and Scheibling 2012, Teagle et al. 2017). 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). 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 (Springer et al. 2010). In lab-grown *N. luetkeana* under ideal conditions (10°C, white light between 80-100 μE.m^2.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).

While many kelp species are perennial, there are annual kelps in geographically disparate areas, such *Saccorhiza polyschides* in southern Europe as well as *Postelsia palmaeformis* and *Nereocystis luekeana* in the northeast Pacific. These kelps often occur in wave swept areas and most mature sporophytes that have already reproduced begin to degrade in the autumn before ultimately being detached by winter storms (Biskup et al. 2014, Blanchette 1996, Springer 2010). 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). However, anecdotal observations suggest that *N. luetkeana* beds in certain locations can persist for multiple growing seasons, even if the individuals themselves only persist for one year.

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 have abundant propagules but be establishment-limited or seed-limited, with unoccupied safe sites (Duncan et al. 2009). For kelp (Laminariales), propagule availability can be difficult to track because this life stage is microscopic and frequently found on the benthos at depths of up to 30 meters (Springer et al. 2010). Also, many macroalgae undergo alternation of heteromorphic generations in which the development and gamete production by a microscopic gametophyte stage occurs 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 and Carpenter 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 *Macrocystis pyrifera* by eliminating space for spore settlement (Reed 1990). At larger life stages, competition via light availability influences macroalgal community structure. Perennial canopy-forming kelp species, such as *M. pyrifera and P. californica*, can reduce available bottom light by 60% and 75% respectively, as compared to levels at the surface. After removal of these canopy species, the cover of an annual brown alga (genus *Desmarestia*) increased significantly and lowered the bottom light even further to ~1% of ambient light (Clark et al. 2004). Adult sporophytes of *Ecklonia radiatia*, a habitat-forming kelp in southern Australia, grow up to 2 meters in height and effectively block light for understory macroalgal species. However, microscopic *E. radiata* sporophytes also cannot grow in 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 Ehrlen 1992). In southern California kelp forests, disturbance from storms may help clear substrate for settlement, recruitment, and growth as well as disperse propagules of *Macrocystis pyrifera* and *Pterygophora californica* (Reed 1992). 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 microscopic propagules may have lower requirements for survival than other life stages. Even if propagules are dispersed in one season, they 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 that persists in the same (or similar) locations from year to year in this particular system. We ask, how does bull kelp, *Nereocystis luetkeana*, maintain persistent kelp beds despite is 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 and 2) competition for space would be more limiting than propagules (spores) to recruitment at sites adjacent to established *N. luetkeana* beds because of the annual life history of *N. luetkeana* as well as the close proximity of reproductive material.

Methods

Study Species

Bull kelp, *Nereocystis luetkeana*, is an annual kelp that exhibits alternation of heteromorphic generations. It occurs on the Pacific coast of North America, from the Aleutian Islands to central California.

One demographic study of *Nereocystis 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.

Study Sites

To track seasonal appearance and survivorship of juvenile *Nereocystis 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, and those individuals did not persist after early spring.

One site for subtidal experimental manipulation of competition (hereafter, “clearing”) and propagule abundance (hereafter, “seeding”) 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. S1A). We established a second site for clearing and seeding near Point Caution on San Juan Island (N 48.56323°, W 123.02555°; 8-10 meters max depth; hereafter, Point Caution; Fig. S1B)

All three sites were accessed via SCUBA. All divers participating in monitoring were trained and accompanied by the lead diver (author) to enhance accuracy of data collection.

Tagging and Tracking Recruits

Using numbered plastic flagging tape (as in Maxell and Miller 1991), 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). Dive length was consistent (~50 minutes), providing a means of standardizing the seasonal appearance of new recruits.

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 *Nereocystis 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 new manipulated plots (n=20 per season, four seasons, for a total of 80 plots) across four seasons at South Shaw 2: spring (April), summer (August), fall (October) 2015, and winter (February) 2016. The same plot setup (n=20 plots) was done three times at Point Caution in two seasons for a total of 60 plots: July and August 2016 (summer) and April 2017 (spring). For statistical analysis, we combined the July and August plot setup and manipulations 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; plots were separated by no less than 0.5 meters. 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 *Nereocystis 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 m^2 subsamples within each cleared 4 m^2 plot; subsampling, using a haphazardly-placed quadrat to minimize sampling bias, was necessary because divers could not swim safely while transporting the large total amount of kelp biomass in each plot. We dried the samples in a drying oven for 24 hours at 60°C to allow comparison of biomass between seasons at each site. We monitored manipulated plots monthly for one year following each initiation, counting the number of kelp in each plot on each survey, except for the spring initiation at Point Caution, which was monitored for three months.

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 design was analyzed separately for each site and each season. The response variable was the maximum count of *Nereocystis luetkeana* observed at any single time in a particular plot to account for the fact that plots were monitored monthly and an average value for the entire study period would overestimate the number of recruits due to turnover. 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 (α=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 *Nereocystis 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 new bull kelp never appeared in many plots. 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 plots because removing macroalgae from uncleared plots would change the treatments. 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 manipulations 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).

Results

Tagging and Tracking Recruits

We tagged and tracked 41 *Nereocystis 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. 1A). On survey dives, we observed at least one new juvenile *N. luetkeana* recruit (stipe length < 30 cm) appearing in every month except February (Fig. 1B).

Manipulation of Competition and Propagule Abundance

Following the spring initiation at South Shaw 2, clearing increased the number of new juvenile *Nereocystis luetkeana* (Fig. 2A; Table 1); the cleared plots grew more individuals (mean ± SE = 23.5 ± 7.2) than the uncleared plots (mean = 0.4 ± 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 in plots within one year following the summer (cleared = 0.3 ± 0.15, uncleared = 0.3 ± 0.2; Fig. 2B), fall (cleared = 0.8 ± 0.33, uncleared = 0.3 ± 0.15; Fig. 2C), and winter (cleared = 3.5 ± 1.46, uncleared = 1.1 ± 0.43; Fig. 2D) experiment at South Shaw 2. Seeding 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. 3A; Table 2) 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* was greater in cleared plots (Fig. 3B) but did not differ between plots with propagule enhancement. The interaction was also not significant.

Among plots in which new recruits appear following experimental manipulations, the time to appearance (in months) at South Shaw 2 varied by season ($F_{3,30}=25.4$, $p<0.001$; Fig 4; Table 3). New *Nereocystis luetkeana* appeared the soonest following the spring experiment (mean ± 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) manipulations (i.e. clearing and seeding). New kelp took longer to appear following the fall manipulation as compared to the winter manipulation, 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 2 ($F_{3,76}=6.09$, $p<0.001$; Fig. 5A; Table 4). The number of juveniles that appeared following the spring manipulation (mean ± 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 manipulation 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 *Nereocystis luetkeana* recruits did not vary by season ($F_{1,57}=1.2$, $p=0.65$; Fig 5B).

Understory macroalgal (potential competitor) biomass, as measured at the time of manipulation (clearing and seeding), varied between seasons at both sites (South Shaw 2: $F_{3,35}$=3.24, p=0.03; Fig. 6A and Point Caution: $F_{1,28}$=8.4, p=0.005; Fig. 6B). 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 (p=0.005).

Discussion

Juvenile *Nereocystis 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 some seasonality in appearance, but that new individuals can begin to grow across seasons. Successful appearance of new sporophytes may be inhibited by competition from other macroalgae, which allows some "offseason" recruits to appear, potentially following a space-clearing disturbance event. Additionally, although disturbances may generate sites for recruitment in a propagule-rich system, especially since microscopic stages can likely persist for extended periods until conditions become favorable, high juvenile mortality also plays a role in determining where recruits persist and mature.

Our results suggest that competition is an important driver of where juvenile bull kelp appear. In our subtidal experiment, more *Nereocystis luetkeana* recruits appeared in cleared plots in the spring at South Shaw and in both spring and summer at Point Caution, when environmental conditions (especially light) are expected to be otherwise favorable for kelp growth. We also quantified a seasonal difference in biomass of potential competitors (understory macroalgae) in keeping with an increase in biomass during the spring/summer growing season. Evidence suggests that the perennial giant kelp (*Macrocystis pyrifera*) may also begin to grow following experimental clearing of understory competitors, suggesting that this other canopy-formers also benefit from the opening of gaps in existing understory to initiate growth (Dayton et al. 1984). The fact that new juvenile *N. luetkeana* can begin to grow in the same location, creating a seemingly persistent kelp bed for multiple years, may be a function of a high level of benthic disturbance in this system. The disturbance may serve to reduce interspecific competition to a low enough level to allow *N. luetkeana* to gain a "foothold" even in a field of perennial kelp species.

The lack of influence of seeding in our manipulated ("seeded" vs. "unseeded") plots indicates that propagule limitation may not be a major factor influencing where *Nereocystis luetkeana* recruit and begin to grow in this system. While we did add fertile sori to "seeded" plots, we did not measure total spore availability; while we did not quantify number or spores or motility in this study, we did achieve spore release from fertile sori followed by successful zoospore settlement in all seasons in the laboratory as part of a temperature growth experiment. Additionally, our plots at both sites were in some cases as close together as 0.5 meters, which may influence the independence of treatments, and were established adjacent (<5 m) to a known *N. luetkeana* beds. 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, as transport distances for *N. luetkeana* zoospores are not well documented but one study that analyzed numerous years of survey data suggested that although environmental factors may play a role, the abundance of bull kelp in one growing season is the crucial predictor of bull kelp presence in a location the following season (Pfister et al. 2018). Bull kelp zoospore dispersal may be similar to *Macrocystis pyrifera* (as are some other aspects of reproductive biology between these two canopy-formers); evidence suggests that *M. pyrifera* propagules can be transported long distances (<1000 m) to potentially maintain or restore populations even when an individual kelp bed disappears (Gaylord et al. 2002, 2006). It is possible that the zoospores of bull kelp may disperse even further due to the manner in which the fertile sori detach from the blade at maturity (Walker 1980). However, Springer (2010) suggests that *N. luetkeana* spores may only move short distances less than 100 meters, so clearly additional work is needed to quantify the dispersal distances of these zoospores in the field, ideally across different areas of the species' large geographic range.

Both our tagging/tracking study as well as our manipulated plots show that young sporophytes can appear during any season, which suggests that not all *N. luetkeana* begin to grow as a cohort in the spring as Maxell and Miller (1991) observed at sites further south in the Salish Sea. Although our results only come from one site (near South Shaw Island in the San Juan Islands of Washington State), the seasonal difference in time to the appearance of the first new bull kelp recruits between spring and other seasons suggests that microscopic *N. luetkeana* life stages can persist for an extended period of time, "waiting" for environmental conditions or competitor-free space to become more favorable. In laboratory experiments with low nutrient levels, *Macrocystis 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 another large, subtidal, annual brown alga *Desmarestia ligulata* var. *ligulata* can persist for up to 15 months in the field (Edwards 2000).

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. 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. Other factors that we did not explore may influence where the microscopic stages of bull kelp settle and complete their life stage transitions; for example, the effects of sedimentation as well as the combination of increased temperature and salinity may negatively influence the settlement and survival of microscopic stages (Deiman et al. 2012; Lind and Konar 2017).

This less regimented life cycle does not mean that *Nereocystis luetkeana* is not correctly classified as an annual species. A particular individual bull kelp still progresses through the life stages of sporophyte germination (following fusion of gametes) through growth to reproduction within an annual period; the primary difference suggested by our results is that germination/appearance can occur in any season, potentially allowing *N. luetkeana* recruits to take full advantage of any gaps in the perennial kelp canopy that appear. This is additionally supported by our anecdotal observations that bull kelp sporophytes of multiple size classes (from 2 cm stipe length to 10 m stipe length) as well as mature sporophytes with fertile sori can be found throughout the year in the San Juan Islands of Washington state.

An improved understanding of competition as an important factor governing the seasonal appearance of new *Nereocystis luetkeana* sporophytes in a propagule-rich system furthers our understanding of bull kelp bed appearance 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. Grazers like the snail *Lacuna vincta* can consume bull kelp, causing damage with their radula (Chenelot and Konar 2007). This type of damage potentially contributes to breakage, and therefore mortality, even when the damage appears very minor (Duggins et al. 2001). 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). Studies of other kelp species suggest that herbivory by urchins and competition from conspecifics or other kelp leads to extreme mortality of juvenile *Macrocystis pyrifera* (Dean et al. 1989) and *Laminaria hyperborea* (Sjotun et al. 2006). Therefore, propagule availability and appearance of juvenile sporophytes in a field of competitors is only the first step toward a thriving bull kelp bed each year; this connection to disturbance as well as large parental investment in quantity of offspring instead of the evolution of chemical or mechanical defenses to prevent juvenile mortality further suggests that *N. luetkeana* is correctly classified when described as a ruderal species.

The intertwined realities of bull kelp's complicated life cycle as well as competition, seasonal variation, and juvenile sporophyte survival all contribute to annual *Nereocystis luetkeana* bed appearance and maintenance. Our results highlight the importance of studying organisms with complex life histories across multiple life stages and in geographically disparate systems, as local populations may exhibit different responses to unique environmental characteristics that do not generalize across the broader geographic range of a species.

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List of abbreviations

Vs. = versus

~ = approximately

Mm = millimeter

Cm = centimeter

M = meter

°C = degrees Celcius

Max = maximum

Statistical Results - Two-Factor Experiment - South Shaw

	Season							
	Spring		Summer		Fall		Winter	
Factor	**$F_{1,16}$**	**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: Clearing and propagule enhancement (main effects) and interactions ($\alpha=0.05$) results of two-factor experiment; $F_{\text{numerator df, denominator df}}$ and p-values from PERMANOVA (Euclidean distances; 9,999 permutations); statistically significant effects are shaded

Statistical Results - Two-Factor Experiment - Point Caution

	Season			
	Spring		Summer	
Factor	**$F_{1,16}$**	**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 2: Clearing and propagule enhancement (main effects) and interactions ($\alpha=0.05$) results of two-factor experiment; $F_{\text{numerator df, denominator df}}$ and p-values from PERMANOVA (Euclidean distances; 9,999 permutations); statistically significant effects are shaded

Pairwise Comparisons Between Seasons (Time to Appearance of New Recruits)

	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 3: Test statistics and p-values for time to appearance of recruits in plots that grew kelp 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)

	Spring		Summer		Fall	
	$F_{1,38}$	p	$F_{1,38}$	p	$F_{1,38}$	p
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 4: Test statistics and p-values for number of recruits that grew per seasonal experimental 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)

Figure Captions

Fig. 1: 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; multiple points in a month indicate multiple surveys

Fig. 2: Appearance of bull kelp (*N. luetkeana*) recruits in A) Spring B) Summer, C) Fall, and D) Winter at South Shaw Island, USA 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

Fig. 3: Appearance of bull kelp (*N. luetkeana*) recruits in following seasonal setups in A) Spring and B) Summer at Point Caution, 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)

Fig. 4: 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.

Fig. 5 Appearance of new bull kelp, *N. luetkeana*, recruits at A) Shaw Island and B) Point Caution, USA A) At South Shaw 2, the most new kelp 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)

Fig. 6: Understory macroalgal biomass across seasons at A) South Shaw 2, 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)

Fig. S1: **Site maps** A) South Shaw 2; "block" indicates the location of the surface site marker and B) Point Caution; "log" indicates a pre-existing structure used in site navigation. In both A) and B), numbered blocks indicate 2x2 m plots.