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# Factors influencing recruitment and appearance of bull kelp, *Nereocystis luetkeana* (phylum Ochrophyta)

Katie Dobkowski

*Bates College*, [kdobkows@bates.edu](mailto:kdobkows@bates.edu)

K. Darby Flanagan

Jessica R. Nordstrom

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1 FACTORS INFLUENCING RECRUITMENT AND APPEARANCE OF BULL KELP, *NEREOCYSTIS*  
2 *LUETKEANA* (PHYLUM OCHROPHYTA)<sup>1</sup>  
3

4 Running Title: Influences on *N. luetkeana* recruitment  
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6 Katie A. Dobkowski<sup>2</sup>, University of Washington and Friday Harbor Laboratories  
7

8 K. Darby Flanagan, University of Washington and Friday Harbor Laboratories  
9

10 Jessica R. Nordstrom, Friday Harbor Labs and Point Defiance Zoo and Aquarium  
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43 1 – Submitted 11/12/2018

44 2 – Current Contact Information: [kdobkows@bates.edu](mailto:kdobkows@bates.edu), Bates College, 44 Campus Ave,  
45 Department of Biology, Lewiston, ME 04240, USA  
46

47 **Abstract**

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

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

## 70 **Introduction**

71           The population dynamics of annual species are strongly tied to their capacity for  
72 recruitment each year. Many annual species have ruderal life history types, characterized  
73 by high reproductive rates and long dispersal distances; instead of competing with other  
74 species, ruderals persist by exploiting different, recently-disturbed areas, each for a limited  
75 period of time (Grime 1977). Some annual or semelparous species may actually generate  
76 their own disturbances that provide suitable free space or resources for the next  
77 generation (Foster 1977, Paine 1979).

78           In the temperate nearshore subtidal zone, kelp forests are ecologically important  
79 because they provide structure for a variety of other organisms and contribute a source of  
80 primary production to food webs within and below the photic zone (Dayton 1985, Duggins  
81 et al. 1989, Siddon et al. 2008, Krumhansl and Scheibling 2012, Teagle et al. 2017). Kelps  
82 (order Laminariales) have a heteromorphic life history consisting of a macroscopic  
83 sporophyte that makes patches of fertile tissue. These sori release swimming zoospores,  
84 which settle and grow into the microscopic gametophyte stage (John 1994). Gametophytes  
85 germinate from swimming zoospores, which are the primary dispersive stage as they are  
86 carried in sori on detached blades and/or swim as single-celled spores. Following  
87 settlement and germination, male gametophytes produce swimming gametes that fertilize  
88 females, from which the juvenile sporophyte grows (Springer et al. 2010). In lab-grown *N.*  
89 *luetkeana* under ideal conditions (10°C, white light between 80-100  $\mu\text{E}\cdot\text{m}^2\cdot\text{s}^{-1}$ ), zoospore  
90 settlement and germination occurs within 24 hours, and germ tubes begin to grow,  
91 branching to form filamentous gametophytes that can become reproductively mature

92 within 10-14 days. After 21 days, microscopic sporophytes (~1 mm length) are visible  
93 (Merrill and Gillingham 1991).

94         While many kelp species are perennial, there are annual kelps in geographically  
95 disparate areas, such *Saccorhiza polyschides* in southern Europe as well as *Postelsia*  
96 *palmaeformis* and *Nereocystis luetkeana* in the northeast Pacific. These kelps often occur in  
97 wave swept areas and most mature sporophytes that have already reproduced begin to  
98 degrade in the autumn before ultimately being detached by winter storms (Biskup et al.  
99 2014, Blanchette 1996, Springer 2010). An annual species such as the bull kelp, *Nereocystis*  
100 *luetkeana*, must complete its lifecycle within a single growing season and deposit  
101 propagules locally to appear in the same location from year to year. In Alaska, experimental  
102 removal of a key consumer (sea urchins) led to colonization by *N. luetkeana* initially, but  
103 this annual kelp was replaced by the perennial kelp *Laminaria groenlandica* in the second  
104 growing season; in this system, *N. luetkeana* is considered a ruderal species that will  
105 eventually be replaced by another more competitively dominant species (Duggins 1980).  
106 However, anecdotal observations suggest that *N. luetkeana* beds in certain locations can  
107 persist for multiple growing seasons, even if the individuals themselves only persist for one  
108 year.

109         Two factors typically govern plant recruitment – propagule (seed) availability and  
110 safe sites suitable for seeding recruitment (Harper et al. 1961, Harper et al. 1965, Grubb  
111 1977). Populations may have abundant propagules but be establishment-limited or seed-  
112 limited, with unoccupied safe sites (Duncan et al. 2009). For kelp (Laminariales), propagule  
113 availability can be difficult to track because this life stage is microscopic and frequently  
114 found on the benthos at depths of up to 30 meters (Springer et al. 2010). Also, many

115 macroalgae undergo alternation of heteromorphic generations in which the development  
116 and gamete production by a microscopic gametophyte stage occurs between successive  
117 generations of macroscopic sporophytes. However, algal propagule availability has been  
118 studied in relation to the spread and persistence of invasive species. Increasing propagules  
119 in disturbed (cleared) plots greatly increased recruitment of the invasive brown alga  
120 *Sargassum muticum*, indicating that propagule-supply drives appearance of this alga when  
121 space is available (Britton-Simmons and Abbot 2008). The presence of the subtidal canopy  
122 kelp, *Eisenia arborea* influences which macroalgal propagules can settle and form a  
123 macroalgal understory (Benes and Carpenter 2015).

124 Another important factor that determines where macroalgae recruit each year is  
125 competition for space and/or light. There may be competition among different kelps even  
126 at microscopic life stages, as *Pterygophora californica* spores have been shown to inhibit  
127 the recruitment of *Macrocystis pyrifera* by eliminating space for spore settlement (Reed  
128 1990). At larger life stages, competition via light availability influences macroalgal  
129 community structure. Perennial canopy-forming kelp species, such as *M. pyrifera* and *P.*  
130 *californica*, can reduce available bottom light by 60% and 75% respectively, as compared to  
131 levels at the surface. After removal of these canopy species, the cover of an annual brown  
132 alga (genus *Desmarestia*) increased significantly and lowered the bottom light even further  
133 to ~1% of ambient light (Clark et al. 2004). Adult sporophytes of *Ecklonia radiata*, a  
134 habitat-forming kelp in southern Australia, grow up to 2 meters in height and effectively  
135 block light for understory macroalgal species. However, microscopic *E. radiata* sporophytes  
136 also cannot grow in high understory algal cover, highlighting the importance of light  
137 availability across different life stages (Tatsumi and Wright 2016).

138           In many instances, plant and macroalgal recruitment are likely influenced by a  
139 combination of both propagule availability and availability of space. In a terrestrial forested  
140 area, experimentally increasing seed supply and availability of safe sites increased  
141 recruitment in numerous species (Eriksson and Ehrlen 1992). In southern California kelp  
142 forests, disturbance from storms may help clear substrate for settlement, recruitment, and  
143 growth as well as disperse propagules of *Macrocystis pyrifera* and *Pterygophora californica*  
144 (Reed 1992). Additionally, seasons are likely to differ in propagule and space availability. In  
145 laboratory experiments, the filamentous kelp gametophytes of numerous kelp species,  
146 including *Saccharina latissima*, *Laminaria setchellii*, and *Laminaria digitata*, survived an 18  
147 month period of darkness at low temperatures between 0°C and 8°C (tom Dieck 1993).  
148 This suggests that microscopic propagules may have lower requirements for survival than  
149 other life stages. Even if propagules are dispersed in one season, they may not begin to  
150 produce gametes immediately, waiting for enhanced light or space availability.

151           Here we use field observations and experiments to examine the factors influencing  
152 the recruitment of an annual species of marine macroalgae serving as major biogenic  
153 habitat that persists in the same (or similar) locations from year to year in this particular  
154 system. We ask, how does bull kelp, *Nereocystis luetkeana*, maintain persistent kelp beds  
155 despite its annual life history? We investigated recruitment dynamics of *N. luetkeana* by  
156 tracking the natural appearance of juveniles and manipulating both propagule and space  
157 availability. We hypothesized that 1) juvenile *N. luetkeana* would exhibit a seasonal  
158 appearance as a cohort in the spring when there is low biomass of macroalgal competitors  
159 and 2) competition for space would be more limiting than propagules (spores) to

160 recruitment at sites adjacent to established *N. luetkeana* beds because of the annual life  
161 history of *N. luetkeana* as well as the close proximity of reproductive material.

## 162 **Methods**

### 163 *Study Species*

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

167 One demographic study of *Nereocystis luetkeana* sporophytes in the field gives an  
168 indication of the timing of major life history events at a subtidal site in southern Salish Sea,  
169 approximately 100 miles south of our study sites (Maxell and Miller 1996). At this site,  
170 recognizable juvenile *N. luetkeana* first appeared in March, stipe growth reached a  
171 maximum in late June, followed by an increase in blade growth, and the first reproductive  
172 individuals were observed in early May. This timing is consistent with reproduction  
173 occurring in summer of one year that results in appearance of juveniles the following  
174 spring. In between these events, *N. luetkeana* goes through its microscopic benthic  
175 gametophyte stage.

### 176 *Study Sites*

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



183 few mature individuals remained during the winter when we established the site, and  
184 those individuals did not persist after early spring.

185 One site for subtidal experimental manipulation of competition (hereafter,  
186 “clearing”) and propagule abundance (hereafter, “seeding”) was located approximately 25  
187 meters from South Shaw 1, further offshore toward the San Juan Channel (N 48.54710°, W  
188 122.95130°; 7-9 m max depth; hereafter, South Shaw 2; Fig. S1A). We established a second  
189 site for clearing and seeding near Point Caution on San Juan Island (N 48.56323°, W  
190 123.02555°; 8-10 meters max depth; hereafter, Point Caution; Fig. S1B)

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

#### 193 *Tagging and Tracking Recruits*

194 Using numbered plastic flagging tape (as in Maxell and Miller 1991), we tagged all of  
195 the juvenile bull kelp that we encountered (stipe length < 30 cm) between June 2014 and  
196 January 2015 at South Shaw 1. We monitored survivorship of these recruits every two  
197 weeks and surveyed for appearance of new *N. luetkeana* recruits during each month of the  
198 year (2014-2015). Dive length was consistent (~50 minutes), providing a means of  
199 standardizing the seasonal appearance of new recruits.

#### 200 *Manipulation of Competition and Propagule Abundance*

201 A two-factor crossed design was used to assess the effects of competition (hereafter  
202 clearing) and propagule availability (hereafter seeding) on appearance of new *Nereocystis*  
203 *luetkeana* sporophytes. Subtidal plots were marked at the corners with bricks and flagging  
204 tape while the edges of each plot were delineated with yellow polypropylene ropes  
205 connecting the bricks. Plot size was 2x2 m and five replicate plots were established for each

206 of the four treatments: cleared and seeded, cleared and unseeded, uncleared and seeded,  
207 and uncleared and unseeded. We established new manipulated plots (n=20 per season,  
208 four seasons, for a total of 80 plots) across four seasons at South Shaw 2: spring (April),  
209 summer (August), fall (October) 2015, and winter (February) 2016. The same plot setup  
210 (n=20 plots) was done three times at Point Caution in two seasons for a total of 60 plots:  
211 July and August 2016 (summer) and April 2017 (spring). For statistical analysis, we  
212 combined the July and August plot setup and manipulations into one group (“summer”)  
213 because of the close proximity of plots, the similarity in cleared biomass, and short (6-  
214 week) interval between setups.

215         Treatments were assigned to plots at random; plots were separated by no less than  
216 0.5 meters. In cleared plots, we reduced competition by clearing attached macroalgae taller  
217 than 5 cm. In seeded plots, we enhanced propagule availability by anchoring fertile sori of  
218 *Nereocystis luetkeana* (five per plot, collected at the surface prior to the dive) to the  
219 substrate in the center of the plot using small rocks already in the subtidal environment.  
220 We collected the cleared macrophytes from 0.3 m<sup>2</sup> subsamples within each cleared 4 m<sup>2</sup>  
221 plot; subsampling, using a haphazardly-placed quadrat to minimize sampling bias, was  
222 necessary because divers could not swim safely while transporting the large total amount  
223 of kelp biomass in each plot. We dried the samples in a drying oven for 24 hours at 60°C to  
224 allow comparison of biomass between seasons at each site. We monitored manipulated  
225 plots monthly for one year following each initiation, counting the number of kelp in each  
226 plot on each survey, except for the spring initiation at Point Caution, which was monitored  
227 for three months.

228 *Data Analysis*

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

231           The two-factor design was analyzed separately for each site and each season. The  
232 response variable was the maximum count of *Nereocystis luetkeana* observed at any single  
233 time in a particular plot to account for the fact that plots were monitored monthly and an  
234 average value for the entire study period would overestimate the number of recruits due to  
235 turnover. The main effects were clearing and seeding and their interaction. These counts  
236 did not meet the assumptions of normality, even after various transformations, and also  
237 were overdispersed relative to Poisson distribution, so we used a resampling approach to  
238 determine statistical significance of the main effects and interactions ( $\alpha=0.05$ ):  
239 PERMANOVA with Euclidean distances and 9,999 permutations.

240           Across seasons at each site we compared the cleared biomass of macroalgae and the  
241 magnitude of juvenile *Nereocystis luetkeana* recruitment, using counts of new recruits, and  
242 the time to appearance of the first *N. luetkeana* in each plot. The time to appearance used  
243 only plots in which juvenile recruits appeared because new bull kelp never appeared in  
244 many plots. Because of the lack of normality and heteroskedastic variances, we analyzed  
245 these data using PERMANOVA (as described above). When a factor was significant, we used  
246 pairwise PERMANOVA to compare all possible combinations and Bonferroni-corrected p-  
247 values as the threshold for significance.

248           We measured the macroalgal biomass only in cleared plots because removing  
249 macroalgae from uncleared plots would change the treatments. The dried biomass data for  
250 South Shaw 2 met the assumptions of normality and we tested for seasonal differences  
251 using a one-way ANOVA followed by a Tukey HSD test. Because Point Caution biomass data

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

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

## 257 **Results**

### 258 *Tagging and Tracking Recruits*

259 We tagged and tracked 41 *Nereocystis luetkeana* recruits in the spring/summer and  
260 10 in the fall/winter at South Shaw 1. Survivorship of juvenile bull kelp recruits was low for  
261 individuals tagged in both seasons, as less than half of tagged individuals survived the  
262 initial two-week observation period (Fig. 1A). On survey dives, we observed at least one  
263 new juvenile *N. luetkeana* recruit (stipe length < 30 cm) appearing in every month except  
264 February (Fig. 1B).

### 265 *Manipulation of Competition and Propagule Abundance*

266 Following the spring initiation at South Shaw 2, clearing increased the number of  
267 new juvenile *Nereocystis luetkeana* (Fig. 2A; Table 1); the cleared plots grew more  
268 individuals (mean  $\pm$  SE =  $23.5 \pm 7.2$ ) than the uncleared plots (mean =  $0.4 \pm 0.4$ ). Seeding  
269 did not influence the appearance of new *N. luetkeana* and the interaction between clearing  
270 and seeding was also not significant. Clearing made no difference in the number of new  
271 individuals in plots within one year following the summer (cleared =  $0.3 \pm 0.15$ , uncleared  
272 =  $0.3 \pm 0.2$ ; Fig. 2B), fall (cleared =  $0.8 \pm 0.33$ , uncleared =  $0.3 \pm 0.15$ ; Fig. 2C), and winter  
273 (cleared =  $3.5 \pm 1.46$ , uncleared =  $1.1 \pm 0.43$ ; Fig. 2D) experiment at South Shaw 2. Seeding  
274 did not significantly impact appearance of new *N. luetkeana* in plots established in summer,

275 fall, or winter. The interaction between clearing and seeding was also not significant in  
276 summer, fall, or winter. At Point Caution, cleared plots had more *N. luetkeana* recruits in  
277 the spring (Fig. 3A; Table 2) but seeding did not change the number of recruits and the  
278 interaction between clearing and seeding was also not significant. In the summer, the  
279 number of new *N. luetkeana* was greater in cleared plots (Fig. 3B) but did not differ  
280 between plots with propagule enhancement. The interaction was also not significant.

281         Among plots in which new recruits appear following experimental manipulations,  
282 the time to appearance (in months) at South Shaw 2 varied by season ( $F_{3,30}=25.4$ ,  $p<0.001$ ;  
283 Fig 4; Table 3). New *Nereocystis luetkeana* appeared the soonest following the spring  
284 experiment (mean  $\pm$  SE =  $1.6 \pm 0.16$  months) as compared to the summer ( $7.3 \pm 2.27$ ), fall  
285 ( $8.5 \pm 0.52$ ), and winter ( $4.5 \pm 0.47$ ) manipulations (i.e. clearing and seeding). New kelp  
286 took longer to appear following the fall manipulation as compared to the winter  
287 manipulation, while the time to appearance of new kelp was statistically indistinguishable  
288 for summer and fall as well as summer and winter.

289         The number of new individuals also varied by season at South Shaw 2 ( $F_{3,76}=6.09$ ,  
290  $p<0.001$ ; Fig. 5A; Table 4). The number of juveniles that appeared following the spring  
291 manipulation (mean  $\pm$  SE =  $23.9 \pm 7.1$ ) was greater than in the summer ( $1 \pm 0.32$ ) or fall  
292 ( $1.4 \pm 0.26$ ). The number that grew in plots following the winter manipulation was greater  
293 than in the summer ( $3.75 \pm 1.1$ ). The number that appeared in spring was not statistically  
294 different than in winter initiations nor between summer and fall or fall and winter. At Point  
295 Caution, the number of new *Nereocystis luetkeana* recruits did not vary by season  
296 ( $F_{1,57}=1.2$ ,  $p=0.65$ ; Fig 5B).

297 Understory macroalgal (potential competitor) biomass, as measured at the time of  
298 manipulation (clearing and seeding), varied between seasons at both sites (South Shaw 2:  
299  $F_{3,35}=3.24$ ,  $p=0.03$ ; Fig. 6A and Point Caution:  $F_{1,28}=8.4$ ,  $p=0.005$ ; Fig. 6B). At South Shaw 2,  
300 the cleared biomass of plots established in the fall was greater than those in the winter  
301 ( $p=0.02$ ), while the pair-wise comparisons of cleared biomass from the plots established in  
302 spring, summer, and fall were all statistically similar. At Point Caution, the cleared biomass  
303 was lower in the spring initiation than the summer initiation ( $p=0.005$ ).

#### 304 **Discussion**

305 Juvenile *Nereocystis luetkeana* represent a life stage whose success is crucial to the  
306 persistence of beds of this annual species from year to year. This kelp's alternation of  
307 heteromorphic generations means that there is always an interval between sporophyte  
308 generations, in which the microscopic life stages occur. Our experimental removal of  
309 competitors and enhancement of propagule availability across multiple seasons suggests that *N.*  
310 *luetkeana* shows some seasonality in appearance, but that new individuals can begin to grow  
311 across seasons. Successful appearance of new sporophytes may be inhibited by competition from  
312 other macroalgae, which allows some "offseason" recruits to appear, potentially following a  
313 space-clearing disturbance event. Additionally, although disturbances may generate sites for  
314 recruitment in a propagule-rich system, especially since microscopic stages can likely persist for  
315 extended periods until conditions become favorable, high juvenile mortality also plays a role in  
316 determining where recruits persist and mature.

317 Our results suggest that competition is an important driver of where juvenile bull kelp  
318 appear. In our subtidal experiment, more *Nereocystis luetkeana* recruits appeared in cleared plots  
319 in the spring at South Shaw and in both spring and summer at Point Caution, when

320 environmental conditions (especially light) are expected to be otherwise favorable for kelp  
321 growth. We also quantified a seasonal difference in biomass of potential competitors (understory  
322 macroalgae) in keeping with an increase in biomass during the spring/summer growing season.  
323 Evidence suggests that the perennial giant kelp (*Macrocystis pyrifera*) may also begin to grow  
324 following experimental clearing of understory competitors, suggesting that this other canopy-  
325 formers also benefit from the opening of gaps in existing understory to initiate growth (Dayton et  
326 al. 1984). The fact that new juvenile *N. luetkeana* can begin to grow in the same location,  
327 creating a seemingly persistent kelp bed for multiple years, may be a function of a high level of  
328 benthic disturbance in this system. The disturbance may serve to reduce interspecific competition  
329 to a low enough level to allow *N. luetkeana* to gain a “foothold” even in a field of perennial kelp  
330 species.

331         The lack of influence of seeding in our manipulated (“seeded” vs. “unseeded”) plots  
332 indicates that propagule limitation may not be a major factor influencing where *Nereocystis*  
333 *luetkeana* recruit and begin to grow in this system. While we did add fertile sori to “seeded”  
334 plots, we did not measure total spore availability; while we did not quantify number or spores or  
335 motility in this study, we did achieve spore release from fertile sori followed by successful  
336 zoospore settlement in all seasons in the laboratory as part of a temperature growth experiment.  
337 Additionally, our plots at both sites were in some cases as close together as 0.5 meters, which  
338 may influence the independence of treatments, and were established adjacent (<5 m) to a known  
339 *N. luetkeana* beds. This close proximity likely contributes to a high natural availability of  
340 propagules in both seeded and unseeded plots. Working at a site more distant from adult *N.*  
341 *luetkeana* might have produced different results, as transport distances for *N. luetkeana*  
342 zoospores are not well documented but one study that analyzed numerous years of survey data

343 suggested that although environmental factors may play a role, the abundance of bull kelp in one  
344 growing season is the crucial predictor of bull kelp presence in a location the following season  
345 (Pfister et al. 2018). Bull kelp zoospore dispersal may be similar to *Macrocystis pyrifera* (as are  
346 some other aspects of reproductive biology between these two canopy-formers); evidence  
347 suggests that *M. pyrifera* propagules can be transported long distances (<1000 m) to potentially  
348 maintain or restore populations even when an individual kelp bed disappears (Gaylord et al.  
349 2002, 2006). It is possible that the zoospores of bull kelp may disperse even further due to the  
350 manner in which the fertile sori detach from the blade at maturity (Walker 1980). However,  
351 Springer (2010) suggests that *N. luetkeana* spores may only move short distances less than 100  
352 meters, so clearly additional work is needed to quantify the dispersal distances of these  
353 zoospores in the field, ideally across different areas of the species' large geographic range.

354 Both our tagging/tracking study as well as our manipulated plots show that young  
355 sporophytes can appear during any season, which suggests that not all *N. luetkeana* begin to  
356 grow as a cohort in the spring as Maxell and Miller (1991) observed at sites further south in the  
357 Salish Sea. Although our results only come from one site (near South Shaw Island in the San  
358 Juan Islands of Washington State), the seasonal difference in time to the appearance of the first  
359 new bull kelp recruits between spring and other seasons suggests that microscopic *N. luetkeana*  
360 life stages can persist for an extended period of time, "waiting" for environmental conditions or  
361 competitor-free space to become more favorable. In laboratory experiments with low nutrient  
362 levels, *Macrocystis pyrifera* gametophytes remained vegetative, delaying reproduction for at  
363 least seven months with low nutrient levels before rapidly producing sporophytes after nutrients  
364 were added (Carney 2011). Gametophytes of another large, subtidal, annual brown alga  
365 *Desmarestia ligulata* var. *ligulata* can persist for up to 15 months in the field (Edwards 2000).



366 However, it is also possible that some of the recruits that appeared after a long delay came from  
367 zoospores that settled after our propagule enhancements. The fact that clearing yielded more  
368 recruits following the summer experimental setup at Point Caution but not at South Shaw may  
369 indicate some subtle effect of site or temporal variation that may be acting on any one of the life  
370 stages. Other factors that we did not explore may influence where the microscopic stages of bull  
371 kelp settle and complete their life stage transitions; for example, the effects of sedimentation as  
372 well as the combination of increased temperature and salinity may negatively influence the  
373 settlement and survival of microscopic stages (Deiman et al. 2012; Lind and Konar 2017).

374 This less regimented life cycle does not mean that *Nereocystis luetkeana* is not correctly  
375 classified as an annual species. A particular individual bull kelp still progresses through the life  
376 stages of sporophyte germination (following fusion of gametes) through growth to reproduction  
377 within an annual period; the primary difference suggested by our results is that  
378 germination/appearance can occur in any season, potentially allowing *N. luetkeana* recruits to  
379 take full advantage of any gaps in the perennial kelp canopy that appear. This is additionally  
380 supported by our anecdotal observations that bull kelp sporophytes of multiple size classes (from  
381 2 cm stipe length to 10 m stipe length) as well as mature sporophytes with fertile sori can be  
382 found throughout the year in the San Juan Islands of Washington state.

383 An improved understanding of competition as an important factor governing the seasonal  
384 appearance of new *Nereocystis luetkeana* sporophytes in a propagule-rich system furthers our  
385 understanding of bull kelp bed appearance from year to year. However, observed low  
386 survivorship of *N. luetkeana* recruits indicates that appearance of new individuals does not  
387 necessarily lead to generation of a kelp bed due to post-recruitment effects such as herbivory and  
388 post-recruitment competition. Grazers like the snail *Lacuna vincta* can consume bull kelp,

389 causing damage with their radula (Chenelot and Konar 2007). This type of damage potentially  
390 contributes to breakage, and therefore mortality, even when the damage appears very minor  
391 (Duggins et al. 2001). Experimentally caged juvenile bull kelp (stipe length < 30 cm) protected  
392 from large local consumers such as kelp crabs (genus *Pugettia*) and urchins (*Strongylocentrotus*  
393 sp.) increased in blade length and mass, while uncaged individuals decreased in both  
394 (Dobkowski 2017). Studies of other kelp species suggest that herbivory by urchins and  
395 competition from conspecifics or other kelp leads to extreme mortality of juvenile *Macrocystis*  
396 *pyrifera* (Dean et al. 1989) and *Laminaria hyperborea* (Sjotun et al. 2006). Therefore, propagule  
397 availability and appearance of juvenile sporophytes in a field of competitors is only the first step  
398 toward a thriving bull kelp bed each year; this connection to disturbance as well as large parental  
399 investment in quantity of offspring instead of the evolution of chemical or mechanical defenses  
400 to prevent juvenile mortality further suggests that *N. luetkeana* is correctly classified when  
401 described as a ruderal species.

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

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- 529

530 List of abbreviations

531

532 Vs. = versus

533 ~ = approximately

534 Mm = millimeter

535 Cm = centimeter

536 M = meter

537 °C = degrees Celcius

538 Max = maximum

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Statistical Results - Two-Factor Experiment - South Shaw

Factor	Season							
	Spring		Summer		Fall		Winter	
	F <sub>1,16</sub>	p	F <sub>1,16</sub>	p	F <sub>1,16</sub>	p	F <sub>1,16</sub>	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

542

543 Table 1: Clearing and propagule enhancement (main effects) and interactions ( $\alpha=0.05$ ) results of  
544 two-factor experiment; F<sub>numerator df, denominator df</sub> and p-values from PERMANOVA (Euclidean  
545 distances; 9,999 permutations); statistically significant effects are shaded  
546  
547



Statistical Results - Two-Factor Experiment - Point Caution  
**Season**

<b>Factor</b>	Spring		Summer	
	<b>F<sub>1,16</sub></b>	<b>p</b>	<b>F<sub>1,35</sub></b>	<b>p</b>
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

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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)

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

554

555

556 Table 3: Test statistics and p-values for time to appearance of recruits in plots that grew kelp  
 557 within one year at South Shaw;  $F_{\text{numerator df, denominator df}}$  and p-values from PERMANOVA  
 558 (Euclidean distances; 9,999 permutations); statistically significant effects are shaded ( $p<0.008$   
 559 with Bonferroni correction)

560

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562

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

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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)

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572 Figure Captions

573 Fig. 1: A) Survivorship and B) Appearance of new bull kelp, *N. luetkeana* recruits at South Shaw  
574 Island, USA in 2014-2015; A) dashed line indicates recruits tagged in the spring/summer and  
575 tracked for 18 weeks; solid line indicates recruits tagged in the fall/winter and tracked for 8  
576 weeks B) new recruits were surveyed in every month except February; multiple points in a  
577 month indicate multiple surveys

578  
579 Fig. 2: Appearance of bull kelp (*N. luetkeana*) recruits in A) Spring B) Summer, C) Fall, and D)  
580 Winter at South Shaw Island, USA A) Spring - the number of new kelp that began to grow  
581 differed between cleared and uncleared plots ( $p=0.0018$ ) but not between seeded and unseeded  
582 plots ( $p=0.21$ ); the clearing \* seeding interaction was also not significant B) Summer, C) Fall, D)  
583 Winter – neither clearing nor seeding significantly increased the appearance of new bull kelp and  
584 the interaction was not significant

585  
586 Fig. 3: Appearance of bull kelp (*N. luetkeana*) recruits in following seasonal setups in A) Spring  
587 and B) Summer at Point Caution, A) The number of recruits that appeared differed between  
588 cleared and uncleared plots ( $p=0.01$ ) but not between seeded and unseeded plots ( $p=0.57$ ); the  
589 interaction was also not significant ( $p=0.85$ ) B) The number of recruits that appeared differed  
590 between cleared and uncleared plots established ( $p=0.04$ ) but not between seeded and unseeded  
591 plots ( $p=0.37$ ); the interaction was also not significant ( $p=0.36$ )

592  
593 Fig. 4: Time to appearance of bull kelp, *N. luetkeana*, recruits following experimental setup in  
594 four seasons at South Shaw Island. The time for new kelp at South Shaw to appear was the  
595 shortest in the spring ( $p<0.001$ ), while the amount of time to first kelp was not distinguishable  
596 between summer and fall and summer and winter; fall and winter were also different ( $p=0.02$ ).  
597 Letters indicate statistically significant differences.

598  
599 Fig. 5 Appearance of new bull kelp, *N. luetkeana*, recruits at A) Shaw Island and B) Point  
600 Caution, USA A) At South Shaw 2, the most new kelp grew following the spring setup  
601 ( $p<0.001$ ), while the number of new kelp that appear following the summer and fall setup and the  
602 winter and fall setup did not differ. Letters indicate statistically significant differences. B) At  
603 Point Caution, there was no statistical difference in kelp that grew between seasons ( $p=0.65$ )

604  
605 Fig. 6: Understory macroalgal biomass across seasons at A) South Shaw 2, where the cleared,  
606 dried biomass was the same between spring, summer, and fall but different between fall and  
607 winter ( $p=0.02$ ) and B) Point Caution, where cleared, dried biomass differed between spring and  
608 summer ( $p=0.005$ )

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

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