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INHERENT TOLERANCE OF EXTREME SEASONAL VARIABILITY IN LIGHT AND SALINITY IN AN ARCTIC ENDEMIC KELP (*LAMINARIA SOLIDUNGULA*)[1]

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The kelp *Laminaria solidungula* is an important foundation species in the circumpolar Arctic. One of the largest populations of *L. solidungula* in the Beaufort Sea occurs in Stefansson Sound, off the north coast of Alaska. We surveyed kelp populations in the Stefansson Sound Boulder Patch and found that inshore sites in close proximity (3.5 km) to river input and increased turbidity exhibited lower sporophyte densities ($0.36 \pm 0.44 \cdot m^{-2}$) than more offshore sites (>7 km) to the west ($0.72 \pm 0.48 \cdot m^{-2}$) and east ($4.72 \pm 1.51 \cdot m^{-2}$). We performed culture experiments to examine the possible combined effects of salinity and light on microscopic sporophyte production. Gametophytes cultured in the low salinity treatment (10) were unable to produce sporophytes regardless of light level. The highest light level tested (40 µmol photons $\cdot m^{-2} \cdot s^{-1}$) produced the greatest sporophyte densities ($0.037 \pm 0.08 \cdot mm^{-2}$) at a salinity of 30. Subsequent experimental work on the effect of salinity on microscopic stages revealed that haploid stages were not capable of producing sporophytes at a salinity of 10, but 3-month-old microscopic sporophytes were able to persist in the lower (10 and 20) salinity treatments. Although *L. solidungula* sporophytes have apparently acclimated to extreme salinity (<5–33) and light variations, the vulnerability of haploid microscopic stages to reduced salinity has the potential to affect future populations as the timing and magnitude of freshwater input to the Arctic Ocean changes.

Key index words: **acclimation; Arctic; freshwater input; kelp; polar; recruitment; salinity; sexual reproduction**

***Abbreviations*: CCA, crustose coralline algae; FOV, field of view; GOM, Gulf of Mexico; PES, Provasoli's Enriched Seawater; RO, reverse osmosis**

Brown seaweeds of the order Laminariales (kelps) play important roles in nearshore marine ecosystems by providing a food source and habitat through their physical structure (Steneck et al. 2002, Graham 2004). Many kelp species play similar ecological roles, but their response to variations in environmental factors differs tremendously. Certain species can adjust timing of their growth and reproduction to periods when conditions are favorable (e.g., *Macrocystis pyrifera*), while other species respond to specific extrinsic factors (i.e., daylight; *Pterygophora californica*, Reed et al. 1996) or possess endogenous rhythms that are linked to daylength (Lüning and Kadel 1993). Endogenous rhythms in kelps are often based on species adaptation to environmental fluctuations over time (temperature, Matson and Edwards 2007; nutrients, Dunton et al. 1982; light, Reed et al. 1996), exemplified in the Arctic endemic kelp, *Laminaria solidungula*.

Known as a "season anticipator" (Wiencke et al. 2006), *Laminaria solidungula* optimizes annual light and nutrient variability by fixing carbon when light is available (summer) and producing new frond tissue during the dark winter period when nitrogen is available in nearshore Arctic waters (Dunton et al. 1982, Dunton and Schell 1986). Ecologically, *L. solidungula* serves as an important foundation species in many parts of the Arctic by providing habitat and a year-round food source for a diverse benthic fauna (Dunton et al. 1982, Dunton and Schell 1987, Filbee-Dexter et al. 2019). Arctic kelp populations are expected to shift in species composition and distribution as waters warm and sea ice retreats (e.g., Krause-Jensen and Duarte 2014). The demographic nature of this response for *L. solidungula* is unknown, but sentinel population biology theory stresses the importance of considering all life-history stages when exploring adult population dynamics (Harper 1977). Therefore, the ability to predict biotic and abiotic controls on all life-history stages of kelp species is a critical step toward understanding population dynamics.

Kelps possess a diplohaplontic life-history strategy for reproduction. Macroscopic sporophytes ($2n$) release microscopic zoospores ($1\ n$; meiospores) that settle onto the substrate, undergo gametogenesis, form gametophytes, and release gametes ($1\ n$). Male gametophytes produce and release spermatozoids that fertilize eggs protruding from female gametophytes. Once fertilization occurs, a microscopic sporophyte ($2n$) is produced. Often, microscopic stages are more vulnerable to changes in environmental conditions and have specific light, temperature, nutrient, and other abiotic demands that differ from adult individuals (Deysher and

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Dean 1986, reviewed in Graham et al. 2007, Harley et al. 2012, Muth et al. 2019), ultimately affecting population persistence (Graham et al. 2007).

The Stefansson Sound Boulder Patch, located on the north coast of Alaska, is an area of rocky substrate composed of boulders and cobbles that provides a habitat for kelp on an otherwise featureless seabed (Fig. 1). The Boulder Patch is a regional hotspot of high floral and faunal diversity and supports a diverse food web (Dunton and Schell 1987, Wilce and Dunton 2014, Dunton and Schonberg 2020). The benthic communities of the Boulder Patch are exposed to considerable seasonal variability, including ice cover, light, and the large pulse of freshwater from the Sagavanirktok River that enters Stefansson Sound every spring. Irradiance is very low or undetectable during the winter months due to low sun angles and thick (up 1.8 m) sediment-laden ice (Dunton 1990). However, relatively "clear" sea ice in some years can allow light to penetrate to the benthos from March to June (up to 5.4 μmol photons $\cdot$ m^{-2} $\cdot$ s^{-1}), which can significantly increase the annual growth of *Laminaria solidungula* (Dunton 1990). Following the spring freshet, ice cover begins to dissipate but nearshore waters are often turbid as winds resuspend sediments in the shallow waters of the Sagavanirktok River Delta and lower light levels (Dunton et al. 1982, Bonsell and Dunton 2018, Muth et al. 2020).

Throughout the Boulder Patch, *Laminaria solidungula* population densities vary, but kelp are present in nearly all areas with rocky substrate. Since observations by divers over several years suggest that there are strong spatial differences in kelp density, we sought to first quantify these differences and secondly examine the potential mechanisms that would affect kelp density and distribution within the Boulder Patch. To address the second objective, we designed experiments to quantify the effects of salinity and light on the haploid and diploid microscopic stages of *L. solidungula*. The rapidly warming Arctic climate presents major challenges for many endemic marine species, especially along circumpolar coasts where oceanographic conditions are likely to change most in response to increased freshwater inputs, nearshore ice retreat, and coastal erosion (Jones et al. 2009, Fichot et al. 2013). For the Arctic endemic kelp *L. solidungula*, the changes in physicochemical conditions may rapidly exceed the physiological tolerances of this ecologically important species. Our work provides an important baseline to assess the tolerance and ultimately the resilience of *L. solidungula* life stages to light and salinity regimes.

MATERIALS AND METHODS

Study sites. We selected three sites that are located at varying distances from the mouth of the Sagavanirktok River: Offshore-East, 9 km (DS-11), Offshore-West, 7 km (W-3), and Inshore, 3.5 km (E-1). These sites (Fig. 1) have been the focus of long-term ecological studies within the Boulder Patch since 1977 (Dunton et al. 1982, Dunton 1990). Rock cover within the Boulder Patch varies greatly, but the boundaries between areas of high density with those of scattered cobbles have been delineated by multiple geophysical surveys (Wilce and Dunton 2014). Data collected at these sites also reveal long-term differences in average salinity levels during spring and summer months (Offshore-East ~29, Offshore-West ~28, Inshore ~27; Dunton and Schonberg 2020) that were first described by Sellmann et al. (1992). Examination of these long-term high frequency measurements shows that salinity levels frequently drop much lower (<10) for sustained periods at inshore locations than are captured in long-term records (Sellmann et al. 1992, Bonsell and Dunton 2021). Benthic light levels also differ among these sites, with daily summer open-water (July–September) values often ranging up to 12 mol photons $\cdot$ m^{-2} $\cdot$ d^{-1} at Offshore-East and the Inshore site but only to 6 mol photons $\cdot$ m^{-2} $\cdot$ d^{-1} at Offshore-West (Bonsell and Dunton 2021).

Kelp densities. To quantify *Laminaria solidungula* densities at the three sites within the Boulder Patch, we acquired 0.05 m^2 photoquadrats with a Nikon 1 AW1 waterproof digital camera in July and August 2016 and 2017. Photographs were taken in a spiral pattern around a central point at each site by divers as described by Bonsell and Dunton (2021). Since kelp propagules mainly recruit to hard stable substrates, we addressed the variance in rock distribution by only selecting surfaces with rock cover >75%. We standardized the density of *L. solidungula* to hard substrate which allowed for direct comparisons of kelp densities among sites. Individuals were counted only if the holdfast was present within the quadrat (overlying blades were not counted). Densities were compared using a Kruskal–Wallis rank sum test and a Dunn test with *P*-values adjusted via the Bonferroni method for pairwise comparisons.

Combined effects of salinity and light culture experiment. To assess the interactive effects of salinity and light levels that both gametophyte and sporophyte generations are exposed in situ, we conducted multi-factor culture experiments in a large growth incubation chamber. Reproductive *Laminaria solidungula* individuals were collected from Endicott Island, Alaska (adjacent to the Boulder Patch) and shipped to the University of Texas Marine Science Institute in October 2017 and maintained at 0°C in aerated filtered seawater for 2 months, ensuring all individuals had been exposed to similar abiotic factors prior to sporulation. Reproductive sori were then placed between layers of damp paper towels, kept in darkness for 24 h, and placed in 10°C seawater to induce sporulation (December 7, 2017). After sporulation, 10 mL of the solution was placed in 45 Petri dishes (50 × 10 mm). After allowing 1 week for zoospore settlement, the solution was replaced with offshore Gulf of Mexico (GOM) seawater (oligotrophic), Provasoli's Enriched Seawater (PES; Provasoli 1968; 20 mL $\cdot$ L^{-1}), and mixed with reverse osmosis (RO) water to attain three salinity (10, 20, and 30) treatments.

We exposed zoospores (meiospores) from each salinity treatment to three different light treatments to create nine salinity/light treatments ($n = 5$ for each treatment, see Appendix S1 in the Supporting Information for experiment schematic). Shade cloth deployed above the dishes was used to achieve light levels of 10, 20, and 40 μmol photons $\cdot$ m^{-2} $\cdot$ s^{-1}. Dishes were randomly arranged in the culture chamber where they were maintained at 0°C in a 10:14-h light:dark regime. Media changes were made on a weekly basis.

Dishes were monitored weekly for microscopic stage development. Initial settlement densities were quantified on

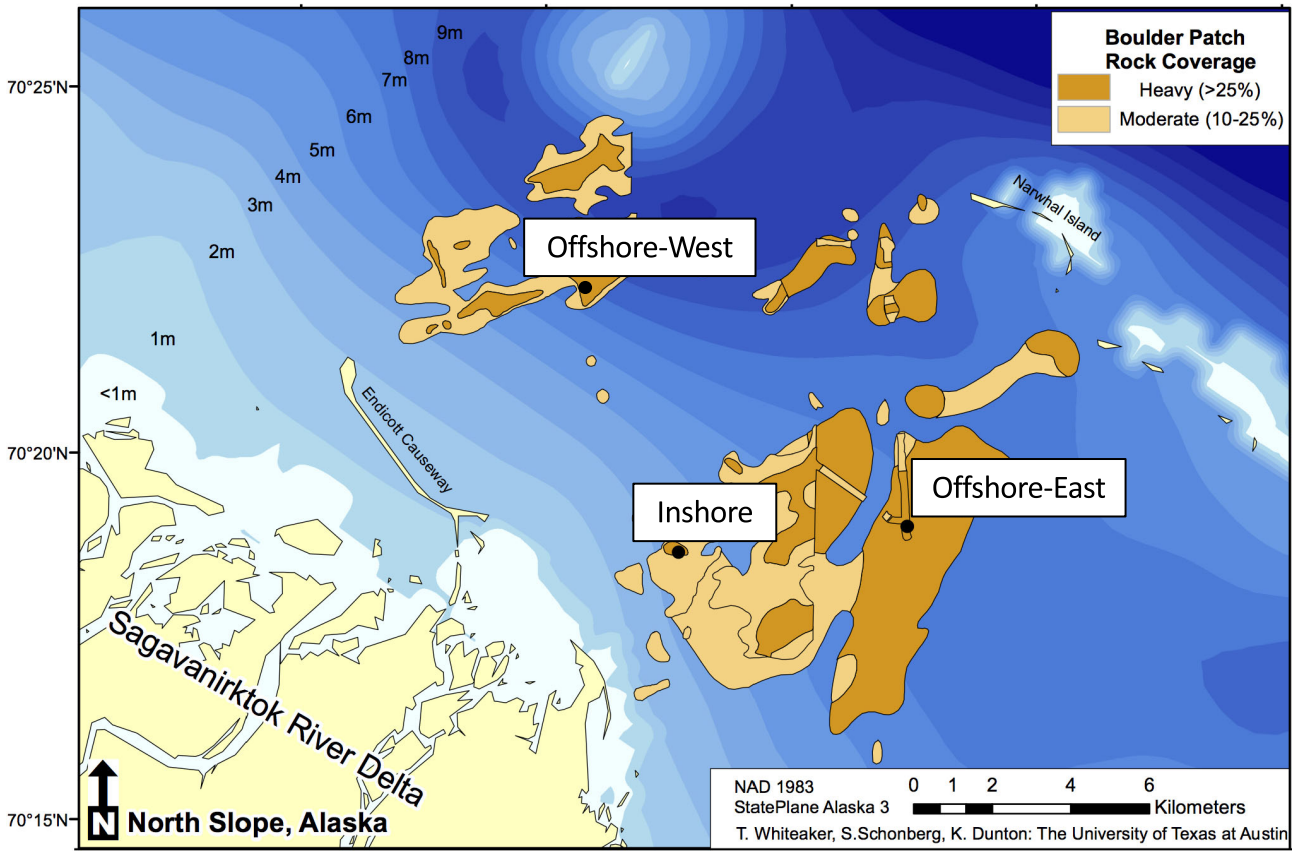

FIG. 1. The Boulder Patch in Stefansson Sound. Rock cover is denoted by brown shading. Densities of *Laminaria solidungula* were measured at the Inshore (E-1), Offshore-West (W-3), and Offshore-East (DS-11) sites. Adapted from Bonsell and Dunton (2018).

December 15, 2017, to ensure all treatments had similar settlement. Gametophyte densities were assessed on January 26, 2018, within a month, young sporophytes developed from the fertilized gametophytes. Sporophyte densities were then assessed biweekly (February 28, March 16 and 27), to track sporophyte production from the original gametophytes. Each dish was observed under 400x magnification for 10 fields of view (FOV; see Appendix S1 for experiment schematic).

Settlement densities of zoospores (assessed on December 15) and gametophytes (assessed on January 26) were compared using two-way ANOVAs among light and salinity levels, and post hoc comparisons were made using Tukey's LSD. Sporophyte abundance was assessed over time (three dates) using a repeated measures ANOVA (time, light, salinity, and light × salinity). The interaction of light and salinity was not significant (Repeated Measures ANOVA, chi-squared$_1$ = 0.2764, p = 0.59) and was removed from the model. All statistics were run using R Version 3.3.1.

Salinity effects on microscopic stages. An additional culture experiment was conducted to explore the sole effects of salinity on the ability of zoospores and newly formed gametophytes to mature and ultimately lead to sporophyte production (see Appendix S1 for experiment schematic).

Zoospores: We released zoospores from five reproductive *Laminaria solidungula* individuals (collected August 2018 from the Boulder Patch) on February 11, 2019, and combined zoospores into one solution. Individuals were not reproductive when collected and additional time in the cold chamber was needed for sori production and to ensure that all individuals were exposed to similar abiotic factors before sporulation. As described above, equal aliquots of zoospore solution (10 mL) were placed onto 18, 50 × 10 mm Petri dishes for 1 week to allow for maximum settlement (salinity of 30, 0°C, 40 µmol photons · m^{-2} · s^{-1} 10:14-h light:dark regime). Settlement densities were quantified for all dishes to ensure similar starting densities (February 18, 2019; 10 FOV at 400x). After 1 week, GOM seawater, 20 mL · L^{-1} of PES and varying amounts of RO water were added to nine dishes to create three salinity treatments (10, 20, and 30, n = 3). The nine remaining dishes were replaced with control solution (30-salinity) and left for further observation once gametophytes were mature (unicellular, pre-egg development). All dishes were monitored, and media changes occurred weekly.

Gametophytes: Once gametophytes were present in the remaining nine dishes (kept at a salinity of 30), salinity treatments were initiated to observe salinity effects on the gametophyte stage (n = 3 for each salinity treatment, March 27, 2019). Sporophytes were observed in the control treatments nearly 6 weeks later (May 6, 2019). The presence and absence of sporophytes was recorded for each treatment (100×, 20 FOV), which enabled us to document the effects of salinity on the ability of the gametophyte to successfully produce sporophytes.

Sporophytes: Survivorship and production of microscopic sporophytes (derived from the control experiment above) was quantified by first assessing densities (50×, entire dish)

for six dishes (May 11, 2019), then initiating salinity treatments ($n = 2$; 10, 20, and 30), and finally measuring sporophyte density in each dish after 1 month (June 12, 2019; see Appendix S1 for experiment schematic). The initial quantity and final quantity of sporophytes were used to calculate percent change in sporophyte densities and to compare densities among salinity treatments. We used a one-way ANOVA to compare the percent change in sporophyte densities.

It is important to note that adults were only observed in field conditions, and microscopic stages were cultured in medium composed of ocean water from the Gulf of Mexico and reverse osmosis freshwater. Culture media was prepared by diluting ocean water, keeping all ion ratios constant. This approach mimics seawater dilution from the addition of freshwater (Kirst 1990), but ion concentrations are different depending on source water values.

RESULTS

Boulder Patch kelp densities. Adult *Laminaria solidungula* densities were significantly different among Boulder Patch sites (Kruskal–Wallis chi-squared$_2$ = 9.908, $P = 0.007$) with kelp densities doubling between the inshore East site and the Offshore East site. Pairwise comparisons showed that Offshore-East ($4.72 \pm 1.51 \cdot m^{-2}$ SE) differed from Inshore ($0.36 \pm 0.44 \cdot m^{-2}$ SE) and Offshore-West ($0.72 \pm 0.48 \cdot m^{-2}$ SE; Dunn Test, Offshore-East × Inshore $P = 0.001$, *Offshore-East* × *Offshore-West* $P = 0.001$, *Inshore* × *Offshore-West* $P = 1.00$; Fig. 2).

Combined effects of salinity and light culture experiment. Initial zoospore settlement densities were not significantly different among salinity and light treatments and ranged from 0.79 to 1.45 zoospores $\cdot$ mm^{-2} (2-way ANOVA, light vs. salinity $F_{3,41} = 0.3293$, $P = 0.80$; Table S1 in the Supporting Information). Based on these data, we assumed that any differences in gametophyte or sporophyte densities are a result of environmental conditions after settlement.

Gametophyte densities were significantly different among salinity treatments, but there was no significant difference among light treatments or the salinity light interactions (2-way ANOVA, salinity $F_{2,41} = 21.67$, $P < 0.001$; Fig. 3). The low salinity (10) treatments had significantly lower densities (0–1.97 $\cdot$ mm^{-2}) than the 20 (0–2.63 $\cdot$ mm^{-2}) and 30 (0–3.28 $\cdot$ mm^{-2}; Fig. 3). Gametophytes apparently did not germinate in the 20 and 40 µmol photons $\cdot$ m^{-2} $\cdot$ s^{-1} light treatments at a salinity of 10, and very low numbers of gametophytes were produced in the 10 µmol photons $\cdot$ m^{-2} $\cdot$ s^{-1} light treatment.

Sporophyte densities were quantified over a period of 4 weeks (February 28 to March 27, 2019), but the effect of time was not significant (*repeated measures ANOVA,* $F_{1,41} = 2.32$, $P = 0.127$). No sporophytes were produced in the 10-salinity treatment, while both the 20 and 30 treatments yielded sporophytes (repeated measures ANOVA: light, chi-squared$_1$ = 6.52, $P = 0.01$; salinity, chi-squared$_1$ = 44.12, $P < 0.001$; Fig. 4). Sporophyte densities were significantly higher in the 40 µmol photons $\cdot$ m^{-2} $\cdot$ s^{-1} light treatments

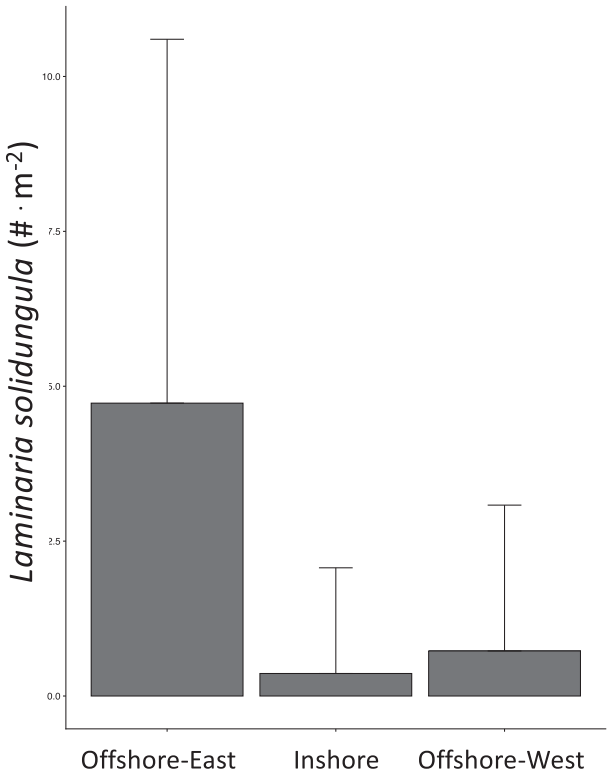

FIG. 2. *Laminaria solidungula* densities (# $\cdot$ m^{-2} $\pm$ SD) at the Inshore (E-1), Offshore-West (W-3), and Offshore-East (DS-11) sites within the Boulder Patch. Densities were quantified using photo quadrats and employed a standardized rock cover (>75%) to minimize the effects of patchy hard substrate occurrence among sites.

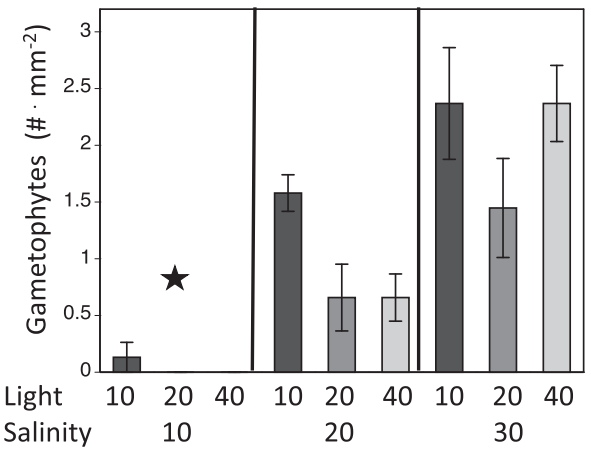

FIG. 3. Gametophyte density assessed on January 26, 2018 (# $\cdot$ mm^{-2}; $x \pm$ SE, $n = 5$), was significantly different ($P < 0.001$) among salinity treatments (10 vs. 20, 10 vs. 30; denoted by a star). Panels represent the salinity treatment levels, 10, 20, and 30. Light ($P = 0.41$) and salinity × light (µmolphotons $\cdot$ m^{-2} $\cdot$ s^{-1}) interaction were not significant ($P = 0.61$).

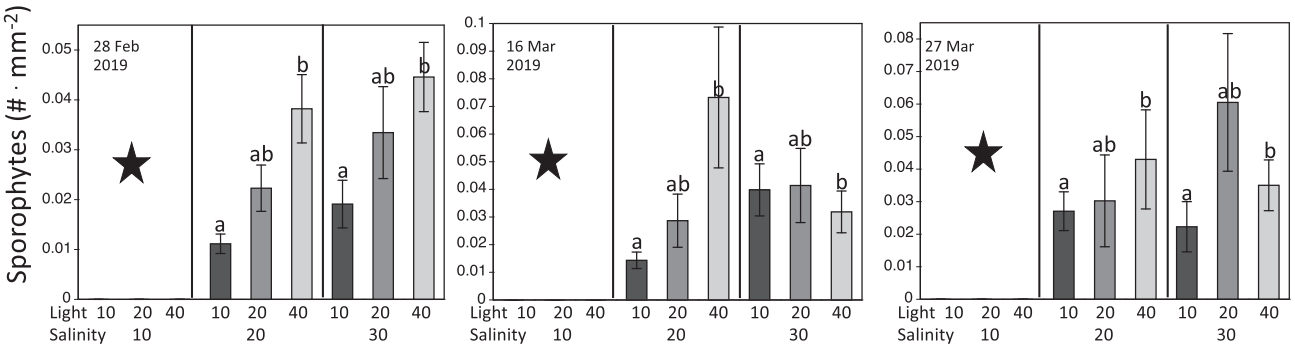

FIG. 4. Sporophyte densities (# · mm^{-2}; $x \pm$ SE, $n = 5$) from February 28, 2019, to March 27, 2019. Densities were significantly ($P = 0.007$; denoted by a and b) lower in the 10 vs. 40 µmol photons · $^{-2}$ · s^{-1}. Sporophytes were not detected in the low salinity treatment (10; denoted by a star), and densities were not significantly ($P = 0.65$) different between the 20 and 30 treatments.

(0.03–0.07 individuals · mm^{-2}) than the 10 µmol photons · m^{-2} · s^{-1} light treatment (0.01–0.25 individuals · mm^{-2}, Tukey LSD, $P = 0.007$; Fig. 4, Table S1). On average, sporophyte densities were greatest on February 28, 2018, in the salinity of 30 and 40 µmol photons · m^{-2} · s^{-1} light treatments (0.03–0.06 · mm^{-2}; Fig. 4, Table S1).

Salinity effects on microscopic stages. Zoospores and gametophytes: Initial zoospore densities did not significantly differ among treatments, which ensured that all treatments began with similar settlement conditions (salinity: 10, 1.02 ± 0.27; 20, 1.53 ± 2.79; 30, 1.60 ± 0.31 zoospores · mm^{-2}; one-way ANOVA $F_{2,21} = 0.265$, $P = 0.7691$). Dishes exposed to salinities of 10 and 20 at the zoospore stage did not ultimately produce sporophytes, while dishes in the 30-salinity treatment were able to complete the fertilization process and produce sporophytes (Table 1). Gametophytes exposed to the low salinity treatment (10) were unable to produce sporophytes, but gametophytes exposed to the higher salinity treatments (20 and 30) were successful in recruitment (Table 1).

Sporophyte production and survivorship: Survivorship of one-month-old sporophytes was compared among salinity treatments after a one-month exposure time.

TABLE 1. Overview of the presence and absence of microscopic sporophytes when salinity treatments (10, 20, and 30) were enacted at the zoospore or unicellular gametophyte stage ($n = 3$ for each salinity treatment).

Salinity treatment	Stage	Sporophyte
10	Zoospore	No
20	Zoospore	No
30	Zoospore	Yes
10	Gametophyte	No
20	Gametophyte	Yes
30	Gametophyte	Yes

No denotes treatments where sporophytes were not ultimately formed, and Yes represents treatments with successful sporophyte production.

The sporophytes in the 10-salinity treatment had initial densities of 15.75 (±3.42 SE) and after 1 month averaged 22 (±4.06 SE) sporophytes per dish. These changes represent a 62.5% increase in sporophytes, highlighting sporophyte survival and continued development in the low salinity treatment. Initial densities in the 20-salinity treatment were 17.75 (±2.62) and increased to 31.5 (±7.97) over 1 month, a 74.5% increase in sporophytes. Although not significant ($F_{1,10} = 1.69$, $P = 0.22$), the salinity of 30 did have the highest percent increase (130.68%), starting at 18 (±4.81) and almost doubling to 37 (±5.21) sporophytes per dish.

DISCUSSION

Tolerance of kelp microscopic life-history stages to environmental stressors often determines species population persistence and distribution (Peteiro and Sanchez 2012, Muth et al. 2019). Low light and temperature tolerances of early life stages are critical adaptations for polar seaweeds (reviewed in Wiencke et al. 2006), and nearshore Arctic species must tolerate extreme salinity variations as they are exposed to large freshwater inputs (Wiencke et al. 2006, McClelland et al. 2012). Results of this study highlight the low light acclimation but disparate salinity tolerances for macro- and microscopic stages of the kelp *Laminaria solidungula*. Our observations show that adult individuals are found throughout the Boulder Patch, despite low salinity (<10) levels at the inshore site (Fig. 5) during the late spring and summer, inferring that zoospore and gametophyte development likely occurred at higher salinities (>10).

Laminaria solidungula *microscopic stages—effects of light and salinity. Laminaria solidungula* adult populations were present at all sites surveyed (Inshore, Offshore-West, Offshore-East; Fig. 1) even when standardized to less available substrate (i.e., rock cover; see Fig. 1). Kelp densities decreased with proximity to the Sagavanirktok River (Inshore and Offshore-West; Fig. 1) where sites experience lower

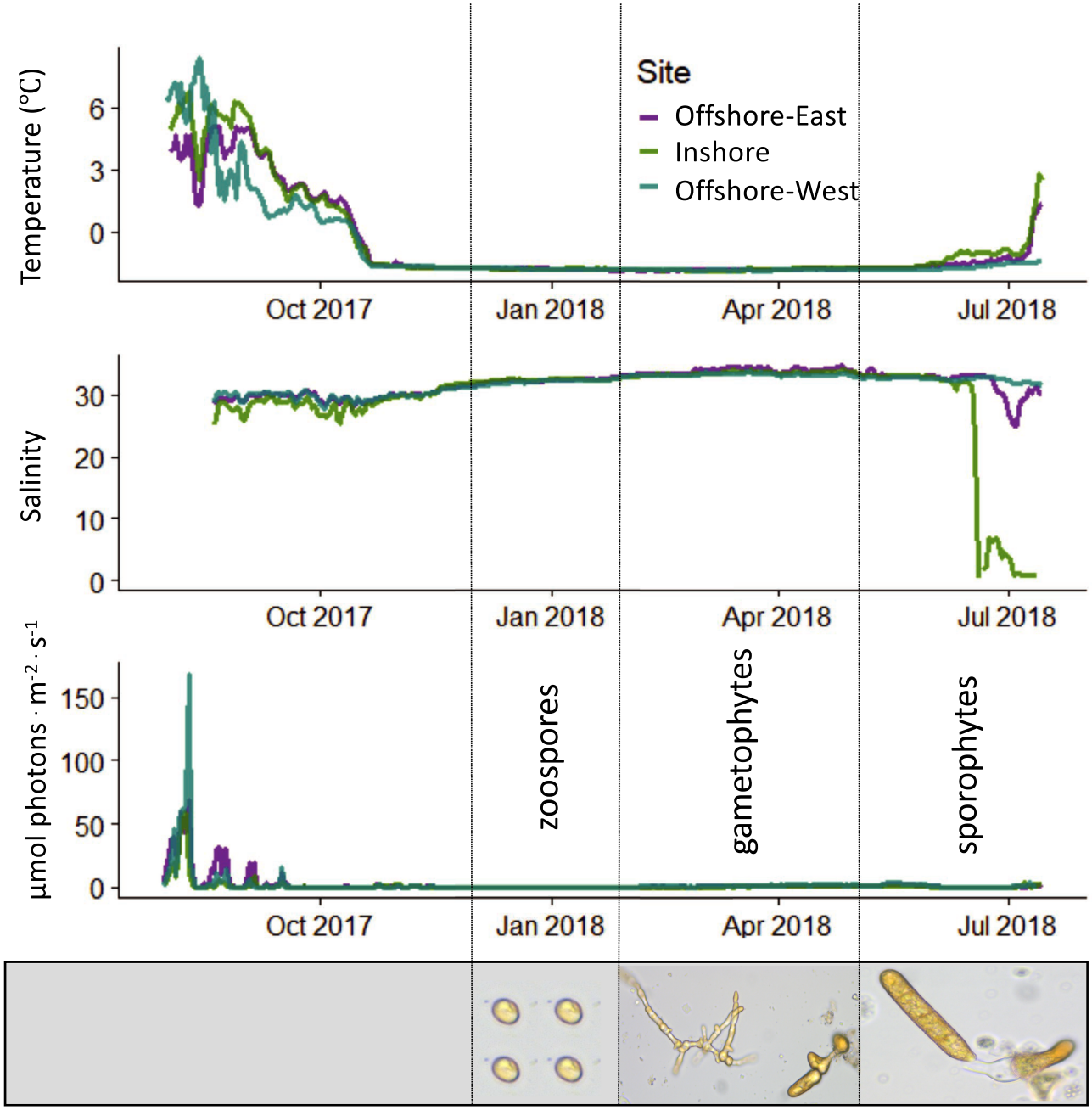

FIG. 5. August 2017–August 2018 temperature (top), salinity (center), and light (bottom) for the Offshore-East (DS-11, purple), Offshore-West (W-3, teal), and Inshore (E-1, green) sites (Dunton and Schonberg 2020). Timing of *Laminaria solidungula* microscopic stage development along the annual patterns of light and salinity highlights that zoospores and gametophytes are developing when ocean salinity levels are stable and sporophytes are present when salinity becomes more variable. In addition, light levels are very low during all microscopic stage development. Adult populations are exposed to low salinity levels when temperatures are increasing, ameliorating osmotic stress, and allowing rapid acclimation to the hyposaline conditions.

salinity and light levels during the spring freshet (Bonsell and Dunton 2018, Bonsell and Dunton 2021), yet *L. solidungula* individuals have persisted at these sites for decades (Dunton 1990). Similarly, adult populations of *L. solidungula* in Kongsfjorden, Svalbard, were tolerant to low salinities (5) as noted by Karsten (2007). However, as Diehl et al. (2020) showed in their culture experiments, lower-than-average salinity (25) and high temperatures (10 and 15°C) were additive physiological stressors on *L. solidungula* juvenile sporophytes, and highlight the importance of examining multiple stressors.

We utilized culture experiments to explore the additive and separate effects of light and salinity on *Laminaria solidungula* sporophyte production. *Laminaria solidungula* was cultured under replete nutrient regimes and settlement densities were very close to $1 \cdot mm^{-2}$ for both culture experiments, which is near the lower limit for successful kelp recruitment (Reed et al. 1996). Lower settlement values (0.78–1.44 zoospores $\cdot mm^{-2}$) within our experiments resulted in lower gametophyte and sporophyte abundances, but were sufficient for successful fertilization and formation of sporophytes. Initial zoospore densities did not affect results since settlement density did not differ among treatments from day one within the treatments. Notably, differences in light affected sporophyte production but did not prevent recruitment from occurring as demonstrated in the salinity treatments (Fig. 4). *Laminaria solidungula* sporophytes are incredibly shade tolerant (Dunton and Jodwalis 1988, Dunton 1990), and this trait is shared among all its life-history stages (tom Dieck 1993). Ecologically, low light levels should not prevent recruitment in the Boulder Patch since these stages develop under ice at extremely low light levels (<2 μmol photons $\cdot m^{-2} \cdot s^{-1}$; Dunton 1990) in their natural environment (Fig. 5). Our work sought to confirm whether low levels of irradiance combined with reduced salinity levels interactively affected microscopic stages.

Our experimental results demonstrated that low salinity (10), not light, was the main determinant factor that caused zoospore loss (or gametophyte germination failure; Fig. 3), which completely precluded sporophyte development (Fig. 4). Did lower sporophyte production respond to diminished gametophyte production or lower salinity? To address this question, we ran a second culture experiment to examine the effects of salinity alone on the life cycle stages. When exposed to the 10- and 20-salinity treatments, zoospores were ultimately unable to mature to produce sporophytes (Table 1). Unicellular gametophytes exposed to the 20- and 30-salinity treatments were able to complete the recruitment process, but as seen in the first experiment with light and salinity, zoospores and gametophytes exposed to the 10-salinity treatment did not yield sporophytes (Fig. 4, Table 1).

Interestingly, sporophyte survivorship was not affected by salinity. In fact, production of additional sporophytes from mature eggs was observed in each treatment. As gametophytes mature, they often become multicellular and each cell is able to produce an egg. In our study, gametophytes continued to grow vegetatively, additional eggs were fertilized, and this resulted in increased sporophyte densities over time, unlike the unicellular, newly formed gametophytes used in the experiment to assess salinity effects on microscopic stages (Gametophytes; Table 1). Sporophyte densities increased in all salinity treatments and were not significantly different among the three salinity regimes ($P = 0.22$). Similar survival patterns were seen in *Macrocystis pyrifera* (previously known as *integrifolia*) individuals in Chile; high salinity levels and low temperatures were required for microscopic stage development, but adults were able to persist in less than optimal conditions (Buschmann et al. 2004). Results from the salinity and light experiment showed trends of high light ameliorating hyposaline conditions in *Laminaria solidungula* sporophyte production. Gametophytes exposed to a salinity of 20 were able to consistently produce more sporophytes (Fig. 4) in the high light treatment (40 μmol photons $\cdot m^{-2} \cdot s^{-1}$). With warming temperatures and reduced sea ice, hyposaline conditions may be less detrimental to kelp gametophytes and sporophyte production if more light is present (Clark et al. 2013).

Since *Laminaria solidungula* individuals from Stefansson Sound were surveyed in situ, but specimens used in laboratory experiments were collected from multiple sites, there is potential for response plasticity attributed to natural genetic variability in populations and site-specific acclimation across the Boulder Patch. For example, zoospores used in the light and salinity culture experiment successfully produced gametophytes that survived in the 20-salinity treatment at all light levels (Fig. 4), but sporophyte development was not observed when zoospores were exposed to the salinity of 20 treatment in the salinity only culture experiment (Table 1). Results from both experiments, years and collection sites, show similar trends of low salinity (10) negatively affecting zoospores and gametophytes and inhibiting sporophyte production.

Scaling up—ecological consequences. Variable salinities within the Boulder Patch have been shown to affect other seaweed species, notably crustose coralline algae (CCA; Schoenrock et al. 2018, Muth et al. 2020). Results from the laboratory experiments presented in this study demonstrate resilience of microscopic sporophytes to low salinities and suggest that other factors, such as post recruitment survival, are affecting *Laminaria solidungula* distributions and limiting sporophyte recruitment. Long-term in situ monitoring studies within the Boulder Patch have revealed that CCA are absent at the Inshore site (Bonsell and Dunton 2021), the site closest to the Sagavanirktok River. Within the Boulder Patch, sites without CCA are characterized by higher red algal biomass (Bonsell and Dunton 2021), potentially affecting *L. solidungula* survival through competition for space. *Laminaria solidungula* were routinely seen attached to CCA (A. Muth, C. Bonsell, K. Dunton, pers. obs.), while CCA inhibited attachment of other algal and invertebrate species, creating available space on the substrate for kelp recruitment and survival. Kelp recruits at the Inshore site were often observed attached to red algal species, a much less stable substrate than CCA (Burek et al. 2018). These interactions could explain why *L. solidungula*

densities vary with salinity values throughout the Boulder Patch, despite tolerance of the sporophytes to wide ranges in salinity.

Arctic nearshore environments experience high annual variability in abiotic factors, but the seasonality in light, temperature, and salinity are relatively consistent annual phenomena (Dunton and Schonberg 2020). *Laminaria solidungula* zoospores and gametophytes within the Boulder Patch appear vulnerable to low salinity (10 and 20) levels, but these stages occur in the winter and spring months when salinity levels are relatively stable and high (~32; Fig. 5). However, large changes in the amplitude or timing of this seasonal variability could be detrimental to *L. solidungula* populations and other species acclimated to long-standing temporal patterns. For example, changes in the timing of break-up, delays in zoospore release, and an increase of freshwater input into the system could cause the overlapping of unfavorable environmental variables with microscopic stage development (i.e., sustained low salinity pulses when haploid microscopic stages are present).

We noted that *Laminaria solidungula* adults were present at the inshore site and showed resilience to low light and salinity levels. Kelp density was reduced at lower salinity sites, but it does not appear that salinity and/or light alone could cause these decreases, as microscopic sporophyte survival was not affected by low salinity levels. The loss of CCA at the inshore sites because of low salinity levels (Muth et al. 2020) may decrease kelp densities through the loss of positive turf/canopy interactions. Work to explore these interactions is ongoing and critical to understanding current *L. solidungula* distributions and how these populations and the species they sustain may be affected by climatic warming and large-scale ice retreat in the Arctic Ocean.

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AUTHOR CONTRIBUTIONS

A.F. Muth: Conceptualization (lead); Data curation (lead); Funding acquisition (supporting); Investigation (lead); Methodology (lead); Writing-original draft (lead). **C. Bonsell:** Conceptualization (supporting); Methodology (supporting); Writing-review & editing (supporting). **K.H. Dunton:** Conceptualization (supporting); Funding acquisition (lead); Methodology (supporting); Writing-review & editing-Equal.

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Supporting Information

Additional Supporting Information may be found in the online version of this article at the publisher's web site:

Table S1. Treatments (salinity: 10, 20, and 30 and light: 10, 20, and 40 µmol photons $\cdot$ m^{-2} $\cdot$ s^{-1}) and average densities for zoospores, gametophytes, and sporophytes for the *Combined Salinity and Light Culture Experiment.*

Appendix S1. Schematics of *Laminaria solidungula* culture experiments.