Elevated temperatures create bottlenecks in the life history of bull kelp (*Nereocystis luetkeana*, Phaeophyceae)

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A thesis

submitted in partial fulfillment of the

requirements for the degree of

Master of Marine Affairs

University of Washington

2025

Committee:

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Program Authorized to Offer Degree:

School of Marine and Environmental Affairs

University of Washington

Abstract

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The bull kelp *Nereocystis luetkeana* has declined in parts of the Salish Sea due to local and global change factors, including rising sea surface temperatures. As a foundation species, its loss has broad impacts on biodiversity and nearshore ecosystem function, underscoring the need to identify and address mechanisms of decline. Elevated temperatures affect all stages of the bull kelp life cycle, but it remains unclear whether some stages are more vulnerable than others. To assess stage-specific sensitivity, I examined the effects of four temperatures (10, 12, 15, and 18°C) on the development of gametophytes and young sporophytes cultured from field-collected sori over four weeks. The density of female gametophytes declined significantly at 15°C and 18°C, while the density of male gametophytes remained consistent across temperatures, leading to greatly reduced sex ratios over time. Gametophyte reproductive success was severely limited at 18°C, suggesting a thermal threshold for successful recruitment. Sporophyte production was reduced at 15°C and nearly absent at 18°C, driven by the reductions in the density of female gametophytes and impaired

reproductive success at elevated temperatures. These findings reveal critical bottlenecks in bull kelp maturation and recruitment, with serious implications for population persistence and ecosystem resilience in a warming ocean.

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Acknowledgements

I am deeply grateful to the mentors, peers, friends, and family who have supported and inspired me throughout my time in graduate school. This journey has been enriched by their generosity, encouragement, and belief in me.

I owe immense thanks to my advisor, Dr. Terrie Klinger, whose guidance and shared enthusiasm for phycology have shaped both my research and my growth as a writer and scientist. I'm grateful to Dr. Ryan Kelly for helping me develop confidence in data analysis, and for reminding me—through example—that science benefits from a healthy sense of humor. I also want to thank Dr. Tom Mumford and Dr. Megan Dethier for their mentorship and for modeling the kind of scientist I strive to become.

The School of Marine and Environmental Affairs, Friday Harbor Laboratories, Phycological Society of America, and Northwest Straits Foundation provided critical support—logistical, financial, and intellectual—that made this research possible and meaningful.

I'm especially thankful to Emily Bews for her dedication and support in both the field and the lab, and to Augustin Kalytiak-Davis and Kaitlyn Tonra for pushing me to grow as an ecologist, thanks to their tenacity and disarming questions.

Above all, I am profoundly grateful to my wife, Fruzsina Nagy. Her support, patience, and sense of adventure have been a constant source of strength throughout this process and beyond.

Introduction

Globally, the marine environment is experiencing rapid and unprecedented transformations due to anthropogenic climate change. Rising global sea surface temperatures and more frequent marine heatwaves are exposing marine organisms to conditions beyond their historical thermal limits (Cooley et al. 2022). These climatic stressors fundamentally disrupt marine ecosystems by impacting foundation species, whose decline can trigger cascading effects throughout the communities they support (Wernberg et al. 2024).

Kelps, large brown macroalgae in the order Laminariales, form subtidal forests along approximately 25% of the world's temperate and subpolar coastlines (Smale 2020). As foundation species, kelps provide biogenic habitat for diverse marine organisms and contribute significantly to primary productivity (Wernberg et al. 2024, Teagle et al. 2017, Duarte et al. 2022). While kelp forests are highly dynamic and capable of recovering from disturbances, the accelerating pace of environmental change raises concerns that their capacity for adaptation may be insufficient to maintain their ecological functions. Over the past 50 years, more than one-third of the world's kelp forests have experienced significant declines in abundance, and although responses vary at regional and local scales (Krumhansl et al. 2016), many losses are associated with ocean warming (Filbee-Dexter & Wernberg 2018, Smale 2020, Berry et al. 2021, Starko et al. 2022, Starko et al. 2024). As seawater temperatures continue to rise, understanding the effects of ocean warming on kelp forest ecosystems is essential for their conservation and management.

Kelps have a biphasic life history that alternates between a macroscopic diploid sporophyte phase and a microscopic haploid gametophyte phase. The responses of kelps to environmental conditions can differ across species and life history stages (e.g., Harley et al. 2012, Lind & Konar 2017, Muth et al. 2019, Fales et al. 2023), suggesting that certain stages may disproportionately

influence population dynamics. The majority of research on environmental stressors in kelps has focused on adult sporophytes, resulting in a significant gap in our understanding of how these factors influence earlier life stages, including zoospores, gametophytes, and juvenile sporophytes (Hollarsmith et al. 2022, Weigel et al. 2023).

Bull kelp, *Nereocystis luetkeana*, is the primary canopy-forming kelp in the fjord-like estuarine system of the Salish Sea. During an annual life cycle, bull kelp sporophytes become reproductive in the late spring and summer, when adult sporophytes release microscopic zoospores that settle on the seafloor and develop into male and female gametophytes (Maxell & Miller 1996). Sexual reproduction occurs when sperm released by male gametophytes fertilizes female oogonia, leading to the formation of juvenile sporophytes. Temperature is a key regulator of kelp reproduction, directly influencing its onset and success (Lüning 1980, Bartsch et al. 2008, González et al. 2018). Bull kelp gametophytes can germinate and survive within a temperature range of 5 to 21°C (Vadas 1972, Lind & Konar 2017, Weigel et al. 2023). Juvenile sporophyte production occurs only at temperatures below 20°C (Vadas 1972), though recruitment success has been shown to decline greatly at 18°C (Muth et al. 2019, Weigel et al. 2023). Because successful recruitment will determine the distribution and abundance of sporophytes, environmental stressors that affect early life stages will influence population persistence and community structure (Lind & Konar 2017).

Bull kelp populations have declined throughout the Salish Sea, often in association with water quality changes such as elevated sea surface temperatures. Particularly severe losses have occurred in the southern Salish Sea, where warm water is entrained within shallow basins with limited tidal flushing (Berry et al., 2021). Similar declines have been observed in British Columbia (Starko et al. 2024), while populations with greater exposure to tidal flow and wave action have persisted

over the same period (Pfister et al. 2018, Starko et al. 2024). Elevated temperatures have been linked to tissue degradation and mortality in adult sporophytes (Fales et al. 2023, Berry et al. 2021) and declines in the densities of attached spores, gametophytes, and sporophytes in laboratory cultures (Lind & Konar 2017, Weigel et al. 2023). Moreover, Veenhof et al. (2022) hypothesize that gametophyte growth and performance are influenced by the temperature conditions experienced during spore production, a process which may coincide with summer sea surface temperature extremes. Concerns about how bull kelp will respond to rising temperatures are especially pressing given that mean sea surface temperatures in the Salish Sea are expected to increase by 1.5 to 3°C by the end of the century (Khangaonkar et al. 2019, Amos et al. 2015). Rapid changes in thermal conditions will have ecosystem-level consequences (Smale 2020), and therefore, resolving how elevated temperatures affect species that are foundational to nearshore ecosystems remains a priority.

This study focuses on the microscopic life stages of bull kelp, from spore germination through gametogenesis, fertilization, and sporophyte production. Understanding the temperature sensitivity of microscopic stages is critical for predicting kelp recruitment success under future climate scenarios. This research investigates (1) whether female and male gametophytes respond differently to elevated temperatures, (2) whether temperature influences sporophyte production, and (3) whether temperature alters the reproductive success of female gametophytes. By examining these fundamental aspects of bull kelp reproduction, this study aims to improve our understanding of the potential impacts of rising ocean temperatures on kelp population dynamics and resilience.

Methods

Kelp gametophyte culturing conditions

Mature bull kelp sori were collected from two sites with persistent kelp beds in the San Juan Channel, WA, in early June 2024: Turn Rock on San Juan Island (48.534876, -122.964101) and the south end of Point George on Shaw Island (48.555938, -122.984821). Sori were gathered from blades held at the surface during low slack tide. At each site, sori from multiple individuals were collected and transported to a 10°C cold room at Friday Harbor Laboratories in seawater-filled containers.

In the laboratory, each sorus was gently scrubbed with a paper towel and rinsed with 1.0 µm filtered, autoclaved (sterile) seawater to remove visible epiphytes. The sori were then surface-sterilized in a dilute solution of Povidone iodine for 30 seconds, rinsed with sterile seawater, and lightly wrapped in paper towels dampened with sterile seawater. To synchronize spore release, the sori were kept in the dark at 10°C for two to four hours (Deiman et al. 2012).

Six ripe sori from each site were rinsed with sterile seawater to remove any prematurely released spores before being placed into glass beakers containing 800 mL of sterile seawater. Sori remained separated by site during the process of spore release. Both solutions became cloudy with swimming zoospores. After one hour, the spent sori were removed, and a sample of each spore solution was examined under a light microscope to confirm the presence of numerous motile zoospores. Zoospore concentrations were quantified using a hemocytometer and diluted to approximately 500 spores mL^{-1} to optimize juvenile sporophyte production (Weigel et al. 2023). At this stage, zoospores from the two sites were combined in an attempt to increase genetic diversity before distributing the zoospores into the treatments.

Experimental temperatures of 10, 12, 15, and 18°C were chosen to span the range from present-day average conditions to the upper thermal limit for bull kelp in the Salish Sea. Four five-gallon aquaria were filled with freshwater and equipped with titanium heaters, heat controllers, temperature-light loggers, and air pumps to maintain stable water temperatures. The dilute zoospore solution was dispensed into 12 six-well plates, with each well containing 12 mL of medium. Gametophyte culture plates were sealed with Parafilm™ to prevent salinity changes due to evaporation or intrusion of fresh water from the water bath. The sealed plates were randomly assigned to a treatment (18 replicate wells per treatment) and placed on stands within the aquaria and partially submerged in the heated water. Samples were left undisturbed in the dark for 36 hours to allow for zoospore settlement and attachment. After settlement, gametophyte cultures were maintained for four weeks under cool white (5000 K) LED lights at an irradiance of 40-65 μmol · m^{-2} · s^{-1} photosynthetically active radiation (PAR), following a 16:8 h light:dark cycle. The culture medium was replaced with sterile seawater enriched with F/2 nutrients after two weeks to maintain sufficient nutrients.

Measurement of response variables

To evaluate the effects of elevated temperature on the microscopic stages of bull kelp, I quantified the density of female and male gametophytes, gametophyte sex ratio, female reproductive success, and sporophyte density. These variables were measured across three optical fields per replicate well using a Nikon Eclipse TE2000-U inverted microscope equipped with either a QImaging MicroPublisher 5.0 (10× magnification = 0.27 mm^2 optical field, week two) or an Infinity8 (10× magnification = 0.55 mm^2 optical field, weeks three to four) microscope camera. Optical fields within wells were selected haphazardly, but if a clear image could not be obtained, the stage

position was adjusted until gametophytes were clearly distinguishable. Images were captured non-destructively at weekly intervals for four weeks (days 7, 14, 21, and 28). A total of 54 photographs were captured per treatment at each time point (18 replicate wells × 3 images per well).

Photographs were analyzed using ImageJ (https://imagej.net/ij/index.html). A microscope calibration slide was used to accurately determine the optical field area (mm^2) for each magnification setting. The counter tool was used to annotate images based on predefined criteria. To ensure accuracy and reproducibility in image annotation, one plate from each treatment was used for observer training (18 images per treatment, 72 images total), and all observations were made by a single individual. Images were re-evaluated 24 hours after annotation to assess agreement with initial counts. Training was considered successful if annotations exceeded 95% agreement, after which final data collection commenced. To minimize bias, the order of image annotation was randomized by treatment and well plate. All images from a given time point were analyzed within one week before proceeding to the next round of calibration and data collection.

Statistical analysis

Data from the three optical fields per replicate were combined, and the density (mm^{-2}) was computed based on the combined area of the fields. Response variables included the densities of female and male gametophytes, gametophyte sex ratio, sporophyte production, and the proportion of sporophyte-bearing female (SBF) gametophytes. The densities of female and male gametophytes were calculated as the number of individuals per mm^2 at each observation point. The gametophyte sex ratio was estimated as the density of female gametophytes versus the density of male gametophytes at each observation point. Sporophyte production was measured as the number of embryonic sporophytes observed at weeks three and four. The proportion of SBF

gametophytes at week four was calculated as the density of SBF gametophytes divided by the density of total female gametophytes.

To assess the effects of temperature on each response variable, I first tested for normality of the data using the Shapiro-Wilk test. For variables that met the assumption of normality, I used one-way analysis of variance (ANOVA) followed by Tukey's Honest Significant Difference (HSD) test to identify pairwise differences between temperature treatments. When the assumption of normality was violated, I applied a Kruskal-Wallis rank sum test, followed by post-hoc pairwise Wilcoxon rank sum tests with p-values adjusted using the Benjamini-Hochberg method. In cases where the data were more appropriately modeled using continuous predictors, I used linear models to evaluate the effects of temperature. For one hypothesis involving paired measurements over time, I used paired t-tests to evaluate whether the change over time was statistically distinguishable from zero. All analyses were conducted in R version 4.4.2.

Results

Effects of temperature on female versus male gametophytes

The mean density of gametophytes varied according to sex (female, male), temperature treatment (10, 12, 15, and 18°C), and development time (two to four weeks). Densities of both female and male gametophytes declined sharply between two and three weeks of development, while changes in density between weeks three and four were variable (**Figure 1**). The density of female gametophytes was highly temperature dependent. Female densities were consistently higher at cooler temperatures (10-12°C) compared to warmer temperatures (15-18°C) throughout the observation period. After four weeks, the density of female gametophytes at 10-12°C was approximately 1.71±0.15 times greater than at 15-18°C, indicating a significant difference by

treatment ($\chi^2(3) = 43.19$, $p < 0.001$). The density of male gametophytes did not depend upon temperature. There was no significant difference in male densities by treatment at the initial ($F_{3,68} = 0.09$, $p = 0.96$) and final ($F_{3,68} = 0.52$, $p = 0.67$) observation points. Males were less dense than females across all temperatures at the initial sampling point and in cooler temperatures throughout the study. However, male densities surpassed female densities by the end of the observation period at 15°C and 18°C.

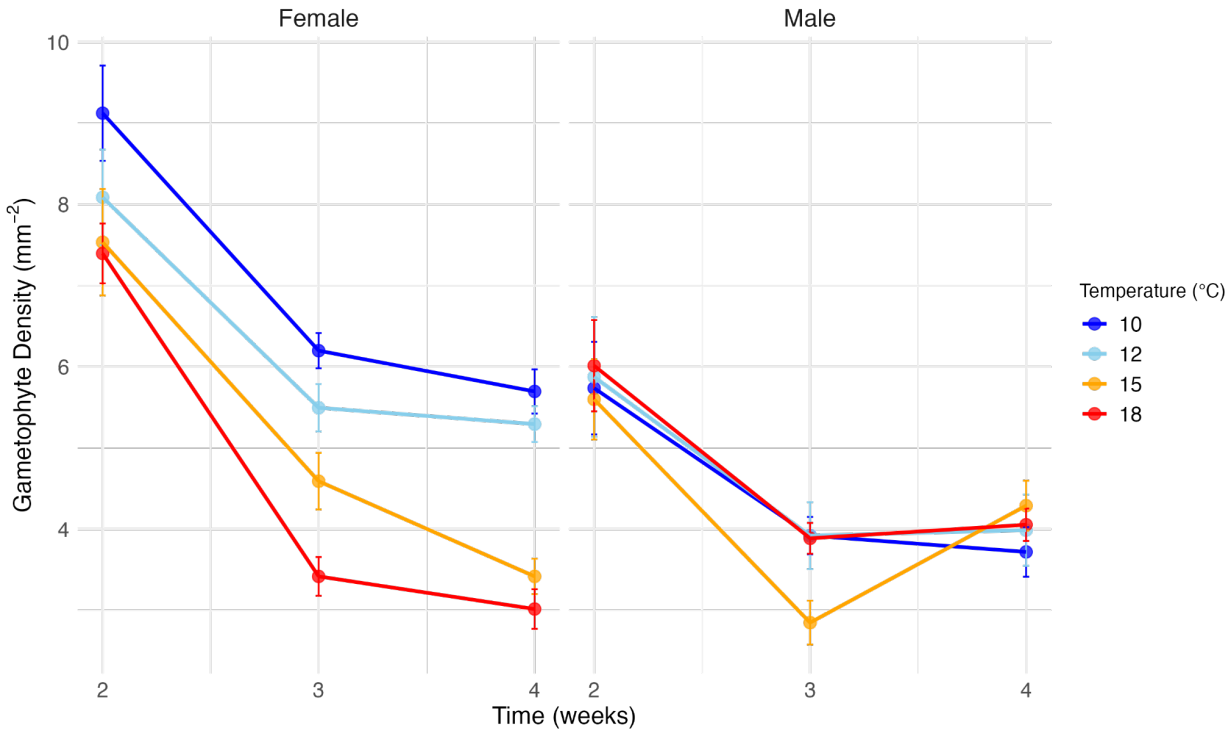

Figure 1. Mean (±SE) densities of female (left) and male (right) gametophytes (gametophytes per mm^2) across temperatures after two, three, and four weeks of development.

The disproportionate effect of elevated temperatures on the density of female gametophytes led to shifts in the relative proportion of female and male gametophytes over time. The gametophyte sex ratio (density of female gametophytes versus density of male gametophytes) over time was consistently female-dominated at cooler temperatures and variable at warmer temperatures (**Figure 2**). The proportion of female gametophytes declined with increasing

temperature and duration of development. At two weeks, the sex ratio was female-dominated across all treatments, and temperature had no significant effect ($F_{3,68} = 0.58$, $p = 0.63$). By three weeks, temperature significantly influenced the sex ratio, with the 18°C treatment exhibiting a significantly lower female-to-male ratio than the other treatments ($F_{3,68} = 5.20$, $p < 0.01$). By four weeks, this effect intensified, as both the 15°C and 18°C treatments shifted toward greater male dominance ($F_{3,68} = 7.88$, $p < 0.001$).

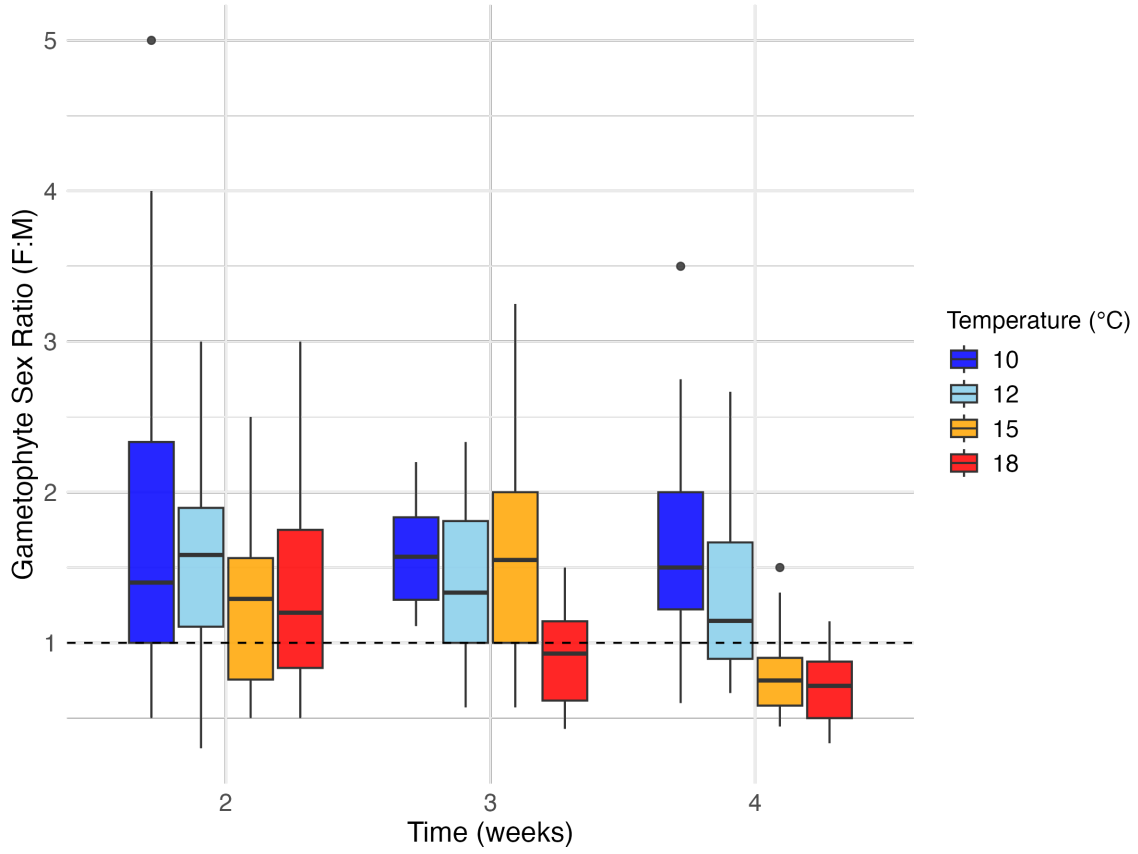

Figure 2. The gametophyte sex ratio (density of female gametophytes versus density of male gametophytes) at two, three, and four weeks of development under experimental temperature conditions. The horizontal dashed line at 1.0 represents an equal ratio of females to males. Values above the line indicate female-biased ratios and values below the line indicate male-biased ratios. Outliers were removed for the purpose of plotting.

Effects of temperature on sporophyte production

Sporophyte production was influenced by temperature, time, and the density of female gametophytes. At three weeks of development, sporophyte density was similar across the 10-15°C treatments ($F_{2,51} = 0.32$, $p = 0.73$; **Figure 3**), although cultures at 15°C showed greater variability, with eight replicates containing no sporophytes. No sporophytes were observed in the 18°C treatment. By week four, sporophyte density was negatively associated with temperature ($F_{3,68} = 14.96$, $p < 0.001$). Fewer sporophytes developed at 18°C compared to cooler treatments. While sporophyte density increased significantly between weeks three and four in the 10°C treatment ($t(17) = -2.87$, $p = 0.01$), there was no significant difference in the 12-18°C treatments.

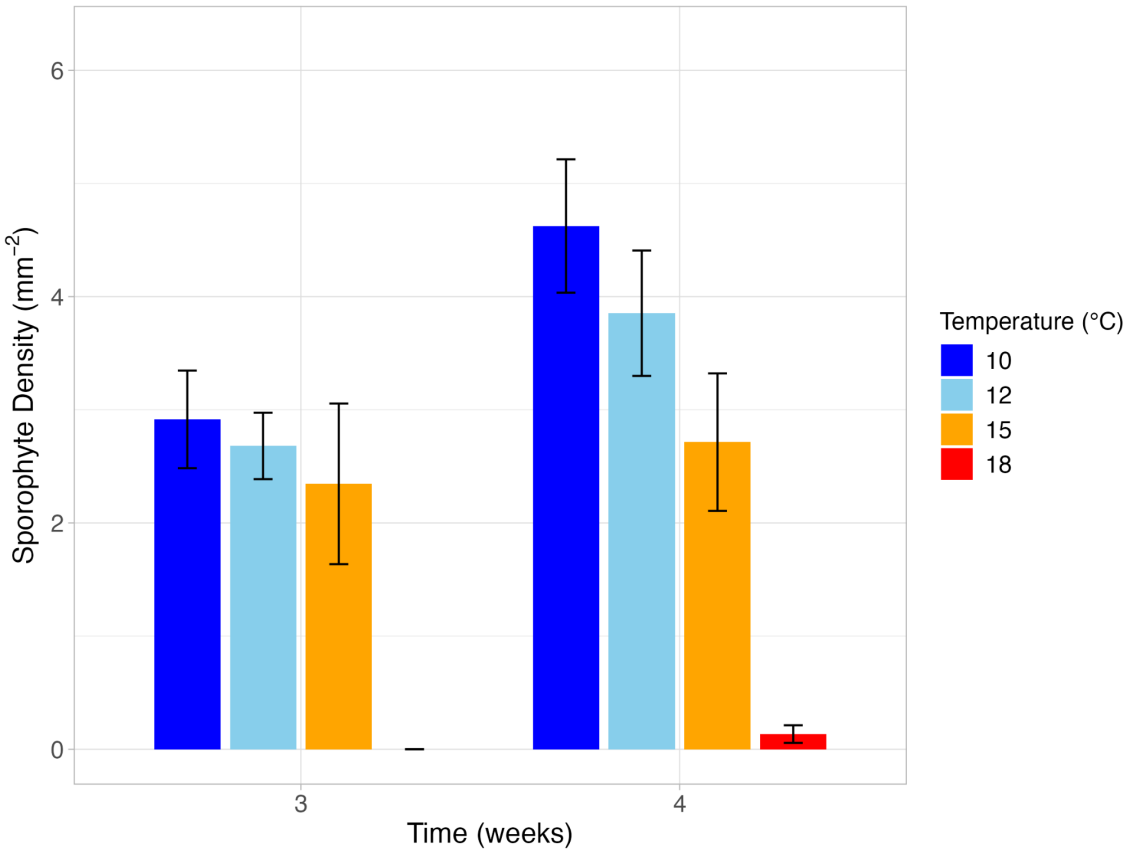

Figure 3. Mean (±SE) sporophyte density (sporophytes per mm^2) across temperatures after three and four weeks of development.

After four weeks of development, sporophyte density was positively associated with female gametophyte density ($F_{1,70} = 22.58$, $p < 0.001$). As expected, sporophyte density was strongly positively associated with the density of SBF gametophytes ($F_{1,70} = 439.3$, $p < 0.001$), which was itself negatively correlated with temperature ($F_{3,68} = 18.66$, $p < 0.001$). Sporophyte density was not associated with the density of male gametophytes ($F_{1,70} = 0.757$, $p = 0.387$), suggesting that the mating system is not sperm-limited.

Effects of temperature on gametophyte reproductive success

The responses of bull kelp to temperature were observed as the microscopic haploid stages matured, underwent sexual reproduction, and produced diploid offspring. Cultures were systematically inoculated with similar densities of zoospores at the start of the experiment. After four weeks of development, the proportion of female gametophytes was significantly higher in the 10-12°C treatments than in the 15-18°C treatments ($F_{3,68} = 13.03$, $p < 0.001$; see **Figure 2**). Of those females that survived to four weeks, the proportion of SBF gametophytes was not significantly different in the 10-15°C treatments ($F_{2,51} = 0.14$, $p = 0.87$; **Figure 4**). However, the proportion of SBF gametophytes was significantly lower at 18°C where little sporophyte production was observed ($F_{3,68} = 12.12$, $p < 0.001$). Despite the influence of temperature on both the density and proportion of female gametophytes and the proportion of SBF gametophytes, temperature did not influence sporophyte production per SBF gametophyte ($F_{3,45} = 0.93$, $p = 0.44$). On average, SBF gametophytes bore between one and two sporophytes, and some individuals were observed to produce as many as five sporophytes in culture.

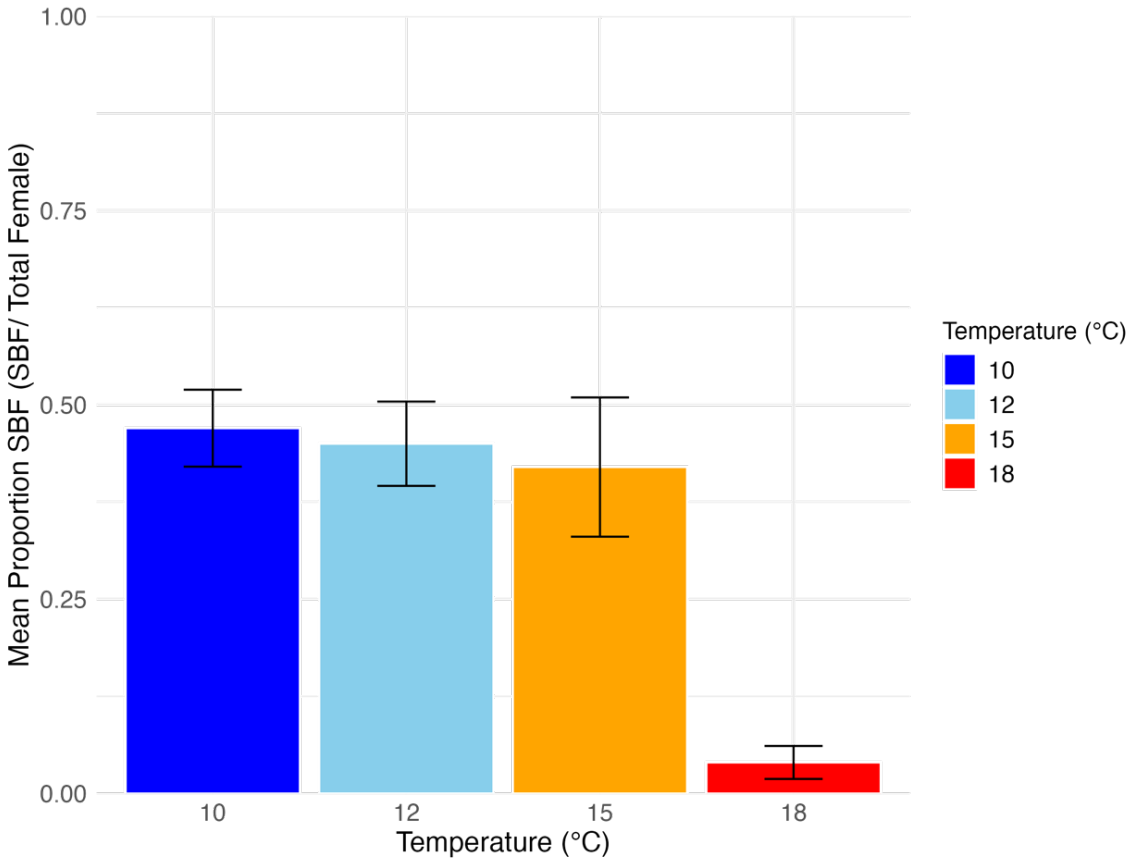

Figure 4. Mean (±SE) proportion of SBF gametophytes (SBF/ Total Female) across temperature treatments after four weeks of development.

Discussion

Bottlenecks in the microscopic stages of bull kelp could limit population growth in the species at elevated temperatures. Differences in the density and proportion of female gametophytes across temperature treatments represent a significant bottleneck that affects the absolute and relative availability of mature female gametophytes to be fertilized. I identified a thermal sensitivity threshold in the survival of female gametophytes between 12 and 15°C. This is noteworthy because sea surface temperatures in this range are already observed in some areas of the Salish Sea during periods when bull kelp is recruiting (Weigel et al. 2023), and water temperatures may regularly occupy this range over the coming decades due to ocean warming and marine heatwave events

(Khangaonkar et al. 2019, Frölicher et al. 2018). Despite differences in the proportion of female gametophytes across treatments, I observed similar proportions of SBF gametophytes from 10-15°C, suggesting that temperature influences sporophyte production across this range by affecting female gametophyte development and survival but not the processes of fertilization or sporophyte production. Consistent with previous studies, sporophyte production was minimal at 18°C, with only a few female gametophytes producing sporophytes (Muth et al. 2019, Weigel et al. 2023). The paucity of SBF gametophytes at 18°C indicates an additional bottleneck that contributes to the lack of recruitment success observed at this temperature. Given that less than five percent of female gametophytes bore sporophytes at 18°C, there is evidence that fertilization success or embryonic development are inhibited at this temperature, although gametophytes persist vegetatively. Notably, sporophyte production by SBF gametophytes was consistent across temperature treatments despite variation in the densities and proportions of female and SBF gametophytes. This indicates that observed differences in density of sporophytes across the range tested are likely not due to direct effects of temperature on sporophyte mortality and are instead the consequence of bottlenecks in female survival and reproductive success.

Consistent with previous research, I documented a negative association between temperature and total gametophyte density (Weigel et al. 2023). However, this study provides new insight by demonstrating that declines in gametophyte density with temperature were driven specifically by the detrimental effects of elevated temperature on female gametophytes. The differing responses of female and male gametophytes resulted in temperature-dependent shifts in the effective gametophyte sex ratio. Although the development of gametophytes into females or males is genetically determined, sex ratios can be influenced by environmental factors such as post-germination mortality of one sex (Oppliger et al. 2011). The sex ratio of a population is a key

factor influencing population dynamics because it directly affects recruitment success. Skewed sex ratios in warming oceans could reduce reproductive success in kelps because the abundance and fertility of females determine overall sporophyte production (Veenhof et al. 2022). Studies on other kelp species have reported mixed results regarding sex-specific thermal responses. For example, sex-dependent temperature effects on the relative abundance of female and male gametophytes were observed in *Macrocystis pyrifera*, *Saccharina latissima*, and *Lessonia variegata* (Rodriguez et al. 2019, Lee & Brinkhuis 1988, Nelson 2005), but not in *Lessonia trabeculata* (González et al. 2018). In the present study, the ratio of female versus male bull kelp gametophytes depended on temperature. At cooler temperatures (10-12°C) and during early development, the sex ratio remained consistently female-biased, suggesting that lower temperatures favor female survival or development. As maturation progressed, higher temperatures (15-18°C) led to increasingly male-biased sex ratios due to the disproportionate decline in female gametophyte density. Male bias is common in dioecious land plants and is expected to intensify under warming conditions, as males are generally more stress tolerant than females (Munné-Bosch 2015). For sexually reproducing species like bull kelp, biased sex ratios reduce the effective population size below the census population size by limiting successful reproduction. The observations made here indicate a demographic shift in the absolute and relative abundance of mature females in the population, which constrains the number of individuals contributing genes to the next generation. Such responses could have cascading effects on population viability and ecosystem function.

Refining our understanding of the life stages and mechanisms by which elevated temperatures affect bull kelp can help guide effective management and restoration strategies. This study adds to the growing body of research on how the microscopic stages of bull kelp respond to environmental stressors. Insights into recruitment dynamics under changing conditions are critical because they

influence population trajectories and potential resilience to ocean warming. Sex ratios, for instance, have been used to inform conservation and management actions in a variety of marine species, including sea turtles, polar bears, and giant kelp (Santidrián Tomillo et al. 2015; Vongraven et al. 2022; Roleda et al. 2012). Similarly, traits such as thermal tolerance have been targeted to enhance resilience and support assisted migration efforts in corals (Van Oppen et al. 2015). In this study, limited but successful sporophyte production was observed at 18°C, suggesting the possibility of selection for individuals with greater tolerance to elevated temperatures. Such individuals represent a subset of the population capable of successful fertilization and sporophyte development under warming conditions, potentially contributing to future adaptive capacity. Moreover, recent evidence of genetically distinct bull kelp populations within the Salish Sea (Gierke et al. 2023) highlights the importance of incorporating genetic diversity into conservation and restoration planning.

This research reveals critical bottlenecks in the bull kelp life cycle and highlights the vulnerability of bull kelp to warming ocean temperatures. These findings emphasize the need for proactive strategies to support bull kelp persistence in the Salish Sea. Restoration efforts may benefit from focusing on cooler, more thermally stable refugia where recruitment success is least likely to be disrupted. Additionally, strategies such as the selective outplanting of heat-tolerant gametophytes and reduction of localized stressors (e.g., nutrient pollution and sedimentation) could enhance resilience against warming conditions. Understanding the temperature thresholds that constrain early life stages is also critical for refining predictive models and conservation plans. As climate change continues to alter nearshore ecosystems, integrating temperature-dependent recruitment dynamics into management frameworks will be essential for sustaining kelp populations and the biodiversity they support.

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