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The Impacts of Climate Change on the Reproduction of Native and Invasive Kelps

By

ANGELA KORABIK
DISSERTATION

Submitted in partial satisfaction of the requirements for the degree of

DOCTOR OF PHILOSOPHY

in

ECOLOGY

in the

OFFICE OF GRADUATE STUDIES

of the

UNIVERSITY OF CALIFORNIA

DAVIS

Approved:

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Committee in Charge

2023

DISSERTATION ABSTRACT

Climate change represents a threat to coastal marine ecosystems through variable effects on community structure and function due to increasing mean sea-surface temperatures (SST), marine heatwaves, variation in salinity, and ocean acidification. Among the most at risk species are California kelps, which have already experienced significant die-offs over the past several years as a result of elevated SST and urchin grazing. However, the effects of these stresses on the very sensitive microscopic kelp life stage (gametophyte) are much less understood. Gametophytes are generally less resilient to changes in abiotic conditions, so global environmental change could result in drastic changes in kelp forest community structure and composition via impacts on this life stage**.** My dissertation research used manipulative laboratory experiments to investigate the interacting role of abiotic stressors on kelp reproduction and community compositions, specifically, the growth and survival of early kelp life stages.

My first chapter focused on the effects of climate-driven temperature increases and ocean acidification on bull kelp (*Nereocystis luetkeana*) gametophytes from Point Arena, CA (Korabik et al. 2023). From 2014 to 2016, the largest marine heatwave in history appeared off the coast of California resulting in large kelp die off events. In this chapter, I asked how increased temperature and lowered pH impact the survival of bull kelp gametophytes and the production of juvenile bull kelp sporophytes. My results showed that increased temperature resulted in a significant decrease in the survival of gametophytes and a lower number of juveniles produced, whereas lowered pH only had a significant effect on the production of juveniles, slowing their rate of development. These results indicate that the predicted increase of marine heatwaves could have devastating effects on the persistence of bull kelp forest ecosystems.

My second chapter considered the interacting effects of climate driven changes in temperature and salinity and interactions with the invasive seaweed (*Sargassum muticum*) on the growth and survival of giant kelp (*Macrocystis pyrifera*) gametophytes from Tomales Bay, CA. In my experiments, I tested: 1) how different salinities and temperatures impact giant kelp early life stages from different sources within Tomales Bay, 2) how the presence of invasive *Sargassum* propagules affect giant kelp gametophyte development, and 3) how the combined effects of salinity, temperature, and *Sargassum* presence affect giant kelp early life stages. My results indicate that 1) the presence of *Sargassum* had little effect on the survival of giant kelp gametophytes, 2) *Sargassum* accelerated development of giant kelp juvenile sporophytes, and 3) high temperatures resulted in the greatest reduction of giant kelp gametophyte survival. These results imply that giant kelp reproduction and presence within estuaries is more influenced by temperature than salinity and microscopic-stage competition with invasive species.

My third chapter examined the effects of increased temperature and lowered salinities on invasive Wakame (*Undaria pinnatifida*) gametophytes in the San Francisco Bay. Previous studies have shown that low salinity can limit the distribution of *Undaria*, but there is no information about these effects on gametophyte stages. Using a full factorial design, I exposed *Undaria* gametophytes to five salinity conditions ranging from low to ambient salinity and two temperatures representing pre-2013 temperature maxima in San Francisco and maximum increased temperatures experienced under the 2014-2016 marine heatwave. I found that *Undaria* microstages were unable to survive below 20 psu and generally survived better under warmer temperatures of 18°C. Climate change in California is predicted to result in higher temperatures and reduced annual rainfall in drought years, which may facilitate future northward expansion of Wakame populations.

With this research, I can better predict the impacts of climate change on kelp ecosystems to help coastal managers prioritize future protection efforts. Early life stages are often the most vulnerable to stress, and in this era of rapid climate change, understanding early life stage responses to stress will allow scientists and managers to better work towards the protection of our planet.

ACKNOWLEDGEMENTS

Doing research takes a village, and dissertation research is no different. This dissertation would not have been possible without the help of many people at the Bodega Marine Lab, but there are a few I owe special thanks to. Without ARG, I never would have gotten my experiments running. Thank you to Carol Vines, who was an amazing guide to microscopy methods, and Jackie Sones, who is always generous with her knowledge of natural history and willingness to loan me supplies. Thank you also to the Boating and Diving Safety teams, especially Jason Herum and Dave Dann. You have been so instrumental in getting me out into the water, and you have also been so patient and willing to answer any questions I've had as I planned field ops. Last but not least, thank you to my two wonderful undergraduate research assistants, Suellen Dias and Genece Grisby, who are amazingly kind, curious, and hardworking, and are responsible for so much data collection that made this dissertation.

I want to extend a full-hearted thank you to my committee members, Jay Stachowicz and Matt Edwards. Jay, you have been so great at asking me the hard questions, like "Why would an ecologist studying birds in the Amazon care about kelp?", which frankly, I still don't know how to answer. But in all seriousness your feedback and questions have been so instrumental in helping me think deeper and more critically about my science and have really helped me strengthen my arguments. Matt, you have been such an amazing resource in kelp ecology and experimental design, and even before you were on my committee, were always so willing to meet and help me work through any experiment issues I was having.

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costumes, and downright silliness, and my best memories of grad school will 100% be of you all. Even though I only actually lived in Davis for two years, y'all have made it so easy to fit back in every time I return, and I hope we can stay in touch no matter where we all end up in the world.

While leaving Davis meant leaving my cohort, I have been so blessed to have developed new communities at not, one but THREE other UC campuses. To the 2020-2021 BML crew, y'all got me through the pandemic, my quals, a presidential election and so much other crazy shit. Even though I haven't been at the lab lately, y'all will always hold a special place in my heart, and I will forever miss our socially distant Casino/movie nights. To my Merced crew, y'all have been such an amazingly warm community and so incredibly welcoming. From going on strike together to struggling to write at Coffee Bandits together, your support and camaraderie has been unwavering. And last, while I've only lived in the Bay area for the past year and a half, I want to extend a special thanks to my friend Tyus and my roommate Kwasi for welcoming me and Jon into the UC Berkeley community. I also have to thank Kwasi because we've been on the same trajectory to graduate and get new jobs since I've moved in, and it's been lovely having someone going through the exact same stuff to check in with and complain to at home.

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CHAPTER 1:

EXAMINING THE REPRODUCTIVE SUCCESS OF BULL KELP (*NEREOCYSTIS LUETKEANA*, PHAEOPHYCEAE, LAMINARIALES) IN CLIMATE CHANGE CONDITIONS

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Abstract:

Climate change is affecting marine ecosystems in many ways including rising temperatures and ocean acidification. From 2014-2016, an extensive marine heat wave extended along the west coast of North America and had devastating effects on numerous species during this period, including bull kelp (*Nereocystis luetkeana*). Bull kelp is an important foundation species in coastal ecosystems that can be affected by marine heat waves and ocean acidification; however, these impacts have not been investigated on sensitive early life stages. To determine the effects of changing temperatures and carbonate levels on Northern California's bull kelp populations, we collected sporophylls from mature bull kelp individuals in Point Arena, CA. At the Bodega Marine Laboratory, we released spores from field-collected bull kelp, and cultured microscopic gametophytes in a common garden experiment with a fully factorial design crossing modern conditions (11.63 ± 0.54°C and pH 7.93 ± 0.26) with observed extreme climate conditions (15.56 ± 0.83°C and 7.64 ± 0.32 pH). Our results found that both increased temperature and decreased pH influenced growth and egg production of bull kelp microscopic stages. Increased temperature resulted in decreased gametophyte survival and offspring production. In contrast, decreased pH had less of an effect, but resulted in increased gametophyte survival and offspring production. Additionally, increased temperature significantly impacted reproductive timing by causing female gametophytes to produce offspring earlier than under ambient temperature conditions. Our findings inform better predictions of the impacts of climate change on coastal ecosystems and provide key insight into environmental dynamics regulating the bull kelp lifecycle.

Introduction:

Globally, marine systems are under pervasive threats from climate change. Chief among these threats are marine heat waves and ocean acidification (OA) (Cooley et al., 2022). Changing temperature and OA have negative impacts on the critical structure-forming foundational species of the world's oceans, namely kelps and corals, especially in terms of reduced reproduction (Smith et al., 2022; Straub et al., 2019) and juvenile mortality (Harvey et al., 2013; Kroeker et al., 2013; Przeslawksi et al., 2014). In the ocean, early life stages are already subject to high mortality rates due to a number of environmental bottlenecks, and increased temperature and decreased pH can further increase juvenile mortality through reduced recruitment and growth of the microscopic-stages of canopy-forming kelps (Gaitan-Espitia et al., 2014; Hollarsmith et al., 2020; Lind & Konar, 2017; Shukla & Edwards, 2017), reduced calcification and increased disease in juvenile invertebrates (Ban et al., 2013; Kroeker et al., 2013; Miner et al., 2018; Small et al., 2016), and altered larval fish behavior (Ferrari, 2011; Munday, 2010).

Kelp forests are critical to temperate, nearshore subtidal, and intertidal marine systems worldwide, and they sustain numerous economically important recreational and commercial fisheries (Bennett et al., 2016; Blamey & Bolton, 2018; Carr & Reed, 2016). In addition, kelp forests provide numerous ecosystem functions and services such as shelter of structural habitat and food sources to surrounding ecosystems, buffering coastlines from wave energy, ameliorating the effects of ocean acidification, reduction of current speeds and larval delivery to the shore, and modification of seawater chemistry (Carrano et al., 2020; Carrano et al., 2021; Hamilton et al., 2022; Malone et al., 2022).

Globally, the effects of marine heat waves are already having extreme effects on kelp forests (Arafeh-Dalmau et al., 2019; Camus et al., 2021, Filbee-Dexter et al., 2020; Straub et al.,

2019). From 2014-2017, Northern California lost 90% of its bull kelp (*Nereocystis luetkeana*) canopy cover over an area of roughly 350 km (Rogers-Bennett & Catton, 2019). This loss of kelp forest cover has been attributed to a dramatic increase in purple urchin (*Strongylocentrotus purpuratus*) density due to loss of keystone predators, coupled with a pervasive system of marine heat waves (McPhearson et al., 2021). The results of such widespread canopy loss were drastic changes in community structure and composition (Beas-Luna et al., 2020) and the collapse of the several fisheries in the area, such as that of the red sea urchin (*Mesocentrotus franciscanus*) (Rogers-Bennett & Okamoto, 2020) and the closure of the world's largest recreational abalone fishery (*Haliotis rufescens*) (Reid et al., 2016; Rogers-Bennett & Catton, 2019).

Numerous studies in recent years have documented the effects of increased temperature on bull kelp canopies (Berry et al., 2021; Hamilton et al., 2020; Rogers-Bennett & Catton, 2019), and these studies have found that decreases in adult bull kelp canopy abundance have been related to local and large-scale processes associated with warm water (Pfister et al., 2017; Schiel et al., 2004). Bull kelp exposure to warm temperatures also reduces adult blade morphological plasticity to changes in hydrodynamic flow regimes (Suprataya et al., 2020), but the physiological impacts of warm waters on bull kelp need to be further studied. Studies of bull kelp microscopic developmental stages in British Columbia and Alaska have found that increased temperatures have resulted in reductions in settlement and reduced germination and growth (Lind & Konar, 2017; Muth et al., 2019; Schiltroth, 2021), but the impact of rising temperatures on microscopic bull kelp stages in the southern portion of their range in northern California remains unclear. California bull kelp populations represent the range extreme of bull kelp, existing in low-latitude areas that are the most exposed to El Niño-Southern Oscillation (ENSO) warm water events compared to more northern populations. As a result, California bull

kelp populations could either be more warm-water adapted than the higher latitude populations previously studied, or they could be existing much closer to the thermal maxima and therefore be very vulnerable. As the bulk of kelp die-offs during the 2014 to 2016 marine heat wave occurred near the lower-latitude portion of kelp species' ranges (Arafeh-Dalmau et al., 2019; Beas-Luna et al., 2020; Cavanaugh et al., 2019; Finger et al., 2021; Rogers-Bennett & Catton, 2019), it is necessary to further study how future marine heat waves may affect the ability of these foundation species to remain in their lower latitude ranges.

In addition to the increasing threat of marine heat waves, coastal temperate ecosystems are also subject to stress from ocean acidification (OA), which, on average, has already caused a global lowering of surface water pH by 0.11 pH units (Feely et al., 2004; Feely et al., 2009; Gattuso et al., 2015a). Variability of pH levels in nearshore systems is normal to a degree as seasonal oceanographic shifts like upwelling bring deep offshore waters to the surface and expose nearshore ecosystems to reduced pH levels. This exposure varies with local bathymetry and coastal topography, which often changes the intensity of upwelling events along the coast (Feely et al., 2008). While pH variation in the California Current System generally stays between 7.720 and 8.413 pH units (Feely et al., 2018), climate change projections predict an increasing frequency and duration of low-pH extremes (Bakun et al., 2015; García-Reyes et al., 2015), which may result in an average decrease of up to 0.4 pH units (Feely et al., 2008). Low pH may impact physiological functions among a variety of organisms. Studies have shown that OA will more disproportionately impact organisms that form calcium carbonate skeletons (Kroeker et al., 2013), but we must also understand how the compounding stress of these combined threats will impact our critical temperate nearshore systems.

Kelps are very efficient at processing multiple carbon species in the water column and require CO_2 for photosynthesis. Kelps are able to uptake CO_2 from the water column either via diffusive entry, or through carbon concentrating mechanisms (CCMs) that allow them to convert the more abundant form of dissolved inorganic carbon, HCO_3^-, into the less abundant CO_2 (Maberly, 1990; Raven, 2003). There is some evidence to suggest that the excess of carbon predicted for future ocean conditions may increase kelp growth in climate change conditions (Brown et al., 2014, reviewed in Veenhof et al., 2021). For example, increased pCO_2 has been shown to have beneficial impacts on mature bull kelp net apparent productivity (Thom, 1996) and growth (Swanson & Fox, 2007). At the microscopic stage, however, the effects of *p*CO2 and pH on kelp can be variable (Edwards, 2022), ranging from having negative effects (Gaitán-Espitia et al., 2014), to no effect (Fernández et al., 2015; Hollarsmith et al., 2020), to positive effects on growth and photosynthesis (Shukla & Edwards, 2017).

Understanding how different life stages respond to environmental stress is critical when trying to predict population resilience to disturbance events. Laminariales, or the large canopy-forming kelps, have a multistage process of development that presents numerous areas for the imposition of bottlenecks from climate stress. However, to our knowledge, no studies have yet investigated the role that pH may play in embryonic sporophyte (sporeling) bull kelp development, nor the combined threats of increased temperature and ocean acidification on any bull kelp life stage.

In this study, we ask how increased temperatures and decreasing pH will affect bull kelp 1) gametophyte development, 2) egg and sporeling production, and 3) sporeling growth. Based on the observed negative effects of the 2014-17 marine heat wave on bull kelp adult sporophytes, we hypothesized that increased temperature will generally result in decreased growth, survival,

and reproduction. In contrast, we hypothesized that decreased pH will have less of an effect than temperature on growth and egg production, but will generally result in increased growth, survival, and reproduction.

Materials and Methods:

Bull Kelp Life Cycle:

In California, one of the dominant canopy-forming kelp species is bull kelp (*Nereocystis luetkeana*). The range of bull kelp extends from the eastern Aleutian Islands, Alaska, in the north to Point Conception, California, in the south. Within its California range, it is considered to be the dominant canopy-forming kelp species in Northern California, between San Francisco and the California-Oregon border. Bull kelp experience sea surface temperatures that annually average between 12 and 15 °C at the southernmost edge of its distribution in Point Conception and between 9 and 12 °C near Point Arena in Northern California (National Data Buoy Center [NDBC], 2023a; NDBC, 2023b). Bull kelp is an annual species and is thought to be a more opportunistic, resilient colonizer, especially in areas with too much wave stress for the persistence of giant kelp (*Macrocystis pyrifera*) (Foster & Schiel, 1985; Graham, 1997; Graham et al., 2007).

Bull kelp have a heteromorphic life cycle consisting of a large diploid sporophyte and a microscopic haploid gametophyte. Adult sporophytes develop patches of sori on their blades at the ocean surface, and at maturity, begin to release spores. The released zoospores then settle on hard substrate at the benthos, where they grow into microscopic male and female gametophytes. The female gametophytes begin to produce eggs, and then release the lamoxirene pheromone to

trigger sperm release from nearby males (Lüning & Müller, 1978). Once the sperm fertilizes the egg, a new sporophyte begins to develop (Reed, 1990).

Collection:

Blades with sori from approximately 10 individuals were collected at the surface by boat from a single kelp bed in Point Arena, California (38.916271°N, 123.725644°W) in October 2017. Sori were cleaned in iodine and fresh water, layered in a cooler with wet paper towels separating individual sori, and transported to the Bodega Marine Laboratory (BML, 38.318164°N, 123.072019°W) for sporulation. Spore densities were determined using a hemocytometer (model number CTL-HEMM-GLDR, LW Scientific, Lawrenceville, U.S.A.), and were introduced into the experimental Petri dishes to facilitate a settlement density of approximately 8 spores/mm^2.

Ex situ culturing experiment:

We conducted a fully factorial common garden experiment that consisted of four treatments representing ambient and high temperature and ambient and low pH, with ten replicates per treatment, for a total of forty experimental Petri dishes (Fisher Brand 100 mm × 15 mm). Temperature was maintained at 15.6 ± 0.8°C and 11.6 ± 0.5°C using walk-in incubators at Bodega Marine Laboratory (BML), and pH was maintained at 7.93 ± 0.26 pH and 7.64 ± 0.32 pH using chemical additions of equal parts 1M HCl and 1M NaHCO3 ($NaHCO3 + HCl \rightarrow NaCl + H2CO3$) (Riebesell et al., 2011). Petri dishes were randomly arranged on shelves within the incubators. Temperatures were chosen to represent ambient sea surface temperatures for our ambient temperature treatment, whereas our high temperature treatment represented the 4°C

increase in SST observed during the 2014-17 marine heat wave (Gentemann et al., 2017). Ambient and low pH were chosen to represent the pH of incoming seawater at BML and pH during an extreme upwelling event (Feely et al., 2008), respectively. Light was set at 14:10 photoperiod and 30-45 umol m^{-2} s^{-1} to mimic summer conditions when the potential for exposure to higher temperatures and lower pH through upwelling is greatest. The pH of incoming, manipulated, and outgoing seawater was measured to 0.01 pH units immediately after collection using a spectrophotometer. Total alkalinity (T_{alk}, μmol kg^{-1}) was measured using potentiometric acid titration. We changed the water in all experimental dishes every 2 to 3 days for the duration of the 27-day experiment in order to maintain low pH conditions and prevent anoxia or nutrient limitation. We added standard 20 mL L^{-1} Provasoli nutrient mix to all treatment water to prevent nutrient limitation during growth (Provasoli, 1968).

Photo Analysis:

Beginning one week after spore inoculation, Petri dishes were photographed weekly with a Micropublisher 5.0 RTV digital camera (QImaging, Surrey, Canada) mounted on an inverted microscope at 40× magnification, resulting in four weeks of photos documenting gametophyte and sporeling growth and reproduction. Within each dish, three points were randomly selected to be photographed, with different points being photographed each week. Each photo encompassed 1.08 mm^2 of the Petri dish (7,853 mm^2 bottom surface area).

After the growth experiment was completed, each photo was analyzed using ImageJ (Rasband, 2019). Week 1 and 2 photos did not contain any gametophytes large enough to identify by sex, so only Weeks 3 and 4 were used for analysis. Count data was obtained from each photo for female gametophytes, male gametophytes, eggs, and sporeling (Figure 1.1). Every

female counted was also categorized as “productive” (having produced at least one egg or sporeling) or “non-productive” (having no eggs or sporelings). The proportion of productive females in each photo was calculated by dividing the number of productive females by the total number of females counted.

Count data were also used to calculate three additional variables: average number of eggs per female, average number of sporelings per female, and average number of offspring per female ((# eggs + # sporelings)/# females). We used these three ratios to distinguish whether differences in numbers of eggs and juveniles were simply a result of differences in parent gametophyte numbers, or whether they were a result of reduced production by females. These three ratios were also used to approximate which stages of reproduction were taking place at Weeks 3 and 4. Sporeling sizes were also obtained by using the freehand trace tool in ImageJ and measuring the number of pixels encapsulated. Sizes were then converted to μm^2 using a conversion factor of 71330 pixels per 62,500μm^2, which was calculated by measuring the area of a photo of a 0.0625 mm^2 hemocytometer cell at 40× magnification.

Statistical Analysis:

All count outcome variables were analyzed using linear mixed models with temperature, pH, and their interaction as fixed effects and Dish ID as a random effect. In order to meet the parametric assumptions of normality of residuals and homogeneity of variances, all count data was subjected to a square-root transformation as needed before being analyzed. We tested the significance of our fixed effects by conducting log-likelihood tests via model comparison using the ANOVA function, where one model included the effect of interest while the other model excluded it.

We analyzed the proportion of productive female gametophytes using a generalized linear mixed model (GLMM) with a beta distribution. Size data were also analyzed with a GLMM using a gamma distribution. GLMMs included temperature, pH, and their interactions as fixed effects, and Petri dish ID as a random effect. Average number of gametophytes per photo in a given dish was also calculated and included in the size model as a covariate to account for possible density dependence. We also separately analyzed the relationship between average size of sporelings per photo and the covariate (average number of gametophytes per photo) using a linear regression model that included only the covariate as a fixed effect.

All count and size data were only analyzed for Week 4 of our experiment, but calculated ratios of eggs per female (eggs/fem), sporelings per female (sporelings/fem), and offspring per female (offspring/fem) were analyzed for both Weeks 3 and 4 in order to draw conclusions about differences in rates of fertilization or maturation. Specifically, we used the ratio of offspring/fem to ask whether females, regardless of treatment, showed equal fecundity, and the ratios of eggs/fem and sporelings/fem were calculated to inform us about which stage reproduction was within each treatment. We tested the significance of our fixed effects via model comparison using the ANOVA function, where one model included the effect of interest while the other model excluded it. Hypothesis testing was conducted via log-likelihood tests for count and offspring ratio LMMs and Chi-squared tests for size GLMMs. All analyses were performed using R version 4.1.2 (R Core Team, 2021) and the packages *nlme* (Pinheiro et al., 2022), *lme4* (Bates et al., 2015), and *glmmTMB* (Brooks et al., 2017).

Results:

Female and Male Gametophyte Development:

High temperature decreased the density of females present after four weeks (Log-Likelihood = 51.1283, DF = 36, $p < 0.0001$) (Figure 1.2, Table 1.1). Neither pH nor the interaction between pH and temperature had a significant effect on female gametophyte numbers (Table A1). Female gametophyte numbers in Week 4 did vary among dishes (Log-Likelihood = 7.8795, $p = 0.005$).

Male density also decreased at high temperatures (Log-Likelihood = 45.393, DF = 36 , $p < 0.0001$), but unlike females, male density increased under lower pH conditions (Log-Likelihood = 8.6378, DF = 36 , $p = 0.0033$). Neither the pH:temperature interaction term nor the variation among dishes had any significant effect on male gametophyte numbers (Table A2). In summary, these results indicate that temperature caused a significant decrease in female and male gametophyte numbers, whereas low pH only caused a significant increase in male gametophyte numbers.

Egg and Sporeling Counts:

After four weeks, high temperatures decreased the numbers of both eggs (Table A3, Log-Likelihood = 33.73, DF = 36, $p < 0.0001$) and sporelings (Table A4, Log-Likelihood = 36.6391, DF = 36, $p < 0.0001$) (Figure 1.3). Low pH increased numbers of eggs (Log-Likelihood = 4.3958, DF = 36, $p = 0.036$), but there were no significant effects on sporeling counts (Log-Likelihood = 1.0702, DF = 36, $p = 0.3009$). The interaction term for pH:temperature was insignificant for counts of both eggs and sporelings. Sporeling counts did not vary among dishes (Log-Likelihood = 3.0544, $p = 0.0805$), but eggs did vary among dishes (Log-Likelihood = 5.2080, $p = 0.0225$). Overall, temperature caused the greatest decreases in both egg and sporeling numbers, whereas low pH caused a significant increase in eggs only.

Proportion of Productive Females:

The proportion of productive females (percent of females producing eggs or sporelings) was uniformly high across all treatments, but the high temperature treatments consistently resulted in nearly 100% of females reaching productivity by Week 4 (Figure 1.4, Table A5). We found that the proportion of productive females was not affected by the interaction between temperature and pH (Chi-Sq = 0. 5117, p = 0.4744) nor the individual effect of pH (Chi-Sq = 1.1619, p = 0.2811). Increased temperature increased in the proportion of productive females (Chi-Sq = 28.187, p < 0.0001).

Ratios of Offspring per Female:

For mean number of eggs per female (egg/fem), we found a marginally significant effect of the interaction between temperature and pH in Week 3 (Log-Likelihood = 3.7737, DF = 36, p = 0.0521) but not Week 4 (Log-Likelihood=0.0976, DF = 36, p = 0.7547) (Table 1.2, Figure 1.5). Investigating temperature and pH individually in Week 3, we found that low pH (Log-Likelihood = 3.7345, DF = 36, p = 0.0533) resulted in a marginally significant decrease in the egg/fem ratio under ambient temperature treatments, but an increased egg/fem ratio under high temperature treatments (Table S6). We did not detect an effect of temperature in Week 3 (Log-Likelihood = 0.1406, DF = 36, p = 0.7077). In Week 4, low pH was found to be significantly associated with a higher egg/fem (Log-Likelihood = 9.3663, DF = 36, p = 0.0022), whereas low temperature resulted in lower egg/fem (Log-Likelihood = 13.114, DF = 36, p = 0.0003). The variation among dishes was insignificant in both Week 3 (Log-Likelihood = 0.2318, p = 0.6302) and Week 4 (Log-Likelihood = 0.5643, p = 0.4525).

High temperatures increased the sporelings per female ratio (sporelings/fem) in both Week 3 (Log-Likelihood = 45.2639, DF = 36, $p < 0.0001$) and Week 4 (Log-Likelihood = 9.1867, DF = 36, $p = 0.0024$). Low pH decreased the sporeling/fem ratio in Week 3 (Log-Likelihood = 16.7485, DF = 36, $p < 0.0001$) but not in Week 4 (Log-Likelihood = 0.1262, DF = 36, $p = 0.7225$). Neither the interaction term pH:temperature nor the variation among Dishes influenced sporelings per female in either week (Table A7).

Ratios of total offspring per female (offspring/fem) increased with high temperatures in Week 3 (Log-Likelihood = 30.4186, DF = 36, $p < 0.0001$) but not Week 4 (Log-Likelihood = 0.2279, DF = 36, $p = 0.6331$), whereas low pH increased offspring/fem in Week 4 (Log-Likelihood = 5.2345, DF = 36, $p = 0.0221$) but not Week 3 (Log-Likelihood = 1.3622, DF = 36, $p = 0.2432$). Neither the interaction between temperature and pH nor the variation among Dishes influenced offspring per female in either week (Table A8).

Across all responses, high temperature had the greatest impacts in Week 3, resulting in lower ratios of sporelings/fem and offspring/fem, whereas low pH was most significant in Week 4, resulting in high eggs/fem and offspring/fem.

Growth of Sporeling Bull Kelp:

When analyzing the global trend across all treatments, we found that sporeling size was significantly influenced by the average number of gametophytes within each dish in Week 4 ($R^2 = 0.639$, $p < 0.0001$), indicating possible density dependence where increased number of gametophytes resulted in significantly smaller sporelings (Table 1.2, Figure 1.6). When included in the GLMM, the 3-way interaction between pH, temperature, and the average number of

gametophytes within each dish was significant (Chi-Sq = 6.3387, p = 0.0118), but all 2-way interactions were insignificant (Table A9).

In order to examine the role of each fixed factor (pH, temperature, and the covariate: average number of gametophytes within each dish) in the 3-way interaction, we subset our model within the two pH and two temperature levels to elucidate the significance of the covariate and the other non-subset factor. When low pH and ambient pH treatments were separately analyzed, the average number of gametophytes within each dish was never independently significant, but high temperatures resulted in a significant increase in size by itself under low pH conditions (Chi-Sq = 10.051, p = 0.0015) and the temperature by covariate interaction was significant under ambient pH conditions (Chi-Sq = 5.3001, p = 0.02132). When the two temperature treatments were analyzed separately, the covariate was again never significant by itself, but low pH resulted in a significant decrease in sporeling sizes under ambient temperature conditions (Chi-Sq = 3.955, p = 0.04673), and the pH by covariate interaction had a significant effect on size under high temperature conditions (Chi-Sq = 6.0391, p = 0.01399) (Figure 1.6). In summary, sporeling sizes were most significantly increased under high temperatures, but both low pH and the number of gametophytes present reduced this effect.

Discussion:

Our results demonstrated that both temperature and pH do significantly impact bull kelp reproduction and development, but the effects were more varying and nuanced than we predicted. Our most consistent finding was that high temperatures decreased the number of gametophytes that survived and/or developed and the total numbers of eggs and sporelings produced. The number of male gametophytes, female gametophytes, eggs, and sporelings were

always lower in high temperature treatments than ambient temperature treatments, regardless of pH. These results align with previous findings that bull kelp exposed to increased temperature conditions had reduced spore germination rates and reduced gametophyte growth (Lind & Konar, 2017; Muth et al., 2019; Schiltroth, 2021). Increased temperatures also result in decreased gametophyte growth and survival and sporophyte recruitment in numerous other kelp species including giant kelp (*Macrocystis pyrifera)* (Camus et al., 2021, Hollarsmith et al., 2020), stalked kelp (*Pterygophora californica*) (Howard, 2014), spiny kelp (*Ecklonia radiata*) (Alsuwaiyan, 2021), paddleweed (*Ecklonia cava*) (Oh et al., 2015), sugar kelp (*Saccharina latissima*), skinny kelp (*Saccharina angutissima*) (Augyte et al., 2019), dragon kelp (*Eualaria fistulosa*) (Lind & Konar, 2017), and other taxa (reviewed in Edwards, 2022). High temperatures can also modulate the ratios of female to male kelp gametophytes, where more equatorward populations may see lower frequencies of males under high temperatures (Leal et al., 2017a; Oppliger et al., 2011). While we did not analyze sex ratios in this study, we did generally see more females than males across treatments for this relatively low latitude population of bull kelp, which may affect fertilization rates of eggs produced.

Low pH had no significant effect on the number of female gametophytes or sporelings in our study, but there was a significant increase in male gametophytes and eggs. Other studies have found varying impacts of pH on kelp gametophyte growth and survival (reviewed in Veenhof et al. 2021 and Edwards, 2022). Several studies have found overall positive effects of low pH on *M. pyrifera* gametophyte growth, survival, and size (Roleda et al., 2012; Leal et al., 2017a), whereas other studies found that elevated *p*CO2 had little effect on rates of growth and photosynthesis (Fernández et al., 2015) or reproduction (Hollarsmith et al., 2020), or even negative effects (Gaitán-Espitia et al., 2014). The variation in kelp organismal responses across

studies, species, and location indicates that while in general ocean acidification does not seem to be a particular factor of concern for kelp, there is much more to be understood about the impacts of ocean acidification on kelp reproduction.

One hypothesized mechanism that may explain our results is that bull kelp female gametophytes become reproductive sooner under high temperature conditions. While the overall number of gametophytes and sporelings declined under high temperature conditions, the female gametophytes that survived were more productive on average, and produced more sporelings earlier than female gametophytes under ambient temperature conditions. We also saw that our results align with this proposed mechanism via slower reproduction and development under ambient temperature conditions. In Week 3, high temperature treatments had higher ratios of both eggs/fem and sporelings/fem than ambient temperature treatments. By Week 4, however, the eggs/fem ratio in ambient temperature treatments exceeded that of high temperature treatments, and the sporelings/fem ratio was similar regardless of temperature treatment. The later increases in egg/fem and sporelings/fem ratios in ambient temperatures and lack of difference in the offspring/fem ratios across treatments in Week 4 seem to indicate that female gametophytes have equal individual reproductive capacity under both our temperature treatments, but females growing under high temperature treatments were progressing through reproduction earlier.

The accelerated timeline of bull kelp microstage development could be due to rate limitation of metabolic processes under lower temperatures. The Q10 coefficient for seaweed metabolic processes, the factor by which a reaction increases for every 10°C rise in temperature, varies by seaweed species, but generally results in a doubling of the rate of active uptake and general cell metabolism, and thus the uptake of carbon for photosynthesis and nitrate and other

nutrients for other processes (Davison, 1991; Hurd et al., 2014; Raven & Geider, 1988). Due to limited amounts of diffusible CO_2 in ocean water, canopy-forming macroalgae generally rely on carbon concentrating mechanisms (CCMs) that utilize and alter enzymatic functions to supply CO_2 to the cell (Hepburn et al., 2011; Raven, 2003). The faster growth rates of kelp microstages at high temperatures may thus be an effect of altered CCMs that change chemical transformations, enzymatic and lipid functions and properties, rates of membrane transport, and thus carbon availability (Davison, 1991; Raven & Geider, 1988). Previous studies have also shown that in other seaweeds, increased temperatures have sped up reproductive timing. In a study examining the effects of temperature on time to egg production in several California kelp species, egg release of bull kelp as well as *M. pyrifera* and *P. californica* occurred much earlier under our high temperature (16°C) than our ambient temperature (12°C) (Howard, 2014). Additionally, the results of Leal et al. (2017b), while not focused on the size and growth of sporelings after fertilization, did find that high temperatures did result in increased gametophyte growth rates leading up to fertilization in *M. pyrifera* and wakame (*Undaria pinnatifida*). While increased rates of development have been seen among many seaweed species, research on the physiology and metabolic processes of bull kelp microstages is lacking and would benefit from further study.

Recent advances in kelp reproduction studies have given needed attention to delayed development of microscopic stages and the resulting "bank of microscopic forms" (Carney & Edwards, 2006; Hoffman & Santelices, 1991; Schoenrock et al., 2021), but less focus has been placed on the factors that may accelerate microscopic kelp development. In terrestrial plants, increased temperatures have been found to result in an acceleration of pollen tube growth and stigma and ovule development, which correspond to an overall reduction of the length of time

females are receptive to pollination (Hedhly et al., 2009). Reviews of other marine organisms, specifically benthic invertebrates, have shown that increased sea surface temperatures may increase the rate and timing of development and spawning (Przeslawski et al., 2008). In order to better understand the ability of populations to recover from extreme climate disturbance events, more research is needed to better understand the effect of climate stressors on survival, time to development, and propagule production.

Our results interestingly reflect natural seasonal fluctuations in northern California's coastal waters (García-Reyes & Largier, 2012). The upwelling season (April to June) is characterized by the upwelling of cold, dense, nutrient rich water that is also more acidic. During relaxation season (July to October), coastal waters become warmer, less acidic, and exhibit less primary productivity and chlorophyll-a (García-Reyes & Largier, 2012). The majority of visible bull kelp juveniles appear in upwelling season and most adults become reproductive by the end of July during the relaxation season, but these two events of visible recruitment and spore release have been observed to occur in all seasons, albeit at much lower rates (Maxell & Miller, 1996; Dobkowski et al., 2019). Consequently, gametophytes and sporelings that develop in the spring will likely be most exposed to low temperatures and low pH, but the vast majority of gametophytes and sporelings that develop in the fall will be exposed to high temperatures. As such, it is conceivable that high temperatures in September and October would affect the first month of sporeling and juvenile development, whereas low pH in the spring would likely be more important for late stage microscopic sporelings and small, visible juveniles.

In contrast, low pH conditions seemed to impact reproductive efforts differently based on temperature conditions. The lowest proportion of productive females was observed in low pH treatments under ambient temperatures (Figure 1.4), and these females seemed to produce more

offspring per female, later in the experiment. Other studies, however, have seen an increase in pre-fertilization gametophyte sizes under low pH conditions for *M. pyrifera* and *U. pinnatifida* (Leal et al., 2017a; 2017b). We did see an increase in post-fertilization bull kelp sporeling size under low pH conditions, but only when temperatures were also increased. The late increase in production of eggs and smaller sporeling sizes under ambient temperatures may potentially signal that a delay in reproduction occurs under low pH and ambient temperature conditions. While the specific mechanisms responsible for lower growth under low pH/increased CO_2 conditions are not well understood, we suggest further study into this area would be an interesting new direction for further research.

Our results potentially contrast with those of Dobkowski et al. (2019) in that we found that low pH (most often seen in the Spring upwelling season) resulted in slower reproduction and growth whereas high temperature (most often seen in late summer and fall) accelerated it. In their study, Dobkowski et al. (2019) witnessed the quickest recruitment of visible bull kelp juveniles (indicating faster microscopic development times) in the spring (upwelling season), and slowest recruitment (implying slower microscopic development times) in the late summer and fall (relaxation season). A potential explanation for the different observed reproductive rates is that Dobkowski et al. (2019) conducted their experiments in the field, where they were exposed to a full array of abiotic conditions, whereas our experiments were conducted in a laboratory setting where only temperature and pH were manipulated, and all other variables were held constant, including nutrients. Previous studies have shown that delayed development of microscopic kelp stages is often closely tied to insufficient nutrient and light regimes (Carney & Edwards, 2010), both of which are present between September to March due to dampened upwelling conditions and reduced daylength. As such, the slow development over winter in

natural populations suggests that changing day length and nutrient supply from upwelling could be more important than temperature and pH fluctuations in promoting the development of microscopic kelp stages.

Our results suggest that there may be some density-dependent effects on sporeling growth at these microscopic stages. The difference in sporeling sizes between treatments was most significantly correlated with temperature, but also showed at least a marginally significant correlation with the number of gametophytes present in both weeks (Figure 1.5). However, due to the fact that high temperatures consistently resulted in significant decreases in gametophyte numbers, the relationships of both temperature and number of gametophytes to gametophyte size are confounded, and direct causation cannot be determined. As a result, more research is needed to see whether these increased sizes were really a result of high temperatures or whether they were a result of lowered density of individuals.

In natural populations, there are numerous density-dependent effects that impact kelp reproduction and recruitment. At initial spore settlement, high densities of gametophytes are needed for fertilization between male and female gametophytes to occur, so Allee effects may occur if spores settle at a density of less than 1 spore/mm^2 (Reed, 1990). The direction of density-dependence then reverses somewhere between the gametophyte stage and the point where a juvenile becomes easily detectable to the naked eye, and numerous kelps, including bull kelp, exhibit subsequent increases in mortality due to competition for space, grazing, and overgrowth of other species until they reach the adult life stage (Dobkowski et al., 2019; Reed et al., 1991; Schiel & Foster, 2006). Due to the number of mortality agents that occur in a natural environment and need for close proximity between gametophytes to allow for fertilization,

reductions in gametophyte numbers and densities from high temperatures could still have detrimental effects on the replenishment of bull kelp forests.

The results of this research indicate that climate change will significantly affect bull kelp reproduction via increased temperatures, and, to a lesser extent, ocean acidification. Increasing frequency and intensity of extreme temperature events such as marine heat waves will likely lead to a massive decrease in the survival of gametophytes and decreased, but accelerated, production of embryonic sporophytes. Lowered pH, mimicking ocean acidification, resulted in an increase in numbers of male gametophytes and sporelings, as well as a slower reproduction rate. Warming waters from climate change will interact with seawater chemistry, and the potentially increased access of kelps to easily diffusive CO_2 molecules or increased rates of carbon concentrating mechanisms under warming climate conditions may have significant impacts on metabolic rates affecting growth and reproduction. The ability of bull kelp to recover from extreme climate events depends on the ability of all lifestages to withstand abiotic stress. In order for managers and scientists to intervene successfully through restoration, an understanding of physiological processes and potential bottlenecks and challenges present at each life stage is necessary. This study informed how bull kelp microstages survive under extreme conditions that are becoming increasingly common, which can help to improve projections for this species into the future and help to explain the consequences of extreme events that lead to major die-offs.

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TABLES AND FIGURES:

Table 1.1: Linear Mixed Model results for count and offspring to female ratio data.

Linear Mixed Model Results

Variable	Variable Type	Effect	Log-Likelihood	DF	P-value
Females	Count	Temperature	51.128	36	**<0.001**
		pH	0.518	36	0.472
		Temperature:pH	0.813	36	0.367
		Petri Dish ID (random)	7.880		**0.005**
Males	Count	Temperature	45.393	36	**<0.001**
		pH	8.638	36	**0.003**
		Temperature:pH	0.016	36	0.901
		Petri Dish ID (random)	1.082		0.298
Eggs	Count	Temperature	33.730	36	**<0.001**
		pH	4.396	36	**0.036**
		Temperature:pH	0.190	36	0.663
		Petri Dish ID (random)	5.208		**0.023**
Juveniles	Count	Temperature	36.639	36	**<0.001**
		pH	1.070	36	0.301
		Temperature:pH	0.199	36	0.656
		Petri Dish ID (random)	3.054		0.081
Eggs per Female (Week 3)	Ratio	Temperature	0.141	36	0.708
		pH	3.735	36	**0.053**
		Temperature:pH	3.774	36	**0.052**
		Petri Dish ID (random)	0.232		0.630
Eggs per Female (Week 4)	Ratio	Temperature	13.114	36	**<0.001**
		pH	9.366	36	**0.002**
		Temperature:pH	0.098	36	0.755
		Petri Dish ID (random)	0.564	36	0.453
Juveniles per Female (Week 3)	Ratio	Temperature	45.264	36	**<0.001**
		pH	16.749	36	**<0.001**
		Temperature:pH	0.067	36	0.796
		Petri Dish ID (random)	0.118		0.731
Juveniles per Female (Week 4)	Ratio	Temperature	9.187	36	**0.002**
		pH	0.126	36	0.723
		Temperature:pH	0.100	36	0.751
		Petri Dish ID (random)	1.145		0.285
Offspring per Female (Week 3)	Ratio	Temperature	30.419	36	**<0.001**
		pH	1.362	36	0.243
		Temperature:pH	1.709	36	0.191
		Petri Dish ID (random)	0.065		0.799
Offspring per Female (Week 4)	Ratio	Temperature	0.228	36	0.633
		pH	5.234	36	**0.022**
		Temperature:pH	0.006	36	0.937
		Petri Dish ID (random)	1.053		0.305

Table 1.2: Generalized Linear Mixed Model results for proportion productive females and size data.

Generalized Linear Mixed Model Results

Variable	Data Subset	Effect	Chi-Sq	DF	P-value
Proportion of Females Productive	All Data	Temperature	28.187	36	<0.001
		pH	1.162	36	0.281
		Temperature:pH	0.512	36	0.474
Size	All Data	# Gametophytes:Temperature:pH	6.339		0.012
	Ambient Temperature	pH	3.955		0.047
		# Gametophytes (covariate)	1.173		0.279
		# Gametophytes:pH	2.267		0.132
	High Temperature	pH	0.081		0.776
		# Gametophytes (covariate)	0.988		0.320
		# Gametophytes:pH	6.039		0.014
	Low pH	Temperature	10.051		0.002
		# Gametophytes (covariate)	0.319		0.572
		# Gametophytes:Temperature	1.611		0.204
	Ambient pH	Temperature	2.082		0.149
		# Gametophytes (covariate)	3.181		0.074
		# Gametophytes:Temperature	5.300		0.021

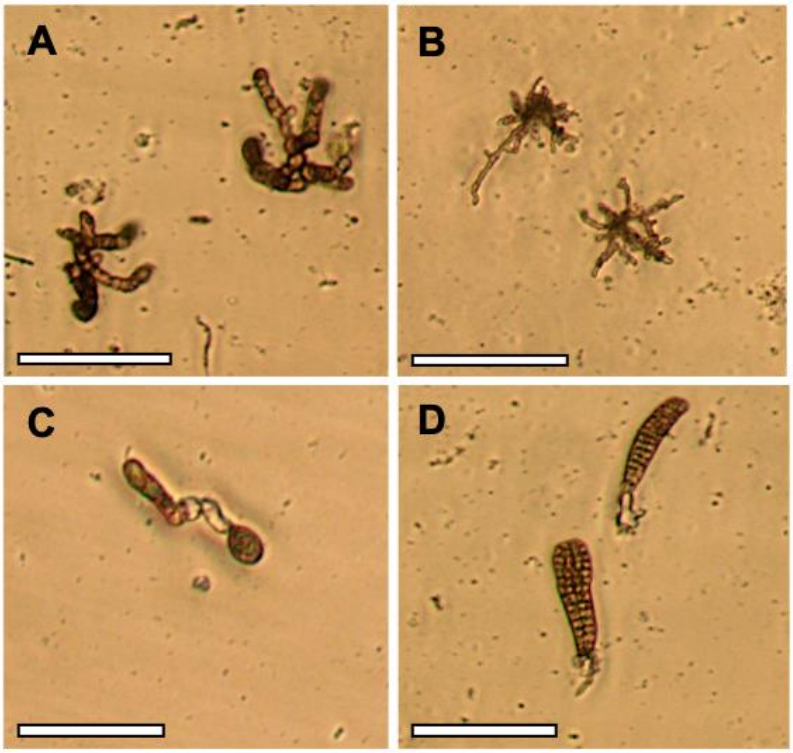

Figure 1.1: The microscopic stages of bull kelp: A) Female gametophyte (image area = 0.065 mm^2); B) Male gametophyte (image area = 0.065 mm^2); C) Female gametophyte producing an egg (image area = 0.077 mm^2); D) Female gametophytes with sporelings (image area = 0.065 mm^2). Scale bars in lower left hand corner represent 0.1mm.

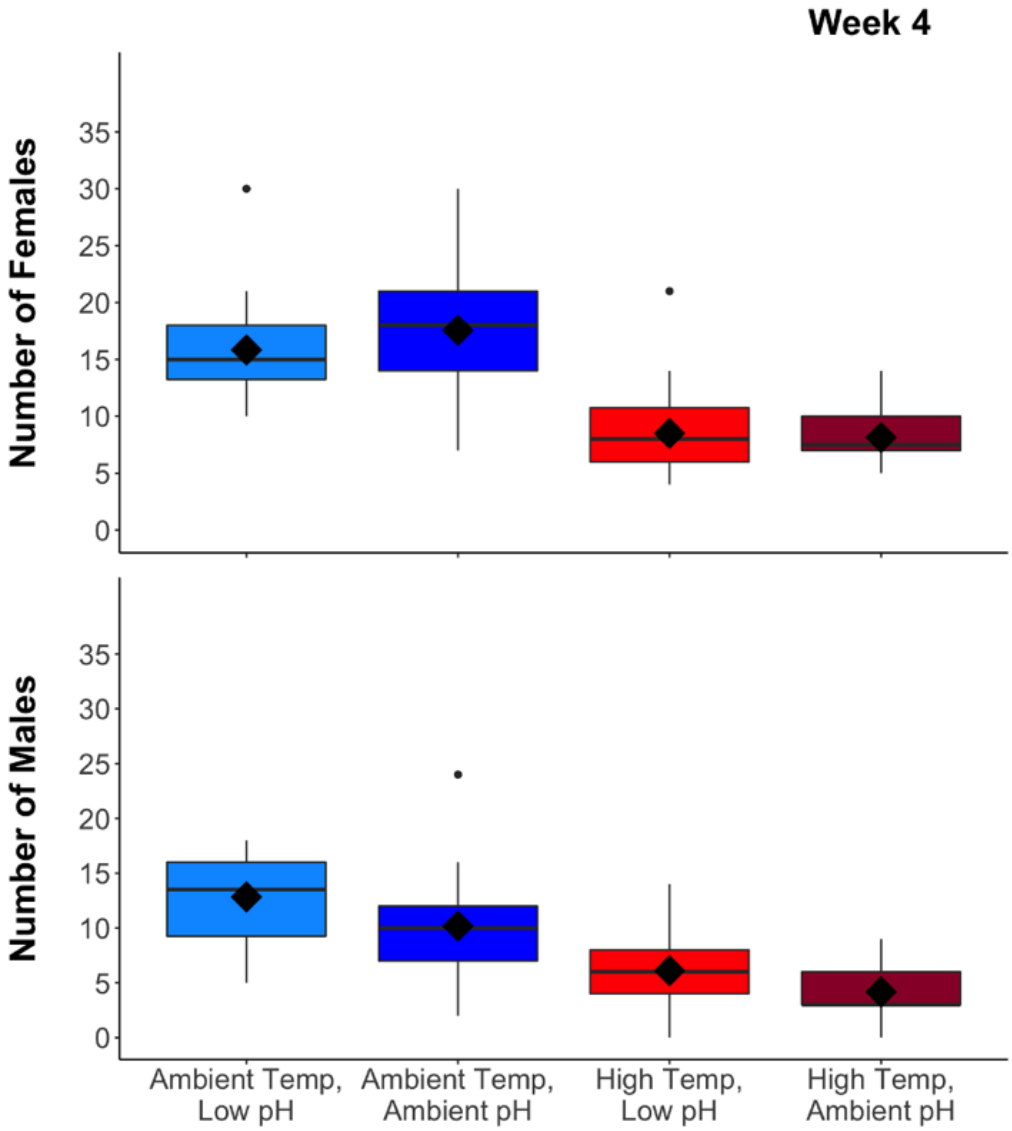

Figure 1.2: Female and male gametophytes present in each photo after 4 weeks of growth. The box plots summarize the mean (diamond) and median (box midline) for each treatment, the first and third quartiles (upper and lower box limits), outliers within 1.5 times the inter-quartile range (vertical lines), and outliers beyond that range (dots).

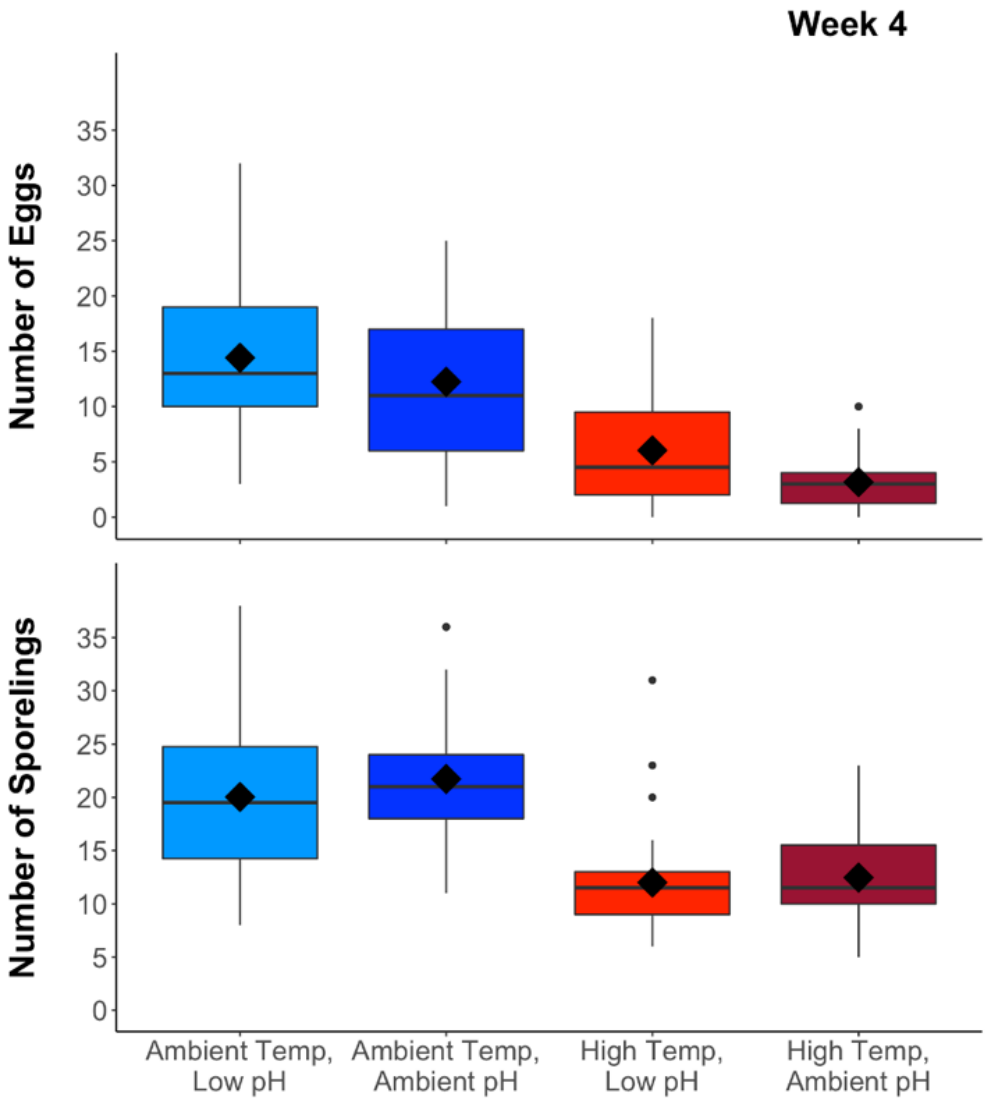

Figure 1.3: Eggs and sporelings present in each photo after 4 weeks of growth. The box plots summarize the mean (diamond) and median (box midline) for each treatment, the first and third quartiles (upper and lower box limits), outliers within 1.5 times the inter-quartile range (vertical lines), and outliers beyond that range (dots).

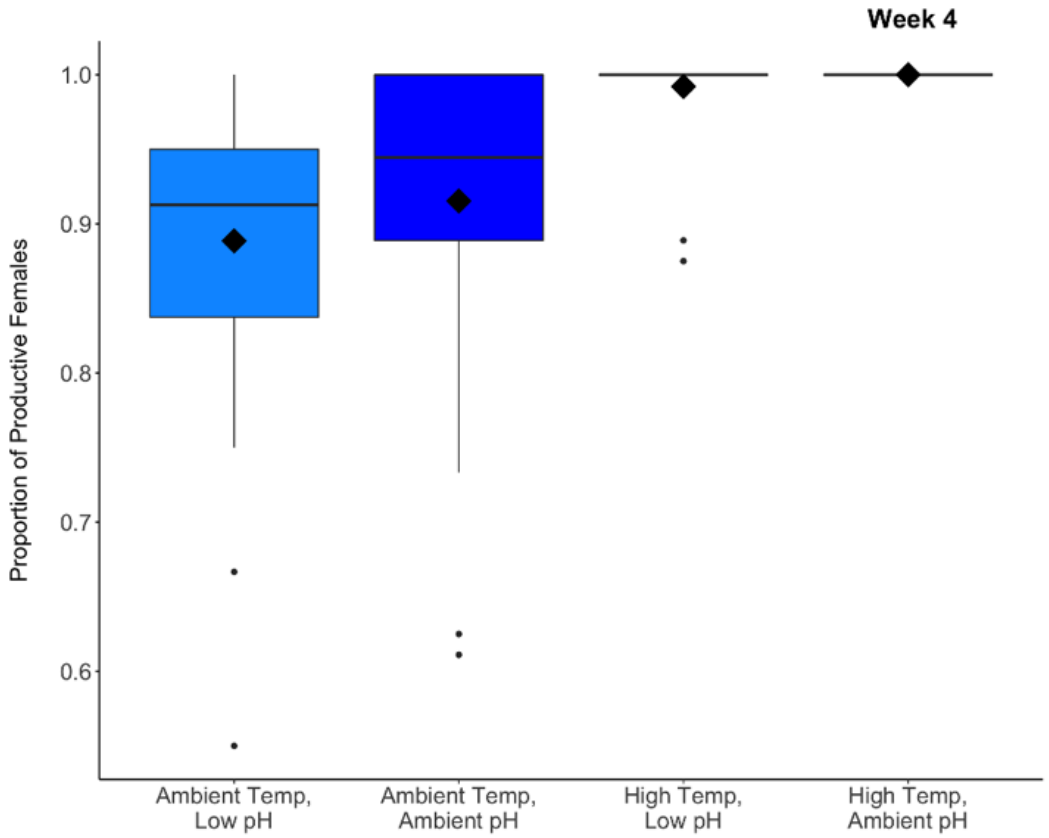

Figure 1.4: Proportion of productive female gametophytes after 4 weeks of growth. The box plots summarize the mean (diamond) and median (box midline) for each treatment, the first and third quartiles (upper and lower box limits), outliers within 1.5 times the inter-quartile range (vertical lines), and outliers beyond that range (dots).

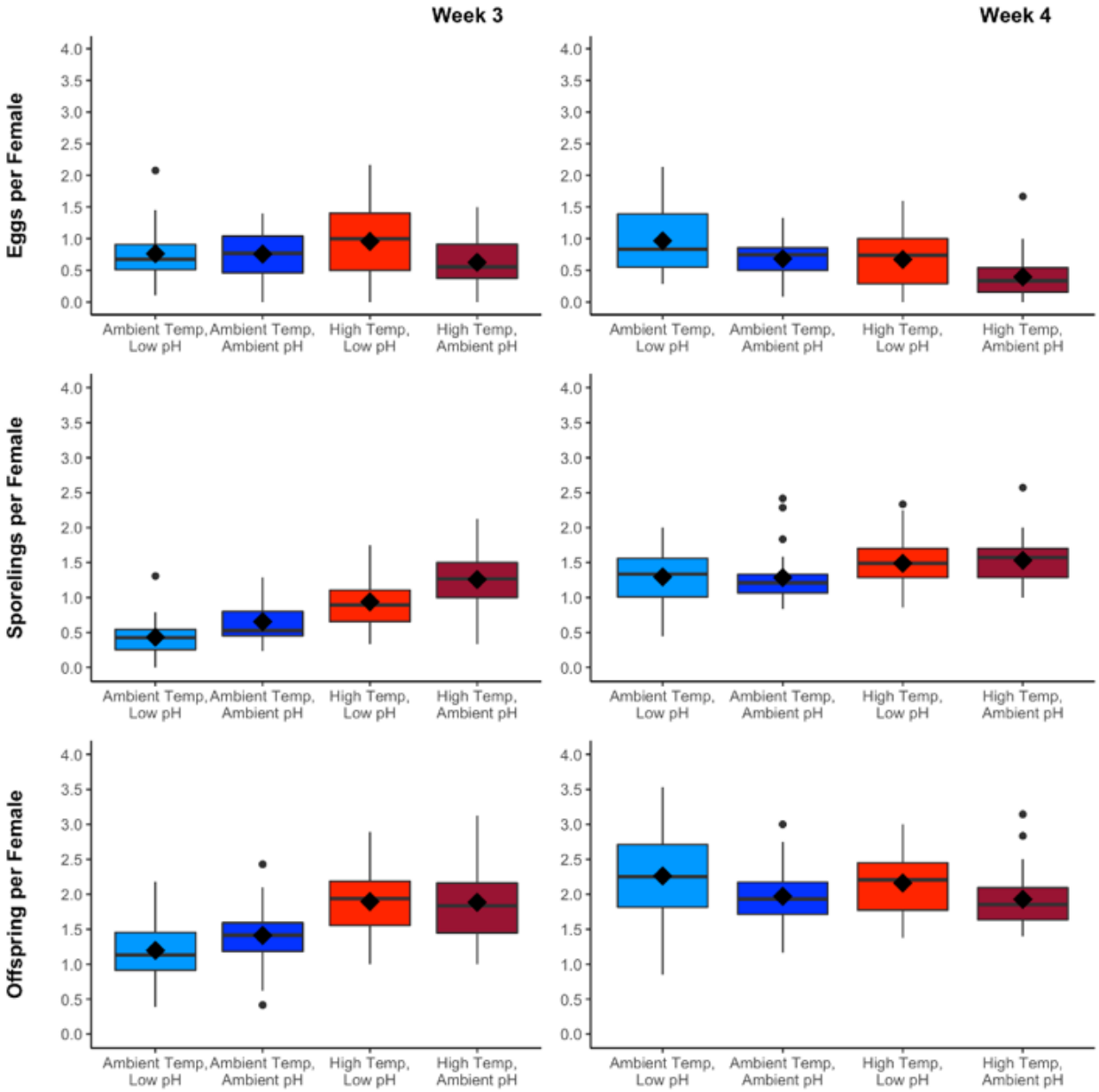

Figure 1.5: Eggs, sporelings, and total offspring (eggs + sporelings) per female after 3 and 4 weeks of growth. The box plots summarize the mean (diamond) and median (box midline) for each treatment, the first and third quartiles (upper and lower box limits), outliers within 1.5 times the inter-quartile range (vertical lines), and outliers beyond that range (dots).

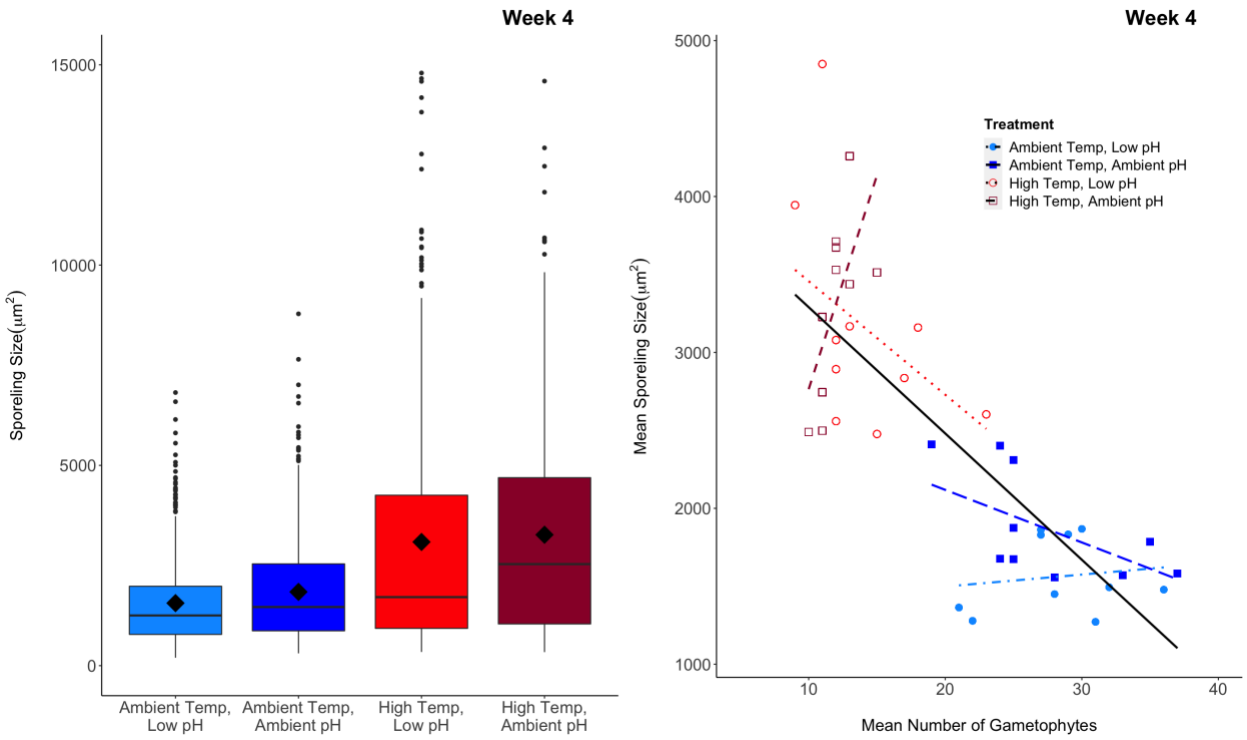

Figure 1.6: Left panel shows the average size of sporelings after 4 weeks of growth. The left panel shows box plots that summarize the mean (diamond) and median (box midline) for each treatment, the first and third quartiles (upper and lower box limits), outliers within 1.5 times the inter-quartile range (vertical lines), and outliers beyond that range (dots). The right panel shows the relationship of the covariate (mean number of gametophytes) to the response variable (mean sporeling size). Data and trends are represented by different dash and dot styles and colors for each treatment: Ambient Temp and Low pH (light blue, solid circles, dot-dash line), Ambient Temp and Ambient pH (dark blue, solid squares, long dash line), High Temp and Low pH (red, open circle, dotted line), and High Temp and Ambient pH (dark red, open square, short dash line).The trend across all groups is represented by the solid black line. Heterogeneous slopes and different ranges of values for each treatment indicate that the different treatments are confounded with differences in the covariate.

APPENDIX A: Chapter 1 Statistical Tables

Data and R code for this manuscript can be accessed at
https://github.com/arkorabik/PublishedData

Table A1: Statistical outcomes for models of female count data

Week 4 Females

Model: lmer(sqrt(Females)~ Temp + pH + Temp:pH + (1|Petri Dish ID), data = pdt)

Random Effects	**Estimate**	**SE**	**Df**	**T-value**	**LLR**	**P-value**
Petri Dish ID	0.08195				7.879457	**0.005**
Residual	0.21277					
Interactions	**Estimate**	**SE**	**Df**	**T-value**	**LLR**	**P-value**
Temperature : pH	-0.213035	0.2478791	36	-0.859432	0.81337	0.3671
Fixed Effects	**Estimate**	**SE**	**Df**	**T-value**	**LLR**	**P-value**
Intercept	2.82775	0.12364	79	22.8702		
Temperature	1.31545	0.1757	36	7.4871	51.1283	< **0.0001**
pH	0.02026	0.17486	36	0.11587	0.51791	0.4717

Table A2: Statistical outcomes for models of male count data

Week 4 Males

Model: lmer(sqrt(Males)~ Temp + pH + Temp:pH + (1|Petri Dish ID), data = pdt)

Random Effects	**Estimate**	**SE**	**Df**	**T-value**	**LLR**	**P-value**
Petri Dish ID	0.04678				1.082005	0.2982
Residual	0.41635					
Interactions	**Estimate**	**SE**	**Df**	**T-value**	**LLR**	**P-value**
Temperature : pH	0.032674	0.2733936	36	0.119513	0.01556	0.9007
Fixed Effects	**Estimate**	**SE**	**Df**	**T-value**	**LLR**	**P-value**
Intercept	1.94558	0.13622	79	14.2825		
Temperature	1.17496	0.19399	36	6.05686	45.393	**< 0.0001**
pH	0.38634	0.19265	36	2.00546	8.63776	**0.0033**

Table A3: Statistical outcomes for models of egg count data

Week 4 Eggs

Model: lmer(sqrt(Eggs)~ Temp + pH + Temp:pH + (1| Petri Dish ID), data = pdt)

Random Effects	**Estimate**	**SE**	**Df**	**T-value**	**LLR**	**P-value**
Petri Dish ID	0.28648				5.207977	**0.0225**
Residual	0.98171					
Interactions	**Estimate**	**SE**	**Df**	**T-value**	**LLR**	**P-value**
Temperature : pH	-0.204592	0.496794	36	-0.411825	0.18959	0.6633
Fixed Effects	**Estimate**	**SE**	**Df**	**T-value**	**LLR**	**P-value**
Intercept	1.52398	0.24773	79	6.15174		
Temperature	1.82336	0.35222	36	5.17672	33.73	**<0.0001**
pH	0.61102	0.35035	36	1.74406	4.39583	**0.036**

Table A4: Statistical outcomes for models of sporeling count data

Week 4 Sporelings

Model: lmer(sqrt(Sporelings)~ Temp + pH + Temp:pH + (1|Petri Dish ID), data = pdt)

Random Effects	**Estimate**	**SE**	**Df**	**T-value**	**LLR**	**P-value**
Petri Dish ID	0.08057				3.054386	0.0805
Residual	0.38809					
Interactions	**Estimate**	**SE**	**Df**	**T-value**	**LLR**	**P-value**
Temperature : pH	-0.122581	0.290655	36	-0.42174	0.19862	0.6558
Fixed Effects	**Estimate**	**SE**	**Df**	**T-value**	**LLR**	**P-value**
Intercept	3.48191	0.14489	79	24.0311		
Temperature	1.13264	0.20614	36	5.49452	36.6391	**<0.0001**
pH	-0.0829	0.20491	36	-0.4047	1.07023	0.3009

Table A5: Statistical outcomes for models of ratios of proportion productive females.

Week 4 Proportion of Productive Females

Model: glmmTMB((Prop_prod-0.00001) ~ Temp*pH +(1|Petri Dish ID), family = beta_family(link="logit"), data = pdt)

Random Effects	**Estimate**	**SE**	**z-value**	**ChiSq**	**P-value**
Petri Dish ID	2.24E-01				
Interactions	**Estimate**	**SE**	**z-value**	**ChiSq**	**P-value**
Temperature : pH	-0.34443	0.47961	-0.718	0.5117	0.4744
Fixed Effects	**Estimate**	**SE**	**z-value**	**ChiSq**	**P-value**
Intercept	4.05985	0.35058	11.58		
Temperature	-1.25286	0.37167	-3.371	28.187	**<0.0001**
pH	-0.08916	0.339	-0.263	1.1619	0.2811

Table A6: Statistical outcomes for models of egg/female ratios.

Week 3 Eggs per Female

Model: lmer(EPF~ Temp + pH + Temp:pH + (1|Petri Dish ID), data = wk3dt)

Random Effects	**Estimate**	**SE**	**Df**	**T-value**	**LLR**	**P-value**
Petri Dish ID	0.00925				0.231782	0.6302
Residual	0.19129					
Interactions	**Estimate**	**SE**	**Df**	**T-value**	**LLR**	**P-value**
Temperature : pH	-0.322532	0.1709	36	-1.88726	3.77374	**0.0521**
Fixed Effects	**Estimate**	**SE**	**Df**	**T-value**	**LLR**	**P-value**
Intercept	0.62774	0.08545	80	7.34626		
Temperature	0.12938	0.12084	36	1.0706	0.14057	0.7077
pH	0.3294	0.12084	36	2.72582	3.73457	**0.0533**

Week 4 Eggs per Female

Model: lmer(log(EPF+1)~ Temp + pH + Temp:pH + (1|Petri Dish ID), data = pdt)

Random Effects	**Estimate**	**SE**	**Df**	**T-value**	**LLR**	**P-value**
Petri Dish ID	0.00455				0.564319	0.4525
Residual	0.05809					
Interactions	**Estimate**	**SE**	**Df**	**T-value**	**LLR**	**P-value**
Temperature : pH	-0.028905	0.098165	36	-0.29445	0.09764	0.7547
Fixed Effects	**Estimate**	**SE**	**Df**	**T-value**	**LLR**	**P-value**
Intercept	0.30672	0.0489	79	6.27227		
Temperature	0.19842	0.06967	36	2.84811	13.114	**0.0003**
pH	0.16569	0.06916	36	2.39591	9.36634	**0.0022**

Table A7: Statistical outcomes for models of sporeling/female ratios.

Week 3 Sporelings per Female

Model: lmer(sqrt(JPF)~ Temp + pH + Temp:pH + (1|Petri Dish ID), data = wk3dt)

Random Effects	**Estimate**	**SE**	**Df**	**T-value**	**LLR**	**P-value**
Petri Dish ID	0.00127				0.11794	0.7313
Residual	0.03731					
Interactions	**Estimate**	**SE**	**Df**	**T-value**	**LLR**	**P-value**
Temperature : pH	-0.01826	0.074029	36	-0.2466	0.06719	0.7955
Fixed Effects	**Estimate**	**SE**	**Df**	**T-value**	**LLR**	**P-value**
Intercept	1.10355	0.03701	80	29.814		
Temperature	-0.313	0.05235	36	-5.9799	45.2639	**<0.0001**
pH	-0.1512	0.05235	36	-2.8877	16.7485	**<0.0001**

Week 4 Sporelings per Female

Model: lmer(sqrt(JPF)~ Temp + pH + Temp:pH + (1|Petri Dish ID), data = pdt)

Random Effects	**Estimate**	**SE**	**Df**	**T-value**	**LLR**	**P-value**
Petri Dish ID	0.00259				1.14462	0.2847
Residual	0.22314					
Interactions	**Estimate**	**SE**	**Df**	**T-value**	**LLR**	**P-value**
Temperature : pH	0.019201	0.063551	36	0.30213	0.10041	0.7513
Fixed Effects	**Estimate**	**SE**	**Df**	**T-value**	**LLR**	**P-value**
Intercept	1.23074	0.03167	79	38.8668		
Temperature	-0.1066	0.04509	36	-2.364	9.18669	**0.0024**
pH	-0.0192	0.04478	36	-0.4516	0.12616	0.7225

Table A8: Statistical outcomes for models of offspring/female ratios.

Week 3 Offspring per Female

Model: lmer(OPF~ Temp + pH + Temp:pH + (1|Petri Dish ID), data = wk3dt)

Random Effects	**Estimate**	**SE**	**Df**	**T-value**	**LLR**	**P-value**
Petri Dish ID	0.00557				0.065118	0.7986
Residual	0.22368					
Interactions	**Estimate**	**SE**	**Df**	**T-value**	**LLR**	**P-value**
Temperature : pH	-0.2254192	0.179037	36	-1.2591	1.70902	0.1911
Fixed Effects	**Estimate**	**SE**	**Df**	**T-value**	**LLR**	**P-value**
Intercept	1.88519	0.08952	80	21.0593		
Temperature	-0.4731	0.1266	36	-3.7368	30.4186	**<0.0001**
pH	0.01056	0.1266	36	0.08344	1.36223	0.2432

Week 4 Offspring per Female

Model: lmer(log(OPF)~ Temp + pH + Temp:pH + (1|Petri Dish ID), data = pdt)

Random Effects	**Estimate**	**SE**	**Df**	**T-value**	**LLR**	**P-value**
Petri Dish ID	0.00612				1.053258	0.3048
Residual	0.05503					
Interactions	**Estimate**	**SE**	**Df**	**T-value**	**LLR**	**P-value**
Temperature : pH	0.007708	0.099264	36	0.07765	0.00619	0.9373
Fixed Effects	**Estimate**	**SE**	**Df**	**T-value**	**LLR**	**P-value**
Intercept	0.63724	0.04946	79	12.8842		
Temperature	0.01849	0.07043	36	0.2625	0.22787	0.6331
pH	0.10749	0.06995	36	1.53682	5.23446	**0.0221**

Table A9: Statistical outcomes for models of sporeling size data (area in um2). The "covariate" refers to the mean number of gametophytes present per photo in a given dish.

Week 4 Sporeling Sizes

Full Model: glmer(I(area_um2/100) ~ Temp*pH*covariate +(1|Petri Dish ID), family = Gamma(link="inverse"), data = wk4dt)

Interactions	**Estimate**	**SE**	**T-value**	**ChiSq**	**P-value**
covariate:Temp:pH	0.48066	0.14353	3.349	6.3387	**0.01181**

Subset Model for Low pH Treatments

Model: glmer(I(area_um2/100) ~ Temp*covariate +(1|Petri Dish ID), family = Gamma(link="inverse"), data = wk4lph)

Variables	**Estimate**	**SE**	**T-value**	**ChiSq**	**P-value**
Petri Dish ID	2.93E-03				
Residual	6.53E+01				
Intercept	7.56E+00	1.86766	4.048		
temp:covariate	0.11974	0.08914	1.343	1.6106	0.2044
temp	-5.40444	20.7699	-2.602	10.051	**0.001523**
covariate	-0.03965	0.06543	-0.606	0.3192	0.5721

Subset Model for Ambient pH Treatments

Model: glmer(I(area_um2/100) ~ Temp*covariate +(1|Petri Dish ID), family = Gamma(link="inverse"), data = wk4hph)

Variables	**Estimate**	**SE**	**T-value**	**ChiSq**	**P-value**
Petri Dish ID	1.33E-03				
Residual	5.21E+01				
Intercept	2.57E+00	1.03042	2.49		
temp:covariate	-0.36249	0.13335	-2.718	5.3001	**0.02132**

temp	3.63827	1.87179	1.944	2.0815	0.1491
covariate	0.10426	0.03703	2.816	3.1812	0.07449

Subset Model for Ambient Temperature Treatments

Model: glmer(I(area_um2/100) ~ pH*covariate +(1|Petri Dish ID), family = Gamma(link="inverse"), data = wk4ltemp)

Variables	**Estimate**	**SE**	**T-value**	**ChiSq**	**P-value**
Petri Dish ID	4.03E-03				
Residual	4.58E+01				
Intercept	2.62E+00	1.57501	1.665		
pH:covariate	-1.46E-01	0.11731	-1.246	2.2666	0.1322
pH	5.05E+00	3.32134	1.521	3.955	**0.04673**
covariate	1.04E-01	0.05653	1.837	1.1728	0.2788

Subset Model for High Temperature Treatments

Model: glmer(I(area_um2/100) ~ pH*covariate +(1|Petri Dish ID), family = Gamma(link="inverse"), data = wk4htemp)

Variables	**Estimate**	**SE**	**T-value**	**ChiSq**	**P-value**
Petri Dish ID	4.86E-04				
Residual	8.07E+01				
Intercept	5.95E+00	1.2176	4.887		
pH:covariate	3.22E-01	0.10705	3.011	6.0391	**0.01399**
pH	-3.90E+00	1.35655	-2.874	0.0811	0.7758
covariate	-2.40E-01	0.09895	-2.427	0.988	0.3202

CHAPTER 2:

INCREASED TEMPERATURES IMPACT THE REPRODUCTION OF LOCALIZED ESTUARINE KELP POPULATIONS MORE THAN INVASIVE SPECIES

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Abstract:

Coastal marine organisms are particularly susceptible to the effects of climate change and other anthropogenic impacts when the natural variation of conditions within an environment is altered. While estuarine habitats in particular experience large variation in abiotic conditions such as temperature and salinity, as well as numerous stresses due to biotic interactions such as the presence of invasive species, the pressure from both abiotic and biotic stresses have been increasing. Along the western shoreline of Tomales Bay, CA, there are several locations where rocky shorelines support dense stands of both the giant kelp *Macrocystis pyrifera* and the invasive brown alga *Sargassum muticum*. *M. pyrifera* is rarely found in estuaries, and while several studies have investigated the interactions of the adult stages of these species, there is little understanding of how microscopic stages of these two species interact or how climate change may influence this interaction. Our research considers the interacting effects of climate driven changes in temperature and salinity and interactions with *S. muticum* on the growth and survival of *M. pyrifera* gametophytes from Tomales Bay, CA. Using kelp culturing experiments, we tested: 1) how different salinities and temperatures impact early life stages *M. pyrifera* from different sources within Tomales Bay, 2) how the presence of invasive *S. muticum* propagules affect *M. pyrifera* gametophyte development, and 3) how the combined effects of salinity, temperature, and *S. muticum* presence affect *M. pyrifera* early life stages. Our results indicate that 1) *M. pyrifera* reproduction is severely reduced under high temperatures, 2) the presence of *S. muticum* had a negative effect on the survival of *M. pyrifera* gametophytes, 3) there were no interactions among these effects, and 4) *M. pyrifera* from Tomales Bay exhibited the greatest reproduction under lower salinities (26 psu), potentially indicating that they may be locally adapted to lower salinities. These results suggest that while *M. pyrifera* may be able to adapt to

local conditions like salinity, higher temperatures from changing climate and the presence of competitors from biological invasions act additively, but not interactively, in their impacts on early life stages of kelp. By determining how foundation species respond to various combinations and levels of abiotic (climate change) and biotic (invasions and habitat loss) stressors, we can better predict how these species will perform in a changing environment and how they will contribute to overall ecosystem resilience.

Introduction:

In an era of global climate change, coastal ecosystems are becoming increasingly stressed by the cumulative impacts of climate-driven abiotic changes such as ocean acidification (Cheresh & Fiechter, 2020; Cooley et al., 2022; Feely et al., 2009), hypoxia (Keeling & Garcia, 2002; Keeling et al., 2010; Sarmiento et al., 1998), rising temperatures (Dunstan et al., 2018; Gentemann et al., 2017; Hansen et al., 2006; Lima & Wethey, 2012; Oliver et al., 2018; Reid & Beaugrand, 2012; Shi et al., 2021), sea level rise (Hilton et al., 2008; Taillie et al., 2019), changing salinity (Chen et al., 2019; Ishii et al., 2006; Hilton et al., 2008; Hong & Shen, 2012), and changes to broader oceanographic processes such as upwelling and oscillation patterns (Bakun et al., 2015; Di Lorenzo et al., 2008; García-Reyes et al., 2015; García-Reyes et al., 2020). The effects of climate change can have a variety of different effects on local organisms and ecosystems, including changes in physiology (Helmuth et al., 2006; Kroeker et al., 2013; Pörtner & Farrell, 2008; Smith et al., 2023), morphology and phenology (Alfonso et al., 2022; Hughes, 2000; Parmesan, 2006), range shifts and invasions (Cheung et al., 2009; Lonhart, 2009; Sanford et al., 2019), community structure and composition (Arafeh-Dalmau et al., 2019; Barry et al., 1995; Beaugrand & Reid, 2003; McCarty, 2001), species interactions (Byrnes et al., 2011; Doney et al., 2012; Ferrari et al., 2011; Edwards & Connell, 2012; Ledger et al., 2013; Vergés et al., 2014; Brown et al., 2014), and genetic changes as a result of local adaptation (Pauls et al., 2013; Sanford & Kelly, 2011). Species that have multiple life stages often have stage-based tolerance ranges to abiotic stress (Shukla & Edwards, 2020; Small & Edwards, 2021), and thus a changing climate increases the number of bottlenecks a multi-stage species experiences during its lifetime for vertebrates (Ferrari, 2011; Munday, 2010), invertebrates (Ban et al., 2013; Byrne et al., 2011; Kroeker et al., 2013; Miner et al., 2018; Small et al., 2016; Przeslawksi et al., 2014),

and primary producers alike (Harvey et al., 2013; Smith et al., 2023; Straub et al., 2019; Veenhof et al. 2021).

Biological invasions are also increasing worldwide (Molnar et al., 2008) and have the potential to interact with climate change to exacerbate changes to local communities. Increasing temperatures and changing abiotic conditions can facilitate increased invasion in marine ecosystems via range-shifts poleward towards cooler temperatures (Sorte et al., 2010; Edwards 2022) and reduced barriers to invasion (Mahanes & Sorte, 2019). Due to the fact that exotic species tend to be more frequently introduced to cooler regions than their native ranges (Bennett et al., 2021) and increasing temperatures inhibit native species to a greater extent than their invasive counter parts (Sorte et al., 2013), marine communities under biotic stress from invasion face the possibility of significant community shifts as a result of changing climate (Vergés et al., 2014; Wernberg et al., 2016: Krause-Jensen & Duarte, 2014). In addition to potentially shifting the composition of native communities, invasive marine species can also change the abundance and behavior of native species (Anton et al., 2019), especially those within the same trophic level (Thomsen et al., 2014). Invasive marine primary producers, such as seaweed, can be particularly disruptive by competing with native primary producers for space and other resources (Gaertner et al., 2009; Thomsen et al., 2009, 2014; Powell et al., 2011; Vilà et al., 2011), altering resource allocation and nutrient acquisition rates (Casoli et al., 2021; Maggi et al., 2015), and loss of biodiversity and ecosystem functions (Sullaway & Edwards, 2020; Li et al., 2023). Consequently, the biomass of consumers that prefer native primary producers for food are also significantly altered by invasions of seaweed (Maggi et al., 2014; Thomsen et al., 2014; Williams & Smith, 2007).

Climate change and biological invasions jointly threaten the giant kelp *Macrocystis pyrifera*, an important foundation species in many temperate coastal ecosystems around the world. Kelp forests are sites of high diversity (Metzger et al., 2019), supporting many species of ecological and economic importance (Graham et al., 2008; Tegner & Dayton, 2000), and impacts of climate change on *M. pyrifera* can cause regime shifts and threaten entire ecosystems. The effects of temperatures greater than 18°C on *M. pyrifera* has have been found to provoke different responses in populations from different regions (Buschmann et al., 2004; Hollarsmith et al., 2020; Rodriguez et al., 2019) but overall negatively affect multiple parts of the reproductive cycle, including spore production and release (Gaitán-Espitia et al,. 2014; Le et al., 2022; Rothäusler et al., 2009), gametophyte survival and growth (Gaitán-Espitia et al., 2014; Hollarsmith et al., 2020; Muñoz et al., 2004; Shukla & Edwards, 2017), gametophyte sex ratios (Shukla & Edwards, 2017), egg production (Hollarsmith et al., 2020; Muñoz et al., 2004), sporeling growth (Fernandez et al., 2021; Hollarsmith et al., 2020; Mabin et al., 2019, Shukla & Edwards, 2017), and physiological processes such as photosynthesis and respiration at the microscopic stage (Fain & Murray, 1982; Mabin et al., 2019). In contrast, few studies have examined the effects of changing salinity regimes on *M. pyrifera*, but studies in Chilean populations of *M. pyrifera* show persistent reproductive output at low salinities (estimated between 20 and 30 psu) in populations that are regularly exposed to variable salinities (Buschmann et al., 2004; Buschmann et al., 2014; Rodriguez et al., 2019). This trend is hypothesized to be the same in North American populations (North et al., 1986), but needs to be better studied in the face of increasingly variable precipitation patterns that affect riverine outflow to estuaries and coasts (Easterling et al., 2017; Gernushov et al., 2017).

In addition to changing climate, *M. pyrifera* populations coincide with the invasive Japanese brown algae known as wireweed, *Sargassum muticum*, along the west coast of North America. First introduced to the United States from Japan in 1944, the range of *S. muticum* extends along the near entirety of the North American west coast, from Ketchikan, Alaska at the northern edge of its range (Scagel et al., 1989; Engelen et al., 2015), to Punta Abreojos in Baja California Sur, Mexico (Espinosa, 1990). Previous studies of *M. pyrifera* and *S. muticum* interactions have found that *S. muticum* shading reduces *M. pyrifera* recruitment, and the removal of *S. muticum* adults resulted in drastic increases in *M. pyrifer*a and other native seaweeds presence and abundance (Ambrose & Nelson, 1982; Steen, 2004; Britton-Simmons, 2004). Altered canopy composition by *S. muticum* can significantly reduce native invertebrate biodiversity via reductions in suitable habitat due to reduced canopy cover (Veiga et al., 2018; Salvaterra et al., 2013), altered abiotic conditions such as temperature and light (Critchley et al., 1990), and *S. muticum* resistance to native bacteria, larvae, and diatom habitation via the high concentration of unique secondary compounds they secrete (Li et al., 2023; Schwartz et al., 2017).

The concern that *S. muticum* can impact native habitat biodiversity is compounded by indications that *S. muticum* propagules have greater physiological tolerance ranges than *M. pyrifera* gametophytes. Similarly to *M. pyrifera*, *S. muticum* reproduction has been seen to continue as low as 20 psu (Hales & Fletcher, 1990; Norton, 1977; Steen, 2004), although salinities of 30-35 psu seem to result in highest rates of reproduction (Hales & Fletcher, 1989; Kerrison and Le, 2016). The tolerance of *S. muticum* to high temperatures, however, is much greater than that of *M. pyrifera*. While *M. pyrifera* reproduction generally declines, or even ceases, beyond 18°C (Buschmann et al., 2004; Gaitán-Espitia et al., 2014; Hollarsmith et al.,

2020; Le et al., 2022; Muñoz et al., 2004; Shukla & Edwards, 2017), *S. muticum* reproduction is able to continue up to 30°C (Hales & Fletcher, 1989), with optimum growth rates occurring between 18-25°C (Hales & Fletcher, 1990; Liu et al., 2013). These greater tolerances to a world that is warmer and subject to more variable salinity and negative impacts on local communities make *S. muticum* a species of concern in many areas. While the interacting effects of invasive species and temperature have been well studied (Lopez et al., 2022), studies of interactions between invasive species and salinity in marine environments are rare (Crain et al., 2008). Even rarer are such studies involving early life stages. In order to predict the future of species in changing environments, it is important to understand how abiotic and biotic stress interact and if these interactions are synergistic, antagonistic, or simply additive.

In this study, we aim to understand the biotic and abiotic dynamics that govern *M. pyrifera* distribution in Tomales Bay via three experiments assessing the role of temperature and salinity stress and the presence of the invasive *S. muticum* on *M. pyrifera* reproduction. First, we investigated how salinity and temperature influence growth, survival, and reproduction in *M. pyrifera* microscopic stages from different source locations within Tomales Bay. For this question, we hypothesized that salinity will have a greater negative impact than temperature on *M. pyrifera* growth and development due to physiological limits to osmotic stress from the different locations. Second, we investigated how competition with *S. muticum* impacts *M. pyrifera* growth, survival, and reproduction under ambient conditions. We hypothesized that under ambient conditions, interspecific competition will have a negative impact on *M. pyrifera* growth and development due to competition for space. Finally, we combined our first two experiments to assess how *M. pyrifera* responds to temperature and salinity stress change under differing *S. muticum* densities. For this final question, we hypothesized that interspecific

competition will be less important as *M. pyrifera* responds to abiotic stress, but that there may be interacting effects of competition and abiotic stress.

Methods:

Tomales Bay:

Tomales Bay is a highly invaded estuary north of San Francisco, located on the northern edge of the Point Reyes peninsula (Byers, 1999; Cheng & Grosholz, 2016; Kruger-Hadfield et al., 2018; Rubinoff & Grosholz, 2022). Tomales Bay is very long and narrow, which provides a relatively linear estuarine gradient, consisting of numerous overlapping abiotic gradients that vary not only with distance into the bay, but also seasonally (Cheng & Grosholz, 2016, Kimbro et al., 2009). From November to May, during California's rainy season, there is a large amount of freshwater input into the bay, and mean salinity decreases (Kimbro et al., 2009, mid bay: 30 psu, inner bay: 26 psu) with distance into the bay, and can drop quite significantly (<10psu) during low salinity events (Cheng & Grosholz, 2016). Mean temperature also slightly increases with sitance into the bay (Cheng & Grosholz, 2016; mid bay: 10.9 °C, inner bay: 11.2 °C), but temperatures remain relatively similar throughout the bay in winter, regardless of site (Dubois et al. 2022). During this time, mixing in the water column from upwelling, wind, and storms result in strong distances in water chemistry parameters with distance into the bay, but little difference at different vertical depths (Hollarsmith et al., 2020). From June-October, during California's dry season, there is little freshwater input into the bay at this time, so salinity generally stays consistent (Kimbro et al., 2009; mid bay: 34 psu, inner bay: 33 psu) throughout the bay but may actually become hypersaline closer to the head in especially dry years, whereas the temperature gradient becomes more pronounced, with water several degrees warmer at the head than the

mouth (Cheng & Grosholz, 2016; mid bay: 15.3 °C, inner bay: 17.8 °C). During this time, depth stratification becomes much more common, and abiotic variables differ with both vertical depth and distance in the bay (Hollarsmith et al., 2020).

In this study we chose two different locations where the two species co-occur within Tomales Bay: White Gulch (38.197534° N, 122.946408° W), which represents an upper-bay more marine influenced location, and Marshall Beach (38.165311° N, 122.915651° W), a mid-bay site that is the most estuarine giant kelp site in the Tomales Bay (Figure 2.1). Over a two week period in August 2019, temperatures near White Gulch averaged around 16.5°C and ranged from 13-19°C (Schiebelhut et al., 2023). At Sacramento Landing, 2km further into the bay than Marshall Beach, temperatures during this same time period averaged 19.1°C and ranged from 18-22°C (Schiebelhut et al., 2023).

Macrocystis and Sargassum Life Cycles:

Tomales Bay also hosts populations of *M. pyrifera* and *S. muticum*. One of the primary canopy formers of kelp forests in California and other temperate locations around the globe, *M. pyrifera* is typically thought of as a coastal species, and is usually absent from estuaries and bays in California. In Tomales Bay, however, *M. pyrifera* stands have been found to establish habitats at least 7 miles into the bay.

M. pyrifera and *S. muticum* possess very different life cycles due to the fact that they belong to different orders (Laminariales and Fucales, respectively). All members of Laminariales are considered kelp, and are defined by a haplodiplontic life cycle consisting of a large diploid sporophyte and a microscopic haploid gametophyte. At maturity, adult kelps develop sporophylls or sori that release spores into the water column, which eventually settle into the benthos where

they develop into male or female gametophytes (Reed, 1990). The female gametophytes begin to produce eggs, and then release the lamoxirene pheromone to trigger sperm release from nearby males (Lüning and Müller, 1978), and once fertilization occurs, a new diploid sporophyte, referred to here as sporelings, begins to develop.

S. muticum on the other hand, is considered a rockweed (order Fucales) and exhibits a diplontic life history in which adults produce sperm and eggs, which undergo fertilization both in the water column and inside the reproductive conceptacles, leading to the formation of zygote/germlings. Like kelps, the large visible stage of rockweeds is diploid, but unlike kelp, gamete development and fertilization can take place entirely on the parent plant in reproductive structures called conceptacles (Norton, 1981). The different reproductive histories of *M. pyrifera* and *S. muticum* allow propagules to be easily distinguishable at the microscopic stage after release. *S. muticum* zygotes average at least 100 μm in diameter (Norton & Fetter, 1981), whereas *M. pyrifera* gametophytes are much smaller, averaging less than 10 μm in diameter (Reed, 1990).

Collection:

We collected reproductive structures from 12 adult individuals of each species via SCUBA from White Gulch and Marshall Beach in July 2020 and May 2021. Collection of *M. pyrifera* sporophylls for the experiment examining only abiotic stress occurred in July of 2020, whereas collection of both *M. pyrifera* sporophylls and *S. muticum* fronds for experiments examining biotic stress from *S. muticum* alone and in combination with abiotic stress took place in May 2021.

Immediately upon collection, *M. pyrifera* sporophylls and *S. muticum* fronds were cleaned in iodine and freshwater, layered in a cooler with seawater-moistened paper towels separating individual sporophylls, and transported to the Bodega Marine Laboratory (BML, 38.318164°N, 123.072019°W) for sporulation. Upon return to BML, *S. muticum* fronds were placed in a bucket of running seawater in the lab's Non-Indigenous Species shed with no light, while the *M. pyrifera* sporophylls were immediately prepared for spore release. The *M. pyrifera* sporophylls were soaked in seawater for 24 hours at either 12°C or 18°C, after which spore densities were determined using a hemocytometer (model number CTL-HEMM-GLDR, LW Scientific, Lawrenceville, U.S.A.). We then pipetted spores into the experimental Petri dishes to facilitate a settlement density of approximately 8 spores/mm^2 for 1x density treatments (minimum densities required for fertilization based on results of Reed, 1991), 16 spores/mm^2 for 2x density treatments, and 32 spores/mm^2 for 4x density treatments. After 24 hours, *S. muticum* receptacles were separated from the vegetative portion of the frond and also soaked in seawater for 24 hours at either 12°C or 18°C. 24 hours after *M. pyrifera* spore introduction to the petri dishes, *S. muticum* zygotes were transferred from the bottom of the collection jars using a pipette and introduced to the petri dishes at densities of 1 zygotes/ 72 mm^2 for 1x density treatments and 1 zygotes/ 36 mm^2 for 2x density treatments. The described densities were chosen in order to standardize biomass of propagules input into the dishes, where one *S. muticum* zygote was assumed to equal the volume of approximately 500 *M. pyrifera* spores.

Propagule Cultivation:

Petri dishes containing *M. pyrifera* spores and *S. muticum* embryos were then assigned to one of three laboratory microcosm studies to investigate the specific effects of 1) Source

location-specific effects of temperature and salinity, 2) density dependent effects of both inter- and intra- specific competition, and 3) the interacting effects of *S. muticum* presence, temperature, and salinity. Each experiment was run for four weeks. Petri dishes were randomly arranged on shelves within the incubators, and light was set at 12:12 photoperiod and 10-20 $\mu mol\ m^{-2}\ s^{-1}$ to mimic the low visibility of Tomales Bay and the fall season when *S. muticum* and *M. pyrifera* propagules have already been released. We changed the water in all experimental dishes every 2 to 3 days for the duration of each experiment in order to prevent anoxia and add standard 20 mL L^{-1} Provasoli nutrient mix to all treatment water to prevent nutrient limitation during growth (Provasoli, 1968). To prevent diatom overgrowth, we also added germanium dioxide at a ratio of 0.5 mL GeO_2 per one liter of seawater at 7 and 14 days after each experiment started (Shea & Chopin, 2007).

*Experiment 1: Location-specific effects of temperature and salinity***:**

Petri dishes containing 1x densities of *M. pyrifera* were placed in a full-factorial experiment crossing two temperatures (12°C and 18°C) and three salinities (20 psu, 26 psu, and 33 psu) based on oceanographic monitoring data collected in 2019 from Sacramento Landing, Tomales Bay (Figure B3). We then replicated each of the six temperature-salinity treatments for *M. pyrifera* propagules from each of the two source locations, White Gulch and Marshall Beach, to determine if there were any differences in *M. pyrifera* reproduction based on location within Tomales Bay. We assigned 10 petri dishes to each temperature-salinity-location cross, for a total of 120 petri dish microcosms.

Experiment 2: Density dependent effects:

To determine how density of competitors, both inter- and intraspecific, impacts *M. pyrifera* propagule growth and survival at ambient temperature and salinities, we developed a second factorial experiment using only *M. pyrifera* and *S. muticum* propagules sourced from White Gulch. In this experiment, we crossed two different densities of *M. pyrifera* (1x = 8 spores/mm^2; 2x = 16 spores/mm^2) with three different densities of *S. muticum* (0x = no *S. muticum*; 1x = 1 zygote/72mm^2; 2x = 1 zygote/36 mm^2) to assess the relative effects of inter and intraspecific competition. We also added one extra treatment with 4x (32 spores/mm^2) *M. pyrifera* and 0x *S. muticum* to compare high density intraspecific competition (4x *M. pyrifera*) with high density interspecific competition (2x *M. pyrifera* + 2x *S. muticum*). Each of the seven treatments was assigned five petri dish replicates each, for a total of 35 petri dishes.

Experiment 3: Interacting effects of S. muticum presence, temperature, and salinity:

To determine the interacting effects of competition and climate variables on *M. pyrifera* development, we set up a third full-factorial experiment crossing salinity and temperature using only propagules sourced from White Gulch. In this design, we grew *M. pyrifera* propagules together with *S. muticum* propagules under two density treatments (1x = 1 zygote/12mm^2; 2x = 1 zygote/6 mm^2) in petri dishes with the same two temperature (12°C and 18°C) and three salinity (20 psu, 26psu, and 33psu) combinations used when investigating abiotic stress alone. All dishes were settled with 1x *M. pyrifera* densities (8 spores/mm^2). Each of the 12 density-salinity-temperature crosses had five petri dish replicates for a total of 60 petri dishes.

Data Collection/Count Methods:

At the end of each experiment, we photographed three random locations within each petri dish using a Micropublisher 5.0 RTV digital camera (QImaging, Surrey, Canada) mounted on an inverted microscope at 40× magnification. Each photo encompassed 1.08 mm^2 of the Petri dish (7,853 mm^2 bottom surface area). *M. pyrifera* gametophytes and sporelings were easily distinguishable by size as they were much smaller than *S. muticum*, and in a photo editor, we counted the number of *M. pyrifera* females, males, sporelings, and eggs. Counts for each of the three photos were then summed and taken as the count for each dish. Since our study was primarily concerned with the effects of *M. pyrifera* reproduction, we did not document the growth and maturity of *S. muticum* over the course of our experiment, but we did count the total number of *S. muticum* within each dish in Week 2 of our experiment to ensure existing *S. muticum* densities matched the intended densities during inoculation (Figures B1 & B2). *M. pyrifera* females were determined to be "productive" if they had an attached egg/sporeling after 4 weeks. If a female did not have an egg/sporeling it was considered to be "non-productive".

Size Methods:

Once the digital images of kelp gametophytes were organized, they were individually imported into the ImageJ software to be measured. Using the measure function and free-hand line selection tool, each sporeling in a given image was traced using a handheld mouse or laptop mousepad. Area was recorded, and represents the total area covered by each sporeling. Area was calculated as the number of pixels highlighted and converted to μm^2 using a conversion factor of 71,330 pixels per 62,500 μm^2, which was calculated by measuring the area of a photo of a 0.0625 mm^2 hemocytometer cell at 40× magnification.

Statistical Methods:

All count and size data failed tests of normality and homoscedasticity, even after data was transformed, so all count outcome variables were analyzed using Generalized Linear Models (GLM, packages '*MASS*' and '*glmmTMB*'; Venables & Ripley, 2002; Brooks et al., 2017) and post-hoc pairwise comparisons (package '*emmeans*', Lenth, 2021) in R version 4.1.2 (R Core Team, 2021). Assumed distributions were determined by visually inspecting the residual plots of all models for homogeneity of variances and normality using the '*DHARMa*' package (Hartig, 2022). Counts for the "Location-specific effects of temperature and salinity (E1)" and "Interacting effects of *S. muticum* presence, temperature, and salinity (E3)" experiments were found to have a Negative Binomial distribution, whereas counts for the "Density dependent effects experiment (E2)" were found to have a Poisson distribution.

Counts for the "Location-specific effects of temperature and salinity (E1)" were modeled as responses to the fixed-effect variables of location, temperature, salinity, and all interactions. Counts for the "Interacting effects of *S. muticum* presence, temperature, and salinity (E3)" were modeled as responses to the fixed-effect variables of *S. muticum* density, temperature, salinity, and all interactions. Data for both "Location-specific effects of temperature and salinity (E1)" and "Interacting effects of *S. muticum* presence, temperature, and salinity (E3)" were originally run as models with 3-way interactions, but the models failed to converge because of the lack of data for specific treatment combinations. As a result, we subset our data to investigate specific 2-way interactions. Specifically, in E1, we subset 1) data from our low temperature treatment to investigate the independent and interacting effects of Source Location and salinity, and 2) data from our White Gulch location to investigate the independent and interacting effects of temperature and salinity. In E3, we subset 1) data from our low temperature treatment to

investigate the independent and interacting effects of *S. muticum* density and salinity, and 2) data from our 1X *S. muticum* treatment to investigate the independent and interacting effects of temperature and salinity. We also used the non-parametric Wilcoxon rank sum test to test whether there were significant differences between high and low temperature treatments in the Marshall Beach and 2X *S. muticum* treatments for E1 and E3, respectively.

Counts for the "Density dependent effects experiment (E2)" were modeled as responses to the fixed-effect variables of *M. pyrifera* density, *S. muticum* density, and all interactions. For all count data in E2, we also ran Welch's two-sample t-tests to assess the strength of intra- versus interspecific competition by comparing treatments with similar overall densities of 2X (1X kelp + 1X *S. muticum* vs. 2X kelp + 0X *S. muticum*), 3X (1X kelp + 2X *S. muticum* vs. 2X kelp + 1X *S. muticum*), and 4X (2X kelp + 2X *S. muticum* vs. 4X kelp + 0X *S. muticum*).

Size data were also analyzed with a GLM using a Gamma distribution for all experiments. Average number of gametophytes per dish was also calculated and included in the size model as a covariate to account for possible density dependence. We also separately analyzed the relationship between average size of sporelings per photo and the covariate (average number of gametophytes per photo) using a linear regression model (package *lme4*; Bates et al., 2015) that included only the covariate as a fixed effect. All statistical outputs from GLMs and pairwise comparisons are presented as supplementary tables in the Appendix.

Results:

*Location-specific effects of temperature and salinity (E1)***:**

Within this experiment, we found that high temperatures had a much larger negative effect than site or salinity on any count variables. We counted a total of one female gametophyte

and no eggs or sporelings (juvenile sporophytes) in all Marshall Beach + 18°C treatments, so we only examined the effects of temperature + salinity within the White Gulch population. Within White Gulch, we found significant temperature by salinity interactions (Table C2) for the number of females ($z = -3.887$, $df = 53$, $p < 0.001$), eggs ($z = -2.569$, $df = 53$, $p = 0.010$), and sporelings ($z = -2.563$, $df = 53$, $p = 0.010$), but not males ($z = -0.002$, $df = 53$, $p = 0.999$). High temperatures resulted in significant declines for all variables (Table C4) in White Gulch regardless of salinity level (except for males in the 20psu treatment, $t = -0.002$, $df = 53$, $p = 0.999$). We also tested the effects of temperature in the Marshall Beach location using non-parametric tests and found significant declines under high temperature for all variables (Table C5).

Using data from only the low temperature (12°C) treatments to better understand the effects of location + salinity, we found no significant interactions between source location and salinity for any count variable (Table C3). Source location also had no individually significant effects on any count variable (Table C7), except for the number of males at 26 psu ($t = -6.074$, $df = 53$, $p < 0.001$) and 33psu ($t = -3.982$, $df = 53$, $p < 0.001$).

We analyzed the independent effects of salinity within all treatments combinations except for the 18°C + Marshall Beach, and results tended to vary for each count variable (Figure 2.2). For both locations, the number of female gametophytes in the low temperature treatment was significantly lower at 33 psu than 20 psu (White Gulch: $t = 4.776$, $df = 53$, $p < 0.001$; Marshall Beach: $t = 3.806$, $df = 53$, $p = 0.001$) or 26 psu (White Gulch: $t = 4.865$, $df = 53$, $p < 0.001$; Marshall Beach: $t = 5.137$, $df = 53$, $p < 0.001$). The number of male gametophytes, on the other hand, was significantly highest in 33psu for all site by temperature combinations (Table C6). At low temperatures for both locations, the number of sporelings was significantly lower at 33 psu than 20 psu (White Gulch: $t = 4.629$, $df = 53$, $p < 0.001$; Marshall Beach: $t = 3.389$, $df = 53$, $p = 0.004$) or

26 psu (White Gulch: t =4.532, df=53, p<0.001; Marshall Beach: t =4.243, df=53, p<0.001). The number of eggs did not vary significantly based on salinity, but similarly to females and sporelings, the mean number of eggs was lower at 33 psu than 20 or 26 psu.

Overall, the size of sporelings exhibited a significant temperature by salinity interaction in White Gulch (Figure 2.3, Table C2, z =-3.887, df=584, p<0.001), but only a significant response to salinity under the Low Temperature subset model (Table C3, z =-3.806, df=1168, p<0.001). Sporelings were significantly larger under high salinities regardless of population or temperature (Figure 2.3, Table C6. Low temperatures resulted in significantly larger sporelings in the White 33 psu treatment specifically (z =3.238, df=584, p=0.0012). There was generally no relationship between size and the number of gametophytes present across treatments, but the 26 and 33 psu Salinity treatments did show a significantly positive relationship (Table C1).

Density dependent effects (E2):

Across treatments, increased numbers of *M. pyrifera* spores led to increased number of gametophytes (Figure 2.4). Both female (z =-2.456, df=26, p=0.0373) and male (z =-4.065, df=26, p=0.0001) gametophytes exhibited significant increases in numbers in petri dishes inoculated with 4X *M. pyrifera* spores (32 spores/mm2), and males also showed a significant increase under 2X *M. pyrifera* (16 spores/mm2) spore inoculation (Table S9, z =-2.493, df=26, p=0.0339). There were no significant effects of individual *S. muticum* densities nor statistical interactions with *M. pyrifera* densities (Table C8).

The number of eggs and sporelings that developed after four weeks showed no significant interactions between initial *M. pyrifera* and *S. muticum* densities (Table C8). While the mean number of eggs was higher under higher kelp spore inoculations (Table 2.1), these increases

were not significant (Table C9). Sporeling numbers, on the other hand, remained relatively independent of initial *M. pyrifera* inoculation density for both 0X and 1X *S. muticum* densities. Under the 2X *S. muticum* treatments, however, number of sporelings in 1X *M. pyrifera* treatments declined significantly under 2X *S. muticum* densities (Table C10, z =3.285, df=26, p=0.0029), but then increased significantly under the 2X *M. pyrifera*, 2X *S. muticum* treatment to levels consistent with the other 2X kelp treatments (Table C10, z =-2.773, df=26, p=0.0154).

Analyses of the relative strength of intra- versus interspecific competition reveal that intraspecific competition between *M. pyrifera* propagules is less important than interspecific competition between *M. pyrifera* and *S. muticum* propagules. In treatments with similarly inoculated total biomass densities, *M. pyrifera* counts of females, males, and eggs were consistently higher under high *M. pyrifera* density treatments (2X kelp + 0X *S. muticum*, 2X kelp + 1X *S. muticum*, 4X kelp) than low *M. pyrifera* high *S. muticum* density treatments (1X kelp + 1X *S. muticum*, 1X kelp + 2X *S. muticum*, 2X kelp + 2X *S. muticum*) (Table 2.1). A closer look at the mean number of male and female gametophytes within each treatment, however, reveals that while the increase in number of gametophytes is not directly proportional to the number of spores; in other words, the increase in the number of gametophytes dampens with increasing spore density. Additionally, the number of sporelings had little relationship with inoculation densities (except when M. pyrifera and S. muticum were at levels of 4X and 2X, respectively), potentially as a result of intraspecific competiton. These results thus indicate that there may be significant intraspecific competition in this study.

There was no significant effect of initial densities of either *M. pyrifera* or *S. muticum* on sporeling size (Figure B4, Tables C8, C9, C10). There was also no relationship between the size and number of gametophytes present across all treatments, except for the 2X *M. pyrifera* + 0X *S.*

muticum treatment, which had a significant positive relationship between gametophyte number and size (Table C1, R2=0.220, df=20, p=0.016).

Interacting effects of S. muticum presence, temperature, and salinity (E3):

Due to poor survival at high temperatures (see Methods) we used the 1X *S. muticum* treatment data to test temperature by salinity interactions and low temperature treatment data to test salinity by *S. muticum* interactions. The number of males and eggs was not significantly affected by any treatment regardless of model. Counts of females and sporelings, however did vary significantly with certain treatments (Figure 2.5).

Within all 1X *S. muticum* treatments, only females showed a significant temperature by salinity interaction (Table C11, z =-2.295, df=23, p=0.022). The number of females and juveniles were both significantly reduced under high temperatures at 26 psu (Table C13), and females also decreased under high temperatures at 20 psu (Table C13, t =-3.125, df=23, p=0.005). Non-parametric tests also showed that numbers of both females and juveniles declined under 18°C in the 2X *S. muticum* treatment (Table C14).

In low temperature treatments, we saw no significant interactions between salinity and *S. muticum* density for any variable (Table C12). *S. muticum* density, however, did have significant effects on M. pyrifera reproduction at low temperatures (Table C16), as the number of females was significantly reduced at 26 psu (t =2.011, df=23, p=0.056) and the number of sporelings was significantly reduced at both 20 psu (t =2.127, df=23, p=0.044) and 26 psu (t =2.069, df=23, p=0.050).

We analyzed the independent effects of salinity within all treatments combinations except for the 18°C + 2X *S. muticum*, but only found significant effects in low temperature treatments,

likely because high temperatures were associated with such low levels of survival. The number of females was significantly higher in 26 psu than 33 psu ($t = 2.617$, $df = 23$, $p = 0.039$) in the 1X *S. muticum* treatment, and the number off sporelings was similarly highest in the 26 psu treatment for both the 1X ($t = 3.455$, $df = 23$, $p = 0.006$) and 2X *S. muticum* treatments ($t = 2.721$, $df = 23$, $p = 0.032$).

The size of sporelings was only significantly impacted by salinity in the 1X S. muticum - 12°C treatment specifically. Sporelings in this treatment grew significantly larger with higher salinities (Figure B5, Table C15), where 33 psu had the largest sporelings, and 20 psu had the smallest. Most treatments had no significant correlation between sporeling size and gametophyte number (Table C1), except the 1X S. muticum + 12°C + 26 psu treatment, which showed a significant positive relationship between sporeling size and gametophyte number ($R^2 = 0.173$, $df = 31$, $p < 0.009$).

Discussion:

Climate change is affecting coastal and estuarine ecosystems worldwide, but localized populations specifically adapted to certain combinations of abiotic variables face a unique threat of extinction. In this study, we examined the responses of a uniquely estuarine population of *M. pyrifera* in Northern California to temperature, salinity, and competitive stress at microscopic life stages. Our results indicate that high temperatures (18°C) have the greatest negative impact on *M. pyrifera* microscopic growth and development, followed to a lesser extent by *S. muticum*. Lower salinity (20-25 psu), in contrast, may enhance reproduction in Tomales Bay populations.

High temperatures result in drastic decreases in reproduction:

The most specific and consistent variable affecting the reproduction of *M. pyrifera* in our study was high temperature (18°C). Across variables, high temperature consistently resulted in dramatic declines in numbers of gametophytes and sporelings, and occasional declines in sporeling size. These results are consistent with numerous other studies that have investigated the effects of temperatures 18°C and above on gametophytes and sporeling development (Buschmann et al., 2004; Gaitán-Espitia et al., 2014; Hollarsmith et al., 2020; Le et al., 2022; Muñoz et al., 2004), and other studies were able to show the same adverse effects we saw at temperatures as low as 15°C (Shukla & Edwards, 2017). These results lead us to believe that one of the primary limiting factors regulating *M. pyrifera* presence in estuaries and bays may be high temperature. While locations in mid-Tomales Bay such as Marshall Beach, the most estuarine kelp site, generally continue to experience lower temperatures even in the summer, sites less than 2km further into the bay, such as Sacramento Landing, regularly experience summer time temperatures that exceed 18°C (Figure B3, Cheng & Grosholz, 2016; Kimbro et al., 2009; Hollarsmith et al., 2020).

Global climate change has been associated with increasing sea surface temperature (Dunstan et al., 2018; Lima & Wethey, 2012; Reid & Beaugrand, 2012), increasing frequency and intensity of marine heatwaves (Gentemann et al., 2017; Oliver et al., 2018; Shi et al., 2021), and changes in upwelling regimes (Bakun et al., 2015; Di Lorenzo et al., 2008; García-Reyes et al., 2015; García-Reyes et al., 2020), all of which affect the temperature profile of coastal ocean waters and resident biological communities (Smale et al., 2019). In this study, we chose to look at two temperatures 6°C apart that represent natural environmental variation in Tomales Bay, but the results of this study may have implications for the fate of *M. pyrifera* populations under climate change, especially in regards to marine heatwaves. Marine heat waves in particular are

expected to dramatically increase in frequency by the end of the 21st century and have already increased in the past three decades (Frölicher et al., 2018; Oliver et al., 2018; Smale et al., 2019). As recently as 2014-2016, a multiyear marine heatwave called "the Blob" resulted in temperature anomalies of up to 5°C off the coast of North America. Throughout the past decade marine heatwaves have resulted in drastic kelp canopy losses globally (McPherson et al., 2021; Filbee Dexter et al., 2020), and shifting ecosystem steady states towards urchin-barrens (Rogers-Bennett & Catton, 2019; Carnell & Keough, 2020). Significant *M. pyrifera* canopy losses have often been seen in areas where marine heat wave temperatures exceed 18°C (Butler et al., 2020; Tait et al., 2021; Arafeh-Dalmau, 2019; Michaud et al., 2020; Tolimieri et al., 2023; Fleischman et al. 2020). In addition to the decline in reproductive output as shown in this study and others (Buschmann et al., 2004; Gaitán-Espitia et al., 2014; Hollarsmith et al., 2020; Le et al., 2022; Leal et al., 2017; Muñoz et al., 2004; Shukla & Edwards, 2017), high temperatures also can cause oxidative damage (Umanzor et al., 2021) and reduce photosynthetic capacity (Sanchez-Barredo et al., 2020; Umanzor et al., 2021), nitrogen acclimation (Fernandez et al., 2021), and growth rates (Umanzor et al., 2021; Fernandez et al., 2021) of *M. pyrifera*. Our results indicate that even with some survival of adults at high temperatures, the dramatic loss of microscopic stages at 18°C may limit recovery of kelp forests if warm temperatures persist.

Ultimately, loss of kelp forests due to increasing temperatures under climate has compounding effects that echo throughout marine ecosystems, including ecosystem state shifts towards urchin barrens (Rogers-Bennett & Catton, 2019; Carnell & Keough, 2020; Tolimieri et al., 2023), loss of commercially and ecologically important fisheries (McPherson et al. 2021; Arafeh-Dalmau, 2019), loss of invertebrate biodiversity (Arafeh-Dalmau, 2019; Michaud et al., 2022), and increased presence of invasive species (Arafeh-Dalmau, 2019; Michaud et al., 2022).

While research is currently being done to see whether thermal acclimation of *M. pyrifera* to high temperatures is possible (Aitken & Whitlock, 2013; Schmid et al., 2020; Fernandez et al., 2021; Fredriksen et al., 2020; Vranken et al., 2021), more research is needed to better protect the status of this important canopy species in a changing world.

Local acclimation to salinity:

We originally hypothesized that low salinities would be extremely stressful for the generally marine species *M. pyrifera* due to adaptation to higher salinity levels, but we ultimately rejected this hypothesis. Instead, lower salinity (20-26 psu) had mixed effects on *M. pyrifera* reproduction, both increasing the number of gametophytes and offspring that we saw and reducing the size of sporelings. These seemingly contrasting results of increased number but reduced size could be a result of either the direct impacts of salinity on kelp physiology, or the indirect effects of salinity on kelp interactions with other organisms, such as microbial symbionts. Assuming the effects of salinity are primarily physiological, we have developed two new potential hypotheses about the effects of salinity on *M. pyrifera* reproduction: 1) Local adaptation to lower salinity is resulting in more gametophytes and sporelings, but osmotic stress under lower salinity is causing reduced growth and smaller sporeling sizes, or 2) more stress from low salinity is causing *M. pyrifera* gametophytes to allocate more effort into reproduction, which is why we are seeing more gametophyte and sporelings at lower salinities but the sporelings are much smaller.

Our first hypothesis that *M. pyrifera* in Tomales Bay may be adapted to local salinity levels is consistent with previous studies that found reproductive persistence under low (20-30 psu) salinity conditions in Chile (Buschmann et al., 2004; Buschmann et al., 2014; Rodriguez et

al., 2019). In other kelps as well, such as *Nereocystis luetkeana*, *Eularia fistulosa*, and *Saccharina latissima*, while lowered salinity (26 psu) did somewhat decrease spore settlement and gametophyte development, these processes were still ongoing at lower salinity (Lind & Konar, 2017). Our second hypothesis that salinity stress is increasing allocation to reproduction is consistent with the results of several other studies that show increased growth or reproductive output under stress. For example, previous studies of the effects of high temperature on *M. pyrifera* and *Undaria pinnatifida* growth found that high temperature stress (16°C) resulted in an increased growth rate in both kelps (Leal et al., 2017). Additionally, in *Nereocystis luetkeana*, temperature stress resulted in more production of eggs and sporelings by females and higher offspring to female ratios (Korabik et al., 2023).

For both hypotheses, osmotic stress may be playing a significant role in limiting either the number or size of *M. pyrifera* microstages, but he relationship between salinity and *M. pyrifera* physiology have not been well studied. Studies of osmotic stress on another kelp species, *Laminaria digitata*, found that exposure to low (20 psu) salinities reduced iodine accumulation, and even at high salinities, the low tissue iodine levels resulted in photoinhibition (Nitschke & Stengel, 2013). In order to truly determine how osmotic stress may impact kelp microstages, the specific physiological effects of lower salinity on *M. pyrifera* reproduction and growth, and kelps in general, still need to be better studied.

California's precipitation regime is jointly controlled by sea surface temperature and atmospheric processes (Hu et al., 2021; Beaudin et al., 2023), both of which are being strongly affected by changing climate. While annual precipitation in California and the North American West has decreased over the past century, the frequency and intensity of extreme precipitation events has been increasing (Easterling et al., 2017; Gernushov et al., 2017). Atmospheric rivers

in particular are expected to increase in both frequency and intensity in the coming century as a result of warmer atmospheres and increasing atmospheric moisture content (Gao et al., 2015; Gershunov et al., 2019; Hagos et al., 2016; Payne & Magnusdottir, 2015; Lu et al., 2018; Warner et al., 2015). Increasing freshwater input to estuarine and coastal ecosystems due to large precipitation events, run-off, and riverine outflow may negatively impact marine and coastal biological communities, if residents have strict salinity tolerances. Our results suggest that even in high precipitation years, *M. pyrifera* populations will be unlikely to experience recruitment failures as a result of average lowered salinity levels.

Increased S. muticum *densities have negative effects on* M. pyrifera *reproduction:*

While the number of studies investigating competition at microscopic kelp stages is increasing, the topic has not been well studied, partially due to difficulties detecting gametophytes in the field and assessing the main mechanisms of competition (reviewed in Edwards, 2022). While several studies have found that competition at kelp microstages can take the form of chemical deterrents or the induction of premature gamete release (Amsler et al., 1992; Maier et al., 2001), competition at kelp microstages has most often been quantified as reduced reproductive output of one species in the presence of another, and outcomes can be influenced by sedimentation, order of species settlement (Traiger & Konar, 2017), temperature (Pereira et al., 2011; Zacher et al., 2019), and competition with understory algae for light (Layton et al., 2020; Tatsumi & Wright, 2016). Previous studies on *M. pyrifera* microstage competition with other species has found that other native kelps such as *Pterygophera californica* and *Ecklonia arborea* can suppress *M. pyrifera* recruitment (Reed, 1990; Reed et al., 1991; Howard, 2014), whereas *M. pyrifera* is able to suppress recruitment of *Nereocystis luetkeana*, *Egregia*

menziesii, and *Alaria marginata* (Howard, 2014; Christensen, 2018). This study provides a first look at the competitive effects of invasive *S. muticum* densities on *M. pyrifera* microstages. While our results show that *S. muticum* propagule density was not a main determinant of *M. pyrifera* gametophyte survival and reproduction, our results indicate that high densities of *S. muticum* can have negative impacts on *M. pyrifera* female gametophyte and new diploid sporeling stages specifically. However, we did not see any interactions between *S. muticum* density and salinity or temperature, and there were no significant effects of *S. muticum* on *M. pyrifera* sporeling size.

While we saw some negative effects of *S. muticum* presence that might reduce kelp abundance, the effect was not great enough that we believe competition from *S. muticum* at the gametophyte and early sporophyte stages threatens to eliminate *M. pyrifera* from any locations. While previous studies have shown that *S. muticum* can reduce *M. pyrifera* populations due to shading (Ambrose & Nelson, 1982; Steen, 2004; Britton-Simmons, 2004), our results are consistent with other studies that found that *S. muticum* populations can have negative or negligible effects on seaweed recruitment and growth (Ambrose & Nelson, 1982), biomass (Wernberg et al., 2004; Sánchez et al., 2005), and cover (DeWreede, 1983). Competition among algal species can lead to strong effects on their populations and this can be augmented by climate change, leading to ecosystem-wide shifts in the abundance of the dominant species (reviewed in Edwards & Connell, 2012).

While no studies have previously investigated the interactions of the microscopic stages of *S. muticum* and *M. pyrifera* or how climate change may influence this interaction, a study of the effects of temperature on *M. pyrifera* and *S. muticum*'s sister species, *S. horneri*, similarly found that *M. pyrifera* microstage development was most greatly influenced by warm

temperatures, and to a lesser extent, *S. horneri* density (Bishop, 2021). These results suggest that while *M. pyrifera* populations may be reduced due to shading by adults, microscopic stage development will likely be more negatively impacted by temperature increases than micro-stage competition with invasive propagules.

Climate Change and Invasion: Less than the sum of their parts?

Bioclimate models show that under a warming climate, invasion intensity is predicted to drastically increase by mid-century (Cheung et al., 2009), and thus understanding how climate change and species interact is critical to predict the future of valuable native ecosystems. Invasive species can have impacts not only on native species that share their same trophic level or niche, but throughout entire communities via effects on multiple trophic levels (Anton et al., 2019; Grosholz & Ruiz, 2009; Thomsen et al., 2014; Maggi et al., 2015). Invasive species are likely to fare better than native species under changing climate regimes (Sorte et al., 2013), and often have the greatest impacts in areas that match, or are slightly cooler than, their thermal range of origin (Bennett et al., 2021). Previous reviews and syntheses have generally found synergistic effects of multiple stressors on natural systems (Crain et al., 2008; Gunderson et al., 2015; Kroeker et al., 2013; Kroeker et al., 2017; Przelawski et al., 2015). A more recent review found that the cumulative effects of bioinvasions and climate change have negative impacts on native communities, but generally the result of interacting stressors are simply additive (equal to the sum of their parts), or often antagonistic (less than the sum of their parts) (Cheng et al., 2015; Lopez et al., 2022). Our results contribute to the body of research indicating that, while invasive species can have negative effects on native species and communities, they are not likely to significantly exacerbate the responses of those species and communities to climate variables.

Rather, whether changing climate variables, such as high temperatures, or species invasions pose the greatest risk to native species and community function will likely be situation-specific.

In this study, we show that high temperatures from changing climate pose a much higher risk to *M. pyrifera* reproduction than the presence of the invasive competitor, *S. muticum*. Our results indicate that in order to accurately identify risks and develop the best ecosystem-based management strategies, managers need to understand the specific impacts of potential local stresses, both abiotic and biotic. While climate change and invasive species effects on native species are not often magnified by each other, in a world experiencing change more rapidly than organisms can adapt, reducing the number of stressors, biotic or abiotic, is still important.

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TABLES AND FIGURES

Table 2.1: Wilcoxon rank sum tests of similar density treatments in E2 to determine the relative importance of inter and intraspecific competition on Macrocystis reproduction.

Variable	Overall Density	Macrocystis Density	Sargassum Density	Mean	df	W	p-value
Females	2X	1X	1X	5.2	8	5.5	0.169
		2X	0X	7.6			
	3X	1X	2X	3.4	8	2.5	**0.044**
		2X	1X	6.8			
	4X	2X	2X	6.6	6	4.5	0.112
		4X	0X	10.0			
Males	2X	1X	1X	4.2	6	1	**0.021**
		2X	0X	8.2			
	3X	1X	2X	3.4	7	5.5	0.168
		2X	1X	5.4			
	4X	2X	2X	6.0	8	2	**0.036**
		4X	0X	11.8			
Eggs	2X	1X	1X	0.0	4	0	**0.007**
		2X	0X	3.4			
	3X	1X	2X	0.4	7	9	0.488
		2X	1X	0.8			
	4X	2X	2X	1.4	5	3.5	0.070
		4X	0X	4.8			
Juveniles	2X	1X	1X	5.0	6	13	1.000
		2X	0X	4.8			
	3X	1X	2X	1.0	6	0.5	**0.014**
		2X	1X	4.2			
	4X	2X	2X	4.0	7	18	0.290
		4X	0X	2.2			
Juvenile Sizes	2X	1X	1X	27630.6	44	382	**0.022**
		2X	0X	16336.1			
	3X	1X	2X	21139.7	2	37	0.680
		2X	1X	18220.1			
	4X	2X	2X	15725.5	28	139	0.145
		4X	0X	9360.2			

Figure 2.1: Map of Tomales Bay. Location of M. pyrifera kelp canopies are highlighted in green along the west shore of Tomales Bay. We collected *M. pyrifera* individuals from two sites in Tomales Bay (White Gulch and Marshall Beach), and *S. muticum* individuals from one site (White Gulch).

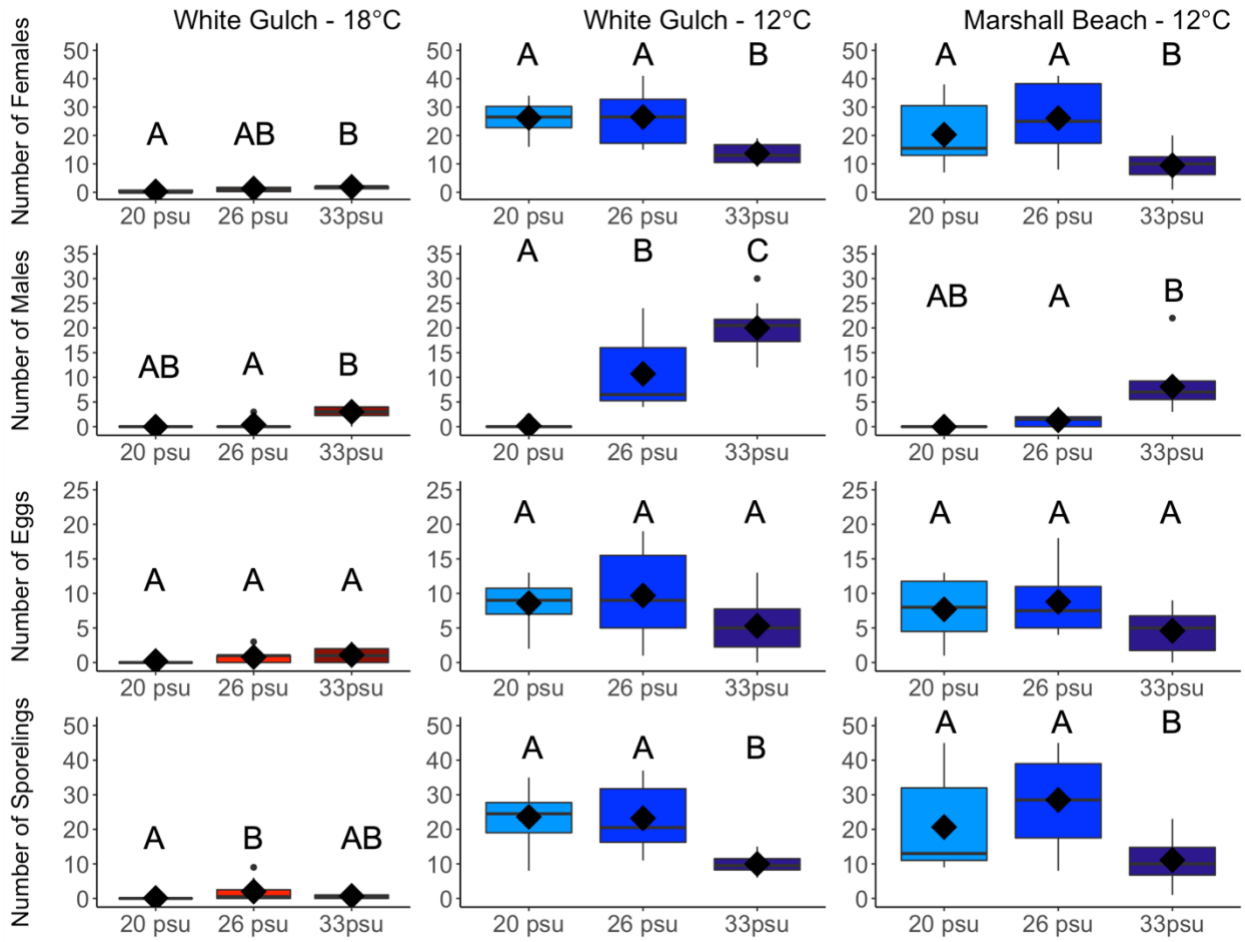

Figure 2.2: Number of gametophytes (female and male) and offspring (eggs and sporelings) summed across three photo replicates after 4 weeks of growth. Top two panels represent treatments sourced from White Gulch, while the bottom two panels represent treatments sourced from Marshall Beach. Left panels represent 12°C temperature treatments, while the right panels represent 18°C temperature treatments. The box plots summarize the mean (diamond) and median (box midline) for each treatment, the first and third quartiles (upper and lower box limits), outliers within 1.5 times the inter-quartile range (vertical lines), and outliers beyond that range (dots). Letters over boxes represent significance of different salinity treatments.

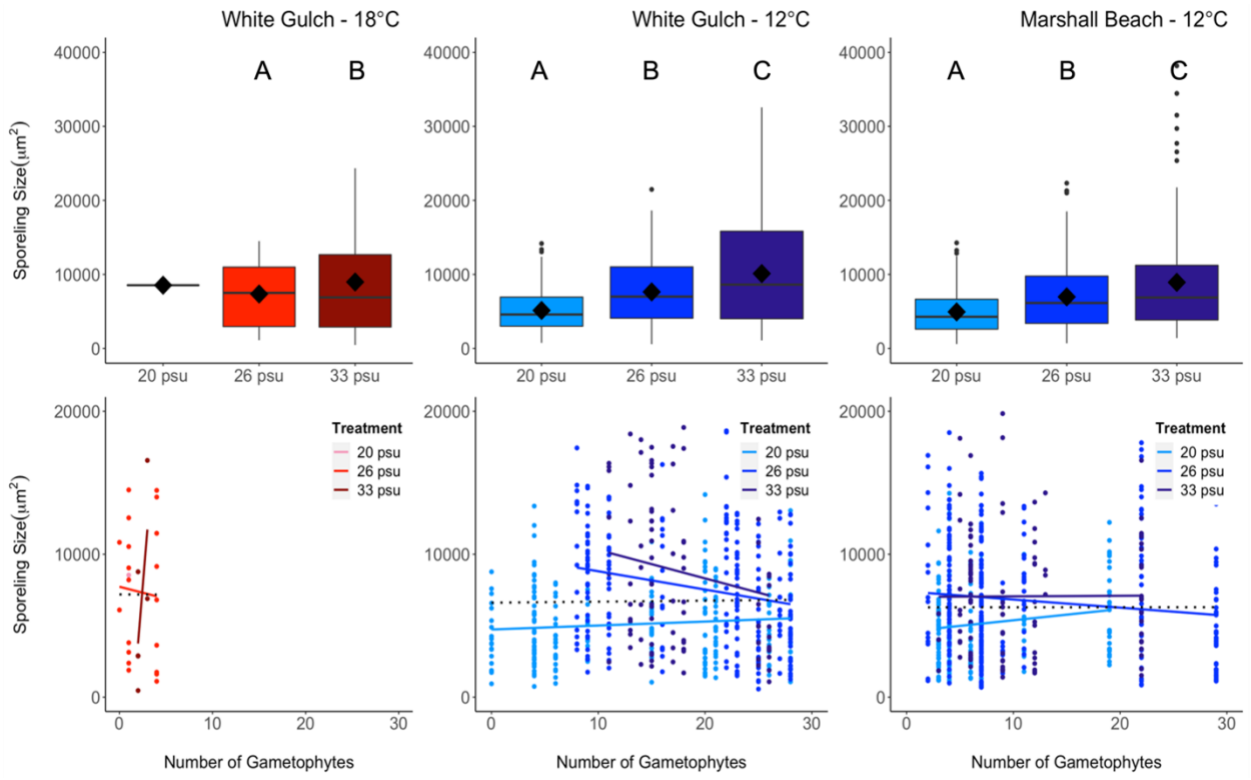

Figure 2.3: Sizes of Sporelings from tests of location-specific effects of temperature and salinity (E1). Top panels show the average size of sporelings after 4 weeks of growth with box plots that summarize the mean (diamond) and median (box midline) for each treatment, the first and third quartiles (upper and lower box limits), outliers within 1.5 times the inter-quartile range (vertical lines), and outliers beyond that range (dots). The bottom panels show the relationship of the covariate (mean number of gametophytes) to the response variable (mean sporeling size). Colored lines represent different salinity treatments within each temperature-location treatment, and the dotted black line represents the overall trend across salinity treatments. Letters over boxes represent significance of different salinity treatments.

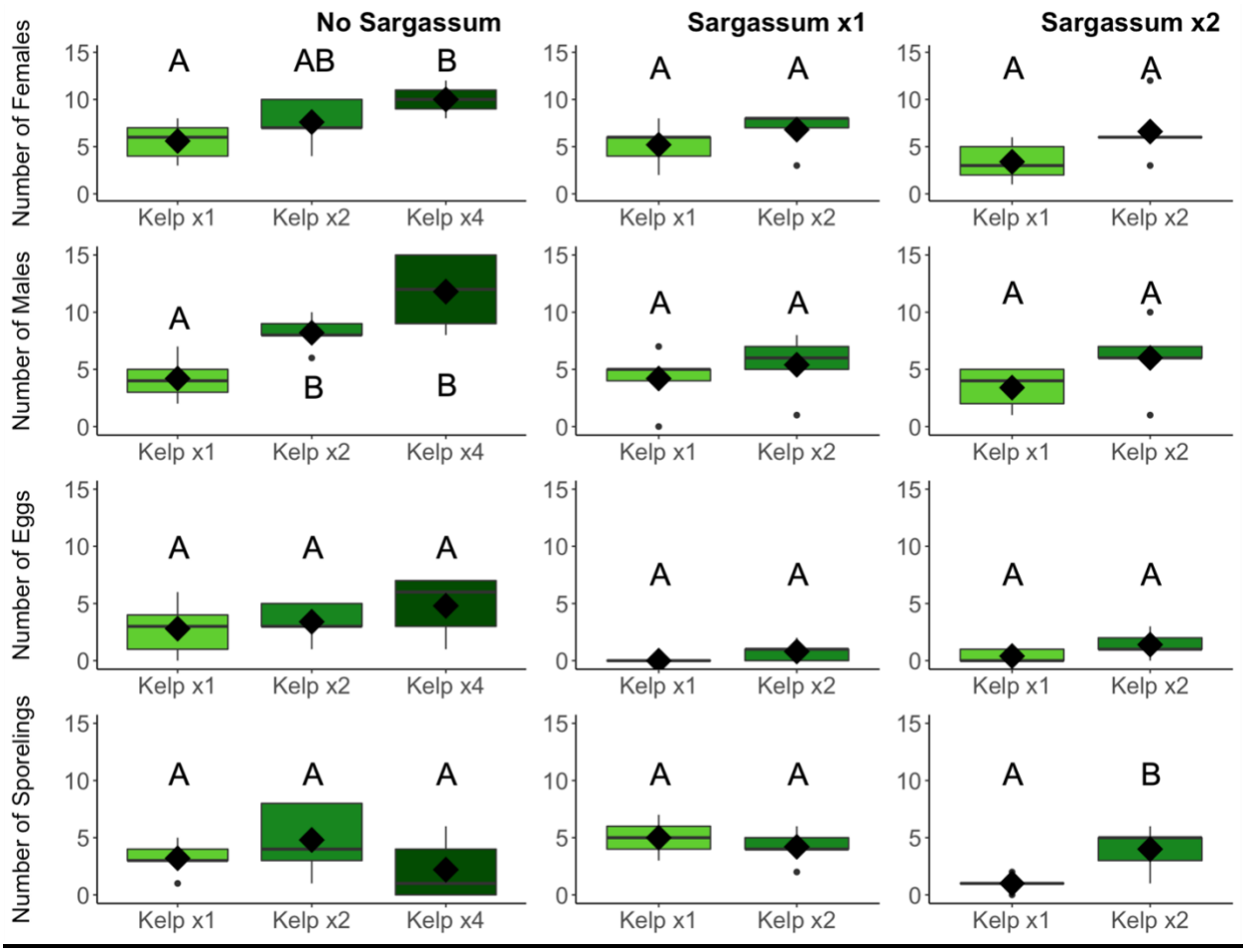

Figure 2.4: Number of gametophytes (female and male) and offspring (eggs and sporelings) summed across three photo replicates after 4 weeks of growth under different initial densities of giant kelp and wireweed inoculation. The box plots summarize the mean (diamond) and median (box midline) for each treatment, the first and third quartiles (upper and lower box limits), outliers within 1.5 times the inter-quartile range (vertical lines), and outliers beyond that range (dots). Letters over boxes represent significance of different kelp density treatments.

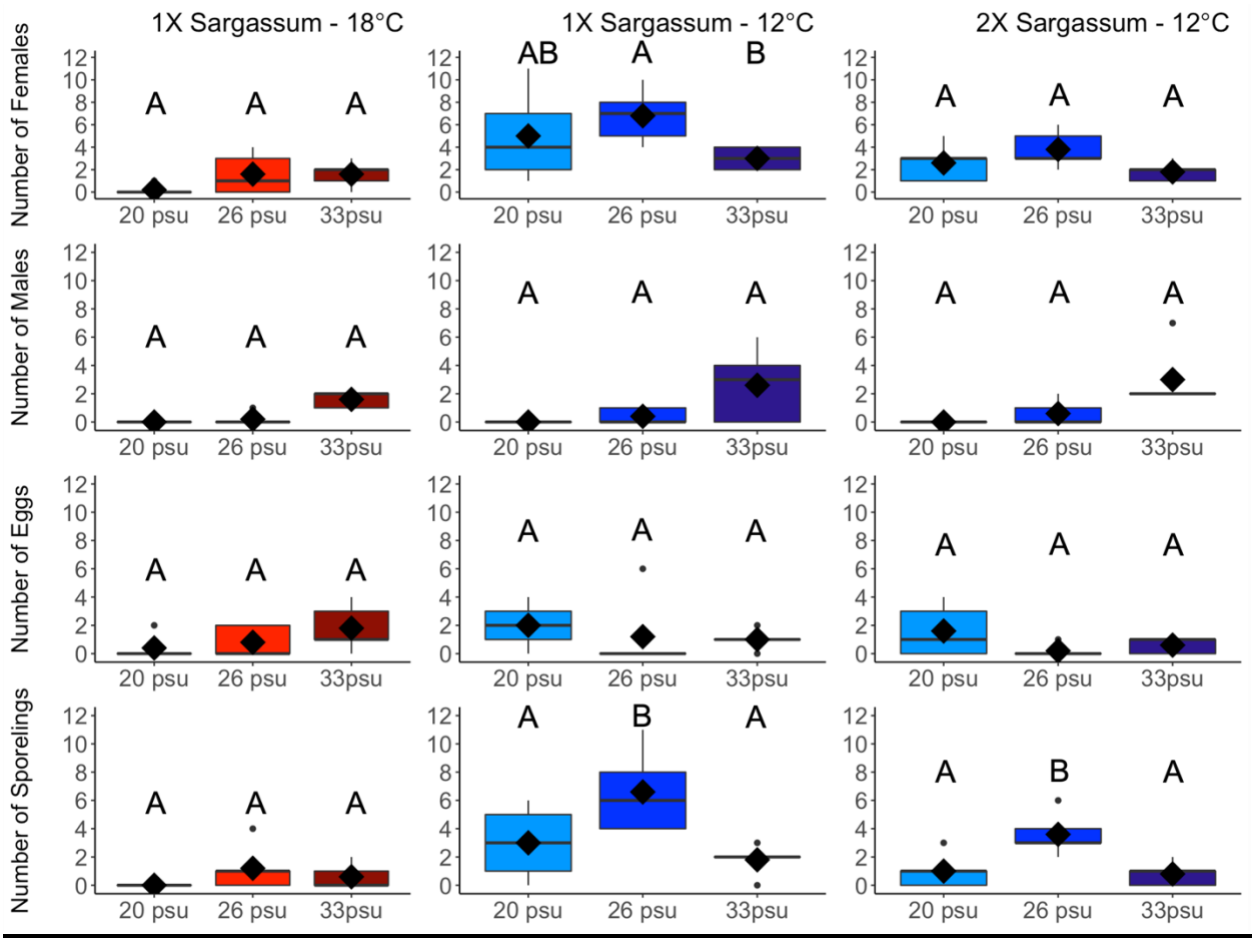

Figure 2.5: Number of gametophytes (female and male) and offspring (eggs and sporelings) summed across three photo replicates after 4 weeks of growth. Top two panels represent treatments inoculated with 1X Sargassum, while the bottom two panels represent treatments inoculated with 2X Sargassum. Left panels represent 12°C temperature treatments, while the right panels represent 18°C temperature treatments. The box plots summarize the mean (diamond) and median (box midline) for each treatment, the first and third quartiles (upper and lower box limits), outliers within 1.5 times the inter-quartile range (vertical lines), and outliers beyond that range (dots). Letters over boxes represent significance of different salinity treatments.

APPENDIX B: Supplementary Figures

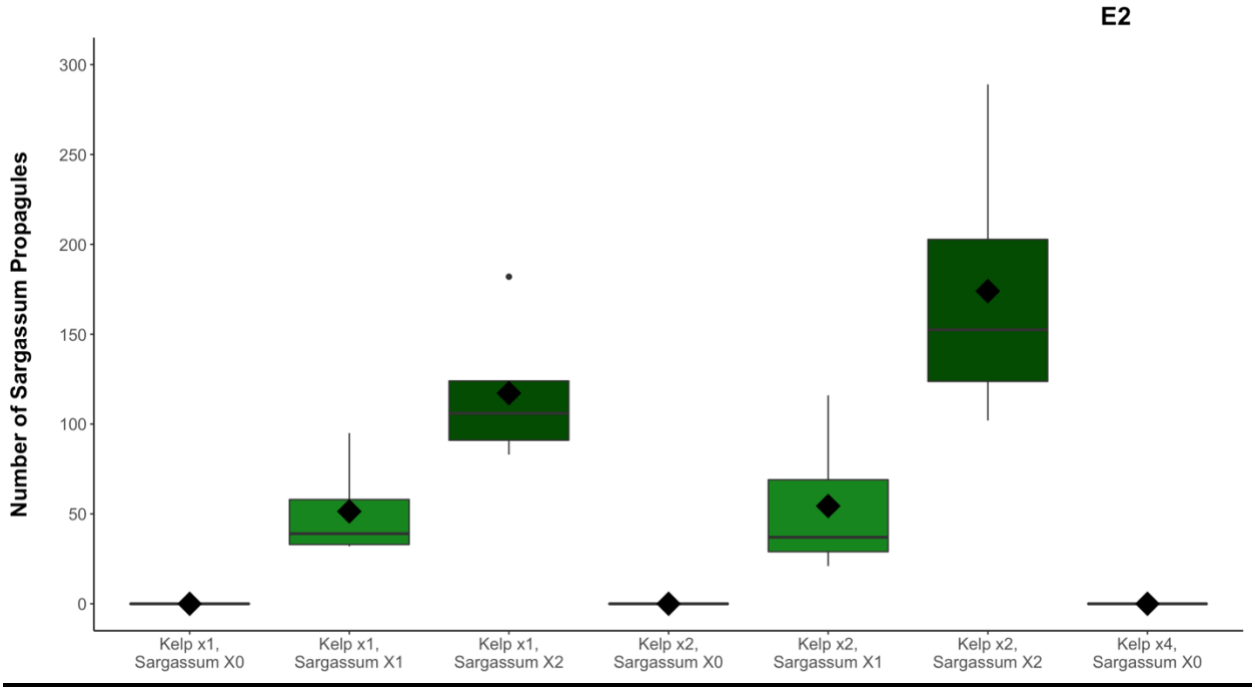

Figure B1: Number of Sargassum propagules present in each dish after 2 weeks of growth under different initial densities of giant kelp and wireweed inoculation. The box plots summarize the mean (diamond) and median (box midline) for each treatment, the first and third quartiles (upper and lower box limits), outliers within 1.5 times the inter-quartile range (vertical lines), and outliers beyond that range (dots).

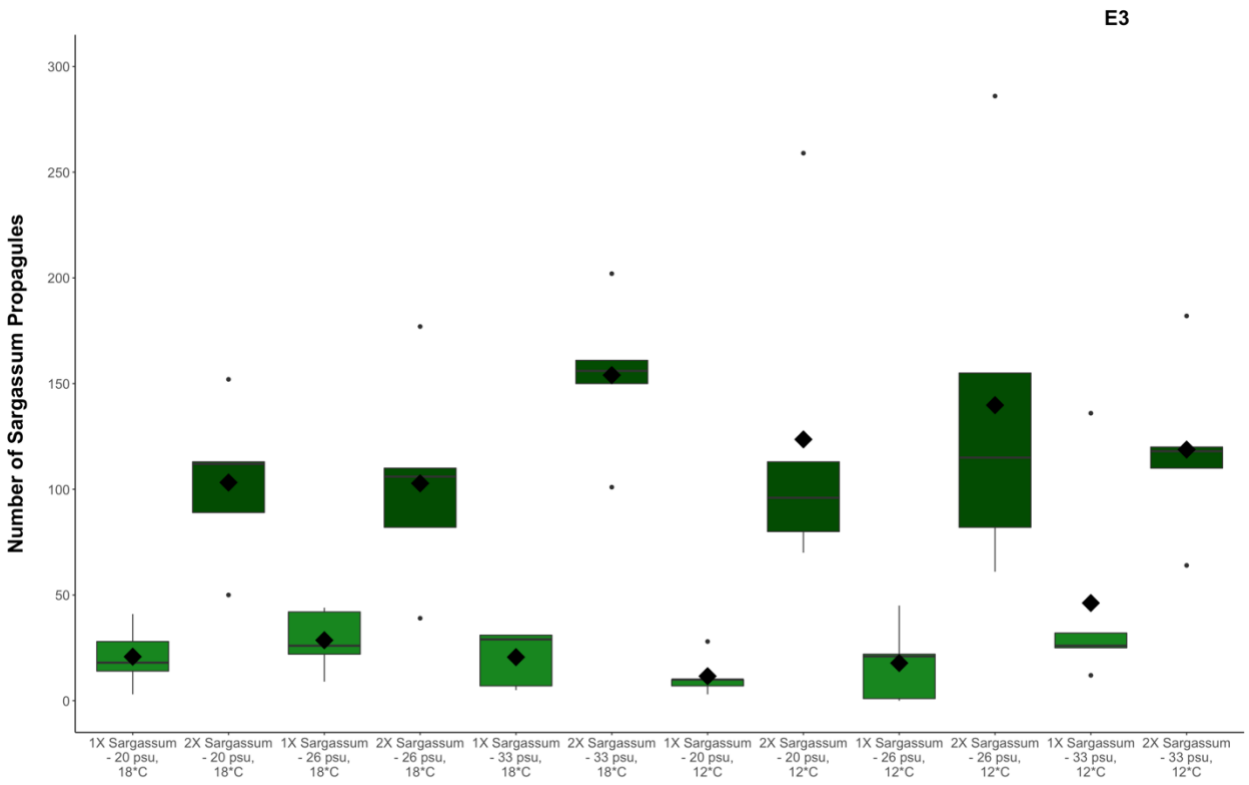

Figure B2: Number of Sargassum propagules present in each dish after 2 weeks of growth in Experiment 3, investigating the interacting effects of S. muticum presence, temperature, and salinity. The box plots summarize the mean (diamond) and median (box midline) for each treatment, the first and third quartiles (upper and lower box limits), outliers within 1.5 times the inter-quartile range (vertical lines), and outliers beyond that range (dots).

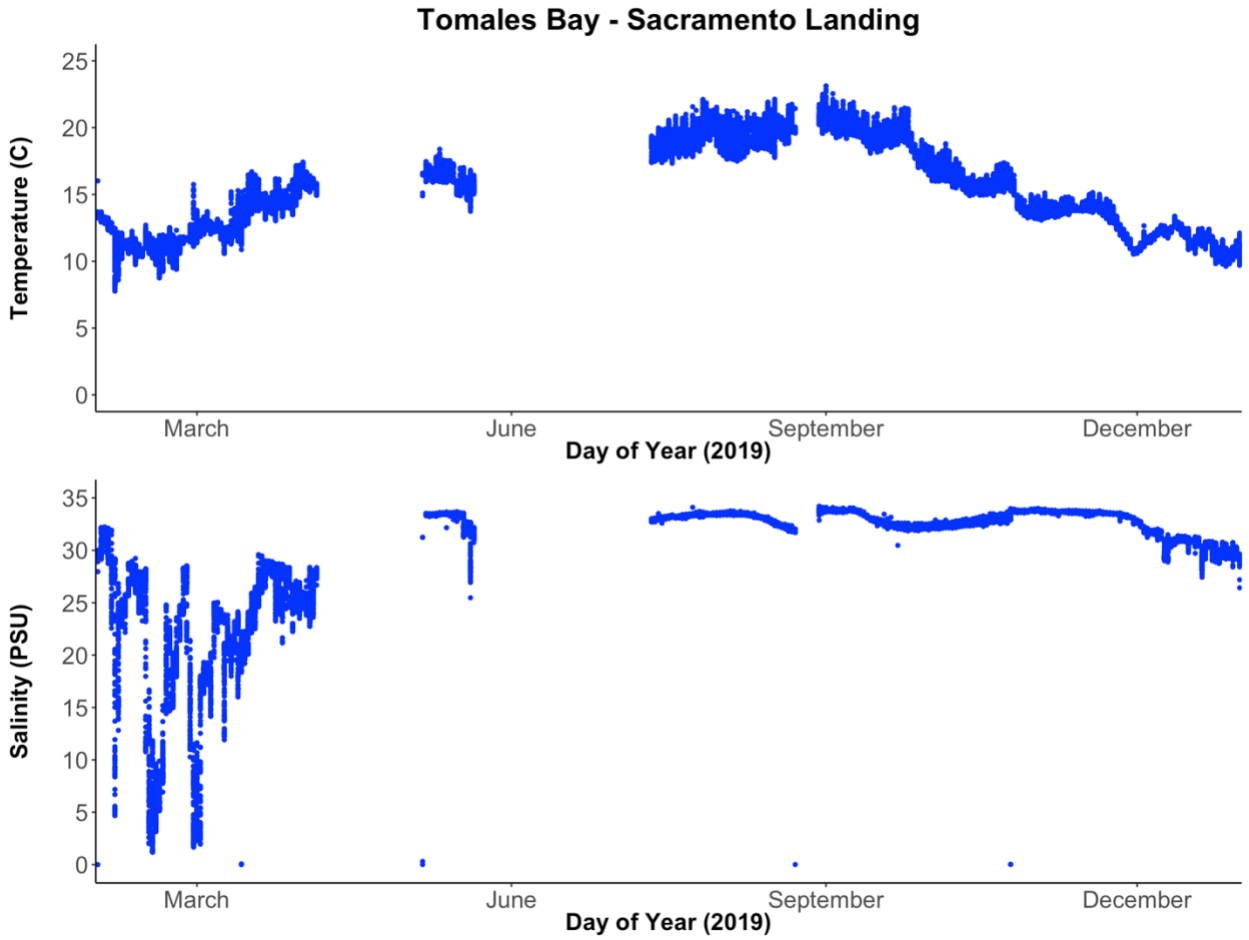

Figure B3: Records of temperature and salinity from Sacramento Landing, Tomales Bay, CA (38.149695°N, 122.905856°W) in 2019. Each blue dot represents a measurement taken at 15 minute intervals using an In-Situ Aqua TROLL 500.

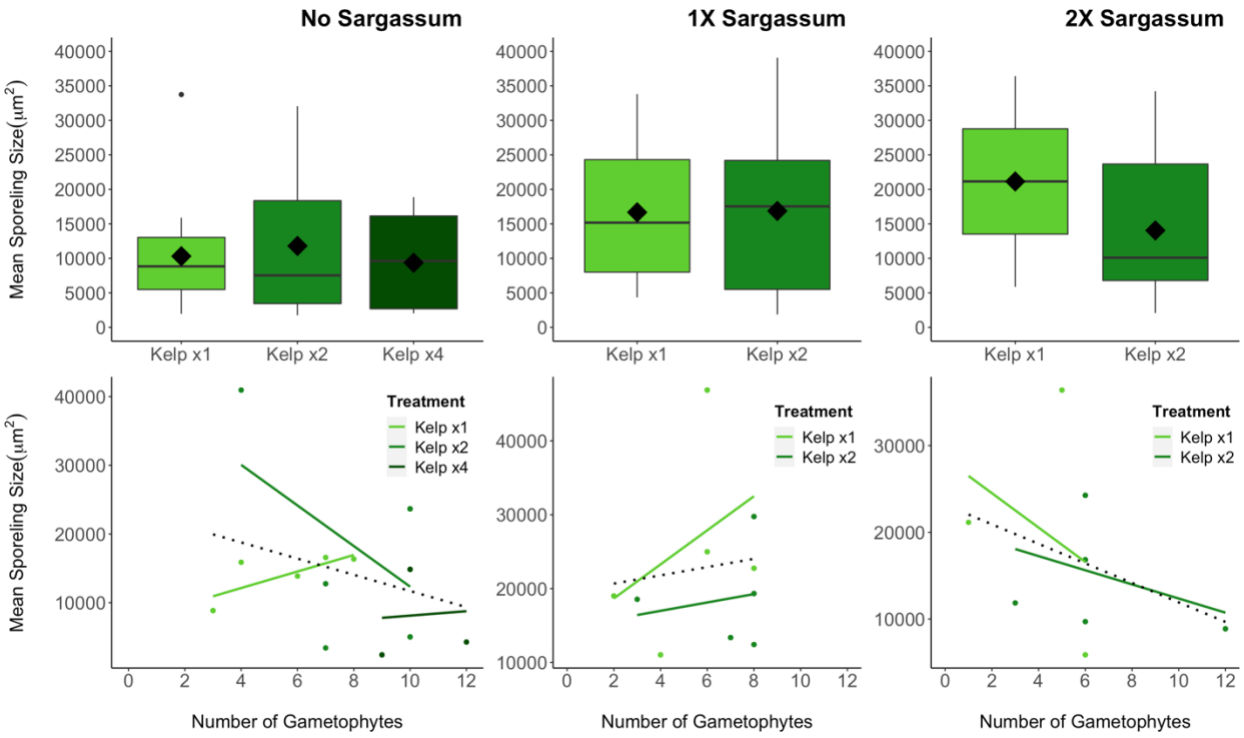

Figure B4: Sizes of Sporelings from tests of density dependent effects (E2). Top panels show the average size of sporelings after 4 weeks of growth with box plots that summarize the mean (diamond) and median (box midline) for each treatment, the first and third quartiles (upper and lower box limits), outliers within 1.5 times the inter-quartile range (vertical lines), and outliers beyond that range (dots). The bottom panels show the relationship of the covariate (mean number of gametophytes) to the response variable (mean sporeling size). Colored lines represent different Kelp densities within each Sargassum density, and the dotted black line represents the overall trend across Kelp densities. Heterogeneous slopes and different ranges of values for each treatment indicate that the different treatments are confounded with differences in the covariate.

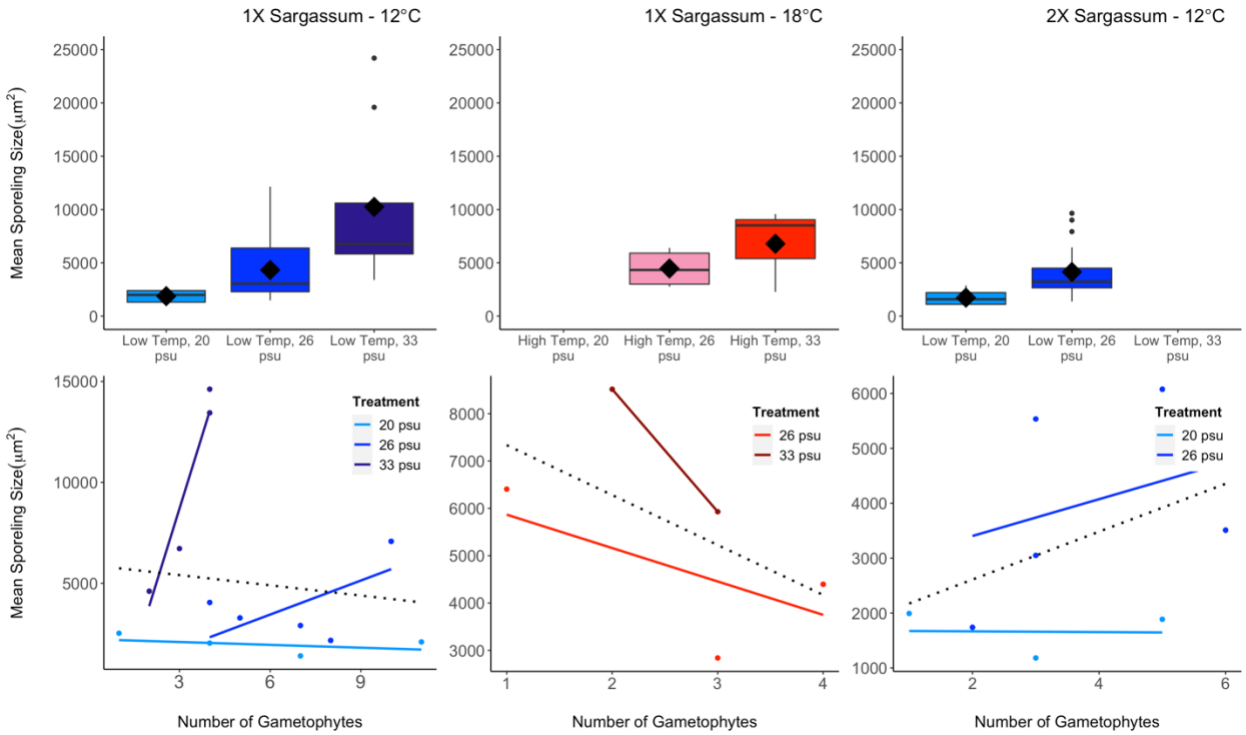

Figure B5: Sizes of Sporelings from tests of the interacting effects of S. muticum presence, temperature, and salinity (E3). Top panels show the average size of sporelings after 4 weeks of growth with box plots that summarize the mean (diamond) and median (box midline) for each treatment, the first and third quartiles (upper and lower box limits), outliers within 1.5 times the inter-quartile range (vertical lines), and outliers beyond that range (dots). The bottom panels show the relationship of the covariate (mean number of gametophytes) to the response variable (mean sporeling size). Colored lines represent different salinity treatments within each temperature-location treatment, and the dotted black line represents the overall trend across salinity treatments. Heterogeneous slopes and different ranges of values for each treatment indicate that the different treatments are confounded with differences in the covariate.

APPENDIX C: Chapter 2 Statistical Tables

Table C1: Linear regression data for the slopes of size vs. the number of gametophytes associated with each treatment. (ND = No Data)

Stage	Model Subset	Predictor	df	R^2	F	*P*
E1	White Gulch, 12˚C	All Salinities	567	-0.002	0.014	0.905
		20 psu	234	0.005	2.141	0.145
		26 psu	231	0.039	10.420	**0.001**
		33 psu	98	0.045	5.663	**0.019**
	White Gulch, 18˚C	All Salinities	26	-0.035	0.087	0.770
		20 psu	ND	ND	ND	ND
		26 psu	18	-0.052	0.062	0.806
		33 psu	5	0.486	6.679	**0.049**
	Marshall Beach, 12˚C	All Salinities	631	0.005	4.390	**0.037**
		20 psu	235	0.004	1.834	0.177
		26 psu	283	0.016	5.631	**0.018**
		33 psu	109	<0.001	1.026	0.313
E2	0X Sargassum	All Macrocystis Densities	47	0.03475	2.728	0.1053
		1X Macrocystis	14	-0.03142	0.5431	0.4733
		2X Macrocystis	20	0.2204	6.938	**0.01591**
		4X Macrocystis	9	-0.01288	0.8728	0.3746
	1X Sargassum	All Macrocystis Densities	44	-0.02214	0.02509	0.8749
		1X Macrocystis	23	-0.006827	0.8373	0.3697
		2X Macrocystis	19	-0.04768	0.08989	0.7676
	2X Sargassum	All Macrocystis Densities	20	0.03844	1.84	0.1901
		1X Macrocystis	1	-0.9283	0.03721	0.8787
		2X Macrocystis	17	0.01418	1.259	0.2775
E3	18˚C, 1X Sargassum	All Salinities	7	0.044	1.372	0.280
		20 psu	ND	ND	ND	ND
		26 psu	4	-0.032	0.844	0.410
		33 psu	1	-0.713	0.168	0.753
	12˚C, 1X Sargassum	All Salinities	51	-0.003	0.821	0.369
		20 psu	9	-0.107	0.038	0.850

		26 psu	31	0.173	7.712	**0.009**
		33 psu	7	0.274	4.013	0.085
	12˚C, 2X Sargassum	All Salinities	20	-0.012	0.745	0.398
		20 psu	2	-0.500	<0.001	0.983
		26 psu	16	-0.043	0.306	0.588
		33 psu	ND	ND	ND	ND

E1 TABLES

Table C2: *Count and Size Responses to Temperature and Salinity Stress for subset White Gulch Data* (Generalized Linear Model with 2-Way Interaction, Distribution = Negative Binomial, Link=Log, Size Distribution = Gamma, '*ref*' = reference)

Lifestage	Variable Type	Variable	Fixed Effects	Estimate	SE	Z	P
Females	Count	Intercept		-1.204	0.5805	-2.074	**0.038**
		Temperature	18 ° C	*ref*	*ref*	*Ref*	*ref*
			12 ° C	4.47	0.5869	7.616	**2.62E-14**
		Salinity	20 psu	*ref*	*ref*	*Ref*	*Ref*
			26 psu	1.466	0.6462	2.269	0.233
			33 psu	1.484	0.6271	2.943	**0.00324**
		Interactions	Temp (12°C): Salinity (26 psu)	-1.455	0.6576	-2.212	**0.0269**
			Temp (12°C): Salinity (33 psu)	-2.949	0.641	-3.887	**0.000101**
Males	Count	Intercept		-20.73	10035.05	-0.002	0.998
		Temperature	18 ° C	*ref*	*ref*	*ref*	*ref*
			12 ° C	19.12	10035.05	0.002	0.998
		Salinity	20 psu	*ref*	*ref*	*ref*	*ref*
			26 psu	19.81	10035.05	0.002	0.998
			33 psu	21.83	10035.05	0.002	0.998
		Interactions	Temp (12°C): Salinity (26 psu)	-15.83	10035.05	-0.002	0.999
			Temp (12°C): Salinity (33 psu)	-17.22	10035.05	-0.002	0.999
Eggs	Count	Intercept		-1.6094	0.7254	-2.219	**0.0265**
		Temperature	18 ° C	*ref*	*ref*	*ref*	*ref*
			12 ° C	3.7612	0.7509	5.009	**5.48E-07**
		Salinity	20 psu	*ref*	*ref*	*ref*	*Ref*

			26 psu	1.3863	0.823	1.684	0.0921
			33 psu	1.7047	0.802	2.126	**0.0335**
		Interactions	Temp (12°C): Salinity (26 psu)	-1.2659	0.8669	-1.46	0.1442
			Temp (12°C): Salinity (33 psu)	-2.1888	0.852	-2.569	**0.0102**
Sporelings	Count	Intercept		-2.303	1.005	-2.291	**0.02196**
		Temperature	18 ° C	*ref*	*ref*	*ref*	*ref*
			12 ° C	5.464	1.012	5.398	**6.73E-08**
		Salinity	20 psu	*ref*	*ref*	*ref*	*ref*
			26 psu	2.996	1.034	2.896	**0.00378**
			33 psu	1.946	1.078	1.804	0.07117
		Interactions	Temp (12°C): Salinity (26 psu)	-3.013	1.048	-2.874	**0.00405**
			Temp (12°C): Salinity (33 psu)	-2.805	1.094	-2.563	**0.01038**
Sporelings	Size	Intercept		-1.204	0.5805	-2.074	**0.038**
		Temperature	18 ° C	*ref*	*ref*	*Ref*	*ref*
			12 ° C	4.47	0.5869	7.616	**2.62E-14**
		Salinity	20 psu	*ref*	*ref*	*Ref*	*Ref*
			26 psu	1.466	0.6462	2.269	0.233
			33 psu	1.484	0.6271	2.943	**0.00324**
		Interactions	Temp (12°C): Salinity (26 psu)	-1.455	0.6576	-2.212	**0.0269**
			Temp (12°C): Salinity (33 psu)	-2.949	0.641	-3.887	**0.000101**

Table C3: *Count and Size Responses to Source Location and Salinity Stress for subset Low Temperature Data* (Generalized Linear Model with 2-Way Interaction, Count Distribution = Negative Binomial, Link=Log, Size Distribution = Gamma, '*ref*' = reference)

Lifestage	Variable Type	Variable	Fixed Effects	Estimate	SE	Z	P
Females	Count	Intercept		3.0106	0.1308	23.025	**2E-16**
		Source Location	Marshall Beach	*ref*	*ref*	*Ref*	*ref*
			White Gulch	0.2551	0.1819	1.403	0.1607
		Salinity	20 psu	*ref*	*ref*	*Ref*	*Ref*
			26 psu	0.2513	0.1819	1.381	0.1672
			33 psu	-0.7593	0.1995	-3.806	**0.000141**
		Interactions	Salinity (26 psu): Location (WG)	-0.2399	0.255	-0.941	0.3468
			Salinity (33 psu): Location (WG)	0.111	0.2743	0.405	0.6858
Males	Count	Intercept		-20.18	7606.7	-0.003	0.998
		Source Location	Marshall Beach	*ref*	*ref*	*ref*	*ref*
			White Gulch	18.57	7606.7	0.002	0.998
		Salinity	20 psu	*ref*	*ref*	*ref*	*ref*
			26 psu	20.44	7606.7	0.003	0.998
			33 psu	22.27	7606.7	0.003	0.998
		Interactions	Salinity (26 psu): Location (WG)	-16.46	7606.7	-0.002	0.998
			Salinity (33 psu): Location (WG)	-17.66	7606.7	-0.002	0.998
Eggs	Count	Intercept		2.04122	0.19283	10.586	**2.00E-16**
		Source Location	Marshall Beach	*ref*	*ref*	*ref*	*ref*
			White Gulch	0.11054	0.2702	0.409	0.682
		Salinity	20 psu	*ref*	*ref*	*ref*	*Ref*

			26 psu	0.13353	0.26971	0.495	0.621
			33 psu	-0.51516	0.2883	-1.787	0.074
		Interactions	Salinity (26 psu): Location (WG)	-0.01317	0.37825	-0.035	0.972
			Salinity (33 psu): Location (WG)	0.03111	0.4025	0.077	0.938
Sporelings	Count	Intercept		3.165476	0.150524	21.03	**2.00E-16**
		Source Location	Marshall Beach	*ref*	*ref*	*ref*	*ref*
			White Gulch	-0.00228	0.212915	-0.02	0.984158
		Salinity	20 psu	*ref*	*ref*	*ref*	*ref*
			26 psu	0.184426	0.211197	0.873	0.382532
			33 psu	-0.758529	0.22384	-3.389	**0.000702**
		Interactions	Salinity (26 psu): Location (WG)	-0.201522	0.300047	-0.672	0.501815
			Salinity (33 psu): Location (WG)	-0.100135	0.318148	-0.315	0.752955
Sporelings	Size	Intercept		3.0106	0.1308	23.025	**2E-16**
		Source Location	Marshall Beach	*ref*	*ref*	*Ref*	*ref*
			White Gulch	0.2551	0.1819	1.403	0.1607
		Salinity	20 psu	*ref*	*ref*	*Ref*	*Ref*
			26 psu	0.2513	0.1819	1.381	0.1672
			33 psu	-0.7593	0.1995	-3.806	**0.000141**
		Interactions	Salinity (26 psu): Location (WG)	-0.2399	0.255	-0.941	0.3468
			Salinity (33 psu): Location (WG)	0.111	0.2743	0.405	0.6858

Table C4: Pairwise comparisons of life stage count and juvenile size responses to temperature in White Gulch, grouped by salinity. (ND = No Data)

Stage	Variable Type	Source Location	Salinity	Temperature Comparison	Estimate	SE	df	Z	*P*
Females	Counts	White Gulch	20 psu	18˚C v. 12˚C	-4.47	0.587	53	-7.616	**<0.001**
			26 psu	18˚C v. 12˚C	-3.01	0.297	53	-10.162	**<0.001**
			33 psu	18˚C v. 12˚C	-1.98	0.259	53	-7.618	**<0.001**
Males	Counts	White Gulch	20 psu	18˚C v. 12˚C	-19.12	1000	53	-0.002	0.9985
			26 psu	18˚C v. 12˚C	-3.29	0.535	53	-6.142	**<0.001**
			33 psu	18˚C v. 12˚C	-1.9	0.256	53	-7.423	**<0.001**
Eggs	Counts	White Gulch	20 psu	18˚C v. 12˚C	-3.76	0.751	53	-5.009	**<0.001**
			26 psu	18˚C v. 12˚C	-2.5	0.433	53	-5.761	**<0.001**
			33 psu	18˚C v. 12˚C	-1.57	0.403	53	-3.906	**0.0003**
Sporelings	Counts	White Gulch	20 psu	18˚C v. 12˚C	-5.46	1.012	53	-5.398	**<0.001**
			26 psu	18˚C v. 12˚C	-2.45	0.273	53	-8.981	**<0.001**
			33 psu	18˚C v. 12˚C	-2.66	0.416	53	-6.393	**<0.001**
Sporelings	Sizes	White Gulch	20 psu	18˚C v. 12˚C	ND	ND	ND	ND	ND
			26 psu	18˚C v. 12˚C	-0.403	1.13	584	-0.357	0.721
			33 psu	18˚C v. 12˚C	19.718	6.09	584	3.238	**0.0012**

Table C5: Wilcoxon rank sum test results for responses to temperature for Marshall Beach. (ND = No Data)

Stage	Source Location	Temperature Comparison	W	*P*
Female Counts	Marshall Beach	18˚C v. 12˚C	0.5	**1.70E-12**
Male Counts	Marshall Beach	18˚C v. 12˚C	210	**5.08E-06**
Egg Counts	Marshall Beach	18˚C v. 12˚C	15	**4.21E-12**
Juvenile Counts	Marshall Beach	18˚C v. 12˚C	0	**1.13E-12**
Juvenile Sizes	Marshall Beach	18˚C v. 12˚C	ND	ND

Table C6: Pairwise comparisons of life stage count and juvenile size responses to salinity, grouped by population and temperature. (ND = No Data)

Stage	Variable Type	Location, Temp	Salinity Comparison	Estimate	SE	df	t	*P*
Females	Count	White Gulch, 12˚C	20 psu v. 26 psu	-0.011	0.122	53	-0.093	0.995
			20 psu v. 33 psu	0.648	0.136	53	4.776	**<0.001**
			26 psu v. 33 psu	0.660	0.136	53	4.865	**<0.001**
		White Gulch, 18˚C	20 psu v. 26 psu	-1.466	0.646	53	-2.269	0.069
			20 psu v. 33 psu	-1.846	0.627	53	-2.943	**0.013**
			26 psu v. 33 psu	-0.380	0.370	53	-1.026	0.564
		Marshall Beach, 12˚C	20 psu v. 26 psu	-0.251	0.182	53	-1.381	0.358
			20 psu v. 33 psu	0.759	0.199	53	3.806	**0.001**
			26 psu v. 33 psu	1.011	0.197	53	5.137	**<0.001**
Males	Count	White Gulch, 12˚C	20 psu v. 26 psu	-3.980	0.732	53	-5.434	**<0.001**
			20 psu v. 33 psu	-4.605	0.729	53	-6.314	**<0.001**
			26 psu v. 33 psu	-0.625	0.203	53	-3.077	**0.009**
		White Gulch, 18˚C	20 psu v. 26 psu	-19.814	1000.000	53	-0.002	1.000
			20 psu v. 33 psu	-21.829	1000.000	53	-0.002	1.000
			26 psu v. 33 psu	-2.015	0.557	53	-3.617	**0.002**
		Marshall Beach, 12˚C	20 psu v. 26 psu	-20.438	7606.696	53	-0.003	1.000
			20 psu v. 33 psu	-22.268	7606.696	53	-0.003	1.000
			26 psu v. 33 psu	-1.829	0.351	53	-5.207	**<0.001**
Eggs	Count	White Gulch, 12˚C	20 psu v. 26 psu	-0.120	0.272	53	-0.442	0.898
			20 psu v. 33 psu	0.484	0.288	53	1.682	0.221

			26 psu v. 33 psu	0.604	0.285	53	2.118	0.096
		White Gulch, 18˚C	20 psu v. 26 psu	-1.386	0.823	53	-1.684	0.221
			20 psu v. 33 psu	-1.705	0.802	53	-2.126	0.094
			26 psu v. 33 psu	-0.318	0.518	53	-0.615	0.813
		Marshall Beach, 12˚C	20 psu v. 26 psu	-0.134	0.270	53	-0.495	0.874
			20 psu v. 33 psu	0.515	0.288	53	1.787	0.184
			26 psu v. 33 psu	0.649	0.285	53	2.272	0.069
Sporelings	Count	White Gulch, 12˚C	20 psu v. 26 psu	0.017	0.169	53	0.101	0.994
			20 psu v. 33 psu	0.859	0.185	53	4.629	**<0.001**
			26 psu v. 33 psu	0.842	0.186	53	4.532	**<0.001**
		White Gulch, 18˚C	20 psu v. 26 psu	-2.996	1.034	53	-2.896	**0.015**
			20 psu v. 33 psu	-1.946	1.078	53	-1.804	0.178
			26 psu v. 33 psu	1.050	0.462	53	2.275	0.068
		Marshall Beach, 12˚C	20 psu v. 26 psu	-0.184	0.211	53	-0.873	0.659
			20 psu v. 33 psu	0.759	0.224	53	3.389	**0.004**
			26 psu v. 33 psu	0.943	0.222	53	4.243	**0.000**
Sporelings	Sizes	White Gulch, 12˚C	20 psu v. 26 psu	-0.434	0.056	584	-7.720	**<0.001**
			20 psu v. 33 psu	-0.699	0.070	584	9.919	**<0.001**
			26 psu v. 33 psu	-0.264	0.072	584	-3.664	**<0.001**
		White Gulch, 18˚C	20 psu v. 26 psu	ND	ND	ND	ND	ND
			20 psu v. 33 psu	ND	ND	ND	ND	ND
			26 psu v. 33 psu	-20.386	6.192	584	-3.292	**0.003**

	Marshall Beach, 12˚C	20 psu v. 26 psu	-0.311	0.057	1189	-5.453	<**0.001**
		20 psu v. 33 psu	-0.679	0.080	1189	-8.516	<**0.001**
		26 psu v. 33 psu	-0.368	0.079	1189	-4.658	<**0.001**

Table C7: Pairwise comparisons of life stage count and juvenile size responses to source location in the low temperature treatment, grouped by salinity. (MB = Marshall Beach, WG = White Gulch)

Stage	Variable Type	Temp	Salinity	Source Comparison	Estimate	SE	df	t	*P*
Females	Counts	12˚C	20 psu	MB v. WG	-0.255	0.182	53	-1.403	0.167
			26 psu	MB v. WG	-0.015	0.179	53	-0.085	0.933
			33 psu	MB v. WG	-0.366	0.205	53	-1.783	0.080
Males	Counts	12˚C	20 psu	MB v. WG	-18.567	7606.696	53	-0.002	0.998
			26 psu	MB v. WG	-2.108	0.347	53	-6.074	**<0.001**
			33 psu	MB v. WG	-0.904	0.227	53	-3.982	**0.000**
Eggs	Counts	12˚C	20 psu	MB v. WG	-0.111	0.270	53	-0.409	0.684
			26 psu	MB v. WG	-0.097	0.265	53	-0.368	0.714
			33 psu	MB v. WG	-0.142	0.298	53	-0.475	0.637
Sporelings	Counts	12˚C	20 psu	MB v. WG	0.004	0.213	53	0.020	0.984
			26 psu	MB v. WG	0.206	0.211	53	0.973	0.335
			33 psu	MB v. WG	0.104	0.236	53	0.441	0.661
Sporelings	Sizes	12˚C	20 psu	MB v. WG	-0.045	0.058	1189	-0.768	0.443
			26 psu	MB v. WG	-0.210	0.065	1189	-3.239	**0.001**
			33 psu	MB v. WG	-1.142	0.102	1189	-1.391	0.164

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Table C8: *Count and Size Responses to Different Sargassum and Macrocystis Densities* (Generalized Linear Model with 2-Way Interaction, Distribution = Poisson, Link=Log, Size Distribution = Gamma, '*ref*' = reference)

Lifestage	Variable Type	Variable	Fixed Effects	Estimate	SE	Z	P
Females	Count	Intercept		1.723	0.189	9.116	**< 0.01**
		Initial Macrocystis Density	1x	*Ref*	*Ref*	*Ref*	*Ref*
			2x	0.305	0.249	1.226	0.220
			4x	0.580	0.236	2.456	**0.014**
		Initial Sargassum Density	0x	*Ref*	*Ref*	*Ref*	*Ref*
			1x	-0.074	0.272	-0.272	0.786
			2x	-0.499	0.307	-1.623	0.105
		Interactions	Macrocystis (2x):Sargassum (1x)	-0.037	0.360	-0.103	0.918
			Macrocystis (2x):Sargassum (2x)	0.358	0.389	0.921	0.357
Males	Count	Intercept		1.435	0.218	6.576	**<0.01**
		Initial Macrocystis Density	1x	*ref*	*Ref*	*Ref*	*ref*
			2x	0.669	0.268	2.493	**0.013**
			4x	1.033	0.254	4.065	**<0.01**
		Initial Sargassum Density	0x	*ref*	*ref*	*Ref*	*Ref*
			1x	1.16E-16	0.309	0.00	1.000
			2x	-0.211	0.326	-0.648	0.517
		Interactions	Macrocystis (2x):Sargassum (1x)	-0.418	0.396	-1.055	0.291
			Macrocystis (2x):Sargassum (2x)	-0.101	0.405	-0.249	0.803
Eggs	Count	Intercept		1.030	0.267	3.852	**<0.01**
		Initial Macrocystis Density	1x	*ref*	*Ref*	*Ref*	*ref*
			2x	0.194	0.361	0.538	0.591
			4x	0.539	0.336	1.603	0.109
			0x	*ref*	*Ref*	*Ref*	*Ref*

		Initial Sargassum Density	1x	-19.332	2556.960	-0.008	0.994
			2x	-19.946	0.756	-2.574	**0.010**
		Interactions	Macrocystis (2x):Sargassum (1x)	17.885	2556.960	0.007	0.994
			Macrocystis (2x):Sargassum (2x)	1.059	0.879	1.204	0.229
Sporelings	Count	Intercept		1.163	0.250	4.653	< **0.01**
		Initial Macrocystis Density	1x	*ref*	*Ref*	*Ref*	*Ref*
			2x	0.406	0.323	1.256	0.209
			4x	-0.375	0.392	-0.957	0.339
		Initial Sargassum Density	0x	*ref*	*Ref*	*Ref*	*Ref*
			1x	0.446	0.320	1.394	0.163
			2x	-1.163	0.512	-2.270	**0.023**
		Interactions	Macrocystis (2x):Sargassum (1x)	-0.580	0.438	-1.324	0.186
			Macrocystis (2x):Sargassum (2x)	0.981	0.595	1.648	0.099
Sporelings	Size	Intercept		1.19E-04	6.21E-05	1.912	0.059
		Initial Macrocystis Density	1x	*ref*	*Ref*	*Ref*	*Ref*
			2x	-1.28E-04	6.71E-05	-1.906	0.059
			4x	1.92E-04	2.59E-04	0.742	0.460
		Initial Sargassum Density	0x	*ref*	*Ref*	*Ref*	*Ref*
			1x	-6.49E-05	6.59E-05	-0.985	0.327
			2x	-8.01E-05	7.45E-05	-1.074	0.285
		Gametophyte #		-7.59E-06	8.99E-06	-0.844	0.401
		Interactions	Macrocystis (2x):Sargassum (1x)	1.44E-04	9.09E-05	1.580	0.117
			Macrocystis (2x):Sargassum (2x)	1.13E-04	8.72E-05	1.296	0.198

Table C9: Pairwise comparisons of life stage count and juvenile size responses to initial Macrocystis densities

Stage	Variable Type	Sargassum Density	Macrocystis Density Comparison	Estimate	SE	df	t/Z	*P*
Females	Counts	0x	1X v. 2X	-0.305	0.249	26	-1.226	0.4377
			1X v. 4X	-0.58	0.236	26	-2.456	**0.0373**
			2X v. 4X	-0.274	0.215	26	-1.275	0.4092
		1X	1X v. 2X	-0.268	0.261	26	-1.03	0.5581
		2X	1X v. 2X	-0.663	0.299	26	-2.222	0.0675
Males	Counts	0x	1X v. 2X	-0.669	0.268	26	-2.493	**0.0339**
			1X v. 4X	-1.033	0.254	26	-4.065	**0.0001**
			2X v. 4X	-0.364	0.203	26	-1.79	0.1729
		1X	1X v. 2X	-0.251	0.291	26	-0.864	0.6632
		2X	1X v. 2X	-0.568	0.304	26	-1.871	0.1471
Eggs	Counts	0x	1X v. 2X	-0.194	0.361	26	-0.538	0.8526
			1X v. 4X	-0.539	0.336	26	-1.603	0.2224
			2X v. 4X	-0.345	0.317	26	-1.088	0.5216
		1X	1X v. 2X	-18.079	2556.958	26	-0.007	1
		2X	1X v. 2X	-1.253	0.802	26	-1.562	0.262
Sporelings	Counts	0x	1X v. 2X	-0.405	0.323	26	-1.256	0.4201
			1X v. 4X	0.375	0.392	26	0.957	0.6043
			2X v. 4X	0.78	0.364	26	2.143	0.0814
		1X	1X v. 2X	0.174	0.296	26	0.589	0.826
		2X	1X v. 2X	-1.386	0.5	26	-2.773	**0.0154**
Sporelings	Sizes	0x	1X v. 2X	6.78E-06	1.78E-05		0.381	0.923
			1X v. 4X	-1.01E-04	8.11E-05		-1.241	0.4288
			2X v. 4X	-1.08E-04	8.05E-05		-1.336	0.3752
		1X	1X v. 2X	-2.26E-05	1.21E-05		-1.87	0.1473
		2X	1X v. 2X	-1.17E-05	4.41E-05		-0.265	0.9619

Table C10: Pairwise comparisons of life stage count and juvenile size responses to initial Sargassum densities

Stage	Variable Type	Macrocystis Density	Sargassum Density Comparison	Estimate	SE	df	t/Z	*P*
Females	Counts	1x	0X v. 1X	0.0741	0.272	26	0.272	0.96
			0X v. 2X	0.499	0.307	26	1.623	0.2359
			1X v. 2X	0.4249	0.312	26	1.362	0.3609
		2X	0X v. 1X	0.1112	0.236	26	0.471	0.8849
			0X v. 2X	0.1411	0.238	26	0.593	0.8239
			1X v. 2X	0.0299	0.244	26	0.122	0.9918
Males	Counts	1x	0X v. 1X	0	0.309	26	0	1
			0X v. 2X	0.211	0.326	26	0.648	0.7937
			1X v. 2X	0.211	0.326	26	0.648	0.7937
		2X	0X v. 1X	0.418	0.248	26	1.685	0.2107
			0X v. 2X	0.312	0.24	26	1.3	0.3951
			1X v. 2X	-0.105	0.265	26	-0.397	0.9167
Eggs	Counts	1x	0X v. 1X	19.332	2556.96	26	0.008	1
			0X v. 2X	1.946	0.756	26	2.574	**0.0271**
			1X v. 2X	-17.386	2556.96	26	-0.007	1
		2X	0X v. 1X	1.447	0.556	26	2.604	**0.025**
			0X v. 2X	0.887	0.449	26	1.976	0.1182
			1X v. 2X	-0.56	0.627	26	-0.893	0.6448
Sporelings	Counts	1x	0X v. 1X	-0.4463	0.32	26	-1.394	0.344
			0X v. 2X	1.1632	0.512	26	2.27	0.06
			1X v. 2X	1.6094	0.49	26	3.285	**0.0029**
		2X	0X v. 1X	0.1335	0.299	26	0.447	0.8958
			0X v. 2X	0.1823	0.303	26	0.602	0.8189
			1X v. 2X	0.0488	0.312	26	0.156	0.9866
Sporelings	Sizes	1x	0X v. 1X	0.0000319	0.0000161		1.984	0.1161
			0X v. 2X	0.00000944	0.0000446		0.211	0.9756
			1X v. 2X	-0.0000224	0.0000427		-0.525	0.8592
		2X	0X v. 1X	0.00000253	0.0000143		0.177	0.9829
			0X v. 2X	-9.06E-06	0.0000165		-0.55	0.8465
			1X v. 2X	-0.0000116	0.0000164		-0.709	0.7585

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Table C11: *Count and Size Responses to Temperature and Salinity Stress in the subset 1X Sargassum treatment* (Generalized Linear Model with 2-Way Interaction, Distribution = Negative Binomial, Link=Log, Size Distribution = Gamma, '*ref*' = reference)

Lifestage	Variable Type	Variable	Fixed Effects	Estimate	SE	t	P
Females	Count	Intercept		-1.609	1.005	-1.601	0.109
		Temperature	18 ° C	*ref*	*ref*	*Ref*	*ref*
			12 ° C	3.219	1.030	3.125	**0.002**
		Salinity	20 psu	*ref*	*ref*	*Ref*	*Ref*
			26 psu	2.079	1.070	1.942	**0.052**
			33 psu	2.079	1.070	1.942	**0.052**
		Interactions	Temp (12°C): Salinity (26 psu)	-1.772	1.112	-1.594	0.111
			Temp (12°C): Salinity (33 psu)	-2.590	1.128	-2.295	**0.022**
Males	Count	Intercept		-21.040	1.66E+04	-0.001	0.999
		Temperature	18 ° C	*ref*	*ref*	*ref*	*ref*
			12 ° C	-6.591	4.11E+05	0.000	1.000
		Salinity	20 psu	*ref*	*ref*	*ref*	*ref*
			26 psu	19.430	1.66E+04	0.001	0.999
			33 psu	21.510	1.66E+04	0.001	0.999
		Interactions	Temp (12°C): Salinity (26 psu)	7.285	4.11E+05	0.000	1.000
			Temp (12°C): Salinity (33 psu)	7.077	4.11E+05	0.000	1.000
Eggs	Count	Intercept		-0.916	0.789	-1.162	0.245

		Temperature	18 ° C	*ref*	*ref*	*ref*	*ref*
			12 ° C	1.609	0.919	1.752	0.080
		Salinity	20 psu	*ref*	*ref*	*ref*	*Ref*
			26 psu	0.693	0.997	0.695	0.487
			33 psu	1.504	0.925	1.626	0.104
		Interactions	Temp (12°C): Salinity (26 psu)	-1.204	1.227	-0.981	0.327
			Temp (12°C): Salinity (33 psu)	-2.197	1.183	-1.857	0.063
Sporelings	Count	Intercept		-21.000	1.62E+04	-0.001	0.999
		Temperature	18 ° C	*ref*	*ref*	*ref*	*ref*
			12 ° C	22.090	1.62E+04	0.001	0.999
		Salinity	20 psu	*ref*	*ref*	*ref*	*ref*
			26 psu	21.180	1.62E+04	0.001	0.999
			33 psu	20.480	1.62E+04	0.001	0.999
		Interactions	Temp (12°C): Salinity (26 psu)	-20.390	1.62E+04	-0.001	0.999
			Temp (12°C): Salinity (33 psu)	-21.000	1.62E+04	-0.001	0.999
Sporelings	Size	Intercept		10.113	1.92E+00	5.270	**<0.001**
		Temperature	18 ° C	*ref*	*ref*	*ref*	*ref*
			12 ° C	-2.537	1.88E+00	-1.350	0.183
		Salinity	20 psu	*ref*	*ref*	*ref*	*ref*
			26 psu	-1.362	2.03E+00	-0.669	0.506
			33 psu	-0.339	8.28E-01	-0.409	0.684
		Gametophyte #		-0.937	6.76E-01	-1.387	0.171

	Interactions	Temp (12°C): Salinity (26 psu)	1.3015	2.0235	0.643	0.5229

Table C12: *Count and Size Responses to Sargassum Density and Salinity Stress in the Low Temperature Treatment* (Generalized Linear Model with 2-Way Interaction, Distribution = Negative Binomial, Link=Log, Size Distribution = Gamma, '*ref*' = reference)

Lifestage	Variable Type	Variable	Fixed Effects	Estimate	SE	t	P
Females	Count	Intercept		1.609	0.202	7.963	**0.000**
		Sargassum Density	1X	*ref*	*ref*	*Ref*	*ref*
			2X	-0.654	0.344	-1.899	**0.058**
		Salinity	20 psu	*ref*	*ref*	*Ref*	*Ref*
			26 psu	0.307	0.267	1.153	0.249
			33 psu	-0.511	0.329	-1.552	0.121
		Interactions	Salinity (26 psu): Sargassum Density (2X)	0.072	0.450	0.160	0.873
			Salinity (33 psu): Sargassum Density (2X)	0.143	0.546	0.262	0.793
Males	Count	Intercept		-21.271	1.86E+04	-0.001	0.999
		Sargassum Density	1X	*ref*	*ref*	*ref*	*ref*
			2X	-6.067	4.08E+05	0.000	1.000
		Salinity	20 psu	*ref*	*ref*	*ref*	*ref*
			26 psu	20.355	1.86E+04	0.001	0.999
			33 psu	22.226	1.86E+04	0.001	0.999
		Interactions	Salinity (26 psu): Sargassum Density (2X)	6.473	4.08E+05	0.000	1.000
			Salinity (33 psu): Sargassum Density (2X)	6.210	4.08E+05	0.000	1.000
Eggs	Count	Intercept		0.693	0.459	1.511	0.131
			1X	*ref*	*ref*	*ref*	*ref*

		Sargassum Density	2X	-0.223	0.668	-0.334	0.738
		Salinity	20 psu	*ref*	*ref*	*ref*	*Ref*
			26 psu	-0.511	0.698	-0.731	0.465
			33 psu	-0.693	0.722	-0.960	0.337
		Interactions	Salinity (26 psu): Sargassum Density (2X)	-1.569	1.354	-1.158	0.247
			Salinity (33 psu): Sargassum Density (2X)	-0.288	1.096	-0.263	0.793
Sporelings	Count	Intercept		1.099	0.258	4.255	**0.000**
		Sargassum Density	1X	*ref*	*ref*	*ref*	*ref*
			2X	-1.099	0.516	-2.127	**0.033**
		Salinity	20 psu	*ref*	*ref*	*ref*	*ref*
			26 psu	0.789	0.311	2.532	**0.011**
			33 psu	-0.511	0.422	-1.212	0.226
		Interactions	Salinity (26 psu): Sargassum Density (2X)	0.493	0.594	0.829	0.407
			Salinity (33 psu): Sargassum Density (2X)	0.277	0.792	0.363	0.717
Sporelings	Size	Intercept		7.575	4.10E-01	18.490	<2e-16
		Sargassum Density	1X	*ref*	*ref*	*ref*	*ref*
			2X	-0.130	7.61E-01	-0.171	0.865
		Salinity	20 psu	*ref*	*ref*	*ref*	*ref*
			26 psu	-0.060	5.34E-01	-0.112	0.911
			33 psu	-0.339	8.72E-01	-0.389	0.699
		Gametophyte #		-0.005	5.09E-02	-0.103	0.918

	Interactions	Salinity (26 psu): Sargassum Density (2X)	0.655048	0.924492	0.709	0.4811

Table C13: Pairwise comparisons of life stage count and juvenile size responses to temperature in the 1X Sargassum treatment, grouped by salinity. (ND = No Data)

Stage	Variable Type	Sargassum Density	Salinity	Temp Comparison	Estimate	SE	df	t	*P*
Females	Counts	1X	20 psu	12˚C v. 18˚C	-3.219	1.030	23	-3.125	**0.005**
			26 psu	12˚C v. 18˚C	-1.447	0.419	23	-3.456	**0.002**
			33 psu	12˚C v. 18˚C	-0.629	0.461	23	-1.363	0.186
Males	Counts	1X	20 psu	12˚C v. 18˚C	6.591	4.11E +05	23	0.000	1.000
			26 psu	12˚C v. 18˚C	-0.693	1.200	23	-0.556	0.584
			33 psu	12˚C v. 18˚C	-0.486	0.500	23	-0.959	0.348
Eggs	Counts	1X	20 psu	12˚C v. 18˚C	-1.609	0.919	23	-1.752	0.093
			26 psu	12˚C v. 18˚C	-0.405	0.813	23	-0.499	0.623
			33 psu	12˚C v. 18˚C	0.588	0.745	23	0.789	0.438
Sporelings	Counts	1X	20 psu	12˚C v. 18˚C	-22.100	1.62E +04	23	-0.001	0.999
			26 psu	12˚C v. 18˚C	-1.700	0.473	23	-3.602	**0.002**
			33 psu	12˚C v. 18˚C	-1.100	0.687	23	-1.600	0.123
Sporelings	Sizes	1X	20 psu	12˚C v. 18˚C	ND	ND	ND	ND	ND
			26 psu	12˚C v. 18˚C	-0.110	0.609	49	-0.181	0.857
			33 psu	12˚C v. 18˚C	-3.280	2.393	49	-1.371	0.171

Table C14: Wilcoxon rank sum test results for responses to temperature in the 2X Sargassum treatment.

Stage	Sargassum Density	Temperature Comparison	W	*P*
Female Counts	2X	18˚C v. 12˚C	9.5	**8.59E-06**
Male Counts	2X	18˚C v. 12˚C	70	**0.023**
Egg Counts	2X	18˚C v. 12˚C	82	0.128
Juvenile Counts	2X	18˚C v. 12˚C	34	**2.25E-04**
Juvenile Sizes	2X	18˚C v. 12˚C	3	0.3478

Table C15: Pairwise comparisons of life stage count and juvenile size response to salinity, grouped by Sargassum density and temperature. (ND = No Data)

Stage	Variable Type	Temp or Sargassum Density	Salinity Comparison	Estimate	SE	df	t	*P*
Females	Counts	18˚C, 1X Sargassum	20 psu v. 26 psu	-2.079	1.070	23	-1.943	0.150
			20 psu v. 33 psu	-2.079	1.070	23	-1.943	0.150
			26 psu v. 33 psu	0.000	0.520	23	0.000	1.000
		12˚C, 1X Sargassum	20 psu v. 26 psu	-0.307	0.267	23	-1.153	0.492
			20 psu v. 33 psu	0.511	0.329	23	1.552	0.286
			26 psu v. 33 psu	0.818	0.313	23	2.617	**0.039**
		12˚C, 2X Sargassum	20 psu v. 26 psu	-0.379	0.362	23	-1.047	0.555
			20 psu v. 33 psu	0.368	0.436	23	0.844	0.680
			26 psu v. 33 psu	0.747	0.407	23	1.837	0.180
Males	Counts	18˚C, 1X Sargassum	20 psu v. 26 psu	-19.430	1.66E+04	23	-0.001	1.000
			20 psu v. 33 psu	-21.510	1.66E+04	23	-0.001	1.000
			26 psu v. 33 psu	-2.080	1.100	23	-1.915	0.157
		12˚C, 1X Sargassum	20 psu v. 26 psu	-20.350	1.86E+04	23	-0.001	1.000
			20 psu v. 33 psu	-22.230	1.86E+04	23	-0.001	1.000
			26 psu v. 33 psu	-1.870	0.800	23	-2.266	0.081
		12˚C, 2X Sargassum	20 psu v. 26 psu	-26.830	4.07E+05	23	0.000	1.000
			20 psu v. 33 psu	-28.440	4.07E+05	23	0.000	1.000
			26 psu v. 33 psu	-1.610	0.700	23	-2.264	0.082
Eggs	Counts	18˚C, 1X Sargassum	20 psu v. 26 psu	-0.693	0.997	23	-0.695	0.769
			20 psu v. 33 psu	-1.504	0.925	23	-1.626	0.255

			26 psu v. 33 psu	-0.811	0.778	23	-1.042	0.559
		12˚C, 1X Sargassum	20 psu v. 26 psu	0.511	0.698	23	0.731	0.748
			20 psu v. 33 psu	0.693	0.722	23	0.960	0.609
			26 psu v. 33 psu	0.182	0.767	23	0.238	0.969
		12˚C, 2X Sargassum	20 psu v. 26 psu	2.079	1.160	23	1.792	0.194
			20 psu v. 33 psu	0.981	0.824	23	1.190	0.471
			26 psu v. 33 psu	-1.099	1.247	23	-0.881	0.657
Sporelings	Counts	18˚C, 1X Sargassum	20 psu v. 26 psu	-21.178	1.62E+04	23	-0.001	1.000
			20 psu v. 33 psu	-20.485	1.62E+04	23	-0.001	1.000
			26 psu v. 33 psu	0.693	0.726	23	0.955	0.612
		12˚C, 1X Sargassum	20 psu v. 26 psu	-0.788	0.311	23	-2.532	**0.047**
			20 psu v. 33 psu	0.511	0.422	23	1.212	0.459
			26 psu v. 33 psu	1.299	0.376	23	3.455	**0.006**
		12˚C, 2X Sargassum	20 psu v. 26 psu	-1.281	0.506	23	-2.534	**0.047**
			20 psu v. 33 psu	0.223	0.671	23	0.333	0.941
			26 psu v. 33 psu	1.504	0.553	23	2.721	**0.032**
Sporelings	Sizes	18˚C, 1X Sargassum	20 psu v. 26 psu	ND	ND	ND	ND	ND
			20 psu v. 33 psu	ND	ND	ND	ND	ND
			26 psu v. 33 psu	0.575	2.382	49	0.241	0.968
		12˚C, 1X Sargassum	20 psu v. 26 psu	-0.656	0.197	49	-3.333	**0.003**
			20 psu v. 33 psu	-3.252	0.665	49	-4.891	**<0.001**
			26 psu v. 33 psu	-2.595	0.652	49	-3.979	**<0.001**
		12˚C, 2X Sargassum	20 psu v. 26 psu	-0.966	0.536	62	-1.804	0.168
			20 psu v. 33 psu	ND	ND	ND	ND	ND

26 psu v. 33 psu	ND	ND	ND	ND	ND

Table C16: Pairwise comparisons of life stage counts responses to Sargassum density in the low temperature treatment, grouped by salinity. (ND = No Data)

Stage	Variable Type	Temp	Salinity	Sargassum Density Comparison	Estimate	SE	df	t	*P*
Females	Counts	12˚C	20 psu	1X v. 2X	0.654	0.344	23	1.899	0.070
			26 psu	1X v. 2X	0.582	0.289	23	2.011	**0.056**
			33 psu	1X v. 2X	0.511	0.424	23	1.206	0.240
Males	Counts	12˚C	20 psu	1X v. 2X	6.067	4.08E+05	23	0.000	1.000
			26 psu	1X v. 2X	-0.405	1.000	23	-0.419	0.680
			33 psu	1X v. 2X	-0.143	0.500	23	-0.287	0.777
Eggs	Counts	12˚C	20 psu	1X v. 2X	0.223	0.668	23	0.334	0.741
			26 psu	1X v. 2X	1.792	1.178	23	1.521	0.142
			33 psu	1X v. 2X	0.511	0.869	23	0.588	0.562
Sporelings	Counts	12˚C	20 psu	1X v. 2X	1.099	0.516	23	2.127	**0.044**
			26 psu	1X v. 2X	0.606	0.293	23	2.069	**0.050**
			33 psu	1X v. 2X	0.811	0.601	23	1.349	0.190
Sporelings	Sizes	12˚C	20 psu	1X v. 2X	0.074	0.530	62	0.139	0.890
			26 psu	1X v. 2X	-0.263	0.227	62	-1.157	0.247
			33 psu	1X v. 2X	ND	ND	ND	ND	ND

CHAPTER 3:

EFFECTS OF CHANGING SALINITY AND TEMPERATURES ON INVASIVE *UNDARIA PINNATIFIDA* REPRODUCTION AT THE NORTHERN EDGE OF ITS RANGE IN NORTH AMERICA

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Abstract:

Climate change represents a threat to many ecosystems via changes in temperature and precipitation. Many coastal ecosystems, including those dominated by kelps, are experiencing variable effects on community structure and function due to increasing mean sea-surface temperatures (SST), marine heatwaves, and variation in salinity due to changing precipitation patterns. The effects of these stresses have been well documented in mature kelps, but effects on the microscopic kelp life stage (gametophyte), which are often the most vulnerable to the effects of environmental change, are much less understood. Wakame (*Undaria pinnatifida*) is a globally invasive kelp first introduced to the West Coast of North America in 2000. Along the West Coast, *Undaria* can be found primarily in ports and harbors from Ensenada, BC, Mexico in the south to San Francisco, CA, USA in the north. We sought to answer the question: how do increased temperatures and low salinities affect the reproduction of *Undaria* individuals at its northern range? In August 2021, we collected reproductively mature individuals of *Undaria* from the San Francisco Small Boat Harbor and brought them back to UC Davis Bodega Marine Laboratory for spore release and cultivation. Using a full factorial design, we exposed *Undaria* gametophytes to five salinity conditions ranging from low to ambient salinity (10, 15, 20, 25, and 33 psu) and two temperatures (15°C and 20°C) representing pre-2013 average maximum temperature in San Francisco and maximum increased temperatures experienced under the 2014-2016 marine heatwave . Each week, we photographed three random points within each petri dish and counted the number of male and female gametophytes and the number of eggs and sporelings produced. After six weeks in culture, we found that microscopic stages of *Undaria* were unable to survive at 10 and 15 psu, but exhibited relatively equal survival and sporeling production rates at 20, 25, and 33 psu. Additionally, we saw significantly higher survival and reproduction of *Undaria*

under warmer temperatures (20°C) than ambient temperature (15°C). Our results indicate that under predicted higher temperatures and reduced annual rainfall and higher salinity in drought years, future northward expansion of *Undaria* populations in California may be likely.

Introduction:

Around the world, biological invasions are increasing and threatening local ecosystems (Molnar et al., 2008). Marine and estuarine environments, in particular, are some of the most heavily invaded ecosystems (Cohen & Carlton, 1995, 1998), primarily as a result of human activity and coastal urbanization. Invasive species are spread through marine environments as a result of ballast water release, hull fouling, intentional or accidental release from aquaria or aquaculture (Ruiz et al., 1997), or via the development of anthropogenic structures such as docks as marinas, that can serve as corridors facilitation the spread of an invasive species (Airoldi et al., 2015; Piola & Johnston, 2008; Dafforn et al., 2009; Airoldi & Bulleri, 2011; Edwards & Stachowicz, 2011; Cordell et al., 2013; Todd et al., 2019). Marine invasive seaweeds can have severe negative consequences on local ecosystems that can be intensified by co-occurring anthropogenic impacts (Grosholz, 2002; Anton et al., 2019), and evolutionary processes can actually increase the potential of an introduced species in its native range (Blakeslee et al., 2019). Invasive seaweeds in particular can have negative impacts on local communities by competing with native primary producers for space and other resources (Gaertner et al., 2009; Thomsen et al., 2009, 2014; Powell et al., 2011; Vilà et al., 2011) and/or altering resource allocation and nutrient acquisition rates (Casoli et al., 2021; Maggi et al., 2015), thus causing changes in the biomass of specialist consumers (Maggi et al., 2014; Thomsen et al., 2014; Williams & Smith, 2007) and loss of biodiversity and ecosystem functions (Sullaway & Edwards, 2020; Li et al., 2023).

Marine ecosystems are also being highly impacted by climate change in addition to biological invasion. The cumulative impacts of climate-driven abiotic changes such as rising temperatures (Dunstan et al., 2018; Gentemann et al., 2017; Hansen et al., 2006; Lima &

Wethey, 2012; Oliver et al., 2018; Reid & Beaugrand, 2012; Shi et al., 2021), changing salinity regimes (Chen et al., 2019; Ishii et al., 2006; Hilton et al., 2008; Hong & Shen, 2012), and changes to broader oceanographic processes such as upwelling and oscillation patterns (Bakun et al., 2015; Di Lorenzo et al., 2008; García-Reyes et al., 2015; García-Reyes et al., 2020) are increasingly stressing marine ecosystems and organisms. The combination of these abiotic factors are resulting in significant ecological changes in native species, such as changes in range shifts and invasion processes (Cheung et al., 2009; Lonhart, 2009; Sanford et al., 2019; Small & Edwards, 2022), community structure and composition (Arafeh-Dalmau et al., 2019; Barry et al., 1995; Beaugrand & Reid, 2003; McCarty, 2001), species interactions (Byrnes et al., 2011; Doney et al., 2012; Ferrari et al., 2011; Ledger et al., 2013; Vergés et al., 2014), and physiology and phenology (Helmuth et al., 2006; Hughes, 2000; Kroeker et al., 2013; Parmesan, 2006; Pörtner & Farrell, 2008; Alfonso et al., 2022; Smith et al., 2023).

Bioclimate models predict that, under a warming climate, invasion intensity is predicted to drastically increase by mid-century (Cheung et al., 2009). While invasion of higher latitude ecosystems has been relatively low due to invasion barriers such as low propagule pressure, extreme and seasonal abiotic conditions, and biotic resistance of relatively intact communities, these barriers are being affected by climate change (Mahanes & Sorte, 2019). Studies of increasing temperature on invasive species have found that higher temperatures can have positive effects on invasive species growth and recruitment rates and may thus facilitate increased dominance of invasive species relative to native species (Cockrell & Sorte, 2013; Stachowicz et al., 2002). Similar to native species, invasive species are undergoing range shifts poleward towards cooler temperatures (Sanford et al., 2019; Sorte et al., 2010; Small & Edwards, 2021). Due to the fact that many invasive species already occupy regions cooler than their native ranges

(Bennett et al., 2021), increasing temperatures and other changing abiotic variables are more likely to negatively impact native than invasive species (Sorte et al., 2013). As a result, invasive species may be uniquely poised to weather increased variance in the abiotic environment and colonize disturbed areas that formerly held native species, thus causing significant community shifts as a result of changing climate (Vergés et al., 2014; Wernberg et al., 2016; Krause-Jensen & Duarte, 2014).

Undaria pinnatifida (henceforth *Undaria*) is a brown algae (family Laminariales) native to Japan and well cultivated for human consumption. Since 1970, however, *Undaria* has been spread worldwide , and is now considered invasive in Australia (Campbell & Burridge, 1998), Tasmania (Hay & Villouta, 1993; Primo et al., 2010), New Zealand (Hay & Luckens, 1987), Western Europe (Castric-Fey et al., 1999; Fletcher & Manfredi; 1995, Salinas et al., 1996), the Mediterranean (Boudouresque et al., 1985; Curiel et al., 1998), Argentina (Martín & Cuevas, 2006), and Mexico (Aguilar-Rosas et al. 2004), and the United States (Silva et al., 2002). In North America, *Undaria* was first introduced to Los Angeles Harbor in 2000 (Silva et al., 2002) and has since expanded its range to San Francisco in the north (Zabin et al., 2009) and Ensenada, Mexico in the south (Aguilar-Rosas et al., 2004; Kaplanis et al., 2016). *Undaria* is mainly confined to ports and harbors along the North American coastline but has also been found among native kelp beds in the Channel Islands (Miller & Engle, 2009).

Undaria is one of two seaweeds (*Caulerpa taxifolia* is the other) to be included in a list of the world's 100 Worst Invasive Species (Lowe et al., 2000). *Undaria* has had numerous negative effects on marine ecosystems by decreasing the abundance and diversity of native seaweeds and invertebrates (Casas et al., 2004; Farrell & Fletcher, 2006), changing community structure (Bunicontro et al., 2018; Williams & Smith, 2007). Additionally, in Tasmania, *Undaria*

has been able to rapidly colonize areas where native kelp canopies were reduced as a result of other disturbances, thus preventing recolonization of ecologically important native species (Valentine & Johnson, 2003, 2004). While *Undaria* is found to be edible by many native herbivores globally (Thornber et al., 2004; Jiménez et al., 2015), often the grazing rate, while able to reduce the extent of *Undaria* canopy, is unable to fully control this species (Edgar et al., 2004; Valentine & Johnson, 2005).

While climate change effects such as rising sea surface temperature and increasing frequency and intensity of marine heatwaves are threatening native kelp species worldwide (McPherson et al., 2021; Filbee-Dexter et al., 2020), *Undaria* possesses a broad tolerance of a wide range of temperatures. The effects of temperature on different *Undaria* life stages have been well studied across the globe. Macroscopic sporophyte stages can survive a broad range of temperatures from 0-27°C, but optimum growth and photosynthetic rates can range from 15 to 20°C (Watanabe et al., 2014; Bollen et al., 2016; Gao et al., 2013a; James & Shears, 2016) and tend to be population-specific and genetically based (Gao et al., 2013b). Microscopic gametophytes, on the other hand, have a narrower range for optimal growth and fertilization between 10 and 20°C, where temperatures greater than 20°C result in inhibited growth and photosynthesis (Epstein & Smale, 2017; Henkel & Hoffman, 2008; Morita et al., 2003; Watanabe et al., 2014). While invasive *Undaria* populations are still limited to specific geographic areas, the geographic area possible for suitable range expansion based on minimum and maximum SSTs is quite extensive (James et al., 2015).

Other abiotic factors such as salinity can also affect size, growth rate, survival, and morphology in *Undaria*. At the microscopic stage, reproduction is generally able to proceed without issue between salinities of 14 and 35 psu, but zoospore germination and gametophyte

survival are able to take place at salinities as low as 3.5 and 6 psu, respectively (Crane et al., 2018; Peteiro & Sanchez, 2012). Comparative studies have also found that adult blades of *Undaria* can be more tolerant to salinity than native kelps, resulting in an increased tolerance to fluctuating environmental conditions and estuarine environments (Bollen et al., 2016). Despite the fact that *Undaria* does have wide salinity tolerances, in nature, it still tends to be found in more marine environments with salinities above 25 psu (Epstein & Smale, 2017; Floc'h et al., 1991; Watanabe et al., 2014).

While the combination of high temperatures and low salinities has been found to have a synergistic effect in reducing *Undaria* photosynthetic capacity in adult sporophyte blades, the interactive effect of salinity and temperature on *Undaria* gametophytes has not been as well studied. The persistence and spread of invasive species depend on the ability of all life stages to tolerate the conditions presented by a new environment, and thus understanding how changing climate regimes may impact early *Undaria* life stages is vital. In this study, we sought to answer the question of how do increasing temperatures and lowered salinities impact *Undaria* pinnatifida microscopic life stages at the northern edge of its North American range? While the tolerances of Undaria microstages to temperature and salinity are well understood separately, the interactive effects of these stressors remains unclear. Based on previous studies of *Undaria* temperature and salinity ranges, we hypothesized that temperature and salinity would have little effect on microstage reproduction, and that *Undaria* populations would be well suited to expand northward under a warmer climate with more variable precipitation.

Methods:

Undaria pinnatifida *in San Francisco Bay:*

San Francisco Bay holds some of the most heavily used ports in the world, and as a result, hosts over 328 invasive species (Fofonoff et al., 2018) and has one of the highest rates of introduction in the world, at one new species being introduced every 32 weeks (Hewitt, 2003). Sea surface temperature (SST) averages from 1990 to 2013 in San Francisco ranged from 10°C (minimum) to 15.5°C (maximum) (James et al., 2015), but the following year, a multiyear marine heat wave began that caused San Francisco water to experience maximum SST anomalies of up to 5°C higher than normal (Gentemann et al., 2017).

Undaria has been present in San Francisco Bay since 2009 (Zabin et al., 2009), where it primarily occupies depths of about 1-3 meters in ports and marinas. In other parts of the world, however, it can be found at depths up to 18 meters (Valentine & Johnson, 2003; Epstein & Smale, 2017). Like all kelps, *Undaria* possesses a heteromorphic lifecycle consisting of a macroscopic diploid sporophyte (1-2 meters in length) and a microscopic haploid gametophyte (~0.2 mm in length). At maturity, adult sporophytes release spores from honeycomb-like sporophylls located below the meristem, which settle onto available substrate and develop into male and female gametophytes. Male gametophytes release sperm that fertilizes eggs produced by female gametophytes, and the fertilized zygote then develops into a new sporophyte (Pang & Wu, 1996). Different populations around the world show different reproductive timing based on sea surface temperatures, and while the seasonal phenology of *Undaria* in San Francisco has not been reported, the population is predicted to be reproductive all year round (James et al., 2015; Primo et al., 2010).

Collection and experimental cultivation:

We collected 15 reproductively mature *Undaria* sporophylls from the San Francisco Small Boat Harbor (37.806612°N, 122.443779°W) on August 16th, 2021, and brought them into the lab for cultivation at the UC Davis Bodega Marine Laboratory, Bodega Bay, CA (38.317979°N, 123.071865°W). Sporophylls were rinsed in iodine and freshwater and manually cleared of epibionts before being soaked in UV-sterilized seawater for 24 hours. After 24 hours, we counted the number of spores suspended in the seawater solutions using a hemocytometer (model number CTL-HEMM-GLDR, LW Scientific, Lawrenceville, U.S.A.), and pipetted spore slurry into experimental petri dishes (pre-filled with the various seawater salinity treatments) at calculated amounts to ensure settlement densities of approximately 8 spores per square millimeter (Reed 1991). We chose 5 different salinity treatments; 5, 10, 15, 20, 25, and 33 (ambient) psu – which were mixed using calculated amounts of UV-filtered seawater and deionized freshwater and verified using a salinity refractometer. After salinity treatments were mixed, we also added 20 mL L^{-1} Provasoli nutrient mix to all water treatments to prevent nutrient limitation during growth (Provasoli, 1968). To achieve a full factorial design, dishes from each salinity treatment were evenly split between two different temperature treatments: 15°C, representing existing maximum temperatures in San Francisco (James et al. 2015), and 20°C, , representing warmer temperatures experienced under extreme heatwaves (Gentemann et al., 2017). Each salinity-temperature combination had 8 petri dish replicates, for a total of 80 petri dishes.

Undaria gametophytes were then cultured for four weeks under a 12:12 diel cycle and light intensities of 31±5 μmol m^{-2} s^{-1}, measured with a LI-COR light meter (LI-250A). The water in each dish was replaced every twice a week to prevent anoxia and replenish nutrient availability. We also added germanium dioxide to seawater mixtures at a ratio of 0.5 mL GeO_2

per liter of seawater at 6 and 16 days into the experiment in order to prevent diatom contamination (Shea & Chopin, 2007).

Data Collection:

Each week, three random points within each dish were chosen and photographed using a Micropublisher 5.0 RTV digital camera (QImaging, Surrey, Canada) mounted on an inverted microscope at 40× magnification. Each photo encompassed 1.08 mm^2 of the Petri dish (7,853 mm^2 bottom surface area). We then counted the numbers of female gametophytes, male gametophytes, eggs, and sporelings in each photo in Weeks 3 and 4. Each female counted was categorized as productive (producing eggs and or sporelings) or non-productive (not yet producing eggs and/or sporelings). These counts were then used to calculate a five different productivity ratios for each dish, including: 1) male to female ratio (# males/# females), 2) proportion of females productive (# productive females/ total # females), 3) eggs per female (# eggs/# females), 4) sporelings per female (# sporelings/ # females), and 5) offspring per female (# eggs and # juveniles / # females). We also measured the sizes of each sporeling in every photo using ImageJ. Area was calculated as the number of pixels and converted to μm^2 using a conversion factor of 71,330 pixels per 62,500 μm^2.

Statistical Methods:

All data was tested for their ability to meet the assumptions of normality and homogeneity of variance using Levene and Shapiro-Wilks tests in R version 4.1.2 (R Core Team, 2021). The three offspring per female ratios (eggs per female, juveniles per female, and total offspring per female) met the parametric assumptions of normality and homoscedasticity, and

were then analyzed with linear models that included temperature and salinity as fixed effects using package '*lme4*' (Bates et al., 2015). The percent of females productive and all count and size data did not meet the assumptions of normality even when transformed, and were subjected to additional tests of homogeneity of variances and normality for other assumed distributions by visually inspecting the residual plots of all models using the '*DHARMa*' package (Hartig, 2022). All count data had a negative binomial distribution (with the exception of males in Week 4, which had a Poisson distribution). The percent of females productive had a beta distribution, and all size data had a gamma distribution. Percent of females productive, sizes, and all count data were subsequently tested using Generalized Linear Models (GLM, packages '*MASS*' and '*glmmTMB*'; Venables and Ripley, 2002; Brooks et al., 2017), where temperature and salinity were included as fixed effects. Size models also included a covariate, the number of gametophytes present in each petri dish, in order to account for any density dependent effects on growth. The relationship between sporeling size and gametophyte number were also analyzed using linear regressions for each temperature by salinity treatment. All linear and generalized linear models were finally analyzed with post-hoc unplanned pairwise comparisons using package '*emmeans*' (Lenth, 2021). The trends and statistical outputs for the count and size data were similar in Weeks 3 and 4, so only Week 4 results are presented here. Results from both Weeks 3 and 4 are presented for all productivity ratios to provide a picture of how different treatments affected when different reproductive stages were reached.

Results:

Gametophyte Numbers:

Temperature by salinity interactions had significant effects on the number of female gametophytes (Table D1, t=-3.296, df=70, p=0.001). In low temperature treatments, female gametophytes at low salinities (10 and 15 psu) were significantly different (Table D3) from high salinities (20 and 25 psu), but not the highest, ambient salinity (33 psu). In high temperature treatments, however, low salinities (10 and 15 psu) were significantly different from high salinities (20, 25, and 33 psu, Table D3). The number of female gametophytes increased significantly under high temperatures (Table D1, t=3.260, df=70, p=0.001) for the 20 psu (Table D2, z=2.541, df=70, p=0.011) and 33 psu treatments (z=3.260, df=70, p=0.001). Salinity also had significant overall effects on the number of females, but only 10 psu had significantly lower numbers of females than all other salinity treatments (Table D1, t=3.602, df=70, p<0.001).

Ratios of Male to Female gametophytes were primarily shaped by the number of females present, as the number of male gametophytes was not significantly influenced by salinity, temperature, or any temperature by salinity interactions (Figure 3.2, Table D1). Male to Female Ratios could not be assessed in salinity treatments lower than 20 psu due to a lack of survival of male gametophytes at these low salinity treatments. In the 20, 25, and 33 psu salinity treatments, ratios were consistently low, and averaged around 3 to 4 males for every 10 females counted in Week 3 and around 1 male for every 10 females counted in Week 4 (Table 3.1).

Egg and Sporeling Numbers:

Temperature by salinity interactions significantly affected the number of eggs (Figure 3.3, Table D1), specifically within the 15 psu (t=2.075, df=70, p=0.038) and 25 psu (t=2.213, df=70, p=0.027) salinity treatments. Under low temperatures, 15 and 25 psu resulted in higher numbers of eggs than ambient (33 psu) salinity, but under high temperatures, the number of eggs

was lower than ambient salinity. The number of eggs was significantly affected by temperature in both Week 4 (Table D1, z=3.404, df=70, p=0.001), where high temperature increased the number of eggs in the 20 (Table D2, z=2.071, df=70, p=0.038) and 33 psu treatments (z=3.404, df=70, p<0.001). Pairwise comparisons reveal that at low temperatures, 10 psu had significantly fewer eggs than both 15 (Table S3, z=-2.815, df=70, p=0.039) and 25 psu (z=-2.918, df=70, p=0.029). In high temperature treatments, there were no significant effects of salinity.

Both temperature and salinity impacted the number of sporelings (Figure 3.4, Table D1), and there were significant interactions between temperature and salinity (t=2.010, df=70, p=0.044). Under high temperature treatments, both 10 and 15psu had significantly lower numbers of sporelings than high salinities (20, 25, and 33 psu), but only 15 psu had significsntly lower numbers of sporelings under the low temperature treatment (Table D3). This change in the significance of the 10 psu treatment, however, is due to extremely low sporeling survival under low temperatures. Across both temperature treatments, therfore, high salinities (20, 25, and 33 psu) resulted in significantly more sporelings than low salinities (10 and 15 psu).

Productivity Ratios:

The percent of females productive were uniformly high across treatments. While there were no significant differences between the percent of females productive in any treatment, low temperature and high salinity treatments in Week 3 showed the most variation in the proportion of females that were productive (Figure 3.5), whereas high temperature treatments resulted in nearly 100 percent female productivity. By Week 4, every female observed was productive (Table 3.1).

Ratios of eggs per female were overall not significantly different from each other in Week 3 (Figure 3.6, Table D1), but 10 psu ($t=2.170$, $df=48$, $p=0.035$) and 15 psu ($t=3.476$, $df=48$, $p=0.001$) were significantly higher than other salinity treatments in Week 4. There was no overall effect of temperature on the ratio of eggs per female in either week, but there were temperature by salinity effects in Week 4 ($t=2.796$, $df=48$, $p=0.007$). Pairwise comparisons revealed that there was only a significant effect of temperature at 10 psu (Table D2, $z=-2.29$, $df=48$, $p=0.026$), where low temperatures resulted in a higher ratio of eggs per female.

Ratios of sporelings per female were generally higher under high temperatures and high salinities (Figure 3.7), but specific trends were influenced by temperature by salinity interactions in both Week 3 (Table D4, $t=2.019$, $df=38$, $p=0.051$) and Week 4 (Table D1, $t=2.053$, $df=48$, $p=0.046$). Specifically, in the Week 3 low temperature treatment, only 25psu had a significantly lower ratio of sporelings per female than 33 psu (Table D6, $z=-2.948$, $df=38$, $p=0.041$), whereas in high temperature conditions, ratios in the 15 psu treatment were significantly lower than in 20 ($z=-3.826$, $df=38$, $p=0.004$), 25 ($z=-3.995$, $df=38$, $p=0.003$), or 33 psu ($z=-4.295$, $df=38$, $p=0.001$). In Week 4 low temperature conditions, 10 and 15 psu ratios were significantly lower than 20 (Table D3, 10 psu: $z=-2.849$, $df=48$, $p=0.048$, 15 psu: $z=-3.573$, $df=48$, $p=0.007$) and 33 psu (10 psu: $z=-3.384$, $df=48$, $p=0.012$, 15 psu: $z=-4.645$, $df=48$, $p<0.001$), but not 25 psu. Under high temperatures in Week 4, however, ratios in 15 psu were significantly lower than all other treatments, including 10 psu ($z=2.962$, $df=48$, $p=0.037$). Temperature was not independently significant for either week, but in Week 3, the ratios of sporelings per female were significantly higher under high temperatures in the 20 (Table D5, $t=3.25$, $df=38$, $p=0.002$) and 25 psu treatments ($t=4.838$, $df=38$, $p<0.001$), and in the 10 (Table D2, $z=2.703$, $df=48$, $p=0.010$) and 25 psu treatments ($z=3.346$, $df=48$, $p=0.002$) in Week 4.

Offspring (eggs + sporelings) per female ratios were generally more even across low temperature treatments, but under higher temperatures generally increased with higher salinities (Figure 3.8). In Week 3, ratios of offspring per female were significantly lower under low temperatures at high salinities (20, 25, and 33 psu) but this only remained true in Week 4 for the 25 psu treatment (Table D2, $z=3.541$, $df=48$, $p<0.001$). Salinity generally had no independent effect on the total offspring per female ratio in either week, with the exception of the Week 3 high temperature treatment, where 15 psu resulted in a significantly lower ratio of offspring to females than 33 psu (Table D6, $z=-3.576$, $df=38$, $p=0.008$). Temperature, on the other hand, did have a significant effect on the ratios of offspring per female in both Week 3 (Table D1, $t=2.667$, $df=38$, $p=0.011$), but not Week 4 (Table D1, $t=1.675$, $df=48$, $p=0.101$).

Sporeling Sizes:

In Week 4, there was no significant effect of salinity or number of gametophytes on sporeling size, but temperature ($z=-2.346$, $df = 450$, $p=0.019$) and a temperature by salinity interaction were significant ($z=2.62$, $df = 450$, $p=0.009$). Specifically, pairwise comparisons showed that high temperature resulted in a significant decline in sporeling size for 33 psu ($t=-2.346$, $df = 450$, $p=0.019$), and that 20 psu resulted in significantly smaller sporelings than 33 psu at low temperature treatments($t=3.008$, $df = 450$, $p=0.014$), but significantly larger sporelings under high temperature treatments ($t=2.942$, $df = 450$, $p=0.0172$). Additionally, there was a significant relationship between sporeling size and the number of gametophytes in a dish for several treatments in Week 4 (Table 3.2). There was no overall relationship between number of gametophytes and sporeling size in the low temperature treatment ($r^2=0.008$, $df=100$, $p=0.674$), but we did see significantly negative relationships between the two variables in the 20

(r^2=0.086, df=36, p=0.041) and 33 psu treatments (r^2=0.143, df=39, p=0.009) specifically (Figure 3.9). In high temperature treatments, there was a significant overall negative relationship between sporeling size and the number of gametophytes (r^2=0.023, df=360, p=0.002). This negative trend was observed in the 33 psu treatment specifically (r^2=0.025, df=169, p=0.021), but in the 20 psu treatment, the relationship was positive (r^2=0.1453, df=100, p<0.001).

Discussion:

Our results show that both temperature and salinity have significant effects on microstage reproduction of *Undaria pinnatifida* sourced from San Francisco Harbor, especially in regards to gametophyte survival. In this study, we saw that both higher temperatures (20°C) and higher salinities (20-33 psu) resulted in higher counts of gametophytes (males and females) and offspring (eggs and females). These results are consistent with previous studies of temperature and salinity ranges that have found that optimal ranges for gametophyte growth and photosynthesis tend to occur between 15 and 20 °C (Epstein & Smale, 2017; Henkel & Hoffman, 2008; Morita et al., 2003; Watanabe et al., 2014) and 14 to 35 psu (Crane et al., 2018; Peteiro & Sanchez, 2012). While other studies noted that gametophyte survival was possible as low at 6 psu (Peteiro & Sanchez, 2012), we saw very few gametophytes develop at 15 psu, and almost none at 10 psu. Generally, we saw that counts of gametophytes and offspring were most similar in low salinities (10 and 15) and at high salinities (20, 25, 33), whereas counts were significantly different between high and low salinities, potentially indicating some salinity threshold between 15 and 20 psu for this population of *Undaria*.

We saw significant temperature by salinity interactions on several stages of *Undaria* reproduction. The number of females, eggs, and sporelings were overall higher at higher

salinities and temperatures, but at low salinities, numbers of females, eggs, and sporelings were actually higher under low temperatures. This varying response to salinity based on temperature may thus indicate that microstages growing under lower temperatures may be associated with more resilience to low salinity.

Across treatments, male to female ratios were biased towards the latter, supporting more female than male gametophytes. We did see that high salinities resulted in a higher male to female gametophyte ratios, whereas low salinities (<20psu) had little to no male gametophyte development. This particular result may indicate that male gametophytes have a different threshold for salinity tolerance than females. Previous studies have found that abiotic conditions such as temperature have the ability to alter gametophyte sex ratios (Luthringer et al., 2014, Oppliger et al., 2011), growth optima (Sato et al., 2020), and molecular markers and gene expression for gametophyte sexes (Bi & Zhou, 2014; Monteiro et al., 2019; Pearson et al., 2019). The effects of salinity on gametophyte sex ratios tend to vary by species (reviewed in Bartsch et al., 2008). For example, Norton and South (1969) saw that lower salinities tended to skew ratios in favor of females for *Sacchoriza polyschides*, but in favor of males for *Chorda filum*. While we did not see a significant effect of temperature on gametophyte sex ratios in this study, salinity clearly affected males and females differently.

We also saw an effect of both temperature and salinity on reproductive timing based on the ratios of offspring per female in weeks 3 and 4. First we saw that low temperature significantly reduced ratios of offspring to female in several cases. These results are consistent with the effects of temperature on the reproductive timing of other kelps, where high temperatures caused increased gametophyte growth rates (Leal et al., 2017) and earlier peaks of egg release and egg per female ratios (Howard, 2014; Korabik et al., 2023). We also saw that

salinity affects rate of production (affecting ratios of eggs per female and sporeling per female) but not overall amount of production (offspring per female) over the course of 4 weeks. Specifically, under low salinities egg production and fertilization occurs later, but is not actually reduced relative to high salinities. The effects of abiotic factors on reproductive timing at microstages could potentially explain population-specific differences in reproductive timing. Previous studies have found that different populations of *Undaria* can have different demographic histories rooted in seasonality, reproductive timing, and sea surface temperature (Primo et al., 2010; James et al., 2015; Hay & Villouta, 1993; Stuart et al., 1999). Other factors such as nutrients and light have also been found to affect development of *Undaria* microscopic stages (Morelisson et al., 2013), and as a result, we hypothesize that the abiotic profile of a given location can determine the timing and seasonality of the *Undaria* life cycle.

California's coastal climate is expected to drastically change due to increasing sea surface temperatures (Dunstan et al., 2018; Lima & Wethey, 2012; Reid & Beaugrand, 2012), increasing frequency and intensity of marine heatwaves (Gentemann et al., 2017; Oliver et al., 2018; Shi et al., 2021), and changes in upwelling regimes (Bakun et al., 2015; Di Lorenzo et al., 2008; García-Reyes et al., 2015; García-Reyes et al., 2020). Marine heatwaves specifically are also resulting in extreme changes to California's coastal ecosystems via native kelp canopy loss (McPherson et al., 2021; Filbee-Dexter et al., 2020), reductions in kelp reproduction (Buschmann et al., 2004; Gaitán-Espitia et al., 2014; Hollarsmith et al., 2020; Korabik et al., 2023; Le et al., 2022; Leal et al., 2017; Muñoz et al., 2004; Shukla & Edwards, 2017), ecosystem state shifts towards urchin barrens (Rogers-Bennett & Catton, 2019; Carnell & Keough, 2020; Tolimieri et al., 2023), loss of commercially and ecologically important fisheries (McPherson et al., 2021; Arafeh-Dalmau, 2019), loss of invertebrate biodiversity (Arafeh-Dalmau, 2019;

Michaud et al., 2022), and increased presence of invasive species (Arafeh-Dalmau, 2019; Michaud et al., 2022).

These changes to sea surface temperature and coastal circulation patterns, combined with changes in atmospheric processes, are also resulting in increasing variability and less predictability in California's precipitation patterns (Hu et al., 2021; Beaudin et al., 2023; Easterling et al., 2017; Gernushov et al., 2017). Atmospheric rivers, in particular, are expected to increase in both frequency and intensity in the coming century as a result of warmer atmospheres and increasing atmospheric moisture content (Gao et al., 2015; Gershunov et al. 2019, Hagos et al., 2016; Payne & Magnusdottir, 2015; Lu et al., 2018; Warner et al., 2015), thus altering coastal and estuarine salinity regimes.

While native kelp species are responding negatively to increasing temperatures (reviewed in Edwards, 2022, and Veenhof et al., 2021; Korabik et al., 2023; Chapter 2), our results and other studies show that *Undaria* reproduction will respond positively to the projected and experienced increases in northern California sea surface temperatures (Watanabe et al., 2014; Bollen et al., 2016; Gao et al., 2013a; Gao et al., 2013b; James & Shears, 2016; Epstein & Smale, 2017; Henkel & Hoffman, 2008; Morita et al., 2003; Leal et al., 2017). As *Undaria* invasion primarily dependent on man-made structures and shipping (Guzinski et al., 2018; Hay, 1990), movement northward is very possible, and several models show that large geographic areas north of *Undaria*'s current California range would be able to support the establishment of populations (James et al., 2015; Murphy et al., 2017). Some other vector, however, would be required to facilitate *Undaria* spread into natural environments. Currently in California, *Undaria*'s expansion to natural areas has been largely limited due to shading from existing *Macrocystis pyrifera* and *Nereocystis luetkeana* canopies (Sandoval-Gil et al., 2023; Veenhof et

al., 2021). However, disturbance of native canopies can open up space for *Undaria* to colonize new areas (Valentine & Johnson, 2003), and as a result, increasing disturbance to native kelp canopies from marine heat waves and excessive urchin grazing may provide more opportunity for range expansion both northward and to natural areas.

In this study, we show that *Undaria* reproduction may benefit from climate change at the northern edge of its introduced range on the West Coast of North America. While extreme low salinities (10-15 psu) have negative effects on *Undaria* reproduction, less intense drops in salinity (down to 20 psu) and increasing temperatures from marine heat waves support increased *Undaria* reproduction. California is expected to see more interannual variation in precipitation under climate change, so the future of *Undaria* reproduction will likely depend on the given water year. In very dry years, *Undaria* reproduction can be expected to thrive, especially if temperatures are warm, whereas in very wet years, *Undaria* reproduction may suffer. As *Undaria* is positioned to potentially benefit from changes to California's climate, managers and scientists should remain wary in preventing the spread of this species.

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TABLES AND FIGURES

Table 3.1: Means and SDs of Productivity Data

Variable	Temperature Treatment	Salinity Treatment	Week 3 Mean	Week 3 SD	Week 4 Mean	Week 4 SD
# Females	15 ° C	10psu	0.25	0.71	0.25	0.71
		15psu	0.12	0.35	3.38	2.72
		20psu	4.25	3.01	5.00	3.16
		25psu	3.50	2.56	5.25	2.43
		33psu	2.00	2.00	4.25	2.76
	20 ° C	10psu	0.12	0.35	0.25	0.71
		15psu	1.62	1.92	1.62	2.56
		20psu	8.62	7.15	12.25	3.58
		25psu	7.00	3.96	9.12	6.94
		33psu	13.12	9.14	13.62	12.40
Male to Female Ratio	15 ° C	10psu	0.00	NA	0.00	NA
		15psu	0.00	NA	0.00	0.00
		20psu	0.06	0.14	0.00	0.00
		25psu	0.30	0.33	0.13	0.23
		33psu	0.38	0.44	0.17	0.25
	20 ° C	10psu	0.00	NA	0.00	NA
		15psu	0.00	0.00	0.00	0.00
		20psu	0.30	0.05	0.00	0.00
		25psu	0.30	0.28	0.03	0.09
		33psu	0.31	0.45	0.23	0.19
Proportion Productive Females	15 ° C	10psu	1.00	NA	1.00	NA
		15psu	1.00	NA	1.00	0.00
		20psu	0.56	0.30	1.00	0.00
		25psu	0.66	0.37	1.00	0.00
		33psu	0.79	0.31	1.00	0.00
	20 ° C	10psu	1.00	NA	1.00	NA
		15psu	0.70	0.28	1.00	0.00
		20psu	1.00	0.00	1.00	0.00
		25psu	0.98	0.05	1.00	0.00
		33psu	0.87	0.35	1.00	0.00

Table 3.2: Linear Regression Statistics for the relationship between Sporeling Size and the number of gametophytes in each dish. (ND=No Data, NS=No Slope)

Week	Temperature	Predictor	df	R-Squared	F	*P*
Week 3	15 ° C	All Salinities	18	0.102	3.158	0.092
		20psu	4	NS	NS	NS
		25psu	ND	ND	ND	ND
		33psu	13	0.060	0.204	0.659
	20 ˚ C	All Salinities	309	0.047	16.200	**<0.001**
		20psu	49	0.06183	4.295	**0.0435**
		25psu	57	0.016	0.094	0.760
		33psu	199	0.062	14.220	**0.000**
Week 4	15 ° C	All Salinities	100	0.008	0.178	0.674
		15psu	1	NS	NS	NS
		20psu	36	0.086	4.474	**0.041**
		25psu	19	0.047	0.109	0.745
		33psu	39	0.143	7.659	**0.009**
	20˚C	All Salinities	360	0.023	9.376	**0.002**
		15psu	2	NS	NS	NS
		20psu	100	0.1453	18.17	**<0.001**
		25psu	84	0.113	0.047	0.830
		33psu	169	0.025	5.438	**0.021**

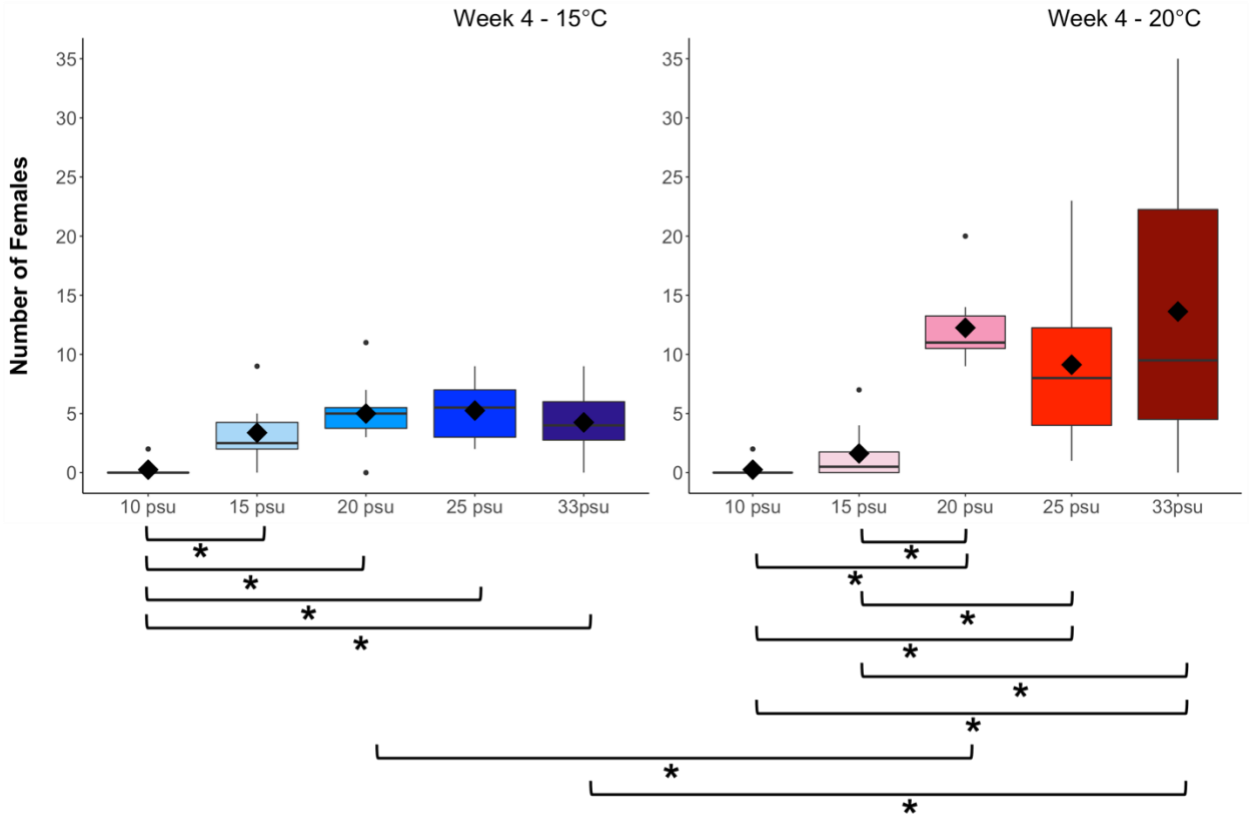

Figure 3.1: Number of female gametophytes summed across three photo replicates. The left panel represents 15°C temperature treatments, while the right panel represents 20°C temperature treatments. The box plots summarize the mean (diamond) and median (box midline) for each treatment, the first and third quartiles (upper and lower box limits), outliers within 1.5 times the inter-quartile range (vertical lines), and outliers beyond that range (dots). Starred brackets beneath the graph signify that two treatments were significantly different from one another.

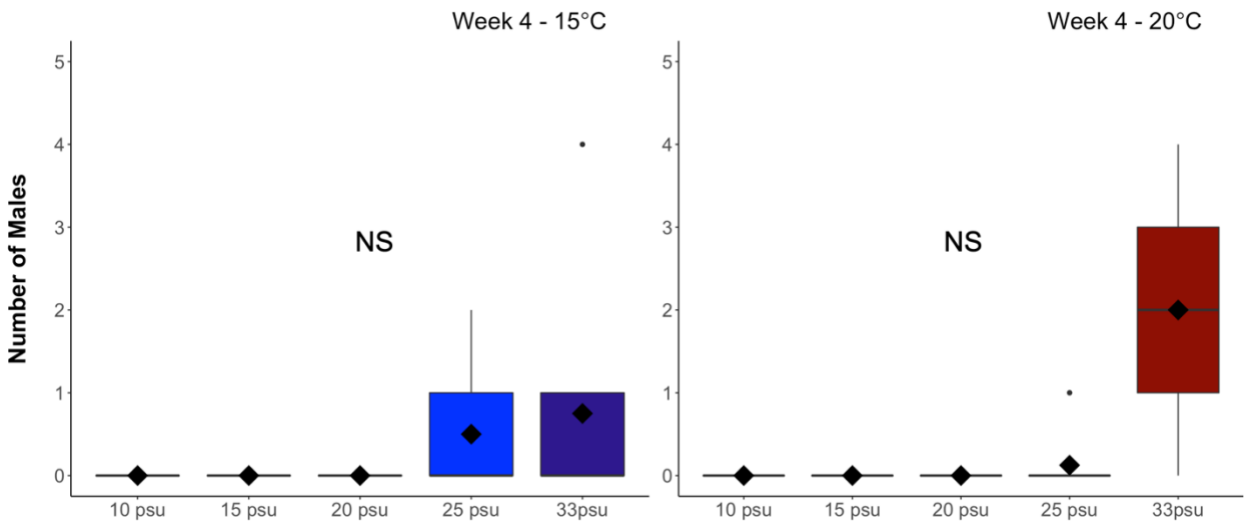

Figure 3.2: Number of male gametophytes summed across three photo replicates. The left panel represents 15°C temperature treatments, while the right panel represents 20°C temperature treatments. The box plots summarize the mean (diamond) and median (box midline) for each treatment, the first and third quartiles (upper and lower box limits), outliers within 1.5 times the inter-quartile range (vertical lines), and outliers beyond that range (dots). Graphs labelled "NS" had no significantly different treatments.

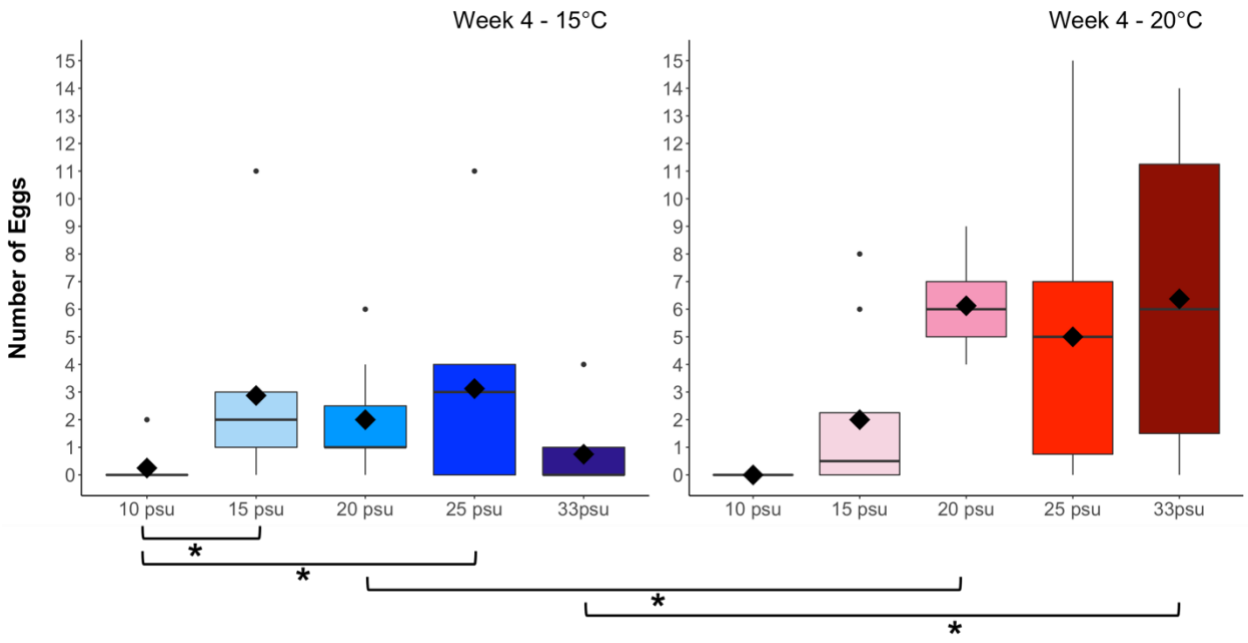

Figure 3.3: Number of eggs summed across three photo replicates. The left panel represents 15°C temperature treatments, while the right panel represents 20°C temperature treatments. The box plots summarize the mean (diamond) and median (box midline) for each treatment, the first and third quartiles (upper and lower box limits), outliers within 1.5 times the inter-quartile range (vertical lines), and outliers beyond that range (dots). Starred brackets beneath the graph signify that two treatments were significantly different from one another.

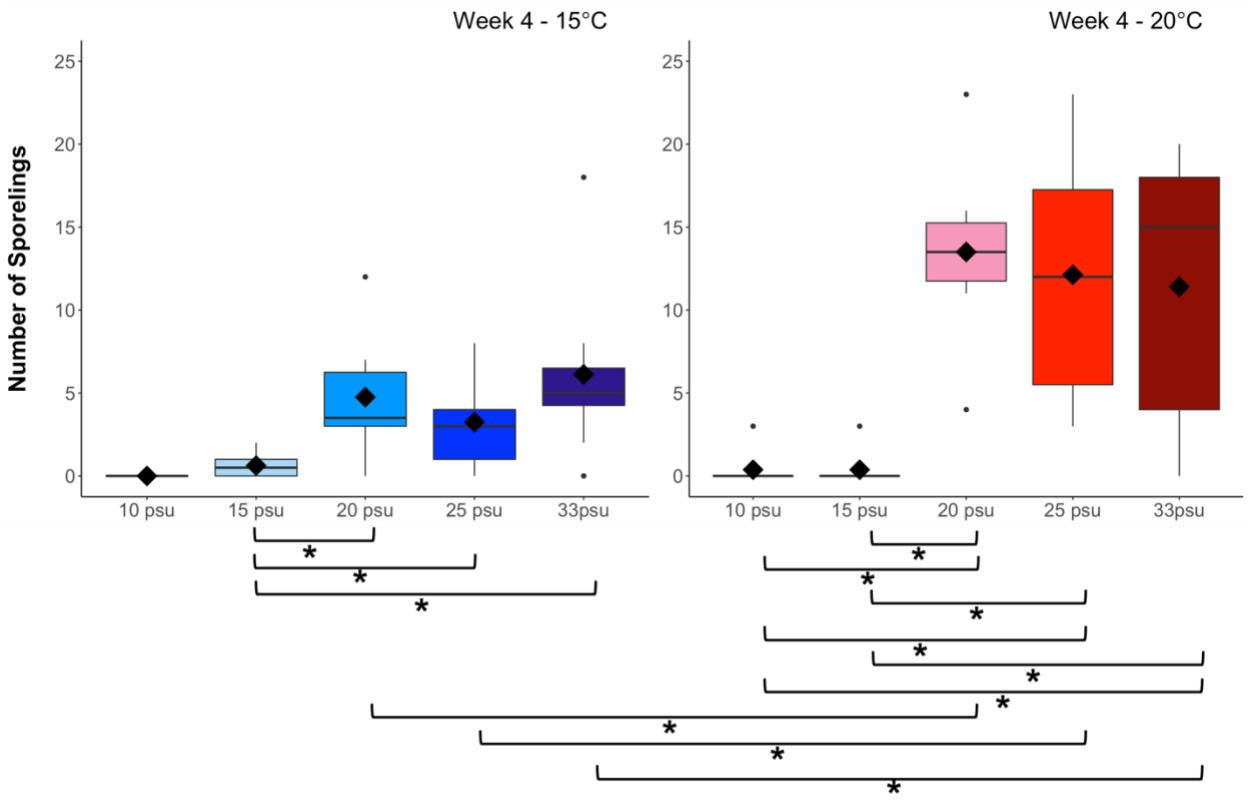

Figure 3.4: Number of sporelings summed across three photo replicates. The left panel represents 15°C temperature treatments, while the right panel represents 20°C temperature treatments. The box plots summarize the mean (diamond) and median (box midline) for each treatment, the first and third quartiles (upper and lower box limits), outliers within 1.5 times the inter-quartile range (vertical lines), and outliers beyond that range (dots). Starred brackets beneath the graph signify that two treatments were significantly different from one another.

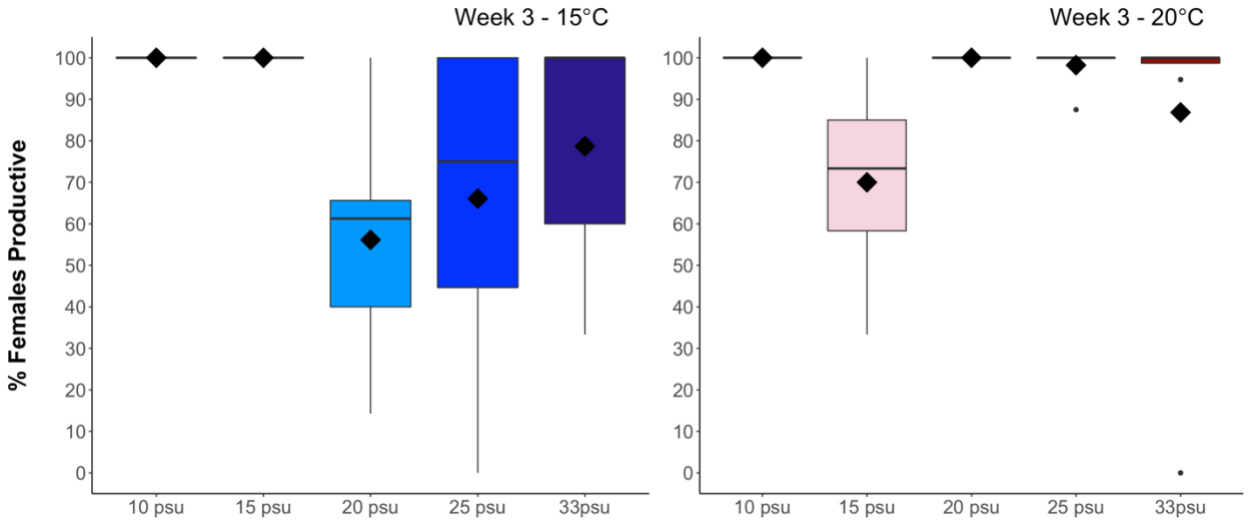

Figure 3.5: Proportion of female gametophytes producing eggs or sporelings in Week 3. The left panel represents 15°C temperature treatments, while the right panel represents 20°C temperature treatments. The box plots summarize the mean (diamond) and median (box midline) for each treatment, the first and third quartiles (upper and lower box limits), outliers within 1.5 times the inter-quartile range (vertical lines), and outliers beyond that range (dots).

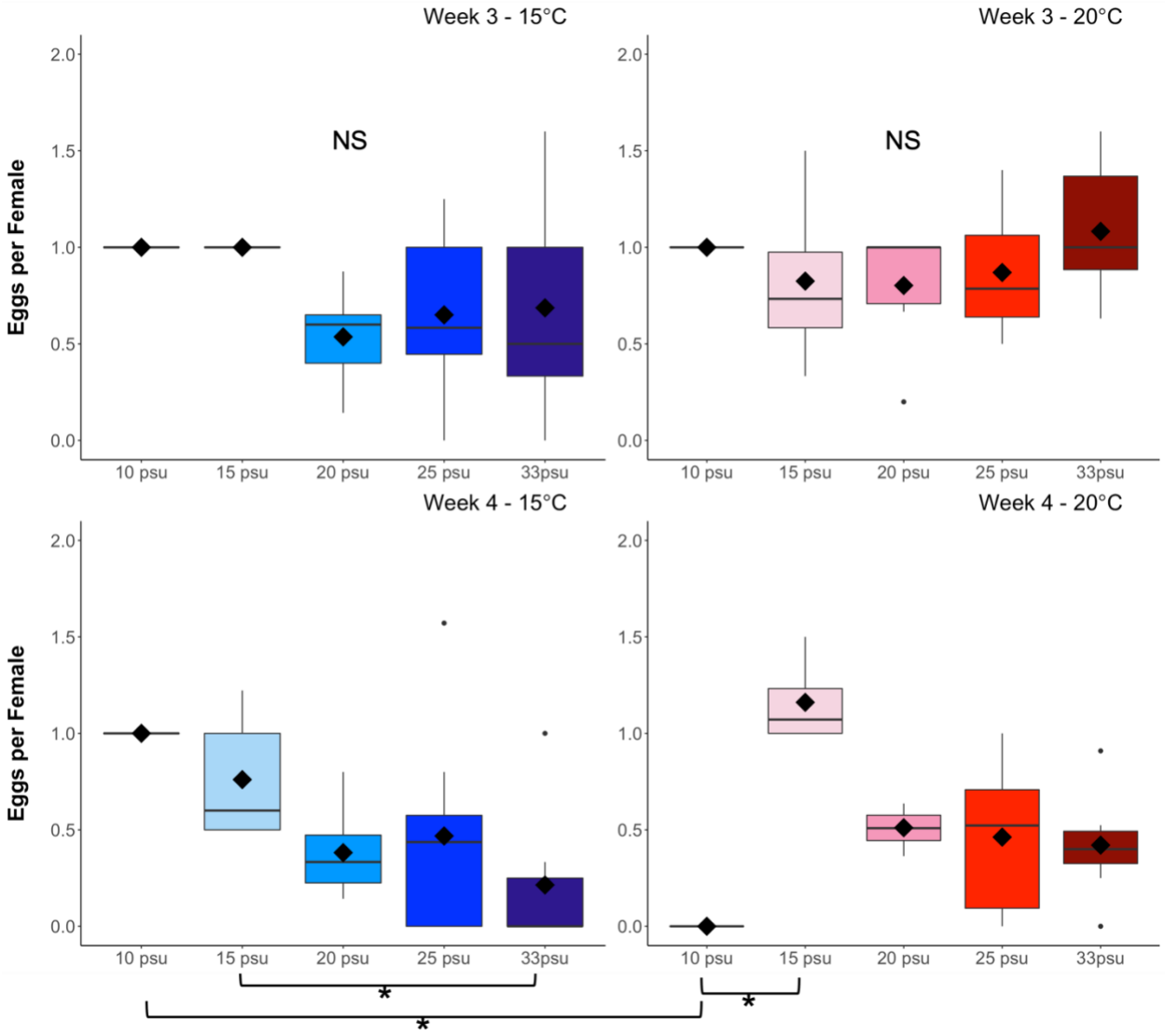

Figure 3.6: Ratio of eggs per female. Top panels represent results from Week 3, while the bottom panels represent results from Week 4. Left panels represent 15°C temperature treatments, while the right panels represent 20°C temperature treatments. The box plots summarize the mean (diamond) and median (box midline) for each treatment, the first and third quartiles (upper and lower box limits), outliers within 1.5 times the inter-quartile range (vertical lines), and outliers beyond that range (dots). Starred brackets beneath the graph signify that two treatments were significantly different from one another. Graphs labelled "NS" had no significantly different treatments.

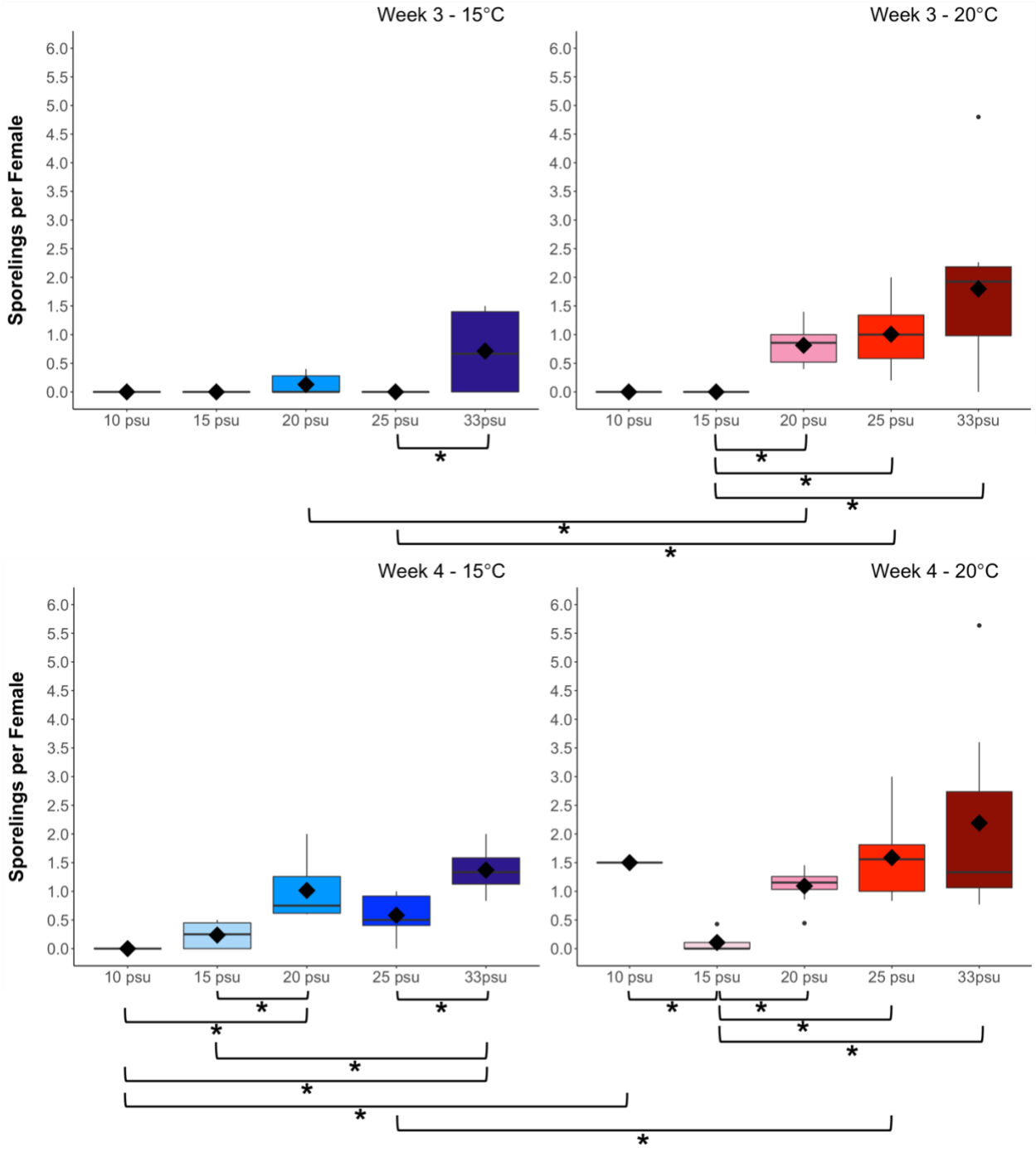

Figure 3.7: Ratio of sporelings per female. Top panels represent results from Week 3, while the bottom panels represent results from Week 4. Left panels represent 15°C temperature treatments, while the right panels represent 20°C temperature treatments. The box plots summarize the mean (diamond) and median (box midline) for each treatment, the first and third quartiles (upper and lower box limits), outliers within 1.5 times the inter-quartile range (vertical lines), and outliers beyond that range (dots). Starred brackets beneath the graph signify that two treatments were significantly different from one another.

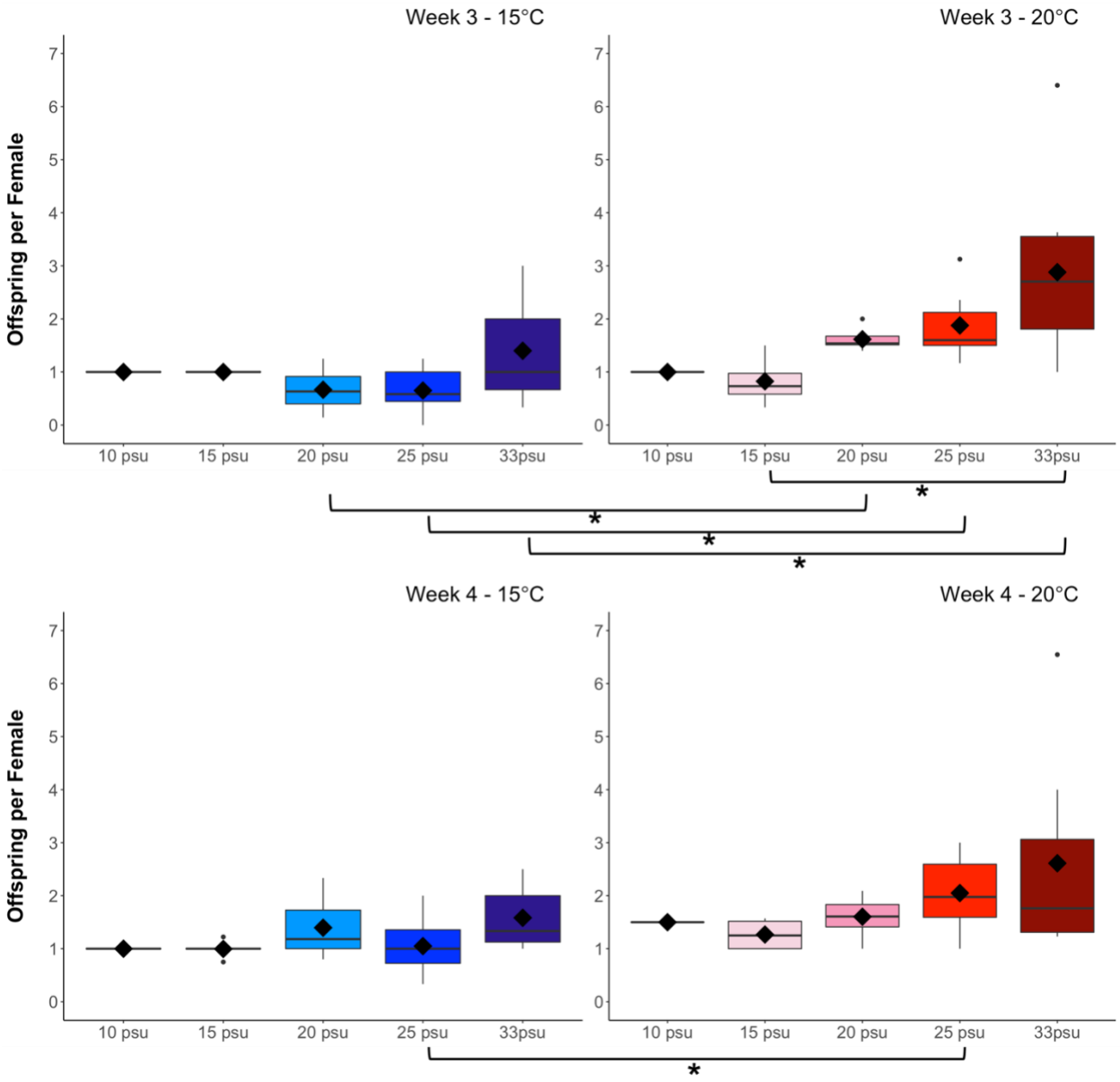

Figure 3.8: Ratio of offspring (eggs + juveniles) per female. Top panels represent results from Week 3, while the bottom panels represent results from Week 4. Left panels represent 15°C temperature treatments, while the right panels represent 20°C temperature treatments. The box plots summarize the mean (diamond) and median (box midline) for each treatment, the first and third quartiles (upper and lower box limits), outliers within 1.5 times the inter-quartile range (vertical lines), and outliers beyond that range (dots). Starred brackets beneath the graph signify that two treatments were significantly different from one another.

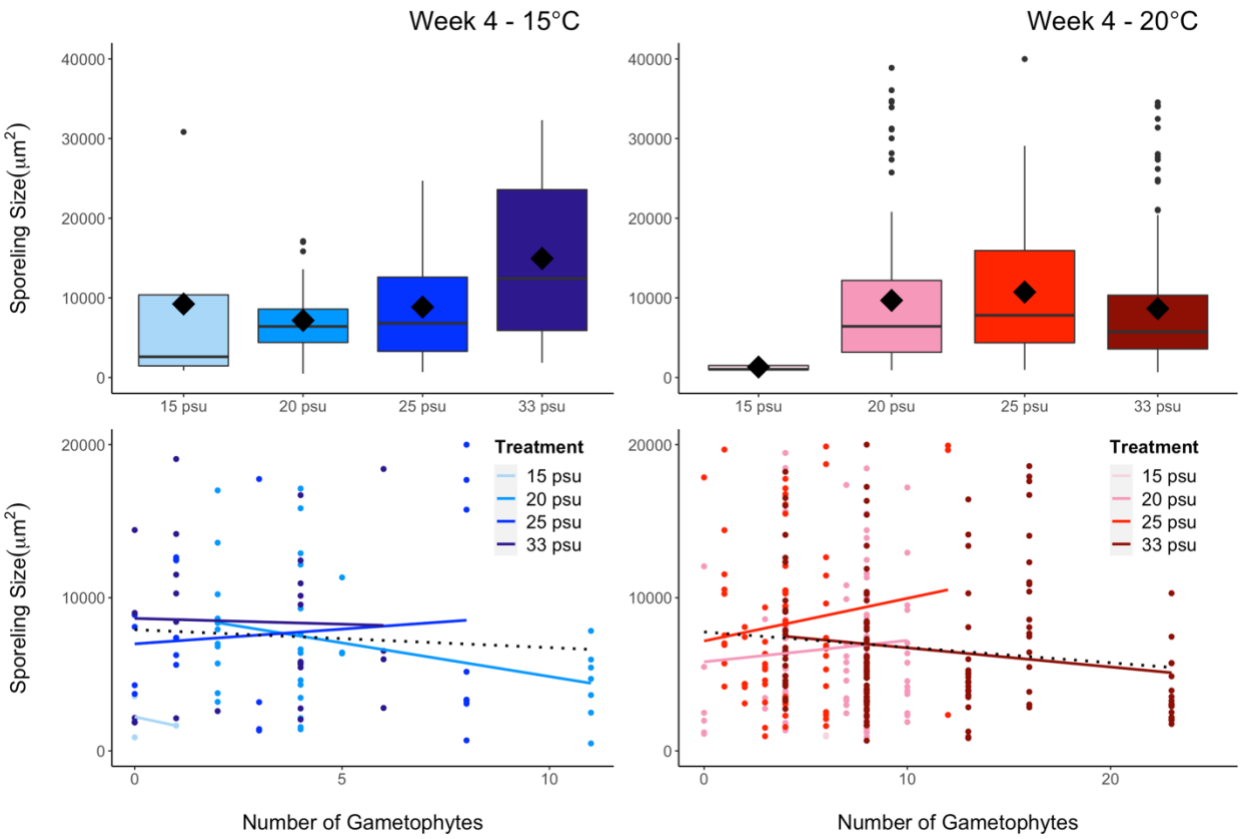

Figure 3.9: Sporeling sizes in Week 4. Left panels represent 15°C temperature treatments, while the right panels represent 20°C temperature treatments. Top panels contain box plots summarize the mean (diamond) and median (box midline) for each treatment, the first and third quartiles (upper and lower box limits), outliers within 1.5 times the inter-quartile range (vertical lines), and outliers beyond that range (dots). The bottom panels show the relationship of the covariate (mean number of gametophytes) to the response variable (mean sporeling size). Colored lines represent different salinity treatments within each temperature-location treatment, and the dotted black line represents the overall trend across salinity treatments. Heterogeneous slopes (R^2 values listed in Table 2) and different ranges of values for each treatment indicate that the different treatments are confounded with differences in the covariate.

APPENDIX D: Chapter 3 Statisitical Tables

WEEK 4 TABLES

Table D1: Week 4 *Count and Size Responses to Temperature and Salinity Stress* (Generalized Linear Model with 2-Way Interaction, Count Distribution = Negative Binomial, Link=Log, Size Distribution = Gamma, '*ref*' = reference)

Lifestage	Variable	Fixed Effects	n	Estimate	SE	z/t	P
Females	Intercept			1.447	0.272	5.320	**<0.001**
	Temperature	15 ° C	40	*ref*	*ref*	*Ref*	*ref*
		20 ° C	40	1.165	0.357	3.260	**0.001**
	Salinity	33 psu	16	*ref*	*ref*	*Ref*	*Ref*
		25 psu	16	0.211	0.377	0.560	0.575
		20psu	16	0.163	0.379	0.429	0.668
		15 psu	16	-0.231	0.394	-0.584	0.559
		10psu	16	-2.833	0.787	-3.602	**<0.001**
	Interactions	Temp (20°C):Salinity (10 psu)	8	-1.165	1.103	-1.056	0.291
		Temp (20°C):Salinity (15 psu)	8	-1.896	0.575	-3.296	**0.001**
		Temp (20°C):Salinity (20 psu)	8	-0.269	0.502	-0.536	0.592
		Temp (20°C):Salinity (25 psu)	8	-0.612	0.504	-1.214	0.225
Males	Intercept			-0.288	0.441	-0.653	0.514
	Temperature	15 ° C	40	*ref*	*ref*	*Ref*	*ref*
		20 ° C	40	0.981	0.533	1.840	0.066
	Salinity	33 psu	16	*ref*	*ref*	*Ref*	*Ref*
		25 psu	16	-0.406	0.687	-0.590	0.555
		20psu	16	-22.920	38730.000	-0.001	1.000
		15 psu	16	-22.920	38730.000	-0.001	1.000
		10psu	16	-22.920	38730.000	-0.001	1.000
	Interactions	Temp (20°C):Salinity (10 psu)	8	-3.458	140000.000	0.000	1.000

		Temp (20°C):Salinity (15 psu)	8	-3.458	140000.000	0.000	1.000
		Temp (20°C):Salinity (20 psu)	8	-3.458	140000.000	0.000	1.000
		Temp (20°C):Salinity (25 psu)	8	-2.367	1.261	-1.878	0.060
Eggs	Intercept			-0.288	0.521	-0.552	0.581
	Temperature	15 ° C	40	*ref*	*ref*	*Ref*	*ref*
		20 ° C	40	2.140	0.629	3.404	**0.001**
	Salinity	33 psu	16	*ref*	*ref*	*Ref*	*Ref*
		25 psu	16	1.427	0.645	2.213	**0.027**
		20psu	16	0.981	0.662	1.482	0.138
		15 psu	16	1.344	0.648	2.075	**0.038**
		10psu	16	-1.099	0.936	-1.174	0.240
	Interactions	Temp (20°C):Salinity (10 psu)	8	-20.578	7133.230	-0.003	0.998
		Temp (20°C):Salinity (15 psu)	8	-2.503	0.843	-2.970	**0.003**
		Temp (20°C):Salinity (20 psu)	8	-1.021	0.829	-1.231	0.218
		Temp (20°C):Salinity (25 psu)	8	-1.670	0.818	-2.041	**0.041**
Sporelings	Intercept			1.812	0.281	6.458	**<0.001**
	Temperature	15 ° C	40	*ref*	*ref*	*Ref*	*ref*
		20 ° C	40	1.279	0.378	3.384	**0.001**
	Salinity	33 psu	16	*ref*	*ref*	*Ref*	*Ref*
		25 psu	16	-0.634	0.419	-1.513	0.130
		20psu	16	-0.254	0.404	-0.629	0.529
		15 psu	16	-2.282	0.581	-3.931	**<0.001**
		10psu	16	-21.959	8380.858	-0.003	0.998
	Interactions	Temp (20°C):Salinity (10 psu)	8	17.887	8380.858	0.002	0.998

		Temp (20°C):Salinity (15 psu)	8	-1.789	0.890	-2.010	**0.044**
		Temp (20°C):Salinity (20 psu)	8	-0.234	0.543	-0.431	0.666
		Temp (20°C):Salinity (25 psu)	8	0.038	0.555	0.068	0.946
Eggs per Female	Intercept			0.284	0.117	2.431	**0.019**
	Temperature	15 ° C	40	*ref*	*ref*	*Ref*	*ref*
		20 ° C	40	0.305	0.165	1.849	0.071
	Salinity	33 psu	16	*ref*	*ref*	*Ref*	*Ref*
		25 psu	16	0.238	0.160	1.492	0.142
		20psu	16	0.312	0.165	1.889	0.065
		15 psu	16	0.574	0.165	3.476	**0.001**
		10psu	16	0.716	0.330	2.170	**0.035**
	Interactions	Temp (20°C):Salinity (10 psu)	8	-1.305	0.467	-2.796	**0.007**
		Temp (20°C):Salinity (15 psu)	8	-0.089	0.254	-0.350	0.728
		Temp (20°C):Salinity (20 psu)	8	-0.189	0.230	-0.822	0.415
		Temp (20°C):Salinity (25 psu)	8	-0.260	0.226	-1.149	0.256
Juveniles per Female	Intercept			1.159	0.121	9.573	**<0.001**
	Temperature	15 ° C	40	*ref*	*ref*	*Ref*	*ref*
		20 ° C	40	0.230	0.171	1.344	0.185
	Salinity	33 psu	16	*ref*	*ref*	*Ref*	*Ref*
		25 psu	16	-0.461	0.166	-2.778	**0.008**
		20psu	16	-0.184	0.171	-1.072	0.289
		15 psu	16	-0.796	0.171	-4.645	**<0.001**
		10psu	16	-1.159	0.343	-3.384	**0.001**
	Interactions	Temp (20°C):Salinity (10 psu)	8	0.995	0.484	2.053	**0.046**

		Temp (20°C):Salinity (15 psu)	8	-0.430	0.264	-1.630	0.110
		Temp (20°C):Salinity (20 psu)	8	-0.173	0.238	-0.726	0.471
		Temp (20°C):Salinity (25 psu)	8	0.306	0.235	1.305	0.198
Offspring per Female	Intercept			0.470	0.145	3.236	**0.002**
	Temperature	15 ° C	40	*ref*	*ref*	*Ref*	*ref*
		20 ° C	40	0.344	0.205	1.675	0.101
	Salinity	33 psu	16	*ref*	*ref*	*Ref*	*Ref*
		25 psu	16	-0.437	0.199	-2.197	**0.033**
		20psu	16	-0.124	0.205	-0.602	0.550
		15 psu	16	-0.385	0.205	-1.875	0.067
		10psu	16	-0.375	0.411	-0.912	0.366
	Interactions	Temp (20°C):Salinity (10 psu)	8	0.031	0.581	0.053	0.958
		Temp (20°C):Salinity (15 psu)	8	-0.135	0.317	-0.427	0.671
		Temp (20°C):Salinity (20 psu)	8	-0.179	0.286	-0.627	0.534
		Temp (20°C):Salinity (25 psu)	8	0.336	0.281	1.196	0.238
Sporeling Sizes	Intercept			9.56E-05	3.37E-05	2.833	**0.00481**
	Temperature	15 ° C	40	*ref*	*ref*	*Ref*	*ref*
		20 ° C	40	-8.35E-05	3.56E-05	-2.346	**0.0194**
	Salinity	33 psu	16	*ref*	*ref*	*Ref*	*Ref*
		25 psu	16	-1.85E-07	5.46E-05	-0.003	0.9973
		20psu	16	-3.19E-06	5.91E-05	-0.054	0.95702
		15 psu	16	-2.43E-05	5.76E-05	-0.422	0.67289
	# Gametophytes		16	-9.68E-06	6.22E-06	-1.555	0.12071
	Interactions	Temp (20°C):Salinity (15 psu)	8	7.28E-04	5.10E-04	1.426	0.15449

	Temp (20°C):Salinity (20 psu)	8	-1.44E-05	6.37E-05	-0.226	0.82111
	Temp (20°C):Salinity (25 psu)	8	4.72E-05	5.79E-05	0.814	0.41584
	Temp (20°C):# Gametophytes	8	1.68E-05	6.39E-06	2.62	**0.00909**
	Salinity (15 psu):# Gametophytes	8	NA	NA	NA	NA
	Salinity (20 psu):# Gametophytes	8	2.11E-05	1.28E-05	1.65	0.09974
	Salinity (25 psu):# Gametophytes	8	1.16E-05	1.07E-05	1.085	0.27871
	Temp (20°C):Salinity (15 psu):# Gametophytes	8	NA	NA	NA	NA
	Temp (20°C):Salinity (20 psu):# Gametophytes	8	-1.24E-05	1.35E-05	-0.918	0.35929
	Temp (20°C):Salinity (25 psu): # Gametophytes	8	-1.79E-05	1.14E-05	-1.575	0.11589

Table D2: Pairwise comparisons of life stage count and juvenile size responses to temperature in Week 4, grouped by salinity. (ND = No Data)

Stage	Salinity	Temperature Comparison	Estimate	SE	df	z/t	*P*
Females	10psu	15°C v. 20°C	3.20E-06	1.044	70	0	1
	15psu	15°C v. 20°C	-7.31E-01	0.451	70	-1.622	0.1048
	20psu	15°C v. 20°C	8.96E-01	0.353	70	2.541	**0.011**
	25psu	15°C v. 20°C	5.53E-01	0.356	70	1.553	0.1203
	33psu	15°C v. 20°C	1.16	0.357	70	3.26	**0.0011**
Males	10psu	15°C v. 20°C	3.441	2.03E+06	70	0	1
	15psu	15°C v. 20°C	-4.203	1.55E+05	70	0	1
	20psu	15°C v. 20°C	-4.203	1.55E+05	70	0	1
	25psu	15°C v. 20°C	-1.386	1.1	70	-1.214	0.2248
	33psu	15°C v. 20°C	0.981	0.5	70	1.841	0.0656
Eggs	10psu	15°C v. 20°C	-18.648	7922.857	70	-0.002	0.9981
	15psu	15°C v. 20°C	-0.363	0.561	70	-0.647	0.5179
	20psu	15°C v. 20°C	1.119	0.54	70	2.071	**0.0383**
	25psu	15°C v. 20°C	0.47	0.524	70	0.898	0.3693
	33psu	15°C v. 20°C	2.14	0.629	70	3.404	**0.0007**
Sporelings	10psu	15°C v. 20°C	19.051	7911.755	70	0.002	0.9981
	15psu	15°C v. 20°C	-0.511	0.806	70	-0.634	0.5263
	20psu	15°C v. 20°C	1.045	0.39	70	2.677	**0.0074**
	25psu	15°C v. 20°C	1.317	0.407	70	3.237	**0.0012**
	33psu	15°C v. 20°C	1.279	0.378	70	3.384	**0.0007**
Eggs per Female	10psu	15°C v. 20°C	-1	0.437	48	-2.29	**0.0264**
	15psu	15°C v. 20°C	0.2161	0.194	48	1.117	0.2697
	20psu	15°C v. 20°C	0.1163	0.16	48	0.728	0.4701
	25psu	15°C v. 20°C	0.0454	0.154	48	0.294	0.7699
	33psu	15°C v. 20°C	0.3051	0.165	48	1.849	0.0706
Sporelings per Female	10psu	15°C v. 20°C	1.225	0.453	48	2.703	**0.0095**
	15psu	15°C v. 20°C	-0.2	0.201	48	-0.997	0.324
	20psu	15°C v. 20°C	0.057	0.166	48	0.344	0.7325
	25psu	15°C v. 20°C	0.536	0.16	48	3.346	**0.0016**
	33psu	15°C v. 20°C	0.23	0.171	48	1.344	0.1854
Offspring per Female	10psu	15°C v. 20°C	0.375	0.544	48	0.689	0.4939
	15psu	15°C v. 20°C	0.209	0.241	48	0.867	0.3904
	20psu	15°C v. 20°C	0.165	0.199	48	0.828	0.4116
	25psu	15°C v. 20°C	0.68	0.192	48	3.541	**0.0009**
	33psu	15°C v. 20°C	0.344	0.205	48	1.675	0.1005
Sporeling Sizes	15psu	15°C v. 20°C	ND	ND	ND	ND	ND
	20psu	15°C v. 20°C	-6.65E-05	4.95E-05	450	-1.342	0.1795

	25psu	15°C v. 20°C	-4.49E-05	4.17E-05	450	-1.076	0.2819
	33psu	15°C v. 20°C	3.81E-05	1.62E-05	450	2.352	**0.0187**

TABLE D3: Pairwise comparisons of life stage count and juvenile size responses to salinity in Week 4, grouped by temperature. (ND = No Data)

Stage	Temperature	Salinity Comparison	Estimate	SE	df	z/t	*P*
Females	15°C	10 psu v 15 psu	-2.6027	0.791	70	-3.289	**0.0089**
		10 psu v 20 psu	-2.9957	0.784	70	-3.823	**0.0012**
		10 psu v 25 psu	-3.0445	0.783	70	-3.889	**0.001**
		10 psu v 33 psu	-2.8332	0.786	70	-3.602	**0.0029**
		15 psu v 20 psu	-0.393	0.389	70	-1.011	0.8505
		15 psu v 25 psu	-0.4418	0.387	70	-1.141	0.7848
		15 psu v 33 psu	-0.2305	0.394	70	-0.584	0.9774
		20 psu v 25 psu	-0.0488	0.371	70	-0.131	0.9999
		20 psu v 33 psu	0.1625	0.379	70	0.429	0.993
		25 psu v 33 psu	0.2113	0.377	70	0.56	0.9807
	20°C	10 psu v 15 psu	-1.8718	0.816	70	-2.294	0.1469
		10 psu v 20 psu	-3.8918	0.774	70	-5.027	**<.0001**
		10 psu v 25 psu	-3.5973	0.776	70	-4.633	**<.0001**
		10 psu v 33 psu	-3.9982	0.774	70	-5.169	**<.0001**
		15 psu v 20 psu	-2.02	0.42	70	-4.811	**<.0001**
		15 psu v 25 psu	-1.7255	0.424	70	-4.07	**0.0005**
		15 psu v 33 psu	-2.1264	0.419	70	-5.08	**<.0001**
		20 psu v 25 psu	0.2945	0.336	70	0.876	0.9058
		20 psu v 33 psu	-0.1064	0.329	70	-0.323	0.9977
		25 psu v 33 psu	-0.4009	0.335	70	-1.198	0.7527
Males	15°C	10 psu v 15 psu	-9.962	1970000	70	0	1
		10 psu v 20 psu	-9.962	1970000	70	0	1
		10 psu v 25 psu	-31.053	1970000	70	0	1
		10 psu v 33 psu	-31.458	1970000	70	0	1
		15 psu v 20 psu	0	26900	70	0	1
		15 psu v 25 psu	-21.091	19000	70	-0.001	1
		15 psu v 33 psu	-21.496	19000	70	-0.001	1
		20 psu v 25 psu	-21.091	19000	70	-0.001	1
		20 psu v 33 psu	-21.496	19000	70	-0.001	1
		25 psu v 33 psu	-0.405	0.7	70	-0.59	0.9766
	20°C	10 psu v 15 psu	-2.318	516000	70	0	1
		10 psu v 20 psu	-2.318	516000	70	0	1
		10 psu v 25 psu	-26.225	493000	70	0	1
		10 psu v 33 psu	-28.998	493000	70	0	1
		15 psu v 20 psu	0	217000	70	0	1

		15 psu v 25 psu	-23.907	154000	70	0	1
		15 psu v 33 psu	-26.68	154000	70	0	1
		20 psu v 25 psu	-23.907	154000	70	0	1
		20 psu v 33 psu	-26.68	154000	70	0	1
		25 psu v 33 psu	-2.773	1.1	70	-2.623	0.0663
Eggs	15°C	10 psu v 15 psu	-2.4423	0.867	70	-2.815	**0.0391**
		10 psu v 20 psu	-2.0794	0.878	70	-2.367	0.1243
		10 psu v 25 psu	-2.5257	0.865	70	-2.918	**0.029**
		10 psu v 33 psu	-1.0986	0.936	70	-1.174	0.7663
		15 psu v 20 psu	0.3629	0.561	70	0.647	0.9673
		15 psu v 25 psu	-0.0834	0.541	70	-0.154	0.9999
		15 psu v 33 psu	1.3437	0.647	70	2.075	0.2307
		20 psu v 25 psu	-0.4463	0.558	70	-0.8	0.9308
		20 psu v 33 psu	0.9808	0.662	70	1.482	0.5745
		25 psu v 33 psu	1.4271	0.645	70	2.213	0.1746
	20°C	10 psu v 15 psu	-20.7276	7922.857	70	-0.003	1
		10 psu v 20 psu	-21.8468	7922.857	70	-0.003	1
		10 psu v 25 psu	-21.6439	7922.857	70	-0.003	1
		10 psu v 33 psu	-21.8868	7922.857	70	-0.003	1
		15 psu v 20 psu	-1.1192	0.54	70	-2.071	0.2325
		15 psu v 25 psu	-0.9163	0.545	70	-1.683	0.4447
		15 psu v 33 psu	-1.1592	0.54	70	-2.148	0.1997
		20 psu v 25 psu	0.2029	0.504	70	0.402	0.9945
		20 psu v 33 psu	-0.04	0.499	70	-0.08	1
		25 psu v 33 psu	-0.2429	0.504	70	-0.482	0.989
Sporelings	15°C	10 psu v 15 psu	-19.6	7911.755	70	-0.002	1
		10 psu v 20 psu	-21.6	7911.755	70	-0.003	1
		10 psu v 25 psu	-21.2	7911.755	70	-0.003	1
		10 psu v 33 psu	-21.8	7911.755	70	-0.003	1
		15 psu v 20 psu	-2.03	0.586	70	-3.463	**0.0049**
		15 psu v 25 psu	-1.65	0.596	70	-2.767	**0.0449**
		15 psu v 33 psu	-2.28	0.581	70	-3.931	**0.0008**
		20 psu v 25 psu	0.379	0.426	70	0.891	0.9004
		20 psu v 33 psu	-0.254	0.404	70	-0.629	0.9704
		25 psu v 33 psu	-0.634	0.419	70	-1.513	0.5543
	20°C	10 psu v 15 psu	-0.000001	0.885	70	0	1
		10 psu v 20 psu	-3.58	0.678	70	-5.288	**<.0001**
		10 psu v 25 psu	-3.48	0.678	70	-5.123	**<.0001**
		10 psu v 33 psu	-4.07	0.675	70	-6.032	**<.0001**
		15 psu v 20 psu	-3.58	0.678	70	-5.288	**<.0001**

		15 psu v 25 psu	-3.48	0.678	70	-5.123	**<.0001**
		15 psu v 33 psu	-4.07	0.675	70	-6.032	**<.0001**
		20 psu v 25 psu	0.107	0.369	70	0.291	0.9984
		20 psu v 33 psu	-0.488	0.363	70	-1.346	0.6622
		25 psu v 33 psu	-0.596	0.364	70	-1.636	0.4744
Egss per Female	15°C	10 psu v 15 psu	0.1426	0.33	48	0.432	0.9925
		10 psu v 20 psu	0.4046	0.33	48	1.226	0.7365
		10 psu v 25 psu	0.4779	0.327	48	1.46	0.5931
		10 psu v 33 psu	0.7163	0.33	48	2.17	0.2084
		15 psu v 20 psu	0.2619	0.165	48	1.587	0.5127
		15 psu v 25 psu	0.3353	0.16	48	2.098	0.2375
		15 psu v 33 psu	0.5737	0.165	48	3.476	**0.0092**
		20 psu v 25 psu	0.0734	0.16	48	0.459	0.9906
		20 psu v 33 psu	0.3118	0.165	48	1.889	0.3369
		25 psu v 33 psu	0.2384	0.16	48	1.492	0.5726
	20°C	10 psu v 15 psu	-1.0734	0.345	48	-3.11	**0.0249**
		10 psu v 20 psu	-0.7118	0.327	48	-2.174	0.2072
		10 psu v 25 psu	-0.5675	0.327	48	-1.733	0.4241
		10 psu v 33 psu	-0.5888	0.33	48	-1.784	0.3946
		15 psu v 20 psu	0.3617	0.189	48	1.913	0.3245
		15 psu v 25 psu	0.506	0.189	48	2.676	0.0726
		15 psu v 33 psu	0.4847	0.194	48	2.505	0.1065
		20 psu v 25 psu	0.1443	0.154	48	0.935	0.8819
		20 psu v 33 psu	0.123	0.16	48	0.77	0.9381
		25 psu v 33 psu	-0.0213	0.16	48	-0.133	0.9999
Sporelings per Female	15°C	10 psu v 15 psu	-0.36381	0.343	48	-1.062	0.8248
		10 psu v 20 psu	-0.97584	0.343	48	-2.849	**0.0483**
		10 psu v 25 psu	-0.69863	0.34	48	-2.056	0.2561
		10 psu v 33 psu	-1.15937	0.343	48	-3.384	**0.0119**
		15 psu v 20 psu	-0.61203	0.171	48	-3.573	**0.007**
		15 psu v 25 psu	-0.33482	0.166	48	-2.019	0.2727
		15 psu v 33 psu	-0.79556	0.171	48	-4.645	**0.0002**
		20 psu v 25 psu	0.27721	0.166	48	1.672	0.4607
		20 psu v 33 psu	-0.18352	0.171	48	-1.072	0.8201
		25 psu v 33 psu	-0.46074	0.166	48	-2.778	**0.0572**
	20°C	10 psu v 15 psu	1.06108	0.358	48	2.962	**0.0365**
		10 psu v 20 psu	0.19189	0.34	48	0.565	0.9795
		10 psu v 25 psu	-0.00997	0.34	48	-0.029	1
		10 psu v 33 psu	-0.16473	0.343	48	-0.481	0.9888
		15 psu v 20 psu	-0.86919	0.196	48	-4.43	**0.0005**

		15 psu v 25 psu	-1.07105	0.196	48	-5.458	**<.0001**
		15 psu v 33 psu	-1.22582	0.201	48	-6.103	**<.0001**
		20 psu v 25 psu	-0.20186	0.16	48	-1.26	0.7165
		20 psu v 33 psu	-0.35662	0.166	48	-2.15	0.2163
		25 psu v 33 psu	-0.15476	0.166	48	-0.933	0.8825
Offspring per Female	15°C	10 psu v 15 psu	0.0105	0.411	48	0.026	1
		10 psu v 20 psu	-0.2511	0.411	48	-0.611	0.9726
		10 psu v 25 psu	0.0623	0.408	48	0.153	0.9999
		10 psu v 33 psu	-0.3747	0.411	48	-0.912	0.8909
		15 psu v 20 psu	-0.2617	0.205	48	-1.274	0.7083
		15 psu v 25 psu	0.0517	0.199	48	0.26	0.999
		15 psu v 33 psu	-0.3853	0.205	48	-1.875	0.3443
		20 psu v 25 psu	0.3134	0.199	48	1.575	0.5201
		20 psu v 33 psu	-0.1236	0.205	48	-0.602	0.9742
		25 psu v 33 psu	-0.437	0.199	48	-2.197	0.1985
	20°C	10 psu v 15 psu	0.1764	0.43	48	0.411	0.9938
		10 psu v 20 psu	-0.0412	0.408	48	-0.101	1
		10 psu v 25 psu	-0.2435	0.408	48	-0.597	0.9748
		10 psu v 33 psu	-0.344	0.411	48	-0.837	0.9176
		15 psu v 20 psu	-0.2176	0.235	48	-0.924	0.886
		15 psu v 25 psu	-0.42	0.235	48	-1.784	0.3943
		15 psu v 33 psu	-0.5205	0.241	48	-2.161	0.2123
		20 psu v 25 psu	-0.2024	0.192	48	-1.053	0.8292
		20 psu v 33 psu	-0.3029	0.199	48	-1.523	0.5532
		25 psu v 33 psu	-0.1005	0.199	48	-0.505	0.9865
Sporeling Sizes	15°C	15 psu v 20 psu	ND	ND	ND	ND	ND
		15 psu v 25 psu	ND	ND	ND	ND	ND
		15 psu v 33 psu	ND	ND	ND	ND	ND
		20 psu v 25 psu	6.55E-05	6.16E-05	450	1.064	0.7117
		20 psu v 33 psu	1.50E-04	4.98E-05	450	3.008	**0.014**
		25 psu v 33 psu	8.42E-05	4.21E-05	450	2.002	0.1871
	20°C	15 psu v 20 psu	ND	ND	ND	ND	ND
		15 psu v 25 psu	ND	ND	ND	ND	ND
		15 psu v 33 psu	ND	ND	ND	ND	ND
		20 psu v 25 psu	4.39E-05	2.00E-05	450	2.193	0.1251
		20 psu v 33 psu	4.52E-05	1.54E-05	450	2.942	**0.0172**
		25 psu v 33 psu	1.22E-06	1.53E-05	450	0.08	0.9998

WEEK 3 TABLES

TABLE D4: Week 3 *Count and Size Responses to Temperature and Salinity Stress* (Generalized Linear Model with 2-Way Interaction, Count Distribution = Negative Binomial, Link=Log, Size

Lifestage	Variable	Fixed Effects	n	Estimate	SE	z/t	P
Females	Intercept			0.693	0.358	1.934	**0.053**
	Temperature	15 ° C	40	*ref*	*ref*	*Ref*	*ref*
		20 ° C	40	1.881	0.452	4.166	**<0.001**
	Salinity	33 psu	16	*ref*	*ref*	*Ref*	*Ref*
		25 psu	16	0.560	0.480	1.167	0.243
		20psu	16	0.754	0.473	1.593	0.111
		15 psu	16	-2.773	1.093	-2.537	**0.011**
		10psu	16	-2.079	0.833	-2.495	**0.013**
	Interactions	Temp (20°C):Salinity (10 psu)	8	-2.575	1.355	-1.900	**0.057**
		Temp (20°C):Salinity (15 psu)	8	0.684	1.189	0.575	0.565
		Temp (20°C):Salinity (20 psu)	8	-1.174	0.616	-1.904	**0.057**
		Temp (20°C):Salinity (25 psu)	8	-1.188	0.624	-1.904	**0.057**
Males	Intercept			-0.288	0.443	-0.650	0.516
	Temperature	15 ° C	40	*ref*	*ref*	*Ref*	*ref*
		20 ° C	40	1.540	0.511	3.016	**0.003**
	Salinity	33 psu	16	*ref*	*ref*	*Ref*	*Ref*
		25 psu	16	0.154	0.607	0.254	0.799
		20psu	16	-1.792	1.107	-1.619	0.106
		15 psu	16	-21.170	16180.000	-0.001	0.999
		10psu	16	-21.170	16180.000	-0.001	0.999
	Interactions	Temp (20°C):Salinity (10 psu)	8	-8.210	500400.000	0.000	1.000
		Temp (20°C):Salinity (15 psu)	8	-8.210	500400.000	0.000	1.000

		Temp (20°C):Salinity (20 psu)	8	-0.847	1.349	-0.628	0.530
		Temp (20°C):Salinity (25 psu)	8	-0.714	0.724	-0.985	0.324
Eggs	Intercept			0.405	0.407	0.997	0.319
	Temperature	15 ° C	40	*ref*	*ref*	*Ref*	*ref*
		20 ° C	40	2.216	0.506	4.377	**<0.001**
	Salinity	33 psu	16	*ref*	*ref*	*Ref*	*Ref*
		25 psu	16	0.348	0.553	0.630	0.529
		20psu	16	0.460	0.548	0.839	0.401
		15 psu	16	-2.485	1.117	-2.225	**0.026**
		10psu	16	-1.792	0.864	-2.073	**0.038**
	Interactions	Temp (20°C):Salinity (10 psu)	8	-2.909	1.386	-2.099	**0.036**
		Temp (20°C):Salinity (15 psu)	8	0.087	1.233	0.071	0.944
		Temp (20°C):Salinity (20 psu)	8	-1.135	0.700	-1.620	0.105
		Temp (20°C):Salinity (25 psu)	8	-1.199	0.707	-1.695	0.090
Sporelings	Intercept			0.629	0.312	2.013	0.048
	Temperature	15 ° C	40	*ref*	*ref*	*Ref*	*ref*
		20 ° C	40	2.653	0.404	6.561	**<0.001**
	Salinity	33 psu	16	*ref*	*ref*	*Ref*	*Ref*
		25 psu	16	-20.420	3036.216	-0.007	0.995
		20psu	16	-1.099	0.513	-2.143	**0.036**
		15 psu	16	-20.420	3036.216	-0.007	0.995
		10psu	16	-20.420	3036.216	-0.007	0.995
	Interactions	Temp (20°C):Salinity (10 psu)	8	-2.653	4293.858	-0.001	1.000
		Temp (20°C):Salinity (15 psu)	8	-2.653	4293.858	-0.001	1.000

		Temp (20°C):Salinity (20 psu)	8	-0.202	0.634	-0.319	0.751
		Temp (20°C):Salinity (25 psu)	8	19.218	3036.216	0.006	0.995
Percent of Females Productive	Intercept			0.969	0.554	1.750	0.080
	Temperature	15 ° C	40	*ref*	*ref*	*Ref*	*ref*
		20 ° C	40	-0.104	0.695	-0.150	0.881
	Salinity	33 psu	16	*ref*	*ref*	*Ref*	*Ref*
		25 psu	16	-0.791	0.710	-1.114	0.265
		20psu	16	-0.728	0.755	-0.964	0.335
		15 psu	16	0.472	1.285	0.367	0.714
		10psu	16	0.472	1.285	0.367	0.714
	Interactions	Temp (20°C):Salinity (10 psu)	8	0.104	1.787	0.058	0.954
		Temp (20°C):Salinity (15 psu)	8	-0.765	1.494	-0.512	0.609
		Temp (20°C):Salinity (20 psu)	8	1.303	0.979	1.331	0.183
		Temp (20°C):Salinity (25 psu)	8	1.283	0.947	1.355	0.175
Eggs per Female	Intercept			0.687	0.175	3.933	**<0.001**
	Temperature	15 ° C	40	*ref*	*ref*	*Ref*	*ref*
		20 ° C	40	0.396	0.223	1.779	0.083
	Salinity	33 psu	16	*ref*	*ref*	*Ref*	*Ref*
		25 psu	16	-0.036	0.223	-0.163	0.871
		20psu	16	-0.150	0.236	-0.636	0.529
		15 psu	16	0.313	0.428	0.733	0.468
		10psu	16	0.313	0.428	0.733	0.468
	Interactions	Temp (20°C):Salinity (10 psu)	8	-0.396	0.595	-0.665	0.510
		Temp (20°C):Salinity (15 psu)	8	-0.571	0.490	-1.165	0.251

		Temp (20°C):Salinity (20 psu)	8	-0.130	0.311	-0.418	0.679
		Temp (20°C):Salinity (25 psu)	8	-0.176	0.301	-0.587	0.561
Sporelings per Female	Intercept			-0.799	0.400	-1.997	**0.053**
	Temperature	15 ° C	40	*ref*	*ref*	*Ref*	*ref*
		20 ° C	40	0.850	0.510	1.666	0.104
	Salinity	33 psu	16	*ref*	*ref*	*Ref*	*Ref*
		25 psu	16	-1.504	0.510	-2.948	**0.005**
		20psu	16	-0.976	0.542	-1.801	0.080
		15 psu	16	-1.504	0.980	-1.534	0.133
		10psu	16	-1.504	0.980	-1.534	0.133
	Interactions	Temp (20°C):Salinity (10 psu)	8	-0.850	1.364	-0.623	0.537
		Temp (20°C):Salinity (15 psu)	8	-0.850	1.123	-0.757	0.454
		Temp (20°C):Salinity (20 psu)	8	0.768	0.713	1.078	0.288
		Temp (20°C):Salinity (25 psu)	8	1.390	0.689	2.019	**0.051**
Offspring per Female	Intercept			1.108	0.153	7.222	<**0.001**
	Temperature	15 ° C	40	*ref*	*ref*	*Ref*	*ref*
		20 ° C	40	0.522	0.196	2.667	**0.011**
	Salinity	33 psu	16	*ref*	*ref*	*Ref*	*Ref*
		25 psu	16	-0.373	0.196	-1.905	0.064
		20psu	16	-0.331	0.208	-1.592	0.120
		15 psu	16	-0.108	0.376	-0.287	0.775
		10psu	16	-0.108	0.376	-0.287	0.775
	Interactions	Temp (20°C):Salinity (10 psu)	8	-0.522	0.523	-0.997	0.325
		Temp (20°C):Salinity (15 psu)	8	-0.643	0.431	-1.494	0.143

		Temp (20°C):Salinity (20 psu)	8	-0.030	0.273	-0.109	0.914
		Temp (20°C):Salinity (25 psu)	8	0.096	0.264	0.364	0.718
Sporeling Sizes	Intercept			3.36E-04	2.06E-04	1.634	0.10318
	Temperature	15 ° C	40	*ref*	*ref*	*Ref*	*ref*
		20 ° C	40	2.08E-05	2.10E-04	0.099	0.920862
	Salinity	33 psu	16	*ref*	*ref*	*Ref*	*Ref*
		25 psu	16	-1.42E-05	8.87E-05	-0.16	0.873042
		20psu	16	3.34E-04	3.02E-04	1.107	0.269256
	# Gametophytes		16	-3.11E-05	1.24E-04	-0.251	0.802065
	Interactions	Temp (20°C):Salinity (20 psu)	16	-4.79E-04	3.06E-04	-1.566	0.118425
		Temp (20°C):Salinity (25 psu)	8	NA	NA	NA	NA
		Temp (20°C):# Gametophytes	8	1.88E-05	1.24E-04	0.152	0.879238
		Salinity (20 psu):# Gametophytes	8	2.30E-05	6.75E-06	3.405	**0.000746**
		Salinity (25 psu):# Gametophytes	8	1.04E-05	8.86E-06	1.176	0.240506
		Temp (20°C):Salinity (20 psu):# Gametophytes	8	NA	NA	NA	NA
		Temp (20°C):Salinity (25 psu): # Gametophytes	8	NA	NA	NA	NA

TABLE D5: Pairwise comparisons of life stage count and juvenile size responses to temperature in Week 3, grouped by salinity. (ND = No Data)

Stage	Salinity	Temperature Comparison	Estimate	SE	df	z/t	*P*
Females	10psu	15°C v. 20°C	-6.93E-01	1.277	70	-0.543	0.5874
	15psu	15°C v. 20°C	2.57E+00	1.099	70	2.333	**0.0197**
	20psu	15°C v. 20°C	7.08E-01	0.419	70	1.688	0.0914
	25psu	15°C v. 20°C	6.93E-01	0.431	70	1.609	0.1075
	33psu	15°C v. 20°C	1.881	0.452	70	4.166	**<0.001**
Males	10psu	15°C v. 20°C	3.429	9.59E+04	70	0	1
	15psu	15°C v. 20°C	-1.455	3.93E+04	70	0	1
	20psu	15°C v. 20°C	0.693	1.25E+00	70	0.555	0.5787
	25psu	15°C v. 20°C	0.827	0.51	70	1.609	0.1075
	33psu	15°C v. 20°C	1.54	0.51	70	3.016	**0.0026**
Eggs	10psu	15°C v. 20°C	-0.693	1.29	70	-0.537	0.591
	15psu	15°C v. 20°C	2.303	1.124	70	2.048	**0.0405**
	20psu	15°C v. 20°C	1.081	0.484	70	2.233	**0.0256**
	25psu	15°C v. 20°C	1.017	0.494	70	2.059	**0.0395**
	33psu	15°C v. 20°C	2.216	0.506	70	4.377	**<0.001**
Sporelings	10psu	15°C v. 20°C	0	4293.858	70	0	1
	15psu	15°C v. 20°C	0	4293.858	70	0	1
	20psu	15°C v. 20°C	2.45	0.488	70	5.027	**<0.001**
	25psu	15°C v. 20°C	21.87	3036.216	70	0.007	0.9943
	33psu	15°C v. 20°C	2.65	0.404	70	6.561	**<0.001**
Percent of Females Productive	10psu	15°C v. 20°C	1.10e-6	1.646	38	0	1
	15psu	15°C v. 20°C	-0.869	1.323	38	-0.657	0.511
	20psu	15°C v. 20°C	1.200	0.688	38	1.742	0.082
	25psu	15°C v. 20°C	1.180	0.641	38	1.838	0.066
	33psu	15°C v. 20°C	-0.104	0.695	38	-0.150	0.881
Eggs per Female	10psu	15°C v. 20°C	0	0.552	38	0	1
	15psu	15°C v. 20°C	-0.175	0.437	38	-0.401	0.6907
	20psu	15°C v. 20°C	0.266	0.217	38	1.225	0.2281
	25psu	15°C v. 20°C	0.219	0.202	38	1.086	0.2842
	33psu	15°C v. 20°C	0.396	0.223	38	1.779	0.0833
Sporelings per Female	10psu	15°C v. 20°C	0	1.265	38	0	1
	15psu	15°C v. 20°C	0	1	38	0	1
	20psu	15°C v. 20°C	1.62	0.498	38	3.25	**0.0024**
	25psu	15°C v. 20°C	2.24	0.463	38	4.838	**<0.001**
	33psu	15°C v. 20°C	0.85	0.51	38	1.666	0.104

Offspring per Female	10psu	15°C v. 20°C	0	0.485	38	0	1
	15psu	15°C v. 20°C	-0.122	0.384	38	-0.317	0.7527
	20psu	15°C v. 20°C	0.492	0.191	38	2.577	**0.014**
	25psu	15°C v. 20°C	0.618	0.178	38	3.479	**0.0013**
	33psu	15°C v. 20°C	0.522	0.196	38	2.667	**0.0112**
Sporeling Sizes	20psu	15°C v. 20°C	ND	ND	ND	ND	ND
	25psu	15°C v. 20°C	ND	ND	ND	ND	ND
	33psu	15°C v. 20°C	0.000209	0.00105	322	0.2	0.8412

TABLE D6: Pairwise comparisons of life stage count and juvenile size responses to salinity in Week 3, grouped by temperature. (ND = No Data)

Stage	Temperature	Salinity Comparison	Estimate	SE	df	z/t	*P*
Females	15°C	10 psu v 15 psu	0.693	1.277	70	0.543	0.9829
		10 psu v 20 psu	-2.833	0.813	70	-3.484	**0.0045**
		10 psu v 25 psu	-2.639	0.817	70	-3.23	**0.0109**
		10 psu v 33 psu	-2.079	0.833	70	-2.495	0.0916
		15 psu v 20 psu	-3.526	1.078	70	-3.272	**0.0094**
		15 psu v 25 psu	-3.332	1.081	70	-3.084	**0.0175**
		15 psu v 33 psu	-2.773	1.093	70	-2.537	0.0826
		20 psu v 25 psu	0.194	0.444	70	0.437	0.9924
		20 psu v 33 psu	0.754	0.473	70	1.593	0.5017
		25 psu v 33 psu	0.56	0.48	70	1.167	0.7705
	20°C	10 psu v 15 psu	-2.565	1.099	70	-2.333	0.1345
		10 psu v 20 psu	-4.234	1.071	70	-3.954	**0.0007**
		10 psu v 25 psu	-4.025	1.072	70	-3.754	**0.0016**
		10 psu v 33 psu	-4.654	1.068	70	-4.356	**0.0001**
		15 psu v 20 psu	-1.669	0.473	70	-3.532	**0.0038**
		15 psu v 25 psu	-1.46	0.476	70	-3.067	**0.0184**
		15 psu v 33 psu	-2.089	0.467	70	-4.47	**0.0001**
		20 psu v 25 psu	0.209	0.405	70	0.515	0.9859
		20 psu v 33 psu	-0.42	0.395	70	-1.063	0.8254
		25 psu v 33 psu	-0.629	0.399	70	-1.575	0.5136
Males	15°C	10 psu v 15 psu	-3.425	95932.92	70	0	1
		10 psu v 20 psu	-22.92	94394.03	70	0	1
		10 psu v 25 psu	-24.866	94394.03	70	0	1
		10 psu v 33 psu	-24.712	94394.03	70	0	1
		15 psu v 20 psu	-19.495	17114.09	70	-0.001	1
		15 psu v 25 psu	-21.441	17114.09	70	-0.001	1
		15 psu v 33 psu	-21.287	17114.09	70	-0.001	1
		20 psu v 25 psu	-1.946	1.1	70	-1.775	0.388
		20 psu v 33 psu	-1.792	1.11	70	-1.619	0.4852
		25 psu v 33 psu	0.154	0.61	70	0.254	0.9991
	20°C	10 psu v 15 psu	1.459	39291.48	70	0	1
		10 psu v 20 psu	-20.184	17080.27	70	-0.001	1
		10 psu v 25 psu	-22.264	17080.27	70	-0.001	1
		10 psu v 33 psu	-22.823	17080.27	70	-0.001	1
		15 psu v 20 psu	-21.643	35384.81	70	-0.001	1

		15 psu v 25 psu	-23.723	35384.81	70	-0.001	1
		15 psu v 33 psu	-24.282	35384.81	70	-0.001	**1**
		20 psu v 25 psu	-2.079	0.79	70	-2.639	0.0635
		20 psu v 33 psu	-2.639	0.77	70	-3.424	**0.0056**
		25 psu v 33 psu	-0.56	0.4	70	-1.414	0.6188
Eggs	15°C	10 psu v 15 psu	0.693	1.29	70	0.537	0.9835
		10 psu v 20 psu	-2.251	0.846	70	-2.66	0.0601
		10 psu v 25 psu	-2.14	0.85	70	-2.517	0.0867
		10 psu v 33 psu	-1.792	0.864	70	-2.073	0.2319
		15 psu v 20 psu	-2.944	1.103	70	-2.67	**0.0585**
		15 psu v 25 psu	-2.833	1.106	70	-2.562	0.0775
		15 psu v 33 psu	-2.485	1.117	70	-2.225	0.1704
		20 psu v 25 psu	0.111	0.525	70	0.212	0.9996
		20 psu v 33 psu	0.46	0.548	70	0.839	0.9184
		25 psu v 33 psu	0.348	0.553	70	0.63	0.9703
	20°C	10 psu v 15 psu	-2.303	1.124	70	-2.048	0.2431
		10 psu v 20 psu	-4.025	1.087	70	-3.703	**0.002**
		10 psu v 25 psu	-3.85	1.089	70	-3.537	**0.0037**
		10 psu v 33 psu	-4.7	1.083	70	-4.34	**0.0001**
		15 psu v 20 psu	-1.723	0.531	70	-3.246	**0.0103**
		15 psu v 25 psu	-1.548	0.534	70	-2.898	**0.0308**
		15 psu v 33 psu	-2.398	0.522	70	-4.59	**<.0001**
		20 psu v 25 psu	0.175	0.451	70	0.389	0.9952
		20 psu v 33 psu	-0.675	0.437	70	-1.546	0.5326
		25 psu v 33 psu	-0.85	0.441	70	-1.929	0.3015
Sporelings	15°C	10 psu v 15 psu	0	4293.858	70	0	1
		10 psu v 20 psu	-19.3218	3036.216	70	-0.006	1
		10 psu v 25 psu	0	4293.858	70	0	1
		10 psu v 33 psu	-20.4204	3036.216	70	-0.007	1
		15 psu v 20 psu	-19.3218	3036.216	70	-0.006	1
		15 psu v 25 psu	0	4293.858	70	0	1
		15 psu v 33 psu	-20.4204	3036.216	70	-0.007	1
		20 psu v 25 psu	19.3218	3036.216	70	0.006	1
		20 psu v 33 psu	-1.0986	0.513	70	-2.143	0.2021
		25 psu v 33 psu	-20.4204	3036.216	70	-0.007	1
	20°C	10 psu v 15 psu	0	4293.858	70	0	1
		10 psu v 20 psu	-21.7728	3036.216	70	-0.007	1
		10 psu v 25 psu	-21.8712	3036.216	70	-0.007	1
		10 psu v 33 psu	-23.0736	3036.216	70	-0.008	1
		15 psu v 20 psu	-21.7728	3036.216	70	-0.007	1

		15 psu v 25 psu	-21.8712	3036.216	70	-0.007	1
		15 psu v 33 psu	-23.0736	3036.216	70	-0.008	1
		20 psu v 25 psu	-0.0984	0.379	70	-0.259	0.999
		20 psu v 33 psu	-1.3008	0.372	70	-3.497	**0.0043**
		25 psu v 33 psu	-1.2024	0.371	70	-3.242	**0.0104**
Percent of Females Productive	15°C	10 psu v 15 psu	1.20e-6	1.646	38	0	1
		10 psu v 20 psu	1.200	1.279	38	0.938	0.882
		10 psu v 25 psu	1.260	1.253	38	1.008	0.852
		10 psu v 33 psu	0.472	1.285	38	0.367	0.996
		15 psu v 20 psu	1.200	1.279	38	0.938	0.882
		15 psu v 25 psu	1.260	1.253	38	1.008	0.852
		15 psu v 33 psu	0.472	1.285	38	0.367	0.996
		20 psu v 25 psu	0.064	0.686	38	0.092	1
		20 psu v 33 psu	-0.728	0.755	38	-0.964	0.871
		25 psu v 33 psu	-0.791	0.710	38	-1.114	0.799
	20°C	10 psu v 15 psu	0.869	1.323	38	0.657	0.965
		10 psu v 20 psu	7.0e-7	1.244	38	0	1
		10 psu v 25 psu	0.084	1.245	38	0.067	1
		10 psu v 33 psu	0.576	1.243	38	0.463	0.991
		15 psu v 20 psu	-0.869	0.768	38	-1.132	0.790
		15 psu v 25 psu	-0.785	0.769	38	-1.021	0.846
		15 psu v 33 psu	-0.294	0.761	38	-0.386	0.995
		20 psu v 25 psu	0.084	0.625	38	0.135	0.999
		20 psu v 33 psu	0.576	0.619	38	0.931	0.885
		25 psu v 33 psu	0.492	0.621	38	0.792	0.933
Egss per Female	15°C	10 psu v 15 psu	0	0.552	38	0	1
		10 psu v 20 psu	0.4637	0.422	38	1.1	0.8056
		10 psu v 25 psu	0.3497	0.414	38	0.844	0.9149
		10 psu v 33 psu	0.3133	0.428	38	0.733	0.9475
		15 psu v 20 psu	0.4637	0.422	38	1.1	0.8056
		15 psu v 25 psu	0.3497	0.414	38	0.844	0.9149
		15 psu v 33 psu	0.3133	0.428	38	0.733	0.9475
		20 psu v 25 psu	-0.114	0.211	38	-0.541	0.9824
		20 psu v 33 psu	-0.1504	0.236	38	-0.636	0.9682
		25 psu v 33 psu	-0.0364	0.223	38	-0.163	0.9998
	20°C	10 psu v 15 psu	1.75E-01	0.437	38	0.401	0.9943
		10 psu v 20 psu	1.98E-01	0.417	38	0.473	0.9893
		10 psu v 25 psu	1.30E-01	0.417	38	0.312	0.9979
		10 psu v 33 psu	-0.0826	0.414	38	-0.199	0.9996
		15 psu v 20 psu	0.0226	0.245	38	0.092	1

		15 psu v 25 psu	-0.0448	0.245	38	-0.183	0.9997
		15 psu v 33 psu	-0.2576	0.239	38	-1.077	0.8169
		20 psu v 25 psu	-0.0674	0.209	38	-0.323	0.9975
		20 psu v 33 psu	-0.2802	0.202	38	-1.387	0.6396
		25 psu v 33 psu	-0.2128	0.202	38	-1.053	0.8288
Juveniles per Female	15°C	10 psu v 15 psu	0	1.265	38	0	1
		10 psu v 20 psu	-0.5279	0.966	38	-0.546	0.9817
		10 psu v 25 psu	0	0.949	38	0	1
		10 psu v 33 psu	-1.5035	0.98	38	-1.534	0.5474
		15 psu v 20 psu	-0.5279	0.966	38	-0.546	0.9817
		15 psu v 25 psu	0	0.949	38	0	1
		15 psu v 33 psu	-1.5035	0.98	38	-1.534	0.5474
		20 psu v 25 psu	0.5279	0.483	38	1.093	0.8092
		20 psu v 33 psu	-0.9756	0.542	38	-1.801	0.388
		25 psu v 33 psu	-1.5035	0.51	38	-2.948	**0.0409**
	20°C	10 psu v 15 psu	0	1	38	0	1
		10 psu v 20 psu	-2.1454	0.956	38	-2.243	0.1862
		10 psu v 25 psu	-2.24	0.956	38	-2.342	0.1541
		10 psu v 33 psu	-2.3531	0.949	38	-2.48	0.1167
		15 psu v 20 psu	-2.1454	0.561	38	-3.826	**0.0041**
		15 psu v 25 psu	-2.24	0.561	38	-3.995	**0.0025**
		15 psu v 33 psu	-2.3531	0.548	38	-4.295	**0.001**
		20 psu v 25 psu	-0.0946	0.478	38	-0.198	0.9996
		20 psu v 33 psu	-0.2077	0.463	38	-0.449	0.9913
		25 psu v 33 psu	-0.1131	0.463	38	-0.244	0.9992
Offspring per Female	15°C	10 psu v 15 psu	0	0.485	38	0	1
		10 psu v 20 psu	0.2226	0.371	38	0.601	0.9741
		10 psu v 25 psu	0.2646	0.364	38	0.727	0.9488
		10 psu v 33 psu	-0.108	0.376	38	-0.287	0.9984
		15 psu v 20 psu	0.2226	0.371	38	0.601	0.9741
		15 psu v 25 psu	0.2646	0.364	38	0.727	0.9488
		15 psu v 33 psu	-0.108	0.376	38	-0.287	0.9984
		20 psu v 25 psu	0.042	0.185	38	0.227	0.9994
		20 psu v 33 psu	-0.3306	0.208	38	-1.592	0.5118
		25 psu v 33 psu	-0.3726	0.196	38	-1.905	0.3321
	20°C	10 psu v 15 psu	0.1217	0.384	38	0.317	0.9977
		10 psu v 20 psu	-0.2692	0.367	38	-0.734	0.9471
		10 psu v 25 psu	-0.3531	0.367	38	-0.963	0.8699
		10 psu v 33 psu	-0.6296	0.364	38	-1.73	0.4283
		15 psu v 20 psu	-0.391	0.215	38	-1.818	0.3783

		15 psu v 25 psu	-0.4749	0.215	38	-2.208	0.1986
		15 psu v 33 psu	-0.7513	0.21	38	-3.576	**0.0081**
		20 psu v 25 psu	-0.0839	0.183	38	-0.457	0.9906
		20 psu v 33 psu	-0.3603	0.178	38	-2.029	0.272
		25 psu v 33 psu	-0.2764	0.178	38	-1.557	0.5332
Sporeling Sizes	15°C	20 psu v 25 psu	-4.40E-06	5.44E-05	322	-0.081	0.9964
		20 psu v 33 psu	8.57E+05	4.25E-05	322	2.019	0.1076
		25 psu v 33 psu	9.01E-05	4.06E-05	322	2.22	0.0678
	20°C	20 psu v 25 psu	ND	ND	ND	ND	ND
		20 psu v 33 psu	ND	ND	ND	ND	ND
		25 psu v 33 psu	ND	ND	ND	ND	ND