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Increased temperatures impact the reproduction of localized estuarine kelp populations more than salinity or invasive species

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ABSTRACT: Estuarine habitats regularly experience large variations in abiotic conditions such as temperature and salinity; however, under climate change and the increasing threat of invasive species, the pressure from both abiotic and biotic stresses has been increasing. Several studies have investigated the interactions of the adult stages of macroalgae; however, there is little understanding of how microscopic stages of *Macrocystis pyrifera* and *Sargassum muticum* interact or how climate change may influence this interaction. Our research considers the effects of climate-driven changes in temperature and salinity and their interactions with *S. muticum* on the growth and survival of *M. pyrifera* gametophytes from Tomales Bay, CA, USA. 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 suggest that *M. pyrifera* may be able to adapt to local conditions like salinity; however, higher temperatures from a changing climate and the presence of competitors from biological invasions act additively, but not interactively, to negatively impact the early life stages of kelp. By determining how foundation species respond to various abiotic and biotic stressors, we can better predict how these species will perform in a changing environment and how they will contribute to overall ecosystem resilience.

KEY WORDS: *Macrocystis pyrifera* · Climate change · *Sargassum* · Kelp forests · Temperature · Salinity · Reproduction

1. 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 (Feely et al. 2009, Cooley et al. 2022), rising temperatures (Reid & Beaugrand 2012, Dunstan et al. 2018), changing salinity (Ishii et al. 2006), and changes to broader oceanographic processes such as upwelling and oscillation patterns (Bakun et al. 2015, García-Reyes et al. 2015). Climate change can have a variety of different effects on local organisms and ecosystems, including changes in physiology (Kroeker et al. 2013, Smith et al. 2023), morphology and phenology (Alfonso et al. 2022), range shifts and invasions (Sanford et al. 2019), community structure and composition (Arafeh-Dalmau et al. 2019), and species interactions (Byrnes et al. 2011). Species that have multiple life stages often have stage-based tolerance ranges to abiotic stress (Shukla & Edwards 2017, Small & Edwards 2021); thus, a changing climate increases the number of bottle-

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necks that a multi-stage species experiences during its lifetime (Straub et al. 2019, Veenhof et al. 2022).

Biological invasions are increasing worldwide (Seebens et al. 2018) and have the potential to interact with climate change to exacerbate changes to local communities. Increasing temperatures and changing abiotic conditions can facilitate invasions in marine ecosystems via poleward range shifts towards cooler temperatures (Sorte et al. 2010, Edwards 2022) and reduced barriers to invasion such as extreme and seasonal abiotic conditions (Mahanes & Sorte 2019). Given that exotic species tend to be more frequently introduced to regions that are cooler than their native thermal ranges (Bennett et al. 2021) and increasing temperatures inhibit native species to a greater extent than their invasive counterparts (Sorte et al. 2013), marine communities under biotic stress from invasion face the possibility of significant community shifts as a result of a changing climate (Vergés et al. 2014, Wernberg et al. 2016). Invasive marine primary producers such as seaweed can be particularly disruptive by competing with native primary producers for space and other resources (Thomsen et al. 2009, 2014, Vilà et al. 2011), altering resource allocation and nutrient acquisition rates (Maggi et al. 2015), and negatively impacting biodiversity and ecosystem functions (Sullaway & Edwards 2020, Li et al. 2023). Consequently, the biomass of consumers that prefer native primary producers for food is also significantly altered by invasions of seaweed (Thomsen et al. 2014, Maggi et al. 2015).

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 (Tegner & Dayton 2000, Graham et al. 2008). The 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* have been found to provoke different responses in populations from different regions (Buschmann et al. 2004, Rodríguez et al. 2019, Hollarsmith et al. 2020a) but overall negatively affect multiple parts of the reproductive cycle, including spore production and release, gametophyte survival and growth, gametophyte sex ratios, egg production, and embryonic sporophyte growth (Gaitán-Espitia et al. 2014, Shukla & Edwards 2017, Mabin et al. 2019, Hollarsmith et al. 2020a, Fernández et al. 2021) as well as physiological processes such as photosynthesis and respiration at the microscopic stage (Mabin et al. 2019). By 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, 2014, Rodríguez 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, Gershunov et al. 2017).

In addition to the changing climate, some habitats occupied by *M. pyrifera* along the west coast of North America have been invaded by the Japanese brown algae known as wireweed, *Sargassum muticum*. First introduced to the USA from Japan in 1944, the range of *S. muticum* now extends along almost the entire North American west coast, from Ketchikan, Alaska, at the northern edge of its range (Engelen et al. 2015) to Punta Abreojos in Baja California Sur, Mexico (Espinoza 1990). Previous studies of *M. pyrifera* and *S. muticum* interactions have found that *S. muticum* shading reduced *M. pyrifera* recruitment, and the removal of *S. muticum* adults resulted in drastic increases in the presence and abundance of *M. pyrifera* and other native seaweeds (Ambrose & Nelson 1982, Britton-Simmons 2004, Steen 2004). *S. muticum* can significantly reduce native invertebrate biodiversity via reductions in suitable habitat due to reduced canopy cover (Salvaterra et al. 2013, Veiga et al. 2018), altered abiotic conditions such as temperature and light (Critchley et al. 1990), and *S. muticum* resistance to native bacteria, larvae, and diatom habitation via secreted unique secondary compounds (Schwartz et al. 2017, Li et al. 2023).

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* reproduces in salinities as low as 20 psu (Norton 1977, Hales & Fletcher 1990, Steen 2004), although 30–35 psu results in the highest rates of reproduction (Hales & Fletcher 1989, Kerrison & Le 2016). The tolerance of *S. muticum* to high temperatures, however, is much greater than that of *M. pyrifera*. While *M. pyrifera* microstage reproduction generally declines, or even ceases, beyond 18°C (Buschmann et al. 2004 Gaitán-Espitia et al. 2014, Hollarsmith et al. 2020a, Le et al. 2022), *S. muticum* reproduces up to 30°C (Hales & Fletcher 1989), with optimum growth rates occurring between 18° and 25°C (Hales & Fletcher 1990, Liu et al. 2013). These

greater tolerances to warmer temperatures and more variable salinity as well as the negative impacts on local communities make *S. muticum* a species of concern. 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), especially in 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 aimed to understand the biotic and abiotic dynamics that govern *M. pyrifera* distribution in Tomales Bay via 3 experiments assessing the role of temperature and salinity stress and the presence of the invasive *S. muticum* on *M. pyrifera* microstage reproduction. Currently, there are no obvious negative impacts of *S. muticum* presence on the persistence of *M. pyrifera* sporophytes in Tomales Bay, but changing climate could impact their coexistence. First, we investigated how salinity and temperature influence growth, survival, and reproduction in *M. pyrifera* microscopic stages from different source locations within Tomales Bay. 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 2 experiments to assess how *M. pyrifera* microstages respond to temperature and salinity stress change under differing *S. muticum* propagule 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.

2. MATERIALS AND METHODS

2.1. Tomales Bay

Tomales Bay is a highly invaded estuary north of San Francisco, located on the northern edge of the Point Reyes peninsula (Cheng & Grosholz 2016, Kruger-Hadfield et al. 2018, Rubinoff & Grosholz 2022). Tomales Bay is long and narrow, and exhibits a generally linear estuarine gradient consisting of numerous overlapping abiotic gradients that vary not only with distance into the bay but also seasonally (Kimbro et al. 2009, Cheng & Grosholz 2016, Hollarsmith et al. 2020b). 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; outer bay: 33 psu; mid bay: 30 psu; inner bay: 26 psu) with distance into the bay and can drop significantly (<10 psu) during low-salinity events (Cheng & Grosholz 2016). Mean temperatures remain largely consistent throughout the bay in winter, regardless of site (DuBois et al. 2022), but may also slightly increase with distance into the bay (Kimbro et al. 2009, Cheng & Grosholz 2016; outer bay: ~11°C; mid bay: 10.9°C; inner bay: 11.2°C). From June to October, during California's dry season, there is little freshwater input into the bay, so salinity generally stays constant throughout the bay (Kimbro et al. 2009; outer bay: 34 psu; mid bay: 34 psu; inner bay: 33 psu) but may become hypersaline closer to the head in especially dry years (Largier et al. 1997). The temperature gradient in the dry season becomes more pronounced, with water several degrees warmer at the head than at the mouth (Kimbro et al. 2009, Cheng & Grosholz 2016; outer bay: ~14°C; mid bay: 15.3°C; inner bay: 17.8°C).

Macrocystis pyrifera is one of the primary canopy-forming kelps in California and other temperate locations around the globe. It 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 (~11 km) into the bay. In this study, we chose 2 different locations where *M. pyrifera* and *Sargassum muticum* co-occur within Tomales Bay: White Gulch (38.197534° N, 122.946408° W), which represents an outer bay, more marine-influenced location, and Marshall Beach (38.165311° N, 122.915651° W), a mid-bay site that hosts the most estuarine giant kelp bed in Tomales Bay (Fig. 1). At White Gulch, the depth ranges of *S. muticum* and *M. pyrifera* overlap between 2.5 and 4 m, and we have observed the 2 species growing within several feet of each other, suggesting that propagules released from both species may be settling in close proximity to each other. At Marshall Beach, however, the 2 species occupy different depth and substrate zones (*S. muticum*, 3–10 feet [1–3 m], sandy bottom; *M. pyrifera*, 10–20 feet [3–6 m], shallow reef), experience high turbidity and reduced light attenuation, and are likely not subjected to competition with each other after propagule settlement.

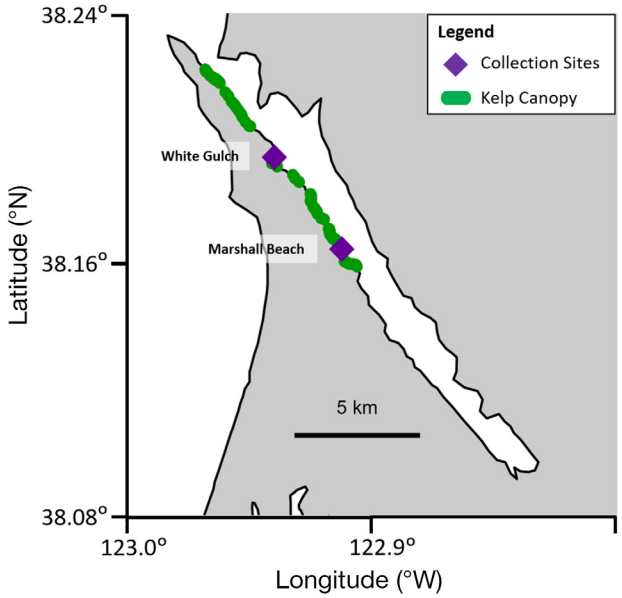

Fig. 1. *Macrocystis pyrifera* kelp canopies (highlighted in green) along the west shore of Tomales Bay. The extent of *Sargassum muticum* presence was not documented, but it has been observed as far north as White Gulch and at least 5 km south of Marshall Beach. We collected *M. pyrifera* individuals from 2 sites in Tomales Bay (White Gulch and Marshall Beach) and *S. muticum* individuals from one site (White Gulch)

2.2. Collection

We collected reproductive structures from 12 adult individuals of each species by SCUBA diving in White Gulch and Marshall Beach in July 2020 (*M. pyrifera* abiotic stress experiments) and in May 2021 (all other experiments). Immediately upon collection, *M. pyrifera* sporophylls and *S. muticum* fronds were cleaned in iodine and freshwater, layered inside 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 the BML, *S. muticum* fronds were placed in a bucket of running seawater in the lab's non-indigenous species quarantine 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 h at either 12° or 18°C, after which spore densities were determined using a hemocytometer (model CTL-HEMM-GLDR; LW Scientific). We then pipetted spores into the experimental Petri dishes (100 × 15 mm polystyrene) to facilitate a settlement density of approximately 8 spores mm^{-2} for 1× density treatments (1 mm^{-2} is the minimum density required for fertilization; Reed et al. 1991), 16 spores mm^{-2} for 2× density treatments, and 32 spores mm^{-2} for 4× density treatments. After 24 h, *S. muticum* receptacles were separated from the vegetative portion of the frond and also soaked in seawater for 24 h at either 12° or 18°C. Then, 24 h 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 zygote per 30 mm^2 for 1× density treatments and 1 zygote per 15 mm^2 for 2× density treatments. The number of *S. muticum* zygotes was small enough and the size large enough that we were able to count them manually using a dissecting microscope. The described densities were opportunistically chosen based on equal collections of fertile adult material and the amount of propagules released within 24 h. We thus standardized the number of propagules inputted into the dishes, assuming one *S. muticum* zygote (250 µm diameter; Deysher & Norton 1981) was equal to approximately 500 *M. pyrifera* spores (<10 µm diameter; Clayton 1992).

2.3. Propagule cultivation

Petri dishes containing *M. pyrifera* spores and *S. muticum* embryos were then assigned to one of 3 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 intraspecific competition, and (3) the interacting effects of *S. muticum* presence, temperature, and salinity. Each experiment was run for 4 wk. Petri dishes were randomly arranged on shelves within the incubators, and light was set at a 12 h light:12 h dark photoperiod and 10–20 µmol m^{-2} s^{-1} to mimic light conditions of Tomales Bay in the fall season when *S. muticum* and *M. pyrifera* propagules are often released. We changed the water in all experimental dishes every 2–3 d for the duration of each experiment to prevent anoxia and added standard 20 ml l^{-1} Provasoli nutrient mix to all treatment water to prevent nutrient limitation during growth. To prevent diatom overgrowth, we also added germanium dioxide at a ratio of 0.5 ml GeO_2 solution (0.894 reagent grade powdered GeO_2 + 200 ml deionized water) per liter of seawater at 7 and 14 d after each experiment started (Shea & Chopin 2007).

2.4. Expt 1: Location-specific effects of temperature and salinity

Petri dishes containing 1× densities of *M. pyrifera* were placed in a full-factorial experiment crossing 2

temperatures (12° and 18°C) and 3 salinities (20, 26, and 33 psu) based on oceanographic monitoring data collected in 2019 from the Bodega Ocean Observing Node Tomales Bay Buoy near Hog Island (1 km further south than White Gulch) and a sonde placed at Sacramento Landing (1.6 km further south than Marshall Beach) (Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m744p033_supp.pdf). We then replicated each of the 6 temperature—salinity treatments for *M. pyrifera* propagules from each of the 2 source locations, White Gulch and Marshall Beach, to determine whether there were any local differences in *M. pyrifera* reproduction within Tomales Bay. We assigned 10 Petri dishes to each temperature—salinity—location cross, for a total of 120 Petri dish microcosms.

2.5. Expt 2: Density-dependent effects

To determine how the 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 2 different densities of *M. pyrifera* (1×: 8 spores mm^{-2}; 2×: 16 spores mm^{-2}) with 3 different densities of *S. muticum* (0×: no *S. muticum*; 1×: ca. 1 zygote per 30 mm^2; 2×: ca. 1 zygote per 15 mm^2) to assess the relative effects of inter- and intraspecific competition. We also added one extra treatment with 4× (32 spores mm^{-2}) *M. pyrifera* and 0× *S. muticum* to compare high-density intraspecific competition (4× *M. pyrifera*) with high-density interspecific competition (2× *M. pyrifera* + 2× *S. muticum*). Each of the 7 treatments was assigned 5 Petri dish replicates each, for a total of 35 Petri dishes.

2.6. Expt 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 2 density treatments (1×: ca. 1 zygote per 30 mm^2; 2×: ca. 1 zygote per 15 mm^2) in Petri dishes with the same 2 temperature (12° and 18°C) and 3 salinity (20, 26, and 33 psu) combinations used when investigating abiotic stress alone. All dishes were settled with 1× *M. pyrifera* densities (8 spores mm^{-2}). Each of the 12 density—salinity—temperature crosses had 5 Petri dish replicates for a total of 60 Petri dishes.

2.7. Data collection and count methods

At the end of each experiment, we photographed 3 random locations within each Petri dish using a Micropublisher 5.0 RTV digital camera (QImaging) mounted on an inverted microscope at 40× magnification. Each photo encompassed 1.08 mm^2 of the 7853 mm^2 bottom surface area of the Petri dish). *M. pyrifera* gametophytes and embryonic sporophytes (new sporophytes) were easily distinguishable by size, as they are much smaller than *S. muticum*. In a photo editor, we counted the number of *M. pyrifera* females, males, embryonic sporophytes, and eggs. Counts for each of the 3 photos were then summed and taken as the count for each dish. As 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 (Figs. S2 & S3).

Gametophyte surface area (μm^2) was measured using ImageJ version 1.53 (National Institutes of Health). Area was calculated as the number of pixels and then converted to μm^2 using a conversion factor of 71 330 pixels per 62 500 μm^2.

2.8. 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 (GLMs, 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 Expt 1 and Expt 3 were found to have a negative binomial distribution, whereas counts for Expt 2 were found to have a Poisson distribution.

Counts for Expt 1 were modeled as responses to the fixed-effect variables of location, temperature, salinity, and all interactions. Counts for Expt 3 were modeled as responses to the fixed-effect variables of *S. muticum* density, temperature, salinity, and all interactions. Data for both Expt 1 and Expt 3 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 Expt 1, 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 Expt 3, 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 1× *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 2× *S. muticum* treatments for Expt 1 and Expt 3, respectively.

Counts for Expt 2 were modeled as responses to the fixed-effect variables of *M. pyrifera* density, *S. muticum* density, and all interactions. For all count data in Expt 2, we also ran Welch's 2-sample *t*-tests to assess the strength of intra- versus interspecific competition by comparing treatments with similar overall densities of 2× (1× kelp + 1× *S. muticum* versus 2× kelp + 0× *S. muticum*), 3× (1× kelp + 2× *S. muticum* versus 2× kelp + 1× *S. muticum*), and 4× (2× kelp + 2× *S. muticum* versus 4× kelp + 0× *S. muticum*). Additionally, in order to assess how observed numbers between treatments varied from the inoculated proportions, we calculated the ratios of observed counts in the 1× *M. pyrifera* treatment to both the 2× and 4× *M. pyrifera* treatments and ran chi-squared goodness-of-fit tests.

Size data were also analyzed with a GLM using a gamma distribution for all experiments. The 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 the average size of embryonic sporophytes 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 in Tables S1–S7.

3. RESULTS

3.1. Location-specific effects of temperature and salinity (Expt 1)

We found that high temperatures had a much larger negative effect than site or salinity on any count variables. The Marshall Beach +18°C treatments exhibited a near 100% mortality rate (we counted a total of one female gametophyte and no eggs or embryonic sporophytes), so we only examined the effects of temperature + salinity within the White Gulch population. Within White Gulch, we found significant temperature and salinity interactions for the number of females, eggs, and embryonic sporophytes, but not males (Table S1). We found that high temperatures resulted in significant declines for every life stage at all salinity levels (except for males in the White Gulch + 20 psu treatment, ANOVA: $F = -0.002$, df = 53, p = 0.999).

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 S2). Source location also had no individually significant effects on any count variable, except for a significant increase in the number of males at 26 psu (pairwise comparison: $t = -6.074$, df = 53, $p < 0.001$) and 33 psu (pairwise comparison: $t = -3.982$, df = 53, $p < 0.001$) in the White Gulch location.

We analyzed the independent effects of salinity within all treatment combinations except for the 18°C + Marshall Beach, and results tended to vary for each count variable. For both locations, the numbers of female gametophytes and embryonic sporophytes in the low-temperature treatment were both significantly lower at 33 psu than at 20 or 26 psu (Table S3). The number of eggs did not vary significantly based on salinity; however, similarly to females and embryonic sporophytes, the mean number of eggs was lower at 33 psu than at 20 or 26 psu. The number of male gametophytes, on the other hand, was significantly highest in 33 psu for all site by temperature combinations (Fig. 2).

Overall, the size of embryonic sporophytes exhibited a significant temperature by salinity interaction in White Gulch (Table S1), but only a significant response to salinity under the low-temperature subset

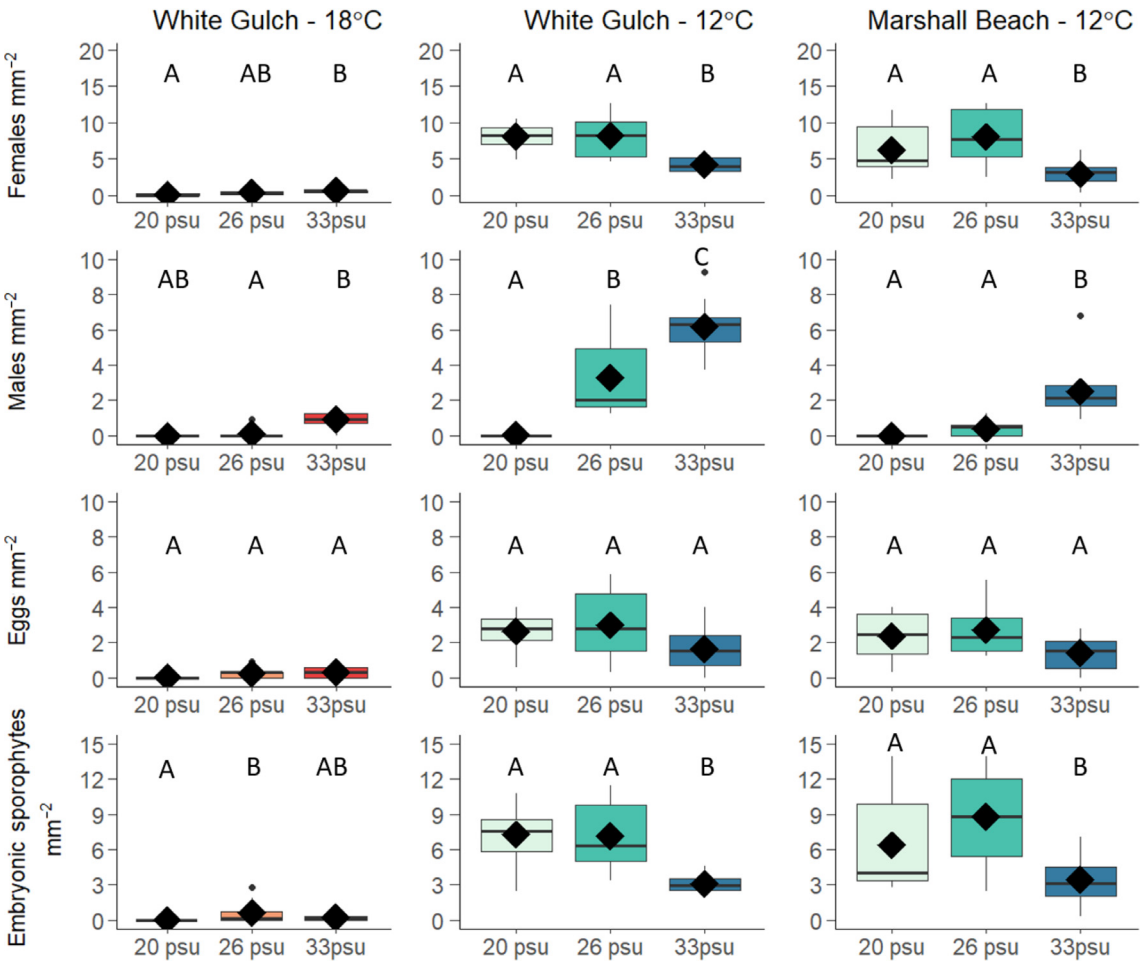

Fig. 2. Number of *Macrocystis pyrifera* gametophytes (female and male) and offspring (eggs and embryonic sporophytes) summed across 3 photo replicates after 4 wk of growth in Expt 1 (n = 10, α = 0.05). Each column represents a different population by temperature treatment, while each row represents a different kelp microstage. No results are shown for the White Gulch −18°C treatment due to near total mortality in that treatment. Boxplot parameters: diamond: mean; midline: median; upper and lower limits: first and third quartiles; vertical lines: outliers (within 1.5× the inter-quartile range); dots: outliers. Letters represent significant differences between salinity treatments

model (Table S2). Embryonic sporophytes were significantly larger under high salinities regardless of population or temperature (Fig. 3, Table S3). 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 significant positive relationship (Table S4).

3.2. Density-dependent effects (Expt 2)

Across life stages, there were no significant interactions between initial *M. pyrifera* and *S. muticum* densities (Table S5). The number of embryonic sporophytes had little relationship with inoculation densities under 0× and 1× *S. muticum* densities and 1× and 2× *M. pyrifera* densities. Under the 2× *S. muticum* treatments, however, the number of embryonic sporophytes in 1× *M. pyrifera* treatments declined significantly (pairwise comparison: $z = 3.285$, df = 26, p = 0.0029) but then increased significantly under the 2× *M. pyrifera* + 2× *S. muticum* treatment to levels consistent with the other 2× kelp treatments (pairwise comparison: $z = -2.773$, df = 26, p = 0.0154). While the mean number of eggs was higher under higher kelp spore inoculations (Table 1), these increases were not significant (Table S5). Across treatments, increased numbers of *M. pyrifera* spores led to increased numbers of gametophytes (Fig. 4).

Analyses of the relative strength of intra- versus interspecific competition revealed that intraspecific competition between *M. pyrifera* propagules had less significant effects than interspecific competition between *M. pyrifera* and *S. muticum* propa-

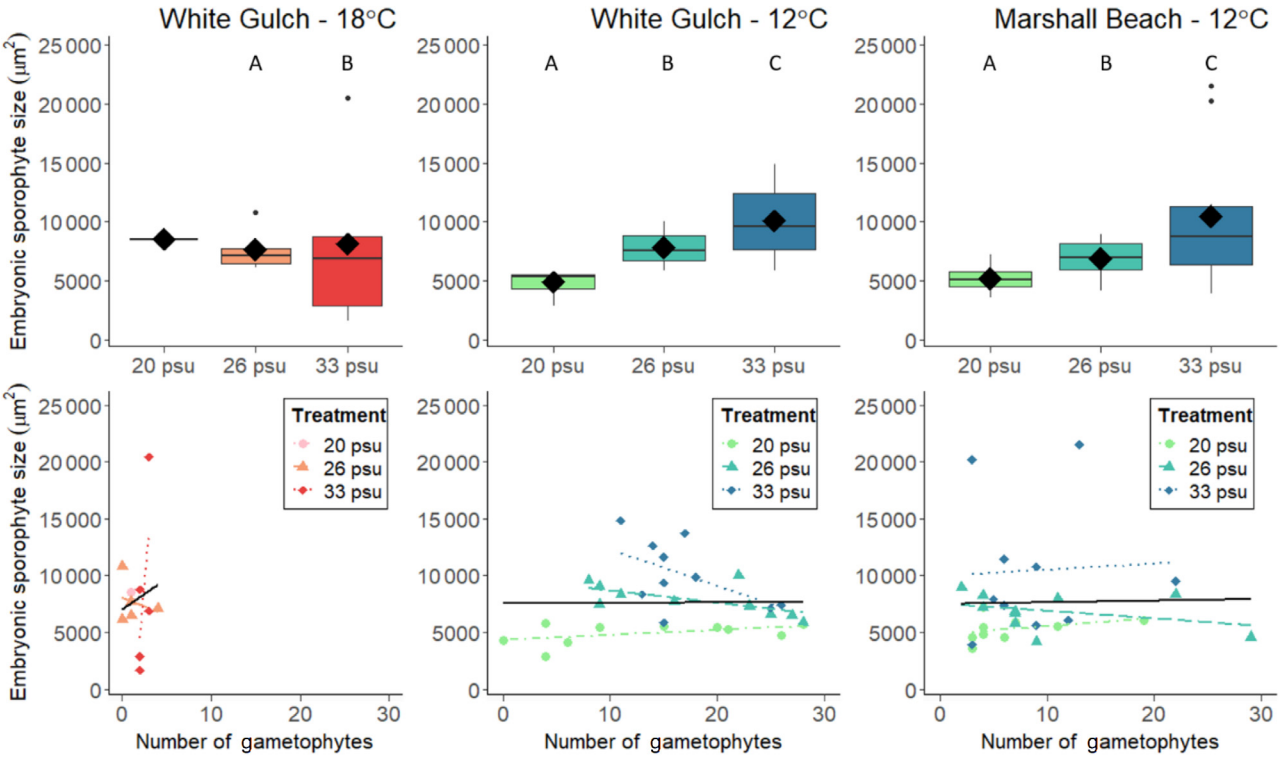

Fig. 3. Sizes of *Macrocystis pyrifera* embryonic sporophytes from tests of location-specific effects of temperature and salinity in Expt 1 ($\alpha = 0.05$). Each treatment had a total of 10 replicates; the number of sporophytes measured in each treatment can be found in Table S8 in the Supplement at www.int-res.com/articles/suppl/m744p033_supp.pdf. Top panels show the average size of embryonic sporophytes after 4 weeks of growth. Boxplot parameters as in Fig. 2; letters represent significant differences between salinity treatments. Bottom panels show the relationship of the covariate (mean number of gametophytes) to the response variable (mean embryonic sporophyte size). Colors represent different temperature treatments (red theme: 18°C; blue theme: 12°C), and point shape and line type represent different salinities within each temperature treatment (circle, dot-dash line: 20 psu; triangle, dashed line: 26 psu; diamond, dotted line: 33 psu). Solid black line: overall trend across salinity treatments. The number of dots in the bottom panels represent the number of replicates in which embryonic sporophytes were observed. No data is shown for the 18°C–20 psu–1× *Sargassum* treatment due to a lack of embryonic sporophytes within that treatment

gules. 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 (2× kelp + 0× *S. muticum*, 2× kelp + 1× *S. muticum*, 4× kelp) than under low *M. pyrifera* high *S. muticum* density treatments (1× kelp + 1× *S. muticum*, 1× kelp + 2× *S. muticum*, 2× kelp + 2× *S. muticum*) (Table 1). While this result is partially because low *M. pyrifera* high *S. muticum* density treatments were inoculated with fewer spores than the high *M. pyrifera* treatments of similar overall densities, chi-squared goodness-of-fit analyses of expected versus observed proportions between density treatments also indicate that intraspecific competition had no significant impact on the observed ratios for any life stage or treatment (Table 2).

There was no significant effect of initial densities of either *M. pyrifera* or *S. muticum* on embryonic sporophyte size (Fig. S4, Table S5). There was also no relationship between the size and number of gametophytes present across all treatments, except for the 2× *M. pyrifera* + 0× *S. muticum* treatment, which had a significant positive correlation between gametophyte number and size (linear regression: $R^2 = 0.220$, df = 20, p = 0.016).

3.3. Interacting effects of *S. muticum* presence, temperature, and salinity (Expt 3)

Due to poor survival at high temperatures, we used the 1× *S. muticum* treatment data to test temperature by salinity interactions and low-temperature treatment data to test salinity by *S. muticum* interactions (see Section 2.8). The number of males and eggs was not significantly affected by any treatment regardless of model. Counts of females and embryonic sporo-

Table 1. Wilcoxon rank sum tests of similar density treatments in Expt 2 to determine the relative importance of inter- and intraspecific competition on *Macrocystis pyrifera* reproduction after 4 wk. **Bold**: significant ($p \leq 0.05$)

Variable	Overall density	*Macrocystis* density	*Sargassum* density	Mean no. of *Macrocystis* mm^{-2}	df	*W*	p
Females	2×	1×	1×	5.2	8	5.5	0.169
		2×	0×	7.6			
	3×	1×	2×	3.4	8	2.5	**0.044**
		2×	1×	6.8			
	4×	2×	2×	6.6	6	4.5	0.112
		4×	0×	10.0			
Males	2×	1×	1×	4.2	6	1	**0.021**
		2×	0×	8.2			
	3×	1×	2×	3.4	7	5.5	0.168
		2×	1×	5.4			
	4×	2×	2×	6.0	8	2	**0.036**
		4×	0×	11.8			
Eggs	2×	1×	1×	0.0	4	0	**0.007**
		2×	0×	3.4			
	3×	1×	2×	0.4	7	9	0.488
		2×	1×	0.8			
	4×	2×	2×	1.4	5	3.5	0.070
		4×	0×	4.8			
Juveniles	2×	1×	1×	5.0	6	13	1.000
		2×	0×	4.8			
	3×	1×	2×	1.0	6	0.5	**0.014**
		2×	1×	4.2			
	4×	2×	2×	4.0	7	18	0.290
		4×	0×	2.2			
Variable	Overall density	*Macrocystis* density	*Sargassum* density	Mean *Macrocystis* embryonic sporophyte size (μm^2)	df	*W*	p
Juvenile sizes	2×	1×	1×	27630.6	44	382	**0.022**
		2×	0×	16336.1			
	3×	1×	2×	21139.7	2	37	0.680
		2×	1×	18220.1			
	4×	2×	2×	15725.5	28	139	0.145
		4×	0×	9360.2			

phytes, however, did vary significantly with certain treatments (Fig. 5). Within all 1× *S. muticum* treatments, only females showed a significant temperature by salinity interaction (Table S6). The number of females (pairwise comparison: $t = 3.456$, df = 23, $p = 0.002$) and embryonic sporophytes (pairwise comparison: $t = 3.602$, df = 23, $p = 0.002$) were both significantly reduced under high temperatures at 26 psu, and females also decreased under high temperatures at 20 psu (pairwise comparison: $t = 3.125$, df = 23, $p = 0.005$).

In low-temperature treatments, we saw no significant interactions between salinity and *S. muticum* density for any variable (Table S7). At low temperatures, *S. muticum* density did significantly reduce the number of *M. pyrifera* females at 26 psu (pairwise comparison: $t = 2.011$, df = 23, $p = 0.056$) and the number of embryonic sporophytes at 20 psu (pairwise comparison: $t = 2.127$, df = 23, $p = 0.044$) and 26 psu (pairwise comparison: $t = 2.069$, df = 23, $p = 0.050$). The 26 psu salinity treatment resulted in the highest number of females in the 1× *S. muticum* treatment (pairwise comparison: $t = 2.617$, df = 23, $p = 0.039$) as well as the highest number of embryonic sporophytes in both the 1× (pairwise comparison: $t = 3.455$, df = 23, $p = 0.006$) and 2× *S. muticum* treatments (pairwise comparison: $t = 2.721$, df = 23, $p = 0.032$).

The size of embryonic sporophytes was only significantly impacted by salinity in the 1× *S. muticum* + 12°C treatment specifically. Embryonic sporophytes in this treatment grew significantly larger with higher salinities (Fig. S5), where 33 psu had the largest embryonic sporophytes (pairwise comparison: $t = 3.979$,

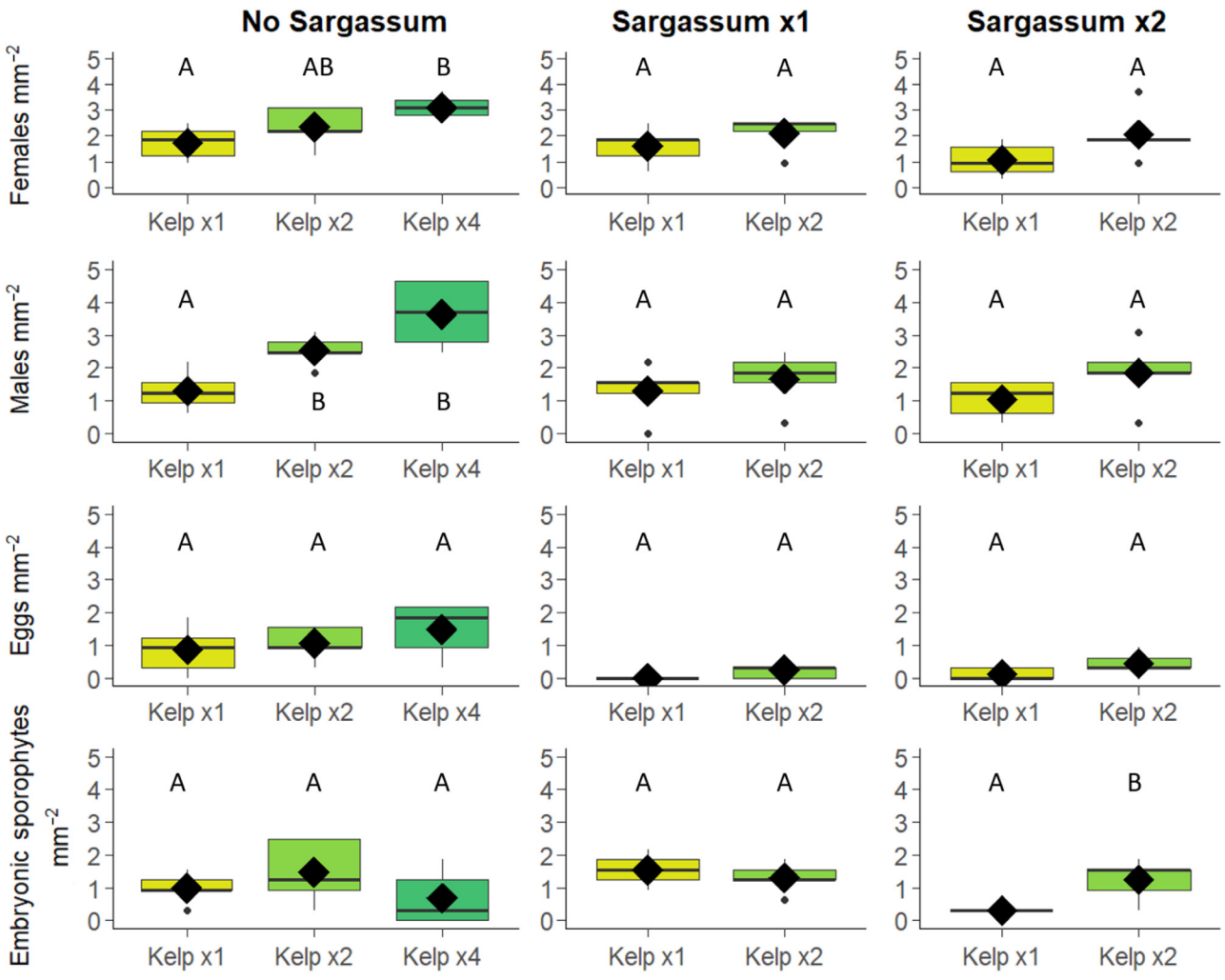

Fig. 4. Number of *Macrocystis pyrifera* gametophytes (female and male) and offspring (eggs and embryonic sporophytes) summed across 3 photo replicates after 4 wk of growth under different initial densities of giant kelp and wireweed inoculation in Expt 2 (n = 5, α = 0.05). Each column represents a different *Sargassum* density treatment, while each row represents a different kelp microstage. Boxplot parameters as in Fig. 2; letters represent significant differences between kelp density treatments

df = 49, p < 0.001) and 20 psu had the smallest (pairwise comparison: t = 3.333, df = 49, p = 0.003). Most treatments had no significant correlation between embryonic sporophyte size and gametophyte number (Table S4), except the 1× *S. muticum* + 12°C + 26 psu treatment, which showed a significant positive relationship between embryonic sporophyte size and gametophyte number (linear regression: R^2 = 0.173, df = 31, p < 0.009).

4. DISCUSSION

Climate change is affecting coastal and estuarine ecosystems worldwide, but locally adapted populations are especially vulnerable to extinction. In this study, we examined the responses of a uniquely estuarine population of *Macrocystis 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 competition with *Sargassum muticum*. Lower salinity (20–25 psu), in contrast, may enhance microstage reproduction in Tomales Bay populations.

4.1. 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

Table 2. Chi-squared goodness-of-fit tests for expected versus observed ratios between density treatments in Expt 2 to determine the effect of intraspecific competition on *Macrocystis pyrifera* reproduction. — : no treatment

Observed means (±SD)

Life stage	*Sargassum* density treatment	*Macrocystis* density treatment 1×	2×	4×
Females	0×	5.6 (2.07)	7.6 (2.51)	10 (1.58)
	1×	5.2 (2.28)	6.8 (2.17)	—
	2×	3.4 (2.07)	6.6 (3.29)	—
Males	0×	4.2 (1.92)	8.2 (1.48)	11.8 (3.27)
	1×	4.2 (2.59)	5.4 (2.7)	—
	2×	3.4 (1.82)	6 (3.24)	—
Eggs	0×	2.8 (2.39)	3.4 (1.67)	4.8 (2.68)
	1×	0 (0)	0.8 (0.84)	—
	2×	0.4 (0.55)	1.4 (1.14)	—
Embryonic sporophytes	0×	3.2 (1.48)	4.8 (3.11)	2.2 (2.68)
	1×	5 (1.58)	4.2 (1.48)	—
	2×	1 (0.71)	4 (2)	—

1× vs. 2× *Macrocystis* density chi-squared goodness of fit

Life stage	*Sargassum* density treatmen	Expected ratios 1×	2×	Observed ratios 1×	2×	χ^2	df	p
Females	0×	0.33	0.67	0.424	0.576	0.040	1	0.841
	1×	0.33	0.67	0.433	0.567	0.048	1	0.826
	2×	0.33	0.67	0.340	0.660	4.52×10^{-4}	1	0.983
Males	0×	0.33	0.67	0.339	0.661	3.43×10^{-4}	1	0.985
	1×	0.33	0.67	0.438	0.563	0.052	1	0.819
	2×	0.33	0.67	0.362	0.638	0.005	1	0.946
Eggs	0×	0.33	0.67	0.452	0.548	0.067	1	0.796
	1×	0.33	0.67	0.000	1.000	0.493	1	0.483
	2×	0.33	0.67	0.222	0.778	0.053	1	0.819
Embryonic sporophytes	0×	0.33	0.67	0.400	0.600	0.022	1	0.882
	1×	0.33	0.67	0.543	0.457	0.206	1	0.650
	2×	0.33	0.67	0.200	0.800	0.076	1	0.782

1× vs. 4× *Macrocystis* density chi-squared goodness of fit

Life stage	*Sargassum* density treatment	Expected ratios 1×	4×	Observed ratios 1×	4×	χ^2	df	p
Females	0×	0.2	0.8	0.359	0.641	0.158	1	0.691
Males	0×	0.2	0.8	0.263	0.738	0.024	1	0.876
Eggs	0×	0.2	0.8	0.368	0.632	0.177	1	0.674
Embryonic sporophytes	0×	0.2	0.8	0.593	0.407	0.963	1	0.326

temperature (18°C). Across variables, high temperature consistently resulted in dramatic declines in the numbers of gametophytes and embryonic sporophytes and occasional reductions in embryonic sporophyte size. These results are consistent with numerous other studies that have investigated the effects of temperatures 18°C and above on gametophyte and embryonic sporophyte development in *M. pyrifera* (Buschmann et al. 2004, Muñoz et al. 2004, Gaitán-Espitia et al. 2014, Hollarsmith et al. 2020a, Le et al. 2022), 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 suggest 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 2 km further into the bay, such as Sacramento Landing, regularly ex-

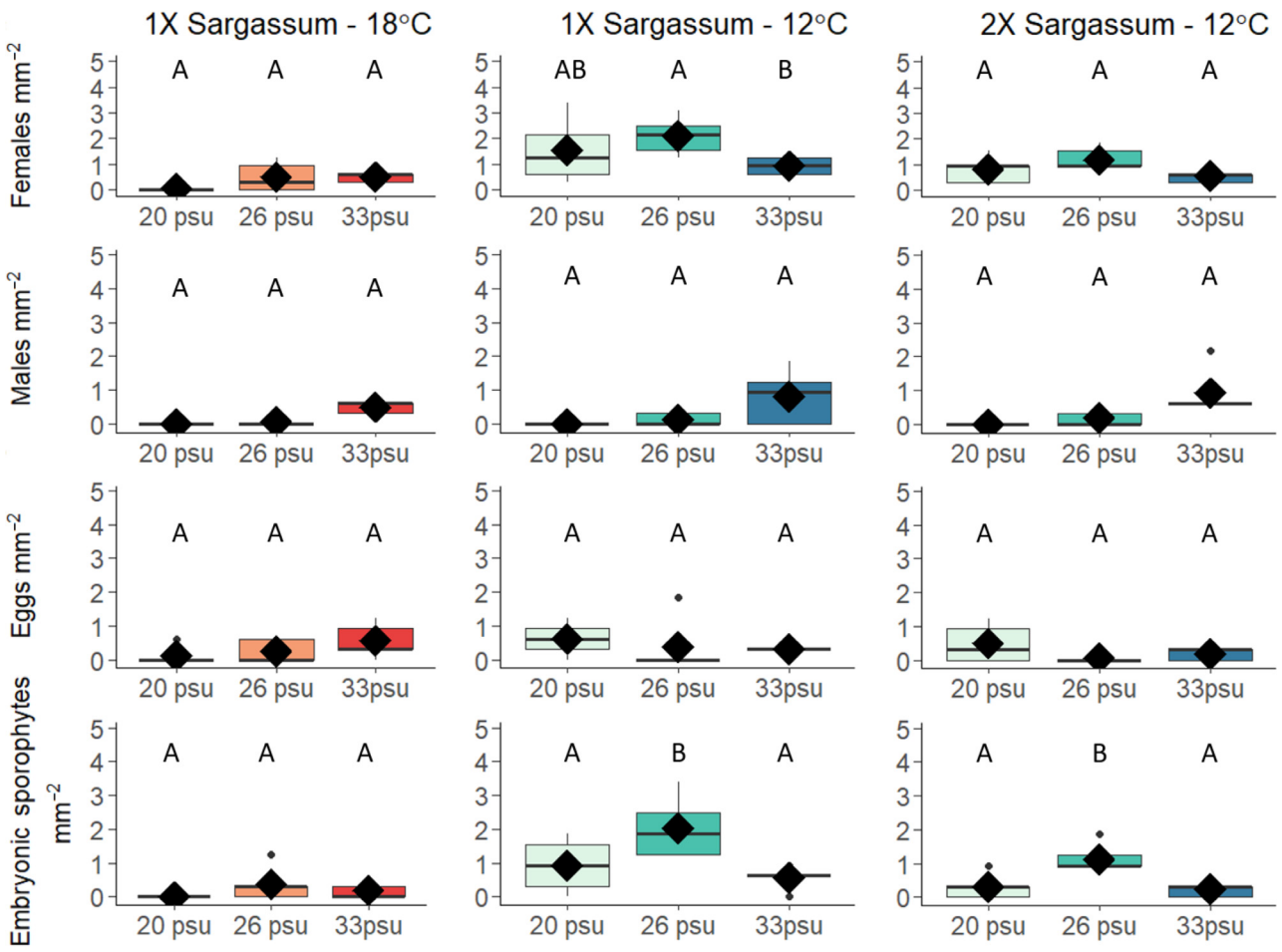

Fig. 5. Number of *Macrocystis pyrifera* gametophytes (female and male) and offspring (eggs and embryonic sporophytes) summed across 3 photo replicates after 4 wk of growth in Expt 3 (n = 5, α = 0.05). Each column represents a different temperature by *Sargassum* density treatment, while each row represents a different kelp microstage. No results are shown for the 2× *Sargassum* 18°C treatment due to near total mortality in that treatment. Boxplot parameters as in Fig. 2; letters represent significant differences between salinity treatments

perience summertime temperatures that exceed 18°C (Fig. S1) (Kimbro et al. 2009, Cheng & Grosholz 2016, Hollarsmith et al. 2020b, Schiebelhut et al. 2023).

Global climate change has been associated with increasing sea surface temperatures (Reid & Beaugrand 2012, Dunstan et al. 2018), 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, García-Reyes et al. 2015), 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 2 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 beyond Tomales Bay, especially in regard to marine heatwaves. Marine heatwaves are expected to dramatically increase in frequency by the end of the 21st century and have already increased in the past 3 decades (Oliver et al. 2018, Smale et al. 2019). As recently as 2014–2016, a multiyear marine heatwave, referred to as 'the Blob', resulted in temperature anomalies of up to 5°C off the Pacific coast of North America. Throughout the past decade, marine heatwaves have resulted in drastic kelp canopy losses globally (Filbee-Dexter et al. 2020, McPherson et al. 2021) and shifting ecosystem steady states towards urchin barrens (Rogers-Bennett & Catton 2019). Significant *M. pyrifera* canopy losses have often been seen in areas where marine heatwave temperatures exceed 18°C (Arafeh-Dalmau et al. 2019, Tolimieri et al. 2023). In addition to the decline in reproductive output as shown in this study and others (Buschmann et al. 2004, Muñoz et al. 2004, Gaitán-Espitia et al. 2014, Shukla & Edwards 2017, Hollarsmith et al.

2020a, Le et al. 2022), high temperatures can also cause oxidative damage and reduce photosynthetic capacity, nitrogen acclimation, and growth rates (Umanzor et al. 2021, Fernández et al. 2021) in the macroscopic juveniles 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 the 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, Tolimieri et al. 2023), loss of commercially and ecologically important fisheries (Arafeh-Dalmau et al. 2019, McPherson et al. 2021), loss of invertebrate biodiversity, and increased presence of invasive species (Arafeh-Dalmau et al. 2019). While research is currently being carried out to determine whether thermal acclimation of *M. pyrifera* to high temperatures is possible (Aitken & Whitlock 2013, Fernández et al. 2021, Vranken et al. 2021), more research is needed to better protect the status of this important canopy species in a changing world.

4.2. Local acclimation to salinity

Previous studies have examined the salinity tolerances of *M. pyrifera* in Chile (Buschmann et al. 2004, 2014, Rodríguez et al. 2019, Fernández et al. 2021) but, to our knowledge, this is the first examination of *M. pyrifera* salinity tolerances in a Northern Hemisphere population. We originally hypothesized that low salinities would be extremely stressful for the generally marine *M. pyrifera*. Contrary to our hypothesis, we found lower salinity (20–26 psu) to have mixed effects on *M. pyrifera* reproduction, both increasing the number of gametophytes and offspring that survived and developed and reducing the size of embryonic sporophytes. 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 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, such as atmospheric rivers, have been increasing (Easterling et al. 2017, Gershunov et al. 2017, 2019, Lu et al. 2018). Increasing freshwater input to estuarine and coastal ecosystems due to large precipitation events, runoff, 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.

Even though recruitment failures are unlikely, osmotic stress may still play a significant role in limiting either the number or size of *M. pyrifera* microstages, but the relationship between salinity and *M. pyrifera* microstage physiology has not been well studied. Decreases in salinity result in the uptake of water and increase of cell volume and turgor. Cells can respond to these changes and osmotically acclimate via the loss of ions and inorganic solutes, or face damage to membranes, organelles, and enzymes (Russell 1987). The regulation of ion and molecule transport can be regulated metabolically using energy reserves or by ion-selective carriers driven by membrane potentials (Karsten 2012). To truly determine how osmotic stress may impact kelp microstages, the specific physiological effects of lower salinity on *M. pyrifera* gametophyte reproduction and growth, and kelps in general, still needs to be better studied.

Based on our results, we hypothesize 2 possible explanatory mechanisms for the physiological effects of salinity on *M. pyrifera* reproduction that require further study. First, we suggest that *M. pyrifera* populations locally adapt to their surrounding salinity regimes. Previous studies have found reproductive persistence under lowered (20–30 psu) salinity conditions in Chile (Buschmann et al. 2004, Rodríguez et al. 2019) and better photosynthetic performance under conditions that *M. pyrifera* individuals are already locally adapted to (Marambio et al. 2023). Our results are consistent with these previous studies in observing location-based tolerances to lowered salinities. To determine whether local adaptation is actually shaping the plasticity of *M. pyrifera* that allows it to inhabit both estuarine and marine environments, further research on the physiological mechanisms and genetic background behind these differentiated responses is required.

A second possible explanatory mechanism for the physiological impacts of salinity on *M. pyrifera* is that osmotic stress from lowered salinities has little effect on *M. pyrifera* survival and fecundity but does reduce growth, which is why we observed more, but much smaller, gametophyte and embryonic sporophytes at lower salinities. Metabolic energy is variably allocated between reproduction, somatic growth, maintenance, and storage, and an increase in energy requirements in one area results in a decreased allo-

cation of energy towards the others. If *M. pyrifera* populations in low salinities are able to maintain survival and reproduction but exhibit a cost in terms of growth, it is possible that they are expending more energy for osmoregulation. Several other studies have documented trade-offs between low salinity tolerance and growth or metabolic processes in *Fucus vesiculosus* (Russell 1987, 1988, Bäck et al. 1992) and *Laminaria digitata* (Nitschke & Stengel 2014). Salinity also influences carbonate and nitrite chemistry and may influence the uptake of nutrients needed for growth or other metabolic processes. Studies of *M. pyrifera* in the Magellan eco-region show that the assimilation of nutrients needed for these processes, such as NO_3^- and CO_2, are impacted by the strength of upwelling, which is associated with higher salinity (Fernández et al. 2021). Furthermore, higher variations in salinity may require adult *M. pyrifera* to generate more photosynthetic activity to maintain plant function, thus utilizing more energy (Marambio et al. 2023). To fully understand the impacts of osmotic stress on ecophysiological adaptation in *M. pyrifera*, further metabolic and cellular physiology studies are needed.

4.3. 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). 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); however, experimentally, 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 (Tatsumi & Wright 2016, Layton et al. 2020). Previous studies on *M. pyrifera* microstage competition with other species have found that other native kelps, such as *Pterygophera californica* and *Ecklonia arborea*, can suppress *M. pyrifera* recruitment (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. Although our study showed 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 the abundance of *M. pyrifera* female gametophyte and new diploid embryonic sporophyte 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* embryonic sporophyte size. The densities used in this experiment were based on the assumption of an equal number of reproductive *M. pyrifera* and *S. muticum* adults, and we assumed that one *S. muticum* zygote (250 µm diameter; Deysher & Norton 1981) was equal to approximately 500 *M. pyrifera* spores (<10 µm diameter; Clayton 1992). These proportional densities may be less than or greater than other natural populations, but likely greatly overestimate the ratio of *S. muticum* to *M. pyrifera* propagules released at the White Gulch population in Tomales Bay. While a single small plant of *S. muticum* may be able to release 500 000 zygotes within its lifetime (Engelen et al. 2015), studies of *M. pyrifera* spore release estimate that a single individual may be able to release 10^8 spores per individual per day (Gaylord et al. 2006).

Our results also suggest that at the densities we used, the presence of *S. muticum* is more detrimental than the presence of more *M. pyrifera*. While we saw *S. muticum* presence reduce *M. pyrifera* abundance in several instances, the effect is unlikely to be great enough that competition from *S. muticum* at the gametophyte and early sporophyte stages threatens to eliminate *M. pyrifera* from any locations within Tomales Bay. While previous studies have shown that *S. muticum* can reduce *M. pyrifera* populations due to shading (Ambrose & Nelson 1982, Britton-Simmons 2004, Steen 2004). Our results are consistent with other studies that found that *S. muticum* populations can also have negative or negligible effects on seaweed recruitment and growth (Ambrose & Nelson 1982), biomass (Wernberg et al. 2004, Sánchez et al. 2005), and cover (De Wreede 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 a sister species of *M. pyrifera* and *S. muticum*, *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 although *M. pyrifera* populations may be reduced due to shading by adults, microscopic stage development will likely be more negatively impacted by temperature increases than microstage competition with invasive propagules.

4.4. 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 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, Kroeker et al. 2013). 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.

We have shown that high temperatures pose a much higher risk to *M. pyrifera* gametophyte 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 stressors, both abiotic and biotic. Although 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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LITERATURE CITED

Aitken SN, Whitlock MC (2013) Assisted gene flow to facilitate local adaptation to climate change. Annu Rev Ecol Evol Syst 44:367–388

Alfonso B, Sansón M, Sangil C, Expósito FJ, Díaz JP, Hernández JC (2022) Herbarium macroalgae specimens reveal a rapid reduction of thallus size and reproductive effort related with climate change. Mar Environ Res 174: 105546

Ambrose RF, Nelson BV (1982) Inhibition of giant kelp recruitment by an introduced brown alga. Bot Mar 25: 265–268

Amsler CD, Reed DC, Neushul M (1992) The microclimate inhabited by macroalgal propagules. Br Phycol J 27: 253–270

Arafeh-Dalmau N, Montaño-Moctezuma G, Martínez JA, Beas-Luna R, Schoeman DS, Torres-Moye G (2019) Extreme marine heatwaves alter kelp forest community near its equatorward distribution limit. Front Mar Sci 6: 499

Bäck S, Collins JC, Russel G (1992) Comparative ecophysiology of Baltic and Atlantic *Fucus vesiculosus*. Mar Ecol Prog Ser 84:71–82

Bakun A, Black BA, Bograd SJ, García-Reyes M, Miller AJ, Rykaczewski RR, Sydeman WJ (2015) Anticipated effects of climate change on coastal upwelling ecosystems. Curr Clim Change Rep 1:85–93

Bates D, Mächler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models using lme4. J Stat Softw 67(1):1–48

Beaudin É, Di Lorenzo E, Miller AJ, Seo H, Joh Y (2023) Impact of extratropical Northeast Pacific SST on US West Coast precipitation. Geophys Res Lett 50:e2022GL10 2354

Bennett S, Santana-Garcon J, Marbà N, Jorda G and others (2021) Climate-driven impacts of exotic species on marine ecosystems. Glob Ecol Biogeogr 30:1043–1055

Bishop AM (2021) Effects of temperature on competition between *Macrocystis pyrifera* and *Sargassum horneri*. MSc thesis, California State University, Monterey Bay, Monterey, CA

Britton-Simmons KH (2004) Direct and indirect effects of the introduced alga *Sargassum muticum* on benthic, subtidal communities of Washington State, USA. Mar Ecol Prog Ser 277:61–78

Brooks ME, Kristensen K, van Benthem KJ, Magnusson A and others (2017) glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. R J 9:378–400

Buschmann AH, Vásquez JA, Osorio P, Reyes E, Filún L, Hernández-González MC, Vega A (2004) The effect of water movement, temperature and salinity on abundance and reproductive patterns of *Macrocystis* spp. (Phaeophyta) at different latitudes in Chile. Mar Biol 145: 849–862

Buschmann AH, Pereda SV, Varela DA, Rodríguez-Maulén J and others (2014) Ecophysiological plasticity of annual populations of giant kelp (*Macrocystis pyrifera*) in a seasonally variable coastal environment in the northern Patagonian inner seas of southern Chile. J Appl Phycol 26: 837–847

Byrnes JE, Reed DC, Cardinale BJ, Cavanaugh KC, Holbrook SJ, Schmitt RJ (2011) Climate-driven increases in storm frequency simplify kelp forest food webs. Glob Change Biol 17:2513–2524

Cheng BS, Grosholz ED (2016) Environmental stress mediates trophic cascade strength and resistance to invasion. Ecosphere 7:e01247

Cheng BS, Bible JM, Chang AL, Ferner MC and others (2015) Testing local and global stressor impacts on a coastal foundation species using an ecologically realistic framework. Glob Change Biol 21:2488–2499

Cheung WWL, Lam VWY, Sarmiento JL, Kearney K, Watson R, Pauly D (2009) Projecting global marine biodiversity impacts under climate change scenarios. Fish Fish 10:235–251

Christensen MS (2018) Chemical competition between microscopic stages of *Macrocystis pyrifera* and five native kelp species: Does giant kelp always lose? MSc thesis, San Jose State University, San Jose, CA

Clayton MA (1992) Propagules of marine macroalgae: structure and development. Br Phycol J 27:219–232

Cooley S, Schoeman DS, Bopp L, Boyd P and others (2022) Ocean and coastal ecosystems and their services. In: Pörtner H-O, Roberts DC, Tignor MMB, Poloczanska ES and others (eds) Climate Change 2022: impacts, adaptation and vulnerability. Contribution of Working Group II to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge and New York, NY

Crain CM, Kroeker K, Halpern BS (2008) Interactive and cumulative effects of multiple human stressors in marine systems. Ecol Lett 11:1304–1315

Critchley AT, De Visscher PRM, Nienhuis PH (1990) Canopy characteristics of the brown alga *Sargassum muticum* (Fucales, Phaeophyta) in Lake Grevelingen, southwest Netherlands. Hydrobiologia 204:211–217

De Wreede RE (1983) *Sargassum muticum* (Fucales, Phaeophyta): regrowth and interaction with *Rhodomela larix* (Ceramiales, Rhodophyta). Phycologia 22:153–160

Deysher L, Norton TA (1981) Dispersal and colonization in *Sargassum muticum* (Yendo) Fensholt. J Exp Mar Biol Ecol 56:179–195

DuBois K, Pollard KN, Kauffman BJ, Williams SL, Stachowicz JJ (2022) Local adaptation in a marine foundation species: implications for resilience to future global change. Glob Change Biol 28:2596–2610

Dunstan PK, Foster SD, King E, Risbey J and others (2018) Global patterns of change and variation in sea surface temperature and chlorophyll *a*. Sci Rep 8:14624

Easterling DR, Kunkel KE, Arnold JR, Knutson T and others (2017) Precipitation change in the United States. In: Wuebbles DJ, Fahey DW, Hibbard KA, Dokken DJ, Stewart BC, Maycock TK (eds) Climate science special report: fourth national climate assessment, Vol 1. US Global Change Research Program, Washington, DC, p 207–230

Edwards M (2022) It's the little things: the role of microscopic life stages in maintaining kelp populations. Front Mar Sci 9:871204

Edwards MS, Connell SD (2012) Competition, a major factor structuring seaweed communities. In: Wiencke C, Bischof K (eds) Seaweed biology: novel insights into ecophysiology, ecology and utilization. Ecological Studies, Vol 219. Springer, Berlin, p 135–156

Engelen A, Serebryakova A, Ang P, Britton-Simmons K and others (2015) Circumglobal invasion by the brown seaweed *Sargassum muticum.* Oceanogr Mar Biol Annu Rev 53:81–126

Espinoza J (1990) The southern limit of *Sargassum muticum* (Yendo) Fensholt (Phaeophyta, Fucales) in the Mexican Pacific. Bot Mar 33:193–196

Feely RA, Doney SC, Cooley SR (2009) Ocean acidification: present conditions and future changes in a high-CO_2 world. Oceanography 22:36–47

Fernández PA, Navarro JM, Camus C, Torres R, Buschmann AH (2021) Effect of environmental history on the habitat-forming kelp *Macrocystis pyrifera* responses to ocean acidification and warming: a physiological and molecular approach. Sci Rep 11:2510

Filbee-Dexter K, Wernberg T, Grace SP, Thormar J and others (2020) Marine heatwaves and the collapse of marginal North Atlantic kelp forests. Sci Rep 10:13388

Gaitán-Espitia JD, Hancock JR, Padilla-Gamiño JL, Rivest EB, Blanchette CA, Reed DC, Hofmann GE (2014) Interactive effects of elevated temperature and pCO_2 on early-life-history stages of the giant kelp *Macrocystis pyrifera.* J Exp Mar Biol Ecol 457:51–58

García-Reyes M, Sydeman WJ, Schoeman DS, Rykaczewski RR, Black BA, Smit AJ, Bograd SJ (2015) Under pressure: climate change, upwelling, and eastern boundary upwelling ecosystems. Front Mar Sci 2:109

Gaylord B, Reed DC, Raimondi PT, Washburn L (2006) Macroalgal spore dispersal in coastal environments: mechanistic insights revealed by theory and experiment. Ecol Monogr 76:481–502

Gentemann CL, Fewings MR, García-Reyes M (2017) Satellite sea surface temperatures along the west coast of the United States during the 2014–2016 northeast Pacific marine heat wave. Geophys Res Lett 44:312–319

Gershunov A, Shulgina T, Ralph FM, Lavers DA, Rutz JJ (2017) Assessing the climate-scale variability of atmospheric rivers affecting western North America. Geophys Res Lett 44:7900–7908

Gershunov A, Shulgina T, Clemesha RES, Guirguis K and others (2019) Precipitation regime change in western North America: the role of atmospheric rivers. Sci Rep 9: 9944

Graham M, Halpern B, Carr M (2008) Diversity and dynamics of Californian subtidal kelp forests. In: McClanahan T, Branch GM (eds) Food webs and the dynamics of marine reefs. Oxford University Press, Oxford, p 103–134

Hales JM, Fletcher RL (1989) Studies on the recently introduced brown alga *Sargassum muticum* (Yendo) Fensholt.

IV. The effect of temperature, irradiance and salinity on germling growth. Bot Mar 32:167–176
Hales JM, Fletcher RL (1990) Studies on the recently introduced brown alga *Sargassum muticum* (Yendo) Fensholt. V. Receptacle initiation and growth, and gamete release in laboratory culture. Bot Mar 33:241–250
Hartig F (2022) DHARMa: Residual diagnostics for hierarchical (multi-level/mixed) regression models. R package version 0.4.6. https://CRAN.R-project.org/package=DHARMa
Hollarsmith JA, Buschmann AH, Camus C, Grosholz ED (2020a) Varying reproductive success under ocean warming and acidification across giant kelp (*Macrocystis pyrifera*) populations. J Exp Mar Biol Ecol 522:151247
Hollarsmith JA, Sadowski JS, Picard MMM, Cheng B, Farlin J, Russell A, Grosholz ED (2020b) Effects of seasonal upwelling and runoff on water chemistry and growth and survival of native and commercial oysters. Limnol Oceanogr 65:224–235
Howard AC (2014) Effects of temperature on sexual competition in kelps: implications for range shifts in foundation species. MSc thesis, San Jose State University, San Jose, CA
Hu F, Zhang L, Liu Q, Chyi D (2021) Environmental factors controlling the precipitation in California. Atmosphere (Basel) 12:997
Ishii M, Kimoto M, Sakamoto K, Iwasaki SI (2006) Steric sea level changes estimated from historical ocean subsurface temperature and salinity analyses. J Oceanogr 62:155–170
Karsten U (2012) Seaweed acclimation to salinity and desiccation stress. In: Weineke C, Bischof K (eds) Seaweed biology. Springer, Berlin, p 87–107
Kerrison P, Le HN (2016) Environmental factors on egg liberation and germling production of *Sargassum muticum.* J Appl Phycol 28:481–489
Kimbro DL, Largier J, Grosholz ED (2009) Coastal oceanographic processes influence the growth and size of a key estuarine species, the Olympia oyster. Limnol Oceanogr 54:1425–1437
Kroeker KJ, Kordas RL, Crim R, Hendriks IE and others (2013) Impacts of ocean acidification on marine organisms: quantifying sensitivities and interaction with warming. Glob Change Biol 19:1884–1896
Krueger-Hadfield SA, Stephens TA, Ryan SH, Heiser S (2018) Everywhere you look, everywhere you go, there's an estuary invaded by the red seaweed *Gracilaria vermiculophylla* (Ohmi) Papenfuss, 1967. Bioinvasions Rec 7: 343–355
Largier JL, Hollibaugh JT, Smith SV (1997) Seasonally hypersaline estuaries in Mediterranean-climate regions. Estuar Coast Shelf Sci 45:789–797
Layton C, Cameron MJ, Tatsumi M, Shelamoff V, Wright JT, Johnson CR (2020) Habitat fragmentation causes collapse of kelp recruitment. Mar Ecol Prog Ser 648:111–123
Le DM, Desmond MJ, Pritchard DW, Hepburn CD (2022) Effect of temperature on sporulation and spore development of giant kelp (*Macrocystis pyrifera*). PLOS ONE 17: e0278268
Lenth RV (2024) emmeans: estimated marginal means, aka least-squares means. R package version 1.10.2. https://CRAN.R-project.org/package=emmeans
Li H, Geng Y, Shi H, Wu C and others (2023) Biological mechanisms of invasive algae and meta-analysis of ecological impacts on local communities of marine organisms. Ecol Indic 146:109763
Liu F, Pang S, Gao S, Shan T (2013) Intraspecific genetic analysis, gamete release performance, and growth of *Sargassum muticum* (Fucales, Phaeophyta) from China. Chin J Oceanology Limnol 31:1268–1275
Lopez BE, Allen JM, Dukes JS, Lenoir J and others (2022) Global environmental changes more frequently offset than intensify detrimental effects of biological invasions. Proc Natl Acad Sci USA 119:e2117389119
Lu J, Xue D, Gao Y, Chen G, Leung LR, Staten P (2018) Enhanced hydrological extremes in the western United States under global warming through the lens of water vapor wave activity. NPJ Clim Atmos Sci 1:7
Mabin CJT, Johnson CR, Wright JT (2019) Physiological response to temperature, light, and nitrates in the giant kelp *Macrocystis pyrifera* from Tasmania, Australia. Mar Ecol Prog Ser 614:1–19
Maggi E, Benedetti-Cecchi L, Castelli A, Chatzinikolaou E and others (2015) Ecological impacts of invading seaweeds: a meta-analysis of their effects at different trophic levels. Divers Distrib 21:1–12
Mahanes SA, Sorte CJB (2019) Impacts of climate change on marine species invasions in northern hemisphere high-latitude ecosystems. Front Biogeogr 11:e40527
Maier I, Hertweck C, Boland W (2001) Stereochemical specificity of lamoxirene, the sperm-releasing pheromone in kelp (Laminariales, Phaeophyceae). Biol Bull (Woods Hole) 201:121–125
Marambio J, Rodríguez Provoste JP, Rosenfeld S, Mendez F and others (2023) New ecophysiological perspectives on the kelp *Macrocystis pyrifera*: generating a basis for sustainability in the sub-Antarctic region. Front Mar Sci 10: 1222178
McPherson ML, Finger DJI, Houskeeper HF, Bell TW, Carr MH, Rogers-Bennett L, Kudela RM (2021) Large-scale shift in the structure of a kelp forest ecosystem co-occurs with an epizootic and marine heatwave. Commun Biol 4: 298
Metzger JR, Konar B, Edwards MS (2019) Assessing a macroalgal foundation species: community variation with shifting algal assemblages. Mar Biol 166:156
Muñoz V, Hernández-González MC, Buschmann AH, Graham MH, Vásquez JA (2004) Variability in per capita oogonia and sporophyte production from giant kelp gametophytes (*Macrocystis pyrifera*, Phaeophyceae). Rev Chil Hist Nat 77:639–647
Nitschke U, Stengel DB (2014) Iodine contributes to osmotic acclimatisation in the kelp *Laminaria digitata* (Phaeophyceae). Planta 239:521–530
North WJ, Jackson GA, Manley SL (1986) *Macrocystis* and its environment, knowns and unknowns. Aquat Bot 26: 9–26
Norton TA (1977) Ecological experiments with *Sargassum muticum*. J Mar Biol Assoc UK 57:33–43
Oliver ECJ, Lago V, Hobday AJ, Holbrook NJ, Ling SD, Mundy CN (2018) Marine heatwaves off eastern Tasmania: trends, interannual variability, and predictability. Prog Oceanogr 161:116–130
Pereira TR, Engelen AH, Pearson GA, Serrão EA, Destombe C, Valero M (2011) Temperature effects on the microscopic haploid stage development of *Laminaria ochroleuca* and *Sacchoriza polyschides*, kelps with contrasting life histories. Cah Biol Mar 52:395–403
R Core Team (2021) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Reed DC, Neushul M, Ebeling AW (1991) Role of settlement density on gametophyte growth and reproduction in the kelps *Pterygophora californica* and *Macrocystis pyrifera* (Phaeophyceae). J Phycol 27:361–366
Reid PC, Beaugrand G (2012) Global synchrony of an accelerating rise in sea surface temperature. J Mar Biol Assoc UK 92:1435–1450
Rodríguez JP, Terrados J, Rosenfeld S, Méndez F, Ojeda J, Mansilla A (2019) Effects of temperature and salinity on the reproductive phases of *Macrocystis pyrifera* (L.) C. Agardh (Phaeophyceae) in the Magellan region. J Appl Phycol 31:915–928
Rogers-Bennett L, Catton CA (2019) Marine heat wave and multiple stressors tip bull kelp forest to sea urchin barrens. Sci Rep 9:15050
Rubinoff BG, Grosholz ED (2022) Biological invasions alter consumer–stress relationships along an estuarine gradient. Ecology 103:e3695
Russell G (1987) Spatial and environmental components of evolutionary change: interactive effects of salinity and temperature on *Fucus vesiculosus* as an example. Helgol Meeresunters 41:371–376
Russell G (1988) The seaweed flora of a young semi-enclosed sea: the Baltic. Salinity as a possible agent of flora divergence. Helgol Meeresunters 42:243–250
Salvaterra T, Green DS, Crowe TP, O'Gorman EJ (2013) Impacts of the invasive alga *Sargassum muticum* on ecosystem functioning and food web structure. Biol Invasions 15:2563–2576
Sánchez Í, Fernández C, Arrontes J (2005) Long-term changes in the structure of intertidal assemblages after invasion by *Sargassum muticum* (Phaeophyta). J Phycol 41:942–949
Sanford E, Sones JL, García-Reyes M, Goddard JHR, Largier JL (2019) Widespread shifts in the coastal biota of northern California during the 2014–2016 marine heatwaves. Sci Rep 9:4216
Schiebelhut LM, Grosberg RK, Stachowicz JJ, Bay RA (2023) Genomic responses to parallel temperature gradients in the eelgrass *Zostera marina* in adjacent bays. Mol Ecol 32:2835–2849
Schwartz N, Rohde S, Dobretsov S, Hiromori S, Schupp PJ (2017) The role of chemical antifouling defence in the invasion success of *Sargassum muticum*: a comparison of native and invasive brown algae. PLOS ONE 12: e0189761
Seebens H, Blackburn TM, Dyer EE, Genovesi P and others (2018) Global rise in emerging alien species results from increased accessibility of new source pools. Proc Natl Acad Sci USA 115:E2264–E2273
Shea R, Chopin T (2007) Effects of germanium dioxide, an inhibitor of diatom growth, on the microscopic laboratory cultivation stage of the kelp, *Laminaria saccharina*. J Appl Phycol 19:27–32
Shi H, García-Reyes M, Jacox MG, Rykaczewski RR, Black BA, Bograd SJ, Sydeman WJ (2021) Co-occurrence of California drought and Northeast Pacific marine heatwaves under climate change. Geophys Res Lett 48: e2021GL092765
Shukla P, Edwards MS (2017) Elevated pCO_2 is less detrimental than increased temperature to early development of the giant kelp, *Macrocystis pyrifera* (Phaeophyceae, Laminariales). Phycologia 56:638–648
Smale DA, Wernberg T, Oliver ECJ, Thomsen M and others (2019) Marine heatwaves threaten global biodiversity and the provision of ecosystem services. Nat Clim Chang 9: 306–312
Small SL, Edwards MS (2021) Thermal tolerance may slow, but not prevent, the spread of *Sargassum horneri* (Phaeophyceae) along the California, USA and Baja California, MEX Coastline. J Phycol 57:903–915
Smith KE, Burrows MT, Hobday AJ, King NG and others (2023) Biological impacts of marine heatwaves. Annu Rev Mar Sci 15:119–145
Sorte CJB, Williams SL, Carlton JT (2010) Marine range shifts and species introductions: comparative spread rates and community impacts. Glob Ecol Biogeogr 19: 303–316
Sorte CJB, Ibáñez I, Blumenthal DM, Molinari NA and others (2013) Poised to prosper? A cross-system comparison of climate change effects on native and non-native species performance. Ecol Lett 16:261–270
Steen H (2004) Effects of reduced salinity on reproduction and germling development in *Sargassum muticum* (Phaeophyceae, Fucales). Eur J Phycol 39:293–299
Straub SC, Wernberg T, Thomsen MS, Moore PJ, Burrows MT, Harvey BP, Smale DA (2019) Resistance, extinction, and everything in between—the diverse responses of seaweeds to marine heatwaves. Front Mar Sci 6:763
Sullaway GH, Edwards MS (2020) Impacts of the non-native alga *Sargassum horneri* on benthic community production in a California kelp forest. Mar Ecol Prog Ser 637: 45–57
Tatsumi M, Wright JT (2016) Understory algae and low light reduce recruitment of the habitat-forming kelp *Ecklonia radiata*. Mar Ecol Prog Ser 552:131–143
Tegner MJ, Dayton PK (2000) Ecosystem effects of fishing in kelp forest communities. ICES J Mar Sci 57: 579–589
Thomsen MS, Wernberg T, Tuya F, Silliman BR (2009) Evidence for impacts of nonindigenous macroalgae: a meta-analysis of experimental field studies. J Phycol 45: 812–819
Thomsen MS, Byers JE, Schiel DR, Bruno JF, Olden JD, Wernberg T, Silliman BR (2014) Impacts of marine invaders on biodiversity depend on trophic position and functional similarity. Mar Ecol Prog Ser 495:39–47
Tolimieri N, Shelton AO, Samhouri JF, Harvey CJ and others (2023) Changes in kelp forest communities off Washington, USA, during and after the 2014–2016 marine heatwave and sea star wasting syndrome. Mar Ecol Prog Ser 703:47–66
Traiger S, Konar B (2017) Supply and survival: glacial melt imposes limitations at the kelp microscopic life stage. Bot Mar 60:603–617
Umanzor S, Sandoval-Gil J, Sánchez-Barredo M, Ladah LB, Ramírez-García MM, Zertuche-González JA (2021) Short-term stress responses and recovery of giant kelp (*Macrocystis pyrifera*, Laminariales, Phaeophyceae) juvenile sporophytes to a simulated marine heatwave and nitrate scarcity. J Phycol 57:1604–1618
Veenhof R, Champion C, Dworjanyn S, Wernberg T and others (2022) Kelp gametophytes in changing oceans. Oceanogr Mar Biol Annu Rev 60:335–372
Veiga P, Torres AC, Besteiro C, Rubal M (2018) Mollusc assemblages associated with invasive and native *Sargassum* species. Cont Shelf Res 161:12–19
Venables WN, Ripley BD (2002) Modern applied statistics with S, 4th edn. Springer, New York, NY
Vergés A, Steinberg PD, Hay ME, Poore AGB and others

(2014) The tropicalization of temperate marine ecosystems: climate-mediated changes in herbivory and community phase shifts. Proc R Soc B 281:20140846

Vilà M, Espinar JL, Hejda M, Hulme PE and others (2011) Ecological impacts of invasive alien plants: a meta-analysis of their effects on species, communities and ecosystems. Ecol Lett 14:702–708

Vranken S, Wernberg T, Scheben A, Severn-Ellis AA and others (2021) Genotype–environment mismatch of kelp forests under climate change. Mol Ecol 30:3730–3746

Wernberg T, Thomsen MS, Staehr PA, Pedersen MF (2004) Epibiota communities of the introduced and indigenous macroalgal relatives *Sargassum muticum* and *Halidrys siliquosa* in Limfjorden (Denmark). Helgol Mar Res 58: 154–161

Wernberg T, Bennett S, Babcock RC, de Bettignies T and others (2016) Climate-driven regime shift of a temperate marine ecosystem. Science 353:169–172

Zacher K, Bernard M, Daniel Moreno A, Bartsch I (2019) Temperature mediates the outcome of species interactions in early life-history stages of two sympatric kelp species. Mar Biol 166:161

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