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ARTICLE

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Food limitation erodes the thermal tolerance of larvae in an ecologically influential marine herbivore

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Abstract

Biologists often use organismal thermal tolerance to help explain or forecast responses of populations to climate change. Yet many studies quantify thermal tolerance under isolated laboratory conditions despite extreme events, such as heatwaves, often coinciding with other stressors such as nutrient or food limitation. These oversights may be consequential as recent theory suggests thermal tolerance itself can be fundamentally altered by food limitation. Here, we experimentally test how food limitation (500–10,000 cells mL^{-1}) affects long-term survival, development, and growth across a present-day range of temperatures (10–20°C) in the most sensitive life stages of an important marine herbivore, purple sea urchins (*Strongylocentrotus purpuratus*). We show food limitation substantially erodes thermal tolerance in terms of survival, but when provided ample food, larvae exhibited robust survival across temperatures currently experienced by larvae in nature. Reductions in food however lowered optimal survival temperatures and shifted survival thresholds to those conditions observed during recent marine heatwaves. These results are consistent with the "metabolic meltdown" hypothesis—shifting optima and upper limits to cooler temperatures—and illustrate how present-day warming coupled with lower productivity may lead to substantial, unexpected declines in larval survival and recruitment. In contrast to survival, developmental rates and time to metamorphic competency, which ranged from 21 to 61 days, were driven largely by temperature with little impact of food concentration. Our findings relate to historical observations of declines in larval supply at the southern edge of the species range. Overall, these results have broad-reaching implications beyond sea urchin populations as sea urchin herbivory is known to control productivity of kelp forest communities. We provide evidence of how laboratory derived thermal reaction norms can be coupled with ecologically relevant food concentrations to inform unexpected vital rate declines of sensitive life stages in a changing climate.

KEYWORDS
climate warming, food availability, morphometrics, planktonic larvae, *Strongylocentrotus purpuratus*, thermal performance

INTRODUCTION

Shifts in global temperatures (Oliver, Donat, et al., 2018) have in many cases led to unfavorable thermal conditions and, in combination with other global and local environmental stressors, have led to organismal adaptation, declines in viability, or risk of local extinction (Chevin et al., 2010; Diffenbaugh & Field, 2013; Seebacher et al., 2015). Assessment of how temperature affects key rates such as mortality, fecundity, and early-stage development can provide insight to understanding historical trends in population dynamics and species' responses to warming (Sinclair et al., 2016; Williams et al., 2016). Yet, for many species, declines in abundance resulting from climate change are based on single-stressor experiments, such as thermal tolerances (Wernberg et al., 2012). Changes in temperature can shift not only organismal physiological rates such as metabolism and development but can also cause and/or co-occur with shifts in exogenous ecological conditions such as resource availability (Brett, 1971). Thus, focusing solely on temperature effects is hypothesized to lead to erroneous predictions when neglecting potential interaction with additional stressors (Gunderson et al., 2016; Kroeker et al., 2017). Furthermore, ocean warming and food limitation may lead to differing responses in southern and northern regions (Bennett et al., 2004).

For ectotherms, metabolic rates increase exponentially with temperature until a critical limit is reached where various physiological functions fail (Huey & Kingsolver, 1989). Yet, as temperatures rise, if organisms cannot increase energy acquisition to meet metabolic demands, declines in performance may occur at cooler thresholds (Brett, 1971; Cheng et al., 2018; Huey & Kingsolver, 2019; Huxley et al., 2022; Koenker et al., 2018; Thomas et al., 2017; Verhille et al., 2015). Although temperature-induced changes in metabolic demands have been examined, a critical knowledge gap exists in understanding how other environmental factors affect thermal reaction norms and the induced trade-offs between maintaining equilibrium states needed for survival and devoting energy to growth or reproduction (Brett, 1971; Huey & Kingsolver, 2019; Huxley et al., 2022; McCue, 2010; Nyamukondiwa & Terblanche, 2009; Scharf et al., 2016). Under low food conditions, the physiological stress of high temperatures may be accentuated (Huey & Kingsolver, 2019; Verhille et al., 2015). The phenomenon where thermal optima and upper tolerance limits shift to lower (cooler) values as resources become limited is known as the "metabolic meltdown" hypothesis (Huey & Kingsolver, 2019). In sockeye salmon (*Oncorhynchus nerka*), for example, the upper thermal limits and optimal temperature for growth declined when food was restricted (Brett, 1971). Similarly, in marine bivalves, individuals acclimated to warmer temperatures and high food environments exhibited higher thermal limits compared to warm-acclimated individuals in low food environments (Cheng et al., 2018). Likewise, in *Aedes* mosquitos, depletions in resources can not only reduce the maximum thermal limits but also shrink the thermal breadth of optimal temperatures (Huxley et al., 2022). Thus, across taxa, temperature and food availability may interact synergistically to dictate shifts in performance.

In the marine realm, many animals are most vulnerable during the planktonic larval life stages (Strathmann et al., 2002), serving as a bottleneck for populations. Changes in temperature or food availability can affect survival and development in early life stages by influencing metabolism, energy demands, and growth (Burgess et al., 2016; Karelitz et al., 2020; Pineda & Lopez, 2002; Przeslawski et al., 2015). Negative effects of warming at sensitive life stages can outweigh benefits of resilience in more robust life stages. Thus, extrapolating from single life stages or food contexts can lead to underestimation of thermal vulnerabilities in a species (Williams et al., 2017). Previous work in echinoderms, more specifically sea urchins, has shown abiotic and biotic factors such as elevated temperatures and food limitation can alter larval survival, physiology, and development (Basch, 1996). Temperature was found to be positively related to rates of larval development and growth across marine taxa (O'Connor et al., 2007; Strathmann et al., 2002); however, beyond a thermal tipping point, survival and development are negatively affected (Karelitz et al., 2016). Variation in oceanographic processes, such as ocean circulation, pH, alkalinity, salinity, and stratification may affect recruitment patterns (Basch, 1996; Bialonski et al., 2016; Gaylord & Gaines, 2000; Padilla-Gamiño et al., 2013). Both biotic and abiotic factors, specifically temperature and food, may interact to influence dispersal distance, larval supply, and recruitment dynamics, which can alter planktonic larval duration and survival and ultimately, species persistence, genetics, and population dynamics (Basch, 1996; Caley et al., 1996; Hoegh-Guldberg & Pearse, 1995; O'Connor et al., 2007;

Rassweiler et al., 2020; Woodson et al., 2012). Experimental studies in the red sea urchin (*Mesocentrotus franciscanus*) found larval thermal tolerance was higher in individuals raised in warmer temperatures, whereas pH did not have a significant effect on thermal tolerance (Wong & Hofmann, 2020). Furthermore, developmental rates in echinoids slowed in cooler temperatures, and the amount of food available during the larval period had a strongly positive effect on juvenile development (Hart & Strathmann, 1994; Miller & Emlet, 1999). Yet a key gap exists in how thermal performance synergistically changes with food availability in the most vulnerable life stage of planktonic ectotherms and the potential implications for recruitment dynamics.

Purple sea urchins (*Strongylocentrotus purpuratus*) are a model organism for understanding how thermal performance shifts depending on food availability. Understanding larval bottlenecks in sea urchins is critical as they drive kelp forest community structure (Rogers-Bennett & Okamoto, 2020). Purple urchins inhabit a large latitudinal range with variations in abiotic and biotic conditions that covary with booms and busts in larval supply, shaping recruitment (Okamoto et al., 2020) and imposing disproportional influence on the ecosystem structure (Filbee-Dexter & Scheibling, 2014; Rogers-Bennett & Okamoto, 2020). Marine heatwaves in northern California have resulted in recent explosions in purple urchin numbers, presumably due to a combination of increased larval supply and loss of urchin predators (Filbee-Dexter & Scheibling, 2014; Rogers-Bennett & Catton, 2019). Marine heatwaves in the region are defined by sea surface temperatures in the 90th percentile for five consecutive days (Hobday et al., 2016). The 2014–2016 marine heatwave in the Southern California Bight had temperature anomalies with daily deviations of +5.8°C and monthly deviations of +4.6°C for 432 days (Hobday et al., 2016; Reed et al., 2016). Similarly, the 1997–1998 El Niño event in California recorded anomalously high ocean temperatures and low chlorophyll and primary production (Chavez et al., 2002). In contrast, marine heatwaves in the southern range (i.e., southern California to Baja California), where temperatures are already warm, have coincided with substantial reductions in larval supply (Okamoto et al., 2020) and adult densities (Arafeh-Dalmau et al., 2019; Beas-Luna et al., 2020; Reed et al., 2016). Within the warm Southern California Bight region, larvae are subject to seasonal fluctuations in temperature and food with higher temperatures often associated with lower food availability (Figure 1). Furthermore, recruitment across the purple sea urchin range displays inconsistent patterns with large increases in the northern regions of California but decreases in recruitment in the southern parts of the range (Ebert, 2010; Ebert et al., 1994). Previous El Niño events and heatwave conditions in the Southern California Bight resulted in reduced recruitment for *S. purpuratus* (Tegner & Dayton, 1991). Yet how ocean warming and food availability shapes sea urchin larval supply and subsequent recruitment remains an open question.

Here, we test how food limitation shapes the thermal reaction norm with respect to survival and development using larval *S. purpuratus*. We use this model system to understand the influence of food availability on temperature-dependent characteristics. Planktonic life history, larval development, survival, and time to metamorphic competency were measured for ecologically relevant temperatures (10–20°C) and food conditions (500–10,000 cells mL^{-1}) to encompass ambient and near future conditions. Our main hypotheses are as follows: (1) elevated temperatures will decrease rates of survival and increase rates of growth and development, (2) food limitation will decrease survival and decrease rates of growth and development, and (3) food condition will have a synergistic interaction with temperature where the food limitation will negatively affect survival and development with elevated temperature. We examine historical marine heatwaves, annual and interannual temperature trends, and chlorophyll abundance in the Southern California Bight to establish minima and maxima for the experimental temperature and food treatments. Specifically, we include temperatures that are slightly above those experienced in extreme heatwave conditions. Our experimental design includes these treatments to provide a basis for uncovering unexplained variation in recruitment trends across the range (Figure 1). We measure larval survival, morphology, and time to competency in relation to relevant temperature and larval food concentrations. We examine the effects of increasing ocean temperatures and food concentrations on larval sea urchins and discuss how this may influence community wide impacts on kelp forests in northern and southern regions.

MATERIALS AND METHODS

Trends in survival, morphometric patterns, and time to metamorphic competency across temperature and food availability treatments were measured in *S. purpuratus* larvae. Larvae were spawned from adult purple urchins collected in Santa Barbara, CA. Effects of temperature and food availability were tested using a 6 × 4 factorial experimental design with six temperature treatments (10, 12, 14, 16, 18, 20°C) and four concentrations of *Rhodomonas* sp. microalgae (500, 2500, 5000, 10,000 cells mL^{-1}) for a total of 24 treatment combinations. Food treatments represented algal concentrations from starvation to ad libitum conditions. Temperature and food treatments were based on historical observations of temperature trends and chlorophyll abundance (Figure 1, Appendix S1: Figure S1).

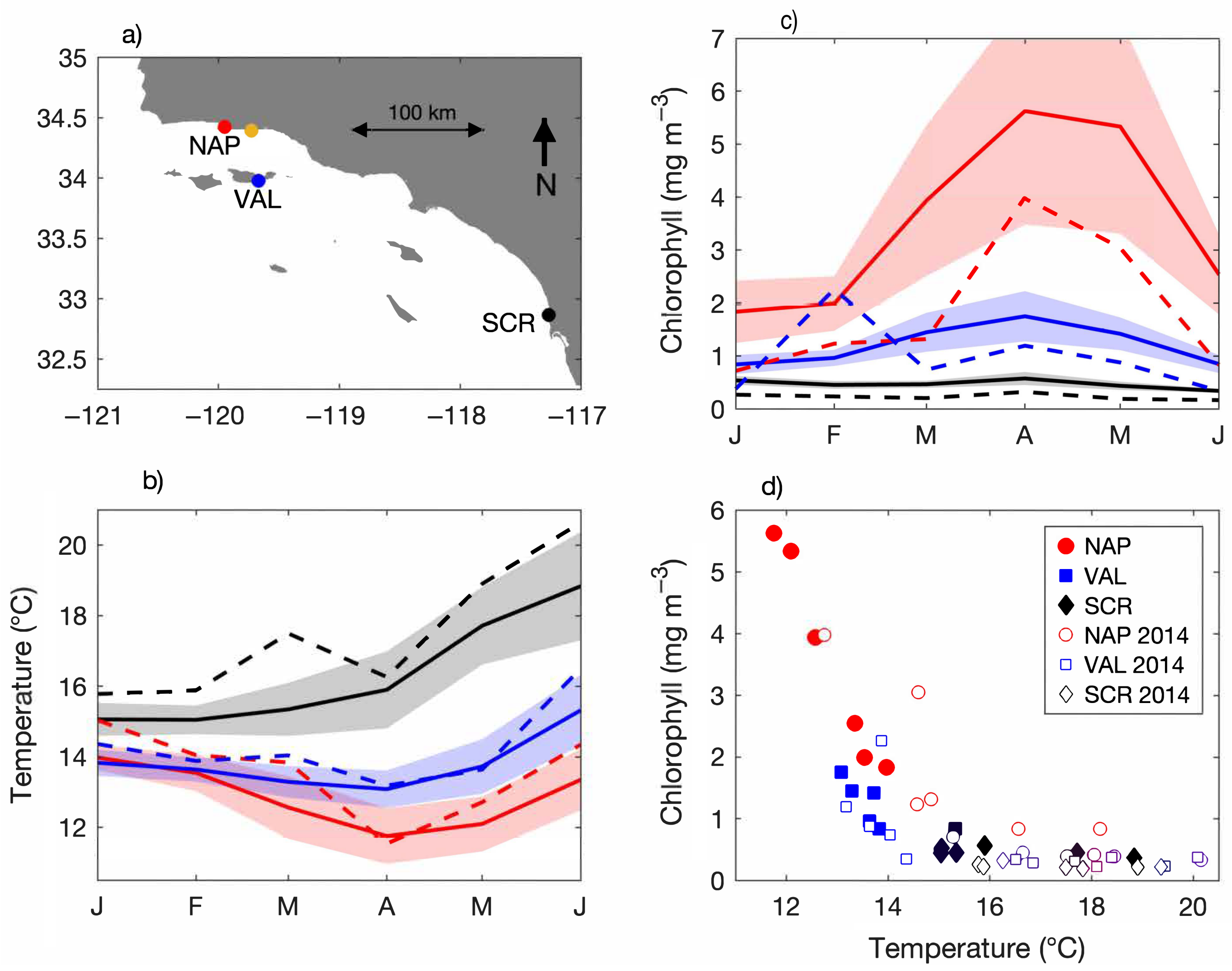

FIGURE 1 Temperature and chlorophyll across the Southern California Bight for January–June when larvae are in the water column. (a) Temperature and chlorophyll locations of Naples (NAP, red circle), Valley (VAL, blue circle), and Scripps Pier (SCR, black circle) and sea urchin collection site at Mohawk Reef, Santa Barbara (yellow circle). (b) Mean annual temperature (monthly average) from 2001 to 2022 at NAP (red), VAL (blue), and SCR (black) locations. Error bars represent ±1 SD of the monthly temperature over 21 years (2001–2022). Dashed lines represent monthly average temperatures for 2014, the warmest, most recent marine heatwave year. (c) Mean annual chlorophyll (in milligrams per cubic meter) concentrations at NAP (red), VAL (blue), and SCR (black) locations. Error bars represent ±1 SD of monthly chlorophyll values over 21 years (2001–2022). Dashed lines represent monthly average chlorophyll concentrations for 2014, the warmest, most recent marine heatwave year. (d) Negative relationship between temperature and chlorophyll concentrations for NAP (red), VAL (blue), and SCR (black) locations. Solid shapes represent averaged monthly values of years between 2001 and 2022 and open shapes represent values for each month of 2014.

Ocean temperature

Spanning the Southern California Bight from north to south, ocean temperature was obtained from three stations, Naples (NAP), Valley (VAL), and Scripps Pier (SCR) (Figure 1a). Ocean temperature at the NAP and VAL stations was obtained from the Santa Barbara Coastal Long-Term Ecological Research site and collected every 20 min at ~15 m depth from 2001 to 2022 (Washburn et al., 2025). Ocean temperature data at the SCR station was obtained from the Scripps Institution of Oceanography Manual Shore Stations program and collected daily from 2001 to 2022 at ~5 m depth (Carter et al., 2022). Annual mean monthly temperature was calculated for each station with confidence bands representing ±1 SD (Figure 1b).

Ocean chlorophyll

Ocean chlorophyll at NAP, VAL, and SCR stations was obtained from satellite-derived 5-day composites of surface chlorophyll *a* concentrations from 2001 to 2022. Surface chlorophyll concentrations were derived from three ocean color sensors, SeaWiFS, MODIS-Aqua, MODIS-Terra, and MERIS, assembled by the Scripps Photobiology Group at U.C. San Diego (Kahru et al., 2012, 2015). Annual mean monthly surface chlorophyll was calculated for each station with confidence bands representing ±1 SD (Figure 1c). Chl *a* concentrations are often used as a proxy for algal biomass due to challenges associated with measuring microalgae directly at large spatial scales (Bialonski et al., 2016; Spaulding et al., 2024). The highest food treatment in the current study is used to reflect a saturating density for optimal larval performance in *S. purpuratus* and reduced for lower food treatments. Previous studies have linked chl *a* concentrations to algal food availability to produce ecologically relevant larval food levels observed in nearshore temperate reefs (Basch, 1996; Basch & Pearse, 1996; Basch & Pearse, 2022). The highest food treatment in the current study is above the saturation value considered for sea urchin larvae, and serial restrictions in food were chosen given the large variation of microalgae in nature.

Field collections

Forty *S. purpuratus* were collected from seasonally urchin barren habitats between 2.2 and 8.8 m from Mohawk Reef in the Santa Barbara Channel, California, in June 2022 (Figure 1a). Kelp is seasonally available to organisms in the area, but there is less food available compared to adjacent reefs. During the month of June 2022, temperature ranged from 12 to 19°C, with an average of 16°C. Before spawning, individuals were held at 13°C for 4 weeks at UC Davis Bodega Marine Laboratory and were fed 20 g of a standardized kelp-based Urchinomics Inc. pelleted food every other day. While this is somewhat cooler than typical Santa Barbara conditions at the time of collection, these temperatures are still well within the natural range that urchins would experience seasonally in Santa Barbara. Importantly, the adults were given sufficient time to acclimate prior to spawning, which minimizes the risk of stress or temperature shock.

Larval culture

A homogeneous pool of fertilized embryos was assigned to temperature treatments. Spawning was induced by injecting 1–2 mL of 0.5 M KCl. Female urchins were placed upside down over 250-mL beakers filled with filtered to 0.1-μm seawater (FSW) at ambient temperature. Eggs were allowed to collect at the bottom of the beakers. Sperm was collected dry from the aboral surface and placed on ice in 2.0-mL microcentrifuge tubes until use. Gamete quality was visually inspected, with eggs assessed for shape, color, and uniform size and sperm for motility. Eggs from four females were pooled and rinsed before being fertilized by sperm from four males. Multiple individuals were chosen from each sex to account for maternal effects and genetic variability present in natural populations. Approximately equal proportions of gametes from each individual within each sex were represented. Successful fertilization was determined by 95% of eggs having a fertilization envelope with no polyspermy. Fertilized eggs were rinsed three times with FSW to remove excess sperm to prevent polyspermy. Approximately 2800 embryos (concentration of ~5.5 embryos mL^{-1}) were placed in each 500-mL glass bottle filled with FSW and placed on roller tables to suspend larvae (Karelitz et al., 2020).

Roller agitation tables were constructed to provide water movement for larval sea urchin cultures. Rollers on free moving axles kept larval culture bottles rotating to prevent larvae from settling to the bottom. Bottles were partially submerged in water baths heated or chilled using Heater/Chillers (TECO US Inc. TK-500) to maintain target temperatures. Embryos were initially stocked in bottles with ambient temperature (16°C) FSW to minimize temperature shock but were immediately placed into water baths to allow embryos to acclimate to target temperatures. Each of the 24 temperature × food treatments had four replicate bottles for a total of 96 bottles. Larvae were fed daily starting at 4 days postfertilization (when larvae were observed to be competent to feed) and water changes and feeding were conducted every 2 days.

Density counts, sampling, morphometrics, and metamorphic competency

Larval sampling was conducted every 2 days to estimate changes in larval density, morphometry, and competency, in conjunction with water changes and feedings. Larval densities were quantified by concentrating larval cultures to 100 mL and counting the number of larvae found in five 1-mL subsamples. Density counts continued until larvae showed signs of metamorphosis, as determined by the presence of a rudiment and exposed tube feet. Larval samples were collected 4, 9, and 15 days postfertilization and fixed in 10% phosphate-buffered saline (PBS) buffered formalin for morphometric analyses. Samples were collected before feeding to minimize the influence of algae on stomach measurements. Fixed larvae were then photographed using an Olympus BX41 compound microscope with a Nikon 3400 DSLR camera at 4× magnification, and postoral arm length, body length, and stomach length/height were measured in 20 randomly selected larvae from each sample using ImageJ software (Schneider et al., 2012). Metamorphic competency was determined when >50% of larvae exhibited tube feet and adhered to the bottle.

Statistical analysis

Morphometrics and development time

We used a Bayesian generalized linear mixed-effects model to estimate how larval morphometrics varied with temperature, food, and time. The model had an interaction between temperature, food, and days postfertilization while adding a hierarchical (random) intercept term by bottle replicate. We used a separate model for each response variable: larval body length, averaged postoral arm length, and stomach area (calculated with area of an oval using stomach height and width). All morphometric models were modeled with a Gamma likelihood and log link. The model including temperature, food, and days postfertilization was selected to maximize predictive accuracy, from which posteriors were analyzed for treatment comparisons. Models were constructed and posteriors were sampled using the *brms* package in R (Bürkner, 2017) as an interface to Stan (Stan Development Team, 2023). We computed the posterior distribution of pairwise differences in parameters within each timepoint using the *emmeans* package (Lenth, 2017). To display the exponential relationship between temperature and time to metamorphic competency, the *nls* function from *stats* in R was used to create a nonlinear weighted least squares estimate for an exponential decay function.

Survival

The effects of each treatment on larval survival rates during each 2-day interval were estimated using a custom Bayesian hierarchical state-space model (see Appendix S1: Supplemental methods for more information). We use this approach because survival is not directly observable and thus must be inferred from subsampled data as an “inverse problem.” A Bayesian approach allows for estimates of survival by handling both process and observation uncertainty, accommodates unbalanced data spaced in time across replicates, and enables probabilistic statements of mortality rates and survival using full posterior distributions. Specifically, larval subsample counts are measured with error, and thus survival from one timepoint to another timepoint is estimated in the presence of measurement error at both timepoints. As a result, to estimate mortality rates within each treatment/time period and among replicates, we require a model that allows for both error in measurement (counts as subsamples of the true density) and error in process (variation in mortality across times and replicates).

Our model approach assumes that (1) survival is not directly observed (inferred from count data), (2) variability comes from sampling error and process error, (3) mortality between timepoints follows an exponential decay, and (4) counts conditional on the true densities follow a Poisson distribution. Core model parameters, hyperparameters, priors, and hyperpriors are detailed in Appendix S1. Models were estimated in Stan via R using *cmdstan*.

RESULTS

The effect of temperature on larval survival and morphometry varied with food. When food was in high quantities, larval survival peaked at temperatures consistent with those experienced in the Southern California Bight (12–16°C; Figure 1b). As temperatures approached the cooler (10°C) and warmer extremes (18 and 20°C), survival sharply decreased. However, when food quantities were low, larval survival was highest at the coolest temperature (10°C) with survival dropping as temperatures increased. Mortality rate changed throughout the experiment for all treatments, with higher mortality in early phases of the experiment and lower mortality as larvae aged. Larval body length, postoral arm length, and stomach area increased with higher temperatures and food availability, with growth trends varying by larval age, where lower temperatures and food resulted in smaller larvae at 9 and 15 days, while stomach area significantly increased with higher food at 9 and 15 days, especially in warmer conditions. In contrast to temperature, time to metamorphic competency decreased exponentially with increasing temperature but did not differ between the two highest food treatments (where survival to competency was sufficiently high for comparison).

Survival

Food and temperature interacted to influence larval survival, decreasing exponentially between 0 and 15 days postfertilization across all treatments. Following the initial phase of mortality, cultures experienced either complete mortality (i.e., bottle level extirpation) or plateaued mortality rates. Larvae in 10 and 12°C reached metamorphic competency last and exhibited mortality rates

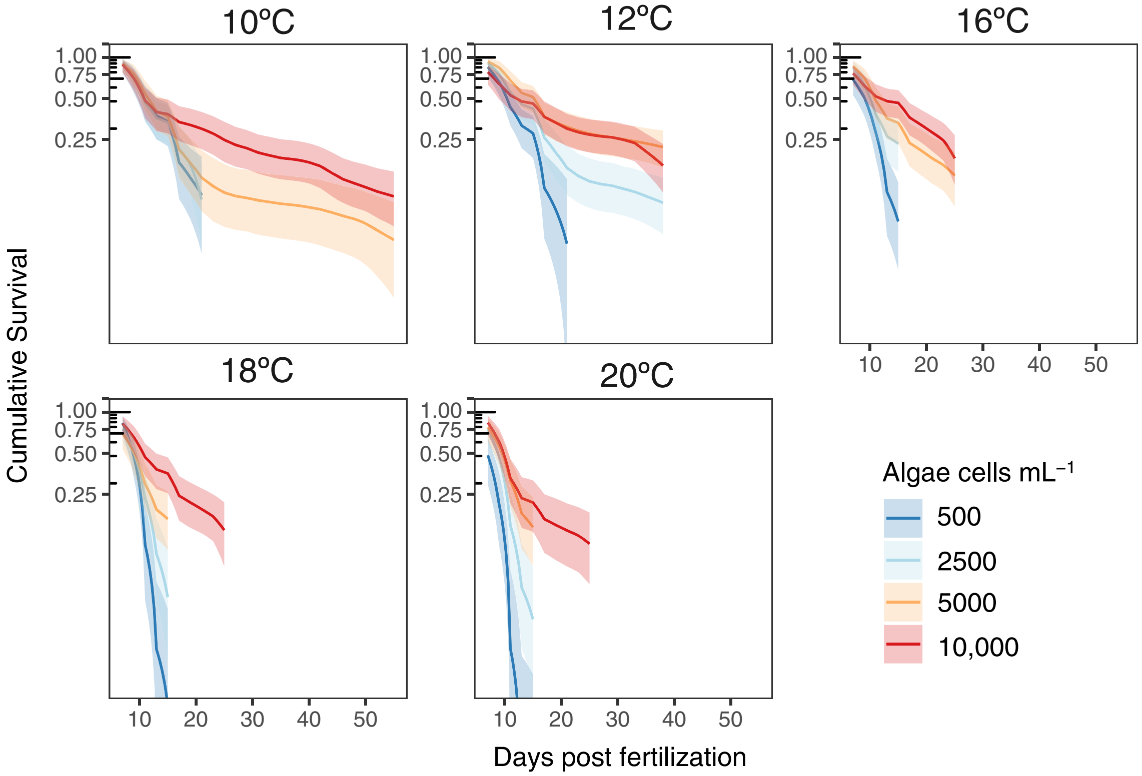

FIGURE 2 The effect of food availability (in algae cells per milliliter) on larval survival with 95% CIs across the duration of the experiment, separated by temperature in each panel. Survival curves terminate either due to total mortality of treatment type or larvae reaching metamorphic competency. Larval survival was greatest in the highest food treatment, 10,000 cells mL^{-1}. Larval survival steeply dropped off and resulted in total mortality at 15 days post fertilization in the lowest food treatment (500 cells mL^{-1}) across temperatures.

that leveled off and remained low from 20 days post-fertilization onward to 61 and 33 days, respectively. Importantly, mortality rates decreased over time, but the qualitative effects of food and temperature remained consistent, which is evident in the survival rates (Figure 2).

Throughout the experiment, survival decreased, but in low food treatments, survival steeply dropped off as opposed to the highest food treatments slowly decreasing over time (Figure 2). The 14°C treatment was excluded from all survival analyses due to equipment malfunction at 10 days post fertilization which resulted in >50% mortality across all replicate bottles. Qualitatively, larval survival in the 14°C treatment tracks similar trends of 12 and 16°C. However, due to equipment failure survival trends in the 14°C were excluded from the analysis. Although the exclusion of data for larvae held at 14°C may have potentially missed the peak precise survival point in the thermal performance curves, the overall trend of how food modulates thermal performance remains consistent despite the 14°C exclusion. Specifically, at the 7-day timepoint, survival in 12°C was 78%, 14°C was 80%, and 16°C was 76%. The 20°C treatment exhibited the lowest survival rates across all timepoints compared to the other temperature treatments (Figure 2). In the lowest food treatment (500 cells mL^{-1}) survival was particularly poor with only 21% surviving at 9 days, dropping to just 2% by 11 days and down to 0.03% by 15 days. Survival rates increased slightly in the 2500 cells mL^{-1} treatment, with 47% surviving at 9 days, decreasing to 15% at 11 days and 3% at 15 days. As food increased to 5000 cells mL^{-1}, survival was 57% at 9 days, 32% at 11 days, and 14% at 15 days. In the highest food treatment of 10,000 cells mL^{-1}, survival was 61% at 9 days, 33% at 11 days, and 22% at 15 days. Cumulative survival rates for each timepoint for all temperatures and food treatments are provided in Munstermann et al. (2025b) in the file named TableS1_surv_mort_perbottle_modeloutput.csv.

At the 15 day timepoint, the shape of thermal performance curves largely differed by food availability with larvae in high food treatments displaying peak survival at mid-range ambient temperatures but decreasing with temperature when food was in low quantities (Figure 3). The 15 days post fertilization was the last timepoint with sufficient larvae from all food and temperature treatments to allow comparisons across treatments (Figure 3). There was a disproportionate reduction in survival as food decreases between temperatures: Within the warmest temperature (20°C) there was a 22% reduction in survival between the highest food treatment and the

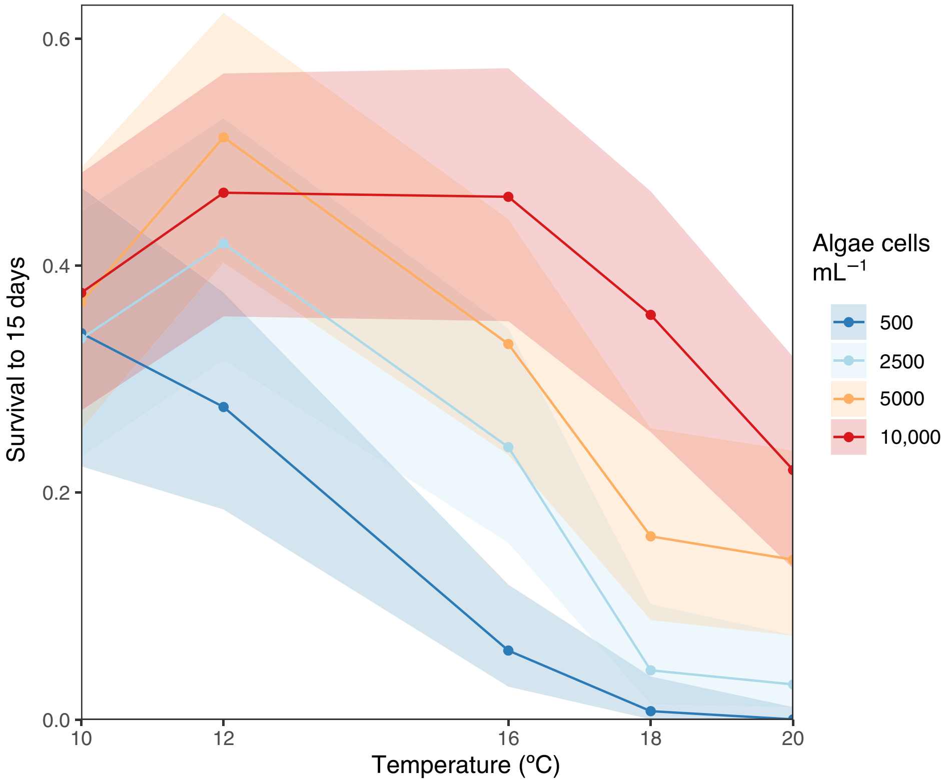

FIGURE 3 Shape of thermal performance curve for survival changes depending on amount of food available at 15 days post fertilization. Lines and points represent posterior mean estimates and bands represent 95% posterior uncertainty intervals. Larval survival was not significantly different across food concentrations at 10°C, indicated by the overlapping CIs, whereas in warmer temperatures, survival differed by the amount of available food. See results for specific contrasts.

lowest food treatment, whereas in 10°C, a temperature that larvae would commonly experience in the wild, there was only a 4% reduction between the highest and lowest food treatment. Survival was similar across food treatments at 10 and 12°C; however, as temperature increased the negative effect of lower food became exacerbated (Figure 3). Pairwise comparisons reveal no differences in survival across food treatments at 10°C (500 cells mL^{-1}: 34% CI [23%–46%], 2500 cells mL^{-1}: 34% CI [24%–45%], 5000 cells mL^{-1}: 37% CI [26%–49%], and 10,000 cells mL^{-1}: 38% CI [27%–49%]). In 12°C, the lowest food treatment of 500 cells mL^{-1} had lower survival at 28% CI (19%–38%) compared to the 42% CI (31%–53%) survival at 2500 cells mL^{-1}, 51% CI (41%–62%) survival at 5000 cells mL^{-1}, and 46% CI (36%–57%) survival at 10,000 cells mL^{-1} food treatments (Bayesian probability = 0.02675, 0.0005, 0.00775, respectively). In 16°C, the lowest food treatment had lower survival of 6% CI (3%–12%) compared to the remaining food treatments (24% CI [15%–34%], 33% CI [24%–44%], and 47% CI [35%–56%], respectively). There was also a significant difference in survival between larvae in the highest food treatment and the 2500 cells mL^{-1} (Bayesian probability = 0.0028) and 5000 cells mL^{-1} food treatments (Bayesian probability = 0.040). In 18°C, the 500 cells mL^{-1} food treatment had the lowest survival of 1% CI (0.03%–4%), 2500 cells mL^{-1} with 5% CI (1%–10%), 5000 cells mL^{-1} with 16% CI (9%–26%), and the 10,000 cells mL^{-1} with the highest survival of 36% CI (26%–47%), all displaying meaningfully different survival rates (Bayesian probability = 0.038, <0.001, <0.001, <0.001, respectively). Lastly, in 20°C, no meaningful differences in survival rates were detected between the two highest food treatments (15% CI [8%–24%] and 22% CI [13%–33%], respectively), whereas survival in the two low food treatments (0.15% CI [0.0001%–1.03%] and 3% CI [1.1%–7%], respectively) were significantly lower compared to the rest of the food treatments (Bayesian probability = 0.0001). All pairwise survival comparisons are provided in Munstermann et al. (2025b) in the file named TableS2_survival_15day_pairwise.csv. In the Southern California Bight system and greater purple urchin range, huge variation exists for temperature and food availability both in time and space. Our data indicate not only that the interaction between temperature and food may affect survival, but also that food restrictions with a slight increase in temperature can lead to significant impairments to survival. In the Southern California Bight, temperatures are rarely above 17°C in the wild when larvae are in the plankton; however, we observe dips in survival even at 16°C when food is limited. Therefore, the effect of food availability on survival across the tested range of temperatures has important ecological implications in explaining the mechanisms in which recruitment and subsequent adult population numbers fluctuate in response to ocean warming or marine heatwave events.

Time to competency

Larvae in higher temperatures had a shorter planktonic larval duration, measured as the time to metamorphic competency, compared to lower temperatures. Not all food treatments had sufficient survival to estimate time to metamorphic competency. Time to metamorphic competency decreased exponentially with temperature, with larvae at 10°C reaching competency in 61 days, larvae at 12°C in 33 days, larvae at 14°C in 29 days, larvae at 16°C in 25 days, larvae at 18°C in 22 days, and larvae at 20°C in 21 days (Table 1, Appendix S1: Table S1). At 61 days in 10°C, 5% and 10% (cumulative survival across replicates) of larvae reached metamorphic competency in the 5000 and 10,000 cells mL^{-1} food treatments, respectively. At 33 days in 12°C, 9%, 22%, and 16% of larvae reached metamorphic competency in 2500, 5000, and 10,000 cells mL^{-1} food treatments, respectively. At 25 days in 16°C, 13% and 18% of larvae reached metamorphic competency in the high food treatments, respectively. At 22 days in 18°C, 16% and 14% of larvae reached metamorphic competency in the high food treatments, respectively. At 21 days in 20°C, 14% and 11% of larvae reached metamorphic competency in the high food treatments, respectively. The lowest food treatment eventually resulted in 100% mortality, regardless of temperature. Within each temperature, time to competency did not differ between the two highest food conditions; however, the 2500 cells mL^{-1} food treatment lagged by 2 days in both 12 and 14°C (Table 1). In 16°C, larvae in 2500, 5000, and 10,000 cells mL^{-1} food treatments all reached competency at 25 days (Table 1). Larvae in warmer temperatures and highest food were in the 8-arm (14–20°C) larval stage, whereas larvae in cooler temperatures and lowest food were in 4-arm (10–14°C) or 6-arm (16–20°C) stages (Appendix S1: Table S1).

TABLE 1 Time to settlement decreased exponentially with increasing temperature and was determined when the majority (>50%) of individuals reached metamorphic competency.

Temperature (°C)	Algal food concentration (cells mL^{-1})	Days to metamorphic competency
10	500	No metamorphosis—died by 23 dpf
	2500	No metamorphosis—died by 25 dpf
	5000	61
	10,000	61
12	500	No metamorphosis—died by 23 dpf
	2500	35
	5000	33
	10,000	33
14	500	No metamorphosis—died by 15 dpf
	2500	31
	5000	29
	10,000	29
16	500	No metamorphosis—died by 15 dpf
	2500	25
	5000	25
	10,000	25
18	500	No metamorphosis—died by 15 dpf
	2500	No metamorphosis—died by 15 dpf
	5000	22
	10,000	22
20	500	No metamorphosis—died by 13 dpf
	2500	No metamorphosis—died by 15 dpf
	5000	21
	10,000	21

Note: Reductions in food concentrations resulted in delays to metamorphic competency. Larval cultures that reached metamorphic competency have the number of days indicated in the right column. Larval cultures that did not survive have the number of days post fertilization (dpf) culture was removed.

Larval morphometrics

Temperature and food had a synergistic effect on larval body length, postoral arm length, and stomach area, with size trends dependent on age. Within each temperature, body length was similar across food treatments at 4 days post fertilization but at 9 and 15 days. Cooler temperatures (10 and 12°C) and lower food resulted in smaller larvae compared to warmer temperatures (18 and 20°C) with high food. At 4 days, temperature had a stronger effect than food on body length. Body lengths in 10°C (all food treatments) were, on average, 1.4× smaller and significantly different from individuals in 12, 14, 16, 18, and 20°C temperatures, which were approximately the same size (Figure 4a, $p < 0.001$). At 9 days and within each temperature, body length was smallest in the lowest food treatment and increased with each increasing food

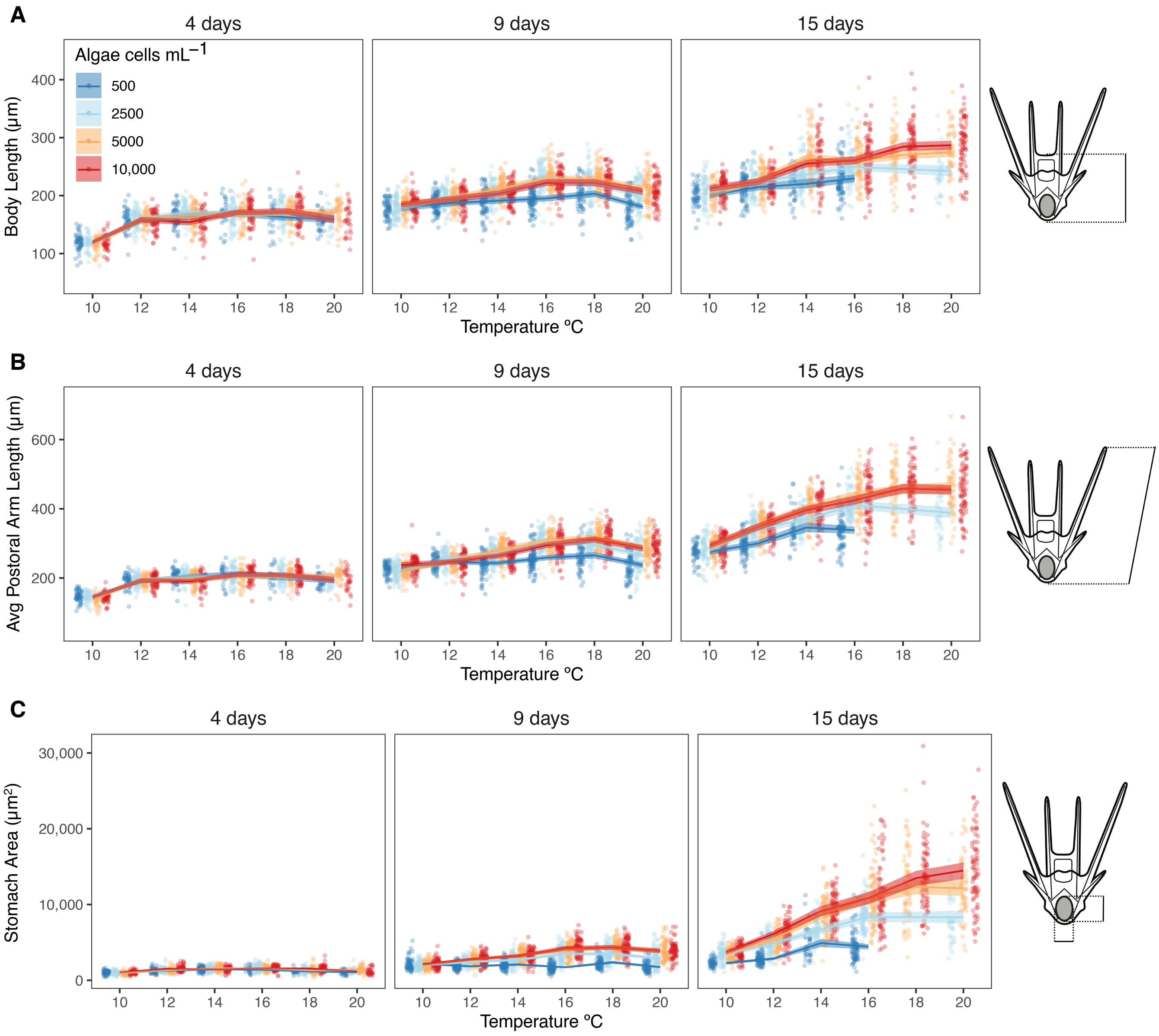

FIGURE 4 Morphometry of larvae at 4-, 9-, and 15-days post fertilization across temperatures ranging from 10 to 20°C and four algal food concentrations (500–10,000 cells mL^{-1}). Three larval body morphometrics were measured: (a) body length (in micrometers), (b) averaged postoral arm length (in micrometers), and (c) stomach area (in square micrometers). Points represent observed body length values for individuals. Trend lines represent Bayesian generalized linear mixed-effects model estimates and 95% CIs. All larval images were illustrated by Sam E. Karelitz.

treatment. In 10°C, body length increased from 177 μm in the lowest food treatment to 184 μm in the highest food treatment; in 12°C body length increased from 186 to 193 μm; in 14°C body length increased from 191 to 202 μm; in 16°C body length increased from 195 to 222 μm; in 18°C body length increased from 202 to 221 μm; and in 20°C, body length increased from 180 to 207 μm (Figure 4a). Although larvae were the same age, all individuals in 10°C (μ = 181 μm) were about the same size as the lowest food treatment in 20°C (180 μm), whereas larvae in warmer, high food treatments were, on average, 1.3× larger (228 μm). At 15 days, body length increased with temperature (Figure 4a), and within each temperature, body length increased with food; however, the magnitude of size differences was 1.4× times greater for high food and warm temperatures compared to the lowest food treatment in 10°C (Figure 4a). All significance values for larval morphometric pairwise comparisons are in Munstermann et al. (2025b) in the file named TableS3_morphometric_pairwise.xlsx.

A similar trend was observed in the postoral arm length averages at day 4 across temperature and food treatments but at 9 and 15 days, cooler temperatures had larvae with shorter arms and warmer temperatures had larvae with longer arms (Figure 4b; TableS3_morphometric_pairwise.xlsx in Munstermann et al., 2025b). Stomach area, however, was a consistent size across temperature treatments at day 4 (Figure 4c; TableS3_morphometric_pairwise.xlsx in Munstermann et al., 2025b), but at 9 days, stomach area increased with food availability (500 cells $\text{mL}^{-1} = 1992\ \mu\text{m}^2$, 2500 cells $\text{mL}^{-1} = 2851\ \mu\text{m}^2$, 5000 cells $\text{mL}^{-1} = 2899\ \mu\text{m}^2$, 10,000 cells $\text{mL}^{-1} = 3451\ \mu\text{m}^2$) but did not differ significantly by temperature (Figure 4c, $p < 0.001$). At 15 days, stomach area in the lowest food treatments remained small across temperatures ($\mu = 3635\ \mu\text{m}^2$), whereas all high food treatments exponentially increased in size, with a 3.7× increase in 18°C (13,552 μm^2) and a 4× increase in 20°C (14,573 μm^2).

DISCUSSION

We present experimental evidence illustrating how food availability modifies temperature impacts on larval survival and development. Co-occurring shifts in food availability and temperature synergistically shape mortality of early life history stages. Even small changes in the proportion of larvae surviving can scale up to large differences in recruitment success due to only a fraction of larvae ever reaching suitable settlement habitats. Thus, larval survival interacts with oceanographic drivers of transport. While currents and oceanographic processes associated with events such as El Niño largely determine whether larvae are delivered to the coast, the size of the larval pool available for transport depends not only on production of larvae but also survival during the planktonic larval period. Historical recruitment failures in purple urchins have been attributed to oceanographic processes limiting delivery and production of larvae (Basch & Tenger, 2007; Okamoto et al., 2025; Simons & Okamoto, 2025), but our results suggest that variation in survival, especially under concurrent shifts in food supply and temperature, may further magnify or buffer those outcomes. As such, larval production, transport, and survival dynamics jointly shape recruitment dynamics, highlighting how changes in ocean conditions can alter urchin population trajectories. While we use larvae of a marine invertebrate to test these hypotheses, these results may hold for many ectotherms, including species in terrestrial, freshwater, and other marine systems (Gunderson & Stillman, 2015; Huxley et al., 2022). Resource availability combined with warming strongly influenced survival of early life stages which may impact later life history stages, and ultimately the productivity and viability of populations. Two main findings emerged from this study: (1) effect of temperature on larval survival shifts to cooler optima under food limitation; (2) while thermal tolerance and survival are influenced by resource availability, developmental rates were governed by temperature with warmer temperatures resulting in a shorter larval planktonic period and larger individuals.

Implications of survival

Our study provides evidence of a shift in the thermal reaction norms associated with reduction of food resources, which directly informs observed historic population dynamics and recruitment patterns. Importantly, this result is consistent with expectations from the "metabolic meltdown" hypothesis (Huey & Kingsolver, 2019). When comparing stressful temperatures to ambient temperatures, there is a disproportionate reduction in survival as food decreases, potentially due to stressful temperatures requiring a greater reliance on food for energy. Larvae were not only smaller in cooler temperatures but also less mature. Because of the lower metabolic costs for smaller, earlier developmental stage larvae, less energy and thus less food may be required to maintain similar functions (Holden et al., 2019; Mogensen & Post, 2012). However, as larvae grow faster and are larger in higher temperatures, they have higher metabolic demands (O'Connor et al., 2007), such that the mortality rate is amplified even with small reductions in food quantity. Variations in larval growth and development are observed between food and temperature treatments; however, we are unable to distinguish if larvae from different treatments had varying body shapes or if individuals were at different developmental stages. Similar results are found for various taxa including fish, gastropods, and sea stars. In larval fish, lower food availability resulted in significantly smaller individuals compared to the full food ration; however, the added stressor of warm temperature had an inverse effect with higher growth rate and survival in late-stage larvae (Koenker et al., 2018). Similarly in whelk, *Nucella ostrina*, individuals exposed to warmer water temperature had higher survival when food was abundant and lower survival when food was scarce (Dahlhoff et al., 2001). In larval asteroids, food availability had a strong effect on development time with the lowest food treatment (500 cells mL^{-1}) resulting in arrested growth at early pre-competent stages, an observation also made in the current study with arrest in the low food treatment of 500 cells mL^{-1} (Basch, 1996). To maintain necessary biological processes, species can also shift energy allocation when exposed to unfavorable conditions to compensate for compounding stressors when food is available (Pan et al., 2015); however, the increased energetic cost of surviving in warmer conditions requires compensation in the form of behavioral changes, energy conservation, or nutrition (Holden et al., 2019; Huey & Kingsolver, 2019; Mogensen & Post, 2012).

Impacts to larval development

In contrast to survival, time to metamorphic competency was largely shaped by temperature, as synthesized in previous work (O'Connor et al., 2007; Strathmann, 1978). In ambient temperatures, 12 and 14°C, all but the lowest food treatment reached competency, whereas in the coldest temperature 10°C and the warmer temperatures 16, 18, and 20°C, only the two highest food treatments reached competency. Development times do not differ above 5000 cells mL^{-1} of food, indicating that temperature determines time to metamorphosis more than food. Temperature extremes may impose stressful conditions that require a certain threshold of food to transition from the larval stage to the juvenile stage, but once that food threshold is achieved there is no difference in developmental response. When temperatures approach stressful levels, low food (2500 cells mL^{-1}) may not have provided adequate sustenance for metamorphosis. In the Southern California Bight, high temperatures are associated with low food availability (Figure 1), indicating that when heatwave conditions are present, time to settlement may be reduced.

The synergistic effect of temperature and food availability on survival, but not development time, imposes an important trade-off. Larvae in cooler temperatures have an extended period of development in the plankton. Thus, larvae must endure a longer vulnerable period in planktonic forms but may also have higher cumulative survival (i.e., independent of predation or other exogenous risks). In contrast, larvae in warmer temperatures have a shorter planktonic larval duration but with lower basal cumulative survival rates. Temporal trends in mortality rate (i.e., decline in mortality as larvae age) and predation on larvae complicate these trade-offs. Furthermore, warmer water associated with lower food concentrations (SCR station) and cooler temperatures with higher food (NAP and VAL stations) indicate that even within the Southern California Bight, larval survival may differ (Figure 1a,d). Avenues for future studies can focus on quantifying the stage in which food limitation affects larval condition and assess phytoplankton communities and survival in nature (Basch & Pearse, 2022). Previous studies have linked El Niño conditions to reductions in primary productivity in Southern California and therefore linking low food concentrations to larval limitations requires direct wild sampling to assess more realistic scenarios.

S. purpuratus span a large latitudinal range over which populations experience highly variable temperature and oceanographic regimes as well as divergent recruitment trends. While our study focused on animals sourced from Santa Barbara, CA, from seasonally barren sites, organisms from kelp-replete or other regions throughout the range may exhibit different thermal reaction norms from those identified here (Azad et al., 2012; Hammond & Hofmann, 2010; Stumpp et al., 2013). In addition to population variability, larvae spawned from a subset of individuals will never fully encompass the genetic variation present in the population. The isolation of the population scale genetic effects lies beyond the scope of this paper and is an area for future research. As a result, future contributions may expand on these insights by replicating results across parental nutritional states, thermal regimes, and/or genotypes. Despite the potential for population differentiation, our work illustrates that food and temperature can interact synergistically to shape survival and must be accounted for in estimating larval survival and delivery of feeding larvae. This result is likely to have implications for purple urchin recruitment trends across the range due to early life history stages dictating the number of successful recruits and subsequent adult population sizes (Ebert, 2010; Pineda, 2000; Woodson et al., 2012).

Dispersal distance and larval duration can directly determine the recruitment and structure of adult populations (Morgan et al., 2009). Oceanographic factors such as eddies, jet formation, upwelling, strong winds, and ocean fronts have influence on water movement and recruitment dynamics by the advection of larvae offshore and return of larvae via eddies and shallow waves in the convergence zone (Connolly & Roughgarden, 1998; Ebert & Russell, 1988; Shanks, 1983; Woodson et al., 2012). The eddies specifically in the Southern California Bight can alter the sea surface temperature, retention of larvae, and ultimately nutrient concentrations, larval delivery, and recruitment patterns (DiGiacomo & Holt, 2001; Siegel et al., 2008). Between 1990 and 1993, purple urchin settlement trends differed between northern and southern CA with settlement densities consistently higher in the south, potentially attributed to opposing oceanographic conditions with weak cross shelf water movement, reduced upwelling conditions, and larval retention in the Southern eddy system (Ebert et al., 1994; Ebert & Russell, 1988). Advective currents may alter the ability of larvae to reach shore and successfully settle (Gaylord & Gaines, 2000). Planktonic dispersal of larval crabs and other larval organisms in the south follows an eddy circulation current pattern and may result in settlement closer to the site of spawning; whereas larvae in northern California seem to follow a different transport mechanism by remaining near shore during the upwelling season by descending below the Ekman transport layer during development and returning to shore by ascending to the surface via wind relaxation events or internal waves (Ebert & Russell, 1988; Gaylord & Gaines, 2000; Morgan et al., 2009). The vertical distribution and behavior of sea urchin larvae in nature remains a research frontier and future work can focus on the modeling and measurement of urchin larval dispersal with the interactions between physiological, demographic, and developmental responses to climate. Historical recruitment failures in purple urchins may be explained by the aforementioned oceanographic processes and changes in transport mechanisms associated with El Niño events.

Prolonged larval duration observed in cooler conditions may increase dispersal potential as well as connectivity and gene flow among populations (Rogers-Bennett & Rogers, 2008) however may lead to transportation of larvae away from favorable settlement conditions (Strathmann et al., 2002). Although we found cumulative survival to be higher in cooler temperatures, development time was longer, spending a significantly greater amount of time in the vulnerable planktonic life stage, potentially reducing the likelihood of returning to nearshore habitats and overall survival due to oceanographic factors (Burgess et al., 2016; Menge, 2000; Pineda, 2000; Strathmann et al., 2002). Conversely, in warmer temperatures or years with marine heatwaves, shorter planktonic larval duration is expected to lead to quicker settlement of larvae that are larger and potentially more successful in the benthos but with lower larval survival. Population connectivity in the California Current system is a function of planktonic larval duration (Mitarai et al., 2008). Fewer days in the plankton coupled with larger size at settlement in warm water may outweigh lower larval survival rates in some oceanographic conditions, at the expense of lower connectivity between populations (Mitarai et al., 2009; O'Connor et al., 2007; Rassweiler et al., 2020).

Oceanographic processes, many of which are affected by El Niño, also play an important role in shaping the spatial and temporal patterns of recruitment. During cooler years, purple urchin recruitment is consistently higher in southern California than northern California (Ebert et al., 1994). However, larval transport, recruitment, and local retention trends can drastically change during El Niño oscillations and can be exacerbated by marine heatwaves (Okamoto et al., 2020). El Niño years are often characterized by warmer sea surface temperatures, relaxed winds, and weakening of seasonal upwelling (Navarrete et al., 2002). As a result, purple urchin recruitment has been observed to decrease in southern California and increase in northern California (Chavez et al., 2002; Ebert et al., 1994; Okamoto et al., 2020; Tegner & Dayton, 1991). Although El Niño conditions have been observed along the coastline, there has not been a clear connection between fluctuations in temperature and food availability and why these effects have resulted in recruitment failure. Effects of warming may be underestimated if shifts in resource availability are not considered and may explain regional declines in urchin recruitment under nonlethal temperature conditions. Our study encompasses ambient and heatwave temperatures to test the organismal response when food is limited. The continued widespread urchin barrens along the northern California coastline following the marine heatwaves are an example of the disruptive, ecosystem-scale consequences of rising temperatures seemingly driving larval recruitment dynamics.

Increases in ocean temperatures and the frequency and severity of marine heatwaves make it crucial to understand the mechanisms of larval response and subsequent recruitment dynamics in response to changing environmental conditions (Leach et al., 2021; Oliver, Lago, et al., 2018). Modest quantities of purple urchins serve an important herbivore role, but extremely high densities of urchins from massive recruitment events can lead to barren habitats. Temperatures tested in the current study encompass the heatwave temperatures experienced in southern California regions (Figure 1, Appendix S1: Figure S1), allowing for an understanding of how food modifies survival and development trends during the previous marine heatwave event. Due to the recent ecosystem transition from kelp-dominated to urchin barren states along the California coastline (Rogers-Bennett & Catton, 2019), understanding purple urchin recruitment and larval supply trends will help inform how kelp forests will respond to future warming events and how these trends can lead to inverse regional responses between northern and southern parts of the range. Furthermore, results from our study can inform mitigation measures along the California coastline by using the larval survival and development data to predict recruitment trends. Climate change can alter the effectiveness of kelp forest restoration practices. Here, we show multiple stressors can synergistically affect larval survival and thereby recruitment of an important marine herbivore which has a disproportionate effect on the dynamics of kelp, a key foundation species. Given the magnitude of the effect observed in our study, models of recruitment and dispersal that have historically been used to design marine protected areas and marine spatial planning with fixed larval life histories may be aided by accounting for multiple stressor effects. Our study highlights how thermal performance optima can shift depending on availability of resources with applications across ectothermic taxa. As global temperatures continue to rise and ecosystems experience shifts in productivity, we will need to understand how population dynamics, community interactions, and ecosystem functions are linked to temperature in the context of resource dynamics.

AUTHOR CONTRIBUTIONS

Maya J. Munstermann, Sam E. Karelitz, Laura Rogers-Bennett, and Daniel K. Okamoto designed the study. Maya J. Munstermann, Sam E. Karelitz, and Rachele Ferraro conducted the experiment. Maya J. Munstermann and Daniel K. Okamoto performed statistical analyses. Rachel D. Simons provided historical datasets and map analyses. Maya J. Munstermann wrote the first draft of the manuscript, and all authors contributed substantially to revisions.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Munstermann et al., 2025a, 2025b) are available in Dryad and Zenodo at https://doi.org/10.5061/dryad.j9kd51cp2 and https://doi.org/10.5281/zenodo.14533775, respectively. Code (Munstermann et al., 2025c) is available in Zenodo at https://doi.org/10.5281/zenodo.14533773.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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