Title: Thermal suppression of gametogenesis explains historical collapses in larval recruitment

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Abstract

Projections for population viability under climate change are often made using estimates of thermal lethal thresholds. These estimates vary across life history stages and can be valuable for explaining or forecasting shifts in population viability. However, sub-lethal temperatures can also lead to declines in vital rates and ultimately shape fluctuations in the reproductive viability of populations. For example, anomalous climatic events can suppress reproduction and lead to recruitment failure well before early life stages or adult stages become affected. These sub-lethal impacts make the effects of climate change more severe than lethal thresholds predict. Despite a growing awareness of this issue, tying sub-lethal effects to observed recruitment failure remains a challenge especially in marine environments. Here, we experimentally show that sub-lethal thermal suppression of female gametogenesis offers a plausible explanation for historical collapses in sea urchin recruitment during marine heatwaves. These sub-lethal thermal sensitivities of reproduction can narrow the thermal envelope for population viability compared to what lethal limits predict.

Introduction

Predicting the impact of warming and extreme heatwaves on ecosystems and populations remains one of the most daunting but important tasks in ecology and conservation. Information about the future dynamics and viability of populations can be gleaned from measuring thermal lethal thresholds (or critical thermal limits - CTLs) in controlled settings, as well as from historical patterns of population performance in nature. For the latter, extrapolating historical patterns without understanding processes that shaped them remains dubious; meanwhile, expectations from CTLs often underpredict the abruptness and magnitude of population responses to warming in nature [1-3]. For example, warming and heatwaves may lead to recruitment failure in populations even when temperatures remain below lethal thresholds [4,5]. Thus, the realized thermal niche of many species (i.e., thermal regimes in which a population exhibits viability over time) is often narrower than expected based on CTLs for individual life stages (gametes, juveniles, adults, etc. - [6]). Combining inference from laboratory studies and historical patterns and analysis can provide a more comprehensive understanding of the processes that shape recruitment and population dynamics.

One pathway by which sub-lethal temperatures can alter population viability is by affecting gametogenesis, maturation, and/or sterility. Reproductive phenology for a diversity of plants and animals responds directly to temperature [7] and as such, temperature can significantly impact reproductive success and thereby fitness and productivity in a warming world. In plants, for example, warmer winters can lead to crop failure by disrupting vernalization pathways. This family of processes, in which plants require specific thermal cues, as well as other environmental patterns or thresholds for induction of flowering and seed/fruit development has long been studied and understood in agricultural and laboratory plant systems e.g., [8,9]. Likewise, a diversity of animal taxa can exhibit infertility or low fecundity at sub-lethal temperatures [10-14].

Yet for animals, and marine organisms with planktonic larvae in particular, it remains unclear if and to what extent patterns of recruitment failure in nature are shaped by sub-lethal thermal suppression of reproduction. This gap remains, in part, for several reasons. First, attributing causality to observed changes in year-class strength remains a challenge for animals with dispersive reproductive propagules. Shifts in recruitment may be explained by variation in

food supply [15], trends in reproductive and mating success [16], shifts in dispersal [17], or a host of other factors that may also be directly or indirectly related to warming. Second, thermal limits are often estimated using constant temperatures; yet in the oceans, temperature is highly dynamic, and those dynamics can shape patterns of reproduction. Thus, while it is well known that sub-lethal temperature can limit reproduction in marine invertebrates [18,19], it remains less well understood if dynamic heatwave trends can induce such limitations and/or plausibly explain collapses in recruitment. If climate change and extreme events in nature lead to suppressed gametogenesis well before lethal limits of organisms are reached (e.g., thermal stress that decreases larval, juvenile, or adult survival), then declines in population viability and contractions in distributions may occur much more quickly than expected from currently established critical thermal limits.

For populations of purple sea urchins (*Strongylocentrotus purpuratus* - an ecologically important herbivore) in Southern California, recruitment tends to collapse during warm El Niño events[20] (Figure 1A). This phenomenon is remarkably consistent over time (extending back at least six decades), even though temperatures during the reproductive season in southern California (late fall and early winter [20,21] Figure 1B) are almost always below those considered to be lethal for adults (~25 °C[22]). Moreover, winter temperatures in the Santa Barbara Channel when larvae are present (~ 11-16°C) are generally well below the thresholds thought to impede multiple phases of larval survival[23] (fertilization and early-phase survival of San Diego, Santa Barbara, and British Columbia animals declines from high to low between 20-22°C - SK, unpublished data). Specifically, purple urchins tend to spawn in the winter and spring, coinciding with favorable (low temperatures and high food availability) conditions for larvae [20]. Larvae persist in the plankton from approximately 28 days to several months depending on food availability and temperature [24,25]. Adult urchins build gonads over the course of the summer and fall with gametogenesis occurring in the fall and early winter. El Niño conditions in Southern California are characterized by warmer water temperatures in summer, fall, and winter than during neutral years or during La Niña conditions, but still exhibit seasonal cooling (Figure 1B). One proposed explanation for decreases in recruitment in southern California during El Niño is that temperatures experienced during these events suppress gametogenesis even though energetic investment in gonads may be sufficient for reproduction [26-28]. Specifically, Pearse [28]

demonstrated that high temperatures decrease gamete production at sub-lethal levels (i.e., at 21°C vs 14°C), but these high temperatures exceed the extreme values experienced in the spawning season.

In this study, we used *S. purpuratus* to test whether historical collapses in larval supply and year-class strength (i.e., abundance for a given young-of-year cohort) can, in part, be explained by sub-lethal thermal suppression of reproduction. Specifically, we used laboratory experiments to ask whether dynamic marine heatwaves that have led to collapses in larval supply also affect reproduction in terms of both gonad production and gametogenesis. We compared effects of simulated heatwaves to simulated historical cool trends, as well as the outcomes under a gradient of constant conditions (i.e., the thermal performance under constant temperatures).

Results

Simulated El Niño and warming conditions led to decreased gonad production as well as suppressed gametogenesis in *S. purpuratus* with no mortalities associated with any treatments. Declines in gonad production associated with high temperatures were consistent for constant exposure to 20°C and the El Niño treatment that shifted from 21 to 18°C with a mean of 20°C (Figure 4). In contrast, the dynamic La Niña treatment (shifting from 18 to 14°C, with a mean of 16°C) led to reduced gonad production compared to a constant mean temperature of 16°C. The effect of treatment on reproductive status differed depending on whether the thermal environment varied over time (El Niño and La Niña versus constant temperatures) and by sex. With a mean of 16°C, we saw no effect of dynamic La Niña or constant temperatures on male or female reproductive status. For females, both constant high temperatures and the El Niño treatment led to a substantial reduction in oogenesis; for males, only the dynamic El Niño treatment affected spermatogenesis, with no change observed across constant temperatures from 10 to 20°C. Below, we detail these results in terms of gonad production and sex-specific gametogenesis, comparing effects among the constant temperature treatments and dynamic El Niño and La Niña treatments.

Gonad production

Exposure to the highest temperatures (for both dynamic and constant treatments with mean of 20°C) negatively affected both male and female gonad production (cumulative gonad

mass, Figure 4) with a 42% decrease (95% highest probability density interval [HPD]: 28-55%) compared to a constant temperature of 16°C. Gonad production did not differ for the El Niño (7.03g [95% HPD: 6.20g – 7.96g]) and constant treatment that shared the same mean value of 20°C (7.2g, [95% HPD: 5.97g – 8.50g]). In contrast, the dynamic La Niña treatment (declining from 18 to 14°C with mean of 16°C) showed a reduction in gonad mass (26% - HPD: 15 – 38%) compared with a constant value of the same mean (16°C - 8.69g [95% HPD: 7.68g– 9.77g] vs 11.84g [95% HPD 10.71g – 13.15g], respectively). The lowest temperature imposed a smaller, but still significant reduction (22% reduction, 95% HPD: 4-39%) compared to that at 16°C. The disparity in gonad production for the El Niño and La Niña was much smaller than when comparing constant temperature treatments of 20°C and 16°C despite having the same mean temperature differential. This reduced effect resulted in part from the aforementioned decline in gonad size in La Niña versus equivalent but constant mean. Model comparison showed >99% stacking weight for the temperature and treatment effects, and no support for differences among sexes in the gonad mass overall or interaction among treatment effects with sex.

Reproductive status

The El Niño treatment led to a significant reduction in gametogenesis for both males and females. Specifically, far fewer females in the El Niño treatment reached Stage IV compared to La Niña treatment for both males and females (Figure 5). Yet this effect was more extreme for females compared to males. Female urchins incubated in La Niña treatment actively produced mature gametes (89% [95% HPD: 77-94%] of females in stage IV, Figure 5 A). In contrast, only 15% [95% HPD: 4-28%] of El Niño females were in stage IV (Figure 5A), while most females were in stage I. This decline in reproductive status associated with El Niño amounted to an estimated 74% reduction for females compared to La Niña (Figure 5 A, HPD: 56-91% decline in females in stage IV). For male urchins, these results were consistent but less extreme. 92% of La Niña males were stage IV [HPD: 77 - 99%] vs 44% of El Niño females [HPD: 23 -67%]– a reduction of 48% [HPD: 23 – 72%] - Figure 5 C). Results were consistent across the four replicate mesocosms for each treatment (Figure 5 C).

Our results also indicate that temperature dynamics, and not just their mean values, can alter reproductive response depending on sex. Simulating a dynamic, historical El Niño trend resulted in a reduction in the proportion of males investing in spermatogenesis in contrast to no

shift under a constant mean temperature. Specifically, male animals subjected to the El Niño treatment (simulated seasonal peak and decrease from 21 to 18°C with a mean of 20°C) compared to a constant 20°C throughout showed substantially lower rates of full maturity (stage IV) with a reduction from 81.2 to 47.8% (a difference of 37% [95% HPD: 8% to 65%], Figure 5 C, D). In contrast, we observed similarly low rates of full maturity for females subjected to the El Niño simulation when compared to constant 20°C (15% for El Niño vs 25% for constant 20°C, Bayesian P = 0.28, (Figure 5A, B). These outcomes are supported by a sex by treatment interaction on top of the temperature by sex estimates (>99% stacking weight from loo cross validation for the full model compared to models without any of the treatment, sex, or interaction terms).

Discussion

Global warming and extreme heatwaves present a significant threat to ecosystems worldwide. It is well understood that range limits contract and abundances decline well before lethal limits for entire populations are reached. Yet mechanistically, explaining how and why such sub-lethal thermal regimes affect populations remains a challenge. In this study, we show how thermal suppression of reproduction can, in part, provide a plausible explanation for historical collapses in larval supply associated with warming events. These results provide two key general conclusions. First, sublethal impacts of warming events on reproduction may lead to recruitment failure and population declines before lethal upper thermal limits for individual life stages are experienced. This insight is derived from the results of our lab experiments in the context of our historical observations of larval supply. Second, dynamic temperature treatments that reflect real world trends in historically observed heatwaves, in comparison to constant temperatures, exert a more pronounced effect on reproductive development; thus, ignoring the dynamics of thermal regimes may underpredict the magnitude of thermal effects. Importantly, these results raise questions regarding physiological processes by which temperature shapes gametogenesis, and how such effects may vary in and among populations over time. These effects will almost certainly interact with other stressors such as food availability for adults sensu [29] or shifts in physical dispersal, gametogenesis, or heatwave conditions.

Heatwave events in both marine and terrestrial settings are often highly dynamic, characterized by rapid fluctuations in temperature. Thus, experiments that utilize constant temperatures ignoring such fluctuations may yield erroneous insights. Here, we show that male but not female stages of maturity differed between constant versus El Niño temperature profiles that shared the same mean value (20°C). This outcome also yields insight into a possible fitness benefit from suppressing gametogenesis during El Niño. Early-stage larval viability (within 48 hours) declines rapidly between 20 to 22°C (SK unpublished data for these subjects as well as for animals from San Diego). Thus, males in the El Niño treatment incubated briefly at 21°C at the onset of the experiment may delay production of mature sperm until temperatures have consistently dropped well below potential thresholds for larval mortality, even though mean temperatures for all treatments at the end of the experiment, and in nature, lie well below such values. Because male gametogenesis may be completed more quickly, these disparities may reflect a more rapid reaction time to decreases in temperature. Females exposed to a constant 18°C proceeded with vitellogenesis and produced mature gametes; those subjected to El Niño treatment that ended at 18°C did not. In contrast, overall gonad production (mass) differed between La Niña and constant temperatures but not for El Niño. These disparities in gonad production appear to result from nonlinear averaging (e.g., Jensen's inequality) associated with dynamics of feeding, metabolism, and/or structural growth allocation [30]. Importantly, our study ended in December, when temperatures approach winter lows (Figure 1). Even in El Niño years, winter temperatures are likely sufficient to facilitate reproduction over the long term (Figure 1). Thus, rather than inducing skip-spawning, thermal suppression of gametogenesis in fall and early winter may instead lead to a shortened spawning season. Because urchin settlement timing aligns with peak phytoplankton production [20], such effects may lead to other negative impacts on recruitment such as match-mismatch dynamics [31]. Moreover, our dynamic treatments are limited to a specific set of trajectories and our constant treatments do not include 21°C or above (the maximum temperature of the El Niño treatment); thus, future work may benefit from assessing how brief or consistent incursions into the 21°C range, and the timing of such incursions, affect male sperm production. Thus, while our study highlights a single process that can plausibly contribute to recruitment failure, it may be one of many interacting factors that shape temporal trends in larval supply. As a result, future studies may benefit from documenting gonad

204 production and stages of maturity over time to assess how and when gamete production proceeds
205 under different heatwave conditions both in the field and in controlled settings.

206 While our experiments were conducted using sea urchins from British Columbia (where
207 waters are cooler than in Southern California), the results are consistent with prior insights from
208 across California. Specifically, field observations in southern California indicated reproduction
209 (assessed via seasonal gamete extrusion [26] and histology[27]) may have been suppressed during
210 analogous high temperature periods, and Cochrane and Engelman[26] suggested that 17°C was the
211 approximate threshold above which gametogenesis may be suppressed. A prior experiment by
212 Pearse[28] in Monterey Bay, California showed that a constant 21°C suppressed male and female
213 gametogenesis compared to constant 14°C. We show that for females, this suppression appears
214 to occur above 18°C but at or below 20°C. Importantly, these results align with the thermal
215 limits of early-stage larvae for animals from both British Columbia and San Diego, California
216 (survival of larvae 48 hr. post fertilization, prior to feeding, declines from near 100% to near 0%
217 in the 20-22°C range - SK unpublished data). Overall, these data highlight a need for further
218 study focused on the processes that regulate suppressed or delayed reproduction. Specifically, do
219 such responses vary by population or geographic region? How do depth, signal amplitude, or
220 acclimatization affect these outcomes? Moreover, how reproductive phenology varies in space
221 and over time has yet to be examined across the range from Baja California to Alaska. Evidence
222 for such variation exists in response to other stressors for this species e.g., [32]. Thus, we argue our
223 experiments demonstrate a thermal sensitivity that represents a plausible explanation for
224 historical collapses in larval supply. Yet examining the genetic and plastic basis of how
225 reproduction may respond to changes in temperature regime remains an important and
226 unanswered question both in this species and more broadly.

227 These experiments present plausible evidence for how and why historical collapses in
228 larval supply occur during marine heatwaves. Yet there are likely a myriad of factors that occur
229 during marine heatwaves that may shape recruitment in addition to, or in synergy with
230 suppression of reproduction. First, food stress occurs during El Niño events in southern
231 California [33]. Such trends might exacerbate the effects of temperature on gamete production as
232 food limitation for adults may alter thermal energetic performance (e.g., via “metabolic
233 meltdown” [29]). In these experiments, we focused on well-fed adult animals to avoid confounding

effects of food availability. But the results shown here raise the question of whether declines in availability and productivity of macroalgae can exacerbate responses of gametogenesis. Second, El Niño events are thought to be coupled with shifts in ocean circulation that might alter patterns of phytoplankton production (i.e., larval food) as well as the delivery of planktonic larvae to suitable settlement sites. These trends may also affect reproduction as urchin spawning may be sensitive to changes in phytoplankton-derived chlorophyll [34,35]. Thus, even in the cases where offspring are produced from successful maturation and spawning, shifts in larval survival and delivery may further compound effects of heatwaves. Finally, we conducted these experiments with healthy animals with no evidence of disease, yet temperature [36] in tandem with density may increase disease prevalence and disease related mortality [37,38]. Therefore, our results focus on one key vital rate among many that may simultaneously respond to abiotic and biotic conditions during extreme events known to alter dynamics of populations.

Marine heatwaves have led to substantial reorganization of ecosystems. This trend has been particularly apparent in recent years in temperate rocky reefs [39-45] with resulting, negative effects on ecosystem services and biodiversity [46]. While extreme events can impose direct and observable effects on mortality, sub-lethal effects, when present, may be far more frequent and insidious because they occur below lethal thresholds and may have less immediately visible or observable impacts e.g., [19]. This study is among the first to show that widespread, historical collapses in larval supply in the field can partially and plausibly be explained by sub-lethal suppression of gametogenesis resulting from marine heatwaves. Moreover, our study demonstrates the value of long-term population studies and quantifying non-lethal physiological and reproductive sensitivities when considering thermal envelopes and the population-level impacts of global warming and heatwaves.

Methods

To quantify how different thermal regimes affect investment in gonads and development of gametes in male and female urchins, we conducted a large-scale 10-week experiment in which 300 animals were incubated in replicate 340L mesocosms that simulated dynamic El Niño (N = 4 mesocosms, 60 animals per treatment) or La Niña (N = 4 mesocosms, 60 animals) conditions based on historical, empirical benthic temperature time series from Scripps Pier in La Jolla,

California[47] (trends: Figure 1B, map: Figure 1C) that coincide with historical collapses in larval supply in Southern California. We paired these treatments with a range of fixed temperature incubations (10, 13, 16, 17, 18, 20 °C, N = 2 mesocosms, 30 animals per treatment), two of which matched the mean temperature of the El Niño (20 °C) and La Niña (16 °C) (Figure 1). We chose this benthic time series rather than satellite derived sea surface temperature information because the latter provides high quality spatial representations of sea surface temperature but not at depths where subtidal animals reside [48]. Experiments were conducted at the Marna Lab at the Hakai Institute's Quadra Island Ecological Observatory in Heriot Bay, British Columbia due to availability of sophisticated seawater systems for careful, replicated temperature manipulations.

Field Collections and Acclimation

We collected sea urchins by hand on SCUBA in the vicinity of Ucluelet, British Columbia, Canada (48.94˚N, 125.56˚ W) from a depth of 20-25 ft relative to mean tide in September 2021 and transported them to the Marna Lab. We transferred sea urchins to flow-through sea tables and allowed them to recover for a period of one week before inserting animals into the mesocosm system. We selected healthy individuals within a constrained size range for incubations (n = 300, mean test diameter = 56.09 mm, range test diameter = 42.12 – 69.46 mm). Finally, we assigned animals to mesocosms at random at ambient temperature and exposed each assigned mesocosm to a temperature ramp, where the ramp reached target temperatures after two weeks from the initial incoming, ambient temperature (mean across all tanks of 13.3˚C, SD = 0.3˚C) to avoid thermal shock. Once initial target temperatures were reached, they were maintained or, for the dynamic treatments, were manually adjusted daily in the AM (~8am each day) as needed by 0.5 °C increments in a scheduled manner to match historical mean El Niño and La Niña daily temperature conditions.

Mesocosm System

We placed urchins in a custom-built array of twenty replicated 340 L acrylic mesocosms supplied with flow-through UV sterilized and filtered seawater (Figure 3: , Integrated Aqua Systems, Inc., Vista, CA, USA). Each mesocosm was capable of independent control of temperature and animals were provided a lighting regime for all mesocosms using LED fixtures (Aquamaxx, CA, USA) programmed to provide 10L:14D with two-hour linear light intensity

292 transition periods for dawn and dusk (0-100% from 07:00 to 09:00 “dawn”, and 100-0% from
293 17:00 to 19:00 “dusk”). Each mesocosm independently maintained temperature treatments using
294 a heat exchanger fitted with a titanium coil regulated by a dual stage digital temperature
295 controller (Resolution = 0.1℃, Dwyer Instruments, LLC.©, Michigan City, IN, USA). The
296 mesocosm system employed central cooling (Aermec Mits Airconditioning Inc., Mississauga,
297 ON, Canada) and heating (boiler array, Viessmann Manufacturing Company Inc., Warwick, RI,
298 USA) to supply independent heat exchangers with on-demand cold and warm glycol loops for
299 down- and up-regulation of water temperature, respectively. We manually checked and re-
300 calibrated sensors, as needed, using digital traceable thermometers twice daily to control
301 potential temperature sensor drift. We randomly assigned mesocosms to the specified treatments.

302 *Animal husbandry*

303 We fed individuals uniform dry pellets combining several macroalgal species formulated
304 for the aquaculture of *S. purpuratus* (Urchinomics Canada Inc., Halifax, NS, Canada). Animals
305 in mesocosms were fed twice per week, and we removed uneaten food and refuse every 72 h.
306 Food rations were determined by trial and error in a prior pilot study to ensure all animals had
307 consistent access to food over time. To optimize access for all mesocosm inhabitants to abundant
308 food, we enclosed subjects and food in aquaculture baskets (two baskets per mesocosm, 7 or 8
309 animals per basket, Thunderbird Plastics) such that food was always readily accessible, and
310 movement was not impeded. Each animal was supplied approximately 2.7 grams of pelleted food
311 twice per week (either 19 or 21 grams per basket for the baskets with 7 and 8 individuals,
312 respectively in each mesocosm) for the duration of the experiment.

313 *Histological and gonad assays*

314 At the end of the experiment, we measured all individuals to test for changes in height
315 and diameter (using precision digital calipers) and wet mass (to the nearest 0.1 g). Animals were
316 then sacrificed to measure gonad and histological properties. After cracking urchin tests, we
317 rapidly removed gonads for sampling. We excised a second gonad from each animal, which was
318 weighed to the nearest 0.01g and categorized the remaining gonads visually for evidence of
319 gamete production (macroscopic egg extrusion or sperm extrusion). Using a clean, sterile scalpel
320 we excised an approximately 2mm cross section from one gonad which we immediately placed

in a histological cassette, preserved in Hartmann's fixative for 24 hours, and transferred to 70% EtOH. Preserved gonads were embedded in paraffin, sliced, stained using eosin and hematoxylin, and mounted. We assessed gonad samples for sex and developmental stage using four visual subsections and the entire sample collectively to ensure agreement among subsamples. Histological slides were scored on a scale of I to IV (sensu [49]), where representative stages are depicted in Figure 1.

Statistical Analyses

We estimated the probability of individuals in each reproductive stage as a function of mean temperature by sex and in response to El Niño and La Niña treatments using a Bayesian regression model with a multinomial likelihood. We modeled the response to mean temperature using a non-parametric Gaussian process smoother. To account for treatment effects, we included a categorical effect of treatment (constant, El Niño, La Niña). Gonad mass was modeled with a Gamma likelihood and log link with the log of test diameter included as a covariate to account for gonad-body size allometry. Because gonad mass was expected to exhibit a concave response to temperature, a 3rd order polynomial was used for mean temperature. For both analyses, intercepts were allowed to vary randomly by mesocosm.

We directly compared parameter posteriors within models and to ensure that comparing parameters within models was robust to model (structural) uncertainty, we conducted model comparison using approximate leave-one-out cross validation (loo) and generated weights using stacking [50-52]. These methods measure the predictive accuracy with a loo approximation and generate weights by generating weights of models that maximize the predictive accuracy of the potential models. The selected models represented >99% of posterior model weight and thus results presented are from these models. We sampled posteriors using brms in R [53,54]. We ran models with vague priors, and conducted sensitivity analyses to ensure varying prior distributions and hyperparameters did not qualitatively affect the results. We ran models for 2000 iterations for each of four chains after a 2000 iteration warmup period, and checked convergence visually and ensuring that that parameters had convergence diagnostics (Rhat) less than 1.001. Data and code from this study are available at https://www.bco-dmo.org/project/818918.

Author contributions:

DKO, NBS, BC, LRB and SS designed the research. DKO, NBS, BC, MJM, SK, KR, DS, IG, EC, MF, and NM conducted mesocosm experiments. RF conducted histological analyses. DKO conducted statistical analyses. DKO wrote the initial draft of the manuscript, and all authors contributed to revisions.

Acknowledgements:

This study was funded with generous support from the Hakai Institute, a program of the Tula Foundation, a grant from the US National Science Foundation to DKO and LRB (OCE nos. 2023649 and 2023664), as well as from the Santa Barbara Coastal (SCB) LTER (NSF OCE no.1831937). We thank Eric Peterson, Christina Munck, as well as the facilities staff at the Quadra Island Ecological Observatory for their generous support. We thank the Coastal Marine Science Inst. and Bodega Marine Lab at UC Davis as well as the California Dept. Fish and Wildlife LRB. Rachel Simons, Wiley Evans, and two anonymous reviewers provided useful feedback on prior versions of the paper.

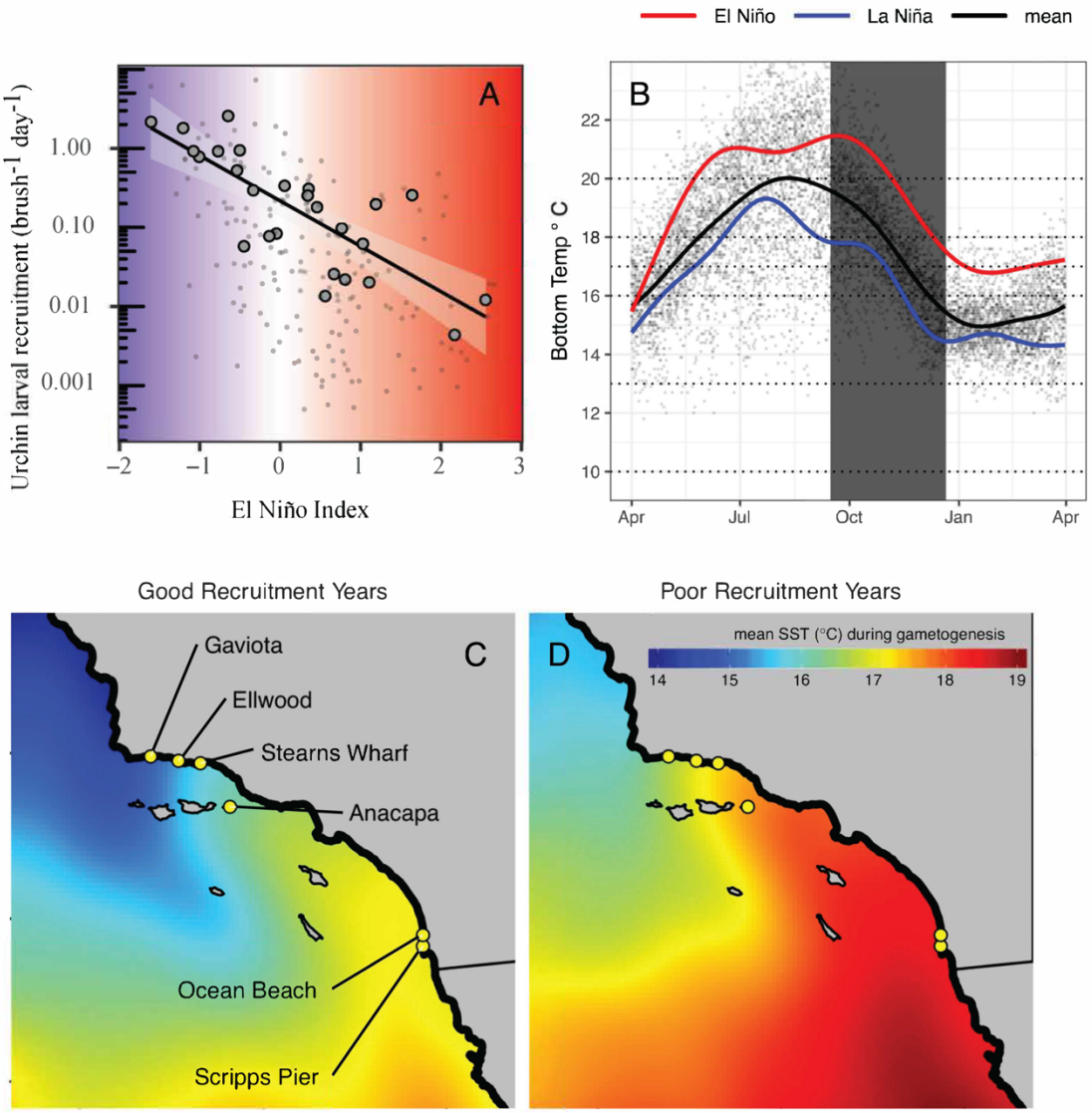

Figure 1: A) Historical mean annual (large points) and monthly mean (small points) larval settlement on standardized brush samplers across six sites in southern California vs Multivariate El Niño Index (MEI) since 1990 (reproduced from Okamoto et al.[20]). Colors correspond to the x-axis representing cooler (negative) and warmer (positive) temperatures associated with the MEI in Southern California. B) Historical benthic temperatures from Scripps Pier [47]. Small points: daily means. Black line: historical seasonal mean. Red and blue lines: historical El Niño & La Niña seasonal trends, respectively, from the data that were simulated in mesocosms (the period simulated in the experiment is indicated by the vertical grey bar). Horizontal dotted lines: constant mean temperatures simulated in replicate mesocosms. C & D) Mean satellite derived sea surface temperature from September through December in four strong (C - 1993, 1996, 1999, & 2010) and poor (D - 1994, 1997, 2004, & 2015) years for larval settlement from 1990 to 2016 [48]. Note that C & D are visualized to show comparative spatial trends, though satellite-derived temperature data may be biased relative to in situ benthic temperature data. Sites in C represent the six historical settlement collection locations that all show negative correlations with the MEI.

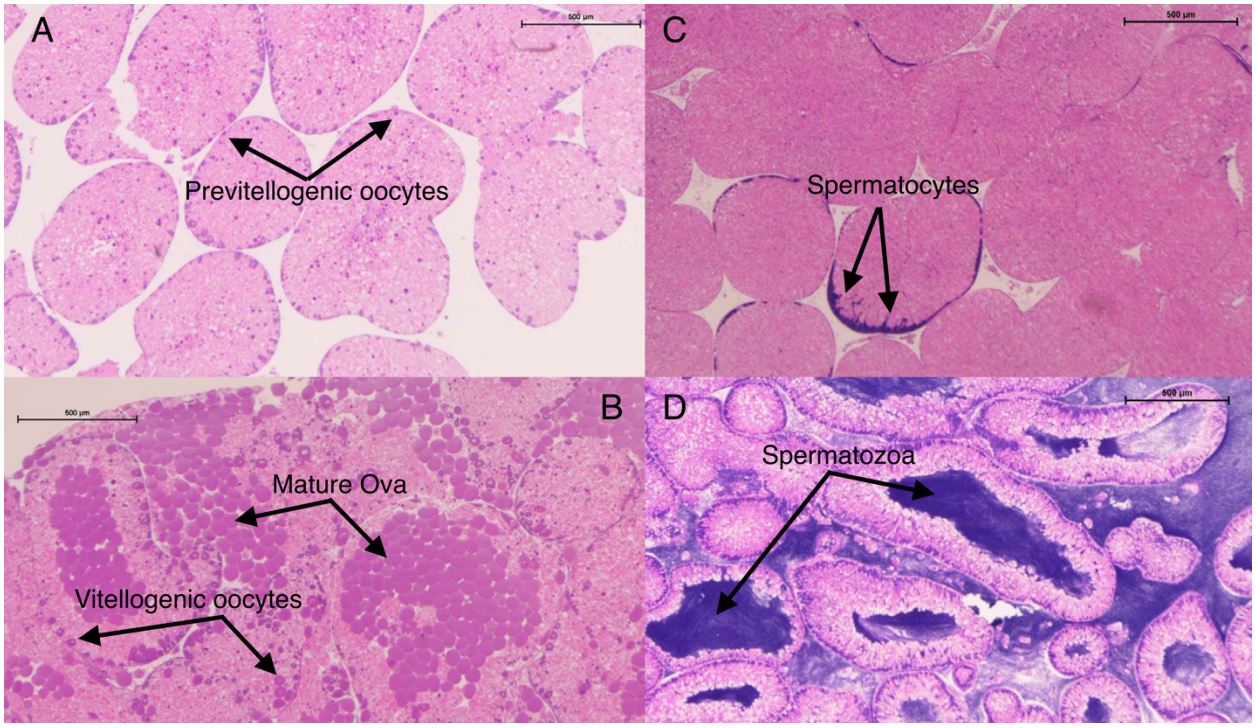

Figure 2: Gonad sections stained with hematoxylin and eosin with scale bar representing 500 µm. A-B Female ovaries in Stage I (A) and Stage IV (B) arrows indicate small previtellogenic oocytes, vitellogenic oocytes in the process of meiosis, and mature ova. C-D. Females in stage I are largely devoid of developing and vitellogenic oocytes with substantial reserves invested in nutritive phagocytes (light pink), Stage II has few developing oocytes, Stage III has some developing oocytes with few, scattered mature eggs, and Stage IV has many mature eggs (dark, solid circles) and some developing oocytes (dark circles with visible, central germinal vesicle). Male testes showing stage I (C) with few developing columns of spermatocytes, and stage IV (D) with large sections of the gonad converted to mature spermatozoa. Males in stage I have few visible developing spermatocytes (columns of dark purple around the margins), males in stage II have dense columns of spermatocytes, males in stage III have few small pockets of spermatozoa, and males in stage IV have large pockets of spermatozoa and rapidly disappearing somatic tissue (light pink).

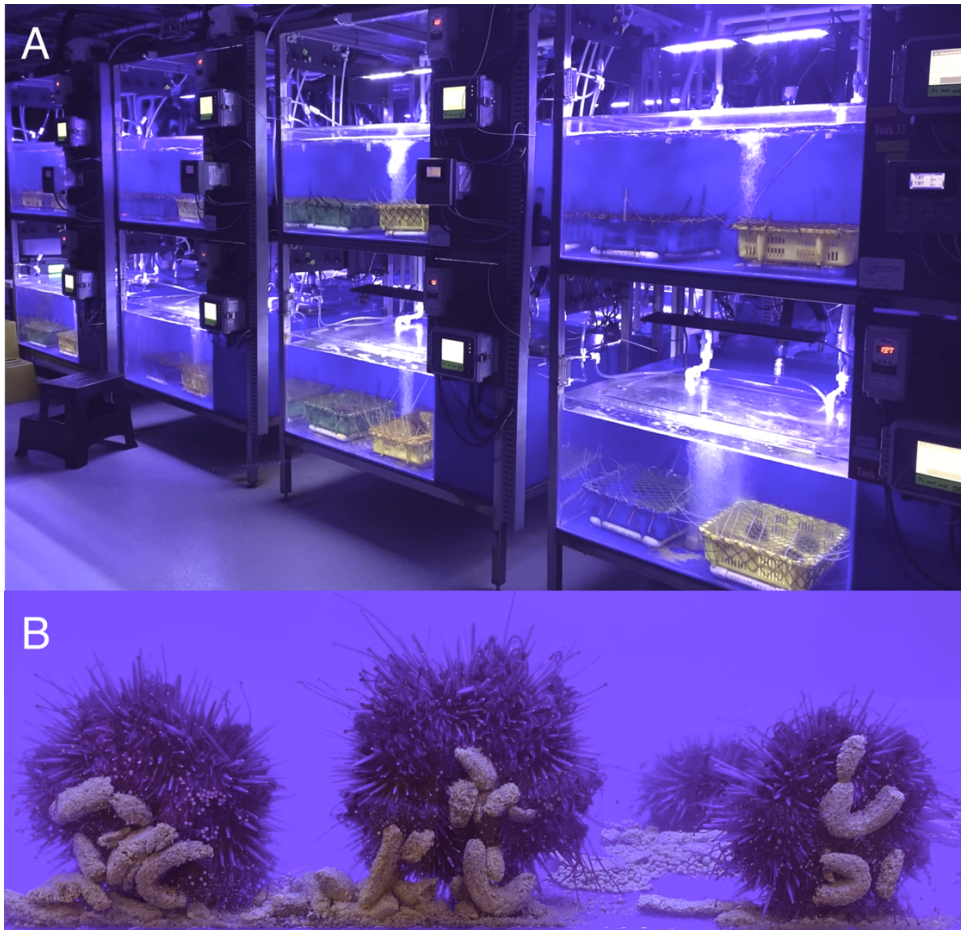

Figure 3: A) Mesocosms at the Hakai Institute's Quadra Island Ecological Observatory with trays holding experimental subjects. B) Experimental subjects consuming controlled, manufactured Urchinomics algal feed pellets.

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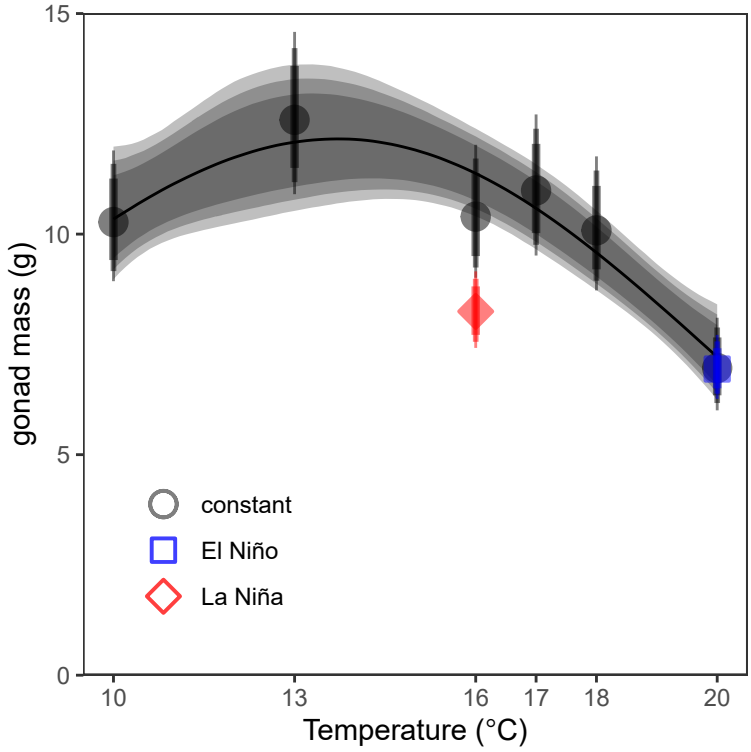

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402 Figure 4: Final gonad mass vs mean temperature. Black circles and the smooth trend represent
403 fixed temperature treatments; the red diamond and blue square represent La Niña and El Niño
404 thermal treatments, respectively. Error bars and bands represent the 80, 90, and 95% highest
405 probability density interval of the posterior.

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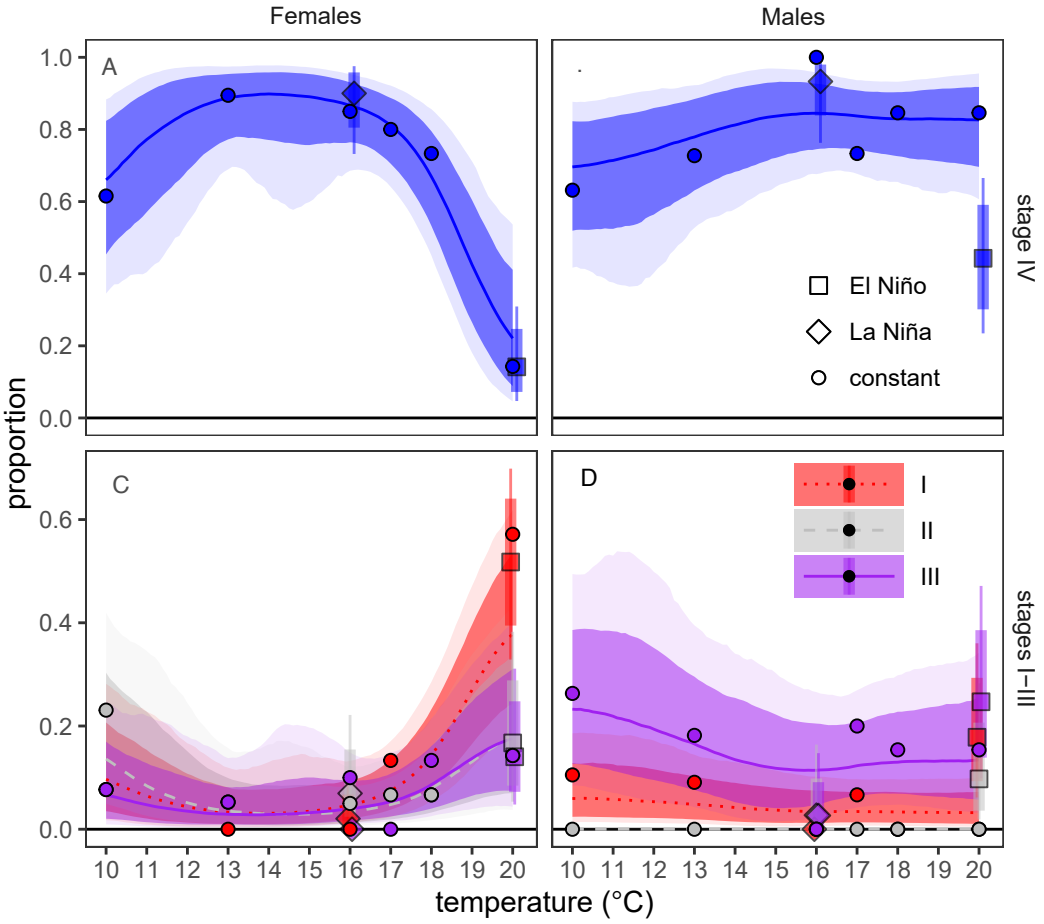

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408 Figure 5: Proportion of adult females (A, B) and males (C, D) in each reproductive stage by
409 treatment (El Niño (squares), La Niña (diamonds), or constant temperature (circles)) and mean
410 temperature. A) Proportion of females in stage IV. B) Proportion of females in stages I (dotted
411 red lines, red points), II (dashed grey lines, grey points, and III (solid purple lines, purple points).
412 C) Proportion of males in stage IV, and D) proportion of males in stages I, II, and III (same
413 symbology as females). Circles represent empirical means for constant temperature treatments,
414 while El Niño and La Niña points represent posterior mean estimates. Constant temperature
415 treatments had two replicate mesocosms per treatment and 15 animals per mesocosm. El Niño
416 and La Niña had four replicate mesocosms and 15 animals per mesocosm. Uncertainty
417 bands/intervals represent 95% (light/thin) and 90% (dark/thick) from the multinomial regression.

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References

1 Braschler, B., Chown, S. L. & Duffy, G. A. Sub-critical limits are viable alternatives to critical thermal limits. *J Therm Biol* **101**, 103106 (2021). https://doi.org:10.1016/j.jtherbio.2021.103106 PMID - 34879920

2 Kinzner, M. T. *et al.* Is temperature preference in the laboratory ecologically relevant for the field? The case of *Drosophila nigrosparsa*. *Global Ecol Conservation* **18**, e00638 (2019). https://doi.org:10.1016/j.gecco.2019.e00638

3 Rezende, E. L., Bozinovic, F., Szilágyi, A. & Santos, M. Predicting temperature mortality and selection in natural *Drosophila* populations. *Science* **369**, 1242-1245 (2020). https://doi.org:10.1126/science.aba9287 PMID - 32883867

4 Oliver, E. C. *et al.* Marine heatwaves off eastern Tasmania: Trends, interannual variability, and predictability. *Progress in oceanography* **161**, 116-130 (2018).

5 Munday, P. L., Jones, G. P., Pratchett, M. S. & Williams, A. J. Climate change and the future for coral reef fishes. *Fish and Fisheries* **9**, 261-285 (2008).

6 Terblanche, J. S., Deere, J. A., Clusella-Trullas, S., Janion, C. & Chown, S. L. Critical thermal limits depend on methodological context. *Proc Royal Soc B Biological Sci* **274**, 2935-2943 (2007).

7 Inouye, D. W. Climate change and phenology. *Wiley Interdiscip Rev Clim Change* **13** (2022). https://doi.org:10.1002/wcc.764

8 Amasino, R. Vernalization, Competence, and the Epigenetic Memory of Winter. *Plant Cell* **16**, 2553-2559 (2004). https://doi.org:10.1105/tpc.104.161070 PMID - 15466409

9 Kim, D.-H. Current understanding of flowering pathways in plants: focusing on the vernalization pathway in *Arabidopsis* and several vegetable crop plants. *Hortic Environ Biotechnology* **61**, 209-227 (2020). https://doi.org:10.1007/s13580-019-00218-5

10 Rogers-Bennett, L., Dondanville, R. F., Moore, J. D. & Vilchis, L. I. Response of Red Abalone Reproduction to Warm Water, Starvation, and Disease Stressors: Implications of Ocean Warming. *J Shellfish Res* **29**, 599-611 (2010). https://doi.org:10.2983/035.029.0308

11 Breckels, R. D. & Neff, B. D. The effects of elevated temperature on the sexual traits, immunology and survivorship of a tropical ectotherm. *J Exp Biol* **216**, 2658-2664 (2013). https://doi.org:10.1242/jeb.084962 PMID - 23531818

12 Paxton, C. W., Baria, M. V. B., Weis, V. M. & Harii, S. Effect of elevated temperature on fecundity and reproductive timing in the coral *Acropora digitifera*. *Zygote* **24**, 511-516 (2016). https://doi.org:10.1017/s0967199415000477 PMID - 26349407

13 Hurley, L. L., McDiarmid, C. S., Friesen, C. R., Griffith, S. C. & Rowe, M. Experimental heatwaves negatively impact sperm quality in the zebra finch. *Proc Royal Soc B Biological Sci* **285**, 20172547 (2018). https://doi.org:10.1098/rspb.2017.2547 PMID - 29343605

14 Parratt, S. R. *et al.* Temperatures that sterilize males better match global species distributions than lethal temperatures. *Nat Clim Change* **11**, 481-484 (2021). https://doi.org:10.1038/s41558-021-01047-0

15 Okamoto, D. K., Schmitt, R. J., Holbrook, S. J. & Reed, D. C. Fluctuations in food supply drive recruitment variation in a marine fish. *Proc Royal Soc B Biological Sci* **279**, 4542-4550 (2012). https://doi.org:10.1098/rspb.2012.1862 PMID - 23015631

16 Stoner, A. W. & Ray-Culp, M. Evidence for Allee effects in an over-harvested marine gastropod: density-dependent mating and egg production. *Mar Ecol Prog Ser* **202**, 297-302 (2000). https://doi.org:10.3354/meps202297

17 Gaines, S. D. & Bertness, M. D. Dispersal of juveniles and variable recruitment in sessile marine species. *Nature* **360**, 579-580 (1992). https://doi.org:10.1038/360579a0

18 Kelly, M. S. Environmental parameters controlling gametogenesis in the echinoid *Psammechinus miliaris*. *Journal of Experimental Marine Biology and Ecology* **266**, 67-80 (2001).

19 Rogers-Bennett, L., Klamt, R. & Catton, C. A. Survivors of climate driven abalone mass mortality exhibit declines in health and reproduction following kelp forest collapse. *Frontiers in Marine Science* **8**, 725134 (2021).

20 Okamoto, D. K., Schroeter, S. C. & Reed, D. C. Effects of ocean climate on spatiotemporal variation in sea urchin settlement and recruitment. *Limnol Oceanogr* **65**, 2076-2091 (2020). https://doi.org:10.1002/lno.11440

21 Ebert, T. A., Schroeter, S. C., Dixon, J. D. & Kalvass, P. Settlement patterns of red and purple sea urchins (*Strongylocentrotus franciscanus* and *S. purpuratus*) in California, USA. *Mar Ecol Prog Ser*, 41-52 (1994).

22 Farmanfarmaian, A. & Giese, A. C. Thermal tolerance and acclimation in the western purple sea urchin, Strongylocentrotus purpuratus. *Physiological Zoology* **36**, 237-243 (1963).

23 Azad, A. K., Pearce, C. M. & McKinley, R. S. Influence of stocking density and temperature on early development and survival of the purple sea urchin, *Strongylocentrotus purpuratus* (S timpson, 1857). *Aquaculture Research* **43**, 1577-1591 (2012).

24 Azad, A. K., Pearce, C. M. & McKinley, R. S. Influence of microalgal species and dietary rations on larval development and survival of the purple sea urchin, *Strongylocentrotus purpuratus* (Stimpson, 1857). *Aquaculture* **322**, 210-217 (2011).

25 Strathmann, M. F. *Reproduction and development of marine invertebrates of the northern Pacific coast: data and methods for the study of eggs, embryos, and larvae*. (University of Washington Press, 2017).

26 Cochran, R. C. & Engelmann, F. Characterization of spawn-inducing factors in the sea urchin, *Strongylocentrotus purpuratus*. *Gen Comp Endocr* **30**, 189-197 (1976). https://doi.org:10.1016/0016-6480(76)90099-x PMID - 992340

27 Basch, L. V. & Tegner, M. J. Reproductive responses of purple sea urchin (*Strongylocentrotus purpuratus*) populations to environmental conditions across a coastal depth gradient. *Bulletin of Marine Science* **81**, 255-282 (2007).

28 Pearse, J. S. in *Advances in invertebrate reproduction* (ed S. Adams W. H. Clark Jr) (1981).

29 Huey, R. B. & Kingsolver, J. G. Climate warming, resource availability, and the metabolic meltdown of ectotherms. *The American Naturalist* **194**, E140-E150 (2019).

30 Spindel, N. B. *Impacts of abiotic and biotic stressors on the energetics and nutritional composition of temperate sea urchins* PhD thesis, Florida State University, ("In Prep").

31 Cushing, D. in *Advances in marine biology* Vol. 26 249-293 (Elsevier, 1990).

32 Kapsenberg, L., Okamoto, D. K., Dutton, J. M. & Hofmann, G. E. Sensitivity of sea urchin fertilization to pH varies across a natural pH mosaic. *Ecology and Evolution* **7**, 1737-1750 (2017).

33 Tegner, M. & Dayton, P. Sea urchins, El Niños, and the long term stability of Southern California kelp forest communities. *Marine ecology progress series. Oldendorf* **77**, 49-63 (1991).

34 Seward, L. C. The relationship between green sea urchin spawning, spring phytoplankton blooms, and the winter-spring hydrography at selected sites in Maine. (2002).

35 Zhadan, P. M., Vaschenko, M. A. & Almyashova, T. N. Spawning failure in the sea urchin Strongylocentrotus intermedius in the northwestern Sea of Japan: Potential environmental causes. *Journal of Experimental Marine Biology and Ecology* **465**, 11-23 (2015).

36 Lester, S. E., Tobin, E. D. & Behrens, M. D. Disease dynamics and the potential role of thermal stress in the sea urchin, *Strongylocentrotus purpuratus*. *Canadian Journal of Fisheries and Aquatic Sciences* **64**, 314-323 (2007).

37 Behrens, M. D. & Lafferty, K. D. Effects of marine reserves and urchin disease on southern Californian rocky reef communities. *Mar Ecol Prog Ser* **279**, 129-139 (2004).

38 Lafferty, K. D. Fishing for lobsters indirectly increases epidemics in sea urchins. *Ecological Applications* **14**, 1566-1573 (2004).

39 Arafeh-Dalmau, N. *et al.* Extreme marine heatwaves alter kelp forest community near its equatorward distribution limit. *Frontiers in Marine Science* **6**, 499 (2019).

40 Filbee-Dexter, K. *et al.* Marine heatwaves and the collapse of marginal North Atlantic kelp forests. *Scientific Reports* **10**, 13388 (2020).

41 McPherson, M. L. *et al.* Large-scale shift in the structure of a kelp forest ecosystem co-occurs with an epizootic and marine heatwave. *Communications biology* **4**, 298 (2021).

42 Michaud, K. M., Reed, D. C. & Miller, R. J. The Blob marine heatwave transforms California kelp forest ecosystems. *Communications Biology* **5**, 1143 (2022).

43 Smale, D. A. Impacts of ocean warming on kelp forest ecosystems. *New Phytologist* **225**, 1447-1454 (2020).

44 Thomsen, M. S. *et al.* Local extinction of bull kelp (*Durvillaea* spp.) due to a marine heatwave. *Frontiers in Marine Science* **6**, 84 (2019).

45 Wernberg, T. in *Ecosystem collapse and climate change* 325-343 (Springer, 2021).

46 Smith, K. E. *et al.* Socioeconomic impacts of marine heatwaves: Global issues and opportunities. *Science* **374**, eabj3593 (2021).

47 Carter, M. L. *et al.* (UC San Diego Library Digital Collections, 2022).

48 Reynolds, R. W. *et al.* Daily High-Resolution-Blended Analyses for Sea Surface Temperature. *J Climate* **20**, 5473-5496 (2007). https://doi.org:10.1175/2007jcli1824.1

49 Byrne, M. Annual reproductive cycles of the commercial sea urchin *Paracentrotus lividus* from an exposed intertidal and a sheltered subtidal habitat on the west coast of Ireland. *Marine Biology* **104**, 275-289 (1990).

50 Vehtari, A., Gelman, A. & Gabry, J. Practical Bayesian model evaluation using leave-one-out cross-validation and WAIC. *Statistics and computing* **27**, 1413-1432 (2017).

51 Yao, Y., Vehtari, A., Simpson, D. & Gelman, A. Using stacking to average Bayesian predictive distributions (with discussion). (2018).

52 Vehtari A *et al.* loo: Efficient leave-one-out cross-validation and WAIC for Bayesian models v. R package version 2.6.0. (2023).

53 Bürkner, P.-C. brms: An R package for Bayesian multilevel models using Stan. *Journal of statistical software* **80**, 1-28 (2017).

54 R Core Team. R: A Language and Environment for Statistical Computing (R Foundation for Statistical Computing, Vienna, Austria., 2023).