Title: Thermal suppression of gametogenesis can explain 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, sublethal temperatures can also depress vital rates and shape fluctuations in the reproductive viability of populations. For example, heatwaves may suppress reproduction, leading to recruitment failure before lethal temperatures are reached. Despite a growing awareness of this issue, tying sublethal effects to observed recruitment failure remains a challenge especially in marine environments. We experimentally show that sublethal suppression of female gametogenesis by marine heatwaves can partially explain historical collapses in urchin recruitment. This response differed by sex but was similar between animals from warmer or cooler regions of their range. Overall, we show sublethal thermal sensitivities of reproduction can narrow the thermal envelope for population viability compared to predictions from lethal limits.

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 as climate change impacts intensify. 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 solely on CTLs for individual life stages (gametes, juveniles, adults, etc. [6]). Combining inference from a mixture of laboratory studies, historical patterns, and analysis of reproductive rates can provide a more comprehensive understanding of the impacts that climate events such as heatwaves have on recruitment and population dynamics.

Sublethal challenges of climate change and warming are impacting recruitment and subsequent population viability[7]. One pathway by which sublethal temperatures can alter population viability is by affecting gametogenesis, sexual maturation, and/or sterility. Changes in temperature can directly affect reproductive phenology for a diversity of plants and animals[8] which can significantly impact reproductive success, 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., [9,10]). Likewise, a diversity of animal taxa can exhibit infertility or low fecundity at sublethal temperatures [11-15].

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 sublethal

64 thermal suppression of reproduction. This knowledge gap remains for several reasons. First,
65 attributing causality to observed changes in year-class strength remains a challenge for animals
66 with highly dispersive reproductive propagules. Shifts in recruitment may be explained by
67 variation in food supply [16], trends in reproductive and mating success [17], shifts in dispersal [18], or
68 a host of other factors that may also be directly or indirectly related to warming. Second, thermal
69 limits are often estimated using constant temperatures; yet in the oceans, temperature is variable,
70 and the dynamics of this variation can shape patterns of reproduction. Thus, while it is well
71 known that sublethal thermal stress can limit reproduction in marine invertebrates [19,20], it remains
72 less well understood if heatwaves can induce such limitations and/or plausibly help explain
73 collapses in recruitment. If climate change and extreme events in nature lead to suppressed
74 gametogenesis well before lethal limits of organisms are reached (e.g., thermal stress that
75 decreases larval, juvenile, or adult survival), then declines in population viability and
76 contractions in distributions may occur and at less extreme temperatures than established under
77 critical thermal limits.

78 For populations of purple sea urchins (*Strongylocentrotus purpuratus* – a key herbivore)
79 in Southern California, recruitment tends to collapse during warm El Niño events [21] (Figure 1A).
80 This phenomenon is remarkably consistent over time (extending back at least six decades), even
81 though temperatures during the reproductive season in Southern California (late fall and early
82 winter [21,22] Figure 1B) are almost always below those considered to be lethal for adults (~25 °C
83 [23], < 0.01% of daily observations since 1990 above this value). Moreover, winter temperatures in
84 the Southern California Bight when larvae are present (~ 11-16°C) are generally well below the
85 thresholds thought to impede multiple phases of larval survival [24] (fertilization and early-phase
86 survival of San Diego, Santa Barbara, and British Columbia animals declines to near zero
87 between 20-22°C - SK, unpublished data). Specifically, purple urchins tend to spawn in the
88 winter and spring, coinciding with favorable conditions (low temperatures and high food
89 availability) for larvae [21]. Larvae persist in the plankton from approximately 28 days to several
90 months depending on food availability and temperature [25,26]. Adult urchins build gonads over the
91 course of the summer and fall with gametogenesis occurring in the fall and early winter. El Niño
92 conditions in Southern California are characterized by warmer water temperatures in summer,
93 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 [27,28]. Specifically, Pearse [28] demonstrated that high temperatures decrease gamete production at sublethal levels (i.e., at 21°C vs 14°C), but the higher temperature exceeded those experienced in the spawning season. Moreover, animals used by Pearse were sourced from cooler regions of the range that rarely experience such temperatures, while animals from southern regions are frequently exposed to temperatures that exceed 21°C.

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 sublethal thermal suppression of reproduction. Specifically, we used two laboratory experiments to ask whether marine heatwaves (prolonged periods of anomalously high temperatures[29] in this case that correspond with well-defined El Niño is events) that have led to collapses in larval supply also affect reproduction in terms of both gonad production and gametogenesis. For the first experiment we compared effects of simulated heatwaves to simulated historical cool trends, as well as responses under a gradient of constant temperatures. For the second experiment we exposed animals from warm and cool regions to the same treatments in a common garden setting to test whether source population (whether via local adaptation or acclimatization) affected patterns of gametogenesis.

Results

Simulated El Niño and warmer conditions in the first experiment led to decreased gonad production as well as suppressed gametogenesis in *S. purpuratus.* 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 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 gametogenesis 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 difference in gametogenesis between La Niña and constant temperatures for males or females. For females,

constant high temperature (20°C) and the El Niño treatment (21-18°C with a mean of 20°C) led to a substantial reduction in oogenesis. For males, only the El Niño treatment affected spermatogenesis, with no change observed across constant temperatures from 10 to 20°C. For the second experiment, we found no differences in gametogenesis among source populations in response to treatments, with qualitatively similar treatment effects as in the first experiment for both males and females. Below, we describe the specific results of each experiment in detail.

Experiment 1: Effects of El Niño, La Niña, and a thermal gradient on gonad production and gametogenesis

Gonad production

In the first experiment, exposure to the highest temperatures (for both variable and constant treatments with mean of 20°C) negatively affected both male and female gonad production (cumulative gonad mass, Figure 4). Specifically, we observed a 42% decrease (95% highest probability density interval [HPD]: 28-55%) in gonad production at 20°C compared to a constant temperature of 13°C (where peak gonad production was observed). Gonad production did not differ for the El Niño (7.03g [95% HPD: 6.20g to 7.96g]) and constant treatment that shared the same mean value of 20°C (7.2g, [95% HPD: 5.97g to 8.50g]). In contrast, the La Niña treatment (declining from 18 to 14°C with mean of 16°C) showed a reduction in gonad mass (26% - HPD: 15 to 38%) compared with a constant value of 16°C (8.69g [95% HPD: 7.68g to 9.77g] vs 11.84g [95% HPD 10.71g to 13.15g], respectively). The lowest temperature (10°C) imposed a smaller, but still significant reduction in gonad mass (22% reduction, 95% HPD: 4-39%) compared to the peak at 13°C. The reduction in gonad production from the La Niña to El Niño (with means of 16°C and 20°C, respectively) was smaller than when comparing constant temperature treatments of 16°C to 20°C (17% [HPD: 3.5 to 32%] vs 38% [HPD: 23 to 39%] respectively) despite having the same mean temperatures. This reduced effect resulted from the aforementioned decline in gonad size in La Niña versus equivalent but constant mean of 16°C. Notably, we saw no difference in gonad production by sex. The final model used for analysis (temperature treatment but no sex or sex x treatment interaction) is supported by Bayes Factors >100 for temperature treatment relative to both the null and to models with sex and interactions. Bayes Factors > 100 are considered decisive evidence of one model over a second, values 10-100 are considered strong evidence [30], while values <1 favor the second model.

Gametogenesis

The El Niño treatment led to a significant reduction in gametogenesis for both males and females, and this effect was more extreme for females compared to males. We scored gametogenesis using a standard staging scale of I to IV where IV is fully mature and I is immature (sensu [31]). Specifically, far fewer individuals in the El Niño treatment reached Stage IV (most mature) compared to the 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 the La Niña treatment actively produced mature gametes (89% [95% HPD: 77 to 94%] of females in stage IV, Figure 5A). In contrast, only 15% [95% HPD: 4 to. 28%] of El Niño females were in stage IV (Figure 5A), while most females were in stage I. This decline in gametogenesis associated with El Niño amounted to an estimated 74% reduction for females compared to La Niña (Figure 5A, HPD: 56 to 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 to 99%] vs 44% of El Niño females [HPD: 23 to 67%]– a reduction of 48% [HPD: 23 to 72%] - Figure 5B). Overall, models that included the treatment, sex, and interaction compared to the models with only sex were supported Bayes Factors >100.

Our results from the first experiment also indicate that temperature dynamics, and not just their mean values, can alter reproductive response depending on sex. Simulating a historical El Niño trend resulted in a reduction in the proportion of males investing in spermatogenesis in contrast to no change in spermatogenesis 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 gonad maturation (stage IV) with a reduction from 81.2 to 47.8% (a difference of 37% [95% HPD: 8% to 65%], Figure 5C, D). In contrast, we observed similarly low rates of full maturity for females subjected to the El Niño simulation and constant 20°C treatment (15% for El Niño vs 25% for constant 20°C, Bayesian P = 0.28, (Figure 5A, B).

Experiment 2: Effects of source population on effects of El Niño on gametogenesis

When comparing populations, we found a similar strong effect of temperature treatment on gametogenesis but did not find a significant difference among populations in these responses

182 (Figure 6). Specifically, we did not find differences in gametogenesis in response to 20°C or El
183 Niño conditions (relative to 10°C) among animals sourced from different populations, including
184 those from warm regions (San Diego County and Santa Barbara County) or a cold upwelling
185 region (Sonoma County). Comparing models using Bayes Factors found no support for the
186 hypothesis that treatment effects varied by source population (Bayes Factor = 19 favoring the
187 reduced model [treatment, sex, and interaction] compared to the full model [with location,
188 treatment, sex and interactions]). The lack of location of origin effect is reinforced by analysis of
189 the full model, where we found no difference among locations in estimated treatment effects for
190 any stage (i.e., 95% credible intervals overlap zero for differences among populations in the log-
191 scale treatment effects for either 20°C or El Niño relative to 10°C by sex); however, we did find
192 consistent effects of each treatment across locations (>95% posterior probability of a difference
193 in proportion of stage IV animals for both 20°C and El Niño relative to 10°C for females and El
194 Niño relative to 10°C only for males). Thus, hereafter we describe analysis using the model
195 without location interactions. Overall, we estimate a combined 75% and 90% reduction in stage
196 IV females and males (respectively) for the El Niño treatment relative to the 10°C treatment
197 (95% HPD = 92% to 61% reduction for females and 99% to 65% reduction for males) and an
198 81% and 96% reduction in stage for IV females and males for the 20°C treatment relative to the
199 10 degree treatment (95% HPD = 96% to 68% reduction for females and 99 to 72% reduction for
200 males). The pooled results are shown as the thick lines/points in Figure 6 D and H for females
201 and males, respectively. While results from the first experiment were conducted with animals
202 sourced from cooler water, gametogenesis trends are similar when comparing animals from
203 warmer versus cooler environments.

204 **Discussion**

205 Global warming and extreme heatwaves present a significant threat to ecosystems
206 worldwide. Characterizing temperature thresholds that cause mortality across life stages can
207 provide essential insight into the impacts of heatwaves. It is well understood that range limits can
208 contract and abundances can collapse well before organismal lethal limits are reached.
209 Mechanistically explaining how and why such sublethal thermal regimes affect populations
210 remains a challenge. In this study, we show how thermal suppression of reproduction can, in

211 part, provide a plausible explanation for historical collapses in larval supply associated with
212 warming events. Our results provide two key general conclusions. First, sublethal impacts of
213 warming events on reproduction may lead to recruitment failure and population declines before
214 lethal upper thermal limits are experienced. This insight is derived from the results of our lab
215 experiments in the context of our historical observations of larval supply. We found these results
216 to be consistent for animals sourced from both warmer and cooler parts of their range. Second,
217 variable temperature treatments that reflect historical observations of heatwaves, in comparison
218 to constant temperatures, exert a more pronounced effect on reproductive suppression. Therefore,
219 ignoring the dynamics of thermal regimes may underpredict the magnitude of sublethal thermal
220 effects. Importantly, these results raise questions regarding physiological processes by which
221 temperature shapes gametogenesis, and how such effects may vary in and among populations
222 over time. These effects will almost certainly interact with other stressors such as food
223 availability for adults (sensu [32]) or shifts in physical dispersal, gametogenesis, or heatwave
224 conditions.

225 Organismal thermal lethal limits can underpredict observed shifts in population-level
226 vital rates. Our experimental results provide plausible evidence that sublethal reproductive
227 failure contributes to collapses in year-class strength. These insights hinge upon a combination of
228 long-term monitoring, historical observational data collection, and incremental prior
229 experimentation. Specifically, our historical data collection in Southern California shows larval
230 supply of purple urchins consistently collapses during marine heatwaves[21]. Prior field
231 observations proposed that temperatures above a 17°C threshold led to suppressed reproduction
232 during a marine heatwave (assessed observationally via seasonal gamete extrusion [33] and
233 histology [27,33]). Additionally, the prior experiment by Pearse [28] in Monterey Bay, California
234 showed that urchins exposed to constant 21°C suppressed male and female gametogenesis
235 compared to constant 14°C. However, 21°C is outside the range of temperatures generally
236 experienced during the spawning season, even during marine heatwaves in Southern California
237 (Figure 1A, Figure 7A,B). Our results suggest a higher limit than 17°C but still support the
238 notion that El Niño can suppress gametogenesis. Specifically, replicating historical marine
239 heatwaves (shifting from 21°C and ending at 18°C with a mean of 20°C) can suppress
240 gametogenesis for both males and females sourced from across a wide latitudinal range. For

241 females, this suppression appears to occur above 18°C but at or below 20°C. Females exposed to
242 a constant 18°C in the first experiment proceeded with vitellogenesis and produced mature
243 gametes, whereas females generally did not when under the El Niño treatment (ending at 18°C)
244 or the constant 20°C treatment. Males exposed to a constant 20°C proceeded with
245 spermatogenesis and produced mature gametes but not those in the El Niño treatments. In
246 contrast to gametogenesis, overall treatment effects on gonad production (mass – a metric of
247 potential fecundity) did not differ by sex. These disparities in gametogenesis patterns among
248 sexes raise several hypotheses that require further investigation. For example, sperm and eggs
249 may differ in their thermal constraints, time required to complete gametogenesis, and/or costs
250 associated with production and maturation. Despite the aforementioned differences, El Niño
251 treatments that ended at 18°C yielded consistent results for gametogenesis among males and
252 females. This final temperature is several degrees lower than what is considered to be lethal for
253 adults and larvae (23-25°C and 20-22°C, respectively). As a result, inferences derived solely
254 from larval or adult survival under laboratory conditions would not predict collapses in year-
255 class strength in association with marine heatwaves.

256 Heatwave events in both marine and terrestrial settings are often highly dynamic,
257 characterized by rapid fluctuations in temperature. We've shown how experiments that test
258 constant temperatures and ignore such fluctuations may yield erroneous conclusions. When
259 comparing variable versus constant temperature treatments, gonad production (and by extension
260 potential male and female fecundity) differed between La Niña and constant temperatures of the
261 same mean. These disparities in gonad production likely result from nonlinear averaging (e.g.,
262 Jensen's inequality) associated with dynamics of feeding, metabolism, and/or structural growth
263 allocation [34,35]. With regards to gametogenesis, male but not female patterns of gametogenesis
264 consistently differed between constant versus El Niño temperature profiles that shared the same
265 mean value (20°C). Thus, the variability, specific time course, and extremes of environmental
266 exposure have the potential to alter reproductive responses to heatwaves and can differ by sex.
267 Importantly, our studies ended in December, when temperatures approach winter lows (Figure 1,
268 Figure 7). Even in El Niño years, winter temperatures are likely sufficient to facilitate
269 reproduction over the long term (Figure 1). Thus, rather than inducing skip-spawning, thermal
270 suppression of gametogenesis in fall and early winter may instead lead to a shortened spawning

271 season. Because urchin settlement timing aligns with peak phytoplankton production[21], such
272 effects may lead to other negative impacts on recruitment such as match-mismatch dynamics
273 with poor survival [36]. Moreover, our variable treatments are limited to a specific set of
274 trajectories and our constant treatments do not include 21°C or above (the maximum temperature
275 of the El Niño treatment); thus, future work may benefit from assessing how brief or consistent
276 incursions into the 21°C range, and the timing of such incursions, affect both male
277 spermatogenesis and female oogenesis. As a result, future studies may benefit from documenting
278 gonad production and gametogenesis under different real-world and forecasted conditions in
279 both controlled settings and among populations across time and space.

280 Many species exhibit spatial and/or population level variation in response to temperature.
281 Purple urchins, for example, can display significant differences in environmental sensitivities
282 among populations (e.g., [37]). Our results suggest that, at least for the populations sampled and
283 treatments applied, impacts of marine heatwaves are consistent between sea urchins sourced
284 from cool and warm regions of the range. These results reflect only these specific contrasts and
285 populations, and thus cannot rule out variation to different contrasts or variation in the response
286 in other populations. Yet with animals ranging from British Columbia to Southern California, we
287 show that marine heatwave effects on sea urchin gametogenesis are likely significant in those
288 regions exposed to warm waters. However, we acknowledge that linking these results to
289 outcomes in the field definitively, rather than logically, requires documenting the spatial and
290 temporal patterns of reproductive phenology and gametogenesis in nature and any association
291 with larval supply. Moreover, the physiological and regulatory processes shaping these patterns
292 have yet to be systematically characterized. Thus, examining the genetic and plastic basis of how
293 reproduction and gametogenic cycles may respond to changes in temperature regimes remains an
294 important objective both in this species and more broadly.

295 These experiments present plausible evidence for how and why historical collapses in
296 larval supply occur during marine heatwaves. Yet there are likely myriad factors that occur
297 during marine heatwaves that may shape recruitment in addition to, or in synergy with
298 suppression of reproduction. First, food stress occurs during El Niño events in Southern
299 California [38]. Such trends might exacerbate the effects of temperature on gamete production as
300 food limitation for adults may alter thermal energetic performance or allocation (e.g., via

301 “metabolic meltdown” [32]). In these experiments, we focused on well-fed adult animals to avoid
302 confounding effects of food availability. The results shown here raise the question of whether
303 declines in availability and productivity of macroalgae can exacerbate responses of
304 gametogenesis in sea urchins. Second, El Niño events are thought to be coupled with shifts in
305 ocean circulation that might alter patterns of phytoplankton production (i.e., larval food) as well
306 as the delivery of planktonic larvae to suitable settlement sites. These trends may also affect
307 reproduction as urchin spawning may be sensitive to changes in phytoplankton-derived
308 chlorophyll [39,40]. Thus, even in the cases where offspring are produced from successful
309 maturation and spawning, shifts in larval survival and delivery may further compound effects of
310 heatwaves. Finally, temperature [41] and animal density may increase disease prevalence and
311 disease related mortality [42,43] in nature in addition to the reproductive effects observed here.
312 Therefore, our results focus on one set of key factors among many that may simultaneously
313 respond to abiotic and biotic conditions during extreme events known to alter dynamics of
314 populations.

315 Marine heatwaves have led to substantial reorganization of ecosystems. This trend has
316 been particularly apparent in recent years in temperate rocky reefs [44-50] with resulting, negative
317 effects on ecosystem services and biodiversity [51]. While extreme events can impose direct and
318 observable effects on mortality, sublethal effects, when present, may be far more frequent and
319 insidious because they occur below lethal thresholds and may have less immediately visible or
320 observable impacts. This suggests that survivors of marine heatwaves may be impaired and
321 reproductively dysfunctional despite being alive [19]. This study is among the first to show that
322 widespread, historical collapses in sea urchin larval supply in the field can at least partially be
323 explained by sublethal suppression of gametogenesis resulting from marine heatwaves.
324 Moreover, our study demonstrates the value of long-term population studies and quantifying
325 non-lethal physiological and reproductive sensitivities when considering sublethal thermal
326 envelopes or thermal fertility limits [52] and the population-level impacts of global warming and
327 heatwaves.

Methods

To quantify how different thermal regimes affect investment in gonads and development of gametes in male and female urchins, we first conducted a 10-week experiment in which 300 animals were incubated in replicate 350L mesocosms that simulated 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 [53,54](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 ºC, N = 2 mesocosms, 30 animals per treatment), two of which matched the mean temperature of the El Niño (20 ºC) and La Niña (16 ºC) (Figure 1). We chose this benthic time series rather than satellite-derived sea surface temperature information because sea surface temperatures can be markedly different than temperatures experienced at depth by benthic organisms[55]. 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 precisely controlled and replicated temperature manipulations. However, animals in this first experiment were sourced from populations found in Ucluelet, British Columbia that rarely if ever experience the high temperatures commonly observed in southern California. Thus, we also conducted a second experiment in which animals were sourced from warm and cool populations and compared responses of urchins to different thermal treatments.

To quantify the degree to which animal source location affected results, we conducted a second 12-week experiment comparing animals from the warmer Southern California bight including San Diego and Santa Barbara with the cool upwelling region of Sonoma County. Seasonal daily temperature data from 2009 (the earliest record at Bodega Marine Lab) for all sites are shown in Figure 7. Seasonal averages from September into December since 2009 are 19ºC, 16.8 ºC, and 13.5 ºC from Scripps Pier (San Diego), Arroyo Burro (Santa Barbara), and Bodega Marine Lab (Sonoma), respectively. The percent of daily observations above 19ºC at these sites since 1990 are 47%, 10%, and <1% at Scripps Pier, Arroyo Burro, and Sonoma, respectively. In this experiment, we exposed animals to the same heatwave treatments (21-18ºC), 10ºC, and 20ºC in a split plot design. See below for experimental details.

For both experiments we used the same general methodologies (food source, feeding regime, containers) but in different settings (Quadra Island Ecological Observatory in experiment 1 and Bodega Marine Lab in experiment 2).

Field Collections and Acclimation

For the first experiment, 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 7-8 m relative to mean low tide in September 2021 and transported them to the Marna Lab via truck in seawater filled coolers with bubblers in less than 24 hours. We transferred sea urchins to flow-through sea tables and allowed them to recover for a period of one week before placing 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 variable treatments, were manually adjusted daily in the AM (~8am each day) as needed by 0.5 ºC increments in a scheduled manner to match historical mean El Niño and La Niña daily temperature trends shown in Figure 1B.

For the second experiment, we collected animals from three locations in California including Stillwater Cove in Sonoma County, Mohawk Reef in Santa Barbara, and Point Loma in San Diego using SCUBA from 3-5 meters mean low water. Urchins were dry transported layered between kelp and transferred via ground transportation and into the ambient flow through sea water tanks at Bodega Marine Lab within 24 hours of collection. Temperature ramps and acclimation periods were manually adjusted in 1ºC increments.

Mesocosm Systems

For the first experiment, we placed urchins in a custom-built array of twenty replicated 214 L [90(L) x 59.5(W) x 40(H) cm] acrylic mesocosms supplied with flow-through UV sterilized and filtered seawater (Figure 3). Each mesocosm was capable of independent control of temperature and animals were provided a lighting regime for all mesocosms using LED fixtures

387 (Aquamaxx, CA, USA) programmed to provide 10L:14D with two-hour linear light intensity
388 transition periods for dawn and dusk (0-100% from 07:00 to 09:00 "dawn", and 100-0% from
389 17:00 to 19:00 "dusk"). Each mesocosm independently maintained temperature treatments using
390 a heat exchanger fitted with a titanium coil regulated by a dual stage digital temperature
391 controller (Resolution = 0.1℃, Dwyer Instruments, LLC.©, Michigan City, IN, USA). The
392 mesocosm system employed central cooling (Aermec Mits Airconditioning Inc., Mississauga,
393 ON, Canada) and heating (boiler array, Viessmann Manufacturing Company Inc., Warwick, RI,
394 USA) to supply independent heat exchangers with on-demand cold and warm glycol loops for
395 down- and up-regulation of water temperature, respectively. We manually checked and re-
396 calibrated sensors, as needed, using digital traceable thermometers twice daily to control
397 potential temperature sensor drift. We randomly assigned mesocosms to the specified treatments.
398 For the second experiment, we placed individuals in a custom-built experimental array at
399 the Bodega Marine Laboratory in which individuals from each population were placed in a split
400 plot design in replicated (N = 4 each 140L - 73 (W) x 66 (H) x 32 (D) cm) acrylic tanks per
401 treatment (Oceans Design Inc). Tanks were fed by sumps fixed with both 0.25hp chillers
402 (Aqualogic Delta Star®) and 1000W heat sticks (TSHTCE-1000S) and temperature controllers
403 to regulate temperature in a partially recirculating flow through system with fresh seawater
404 allocated to each system at a rate of 0.5L/min (approx. 5x turnover per day). Each sump was
405 affixed with protein skimmers, UV filter, and bio-ball filters such that water was first filtered and
406 then UV sterilized upon recirculation. Temperatures were set by hand each day for the heatwave
407 treatments and checked with temperature probes for all treatments. We ran experiments from
408 September 15, 2023, to December 19, 2023.
409

410 *Animal husbandry*

411 For both experiments, animals were fed on the same feeding regime and the same food as
412 above, also housed in the same density and same trays for consistency. We fed individuals
413 uniform dry pellets combining several macroalgal species formulated for the aquaculture of *S.*
414 *purpuratus* (Urchinomics Canada Inc., Halifax, NS, Canada). Animals in mesocosms were fed
415 twice per week and we removed uneaten food and refuse every 72 h. Food rations were
416 determined by trial and error in a prior pilot study to ensure all animals had consistent access to

417 food over time. To optimize access for all mesocosm inhabitants to abundant food, we enclosed
418 subjects and food in aquaculture baskets (two baskets per mesocosm, 7 or 8 animals per basket,
419 Thunderbird Plastics 48 x 33.5 x 10 cm Fish Farm Tray) such that food was always readily
420 accessible, and movement was not impeded. Each animal was supplied approximately 2.7 grams
421 of pelleted food twice per week (either 19 or 21 grams per basket for the baskets with 7 and 8
422 individuals, respectively in each mesocosm) for the duration of the experiment.

423 *Histological and gonad assays*

424 At the end of the first experiment, we measured all individuals to test for changes in
425 height and diameter (using precision digital calipers) and wet mass (to the nearest 0.1 g). Full
426 growth measurements are reported by Spindel et al. (2023)[34]. Animals were then sacrificed to
427 measure gonad and histological properties. After opening urchin tests, we immediately removed
428 gonads for sampling. We excised one gonad from each animal for histological analyses; a second
429 gonad was excised and carefully weighed to the nearest 0.01 g. Using a clean, sterile scalpel we
430 excised an approximately 2 mm cross section from the first gonad which we immediately placed
431 in a histological cassette, preserved in Hartmann's fixative for 24 hours, and transferred to 70%
432 EtOH. Preserved gonads were embedded in paraffin, sliced, stained using eosin and hematoxylin,
433 and mounted. We assessed gonad samples for sex and developmental stage using four visual
434 subsections and the entire sample collectively to ensure agreement among subsamples.
435 Histological slides were scored on a scale of I to IV (sensu [31]), where representative stages are
436 depicted in Figure 2. For the second experiment, we only report analyses of histological data in
437 this paper.

438 *Statistics and Reproducibility*

439 For the first experiment, we estimated the probability of individuals in each reproductive
440 stage as a function of mean temperature by sex and in response to El Niño and La Niña
441 treatments using a Bayesian multinomial logistic regression model. We modeled the response to
442 mean temperature using a non-parametric Gaussian process smoother. To account for treatment
443 effects, we included a categorical effect of treatment (constant, El Niño, La Niña). Gonad mass
444 was modeled with a Gamma likelihood and log link with the log of test diameter included as a
445 covariate to account for gonad-body size allometry. Because gonad mass was expected to

potentially exhibit a concave response to temperature (i.e., consistent with a constrained thermal performance curve), a 3rd order polynomial was used for mean temperature. For both analyses, intercepts were allowed to vary randomly by mesocosm. For the second experiment, we used the same model structure for reproductive stage but with no smoother effects (only categorical terms for constant 10˚C, constant 20˚C, or El Niño) and included location of collection as a random effect.

For both datasets, 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 Bayes Factors[56] (as hypothesis tests of the full versus null models). For Bayes Factors we estimated the marginal likelihood using bridge sampling[57] via the R package bridgesampling[30]. Because Bayes Factors can be sensitive to prior construction, we ensured our analyses are robust by simulating 200 datasets from both the full and null model under the same prior construction to ensure that Bayes Factor would consistently reject the null when simulating from the full model and vice versa. We sampled posteriors in Stan[58] (via brms[59] for Gamma regressions for gonads or coded directly for multinomial models of histology) in R. We ran models with vague priors, and conducted sensitivity analyses to ensure varying prior distributions and hyperparameters did not qualitatively affect the results. For the multinomial models, we provided stage proportions by treatment for the multinomial models vague Dirichlet priors (all concentration parameters = 1 yielding equal prior odds with high uncertainty). Location random effects were provided logit-scale normal effects (with mean zero) from the mean stage proportions where the scale hyperparameter was provided a folded student-t (df = 3, lower bound = 0, scale = 0.1) hyperprior. Finally, for the Marna Lab dataset, the logit-scale Gaussian process model was given a squared exponential covariance and with length and scale hyperparameters having folded normal hyperpriors (both with sd = 1 and mean and lower bound of 1 and 0, respectively). We ran models for 12000 iterations for each of four chains after a 2000 iteration warmup period and checked convergence visually, that parameters had convergence diagnostics (Rhat) less than 1.001. Data and metadata from this study are available at https://www.bco-dmo.org/project/818918 and analysis and code is available at https://doi.org/10.5281/zenodo.15420518.

Author contributions:

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

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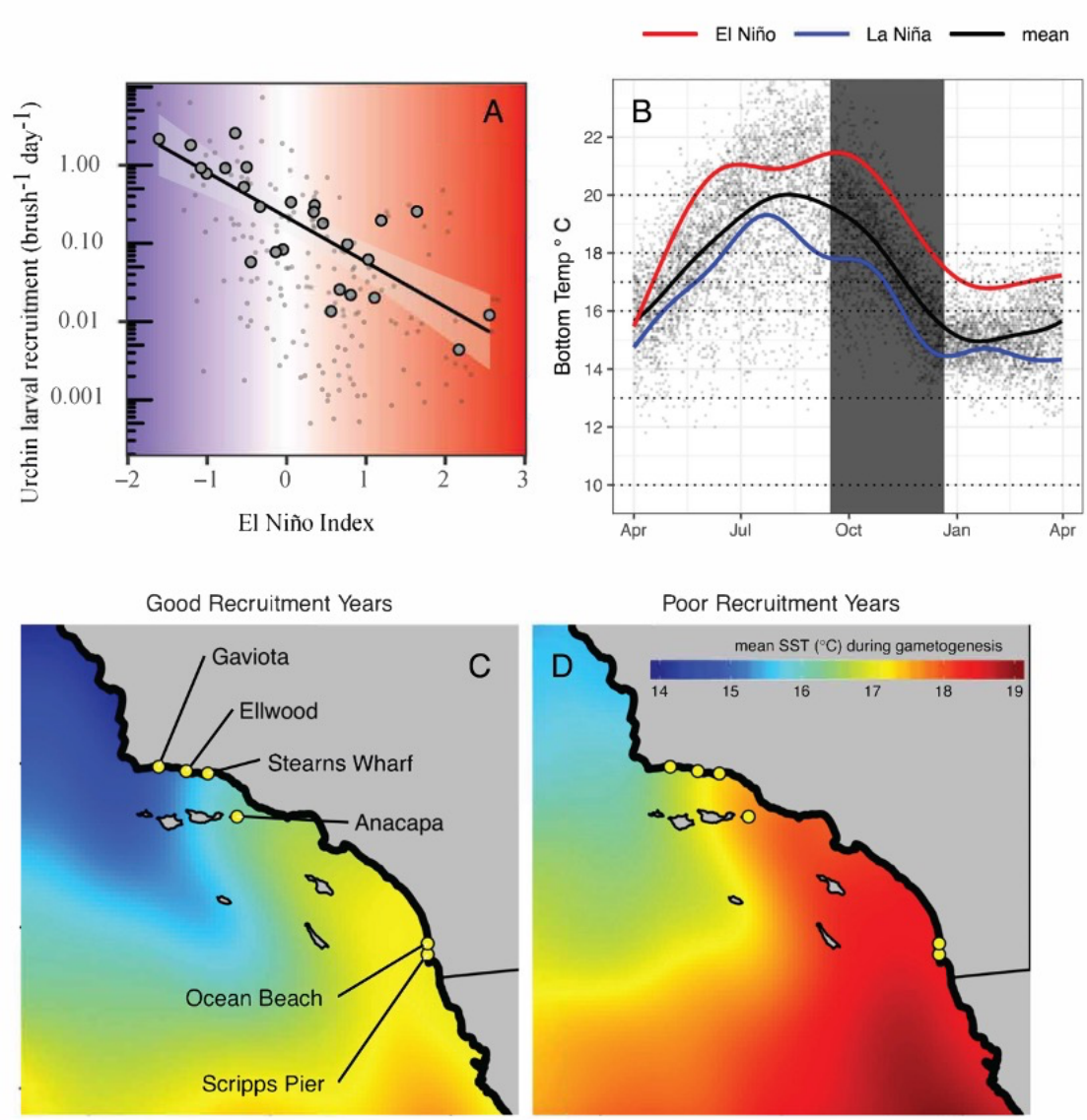

Figure 1: A) Historical mean annual (large points) and monthly mean (small points) larval settlement on standardized brush samplers across six sites in Southern California vs Multivariate El Niño Index (MEI) since 1990 (reproduced from Okamoto et al. [21]). Colors correspond to the x-axis representing cooler (negative) and warmer (positive) temperatures associated with the MEI in Southern California. B) Historical benthic temperatures from Scripps Pier[53,54]. 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 [55]. 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.

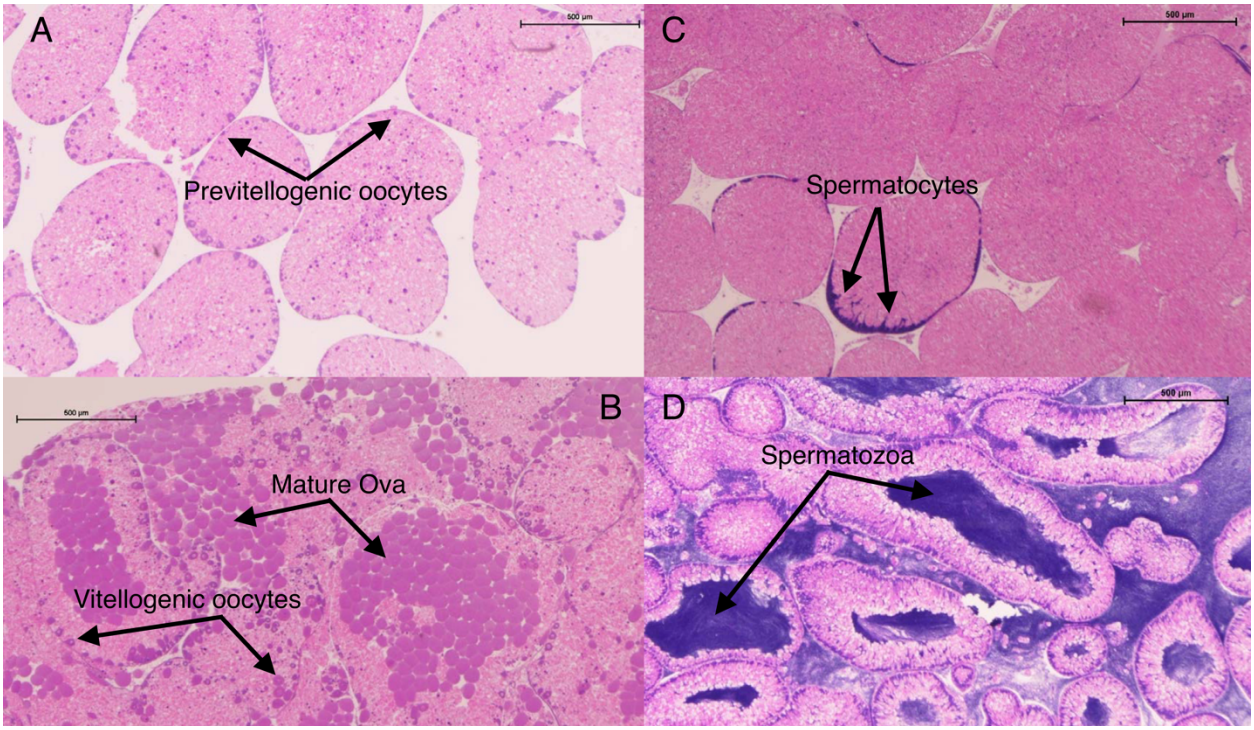

Figure 2: Gonad sections stained with hematoxylin and eosin with scale bar representing 500 µm. A-B Female ovaries in Stage I (A) and Stage IV (B) arrows indicate small previtellogenic oocytes, vitellogenic oocytes in the process of meiosis, and mature ova. C-D. Females in stage I are largely devoid 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.

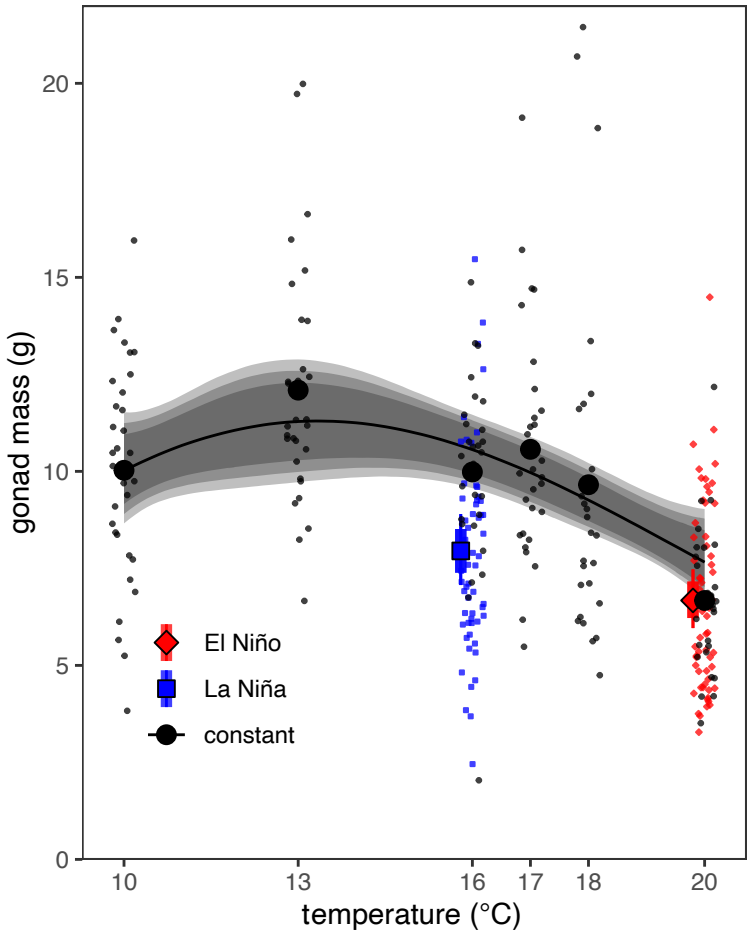

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Figure 4: Final gonad mass vs mean temperature. Black circles and the smooth trend represent fixed temperature treatments; the red diamond and blue square represent El Niño and La Niña thermal treatments, respectively. Small points represent individual observations (standardized to 50 mm diameter individual for consistency). Error bars and bands represent the 90, and 95% highest probability density interval of the posterior. Results are shown for males and females combined with no evidence for a difference between sexes in the response (see Results).

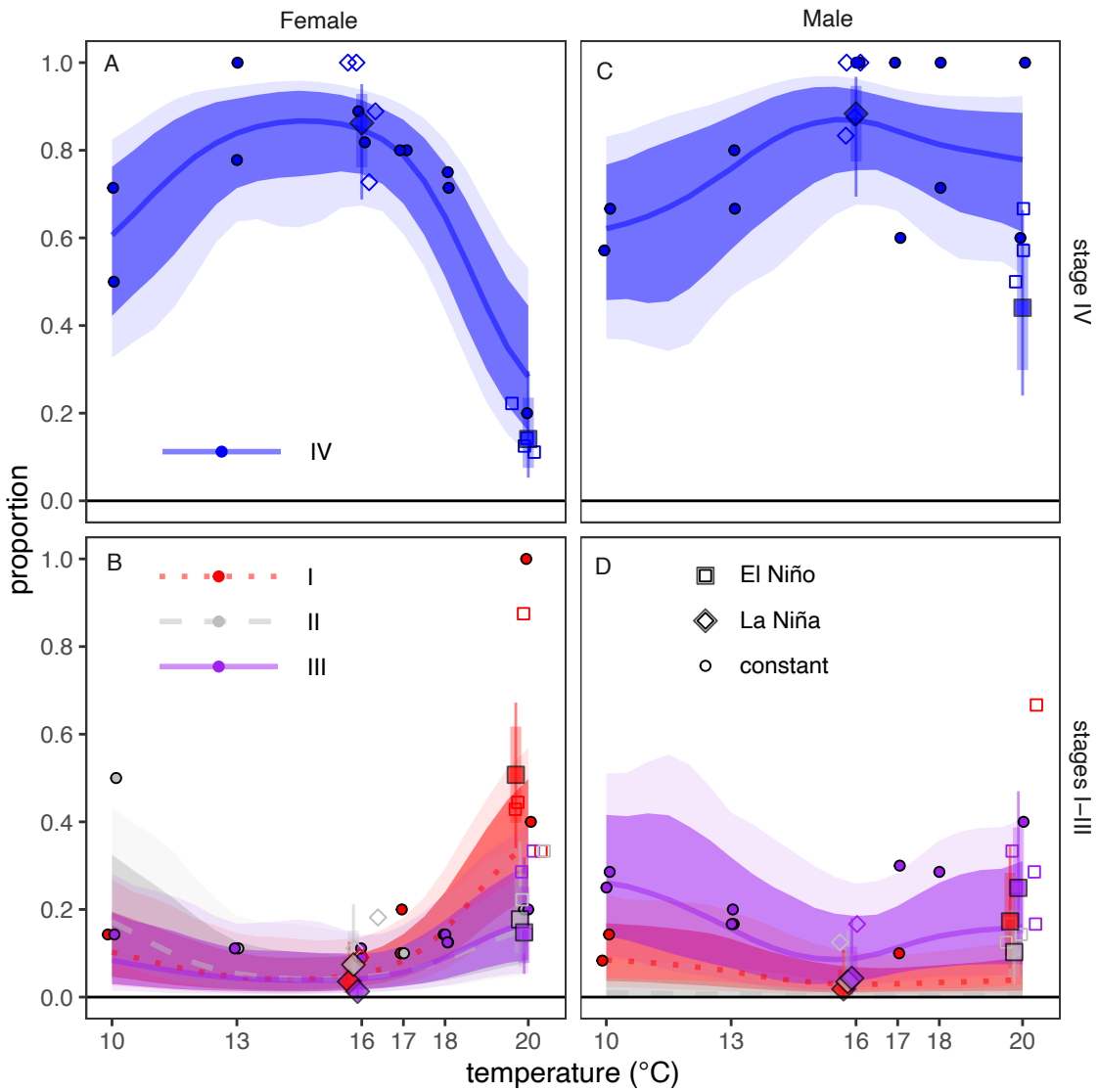
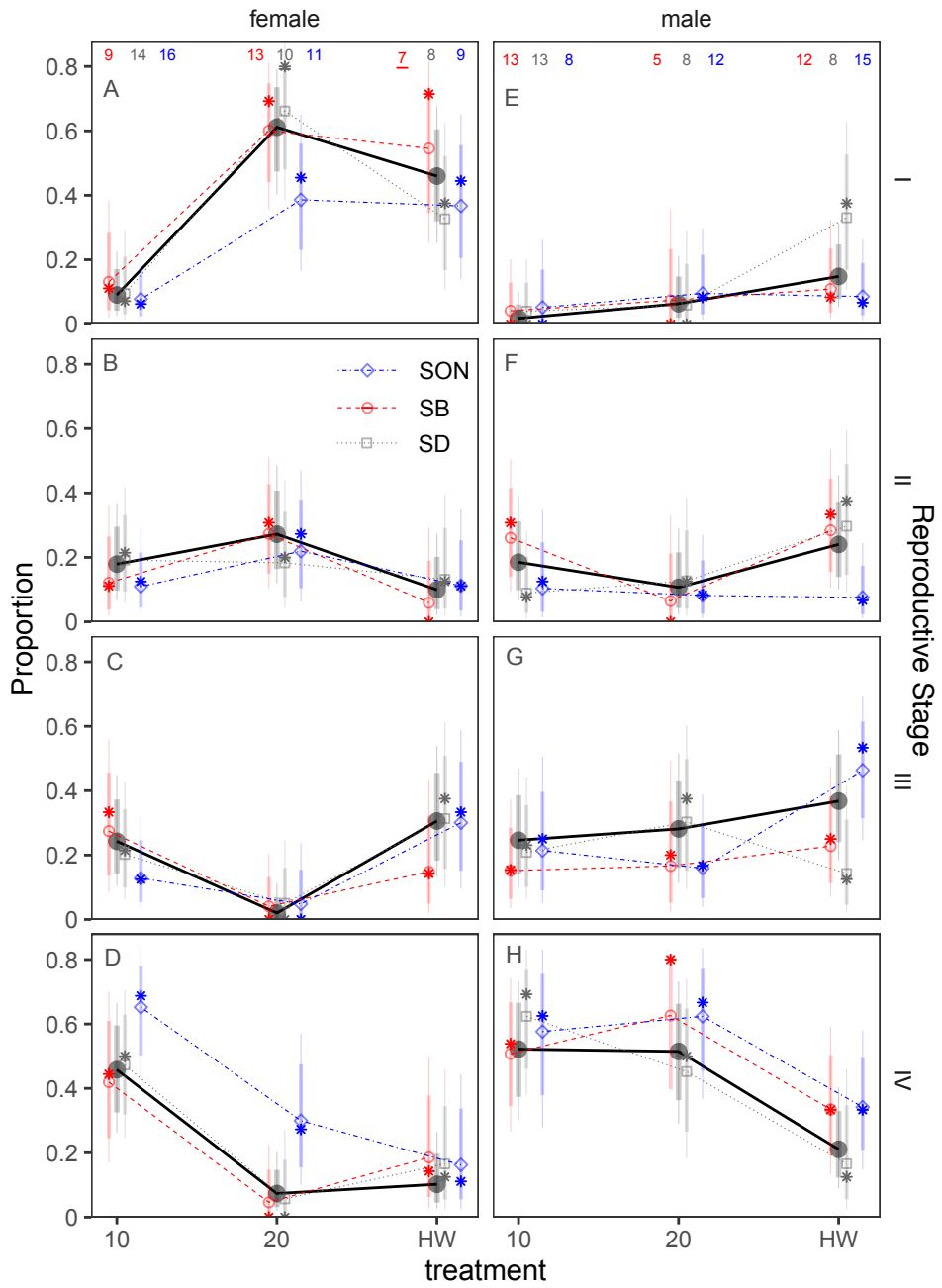


Figure 5: Proportion of adult females (A, B) and males (C, D) in each reproductive stage by treatment (El Niño (squares), La Niña (diamonds), or constant temperature (circles)) and mean temperature. A) Proportion of females in stage IV. B) Proportion of females in stages I (dotted red lines, red points),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



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548 Figure 6: Estimated proportions of each stage (rows) for each sex (columns) for each treatment
549 from the population comparison experiment (Sonoma, Santa Barbara, San Diego). Points
550 represent mean and error bars 90/95% credible intervals. The model with no location interaction
551 is indicated by black circles while other symbols/colors reflect the model with location
552 interaction with sex/treatment (red circles - SB = Santa Barbara County, grey squares - SD = San
553 Diego, and blue diamonds - SON = Sonoma). All estimates are derived from Bayesian ordinal
554 logistic regressions with random effects of location and vague priors on the estimated means.
555 Sample sizes are shown in panels A and E for males and females, respectively. Asterisks
556 represent empirical mean proportions.

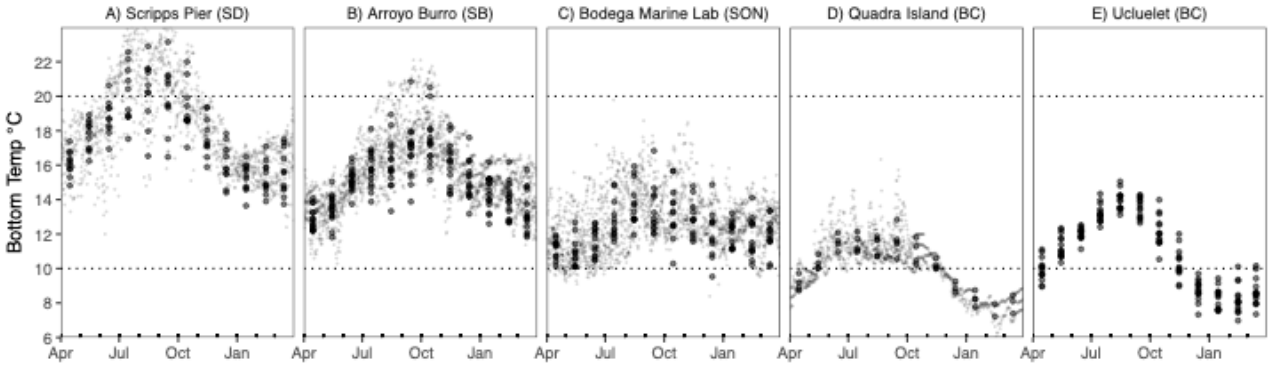

Figure 7: Daily benthic temperatures from San Diego (Scripps Pier), Santa Barbara (Arroyo Burro SBC LTER), Sonoma (Bodega Marine Lab), D) the Quadra Island Ecological Observatory, BC (the site of the Marna experimental work) and E) surface temperatures for the Amphitrite Point lighthouse in Ucluelet, BC (the source of the animals for the Marna experimental work). Small points represent daily means (except in E where original data are monthly values) and large points represent monthly means. For consistency, data are shown only since 2015 (the inception of the Quadra Island time series).

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