Seasonally variable thermal performance curves prevent adverse effects of heatwaves

A Preprint

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Abstract

The increasing frequency and intensity of heatwaves may represent a significant challenge for organisms in a warming ocean. The direct impacts of heatwaves on populations depend on the relative position of environmental temperatures to the thermal performance curve optima. The effects of heatwaves may therefore vary seasonally along the annual temperature cycle. However, this seasonal variation in the effects of heatwaves may be dampened by corresponding variation in thermal performance curves. In organisms with relatively short generation times, these changes may be driven by phenotypic plasticity as well as genetic differentiation. We investigate the effects of seasonal timing and duration on the impacts of heatwaves in the ecologically important copepod Acartia tonsa. We show that thermal performance curves are seasonally variable in the field, and that this variation buffers against negative effects of simulated heatwaves. Further, the offspring of individuals that experienced the simulated heatwaves were raised in the laboratory to examine trans-generational effects of heatwaves on body size and reproductive output. The lack of a clear pattern in the trans-generational effects may indicate that seasonal variation in thermal performance curves also buffers against indirect effects of heat waves by reducing the effects of parental stress on the offspring. Our results show that seasonal variation in thermal performance curves has the potential to limit the adverse effects of heatwaves on populations of short-lived organisms.

***K*eywords** Heat wave · Climate change · Copepod · Transgenerational plasticity · Seasonal variation · Thermal performance

Introduction

Heatwaves are increasing in frequency and intensity across marine ecosystems (Frölicher et al. 2018; Oliver et al. 2018, 2019). These periods of anomalously high temperatures present severe challenges to marine biota (Smale et al. 2019). Both lethal and non-lethal temperature effects on organisms have strong potential to alter community composition and ecosystem functions (REF). In order to predict how communities may respond to both long-term warming and the increasing effects of heatwaves, there is an urgent need to understand what determines relative vulnerability to heatwaves. [Why look at closely related species?]

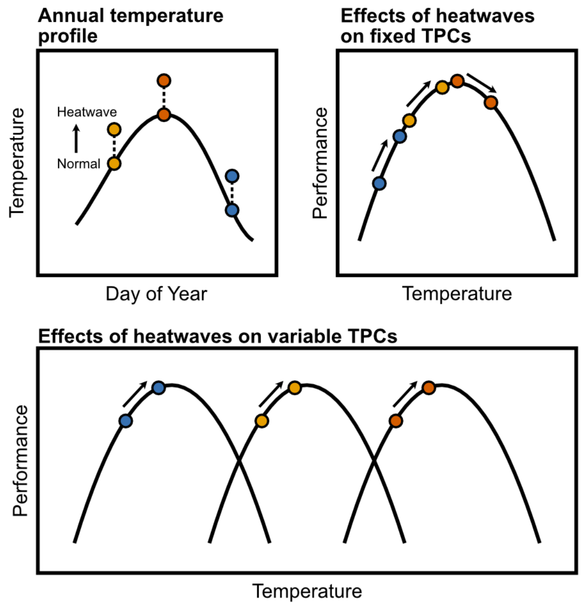


Figure 1: Caption

In marine communities, autotrophs (e.g. phytoplankton) and primary consumers (e.g. copepods) typically have generation times on the order of days to weeks. As such, the response of these key groups to heatwaves may vary over seasonal timescales, reflecting either acclimatization or adaptation to different seasonal conditions (Sasaki and Dam 2020; Adaptive tracking paper). Whether there is or is not seasonal variation in thermal performance curves will play an important role in determining the effects of heatwaves on a population (Figure 1). While past work has shown that heatwaves can have drastic effects on individual biology and population dynamics (REF), much of this work assumes performance curves are fixed (i.e. - there is no seasonal variation in TPCs). In this case, the effect of heatwaves will vary seasonally as the relative position of environmental temperature to TPC optimum and lethal thermal limits varies. Alternatively, variation in TPCs over seasonal timescales may act as a buffer against negative effects of heatwaves if optimum temperatures track environmental temperatures, preventing environmental temperatures from exceeding thermal optima.

- The effects of heat waves may also extend beyond direct effects on individuals; Transgenerational effects also need to be considered (maternal effects, transgenerational plasticity, etc.), as exposure to high temperature is known to affect offspring phenotypes and performance (REF).
- To summarize, the relative vulnerability of closely related species, seasonal variation in TPCs, and the magnitude of transgenerational effects are all important to consider in predictions about how the increasing threat of heatwaves may affect marine communities. [Copepods as a model system].

Here we examine the potential for seasonal variation in thermal performance curves to buffer populations of short-lived organisms against negative effects of heatwaves. We examined how thermal performance curves for key fitness related traits (egg production, hatching success, and survivorship) varied over the course of the seasonal temperature cycle in the ecologically important copepod species *Acartia hudsonica* and *A. tonsa*. We also quantified both direct and indirect (e.g. - transgenerational) effects of heatwaves on these copepods in the laboratory using a series of simulated heatwave experiments. We test two hypotheses: 1) there is seasonal variation in the thermal performance curves of key fitness related traits in *A. hudsonica* and *A. tonsa*; and 2) when TPC parameters track changes in environmental temperatures, the effects of simulated heatwaves do not vary over the course of the year. By integrating experiments with field-collected and lab-reared organisms, we show that TPCs of *A. tonsa* are highly variable across seasons and this variation allows the population to maintain a relatively constant margin between optimum temperatures and ambient environmental temperatures. The mechanisms that produce seasonally variable TPCs, whether genetic or plastic, therefore reduce the potential for heatwaves to adversely affect population dynamics and thus increase resilience in the face of climate change.

Methods

Generating Field TPCs

Copepods were collected from Long Island Sound, near the University of Connecticut, Avery Point Campus at several times throughout the year using surface tows of a __ um mesh plankton net. Mature *Acartia hudsonica* or *Acartia tonsa* females were isolated from the contents of the plankton tow and isolated individually in petri dishes for egg production and hatching success assays. During these assays, females were fed __. Females produced eggs for __ days, after which the female was removed. Eggs were given three additional days before hatching frequency was assessed. These assays were performed across a range of temperatures (10-30 degrees C for *A. tonsa* and 4-24 degrees C for *A. hudsonica*).

Will need substantial input from other people to fill in the methods section.

Table 1: Caption

Month	Date	Temperature	Species
January	January 21st 2015	2.1	Acartia hudsonica
February	February 21st 2015	-0.4	Acartia hudsonica
March	March 16 2015	4.0	Acartia hudsonica
April	April 21st 2015	9.2	Acartia hudsonica
May	May 14th 2015	12.0	Acartia hudsonica
June	June ___ 2015	18.6	Acartia hudsonica
July	July 29th 2014	20.0	Acartia tonsa
August	August 13th 2014	18.0	Acartia tonsa
September	September 11th 2014	18.0	Acartia tonsa
October	October 22nd 2014	16.0	Acartia tonsa
November 1	November 4th 2014	14.5	Acartia tonsa
November 2	November 19th 2014	11.0	Acartia tonsa

TPCs for egg production, hatching success, and production were then generated using the framework outlined by Padfield et al. (2021). Egg production, hatching success, and production data were modeled using a Guassian equation. Survivorship was modeled using a logistic regression of individual survivorship against stress temperature.

Simulated Heat Waves

To test our second hypothesis (that varying thermal performance curve parameters reduce vulnerability to heatwaves) we collected *Acartia tonsa* again in 2015 for use in laboratory simulated heatwave experiments. In order to test the effects of a heatwave against the seasonally shifting baseline of ambient temperature, three collections were made before, during, and after peak environmental temperatures, corresponding to late June, late July, and early December (Table 2). These experiments examined both direct and indirect (e.g. transgenerational) effects of heatwaves. To examine the direct effects, egg production rate, hatching success, and production were measured for around 60 females per collection split into two groups (control and heatwave). These assays were performed as described in the Field TPC section, with females isolated in individual petri dishes and provided with food *ad libitum*. The control group remained at a temperature near the current ambient temperature in Long Island Sound while the Heatwave group experienced temperatures 5 degrees C above the ambient temperature (Table 3). Traits were measured over two periods to examine the effects of short and long heatwave events - Days 1-3 and Days 5-7, respectively. Females were moved into petri dishes with fresh food solution on Days 3 and 5. Eggs produced in between the two time periods were not examined.

Table 2: Caption

Period	Date	Field Temp.	Control Temp.	Heatwave Temp.
Early	June 27th 2015	17.8	17	22
Mid	July 29th 2015	22.4	22	27
Late	December 1st 2015	12.0	12	17

Transgenerational Experiments

In addition to the individuals maintained in petri dishes to measure direct effects of heatwaves, several hundred adult copepods were also placed into each of eight 4L buckets of filtered seawater and provided with food ad libitum (four each, maintained at control and heatwave temperatures). Water in each bucket was kept oxygenated using a small aquarium pump. Eggs were collected from each bucket following the same schedule as the direct effect experiments - eggs were collected on Day 3 and Day 7 for the short and long heatwave exposures, respectively. Eggs were discarded on Day 5 to ensure all individuals reflected the correct exposure periods. These eggs were then split into three groups which developed at one of three different temperatures (12, 17, or 22 degrees C). After these individuals matured, body size and the three reproductive traits (egg production, hatching success, and production) were measured at the temperature individuals developed at. Within developmental temperatures, differences between the Heatwave and Control treatment groups should reflect the indirect effects of heatwaves: these individuals represent eggs produced by parents experiencing the heatwave conditions, but that developed at the same temperatures as the Control individuals.

Results

Seasonal Variation in Field TPCs

There was abundant variation in TPCs for Egg Production Rate (EPR), Hatching Success (HS), and production (the product of Hatching Success and Total Egg Production - the number of offspring per female per day) for copepods collected throughout the year. EPR TPCs had higher optimum temperatures and maximum values in warmer months (July, August, and September) than in cooler months (October and November). Peaks were generally less distinct for HS than EPR. However, hatching success was generally higher in warmer months than cooler months, regardless of incubation temperature. When combined, the variation in optimum temperatures and maximum values for EPR and HS curves yielded Production curves that were highly variable. Collections from warmer months generally had slightly higher optimum temperatures as well as higher maximum production values. Thermal survivorship curves also varied significantly between collections.

Many of these traits tracked collection temperatures. Collection temperature never exceeded optimum temperatures, suggesting that at all times, additional warming (e.g. - a heatwave) would increase egg production. Indeed, the safety margin between environmental temperatures and TPC optima was relatively constant over time. The one outlier was the second November collection, which was collected at 11 degrees C. This is around the threshold for resting egg production in *A. tonsa*. The extremely high estimated production optimum temperature may reflect the difference in hatching requirements between resting and subitaneous eggs. Thermal tolerance also increased with collection temperature, but this trend was not significant. The difference between environmental temperatures and thermal tolerance decreased as waters warmed. However, even during the warmest times, thermal tolerance values were always more than 8 degrees higher than water temperatures.

To summarize, there is a seasonally variable TPC for multiple traits in the Long Island Sound population of *A. tonsa*, keeping the optimum temperature and thermal tolerance values well above the environmental temperature. As a result, we'd predict heat waves should have a beneficial effect, regardless of seasonal timing, by moving the population towards its optimum temperature. However, strong heatwaves during the warmest times may have an adverse effect on survivorship, unless other mechanisms (e.g. - acclimation and phenotypic plasticity) adjust thermal tolerance.

Effects of Simulated Heatwaves

The second component of this project examined the effects of heatwaves across generations. This necessarily began with reassessing the field collected F0. We examined the effects of short or long duration artificial heatwaves, during different collection months on EPR, HS, and production. We will focus the analysis on production, as it integrates the other traits. The ANOVA indicated no significant overall effect of heatwaves on production (p-value = 0.38). There was, however, a significant interaction between treatment and collection month (p-value = 0.01), indicating different effects of heatwaves across months. The different trial duration and collection months were also significantly different, with a significant interaction term as well. ANOVA results are shown in Supp. Table 1.

The effect sizes (the difference between heatwave and control trials, or between long and short duration trials) and confidence intervals were estimated using non-parametric bootstrap resampling. These estimates are

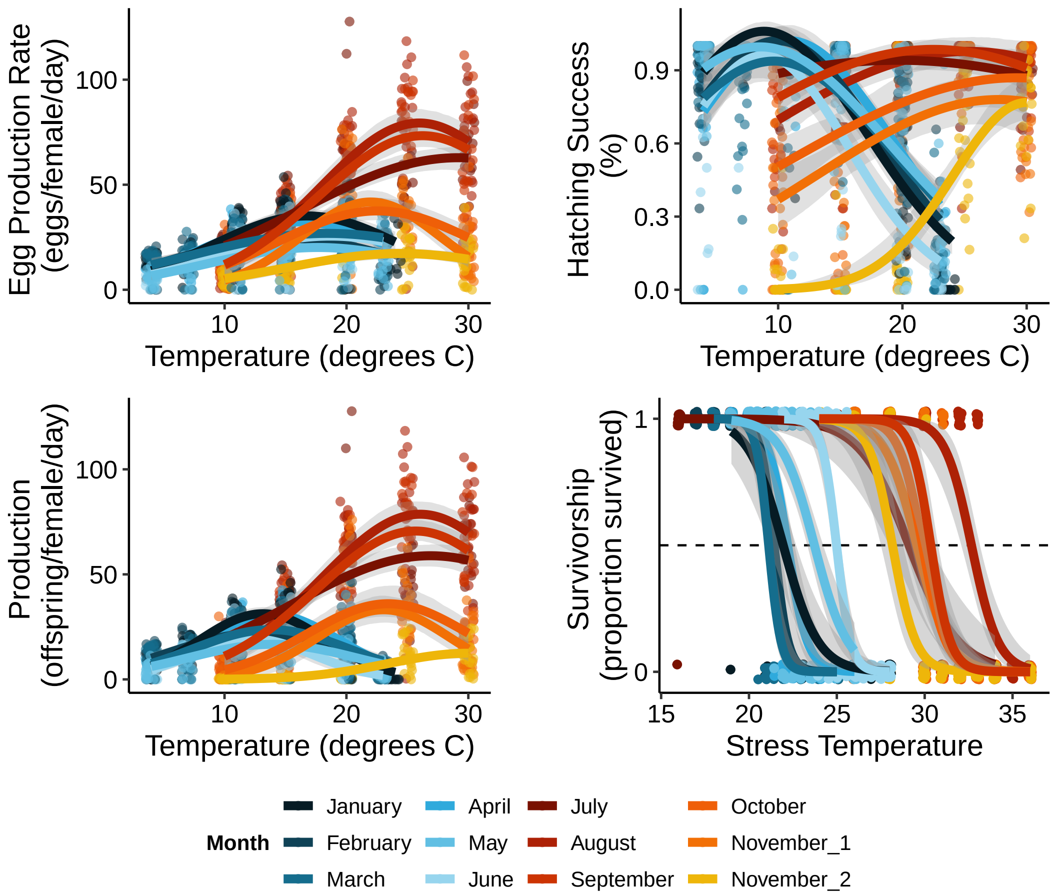


Figure 2: caption

shown below for the effects of treatment and the effect of duration. Short and long duration trials are shown in white and black symbols, respectively, in the first panel. The control and heatwave treatments are shown with different shapes in the second panel. Full Gardner-Altman estimation plots are shown in Supp. Fig 1 and 2. Effects of heatwaves were generally weak; only long heatwaves in June and short heatwaves in August had confidence intervals that did not (or nearly did not) overlap zero. In contrast, there were strong decreases in long duration trials relative to short trials, in both control and heatwave treatments.

Transgenerational Effects of Simulated Heatwaves

We also examined the effects of parental exposure to heatwaves on offspring traits. Comparing between Control and Heatwave treatments now examines not the direct effects of increased temperature, but the indirect effect on offspring of parental exposure to heatwaves. In both panels, the gray boxes indicate the developmental temperature most similar to that experienced by offspring of the parental generation in the field.

Body Size - Offspring body size generally decreased with developmental temperature, as expected (Supp. Fig. 4). Within individual developmental temperatures, parental exposure to heatwaves also generally resulted in small decreases in body size. Short and long duration events are shown with open and filled circles respectively.

Fecundity - There were no consistent patterns in the effects of parental exposure to heatwaves across developmental temperatures, heatwave duration, or time of year.

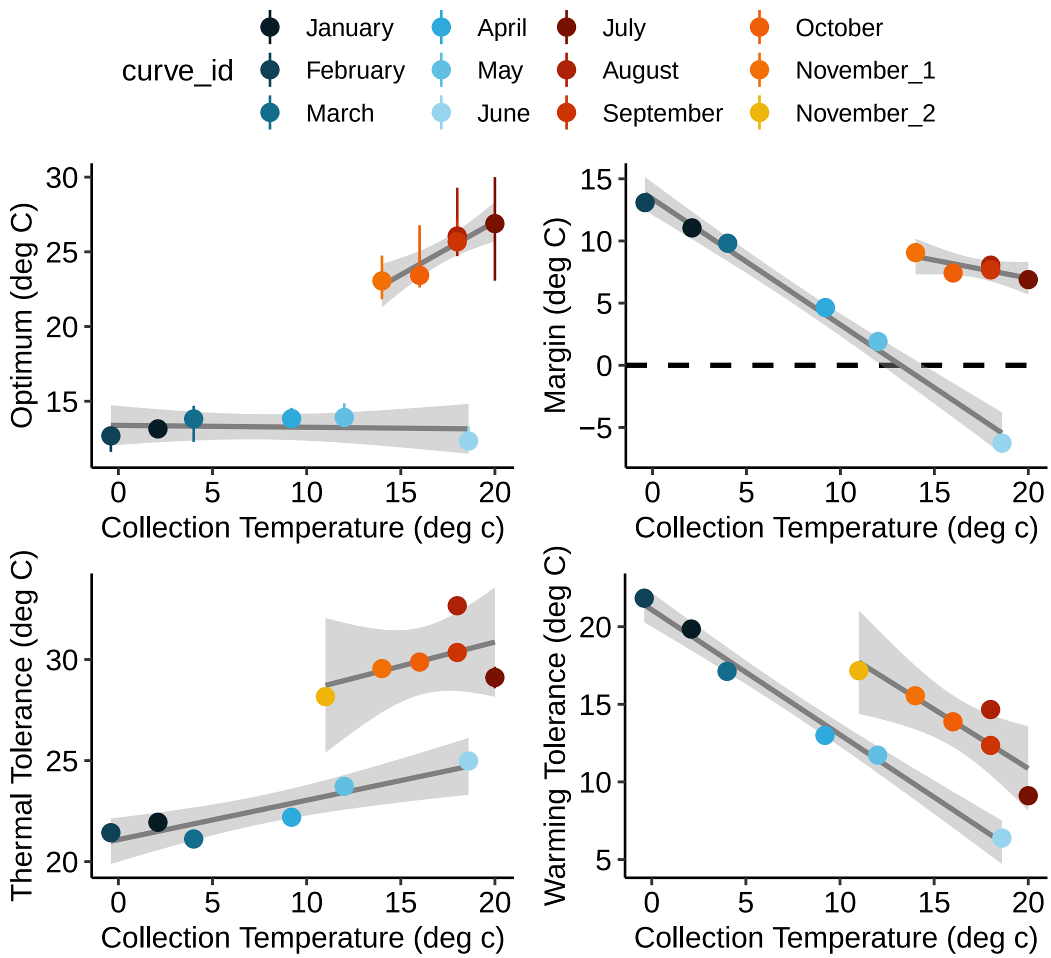


Figure 3: caption

Discussion

General patterns are scare in this data. Parental exposure to heat waves generally decreased offspring body size, but had no consistent effects on F1 production rates. Effects were particularly small when looking just at the developmental temperatures the offspring would experience in the field - At these temperatures, only parental exposure to heatwaves in August resulted in a decrease in offspring production or reduced body sizes.

The expectation is that production should decrease as body size decreases due to the effects on EPR. However, the changes in production were independent of changes in body size (Supp. Fig. 6). Instead, the observed effects are more likely to be the result of other mechanisms (such as maternal effects or transgenerational plasticity).

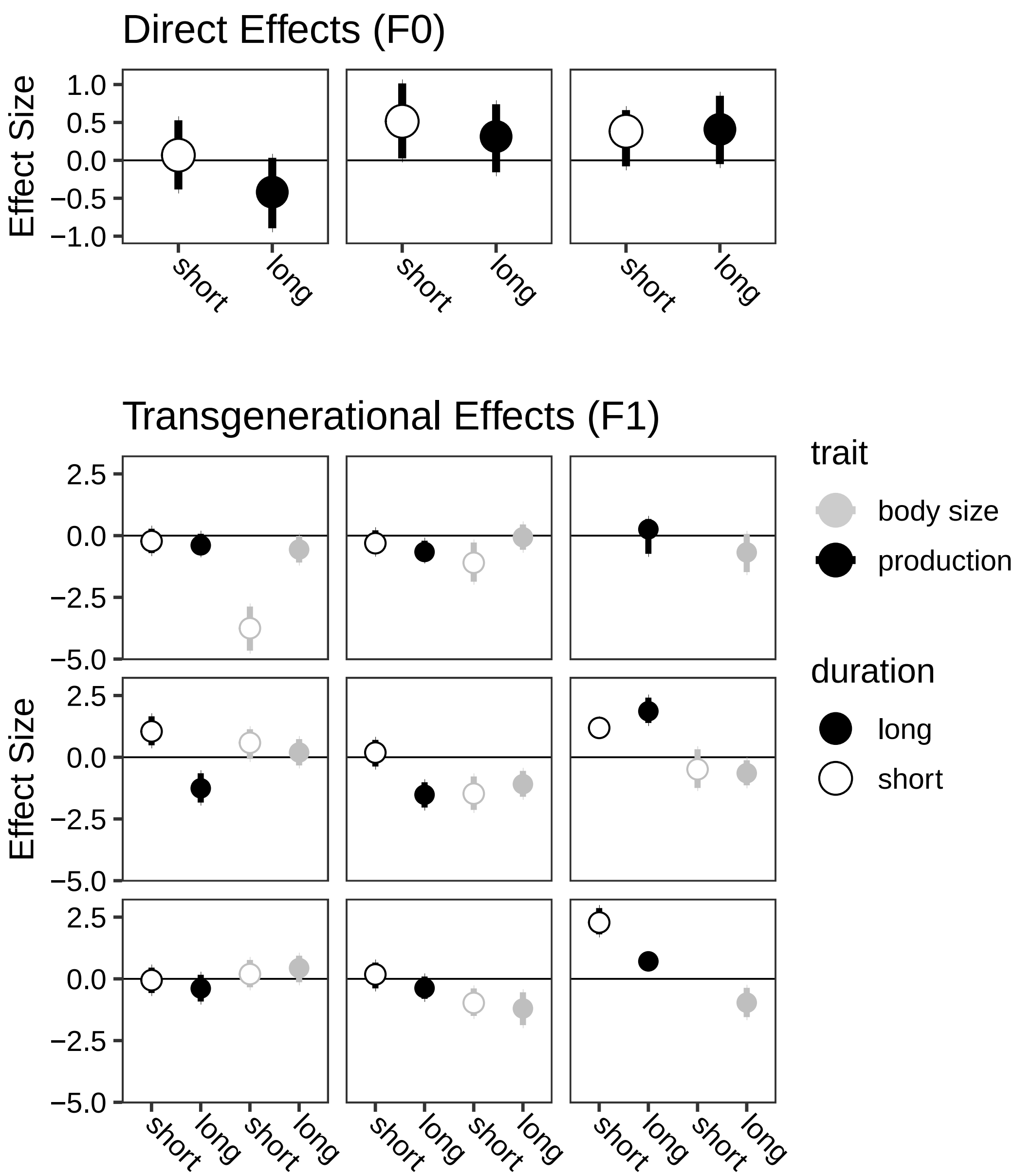
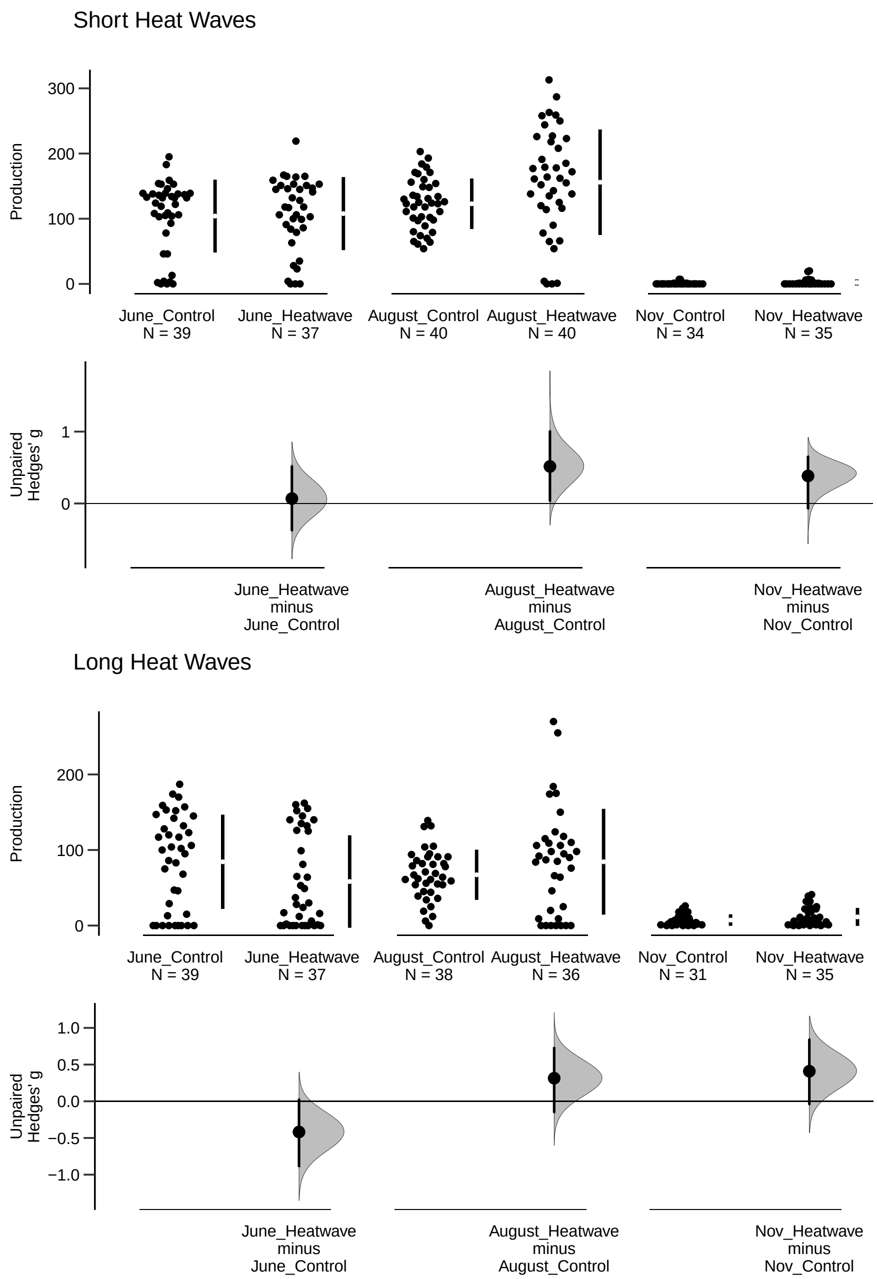


Figure 4: caption

Supplemental Information

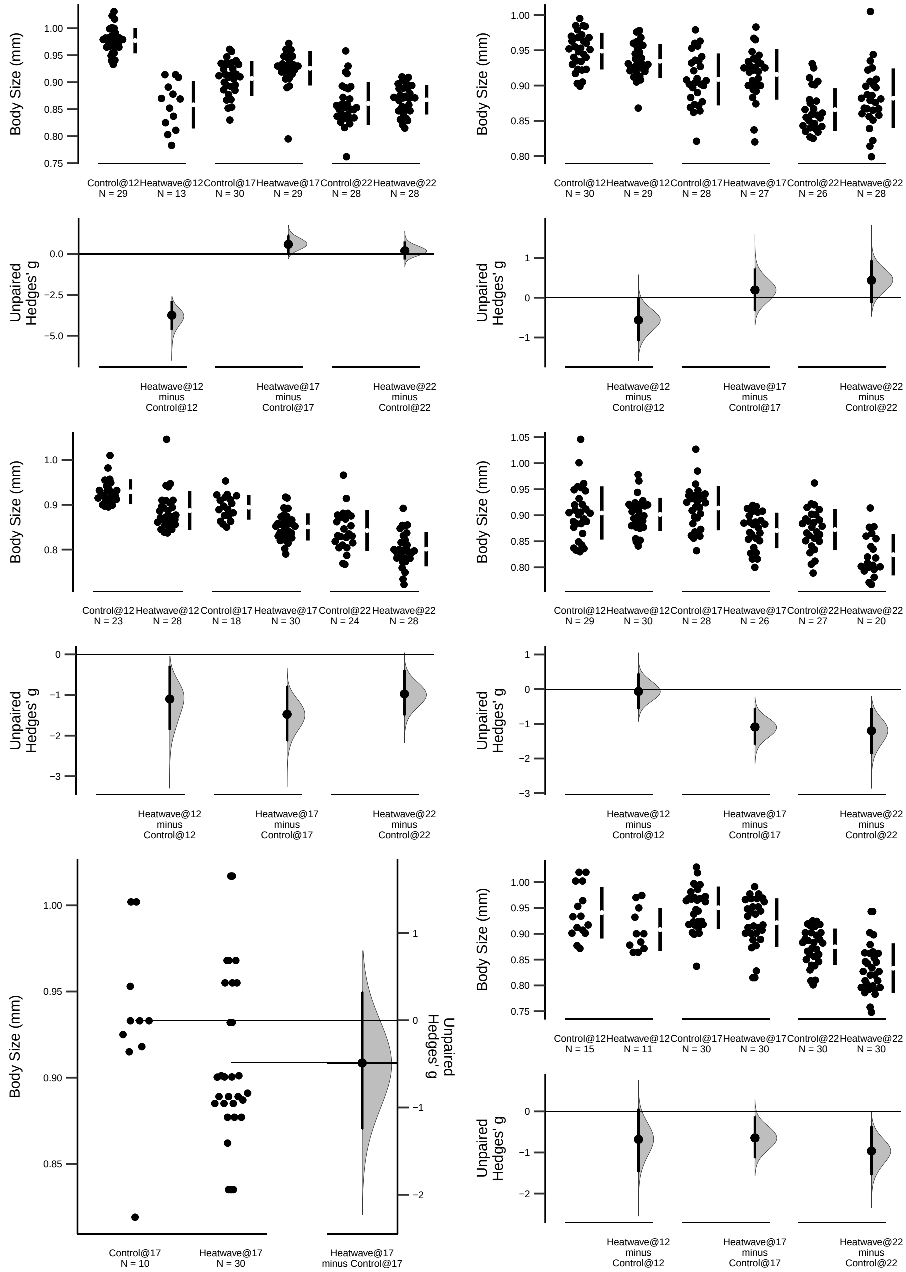
Supp. Fig. 1

These plots follow best practices for the visualization of differences between groups. The top half of each figure shows the underlying data points in a swarm plot. To the right of each each swarm is the mean and standard deviation of the group, represented using a gapped bar (gap = mean value). Below the raw data, the effect size and 95% confidence intervals are shown, which were obtained using non-parametric bootstrap resampling. Confidence intervals that do not cross the 0 effect size line indicate significant differences between groups.



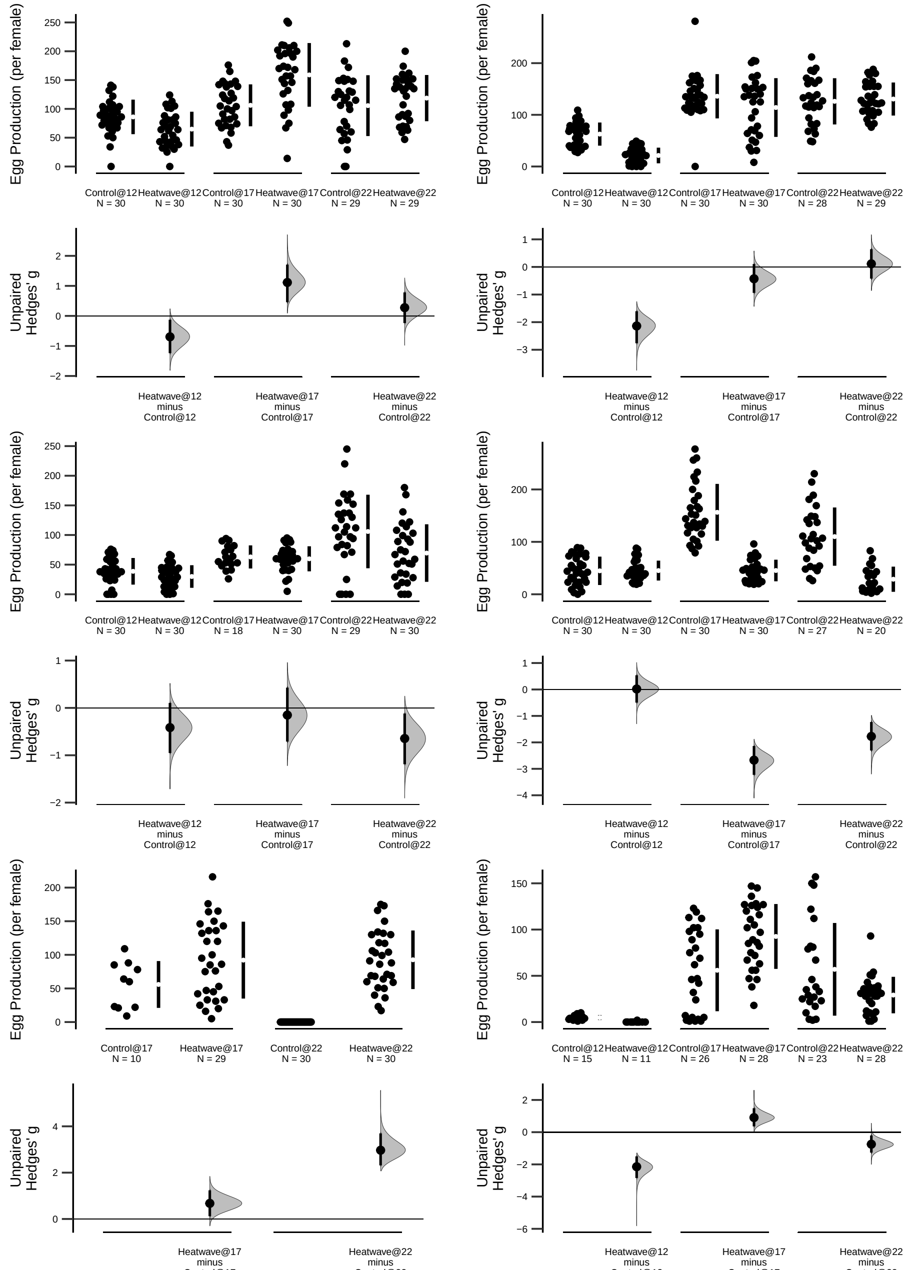
Supp. Fig. 2

Effects of parental exposure to heatwaves on F1 body size at different developmental temperatures.



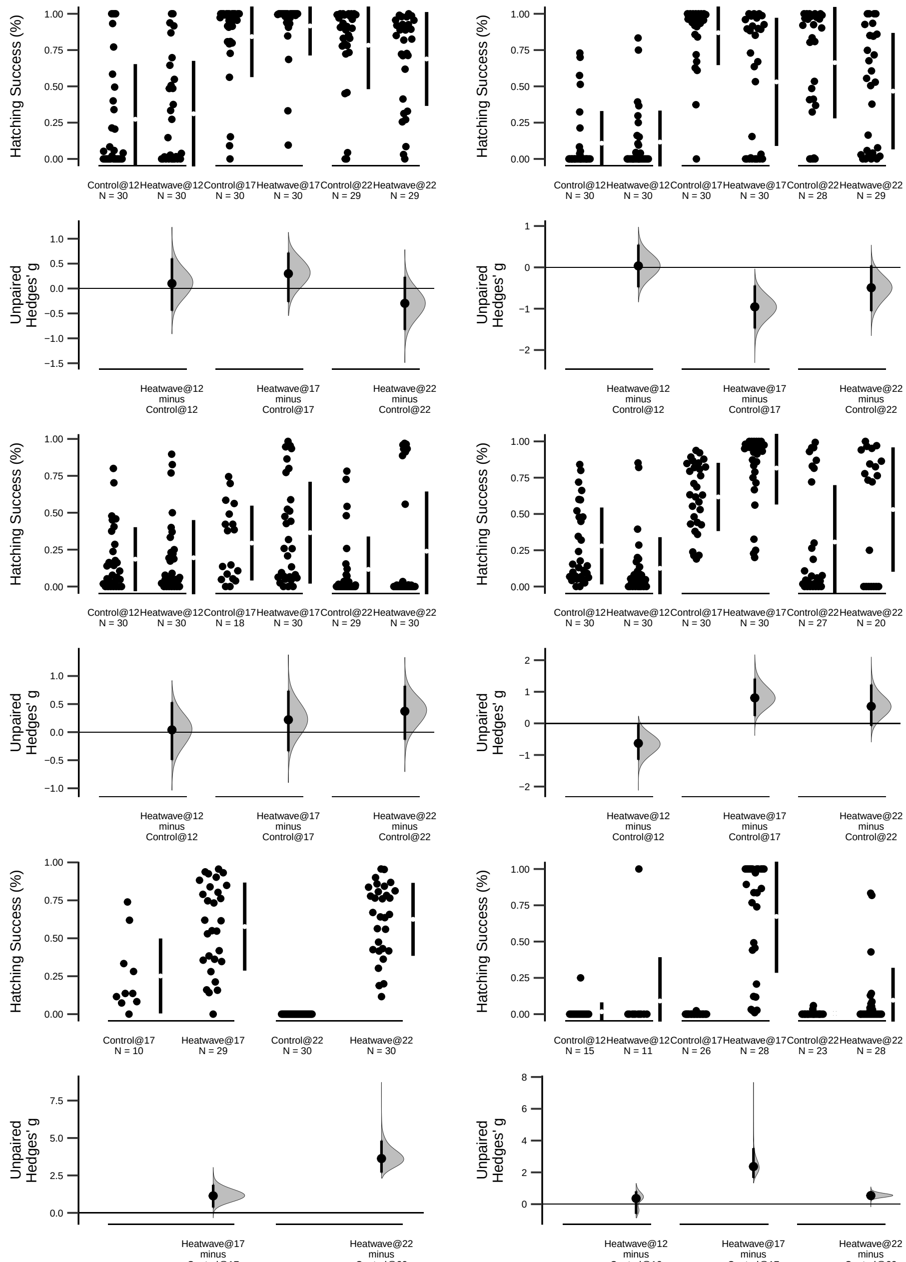
Supp. Fig. 3

Effects of parental exposure to heatwaves on F1 egg production at different developmental temperatures.



Supp. Fig. 4

Effects of parental exposure to heatwaves on F1 hatching success at different developmental temperatures.



Supp. Fig. 5

Effects of parental exposure to heatwaves on F1 production at different developmental temperatures.