
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.

Keywords Heat wave · Climate change · Copepod · Transgenerational plasticity · Seasonal variation · Thermal performance

1 Introduction

Marine heatwaves are increasing in frequency and intensity across marine ecosystems (Frölicher et al. 2018; Oliver et al. 2018, 2019) and present severe challenges to marine organisms (Smale et al. 2019).

The acute nature of these events has large effects on organisms and need to be taken into account when predicting organismal responses to climate change. - While past work has shown that heatwaves can have drastic effects on individual biology and population dynamics, and that the effects of heatwaves can vary across seasons, much of this is based on the perspective of fixed performance curves (i.e. - that the effect of

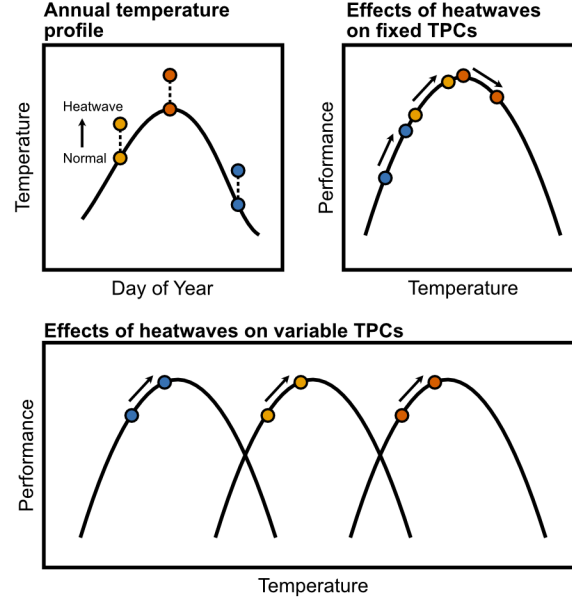


Figure 1: Schematic

heatwaves varies because the relative position of environmental temperature to TPC optimum varies). TPCs can be highly variable though, even over seasonal timescales. Variation in TPCs over seasonal timescales may act as a buffer against the negative effects of heatwaves on populations, as illustrated in the conceptual schematic below.

- Sources of variation in TPCs: 1) Genetic variation, balanced polymorphism fluctuating selection, etc. etc., 2) phenotypic plasticity.
- 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.).
- 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 *Acartia 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. tonsa*; and 2) TPC parameters track changes in environmental temperatures and as a result the effects of simulated heatwaves on *A. tonsa* do not vary over the course of the year. By integrating experiments with field-collected and lab-reared organisms, we show that TPCs 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, be they genetic or plastic, therefore reduce the potential for heat waves to adversely affect population dynamics increase resilience in the face of climate change

2 Methods

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

2.1 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 $_\mu\text{m}$ mesh plankton net. Mature *Acartia tonsa* individuals were isolated from the contents of the plankton tow and $_\$.

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

TPCs for egg production, hatching success, and production were generated using the framework outlined by Padfield et al. (). A quadratic equation of form $y = ax^2 + bx + c$ was used to model the data, with parameters estimated with $_\$.

2.2 Simulated Heat Waves

The following year, copepods were collected again, as described above, 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. The simulated heatwave (ambient +5 degrees C) tracked ambient temperatures over the course of the season.

Period	Date	Temperature
Early	June 27th 2015	17.8
Mid	July 29th 2015	22.4
Late	December 1st 2015	12.0

2.3 Transgenerational Experiments

In addition to the mature individuals maintained in petri dishes to measure direct effects of heatwaves, several hundred adult copepods were also placed into each of four 4L buckets of filtered seawater and provided with food ad libitum. 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 (collected after Day 3 and Day $_\$). 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 Heatwave individuals only experienced the increased temperatures of the simulated heatwaves during the initial laying phase).

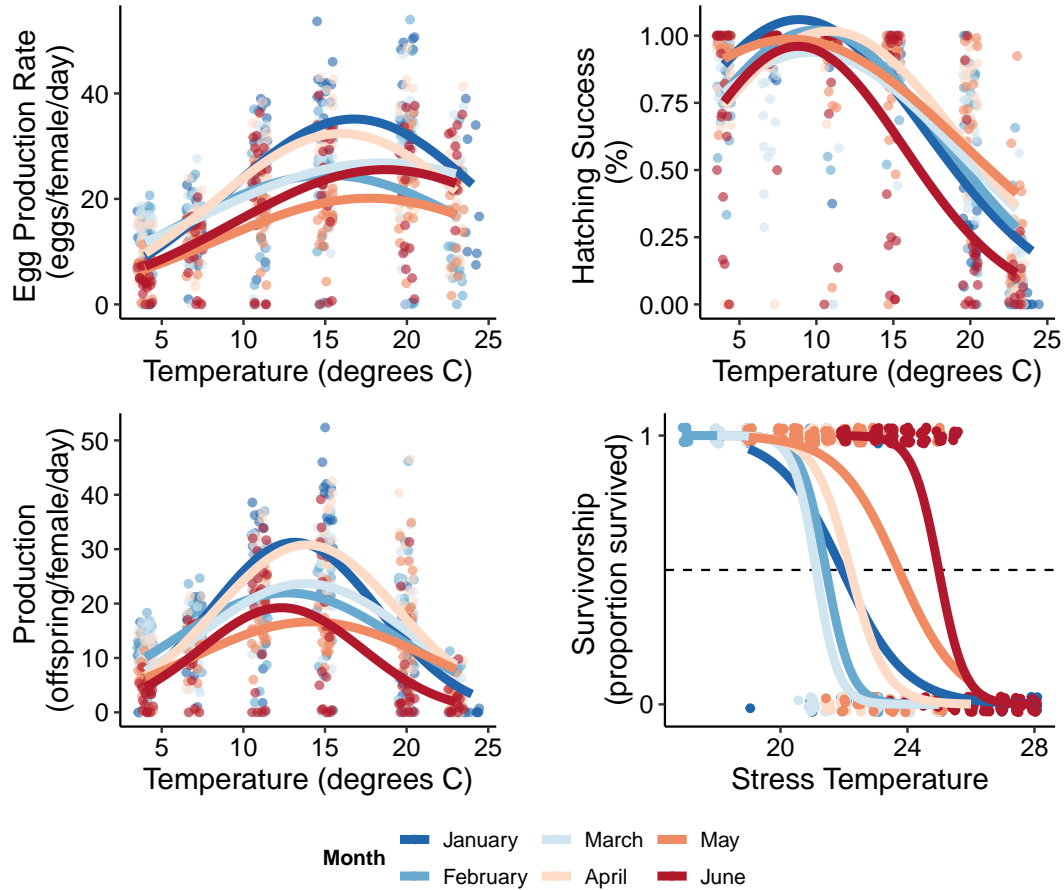
Period	Treatment	Temperature
Early	Control	17
Early	Heatwave	22
Mid	Control	22
Mid	Heatwave	27
Late	Control	12

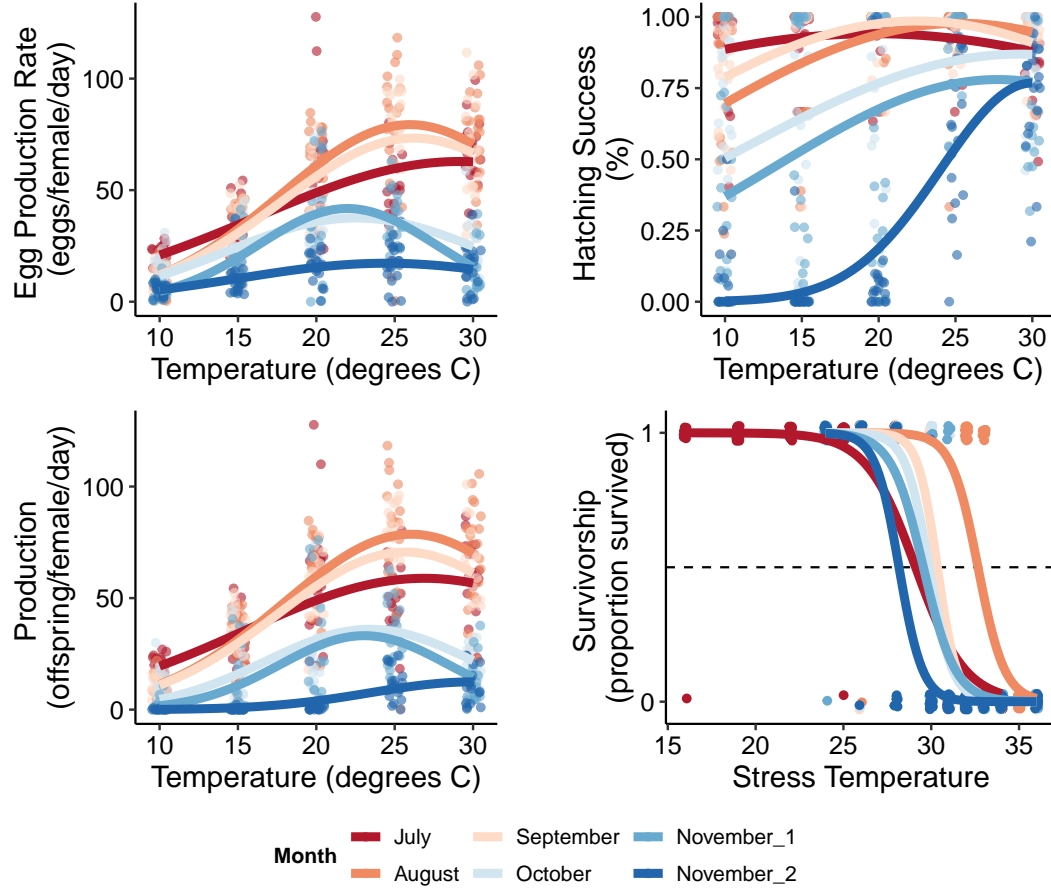
Period	Treatment	Temperature
Late	Heatwave	17

3 Results

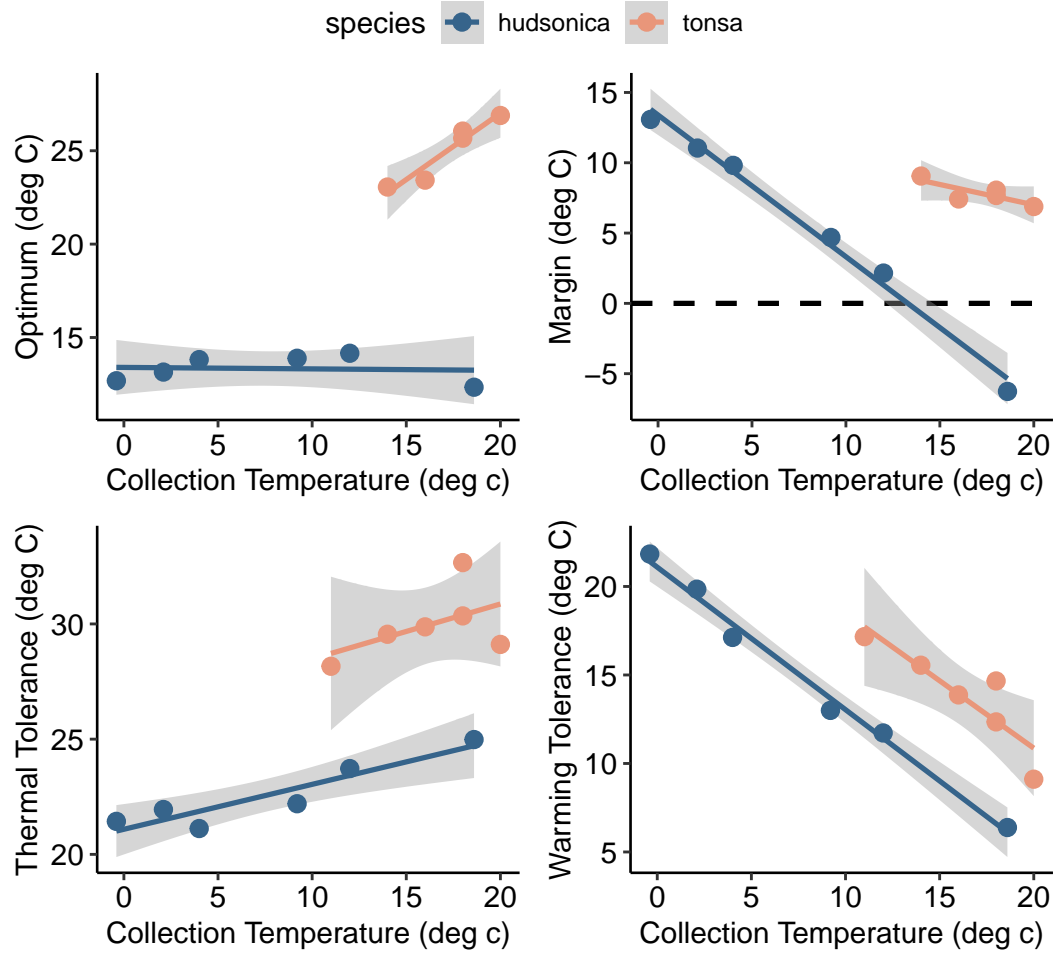
3.1 Seasonal Variation in Field TPCs

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.

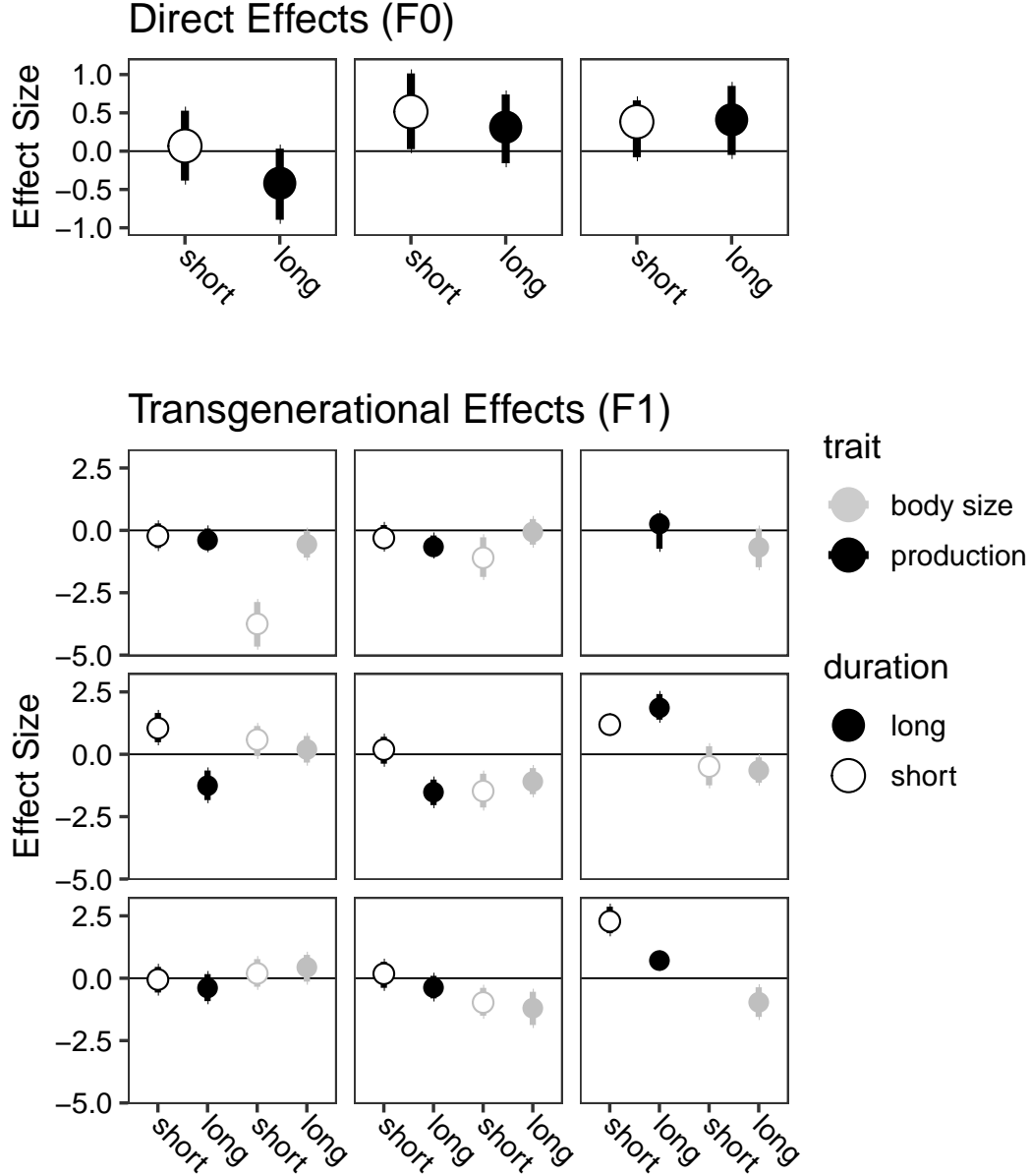
3.2 Effects of Simulated Heatwaves

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 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.

3.3 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.

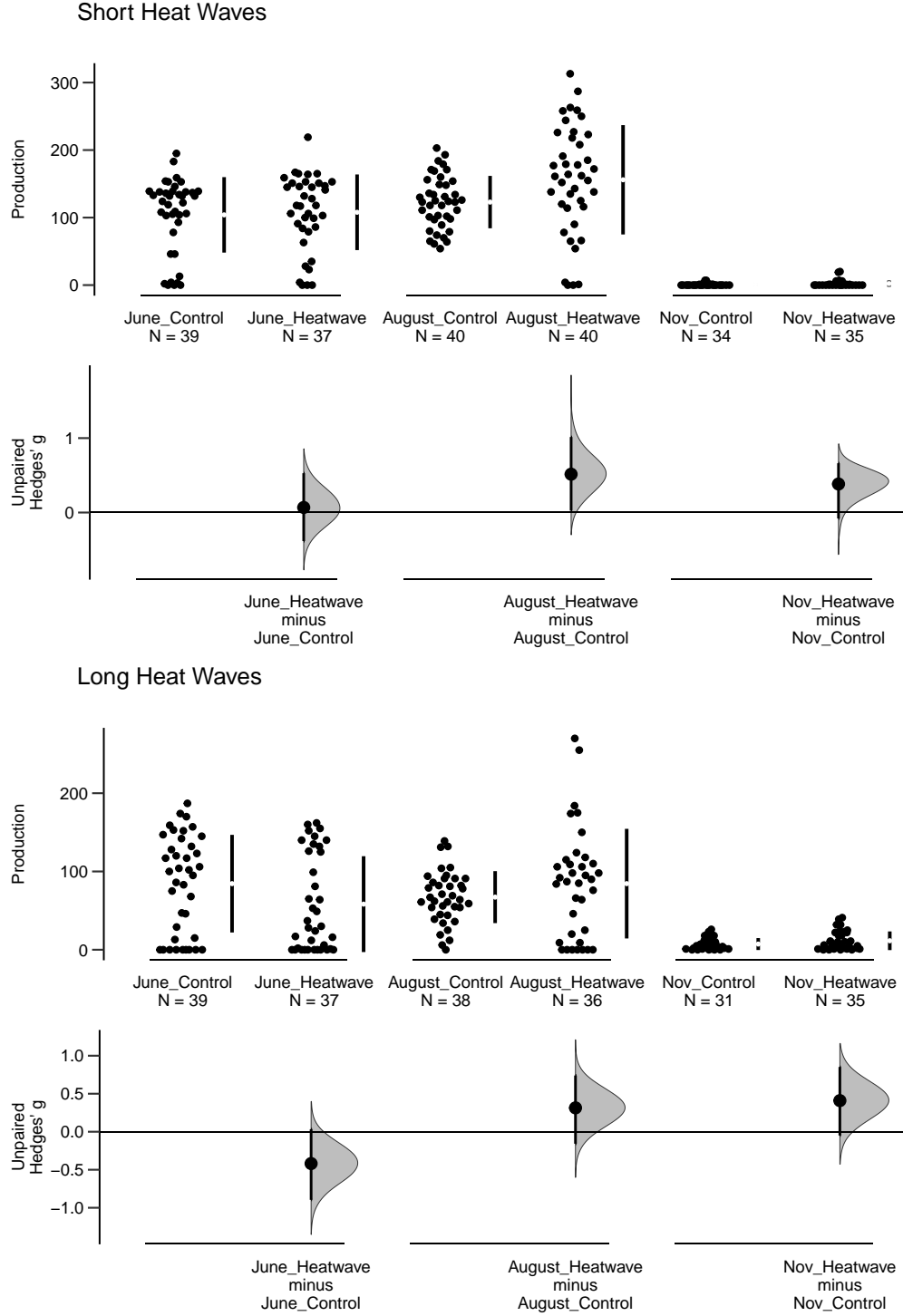
3.4 Discussion

General patterns are scarce 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.

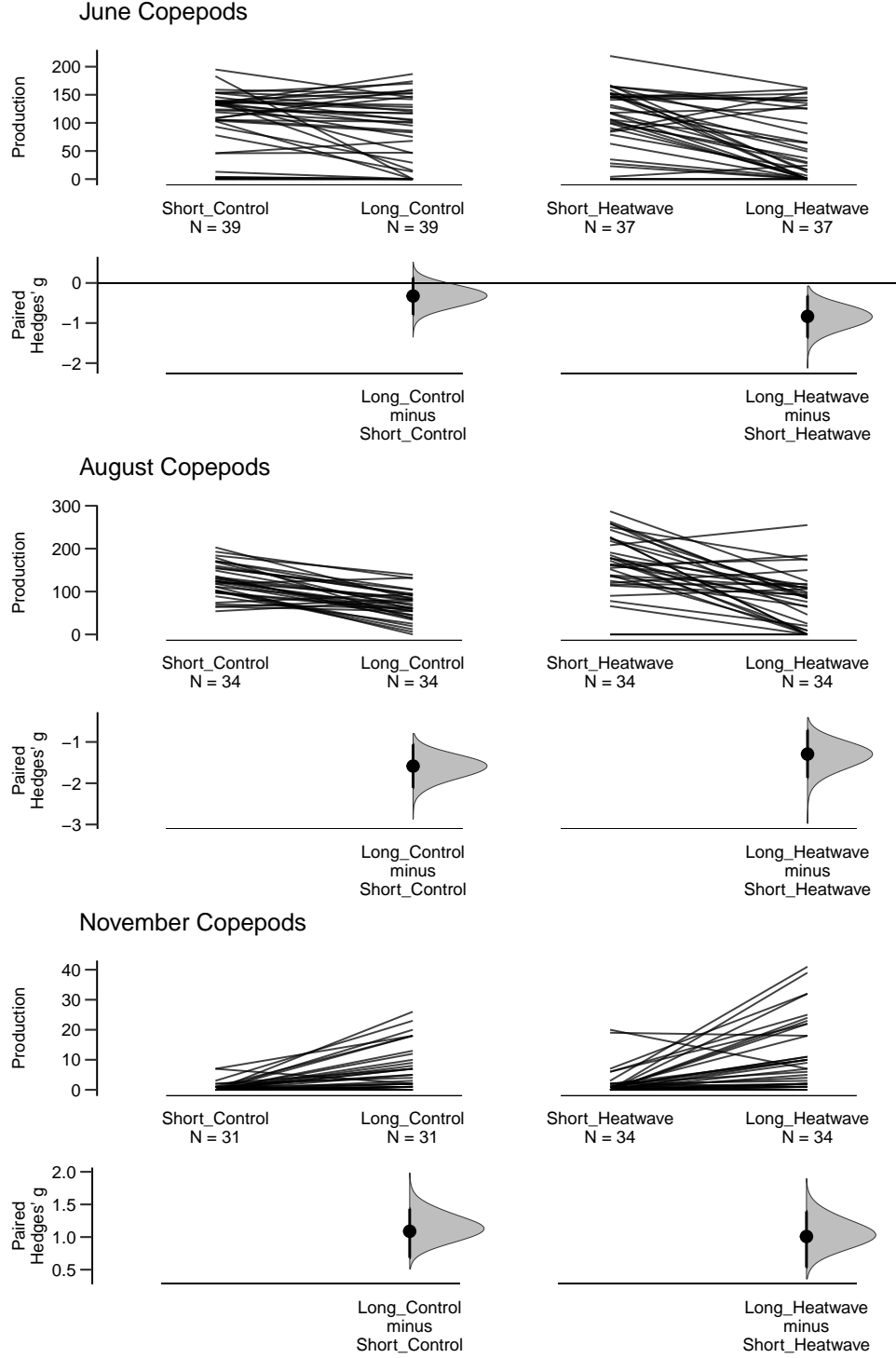
The expectation is that production should decrease as body size decreases due to the effects on EPR. However, the changes in production were independent of changes in body size (Supp. Fig. 6). Instead, the observed effects are more likely to be the result of other mechanisms (such as maternal effects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

4 Supplemental Information

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 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.



Here, the Gardner-Altman plot has been modified to show the repeated measures for each female using a Tuftes slopegraph instead of a swarmplot. Production was generally lower in Days 5 to 7 than during days 1 to 3, regardless of treatment (heat wave vs. control), although not for all collections (production increased in the longer trials in November) - However, note the y-axis scale for the female responses relative to those from the other months. A similar decrease in both control and heatwave treatments might suggest effects of aging on female reproductive output. A stronger decrease in the heatwave treatment than in the control, might indicate cumulative effects of the increased temperature. An increase in production over time might be expected from the effects of beneficial acclimation.



The effects of parental heatwave exposure varied strongly between collections, heatwave duration, and offspring temperature. As a reminder, these represent carry-over effects of heat waves - differences observed here do not represent the direct effects of heat waves, but rather indirect effects of parental exposure to heat waves. In June, Short heatwaves increased production relative to controls at intermediate offspring temperatures, while long heat waves decreased production relative to controls. In August, short heat waves had very little effect on production, while long heat waves generally decreased production. In November, both long and short heatwaves had positive effects on production at intermediate temperatures. Short heatwaves also increased production at high offspring temperatures relative to the control.

