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RESEARCH ARTICLE

Marine Heatwaves Special Feature

Seasonally variable thermal performance curves prevent adverse effects of heatwaves

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Abstract

1. Differential vulnerability to heatwaves may affect community dynamics in a changing climate. In temperate regions, this vulnerability to heatwaves depends on the interactions between seasonal temperature fluctuations and the capacity to rapidly shift thermal performance curves.
2. Here we investigate how these dynamics affect the vulnerability of two ecologically important copepod congeners, *Acartia tonsa* and *A. hudsonica*, to heatwaves of different durations. Using a combination of field observations and simulated laboratory heatwave experiments, we uncover strong seasonal variation in the performance curves of *A. tonsa* but not *A. hudsonica*. This translated to species-specific seasonal patterns of vulnerability to heatwaves, with increased vulnerability in *A. hudsonica*.
3. By reducing parental stress during simulated heatwaves, seasonal performance curve shifts likely reduced indirect, transgenerational effects of these events on offspring performance in *A. tonsa*.
4. Our results illustrate how different levels of seasonal variation in thermal performance curves will affect population persistence in a changing climate

KEYWORDS
climate change, copepod, heatwave, seasonal variation, thermal performance, transgenerational plasticity

1 | INTRODUCTION

Heatwaves are increasing in frequency and intensity in aquatic ecosystems (Frölicher & Laufkötter, 2018; Oliver et al., 2018; Tassone et al., 2022). These periods of anomalously high temperatures are typically expected to present severe challenges to marine biota (Smale et al., 2019). The factors shaping the effects of these events on communities are, however, complex—whether heatwaves increase or decrease performance relative to typical conditions will be strongly dependent on the current proximity of ambient temperature to an organism's thermal optimum, the amount of intraspecific diversity within a population, the relative vulnerabilities of the different component taxa to increased temperatures (e.g. inter-specific variation in thermal performance curves), previous thermal history (e.g. King et al., 2024; Samuels et al., 2021), and interactive effects of temperature and other stressors (e.g. hypoxia, nutrient limitation, etc.). Understandably, much attention has been focused on macro-organisms like coral, kelp and fish, on which heatwaves have had significant, highly visible effects (Joyce et al., 2024; Smith et al., 2023). Heatwaves can also have profound effects on planktonic communities (Brown et al., 2024), shaped by temperature-driven changes in metabolism, reproduction, competitive ability and survival (Evans et al., 2020; Maazouzi et al., 2008; McKinstry et al., 2022). By altering the dynamics and the distributions of planktonic communities, the impacts of heatwaves may manifest across the food web (Gomes et al., 2024).

Characterizing the thermal sensitivity of planktonic taxa is crucial for predicting the effects of marine heatwaves on food webs and ecosystem functioning. Thermal performance curves provide key insights into the direct effects of increased temperature on organisms and population dynamics (Angilletta, 2009; Arroyo et al., 2022; Deutsch et al., 2022; Hochachka & Somero, 2002). However, there is often key variation in thermal performance within populations of planktonic taxa (e.g. Samuels et al., 2021), and in taxa with short generation times, seasonal acclimatization and genetic differentiation can rapidly change thermal performance curves to track environmental temperatures (Rudman et al., 2022; Sasaki & Dam, 2020), altering patterns in vulnerability (Williams et al., 2008). Further, the effects of heatwaves on populations may also be propagated across generations by mechanisms like trans-generational plasticity and maternal effects, which can have important effects on offspring performance (Dinh et al., 2021; Truong et al., 2022). These fine-scale temporal dynamics need to be accounted for when predicting the effects of heatwaves on populations of planktonic and other short-lived taxa.

Vulnerability to adverse effects of heatwaves is often assumed to be largest during the warmest seasons when environmental temperatures are nearest to organismal thermal optima (although studies examining vulnerability during cooler seasons are dramatically underrepresented in the literature; Dinh et al., 2023). This can be modified, however, by seasonal variation in thermal performance (Tran & Johansen, 2023). In planktonic taxa, this seasonal variation may be underlain by acclimatization within generations (Hahn & Brennan, 2024), transgenerational effects across generations and seasonal genetic differentiation (Sasaki & Dam, 2020). Regardless of mechanism, this variation may play an important role in determining the effects of heatwaves on a population (Figure 1). Much of the past work on the effects of heatwaves assumes performance curves are fixed (i.e. there is no seasonal variation in TPCs). In this case, the effect of heatwaves would be predicted to change over the course of the season as the relative position of environmental temperatures to TPC optimum temperature and upper thermal limit varies. Under these conditions, heatwaves during cooler seasons may result in increased performance, as temperatures shift closer to the thermal optimum. The realized effect of these increases in performance depends heavily on life history; for taxa that enter diapause or dormancy during cooler periods, for example, increases in performance during a winter heatwave may actually reduce individual fitness via depletion of lipid reserves and changes in phenology (Wilson et al., 2016). Alternatively, variation in TPCs over seasonal timescales may act as a buffer against negative effects of heatwaves if optimum temperatures maintain a fixed position above environmental temperatures, limiting exposure to temperatures in excess of thermal optima. Differences in the magnitude of seasonal variation in TPCs between taxa may therefore play a key role in shaping patterns in relative vulnerability of community members to heatwaves.

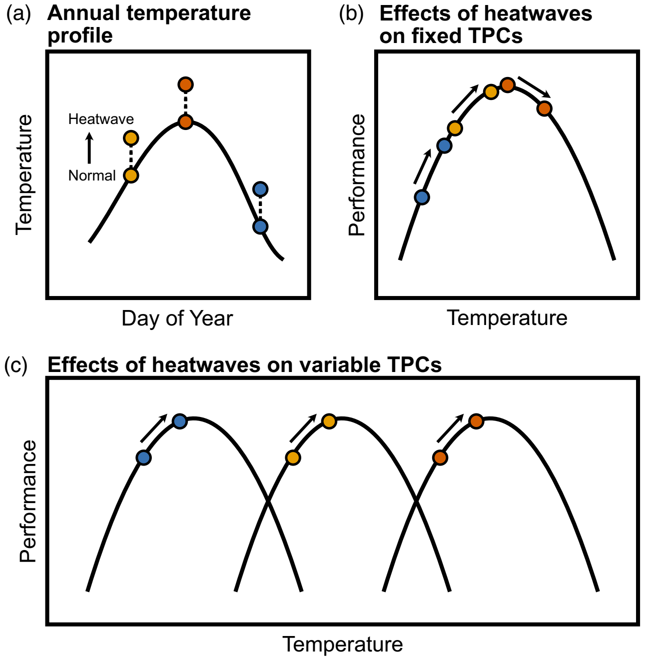

FIGURE 1 Schematic illustrating the effects of heatwaves on performance. (a) Heatwaves may occur at various times throughout the year, resulting in acute increases in temperature against a seasonally variable baseline temperature (shown here for a hypothetical example in the Northern Hemisphere). (b) Static thermal performance curves result in seasonally variable effects of heatwaves on performance. Heatwaves that occur when temperatures are low relative to the optimum would be expected to increase performance (a beneficial effect). Heatwaves that occur when temperatures are near or past the thermal optimum may decrease performance (a detrimental effect). (c) Variable thermal performance curves reduce seasonal variation in the effects of heatwaves on performance, when thermal optima are positively correlated with environmental temperatures. An increase in temperature would then be expected to increase performance, regardless of the seasonal timing of the heatwave.

Given their short generation times, large abundance and ecological importance in marine systems (Dam, 2013), copepods are an ideal model system to examine the interplay between seasonal variation in thermal performance curves and the direct and indirect effects of heatwaves. Here we characterize how thermal performance curves for key fitness related traits (egg and offspring production, hatching success and survivorship) of the ecologically important copepod species *Acartia hudsonica* and *A. tonsa* change over the season of occurrence, and how this variation shapes vulnerability to heatwaves. We also quantified seasonal variation in both direct and trans-generational effects of heatwaves on one of the species (*A. tonsa*) 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 *A. hudsonica* and *A. tonsa*; and (2) that seasonal variation in TPCs will minimize negative transgenerational effects of heatwaves.

2 | MATERIALS AND METHODS

2.1 | Generating field TPCs

All analyses were performed in R version 4.1.3 (R Core Team, 2021). Copepods were collected from eastern Long Island Sound, USA (41.31, −72.07) several times throughout the year using surface tows of a 200 μm mesh plankton net (Table 1). No special permissions were required for this field work, and no elements of this study required ethical approval. Mature *Acartia hudsonica* or *Acartia tonsa* females were isolated from the contents of the plankton tow during their respective seasons of occurrence, and placed individually in petri dishes for egg production and hatching success assays. Typically *A. hudsonica* is only abundant during the winter and spring, while *A. tonsa* dominates the summer and fall plankton community. During these assays, females were fed maximum rations of a mixture of *Tetraselmis* spp. and *Thallasiosira weissfloggi*. This diet has been used to maintain large cultures of these copepods for many generations (Dam et al., 2021; Sasaki & Dam, 2021). Females produced eggs for 3 days, after which the female was removed. Eggs were given three additional days to hatch. Egg production (EPR; the total number of eggs produced per female per day), the hatching success (HS; percentage of eggs produced that hatched) and the total offspring production (OP; the number of nauplii produced per female per day, which integrates the egg production rate and the hatching success values) were measured for each individual. These assays were performed across a range of temperatures (10–30°C for *A. tonsa* and 4–24°C for *A. hudsonica*) using stand up incubators (Fisher Scientific Model #3720), with temperature ranges selected for the two species to cover the range of temperatures typically experienced during their respective seasons of occurrence. Maximum trait values and thermal optima were extracted from thermal performance curves (TPCs) for egg production, hatching success and offspring production, modelled using a Gaussian equation (Lynch & Gabriel, 1987; Padfield et al., 2021),

$$\text{trait} = r_{\max} * \exp^{\left(-0.5\left(\frac{|\text{temp}-t_{\text{opt}}|}{a}\right)^2\right)}$$

Here, $r_{\max}$ refers to the maximum trait value, observed at the thermal optimum (t_{opt};°C). Assay temperature (°C) is indicated by temp. The parameter *a* is related to the width of the performance curve.

Thermal survivorship curves were also determined for each of these collections by exposing individual females to an acute 24-h heat shock across a range of temperatures (Sasaki & Dam, 2019). Individual females were placed in a 2.5 mL microfuge tube with 0.2 μm filtered seawater, and moved to 15-well drybaths (USA Scientific). Each drybath was set to a single temperature, ranging from 17 to 28°C for *A. hudsonica* and 16–36°C for *A. tonsa*. In both species, these ranges extend from a low temperature with 100% survival to a high temperature with 0% survival. The lower temperature was selected to ensure 100% survival in both the cold-adapted *A. hudsonica* and warm-adapted *A. tonsa*. The maximum temperature used differs between the two species, reflecting the higher thermal tolerance in *A. tonsa* than *A. hudsonica*. Survivorship was checked after 24 h. Each female experienced only one temperature during the assay, with survivorship curves then modelled using a logistic regression of individual survivorship against stress temperature. Note that these survivorship curves are different from other forms of survival analyses (e.g. monitoring survival under fixed conditions over time). Survivorship curves were estimated separately for each collection and used to estimate thermal tolerance (as LD50, the temperature of 50% mortality).

To determine whether TPC parameter variation tracked seasonal temperature changes, we regressed the TPC parameters against the temperature at the time of collection. A significant, positive relationship between collection temperature and TPC parameters (especially thermal optimum and thermal tolerance) would indicate that TPCs varied in relation to the seasonal temperature cycle.

TABLE 1 Details for the field thermal performance curve collections.

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

Note: The date and water temperature at the time of collection are provided for each group, along with which species was collected. The exact date for the June 2015 collection of *Acartia hudsonica* was not available.

2.2 | Simulated heat waves

To examine transgenerational effects of heatwaves, we collected *Acartia tonsa* from the same site 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 the peak environmental temperatures, corresponding to late June, late July, and early December (Table 2). These experiments examined both direct and transgenerational effects of heatwaves. To examine the direct effects, EPR, HS, and OP were measured for around 60 females per collection, split into two groups (control and heatwave; sample sizes provided in Table 2). 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°C above the ambient temperature (Table 2). A 5°C increase in temperature represents a substantial heatwave event, reflecting the expected near-term increase in heatwave intensity in this region. During the simulated heatwave, traits were measured after two periods to examine the effects of short and long heatwave events. Eggs were first collected on day 3 and females were moved into petri dishes with fresh food solution. On day 5, females were again moved to petri dishes with fresh food solution. Eggs produced during the intervening period were not examined. Finally, eggs were collected again on day 7, representing eggs produced after exposure to a longer heatwave. To summarize, the effects of short and long heatwave events were examined by collecting eggs produced from days 1–3 and days 5–7, respectively. Eggs were given an additional 3 days after collection to hatch before measurements were made.

We used effect sizes (Hedge's *g*) to examine how heatwaves and the duration of exposure affected copepod performance (Berner & Amrhein, 2022; Gardner & Altman, 1986; Ho et al., 2019). Two sets of effect sizes were estimated within each collection: the effect of duration within treatments (long control vs. short control and long heatwave vs. short heatwave), and the effect of treatment (short heatwave vs. short control and long heatwave vs. long control). A negative effect size represents a reduction in the variable of interest as either (1) experimental duration increases, or (2) when copepods were exposed to heatwave conditions. Each effect size estimate also included a 95% confidence interval (CI), estimated by non-parametric bootstrapping (Ho et al., 2019). Hedge's *g* was used instead of mean or median difference to account for the drastic seasonal differences in the magnitude and variation of egg production and hatching success observed between collections.

2.3 | Transgenerational effects

In addition to the direct effects of heatwaves, we also examined the effects of parental exposure to increased temperature on offspring performance (i.e. transgenerational effects). From the same collections described above, several hundred adult *A. tonsa* were placed into each of eight 4 L buckets of filtered seawater, which were split between the control and heatwave temperatures for that collection ($n = 4$ buckets per temperature). Cultures were provided with food ad libitum and kept oxygenated using a small aquarium pump. Eggs were collected from each bucket following the same schedule as the direct effect experiments (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. For each collection, we therefore had four groups of offspring, those with parents exposed to control and heatwave temperatures for either 3 or 7 days.

Eggs for each time period were pooled together and then split into three groups which developed at either 12, 17, or 22°C. These rearing temperatures were used for all three collections, and reflect the temperatures observed at the times of collection. During development, individuals were maintained in 4 L buckets of filtered seawater and fed ad libitum. After these individuals matured, body size and the three reproductive traits (egg production, hatching success and offspring production) were measured at the respective rearing temperature.

As for the F0 generation, we used effect size estimates (Hedge's *g*) to examine how parental conditions affected offspring traits. For each seasonal collection we examined the effect of treatment within each developmental temperature (short heatwave vs. short control and long heatwave vs. long control). As offspring of the different batches of parents developed under identical conditions within each temperature, an effect of treatment in these comparisons indicates a transgenerational effect of parental exposure to heatwave conditions. As before, a negative effect size indicates a trait reduction when parents were exposed to heatwave conditions, and a positive effect size indicates a trait increase when parents were exposed to heatwave conditions.

TABLE 2 Details for the simulated heatwave collections.

Period	Date	Field temp.	Control temp.	Simulated heatwave temp.	Sample sizes (control, heatwave)
Early	27 June 2015	17.8	17	22	39, 37
Mid	29 July 2015	22.4	22	27	38, 36
Late	1 December 2015	12.0	12	17	31, 35

Note: The date and water temperature at the time *A. tonsa* individuals were collected from the field is provided for each group, along with the temperatures used for the control and heatwave exposures.

Variation in F1 offspring body sizes was also examined using a linear model (size as a function of parental treatment, duration, offspring temperature, and month, with all interactions). Model assumptions (posterior predictive checks, linearity, homogeneity of variance, influential outliers, and the normality of residuals) were checked with the performance package (Lüdecke et al., 2021) and are visualized in Figure S1. Two sets of posthoc contrasts were determined using emmeans (Lenth, 2024): (1) all contrasts between control and heatwave treatments for each duration, rearing temperature and month combination; and (2) the body size—offspring temperature trend for each parental treatment, duration and month combination.

3 | RESULTS

3.1 | Seasonal variation in field TPCs

TPCs for the two species were strongly diverged. There was also noticeable seasonal variation in the TPCs of *Acartia tonsa* (Table S1). *Acartia hudsonica* egg production rate (EPR) TPCs had lower thermal optima and varied less across the season than those of *A. tonsa* (Figure 2). Across *A. tonsa* TPCs, EPR optimum temperatures tended to be higher in warmer months (Figures 2 and 3). Hatching success (HS) TPCs for *A. hudsonica* were also narrower and less seasonally variable than those of *A. tonsa*. Hatching success was higher for *A. tonsa* in warmer months than cooler months, regardless of incubation temperature. This is especially evident for the second November collection of *A. tonsa*, which exhibited very low hatching success at all but the highest temperatures used in the assays. When combined, the variation in EPR and HS TPCs yielded offspring production (OP) curves that were highly variable in *Acartia tonsa*. Collections from warmer months generally had higher maximum production values and slightly higher optimum temperatures, although the narrow hatching success TPC of the second November collection produces a production TPC strongly skewed towards warmer temperatures, going against this trend. The complete set of EPR, HS and OP maximum rates and thermal optima are provided in Table S1.

Thermal optima of the OP TPCs were related to collection temperature for *A. tonsa* but not *A. hudsonica* (Figure 3). The values from the second November collection of *A. tonsa*, which had the highest production thermal optimum despite being collected at the lowest temperature, were excluded from this analysis; these copepods were collected at 11°C, which is around the threshold for resting egg production in *A. tonsa* (Holste & Peck, 2006). The extremely high estimated optimum temperature for production in this collection may

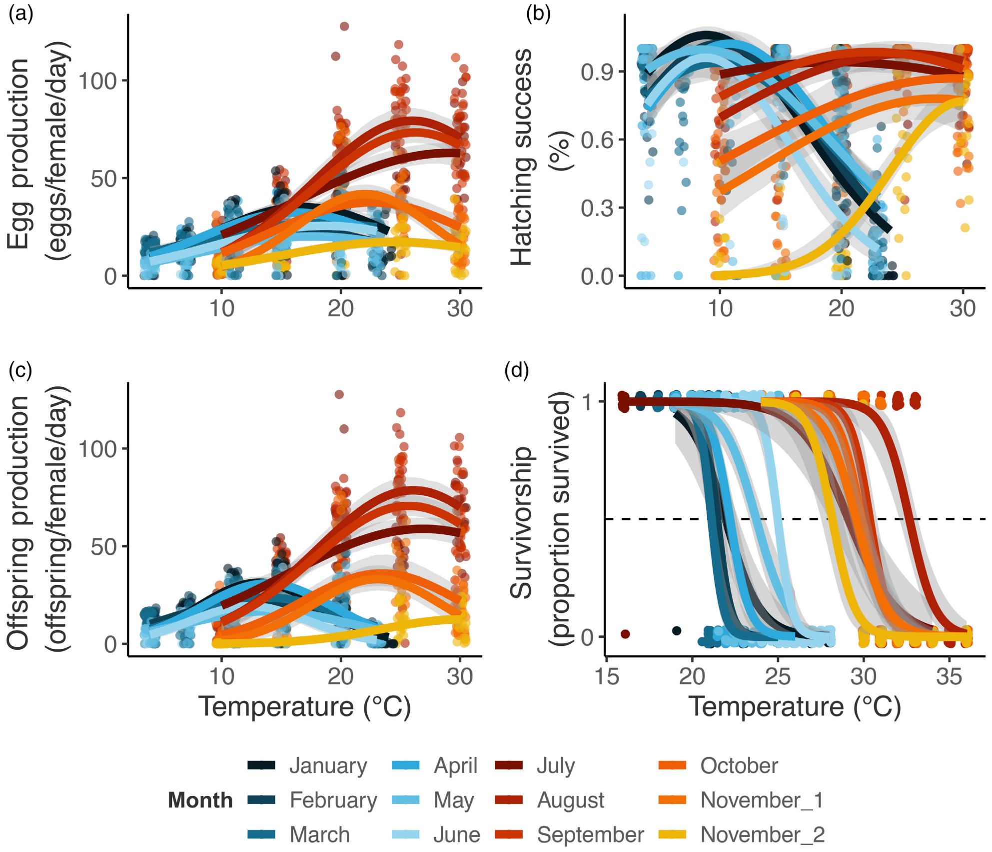

FIGURE 2 Thermal performance curves for each of the collections, each shown in a different colour. Curves in the blue range (January through June) are for *Acartia hudsonica*, while curves in the red range (July through November) are for *A. tonsa*. (a–c) show points for each individual measurement along with the estimated Gaussian regression line. (d) shows individual survivorship measurements following a 24-h acute heat stress. Survivorship curves are estimated as logistic regressions. Note that the *x*-axis range differs in (d).

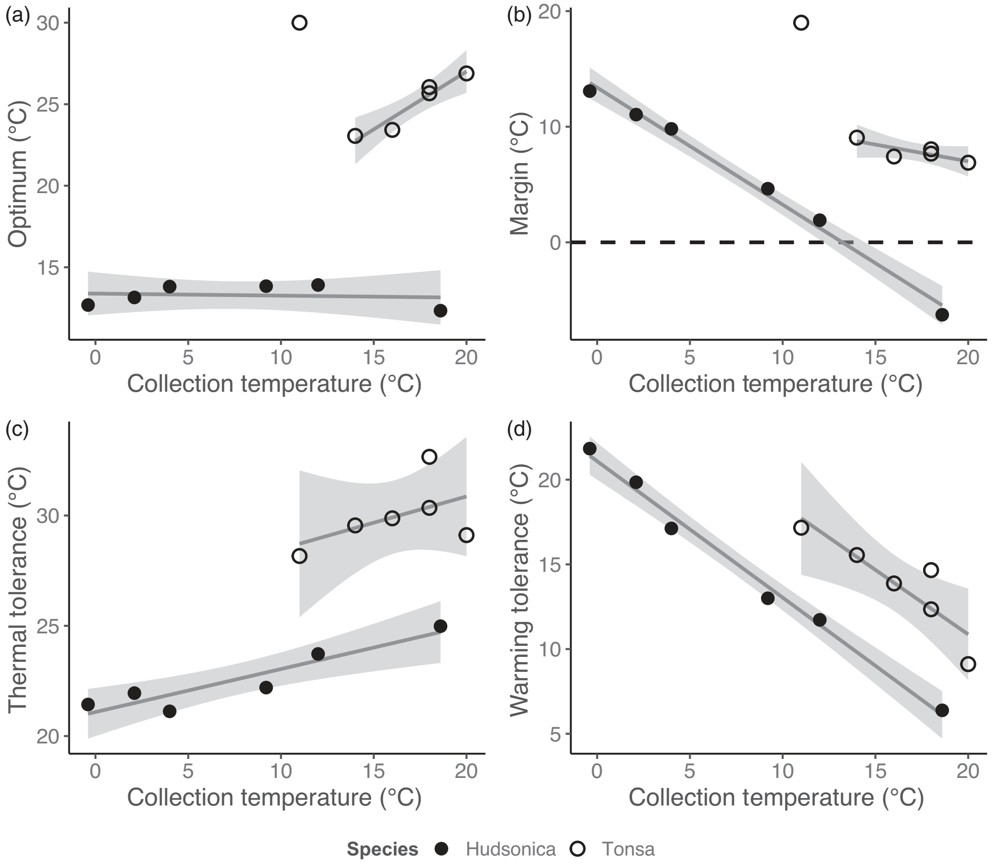

FIGURE 3 Relationships between (a) thermal optimum, estimated from the offspring production thermal performance curves, and collection temperature; (b) the thermal safety margin (calculated as the difference between thermal optimum and collection temperature) and collection temperature; (c) thermal tolerance, measured as LD50 and collection temperature; and (d) warming tolerance (calculated as the difference between thermal tolerance and collection temperature) and collection temperature. The two Acartiid species are shown with different symbols. Linear regressions with confidence intervals are included.

therefore reflect the difference in hatching requirements between resting and subitaneous eggs. Thermal survivorship curves were variable in both species, with a range of LD50 values around 5°C in both species. Thermal tolerance increased with collection temperature in both species. Vulnerability to heatwaves was estimated using two metrics: thermal safety margins for offspring production (the difference between thermal optimum and collection temperature) and warming tolerance for survivorship (difference between thermal tolerance, LD50 and environmental temperature; Deutsch et al., 2008). Thermal safety margins of the two species responded differently to changes in collection temperature (Table S2). The invariant OP thermal optima for *A. hudsonica* results in a strong decline in thermal safety margins as water temperatures increase (Figure 3; Figure S2). Indeed, the warmest collection of *A. hudsonica*, occurring ~19°C, appears to have been above the population's thermal optimum. By contrast, the seasonally variable *A. tonsa* production TPCs resulted in relatively stable thermal safety margins (Figure 3; Figure S2). Throughout its season of occurrence, *A. tonsa* maintained a safety margin of at least 5°C. In both species, warming tolerance responded in a similar manner to changes in collection temperature (Table S3; Figure S2), with decreases in warming tolerance as water temperatures increased (Figure 3; Figure S2). While collection temperatures never exceeded thermal tolerance for either species, the lower thermal tolerance of *A. hudsonica* translated to reduced warming tolerance relative to *A. tonsa*.

3.2 | Effects of simulated heatwaves

The second component of this project examined the effects of simulated heatwaves across generations in seasonal collections of *Acartia tonsa*. This began by assessing the impact of a simulated warming event on field collected (F0) individuals. We examined the effects of warming for 1–3 days (short duration) and 5–7 days (long duration) on EPR, HS and OP (Figure 4; Figures S3 and S4a) although we will focus on the effects of offspring production as this integrates across the other two traits. The impact of these warming events was assessed using an effect size estimate (Hedge's *g*), comparing the warming to the control treatment. Simulated heatwaves of both durations generally had a small positive effect on offspring production (positive effect size), with the exception of long heatwaves in June, which had a small negative effect (negative effect size; Figure 4, top

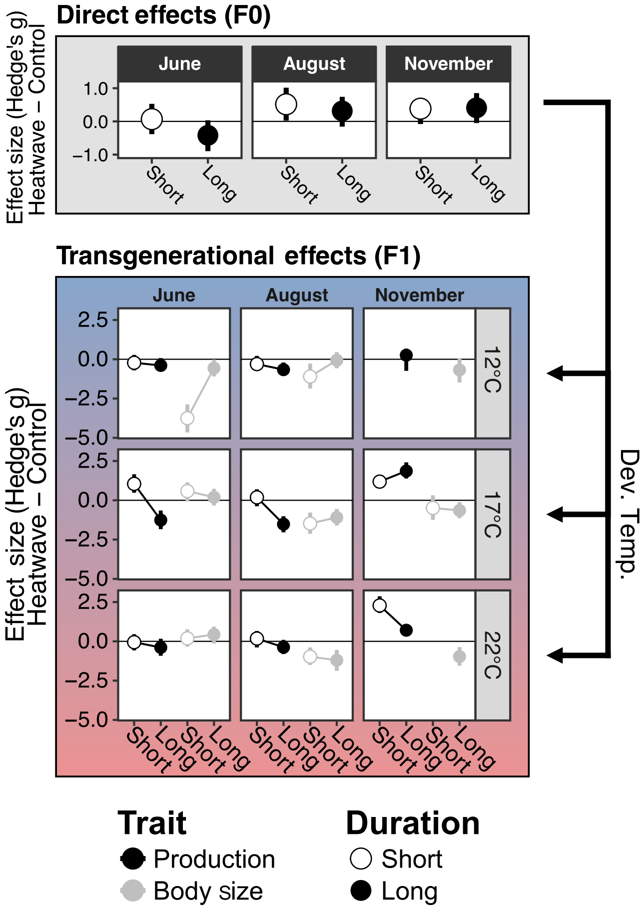

FIGURE 4 The effects of simulated heatwaves on offspring production and body size. (a) The direct effects of elevated temperature (field-caught F0 individuals), estimated as the effect size (Hedge's *g*) calculated for the comparison between offspring production by copepods exposed to heatwave and control treatments. A negative effect size indicates exposure to elevated temperature decreased offspring production. The two different durations, short and long events, are shown with different symbols. (b) The indirect, transgenerational effects of parental exposure to elevated temperature were also estimated as an effect size using Hedge's *g*. Each panel shows data for 1 month and one developmental temperature. The different durations are again represented with different symbols, while offspring body size and production are shown in different colours. Here, a negative effect size indicates that parental exposure to elevated temperature decreased offspring production or body size relative to individuals whose parents did not experience elevated temperatures. A positive effect size indicates that parental exposure to heatwave conditions increased the trait value.

row). Results for the other traits were highly variable across collection and duration (Figure S4a), but effect sizes tended to be fairly small (Hedge's *g* between −1 and 1; Figure 4). For the June collection, there was a small increase in EPR in response to acute warming, and a small decrease in HS in response to the longer duration event (Figure S4a). Offspring production, integrating both EPR and HS, exhibited only a small decrease in the longer duration warming treatment. In the August copepods, there was a small increase in EPR and a small decrease in HS during both short and longer events (Figure S4a). The increase in EPR was large enough, however, to result in a small increase in OP during both short and long events. In November, warming resulted in a large increase in EPR (Figure S4a) regardless of the duration of the event (Hedge's $g > 1$). There was no effect of warming on HS, however, limiting the increase in OP.

We also examined the effect of warming duration (the comparison between long and short events within treatment) on the three traits. Here, we observed similar effects of duration on OP in both control and warming groups, in all 3 months (Figure S5); in all cases there were slight decreases in production over time for the June and August collections and an increase in production for the November collection. The similarities in the effect of duration between the control and heatwave treatments suggests that seasonal variation in the effects of warming may be more consequential than differences between short and long events (at least at the daily to weekly timescales examined here).

3.3 | Transgenerational effects of simulated heatwaves

For the transgenerational experiments, the comparison between control and heatwave treatments examines the indirect effect of parental exposure to heatwaves on offspring performance. Results were again highly variable across developmental temperatures, parental exposure duration and monthly collections. For the June and August collections, effect sizes were often similar across all three reproductive traits (Figure S4b; see June copepods at 17°C and 22°C, and August copepods at 12°C). When effect sizes differed between traits, EPR tended to be most strongly affected by parental exposure to warming (see June copepods at 18°C and August copepods at 17 and 22°C). Differences in the effects of parental exposure to heatwaves on EPR and HS often ameliorated the overall effect size on OP, which was generally smaller than those for the other traits. There were, however, significant decreases in production driven by parental exposure to longer duration warming in offspring developed at 17°C for both June and August collections. A small increase in production resulted from parental exposure to short duration warming in the June copepods reared at 17°C. This was the only observation in the effect size comparisons of a positive effect of parental exposure to warming on production for the June and August copepods.

Effects of parental exposure to elevated temperature on November copepods were drastically different from those observed in June and August copepods. Instead of primarily affecting EPR, parental exposure to heatwave conditions generally had large effects on HS in the November copepods (Figure S4b). Additionally, unlike in June and August, there were no negative effects of parental exposure to warming on production values (Figure 3). However, nauplii in the 12°C developmental temperature group produced by parents exposed to short heatwaves did not successfully reach adulthood, potentially indicating strong lethal effects of parental exposure on offspring survival.

In all three collections, parental exposure to the heatwave conditions generally (but not always) reduced offspring body size. The effects of parental exposure to warming on production and body size were not correlated (Figure S6). Offspring body size generally decreased with developmental temperature (Figure S7). However, there were, at times, substantial differences in the observed temperature sensitivity of offspring body size between the two treatments; in June, parental exposure to heatwaves slightly decreased the temperature sensitivity of offspring body size, while a long heatwave during August increased the temperature sensitivity. The results of the linear model were largely concordant with the effect size estimates for body size, with parental exposure to longer heatwaves generally decreasing body size in the F1 individuals (Figure S8).

4 | DISCUSSION

The rapid, intense warming associated with heatwaves and other extreme events may have dire consequences for ecological dynamics in aquatic systems. Responses to these acute events are determined by the position of thermal optima and limits relative to environmental temperatures and are therefore mediated by processes that can shift the thermal performance curve. In taxa with short generation times, phenotypic plasticity and genetic differentiation may result in TPC variation that tracks ambient temperatures, maintaining a buffer against detrimental effects of heatwaves. Further, exposure to elevated temperatures during heatwaves may have indirect, transgenerational effects on offspring that are important to account for. We show that TPCs of *Acartia tonsa* but not *A. hudsonica* vary across seasons and that this variation allows the population of *A. tonsa* in Long Island Sound to maintain a relatively constant margin between optimum temperatures and ambient environmental temperatures. In *Acartia tonsa*, the mechanisms that produce seasonally variable TPCs, whether genetic or plastic, reduced the potential for heatwaves to adversely affect population dynamics and thus increase resilience in the face of climate change. We also used a series of simulated heatwave experiments to compare the transgenerational effects of short and long duration events throughout the year in *Acartia tonsa*. We observed significant variation in the transgenerational effects of heatwaves between collections, but results generally suggest only minimal deleterious effects of heatwaves on population dynamics across all seasonal collections. It may be that seasonal variation in thermal performance curves reduces parental stress during exposure to heatwave conditions, thus mitigating transgenerational effects on offspring performance.

Differing seasonal patterns in variation of thermal performance curves may affect which species will be most strongly affected by the increasing frequency and intensity of heatwaves. As a result of invariant TPCs, we observed strong seasonal variation in the vulnerability of *A. hudsonica* to heatwaves; as ambient temperature increases, it approaches the population's relatively static thermal optimum. Indeed, late in the season of occurrence, ambient water temperatures actually exceed *A. hudsonica's* thermal optimum. A heatwave at this point would be expected to strongly decrease population performance. By contrast, the variable TPC of *Acartia tonsa* produces relatively stable thermal safety margins, regardless of seasonal timing. As a result, we would predict that heatwaves would increase production by pushing environmental temperatures closer to the thermal optimum of this population. Importantly, the strong seasonal variation in TPCs is critical context for the widespread notion that *A. tonsa* constitutes a eurythermal species (González, 1974; Rahlff et al., 2017)—rather than a broad but fixed thermal performance curve, the large seasonal range of temperatures this population withstands is likely to be strongly affected by rapid shifts in the TPC. By focusing on short time scales, this and other studies highlight that variation in the TPC is fundamental to shaping temporal occurrence in planktonic taxa (Anderson & Rynearson, 2020; Sasaki & Dam, 2020) and will likely play an important role in determining the response of taxa to climate change. Controlled laboratory studies are needed to disentangle the relative contributions of rapid adaptation and phenotypic plasticity to seasonal shifts in the TPCs of *A. tonsa* (Sasaki & Dam, 2019, 2020) and could shed light on the factors limiting seasonal variation in *A. hudsonica* (limited genetic diversity, reduced developmental plasticity, etc.). Ultimately, a more robust understanding of the physiological and genetic mechanisms underlying TPC variation is needed in order to examine why some species can shift their TPCs while others cannot.

Given what was observed in the natural populations of these two species, the increasing incidence of heatwaves may reduce the seasonal occurrence of the cold-water dominant *A. hudsonica* as the thermal optimum is exceeded more frequently. By contrast, performance of the warm-water dominant *A. tonsa* would be expected to increase during mild heatwaves as the increased temperature shifts conditions towards the thermal optimum. These effects may, however, depend on how these two species respond to recurring heatwaves or to smaller, chronic changes in ambient conditions preceding the heatwave. The interactive effects between genetic diversity and exposure history may shape how populations respond to thermal stress (Redana et al., 2024; Samuels et al., 2021), shaping long-term dynamics in a changing climate.

Latitudinal patterns in vulnerability to heatwaves might also be affected by the relative capacity for populations to adjust TPCs. At high latitudes, cold-specialists may lack the capacity to adjust TPCs (Peck et al., 2014), while at low latitudes, the presence of hard upper limits to physiological acclimation (Hoffmann & Sgrò, 2011; Stillman, 2003) may prevent shifts in TPCs to accommodate warming. In both cases, static TPCs would be expected to contribute to heightened vulnerability to heatwaves, similar to what we observed in *A. hudsonica*. An increased vulnerability to warming at low latitudes is observed at both the species- and population-levels (Barley et al., 2021; Morley et al., 2019; Nguyen et al., 2011; Sasaki et al., 2022). It is still an open question, however, how reduced capacity to adjust TPCs may affect the ability of tropical taxa to shift distributions polewards into more variable environments. While TPCs shifted towards higher temperatures will reduce vulnerability to extreme temperatures even during the warmest seasons, inflexible TPCs may result in significant fitness costs during cooler seasons due to a reduction in organismal performance. Additional work is needed on how the relative capacity for variation in thermal performance curves may shape broader biogeographic range shifts by modifying vulnerability to both high and low temperatures.

The transgenerational effects of heatwaves we observed varied in two main respects—the effect of the duration of parental exposure to increased temperatures across offspring developmental temperature treatments and the pattern of this variation across collections. These results indicate that the effects of parental exposure to heatwaves are highly context specific (e.g. that the effects of parental exposure to heatwaves will depend on the exposure history of the parents to other temperature fluctuations), reinforcing that caution is warranted when extrapolating the results of both acute warming and short heatwave events from laboratory experiments to the response of natural populations. However, the general lack of strong detrimental effects does suggest that seasonal variation in TPCs may reduce transgenerational effects of heatwaves by preventing parental stress during these events.

Against the background variation in the effects of parental exposure to heatwaves across collections, however, there were at least superficial similarities between the effects in the June and August collections, and strong differences between these and the November copepods. Past work has shown that seasonal variation in thermal performance has a genetic basis in *A. tonsa* (Sasaki & Dam, 2020). This highlights the importance of considering not only seasonal variation in TPCs, but the mechanistic underpinnings of the variation. In scenarios where seasonal variation is entirely due to plasticity, we would expect broad similarities in the transgenerational effects of heatwaves regardless of offspring developmental temperature. However, where variation in TPCs is produced by genetic changes (or epigenetic differences; Bogan & Yi, 2024), transgenerational effects may also differ, reflecting the interplay between previous environmental exposure history, parental stress, developmental effects, and differing genetic backgrounds. This context dependence is a crucial yet largely unexplored dimension of the response of marine taxa to heatwaves, and experiments manipulating these various factors are much needed.

The increasing frequency of heatwaves is just one of the aspects of climate change, and the ultimate impacts of heatwaves on population dynamics will represent the cumulative effects of multiple factors including, acidification, deoxygenation and changes in food quality and quantity. These multi-stressor interactions have important consequences on evolutionary adaptation (Dam et al., 2021), and may play similar roles in the seasonal vulnerability to heatwaves. In particular, animals in our experiments were fed ad libitum and may have been able to maintain the energetic demands of a robust stress response via increased consumption. Alterations of thermal performance curves by reduced food availability may have strong impacts on population responses to increased temperatures (Huey & Kingsolver, 2019; Rueda-Moreno & Sasaki, 2023). In addition to the organismal basis for observed changes in thermal performance curves (plasticity vs. seasonal genetic differentiation for example), it will be important to identify the environmental drivers for patterns in variation over these relatively short timescales in order to better contextualize the nature of physiological stress (Dowd & Denny, 2020).

Overall, our results highlight that rapid shifts in thermal performance curves, whether plastic or genetic in basis, can buffer populations of short-lived taxa against the deleterious effects of heatwaves that plague longer lived taxa (Smith et al., 2023). Differences in the relative capacity to shift TPCs on ecologically relevant timescales may therefore contribute strongly to the response of community dynamics to heatwaves by affecting the relative vulnerability of community members. Given the critical role planktonic taxa play in the ecological and biogeochemical dynamics of aquatic systems, a more robust, species-specific understanding of the factors that affect vulnerability to heatwaves is important for predictions about the response of these systems to a changing climate.

AUTHOR CONTRIBUTIONS

Hans G. Dam and Michael Finiguerra designed the experiments and acquired funding to support the project. Michael Finiguerra and Matthew Sasaki carried out the experiments. Matthew Sasaki performed analyses, made the graphics and led the writing of the manuscript. All authors contributed substantially to the revision process.

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CONFLICT OF INTEREST STATEMENT

The authors of this manuscript declare no competing interests.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available from a GitHub repository (https://github.com/ZoopEcoEvo/LIS_heatwave). This repository is also archived on Zenodo: https://doi.org/10.5281/zenodo.13988768 (Sasaki et al., 2024).

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SUPPORTING INFORMATION

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

Table S1. Estimated thermal performance curve parameters (thermal optimum and maximum rate value) for egg production (EPR), hatching success (HS), and offspring production (Off. Prod.) for each collection.

Table S2. ANOVA results for a linear regression examining the relationship between thermal safety margin (the difference between thermal optimum of the offspring production TPCs and collection temperature) and collection temperature for the two Acartiid species examined.

Table S3. ANOVA results for a linear regression examining the relationship between warming tolerance (difference between thermal tolerance and collection temperature) and collection temperature for the two Acartiid species examined.

Figure S1. Model diagnostic plots for the linear model examining patterns in the F1 generation body size data, generated using the ‘performance’ package in R: Lüdecke et al. (2021). performance: An R Package for Assessment, Comparison and Testing of Statistical Models. *Journal of Open Source Software*, 6(60), 3139. https://doi.org/10.21105/joss.03139.

Figure S2. Comparison of the (A) safety margin (difference between thermal optimum for offspring production and collection temperature) versus collection temperature slopes and (B) warming tolerance versus collection temperature slopes for the two Acartia species, ±95 percent confidence intervals.

Figure S3. Measured egg production, hatching success, and offspring production values for the F0 and F1 generations in the simulated heatwave experiments (A–C, respectively).

Figure S4. The effects of simulated heatwaves on all four measured traits: body size, production (OP), hatching success (HS), and egg production rate (EPR).

Figure S5. Effect size comparisons between short and long duration events for each collection, along with 95% confidence intervals.

Figure S6. The relationship between the effects of parental exposure to warming on offspring body size and production.

Figure S7. (A) The relationship between offspring developmental temperature and adult body size for individuals produced by parents exposed to different heatwave conditions (control vs. heatwave; short vs. long events). Data is presented split between short and long duration events for each of the three months, with data for offspring of parents exposed to different treatments are shown in different colors. (B) The slopes of body size versus temperature shown in the panel A.

Figure S8. Observed posthoc contrasts from a linear model examining the effects of heatwave exposure and duration on offspring body size when reared at different temperatures.

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