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Can *Acartia* spp. Adapt to Climatic Warming? Heritable within-Population Genetic Variation in Life History Traits

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Can *Acartia* spp. Adapt to Climatic Warming? Heritable Within-Population Genetic
Variation in Life History Traits

Benjamin L. Cournoyer

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Can *Acartia spp.* Adapt to Climatic Warming? Heritable Within-Population Genetic
Variation in Life History Traits

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Abstract

To predict the response of the biota to environmental change requires information on intrapopulation variation in life history traits and the proportion of phenotypic variation attributable to genes, heritability. Yet, knowledge of these parameters in marine populations is very limited. In the present study, I consider phenotypic plasticity and heritability of temperature-dependent, fitness-related life history traits in two coastal copepod species, *Acartia tonsa* and *Acartia hudsonica*, from Long Island Sound, a temperate estuary on the east coast of the USA. *Acartia hudsonica* is a purportedly cold-adapted species and *A. tonsa* a warm-adapted one. I used a full-sibling, split family design to measure egg production rate, adult longevity, and estimated lifetime fecundity at 16°C and 18°C (*Acartia hudsonica*) and 22°C and 24°C (*Acartia tonsa*). Treatment temperatures represent projected increases of +2°C and +4°C by the end of the century relative to mean temperature values experienced by these species, respectively, in Long Island Sound. In *A. tonsa*, egg production, adult life span, and lifetime fecundity displayed significant sibship-environment interaction ($p < 0.05$) and heritability, (0.69 ± 0.18 , 0.39 ± 0.15 , and 0.26 ± 0.19 , respectively). In contrast, no significant sibship-environment interaction was evident for *A. hudsonica*. Selection differentials, the expected change in fitness with a change in phenotype, for traits of *A. tonsa* were positive. Evolutionary rates in *A. tonsa* were moderate, ranging from 0.13 (lifetime fecundity) to 0.23 haldanes (egg production). These results indicate that *A. tonsa* in Long Island Sound has the potential to evolutionarily cope with predicted increases in global temperature whereas *A. hudsonica* does not.

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Introduction

Copepods are the most abundant metazoans in the ocean and arguably on the planet (Humes 1994). Copepods play a significant role in the control of primary production in the ocean (Banse 1995, Calbet 2008), link the microbial loop to upper trophic levels (Sherr et al. 1985, Calbet and Saiz 2005), and represent an important component of the biological pump (Longhurst 1991, Dam et al. 1995, Landry et al. 1997).

Global increases in temperature of 2-4°C are projected by the end of this century (IPCC 2007). A key challenge to marine ecologists is to ascertain whether the marine biota can adapt to the pace of global environmental change (Dam 2013). Copepods are excellent sentinels for the response of marine organisms to climate change because they are ectotherms and have short generation times (Dam 2013). Populations can adapt to changes in the environment through phenotypic plasticity or evolution. Phenotypic plasticity arises when a genotype's performance (e.g., reproduction, survival) changes in different environments (e.g., as temperature changes). Change in performance in this case is understood to happen within a generation. Alternatively, genotype performance might change from generation to generation via evolutionary processes such as natural selection (Pigliucci 2001, Whitman & Agrawal 2009). This response is considered to be evolutionary adaptation. Understanding and predicting responses of the biota to climate change require that we distinguish between phenotypic and evolutionary responses. Phenotypic responses have been widely studied in copepods (Holste and Peck 2006, Isla et al. 2008, Ji et al. 2010). Yet,

relatively few studies have examined evolutionary adaptation to climate change in copepods (reviewed in Dam 2013) despite their potential for fast evolution (Peijnenburg and Goetz 2013).

Phenotypic variation in a trait is a function of genetic and environmental factors and the interaction of these two factors (Falconer and McKay 1996). The interaction term is important because it represents the genetic variation for phenotypic plasticity (Roff 1997), which is essential for the evolution of performance in a population via natural selection (Angilleta 2009, Whitman & Agrawal 2009). Significant gene-environment interactions for fitness-related traits have been demonstrated in marine copepods (Bradley & Ketzner 1982, Bradley 1986, Lee & Petersen 2002, Avery 2005). However, for performance to evolve the phenotypic variable must be heritable-- passed from parent to offspring. Heritable, temperature-dependent life history traits in copepods have been documented (McLaren 1976, Bradley & Ketzner 1982, Bradley 1986, Avery 2005). Properly designed experiments for the study of phenotypic plasticity also allow the quantification of heritability, the fraction of the total phenotypic variation in a trait attributable to genes (Roff 1997).

Global increases in temperature of 2-4°C are projected by the end of this century (IPCC 2007). A challenge is to find if species can adapt to the projected temperature increases. One approach is to determine the critical rate of warming a species can tolerate before it goes to extinction and compare that rate to the different projections of thermal increase (Chevin et al. 2010). This rate is directly dependent on heritability and the phenotypic variance of a trait in the population (Eq. 1 in Chevin et al. 2010). Alternatively, one can determine the evolutionary response (r) of a trait with the

breeder's equation (Eq. 1). The response is directly proportional to heritability (h^2) and the selection gradient (S), a change in fitness with a small change in phenotype.

$$r = h^2 S \quad (\text{Eq. 1})$$

Therefore, heritability is a key parameter in predicting whether species can adapt to environmental change.

Heritability is the proportion of genetic variance to total phenotypic variance, of which there are two types (Roff 1997, Falconer and McKay 1996). Broad sense heritability (H^2) is the proportion of all genetic variance; which includes variance due to additive, epistasis, dominance, and maternal effects, to total phenotypic variance.

Narrow sense heritability (h^2) is the proportion of additive genetic variance, variance attributable to alleles, to total phenotypic variance (Falconer and McKay 1996).

Heritability is a powerful indicator of the ability of a trait to evolve because of its scale. Large heritability values enable traits to evolve quickly, while small heritability values can drastically increase the time needed for evolution, making that population more susceptible to extinction in the face of a changing environment.

Excluding the present study, as well as the literature on *Daphnia*, 18 studies have calculated heritability in ten species of zooplankton (Appendix 1). Of these, only four studies have calculated heritability in marine copepods, encompassing four species and six traits. With the exception of mortality before maturity (McLaren 1976), none of the measured traits are direct correlates (i.e., survival or fecundity) of population fitness. The goal of this study is to determine if temperate coastal copepods of the genus *Acartia* contain heritable genetic variation for temperature-dependent life history traits

related to population fitness. If such variation is present, it may allow species to adapt to the projected climatic warming.

Environment and Organisms:

Over the last century, average water temperature increases of 1.2°C have been observed in many New England estuaries (Nixon et al. 2004). The increase in temperature includes Long Island Sound, where the rate of winter warming exceeded the rate of summer warming (Stachowicz et al. 2002, Keser et al. 2005). Global climate change is predicted to increase the average ocean temperature by at least 2° to 4°C by 2100 (IPCC 2007), which can have a large effect on the biota. Zooplankton are ectothermic; their body temperatures and physiological rates are dependent upon the temperature of the water they inhabit. Small changes in temperature can cause significant fluctuations in fecundity, life span, and other life history traits (Mauchline 1998). Furthermore, small changes in fitness, induced by temperature increases, can lead to drastic changes in the phenology and abundance of species in both the zooplankton community, and in the community at large (Richardson 2008, Ji et al. 2010, Hoffmann and Sgro 2011).

Numerically, copepods of the *Acartia* complex dominate zooplankton communities within estuaries of the Eastern United States. *Acartia tonsa* is a subtropical/temperate species ranging from Florida to southern New England, whereas *Acartia hudsonica* is a boreal species ranging from the Mid-Atlantic to southern Canada. Long Island Sound is situated where these two distributions overlap (Fig.1). Thus, in Long Island Sound, community structure changes seasonally, and is dominated by *A. tonsa* in the summer and fall, and by *A. hudsonica* in the winter and spring (Peterson

1986, Capriulo et al. 2002). The genus *Acartia* has been suggested as a model for research on the physiological response of zooplankton to climate change because species in the genus dominate their seasonal assemblages, can be successfully reared in the lab for multiple generations, and have relatively short generation times (Ji et al. 2010). Furthermore, physiological rates reflect recent environmental history because both *Acartia* species contain minimal energy stores in the form of lipids, and lack pre-adult dormancy (Ji et al. 2010).

Materials and Methods

To test the hypothesis that coastal copepods of the genus *Acartia* contain heritable within-population genetic variation in temperature-dependent life history traits, a split-family experimental design was used. This design allows one to attribute variation in life history traits to environmental and to family (i.e., genetics) sources, similar to the approach in Avery (2005) and Lee and Peterson (2003). A genotype is the genetic makeup of an organism, while a phenotype of an organism is the manifestation of its genotype in an environment (Roff 1997). Typically, life history measurements are made on individuals within populations and represent phenotypic variables, as measurements have both environmental and genetic components. In order to separate these components, the portion of the total phenotypic variance (V_P), comprised of genetic variance (V_G) compared to environmental variance (V_E) or the interaction of the two ($V_{G \times E}$) must be calculated. $V_P = V_G + V_E + V_{G \times E} + \text{error}$ (Falconer and McKay, 1996). This equation can be simplified by normalizing environmental variance by raising individuals in the same environment (common garden) for more than one generation; thus eliminating any variation caused by the environment (i.e. $V_E = 0$ and $V_{G \times E} = 0$) (Roff 1997). The initial equation then reduces to $V_P = V_G + \text{error}$; any difference in response is attributable to V_G or random error. Common garden experiments within a population can hence identify family effects and family-by- environment-interaction effects.

Copepods collected from Long Island Sound were grown in a common environment (*A. hudsonica* at 14 °C and *A. tonsa* at 20 °C) in duplicate 20 L containers for two generations, with non-limiting food and 12:12 light/dark cycle, to remove

environmental variation and maternal effects (Roff 1997, Avery 2005). Eggs from actively swimming females were collected to start full-sibling families and raised under the aforementioned conditions. Once the siblings matured, 6-8 females per family per temperature-treatment were individually isolated in petri dishes where life-history traits related to fitness were measured, including average daily egg production, adult lifespan, and lifetime fecundity. Individuals were fed a non-limiting diet of microalgae, 50% *Tetraselmis* sp. ($\sim 7\mu\text{m}$ diameter, $\sim 4 \times 10^{-5} \mu\text{gC cell}^{-1}$) and 50% *Thalassiosira weissflogii* ($\sim 11\mu\text{m}$ diameter, $\sim 4.5 \times 10^{-5} \mu\text{gC cell}^{-1}$). Food was kept $\geq 600\mu\text{gC L}^{-1}$, above the limiting concentration for both species (Besiktepe and Dam 2002; Colin and Dam 2007). Daily egg production was calculated as the average of three days. Families were kept under identical conditions until death of all individuals to determine adult lifespan. Lifetime fecundity, a proxy for fitness, was then estimated by multiplying daily egg production and adult life span for each individual. Ten and thirteen families were represented in these experiments, for *A. hudsonica* and *A. tonsa* respectively. Increasing the number of families, instead of the number of individuals within a family, gives the best estimate of among-family variance (Roff 1997). Using six to eight females per family per temperature provides an adequate estimate of life-history traits while keeping sample size manageable. Avery (2005) was able to statistically differentiate among-family differences using three to five siblings per temperature. Due to the large sample sizes required, experiments were performed at only two temperatures corresponding to 2°C and 4°C above the current mean surface temperature experienced in Long Island Sound by each species, 16°C and 18°C for *A. hudsonica* and 22°C and 24°C for *A. tonsa*.

A reaction norm is the phenotypic expression of a genotype in different environments. Here each family was considered to be a phenotype and the temperature treatments correspond to different environments. Reaction norms among families were compared using a nested two-way ANOVA, with the temperature effect nested within family effect (Roff 1997). A significant nested temperature-family effect indicates a significant sibship-environment interaction; i.e., the response of families is significantly different between the two temperature treatments. Therefore, genetic variation that can be acted upon by natural selection exists for that trait (Roff, 1997). For example, if the lifetime fecundity of a family of *A. hudsonica* is significantly greater at 18°C than 16°C, then that family is expected to outperform others that either do not respond or decrease egg production as temperature increases. The sibship-environment interaction is a comparison tested by the split-family design; it is not an interaction term in the nested ANOVA calculation.

The parameters of the ANOVA (Table 1) partition variance both among and between families. This allows for calculation of h^2 with standard error (Roff, 1997), which has been done in a different study for *A. hudsonica* by Avery (2005). The full sib design does not separate additive genetic variance from maternal effects (here maternal effects were eliminated or minimized by raising animals in common environments for two generations prior to the experiments), dominance, or epistatic variance; therefore, our calculation of h^2 is close to a maximum estimate of heritability (Roff 1997, Falconer and McKay 1996). However, given the common rearing conditions, other types of genetic variance are assumed to be minimal. Heritability, h^2 , was calculated using equation 2, and the standard error of h^2 , $SE(h^2)$, was calculated using equation 3. Equation 4 was

used to calculate a representative sample size, k , if treatments contained unequal sample sizes.

$$h^2 = \frac{V_G}{V_P} = \frac{2V_{AF}}{V_{AF} + V_{AP} + V_{WC}} = \frac{2\left(\frac{MS_{AF} - MS_{AP}}{kC}\right)}{\left(\frac{MS_{AF} - MS_{AP}}{kC}\right) + \left(\frac{MS_{AP} - MS_{WC}}{k}\right) + MS_{WC}} \quad \text{Eq. 2}$$

$$SE(h^2) = 2\left(1 - \frac{h^2}{2}\right)\left(1 + (k - 1)\frac{h^2}{2}\right)\left(\frac{2(T-1)}{k^2(T-n)(n-1)}\right)^{\frac{1}{2}} \quad \text{Eq. 3}$$

$$k = \frac{\sum_i^{N_c} n_i - \left(\sum_i^{N_c} n_i^2\right) \left(\sum_i^{N_c} n_i\right)^{-1}}{N_c - 1} \quad \text{Eq. 4}$$

Trade-offs

A trade-off arises if an increase in one trait leads to a reduction in another (Fry 2003). Daily egg production vs. adult life span for each temperature nested within family treatment was analyzed by regression. Negative correlation/slope indicates a trade-off between egg production and adult life span.

Estimated generation-scale response to selection

To simulate the evolutionary response of daily egg production and adult lifespan we used the breeder's equation (Eq. 1). Heritability was calculated from the split family experiment. The selection differential was estimated as the difference between the

mean trait value before and after selection (Lande and Arnold 1983). For our calculation, each individual was considered to be a phenotype, the mean trait value before selection was the average of trait values for each phenotype, and the mean trait value after selection was the average of the trait values weighted by each individual's calculated fitness (Appendix 2). Selection differentials were calculated for both temperature treatments. Each selection differential was multiplied by its corresponding heritability to compute the trait response. Responses were calculated in measured trait values and haldanes (H_0), the number of standard deviations the mean trait value changed per generation (Gingerich 1993). A detailed explanation of the calculations is found in Appendix 2.

Statistical analysis:

The split-family ANOVAs were analyzed using general linear model in Minitab with family and temperature nested within family as the main effects. Family was considered to be a random variable because families included in the experiment were randomly chosen from laboratory populations (Roff 1997). The tradeoff analysis used ordinary linear regression (Fry 2003, Roff 1997).

Results

For *Acartia tonsa* sixteen (egg production), thirteen (adult life span), and thirteen (lifetime fecundity) families met the desired sample size for statistical analysis.

Variability both within and among families was large for all three traits (Fig 2a-c). Daily egg production ranged from 10 to 110 eggs per day. Adult lifespan ranged from 10 to 45 days. Lifetime fecundity ranged from 200 to 3500 eggs. Significant sibship-environment interactions were found between 22° and 24 °C for all traits ($p= 0.020, 0.030, \text{ and } 0.009$, respectively) (Fig 3). In the analysis of adult lifespan three of the thirteen families did not have equal variances, which may increase the probability of falsely reporting a significant difference (Zar 1984). Because removal of these families from the analysis did not change the significance of the overall test and because our sample sizes were balanced, these three families were included in the analysis reported here. A square-root transformation was applied to the lifetime fecundity data to correct for the inequality of variances. After transformation, all but one family showed equal variances. As with adult lifespan, removal of this family did not alter the significance of the overall test and was included in the analysis reported here. Heritability of traits was calculated to be $0.69\pm 0.18, 0.39\pm 0.15, \text{ and } 0.26\pm 0.19$, respectively (Table 2).

For *Acartia hudsonica*, eleven (egg production), eleven (adult life span), and ten (lifetime fecundity) families were used in the analysis. Variability both within and among families was large for all three measures (Fig. 2 d-f). Daily egg production ranged from near zero to over 40 eggs per day. Adult life span ranged from almost zero to nearly 50 days. Lifetime fecundity ranged from 100 to 1200 eggs per lifetime. Sibship-environment

interactions in egg production ($p= 0.347$), adult longevity ($p=0.325$), and estimated lifetime fecundity ($p=0.826$) were not statistically significant (nested ANOVA). Because the nested ANOVAs did not indicate the existence of sibship-environment interactions, heritability could not be calculated for any of the traits. This outcome was not changed by relaxing the sample size requirement of the test to five siblings per temperature family treatment, which increased the number of families to 13.

Tradeo-offs

The relationship between egg production and adult life-span was similar for both species. Of the 20 treatments for *A. hudsonica*, 17 showed no correlation between daily egg production and adult life span. Of the 26 treatments for *A. tonsa*, 22 indicated no correlation between daily egg production and adult life span, whereas four did. All significance treatments showed positive correlations. Significance was equally split between the temperature treatments for each species. With the exception of family 9 from the *A. tonsa* study, no family showed significant correlations at both temperature treatments. When family data were pooled within species and temperature, no significant correlations were found for *A. tonsa* regardless of temperature. At both temperature treatments, *A. hudsonica* displayed positive correlations between egg production and adult lifespan, $p= 0.021$ for 16°C and $p= 0.002$ for 18°C (Fig. 4). In summary, a tradeoff between egg production and adult life-span was not evident for either copepod species.

Estimated evolutionary response

All calculated responses to increased temperature for *A. tonsa* were significantly greater than zero. Average daily egg production per family is expected to increase by 4.96 ± 1.30 and 4.32 ± 1.13 eggs per day, adult lifespan is expected to increase by 1.45 ± 0.55 and 1.22 ± 0.48 days, and lifetime fecundity is expected to increase by 107.46 ± 78.53 and 75.51 ± 55.17 eggs per lifetime, for 22°C and 24° respectively (Table 3). When calculated in haldanes, responses ranged from 0.13 to 0.23 for all traits. Error in trait responses was derived from the error associated with heritability. Trait responses were not different between the temperature treatments for any of the traits measured (Table 3). Responses could not be calculated for *A. hudsonica* because no significant variation was observed in the split-family experiment.

Discussion

Two prerequisites for the evolution of a trait, via natural selection, are the presence of genetic variation within a population and the ability of that variation to be passed from parent to offspring, i.e. heritability (Roff 1997). There are many other requirements for evolution to occur, and even more factors governing the rate and magnitude of an evolutionary response (Hansen et al. 2003, Houle 1992). We have not attempted to reduce the complexity of this process down to a mere two variables, rather we have chosen to explore an understudied evolutionary parameter in marine zooplankton to constrain the potential evolutionary outcomes and draw inferences from the remaining possibilities.

Our calculated heritabilities are, to our knowledge, the first for fecundity-related life history traits in copepods. Based on the split-family experiments, it is clear that even closely related species can have different within-population genetic variation and heritability among traits. *Acartia tonsa* was found to contain significant sibship-environment interactions and heritability for daily egg production, adult life span, and lifetime fecundity and is likely able to evolve in response to projected temperature increases. Given the magnitude of the calculated heritability, all other factors being equal, we expect daily egg production to evolve at a much quicker pace than adult life span or lifetime fecundity in the Long Island Sound population. However, when accounting for our calculated selection differentials, it appears all traits have the potential to evolve at similar rates. Conversely, we failed to find significant sibship-environment interactions in any of the life history traits measured for *Acartia hudsonica*;

thus heritability could not be calculated. We conclude that the population of *A. hudsonica* in Long Island Sound is unlikely to be able to evolve in response to projected temperature increases of 2°C to 4°C. Moreover, it is unlikely that our results are a statistical anomaly. We used a large number of families with a sample size of six to eight siblings per temperature family treatment, which accurately characterizes family variation. Avery (2005), who also worked on *A. hudsonica*, was able to discern significant differences in embryonic dormancy induction with as few as six families and three to six siblings per nested treatment. The experiments in this study contain eleven to 16 families with between six to eight siblings per temperature family treatment.

Circumstantial evidence from the winter months supports our results. In Long Island Sound, as in many other temperate estuaries, the rate of winter warming exceeds the rate of summer warming (Keser et al. 2005, Stachowicz et al. 2002). Although the two species described here share a habitat spatially, their phenology causes each to experience different thermal increases. *A. tonsa* is the dominant species in the summer-mid autumn, with Long Island Sound being near the northern extent of its range (Fig 1). Historically this species disappeared from the water column during the winter months and reappeared every summer, presumably due to cold-sensitivity. Recently, *A. tonsa* has been observed to persist in Long Island Sound throughout the winter months (Dam and McManus unpublished data). It is possible that the decreased seasonal temperature differential has enabled cold-resistant phenotypes to survive the warmer winter months. In contrast, *A. hudsonica* is a cold-adapted species that appears seasonally in Long Island Sound (Fig. 1); it is expected to react differently than its warm-adapted congener. Since *A. hudsonica* is not found farther south than

Chesapeake Bay (approximately 38.5 °N), *A. hudsonica* in Long Island Sound is likely close to its thermal maximum. Thermal reaction norms have a characteristic unimodal shape, skewed toward increasing temperature (Angilletta 2009). Thus, beyond a species' optimal temperature survival and other metabolic indicators decline rapidly. Given the recent magnitude of winter warming, it is possible that the population of *A. hudsonica* in Long Island Sound has already been selected for the upper limit of its thermal tolerance. This would have reduced the amount of genetic variation contained within the population, leading to our inability to determine any significant variation in temperature-dependent life history traits and heritability (Somero 2010). Our results also imply that further thermal increase will likely lead to a reduction or local extinction of the *A. hudsonica* population in Long Island Sound. This hypothesis remains untested. Overall, this line of reasoning suggests that species that are already near the upper limit of thermal tolerance may suffer most from the effects of global temperature increases, as has been suggested previously (Hoffmann and Sgro 2011).

Our results indicate the importance of determining heritability in marine zooplankton, as it is not constant among species or traits. The multiplicative nature of heritability in the breeder's equation has a major effect on the magnitude of an evolutionary response. In the case of *A. hudsonica*, the lack of heritable variation in temperature-related traits means that its evolutionary response is nil. For species containing heritable variation among traits, such as *A. tonsa*, it is important to note that not all traits have similar heritability and are, therefore, likely to evolve at different rates if selection differentials are similar. It would be inappropriate to assume that heritability among species, among populations, or even within a population over time is similar.

Acartia tonsa, for example, has recently been shown, using mitochondrial 16S rRNA as a marker, to be a series of spatially isolated populations that may be cryptic species (Chen and Hare 2008). Regional populations contain 10% to 14% sequence difference between haplotypes in this region (Caudill and Bucklin 2004), similar to the 10% to 20% differences in the same region among morphologically distinct species of calanoid copepods (Bucklin et al. 1998). It is very likely that these regional populations will respond differently when faced with temperature increases. It is, thus, critical to have knowledge of genetic variability for each of these different populations in order to predict how they will respond to increases in mean temperature. Similarly, consider a seasonal population of *A. tonsa*. The first individuals to emerge from resting eggs have drastically different life-history and will face much cooler conditions than individuals hatched from subitaneous eggs during the end of the summer. Thus, even cohorts within a population could respond differently to temperature changes. If we are to make informed decisions, environmental managers and modelers should obtain evolutionary parameters from key populations within the ecosystem they wish to manage.

Trade-offs can confound predictions on the evolution of traits within a population. Only five of the forty-six treatment combinations showed significant correlations between adult lifespan and daily egg production rate ($p < 0.05$). All of these correlations, however, were positive; therefore, no trade-offs were apparent. When data among all families was partitioned by species and temperature no significant correlations were found for *A. tonsa* (Fig. 4). This result is an important requirement for our calculation of evolutionary responses. On the other hand, significant positive correlations were found at both temperature treatments for *A. hudsonica* when the data were pooled (Fig. 4).

Outside the confines of family, longer lived-individuals tended to have higher average daily egg production.

Our estimated responses for *Acartia tonsa* were on the order of 0.05 to 0.3 H_0 (Table 3). These rates are comparable to the evolution of increased temperature in *Daphnia magna* (0.45-1.30 H_0 , Van Doorslaer et al. 2009) and the rate of divergence in resistance to toxic algae (0.17 ± 0.06 , Jiang 2010). Similar rates have also been found outside of zooplankton, such as the evolution of size in Cenozoic mammals ($\sim 0.2 H_0$, Gingerich 2001), molar formation from *Hyracotherium grangeri* to *H. aemular* (0.225 H_0), and spire length shortening in *Littorina obtusata* (0.064-0.319 H_0 , Gingerich 1993). In our study, evolutionary rates were not significantly different among traits. This is surprising, as the reproductive cycle of many small copepods including *A. tonsa* is less than thirty days and mortality in the field is thought to be high (Hirst et al. 2002). It is thus unlikely that copepods in the field die of old age. It seems in the absence of external causes of mortality, egg production rates and lifespan respond evolutionarily at equal magnitude. Furthermore, because daily egg production and adult lifespan were uncorrelated, we expect our findings to be relevant to natural populations in situ if mortality is random and therefore also uncorrelated with daily egg production rate.

Considering *A. hudsonica*, we were unable to find significant temperature-dependent variation for any of the measured traits. Therefore, its response to increases temperature can be inferred from a thermal reaction norm alone (Fig. 5). This reaction norm is for temperature-dependent egg production in Narragansett Bay, an adjacent estuary. The lack of variation for that population in egg production between 14 °C and 16 °C mirrors our findings. Egg production begins to decrease above 14 °C and

dramatically decreases beyond 19°C. We can thus expect to see a dramatic decrease in fitness as the temperature exceeds 19°C, with no evidence of the population having reserves of genetic variation for selection to act upon. This does not mean the population is safe until the average temperature reaches 19°C. By applying a 2°C and 4°C increase to the growth season of *A. hudsonica*, we see that the time favorable for the species shrinks by approximately 14 and 26 days, respectively (Fig 5). Even small increases in temperature can thus lead to local extinction by decreasing the season of growth. With no means to evolve, the fate of this population of *A. hudsonica* is entirely dependent on physical factors.

Our approach to predicting the response of zooplankton to changing temperature is in stark contrast to temperature dependent production as described by Huntley and Lopez (1992). That study used data derived from field studies and, therefore, only represents temperature-dependent production of copepod species thriving in particular environments. It indicates that maximum production among species in the copepod community follows an exponential increase. It has no means to account for production of individual species at temperatures outside species' normal range, conditions likely to be produced by climate change. By their exponential model, we would expect an increase in our measured traits as they are related to production. However, physiological rates follow a unimodal curve with increasing temperature, not an exponential (Angilletta 2009). Our approach (Roff 1997) is more reliable for characterizing the temperature dependence of traits in an unstable environment.

Evolution was historically thought to occur at slow rates over long periods of time, but we now know that when sampled on generational timescales, gene frequencies can

fluctuate much more quickly than when calculated from multigenerational data (Gingerich 2009, Hairston et al. 2005), putting ecology and evolution on the same timescale. This enables evolution to play a pivotal role in ecosystem dynamics on the human time-scale of anthropogenic changes, such as global warming.

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Table 1: Definition of terms for heritability calculations. Equations from Roff (1997).

Symbol	Definition
V_P	Total Phenotypic Variance
V_G	Variance Attributed to Genetics
V_E	Variance Attributed to Environment
$V_{G \times E}$	Variance Attributed to the Interaction of Genetics and Environment in the Field
V_{AF}	Variance Among Sibships
V_{AC}	Variance Among Temperatures within Sibships
V_{WC}	Variance Within Temperatures
MS_{AF}	Mean Square Among Sibships
MS_{AC}	Mean Square Among Temperatures within Sibships
MS_{WC}	Mean Square Within Temperatures
k	Weighted estimate of Temperature within Sibship Size
c	Number of Temperature Treatments
N	Number of Sibships
n_i	The size of the i th Temperature within Sibship Treatment
T	Total number of individuals

Table 2. Estimates of heritability \pm SE of the mean trait values for two *Acartia* spp.

	Egg Production (eggs/day)	Adult life span (days)	Lifetime fecundity (eggs/lifetime)
<i>A. tonsa</i> (22°C - 24°C)			
Number of sibships	16	13	13
Weighted mean number per sibship, k	7.28	7.23	7.34
Mean square among sibships	2721.70	285.55	343.70
Mean square among temperatures within sibships	507.10	93.15	163.51
Mean square within temperatures	264.00	48.28	71.60
Heritability, h^2	0.69	0.39	0.26
Standard error	0.18	0.15	0.19
<i>A. hudsonica</i> (16°C - 18°C)			
Number of sibships	11	11	10
Weighted mean number per sibship, k	7.50	6.95	7.00
Mean square among sibships	301.48	165.13	214632.00
Mean square among temperatures within sibships	60.70	62.48	33536.00
Mean square within temperatures	54.01	54.09	57571.00
Heritability, h^2	-	-	-
Standard error	-	-	-

Table 3. Trait means, selection gradients, and responses to *Acartia tonsa* projected values. All values are the trait unless otherwise specified. Responses are from the associated heritable

Trait	Temperature (°C)	Trait Mean±SE	Selection Differential	Response±SE (trait units)	Response±SE (haldanes)
Egg Production	22	53.82±2.04	7.19	4.96±1.30	0.23±0.06
(eggs/day)	24	57.91±1.90	6.26	4.32±1.13	0.22±0.05
Adult Life Span	22	23.65±0.89	3.71	1.45±0.55	0.17±0.06
(days)	24	21.52±0.79	3.14	1.22±0.48	0.16±0.07
Lifetime Fecundity	22	1302.91±74.13	413.31	107.46±78.53	0.15±0.11
(eggs/lifetime)	24	1285.25±62.09	290.41	75.51±55.17	0.13±0.09

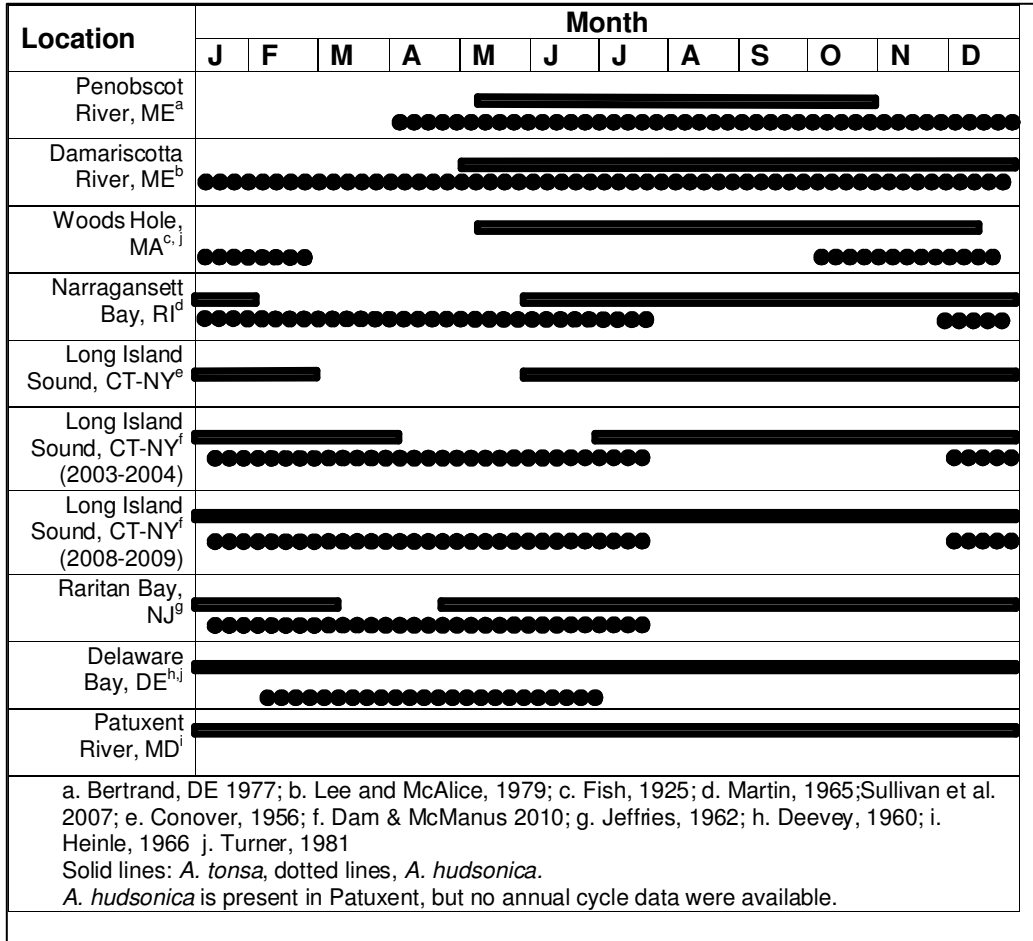


Fig. 1. Temporal distribution of *Acartia* spp. in estuaries along the northeast coast of the USA. Solid lines indicate presence of *A. tonsa* adults or copepodites. Dotted lines indicate presence of *A. hudsonica* (*clausi*) adults or copepodites. The estuaries are sorted approximately according to latitude, north (top) to south (bottom).

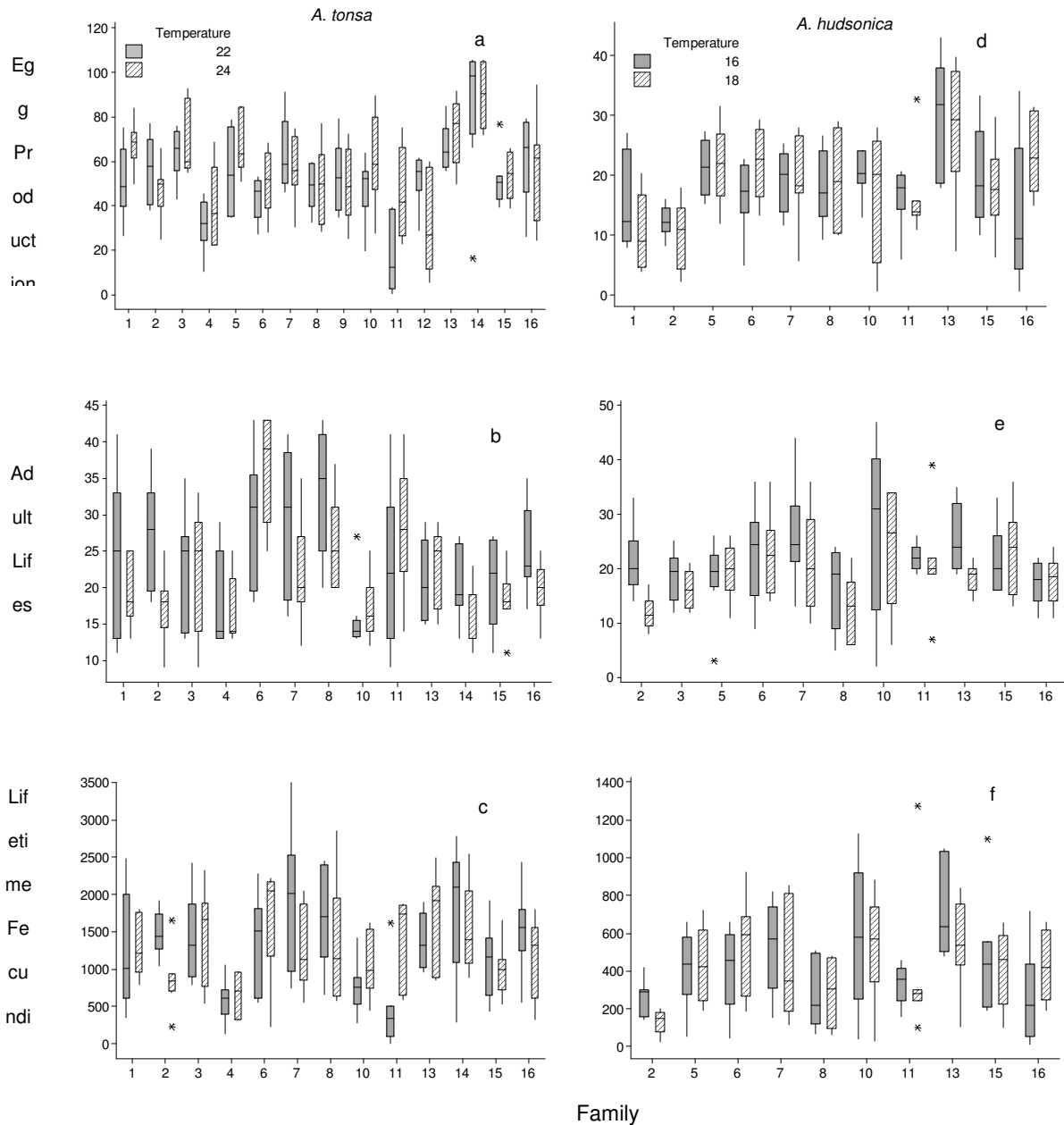


Fig. 2. Box plots of egg production (a,d), adult life span (b,e), and lifetime fecundity (c, f) for each temperature nested within family treatment. The nested ANOVAs indicate significant variation among families of the warm-adapted *Acartia tonsa* (A-C, $p=0.020$, 0.030 , 0.027), but not the cold-adapted *A. hudsonica* (D-F, $p=0.347$, 0.325 , 0.826). Asterisks denote outliers on the boxplots, not significant differences.

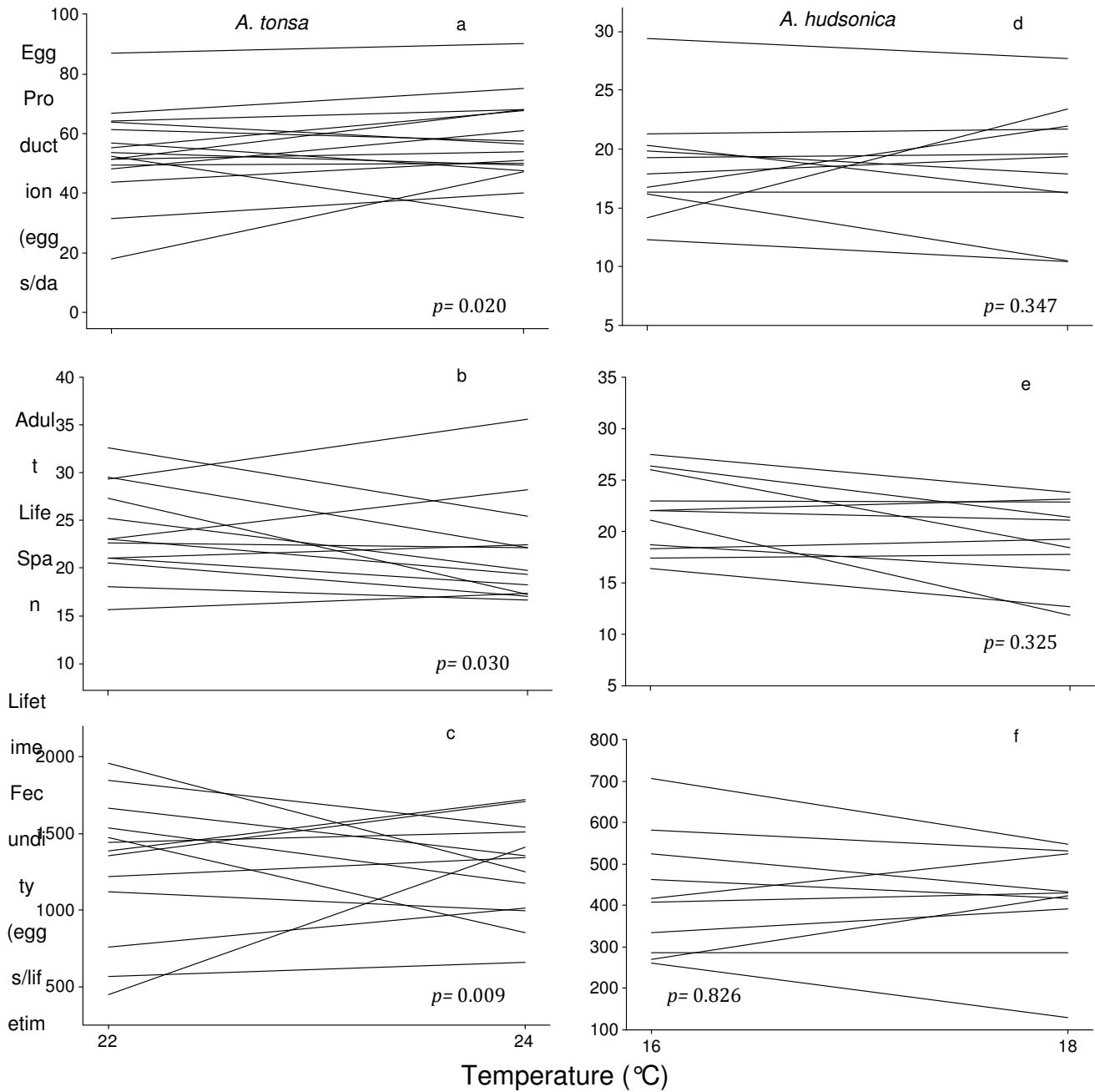


Fig. 3. Reaction norm plots for *Acartia tonsa* (a-c) and *Acartia hudsonica* (d-f). Each line represents the reaction norm of one family, corresponding to the families in Fig. 2. *p-values* indicate the significance of the sibship-environment interaction.

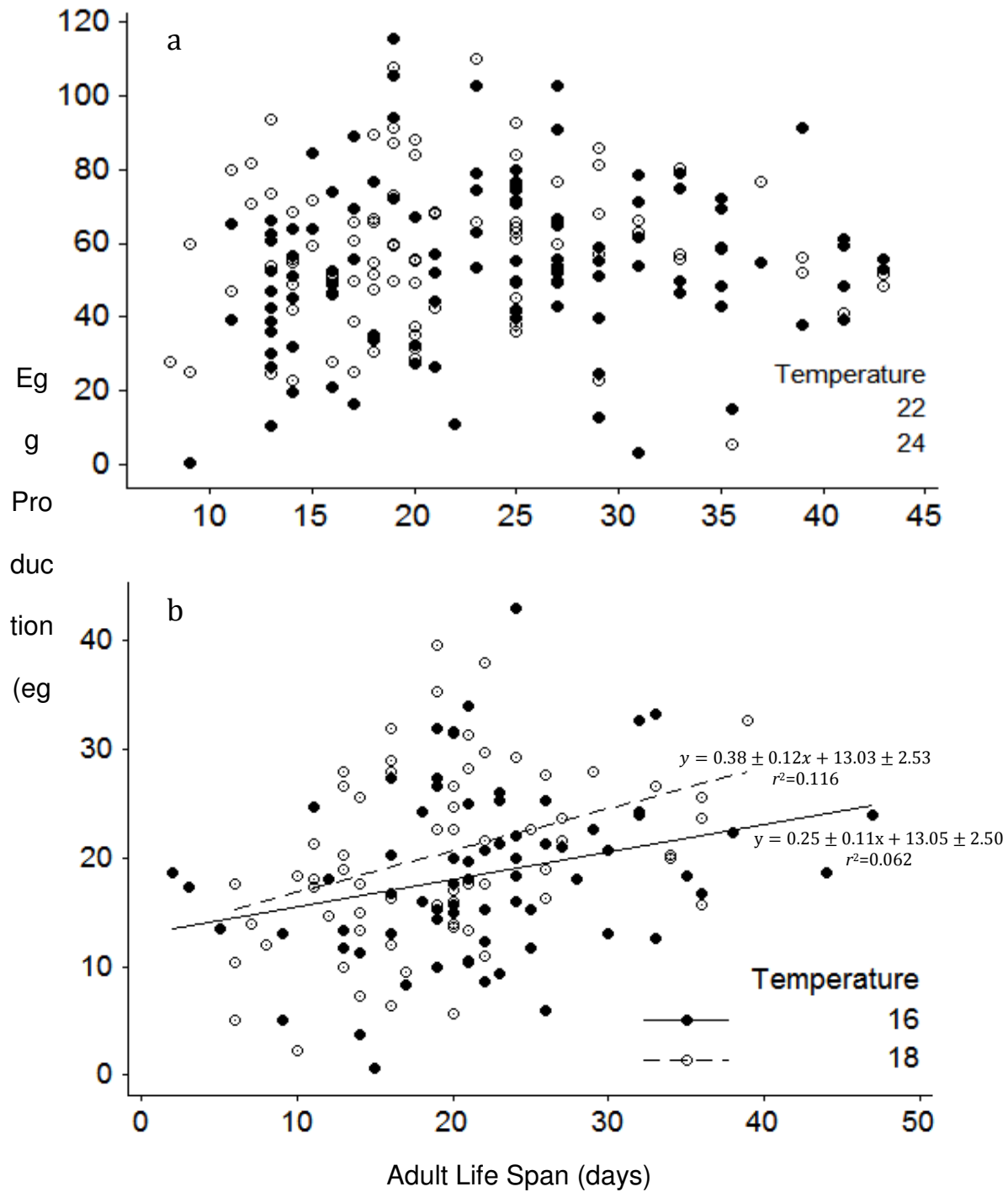


Fig. 4. Egg production versus adult life span. Each point corresponds to an individual copepod. For *Acartia tonsa* (a), no tradeoffs were observed, as neither linear regression was significant, $p = 0.185$ for 22°C and $p = 0.396$ for 24°C. For *A. hudsonica* (b), both temperature-treatment yielded weak, but positive linear relationships between adult life span and egg production (16°C $p = 0.021$ and for 18°C $p = 0.002$).

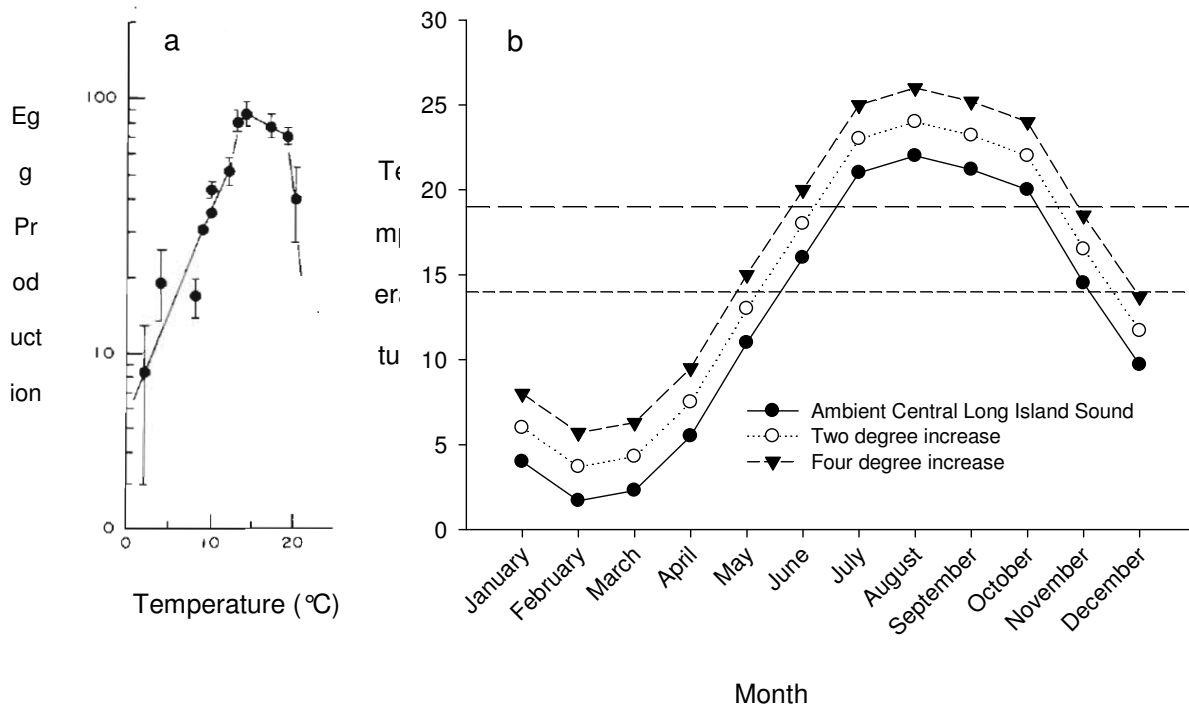


Fig. 5. a) Thermal reaction norm of *Acartia hudsonica* (Sullivan and McManus (1986). Daily egg production peaks around 14°C and sharply decreases above 19°C. b) Average surface water temperature \pm SE for central Long Island Sound between 2000 and 2011, with additional curves indicating a +2° and +4°C increase in temperature. Standard errors for each month are located within the symbols. The long dashed horizontal line and short dashed line depict 19° and 14°C, respectively.

Appendix 1. Studies of heritability in zooplankton. * indicates the same value down, ~ indicates the same value to the right, - denotes no value. All error measurements are in standard error with the exception of Tepper and Bradley 1989 in standard deviation and Ellner et al. 1999 in 95% confidence

Study	Species	Location	Trait	Source of Variation/Regression	Condition Raised	Treatment	Heritability±SE
This study	<i>Acartia tonsa</i>	Long Island Sound, CT	daily egg production	female offspring to temperature	20°	22-24°	0.69±0.18
			adult lifespan	*	20°	22-25°	0.39±0.15
Avery 2005	<i>Acartia hudsonica</i>	Cudy's Harbor, ME	lifetime fecundity*	*	20°	22-26°	0.26±0.19
			% dormant eggs	temperature & light cycle	12°; 12L:12D	~	0.91±0.20
McLaren and Corkett 1978	<i>Pseudocalanus</i>	Nova Scotia, Canada	*	between sires	17°; 12L:12D	~	1.10±0.16
			*	between dams, within sires	17°; 15L:15D	~	0.08±0.21
			*	between sires	13.5°; 12L:12D	~	0.95±0.28
			*	between sires	17.5°; 12L:12D	~	0.25±0.38
			*	between sires	10°	~	0.92
Lobon et al. 2011	<i>Alkopleura dioica</i>	Gijon, Spain	age of maturity	between dams, within sires	*	~	0
			time, N+C1	between sires	*	~	0.56
			intrinsic rate of r	between dams, within sires	*	~	0.59
			parental/offspring variation	between sires	*	~	0
			offspring variation	between dams, within sires	*	~	1.47
			lifespan	intrinsic rate of r	15°; 12L:12D	~	0.69±0.40
			clutch size	*	*	~	0.89±0.47
			egg diameter	*	*	~	0.27±0.32
Shirdhankar et al. 2004	<i>Artemia franciscana</i>	*	trunk length	*	*	~	0.18±0.28
			gonad length	*	*	~	0.37±0.25
			house size	*	*	~	0.00±0.08
			tail length	*	*	~	0.39±0.23
			offspring sex	*	*	~	0.50±0.31
			length at three days*	male	male	~	0.59±0.22
			length at six days*	female	female	~	0.38±0.19
			length at first brood*	male	female	~	0.33±0.37
pre-reproductive*	female	female	~	0.12±0.38			
first brood offspring*	male	male	~	0.50±0.25			
	female	female	~	0.02±0.30			
	female	female	~	0.04±0.11			
	female	female	~	0.32±0.29			
	female	female	~	0.34±0.22			

Study	Species	Location	Trait	Source of Variation/Regression	Condition Raised	Treatment	Heritability	SE	p
McLaren 1976	<i>Eurytemora herdmani</i>	Halifax, NS	time to maturity	temperature, offspring sex, parental variation	♂; male, sires	~	0.1	0.45	
					♂; male, dames (within sires)	~	0.42	0.06	
					♀; female, sires	~	0.2	0.3	
					♀; female, dames (within sires)	~	0	0.5	
					♂; male, sires	~	0	0.68	
					♂; male, dames (within sires)	~	113	<0.0001	
					♀; female, sires	~	0.71	0.05	
					♀; female, dames (within sires)	~	0.72	<0.001	
					♂; male, sires	~	0	0.52	
					♂; male, dames (within sires)	~	0.75	0.01	
					♀; female, sires	~	0.24	0.35	
					♀; female, dames (within sires)	~	0.93	0.02	
					♂; male, sires	~	0.97	0.04	
					♂; male, dames (within sires)	~	0.76	0.001	
					♀; female, sires	~	0.38	0.14	
					♀; female, dames (within sires)	~	0.48	<0.001	
					temperature, offspring sex, parental regression	♂; male, mean parent	~	0.83±0.104	-
					♂; male, male	~	-0.36±0.181	-	
					♂; male, female	~	0.47±0.151	-	
					♂; female, mean parent	~	0.17±0.061	-	
					♀; female, male	~	-0.63±0.209	-	
					♀; female, female	~	0.89±0.161	-	
					♂; male, mean parent	~	0.19±0.046	-	
					♀; female, mean parent	~	0.19±0.062	-	
					♂; male, mean parent	~	0.61±0.118	-	
					♂; male, male	~	0.74±0.107	-	
					♂; male, female	~	0.39±0.378	-	
♀; female, mean parent	~	0.51±0.153	-						
♀; female, male	~	0.65±0.149	-						
♀; female, female	~	0.41±0.399	-						
temperature, parental variation	♂; sires	~	0.01±0.107	-					
♂; dames (within sires)	~	0.08±0.111	-						
♂; sires	~	0.02±0.043	-						
♂; dames (within sires)	~	0.13±0.101	-						
sex ratio in offspring	♂; sires	~	0.11±0.218	-					
♂; dames (within sires)	~	0.13±0.221	-						
♂; sires	~	0.27±0.153	-						
♂; dames (within sires)	~	0.33±0.171	-						

Study	Species	Location	Trait	Source of Variation/Regression	Condition Raised	Treatment	Heritability±SE
Bradley 1996	<i>Acartia hudsonica</i>	Narragansett Bay, RI	high temperature tolerance	temperature & sex	15°; male	32-36.5°	0.69±0.39
					23°; male	32-36.5°	0.83±0.43
					15°; female	32-36.5°	0.34±0.23
					23°; female	32-36.5°	0.41±0.25
					sex & salinity	32-36.5°	0.35±0.30
						32-36.5°	0
						32-36.5°	0.57±0.27
						32-36.5°	0.90±0.43
						32-36.5°	0.64±0.26
						32-36.5°	0.68±0.27
						32-36.5°	0.38±0.20
						32-36.5°	0.66±0.26
						32-35°	0.40±0.18
						32-35°	0
Bradley 1978	<i>Eurytemora affinis</i>	Chesapeake Bay	offspring sex & parental variation	females, sires (half-siblings)	32-35°	0.20±0.09	
				females, sires (half-siblings)	32-35°	0.84±0.35	
				female, mean parent (full-sibling)	32-35°	0.73±0.32	
				male, sires (half-siblings)	32-35°	0.79±0.24	
				male, sires (half-siblings)	32-35°	0.11±0.10	
				male, joint estimates (full-sibling)	32-35°	0.89±0.45	
				female, single pair matings	32-35°	0.28±0.18	
				male, single pair matings	32-35°	0.78±0.29	
				female half broods partitioned by hatching	~	0.995	
				male half broods partitioned by hatching	~	0.953	
				female, genetal segmanet width	~	0.899	
				female, genetal segmanet shape	~	1.000	
				female, antennule proportions	~	1.000	
				male, 5th leg, right exopod 1	~	0.205	
male, 5th leg, right exopod 2	~	0.380					
male, 5th leg, left basipod 2	~	0.254					
male, 5th, leg proportions	~	0.28±0.08					
male, antennule proportions	~	0.14±0.10					
20°; 12L; 12D	~	0.42±0.10					
Edmonds and Harrison 2003	<i>Tigriopus californicus</i>	West Coast USA	Life-history & Morphological traits	All populations	~	0.52±0.14	
				Northern Populations	~	0.11±0.15	
				Southern Populations	~	0.93±0.18	
				All populations	~	0.21±0.09	
				All populations	~	0.15±0.13	
				All populations	~	0.12±0.09	
				All populations	~		
				All populations	~		
				All populations	~		
				All populations	~		
				All populations	~		
				All populations	~		
				All populations	~		
				All populations	~		
All populations	~						

Study	Species	Location	Trait	Source of Variation/Regression	Condition Raised	Treatment	Heritability±SE
Shirdhankar and Thomas 2003	<i>Artemia franciscana</i>	Great Salt Lake, USA	naupliar length	generation, offspring/parent variation, n, line	0, male offspring by sire, SNS	~	0.59±0.22
					1, male offspring by sire, SNS	~	0.38±0.23
					2, male offspring by sire, SNS	~	0.18±0.25
					3, male offspring by sire, SNS	~	-0.13±0.35
					4, male offspring by sire, SNS	~	0.46±0.43
					5, male offspring by sire, SNS	~	0.10±0.68
					6, male offspring by sire, SNS	~	0.38±0.34
					pooled, male offspring by sire, SNS	~	0.21±0.08
					0, male offspring by sire, BNS	~	0.59±0.22
					1, male offspring by sire, BNS	~	0.26±0.21
					2, male offspring by sire, BNS	~	0.08±0.31
					3, male offspring by sire, BNS	~	0.69±0.47
					4, male offspring by sire, BNS	~	1.18±0.53
					5, male offspring by sire, BNS	~	1.35±0.28
					pooled, male offspring by sire, BNS	~	0.58±0.12
					0, female offspring by dame, SNS	~	0.36±0.19
					1, female offspring by dame, SNS	~	0.32±0.23
					2, female offspring by dame, SNS	~	0.69±0.30
					3, female offspring by dame, SNS	~	0.30±0.43
					4, female offspring by dame, SNS	~	0.12±0.38
5, female offspring by dame, SNS	~	0.39±0.44					
6, female offspring by dame, SNS	~	0.46±0.46					
pooled, female offspring by dame, SNS	~	0.39±0.11					
0, female offspring by dame, BNS	~	0.38±0.19					
1, female offspring by dame, BNS	~	0.02±0.22					
2, female offspring by dame, BNS	~	0.31±0.32					
3, female offspring by dame, BNS	~	0.22±0.48					
4, female offspring by dame, BNS	~	1.08±0.50					
5, female offspring by dame, BNS	~	0.95±0.45					
pooled, male offspring by dame, BNS	~	0.34±0.12					
Hairston and Dillon 1990	<i>Diaptomus sanguineus</i>		diapause photo period sensitivity	parental/offspring variation, n, method	mother-daughter pooled, Falconer	~	0.48±0.14
					mother-daughter mean, Falconer	~	0.58±0.30
					mother-daughter pooled, Adjusted Falconer	~	0.5
					mother-daughter mean, Adjusted Falconer	~	0.60±0.31
					mother-daughter pooled, Bulmer	~	0.63
					mother-daughter mean, Bulmer	~	0.60±0.35
					siblings pooled, Falconer	~	0.47±0.23
					siblings mean, Falconer	~	0.44±0.24
					siblings pooled, adjusted Falconer	~	0.5
					siblings mean, adjusted Falconer	~	0.60±0.28
					siblings pooled, Bulmer	~	0.41
					siblings mean, Bulmer	~	0.43±0.24

Study	Species	Location	Trait	Source of Variation/Regression	Condition Raised	Treatment	Heritability±SE
Shirodhankar and Thomas 2003	<i>Artemia franciscana</i>	Great Salt Lake, USA	naupliar length	generation, offspring sex, line	0, male, SNS	~	14.7±0.09
					1, male, SNS	~	14.1±0.10
					2, male, SNS	~	1.10±0.13
					3, male, SNS	~	1.13±0.13
					4, male, SNS	~	1.29±0.17
					5, male, SNS	~	1.32±0.17
					6, male, SNS	~	1.36±0.15
					pooled, male, SNS	~	1.33±0.05
					0, male, BNS	~	14.7±0.09
					1, male, BNS	~	1.04±0.15
					2, male, BNS	~	1.00±0.14
					3, male, BNS	~	1.27±0.14
					4, male, BNS	~	1.20±0.24
					5, male, BNS	~	1.12±0.23
					pooled, male, BNS	~	1.26±0.06
					0, female, SNS	~	1.39±0.10
					1, female, SNS	~	1.11±0.14
					2, female, SNS	~	1.06±0.12
					3, female, SNS	~	1.11±0.14
					4, female, SNS	~	0.84±0.18
5, female, SNS	~	1.11±0.15					
6, female, SNS	~	0.39±0.20					
pooled, female, SNS	~	1.10±0.05					
0, female, BNS	~	1.39±0.10					
1, female, BNS	~	1.17±0.14					
2, female, BNS	~	1.24±0.13					
3, female, BNS	~	1.37±0.13					
4, female, BNS	~	1.50±0.14					
5, female, BNS	~	1.62±0.09					
pooled, female, BNS	~	1.42±0.04					
Voordouw and A. rholt 2002	<i>Tigriopus californicus</i>	British Columbia	sex tendency	corrected, season, temperature	~	0.12±0.04	
				uncorrected, summer, 15°	~	0.00±0.02	
				uncorrected, summer, 22°	~	0.24±0.06	
				uncorrected, fall, 15°	~	0.16±0.05	
				uncorrected, fall, 22°	~	0.10±0.03	
				corrected, summer, 15°	~	0.00±0.01	
				corrected, summer, 22°	~	0.19±0.05	
				corrected, fall, 15°	~	0.12±0.04	
				corrected, fall, 22°	~	0.12±0.04	

Study	Species	Location	Trait	Source of Variation/Regression	Condition Raised	Treatment	Heritability±SE
Elmer et al. 1999	<i>Diplotomus sanguineus</i>	Rhode Island, USA	diapause egg production timing	model	-	-	154±108
Hunte and Myers 1984	<i>Gammarus lawrencianus</i>	Nova Scotia, Canada	loss of pho toposity	offspring variation with age	21; fgsu, 2L; 2D	~	0.20
Miehls et al. 2011	<i>Bythotrephes longimanus</i>	Lake Michigan, USA	distal spine length	time period	2007 September	~	0.76
					2008 Combined	~	0.48
					2010 July	~	0.27
					2008 July	~	0.3
					2008 September	~	0.48
					2010 July	~	0.13
Tepper and Bradley 1989	<i>Eurytemora affinis</i>	Chesapeake Bay, USA	high temperature tolerance	offspring sex, month	male, March	~	0.32±0.19
					female, May	~	0.72±0.19
					female, March	~	0.90±0.19
			width		male, May	~	0.74±0.18
					male, March	~	1.8±0.11
					female May	~	1.09±0.17
					female, March	~	1.22±0.17
			m-brood		female, May	~	0.99±0.17
			r-brood		female, March	~	0.91±0.19
			proportion hatched		female, May	~	1.6±0.15
					female, March	~	1.07±0.18
					female, May	~	1.4±0.12
					female, March	~	1.30±0.15
Voordouw et al. 2005				parent, offspring, raw/corrected	paternal grandfathers, F2 fathers, raw	~	0.92±0.26
					paternal grandfathers, F2 fathers, corrected	~	0.80±0.27
					paternal grandmothers, F2 fathers, raw	~	-0.01±0.30
					paternal grandmothers, F2 fathers, corrected	~	0.09±0.28
					paternal grandfathers, F2 mothers, raw	~	0.78±0.22
					paternal grandfathers, F2 mothers, corrected	~	0.70±0.20
					paternal grandmothers, F2 mothers, raw	~	0.32±0.29
					paternal grandmothers, F2 mothers, corrected	~	0.24±0.33
					F2 fathers, F3 offspring, raw	~	-0.08±0.21
					F2 fathers, F3 offspring, corrected	~	0.19±0.17
					F2 mothers, F3 offspring, raw	~	-0.07±0.21
					F2 mothers, F3 offspring, corrected	~	0.01±0.17
					paternal grandparents, F2 fathers, raw	~	0.45±0.19
					paternal grandparents, F2 fathers, corrected	~	0.38±0.18
					maternal grandparents, F2 mothers, raw	~	0.58±0.17
					maternal grandparents, F2 mothers, corrected	~	0.50±0.16
					F2 parents, F3 offspring, raw	~	-0.06±0.13
					F2 parents, F3 offspring, corrected	~	0.06±0.11

Appendix 2

Determining an evolutionary response from the breeder's equation

In order to determine the evolutionary response of traits to thermal increase, we used the breeder's equation (Eq. 1), which requires knowledge of heritability and the selection differential. Heritability for each trait was determined from the split family experiments, whereas trait-specific selection gradients were established by weighting the trait values by our measurement of fitness (λ). A selection gradient (s), referred to by Lande and Arnold (1983) as a directional selection differential, is the change in the mean value of a phenotypic character (trait) induced by selection over the course of one generation (Eq. A1), where \bar{Z} and \bar{Z}^* are the mean trait values before and after selection.

$$S = \bar{Z}^* - \bar{Z} \quad \text{Eq. A1}$$

Individual trait values (z_i) are each considered to be a phenotype in the population. The mean trait value before selection was calculated as the mean of the observed individual's trait values. The mean trait value after selection was calculated in a different manner than described in Lande and Arnold (1983). The trait value of each individual was weighted by an estimate of individual fitness, λ (equ Eq. A2).

$$\bar{Z}^* = \frac{z_i(z_i\lambda_i)}{(\bar{z}\bar{\lambda})} \quad \text{Eq. A2}$$

Individual fitness (λ)

Fitness was calculated as the principal eigenvalue of the age-structured population projection matrix for each individual (McGraw and Caswell 1996). The first

row of each individual projection matrix being n zeros corresponding to the number of days (n) it took for an individual to mature and k values corresponding to the number of days alive in the adult stage (k). Each value k corresponds to the egg production rate of the individual. For example, the first row of the projection matrix of a copepod that matured in twelve days, lived for twenty days as an adult, and produced forty eggs per day would be twelve zeros followed by twenty forties. The total row length would be 32 corresponding to the copepod's total longevity. This method gives an estimation of individual fitness as it incorporates all measured life history traits.

Individual fitness ranged from approximately 1.22 to 1.45 (Fig. A2-1a). Fitness within families displayed a high variability, with families clustering around fitness values of ~ 1.27 or ~ 1.40 (Fig. A2-1b). Sibship-environment interactions could not be calculated for fitness as time to maturity was determined at a constant temperature for all siblings before the split-family experiment began. Individual fitness values are shown in table A2-1.

Selection differentials were calculated for the traits of *Acartia tonsa* at both treatment temperatures. This method uses data on a trait from one generation to infer the mean value of that trait after selection. Here, I walk the reader through the calculation of a selection differential for daily egg production of *Acartia tonsa* at 22°C (Table A2-2). Family (1-16) is located in the first column. Daily egg production rate and calculated fitness for each individual used in the experiment are in the next two columns to the right. Average EPR and fitness for the population are at the bottom of these columns. Average EPR for the population is the mean trait value before selection (\bar{Z}). EPR and fitness of each individual were multiplied. This product was divided by the

product of EPR and fitness for the population, yielding the relative contribution of each individual to the next generation. The relative contribution of each individual was multiplied by its EPR to determine its adjusted EPR. The average of the adjusted EPRs for the population gives the mean trait value after selection (\bar{Z}^*). Finally, the difference between the mean trait values gives the selection differential.

Table A2-1: Individual Fitness Values

Family	Temperature	Individual	Fitness	Family	Temperature	Individual	Fitness
1	22	1	1.4345	1	24	1	1.3791
1	22	2	1.3334	1	24	2	1.3685
1	22	3	1.4551	1	24	3	1.4088
1	22	5	1.4088	1	24	4	1.4088
1	22	6	1.3494	1	24	5	1.3791
1	22	7	1.3494	1	24	6	1.3494
1	22	8	1.4088	1	24	7	1.3886
2	22	1	1.3791	2	24	1	1.3886
2	22	3	1.4088	2	24	2	1.4088
2	22	4	1.4287	2	24	3	1.3791
2	22	5	1.4287	2	24	4	1.3791
2	22	7	1.3886	2	24	5	1.3131
2	22	8	1.4503	2	24	6	1.3791
3	22	1	1.4159	2	24	7	1.3685
3	22	2	1.3685	2	24	8	1.3563
3	22	3	1.3494	3	24	1	1.4088
3	22	4	1.4088	3	24	2	1.3563
3	22	5	1.4401	3	24	3	1.4345
3	22	6	1.4088	3	24	4	1.3886
3	22	7	1.3494	3	24	5	1.4225
3	22	8	1.4159	3	24	6	1.3131
4	22	1	1.3791	3	24	7	1.4088
4	22	2	1.4225	4	24	1	1.4088
4	22	3	1.3563	4	24	2	1.3563
4	22	4	1.4088	4	24	4	1.3494
4	22	6	1.3494	4	24	5	1.3563
4	22	7	1.3494	4	24	6	1.3886
4	22	8	1.3563	4	24	7	1.3563
5	22	1	1.4225	5	24	2	1.4401
5	22	2	1.4345	5	24	3	1.4088
5	22	3	1.3886	5	24	4	1.4088
5	22	4	1.3791	5	24	6	1.3791
5	22	5	1.3563	5	24	7	1.4503
5	22	7	1.4159	6	24	1	1.4088
6	22	1	1.4345	6	24	2	1.4287
6	22	3	1.3886	6	24	3	1.4503
6	22	4	1.3791	6	24	4	1.4503
6	22	5	1.4597	6	24	5	1.4225
6	22	6	1.4225	6	24	6	1.4597
6	22	7	1.4345	6	24	7	1.4597
7	22	1	1.4453	7	24	2	1.3791
7	22	2	1.4503	7	24	3	1.4401
7	22	3	1.4401	7	24	4	1.4088
7	22	4	1.4159	7	24	5	1.4159
7	22	5	1.4551	7	24	6	1.3418
7	22	6	1.3685	7	24	7	1.3791
7	22	7	1.3685	7	24	8	1.3886
7	22	8	1.4088	8	24	2	1.4287
8	22	1	1.4401	8	24	3	1.3886
8	22	2	1.4551	8	24	4	1.4088
8	22	3	1.3886	8	24	5	1.4088
8	22	5	1.4088	8	24	6	1.4453
8	22	6	1.4597	8	24	7	1.3886
8	22	7	1.4225	8	24	8	1.3886
8	22	8	1.4401	9	24	1	1.4345

Family	Temperature	Individual	Fitness	Family	Temperature	Individual	Fitness
9	22	1	1.4088	9	24	2	1.4287
9	22	2	1.4159	9	24	3	1.4453
9	22	3	1.4551	9	24	7	1.4225
9	22	5	1.4503	9	24	8	1.4088
9	22	6	1.3494	10	24	1	1.4088
10	22	1	1.3563	10	24	3	1.3563
10	22	2	1.3563	10	24	4	1.3418
10	22	3	1.3685	10	24	5	1.3791
10	22	4	1.4159	10	24	6	1.3685
10	22	5	1.3494	10	24	7	1.3685
10	22	6	1.3563	10	24	8	1.3886
10	22	7	1.3494	11	24	2	1.3563
10	22	8	1.3563	11	24	3	1.4551
11	22	1	1.4225	11	24	4	1.4159
11	22	2	1.4551	11	24	5	1.4225
11	22	3	1.3494	11	24	7	1.4345
11	22	5	1.3685	11	24	8	1.4088
11	22	6	1.3131	12	24	1	1.3791
11	22	7	1.3972	12	24	2	1.3791
11	22	8	1.4287	12	24	3	1.3563
12	22	3	1.4088	12	24	4	1.3563
12	22	5	1.4159	12	24	5	1.3563
12	22	6	1.4088	12	24	6	1.3563
12	22	7	1.3131	12	24	7	1.4503
12	22	8	1.3494	13	24	1	1.2523
13	22	1	1.2523	13	24	3	1.2826
13	22	2	1.2871	13	24	4	1.26
13	22	3	1.26	13	24	5	1.2667
13	22	4	1.2725	13	24	6	1.2871
13	22	5	1.2826	13	24	7	1.2912
13	22	6	1.2523	13	24	8	1.2826
13	22	7	1.2912	14	24	1	1.26
13	22	8	1.2667	14	24	2	1.2667
14	22	2	1.2432	14	24	3	1.2318
14	22	3	1.2871	14	24	4	1.2778
14	22	4	1.2778	14	24	5	1.2667
14	22	5	1.2667	14	24	6	1.2523
14	22	6	1.2871	14	24	7	1.2667
14	22	7	1.2667	14	24	8	1.2432
14	22	8	1.2667	15	24	1	1.26
15	22	1	1.2318	15	24	2	1.2667
15	22	2	1.2432	15	24	3	1.26
15	22	3	1.2871	15	24	4	1.2826
15	22	4	1.2826	15	24	5	1.2667
15	22	5	1.2725	15	24	6	1.2725
15	22	6	1.2778	15	24	7	1.26
15	22	7	1.2725	15	24	8	1.2318
15	22	8	1.2871	16	24	1	1.2778
16	22	1	1.26	16	24	2	1.2826
16	22	2	1.2778	16	24	3	1.2667
16	22	3	1.2912	16	24	4	1.2667
16	22	4	1.3021	16	24	5	1.2725
16	22	5	1.2951	16	24	6	1.26
16	22	6	1.2778	16	24	7	1.2432
16	22	7	1.2778	16	24	8	1.2725
16	22	8	1.2725				

Table A2-2: Selection Differential Calculation

Family	Egg Production Rate (EPR)	Fitness	EPR*Fitness	Relative Contribution	Adjusted EPR
1	75.00	1.43	107.59	1.47	109.94
1	65.33	1.33	87.11	1.19	77.54
1	48.67	1.46	70.82	0.96	46.96
1	55.33	1.41	77.95	1.06	58.76
1	26.67	1.35	35.99	0.49	13.08
1	47.00	1.35	63.42	0.86	40.61
1	40.00	1.41	56.35	0.77	30.71
.
.
.
16	69.33	1.26	87.36	1.19	82.52
16	79.33	1.28	101.37	1.38	109.57
16	55.33	1.29	71.44	0.97	53.86
16	43.00	1.30	55.99	0.76	32.80
16	78.67	1.30	101.89	1.39	109.21
16	74.33	1.28	94.98	1.29	96.19
16	63.00	1.28	80.50	1.10	69.10
16	26.33	1.27	33.50	0.46	12.02
	53.82	1.36	73.39		61.73
	Avg. EPR (\bar{Z})	Avg. Fitness			\bar{Z}^*
		$S = \bar{Z}^* - \bar{Z}$			
		Selection Differential	7.91		

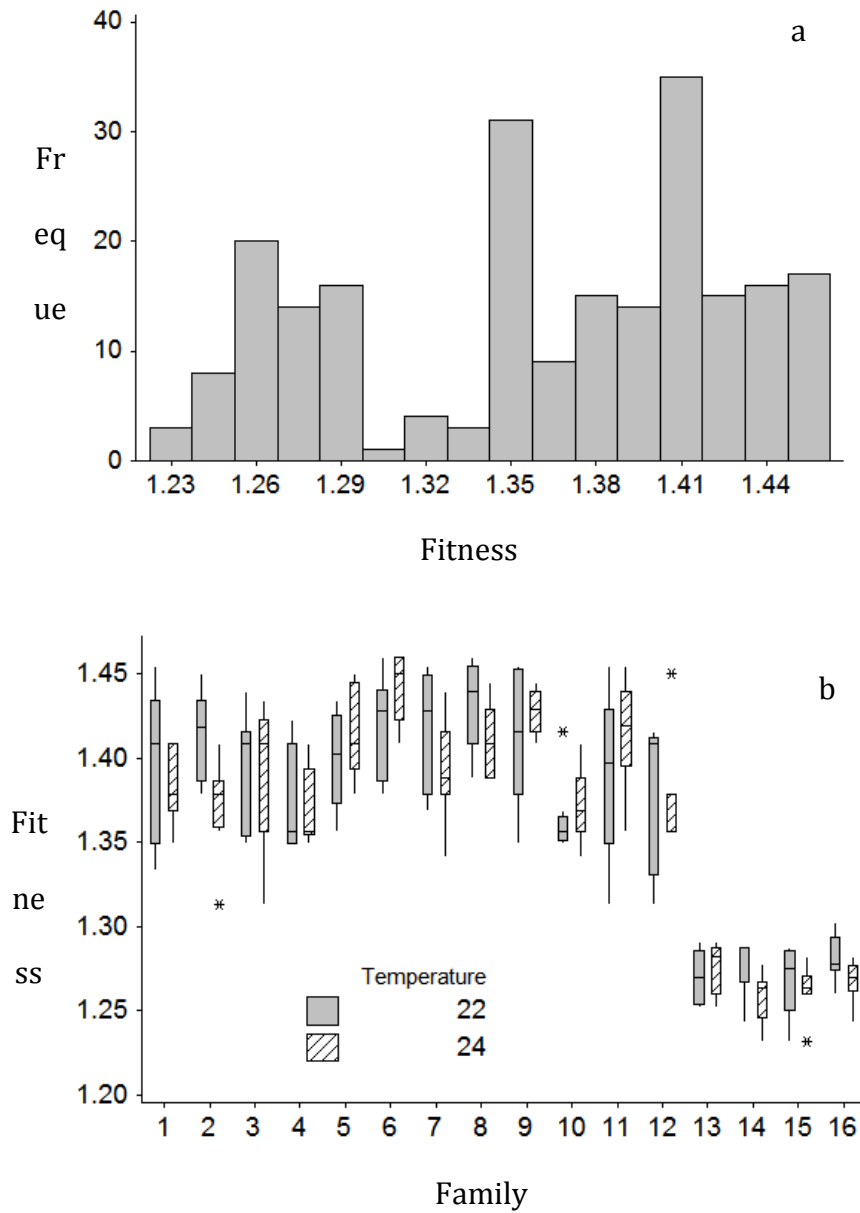


Fig. A2-1. a) *Acartia tonsa*: Individual fitness values binned over family and temperature. b) Box plots of individual fitness partitioned by family and temperature. A sibship-environment interaction was not tested because the fitness calculation includes time to maturity, which was not subject to the treatment temperatures.