8-20-2013

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

Benjamin L. Cournoyer
Benjamin.Cournoyer@gmail.com

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

Benjamin L. Cournoyer

B.S., Eckerd College, 2010

A Thesis

Submitted in Partial Fulfillment of the

Requirements for the Degree of

Master of Science

at the

University of Connecticut

2013

Approval Page

Master of Science Thesis

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

Presented by

Benjamin L. Cournoyer, B.S.

Major Advisor _____
Hans G. Dam

Associate Advisor _____
David E. Avery

Associate Advisor _____
George B. McManus

University of Connecticut

2013

Acknowledgements

I'd like to thank my advisor Hans Dam for allowing me to pursue zooplankton ecology unhindered, guiding me without directly pointing out where the doors were, and keeping my idealistic nature in check. I'd like to thank my committee members David Avery and George McManus for providing me with conceptual assistance and a broad knowledge base with which to understand how my project fits into the big picture of zooplankton ecology and oceanography. I am thankful to Dr. Avery for providing Fig. 1.

In addition I'd like to thank the entire Dam Lab, including: Michael Finiguerra, Tina Senft-batoh, Zair Burris, Gihong Park, Lydia Norton, Charlotte Kading, Silvana Luongo, Caleb Rose, and Nick Stanley. Without their help and daily shenanigans none of this would have been possible.

Finally, I'd like to thank Deb Schuler and Pat Evens. Their expertise in facilitating the daily operations of the Marine Science Department made my life so much easier.

Table of Contents

Title Page ……..… i

Approval Page …… ii

Acknowledgements ……..…. iii

Abstract ……..……v

List of Tables ……..…… vi

List of Figures ……vii

List of Equations ……..…. vii

Introduction ……..…… 1

Materials and Methods ……..… 6

Results ……..…… 11

Discussion ……..… 14

References …… 21

Appendix 1 ……..…… 36

Appendix 2 …….. 42

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^{o}C and 18^{o}C (*Acartia hudsonica*) and 22^{o}Cand 24^{o}C (*Acartia tonsa*). Treatment temperatures represent projected increases of +2^{o}C and +4^{o}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.

List of Tables

Table 1.	Definition of calculation terms	28
Table 2.	Estimates of heritability for *Acartia* spp.	29
Table 3.	Treatment means, selection gradients, and responses	30
Table A2-1.	Individual fitness values	45
Table A2-2.	Selection differential calculation	47

List of Figures

Figure 1. Temporal distribution of *Acartia* spp. in estuaries along the northeastern USA. 31

Figure 2. Box plots of measured traits. 32

Figure 3. Thermal reaction norms. 33

Figure 4. Egg Production vs. Adult Life Span. 34

Figure 5. Reaction norm *of Acartia hudsonica* and temperature climatology in Long Island Sound. 35

Figure A2-1. Frequency distribution and boxplots of fitness values. 48

List of Equations

Equation 1.	Breeder's Equation.	3
Equation 2.	Heritability determination from ANOVA parameters.	9
Equation 3.	Standard error calculation for heritability.	9
Equation 4.	Unequal sample size correction.	9
Equation A2-1.	Selection differential calculation.	42
Equation A2-2.	Approximation of mean trait value after selection.	42

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^{o}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^{o}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.

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

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℃ 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℃ 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_{GxE}) must be calculated. $V_P = V_G + V_E + V_{GxE}$ + 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 $V_{GxE}=0$) (Roff 1997). The initial equation then reduces to $V_P = V_G$+ 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*. (~7μm diameter, ~4 X 10^{-5} μgC $cell^{-1}$) and 50%*Thalassiosira weissflogii* (~11μm diameter, ~4.5 X 10^{-5} μgC $cell^{-1}$). Food was kept ≥ 600μgC 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 where 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℃ and 4℃ above the current mean surface temperature experienced in Long Island Sound by each species, 16℃ and 18℃ for *A. hudsonica* and 22℃ and 24℃ 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.

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

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

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

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 affects. 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, 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±0.18, 0.39±0.15, and 0.26±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 it 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_o (Table 3). These rates are comparable to the evolution of increased temperature in *Daphnia magna* (0.45-1.30 H_o, 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 (~0.2 H_o, Gingerich 2001), molar formation from *Hyracotherium granger* to *H. aemular* (0.225 H_o), and spire length shortening in *Littorina obtusata* (0.064-0.319 H_o, 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℃ and 16℃ mirrors our findings. Egg production begins to decrease above 14℃ and

dramatically decreases beyond 19℃. We can thus expect to see a dramatic decrease in fitness as the temperature exceeds 19℃, 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℃ and 4℃ increase to the growth season of *A. hudsonic*a, 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.

References

Angilletta, M.J., 2009. Thermal adaptation: A theoretical and empirical synthesis. Oxford University Press.

Hoffman, A.A. and and C.M. Sgro. 2011. Climate change and evolutionary adaptation. Nature 470: 479-485.

Avery, D., 2005. Induction of embryonic dormancy in the Calanoid copepod *Acartia hudsonica*: heritability and phenotypic plasticity in two geographically separated populations, J Exp Biol Ecol 314: 215-225.

Avery, D.E. and Dam. H.G. 2007. Newly discovered reproductive phenotypes of a marine copepod reveal the costs and advantages of resistance to a toxic dinoflagellate. Limnol. Oceanogr. 52: 2099-2108.

Banse K. 1995. Zooplankton: pivotal role in the control of ocean production. I. Biomass and production. ICES J. Mar. Sci. 52:265–77.

Bertrand, D.E. 1977. Seasonal succession of the plankton of Penobscot Bay, Maine. M.S. Thesis, Graduate school of Oceanography, University of Rhode Island. 124 pp.

Besiktepe, S. and Dam, H.G. 2002. Coupling of ingestion and defication as a function of diet in the calanoid copepod *Acartia tonsa*. Mar Ecol Prog Ser. 229: 151-164.

Bradley B.P., 1978. Genetic and physiological adaptation of the copepod *Eurytempora affinis* to seasonal temperatures. Genetics 90: 193-205.

Bradley. B.P. and Ketzner. P.A. 1982. Genetic and non-genetic variability in temperature tolerance of the copepod *Eurytemora affinis* in five temperature regimes. Biological Bull. 162: 233-245.

Bradley B.P., 1986. Genetic expression of temperature tolerance in the copepod *Eurytemora affinis* in different salinity and temperature environments. Marn. Biol. 91: 561-565.

Bucklin, A., C. C. Caudill & A. M. Bentley, 1998. Population genetics and phylogeny of marine planktonic copepods. In Cooksey, K. C. (ed.), Molecular Approaches to the Study of the Ocean. Chapman Hall, London: 303–318.

Calbet, A. 2001. Mesozooplankton grazing effect on primary production: a global comparative analysis in marine ecosystems. Limnol. Oceanogr. 46: 1824-1830.

Calbet, A. and E. Saiz. 2005. The ciliate-copepod link in marine ecosystems. Aquatic Microbial. Ecol. 38:157-167

Capriulo, G.M., Smith, G., Troy, R., Wikfords, G.H., Pellet, J., and Yarish, C. 2002. The planktonic food web structure of a temperate zone estuary, and its alteration due to eutrophication. Hydrobiologia. 475/476: 263-333.

Caudill C., and Bucklin A., 2004. Molecular phylogeography and evolutionary history of the estuaring copepod, *Acartia tonsa*, on the Northwest Atlantic coast. Hydrobiologia 511: 91-102.

Chen, G. and Hare M.P. (2008). Cryptic ecological diversification of a planktonic estuaring copepod, *Acartia tonsa*. *Molecular Ecology* 17: 1451-1468.

Chevin L-M, Lande R, Mace GM. 2010. Adaptation, plasticity, and extinction in a changing environment: towards a predictive theory. PLoS Biol. 8:e1000357

Colin, S.P. and Dam, G.H. 2007. Comparison of the functional and numerical responses of resistant versus non-resistant populations of the copepod *Acartia hudsonica* fed the toxic dinoflagellate *Alexandrium tamarense.* Harmful Algae. 6: 875-882.

Dam, H.G., 2013. Evolutionary Adapation of Marine Zooplankton to Global Change. Annual Review of Marine Sciences 5: 349-370.

Dam, H.G., Zhang, X., Butler, M. and Roman, M.R. 1995. Mesozooplankton grazing and metabolism at the equator in the central Pacific: implications for carbon and nitrogen fluxes. Deep-Sea Res. II 42:735–56.

Deevey, G.B. 1960. The Zooplankton of the surface waters of the Delaware Bay region. Bull. Bingham Oceanogr. Coll. 17: 5-53.

Edmands, S. and Harrison, J.S. 2003. Molecular and quantitative trait variation within and among populations of the intertidal copepod *Tigriopus californicus.* Evolution. 57: 2277-2285.

Ellner, S.P., Hairston, N.G., Kearns, C.M. and Babai, D. 1999. The roles of fluctuating selection and long-term diapause in microevolution of diapause timing in a freshwater copepod. Evolution: 53: 111-122.

Falconer, D. and Mackay, T. 1996. Introduction to Quantitative Genetics. Longman, Essex, England.

Fish, C.J. 1925. Seasonal distribution of the plankton of the Woods Hole region. Bull. U.S. Bur. Fish. 41: 91-179.

Fry, J.D. 2003. Detecting Ecological trade-offs using selection experiments. Ecology. 84: 1672-1687.

Gingerich, P.D. 2009. Evolutionary rates. Annual Review of Ecology, Evolution, and Systematics 40: 657-675.

Gingerich, P.D. 2001. Rates of evolution on the time scale of the evolutionary process. Genetica 112-113: 127-144.

Gingerich, P.D. 1993. Quantification and comparison of evolutionary rates. American Journal of Science 293A: 453-478.

Hairston, N.G, Ellner, S.P., Geber, M.A., Yoshida, T. and Fox, J.A. 2005. Rapid evolution and the convergence of ecological and evolutionary time. Ecology Letters 8: 1114-1127.

Hairston, N.G. and Dillon, T.A. 1990. Fluctuating selection and response in a population of freshwater copopods. Evolution. 44: 1796-1805.

Hansen, T.F., Armbruster W.S., Carlson M.L. and Pelabon, C. 2003. Evolvability and genetic constraint in *Dalechampia* blossoms: Genetic correlations and conditional evolvability. Journal of experimental zoology 296B: 23-39.

Hirst, A.G., Kiørboe, T., 2002. Mortality of marine planktonic copepods: global rates and patterns. Mar. Ecol. Prog. Ser. 230, 195–209.

Heinle, D.R. 1966. Production of a calanoid copepod, *Acartia tonsa,* in the Patuxent River estuary. Chesapeake Sci. 7: 59-74.

Hoffmann, A.A. and Sgro, C.M. 2011. Climate change and evolutionary adaptation. Nature 470: doi:10.1038/nature09670.

Houle, D. 1992. Comparing evolvability and variability of quantitative traits. Genetics society of America 130: 195-204.

Holste, L. and Peck, M.A. 2006. The effects of temperature and salinity on egg production and hatching success of Baltic *Acartia tonsa* (Copepoda: Calanoida): a laboratory investigation. Mar. Biol. 148: 1061-1070.

Humes, A.G. 1994. How many copepods? Hydrobiologia. 292/293: 1-7.

Huntley, M.E. and Lopez, M.D.G. 1992. Temperature-dependent production of marine copepods: A global synthesis. The American Naturalist 140: 201-242.

Intergov. Panel Clim. Change. 2007. Summary for policymakers. InClimate Change 2007: The Physical Science Basis: Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change, ed. S Solomon, D Qin, M Manning, Z Chen, M Marquis, et al., pp. 1–18. Cambridge: Cambridge Univ. Press

Isla, J.A., K. Lengfellner and Sommer, U. 2008. Physiological responses of the copepod *Pseudocalanus* sp. In the Baltic Sea at different thermal scenarios. Global Change Biol. Global Change Biology 14: 895-906.

Jeffries, H.P. 1962. Succession of two *Acartia* species in estuaries. Limnology and Oceanography. 7: 354-364.

Jiang, Xiadong, D.J. Lonsdale and C. Gobler. 2011. Rapid gain and loss of evolutionary resistance to the harmful dinoflagellate *Cochlodinium polykrikoides* in the copepod *Acartia tonsa. Limnol. Oceanogr., 56: 947–954.*

Ji, R., Edwards, M., Mackas, D., Runge, J. and Thomas, A. 2010. Marine plankton phenology and life history in a changing climate: current research and future directions. J Plankton Research 32: 1355-1368.

Keser, M., Swenartson, J. and Foertch, J. 2005. Effects of thermal input and climate change on growth of *Ascophyllum nodosum* (Fucales, Pheophyceae) in eastern Long Island Sound. J Sea Res 54: 211-220.

Landry, M.R., Barber, R.T., Bidigare, R.R., Chai, F., Coale, K.H., et al. 1997. Iron and grazing constraints on primary production in the central equatorial Pacific: an EqPac synthesis. Limnol. Oceanogr. 42:405-418.

Lande, R. and Arnold, S.J. 1983. The measurement of selection on correlated characters. Evolution 37:1210–26.

Lee, W.L. and McAlice B.J. 1979. Seasonal Succession and Breeding Cycles of three species of Acartia (Copepoda: Calanoida) in a Maine Estuary. Estuaries. 2: 228-235.

Lee, C.E. and Frost, B.W. 2002. Morphological stasis in the *Eurytemora affinis* species complex (Copepoda: Temoridae). Hydrobiologia. 480: 111-128.

Lee, C.E. and Peterson, C.H. 2002. Genotype-by-environment interaction for salinity tolerance in the freshwater-invading copepod *Eurytemora affinis*. Physiological and Biochemical Zoology. 75: 335-344.

Lobon, C.M., Acuna, J.L., Lopez-Alvarez, M. and Capitanio, F.L. 2011. Heritability of morphological and life history traits in a pelagic tunicate. Mar Ecol Prog Ser. 422: 145-154.

Longhurst, A.R. 1991. Role of the marine biosphere in the global carbon cycle. Limnol. Oceanogr. 36:1507–26.

Longhurst, A.R., Bedo, A.W., Harrison, W.G., Head, E.J.H., Sameoto, D.D. 1990. Vertical flux of respiratory carbon by oceanic diel migrant biota. Deep-Sea Res. I 37:685–94

Martin, J.H. 1965. Phytoplankton-Zooplankton relationships in Narragansett Bay. ASLO. 2: 185-191.

Mauchline, J. 1998. The biology of calanoid copepods.

McLaren, I.A. 1976. Inheritance of demographic and production parameters in the marine copepod *Eurytemora herdmani.* Biol. Bull. 151: 200-213.

McLaren, I. and Corkett, C.J. 1978. Unusual genetic variation in body size, development times, oil storage, and survivorship in the marine copepod *Pseudocalanus.* Biol. Bull. 155: 347-359.

Miehls, A.L.J., Peacor, S.D. and McAdam, A.G. 2011. Genetic and maternal effects on tail spine and body length in the invasive spiny water flea (*Bythotrephes longimanus).* Evolutionary Applications. 5: 306-316.

Nixon, S., Granger, S., Buckley, B., Lamont, M. and Rowell, B. 2004. A one hundred and seventeen year coastal water temperature record from Woods Hole, Massachusetts, Estuaries 27: 397-404.

Parrish, K.K. and Wilson, D.F. 1978. Fecundity studies on *Acartia tonsa* (Copepoda: Calanoida) in standardized culture. Marn. Biol. 46: 65-81.

Peijnenburg, K.T.C.A. and Goetze, E. 2013. High evolutionary potential of marine zooplankton. Ecology and Evolution. Doi: 10.1002/ece3.644.

Peterson, W. 1986. The effect of seasonal variation in stratification on plankton dynamics in Long Island Sound. In: Bowman, M., Yentsch, C., Peterson, W. (Eds.), Tidal Mixing and Plankton Dynamics. Springer-Verlag, New York.

Pigliucci, M. 2001. Phenotypic Plasticity: Beyond Nature and Nurture. Baltimore: Johns Hopkins Univ. Press

Richardson, A. 2008. In hot water: Zooplankton and climate change. ICES J Mar Sci 65: 279-295.

Roff, D. 1997. Evolutionary Quantitative Genetics. Chapman Hall, New York.

Sherr, E.B., B.F. Sherr and G.A. Paffenhöfer. 1985. Phagotrophic protozoa as food for metazoans: a “missing” trophic link in marine pelagic food webs? Marine Microbial Food Webs. 1: 61-69.

Shirdhankar, M.M. and Thomas, P.C. 2003. Heritability estimates of naupliar length in *Artemia franciscana* using different methods. Asian Fisheries Science. 16: 69-76.

Shirdhankar, M.M., Thomas, P.C. and Barve, S.K. 2004. Phenotypic estimates and heritability values of *Artemia franciscana.* Aquaculture Research. 35: 35-39.

Stachowicz J., Terwin, J., Whitlatch, R. and Osman, R. 2002. Linking climate change and biological invasions: Ocean warming facilitates nonindigenous species invasions. Proc Nat Acad Sci 99: 15497-15500.

Somero, G.N. 2010. The physiology of climate change: how potentials for acclimatization and genetic adaptation will determine “winners” and “losers.” J. Exp. Biol. 213:912–20.

Sullivan, B.K., Costello, J.H. and Van Keuren, D. 2007. Seasonality of the copepod Acartia hudsonica and *Acartia tonsa* in Narragansett Bay, RI, USA during a period of climate change. Estuarine Coastal and Shelf Science. 73: 259-267.

Turner, J.T. 1981. Latitudinal patterns of calanoid and cyclopoid copepod diversity in estuarine waters of Eastern North America. Journal of Biogeography. 8: 369-382.

Tepper, B. and Bradley, B.P. 1989. Temporal changes in a natural population of copepods. Biol. Bull. 176: 32-40.

Van Doorslaer, W., Stoks, R., Divovier, C., Bednarska, A. and DeMeester, L. 2009. Population dynamics determine genetic adaptation to temperature in *Daphnia*. Evolution. 63: 1867-78.

Voordouw, M.J. and Anholt, B.R. 2002. Heritability of sex tendency in a harpacticoid copepod, *Tigriopus californicus*. Evolution. 56: 1754-1763.

Voordouw, M.J., Robinson, H.E. and Anholt, B.R. 2005. Paternal inheritance of the primary sex ratio in a copepod. J. Evol. Biol. 18: 1304-1314.

Walker, C.H., Hopkin, S.P., Sibly, R.M., and Peakall, D.B. 2001. Principles of ecotoxicology, 2nd ed. Taylor & Francis.

Whitman, W.A. and Agrawal A.A. 2009. What is phenotypic plasticity and why is it important? In Phenotypic Plasticity of Insects: Mechanisms and Consequences, ed. DW Whitman, TN Ananthakrishan, pp. 1–63. Enfield, NH:Sci. Publ

Zar, J.H. 1984. Biostatistical Analysis 2nd ed. Prentice-Hall, Inc., Englewood Cliffs, New Jersey USA.

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_{GxE}	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 ith Temperature within Sibship Treatment
T	Total number of individuals

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

A. tonsa (22°C - 24°C)	Egg Production (eggs/day)	Adult life span (days)	Lifetime fecundity (eggs/lifetime)
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
A. hudsonica (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. Tr
means, se
gradient
respons
Acartia to
projected v
All values
the trait
unless oth
specified.
responses
from the
associate
heritab

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

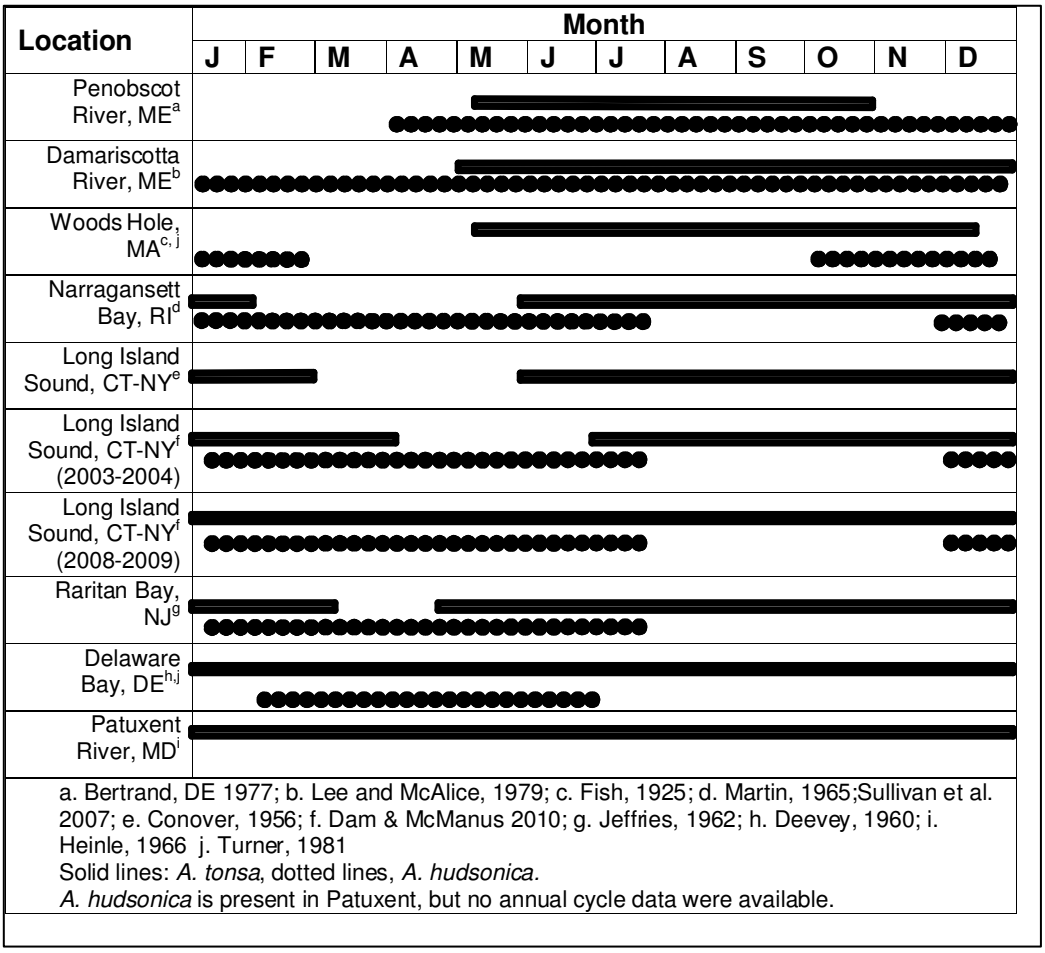

Fig. 1. Temporal distribution of *Acartia* spp. in estuaries along the northeast coast of the USA. Solid lines indicate presence of *A. tonsa* adults or copepodites. Dotted lines indicate presence of *A. hudsonica* (*clausi*) adults or copepodites. The estuaries are sorted approximately according to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

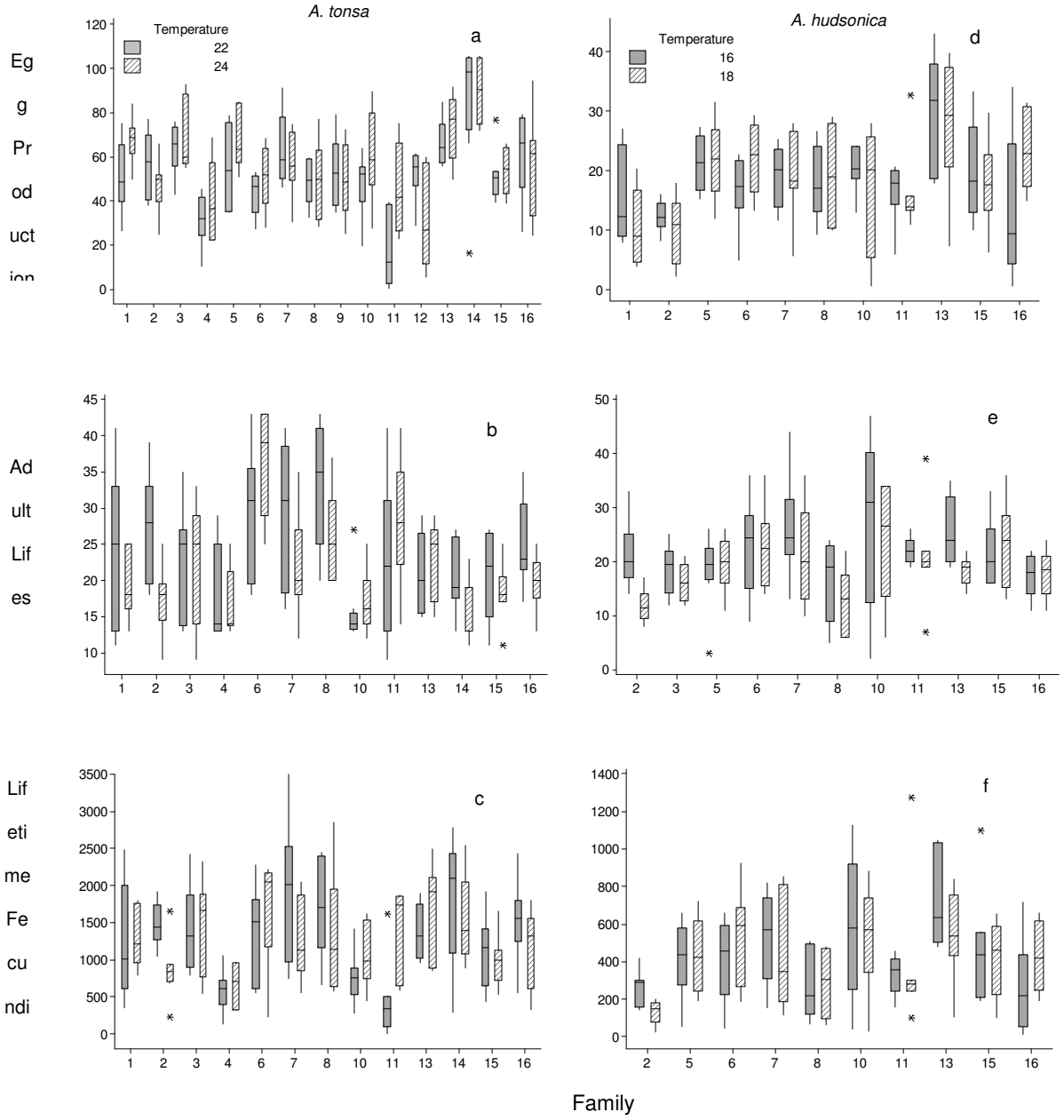

Fig. 2. Box plots of egg production (a,d), adult life span (b,e), and lifetime fecundity (c, f) for each temperature nested within family treatment. The nested ANOVAs indicate significant variation among families of the warm-adapted *Acartia tonsa* (A-C, p= 0.020, 0.030. 0.027), but not the cold-adapted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

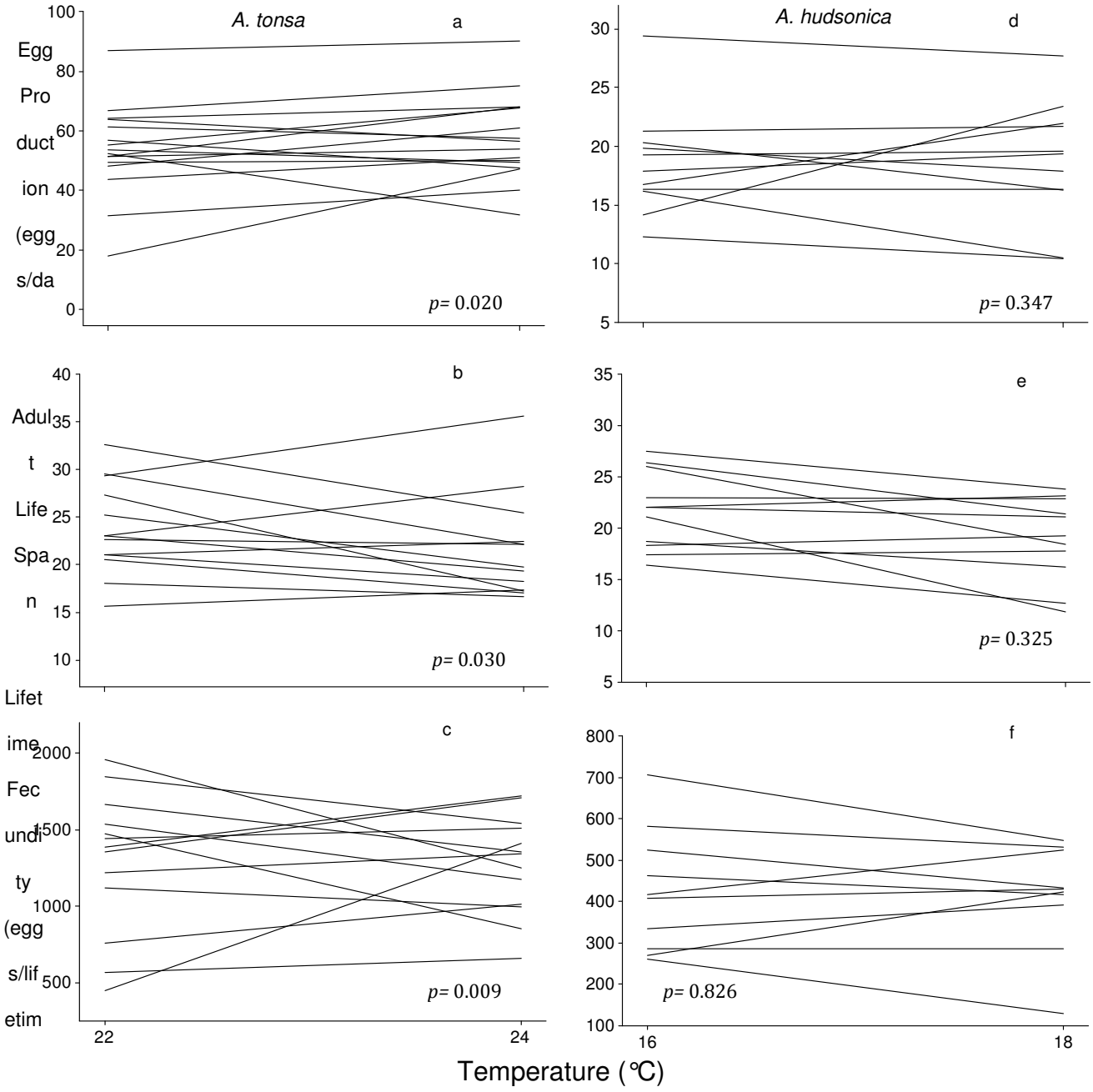

Fig. 3. Reaction norm plots for *Acartia tonsa* (a-c) and *Acartia hudsonica* (d-f). Each line represents the reaction norm of one family, corresponding to the families in Fig. 2. *p-values* indicate the significance of the sibship-environment interaction.

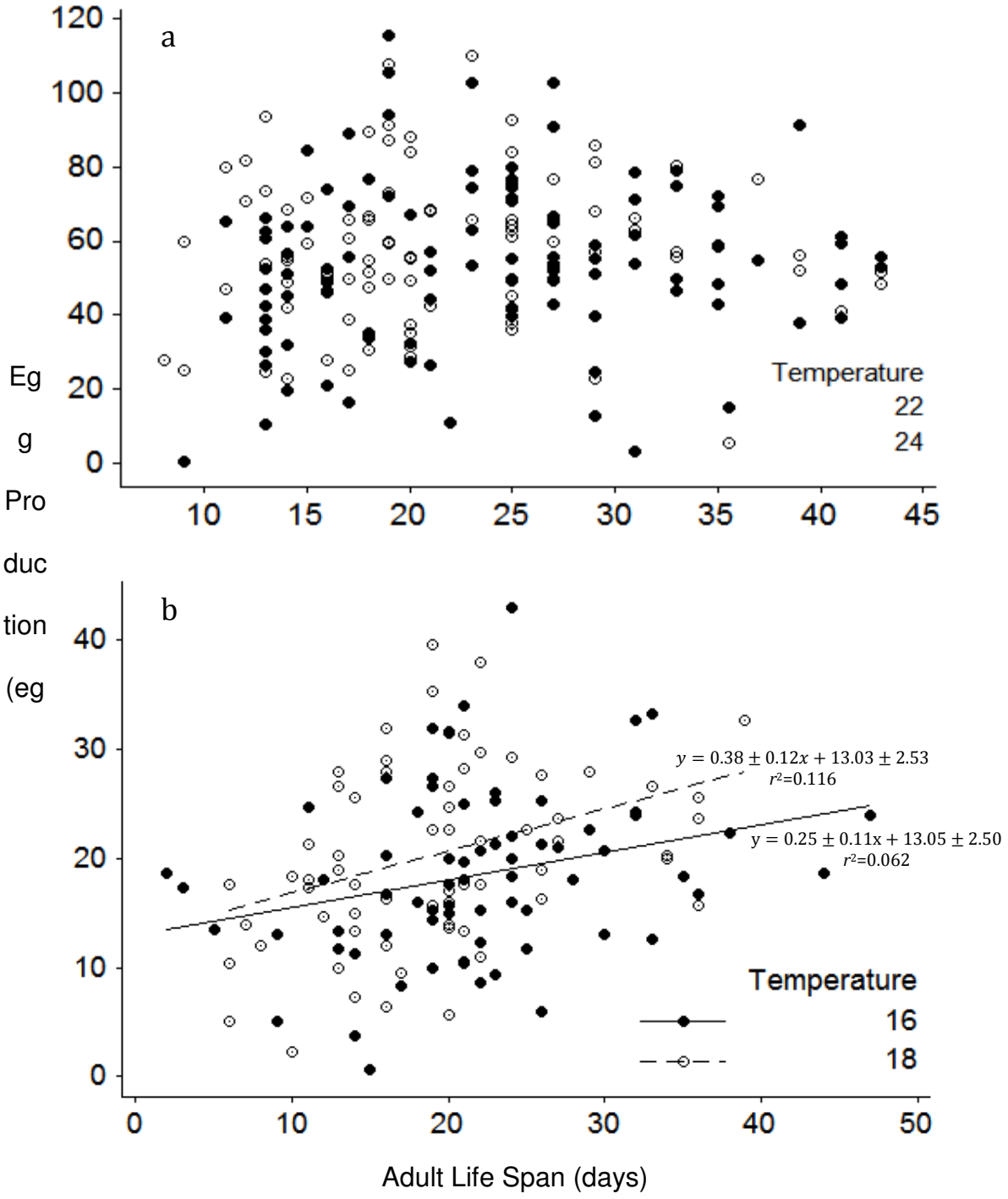

Fig. 4. Egg production versus adult life span. Each point corresponds to an individual copepod. For *Acartia tonsa* (a), no tradeoffs were observed, as neither linear regression was significant, p= 0.185 for 22°C and p= 0.396 for 24°C. For *A. hudsonica* (b), both temperature-treatment yielded weak,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

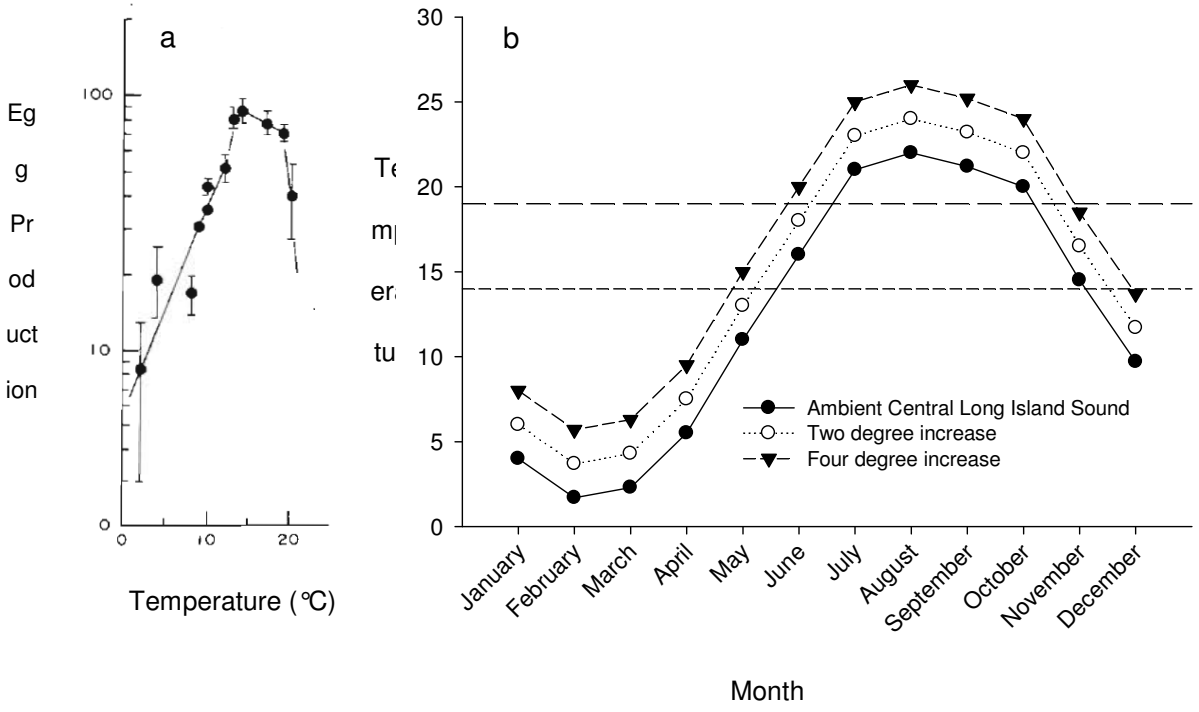

Fig. 5. a) Thermal reaction norm of *Acartia hudsonica* (Sullivan and McManus (1986). Daily egg production peaks around 14°C and sharply decreases above 19°C. b) Average surface water temperature±SE for central Long Island Sound between 2000 and 2011, with additional curves indicating a +2° and +4°C 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	*Acartia tonsa*	Long Island Sound, CT	daily egg product	female offspring to temperature	20°	22-24°	0.69±0.18
*	*	*	adult lifespan	*	20°	22-25°	0.39±0.15
*	*	*	lifetime fecundity	*	20°	22-26°	0.26±0.19
Avery 2005	*Acartia hudsonica*	Cudy's Harbor, ME	%dorman eggs	temperature & light cycle	12°; 12L:12D	~	0.91±0.20
*	*	*	*	*	17°; 12L:12D	~	1.10±0.16
*	*	*	*	*	17°; 15L:15D	~	0.08±0.21
*	*	Narragansett Bay, RI	*	*	13.5°; 12L:12D	~	0.95±0.28
*	*	*	*	*	17.5°; 12L:12D	~	0.25±0.38
McLaren and Corkett 1978	*Pseudocalanus*	Nova Scotia, Canada	body size	between sires	10°	~	0.92
*	*	*	*	between dams, within sires	*	~	0
*	*	*	age of maturity	between sires	*	~	0.56
*	*	*	*	between dams, within sires	*	~	0.59
*	*	*	time, N1-C1	between sires	*	~	0
*	*	*	*	between dams, within sires	*	~	1.47
Lobon et al. 2011	*Oikopleura dioica*	Gijon, Spain	intrinsic rate of ir	parental/offspring variation	15°; 12L:12D	~	0.69±0.40
*	*	*	lifespan	*	*	~	0.89±0.47
*	*	*	clutch size	*	*	~	0.27±0.32
*	*	*	egg diameter	*	*	~	0.18±0.28
*	*	*	trunk length	*	*	~	0.37±0.25
*	*	*	gonad length	*	*	~	0.00±0.08
*	*	*	house size	*	*	~	0.39±0.23
*	*	*	tail length	*	*	~	0.50±0.31
Shirdhankar et al. 2004	*Artemia franciscana*	*	*	offspring sex	male	~	0.59±0.22
*	*	*	*	*	female	~	0.38±0.19
*	*	*	length at three da	*	male	~	0.33±0.37
*	*	*	*	*	female	~	0.12±0.38
*	*	*	length at six days	*	male	~	0.50±0.25
*	*	*	*	*	female	~	0.02±0.30
*	*	*	length at first bro	*	female	~	0.04±0.11
*	*	*	pre-reproductive	*	female	~	0.32±0.29
*	*	*	first brood offsp	*	female	~	0.34±0.22

Study	Species	Location	Trait	Source of Variation/Regression	Condition Raised	Treatment	Heritability±SE	*p*
McLaren 1976	*Eurytemora herdmani*	Halifax,NS	time to maturity	temperature, offspring sex, parental variation	10°, male, sires	~	0.1	0.45
*	*	*	*	*	10°, male, dames (within sires)	~	0.42	0.06
*	*	*	*	*	10°, female, sires	~	0.2	0.3
*	*	*	*	*	10°, female, dames (within sires)	~	0	0.5
*	*	*	*	*	15°, male, sires	~	0	0.68
*	*	*	*	*	15°, male, dames (within sires)	~	1.13	<0.0001
*	*	*	*	*	15°, female, sires	~	0.71	0.05
*	*	*	*	*	15°, female, dames (within sires)	~	0.72	<0.001
*	*	*	adult size of offspring	*	10°, male, sires	~	0	0.52
*	*	*	*	*	10°, male, dames (within sires)	~	0.75	0.01
*	*	*	*	*	10°, female, sires	~	0.24	0.35
*	*	*	*	*	10°, female, dames (within sires)	~	0.93	0.02
*	*	*	*	*	15°, male, sires	~	0.97	0.04
*	*	*	*	*	15°, male, dames (within sires)	~	0.76	0.001
*	*	*	*	*	15°, female, sires	~	0.38	0.14
*	*	*	*	*	15°, female, dames (within sires)	~	0.48	<0.001
*	*	*	*	temperature, offspring sex, parental regression	10°, male, mean parent	~	0.18±0.104	-
*	*	*	*	*	10°, male, male	~	-0.36±0.181	-
*	*	*	*	*	10°, male, female	~	0.47±0.151	-
*	*	*	*	*	10°, female, mean parent	~	0.17±0.061	-
*	*	*	*	*	10°, female, male	~	-0.63±0.209	-
*	*	*	*	*	10°, female, female	~	0.89±0.161	-
*	*	*	*	*	12.5°, male, mean parent	~	0.19±0.046	-
*	*	*	*	*	12.5°, female, mean parent	~	0.19± 0.062	-
*	*	*	*	*	15°, male, mean parent	~	0.61±0.118	-
*	*	*	*	*	15°, male, male	~	0.74±0.107	-
*	*	*	*	*	15°, male, female	~	0.39±0.378	-
*	*	*	*	*	15°, female, mean parent	~	0.51±0.153	-
*	*	*	*	*	15°, female, male	~	0.6±0.149	-
*	*	*	*	*	15°, female, female	~	0.41±0.399	-
*	*	*	mortality before maturity	temperature , parental variation	10°, sires	~	0.01±0.107	-
*	*	*	*	*	10°, dames (within sires)	~	0.08±0.111	-
*	*	*	*	*	15°, sires	~	0.02±0.043	-
*	*	*	*	*	15°, dames (within sires)	~	0.13±0.101	-
*	*	*	sex ratio in offspring	*	10°, sires	~	0.11±0.218	-
*	*	*	*	*	10°, dames (within sires)	~	0.13±0.221	-
*	*	*	*	*	15°, sires	~	0.27±0.153	-
*	*	*	*	*	15°, dames (within sires)	~	0.33±0.171	-

Study	Species	Location	Trait	Source of Variation/Regression	Condition Raised	Treatment	Heritability±SE
Bradley 1986	*Acartia hudsonica*	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	male, acute 5psu	32- 36.5 °	0.35±0.30
*	*	*	*	*	female, acute 5psu	32- 36.5 °	0
*	*	*	*	*	male, acute 12 psu	32- 36.5 °	0.57±0.27
*	*	*	*	*	female, acute 12 psu	32- 36.5 °	0.90±0.43
*	*	*	*	*	male, chronic 5psu	32- 36.5 °	0.64±0.26
*	*	*	*	*	female, chronic 5psu	32- 36.5 °	0.68±0.27
*	*	*	*	*	male, chronic 12 psu	32- 36.5 °	0.38±0.20
*	*	*	*	*	female, chronic 12 psu	32- 36.5 °	0.66±0.26
Bradley 1978	*Eurytemora affinis*	Chesapeak Bay	*	offspring sex & parental variation	female, sires (half-siblings)	32-35 °	0.40±0.18
*	*	*	*	*	female, dames (half-siblings)	32-35 °	0
*	*	*	*	*	female, mean parent (full-sibling)	32-35 °	0.20±0.09
*	*	*	*	*	male, sires (half-siblings)	32-35 °	0.84±0.35
*	*	*	*	*	male, dames (half-siblings)	32-35 °	0.73±0.32
*	*	*	*	*	male, joint estimates (full-sibling)	32-35 °	0.79±0.24
*	*	*	*	*	female, single pair matings	32-35 °	0.11±0.10
*	*	*	*	*	male, single pair matings	32-35 °	0.89±0.45
*	*	*	*	*	female half broods partitioned by hatching	32-35 °	0.28±0.18
*	*	*	*	*	male half broods partitioned by hatching	32-35 °	0.78±0.29
Lee and Frost 2002	*Eurytemora affinis*	globally sampled	morphological characters	sex, morphological character	female, genetal segmanet width	~	0.995
*	*	*	*	*	female, genetal segmanet shape	~	0.353
*	*	*	*	*	female, antennule proportions	~	0.899
*	*	*	*	*	male, 5th leg, right exopod 1	~	1.000
*	*	*	*	*	male, 5th leg, right exopod 2	~	1.000
*	*	*	*	*	male, 5th leg, left basipod 2	~	0.205
*	*	*	*	*	male, 5th, leg proportions	~	0.380
*	*	*	*	*	male, antennule proportions	~	0.254
Edmands and Harrison 2003	*Tigriopus californicus*	West Coast USA	Life-history & Morphological traits	All populations	20°; 12L:12D	~	0.28±0.08
*	*	*	*	Northern Poplations	*	~	0.14±0.10
*	*	*	*	Southern Populations	*	~	0.42±0.10
*	*	*	Life-history traits	All populations	*	~	0.52±0.14
*	*	*	*	Northern Poplations	*	~	0.11±0.15
*	*	*	*	Southern Populations	*	~	0.93±0.18
*	*	*	Morphological Characters	All populations	*	~	0.21±0.09
*	*	*	*	Northern Poplations	*	~	0.15±0.13
*	*	*	*	Southern Populations	*	~	0.12±0.09

Study	Species	Location	Trait	Source of Variation/Regression	Condition Raised	Treatment	Heritability±SE
Shirdhankar and Thomas 2003	*Artemia franciscana*	Great Salt Lake, USA	naupliar length	generation, offspring/parent variation, 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	~	0.38±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 Dillion 1990	*Diaptomus sanguineus*	*	diapause photoperiod sensitivity	parental/offspring variation, 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
Shirdhankar and Thomas 2003	*Artemia franciscana*	Great Salt Lake, USA	naupliar length	generation, offspring sex, line	0, male, SNS	~	1.47±0.09
*	*	*	*	*	1, male, SNS	~	1.41±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	~	1.47±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 Anholt 2002	*Tigriopus californicus*	British Columbia	sex tendency	corrected, season, temperature	uncorrected, summer, 15°	~	0.12±0.04
*	*	*	*	*	uncorrected, summer, 22°	~	0.00±0.02
*	*	*	*	*	uncorrected, fall, 15°	~	0.24±0.06
*	*	*	*	*	uncorrected, fall, 22°	~	0.16±0.05
*	*	*	*	*	corrected, summer, 15°	~	0.10±0.03
*	*	*	*	*	corrected, summer, 22°	~	0.00±0.01
*	*	*	*	*	corrected, fall, 15°	~	0.19±0.05
*	*	*	*	*	corrected, fall, 22°	~	0.12±0.04

Study	Species	Location	Trait	Source of Variation/Regression	Condition Raised	Treatment	Heritability±SE
Ellner et al. 1999	*Diaptomus sanguineus*	Rhode Island, USA	diapause egg production timing	model	-	-	1.54±1.08
Hunte and Myers 1984	*Gammarus lawrencianus*	Nova Scotia, Canada	loss of photopositivity	offspring variation with age	21°, 16psu, 12L:12D	~	0.210
Miehls et al. 2011	*Bythotrephes longimanus*	Lake Michigan, USA	distal spine length	time period	2007 September	~	0.76
*	*	*	*	*	2008 Combined	~	0.48
*	*	*	*	*	2010 July	~	0.27
*	*	*	body length	*	2008 July	~	0.3
*	*	*	*	*	2008 September	~	0.48
*	*	*	*	*	2010 July	~	0.13
Tepper and Bradley 1989	*Eurytemora affinis*	Chesapeak Bay, USA	high temperatuer 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	~	1.18±0.11
*	*	*	*	*	female,May	~	1.09±0.17
*	*	*	*	*	female, March	~	1.22±0.17
*	*	*	m-brood	*	female, May	~	0.99±0.17
*	*	*	*	*	female, March	~	0.91±0.19
*	*	*	r-brood	*	female, May	~	1.16±0.15
*	*	*	*	*	female, March	~	1.07±0.18
*	*	*	proportion hatched	*	female, May	~	1.41±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	~	0.16±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.

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

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℃ (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**

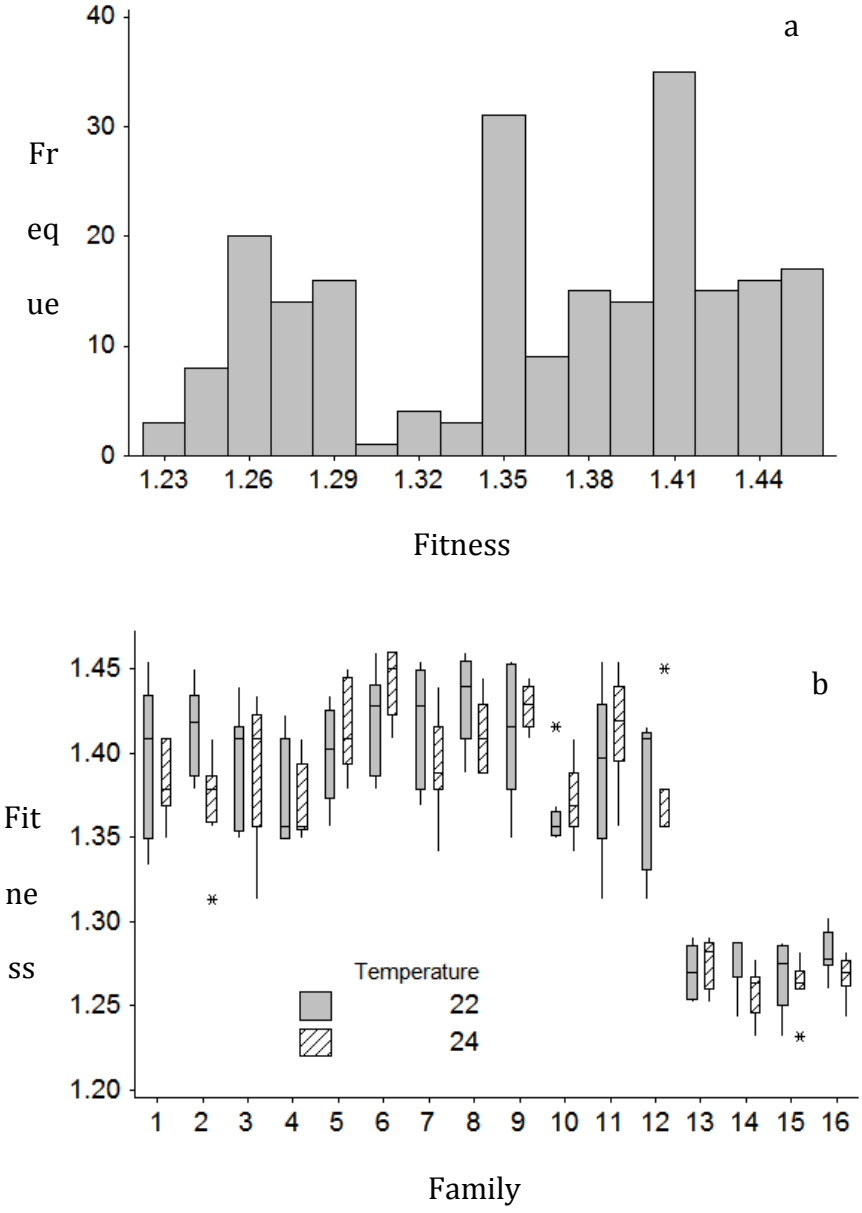

Fig. A2-1. a) *Acartia tonsa*: Individual fitness values binned over family and temperature. b) Box plots of individual fitness partitioned by family and temperature. A sibship-environment interaction was not tested because the fitness calculation includes time to maturity, which was not subject to the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