

Thermal Transgenerational Plasticity and Its Effect on  
Competitive Ability and Consumer-Resource  
Dynamics in a Population of  
*Daphnia ambigua*

by

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I dedicate this thesis to my children, Abigail and Ian. It was your birth, Abigail, that caused me to change careers, and yours Ian, that motivated me to cross the finish line.

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Abstract

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Global temperature increases are predicted to quicken in pace this century, and with them so will the likely impact on natural populations. The extent to which organisms will be able to keep pace with and adapt to these environmental changes is an unanswered question. It has been demonstrated that changing environments can induce changes in phenotypes that persist across generations. TGP may be an important means for populations to cope with climate change stress, but our understanding of these interactions is incomplete. Prior work showed that *Daphnia* program their offspring for faster development when reared under cooler temperatures. Here I tested the impact of thermal TGP in development on population dynamics and competitive interactions in a species of zooplankton (*Daphnia ambigua*) from a lake in Connecticut. I found that populations whose parents were reared at cool temperatures had greater rates of population increase when their offspring were transferred to a warmer temperature compared with treatments that experienced consistently warm conditions. This link between parental rearing temperature and rates of population growth are thus likely due to divergent transgenerational effects of temperature on the expression of life history

traits. Though, this link between transgenerational responses and population dynamics were much weaker (and non-significant) when the populations were reared in larger mesocosms. My findings call for more research into the relationship between TGP and population dynamics and community interactions.

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## Chapter 1

### Introduction

The ability of an organism to alter traits in response to changes in environmental conditions has been known for decades (Bradshaw 1965). The ecological importance of such “phenotypic plasticity” is well established as it can alter direct and indirect ecological interactions with a cascading influence on the properties of populations and communities (Miner et al. 2005). For example, behavioral plasticity can result in trophic cascades (Schmitz et. al. 1997) and changes in competitive interactions (Werner & Anholt 1996). Morphological plasticity can facilitate shifts in resource use (de Kroons & Hutchings 1995) or consumer interactions (Young et. al. 2003). Phenotypic plasticity can also influence predator-prey interactions via inducible defenses (Padilla 2001) or by occurring in traits that govern predator avoidance (Loose & Dawidowicz 1994). For example, tadpoles of *Hyla versicolor*, the gray tree frog, respond to the threat of predation by exhibiting greater swimming speed and reduced activity to avoid predation, which results in reduced algae consumption (Buskirk 2000). This change in behavior is significant because *H. versicolor* tadpoles play a role in food-web dynamics because its grazing activity influences the structure of algae communities in the ponds it inhabits (Harding 1997). It is thus clear that plasticity can alter interactions across species and trophic levels (Yorke & Metaxas 2011).

Research performed over the past two decades has shown that environmental signals can also induce changes in phenotypes that persist for multiple generations (Jablonka & Raz 2009, Agrawal et. al. 1999). This “transgenerational plasticity” (TGP) occurs when the environment experienced by parents causes phenotypic changes in offspring and future generations (Fox & Mousseau 1998). Transgenerational plasticity has been documented in organisms spanning the tree of life in response to numerous

environmental stressors (Jablonka & Raz 2009). This includes transgenerational responses that are induced by variation in temperature (Salinas & Munch 2011; Walsh et al. 2014), resource limitation (Bashey 2006), predator exposure (Walsh et al. 2015), and canopy shading (Galloway & Etterson 2011). Similar to phenotypic plasticity that occurs during development (i.e., within generation plasticity), researchers have speculated that transgenerational plasticity has potentially far reaching consequences for populations, communities, and ecosystems (Herman and Sultan 2011, Mondor et. al. 2004, Sultan et. al. 2009).

There are several reasons why transgenerational plasticity may provide a link to ecological processes (Abrams 1995). Environmental signals often induce transgenerational responses in life-history traits (Galloway & Etterson 2007, Mousseau & Fox 1998, Marshal 2008). Life history traits strongly contribute to rates of population growth (Gotelli 1995). Thus, across-generation shifts in life history traits may alter community interactions and food-web dynamics (Chase 1999). For instance, the cotton aphid, *Aphis gossypii* produces winged offspring when exposed to predator search cues (Mondor et. al. 2005). The winged morphs, in turn, produce offspring that are yellow, wingless and about  $\frac{1}{4}$  the size of the parents. This yellow dwarf has a reduced growth rate and intrinsic rate of increase (Watt & Hales 1996). This maternal effect offers the clear potential to alter numerous cascading ecological interactions. Additionally, ant tended aphids produce a light-green, wingless morph that is resistant to parasitism and has an intermediate intrinsic rate of increase, benefiting the ants by producing the optimal amount of honeydew (Mondor et. al. 2008). Such results foreshadow that phenotypic responses that persist for multiple generations may have broad ecological ramifications. However, the importance and generality of this link between multi-generation responses and community and ecosystem processes is unclear.

## 1.2 Study Organism

*Daphnia* are freshwater planktonic crustaceans that are a ubiquitous feature of lentic environments (Fernando 2002). *Daphnia* have long been used as a model organism for outstanding ecological and evolutionary questions (Colbourne et. al. 1998, Lynch 1984, Brooks 1957, Hu & Tessier 1995, Allan 1977, Sinko & Streifer 1969). This is because they have well established ecological roles as the primary grazer of phytoplankton (Lathrop & Carpenter 1992), and they exhibit many characteristics that make them accessible for experimental manipulation (i.e. short generation time, traits that are easily quantifiable). *Daphnia* are also well known to modify their traits and thus exhibit phenotypic plasticity in response to many common environmental variables including temperature (Sakwinska 1998), resource availability (Walls et. al. 1997, Ebert 1993), competition, and predation (Tollrian 1995).

Recent work has shown that *Daphnia* respond to environmental signals by modifying traits across generations (Agrawal et al. 1999; Harris et al. 2012; Walsh et al. 2014). Walsh et al. (2014) evaluated patterns of thermal transgenerational plasticity in *Daphnia ambigua* from lakes in Connecticut. They reared *Daphnia* across a range of temperatures that mimic the known differences between spring and summer in lakes and found that *Daphnia* reared at cooler temperatures program their offspring for faster development while the opposite response was observed when *Daphnia* were reared under warmer conditions that mimic summer temperatures in lakes. Given the well-known connection between life history traits and rates of population growth (Gotelli 1995), and the use of intrinsic rate of increase as an indicator of fitness (Lampert & Trubetskova 1996), this finding foreshadows an ecological importance of thermal TGP and allows for a clear test of the link between TGP and ecological processes.

### 1.3 Hypothesis

This project tested the connection between thermal transgenerational plasticity and population dynamics and community interactions. I reared *Daphnia* across a range of temperatures and then manipulated the temperature experienced in the subsequent generation to examine the connection between parental temperature and subsequent ecological processes. I first tested the influence of contrasting parental rearing temperature on inter- and intraspecific competitive interactions in highly controlled experimental units (see 'Competitive ability experiment'). The second approach then examined the link between parental temperature and consumer-resource dynamics in larger lab mesocosms (see 'consumer-resource dynamics experiment').

#### *Objective 1*

Test the influence of thermally induced TGP on competitive ability.

Based upon previous work showing that parental exposure to cooler temperatures is associated with significantly faster rates of development the following generation (Walsh et al. 2014), I predicted that the offspring of *D. ambigua* reared under cooler temperatures will exhibit faster population growth rates and enhanced competitive ability than the offspring of *Daphnia* reared at warmer temperatures. (See Fig 1).

#### *Objective 2:*

Test the influence of thermally induced TGP on consumer-resource dynamics.

Given the link between parental temperature and population growth (Walsh et al. 2014), I also predicted that *Daphnia* reared at cooler temperatures will yield faster rates of population growth (see Fig. 1), and faster declines in algal abundance compared with experimental units whose parents were reared at warmer temperatures (see Fig. 1).

## Chapter 2

### Methods

#### 2.1. Overview

This project leveraged the known existence of thermal TGP in *D. ambigua* to explore the effects of TGP on competitive interactions and consumer-resource dynamics. This overall goal was accomplished by creating four contrasting temperature treatments and then exploring the ecological consequences of these treatments. Common garden reared *Daphnia* were reared under contrasting temperature regimes (cool vs. warm) and then offspring were exposed to the same or opposite conditions as their parents. I then assessed rates of population growth (and declines in algae for a subset of the experiments). Below I describe all experiments in detail.

#### 2.2 Establishment of Study Organisms

For these experiments, multiple clones of *Daphnia* were first hatched from resting eggs and all lineages were then reared for three generation under highly controlled conditions to eliminate previous environmental and maternal effects. These experiments used clones of *D. ambigua* that were collected from Gardner Lake in Connecticut, USA using an Ekman grab (see Post et al. 2008 for map). This population was targeted because clones from this lake are known to respond strongly to changes in temperature by modifying traits across generations (Walsh et al. 2014). Seven clones were hatched from sexual resting eggs and reared individually in 90-ml jars at 19°C containing COMBO media (Kilham et al. 1998) and fed specified quantities of high-quality algae, *Scenedesmus obliquus* (concentration of 0.2 mg C L<sup>-1</sup>). COMBO and algae were replaced every other day. To generate the second and then third common garden reared generations, offspring were pulled from the second clutch of each clone and reared under

the same conditions as described above. One distinction between the second and third laboratory generations is that multiple individuals were collected from the second clutch of clones and reared individually to begin to increase the number of animals available for the TGP experiments.

### 2.3 Experimental Design, Intraspecific Competitive Ability

This experiment compared growth rates and population densities among treatments that experienced contrasting temperature histories. To induce thermal transgenerational responses (Walsh et al. 2014), approximately 20 neonates were collected from the second clutch (or later) per clone from the third generation lab reared generation. These individuals formed the  $F_0$  generation in the experimental design (see Fig. 2). These animals were reared individually and randomly placed in incubators set to 15°C (i.e., 'high temperature') or 23°C (i.e., 'low temperature') (see Fig. 2). These temperatures reflect the average differences between spring and summer in lakes and were used to induce TGP in *Daphnia* (Walsh & Post 2011). COMBO and algae were replaced every third day. All individuals were then checked daily for maturation (defined as the release of the first clutch into the brood chamber). The offspring of these individuals then formed the basis of the competitive ability trials. I evaluated the influence of parental temperature regime on intraspecific competitive ability by collecting newly born fourth generation lab reared individuals from clutch number 2-5 per clone (i.e.,  $F_0$  generation in Fig. 2). These individuals were either raised in the same temperature as their parent or transferred to the opposite temperature regime. This yields 4 unique combination of temperatures experienced by parent and offspring: (1) high-high (HH), (2) high-low (HL), (3) low-high (LH), (4) low-low (LL). These temperature treatments were crossed with a density treatment that manipulated the starting density of *D. ambigua* (10

versus 20 individuals) to yield 8 overall experimental treatments: high-high-10 (HH-10), high-high-20 (HH-20), low-high-10 (LH-10), low-high-20 (LH-20), high-low-10 (HL-10), high-low-20 (HL-20), low-low-10 (LL-10), and low-low-20 (LL-20). (See Fig. 2.). Each replicate was created by equally representing all clonal lineages across temperature and density treatments. All treatments were reared in 500-ml jars containing 400-ml of COMBO and 0.2 mg C L<sup>-1</sup> algae. Each combination of density and temperature was replicated 5 times to yield a total of 40 experimental units for this experiment. All experimental units were transferred to fresh media and algae every other day and resource availability was maintained at limiting levels throughout the duration of the experiment (0.2 mg C L<sup>-1</sup>). The abundances of *Daphnia* were evaluated every third day throughout the duration of the experiment, which was 16 days for HL and LL trials, and 31 days for LH and HH trials to accommodate contrasting rates of growth in high and low temperature environments, respectively.

To assess rates of population growth, exponential curves were fit to the *Daphnia* data using the abundances for each jar from day 1 (when *Daphnia* were born) to the end of the experiment (Walsh et. al. 2012). These curves provided a strong fit to the data; the values for R square and adjusted R square were above 0.95 for starting densities of 10, and above .82 for starting densities of 20.

#### 2.4 Dependent Variables, Intraspecific Competitive Ability

All dependent variables were analyzed using general linear models (SPSS v 22). The dependent variables in the intraspecific trials of this experiment were (1) intrinsic rates of increase, (2) abundances of *D. ambigua* at the end of the trials, and (3) ephippia production in the low-temperature treatments (ephippia are not produced in warmer temperatures). These variables were analyzed using general linear models with

temperature (HH, HL, etc.), starting density (x10, x20), and the temperature x density interaction entered as fixed effects. All variables were evaluated for normality and homogeneity of variances prior to testing main effects. Tests of simple main effects followed any significant ( $p < 0.05$ ) 'temperature x density' interactions to compare the temperature treatments independent of density. Here I used the Bonferroni correction to correct for multiple comparisons and accepted a p-value  $< 0.025$  as being 'significant' (2 comparisons;  $0.05/2 = 0.025$ ). Post-hoc Tukey tests were used to compare the 'HH vs LH' and 'LL vs. HL' treatments in this experiment as well as all following experiments.

### 2.5 Experimental Design, Interspecific Competitive Ability

I next tested the influence of divergent temperature histories on interspecific competitive ability in *Daphnia*. These trials began using the same rearing conditions described above to establish the contrasting temperature treatments with the key differences being that this experiment included a single starting density of *D. ambigua* and all temperature treatments were initiated in the presence or absence of a competitor (10 individuals of *Daphnia pulex*). This yielded 4 unique combinations of temperature history and exposure to interspecific competition: high-high-*pulex* (HH-P), low-high-*pulex* (LH-P), high-low-*pulex* (HL-P), and low-low-*pulex* (LL-P). (See Fig. 3). These interspecific trials used a single clone of *D. pulex* that was reared in 90 ml jars at an intermediate temperature (19°C) for a single generation prior to the start of the experiment. Individuals of *D. pulex* used in the interspecific trials were neonates born on the same day as the *D. ambigua* individuals. All treatments were replicated 5x (4 treatments x 5 replicates) = 20 experimental units). All experimental units maintained and evaluated in the same manner as described above.

## 2.6 Dependent Variables, Interspecific Competitive Ability

The dependent variable in the interspecific trials was the ending population density of adult *D. ambigua*. Variation in population size was analyzed using general linear models with temperature (HH, HL, etc.) entered as a fixed effect.

## 2.7 Experimental Design, Consumer-Resource Dynamics

I tested the potential link between TGP and ecological processes by evaluating rates of *Daphnia* growth and declines in algal abundances in larger experimental units where the resource (i.e., algae) was not maintained at nearly constant levels. This experiment used the same lab-reared animals as described above. The experiment commenced with third generation ( $F_0$ ) lab reared neonates. Similar to the competition trials, 160 newly born *Daphnia* were individually placed into 90-mL jars and evenly split between 15°C (low) and 23°C (high) temperature treatments (see Fig. 4). All jars were transferred to fresh media and algae every other day. *Daphnia* were also fed specified quantities of a single species of algae, *Scenedesmus obliquus* (concentration: 0.2 mg C L<sup>-1</sup>). Offspring ( $F_1$  generation) were collected from the second or third clutch from each parent and reared in jars for a standard number of days for the cool (7 days) and warm (4 days) temperature treatments. This initial period of rearing was designed to align the timing of maturation between the temperature treatments with the start of the mesocosm experiments. That is, *Daphnia* in the cool and warm temperatures were placed in experimental units at nearly identical life history stages (i.e., maturation). Following this initial phase of rearing, all individuals were placed into 9.5-l aquaria containing 7.5-l of COMBO and a 0.2 mg C L<sup>-1</sup> concentration of algae at a density of 20 *Daphnia*. This experiment again used seven clones of *Daphnia* and representatives of each clone were

evenly distributed across all treatments. The offspring of parents reared at low or high temperatures were randomly allocated to one of four treatments: high-high (HH), high-low (HL), low-low (LL), and low-high (LH). (See Fig. 4). Each temperature treatment was replicated 5x (4 treatments x 5 replicates = 20 aquaria). The volume of each tank was maintained at 7.5 L by periodically adding COMBO (Kilham et al. 1998). No algae was added after the initial amount, and algae were re-suspended daily.

*Daphnia* and algae abundances were regularly monitored throughout the duration of the experiment. Sampling began 10 days after the addition of *Daphnia* to each tank and continued three times per week thereafter. After each tank was stirred, 350 ml of water (5% of overall tank volume) was collected from each tank and filtered through a 70 $\mu$ m filter. *D. ambigua* from each sample was preserved in 70% ethanol (Black and Dodson 2003). Each sample was subsequently counted using a Bogorov counting chamber. The total number of individuals, males, juveniles, and ephippia were recorded for each sampling episode. Algal density was concurrently sampled by taking a 10 mL aliquot. The sample was preserved with Lugol's iodine, and cell density was counted using a Sedgewick Rafter chamber.

## 2.8 Dependent Variables, Consumer-Resource Dynamics Experiment

The dependent variables that were measured in this experiment were (1) intrinsic rates of increase ( $r$ ), (2) peak abundance, (3) average *Daphnia* length at each sampling episode, (4) algal abundances, and (5) rates of algal decay. To evaluate intrinsic rates of increase or decay, exponential curves were fit to the *Daphnia* and algal growth data using the abundance estimates for each tank from day 1 (when the F<sub>1</sub> generation was born) to the peak population density for each tank (Walsh et. al. 2012). Peak abundance was defined as the sampling date with the highest population density before populations

began to decline. Variation in *Daphnia* length was assessed by taking photographs of *Daphnia* from the preserved samples, measurements from which were then averaged over the course of the experiment to the date of peak abundance. Approximately five adult female individuals were photographed per sample when present (defined as individuals with a clutch of developing embryos). Algae density was determined based on number of cells present in 3 to 10 mm<sup>3</sup> (a minimum of 100 cells were counted, until 10 mm<sup>3</sup> were reached).

Temperature treatment (HH, HL, LH, LL) was entered as a fixed effect. All variables were first evaluated for normality and homogeneity of variances prior to testing the main effect. Post hoc Tukey tests followed significant main effects. Data points greater than 3 standard deviations were determined to be outliers and were removed. The presence and removal of outliers did not alter the overall trends or significance of the results.

## Chapter 3

### Results

The results of this series of experiments demonstrated that the temperature experienced by parents significantly ( $p < 0.05$ ) affected subsequent rates of population growth and population densities. In particular, the results of the intra-specific competition trials showed that rates of population growth depended strongly upon whether *Daphnia* consistently experienced the same temperature regime throughout the experiment or experienced shifts in temperature between parent and offspring generations (Table 1, Fig. 5). Below, I fully describe the results of all experiments and analyses.

#### 3.1 Intraspecific Competitive Ability Results

##### *Temperature effects*

There was an overall significant ( $p < 0.05$ ) effect of temperature treatment on rates of increase and final population density (Table 1). *Daphnia* in the LH treatment had a rate of increase that was 46% higher and a final population density 135% higher than in the HH treatment. *Daphnia* in the HL treatment had an intrinsic rate of increase 10% higher and a final population density 6% higher than in the LL treatment.

##### *Density effects*

I observed a significant ( $p < 0.05$ ) effect of density on rates of increase and final population density (Table 1). *Daphnia* in the treatments with a starting population of 10 versus 20 individuals had a rate of increase 57% higher while a starting density of 20 individuals yielded a final population density that was 28% higher than the treatments that started with 10 individuals.

### *Temperature x density interaction*

I observed a significant ( $p < 0.05$ ) interaction between temperature treatment and initial density for intrinsic rates of increase and final population density (Table 1). This is because the differences among the temperature treatments varied as a function of the initial density. For intrinsic rates of increase, small differences were observed between the HL and LL treatments across both starting densities. However, the LH treatment exhibited a higher intrinsic rate of increase and such a difference was larger when all containers started the experiment with 20 individuals. The intrinsic rate of increase was 30% higher in the LH treatment compared with the HH treatment when all containers were started with 10 individuals and such differences increased to 74% when all treatments received 20 individuals.

The trends for the final population density were more variable. *Daphnia* from the LH treatment attained larger population densities than the HH treatment, but such differences were only apparent in the higher density treatment. The density of individuals in the LH treatment was 13% higher than the HH treatment under low density starting conditions and these differences increased to 323% when all containers were started with 20 individuals. The differences between the HL and LL treatments reversed across the density treatments; *Daphnia* were 40% more abundant in the HL treatment in the low density treatment but *Daphnia* from the LL treatment were 22% more abundant in the high density treatment.

### *Tests of simple main effects*

Because I observed a significant temperature x density interaction for both parameters, I performed tests of simple main effects to explore the difference amongst

the temperature treatments separately across each density treatment. This approach revealed significant effects ( $p < 0.025$ ;  $p$ -value corrected for multiple comparisons) of temperature for both intrinsic rate of increase and final population density at both starting population sizes (Table 2). Post hoc Tukey tests revealed significant ( $p < 0.05$ ) differences between the HH and LH treatments for both intrinsic rate of increase and final population density (Fig. 5).

### 3.2 Effect on Interspecific Competitive Ability

This experiment revealed a significant effect of temperature treatment on final population size (See Table 1, Fig. 6). Small differences were observed between *Daphnia* from the HH and LH treatment. *Daphnia* from the LL treatment, however, attained a peak population density that was 1300% larger than *Daphnia* from the HL treatment. Post hoc Tukey tests revealed significant differences between the HL and LL treatments (See Fig. 6).

### 3.3 Effect of Temperature on Consumer-Resource Dynamics

The effect of temperature treatment on intrinsic rates of increase or peak population density was not significant (Table 1). Intrinsic rates of increase and peak population densities differed little between the HL and LL treatments, but *Daphnia* whose parents were reared under cold temperatures and were transferred to warm temperatures (LH) exhibited qualitatively faster rates of population growth than *Daphnia* reared consistently under warm temperatures. (Fig. 7). There was no significant influence of temperature on *Daphnia* size over the course of the experiment. The mean length of *Daphnia* for the temperature treatments were 1.58 mm for HH, (standard deviation = 0.20), 1.52 mm for HL, (standard deviation = 0.21), 1.60 mm for LH, (standard deviation =

0.19) and 1.63 mm for LL, (standard deviation = 0.18). The mean areas for the treatments were 1.13 mm<sup>2</sup> for HH, (standard deviation = 0.30), 1.08 mm<sup>2</sup> for HL, (standard deviation = 0.30), 1.11 mm<sup>2</sup> for LH, (standard deviation = 0.28), and 1.22 mm<sup>2</sup> for LL, (standard deviation = 0.28). Qualitatively faster rates of *Daphnia* growth in the LH versus HH treatments were correlated with significantly lower densities of algae (Table 1). Post hoc Tukey tests did not reveal any significance between treatments.

## Chapter 4

### Discussion

My results provide evidence that temperatures experienced by parents can influence subsequent ecological dynamics (Fig. 5, Fig. 6). This is because *Daphnia* reared under cool conditions yielded significantly faster rates of growth when transferred to warmer conditions compared with *Daphnia* that experienced consistently warm conditions. These results were only apparent, however, under highly controlled conditions in relative small experimental units. Experiments performed in larger aquaria provided trends that were qualitatively similar but not statistically significant. Below, I discuss the extent to which my results are best explained by thermally-induced changes in the traits of organisms and discuss why the trends lacked consistency across all experiments.

#### 4.1 Competitive Ability

The clearest result obtained by this series of experiments is that parents of *Daphnia* reared under cool conditions yielded faster rates of growth when transferred to much warmer conditions than when compared with lineages that were maintained under consistently warm conditions. Previous work has shown that *Daphnia* reared under cool conditions program their offspring for faster rates of development in the following generation (Walsh et al. 2014). Such maternal effects may, in turn, provide a link to population growth. Thus, the most logical explanation for these differences in population growth is that the temperature experienced by parents induced changes in traits that persisted for multiple generations. However, it is also important to note that the divergent temperature treatments did not lead to differences in growth when all clones were surveyed under warm conditions. This lack of an effect of parental temperature on subsequent rates of growth were contrary to my expectations and could potentially be

explained by the observed differences in the magnitude of TGP in cool versus warm conditions; parental exposure to the cool environment caused *Daphnia* to mature 5.5 days faster in the cool environment, and only 2.5 days faster in the warm environment (Walsh et al. 2014). An alternative possibility is that high metabolic costs and shorter life spans observed at higher temperatures mitigate the pathway from parental effects to ecological processes (Giebelhausen & Lampert 2001, Seidl 2005).

The trends observed in the intra- competition trials did not necessarily parallel the results obtained for the interspecific experiments. This is because the performance of *Daphnia* that experienced consistently cool temperatures (LL) exceeded all other treatments in the presence of another species of *Daphnia* (*D. pulex*) (Fig. 6). It is well known that larger *Daphnia* species, such as *D. pulex*, are superior competitors (Kreutzer & Lampert 1999, MacIsaac & Gilbert 1989). The results of these trials indicate that the treatments that experienced a transition between warm and cool temperatures (and vice versa) were poorer interspecific competitors (at least under cool conditions). One possible explanation for this result is that the cold temperature treatment used in this experiment is outside the thermal optimum for young production in *D. pulex* (Goss & Bunting 1983). Such a possibility would allow *Daphnia ambigua* continually exposed to cool conditions to compete more strongly with *D. pulex* under cool conditions but not warm conditions.

#### 4.2 Consumer-Resource Dynamics

The results of my experiments performed in larger aquaria where resource availability was not controlled yielded results that, in part, parallel the trends observed in the smaller experimental units, but such trends were not significant. That is, *Daphnia* whose parents were reared under cool temperatures yielded qualitatively faster rates of

growth when transferred to the warm temperature when compared with the treatments that experienced consistently warm temperatures. These qualitative differences in population growth were also correlated with marginally significant differences in algal density (Fig. 8). One potential explanation for the weak trends observed in the aquaria experiments is that the pathway between TGP and ecological processes is swamped by the effects of unlimited food availability (at the onset of the experiment). In these experiments, algae was allowed to grow and was not maintained at controlled levels as in the competition trials. Research has shown that the magnitude of TGP is amplified under food stress (Frost et. al. 2010; Valtonen et al. 2012). It is thus possible that a stronger connection between TGP and population size was detected in the competition trials due to more severe food stress.

#### 4.3. Climate change implications

The ability of organisms to adapt to a changing climate is becoming increasingly important. In 2007, the International Panel on Climate Change published predictions stating that if greenhouse gas emission continue at current rates, changes in the global climate system will be larger this century than in the 20<sup>th</sup> century (Solomon 2007). Global temperature averages at the end of this century could be 1.5 °C higher than averages from the end of the 17<sup>th</sup> century (Collins 2013). As climate change continues, an increased understanding of how different taxa adapt to this rising temperatures is paramount. Climate change can influence developmental responses (Nicotra et. al. 2010), and it can affect life-history strategies through changes in temperature (Bale et. al. 2002). The results of this study offer an additional mechanism that may allow organisms to respond and persist in the face of ongoing climate change. *Daphnia* from a mixed temperature treatment (transferred from cool to warm) clearly outperformed those

treatments that experienced consistently warm conditions in the competition trials performed in this study. This means that thermal TGP in life-history traits could contribute to an organism's ability to adapt to future changes in climate.

#### 4.4 Conclusions

These results build upon a growing body of literature demonstrating that previous environmental conditions are a key predictor of future ecological processes. For instance, carryover effects are now well known (Burgess & Marshall 2011, Duckworth 2015, Lee et al. 2013), and they occur when a transition between environments during development differentially alters population and community processes (Van Allen & Rudolf 2015). Carry-over effects also occur when a species inhabits different niches at different life stages (Van Allen et al. 2010). TGP can be thought of as a form of the more general carryover effect, with the clear distinction being that the effect of the environment on phenotype are propagated across generations. The results of this study provide some evidence that variation in thermal regimes induce transgenerational responses which, in turn, alter aspects of plankton ecology. However, increased understanding of links between environmental signals, TGP, and interactions within and across trophic levels is needed. In particular, my work calls for more research to be done on TGP and its impact on population dynamics and community interactions. An understanding of TGP is important for projecting changes in ecosystems that are driven by rapid, ongoing shifts in climate.

Appendix A  
Figures

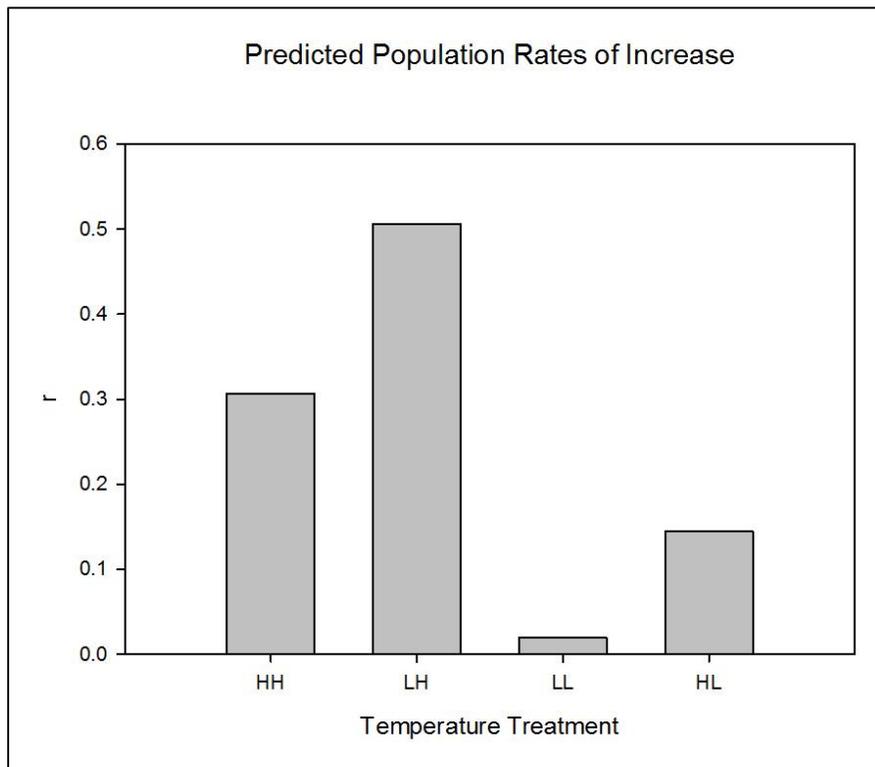


Fig. 1 Predicted Population Rates of Increase

Predicted intrinsic rates of increase ( $r$ ) for *Daphnia*. HH – *Daphnia* reared at consistently warm temperatures across generations. LL – *Daphnia* reared at consistently cool temperatures across generations. HL – Parents are reared at the warm temperatures but offspring are transferred to the cool temperature. LH – Parents are reared at the cool temperature but offspring are transferred to the warm temperature. “L” – 13 °C. “H” – 25 °C. These predictions were generated using life-table data from Walsh et al. 2014.

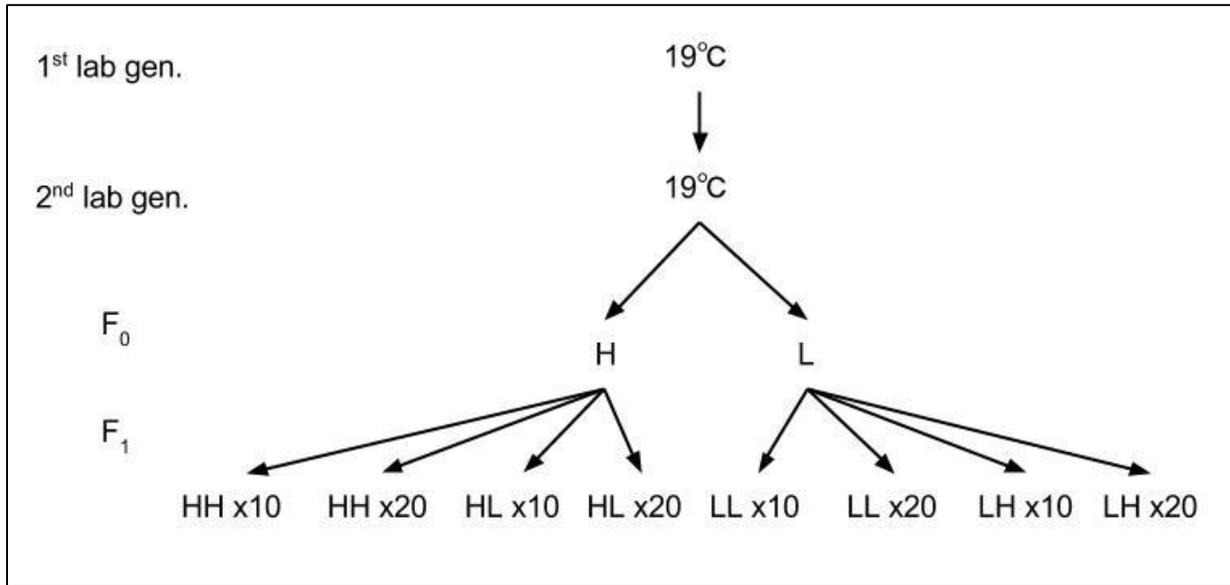


Fig. 2 Intraspecific Competition Experimental Design

Experimental design for evaluating effect of thermal transgenerational plasticity on intra-specific competition. HH – *Daphnia* reared at consistently warm temperatures across generations. LL – *Daphnia* reared at consistently cool temperatures across generations. HL – Parents are reared at the warm temperatures but offspring are transferred to the cool temperature. LH – Parents are reared at the cool temperature but offspring are transferred to the warm temperature. “L” – Low temperature (15°C). “H” – High temperature (23°C). “x10” – Starting population size of 10 *D. ambigua*. “x20” – Starting population size of 20 *D. ambigua*. F<sub>0</sub> and F<sub>1</sub> are the first and second generations of the experiment.

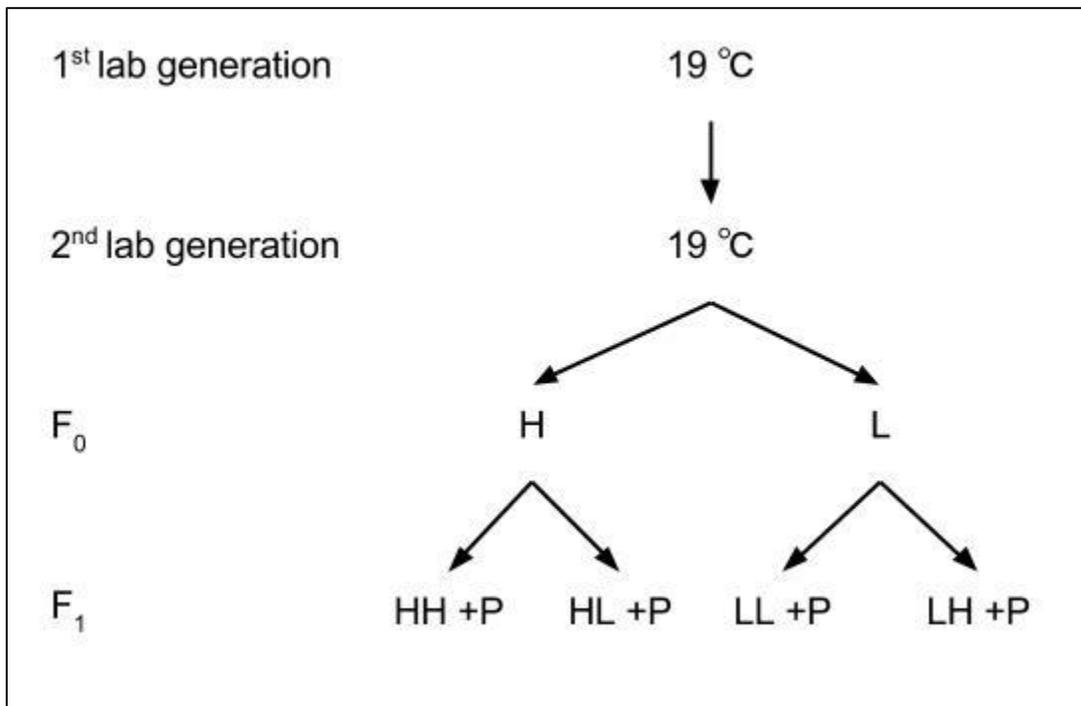


Fig. 3 Interspecific Competition Experimental Design

Experimental design for evaluating effect of thermal transgenerational plasticity on inter-specific competition. HH – *Daphnia* reared at consistently warm temperatures across generations. LL – *Daphnia* reared at consistently cool temperatures across generations. HL – Parents are reared at the warm temperatures but offspring are transferred to the cool temperature. LH – Parents are reared at the cool temperature but offspring are transferred to the warm temperature. “L” – Low temperature (15°C). “H” – High temperature (23°C). “+P” – Presence of *D. pulex*. F<sub>0</sub> and F<sub>1</sub> are the first and second generations of the experiment.

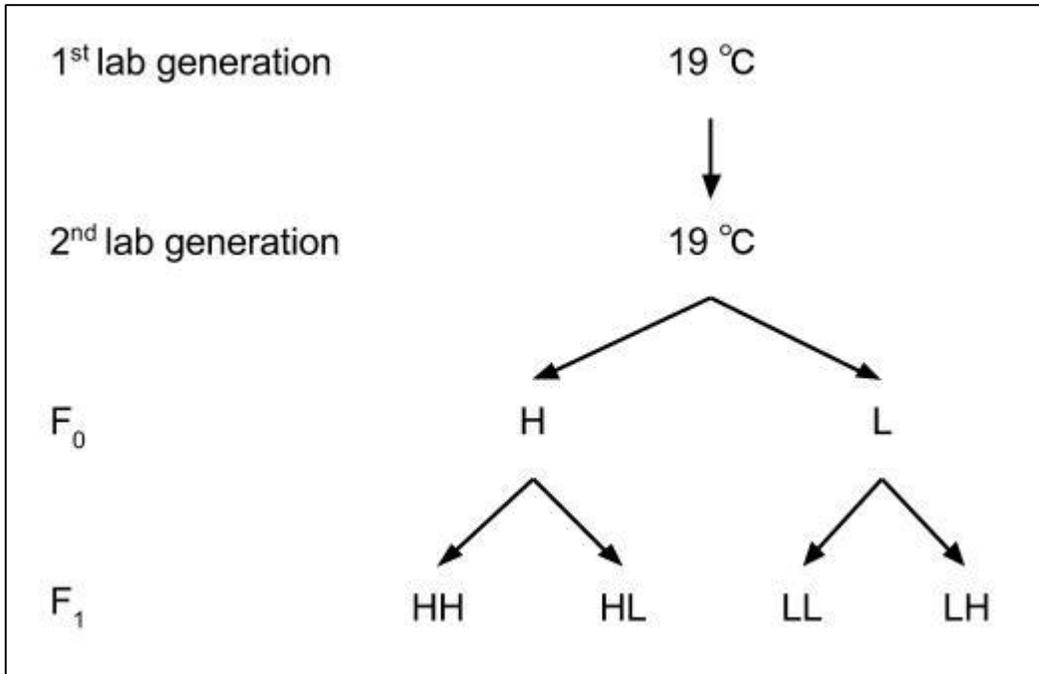


Fig. 4 Consumer-Resource Dynamics Experimental Design

Experimental design for evaluating effect of thermal transgenerational plasticity on consumer-resource dynamics. HH – *Daphnia* reared at consistently warm temperatures across generations. LL – *Daphnia* reared at consistently cool temperatures across generations. HL – Parents are reared at the warm temperatures but offspring are transferred to the cool temperature. LH – Parents are reared at the cool temperature but offspring are transferred to the warm temperature. “L” – Low temperature (15°C). “H” – High temperature (23°C). F<sub>0</sub> and F<sub>1</sub> are the first and second generations of the experiment.

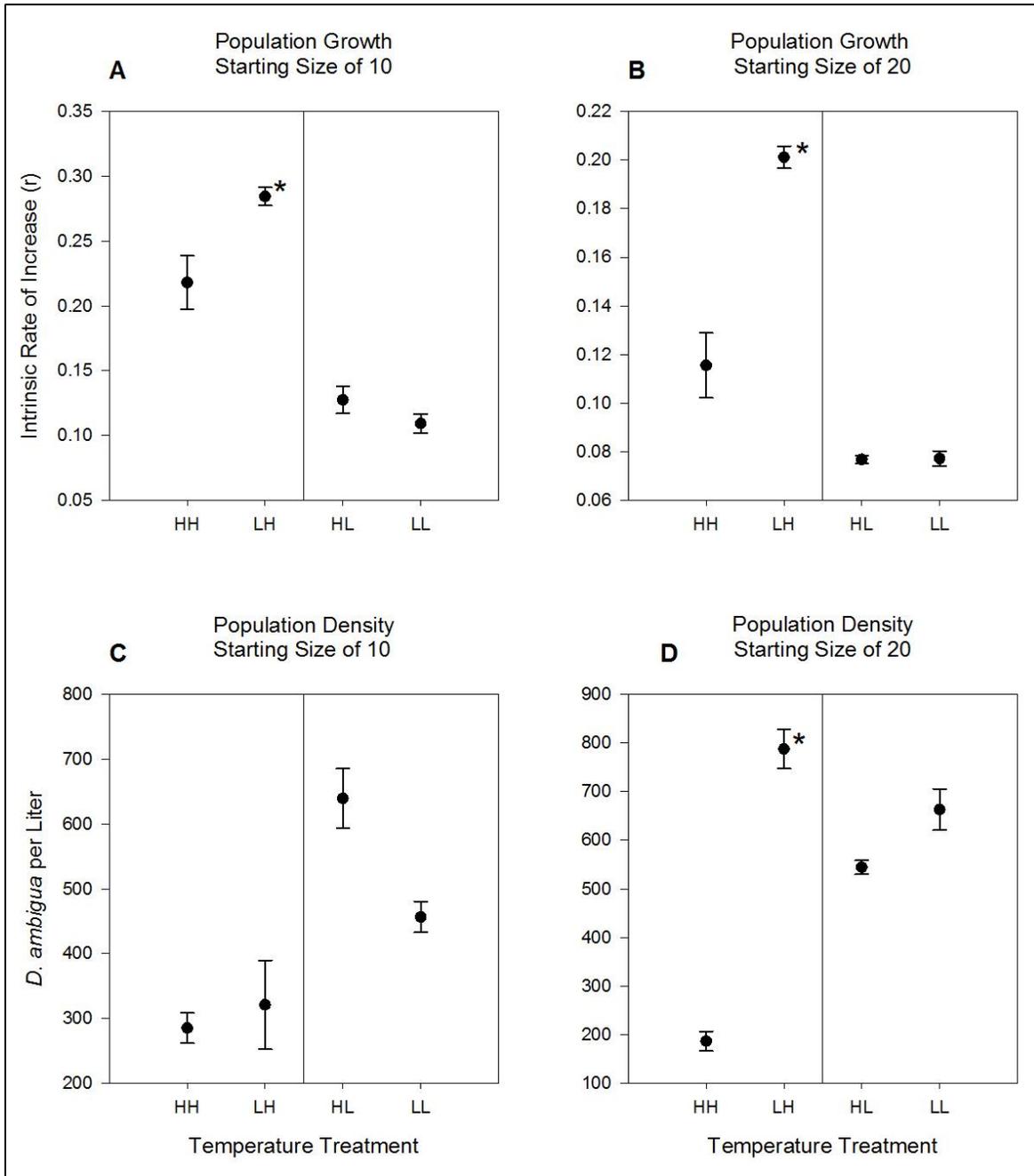


Fig. 5 Intraspecific Competition Results

Fig. 5. Effects of parental temperature (F<sub>0</sub> generation) on offspring's intrinsic rate of increase (r) at a starting density of 10 (A) and a starting density of 20 (B), and population density at the end of the experiment with a starting density of 10 (C) and a starting density of 20 (D). HH indicates *Daphnia* were reared at high temperatures during the F<sub>0</sub> generation and high temperatures during the F<sub>1</sub> generation. LL indicates *Daphnia* were reared at low temperatures during the F<sub>0</sub> generation and low temperatures during

the F<sub>1</sub> generation. HL indicates *Daphnia* were reared at high temperatures during the F<sub>0</sub> generation and low temperatures during the F<sub>1</sub> generation. LL indicates *Daphnia* were reared at low temperatures during the F<sub>0</sub> generation and low temperatures during the F<sub>1</sub> generation. "H" - 23 °C, "L" - 15 °C. An asterisk (\*) represent significant (p<0.05) differences among treatments in the same current environment (example:

HH and LH) based on post hoc tests. Error bars = ± 1 s.e.

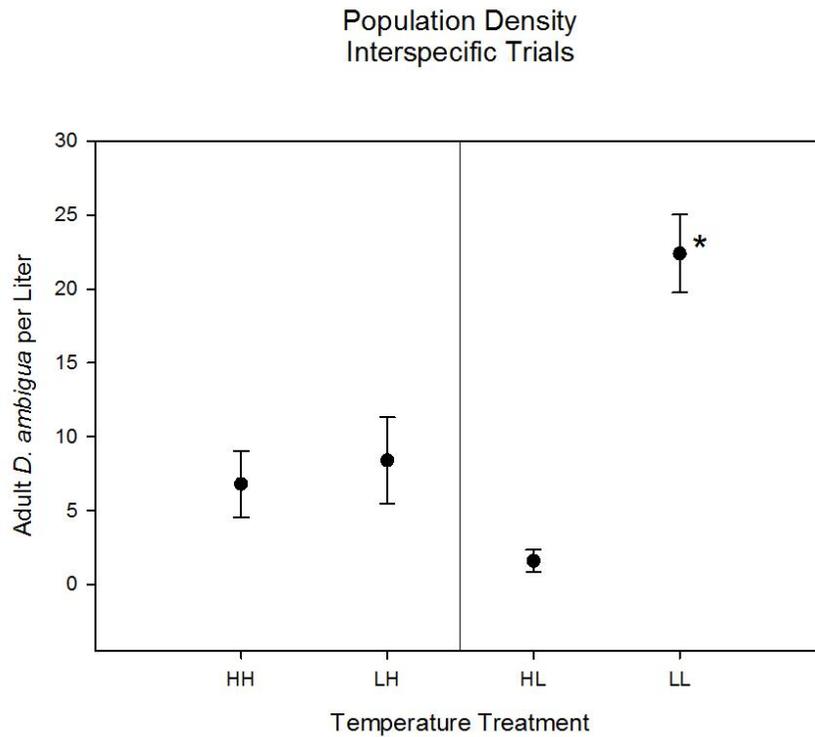


Fig. 6 Intraspecific Competition Results

Fig. 6. Final *D. ambigua* density in the interspecific competitive ability trials. HH indicates *Daphnia* were reared at high temperatures during the F<sub>0</sub> generation and high temperatures during the F<sub>1</sub> generation. LL indicates *Daphnia* were reared at low temperatures during the F<sub>0</sub> generation and low temperatures during the F<sub>1</sub> generation. HL indicates *Daphnia* were reared at high temperatures during the F<sub>0</sub> generation and low temperatures during the F<sub>1</sub> generation. LL indicates *Daphnia* were reared at low temperatures during the F<sub>0</sub> generation and low temperatures during the F<sub>1</sub> generation. H" - 23 °C, "L" - 15 °C. Asterisk (\*) represent significant (p<0.05) difference among treatments in the same current environment (example:

HH and LH) based on post hoc tests. Error bars = ± 1 s.e.

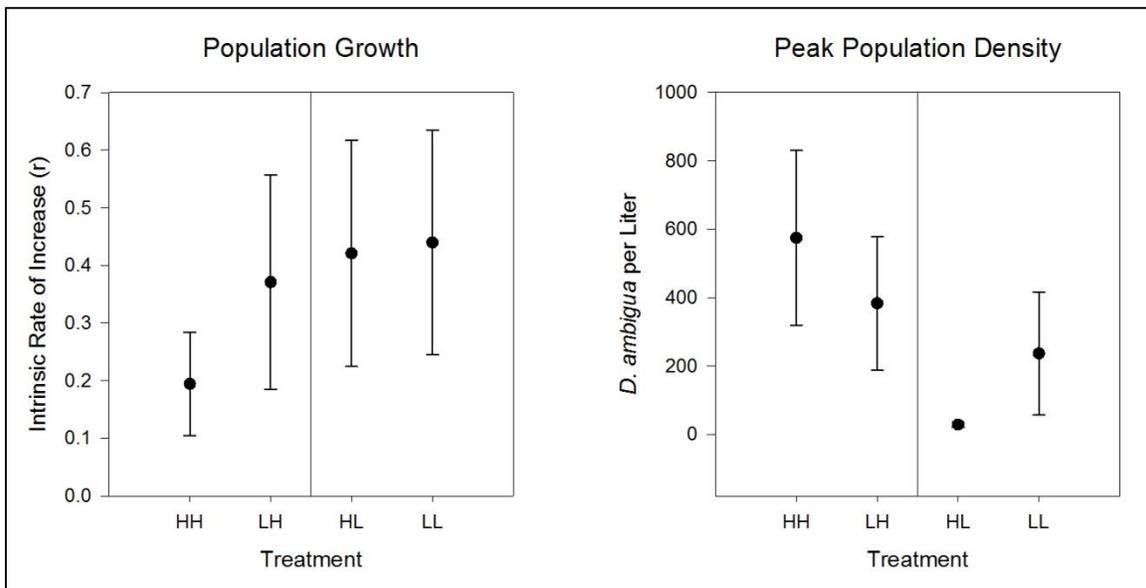


Fig. 7 Consumer-Resource Dynamics Results

Fig. 7. Effects of parental temperature ( $F_0$  generation) on offspring's intrinsic rates of increase ( $r$ ) and peak population density. HH indicates *Daphnia* were reared at high temperatures during the  $F_0$  generation and high temperatures during the  $F_1$  generation. LL indicates *Daphnia* were reared at low temperatures during the  $F_0$  generation and low temperatures during the  $F_1$  generation. HL indicates *Daphnia* were reared at high temperatures during the  $F_0$  generation and low temperatures during the  $F_1$  generation. LL indicates *Daphnia* were reared at low temperatures during the  $F_0$  generation and low temperatures during the  $F_1$  generation. "H" - 23 °C, "L" - 15 °C. There were no significant differences among temperature treatments. Error bars =  $\pm 1$  s.e.

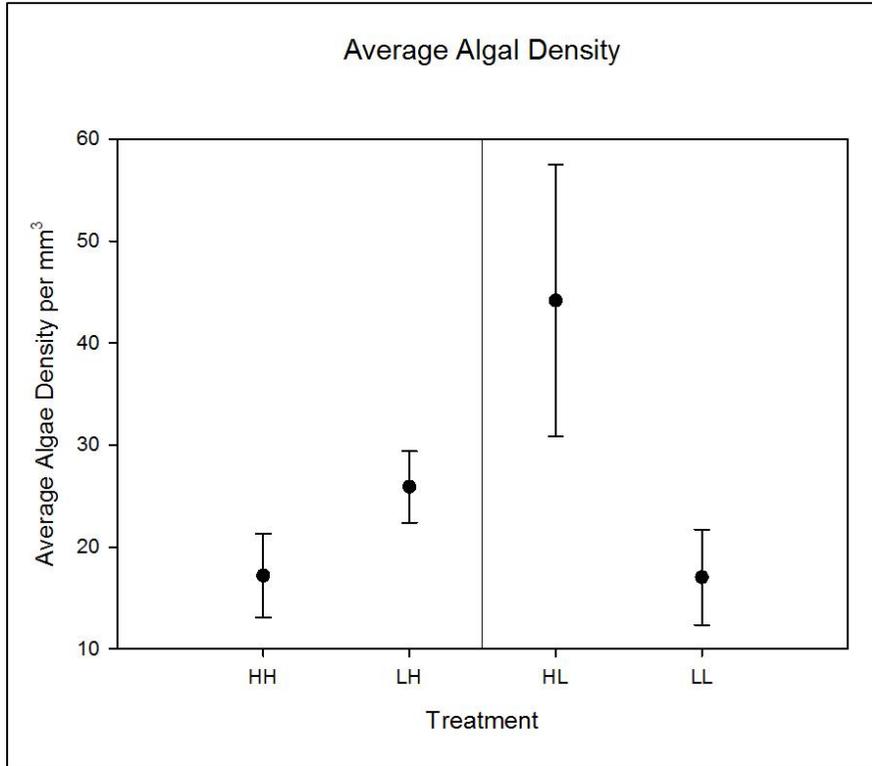


Fig. 8. Consumer-Resource Dynamics Results - Algae Densities

Fig. 8. Peak population densities for algae in the consumer-resource dynamics experiment. HH indicates *Daphnia* were reared at high temperatures during the F<sub>0</sub> generation and high temperatures during the F<sub>1</sub> generation. LL indicates *Daphnia* were reared at low temperatures during the F<sub>0</sub> generation and low temperatures during the F<sub>1</sub> generation. HL indicates *Daphnia* were reared at high temperatures during the F<sub>0</sub> generation and low temperatures during the F<sub>1</sub> generation. LL indicates *Daphnia* were reared at low temperatures during the F<sub>0</sub> generation and low temperatures during the F<sub>1</sub> generation. “H” - 23 °C, “L” - 15 °C. Differences in algal density were marginally significant (p=0.047) Error bars = ± 1 s.e.

Appendix B

Tables

**Table 1.** Analysis of Intrinsic Rates of Increase (r) and Population Densities. General linear models were used with temperature and density treatments as fixed effects and r and population densities entered as dependent variables. F statistics, degrees of freedom, and p-values are reported.

	Intraspecific - r			Intraspecific - Final Density			Interspecific - Final Density			Mesocosm Peak Density			Mesocosm - r			Algae Average Density		
Fixed Effects:	F	df	P	F	df	P	F	df	P	F	df	P	F	df	P	F	df	P
Temperature Treatment	90.192	(3,32)	0.000	38.310	(3,32)	0.000	12.166	(3,16)	0.000	2.397	(3,15)	0.109	1.087	(3,14)	0.387	3.148	(3,15)	0.047
Density	84.503	(1,32)	0.000	26.959	(1,32)	0.000	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a
Temperature X Density	4.728	(3,32)	0.008	23.757	(3,32)	0.000	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a

**Table 2.** Tests of Simple Main Effects: Intraspecific Competition Trials

Analysis of test of simple main effects for intrinsic rate of increase ( $r$ ) and final population density for intraspecific competition trials. Data was divided by starting population size. General linear models were used with temperature treatment was entered as a fixed effect and final population density and  $r$  were entered as dependent variables. P-values were considered significant if less than 0.025 due to Bonferroni correction for multiple comparisons.

Test of Simple Main Effects - Intraspecific Competition						
	$r$			Final Population Density		
Fixed Effects:	F	df	P	F	df	P
Starting Size of 10	41.799	(3,16)	0.000	41.799	(3,16)	0.000
Starting Size of 20	64.476	(3,16)	0.000	64.476	(3,16)	0.000

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### Biographical Information

Julian Holmes was born in Alpine, Texas in 1978. He received his Bachelor of Science in Journalism at Texas A&M University – Commerce in 2002. He has two children with his wife Jana. Abigail was born in October of 2009, and Ian was born in June of 2015. He has been a journalist and an 8<sup>th</sup> grade teacher, but his passion is science and the environment. After graduating, he wants to work as an ecologist or an environmental scientist and fulfill a calling to protect the environment.