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Thermal plasticity within and across generations and its relevance to contemporary evolution

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Abstract of the Dissertation

Thermal plasticity within and across generations and its relevance to contemporary evolution

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Understanding and predicting how populations will react to changes in the environment is a long-standing goal in evolutionary ecology. It is also of considerable practical importance, as anthropogenic changes stress species worldwide. The relevance of phenotypic plasticity is becoming more apparent as species are forced to cope with rapid changes in the environment. This dissertation explores ways in which phenotypic plasticity will play a major role in determining the future of populations.

In Chapters 1 and 2, I evaluate a modeling framework that could be used to predict plastic changes in key life history traits of ectotherms brought about by temperature. This work, based on the metabolic theory of ecology (MTE), assumes that biological rates scale exponentially with temperature. I first show the validity of the MTE for predicting lifespan gradients within species and then apply this temperature-life history relationship to predict changes in ectotherms resulting from global temperature increases over the next 50 years.

In Chapter 3, I experimentally test the plastic response of sheepshead minnows, Cyprinodon variegatus, an estuarine fish common to the east coast, to combinations of temperature (24, 29, 34°C) and food availability (60, 80, or 100% of maximum consumption). The thermal response of juvenile growth rate was mediated by food availability, while the age at maturation was independently affected by temperature and food. Notably, and despite very different thermal and feeding regimes, the fish matured within a small size window.

In Chapters 4 and 5, I explore transgenerational plasticity (TGP) as a means to cope with temperature changes. When the temperature experienced by the parents acts as a reliable indicator of thermal offspring environment, a parent can "pre-program" offspring traits appropriate for the predicted environment. This transfer of information from parent to offspring has been termed TGP, and is well studied in plants and invertebrates. In these chapters, I show that thermal TGP has a strong effect in larval growth of sheepshead minnows. I also explore how transgenerational and phenotypic plasticity interact to shape the size of fish throughout life, and provide evidence suggesting that the TGP effect lasts for at least 2 generations.

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Preface

No one would argue the key role the environment plays in shaping the phenotype. However, and ever since the modern synthesis, evolutionary biologists have been fascinated with genes and their frequencies (Mayr and Provine 1980). Any effect of the environment on organisms was simply dismissed as noise obscuring the fundamental process of gene selection (Sultan 1992). In the last two decades, genotype-environment interactions have enjoyed great interest. This is evident from the plethora of recent empirical and theoretical papers (reviewed in Schlichting and Pigliucci 1998, Pigliucci 2001, De Witt and Scheiner 2004).

Understanding and predicting how populations will react to changes in the environment is a long-standing goal in evolutionary ecology. It is also of considerable practical importance as anthropogenic changes stress species worldwide (Palumbi 2001, Hendry et al. 2008). Thus, the relevance of phenotypic plasticity, the ability of a given genotype to produce different phenotypes in response to distinct environmental conditions (Pigliucci 2001), is becoming more apparent as species are forced to cope with rapid changes in the environment.

This dissertation explores ways in which plasticity within and across generations will play a major role in determining the future of ectotherm populations.

Acknowledgments

I hate this thesis. Well, I hate the fact that some antiquated convention forces me to use the first-person, singular personal pronoun ("I", "me"). Nothing could be further from the truth: everything that you will read here was a "we", a collaboration between Stephan Munch, my advisor, and myself. I owe Steve a great deal. He supported me and encouraged me to explore (oy, those African fish…), always humoring me by discussing my half-baked ideas. He was a patient teacher who treated me as a colleague. You cannot ask for more in a Ph.D. advisor.

I also wish to thank my committee members, David Conover, Douglas Futuyma, Darcy Lonsdale, and Joseph Travis. The time and dedication they put in every interaction with a lowly graduate student like myself will be forever appreciated. All their comments improved this thesis considerably. All our discussions helped me grow as a scientist.

I became who I am academically, in large part, due to some amazing teachers. My thanks to those who sparked my desire to know at Complejo Educativo Gurruchaga (Rosario, Argentina), Lester B. Pearson College of the Pacific (Victoria, BC), and College of the Atlantic (Bar Harbor, ME).

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None of this work would have been completed without the generous help of many undergraduate students at Stony Brook University. These include Christian Castro, Frank Chin, Christina Lotito, Long Ng, Jo Anne Siskidis, and Alison Yee.

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A lot of the work I conducted lies at the intersection of genes and environment. Naturally, then, families play a profound role in shaping an individual. I thank [insert deity of choice] for giving me the absolute best family I could have ever hoped for. I will never be able to express how deeply grateful I am for everything they have given me, or how proud I am of their idealism and accomplishments. Gracias totales.

Finally, I must thank Jessica Glynn. I could list the reasons why, but that would take longer than the 110 pages in this dissertation. All you need to know, my dear reader, is that this woman is a saint. Except early in the morning, better avoid her then. (J, we finally made it).

Chapter 1

Latitudinal variation in lifespan within species is explained by the metabolic theory of ecology

Abstract

Many ectotherms exhibit striking latitudinal gradients in lifespan. However, it is unclear whether lifespan gradients in distantly related taxa share a common mechanistic explanation. I compiled data on geographic variation in lifespan in ectotherms from around the globe in order to determine how much of this intraspecific variation in lifespan may be explained by temperature using the simple predictions of the metabolic theory of ecology. I found that the metabolic theory accurately predicts how lifespan varies with temperature within species in a wide range of ectotherms in both controlled laboratory experiments and free-living populations. After removing the effect of temperature, only a small fraction of species showed significant trends with latitude. There was, however, considerable residual intraspecific variation indicating that other, more local factors are likely to be important in determining lifespan within species. These findings suggest that, given predicted increases in global temperature, lifespan of ectotherms may be substantially shortened in the future.

Introduction

Many phenotypic traits covary with latitude, particularly among ectotherms. For instance, relative to individuals from low latitudes, high latitude individuals tend to have higher growth rates and larger body size (Arendt 1997, Blackburn et al. 1999), produce larger eggs (Lonsdale and Levinton 1985), have relatively shorter extremities (Nudds and Oswald 2007), and more vertebrae (McDowall 2008). Lifespan also varies with latitude in a wide variety of ectotherms. For example, lifespan increases with latitude in the yellow clam (*Mesodesma mactroides*, Fiori and Defeo 2006), oegopsin squid (suborder Oegospina, Arkhipkin 2004), and many fish species (Heino et al. 2005, Roni and Quinn 1995, Duchesne and Magnan 1997, Blanck and Lamouroux 2007). One example is particularly striking: pearl mussels (*Margaritifera margaritifera*) found in Spain (43°N) have maximum lifespans of 29 years while those in Russia (66°N) live nearly 200 years (Bauer 1992, Ziuganov et al. 2000). The purpose of this study is to determine whether this ubiquitous geographical variation in lifespan has a common physiological basis in temperature.

Temperature has long been known to influence lifespan (Loeb and Northrop 1917, Pearl 1928). For example, *Drosophila melanogaster* from Brazil raised at 31.2°C lived up to 29 days, while flies from the same population reared at 12°C lived up to 247 days (Trotta et al. 2006). Although the temperature-lifespan relationship has been known for nearly a century, most of our knowledge on this relationship is derived from laboratory experiments on short-lived invertebrates (e.g., Carey 2003). Studies on natural variation in lifespan with temperature have largely been limited to cross-taxa comparisons (Gillooly et al. 2001, Pauly 1980). As a consequence, the role of temperature in controlling geographic variation in lifespan within

species is unclear; it is easy to imagine how geographic variation in the abundance of predators, availability of resources, fluctuations in environmental conditions, and local adaptation might obscure any relationship between temperature and lifespan in wild populations.

The metabolic theory of ecology (MTE, Brown et al. 2004) has been used to link metabolism to a wide range of physiological and macroecological processes. Growth trajectories and life histories (Charnov and Gillooly 2004), population dynamics (Savage et al. 2004), geographic patterns in species richness (Allen et al. 2002), and community dynamics (Enquist and Niklas 2001) all scale with body size and temperature in a manner surprisingly consistent with predictions made by the MTE. Since metabolism is known to influence lifespan (Van Voorhies 2001), the MTE makes strong, quantitative predictions about the relationship between lifespan and temperature. In fact, Gillooly and colleagues (Gillooly et al. 2001, McCoy and Gillooly 2008) have already used the MTE to predict variation in lifespan *across* species. However, the MTE has been criticized by many authors because it appears to lack predictive power at lower taxonomic levels (Tilman et al. 2004), possibly because of the relatively small range of sizes within species. Nonetheless, many species exist over a wide range of temperatures, suggesting the MTE may yet be useful for predicting intraspecific patterns even in the absence of body size variation. In support of this, pelagic larval duration within marine fish and invertebrate species was found to be tightly coupled to temperature and accurately predicted by an MTE-based model (O'Connor et al. 2007a).

Other concerns have also been raised. For example, O'Connor et al. (2007b) question that the concept of activation energy (the difference in free energy, in simple reactions, between the

reactants and an intermediate) is applicable at the macroscopic level, and many (e.g., Cyr and Walker 2004, Marquet et al. 2004, Clarke 2006) have argued that the observed Boltzmann relationship between temperature and whole-organism metabolic rate is only an approximation of a much more complicated set of phenomena. Here, I hypothesize that geographic variation in lifespan within species may be explained by temperature using the MTE.

Methods

To evaluate whether intraspecific variation in lifespan can be explained by the MTE and whether the temperature-lifespan relationship is apparent in natural populations, I synthesized all available data on intraspecific variation in lifespan from a diverse group of ectothermic taxa. Because field estimates of lifespan may be influenced by many factors including variation in predation, food availability, local adaptation, population density, and sampling variability, I began by testing the MTE using lifespan data from controlled laboratory experiments in which individuals from a single source population were reared under various temperatures. I then evaluated whether variation in temperature affects lifespan in wild populations as predicted by the MTE.

In keeping with previous work (Gillooly et al. 2001), I expect lifespan, l, to scale as

$$l \propto m^{1/4} \exp\left(\frac{E}{kT}\right)$$

where m is body mass, E is activation energy, k is Boltzmann's constant (8.62×10^{-5} eV/K) and T is temperature in K. The chief unknown in this model is the activation energy which, based on previous work, is presumed to range from 0.2 to 1.2 eV (Gillooly et al. 2001, Downs et al. 2008).

I tested the MTE by multiple regression of log-lifespan on log-mass and inverse temperature, fitting

$$\ln[l] = \text{const} + \alpha \ln(m) + \frac{\beta}{kT}$$

to 29 species for which I found intraspecific data on both size and mean annual temperature. However, temperature but not size data were found for an additional 38 species. By dropping mass from the model, I found that the inclusion of mass does not generally affect the slope for temperature, allowing me to analyze this much larger data set (n = 67 wild species). Given the range of values for E (0.2 to 1.2 eV), I consider the MTE supported if slopes (b) of the regression of ln(l) on $\frac{1}{kT}$ are not significantly outside of this range.

Data set. To construct my data set, I queried all major databases (Web of Science, Google Scholar, PubMed, and Biological Abstracts) with appropriate combinations of keywords. I extended this initial collection with additional citations from sampled papers. I first collected data from controlled laboratory experiments in which individuals from a single source population were reared until natural death under at least 4 temperatures. Average lifespan was reported for all lab data. I then reviewed literature for wild populations in which estimates of either maximum

lifespan or average lifespan were provided. After all data for a given species were identified, I screened them against the following criteria: (i) species studied was ectothermic, and (ii) longevity data were reported for at least 5 populations spanning at least 0.25 degrees of latitude. I also collected all other biological (e.g., body size) and physical (e.g., elevation) information, as well as numbers of individuals assayed, when available. I aimed to include the largest possible range of taxa; however, longevity estimates in some groups are scarce (e.g., reptiles, Kardong 1996).

Annual average temperatures experienced by populations were gathered directly from the source when available. When not presented, geographic coordinates were obtained from the source publication or author and 30-year temperature averages estimated from the NCEP Reanalysis Database (Kalnay et al. 1996) for marine species and the National Climatic Data Center (http://www.ncdc.noaa.gov/oa/ncdc.html) database for freshwater and terrestrial species. Since the species in this study were all ectotherms, I assumed that the local ambient temperature was a reasonable approximation to the individual body temperature. Given the uncertainty associated with these estimates of temperature, I evaluated the dependence of lifespan on temperature for wild species with reduced major axis (model II) regression (Sokal and Rohlf 1994).

Because intra-annual variation in temperature typically varies with latitude, I tested whether including variation within a year in my model would yield different results than mean annual temperature alone. Mean annual temperature and the second-order approximation proposed by Savage (Savage 2004), which includes intra-annual variance in temperature, yielded

very similar results. I compared Boltzmann's factors calculated with gathered annual temperatures as exp[E/kT] and using the approximation exp[E/kT]{1+[E/kT(E/kT-1)]Var(T)} [1+($\frac{E}{kT}\left(\frac{E}{2kT}-1\right)$ Var)]with variances I obtained for 354 sites. Because of a high correlation between the two Boltzmann's factors (correlation coefficient = 0.959) and a paucity of annual temperature variance data, I used 30-yr mean annual temperatures.

To test that body size could be safely omitted, I compared estimated temperature-log lifespan slopes with and without body mass information for 29 species. For some taxa, sizes were only available in terms of length and were converted to mass using species-specific conversions. Temperature slopes for models with and without mass were obtained through multiple regression analysis. I then created 100 bootstrap lifespan, mass, and temperature data sets for each species and calculated regression slopes for each. I compared the original temperature slope obtained without accounting for body mass to the 95% confidence interval of the bootstrapped sample of slopes.

I also compared the relationship between ln(lifespan) and temperature assuming a variety of other models. The models I evaluated via second order Akaike Information Criterion (AICc; Burnham and Anderson 2002) included the inverse temperature model presented above, a log-log model [$\ln(l) = a + b \cdot \ln(T)$; Clarke 2003], a quadratic model [$(\ln(l) = a + \frac{b}{kT} + \frac{c}{kT^2})$], and a linear one [$\ln(l) = a + bT$]. All first order models were statistically indistinguishable and the estimated slopes were highly correlated (r>0.98). The quadratic model was never best under AICc.

Results

I compiled data for 30 species under laboratory conditions and for 67 free-living species (1,081 populations). These data represent 4 phyla and 23 orders from around the globe. The data set contained representatives from terrestrial, freshwater, and marine environments and of widely different average longevities (minimum average lifespan 11.6 d [*Acartia tonsa*], maximum 74.0 yrs [*Margaritifera margaritifera*]). Latitude and lifespan were positively correlated in 85% of the species, although the relationship was statistically significant in only 39% of the cases. It is worth noting that under a null model without a latitudinal gradient in lifespan, the chances of obtaining 85% positive slopes are exceedingly small (χ^2=27.597, p<0.0001). Moreover, for all species with significant regressions, lifespan increased with latitude. As discussed below, it appears that much of this latitudinal variation may be explained by temperature using the MTE.

Body size had no apparent influence on lifespan. Among the 29 species for which I had population-specific estimates of body size, 70% exhibited no significant variation in lifespan with size. The temperature slopes (b) estimated for these species did not change significantly when mass was excluded from the regression in all cases except *Stizostedion canadense*. Importantly, this species is also known to exhibit a latitudinal gradient in the genetic capacity for growth (Braaten and Guy 2002), which can potentially generate an interaction between the effects of temperature and mass that is not accounted for in standard MTE analyses. All subsequent results refer to regressions including only temperature.

Laboratory species. For the 30 species examined to test the MTE under controlled laboratory experiments, 80% of temperature-log lifespan slopes were within the predicted range (mean slope = 0.57; Fig. 1, Table 1) and none was significantly outside the range, strongly validating its use at the intraspecific level.

Wild species. Having shown that the MTE accurately predicts intraspecific variation in lifespan under controlled conditions, I tested the MTE on field data from 67 species. Wild populations also showed predictable and consistent variation with temperature. Lifespan in 87% of the species studied varied as predicted by the MTE (Fig. 2, Table 1). Forty-six species (69%) fit precisely within the MTE-specified interval of slopes, 12 (18%) were outside the range but their slopes did not significantly differ from the predicted range, and 9 (13%) were significantly outside of the predicted range. As expected, coefficients of determination for wild populations were much smaller than those for laboratory populations (wild spp. $\overline{r^2}$ = 0.39, SD = 0.34, lab spp. $\overline{r^2}$ = 0.82, SD = 0.27). Overall, 70% of the species sampled had slopes that were significantly different from zero. Of these, 89% were within the range predicted by the MTE, 2% were significantly greater, and 9% were significantly less than predicted.

Because some studies reported maximum lifespan (n = 43) while others reported average lifespan (n = 24), I determined whether this difference had any effect on the estimated slope. There was no significant difference between them: mean slope = 0.463 (SD = 0.717) for average lifespan data and 0.596 (SD = 1.031) for maximum lifespan data (ANOVA: F-ratio = 0.321, df = 1, p = 0.573). However, r^2 values were substantially greater for the average lifespan data ($\overline{r^2}$ =

0.58) than for maximum lifespan data ($\overline{r^2}$ = 0.28). This is not surprising given the much greater sampling variance for maxima than for means.

To further explore the observed variation among species, I regressed the slopes of the temperature-log lifespan regression on the geographic range, mean temperature, average lifespan, and number of populations included in the analysis. I found a significant correlation between mean temperature and b ($r^2 = 0.186$, $p < 0.001$). Geographic range, as measured by the latitude and temperature range for each species, was not significantly correlated with b (lat.: $r^2 = 0.001$, $p = 0.835$; temp.: $r^2 = 0.022$, $p = 0.230$), nor was average lifespan ($r^2 = 0.001$, $p = 0.784$) or number of populations sampled ($r^2 = 0.005$, $p = 0.576$).

I also examined whether there was any consistent pattern in the slopes arising from phylogeny (i.e., class) or environment (i.e., terrestrial, freshwater, marine). Because of limited samples across these two factors (e.g., there are very few marine insects), I addressed both of these factors via one-way ANOVA. I found that there was no significant taxonomic variation in slopes ($F = 2.05$, $df = 8$, $p = 0.056$). The almost-significant difference arises solely due to differences between the Gymnolaemata, an encrusting bryozoan, and all other taxa (Games-Howell pairwise multiple comparison test). I further explored this question accounting for phylogenetic non-independence by partitioning variance within species, genera, families, orders, classes and phyla via a nested ANOVA (Harvey and Pagel 1991). None of the nested sets significantly explained the observed variation (all p values > 0.05). There were also no significant differences in slopes across environments ($F = 0.726$, $df = 2$, $p = 0.488$).

After accounting for temperature, only 8 species showed significant residual variation with latitude, and multiple regression models which included both latitude and temperature had significant effects of latitude in only 7 cases.

Discussion

In this study, I show that the ubiquitous observation that ectotherms live longer at higher latitudes can be primarily explained by temperature in a manner remarkably consistent with the MTE. Previous studies have suggested that the MTE lacks predictive power at the intraspecific level because of the relatively small range of body sizes found within species (Tilman et al. 2004). My analyses show that variation in lifespan at this taxonomic level is well explained by the MTE's Arrhenius model for thermal scaling both in laboratory studies and in wild populations, but is independent of mass. It appears, therefore, that within species temperature is a more important driver of population-level variation than mass. This is to be expected, as intraspecific variation in body mass tends to be relatively small (Belk and Houston 2002).

Although the slopes are remarkably consistent with the MTE, it should be noted that considerable residual variation does remain (Fig. 3). Other factors, like local adaptation (Schmidt et al. 2005), diet (Lin et al. 2002), and environmental stressors (Lithgow and Walker 2002), may also play important roles in determining lifespan within species. Activity level, through its effects on metabolic rate, could also influence lifespan, something that is starting to be

appreciated (Glazier 2009, 2010). A detailed account of intra-specific lifespan variation is simply unattainable with the MTE.

Others have noted that the Arrhenius temperature dependence of the MTE is not the only model that could be used (Clarke 2006). I found that alternative regressions using temperature and log-temperature as independent variables were statistically indistinguishable from the Arrhenius model using the sample size corrected version of AIC (Burnham and Anderson 2002). These simpler models were always better than one with a quadratic temperature dependence. My main finding, that the temperature dependence of lifespan within species is highly consistent across widely different taxa, remains valid regardless of the model used. Moreover, the overall mean slopes for lab and wild species (0.57 and 0.55) are not significantly different from the value of 0.65 predicted under the MTE (Gillooly et al. 2006).

Given the general success of the MTE, I suggest that departures from it may, in fact, be quite informative. Assuming that other environmental gradients are of secondary importance, this framework might be used to assess local adaption in lifespan. For instance, the fact that species whose slopes are outside of the predicted range all occur at relatively low temperatures is consistent with the metabolic cold adaptation hypothesis; i.e., cold-adapted populations tend to have higher metabolic rates than warm-adapted populations (Clarke 2003), reducing the slope of the apparent temperature-log(lifespan) relationship. Moreover, temperature compensation is thought to evolve in response to size-dependent winter mortality (Alvarez et al. 2006, Chown and Gaston 1999) and several of the species with significantly flatter slopes (e.g., *Coregonus*

clupeaformis, *Clupea harengus*) do, in fact, exhibit this type of winter mortality (Pangle et al. 2004, Cohen and Lough 1983). Another relevant outlier is *Stizostedion canadense,* for which there appeared to be a significant interaction between temperature and mass. I suspect that this result arises from local adaptation in growth rate (Braaten and Guy 2002), which is currently unaccounted for in applications of the MTE.

Given the intense current interest in the effects of climate change, it is interesting to consider how lifespan is likely to change, especially given that small changes in temperature will result in relatively large changes in lifespan because of their exponential relationship. Under extremely conservative climate change scenarios, temperatures are expected to rise by 1.1 to 2.9°C in the next 100 years (IPCC 2007). Based on this temperature change and the 0.2 to 1.2 slope predicted by the MTE, ectotherm lifespans may be expected to shorten by 3-19% (under a 1.1°C increase) to 8-42% (2.9°C increases). These changes in lifespan among ectotherms may have widespread consequences, including compensatory responses in life history (Roff 2002) and higher extinction risk (Reynolds et al. 2005). Further, and given the importance to food web dynamics of the interaction between ectotherms and endotherms (Yodzis and Innes 1992, Brose et al. 2005), my results suggest that substantial changes to ecosystem structure and stability are likely if the generation times of ectotherms shift to accommodate changes in climate while generation times of endotherms do not.

Tables

Table 1. Summary of results for both laboratory and wild species.

	Laboratory species (model I regressions)	Wild species (model II regressions)
N	30	67
Mean slope (SD)	0.57 (0.38)	0.55 (0.92)
Mean r^2 (SD)	0.82 (0.27)	0.39 (0.34)
Percent within range	80	69
Percent not significantly outside	100	87

Table 2. Summary of results for all wild species. Slope, intercept, and r^2 values are those obtained from regressing 1/temp(in K)*Boltzmann's constant and ln(lifespan). N indicates the number of populations. Lifespan measure denotes whether maximum or average lifespan was obtained for that species. Mean temperature is the average of all 30-yr average temperature records from where the populations originate. Temperature and latitude ranges were calculated as max_{temp}-min_{temp} and max_{lat}-min_{lat}, respectively (some studies reported temperature only). Order of species mimics Figure 2 (see that figure for phylum, class, and order of each species).

Species	Slope	Intercept	r^2	N	Lifespan measure	Mean temp. (°C)	Temp. range	Lat. Range
Inversiula nutrix	-1.478	62.569	0.645	6	avg	-0.43	3.70	13.42
Celleporella bougainvillei	-1.510	63.834	0.630	5	avg	-0.32	3.70	13.42
Mytilus edulis	0.326	-10.932	0.062	22	max	9.33	15.50	15.58
Placopecten magellanicus	0.327	-11.092	0.923	5	max	5.20	10.00	8.85
Siliqua patula	0.784	-30.347	0.719	10	avg	6.93	11.00	25.27
Dreissena polymorpha	1.783	-72.052	0.122	17	max	6.50	6.13	
Macoma balthica	0.642	-24.683	0.165	15	max	5.59	20.00	27.58
Margaritifera margaritifera	0.680	-23.866	0.599	29	max	8.42	24.90	27.34
Nototodarus gouldi	0.825	-27.451	0.000	5	max	16.04	6.40	9.97
Tegula funebralis	1.226	-47.460	0.372	10	max	12.03	7.33	12.30
Carcinus maenas	0.559	-21.364	0.076	9	max	9.68	6.83	18.13
Emerita brasiliensis	0.505	-17.598	0.672	6	max	21.18	6.63	11.65
Euphausia pacifica	0.384	-15.492	0.196	8	avg	6.88	15.50	18.78
Meganyctiphanes norvegica	0.432	-17.327	0.696	6	avg	6.32	15.00	31.00
Thysanoessa inermis	-0.117	5.891	0.007	11	avg	-7.16	39.90	30.52
Thysanoessa raschii	0.099	-3.742	0.009	7	avg	-10.91	39.70	29.42

Acartia clausi	0.611	-21.617	0.824	14	avg	14.11	10.00	
Acartia tonsa	0.701	-25.382	0.675	15	avg	20.10	18.70	
Acartia californiensis	0.849	-31.295	0.599	16	avg	17.46	7.80	
Eurytemora herdmanni	0.838	-31.057	0.974	5	avg	10.00	13.00	
Calanus finmarchicus	0.920	-33.766	0.935	10	avg	8.70	16.00	
Calanus pacificus	0.932	-34.522	0.856	13	avg	14.50	9.00	
Calanus sinicus	0.658	-23.300	0.973	5	avg	15.20	9.90	
Neocalanus cristatus	-0.621	30.645	0.000	6	avg	3.00	2.00	
Pseudocalanus elongatus	0.760	-27.622	0.965	10	avg	9.94	9.60	
Pseudocalanus minutus	0.641	-22.725	0.930	10	avg	10.71	8.50	
Sinocalanus tenellus	0.831	-30.289	0.973	6	avg	16.80	20.90	
Temora longicornis	0.789	-28.770	0.956	11	avg	13.36	6.50	
Oithona similis	0.458	-15.015	0.621	5	avg	9.20	9.00	
Clupea harengus	-0.660	29.936	0.014	12	max	7.60	11.40	21.00
Macrhybopsis meeki	1.444	-58.522	0.465	10	max	9.83	7.90	9.56
Catostomus commersoni	0.911	-34.795	0.062	53	max	10.72	8.50	9.00
Carpiodes carpio	0.520	-19.291	0.046	30	max	11.24	13.73	14.07
Rutilus rutilus	1.472	-58.381	0.004	7	avg	6.76	1.30	3.98
Notropis atherinoides	1.091	-44.303	0.604	15	max	9.25	7.90	9.53
Ictalurus punctatus	0.486	-17.528	0.105	16	max	13.93	8.58	10.80
Esox lucius	0.476	-17.586	0.643	24	max	2.17	21.42	26.43
Perca flavescens	0.827	-32.371	0.013	29	max	7.43	13.33	14.53
Perca fluviatilis	0.524	-19.455	0.176	75	max	6.18	17.40	27.12
Stizostedion canadense	0.859	-33.561	0.181	27	max	8.36	12.29	13.72
Stizostedion vitreum	0.510	-19.009	0.296	70	max	8.00	24.30	29.50
Pomoxis nigromaculatus	-0.509	22.406	0.002	32	max	12.60	15.04	16.96
Pomoxis annularis	0.683	-25.916	0.013	43	max	13.49	12.79	12.96
Lepomis macrochirus	0.565	-21.413	0.240	52	max	10.75	13.38	12.98
Lepomis gibbosus	-0.744	30.735	0.101	5	max	22.98	12.18	12.15
Micropterus salmoides	0.724	-28.154	0.235	35	max	6.71	12.00	13.23
Micropterus dolomieui	0.779	-29.898	0.448	26	max	10.32	10.38	11.60
Morone chrysops	0.610	-23.127	0.359	18	max	12.49	10.13	10.90
Acanthurus	1.608	-59.570	0.928	10	max	26.06	5.50	56.00

bahianus								
Ctenochaetus striatus	1.056	-37.747	0.514	5	max	26.80	4.00	19.00
Stegastes planifrons	5.629	-215.792	0.379	7	max	26.57	3.00	18.37
Aldrichetta forsteri	0.141	-3.736	0.018	7	max	16.37	8.00	10.20
Gasterosteus aculeatus	1.106	-44.937	0.121	32	max	8.80	15.50	24.00
Microstomus pacificus	-0.230	13.175	0.366	5	max	8.66	6.60	18.00
Oncorhynchus keta	0.223	-7.521	0.010	26	max	9.05	20.60	24.58
Oncorhynchus kisutch	0.202	-7.145	0.235	8	max	7.89	14.90	16.80
Oncorhynchus clarkii	0.773	-30.338	0.120	12	max	6.26	12.38	10.13
Oncorhynchus tshawytscha	0.142	-4.017	0.793	8	max	5.81	15.00	17.28
Salmo trutta	1.033	-40.832	0.104	21	avg	6.22	6.30	11.53
Coregonus clupeaformis	-0.279	14.456	0.712	7	max	3.34	19.40	9.80
Cynops pyrrhogaster	1.160	-44.642	0.457	12	max	12.16	6.30	0.27
Bufo bufo	-0.363	17.197	0.015	5	max	8.67	8.67	19.91
Bufo calamita	0.892	-34.341	0.053	11	max	10.85	5.40	12.67
Bufo hemiophrys	-0.916	40.738	0.029	9	max	1.33	8.38	9.03
Rana temporaria	-1.186	50.667	0.002	10	max	10.12	6.60	12.97
Rana sylvatica	0.331	-12.286	0.551	5	avg	5.60	17.90	17.70
Varanus niloticus	0.860	-30.020	0.501	5	avg	25.18	7.96	2.18

Figures

Figure 1. The relationship between mean lifespan of single-population individuals of 30 species raised at various temperatures (left panel). Slope and 95% confidence intervals for these species are shown on the right panel, along with the MTE predicted range (dashed lines).

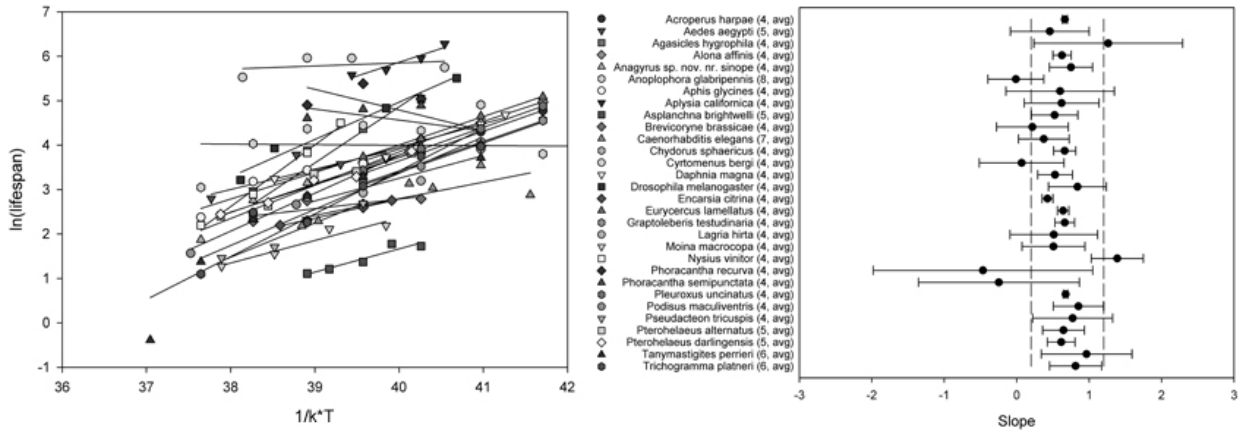


Figure 2. Point estimates and 95% confidence intervals for the temperature-log lifespan slopes for 67 ectotherms from natural populations. Vertical bars to the left indicate phylum, class, and order; parentheses following the species name are number of populations and whether lifespan estimate was average or maximum. * designates estimates that are significantly outside of the predicted range. See supporting information for plots of the raw data.

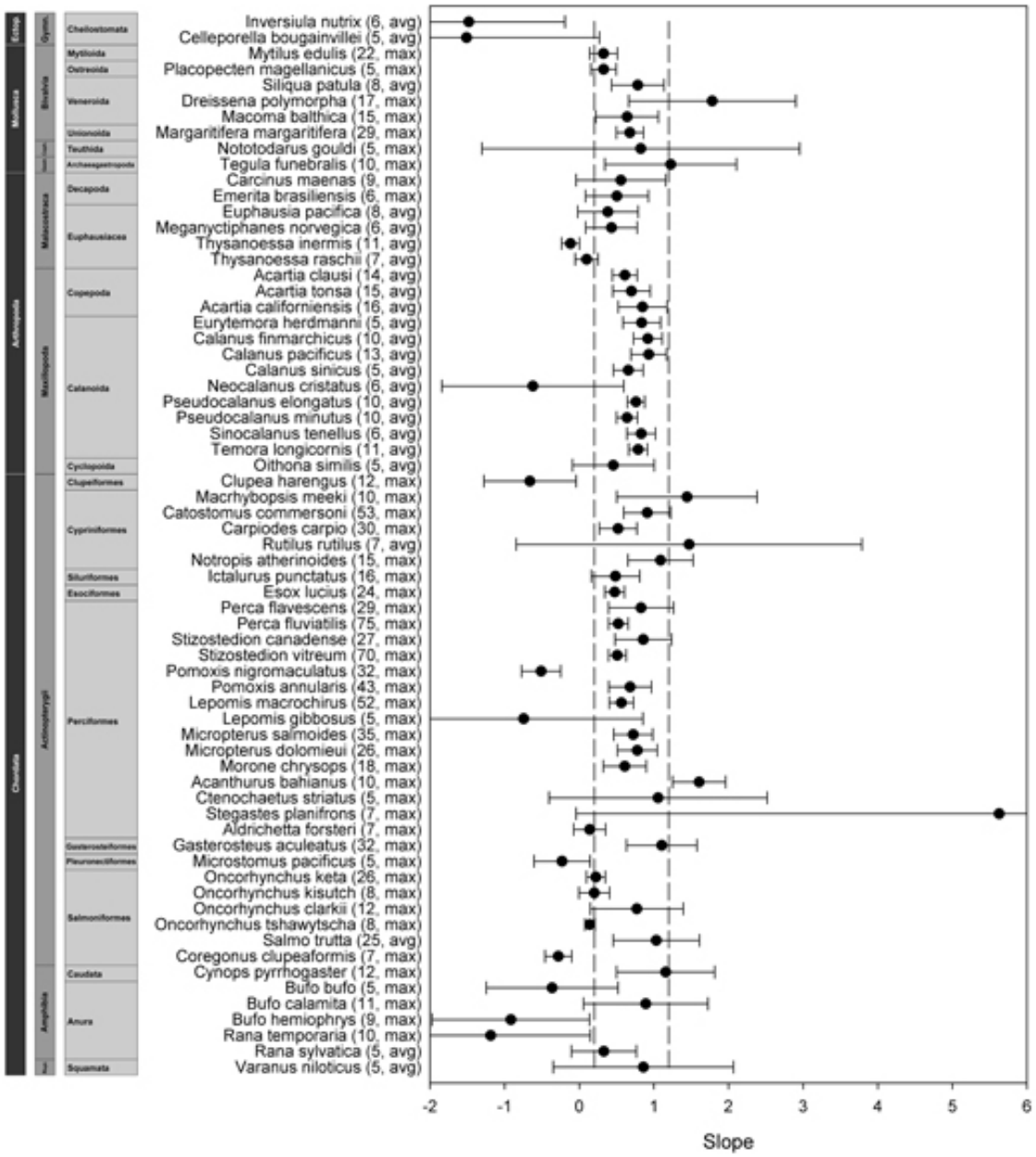
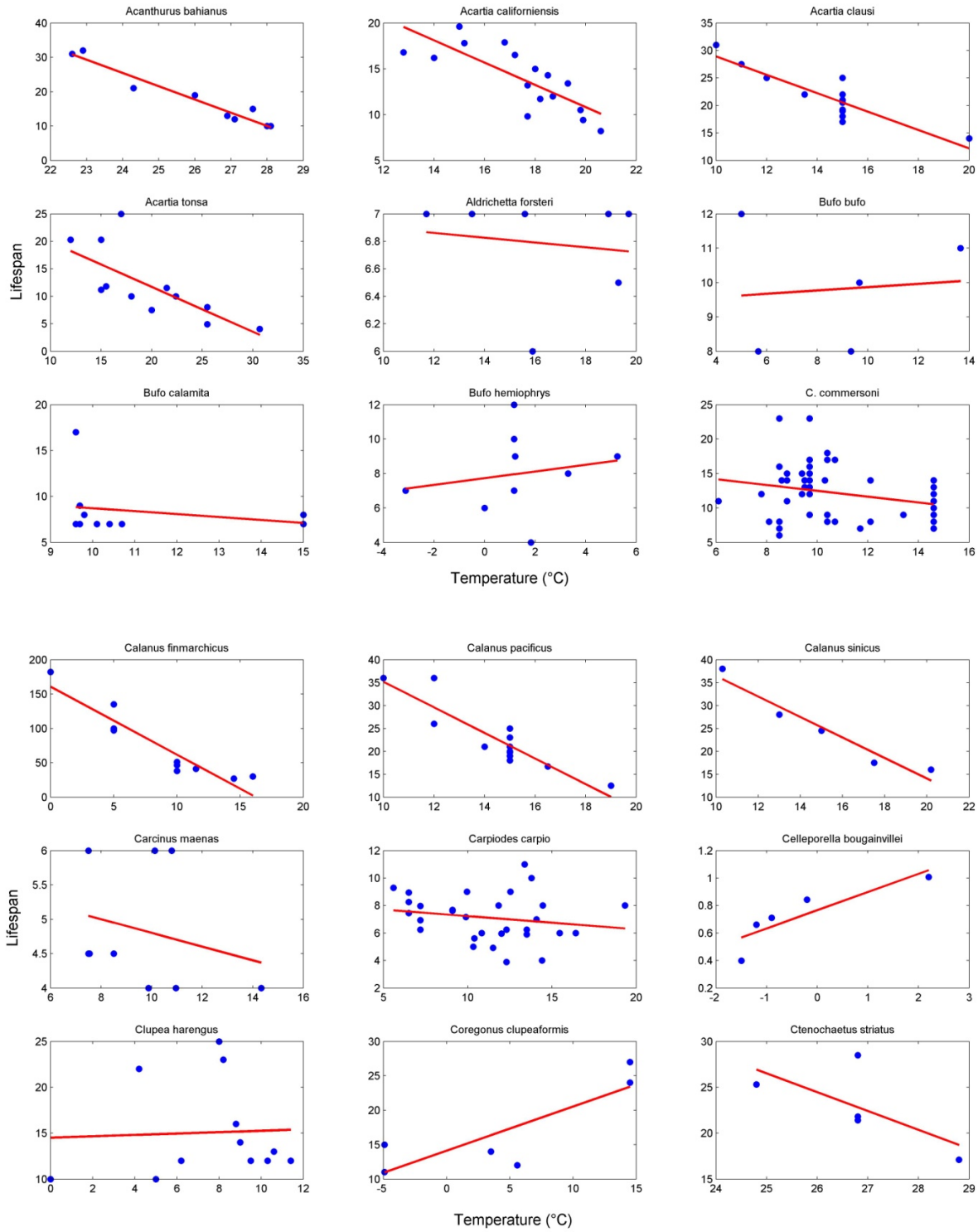
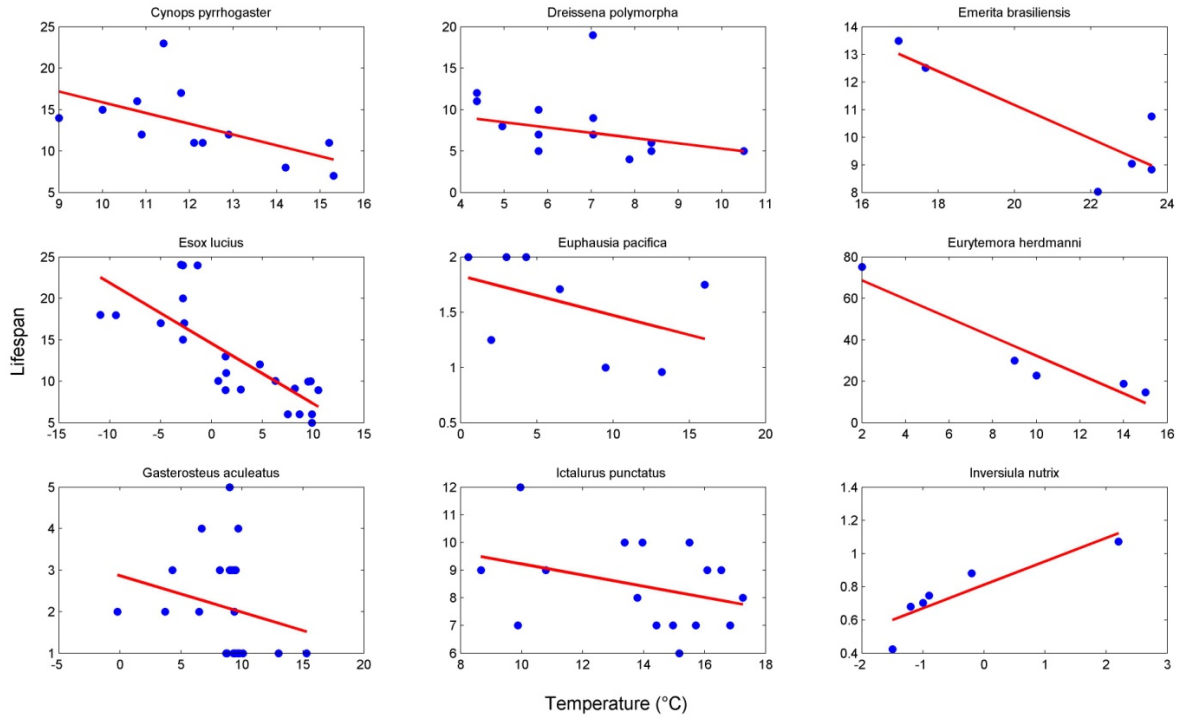
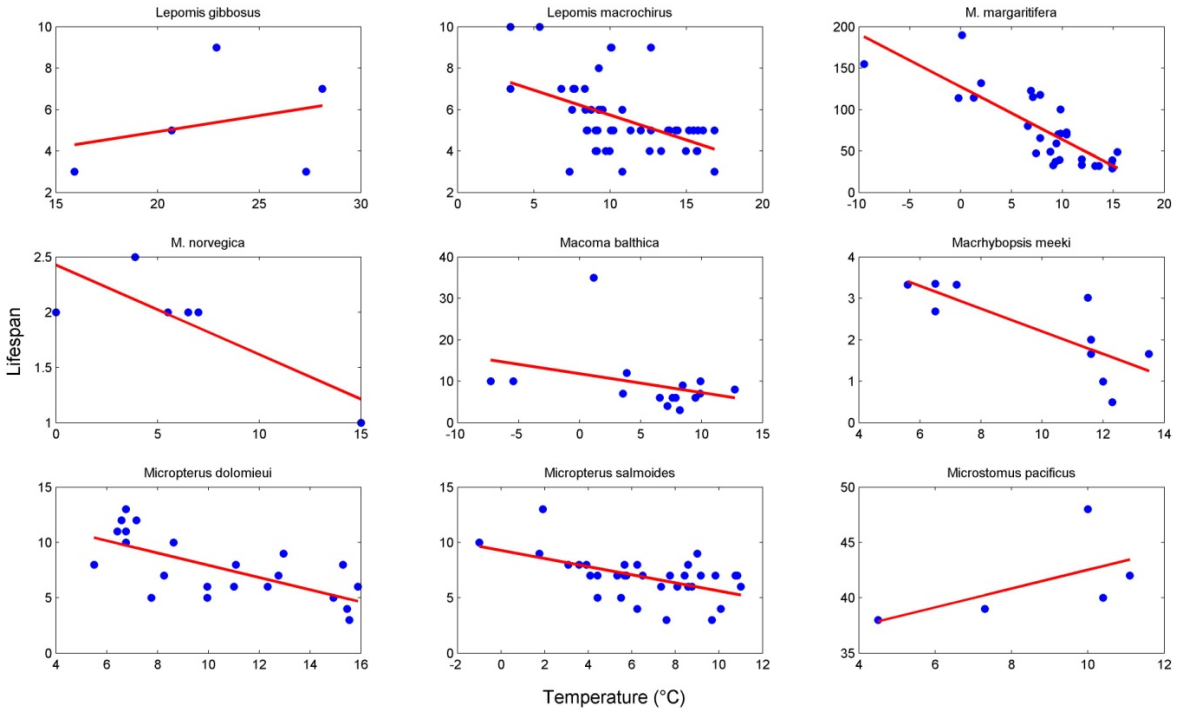
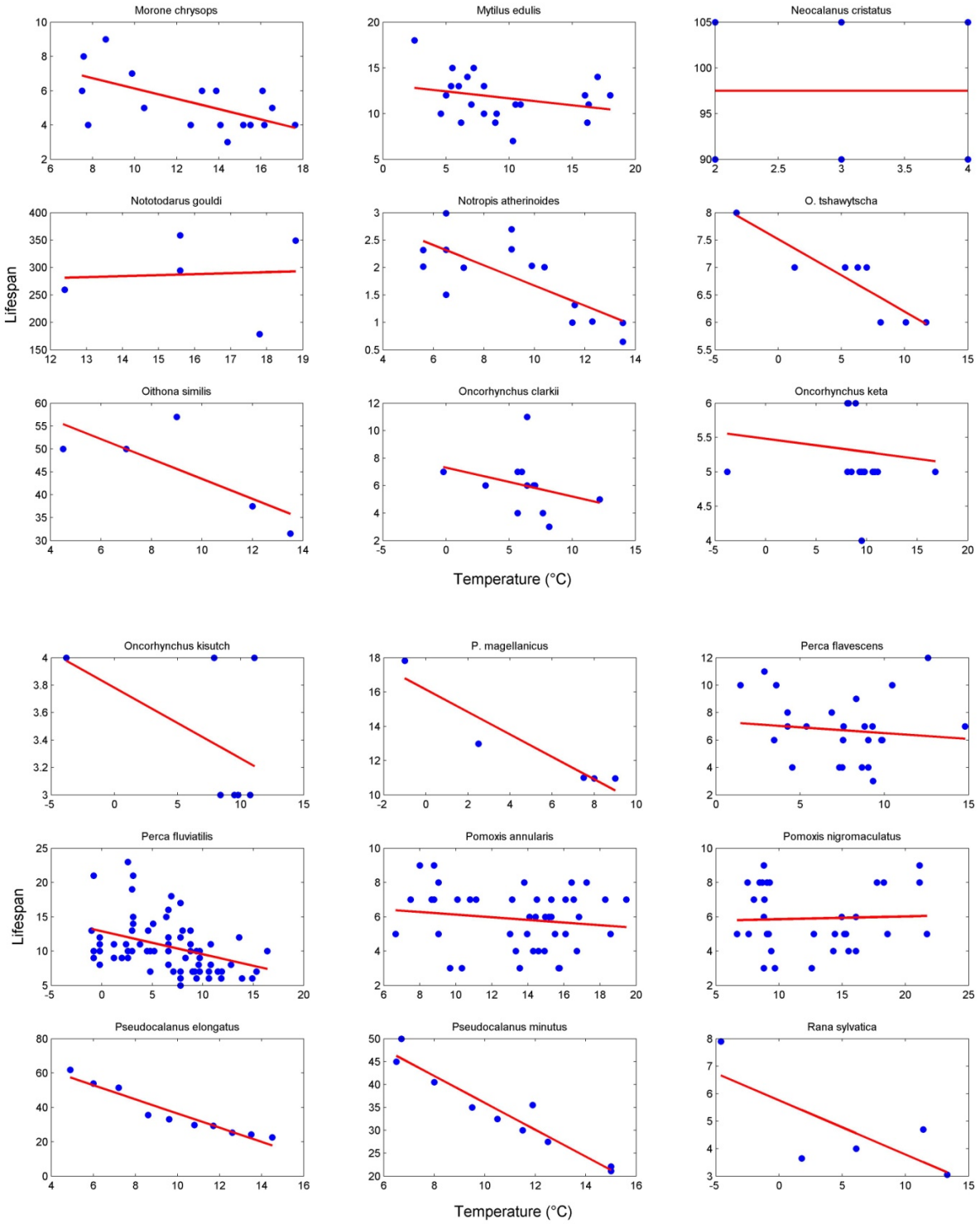


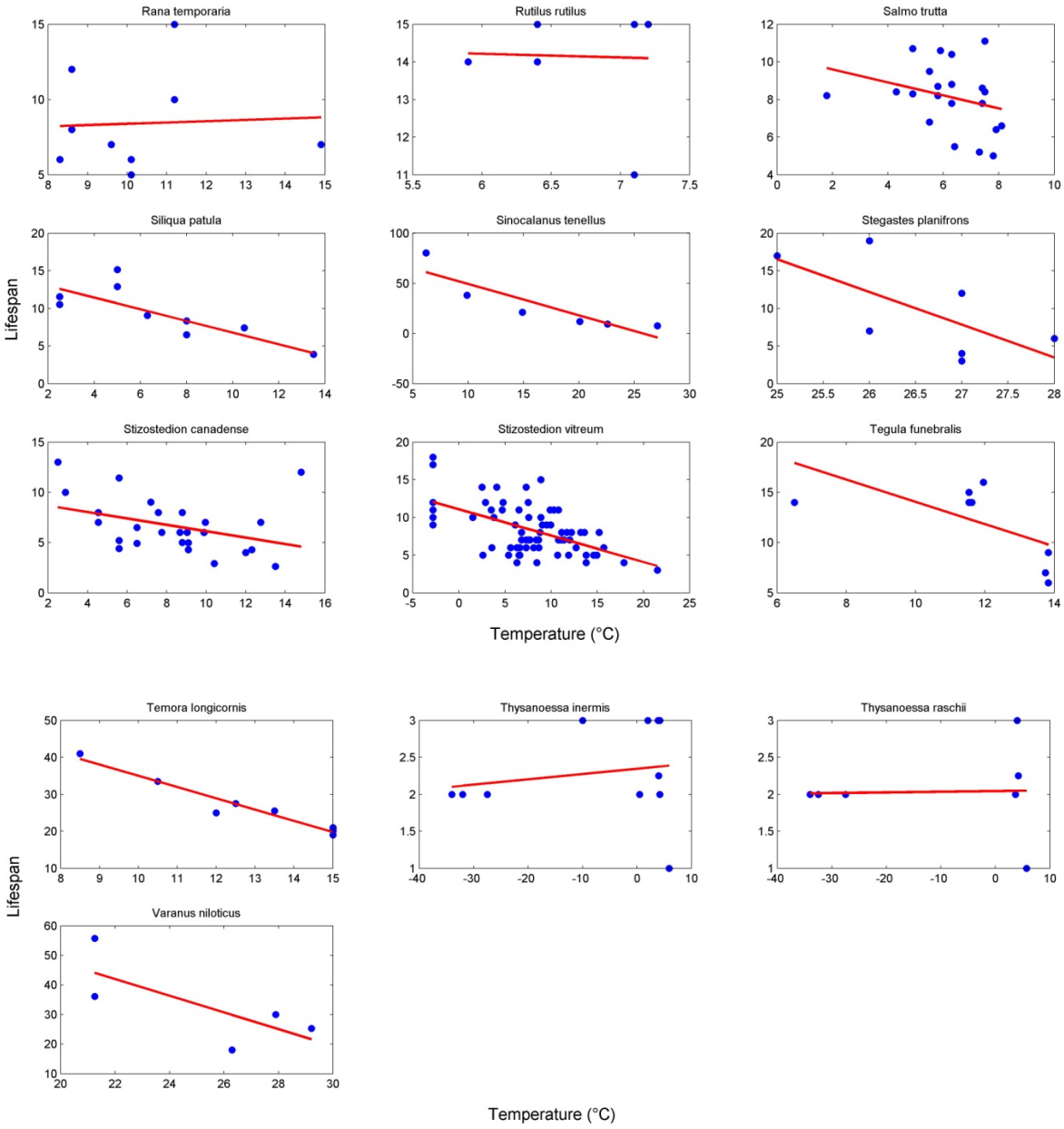
Figure 3. Temperature-lifespan plots for the 67 wild species. Each data point represents one population.




Cynops pyrrhogaster
Dreissena polymorpha
Emerita brasiliensis
Esox lucius
Euphausia pacifica
Eurytemora herdmanni
Gasterosteus aculeatus
Ictalurus punctatus
Inversiula nutrix
Lifespan
Temperature (°C)


Lepomis gibbosus
Lepomis macrochirus
M. margaritifera
M. norvegica
Macoma balthica
Macrhybopsis meeki
Micropterus dolomieui
Micropterus salmoides
Microstomus pacificus
Lifespan
Temperature (°C)


Morone chrysops
Mytilus edulis
Neocalanus cristatus
Nototodarus gouldi
Notropis atherinoides
O. tshawytscha
Oithona similis
Oncorhynchus clarkii
Oncorhynchus keta
Oncorhynchus kisutch
P. magellanicus
Perca flavescens
Perca fluviatilis
Pomoxis annularis
Pomoxis nigromaculatus
Pseudocalanus elongatus
Pseudocalanus minutus
Rana sylvatica
Lifespan
Temperature (°C)


Rana temporaria
Rutilus rutilus
Salmo trutta
Siliqua patula
Sinocalanus tenellus
Stegastes planifrons
Stizostedion canadense
Stizostedion vitreum
Tegula funebralis
Temora longicornis
Thysanoessa inermis
Thysanoessa raschii
Varanus niloticus
Lifespan
Lifespan
Temperature (°C)
Temperature (°C)

Chapter 2

Climate change, metabolism, and the future of life histories

Abstract

A worldwide increase in temperature is expected in the near future. This increase in temperature will not be uniform: some parts of the world will be up to 10°C warmer over the next 50 years, while others will be completely unaffected. Because of this heterogeneity in temperature increases, there is a growing need to develop a general, quantitative framework to predict the effects of warming on key life-history traits. Here, I present such a framework. I use the metabolic theory of ecology to estimate changes in ectotherms on a worldwide scale, and find that growth rates will be greatly increased in much of the world, averaging 15.9-24.9% more in 50 years. Development time and lifespan, on the other hand, are expected to decrease by a global average of 12.5-17.5%. This dramatic increase in the pace of ectotherm life is expected to have important consequences to ecosystem stability and human-ectotherm interactions.

Introduction

The Earth's climate is expected to change substantially in the next 50 years, with an increase in global mean temperature of as much as 2.1°C (IPCC 2007). However, much regional variation in warming is expected: northern Russia is predicted to warm by up to 5.2°C, while southern South America will only change by 1.0°C (IPCC 2007). Changes in ambient temperature will have a profound effect on ectotherms, and will affect global agriculture, pest control programs, productivity of harvested populations, biodiversity, and the conservation of threatened species (IPCC 2007). Predicting these changes is critical.

Much of the current research on how climate change will influence organisms and ecosystems has focused on predicting shifts in species distributions (Parmesan et al. 1999, Root et al. 2003, Thomas et al. 2004). This is clearly important, yet studies of this kind typically show that the movement of species in contemporary time scales is not large. For instance, the range of the sooty copper butterfly, *Heodes tityrus*, has been expanding in the north and contracting in the south over the last half century (Parmesan et al. 1999). The total distance shifted is roughly 66 km in the south and 102 km in the north. Though seemingly substantial, this distance is only 8% of the species' latitudinal range. Studying fish species from the North Sea, Perry et al. (2005) found that 6 out of 12 species shifted their southern boundary northward. The largest boundary shift was exhibited by blue whiting, *Micromesistius poutassou* (816 km). Based on its distribution, this constitutes ~12% of its entire latitudinal range. These are important changes in species distributions. However, from the few studies to survey the entire range of a species, it could be said that most regions of the world are unlikely to be confronted with local extinction

due to range shifts (i.e., the majority of a species' range will remain occupied by that species).

Local changes in life history characters, on the other hand, are expected to be quite common (Gienapp et al. 2008), including, e.g., growth rate and lifespan, major determinants of the resilience of a population. Consequently, there is a clear need for robust predictions of the effects of climate change on critical life history traits in local populations.

In addition, many important management decisions are based on life history traits. In fishery models, for instance, natural mortality is (ironically) one of the most vital parameters. Direct estimates of mortality are seldom available because of logistical difficulties, however, and most fishery scientists rely on approximations derived from longevity data (Vetter 1988). In management and recovery plans, changes in longevity (and, consequently, natural mortality) both spatially and temporally are seldom included (NRC 1998), even though they exist (Maunder et al. 2009). Any method capable of producing location-specific estimates of life history traits, however coarse, could improve the successful implementation of these plans.

Predicting responses of traits to climate change is currently only possible for species with long-term data (Charmantier et al. 2008) and is typically done on a species-by-species basis. Focusing on temperature as the major climatic driver of life history variation (Johnston and Bennett 1996), I use the metabolic theory of ecology (MTE; Brown et al. 2004) to make spatially-explicit, worldwide predictions for changes in somatic and population growth rate, development time, and lifespan driven by anticipated warming over the next 50 years.

Of course, using the MTE to make life history predictions should be viewed as a first attempt, particularly useful in data-poor cases. The MTE can only, for example, forecast changes in the positively-sloped region of a reaction norm or performance curve. If a species is at the thermal optimum, an increase in temperature will lead to decreased performance (and not to an exponential increase). Most species do occur on the left of this thermal optimum, although exceptions exist (Deutsch et al. 2008). Some fundamental issues within the MTE framework are still being explored (Cyr and Walker 2004, Marquet et al. 2004, Clarke 2006, O'Connor et al. 2007b; see Chapter 1 for details). Despite these concerns, I contend that even general estimates of spatial or temporal variation in life history traits brought about by temperature (if obtained from a tested and sufficiently robust framework) could improve the successful implementation of conservation and management plans.

Methods

Under the MTE, the effect of temperature on biological rates (e.g., somatic growth rates, population growth rates) is described by Boltzmann's factor, exp(-E/kT), where E is the activation energy (estimated as 0.63; Brown et al. 2004), k is Boltzmann's constant (8.62×10^{-5} eV/K), and T is temperature in Kelvin. Analogously, biological times (e.g., development time, lifespan) scale as the inverse of Boltzmann's factor, exp(E/kT). This model has previously been used to explain variation in life history traits across species (Brown et al. 2004). For lifespan (Munch and Salinas 2009) and pelagic larval duration (O'Connor et al. 2007a), it holds within species as well. It is also worth noting that Dell et al. (2011) analyzed the temperature dependence of 112 traits relevant to species interactions (e.g., gut clearance rate, escape body

velocity, grazing rate), finding that 87% fit the Boltzmann-Arrhenius model. Here, I extend these within-species results to other critical life history characters including population growth, somatic growth, and development.

I followed the same procedure as in Munch and Salinas (2009) to determine whether development time and growth rates agree with predictions of the MTE at the intraspecific level. I regressed log-transformed values of traits against 1/kT for each population and considered the MTE supported if the slope was between -0.2 and -1.2 for somatic and population growth rates and 0.2 and 1.2 for development time (Gillooly et al. 2001). Data for development time representing 29 species and a total of 129 populations were taken from Gillooly and Dodson (2003) and Pauly and Pullin (1988). Population growth rates were acquired from Savage et al. (2004) (13 species, 63 populations) and somatic growth rates from the database in Munch and Salinas 2009 (20 species, 580 populations). This is by no means an exhaustive database for these traits. The goal is to ascertain, in general terms, that intraspecific variation in somatic growth rate, population growth rate, and development time could be explained by the MTE in a representative sample of ectotherms. I also tested whether including log-body size provided additional information to the trait-specific models. Temperature slopes for models with and without mass were obtained through multiple regression analysis. I then created 100 bootstrap lifespan, mass, and temperature data sets for each species and calculated regression slopes for each. I compared the original temperature slope obtained without accounting for body mass to the 95% confidence interval of the bootstrapped sample of slopes.

I then calculated percent changes in growth rate, development time, and lifespan using

the Community Climate System Model's (version 3; http://www.ccsm.ucar.edu) 10-year surface temperature averages from 1990 to 1999 as the baseline and the predicted 2045-2054 averages as the endpoint, at a resolution of ca. 1.4° latitude by 1.4° longitude. This and all other models in existence are able to capture effectively global temperature dynamics, with correlation coefficients of predicted and observed annual temperatures for individual models ≈ 0.98 (Randall et al. 2007). Two sets of temperatures, arising from different assumptions of future emissions scenarios, were used: a more conservative set (scenario B1 (IPCC 2007)) and a more extreme one (scenario A2 (IPCC 2007)).

I also tested whether accounting for intra-annual variation in temperature would yield different results than when using mean annual temperature. A second order approximation to the Boltzmann's factor including variance is given by $\exp[E/kT]\{1+[E/kT(E/kT-1)]\mathrm{Var}(T)\}$ (Savage 2004). I found that the two approaches were statistically indistinguishable (correlation coefficient of Boltzmann's factors in scenario A2: 0.99997, in scenario B1: 0.99997) and used mean temperature throughout the analysis.

Results

Development rate, somatic growth rate, and population growth rate scale as predicted by the MTE. 100% of the species in the development time and population growth rate analyses are within the MTE-specified range, while 89% of species fall within the range for somatic growth rate (Fig. 1).

Growth rates are, on average, expected to increase by 15.9 (B1 scenario) to 24.9% (A2 scenario) worldwide in the next 50 years (uncertainty for B1 scenario, based on interquartile range of slopes in Munch and Salinas (Munch and Salinas 2009) after removal of two Antarctic bryozoans: 7.8-22.8%; A2: 11.7-36.6%). Ectotherms living at extreme latitudes will be affected more severely (Fig. 2a, 2b), with a maximum change of ~200% at the highest northern latitudes under the A2 scenario. The mean change is roughly 10% near the tropics and increases considerably after 20°N and 60°S (Fig. 3a).

To make the analyses more concrete, it is instructive to use the Pacific razor clam, *Siliqua patula*, with data from Alaska to California, USA (Lassuy and Simons 1989) as a case study. Clams from northern British Columbia, Canada (an approximate midpoint) are predicted to grow at 7.8% (B1) to 14.3% (A2) more than they currently do (current growth rate: 14.3 mm/year), leading to a predicted growth rate of 15.4 to 16.3 mm/year. The predicted growth rates are equivalent to present-day growth rates of clams ~950 km further south, in mid-Washington, USA.

Lifespan, conversely, is expected to decrease by 12.5% (-6.8 - -16.4%) to 17.5% (-9.8 - -22.6%) worldwide with reductions of 10-20% throughout most of the world and much larger changes at high latitudes (e.g., -42.1% at 80°N; Fig. 1c, 1d; Fig. 3b). In the Pacific razor clam this means a reduction in average lifespan for British Columbian clams from 9.05 to 7.9-8.4 years, similar to that of clams in northern California today.

As found previously (Munch and Salinas 2009), including log-body size in the regression

model provided very little additional information and did not alter the estimated temperature dependence: the correlation of estimated Boltzmann's factor from a model including size and the model excluding it was 0.999. The same multiple regression/bootstrap method used in Munch and Salinas (2009) to test for significant differences in temperature dependence across the two models was employed here. For no species was the estimated temperature dependence different when body mass was included.

Discussion

It appears that in most parts of the world, climate change will speed the pace of life among ectotherms by as much as 15.9-24.9%. As others have noted (Vasseur and McCann 2005), disparate changes in the pace of life between ectotherms and endotherms may destabilize ecosystems, leading to substantial changes in community composition and ecosystem dynamics. This includes interactions with humans: substantial changes will be required to maintain the effectiveness of control and management programs in the face of climate-driven changes in the productivity of harvested populations and the increase of population growth in agricultural pests. For example, the predicted 24.9% increase in the growth rates of pests would necessitate a global increase in pesticide application of ~6.3% (Talpaz and Borosh 1974). Given current pesticide use (Kiely et al. 2004), this would represent 107.5 million more pounds of pesticide-per-acre. In fisheries, a commonly used relationship between natural mortality and lifespan (to estimate M) is that derived empirically by Hoenig (1983). This relationship is, in fact, partly used to estimate natural mortality in skates of the Bering Islands and Aleutian Islands (all species are managed as a complex; NPFMC 2011). Given the changes calculated here, natural mortality could increase

from 0.13 to 0.17-0.19 in the next 50 years, with important implications to the fishery and sustainable harvest of the complex. One more example may prove illuminating. Fangue et al. (2009) measured oxygen consumption (a trait related to somatic growth; Jobling 1981) of 25°C-acclimated *Fundulus heteroclitus* at various temperatures ranging from 2 to 37°C. If given the dataset with O_2 consumption data up to 30°C, how closely would the performance curve-derived estimates be (by fitting, as the authors did, an exponential curve to the data) to the %-change estimates obtained from the framework presented here to the actual values measured at 35 and 37°C? The answer is that the MTE-Boltzmann outperformed the experimentally derived relationship in both cases (true value at 35°C=768, performance curve estimate=1,468.9, % change estimate=1,135.7 pmol sec^{-1} mg^{-1}; true value at 37°C=1,152, performance curve estimate=1,758.6, % change estimate=1,323.3 pmol sec^{-1} mg^{-1}). These admittedly simple examples make it clear that long-term management of harvested populations and recovery plans for threatened species, which are typically developed for 50- to 100-year horizons, need to account for climate-driven life history changes, and that the Arrhenius thermal scaling could be used when very little other information is available.

In addition, many factors, including food availability, competition, and predation, as well as local adaptation, could obscure the temperature dependence of these rate and time variables in wild populations. However, I have previously shown that the mean response to temperature is largely invariant across a wide range of poikilotherm species from disparate habitats (Munch and Salinas 2009). Moreover, the mean response to temperature is roughly the same for both laboratory experiments and field data; the addition of other environmental drivers increases residual variability rather than altering the mean response (Munch and Salinas 2009). This

invariance allows me to make robust predictions for changes in growth rate, development, and lifespan under different climate scenarios, approximately independently of the effects of other variables.

Importantly, this approach ignores behavioral thermoregulation (Kearney et al. 2009) and consequently represents an upper bound on expected temperature-driven changes. In addition, I assume that populations are not at the peak of their thermal performance curves (i.e., that a small increase in temperature would not lead to reduced performance). Supporting this assumption, a recent review of thermal optima of insects, turtles, lizards, and frogs indicates that most temperate species are currently below their thermal optima (exceptions to this are tropical species [~20°S-20°N]; Deutsch et al. 2008). Moreover, plastic responses to climate change are common (Parmesan 2006, Giennap et al. 2008) and more important than evolutionary change, at least in cases when the contributions of plasticity and evolutionary change were successfully disentangled (Hoffmann and Sgrò 2011).

A thorough understanding of phenotypic plasticity is clearly important to better predict shifts in species distributions (Helmuth et al. 2005) or invasions (Chown et al. 2007). However, only in a few well-studied species do we know enough about plasticity to aid in climate change predictions. The MTE represents a way to include plasticity when little is known about a species and should serve as a robust baseline for making predictions in the data-poor situations common in conservation biology.

Figures

Figure 1. Slope and 95% confidence intervals for the slopes of temperature vs. development time (a), somatic growth rate (b), and population growth rate (c). The phylum, class, and order of each species is indicated.

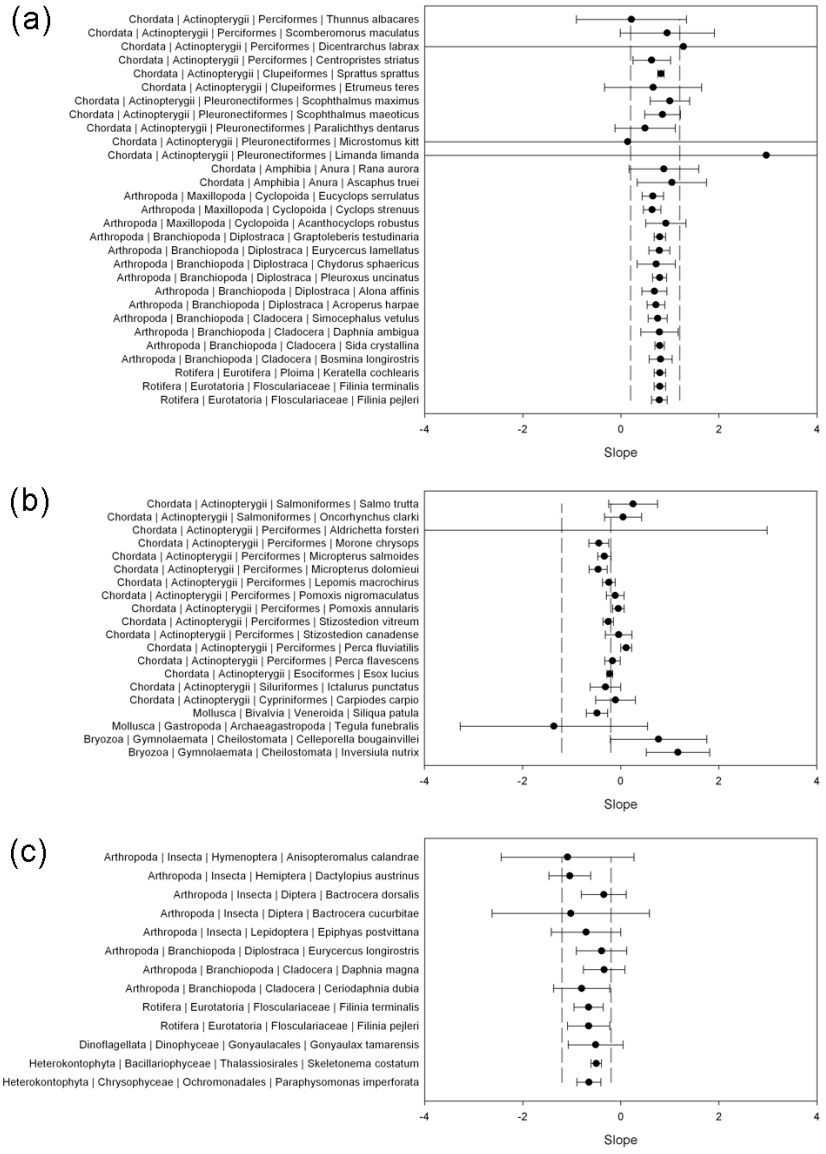


Figure 2. Percent changes in somatic and population growth rates (top) and development time and lifespan (bottom) in 50 years for two of the IPCC scenarios: A2, most extreme (a, c), and B1, most conservative (b, d).

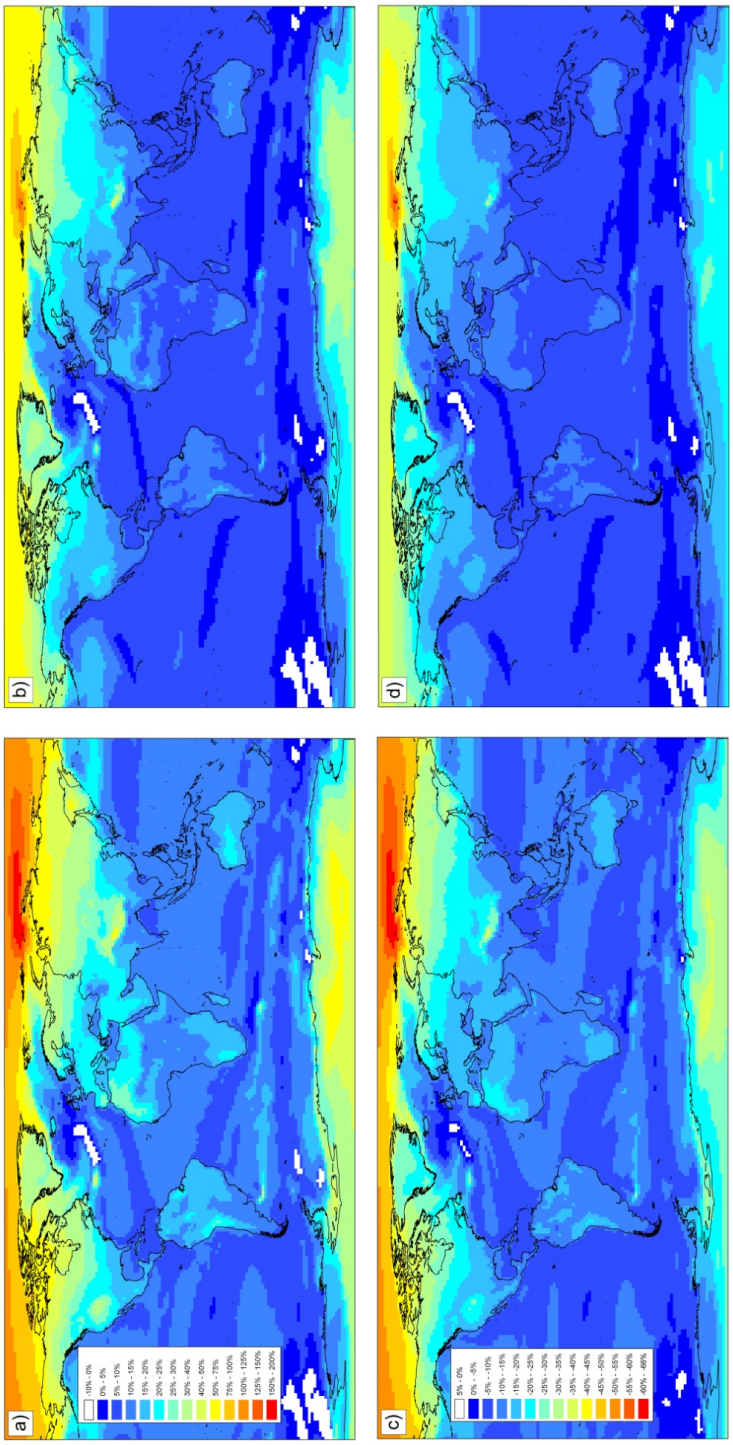
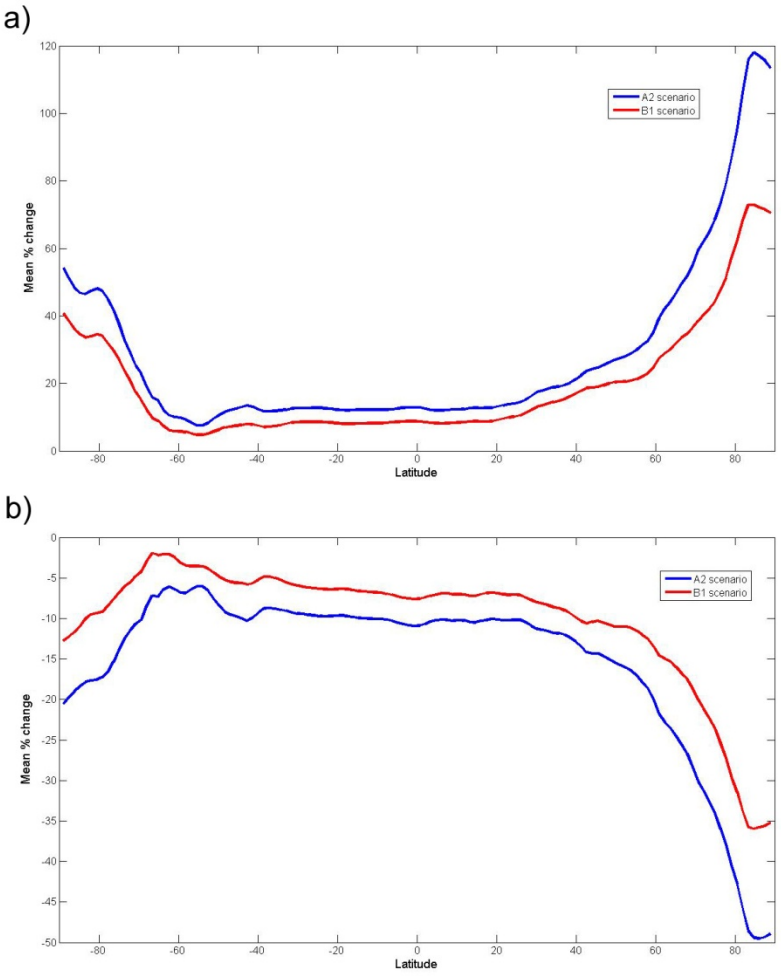


Figure 3. Longitude-averaged percent changes of a) Boltzmann factor and b) inverse Boltzmann factor under both scenarios.



Chapter 3

Interactive effects of temperature and food availability on growth, maturation, and other life history traits in sheepshead minnows, *Cyprinodon variegatus*

Abstract

Environments change. Despite most plasticity studies varying only one environmental variable, far more common is for populations to experience multiple changes at once. For ectotherms, perhaps the two most significant environmental variables are temperature and diet. I studied the response of growth, age and size at maturation, gonadosomatic and hepatosomatic indices, and morphometric shape of the sheepshead minnow, *Cyprinodon variegatus*, to different combinations of temperature (24, 29, 34°C) and food availability (60, 80, or 100% of maximum consumption). These variables appear to affect the traits studied in different ways. The thermal response of juvenile growth rate was mediated by food availability (i.e., there was a statistical interaction between the two), while age at maturation is independently affected by temperature and food. Size at maturation was, surprisingly, very close across all the treatments. Finally, changes in shape were predominantly a result of temperature. As this study illustrates, accurate predictions of plastic responses of populations to changes in the environment will be obtained only through empirical examination of reaction norms under interacting variables. In addition, that temperature and food availability can produce marked changes in the timing of maturation, independent of growth, has important consequences for the probabilistic maturation reaction norm.

Introduction

Environments change. Despite an early disregard of such a fact (Sultan 1992, Sarkar 2004), evolutionary ecology has now embraced it. Many are the current studies on phenotypic plasticity, the expression of different phenotypes under an environmental gradient (DeWitt and Scheiner 2004). However, most of these concentrate on phenotypic differences under various levels of *one* environmental variable (Pigliucci 2001). Though convenient, erroneous interpretations may arise from these univariate reaction norms, especially if they are to be used to predict how populations will react to environmental changes (Kingsolver et al. 2006).

For ectotherms, perhaps the two most significant environmental variables are temperature and diet. Temperature has a strong and inescapable impact on the rate of functions at all levels of organization (Hochachka and Somero 2002, Angilletta 2009). Diet, in the form of food availability, also has clear implications for individuals (Nylin and Gotthard 1998).

Studies of fishes that analyzed thermal reaction norms have repeatedly shown that food mediates the response to temperature (growth-specific examples include Brett et al. 1969, Wurtsbaugh and Cech 1983, Fonds et al. 1992, Reznick 1993, Hutchings et al. 2007). Maturation decisions also depend on temperature and food availability (i.e., how an organism arrives at its current size matters). It may be expected that a decrease in temperature and a decrease in food availability will have the same effect on age and size at maturity, through their effects on growth rate. Empirical studies, however, indicate that a decrease in temperature results in delayed maturation at a *larger* size, while a decrease in food causes later maturation at *smaller* size

(Atkinson 1994, Berrigan and Charnov 1994, Thorpe 2004). Berrigan and Charnov (1994) suggested that the explanation to this "puzzle" could be found in how temperature and food availability affect juvenile growth rate and asymptotic size. They observed that food availability does not alter asymptotic size, which leads to a negatively-sloped reaction norm of age and size at maturity, whereas temperature does result in changes of asymptotic size across individuals, creating a positively-sloped reaction norm, and they presented a simple optimality model that supported this view. Perrin (1995) later pointed out that this hypothesis had already been proposed by von Bertalanffy. Ernsting (1995) and Sevenster (1995) objected to this explanation, claiming that some assumptions in the Berrigan and Charnov's model were unrealistic (e.g., food could affect asymptotic size, choice of parameters determines conclusions), and no consensus explanation has emerged. A careful empirical examination of the effects of temperature and food availability on juvenile growth rate, age and size at maturation, and asymptotic size within one population could add significant insight to this question, which has been tackled primarily via meta-analyses and modeling (Atkinson and Sibly 1996).

When to mature is one of the most important life history determinations (Roff 1992, Stearns 1992). Age and size at maturity are closely tied to fitness, and trade-offs between early and late maturation shape the life histories of many populations (Kozlowski 1992). Stearns (1983) graphically summarized rules that individuals could follow depending on growth conditions (Fig. 1). Individuals could "mature at a fixed size", which would lead to maturation of organisms along a horizontal line, they could "mature at a fixed age", depicted by the vertical line in Fig. 1, or they could follow intermediate rules, represented by curves m1, m2, and m3. Clearly, and although partly under genetic control (Friars and Smith 2001), both age and size at

maturity are highly sensitive to environmental conditions (see examples in Stearns and Koella 1986).

The interaction of food and temperature in maturation decisions could also illuminate the current debate in fishery science over how to disentangle plasticity and evolution. Harvested fish populations are in a deplorable state (Rogers and Laffoley 2011, but see Hilborn and Hilborn 2012). Besides problems like overfishing (Jackson et al. 2001, Daskalov 2002) and climate change (IPCC 2007, FAO 2008), fish stocks are thought to be experiencing evolutionary changes brought about by selective fishing. Many theoretical (e.g., Law and Grey 1989, Gårdmark and Dieckmann 2006), experimental (e.g., Silliman 1975, Conover and Munch 2002), and field (e.g., Haugen 2000a, 2000b, Reznick and Ghalambor 2005, Edeline et al. 2007) studies have proposed that capturing the largest individuals (as most fisheries do; Law 2007) is causing populations to evolve smaller sizes-at-age or younger ages-at-maturity.

However, phenotypically plastic responses of fishes to exploitation occur in the same direction as evolutionary changes expected from life history theory. For instance, fishing causes a reduction in population density, which in turn creates higher food availability and a concomitant speeding of growth and earlier maturation. Plastic changes thus parallel the adaptive changes expected from life history theory. Disentangling phenotypically plastic responses from evolutionary ones is an important first step in devising management and recovery plans. Recently, the probabilistic maturation reaction norm (PMRN) has been proposed as a tool to do just that, by accounting for phenotypic plasticity in body size at maturation (Heino et al. 2002, Dieckmann and Heino 2007, Heino and Dieckmann 2008). In this approach, the environment is

integrated in an individual's growth trajectory ("to characterize the macroenvironment in terms of the growth trajectory it engenders"; Dieckmann and Heino 2007). Essentially, then, it is assumed that most environmental variation is captured in the growth trajectory, and that maturation decisions are independent of environment beyond that.

Despite its widespread use (reviewed in Heino and Dieckmann 2008), this foundational assumption of the PMRN approach, that the manner in which a fish attains a certain size is irrelevant in determining maturation, may not be well supported. Temperature (Kuparinen et al. 2011), food quantity (Uusi-Heikkilä et al. 2011), growth history (Morita and Fukuwaka 2006), and pollutants (Kraak 2007) could influence age and size at maturation independently of their effects on growth. Thus, studies that evaluate the relative contribution of growth rate vs. other important determinants of maturation could help resolve whether that is an untenable assumption.

Here, I evaluate empirically how maturation and other life history characters (growth, gonadosomatic index, hepatosomatic index, and body shape) are affected by variation in food availability and temperature. I used a factorial experimental design with 3 temperature and 3 food availability treatments and followed sheepshead minnows, *Cyprinodon variegatus*, individually over ~6 months.

Methods

The fish used in the experiment originate from the Gulf Islands National Seashore, Florida. I collected wild adults in August 2009, bred them in the rearing facility at Stony Brook University, and maintained the F1 generation at ~22°C, 20 psu, and *ad libitum* feeding. To begin the experiment, I acclimated (over several hours) size-matched adults to one of three temperatures: 24°C, 29°C, and 34°C. After 7 days, I introduced spawning mats and collected the eggs that would become the experimental fish. I maintained the larvae fed brine shrimp nauplii twice a day until the food treatment allocation day. Due to low hatching success in the 24°C eggs, I re-spawned parents to create a second batch of experimental fish, which also allowed me to begin measuring length at comparable ages.

I started the experiment with 23-day old larvae (29°C and 34°C) and 39- and 25-day old larvae (first and second batch of 24°C). I randomly separated fish from each of the temperatures to individual containers and assigned each a food availability treatment: 60, 80, or 100% of maximum consumption (see Table 1 for sample sizes at the beginning of the experiment). Containers were constructed with cylindrical 140-mm diameter dishes, 2-mm mesh walls, and a subdivision along the center of the dish (each container housed 2 individuals). Daily care followed standard protocols (Cripe et al. 2009).

I conducted two separate maximum consumption trials (n=12 and n=13) prior to the experiment to derive a relationship between length and maximum consumption. During the trial day, each fish was fed TetraMin flake food at small increments (0.02 g) until satiation 4 different

times a day, and then summed all the food consumed over one day. The length range of the fish tested was 11.22-40.31 mm (mean=26.83, SD=9.71). Both trials produced very similar relationships (ANCOVA interaction term test; p=0.881), so I combined the data from the two trials and estimated the relationship as MaxFood = 0.0006*TotalLength+0.0076 (Fig. 2). I fed fish flake food 4 times a day throughout the experiment.

Approximately every 7 days, I digitally photographed all fish with a 10.1-megapixel EOS 40D Canon camera and a macro lens mounted on a tripod (calibration photos were taken at the beginning of each session and the tripod never moved within sessions). The following day, I measured the fish using ImagePro Plus (Media Cybernetics, Bethesda, MD), determined 4- and 3-day food consumptions based on the formula above, and weighed the corresponding food allocation for each fish. Calculating and weighing 4- and 3-day food allocations separately allowed me to better control the amount given at each of the 4 daily feedings.

After day 45 post-hatch, I started conducting daily maturation checks. For males I checked for signs of secondary sexual coloration (male sheepshead minnows turn iridescent blue on their dorsal side and orange on their ventral side). Females, on the other hand, are more cryptic after becoming mature. Thus, I visually inspected females for signs of enlarged gonad cavity daily. If I suspected a female had matured, I gently compressed her abdomen and only counted her as mature if eggs were released. I also checked for eggs on several occasions when I did not suspect females had matured. All these checks resulted in no eggs.

At the conclusion of the experiment, I sacrificed each individual by tricaine methanesulfonate (MS-222) immersion. Shortly after death, I photographed the fish for geometric morphometric analysis. All 235 fish that survived to the end of the experiment were laterally photographed under identical lighting and exposure conditions with the same digital camera used for length measurements. After photographing, I weighed the fish and then removed and weighed both gonad and liver to calculate gonadosomatic and hepatosomatic indices (GSI and HSI, respectively). GSI is a measure of energy devoted to reproduction (calculated as gonad mass/body mass) while HSI is typically used as a condition index (liver mass/body mass) (Helfman et al. 1997). I was able to obtain GSI estimates for 224 individuals and HSI ones for 235.

Statistical analyses

After inspection of the growth trajectories, I noticed 6 instances of measurement error (clear dips in size along curves). I re-measured these 6 photographs, all of which came from the 24°C treatment on the 8th measurement day, and used the new values in all analyses. To summarize an individual's growth trajectory, I performed a principal component analysis on the collection of growth trajectories from the entire experiment and used the two dominant principal components. I chose to use principal components over von Bertalanffy parameters because of the noticeable differences in growth trajectory before and after maturation—differences that von Bertalanffy curves would not have represented well.

I statistically analyzed the relationship between age at maturation and all variables via a generalized linear mixed model (GLMM). The statistical model consisted of age at maturation as the response variable; temperature, food, sex, and all possible two- and three-way interactions as predictors; and the two most dominant principal components (as indices of growth) as the random effects. I used a negative binomial distribution for the response variable (with a log link function) after visual exploration of the data. Because of its robustness (Bolker et al. 2009), I chose the Laplace method to approximate the likelihood. Similarly, the gonadosomatic and hepatosomatic indices were analyzed via GLMMs (with arcsine-transformed data and a normal distribution and identity link).

For the geometric morphometric analysis, I first digitized 12 landmarks for each individual (Fig. 3) using tpsDIG2 (Rohlf 2004). These landmarks represent standard characters used to compare shape variation in fishes (Cadrin 2000). Then, I performed a full Procrustes fit to the data to obtain shape variables independent of size, translation, and rotation (Zelditch et al. 2004). This and all subsequent morphometrics analyses were performed in MorphoJ (Klingenberg 2011). Outlier analysis revealed that 2 fish strongly deviated from the mean shape, and were removed from all successive analysis. I analyzed the remaining 233 samples via canonical variate analysis with food and temperature treatments as the grouping variables. In addition, I computed pairwise comparisons among all treatments based on Mahalanobis distances, a measure of the distance between centroids on a scale adjusted to the within-group variance in the direction of the group difference (Strauss 2010).

Results

Of the 246 fish that started the experiment, 236 (96%) survived to the last day of the experiment (Table 1). Growth trajectories were generally more variable at lower temperatures, with coefficients of variation of final length being approximately twice as large for fish at 24°C compared to those at 34°C (Table 2; Fig. 4). Growth was fastest at 29°C, regardless of food treatment, and at high food (100% of maximum consumption), regardless of temperature (Fig. 5).

Juvenile growth rate, defined as growth between days 23-59 post-hatch for the 29 and 34°C treatments and 25-60 for the 24°C treatments (a period during which growth was linear for all fish; Fig. 4), was sensitive to temperature, food availability, and their interaction (Fig. 6, Table 3). In addition, growth before and after maturation (comparing slopes of linear regressions before and after maturation) was uncorrelated (Fig. 7). However, 24°C fish appear to have the capacity for faster growth after maturation, compared to individuals at 29 and 34°C (Fig. 7 inset).

Age at maturation was independently affected by temperature and food availability (Figs. 8-9, Table 4). There was, however, no interaction between the two variables (Table 4). Fish matured earliest in the 29°C-high food (mean=68.3 d, SD=10.0) and latest in the 24°C-low food treatments (mean=89.4 d, SD=23.0; Fig. 9). Age at maturation, like juvenile growth rate, was much more variable at lower temperatures (Fig. 8).

Despite the variability observed (Fig. 8), sheepshead minnows in all treatments matured at very similar sizes (mean=31.5 mm, SD=2.9), this being especially clear in the 24°C treatments (Fig. 9). Multiple comparison testing suggests that only 34-mid food and 34-low food are statistically different than the rest in size at maturity. To further explore the relative contribution of age vs. size in the maturation decision, I plotted juvenile growth rate (calculated linearly between the last measurement before maturation and the length at first measurement) against the slope of age vs. size at maturation for each of the 9 treatments (Fig. 10). The ratio of the slope to growth rate is less than 1 in all cases, suggesting that achieving a specific size is more important in this species. This rule, however, becomes less strict among slow-growing fish, as the ratios were highest in the low food and low temperature treatments.

The gonadosomatic index (GSI) only showed differences between sexes, as females tended to allocate more to reproduction (Fig. 11, Table 4). The hepatosomatic index (HSI) also differed between males and females, the latter being in relatively better condition (Fig. 12, Table 4). HSI was also statistically different among temperature treatments, but not, somewhat surprisingly, to food availability (Fig. 12, Table 4).

Fish shape was closely linked to temperature (MANOVA $p<0.001$, Fig. 13, Table 5). Food environment, on the other hand, was of little relevance in shaping individuals (MANOVA $p=0.246$, Fig. 13, Table 5). The first canonical variate axis, which explains 62.6% of the variation, appears to separate fish from each of the three temperatures evenly, with the 24°C fish on the "stockier" side (particularly on the caudal peduncle). The second canonical variate axis,

explaining 17.1% of variation, divides the 29°C from the 24 and 34°C, which appear to be similar in this dimension (Fig. 13).

Discussion

Organisms live in complex worlds, facing combinations of various environmental factors. Here, I studied the response of several life history traits of the sheepshead minnow to different combinations of temperature (24, 29, 34°C) and food (60, 80, or 100% of maximum consumption). These variables appear to affect the traits studied in different ways. The thermal response of juvenile growth rate, for example, was mediated by food availability (i.e., there was a statistical interaction between the two). Interactions between the effects of food and temperature are common in ectotherms (Petersen et al. 2000, Giebelhausen and Lampert 2001, Kingsolver et al. 2006, Stillwell et al. 2007).

Age at maturation was influenced by temperature and food, but not their interaction. On the other hand, size at maturation in sheepshead minnows grown at very different thermal and diet regimes appears to occur within a remarkably small size window, regardless of when that size is achieved. This pattern is in stark contrast with those seen in other fish species. Size at maturation tends to decrease with increasing temperature (e.g., Japanese flounder, Seikai et al. 1986; sailfin molly, Trexler et al. 1990; Eastern mosquitofish, Meffe 1992; medaka, Dhillon and Fox 2004) and with decreasing food availability (reviewed in Reznick 1993, Thorpe 2004). The mature-at-a-fixed-size rule implies that, for slow-growing fish, the mortality risk is highly exacerbated (slow growers need considerably more time to mature, in this experiment ~30 days)

and are thus exposed to mortality for longer at a vulnerable period; Stearns 1992). Why would sheepshead minnows mature when a specific size (~30-35 mm) is achieved? Perhaps it is related to a physiological constraint, or an ontogenetic change in diet or habitat use, as is the case in the onset of metamorphosis in starry flounder (Policansky 1983). Another potential reason is that, at least for males, a small size at maturity allows for sneaking breeding behavior, which has been observed in sheepshead minnows (Leiser and Itzkowitz 2004), thus maturing as soon as physiologically possible may be beneficial.

In addition to growth and maturation, changes in fish shape due to temperature were apparent, as evidenced by geometric morphometric analysis. In general, the most pronounced feature was the depth of the body, as fish grown at higher temperatures tended to be deeper. This finding appears to be common in fishes (e.g., Atlantic cod, Marcil et al. 2006; European sea bass, Georgakopoulou et al. 2007; zebrafish, Georga and Koumoundouros 2010, Sfakianakis et al. 2011). Food availability had little impact on determining shape, even though it was found to be important in other species (e.g., Chinook salmon and rainbow trout, Currens et al. 1989; pearl cichlid and redhump eartheater, Wimberger 1992; Atlantic cod, Marcil et al. 2006). Colder temperatures may lead to shallower, more slender bodies (which are less energetically costly during swimming; Hunt von Herbing 2002) in response to lowered physiological rates or it could be a response to different habitat use at different temperatures (deeper bodies are associated with hovering and manoeuvrability; Peres-Neto and Magnan 2004). Further work is needed to explain the causal link between temperature and body shape in sheepshead minnows.

Based on a generalized linear mixed model analysis that included growth as a random effect, I found that age at maturation depends on temperature and food availability independent of their effects on growth. This has important consequences for the probabilistic maturation reaction norm (Heino et al. 2002). The PMRN technique was designed to disentangle plastic from evolutionary changes in age at maturation by assuming that plasticity in maturation could be accounted for by plasticity in growth. As shown here, and in recent studies on white-spotted charr (Morita et al. 2009), ninespined sticklebacks (Kuparinen et al. 2011), and zebrafish (Uusi-Heikkilä et al. 2011), this assumption is untenable. It is thus necessary to incorporate the effects of plasticity on maturation in PMRN models.

The interaction of multiple environmental variables to determine specific trait values is undoubtedly complex. However, accurate predictions of plastic responses of populations to changes in the environment will be obtained only through empirical examination of reaction norms under interacting variables. In particular, both temperature and food available to individuals in coastal and marine food webs are likely to change (Harley et al. 2006, Wiklund et al. 2009). This broader ecological view is required to successfully predict population responses to climate change (Angilletta 2009).

Temperature and conspecific density (typically correlated with food availability) were found to interactively affect Chinook salmon body size across a large spatial and temporal scale (Crozier et al. 2010). Predicting the effects of temperature increases on body size based solely on thermal reaction norms would have resulted in poor forecasts. Further, understanding interactive reaction norms across populations (here I presented results for one population) could shed light

on the evolution and constraints of phenotypic plasticity (David et al. 2004, Stillwell et al. 2007), particularly in this study system. Sheepshead minnow growth appears to be phenotypically plastic with respect to temperature along the U.S. east coast (Berry 1987), while mummichog, *Fundulus heteroclitus*, growth exhibits local adaptation (Schultz et al. 1996) despite their physiological, ecological, and geographic-structural similarities (Collette and Klein-MacPhee 2002, Nordlie 2006, Haney et al. 2007). A comparative study of plasticity in these two species could illuminate conditions favoring the evolution of phenotypic plasticity vs. those leading to local adaptation, an area that has enjoyed much theoretical but little empirical attention.

Tables

Table 1. Sample sizes of fish surviving to the end of the experiment and those at the start (in parenthesis).

Temperature	Food ration		
	Low	Medium	High
24°C	28 (28)	27 (27)	26 (27)
29°C	27 (28)	23 (27)	27 (27)
34°C	26 (28)	26 (27)	26 (27)

Table 2. Coefficients of variation at final length.

Temperature	Food ration		
	Low	Medium	High
24°C	0.066	0.080	0.085
29°C	0.067	0.062	0.062
34°C	0.041	0.053	0.043

Table 3. Three-way ANOVA for the effects of temperature, food availability, sex, and their interactions on juvenile growth rate.

Trait	Source	Sum sq.	d.f.	Mean sq.	F	p
Growth rate	Temp	0.116	2	0.058	20.94	**<0.001**
	Food	0.293	2	0.147	53.05	**<0.001**
	Sex	0.006	1	0.006	2.18	0.141
	Temp*Food	0.032	4	0.008	2.92	**0.022**
	Temp*Sex	0.002	2	0.001	0.37	0.688
	Food*Sex	0.001	2	0.001	0.21	0.814
	Temp*Food*Sex	0.022	4	0.006	2	0.096
	Error	0.561	203	0.003		
	Total	1.057	220			

Table 4. Generalized linear mixed model results for age at maturation, GSI, and HSI.

Trait	Variable	d.f.	Den. d.f.*	F	P
Age at mat.	Temp	2	214	21.88	**<0.001**
	Food	2	214	8.10	**<0.001**
	Sex	1	214	0.72	0.397
	Temp*Food	4	214	0.71	0.588
	Temp*Sex	2	214	2.72	0.068
	Food*Sex	2	214	0.25	0.776
	Temp*Food*Sex	4	214	0.38	0.822
GSI	Temp	2	91	0.63	0.534
	Food	2	91	0.59	0.554
	Sex	1	91	176.65	**<0.001**
	Temp*Food	4	91	0.70	0.596
	Temp*Sex	2	91	2.82	0.065
	Food*Sex	2	91	0.27	0.765
	Temp*Food*Sex	4	91	0.30	0.876
HSI	Temp	2	214	3.91	**0.021**
	Food	2	214	0.91	0.404
	Sex	1	214	54.21	**<0.001**
	Temp*Food	4	214	0.92	0.456
	Temp*Sex	2	214	1.33	0.267
	Food*Sex	2	214	1.29	0.277
	Temp*Food*Sex	4	214	0.89	0.470

Table 5. p-values from permutation tests (10,000 permutation rounds) for Mahalanobis distances among groups.

	24-H	24-M	24-L	29-H	29-M	29-L	34-H	34-M
24-M	0.230							
24-L	0.981	0.534						
29-H	**<0.001**	**<0.001**	**<0.001**					
29-M	**<0.001**	**<0.001**	**<0.001**	**0.020**				
29-L	**<0.001**	**<0.001**	**<0.001**	0.347	0.224			
34-H	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**		
34-M	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	0.076	
34-L	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**

Figures

Figure 1. Stearns' (1983) graphical representation of maturation decision rules.

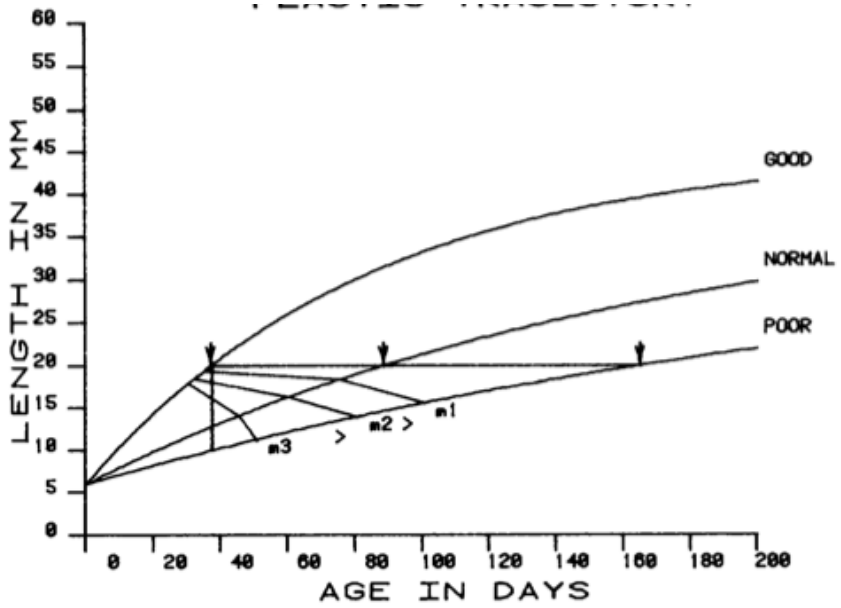


Figure 2. Maximum consumption trials.

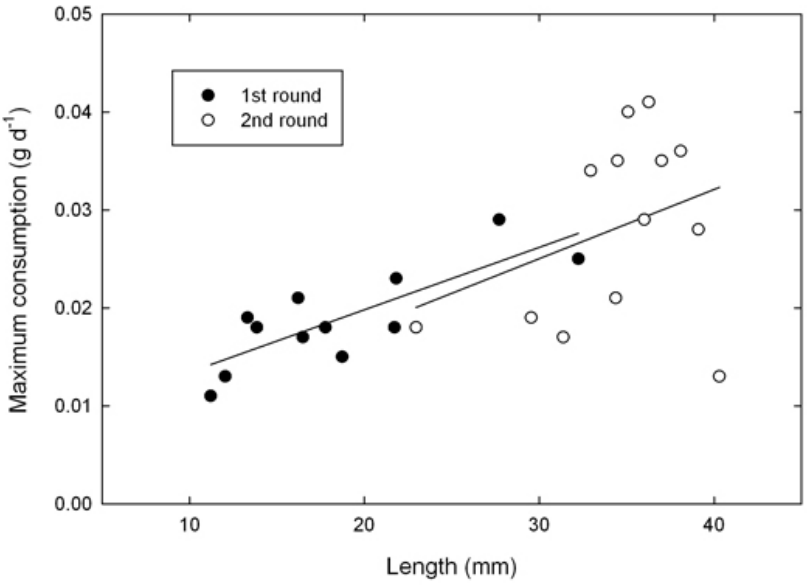


Figure 3. Landmarks (n=12) used in geometric morphometric analysis.

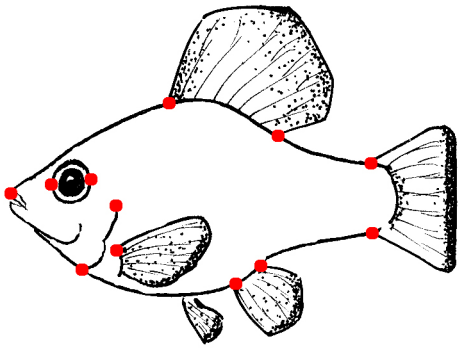


Figure 4. Individual growth trajectories for all 9 treatments. Red circles indicate where, along the curve, each fish matured.

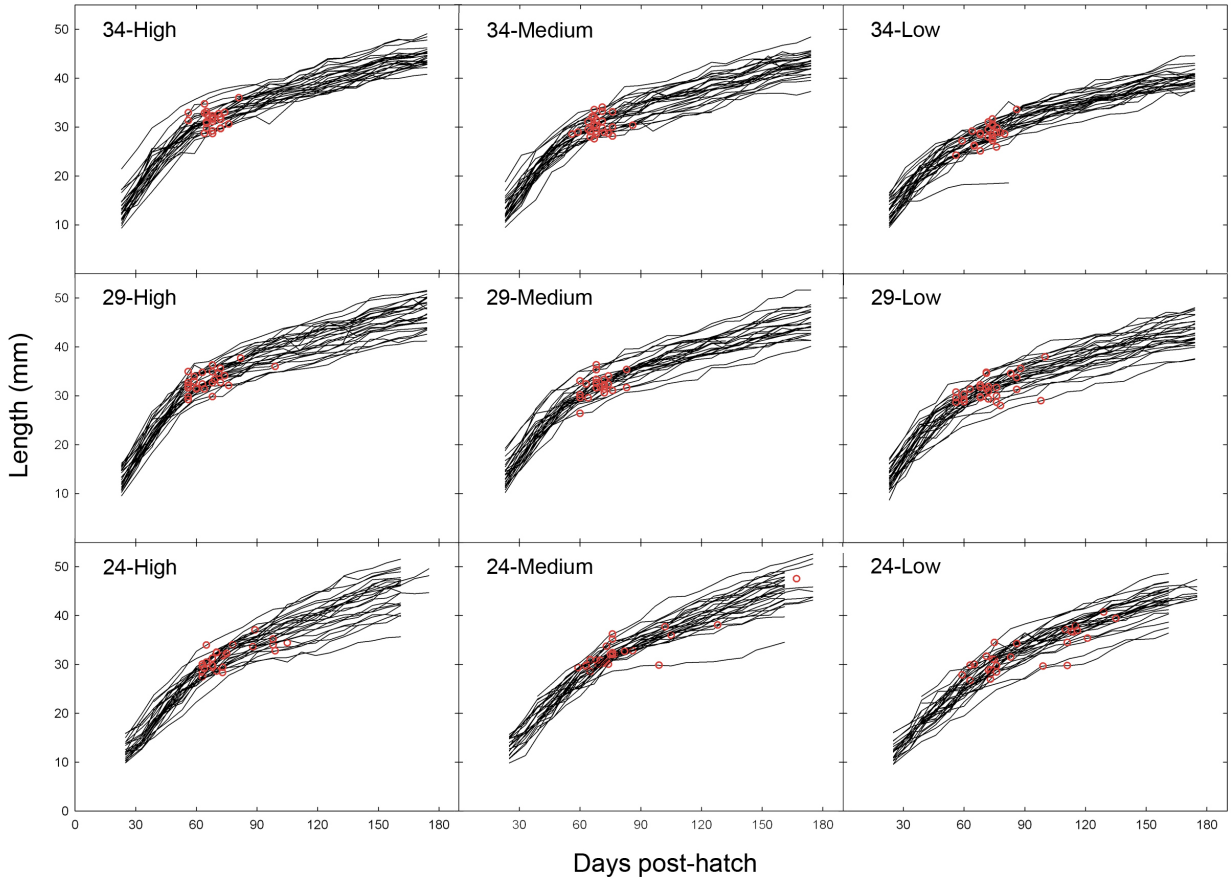


Figure 5. Mean (±SE) growth trajectories.

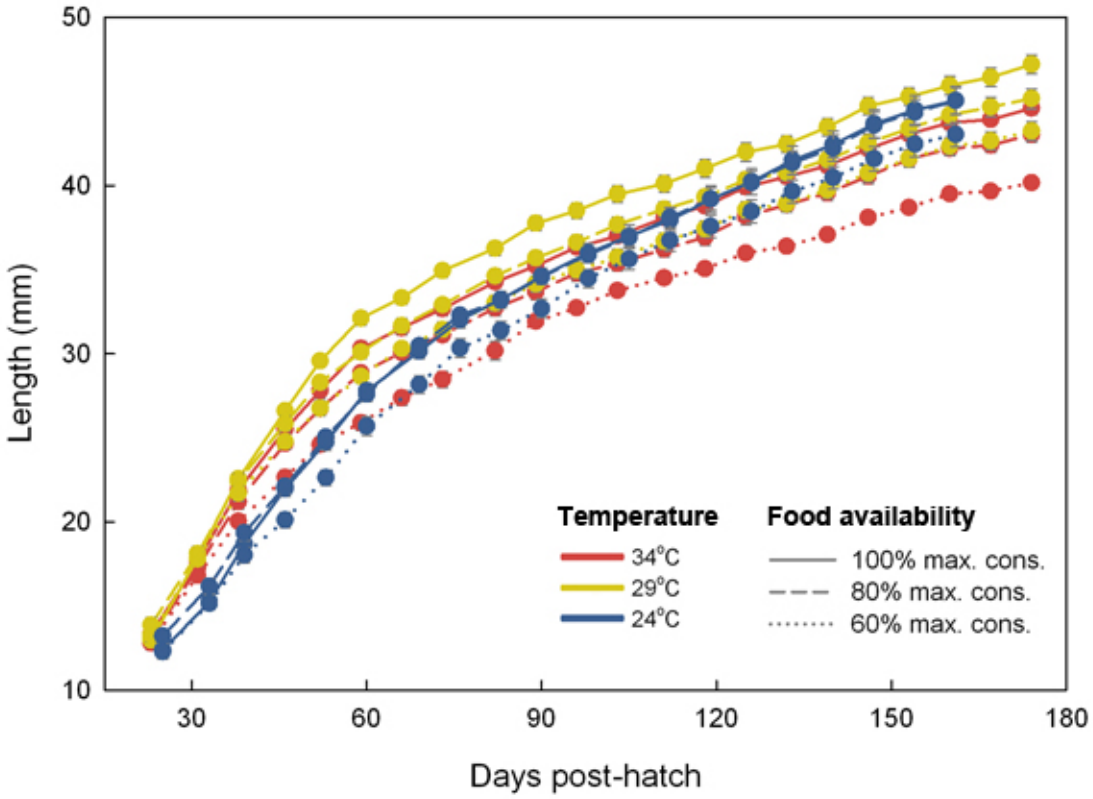


Figure 6. Reaction norms for juvenile growth rate (±1 SE, measured from days 23-59 for the 29 and 34°C treatments and 25-60 for the 24°C treatments).

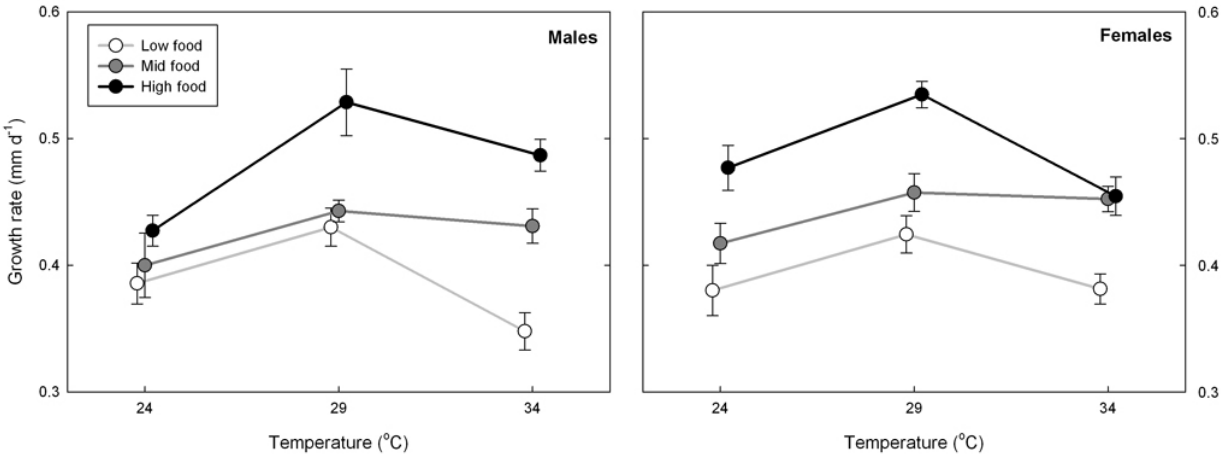


Figure 7. Linear regression slopes for data before and after maturation for all fish in the experiment. All slopes are below the 1:1 line. Inset: Slopes coded by treatment. Color indicates treatment (red=34°C, yellow=29°C, blue=24°C). Filling represents food treatment (full=100% of maximum consumption, half-filled=80%, no fill=60%).

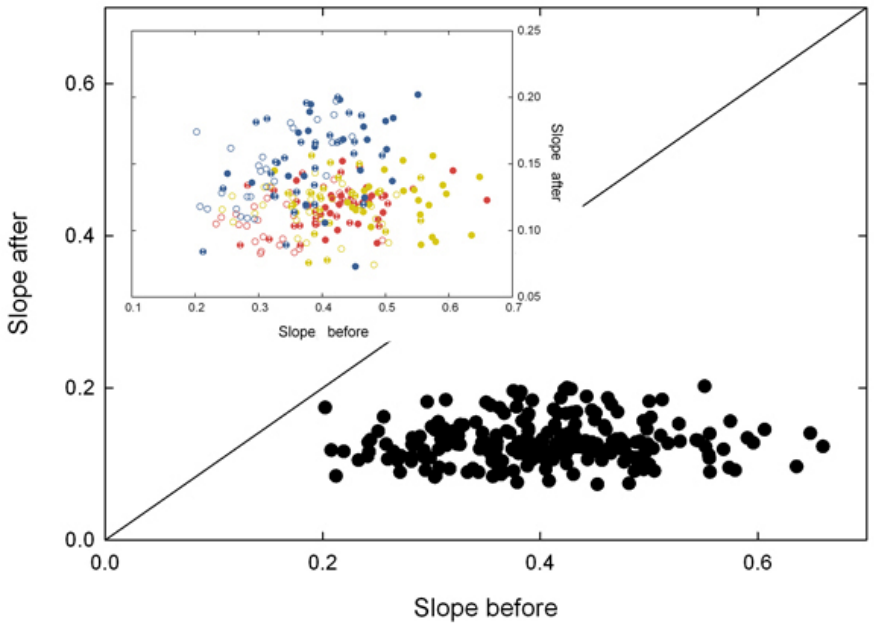


Figure 8. Age and length at maturation for all individuals in the study.

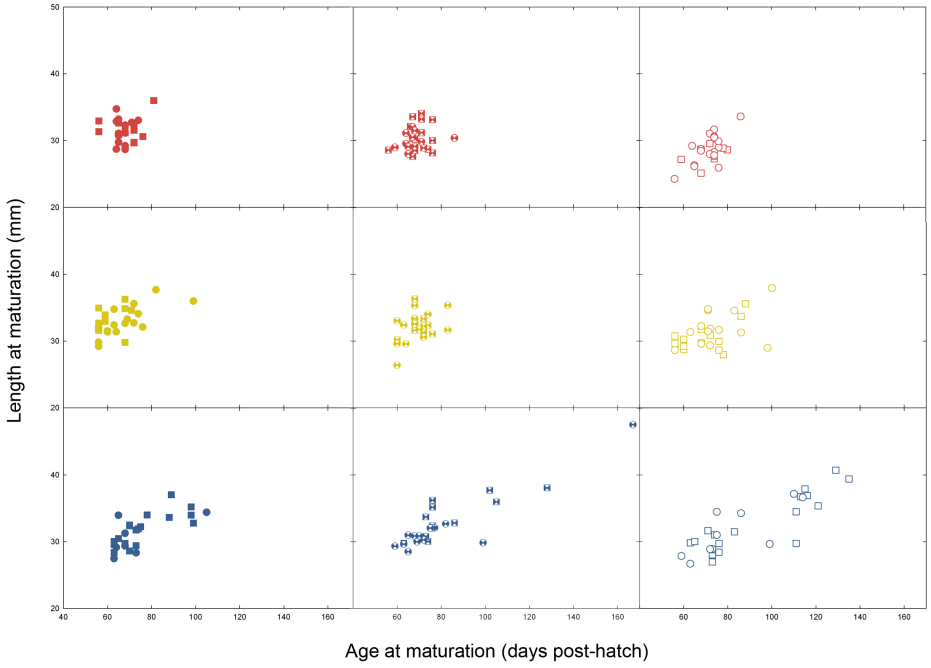


Figure 9. Mean (±SE) age and size at maturation. Color indicates treatment (red=34°C, yellow=29°C, blue=24°C). Filling represents food treatment (full=100% of maximum consumption, half-filled=80%, no fill=60%). Shape of symbol specifies sex (square=male, circle=female).

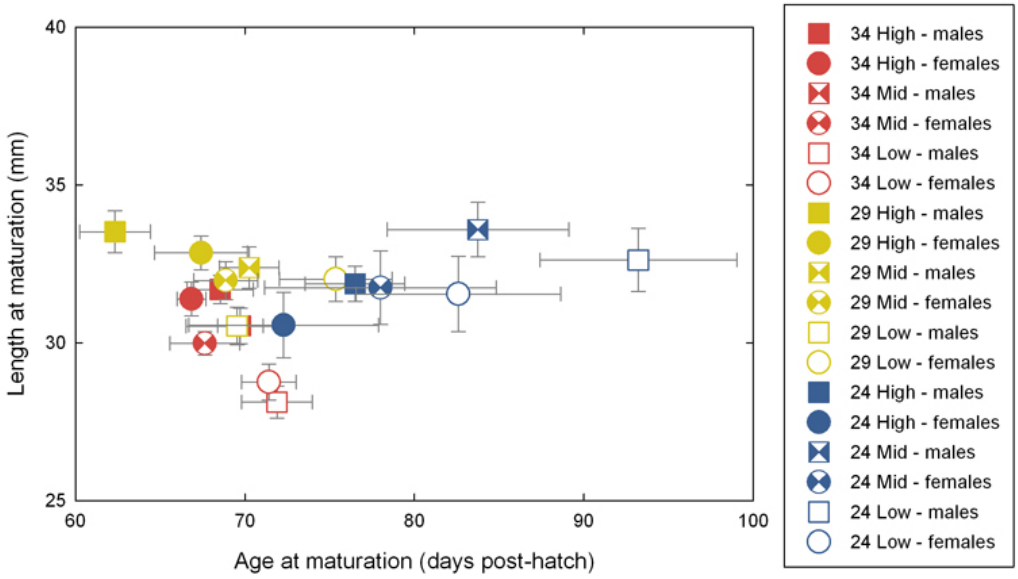


Figure 10. Juvenile growth rate vs. the slope of age and size at maturation for each of the 9 treatments. Color indicates treatment (red=34°C, yellow=29°C, blue=24°C). Filling represents food treatment (full=100% of maximum consumption, half-filled=80%, no fill=60%).

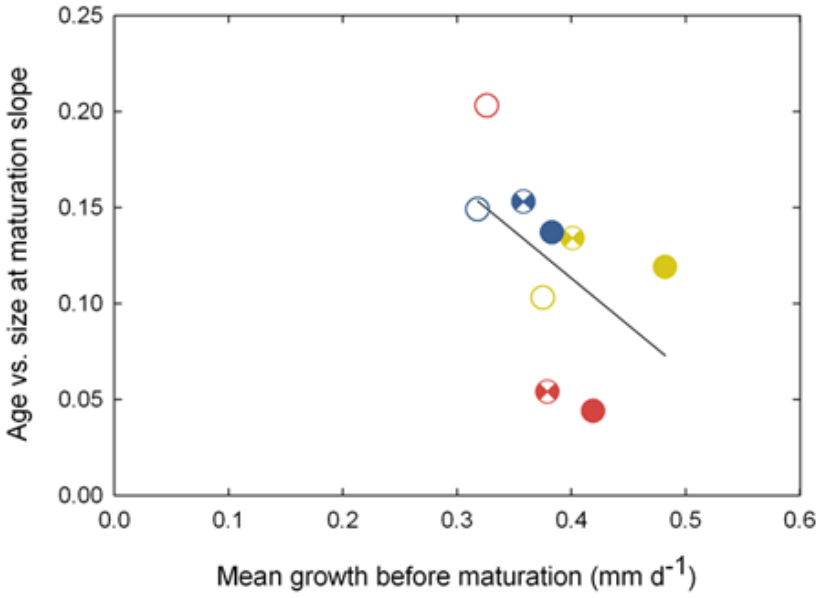


Figure 11. Reaction norms for GSI (±1 SE).

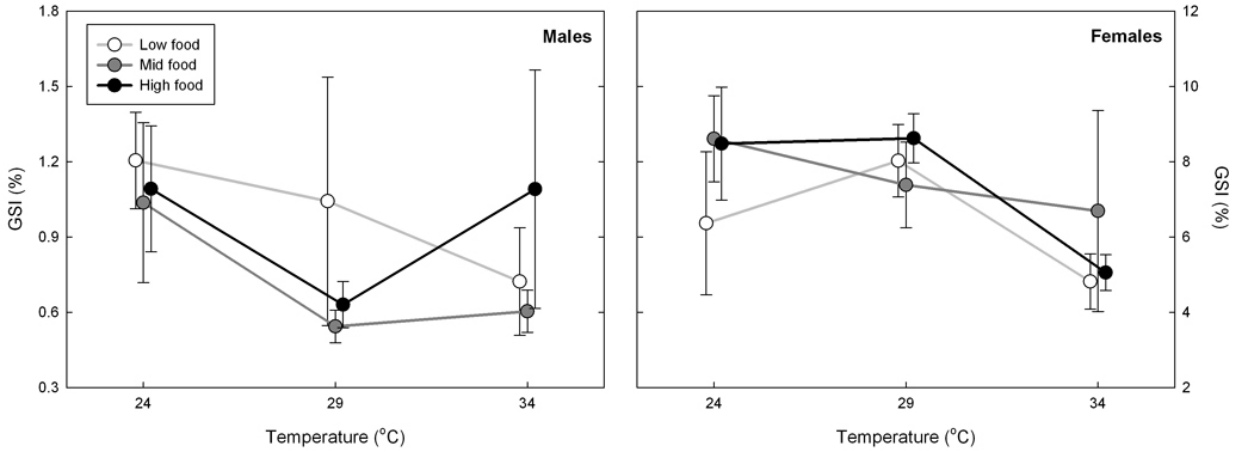


Figure 12. Reaction norms for HSI (±1 SE).

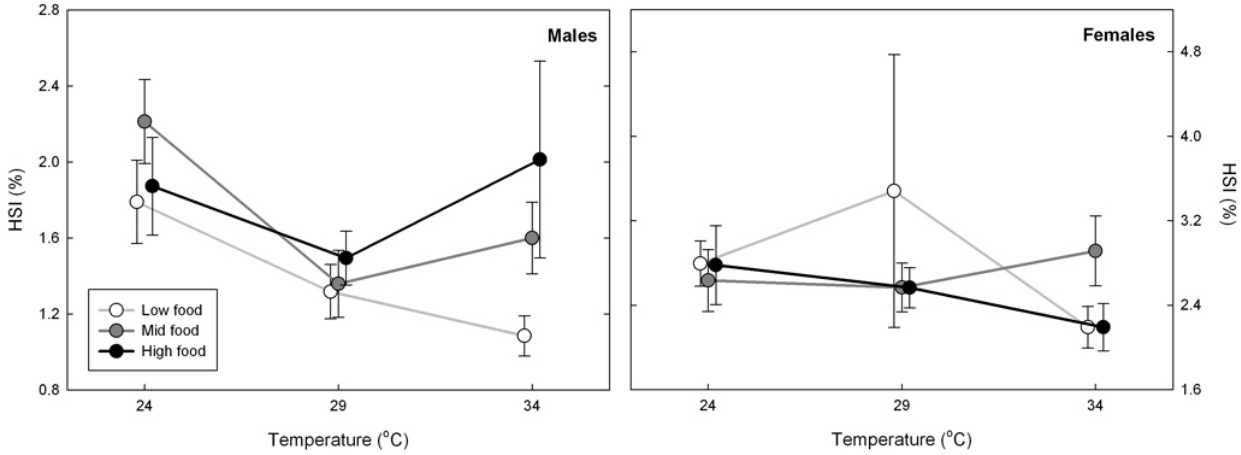
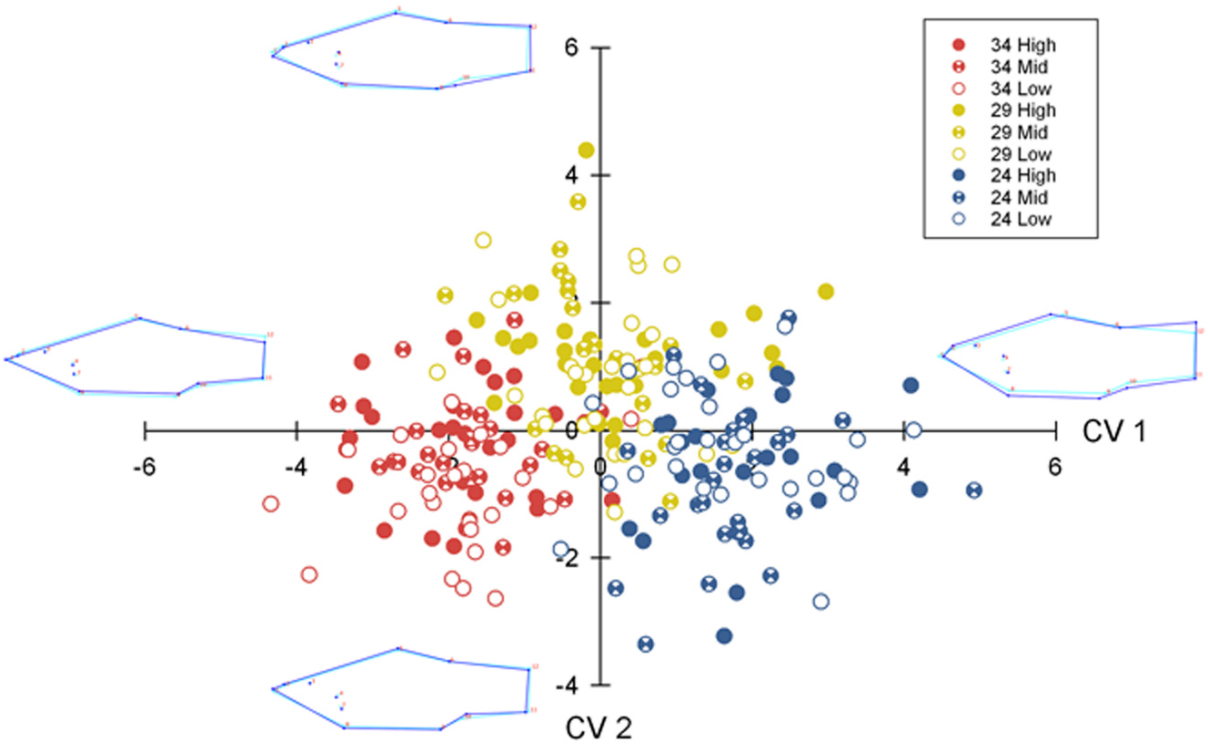


Figure 13. Canonical variate analysis based on the 12 landmarks depicted in Fig. 2. Deformations, superimposed to the mean shape, correspond to each of the extreme values in both axes.



Chapter 4

Thermal legacies: transgenerational effects of temperature on growth in a vertebrate

Abstract

Transgenerational plasticity, a generalization of more widely studied maternal effects, occurs whenever environmental cues experienced by either parent prior to fertilization result in a modification of offspring reaction norms. Such effects have been observed in many traits across many species. Despite enormous potential importance—particularly in an era of rapid climate change—transgenerational plasticity in thermal growth physiology has never been demonstrated for vertebrates. Here, I provide the first evidence for thermal transgenerational plasticity in a vertebrate: given sufficient time, sheepshead minnows, *Cyprinodon variegatus*, adaptively program their offspring for maximal growth at the present temperature. The change in growth over a single generation (~30%) exceeds the single-generation rate of adaptive evolution by an order of magnitude. If widespread, transgenerational effects on thermal performance may have important implications for physiology, ecology, and contemporary evolution, and may significantly alter the extinction risk posed by changing climate.

Introduction

Significant changes in climate are expected in the near future (IPCC 2007). Assuming that species' climate envelopes are maintained, this climate shift is predicted to cause extinctions in a wide range of taxa (Thomas et al. 2004). Because of temperature's dominant role in shaping metabolism (Hochachka and Somero 2002), lifespan (Munch and Salinas 2009) and population dynamics (Savage et al. 2004), particularly for ectotherms, a mechanistic understanding of responses to changing temperatures is needed (Chown et al. 2010). To date, attempts to address this issue have focused exclusively on evolutionary change and phenotypic plasticity (e.g., Gienapp et al. 2008). Here, I highlight a third potential mechanism for rapid responses to climate shifts: transgenerational plasticity.

Transgenerational plasticity (TGP) occurs when the environment experienced by the parents prior to fertilization directly translates, without DNA sequence alteration, into significant changes in the shape of offspring reaction norms (Fox and Mousseau 1998), resulting in a significant interaction between parental and offspring environment effects. In instances where the mother's environment drives the response, TGP may be thought of as a type of maternal effect. However, since paternally inherited environmental effects also exist (e.g., Etterson and Galloway 2002) I adopt the current vernacular of 'trangenerational plasticity' to denote the role of the parental environment in shaping the reaction norm of the offspring.

Evidence for non-genetic transgenerational inheritance spans the tree of life, from plants and fruit flies to humans (Jablonka and Raz 2009). Through TGP, parents may provide offspring

with increased tolerance of environmental perturbations such as contaminants (Marshall 2008), food shortages (Bashey 2006), desiccation (Yoder et al. 2006), and shading (Galloway and Etterson 2007).

Transgenerational plasticity may provide an important and understudied mechanism for coping with rapid environmental variation, including climate change (Rando and Verstrepen 2007). For instance, TGP in desiccation tolerance in a tick (*Dermacentor variabilis*; Yoder et al. 2006) or drought tolerance in a weed (*Polygonum persicaria*; Sultan et al. 2009) may facilitate acclimation to shifting patterns of precipitation. For many ectotherms, particularly those in aquatic systems, the more relevant climate driver will be temperature (Chown et al. 2010). Yet, despite the fact that variation in temperature is important in all aspects of ectotherm biology, very little is known about transgenerational effects on thermal physiology.

While TGP in lethal temperatures has been found in several species (Jablonka and Raz 2009), thermal TGP in growth, a key life history trait, has thus far only been detected in three species: two insects (Groeters and Dingle 1988; Steigenga and Fischer 2007) and a plant (Blödner et al. 2007; Whittle et al. 2009). Thus, knowing whether ectothermic vertebrates have the capacity for thermal TGP will prove important in forecasting species' responses to fluctuations in temperature (e.g., predicted increases in temperature). If present, thermal TGP could also play a role in a number of size-related phenomena (mortality, predation, movement, etc.) I provide, to my knowledge, the first evidence for thermal TGP in the life history of a vertebrate.

Methods

Sheepshead minnows (*Cyprinodon variegatus*) are a small fish common to nearshore marine and estuarine waters throughout the US east coast and the Caribbean. They mature in approximately 2-3 months, live up to 3 years, breed nearly continuously under laboratory conditions, and are an integral part of estuarine food webs (Raimondo et al. 2009). I collected several hundred adult sheepshead minnows from the Gulf Islands National Seashore (Gulf Breeze, Florida, USA) and brought them to the fish facility at Stony Brook University in August 2009. I bred the fish over multiple days, producing thousands of eggs which were then subsampled at random. I kept the progeny in aquaria at 21-22°C until the start of the experiment. These fish, that spent their entire lives in the laboratory at constant temperature and fed *ad libitum* four times a day, were the parental generation in my experiments.

To test for thermal TGP in growth, I randomly placed 24 size-matched females and 18 size-matched males into sea tables at each of the experimental temperatures: 24, 29, and 34°C (one sea table per temperature). These temperatures represent the range experienced by sheepshead minnows from Florida during a normal breeding season; The nearby NOAA station PCLF1 in Pensacola, FL routinely records water temperatures greater than 33°C in July and August and the fish experience still warmer temperatures because of their preference for very shallow waters (Raimondo et al. 2009). In fact, sheepshead minnows are among the most eurythermal of all fishes, tolerating temperatures between -1.5 and 41.6°C (Bennett and Beitinger 1997).

To control for early developmental effects and other potential artifacts, the experiment was repeated on two occasions with distinct sets of parents; the first immediately following a week of acclimation to test temperatures and the second after 30 days of exposure. No mortality occurred during the parental exposure period, and size remained similar in all treatments (ANOVA, females: $p=0.707$; males: $p=0.449$).

On parental exposure days 7 and 30, I introduced egg-collecting mats prior to spawning and replaced them every 2 h thereafter. Thus, fertilized eggs were exposed to parental temperatures for <2 hours prior to collection. Eggs from a common parental temperature were collected from the mats, pooled, and subdivided in thirds to be transferred to either 24, 29, or 34°C (see Fig. 1). More than 250 eggs were collected from each group of parents. Since each female produces roughly 10-15 eggs per clutch, at least 70% of the females participated in each spawning.

Upon collection, I photographed eggs to measure diameters (±0.045 mm). Juvenile densities were standardized post-hatch (6 fish per replicate) and growth in length was measured over 4-6 weeks by digital photography (±0.5 mm) with ImagePro Plus®. Each parental temperature-offspring temperature combination was triplicated for the 7-day exposure, and replicated 6 times for the 30-day exposure. Due to very low hatching success, the 34°C parent-34°C offspring treatment in the 7-day exposure consisted of 2 replicates, while the 34°C parent-24°C offspring treatment in the 30-day exposure consisted of only one replicate. The 7-day treatment continued until day 41 post hatch and the 30-day treatment continued until 51 days (fish in the 30-day treatment were also photographed on day 37). Growth was calculated as the

difference in length at the end of the experiment and length at day 16, divided by time (growth was linear over this period). Because fish within replicates are not independent, the mean for each replicate was used as the response variable in the statistical analysis. I analyzed the growth data for the 7-day and 30-day treatments using a two-way ANCOVA, treating parent and offspring temperatures as fixed effects and using egg diameter as a covariate to control for maternal provisioning effects (Janhunen et al. 2010; Kjærsgaard et al. 2010; Radmacher and Strohm 2010). I note, however, that egg size may not be a good proxy for maternal effects that arise from, for example, content of the eggs, and that digital measurements of diameter are not extremely precise compared to the small differences found.

Feeding and daily care followed standard protocols (Cripe et al. 2009). Larvae were fed *Artemia* nauplii until they were 15 mm and then switched to TetraMin® flakes. All feeding was *ad libitum* 4 times a day. Throughout the duration of the experiment, artificial seawater was maintained at 20 psu and photoperiod at 14L:10D, mimicking conditions in northern Florida.

Results

I found that, after 7 days of parental temperature exposure, the temperature dependence of offspring growth was parallel for all parents (in a two-way ANCOVA, the parent T x offspring T interaction was not significant, $p=0.958$; Fig. 2a, Table 1). Moreover, there was no direct effect of parent temperature ($p=0.729$). After 30 days of exposure, however, the interaction between parent and offspring temperature was abundantly clear (interaction term $p<0.001$; Fig. 2b, Table 1), demonstrating a shift in reaction norms of juveniles driven by temperature prior to

fertilization. Egg size, though variable, failed to explain the results ($p=0.217$; Table 1, Table 2). Moreover, these results for the 30-day exposure period were not driven by the final measurement date or the small sample of fish in the 34°C parent-24°C offspring treatment. I repeated the analysis for the 30-day treatment with lengths on day 37 and obtained qualitatively identical results (interaction term of two-way ANCOVA $p<0.001$, egg diameter as a covariate $p=0.755$). Repeating the analysis excluding the 34°C parent-24°C offspring treatment (interaction term of two-way ANCOVA $p<0.001$, egg diameter as a covariate $p=0.217$) and excluding the entire 34°C parent block (i.e., all offspring originating from 34°C parents) (interaction term of two-way ANCOVA $p<0.001$, egg diameter as a covariate $p=0.065$) yielded the same results.

Discussion

Here, I have shown that, provided sufficient exposure time, sheepshead minnow parents modify the response to temperature in their offspring. Although I have not measured fitness directly, faster growth during the early stages generally leads to increased survival in fishes (Sogard 1997) and fecundity is strongly correlated with body size (Wootton 1999). Offspring from high (34°C) and low (24°C) temperature parents grew best at high and low temperature, respectively, suggesting an adaptive response (Fox and Mousseau 1998).

Interestingly, reaction norms for the 7-day treatment are different from the juvenile growth rate reaction norms obtained in Chapter 3 (Fig. 6 in that chapter) and from the 30-day treatment. Obtaining parallel reaction norms for all parent-by-offspring treatments in the 7-day fish is highly unlikely, and thus not an artifact. Parents in the maturation/Chapter 3 experiment

(which were also obtained from wild adults and kept in the laboratory their entire lives) were held for a longer period of time as compared to the TGP fish. In addition, the length measurements were taken at slightly different ages, although re-analysis trying to match beginning and ending ages across the two experiments indicated no differences. Finally, unintended experimental manipulation ("demonic intrusion", *sensu* Hurltberg [1984]) could have led to the differing reaction norms. This observation may question the generality of TGP if reaction norms are truly this labile.

Growth rates in the 30-day treatment differed by as much as 32% (0.60 vs. 0.46 mm d^{-1} for offspring at 34°C). These changes are quite large. Although I am clearly not measuring evolutionary change, it is nevertheless of interest to compare these results with other studies of trait change across generations. I observed a rate of change of 3.0 haldanes, which is roughly an order of magnitude greater than the single-generation rate reported by Gingerich (2009; 0.3 haldanes). Moreover, the rate of change reported here is roughly 2 orders of magnitude greater than the median rate of phenotypic change found in a review of the subject (0.034 haldanes; Hendry and Kinnison 1999). Although not exactly analogous, food production programs, which attempt to maximize rates of evolution through selective breeding, typically achieve sustained changes of 1-2% per generation (Hill and Kirkpatrick 2010). Thus, the response I observed over one generation would require ten generations of "average" contemporary evolution (though the response is obviously non-genetic). Experiments to elucidate how the magnitude of transgenerational responses decrease with time are currently underway.

The prevalence of thermal TGP in growth is currently unknown. To date, thermal TGP in growth has only been demonstrated for milkweed bugs (*Oncopeltus fasciatus*; Groeters and Dingle 1988), butterflies (*Bicyclus anynana*; Steigenga and Fischer 2007) and thale cress (*Arabidopsis thaliana*; Blödner et al. 2007, Whittle et al. 2009). In all cases, offspring growth is maximized at the temperature experienced by the parents. In *A. thaliana*, the effect persists in grand-offspring, eliminating cytoplasmic inheritance as the mechanism of transfer (Whittle et al. 2009). Interestingly, no thermal TGP was found in development of dung flies (*Scathophaga stercoraria*; Scharf et al. 2010). In *Drosophila melanogaster*, parental temperature changed the elevation of offspring reaction norms but not the shape (Gilchrist and Huey 2001).

Although very few studies have directly addressed the interactive effects of parent and offspring temperature simultaneously, many studies have addressed them separately, providing indirect support for the prevalence of thermal TGP in ectotherms. Mothers under different temperatures produce eggs of different sizes in diverse taxa, including, e.g., fishes (Bownds et al. 2010), gastropods (Collin and Salazar 2010) and butterflies (Steigenga and Fischer 2007), while egg size effects are modified by offspring temperature in, e.g., Arctic char (*Salvelinus alpinus*; Janhunen et al. 2010), turtles (*Podocnemis lewyana*; Páez et al. 2009), bees (*Osmia bicornis*; Radmacher and Strohm 2010), and fruit flies (*Drosophila melanogaster*; Kjærsgaard et al. 2010). Interannual variation in maturation reaction norms in North Sea sole (*Solea solea*), which typically mature at age 3, depends significantly on temperature in their birth year (Mollet et al. 2007) suggesting either thermal TGP or an early developmental effect.

Although the prevalence of thermal TGP remains an open question, I expect that it is both more common and more important than currently appreciated. If this is the case, many disciplines may be affected: thermal TGP in life history traits could easily generate complex population dynamics through time lags (Plaistow et al. 2006), the appearance of rapid rates of contemporary evolution (Olsen et al. 2004), and spuriously high estimates of heritability in wild populations (Swain et al. 2007). I speculate that some instances of apparent extremely rapid contemporary evolution may be the result of TGP. For example, temperature tolerance evolved rapidly in sticklebacks (Barrett et al. 2011), a trait linked to gestational temperature in a viviparous fish (Travis et al. 1999) and known to exhibit TGP in protists (Jollos 1921, as cited in Jablonka and Raz 2009). Further, temperature dependence of growth is typically treated as fixed in bioenergetics models (Chipps and Wahl 2008), and temperature-growth relationships are the foundation for ecosystem models in which temperature-adjusted consumption rates govern species interactions (Cury et al. 2008). These, as well as attempts to predict the responses of species to climate change (Pereira et al. 2010) and to disentangle climate effects from evolution in harvested populations (Olsen et al. 2004), will need to be reconsidered if thermal TGP is common.

Importantly, TGP may allow for a rapid response to environmental changes (Bossdorf et al. 2008). Changes in precipitation may be counteracted via TGP in desiccation tolerance in invertebrates (Yoder et al. 2006) or drought tolerance in plants (Sultan et al. 2009). Higher CO_2 concentrations have been shown to elicit a TGP response in three plants species (Lau et al. 2008) and to alter predator-induced TGP responses in aphids (Mondor et al. 2004). Increased parental temperatures affect dispersal ability in a bryozoan (Burgess and Marshall 2011). Thus, changes

in growth constitute a small part of the overall transgenerational response to changing climate. Many traits, including maturation timing, fecundity and lifespan may also be affected. At present, it is unclear how evolution, phenotypic plasticity, and TGP interact to generate long-term responses. Limits and costs of TGP are also relatively unknown, although they may be similar to those of within-generation phenotypic plasticity (DeWitt et al. 1998). Disentangling these factors is an area of active current research that may qualitatively change projections for extinction risk and other climate impacts.

Tables

Table 1. ANCOVA results for growth (mm d-1) after 7 days of parental temperature exposure and after 30 days.

7-DAY TREATMENT

Source	DF	Adj. SS*	Adj. MS	F	P
Egg diameter (mm)	1	0.002	0.002	0.33	0.576
Parent temp (°C)	2	0.005	0.002	0.32	0.729
Offspring temp (°C)	2	0.407	0.204	26.61	<0.001
Parent temp x Offspring temp	4	0.005	0.001	0.16	0.958
Error	16	0.122	0.008		
Total	25				

30-DAY TREATMENT

Source	DF	Adj. SS*	Adj. MS	F	P
Egg diameter (mm)	1	0.003	0.003	1.57	0.217
Parent temp (°C)	2	0.004	0.002	1.07	0.353
Offspring temp (°C)	2	0.184	0.092	45.23	<0.001
Parent temp x Offspring temp	4	0.085	0.021	10.46	<0.001
Error	39	0.079	0.002		
Total	48				

* Adj. SS is the adjusted (Type III) sums-of-squares.

Table 2. Egg size results.

7-DAY TREATMENT

Parent temp (°C)	Mean egg diameter (mm)	SD	N
24	1.39	0.08	416
29	1.40	0.08	270
34	1.31	0.08	415

30-DAY TREATMENT

Parent temp (°C)	Mean egg diameter (mm)	SD	N
24	1.33	0.12	340
29	1.23	0.14	249
34	1.21	0.12	355

Figures

Figure 1. Experimental design used to assess transgenerational plasticity.

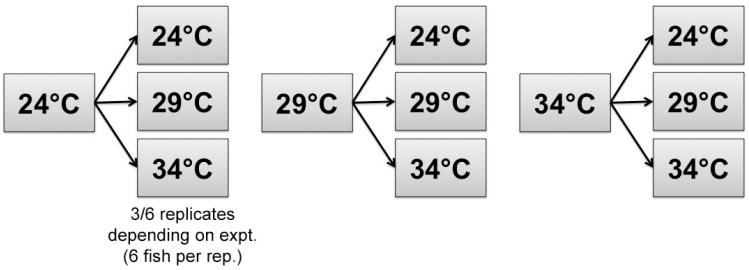
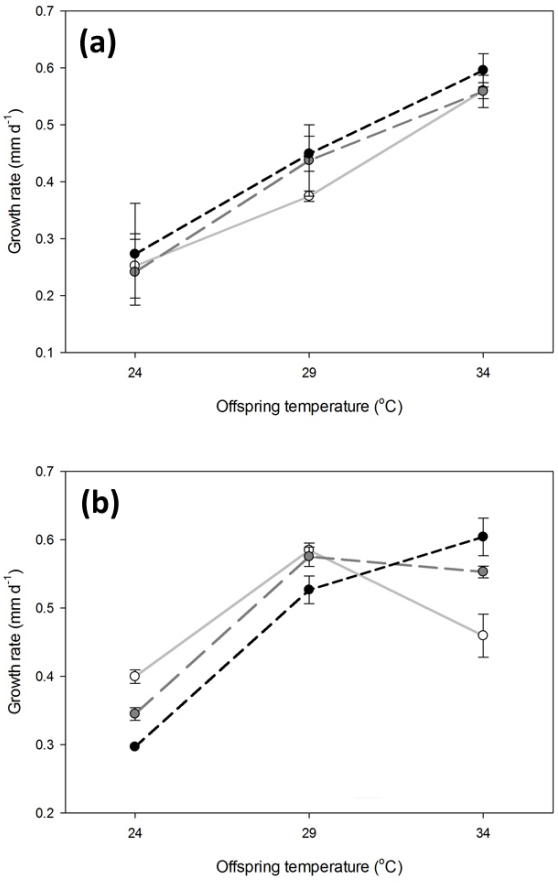


Figure 2. a) Offspring growth vs. temperature for parents held for 7 days at 24, 29, or 34°C (white, gray, and black circles respectively). Growth is parallel across parent temperatures, i.e., there is no effect of parent temperature on growth ($p=0.73$). b) Offspring growth vs. temperature for parents held for 30 days at 24, 29, or 34°C (white, gray, and black circles respectively). The interaction between offspring and parent temperatures is significant ($p<0.0001$).



Chapter 5

Transgenerational and phenotypic thermal plasticity throughout the life-cycle of sheepshead minnows, *Cyprinodon variegatus*

Abstract

When the environment experienced by the parents acts as a reliable indicator of the environment the offspring will experience, a parent can "pre-program" offspring traits appropriate for the predicted environment. This transfer of information from parent to offspring has been termed transgenerational plasticity (TGP). Recent evidence suggests that TGP may be an important mechanism to cope with rapid changes in temperature. In a recent experiment, sheepshead minnow (*Cyprinodon variegatus*) parents pre-conditioned offspring to grow fastest at the temperature that they (the parents) experienced prior to spawning. Growth was measured during the juvenile stage in this experiment, and thus whether phenotypic plasticity can counteract the negative effects of being from parents at the "wrong" temperature remains unknown. Here, I present results from the continuation of the sheepshead minnow experiment. I continued to rear the fish for a total of ~5.5 months, while periodically measuring length. I also explored whether the effects are seen in the F2 generation. Results indicate that phenotypic plasticity does indeed compensate in cases where a wrong cue was experimentally provided. This was true in all cases except in offspring at low temperature from high temperature parents, which could not fully recover. In addition, I found evidence for grand-offspring effects, strongly suggesting that an epigenetic mechanism mediates the phenomenon, as opposed to a protein/hormone transfer. Empirical examinations of plasticity should therefore explore both the entirety (or majority) of the expression of a trait in an organism and also the expression of that trait across generations.

Introduction

Many marine species are undergoing changes in phenotype in response to temperature (Hays et al. 2005, Harley et al. 2006, Byrne 2011). As these changes continue, there is a pressing need to understand and forecast their consequences for biodiversity conservation and the management of harvested populations. Temperature plays a fundamental role in the lives of ectotherms (Angilletta 2009), shaping, for example, metabolism (Hochachka and Somero 2002), lifespan (Munch and Salinas 2009), and population dynamics (Savage et al. 2004). This group is thus particularly vulnerable to thermal perturbations (Dillon et al. 2010).

Recently, transgenerational plasticity (TGP; Mousseau and Dingle 1991, Fox and Mousseau 1998) has been proposed as a mechanism to cope with the expected rapid changes in temperature (Loarie et al. 2009). When the environment experienced by the parents acts as a reliable indicator of the environment the offspring will experience, a parent can "pre-program" offspring traits appropriate for the predicted environment. This transfer of information from parent to offspring has been termed TGP (Fox and Mousseau 1998). Thermal TGP had gone largely unnoticed until recently, likely due to the paucity of studies (Räsänen and Kruuk 2007, Ho and Burggren 2010). Salinas and Munch (2012) showed that sheepshead minnow, *Cyprinodon* variegatus, parents can pre-condition offspring to grow fastest at the temperature that they (the parents) experienced prior to spawning. Growth was measured during the juvenile stage, a period during which size-dependent mortality is extremely high (Sogard 1997). The existence of TGP in thermal physiology in fishes was also recently demonstrated in the tropical damselfish, *Acanthochromis polyacanthus*. Donelson et al. (2012) evaluated whether resting and

maximum metabolic rates would be impacted by the thermal history of the parents via closed respirometry. They found that transgenerational acclimation allowed for a complete compensation in aerobic scope, whereas fish not at the temperatures experienced by the parents suffered a 15-30% decrease in scope (Donelson et al. 2012). Only 3 other instances of thermal TGP in growth have been detected: twice in insects (Groeters and Dingle 1988, Steigenga and Fischer 2007) and once in a plant (Blödner et al. 2007, Whittle et al. 2009).

Because previous work (Salinas and Munch 2012) concentrated on juvenile growth, an important question that remains unanswered is whether phenotypic plasticity can counteract the negative effects of being from parents at the "wrong" temperature. Compensatory growth, accelerated growth once conditions improve after a stressful period, is common in fishes (Ali et al. 2003). It is possible that fish from the slow-growing treatments could catch-up and attain sizes similar to those of fast-growing fish.

Moreover, it will be important to know whether TGP effects remain after the first generation. Temperature is expected to become more variable in the future (IPCC 2007), so the medium-term response of populations to changes in climate will be necessarily tied to how long the effect persists. It will also help elucidate the underlying mechanism of TGP. If the response is only seen after one generation, with a "resetting" after that, a hormonal/protein/RNA transfer via gametes or cytoplasm would be suspected (Bonduriansky and Day 2009). On the other hand, if grand-offspring growth still depends on the temperature experienced by grand-parents, an epigenetic mechanism (e.g., DNA methylation, chromatin structure modification) would likely be at work (Bonduriansky and Day 2009). These different mechanisms will lead to, for example,

different short-term evolutionary outcomes (Ho and Burggren 2010, Shea et al 2011). In addition, having a clear answer would be of major importance in trying to predict population dynamics. It is well known that typical maternal effects can create delayed density dependence (Ginzburg and Taneyhill 1994, Ginzburg 1998, Kendall et al. 2005). TGP acts in much the same way, as was empirically demonstrated by Plaistow et al. (2006) with the soil mite *Sancassania berlesei*.

Here, I present results from the continuation of the experiment first reported in Salinas and Munch (2012). I continued to rear the fish for a total of ~5.5 months, while periodically measuring length. I also explored whether the effects are seen in the F2 generation by crossing specific treatments and growing the resulting offspring.

Methods

This work is a continuation of the previously published study by Salinas and Munch (2012). Briefly, adult sheepshead minnows, raised in the laboratory their entire lives at 21-22°C, were placed into sea tables at each of the experimental temperatures: 24, 29, and 34°C (n=24 females, 18 males at each temperature). Two sets of parents were used, one that spent an acclimation period of 7 days at the designated temperature, and another that spent 30 days at the assigned temperature. After this acclimation period, I collected eggs every 2 hours to ensure that fertilized eggs were exposed to parental temperatures for as little time as possible. Eggs from a common parental temperature were collected, pooled, and subdivided in thirds to be transferred to either 24, 29, or 34°C. I then photographed eggs to measure diameters (±0.045 mm), which

were used as a covariate in the analysis. Juvenile densities were standardized post-hatch (6 fish per replicate). Each parental temperature-offspring temperature combination was triplicated for the 7-day exposure, and replicated 6 times for the 30-day exposure. Due to very low hatching success, the 34°C parent-34°C offspring treatment in the 7-day exposure consisted of 2 replicates, while the 34°C parent-24°C offspring treatment in the 30-day exposure consisted of only one replicate. Feeding and daily care followed standard protocols (Cripe et al. 2009). Larvae were fed *Artemia* nauplii until they were 15 mm and then switched to TetraMin® flakes. All feeding was *ad libitum* 4 times a day. Throughout the duration of the experiment, artificial seawater was maintained at 20 psu and photoperiod at 14L:10D.

Approximately every 7 days, I measured fish length by digital photography (±0.5 mm) with ImagePro Plus®. I reared the fish for 160 (30-day treatment) and 168 (7-day treatment) days. I analyzed growth trajectories in two ways. First, 3 growth time periods were selected and analyzed independently. The first period was the one presented in the previous paper (up to 51 days in the 30-day treatment and up to 41 days in the 7-day treatment; Salinas and Munch 2012). The second period consisted of days 51 to 117 in the 30-day fish and days 41-118 in the 7-day individuals, while the third encompassed days 117-160 and 118-168, respectively. Growth was calculated linearly and analyzed via two-way ANCOVA with parent and offspring temperature as fixed effects and egg diameter as covariate. In addition, I analyzed the entire growth trajectories using a function-valued approach (Kingsolver et al. 2001). Function-valued or infinite-dimensional approaches, unlike multivariate ones, analyze the entire shape of the growth trajectory by decomposing a covariance matrix of size into a number of bases. I used a Legendre polynomial as the basis function expansion with 5 terms. I then projected each individual

(container) growth trajectory onto the basis set and analyzed the set via MANCOVA with parent and offspring temperatures as fixed effects and egg diameter as a covariate. I also analyzed the coefficients of each of the replicates via canonical variate analysis.

To test for the presence of an effect in the grand-offspring generation, I crossed fish from the (parent-offspring) 24-34 and 34-34 treatments and followed the same protocol (<2 hours, eggs split into batches and placed at either 24 or 34°C, measured every 7 days, etc.). The number of replicates were as follows (parent-offspring-grand-offspring): 24-34-24, n=6; 24-34-34, n=6; 34-34-24, n=4; 34-34-34, n=4. I should note that the various replicates for each treatment were not conducted at the same time, so, for example, the 24-34-24 replicates were obtained over 3 different spawning days, with 2 sub-replicates per day. Number of fish per replicate depended on the number of hatchlings at each of the spawning days (range 3-5 fish per replicate). I estimated growth linearly and analyzed it via two-way ANCOVA with parent and grand-offspring temperature as fixed effects and egg diameter as covariate.

Results

Results from the 3-period ANCOVA analysis indicate that offspring of parents kept at each of the temperatures for 7 days were never different from each other within a rearing temperature (Fig. 1). This was true at day 41 ($p=0.958$), day 118 ($p=0.560$), and day 168 ($p=0.774$). Egg diameter was not significant as a covariate in any of the tests, either ($p>0.05$). On the other hand, a parent-by-offspring temperature interaction still remained in the 51-117 day period in the 30-day treatment ($p=0.014$), just as it was in the period up to 51 days ($p<0.001$).

The 117-160 day period, however, showed no interaction effect ($p=0.980$) indicating no parent-by-offspring growth determination (Fig. 2). Size at day 160, however, was different among offspring grown at 34°C (ANOVA: $p=0.013$; Fig. 2), as the fish originating from parents at 24°C were smaller than those from 29 and 34°C parents. In the 24 and 29°C offspring, final size was similar regardless of parental origin (ANOVA: $p=0.388$ and $p=0.522$, respectively).

Multivariate analysis of covariance of the coefficients obtained from the function-valued trait analysis suggests that the growth trajectories were different with respect to the parent-by-offspring temperature interaction ($p<0.001$). Trajectories were also different among offspring temperatures, as expected ($p<0.001$), but not among parental temperature ($p=0.055$). Power to detect differences was high in all cases (>0.8) and egg diameter not significant as a covariate ($p=0.672$). In the canonical variate analysis, the most dominant canonical variate, which groups trajectories mainly among offspring temperature, explains 86.2% of the variation (Fig. 3). Canonical variate axis 2, in turn, explains an additional 6.2% (92.5% for the first two CVs) and appears to separate groups based on parent-by-offspring temperature interaction (Fig. 3).

Larval growth in the grand-offspring generation depended on the interaction of parent (P generation) and grand-offspring (F2 generation) temperatures ($p=0.031$). The effect observed was in the expected direction: grand-offspring from parents that experienced 34°C water grew 15% faster at that temperature compared to offspring at 24°C (Fig. 4). Egg diameter was again not a significant covariate in the analysis ($p=0.617$).

Discussion

Growth is a highly plastic trait that can be affected by phenotypic (Berry 1987) and transgenerational (Salinas and Munch 2012) plasticity. As demonstrated here, phenotypic plasticity could in fact erase the early advantage provided by TGP under some thermal regimes. In this experiment, conclusions would have been very different if the focus had been on early-life vs. whole-life responses. Compensatory growth is thus an important phenomenon in the interaction of phenotypic and transgenerational plasticity. Compensation after a brief period of poor thermal-related growth has been observed in Atlantic salmon (Mortensen and Damsgård 1993, Nicieza and Metcalfe 1997), Arctic charr (Mortensen and Damsgård 1993), Mozambique tilapia (Ali et al. 2003), and three-spined stickleback (Lee et al. 2010). Costs to compensatory growth, both in the short- and long-term, are common and take many forms (Metcalfe and Monaghan 2001). A careful consideration of them would lead to a more holistic understanding of TGP.

In addition, it is likely that TGP responses are mediated by food availability. The interaction of temperature and food is known to influence optimal trait allocation in sheepshead minnows (Chapter 3). Moreover, typical maternal effects are closely linked to parental food environment (Reznick et al. 1996, Green 2008), and examples of TGP with food as the environmental variable (as opposed to temperature) do exist (e.g., Bashey 2006, Hafer et al. 2011). Understanding how other traits and other environmental variables interact with growth and temperature will also lead to a broader appreciation of TGP as a mechanism in population changes.

There also appears to be evidence of TGP effects persisting in the grand-offspring generation. Epigenetic mechanisms are thus likely at work in sheepshead minnows, as opposed to other forms of protein/hormone transfer that would not persist after one generation. Molecularly, the best-studied mechanism of epigenetic inheritance is DNA methylation. It involves the addition of a methyl group to cytosines in CpG sites (where a cytosine nucleotide occurs next to a guanine along its length), which are typically associated with regulatory regions of genes. A methyl group often has a silencing effect on the gene on which it is placed (Jaenisch and Bird 2003, Bender 2004). Another important mechanism of epigenetic inheritance is histone modification. Histones are proteins that provide structure for and mediate the folding of DNA strands. Histones have tails that can be modified by acetylation, phosphorylation, ubiquitination, or methylation (Bernstein et al. 2007). These histone modifiers impact how tightly the DNA is wound, which in turn influence gene activity, with tightly packed genes being less active and vice versa (Ng and Bird 1999, Li et al. 2007). It is now clear that epigenetic modifications to the DNA can be inherited (Whitelaw and Whitelaw 2006, Jirtle and Skinner 2007). During DNA replication, methylation patterns are carefully reconstructed on both strands thanks to an enzyme, methyltransferase, that recognizes previously methylated genes and adds methyl groups to complementary strands (Bender 2004, Jablonka and Lamb 2005). The type of inheritance system, along with the reliability of the cue, the effectiveness of the sensory mechanism, and the fidelity of the information transfer, has important consequences to the evolution of growth under thermally changing environments (Badyaev and Uller 2009, Shea et al. 2011).

Tables

Table 1. ANCOVA results for growth (mm d^{-1}) after 7 days of parental temperature exposure for the two time periods analyzed.

7-DAY TREATMENT — 41-118 DAY PERIOD

Source	DF	Adj. SS*	Adj. MS	F	P
Egg diameter (mm)	1	<0.001	<0.001	0.31	0.587
Parent temp (°C)	2	<0.001	<0.001	0.01	0.991
Offspring temp (°C)	2	0.006	0.006	3.04	0.080
Parent temp x Offspring temp	4	0.003	0.003	0.77	0.560
Error	14	0.014	0.014		
Total	23				

7-DAY TREATMENT — 118-168 DAY PERIOD

Source	DF	Adj. SS*	Adj. MS	F	P
Egg diameter (mm)	1	0.007	0.007	4.07	0.065
Parent temp (°C)	2	<0.001	<0.001	0.12	0.888
Offspring temp (°C)	2	0.008	0.004	2.17	0.154
Parent temp x Offspring temp	4	0.003	0.001	0.45	0.774
Error	13	0.023	0.002		
Total	22				

* Adj. SS is the adjusted (Type III) sums-of-squares.

Table 2. ANCOVA results for growth (mm d^{-1}) after 30 days of parental temperature exposure for the two time periods analyzed.

30-DAY TREATMENT — 51-117 DAY PERIOD

Source	DF	Adj. SS*	Adj. MS	F	P
Egg diameter (mm)	1	0.001	0.001	0.46	0.504
Parent temp (°C)	2	0.004	0.002	1.10	0.343
Offspring temp (°C)	2	0.022	0.011	6.97	0.003
Parent temp x Offspring temp	4	0.023	0.006	3.59	0.014
Error	39	0.063	0.002		
Total	48				

30-DAY TREATMENT — 117-160 DAY PERIOD

Source	DF	Adj. SS*	Adj. MS	F	P
Egg diameter (mm)	1	<0.001	<0.001	0.03	0.864
Parent temp (°C)	2	0.002	0.001	0.35	0.704
Offspring temp (°C)	2	0.003	0.001	0.62	0.541
Parent temp x Offspring temp	4	0.001	<0.001	0.10	0.980
Error	39	0.086	0.002		
Total	48				

* Adj. SS is the adjusted (Type III) sums-of-squares.

Figures

Figure 1. Growth trajectories for offspring at the three temperature treatments from parents exposed to each of the temperatures for 7 days (mean length ±1 SD). Black arrows indicate the times of the three periods analyzed via ANCOVA.

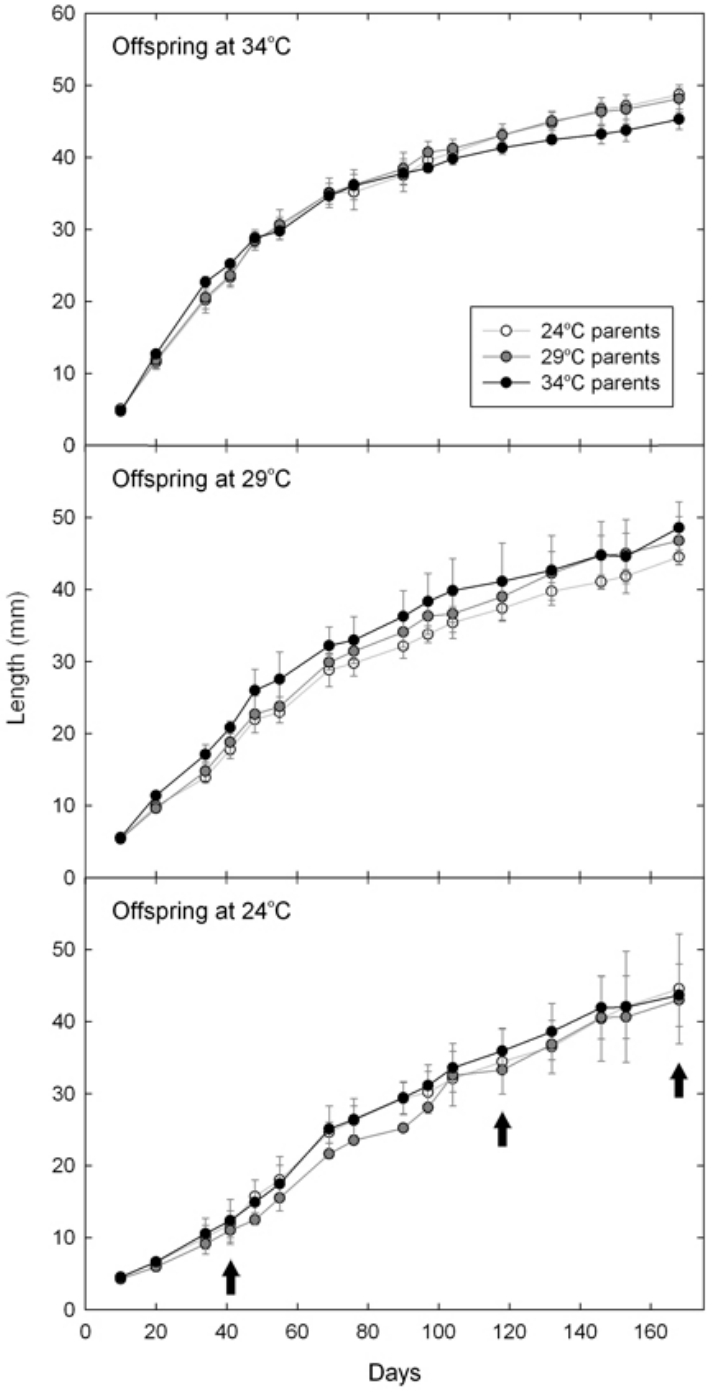


Figure 2. Growth trajectories for offspring at the three temperature treatments from parents exposed to each of the temperatures for 30 days (mean length ±1 SD). Black arrows indicate the times of the three periods analyzed via ANCOVA.

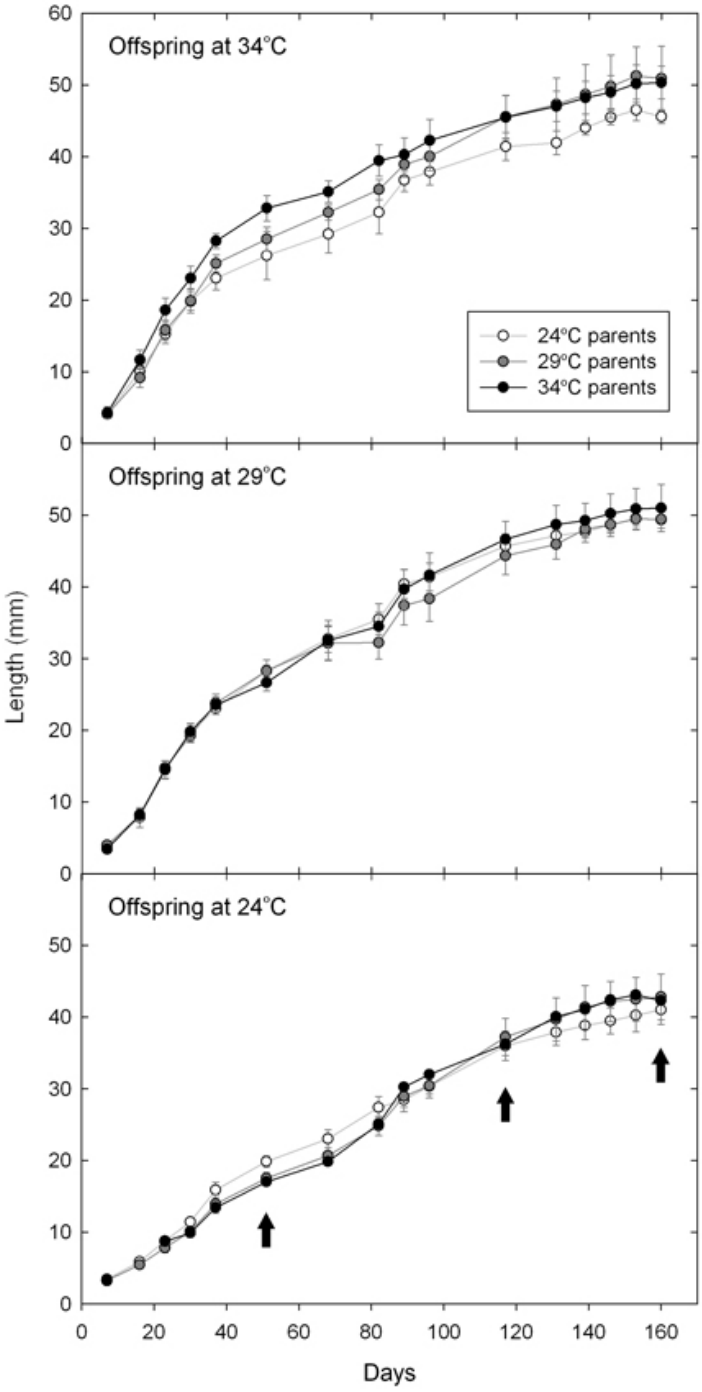


Figure 3. Coefficients for the 5 basis obtained from the function-valued trait analysis separated via canonical variate analysis. The two most dominant CVs are plotted. Color coding: the left side of the point indicates parental temperature while the left side indicates offspring temperature, with blue = 24°C, yellow = 29°C, red = 34°C (e.g., a point with blue on the left and yellow on the right would represent 24°C parents - 29°C offspring). The axes in the CV plot were re-scaled to reflect total variance. Figures at top right represent the extremes of the CVs (gray line = mean growth trajectory, black line = extreme of CV).

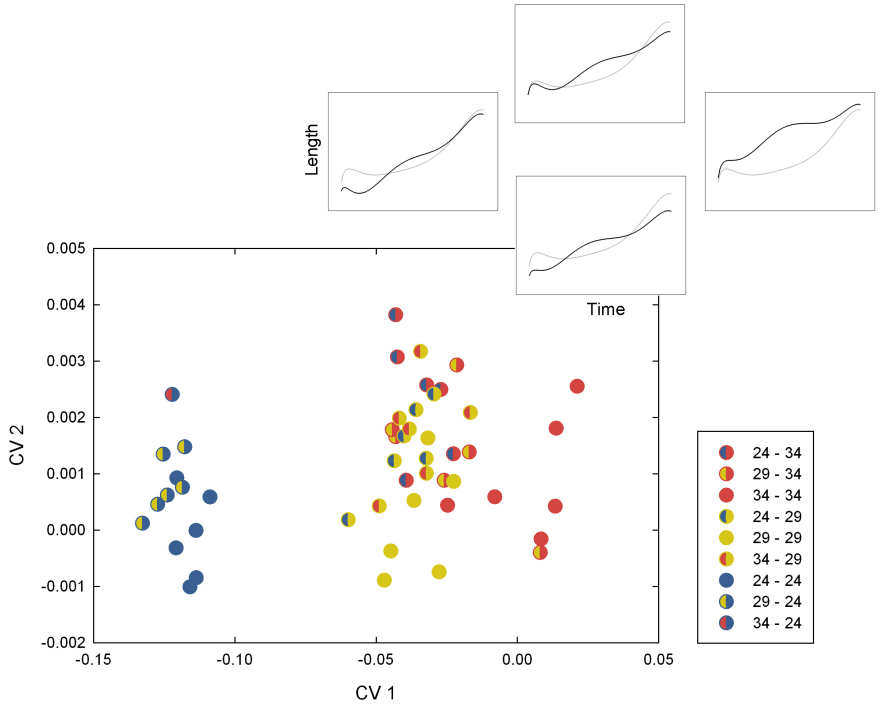
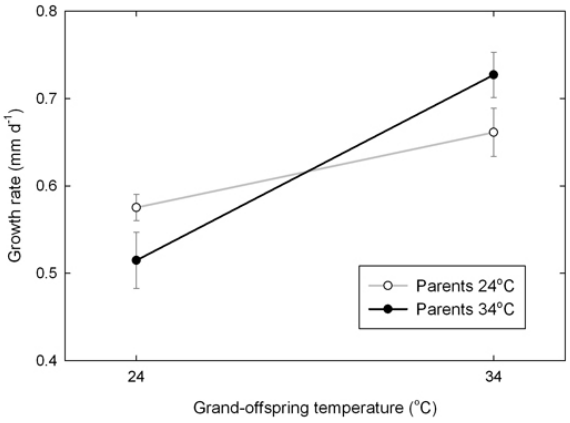


Figure 4. Growth rate (±1 SE) of grand-offspring at 24 and 34°C from parents at either 24 (white points, gray line) or 34°C (black points, black line). Offspring were all grown at 34°C.



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