ECOLOGY LETTERS

Ecology Letters, (2012) **15**: 159–163 doi: 10.1111/j.1461-0248.2011.01721.x

LETTER

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

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Abstract

Transgenerational plasticity (TGP), a generalisation of more widely studied maternal effects, occurs whenever environmental cues experienced by either parent prior to fertilisation results 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—TGP in thermal growth physiology has never been demonstrated for vertebrates. We provide the first evidence for thermal TGP in a vertebrate: given sufficient time, sheepshead minnows adaptively program their offspring for maximal growth at the present temperature. The change in growth over a single generation (*c.* 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 on physiology, ecology and contemporary evolution, and may significantly alter the extinction risk posed by changing climate.

Keywords

Cyprinodon variegatus, ecological epigenetics, maternal effects, sheepshead minnow.

Ecology Letters (2012) **15:** 159–163

INTRODUCTION

Significant changes in climate are expected in the near future [Intergovernmental Panel on Climate Change (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 & Somero 2002), lifespan (Munch & 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, we highlight a third potential mechanism for rapid responses to climate shifts: transgenerational plasticity (TGP).

TGP occurs when the environment experienced by the parents prior to fertilisation directly translates, without DNA sequence alteration, into significant changes in the shape of offspring reaction norms (Fox & 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, as paternally inherited environmental effects also exist (e.g. Etterson & Galloway 2002) we 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 & 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 & Etterson 2007).

TGP may provide an important and understudied mechanism for coping with rapid environmental variation, including climate change (Rando & 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.

Although TGP in lethal temperatures has been found in several species (Jablonka & Raz 2009), thermal TGP in growth, a key life history trait, has thus far only been detected in three species: two insects (Groeters & Dingle 1988; Steigenga & 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.) We provide, to our 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 USA 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). We collected several hundred adult sheepshead minnows from the Gulf Islands National Seashore (Gulf Breeze, Florida, USA) and brought them to our fish facility at Stony Brook University in August 2009. We bred the fish over multiple days, producing thousands of eggs which were then subsampled at random. We 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 our experiments.

To test for thermal TGP in growth, we 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, Florida 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 (Bennet & 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 mortalities 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, we introduced egg-collecting mats prior to spawning and replaced them every 2 h thereafter. Thus, fertilised eggs were exposed to parental temperatures for < 2 h 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 Figure S1). More than 250 eggs were collected from each group of parents. As each female produces roughly 10–15 eggs per clutch, at least 70% of the females participated in each spawning.

Upon collection, we photographed eggs to measure diameters (± 0.045 mm). Juvenile densities were standardised 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® (Media Cybernetics, Bethesda, MD, USA). Each parental temperature-offspring temperature combination was triplicated for the 7-day exposure, and replicated six 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, whereas 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). As fish within replicates are not independent, the mean for each replicate was used as the response variable in our statistical analysis. We analysed 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 & Strohm 2010). We 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 with 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® (Tetra Holding, Blacksburg, VA, USA) flakes. All feeding was *ad libitum* four 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

We 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. 1a, 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. 1b, Table 1), demonstrating a shift in reaction norms of juveniles driven by temperature prior to fertilisation. Egg size, though variable, failed to explain the results ($P = 0.217$; Table 1, Table S1). 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. We repeated the analysis for the 30-

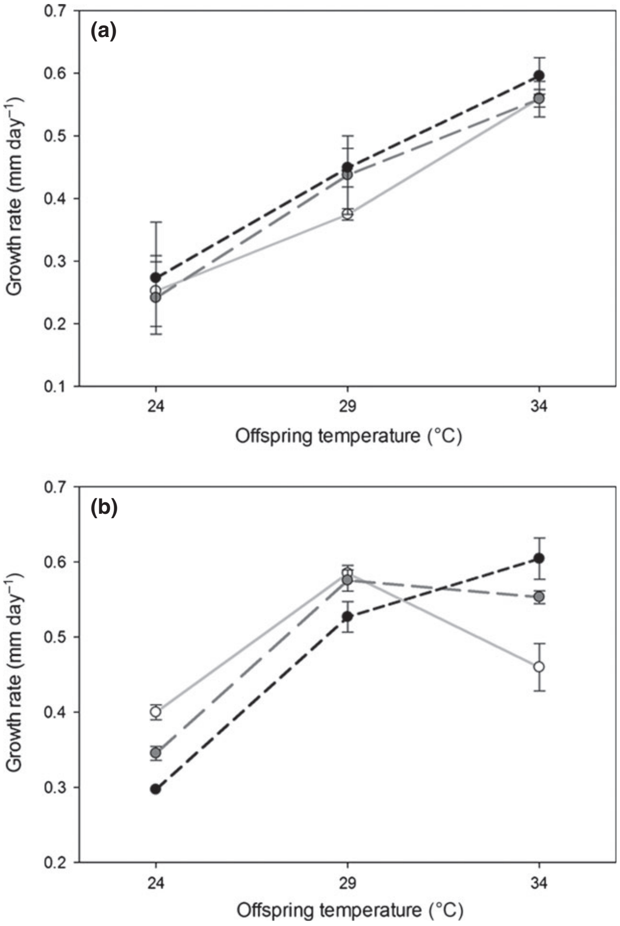

Figure 1 (a) Offspring growth vs. temperature for parents held for 7 days at 24, 29, or 34 °C (white, grey and black circles respectively). Growth is parallel across parent temperatures, i.e. there is no effect of parent temperature on growth ($P = 0.73$). (b) Offspring growth vs. temperature for parents held for 30 days at 24, 29 or 34 °C (white, grey and black circles respectively). The interaction between offspring and parent temperatures is significant ($P < 0.001$).

Table 1 ANCOVA results for growth (mm day^{-1}) after 7 days of parental temperature exposure and after 30 days

Source	d.f.	Adj. SS*	Adj. mean square	*F*	*P*
Seven-day treatment					
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 × offspring temp	4	0.005	0.001	0.16	0.958
Error	16	0.122	0.008		
Total	25				
Thirty-day treatment					
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 × 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.

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, we have shown that, provided sufficient exposure time, sheepshead minnow parents modify the response to temperature in their offspring. Although we 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 & Mousseau 1998).

Growth rates differed by as much as 32% (0.60 vs. 0.46 mm day^{-1} for offspring at 34 °C). These changes are quite large. Although we are clearly not measuring evolutionary change, it is nevertheless of interest to compare these results with other studies of trait change across generations. We 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 two orders of magnitude greater than the median rate of phenotypic change found in a review of the subject (0.034 haldanes; Hendry & Kinnison 1999). Although not exactly analogous, food production programs, which attempt to maximise rates of evolution through selective breeding, typically achieve sustained changes of 1–2% per generation (Hill & Kirkpatrick 2010). Thus, the response we 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 & Dingle 1988), butterflies (*Bicyclus anynana*; Steigenga & Fischer 2007) and thale cress (*Arabidopsis thaliana*; Blödner *et al.* 2007; Whittle *et al.* 2009). In all cases, offspring growth is maximised 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 & 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 & Salazar 2010) and butterflies (Steigenga & Fischer 2007), whereas 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 & 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 three, 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, we 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). We 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 & Raz 2009). Further, temperature dependence of growth is typically treated as fixed in bioenergetics models (Chipps & 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 & 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.

ACKNOWLEDGEMENTS

We thank Jo Anne Siskidis for experimental assistance, Tom Hurst for inspiring discussions, and Eric Anderson, Doug Futuyma, Marc Mangel, Sarah Newkirk, Kestrel Perez, Stephen Sabatino, Will Satterthwaite, Sue Sogard, Mark Sokolowski, George Somero and Masatoshi Sugeno for comments on a previous version of the manuscript. S. S. was supported by a W. B. Turner Dissertation Fellowship.

S.S. and S.B.M. conceived and designed the study, performed the research, and wrote the manuscript.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Figure S1 Experimental design used to assess transgenerational plasticity.
Table S1 Egg size results.

Editor, Mikko Heino
Manuscript received 29 August 2011
First decision made 2 October 2011
Second decision made 15 November 2011
Manuscript accepted 22 November 2011