

## Zebrafish take their cue from temperature but not photoperiod for the seasonal plasticity of thermal performance

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Accepted 6 August 2010

### SUMMARY

**Organisms adjust to seasonal variability in the environment by responding to cues that indicate environmental change. As most studies of seasonal phenotypic plasticity test only the effect of a single environmental cue, how animals may integrate information from multiple cues to fine-tune plastic responses remains largely unknown. We examined the interaction between correlated (seasonally matching) and conflicting (seasonally opposite) temperature and photoperiod cues on the acclimation of performance traits in male zebrafish, *Danio rerio*. We acclimated fish for 8 weeks and then tested the change in thermal dependence of maximum burst swimming and feeding rate between 8 and 38°C. We predicted that correlated environmental cues should induce a greater acclimation response than uncorrelated cues. However, we found that only temperature was important for the seasonal acclimation of performance traits in zebrafish. Thermal acclimation shifted the thermal performance curve of both traits. For maximum burst swimming, performance increased for each group near the acclimation temperature and reduced in environments that were far from their acclimation temperature. The feeding rate of cold-acclimated zebrafish was reduced across the test temperature range compared with that of warm-acclimated fish. Our study is the first that has found no effect of the covariation between temperature and photoperiod acclimation cues on locomotor performance in fishes. Our results support the intuitive idea that photoperiod may be a less important seasonal cue for animals living at lower latitudes.**

Key words: acclimation, temperature, photoperiod, thermal performance curve.

### INTRODUCTION

Many vertebrates are exposed to large seasonal changes in their environment that can affect the performance of behavioural and physiological traits. Any environmentally induced change in an organism's phenotype is known as phenotypic plasticity (Stearns, 1989) and many organisms have the capacity to reversibly alter the expression of phenotypic traits between seasonal environments (Wilson and Franklin, 2002; Piersma and Drent, 2003; Angilletta, 2009). Seasonal changes in plastic traits are induced by cues from the environment that can signal both current conditions and the likelihood of coming changes in the environment. For example, many animals adjust their behaviour in response to the daily warming and cooling of the environment, while decreasing photoperiods over several weeks may signal the onset of seasonal cooling to an organism before average daily temperatures have reduced. A failure to recognise and respond to cues can result in an organism either not altering its phenotype, despite changes in the environment, or producing one that is not well suited to new conditions (DeWitt et al., 1998; Gabriel, 2005). If a phenotype–environment mismatch reduces survival, an organism may have reduced fitness until either the environment changes again or the phenotype can be altered (DeWitt et al., 1998; Auld et al., 2009).

Combining information from both temperature and photoperiod cues is predicted to be important for the expression of alternative seasonal phenotypes in ectotherms (Bradshaw and Holzapfel, 2008). Photoperiod is a cue for the annual timing of many traits in ectotherms including reproduction, development, diapause, migration and sexual maturity (Bradshaw and Holzapfel, 2007). Temperature cues also induce large changes in behaviour,

performance and physiology both in the laboratory (Fry and Hart, 1948; Johnson and Bennett, 1995; Wilson and Franklin, 1999; Condon and Wilson, 2006) and under natural seasonal conditions (Guderley and St-Pierre, 1999). When multiple correlated cues such as temperature and photoperiod can be used together to estimate seasonal variability, the reliability of the information should be greater than that from a single cue alone (Visser et al., 2004; Seko and Nakasuji, 2006; Bradshaw and Holzapfel, 2008). While it is likely that many environmental signals of seasonality (e.g. light, temperature, food availability) are used to estimate the rate of seasonal change, currently little is known about how information from multiple cues is used and combined in plastic phenotypic responses to the environment (Weinig and Delphi, 2001; Cipollini, 2004; Auld et al., 2009).

Thermal acclimation has frequently been found to induce large and reversible plastic changes in the behaviour, physiology and performance of fishes (Fry and Hart, 1948; Beddow et al., 1995; Johnson and Bennett, 1995; Temple and Johnston, 1998; Condon and Wilson, 2006; Wilson et al., 2007b). In thermal acclimation studies, temperature is frequently manipulated without a correlated change in photoperiod, thereby breaking the natural covariation that exists between these cues. However, the few studies that have examined the covariation between temperature and photoperiod cues in fishes have found that the interaction can induce large changes in performance and physiological traits (Kolok, 1991; Smiley and Parsons, 1997; Guderley et al., 2001; Day and Butler, 2005). These studies have largely tested the covariation in seasonal cues under semi-natural conditions where one of the cues was manipulated to produce uncorrelated cue treatments. Although these studies are ecologically relevant tests of the effect of acclimatisation to

seasonality on performance and physiological traits, the direct effect of temperature and photoperiod cues is difficult to determine. By manipulating both temperature and photoperiod cues under controlled conditions, we sought to directly test whether the interaction of multiple cues influences the reversible plasticity of performance traits in the zebrafish, *Danio rerio*.

The zebrafish is a free spawning minnow native to South Asia and has a wide tropical and sub-tropical geographic distribution that extends over eastern India, north to Nepal and across Bangladesh into northern Burma (Laale, 1977). Recent habitat surveys in Bangladesh revealed that zebrafish are typically found in floodplain areas in open, shallow lakes and waterlogged rice fields (Spence et al., 2006). Although this species is an important model organism in developmental biology and genomic research, until recently relatively little was known of zebrafish ecology and behaviour (Spence et al., 2008). We have found that 4 weeks of thermal acclimation of *D. rerio* induces large changes in maximum burst swimming performance (C.H.C. and R.S.W., unpublished), but a lack of cold acclimation of sustained locomotor performance has also previously been reported (McClelland et al., 2006). Photoperiod is also known to regulate reproduction and spawning in female *D. rerio* (Spence et al., 2008), while the interaction between the two cues influences factors that can affect endocrine function (Jin et al., 2010).

Here we examined whether the interaction between temperature and photoperiod cues alters the acclimation response of two whole-animal performance traits (maximum swimming performance and feeding rate) in the zebrafish. We exposed male *D. rerio* to either a sub-tropical winter or a summer temperature (16 or 30°C) and one of three photoperiods (short day, long day or 12 h:12 h light:dark, L:D). These treatments were used to replicate correlated (seasonally matching) temperature and photoperiod cues, and uncorrelated (seasonally opposite) cues. We also used a standard acclimation treatment where temperature was altered but not photoperiod. After an 8 week acclimation period, we examined the thermal dependence of maximum burst swimming performance ( $U_{\max}$ ), as a measure of maximum escape velocity, and feeding rate, as a measure of voluntary activity. We predicted that correlated cues would provide increased reliability about seasonal conditions and induce the greatest acclimation response. Uncorrelated temperature and photoperiod cues were predicted to constrain the acclimation response. Finally, we tested the acclimation response of maximum burst swimming velocity and feeding performance as functional traits to examine any differences in the effect of the treatments on the thermal performance of each trait.

#### MATERIALS AND METHODS

We purchased 500 zebrafish *Danio rerio* (Hamilton 1822) from a commercial supplier (Bayfish Inc., Narangba, QLD, Australia) and these animals were held in mixed sex groups at a density of 0.5 fish l<sup>-1</sup> at the University of Queensland for 2 months prior to the beginning of the study. Fish were fed *Artemia nauplii ad libitum* daily throughout the experiment except on days when feeding trials took place. All experiments were authorised by the University of Queensland Animal Ethics Committee (SIB/841/07).

We used a 2×3 factorial design to examine the interaction of temperature and photoperiod on the thermal dependence of performance in 94 male zebrafish. Fish were kept at 16 or 30°C and one of three photoperiod treatments for 8 weeks. Previous studies have shown that acclimation responses of whole-animal performance traits in fishes are typically induced by 4–6 weeks of exposure to a new environment (Johnston and Lucking, 1978; Hammill et al.,

2004; Wilson et al., 2007a). All animals were housed individually in 3.5 l opaque plastic tanks with a 1 cm gravel bed and provided with constant aeration. Acclimation tanks were placed in three constant temperature rooms in 100 l water baths that were heated with two 60 W glass aquarium heaters (30±1°C) or were cooled to room temperature (16±1°C). Illumination in each constant temperature room was provided by six ceiling fluorescent bulbs and controlled by automatic timers set to 10 h:14 h, 12 h:12 h or 14 h:10 h L:D regimes. The seasonal temperature × photoperiod acclimation treatments were: correlated cues (16°C and 10 h:14 h L:D, N=17; 30°C and 14 h:10 h L:D, N=17), opposite cues (16°C and 14 h:10 h L:D, N=12; 30°C and 10 h:14 h L:D, N=17) and two treatments representing a standard lab acclimation procedure (16°C and 12 h:12 h L:D, N=15; 30°C and 12 h:12 h L:D, N=16). Photoperiod and temperature treatments were derived from summer, equinox and winter mean air temperature and day length data from Lucknow, India (26°51'0"N, 80°55'0"E) within the native range of the zebrafish. Standard length did not differ between groups (range: 25–30 mm, ANOVA:  $F_{5,88}=0.4087$ ,  $P=0.8$ ).

#### Thermal dependence of maximum burst swimming performance

After the 8 week acclimation period, the maximum burst swimming velocity ( $U_{\max}$ ) of each zebrafish was tested at 10 temperatures between 8 and 38°C. Fish were removed from aquariums and placed into 0.5 l plastic containers that were submerged in water baths at the initial test temperature of 26°C for a minimum of 1 h prior to the start of burst swimming tests. Burst swimming performance was tested across the temperature range on a single day in the order 26, 14, 10, 32, 34, 8, 20, 36, 29 and 38 (±0.5)°C. Each fish was exposed to the test environment for approximately 1 h prior to testing except at the test temperature of 38°C, where they were tested after 15 min because of the potentially lethal effects of prolonged exposure to high temperature. Fish that lost the ability to remain upright prior to testing (in either the warm or cold water temperature) were immediately removed from the waterbath and performance was recorded as zero. The temperature order was determined randomly once and all fish underwent the same order of testing. However, the first and last temperatures were not randomised. The first was chosen as intermediate between the levels of the temperature treatments and the last because of the effect of high temperature.

Burst swimming sequences were filmed using a high-speed digital video camera that recorded escape responses inside a swimming arena (30 cm×20 cm×5 cm). The temperature of the arena was maintained by the flow of heated or cooled water from a controlled temperature water bath (Heto, CB 8-30E; Allerod, Denmark) through a submersed metal rod. We elicited the startle response by tapping the side of the swimming arena – a stimulus that frequently induced the fish to burst rapidly away using a C-start. Only these C-starts – a stereotypical contraction of all muscle on one side of the fish curving the body into a 'C' shape followed by one or more propulsive tail strokes, used during escape from predators – were analysed (Eaton et al., 1977; Beddow et al., 1995; Temple and Johnston, 1998; Hammill et al., 2004). A high-speed digital camera recording at 200 Hz (Redlake Imaging Cooperation, Tucson, AZ, USA) filmed fish ventrally from 1.5 m away, capturing the image from a mirror at 45 deg beneath the glass-bottomed arena. The central region of the head was digitised and the first 40 ms of swimming sequences analysed to determine instantaneous measures of burst swimming velocity. We calculated  $U_{\max}$  by adjusting instantaneous velocity data with a three-point moving average filter (Wilson et al., 2000). At least three C-start responses were recorded and

analysed for each fish at each temperature. The highest  $U_{\max}$  recorded at each temperature was used to determine the thermal dependence of maximum burst swimming performance for each individual.

#### Thermal dependence of feeding rate

One week after the completion of swimming trials, the feeding performance of 69 males was assessed at eight temperatures between 13 and 36°C. As satiation would alter the rate of feeding, all animals were tested at a single temperature on each day with at least 48 h between observations. All fish were tested in the random order 22, 30, 15, 36, 34, 13, 28 and 18 ( $\pm 0.5$ )°C. Fish were placed in 41 glass observation tanks (15 cm  $\times$  15 cm  $\times$  20 cm) within a temperature controlled room set to the test temperature at least 12 h before the commencement of feeding trials. Feeding trials took place over 3 weeks and all animals were fasted for 24 h prior to testing.

To determine feeding rate, fish were fed live fourth instar *Aedes aegypti* mosquito larvae. *Aedes aegypti* eggs were obtained from a colony within the University of Queensland and hatched and reared at 24°C. *Aedes aegypti* larvae were fed ground fish food pellets (TetraMin Tropical Tablets, Tetra, Melle, Germany) for 5 days or until approximately 1 cm in length. Ten larvae were added to each observation tank and the feeding behaviour of the fish was observed for 1 min. The number of seconds each fish took to eat all of the larvae was recorded. Recordings lasted until all of the larvae were eaten or until 1 min had elapsed. Observations were recorded using ETHOM 1.0 (Shih and Mok, 2000) installed on a laptop computer.

#### Statistical analysis

Linear mixed effect models were used to analyse thermal performance functions for both performance traits. Acclimation temperature and photoperiod were treated as fixed effects while a random effect of subject was used to account for repeated measurements of an individual's performance across the temperature range. We attempted to fit up to fourth order polynomials for each trait to examine the non-linear relationship of performance as a function of environmental temperature. However, models including fourth order terms did not converge for either burst swimming or feeding performance data. From the linear, quadratic and cubic models that did converge, Akaike's information criterion (AIC) score was used to determine the polynomial model that best fitted our data. All analyses were completed using the MIXED procedure in SAS (Version 9.2, SAS Institute Inc. 2004) and significance was taken at the level of  $P < 0.05$ .

## RESULTS

#### Maximum burst swimming performance

The thermal dependence of  $U_{\max}$  was skewed and performance increased with increasing temperature in all treatments (Fig. 1A). A cubic polynomial model was found to provide the best fit for  $U_{\max}$  performance data. No significant interaction between temperature and photoperiod acclimation was present ( $F_{2,88}=1.00$ ,  $P=0.37$ ; Table 1A, Fig. 1A). Furthermore, photoperiod alone did not affect burst swimming ( $F_{2,88}=0.26$ ,  $P=0.77$ ). However, there was a highly significant effect of temperature acclimation treatment on performance ( $F_{1,88}=122.53$ ,  $P < 0.0001$ ). We found that the temperature cue alone induced a large shift in the thermal dependence of  $U_{\max}$  extending the capacity for escape performance of fish into harsher environments close to their acclimation temperature. A significant interaction between the thermal acclimation treatment and the cubic term of the model indicated that different shaped cubic functions were used to predict performance for fish acclimated to 16 and 30°C ( $F_{1,88}=108.09$ ,

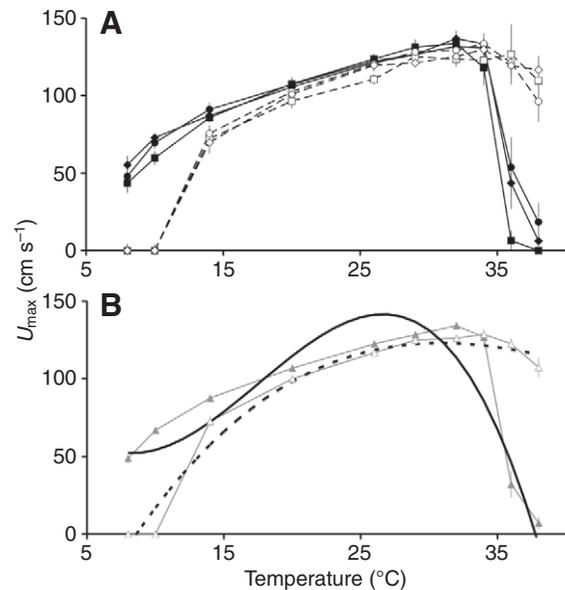


Fig. 1. (A) Thermal dependence of maximum burst swimming velocity  $U_{\max}$  for male zebrafish *Danio rerio* acclimated to 16°C (solid lines, filled symbols) and 30°C (broken lines, open symbols) and short day (square), equal (diamond) and long day (circle) photoperiods for 8 weeks. Analysis showed a highly significant effect of acclimation temperature on performance (Table 1:  $F_{1,88}=108.09$ ,  $P < 0.0001$ ), whereas photoperiod exposure had no effect on thermal performance ( $F_{2,88}=0.26$ ,  $P=0.77$ ). (B) Thermal dependence of  $U_{\max}$  in zebrafish showing only the significant difference between acclimation (grey lines) to either 16°C (filled triangles) or 30°C (open triangles). Black lines are the best fitting (cubic) polynomial functions for 16°C acclimated (solid) and 30°C acclimated (broken) treatments. For both graphs, vertical bars represent  $\pm 1$  s.e.m. of maximum burst swimming performance for each treatment group at each temperature. Where s.e.m. are not visible, they are smaller than the symbol size.

$P < 0.0001$ ; Fig. 1B). The width of the thermal performance curve appears to be constrained as increasing performance at one end of the thermal range reduced  $U_{\max}$  at the opposite end for both thermal acclimation treatments.

#### Feeding rate

A quadratic model provided the best fit for the thermal dependence of feeding rate. As for burst swimming, we found no effect of photoperiod or of an interaction between temperature and photoperiod on the thermal dependence of feeding rate (photoperiod:  $F_{2,71}=0.08$ ,  $P=0.92$ , interaction:  $F_{2,71}=0.66$ ,  $P=0.52$ ; Table 1B, Fig. 2A). However, as with burst swimming performance, there was a highly significant effect of acclimation temperature on feeding performance ( $F_{1,71}=40.98$ ,  $P < 0.0001$ ). Differences in feeding rate induced by thermal acclimation also altered the shape of the quadratic functions fitted to fish acclimated to 16 and 30°C ( $F_{1,71}=16.59$ ,  $P=0.0001$ ; Fig. 2B).

#### DISCUSSION

Multiple environmental cues are predicted to be important for ectotherms to respond to seasonal changes in the environment (Bradshaw and Holzapfel, 2008). We examined the interaction between correlated (seasonally matching) and conflicting (seasonally opposite) temperature and photoperiod cues on the acclimation of performance traits in male zebrafish. We found that the covariation

between temperature and photoperiod did not affect the thermal dependence of zebrafish maximum burst swimming performance or feeding rate. Photoperiod had no effect at all on the performance of either trait whereas acclimation to temperature treatments induced a large change in performance. Our results contrast with previous studies that have detected either an effect of photoperiod acclimation on locomotor performance or a significant interaction between correlated temperature and photoperiod cues in fishes. Kolok (Kolok, 1991) found that bass (*Micropterus salmoides*) acclimated to both 5 and 10°C and a 12h:12h photoperiod had reduced sustained swimming performance compared with fish acclimated to correlated temperate winter (5°C) and early summer (10°C) temperature and photoperiod cues. However, in the same study photoperiod had no effect on locomotor performance at higher temperatures. Day and Butler (Day and Butler, 2005) saw a similar increase in sustained performance in trout acclimated to correlated rather than uncorrelated seasonal cues at 5 and 15°C. The acclimation of three-spine sticklebacks (*Gasterosteus aculeatus*) to 8 and 23°C under natural decreasing photoperiod also decreased growth and burst swimming performance relative to that of fish acclimated to increasing day lengths in spring (Guderley et al., 2001). Tests of physiological traits have found higher oxidative capacity of red muscle in rainbow trout (*Oncorhynchus mykiss*) acclimated to outdoor ponds in winter than in those acclimated in summer (St-Pierre et al., 1998), while a further experiment revealed that acclimation to both cold temperature and short photoperiod induced this response in the same species (Martin et al., 2009). We found a complete lack of photoperiod acclimation in zebrafish despite testing performance as a functional trait for two types of swimming locomotion across a wide thermal range.

Why are temperature and photoperiod cues not used in a coordinated fashion for plasticity of performance traits in zebrafish? Most research in this area to date has used species, such as trout and sticklebacks, from temperate climates, which commonly experience cold winters and mild to extreme summer temperatures (St-Pierre et al., 1998; Guderley et al., 2001). Although photoperiod is a highly stable indicator of long-term average conditions in temperate regions, other seasonal indicators may be equally important at lower latitudes.

Table 1. Mixed effects models testing the independent and combined effects of acclimation temperature and photoperiod on (A) maximum burst swimming performance and (B) feeding rate in *Danio rerio*

Effect	F-value	P
(A) Maximum burst swimming performance		
Acclimation temperature	$F_{1,88}=122.53$	<b>&lt;0.0001</b>
Photoperiod	$F_{2,88}=0.26$	0.77
Acclimation temperature × photoperiod	$F_{2,88}=1.00$	0.37
Test temperature × acclimation temperature	$F_{1,88}=92.76$	<b>&lt;0.0001</b>
Test temperature <sup>2</sup>	$F_{1,88}=30.81$	<b>&lt;0.0001</b>
Test temperature <sup>2</sup> × acclimation temperature	$F_{1,88}=95.39$	<b>&lt;0.0001</b>
Test temperature <sup>3</sup>	$F_{1,88}=80.30$	<b>&lt;0.0001</b>
Test temperature <sup>3</sup> × acclimation temperature	$F_{1,88}=108.09$	<b>&lt;0.0001</b>
(B) Feeding rate		
Acclimation temperature	$F_{1,71}=40.98$	<b>&lt;0.0001</b>
Photoperiod	$F_{2,71}=0.08$	0.92
Acclimation temperature × photoperiod	$F_{2,71}=0.66$	0.52
Test temperature	$F_{1,71}=86.13$	<b>&lt;0.0001</b>
Test temperature × acclimation temperature	$F_{1,71}=29.71$	<b>&lt;0.0001</b>
Test temperature <sup>2</sup>	$F_{1,71}=72.74$	<b>&lt;0.0001</b>
Test temperature <sup>2</sup> × acclimation temperature	$F_{1,71}=16.59$	<b>0.0001</b>

P-values in bold are significant.

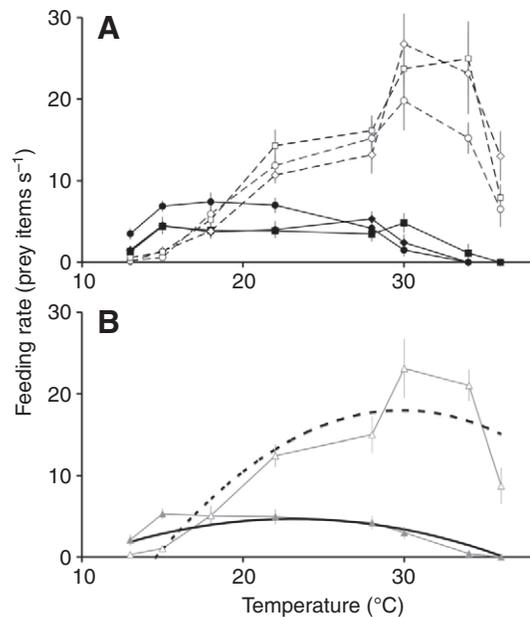


Fig. 2. (A) Thermal dependence of feeding rate for male zebrafish, *D. rerio*, acclimated to 16°C (solid lines, filled symbols) and 30°C (broken lines, open symbols) and short day (square), equal (diamond) and long day (circle) photoperiods for 8 weeks. Acclimation temperature had a highly significant effect on feeding rate ( $F_{1,71}=16.59$ ,  $P=0.0001$ ), while no difference was detected between photoperiod treatments ( $F_{2,71}=0.08$ ,  $P=0.92$ ). (B) Thermal dependence of feeding rate of *D. rerio* showing only the significant difference between acclimation (grey lines) to either 16°C (filled triangles) or 30°C (open triangles). Black lines are the best fitting (quadratic) polynomial function for 16°C acclimated (solid) and 30°C acclimated (broken) treatments. For both graphs, vertical bars represent  $\pm 1$  s.e.m. of feeding rate for each treatment group at each temperature. Where s.e.m. are not visible, they are smaller than the symbol size.

Zebrafish are native to sub-tropical areas of South Asia and do not experience as large a variability in photoperiod as fish from higher latitudes. We suggest that because of the geographical distribution and floodplain habitat of zebrafish (Spence et al., 2006), other environmental cues such as rainfall may be more reliable cues for the seasonal plasticity of performance traits in this species. Additionally, photoperiod may be a more important long-range predictor for upcoming environmental change when the length of the warm summer season is far reduced in temperate species compared with tropical organisms. Annual changes in photoperiod are often thought to be too small to induce plasticity in tropical organisms; however, equatorial birds have been shown to use slight variation in photoperiods as cues for seasonal activity (Hau et al., 1998; Hau, 2001). A lack of photoperiod response has also been found in the activity level of sub-tropical turtles; however, differences between seasonal temperature and photoperiod responses were found in several cardiovascular and metabolic traits (Southwood et al., 2003). While we found no effect of photoperiod on whole-animal performance in zebrafish, it would be interesting to explore whether differences in the photoperiod treatments could be detected in physiological traits that underlie locomotor performance in this species.

As a result of choosing a tropical study species, our summer and winter appropriate acclimation temperatures were much higher than those used in past research. The cold acclimation temperature of 16°C used in this study was approximately  $\pm 1^\circ\text{C}$  from the summer acclimation temperature used for some temperate species (St-Pierre

et al., 1998; Day and Butler, 2005), and our study is also the first to test acclimation to multiple seasonal cues above 23°C (Guderley et al., 2001). Interestingly, Kolak (Kolak, 1991) found no effect of photoperiod for bass acclimated to spring conditions of 17°C in the field or to 15 or 19°C under controlled conditions. However, a large effect of photoperiod was found at cooler acclimation temperatures. These results suggest that long-range predictors of the environment may be more important during acclimation to colder temperatures.

In contrast to previous studies of cue variation, we tested the effect of multiple seasonal cues by comparing acclimated phenotypes as functional traits across a temperature range. The shape of the thermal performance functions differed between the thermal acclimation treatments for both traits. Thermal acclimation increased  $U_{\max}$  near the acclimation temperature but this resulted in a decrease in performance in temperatures far from the acclimation environment. A similar trade-off in escape performance at opposite ends of the thermal range has previously been described in fish and other ectotherms following thermal acclimation (Kaufmann and Bennett, 1989; Temple and Johnston, 1998; Wilson et al., 2000; Johnston and Temple, 2002). Voluntary performance traits, such as feeding rate, are not frequently studied as they are measures of aerobic performance that are largely motivationally based and do not represent maximum aerobic metabolic capacity (O'Steen and Bennett, 2003). However, these traits are likely to be important for overall fitness because they are routinely used for resource acquisition including both food and mates. In contrast, burst swimming performance is a largely anaerobically powered trait and ideally is a measure of an animal's maximum escape velocity with little error due to motivation. Differences in thermal performance functions between these traits are likely to reflect differences in the behaviour and physiological basis of each type of performance.

In summary, our study found no effect of the covariation between temperature and photoperiod cues on locomotor performance in zebrafish. Our results indicate that photoperiod may be a less important seasonal cue for fish living at lower latitudes.

#### ACKNOWLEDGEMENTS

We would like to thank Billy Bywater, Candice Bywater, Skye Cameron, Amanda Niehaus, Conor McMeniman and two anonymous reviewers for valuable comments on the manuscript.

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