

Response of largemouth bass (*Micropterus salmoides*) from different thermal environments to increased water temperature

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Abstract Due to concerns of global climate change, additional research is needed to quantify the thermal tolerance of species, and how organisms are able to adapt to changes in thermal regime. We quantified the thermal tolerance and thermal stress response of a temperate sportfish from two different thermal environments. One group of largemouth bass (*Micropterus salmoides*) inhabited thermally enhanced reservoirs (used for power plant cooling), with water temperatures typically 2–5 °C warmer than nearby reservoirs. We tested fish for chronic thermal maxima and reaction to an 8 °C heat shock using three common physiological indices of stress. We observed no evidence of differences between groups in thermal maxima. We observed no differences in thermal maxima between fish from artificially warmed and natural systems. Our results disagree with research, suggesting differences due to adaptation to different

thermal environments. We speculate that behavioral modifications, lack of adequate time for genetic divergence, or the robust genetic plasticity of largemouth bass explain the lack of difference between treatment groups.

Keywords Temperature tolerance · Heat shock · Largemouth bass · Plasma cortisol · Plasma glucose · Chronic thermal maxima

Introduction

Thermal tolerance assessments on individual fish and fish populations have been used to address a range of questions, including home-range expansion and contraction, and suitability of new habitats to colonization (Kimball et al. 2004; Dunham et al. 2003; Hostetler 1991). Knowledge of preferred temperatures is also important to the development of bioenergetics models (Chipps and Wahl 2008; Hansen et al. 1993). Intraspecific differences have also been used to answer questions concerning the effects of stressors (Morgan et al. 2001), latitudinal variation (Eliason et al. 2011; Fanguie et al. 2006), and effects of fish size (Rodnick et al. 2004). With the growing concern of impending climate change, temperature tolerances of many cold and cool water species have been used to predict effects on fish communities (Britton et al. 2010; Somero 2010; Mohseni et al. 2003; Eaton and Scheller 1996).

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Due to uncertainties concerning the effects of a changing climate on fish populations, evaluation of the stress response of organisms to environmental variables subject to shift in the near future is necessary. Predicting how organisms may respond to a warmer environment is also needed, and examining differences in populations from variable thermal regimes can inform these predictions. Beneficial acclimation theory suggests that fish from warmer systems will be best adapted to those systems (LeRoi et al. 1994) and therefore should demonstrate higher temperature tolerance and potentially a different physiological response to thermal stress than fish from cooler water bodies. However, there are questions concerning the generality of this theory (Huey et al. 1999). Chronic exposure to poor environments, potentially those with disruptively high temperatures, may cause a steady decrease in organismal condition (Woods and Harrison 2002) and mask any beneficial acclimation to the environment.

Predicting the effects of climate change, and how organisms may adapt, is also problematic because of difficulties recreating climate change scenarios to test hypotheses (Meyer et al. 1999). Most predictive studies are based on laboratory experiments and models, as forecasting changes to long-term temperature shifts is logistically difficult. For this study, we have proposed new study systems to be used as surrogates for aquatic environments affected by climate change. For decades, large reservoirs have been used to cool electric generators of power plants, causing water temperatures to be warmer than ambient. Research has demonstrated that power plant effluent can have effects on fish distribution and behavior (Cooke et al. 2004), reproductive success (Luksiene et al. 2000), and thermal tolerance (Meffe et al. 1995). However, using these warmed systems as a proxy for future lake conditions is a somewhat novel approach. The power plants on our study lakes have been in use for half of a century, so resident biota have been chronically exposed to a warmer, artificial temperature regime for decades. This makes these systems ideal for examining how organisms may be affected by a different temperature regime, since nearby lakes have fish communities with a similar genetic composition, but have had a different thermal experience for generations.

Many questions concerning the impacts of climate change on organisms are highly dependent on

characteristics of the organism in question. As climate regimes shift, organisms that are the most able to rapidly adapt physiologically (Hoffman and Sgro 2011; Somero 2010), or migrate to remain in optimal climates (La Sorte and Jetz 2012; Angert et al. 2011), will be the most successful in a changing world. Species currently inhabiting a wide range of habitats and temperature regimes are the most likely to exhibit these traits and are therefore excellent model organisms to study for physiological adjustments and tolerance to habitat variables. Largemouth bass, *Micropterus salmoides* (Lacepede 1802), are a prominent sportfish throughout North America and have been introduced worldwide. Although a temperate species, they have been shown to thrive in a variety of environments, from Canadian Shield lakes to Mediterranean wetlands (Page and Burr 2011; Scalici et al. 2009). Previous research has established that largemouth bass demonstrate plasticity sufficient to adjust its metabolic rate and temperature dynamics to maximize growth and survival in markedly different climates (Gaulke et al. In Press; Venables et al. 1977). Largemouth bass are likely to be better adjusted to deal with a changing climate than many other fishes, as their range and plasticity are traits needed to adapt to rapid change (Somero 2010). Like other widespread eurythermal species, largemouth bass also demonstrate significant phenotypic plasticity, as life history variation can be a consequence of different developmental environments (Meffe 1992). Because of the ability of this eurythermal fish to flourish in variable environments, it is an ideal candidate for studying the adaptive ability of a fish to a changing climate.

There have been a variety of methods used to characterize temperature tolerance and temperature-induced stress. Whole-body responses to temperature treatments have used thermal maxima treatments (first described by Cowles and Bogert (1944)) to ascertain tolerance. Typically, these types of experiments subject individuals to progressively greater temperatures until a response (loss of equilibrium or death) is induced. Because starting temperatures and rate of heating can be variable, the chronic thermal maxima of fish are relative values and artifacts of a given experimental design. However, it is an effective method for characterizing the temperature tolerance of fish (Becker and Genoway 1979) and commonly used to test for differences between fish species and populations (Galbreath et al. 2004; Currie et al.

1998; Fields et al. 1987). Another common practice to assess stress caused by disturbances such as elevated temperatures is to measure physiological parameters (Diaz et al. 2007; Suski et al. 2006; Vanlandeghem et al. 2010). For example, the steroid hormone cortisol, which promotes energy metabolism and is a widely used indicator of stress in fish (Wendelaar Bonga 1997), increases in fish exposed to a stressor, including hypoxia and undesirable temperatures (Vanlandeghem et al. 2010; Tanck et al. 2000; Cataldi et al. 1998), as well as angling, handling, and confinement (Rapp et al. 2012; Suski et al. 2003; Carmichael et al. 1984). Plasma hemoglobin and packed cell volume can also be informative for characterizing secondary responses to sub-lethal stressors (Furimsky et al. 2003), and blood glucose levels have also been shown to rise in response to acute temperature stress (Mesa et al. 2002).

Our goal was to evaluate the response of a temperate teleost fish to multiple temperature stressors from systems that differ significantly in their respective thermal regime. We used largemouth bass as our study organism and compared fish from artificially warmed systems to others from systems of similar size and location, but without an artificial thermal regime. We assessed fish for thermal maxima and three common physiological parameters associated with response to stressful conditions.

Methods

Study systems

To quantify differences in thermal tolerance between fish from different thermal regimes but similar latitudes, we used two artificially heated reservoirs. Clinton Lake (1983 ha., DeWitt Co., IL) and Newton Lake (688 ha., Jasper Co., IL) function as power plant cooling lakes and typically have water temperatures 2–8 °C greater than nearby water bodies (Fig. 1). The nuclear power plant at Clinton Lake has been in use since 1987, and the coal plant at Newton Lake has been operational since 1977. Each power plant lake was then paired with a control lake of similar size and location not receiving thermal effluent. Lake Shelbyville (4492 ha., Shelby Co., IL) was paired with Clinton Lake, and Forbes Lake (226 ha., Marion Co., IL) was paired with Newton Lake. Using a two-by-two

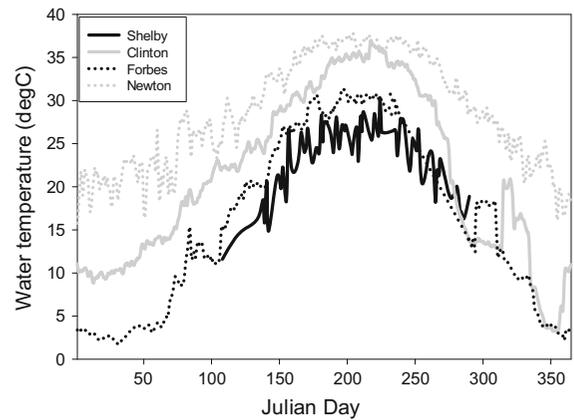


Fig. 1 Average annual temperature regime for heated (gray lines) and natural lakes (black lines)

experimental design, we were able to isolate the effects of thermal regimes on resident populations without the influence of regional differences.

Quantification of the temperature regime of each system was accomplished using temperature loggers (HOBO Pendant Temperature/Alarm Data Logger 8 K—UA-001-08, Onset Computer Corporation, Bourne, MA) stationed centrally in each lake at a depth of 1 meter. Loggers were active on Clinton Lake from 2009 to 2012, Newton Lake from 2003 to 2006, and Forbes Lake from 2006 to 2010, and were programmed to record temperature measurements every hour. Loggers were not installed on Lake Shelbyville, but temperatures at 1 m were taken biweekly from 1999 to 2012. Average temperatures for each Julian day were then calculated for each lake for standardization across years. Treatment lakes were about 5 °C warmer than controls during the summer and fall, and much greater (>7°) during the winter and spring (Fig. 1).

We chose largemouth bass (*Micropterus salmoides*) as our study organism due to their widespread range, prevalence in nearly all regional water bodies, and value as a sportfish (Schramm et al. 1991; Siepker et al. 2007). All bass used in experiments were collected using standard electrofishing procedures from 2009 to 2011, brought to the Kaskaskia Biological Station (Moultrie Co., IL) and acclimated for one to 3 weeks at 25 °C. Fish were captured in shallow, near-shore areas, and fish from heated systems were collected in the arm of the lake receiving effluent. To minimize differences associated with fish

size, all fish were between 250 and 370 mm. Fish were fed to satiation with fathead minnows (*Pimephales promelas*) three times per week and starved for 48 h prior to experimental use.

Thermal maxima

Thermal maxima experiments were conducted in an environmental chamber with temperature and light control. The chamber contained 16 (75 L) aerated aquaria wrapped in black plastic to eliminate visual disturbance. We chose to use a slow heating rate of 2 °C per day to determine chronic thermal maxima (Beitinger et al. 2000; Galbreath et al. 2006), as gradual heating rates are more sensitive for detecting differences between populations, specifically with fish of the same species (Galbreath et al. 2004).

Each trial included eight fish from one of the power plant lakes and eight fish from its associated control lake. Four trials were conducted so that each lake pair was completed twice. Because of inherent seasonal changes in physiology that influence thermal tolerance (Chipps et al. 2000), data analysis included each trial as a block. Because larger fish have been shown to sometimes have lower thermal tolerances (Currie et al. 1998; Rodnick et al. 2004), fish length was also recorded for use as covariate.

Experimental fish for each trial were randomly distributed among the environmental chamber aquaria and allowed to acclimate an additional 24 h at 25 °C. The treatment was then administered, and fish were checked every 4 h for loss of equilibrium, when time and temperature were recorded. Dissolved oxygen concentrations in the aquaria were also monitored, with lower oxygen concentrations observed at higher temperatures, mirroring natural processes (Cross and Rawding 2009). Throughout the trial period, 25 % of the water in each aquaria was replaced each day with fresh water of equal temperature. Each trial persisted until all fish had lost equilibrium.

Physiological comparison

Physiological parameters were measured in response to an acute 8 °C heat shock (25–33° C) sustained for six hours. The magnitude of the heat shock was chosen to be large enough to illicit a stress response, but based on preliminary trials not too severe to lead to mortality in largemouth bass. Although it is unlikely that fish

would encounter a rapid temperature increase of this magnitude in the wild, differences in physiological reaction may provide valuable insights on how these fish populations may respond to climatic changes (Somero 2011). The heat shock was administered by a closed-circuit system designed so that water temperatures in eight 18-L plastic aquaria could be closely regulated, similar to the methods used by Suski et al. (2007). Each aquarium was aerated, covered, and isolated from one another with plastic dividers so that treatment fish were not visually disturbed. Water from one of two large, central basins was pumped into all aquaria and allowed to overflow into fiberglass raceways holding these containers. The raceways then returned water to the central basin, thus closing the system. One basin contained water kept at 25 °C, and the other held heated water maintained at 33 °C. A valve in the flow-through system allowed for changing of the active basin.

Eight fish from each lake were randomly designated to receive the heat-shock treatment, and eight others were used as controls. Each trial could accommodate eight fish, so four fish from each lake of the two lake pairs were included in each experimental run that was either a control or heat-shock treatment. Experimental fish were placed into one of the eight aquaria and allowed to acclimate to the new environment, during which water was constantly flowing from the 25° basin. After 24 h of acclimation in heat-shock treatment runs, temperatures were quickly raised by 8° and held constant at 33° for 6 h. In control runs, temperatures were held constant at 25° for the complete 30-h period. After the allotted time, flow to individual containers ceased and each fish was euthanized with a lethal dose (250 mg/L) of 3-aminobenzoic acid ethyl ester methanesulfonate (MS-222) buffered with 500 mg/L of sodium bicarbonate (Summerfelt and Smith 1990). Following cessation of opercular movement, a 20-gauge hypodermic needle rinsed with lithium heparin (Houston 1990) was used to draw blood from the gill arch of each fish. To assess packed cell volume (PCV %), a portion of the blood was put into microcapillary tubes in duplicate and centrifuged at 15,800 rpm for 3 min using a hematocrit microcentrifuge, and the PCV % was ascertained using a hematocrit reader (CritSpin Models CS22 and CSD2, Iris International Inc., Chatsworth, CA). The remaining blood was centrifuged at 2,000 × gravity for 2 min to separate plasma from red blood cells. Plasma

was pipetted out and put into two 1.5-mL microcentrifuge tubes and then immediately stored in $-197\text{ }^{\circ}\text{C}$ liquid nitrogen until laboratory processing (Iwama et al. 1998). Plasma cortisol concentration was determined using a commercially available kit (Kit # 900-071; Assay Designs, Ann Arbor, MI, USA) previously validated for use on largemouth bass (Sink et al. 2008). Plasma glucose was determined enzymatically following the methods of Lowry and Passonneau (1972) using a spectrophotometer (Spectra Max Plus 384, Model # 05362; Molecular Devices, Union City, CA, USA).

Statistical analysis

For chronic thermal maxima analyses, time from beginning of a given trial to cessation of opercular movement was used as the response variable. Use of time instead of temperature eliminates error associated with minor deviations from the linear heating rate of $2\text{ }^{\circ}\text{C}/\text{day}$ as suggested by Galbreath et al. (2004). Because chronic thermal maxima trials were conducted at different times during the year, and because of seasonal variation expected in fish physiology and metabolism regardless of acclimation temperatures (Chippis et al. 2000), each trial was treated as a block. Because each trial only contained fish from one of the two possible lake pairs, a one-way analysis of variance (ANOVA) was conducted for each lake pair, blocked by trial, with fish length as a covariate, since fish size has been shown to influence thermal tolerance in some cases (Cook et al. 2006; Galbreath et al. 2006; Becker and Genoway 1979).

Because of the relative temporal proximity of trials assessing physiological response to heat shock, blocking by trial was ineffective and therefore not used in subsequent analyses. For each physiological variable measured, an ANOVA was conducted that included thermal environment and treatment type (heat shock vs. control) as binary class variables, the interaction between the two, and lakes nested within environments. In this way, we could test for differences in physiological parameters between thermal environments for baseline levels and the relative change in these levels between control and treatment trials. All statistical analyses were conducted using SAS statistical software, Version 9.3 (SAS Institute, Cary, NC, USA), and significance was determined at $P = 0.05$.

Results

No differences in fish length were observed between Clinton Lake and Lake Shelbyville ($P = 0.98$), or between Forbes Lake and Newton Lake ($P = 0.35$). Fish length was also tested as a covariate and was not different between thermal environments ($P = 0.98$). No significant differences were observed between fish from the different thermal environments in chronic thermal maxima (Fig. 2). Chronic thermal maxima experiments showed no significant differences between either lake pair. The average time until cessation of opercular movement was slightly greater for the warmed Newton Lake (156.2 h) than for the control lake of Forbes (144.8 h), but this difference was not statistically significant ($P = 0.16$, Fig. 2). The average times for thermally enriched Clinton Lake (137.6 h) and control Lake Shelbyville (139.3 h) were also not statistically different ($P = 0.75$, Fig. 2). For both comparisons, the blocking factors were highly significant. One trial was also conducted without the thermal treatment to test whether stress associated with confinement in experimental aquaria caused mortality independent of temperature. This trial lasted 168 h and did not result in mortality.

Physiological variables also showed no differences between heated and control lakes. PCV values were not statistically different between environments for baseline values ($P = 0.12$) or response to treatment ($P = 0.53$, Fig. 3). Cortisol levels were similar between environments for baselines ($P = 0.20$) and

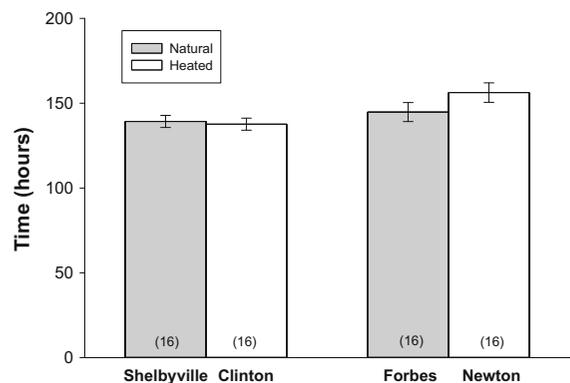


Fig. 2 Elapsed time from the onset of chronic thermal maxima experiments until cessation of opercular movement for largemouth bass (*Micropterus salmoides*) from natural (gray bars) and heated (open bars) lakes. Sample sizes (n) are included below each bar

reactions to heat shock ($P = 0.45$). Likewise, the heat shock did not induce different blood glucose responses ($P = 0.81$) nor were the initial baseline levels different ($P = 0.39$, Fig. 3). Among all fish, the heat shock caused a significant increase in blood glucose levels

($P = 0.04$), but there was no change in PCV ($P = 0.89$) or plasma cortisol ($P = 0.87$) as a result of the treatment.

Discussion

Contrary to our expectations, we saw little evidence of differences in thermal tolerance between fish from lakes with different thermal regimes. Based on the variables measured, we conclude that the populations assessed are not different in their response to rapid heat shock or to gradually rising temperatures. Other studies have suggested that animals raised at different temperatures should demonstrate different tolerance at some level (Ayrinhac et al. 2004; Sokolova and Portner 2003; Tomanek and Somero 1999). Our results also disagree with other studies examining response to thermal challenges for different fish populations of the same species, including research conducted on sockeye salmon (*Oncorhynchus nerka*) (Eliason et al. 2011) and tropical fishes (Newton et al. 2010).

Several plausible explanations exist for why largemouth bass populations from different thermal environments demonstrated similar thermal tolerance. Beneficial acclimation theory, suggesting that fish from warmer systems should perform better in tolerance tests due to their acclimation to higher temperatures, has been scrutinized and failed to have been supported in many cases (Woods and Harrison 2002; Huey et al. 1999). The ability to flourish in a variety of thermal environments has been linked to ideal temperatures during early life stages (Cohet and David 1978). The ‘optimal developmental temperature hypothesis’ could explain our results, if the temperature regime in power plant reservoirs is sub-optimal (i.e., too warm) during the early development of largemouth bass. Differences between populations may also not be present due to behavioral modifications of fish in the warmed environments, referred to as the Bogert effect (Huey et al. 2003). In the power plant lakes, resident fish may be actively avoiding uncomfortably warm water (Zimmerman et al. 1989; Block et al. 1984) and spawning earlier. This would ensure that young are past the critical development stage by the warmest summer temperatures. This seems likely because cooling reservoirs, including those in this study, are characterized as having a temperature

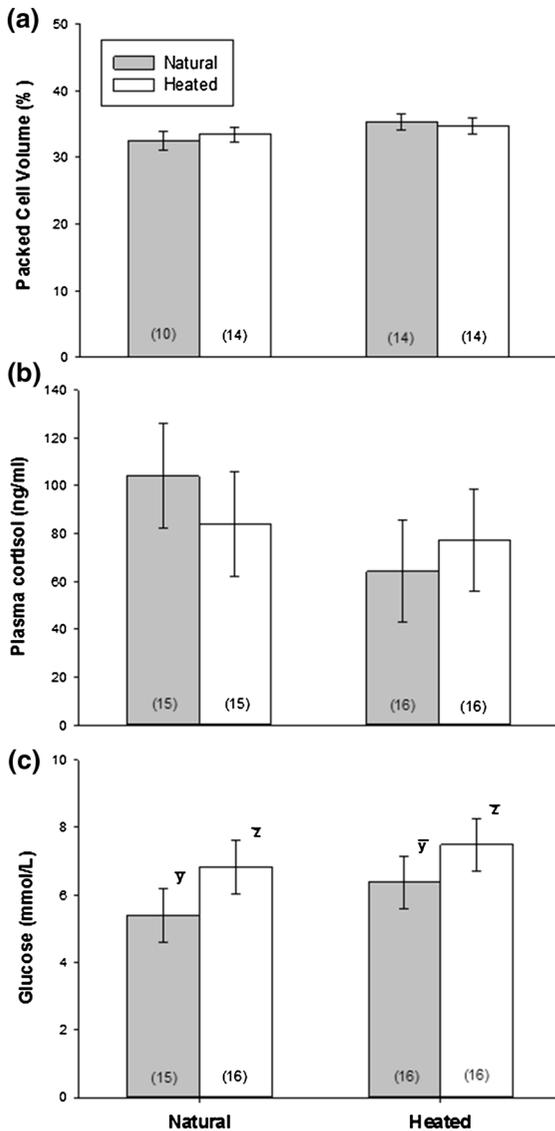


Fig. 3 Packed cell volume (a), and plasma cortisol (b) and glucose (c) concentrations of largemouth bass (*Micropterus salmoides*) held at a control temperature of 25 °C (gray bars) and heat shocked for 6 h at 33 °C (open bars). No significant differences existed between environments for either baseline values (control), or relative reaction to heat shock (treatment \times environment) in any of the measured variables. A significant positive effect of treatment on glucose concentration is indicated with different letters. Samples sizes (n) are included below each bar

gradient across the lake, in which the warmest temperatures are found at the effluent outflow, and gradually drop with distance from the outflow. Previous research has demonstrated that fish captured close to power plant effluent have lower body condition than fish captured farther away (Gibbons et al. 1978). Also, we have observed that juvenile bass are larger in the early summer in power plant lakes when compared to their cooler counterparts, possibly indicating that spawning occurs earlier in the power plant reservoirs (Mulhollem et al. 2014) or that food is more readily available to juvenile bass due to the altered thermal regime. We also may not have observed differences in the populations due to the relatively short evolutionary time scale (25–35 years) in which the power plants have been operating. Even if the unnatural temperature regime is causing changes in fish populations, it is possible that additional time is needed before changes are detectable.

It is possible that the populations differ in response to thermal stressors, but these differences were not measurable by our methods. Both of our techniques for determining temperature tolerance used a rapid change in temperature that is not necessarily indicative of the environmental conditions experienced by fish in cooling reservoirs. Largemouth bass are quite resilient in response to a moderate heat shock, and evidence suggests that short-term changes in physiological parameters may have returned to baseline levels during the six hour exposure to the stressor (Vanlandeghem et al. 2010). However, we induced a response in glucose that should have allowed us to detect differences if they existed. More lake pairs may be useful in eliminating random variation between populations, regardless of local thermal regime. Other physiological parameters may also identify differences that were undetected in our study. Heat-shock proteins, for example, initiate cellular responses as a result of a stressor and are not completely dependent on hormones released in the primary stress response (i.e., cortisol) (Iwama et al. 1998). Differences in heat-shock protein may exist between populations that may have masked differences in the variables we measured. Still, we would expect any physiological variation between the populations to be manifested in the whole-body temperature tolerance experiment, in which we detected no differences.

Our research demonstrated the plasticity in largemouth bass that may signify the ability of the species

to thrive despite a changing climate (Somero 2011). Fish taken from two distinctly different environments demonstrated little difference in their response to a thermal stressor and overall temperature tolerance. We speculate that similar studies with eurythermal species would generate similar results, potentially indicating the hardiness of the species to adapt to varying environmental conditions. Results contrary to ours, in which organisms of the same species but inhabiting different environments reacted differently to a stressor, may indicate that one (or both) populations are occupying a sub-optimal environment. This may suggest that a population is at or near a threshold for some environmental variable and that even minor changes in that variable could have significant effects on the population. Alternatively, it may simply mean that the two populations are genetically distinct stocks that have evolved to different environmental conditions.

Assessing thermal tolerance among organisms has resurfaced as an important research area due to growing concerns about global climate change (Portner and Knust 2007). It has been predicted that fishes most adaptive to changing temperature will be the most likely to flourish despite climatic changes (Matthews and Zimmerman 1990). Future research should focus on the fitness of fish species in response to shifts in thermal regimes, and how changing temperatures may affect populations in ways other than those measured here. Such areas of study include timing queues of reproduction and other life processes, as well as adjustments in behavior. Determining thermal thresholds, those at which significant impairment occurs, for different fish species is needed so that populations at risk can be identified and protected, particularly if local temperatures continue to rise.

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