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Effects of thermal increase on aerobic capacity and swim performance in a tropical inland fish

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ABSTRACT

Rising water temperature associated with climate change is increasingly recognized as a potential stressor for aquatic organisms, particularly for tropical ectotherms that are predicted to have narrow thermal windows relative to temperate ectotherms. We used intermittent flow resting and swimming respirometry to test for effects of temperature increase on aerobic capacity and swim performance in the widespread African cichlid *Pseudocrenilabrus multicolor victoriae*, acclimated for a week to a range of temperatures (2 °C increments) between 24 and 34 °C. Standard metabolic rate (SMR) increased between 24 and 32 °C, but fell sharply at 34 °C, suggesting either an acclimatory reorganization of metabolism or metabolic rate depression. Maximum metabolic rate (MMR) was elevated at 28 and 30 °C relative to 24 °C. Aerobic scope (AS) increased between 24 and 28 °C, then declined to a level comparable to 24 °C, but increased dramatically 34 °C, the latter driven by the drop in SMR in the warmest treatment. Critical swim speed (U_{crit}) was highest at intermediate temperature treatments, and was positively related to AS between 24 and 32 °C; however, at 34 °C, the increase in AS did not correspond to an increase in U_{crit}, suggesting a performance cost at the highest temperature.

1. Introduction

Over the past century global mean temperatures have risen significantly, as has the rate of global warming (IPCC, 2013). The persistence of species on a warming planet will depend on their capacity to shift their distributions to more favourable environments or adapt to their current environment through genetic change and/or phenotypic plasticity. An ectotherm's overall performance can be greatly influenced by environmental temperature (T_{env}) and therefore it is likely that this group will be particularly sensitive to climate change (McNab, 2002). The ability of an ectotherm to carry out vital functions over a range of temperatures is defined as their thermal performance window (Brett, 1971; Huey and Stevenson, 1979) that results from temperature-dependent trade-offs at all levels of functioning (Pörtner, 2010). Beyond the limits of their thermal windows (upper and lower critical temperatures), ectotherms will start to exploit their passive range of tolerance but can only do so for limited time because important processes (*e.g.*, feeding and reproductive behaviours), and thus their long-term fitness, are gradually reduced (Pörtner and Knust, 2007; Pörtner, 2010). Thus, with shifting thermal regimes due to climate change, ectotherms are at risk of being forced to perform at sub-optimal temperatures or at those beyond their thermal windows (Huey et al., 2009).

Tropical ectotherms may be particularly sensitive to climate warming relative to temperate species because they have evolved in a relatively aseasonal thermal environment, which may select for narrow thermal windows (Janzen, 1967; Huey and Hertz, 1984; Hoegh-Guldberg et al., 2007; Tewksbury et al., 2008). In addition, they may have a more limited capacity to adjust their thermal sensitivities and upper thermal limit *via* acclimation than temperate ectotherms, a trend supported in salamanders (Feder, 1982), *Sceloporus* lizards (Tsuji, 1988), porcelain crabs (Stillman, 2003), *Eucalyptus* trees (Drake et al., 2014), and cleaner shrimps (Rosa et al., 2014). Studies on various tropical ectotherms also indicate a relatively small or negligible “thermal safety margin”, characterized as the difference between the thermal optimum for performance and the average environmental temperature (Deutsch et al., 2008), meaning they may need to rely on behaviour to avoid overheating under high temperatures (Sunday et al., 2014). Thus, small increases in environmental temperature may pose a significant risk.

In aquatic systems, distributional shifts of ectothermic vertebrates associated with climate change suggest a strong pattern of poleward movement. Perry et al. (2005) determined that two thirds of 90 North Sea marine fish species, had undergone depth or latitudinal shifts in response to seawater temperature increases, specifically, deeper and/or northward. Additionally, in a recent study using distribution models to project effects of climate change, Jones and Cheung (2014) found that 93–97% of 802 species of harvested marine fish and invertebrate species were predicted to demonstrate poleward shifts to higher latitudes by

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the year 2059. These results for marine systems are striking; however, freshwater species may have fewer options for northern distributional shifts, since they are often trapped within landlocked water bodies and therefore are more likely to need to adapt and/or acclimate *in situ* to warming, and may experience a faster rate of warming than surrounding ocean waters (Kintisch, 2015). These trends highlight the need for studies targeting effects of warming on freshwater fishes, particularly in tropical latitudes, where ectotherms may be particularly sensitive to warming waters. Here, we address this need by quantifying effects of ecologically-relevant thermal increases on aerobic performance of a widespread freshwater tropical fish.

A key measure of metabolic performance in fishes is aerobic scope (AS), defined as the increase in fish's oxygen consumption from its standard (SMR) to maximal metabolic rate (MMR) (Fry, 1947, 1971). A large AS indicates that energy is available to fuel essential performance-related activities (*e.g.*, growth, reproduction), therefore changes in AS are predicted to influence overall fitness. AS is hypothesized to be tightly linked to the thermal window, described in a theoretical framework known as oxygen- and capacity-limited thermal tolerance (OCLTT) (Fry and Hart, 1948; Pörtner, 2001, 2010; Pörtner and Peck, 2010). OCLTT predicts that as temperature increases, oxygen delivery systems cannot keep pace with the rise in resting metabolism, and AS is expected to decline. The OCLTT concept has been successful in explaining changes in the distribution of eelpout *Zoarces viviparus* (Pörtner and Knust, 2007); in predicting success of spawning migrations in sockeye salmon *Oncorhynchus nerka* (Farrell et al., 2008); and in explaining variation in AS in coral reef fishes (Gardiner et al., 2010; Johansen and Jones, 2011; Rummer et al., 2014). However, some recent results are not in agreement with OCLTT predictions including recent studies on barramundi (*Lates calcifer* (Norin et al., 2014)), Atlantic halibut (*Hippoglossus hippoglossus* (Gräns et al., 2014)), python (*Python regius* (Fobian et al., 2014)), and a species of tropical freshwater shrimp (*Macrobrachium rosenbergii*, (Ern et al., 2014)), emphasizing the need for greater geographic and phylogenetic breadth in studies evaluating temperature effects on AS.

According to OCLTT, SMR increases at temperatures above T_{opt} in order to meet increasing aerobic energy requirements, which arise due to elevated cellular respiration, thereby driving the decline in aerobic scope (Pörtner, 2010). In support of this prediction, many studies using short-term acclimations have observed an increase in SMR in fish with increasing temperature (Ott et al., 1980; Claireaux and Lagardère, 1999; Lapointe et al., 2014). MMR represents the maximum metabolic rate (Fry, 1971; Beamish, 1978; Clark et al., 2011) and is often measured at the critical swimming speed of a fish during prolonged swimming (Schurmann and Steffensen, 1997; Korsmeyer and Dewar, 2001; Roche et al., 2013). OCLTT predicts that MMR will not increase significantly at temperatures beyond T_{opt}; thus AS will decline if SMR is positively correlated with T_{env} (Farrell, 2009). Studies testing this prediction across a wide temperature range are few, and patterns vary across studies and acclimation times. In their study of two cardinalfishes (*Ostorhinchus cyanosoma* and *O. doederleini*) and three damselfishes (*Dascyllus anuarus*, *Chromis atripectoralis*, and *Acanthochromis polyacanthus*) from the Great Barrier Reef, Australia, Nilsson et al. (2009) found that MMR did not increase or fell with 1-week acclimation to a range of temperatures between 29 and 33 °C. In contrast, Norin et al. (2014) reported an increase in MMR with temperature in barramundi (*Lates calcifer*) after short-term exposure, but found a 32% reduction in MMR after a 5-week acclimation. Interestingly, shorthorn sculpins (*Myoxocephalus scorpius*) also showed significant decrease in MMR after an 8-week acclimation period under high temperatures, which did not occur under shorter acclimation periods (1 or 4 weeks) (Sandblom et al., 2014). In this same study, however, an increased SMR measured after one-week acclimation to 16 °C was reduced after the 8-week acclimation, to levels similar to those measured at the pre-exposure temperature (10 °C).

Swimming is often a major component of the energy budget of active fishes; and high intensity swimming can comprise a very significant proportion of a fish's aerobic scope (Fry, 1971; Claireaux and Lefrançois, 2007). One of the most widely used swim performance metrics in fishes, critical swim speed (U_{crit}), is a useful measure of prolonged aerobic swimming capacity (Farrell et al., 1998; Kolok, 1999; Reidy et al., 2000; Plaut, 2001). U_{crit} is determined by forcing a fish to swim against a laminar flow in a swim tunnel while increasing the water velocity incrementally at regular time intervals until the fish fatigues (Brett, 1964; Beamish, 1978; Plaut, 2001). The effects of temperature on U_{crit} have been widely studied, with variable results from no temperature effect on U_{crit} (Jones et al., 1974; Kieffer et al., 1998), increased U_{crit} with rising temperature acclimation (Beamish, 1978; Keen and Farrell, 1994; Adams and Parsons, 1998); and the highest U_{crit} at intermediate water temperatures (Taylor et al., 1996).

Measuring these metabolic and performance parameters in parallel across a wide thermal range provides an excellent opportunity to (1) test a series of predictions of OCLTT framework in a tropical freshwater fish and (2) determine thermal sensitivities of a suite of important physiological factors involved in whole-fish functioning. In this study we measured the effects of ecologically-relevant thermal increases on aerobic metabolism (AS, SMR, MMR) and U_{crit}, in a widespread African cichlid, *Pseudocrenilabrus multicolor victoriae* Seegers. We predicted (a) AS would decrease with increased acclimation temperature, primarily driven by a rise in SMR and (b) U_{crit} would peak at intermediate acclimation temperatures and decline at high temperatures due to the predicted decline in AS.

2. Methods

2.1. Study species and sites of origin

Pseudocrenilabrus multicolor victoriae is a small African cichlid fish, found throughout the Lake Victoria basin of East Africa across habitats that encompass a broad thermal range from 18.1 °C in the dense interior of papyrus swamps to 30.8 °C (Chapman et al., 2002; Friesen et al., 2012) in warm ecotonal waters of lakes. This study measured the effect of temperature on aerobic performance in laboratory-acclimated stock *P. multicolor*. We used only male *P. multicolor*, because the metabolic rate is significantly elevated in brooding females relative to non-brooders and males (Reardon and Chapman, 2010). To achieve a sample size of male *P. multicolor* adequate for our repeated measures study, we used six males caught from the Bwera site within the papyrus (*Cyperus papyrus*) dominated Kiaraguru Swamp of the Mpanga River system of western Uganda (0°0′34.55″S, 29°43′52.98″E) and three males from Lake Kayanja, where *P. multicolor* can be found in the ecotonal waters adjacent to *Miscanthidium*-dominated swamp (0°16′60.00″S, 31°52′ 0.00″E). Water temperature and dissolved oxygen (DO) at the Bwera site averages 21.7 °C (range = 17.3 to 25.7 °C) and 0.28 mg L^{-1}, respectively (Crispo and Chapman, 2010; Friesen et al., 2012); while at the Lake Kayanja ecotone, water temperature and DO are both higher, 25.3 °C (range = 21.6 to 31.1 °C) and 6.97 mg L^{-1}, respectively (McDonnell and Chapman, 2015). *P. multicolor* were live-transferred to McGill University in either July 2011 (Bwera) or July 2013 (Kayanja). Fish were held under normoxic conditions (>6.5 mg L^{-1}) at 23 °C (range = 22.2 to 23.6 °C), a temperature approximating the average temperature of the two sites for at least six months prior to initiating the thermal acclimation protocol described below, and they were held close to these levels between transfer from Uganda and initiation of the six-month common acclimation period. In common garden experiments, *P. multicolor* from both sites reared under high or low DO have demonstrated high levels of phenotypic plasticity in morpho-physiological and biochemical traits to their environments, and therefore a six-month holding period should have reduced population effects related to their habitat of origin (Chapman et al., 2000, 2002, 2008; Martínez et al., 2009; Crispo and Chapman, 2010; Crocker et al.,