



# The influence of lifestyle and swimming behavior on metabolic rate and thermal tolerance of twelve Amazon forest stream fish species



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## ARTICLE INFO

### Keywords:

Tropical fishes  
Factorial aerobic scope  
Lifestyle  
Stenothermal

## ABSTRACT

The metabolism of fishes is profoundly affected by environmental factors such as temperature, oxygen concentration, and pH levels. Also, biotic elements, for instance, activity levels of species, have been suggested to affect the energy demand, driving their capacity to support environmental challenges. The present work aims to investigate the effects of the lifestyle and swimming activities levels of fishes living in Amazon forest stream on the aerobic metabolism and thermal tolerance. Intermittent flow respirometry was used to measure routine metabolic rate and thermal maximum metabolic rate with a thermal ramp methodology. Critical thermal tolerance, thermal aerobic scope, and thermal factorial aerobic scope were calculated for twelve species belonging to different families. Our findings showed a correlation between routine and thermal maximum metabolic rate and, between metabolic rate and activity levels. Species belonging to Characidae and Crenuchidae families have high resting metabolic rates, which decrease their factorial aerobic scope and reduce their abilities to cope with warming events. Therefore, these species have low thermal tolerance. Instead, species from families Rivulidae and Cichlidae showed opposite metabolic results and larger thermal windows. We hypothesize that these responses are related to an evolutionary trade-off between lifestyle and energetic requirements and warming will favor species with low activity performance.

## 1. Introduction

Aerobic plasticity is particularly important to animal performance with potential implications for growth rate, reproduction and survival (Clarke, 2004; Killen et al., 2010; Metcalfe et al., 2016). The aerobic metabolism of ectothermic animals is affected by environmental factors such as temperature, oxygen concentration, and pH levels (Clarke and Fraser, 2004; Clarke and Pörtner, 2010; Kochhann et al., 2015). In Addition, biotic factors have been suggested to affect the routine and maximum metabolic rate, driving animal abilities to face environmental challenges. For instance, fishes living in the deep ocean have lower resting metabolic rates than those living in more shallow waters, possibly because they have lower energetic requirements to avoid predation (Clarke and Johnston, 1999; Seibel and Drazen, 2007). Thus, more active species tend to have a higher routine and maximum metabolic rates; these traits allow a greater absolute aerobic scope, and hence more active lifestyles (Clarke, 2004). These metabolic differences may be caused by variation in mitochondrial concentration or membrane proliferation, but also by higher costs of cardiovascular work or muscle tonus that improve athletic performance (Morris and North, 1984; Zimmerman and Hubold, 1998). A higher metabolic rate may

also allow a rapid response to an environmental challenge. However, if this is an evolutionary advantage, it remains in a great discussion, since an elevated aerobic capacity demands important energy costs, which may cause a limitation of factorial aerobic scope (Killen et al., 2010; Stoffels, 2015).

Limitations on aerobic scope have been pointed out as a factor that constrains the ability of an organism to perform various ecological functions, what led to the hypothesis that fishes living at the boundaries of their thermal limits are unable to maintain sufficient oxygen supply for their routine metabolism due to the temperature-induced cardiorespiratory constraints (Pörtner and Knust, 2007; Farrell, 2007; Eliason et al., 2011). According to the so-called OCLTT (oxygen- and capacity-limited thermal tolerance) hypothesis, the aerobic scope is limited by insufficient oxygen supply at both sides of the thermal window and sets the performance in animals, with an optimum close to the upper pejus temperature ( $T_p$ ) (e.g., Pörtner and Knust, 2007; Pörtner and Farrell, 2008; Pörtner et al., 2010). Therefore, it provides access to understanding the physiological mechanisms that limit the performance, integrating whole-organism and tissue levels. Thermal limitation results from insufficient capacity reflected in a decrease in systemic oxygen levels (hypoxemia) and, finally, a transition to anaerobic metabolism.

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Consequently, the organismal thermal tolerance is determined by the animal ability to extract oxygen and to efficiently deliver it to tissues. Accordingly, an optimization of species oxygen supply mechanisms that can be translated in high aerobic scope would bring it a broader thermal tolerance window (Pörtner, 2001; Claireaux and Lefrançois, 2007; Pörtner and Farrell, 2008; Farrell et al., 2008; Cucco et al., 2012). However, the potential relationship between lifestyle and aerobic plasticity, which might set the thermal tolerance in stable habitats, has not been studied.

Thermal limits have been considered one approach to compare the physiological mechanism of adaptation between species and has been extensively applied to investigate the thermal ecology in congeneric species inhabiting thermal gradients (Hochachka and Somero, 2002; Gilman et al., 2006; Helmuth et al., 2006; Helmuth, 2009; Campos et al., 2017). It is well known that fishes experiencing high seasonal thermal variations in their habitats show higher metabolic plasticity and a wider thermal window (Magozzi and Calosi, 2014). Unlike seasonal environments, Amazonian forest stream areas form complex hydrological networks (Junk, 1983) with the vast majority running through the dense forest and presenting high oxygen concentration and small temperature variation (range between 25 and 28 °C) (Espírito-Santo et al., 2009; Costa et al., 2015). Temperature is predicted to increase up to 4 °C due to climate change and may reach a 7 °C increase in some areas of the Earth Planet (IPCC et al., 2014). As described to other tropical fishes (Tewksbury et al., 2008) we might expect that Amazonian species will be vulnerable to such changes, once they evolved in a relatively stable thermal environment, and supposedly live close to the thermal maxima.

Amazon forest streams are stable thermal habitats that contain one of the greatest diversity of fish species in the world with different lifestyles which results in different energy plasticity. Such ecological difference in energy demands may influence their oxygen supply and delivery capacities, playing a pivotal role in determining their thermal limits. In the present work, we investigated the potential effects of lifestyle and swimming behavior on metabolic rate and thermal tolerance of Amazon stream fishes, a group that presents great ecological niche diversity. These characteristics make these fish species ideal for examining the constraints of ecological influences on metabolic rate and thermal tolerance. Herein, we considered the difference in routine metabolic rate and thermal maximum metabolic rate of twelve fish species of first- and second-order streams and correlated this parameter to species' swimming activities levels and their consequence to thermal limits. The present work aimed to determine the critical thermal maximum of fish of Amazon forest streams, and verify if the effects of metabolic rate on their thermal tolerance are related to their lifestyles and swimming behavior.

## 2. Materials and methods

### 2.1. Collection and maintenance of fish

The study was conducted in first- and second-order streams (*sensu* Petts, 1994) at Reserva Ducke (02°53'S, 59°58'W), a protected area located in the central Brazilian Amazon near the confluence of the Negro and Solimões rivers and bordering Manaus. Fish were collected by hand and seine nets (2-mm mesh); the stream extent (1 m ± 0,5) was closed at its margins with block nets (5-mm mesh) to prevent fish movements into or out of the reach; the operators then moved upstream along the range attempting to cover all areas systematically within 1-h period, fishes were also collected in ponds with hand nets (Mendonça et al., 2005). Captured fish were maintained in a container with stream water and aeration. Then they were transferred to 150-L tanks (Fortlev®) with constant aeration until experiments started. Half of the water was replaced every 12 h. The fish were maintained in this resting tank for at least 48 h, to avoid measuring metabolic rate during the digestion phase. The temperature was 25 ± 0.5 °C. All experimental

setups were conducted with stream water in the Reserva Ducke laboratories. The experimental sets are in accordance with CONCEA Brazilian Guide for Animal Use and Care and were authorized by INPA's Council for Ethics in Animal Use (CEUA - protocol number 027/2015).

### 2.2. Metabolic rate in a thermal ramp

We measured routine metabolic rate in a thermal ramp with the use of Intermittent-flow respirometry in an automated apparatus DAQ-M (Loligo Systems, Tjele, Denmark) in individuals (n = 8–6) of each of the twelve species collected. This apparatus consists of a recirculating circuit with three phases: flush, wait, and measurement. The time phases were 180 s flush, followed by 120 s wait, and 600 s measurement. Thus, the duration of an entire 'loop' (flush + wait + measurement) was 15 min. The fall of oxygen inside the chamber never dropped more than 1 mg l<sup>-1</sup> at each loop. The experimental sets were made for each single species, where fishes were individually placed in a 70-mL respirometer chamber immersed in a larger water bath containing a heater with digital thermostat to control temperature (TIC-17RGT, FullGauge, ± 0.01 accuracy) and left for six hours to handily recovery at the natural temperature of streams (25 °C). Subsequently, the metabolic rate was measured for four loops (routine metabolic rate) and the thermal ramp was initiated with an increase of 0.25 °C at each loop (15 min) of recirculating circuit reaching 1 °C h<sup>-1</sup> following the protocol suggested by Vinagre et al. (2014) and tested by Campos et al. (2016) to tropical fishes. Thermal limits were estimated using critical thermal methodology (CTM) (Lutterschmidt and Hutchison, 1997). The critical thermal maximum was defined as the temperature at which 50% of fish presented a final loss of equilibrium, or LOE (inability to maintain dorsal-ventral orientation for at least 1 min, Beitinger et al., 2000). After the thermal ramp, fish were allowed to recover in rest tank with streams temperature water and, after 24 h, all fish were returned to their environment.

In the present work, we refer to routine metabolic rate (mean values at 25 °C) measured at the acclimatization temperatures of the Amazonian streams (25 °C) during the thermal ramp assay as RMR. TMMR refers to the maximum metabolic rates observed during this thermal ramp, which, in this work, occurred before thermal limits. The difference between TMMR and RMR is termed as *Tscope* based on former work of Jayasundara and Somero (2013). Factorial aerobic scope (FAS) was calculated as the ratio of TMMR to RMR (TMMR: RMR) for each individual. According to these authors, this approach assumes that the increase in oxygen consumption is exclusively due to the effects of temperature variations on metabolic processes and it is useful to test thermal limitations based on oxygen supply.

### 2.3. Measuring swimming activity levels on Amazonian streams fishes (lifestyles and swimming behavior)

Morphology data have been extensively used as a proxy to predict fundamental niche of fish species in streams; caudal fin morphology has been specially applied in studies investigating swimming behavior (or capacity). Caudal fin aspect ratio describes the shape of the tail, which is used to propel fish while swimming and is a correlate of average activity level across fish's species (*sensu* Pauly, 1989). It is calculated as

$$A = h^2/s$$

where *A* is the aspect ratio, *h* is the height of the caudal fin, and *s* is the square area of the caudal fin. Caudal fin aspect ratio is directly correlated with activity levels in fish species and has been used as a powerful index of lifestyle and swimming behavior, where high values indicate high swimming activity levels (Pauly, 1989).

### 2.4. Statistical analyses

Statistical analyses were performed through Sigma Stat software

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