Comparative Biochemistry and Physiology, Part A 195 (2016) 32–38

Contents lists available at ScienceDirect

Comparative Biochemistry and Physiology, Part A

journal homepage: www.elsevier.com/locate/cbpa

The effect of temperature on postprandial metabolism of yellowfin tuna (*Thunnus albacares*)

Dane H. Klinger [a,*], Jonathan J. Dale [b], Adrian C. Gleiss [b], Tyler Brandt [c], Ethan E. Estess [c], Luke Gardner [b], Benjamin Machado [b], Alex Norton [c], Luis Rodriguez [c], James Stiltner [c], Charles Farwell [c], Barbara A. Block [b]

[a] Emmett Interdisciplinary Program in Environment and Resources, Stanford University, Stanford, CA 94305, USA
[b] Department of Biology, Hopkins Marine Station, Stanford University, Pacific Grove, CA 93950, USA
[c] Tuna Research and Conservation Center, Monterey Bay Aquarium, Monterey, CA 93940, USA

ARTICLE INFO

Article history:
Received 13 October 2015
Received in revised form 5 January 2016
Accepted 7 January 2016
Available online 12 January 2016

Keywords:
Digestion
Energetics
Respiration
SDA
Temperature
Thunnus albacares
Yellowfin tuna

ABSTRACT

Specific dynamic action (SDA), the increase in metabolic expenditure associated with consumption of a meal, represents a substantial portion of fish energy budgets and is highly influenced by ambient temperature. The effect of temperature on SDA has not been studied in yellowfin tuna (*Thunnus albacares*, Bonnaterre 1788), an active pelagic predator that occupies temperate and subtropical waters. The energetic cost and duration of SDA were calculated by comparing routine and post-prandial oxygen consumption rates. Mean routine metabolic rates in yellowfin tuna increased with temperature, from 136 mg O_2 kg^{-1} h^{-1} at 20 °C to 211 mg O_2 kg^{-1} h at 24 °C. The mean duration of SDA decreased from 40.2 h at 20 °C to 33.1 h at 24 °C, while mean SDA coefficient, the percentage of energy in a meal that is consumed during digestion, increased from 5.9% at 20 °C to 12.7% at 24 °C. Digestion in yellowfin tuna is faster at a higher temperature but requires additional oxidative energy. Enhanced characterization of the role of temperature in SDA of yellowfin tuna deepens our understanding of tuna physiology and can help improve management of aquaculture and fisheries.

1. Introduction

Yellowfin tuna (*Thunnus albacares*, Bonnaterre 1788) occupy a pelagic habitat primarily inclusive of warm temperate to tropical waters around the globe (Block and Stevens, 2001; Miyake et al., 2010) and are among the fastest growing members of the family Scombridae (Juan-Jordá et al., 2013). Like all tunas, they move with a unique thunniform mode of swimming that enables tuna to efficiently cross large expanses of ocean. Yellowfin have higher metabolic rates than ectothermic members of the family Scombridae (Blank et al., 2007a; Korsmeyer and Dewar, 2001) and have significant cardiac capacity, with specializations that improve frequency of heart rate (Graham and Dickson, 2004). Yellowfin tuna also utilize both warm surface waters and the cooler mixed layer (Block and Stevens, 2001; Graham and Dickson, 2004; Shadwick et al., 2013; Weng et al., 2009). These adaptations may allow for increased foraging rates and, as such, digestion likely plays an important role in the total energetic budget of yellowfin.

Specific dynamic action (SDA) describes the metabolic processes of digestion and refers to the increase in metabolism associated with "ingestion, digestion, absorption and assimilation of a meal" (Secor, 2009). SDA represents a substantial portion of fish energy budgets and often accounts for up to 50% of total metabolic expenditure and 20% of ingested energy (Secor, 2009). Multiple factors influence SDA, including meal composition, meal type, meal size, body size, and temperature (Secor, 2009; Wang et al., 2001), although temperature is often considered a primary determinant (Jobling, 1981).

The characteristics of SDA that are known to be affected by temperature include peak metabolic rate during digestion, duration of SDA, factorial scope (peak metabolic rate divided by the fasted metabolic rate), and SDA coefficient (the percentage of meal energy consumed in SDA)(McCue, 2006). In most fish, increased temperatures result in elevated routine metabolic rates, elevated peak metabolism during SDA, and decreased duration of SDA (as reviewed in McCue, 2006; Secor, 2009; Secor, 2011; Seth et al., 2011). Factorial scope does not change with temperature, as both routine metabolic rate and peak metabolism increase with increasing temperature, except where an organism is near the edge of its thermal tolerance range and total aerobic scope is limited (Secor, 2009). The influence of temperature on the SDA coefficient varies between species, with studies reporting no effects (Frisk et al., 2013; Jobling and Davies, 1980; Johnston and Battram, 1993; Peres and Oliva-Teles, 2001; Pérez-Casanova et al., 2010; Pirozzi and Booth,

Abbreviations: SDA, Specific dynamic action; RMR, Routine metabolic rate; SMR, Standard metabolic rate; $\dot{M}o_2$, Oxygen consumption rate; $\dot{M}o_{2peak}$, Peak metabolic rate during digestion; $\dot{M}o_{2dur}$, Duration of postprandial metabolic increase.

* Corresponding author at: Department of Ecology and Evolutionary Biology, Princeton University, Princeton, NJ, 08544, USA.
E-mail address: dklinger@princeton.edu (D.H. Klinger).

http://dx.doi.org/10.1016/j.cbpa.2016.01.005
1095-6433/

2009), increases (Guinea and Fernandez, 1997; Khan et al., 2015; Luo and Xie, 2008; Pang et al., 2010; Peck et al., 2003; Tirsgaard et al., 2014; Vanella et al., 2010; Yang and Xu, 2011), and decreases (Cui and Wootton, 1988; Yang et al., 2014) in SDA coefficients with increased temperatures. Direct comparison among species is complicated by variation in study designs, including different meal types, respiration equipment and protocols, and environmental conditions.

Despite their importance in energy budgets, SDA and the effects of temperature on SDA have not been measured in yellowfin tuna (see Clark, 2015 for a review of tuna energetics). This is in part due to the challenges of holding pelagic tunas in captivity and conducting metabolic experiments. SDA has recently been measured in two other *Thunnus* species, Pacific bluefin (*Thunnus orientalis*) and southern bluefin (*Thunnus macoyii*) (Clark et al., 2010; Fitzgibbon et al., 2007). Bluefin tunas serve as an informative comparison to yellowfin tuna due to the substantial differences in their physiology (Blank et al., 2007a) and because both bluefin and yellowfin tunas are candidate species for aquaculture (Carter et al., 2010; Masuma et al., 2011). Bluefin tuna are more endothermic than yellowfin tuna (Dickson and Graham, 2004) and employ greater use of countercurrent heat exchange to capture heat in their viscera, brain, eyes, and muscles (Block and Stevens, 2001). Recent studies of wild yellowfin tuna have shown that they inhabit warmer temperatures than bluefin tuna (Schaefer et al., 2011, Block et al., 2011). Endothermy allows bluefin tuna to forage actively in cold waters (Carey and Teal, 1966) but also results in metabolic rates that are on average 20% higher than similarly sized yellowfin tuna, measured at 20 °C (Blank et al., 2007a).

In experiments conducted at similar temperatures, Clark et al. found that SDA in *T. orientalis* accounted for 9.2% of the energy ingested (Clark et al., 2010), while Fitzgibbon et al. found that SDA in *T. macoyii* accounted for 35% of the energy ingested (Fitzgibbon et al., 2007). Pacific and southern bluefin tuna are closely related species (Collette et al., 2001), and the discrepancy in these measurements is likely a result of different experimental designs and equipment. Specifically, Clark et al. used an 871 L intermittent-flow, swim tunnel respirometer to measure postprandial metabolism in individual tuna at a controlled swimming speed, while Fitzgibbon et al. used a 350,000 L mesocosm respirometer with small groups of tuna that were able to swim at a variety of speeds (Clark et al., 2010; Fitzgibbon et al., 2007). The discrepancy may be explained by the resulting difference in the ratio of tuna mass to water volume (1:86 in Clark et al. vs. 1:12,000 in Fitzgibbon et al.) (Clark et al., 2010) or the different behavioral patterns and swimming speeds in Fitzgibbon et al. as tuna interacted with conspecifics in the mesocosm, potentially increasing oxygen consumption.

In this study, intermittent respirometry at a controlled swimming speed is used to determine fasted and digesting oxygen consumption rates. The influence of temperature on SDA (SDA peak, duration, factorial scope, and coefficient) is tested and compared to other fish species, including other *Thunnus* species. An improved understanding of SDA in yellowfin can help inform better management of yellowfin tuna aquaculture and fisheries.

2. Materials and methods

2.1. Animal capture and handling

Ten yellowfin tuna were caught in the California Current between July and September in 2010 (4 fish), 2012 (3 fish), and 2013 (3 fish). Surface temperatures at collection locations were between 18 and 22 °C. Experiments were conducted within 9 months of collection from the wild. For a detailed description of tuna collection techniques and husbandry practices see Farwell (2001). In brief, wild tuna were collected onboard the F/V Shogun with rod and reel and barbless hooks. Tunas were held on board the vessel for several days in circulating wells with seawater, before being transported to the Tuna Research and Conservation Center (TRCC) in Monterey, CA, USA, in a trailered transport tank. At the TRCC, fish were maintained in a 109 m^3 holding tank and fed a mix of sardines, squid, and vitamin-enriched gelatin three times per week at a target diet of 176 kJ per kg. Fish were acclimated to the TRCC tank for at least 3 months before experiments began. For identification, individual fish were tagged with passive integrated transponder tags (Avid Identification Systems, California, USA) and external identification tags (Hallprint Tags, Victor Harbor, Australia) in the dorsal musculature. Mean (±S.E.M.) body mass and body length (BL) of the ten fish were 8.3 ± 0.4 kg and 76.4 ± 1.6 cm, respectively. All procedures were approved by the Stanford University Animal Care and Use Committee.

2.2. Respirometry and fish training

Respiration trials were conducted in an intermittent flow swim tunnel respirometer (modified from Loligo Systems, Tjele, Denmark) that has been described previously (Blank et al., 2007a; Blank et al., 2007b; Clark et al., 2010). The respirometer had a volume of 871 L and working section size of 135 cm × 45 cm × 45 cm (length × width × depth), with a removable lid for introduction and removal of the fish. The entire respirometer was submerged in a 1500 L reservoir for thermal insulation. Water velocity in the flume was maintained by a propeller and variable-speed motor, and swimming speeds in all experiments were maintained at 1 body length per second (BL s^{-1}). The solid blocking effect of individual fish was factored into velocity calculations, as described by Bell and Terhune (1970) and Blank et al. (2007a). The respirometer had intermittent flow, meaning it was repeatedly flushed for 10 min with seawater saturated with air and then sealed for 10 min. The concentration of dissolved oxygen was measured with a fiberoptic dipping probe (Presens, Germany). Oxygen consumption rates ($\dot{M}o_2$) were determined based on the decline in dissolved oxygen concentrations in the respirometer during the 10 min closed periods. Intermittent flow enables measurements to be taken over an extended period of time without depleting dissolved oxygen concentrations in the respirometer below normoxic concentrations.

To conduct an SDA experiment, a yellowfin tuna swimming in the 109 m^3 holding tank was captured by lowering the water level of the entire tank to less than a meter and a small school or an individual fish was corralled with a vinyl crowder (see Farwell, 2001) and then caught in an envelope of water held by a vinyl sling with two experienced handlers. The fish was never touched and was transferred in the water-filled vinyl sling. The sling was passed to two researchers who then transferred the fish from the sling to the respirometer. The respirometer and reservoir were surrounded by plastic blackout curtains to eliminate external stimuli, such as light and movement.

Swim tunnel experiments with individual fish can be technically difficult (Ellerby and Herskin, 2013). As such, the tuna used in this experiment were 'trained' in the respirometer following a protocol developed in previous individual tuna respirometr studies (Blank et al., 2007a; Blank et al., 2007b; Clark et al., 2010). During training, tunas were introduced to the respirometer and observed closely for 4–8 h to ensure the acclimation and safety of the tuna. For each tuna that was able to acclimate to the respirometer and maintain steady swimming, 1–2 did not swim well and could not be used in the experiments.

2.3. Experimental protocol

Each fish was subjected to both a 'fasted' and 'digesting' respiration trial. In the fasted trial, fish were not fed for 48–72 h and were then transferred to the respirometer by the same protocol used in training. To measure routine oxygen consumption, the fasted, "trained" fish remained in the respirometer for 48 h, swimming at 1 BL s^{-1} in 20 °C (N = 7) or 24 °C (N = 3) seawater. For each temperature treatment, fish were acclimated to either 20 or 24 °C in the 109 m^3 holding tank for at least 3 weeks.