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

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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.

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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.

Table 1
Nutritional content of squid (*Loligo opalescens*) and sardines (*Sardinops sagax*) fed to yellowfin tuna (*Thunnus albacares*), relative to wet mass.

	2010		2013		2014	
Constituent	Squid	Sardine	Squid	Sardine	Squid	Sardine
Lipid (%)	2.0	18.1	1.5	18.6	2.0	8.3
Protein (%)	16.7	11.3	14.3	14.3	18.0	18.4
Energy (kJ kg^{-1})	4677	9064	3684	9747	4840	7051

For the digesting trials, which were conducted at least one week after the fasted trials, fish were fed in the 109 m^3 holding tank, one piece of food with a known mass at a time, while observers monitored how many pieces were consumed by individual fish. Fish were fed a mix of market squid (*Loligo opalescens*) and Pacific sardines (*Sardinops sagax*). The mass of each piece of food was determined prior to feeding and the energy content of different food types was determined by proximate analyses and bomb calorimetry of subsamples (Table 1; N.P. Analytical Laboratories, St. Louis, MO, USA). The mass ingested and the energy content of individual food types were used to determine the meal intake as a percentage of the tuna's body mass and the kJ consumed. Fish could not be fed in the respirometer or placed in the respirometer immediately after feeding due to equipment and experimental constraints. To avoid regurgitation of food pieces, tunas were not handled until 60–120 min after feeding. Tunas were then transferred to the respirometer by the same protocol used in training and fasted trials. No tunas regurgitated their meal using this protocol. Measurements began shortly after introduction to the respirometer and tuna remained in the respirometer for 48 h, swimming at 1 BL s^{-1} in 20 or 24 °C seawater, to measure the $\dot{M}o_2$ during digestion.

Tailbeat frequency was measured by an observer through live video display of the tuna from a camera placed above the working section of the respirometer. Each hour, three counts of sixty tailbeats were timed to calculate the number of tailbeats per minute. The average of the three counts was taken as the observed tailbeat frequency (Blank et al., 2007a; Clark et al., 2010).

2.4. Data analyses and statistics

For the purposes of comparing SDA in yellowfin and bluefin, data analyses were similar to those used by Clark et al. to measure SDA in bluefin tuna (Clark et al., 2010). For each fish, routine metabolic rate (RMR) was calculated as the lowest mean $\dot{M}o_2$ over a continuous 3 h period during the fasted trial. Peak metabolic rate during digestion ($\dot{M}o_{2peak}$) was calculated as the highest mean $\dot{M}o_2$ during any 3 h period, post-feeding, once $\dot{M}o_2$ stabilized after transport to the respirometer (typically starting ~30 min post-transport). The duration of postprandial increase in $\dot{M}o_2$ ($\dot{M}o_{2dur}$) was calculated as the time between cessation of feeding and the return of $\dot{M}o_2$ to RMR levels, when digestion was considered to be complete. $\dot{M}o_2$ was considered to be at RMR levels when two criteria had been met: First, individual $\dot{M}o_2$ measurements for a fish were within one standard deviation of the RMR recorded during the fasted trial for that fish, and second, the slope of $\dot{M}o_2$ relative to time over a 3 h period was no longer negative.

SDA was calculated in two parts. First, the primary component of SDA (SDA_{part}) was calculated as the amount of energy expended above RMR during the digesting trial, once the fish was introduced to respirometer. There was a clear and easy to measure signal from the SDA event in all yellowfin tuna. However, the period immediately following consumption of food in the tank and before introduction to the respirometer (1.65 ± 0.17 h) was not directly measured, and we followed the convention of Clark et al. (2010) and modeled this short period as a linear increase from RMR to $\dot{M}o_{2peak}$. Both SDA_{part} and SDA with the estimated pre-respirometer period are reported. The SDA coefficient was calculated as the percentage of energy from a meal that was expended during SDA. $\dot{M}o_2$ was converted to energy equivalents assuming 14.32 J of energy per 1 mg of oxygen consumed (Beamish and Trippel, 1990).

Statistical tests were performed using R 2.14.0 software (R Foundation for Statistical Computing, Vienna, Austria). Linear regression analyses were used to describe yellowfin SDA results within temperatures. Mann–Whitney–Wilcoxon tests were used to compare yellowfin results between 20 and 24 °C and between this study and results of a previous study on bluefin tuna SDA at 20 °C (Clark et al., 2010). Paired t-tests were used to compare tailbeats between routine and digesting trials.

3. Results

All ten yellowfin tunas used in the experiments were well trained to swim in the respirometer and successfully completed the experimental trials. During the RMR trials, fish recovered quickly from the $\dot{M}o_2$ increase associated with handling (~1 h). At 20 °C, mean RMR was 136 ± 7 mg $\dot{M}o_2$ kg^{-1} h^{-1} (Table 2) and mean tailbeat frequency was 104 ± 3 beats min^{-1}. At 24 °C, mean RMR was 211 ± 15 mg O_2 kg^{-1} h^{-1} (Table 3) and mean tailbeat frequency was 105 ± 4 beats min^{-1}. The $Q10_{20–24}$ for RMR in yellowfin tuna was 2.99. Tailbeats remained similar.

Each yellowfin tuna had higher $\dot{M}o_2$ upon entry to the respirometer after feeding than in a fasted state, indicating that SDA had initiated prior to the first oxygen consumption measurements in the flume (e.g. Fig. 1). The maximal increase in $\dot{M}o_2$ during digestion ($\dot{M}o_{2peak}$) was significantly different between temperatures, with a mean $\dot{M}o_{2peak}$ of 248 ± 8 O_2 kg^{-1} h^{-1} at 20 °C and 399 ± 21 at 24 °C ($Q10_{20–24}$ = 3.28; $P < 0.05$)(Table 2). $\dot{M}o_{2peak}$ was typically maintained for several hours before $\dot{M}o_2$ began to decrease toward RMR. The mean factorial scope between RMR and $\dot{M}o_{2peak}$ was not significantly different between 20 and 24 °C (1.8 ± 0.1 at 20 °C and 1.9 ± 0.1 at 24 °C; $Q10_{20–24} = 1$; $P = 0.723$). The duration between feeding and the return to baseline levels ($\dot{M}o_{2dur}$) was significantly different between trials and was 40.2 ± 1.1 h at 20 °C and 33.1 ± 1.5 h at 24 °C ($P < 0.05$; $Q10_{20–24}$ = 0.62). There was no significant relationship between $\dot{M}o_{2dur}$ and meal size at either temperature. Average tailbeat frequencies were not significantly different between fasted and digesting runs and were 104 ± 3 and 105 ± 3 at 20 °C, respectively, and 105 ± 4 and 106 ± 2 at 24 °C, respectively ($Q10_{20–24} = 1$; paired t-test, $P > 0.1$ at 20 °C and $P > 0.1$ at 24 °C).

Mean SDA was 278 ± 19 kJ at 20 °C and 378 ± 25 at 24 °C ($Q10_{20–24} = 2.16$). SDA was linearly related to meal energy at both temperatures with larger meals requiring more digestive energy (at 20 °C: SDA = 0.0672 * meal energy − 36.592, $r^2 = 0.711$, $P < 0.05$; at 24 °C: SDA = 0.0818 * meal energy + 126.44, $r^2 = 0.999$, $P < 0.05$; Fig. 2). The mean SDA coefficient, the percentage of energy in a meal that is expended during SDA, was 5.9 ± 0.2% at 20 °C and 12.4 ± 0.4% at 24 °C and was significantly different between temperatures ($P < 0.05$; $Q10_{20–24} = 6.40$).

4. Discussion

Tunas are open ocean predators that are difficult to study in the laboratory. Metabolic measurements that have been made on a variety of active fishes (e.g. salmon, trout, yellowtail) have been challenging to acquire on tunas due to the difficulty of making routine metabolic measurements in captivity. Tunas have to be captured at sea, transported to the lab, and maintained at high effort and expense. As facilities to hold tunas have improved and increased (e.g. Farwell, 2001; Masuma et al., 2011; Wexler et al., 2003), the opportunities to obtain important physiological parameters that enable a better understanding of energetic costs are also increasing.

Table 2
Morphometric, meal, and metabolic values for fasted and digesting yellowfin tuna (*Thunnus albacares*) at 20 °C.

Year	Fish mass (kg)	Fish length (cm)	RMR (mg O_2 kg^{-1} h^{-1})	Meal constituents (sq./sard.) (%)	Meal mass (kg)	Meal size (% tuna mass)	Meal protein content (kg)	Meal lipid content (kg)	Meal energy (kJ)	$\dot{M}o_{2peak}$ (mg O_2 kg^{-1} h^{-1})	Factorial scope ($\dot{M}o_{2peak}$ /RMR)	SDA duration (hrs)	SDA_{part} (KJ)	SDA (kJ)	SDA coefficient (%)
2010	8.7	78	145	71/29	0.74	8.5	0.11	0.05	4899	249	1.7	38.0	248	256	5.2
2010	6.4	72	139	62/38	0.59	9.2	0.09	0.05	3736	256	1.8	37.4	200	205	5.5
2010	7.0	77	124	60/40	0.66	9.4	0.10	0.06	4820	260	2.1	39.4	285	293	6.1
2010	7.6	80	121	48/52	0.63	8.3	0.09	0.07	4419	219	1.8	40.5	227	235	5.3
2013	9.0	74	123	19/81	0.68	7.5	0.10	0.10	5827	229	1.9	41.8	356	363	6.2
2013	6.5	69	124	10/90	0.52	8.0	0.07	0.09	4745	239	1.9	45.6	286	291	6.1
2013	10.0	84	173	57/43	0.69	6.9	0.10	0.06	4312	283	1.6	38.5	294	302	7.0
Mean	7.9	76	136		0.64	8.3	0.09	0.07	4680	248	1.8	40.2	271	278	5.9
S.E.M.	0.5	2	7		0.03	0.3	0.00	0.01	243	8	0.1	1.1	19.4	19.4	0.2

Table 3
Morphometric, meal, and metabolic values for fasted and digesting yellowfin tuna (*Thunnus albacres*) at 24 °C.

Year	Fish mass (kg)	Fish length (cm)	RMR (mg O_2 kg^{-1} h^{-1})	Meal constituents (sq./sard.) (%)	Meal mass (kg)	Meal size (% tuna mass)	Meal protein content (kg)	Meal lipid content (kg)	Meal energy (kJ)	$\dot{M}o_{2peak}$ (mg O_2 kg^{-1} h^{-1})	Factorial scope ($\dot{M}o_{2peak}$ /RMR)	SDA duration (hrs)	SDA_{part} (KJ)	SDA (kJ)	SDA coefficient (%)
2014	10.5	79	188	49/51	0.45	4.3	0.08	0.02	2693	360	1.9	30.8	321	345	12.8
2014	9.4	79	205	80/20	0.69	7.4	0.13	0.02	3664	430	2.1	32.5	396	426	11.6
2014	8.3	72	240	71/29	0.49	5.9	0.09	0.02	2864	408	1.7	36.0	343	362	12.7
Mean	9.4	77	211		0.54	5.9	0.10	0.02	3074	399	1.9	33.1	353.3	377.9	12.4
S.E.M.	0.6	2	15		0.08	0.9	0.01	0.00	299	21	0.1	1.5	22.3	24.5	0.4

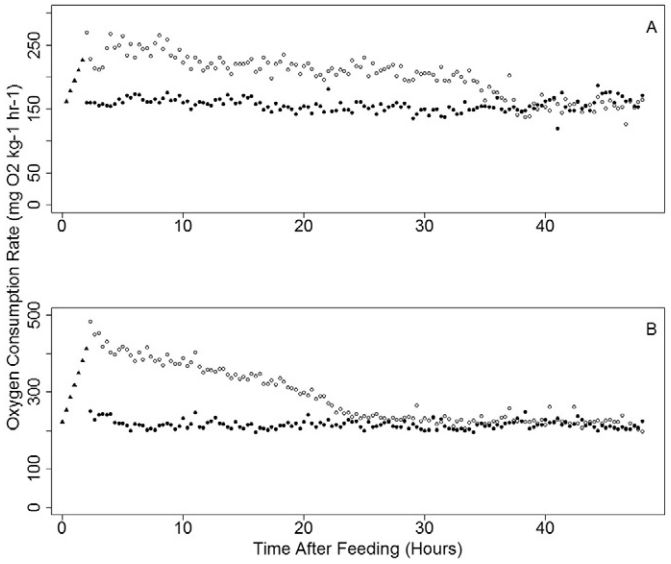

Fig. 1. Representative oxygen consumption rates of yellowfin tuna (*Thunnus albacares*) acclimated to 20 °C (panel A) and 24 °C (panel B) seawater. Fish swam at 1 body length per second during fasted trials (filled circles) and digesting trials (unfilled circles). Estimated post-prandial oxygen consumption prior to entrance to respirometer (filled triangles) is also included.

4.1. Routine metabolic rate

Standard metabolic rate (SMR), the metabolic rate of a fasted, stationary animal, is often used to compare metabolic rates among teleosts. Yellowfin tuna are obligate ram ventilators, meaning they must continuously swim to oxygenate their gills and tissues, making a stationary SMR biologically irrelevant. Instead, RMR, which incorporates the routine movement necessary for ram ventilation, is frequently used to compare metabolic rates among obligate ram ventilators (Korsmeyer and Dewar, 2001). Mean RMR at 20 °C recorded in this study (136 mg O_2 kg^{-1} h^{-1} for tuna with a mean mass of 7.9 kg) at 1 BL s^{-1} is similar to the mean RMR obtained using comparable protocols at 20 °C (203 mg O_2 kg^{-1} h^{-1} for smaller yellowfin tuna with a mean mass of 5.4 kg)(Blank et al., 2007a). This value, when adjusted for body mass, results in a metabolic rate scaling to mass$^{0.5}$, which is similar to the exponent of 0.4 that was found with smaller yellowfin (Dewar and Graham, 1994). RMR may be lower at slower swimming speeds (Blank et al., 2007a). The mean tailbeat frequency of yellowfin at 20 °C at 1 BL s^{-1} was consistent with a previous study at the same swimming speed (103.6 beats min^{-1} in this study vs. 103.3 in (Blank et al., 2007a).

RMR at 24 °C in this study was lower than previous measurements conducted at similar temperatures (211 mg O_2 kg^{-1} h^{-1} at 24 °C in this study and 436 mg O_2 kg^{-1} h^{-1} at 25 °C in Dewar and Graham, 1994), but the difference is likely due to allometric scaling of metabolic rate (yellowfin were 69–84 cm in this study and 30–57 cm in Dewar and Graham, 1994) and faster swimming speeds (1 BL s^{-1} in this study and >1 BL s^{-1} in Dewar and Graham, 1994). Moreover, the fish in this study were trained to swim in the flume, which likely reduced the stress of flume swimming and associated increases in $\dot{M}o_2$. The RMR measurements presented here are also lower than previous estimates with smaller yellowfin (30–50 cm) conducted through fasted energy loss (>600 mg O_2 kg^{-1} h^{-1}) (Boggs and Kitchell, 1991). The lower RMR in this study is likely due to allometric scaling and differences in methodology. Fasted energy loss experiments compare the energy content of groups of fish before and after a period of fasting and assume that the difference must be due to routine metabolic expenditures. The protocol in Boggs and Kitchell did not standardize the behavioral habits of the fish during the fasting period, meaning that swimming speeds could have been higher than 1 BL s^{-1}, resulting in a higher measured RMR.

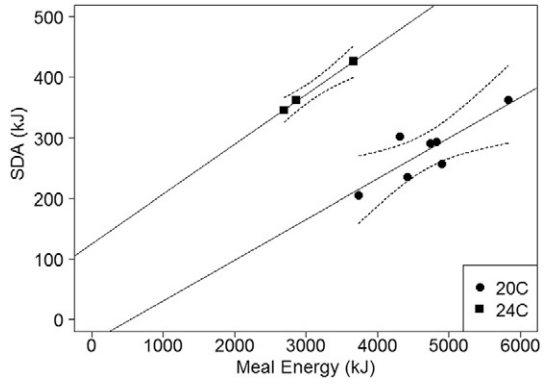

Fig. 2. Relationship between meal energy and the energy consumed by SDA in yellowfin tuna (*Thunnus albacares*) at 20 °C (circles) and 24 °C (squares). Linear regressions are presented as solid lines for SDA at 20 °C (SDA = 0.703 * meal energy − 15.789; r^2 = 0.723, P < 0.05) and at 24 °C (SDA = 0.1162 * meal energy + 28.057; r^2 = 0.998, P < 0.05). Dashed lines are 95% confidence intervals.

4.2. SDA in yellowfin tuna relative to other fish species

This study is the first measurement of SDA in *T. albacares*. At both 20 °C and 24 °C, energy expended on SDA increased linearly with meal energy (Fig. 2), similar to SDA in other species (Clark et al., 2010; Secor, 2009). At both the 20 and 24 °C acclimation temperatures, the total duration of digestion in yellowfin was shorter than the mean for other species of fish fed similar meals, as reviewed by Secor, 2009 (40.2 ± 1.1 h mean at 20 °C and 33.1 ± 1.5 h at 24 °C in this study vs. 47 h). The mean SDA coefficient (5.9 ± 0.2% at 20 °C and 12.4 ± 0.4% at 24 °C) was lower than the mean for other fish surveyed by Secor (2009) (16%). These results indicate that yellowfin tuna use a relatively small amount of energy to rapidly digest meals, a factor that potentially contributes to rapid growth in yellowfin (Juan-Jordá et al., 2013).

4.3. Temperature effects on SDA in yellowfin tuna

An increase in acclimation temperature from 20 °C to 24 °C caused a statistically significant increase in $\dot{M}o_{2peak}$ (P < 0.05) and a statistically significant decrease in $\dot{M}o_{2dur}$ (P < 0.05). Numerous studies report a similar influence of increasing temperature on SDA peak and duration in fish (as reviewed in Secor, 2009). Factorial scope was similar at 20 °C and 24 °C (1.8 ± 0.1 and 1.9 ± 0.1, respectively), meaning that RMR and $\dot{M}o_{2peak}$ increased proportionally with temperature. SDA coefficient also significantly increased with temperature (P < 0.05).

Reports of the influence of ambient temperature on SDA coefficient are mixed, with studies showing no change, increases, and decreases in SDA coefficients with increasing temperatures (Secor, 2009). The increase in SDA coefficient with temperature in this study could be the result of several factors. The yellowfin used in this experiment, collected from the California Current waters, could represent a cold-adapted population who has evolved temperature-sensitive enzymes and cellular components at a thermal optimum closer to 20 °C than 24 °C (Hochachka and Somero, 2002). While the optimal temperature for metabolic function is unknown in yellowfins, a study of Pacific bluefin found that metabolic rate increases below and above the thermal optimum of 15–20 °C (Blank et al., 2007b). Electronic tagging studies show that yellowfin in the California Current inhabit warm waters from 16 to 31 °C with a mean of 21 °C (Block et al., 2011). Another possible explanation for the greater SDA coefficient could be the greater proportion of squid in the meals at 24 °C (49–80% squid at 24 °C vs. 10–71% squid at 20 °C). Squid had lower lipid content than sardines, meaning meals rich in squid were lower in lipid content (mean lipid

mass of 0.02 ± 0.00 kg at 24 °C vs. 0.07 ± 0.01 kg at 20 °C); decreased lipid content can result in an increased SDA coefficient, although there are exceptions (Secor, 2009). The difference between trials in fish mass (7.9 kg at 20 °C vs. 9.4 kg at 24 °C), meal mass (8.3% body weight at 20 °C vs. 5.9% at 24 °C), or meal energy (4680 kJ at 20 °C vs. 3074 kJ at 24 °C) could also explain the increase, as all are associated with greater SDA values in fish (Secor, 2011). Fish in each trial were fed ad libitum, but yellowfin consumed greater amounts of food at 20 °C than 24 °C. Future studies should seek to standardize across fish mass, meal mass, meal energy, and dietary components.

4.4. Comparisons of SDA in yellowfin and bluefin tuna

This experiment was conducted with similar protocols to a previous analysis of SDA in Pacific bluefin (Clark et al., 2010), making the results directly comparable. Yellowfin tuna at 20 °C had significantly lower RMR relative to bluefin tuna in Clark et al., 2010 (136 ± 7.2 mg O_2 kg^{-1} h^{-1} in yellowfin with a mean mass of 7.9 kg vs. 174 ± 9 mg O_2 kg^{-1} h^{-1} in bluefin tuna with a mean mass of 10.4 kg, $P < 0.05$), similar to a previous comparative study of yellowfin and bluefin (Blank et al., 2007a). RMR in yellowfin at 24 °C was not significantly different than RMR in bluefin at 20 °C in Clark et al., 2010 (210 ± 15 mg O_2 kg^{-1} h^{-1} in yellowfin with a mean mass of 9.4 kg vs. 174 ± 9 mg O_2 kg^{-1} h^{-1} in bluefin with a mean mass of 10.4 kg). Bluefin tuna of this body size are known to maintain internal body temperatures several degrees above ambient water temperature (Clark et al., 2010; Kitagawa et al., 2006), and differences in metabolism may relate to warmer internal temperatures in bluefin, which are due to increased heat retention in red muscle and visceral tissues.

$\dot{M}o_{2peak}$ was significantly lower in yellowfin at 20 °C than bluefin at 20 °C (248 ± 8 in yellowfin vs 345 ± 23 mg O_2 kg^{-1} h^{-1} in bluefin, $P < 0.01$), but not in yellowfin at 24 °C (399 ± 20 mg O_2 kg^{-1} h^{-}) relative to bluefin at 20 °C. SDA_{dur} was significantly longer in yellowfin at 20 °C than bluefin at 20 °C (40.2 ± 1.1 in yellowfin at 20 °C vs. 28.9 ± 1.5 h in bluefin, $P < 0.001$) but not in yellowfin at 24 °C (33 ± 1.5 h) relative to bluefin at 20 °C. Differences in metabolic rates and digestion times of yellowfin and bluefin could be a result of greater capacity for regional endothermy and associated thermal excess in bluefin tuna (TRCC unpublished data; Whitlock et al., 2013). As regionally endothermic bluefin are able to maintain gut temperature within an optimal temperature range for enzyme function, thermally dependent digestive enzymes in bluefin, such as trypsin and chymotrypsin, are able to digest meals faster (Stevens and McLeese, 1984). Potentially, the yellowfin at 20 °C are below their optimal temperature and thus enzymatic function is not operating at its maximal capacity.

Between yellowfin and bluefin, the coefficient of SDA was significantly lower in yellowfin at 20 °C (5.9 ± 0.2% in yellowfin vs. 9.2 ± 0.7% in bluefin, $P < 0.01$) and significantly higher in yellowfin at 24 °C (12.4 ± 0.4% in yellowfin vs 9.2 ± 0.7% in bluefin, $P < 0.05$). Yellowfin at 20 °C spend less energy on digestion than bluefin at 20 °C, and yellowfin at 24 °C spend more energy than bluefin at 20 °C. As described above, the increased SDA coefficient in 24 °C yellowfin could be the result of a cold-adapted population or a lower lipid diet.

Bluefin tuna increase their metabolic rates at low temperatures to increase heat generation and maintain a higher thermal excess (Blank et al., 2007b). Both mammals and birds have been shown to use thermal substitution to reduce energy expenditure, whereby the energy required for thermoregulation is substituted for heat generated during the digestive process (Humphries and Careau, 2011). This mechanism can result in an underestimation of the SDA response (Lovvorn, 2007), and may also be at play in regionally endothermic tuna. However, given that heat generation in pre-prandial tuna is a by-product of muscular contraction which is proportional to swimming speed or tail-beat frequency, we assume this effect to be negligible as fish exercised at similar intensity and no significant difference in tail-beat frequencies in pre- and post-prandial conditions were found in yellowfin tuna. We do, however, acknowledge that at very low temperatures, where metabolic rates rise to increase heat generation, tuna may take advantage of such thermal substitution. Future experiments should attempt to measure the post-prandial responses of fish at these lower temperatures for comparison to the responses at nominal temperatures.

5. Context

This study reveals that temperature plays a substantial role in the duration and coefficient of SDA in yellowfin tuna. Digestion at 24 °C is faster but requires additional oxidative energy, relative to digestion at 20 °C, indicating that 24 °C may be outside the thermal optimum range for digestion for these California Current collected yellowfin tuna. Improved knowledge of the relationship between temperature and SDA for individual species is important for optimizing feeding regimes in aquaculture (Secor, 2009), comparing the desirability of candidate aquaculture species (Jobling et al., 2012), and for improving bioenergetic sub-models used in fishery stock assessments and ecosystem models (Jusup et al., 2011; Politikos et al., 2011).

With this knowledge, aquaculturists can adjust feeding practices and increase feeding efficiency by minimizing the duration and coefficient of SDA (Alanärä et al., 2001). Future measurements of SDA at additional temperatures would help determine the full thermal performance curves and optimum temperature for digestion and develop specific, robust recommendations for aquaculturists (Angilletta, 2009; Sandblom et al., 2014; Tirsgaard et al., 2014). The comparative role of SDA in energy budgets of candidate aquaculture species can also help aquaculture enterprises evaluate the tradeoffs between farming different species and at different temperatures. When comparing yellowfin and bluefin tuna for aquaculture, yellowfin spent less energy on digestion at 20 °C. However, bluefin complete digestion faster, meaning they could be fed more often and potentially have faster growth. To help farmers evaluate the complete energy efficiency of candidate species, future SDA studies should be combined with measurements of meal energy loss and absorption to determine species' energy budgets.

Improved understanding of the relationship between SDA and temperature is also important for fisheries models. The movement toward ecosystem based management in wild-capture fisheries (Pikitch et al., 2004) requires increasingly sophisticated bioenergetic models at the individual and population level, which often include estimations of SDA (Latour et al., 2003; van Poorten and Walters, 2016). This study shows that a four degree increase in temperature can double the SDA coefficient for yellowfin. Fish encounter numerous temperature regimes in the wild, and bioenergetics models of yellowfin tuna with greater accuracy can help improve fishery models and optimize fisheries management decisions.

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References

Alanärä, A., Kadri, S., Paspatis, M., 2001. Feeding management. In: Houlihan, D., Boujard, T., Jobling, M. (Eds.), Food Intake in Fish. Blackwell Science Ltd.
Angilletta, M.J., 2009. Thermal Adaptation: A Theoretical and Empirical Synthesis. Oxford University Press.
Beamish, F.W.H., Trippel, E.A., 1990. Heat increment: a static or dynamic dimension in bioenergetic models? Trans. Am. Fish. Soc. 119, 649–661.
Bell, W.H., Terhune, L.D.B., 1970. Water tunel design for fisheries research. Fisheries Research Board of Canada: Technical Report 195, pp. 1–69.

Blank, J.M., Farwell, C.J., Morrissette, J.M., Schallert, R.J., Block, B.A., 2007a. Influence of swimming speed on metabolic rates of juvenile Pacific bluefin tuna and yellowfin tuna. Physiol. Biochem. Zool. 80, 167–177.
Blank, J.M., Morrissette, J.M., Farwell, C.J., Price, M., Schallert, R.J., Block, B.A., 2007b. Temperature effects on metabolic rate of juvenile Pacific bluefin tuna *Thunnus orientalis*. J. Exp. Biol. 210, 4254–4261.
Block, B.A., Stevens, E.D., 2001. Tuna: Physiology, Ecology and Evolution. Academic Press, San Diego, CA, p. 468.
Block, B.A., Jonsen, I.D., Jorgensen, S.J., Winship, A.J., Shaffer, S.A., Bograd, S.J., Hazen, E.L., Foley, D.G., Breed, G.A., Harrison, A.L., Ganong, J.E., Swithenbank, A., Castleton, M., Dewar, H., Mate, B.R., Shillinger, G.L., Schaefer, K.M., Benson, S.R., Weise, M.J., Henry, R.W., Costa, D.P., 2011. Tracking apex marine predator movements in a dynamic ocean. Nature 475, 86–90.
Boggs, C.H., Kitchell, J.F., 1991. Tuna metabolic rates estimated from energy losses during starvation. Physiol. Zool. 64, 502–524.
Carey, F.G., Teal, J.M., 1966. Heat conservation in tuna fish muscle. Proc. Natl. Acad. Sci. U. S. A. 56, 1464–1469.
Carter, C., Nowak, B., Clarke, S., 2010. The tunas (family: Scombridae). In: Francois, N.R.L., Jobling, M., Carter, C.G., Blier, P.U. (Eds.), Finfish Aquaculture Diversification. CABI, Wallingford, UK, pp. 432–449.
Clark, T.D., 2015. In: Kitagawa, T., Kimura, S. (Eds.), Metabolic Limits and Energetics. CRC Press, Biology and Ecology of Bluefin Tuna, pp. 261–273.
Clark, T., Brandt, W., Nogueira, J., Rodriguez, L., Price, M., Farwell, C., Block, B., 2010. Postprandial metabolism of Pacific bluefin tuna (*Thunnus orientalis*). J. Exp. Biol. 213, 2379–2385.
Collette, B.B., Reeb, C., Block, B.A., 2001. Systematics of the tunas and mackerels (Scombridae). In: Block, B., Stevens, E. (Eds.), Tuna: Physiology, Ecology, and Evolution.Academic Press, pp. 1–33
Cui, Y., Wootton, R.J., 1988. The metabolic rate of the minnow, *Phoxinus phoxinus* (L.) (Pisces: Cyprinidae), in relation to ration, body size and temperature. Funct. Ecol. 2, 157–161.
Dewar, H., Graham, J., 1994. Studies of tropical tuna swimming performance in a large water tunnel. J. Exp. Biol. 192, 13–31.
Dickson, K.A., Graham, J.B., 2004. Evolution and consequences of endothermy in fishes. Physiol. Biochem. Zool. 77, 998–1018.
Ellerby, D.J., Herskin, J., 2013. Swimming flumes as a tool for studying swimming behavior and physiology: current applications and future developments. In: Palstra, A.P., Planas, J.V. (Eds.), Swimming Physiology of Fish. Springer-Verlag, Berlin, pp. 345–375.
Farwell, C.J., 2001. Tunas in captivity. In: Block, B., Stevens, E. (Eds.), Tuna: Physiology, Ecology, and Evolution.Academic Press, pp. 391–412
Fitzgibbon, Q.P., Seymour, R.S., Ellis, D., Buchanan, J., 2007. The energetic consequence of specific dynamic action in southern bluefin tuna *Thunnus maccoyii*. J. Exp. Biol. 210, 290–298.
Frisk, M., Steffensen, J.F., Skov, P.V., 2013. The effects of temperature on specific dynamic action and ammonia excretion in pikeperch (*Sander lucioperca*). Aquaculture 404–405, 65–70.
Graham, J.B., Dickson, K.A., 2004. Tuna comparative physiology. J. Exp. Biol. 207, 4015–4024.
Guinea, J., Fernandez, F., 1997. Effect of feeding frequency, feeding level and temperature on energy metabolism in *Sparus aurata*. Aquaculture 148, 125–142.
Hochachka, P.W., Somero, G.N., 2002. Biochemical Adaptation: Mechanism and Process in Physiological Evolution. Oxford University Press.
Humphries, M.M., Careau, V., 2011. Heat for nothing or activity for free? Evidence and implications of activity-thermoregulatory heat substitution. Integr. Comp. Biol.
Jobling, M., 1981. The influences of feeding on the metabolic rate of fishes: a short review. J. Fish Biol. 18, 385–400.
Jobling, M., Davies, P.S., 1980. Effects of feeding on metabolic rate, and the specific dynamic action in plaice, Pleuronectes platessa L. J. Fish Biol. 16, 629–638.
Jobling, M., Alanärä, A., Kadri, S., Huntingford, F., 2012. Feeding biology and foraging. In: Huntingford, F., Jobling, M., Kadri, S. (Eds.), Aquaculture and Behavior.Wiley-Blackwell, pp. 121–149
Johnston, I.A., Battram, J., 1993. Feeding energetics and metabolism in demersal fish species from antarctic, temperate and tropical environments. Mar. Biol. 115, 7–14.
Juan-Jordá, M., Mosqueira, I., Freire, J., Dulvy, N., 2013. Life in 3-D: life history strategies in tunas, mackerels and bonitos. Rev. Fish Biol. Fish. 23, 135–155.
Jusup, M., Klanjscek, T., Matsuda, H., Kooijman, S.A.L.M., 2011. A full lifecycle bioenergetic model for bluefin tuna. PLoS One 6, e21903.
Khan, J.R., Pether, S., Bruce, M., Walker, S.P., Herbert, N.A., 2015. The effect of temperature and ration size on specific dynamic action and production performance in juvenile hapuku (*Polyprion oxygeneios*). Aquaculture 437, 67–74.
Kitagawa, T., Kimura, S., Nakata, H., Yamada, H., 2006. Thermal adaptation of Pacific bluefin tuna *Thunnus orientalis* to temperate waters. Fish. Sci. 72, 149–156.
Korsmeyer, K.E., Dewar, H., 2001. Tuna metabolism and energetics. In: Block, B., Stevens, E. (Eds.), Tuna: Physiology, Ecology and Evolution.Academic Press, pp. 35–78
Latour, R.J., Brush, M.J., Bonzek, C.F., 2003. Toward ecosystem-based fisheries management. Fisheries 28, 10–22.
Lovvorn, J.R., 2007. Thermal substitution and aerobic efficiency: measuring and predicting effects of heat balance on endotherm diving energetics. Philos. Trans. R. Soc. Lond. Ser. B Biol. Sci. 362, 2079–2093.
Luo, Y., Xie, X., 2008. Effects of temperature on the specific dynamic action of the southern catfish, *Silurus meridionalis*. Comp. Biochem. Physiol. A Physiol. 149, 150–156.
Masuma, S., Takebe, T., Sakakura, Y., 2011. A review of the broodstock management and larviculture of the Pacific northern bluefin tuna in Japan. Aquaculture 315, 2–8.
McCue, M.D., 2006. Specific dynamic action: a century of investigation. Comp. Biochem. Physiol. A Physiol. 144, 381–394.
Miyake, M.P., Guillotreau, P., Sun, C.-H., Ishimura, G., 2010. Recent Developments in the Tuna Industry: Stocks, Fisheries, Management, Processing, Trade and Markets. Food and Agriculture Organization of the United Nations, Rome, p. 125.
Pang, X., Cao, Z.-D., Peng, J.-L., Fu, S.-J., 2010. The effects of feeding on the swimming performance and metabolic response of juvenile southern catfish, *Silurus meridionalis*, acclimated at different temperatures. Comp. Biochem. Physiol. A Physiol. 155, 253–258.
Peck, M.A., Buckley, L.J., Bengtson, D.A., 2003. Energy losses due to routine and feeding metabolism in young-of-the-year juvenile Atlantic cod (*Gadus morhua*). Can. J. Fish. Aquat. Sci. 60, 929–937.
Peres, H., Oliva-Teles, A., 2001. Effect of dietary protein and lipid level on metabolic utilization of diets by European sea bass (*Dicentrarchus labrax*) juveniles. Fish Physiol. Biochem. 25, 269–275.
Pérez-Casanova, J.C., Lall, S.P., Gamperl, A.K., 2010. Effects of dietary protein and lipid level, and water temperature, on the post-feeding oxygen consumption of Atlantic cod and haddock. Aquac. Res. 41, 198–209.
Pikitch, E.K., Santora, C., Babcock, E.A., Bakun, A., Bonfil, R., Conover, D.O., Dayton, P., Doukakis, P., Fluharty, D., Heneman, B., Houde, E.D., Link, J., Livingston, P.A., Mangel, M., McAllister, M.K., Pope, J., Sainsbury, K.J., 2004. Ecosystem-based fishery management. Science 305, 346–347.
Pirozzi, I., Booth, M.A., 2009. The effect of temperature and body weight on the routine metabolic rate and postprandial metabolic response in mulloway, *Argyrosomus japonicus*. Comp. Biochem. Physiol. A Physiol. 154, 110–118.
Politikos, D., Triantafyllou, G., Petihakis, G., Tsiaras, K., Somarakis, S., Ito, S.-I., Megrey, B., 2011. Application of a bioenergetics growth model for European anchovy (*Engraulis encrasicolus*) linked with a lower trophic level ecosystem model. Hydrobiologia 670, 141–163.
Sandblom, E., Gräns, A., Axelsson, M., Seth, H., 2014. Temperature acclimation rate of aerobic scope and feeding metabolism in fishes: implications in a thermally extreme future. Proc. R. Soc. Lond. B Biol. Sci. 281, 1–9.
Schaefer, K.M., Fuller, D.W., Block, B.A., 2011. Movements, behavior, and habitat utilization of yellowfin tuna (Thunnus albacares) in the Pacific Ocean off Baja California, Mexico, determined from archival tag data analyses, including unscented Kalman filtering. Fish. Res. 112, 22–37 http://www.sciencedirect.com/science/article/pii/S016578361100275X.
Secor, S.M., 2009. Specific dynamic action: a review of the postprandial metabolic response. J. Comp. Physiol. B. 179, 1–56.
Secor, S.M., 2011. Food acquisition and digestion: Cost of digestion and assimilation. In: Farrell, A.P. (Ed.), Encyclopedia of Fish Physiology. Academic Press, San Diego, pp. 1608–1616.
Seth, H., Axelsson, M., Farrell, A.P., 2011. The circulation and metabolism of the gastrointestinal tract. In: Grosell, M., Farrell, A.P., Brauner, C.J. (Eds.), Fish Physiology: The Multifunctional Gut of Fish.Academic Press, pp. 351–393
Shadwick, R.E., Schiller, L.L., Fudge, D.S., 2013. Physiology of swimming and migration in tunas. In: Palstra, A.P., Planas, J.V. (Eds.), Swimming Physiology of Fish. Springer, Berlin Heidelberg, pp. 45–78.
Stevens, E.D., McLeese, J.M., 1984. Why bluefin tuna have warm tummies: temperature effect on trypsin and chymotrypsin. Am. J. Physiol. Regul. Integr. Comp. Physiol 246, R487–R494.
Tirsgaard, B., Svendsen, J., Steffensen, J., 2014. Effects of temperature on specific dynamic action in Atlantic cod *Gadus morhua*. Fish Physiol. Biochem. 1-10.
van Poorten, B.T., Walters, C.J., 2016. How can bioenergetics help us predict changes in fish growth patterns? Fish. Res.
Vanella, F.A., Boy, C.C., Lattuca, M.E., Calvo, J., 2010. Temperature influence on postprandial metabolic rate of sub-antarctic teleost fish. Comp. Biochem. Physiol. A Physiol. 156, 247–254.
Wang, T., Busk, M., Overgaard, J., 2001. The respiratory consequences of feeding in amphibians and reptiles. Comp. Biochem. Physiol. A Mol. Integr. Physiol. 128, 533–547.
Weng, K.C., Stokesbury, M.J.W., Boustany, A.M., Seitz, A.C., Teo, S.L.H., Miller, S.K., Block, B.A., 2009. Habitat and behaviour of yellowfin tuna *Thunnus albacares* in the Gulf of Mexico determined using pop-up satellite archival tags. J. Fish Biol. 74, 1434–1449.
Wexler, J.B., Scholey, V.P., Olson, R.J., Margulies, D., Nakazawa, A., Suter, J.M., 2003. Tank culture of yellowfin tuna, *Thunnus albacares*: developing a spawning population for research purposes. Aquaculture 220, 327–353.
Whitlock, R.E., Walli, A., Cermeño, P., Rodriguez, L.E., Farwell, C., Block, B.A., 2013. Quantifying energy intake in Pacific bluefin tuna (*Thunnus orientalis*) using the heat increment of feeding. J. Exp. Biol. 216, 4109–4123.
Yang, G., Xu, S., 2011. Effects of temperature on the SDA of the brook trout,. 2011 International Symposium on IT in Medicine and Education (ITME), pp. 653–657.
Yang, G., Yuan, D., Xu, S., 2014. Effects of temperature on the SDA of the taimen. In: Li, S., Jin, Q., Jiang, X., Park, J.J. (Eds.), Frontier and Future Development of Information Technology in Medicine and Education.Springer Netherlands, pp. 2631–2636