

The energetic consequence of specific dynamic action in southern bluefin tuna *Thunnus maccoyii*

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Summary

The effect of feeding on the rate of oxygen consumption (\dot{M}_{O_2}) of four groups of three southern bluefin tuna *Thunnus maccoyii* (SBT) was examined in a large static respirometer at water temperatures of 18.2–20.3°C. Six feeding events of rations between 2.1–8.5% body mass (% M_b) of Australian sardines (*Sardinops neopilchardus*) were recorded (two of the groups were fed twice). Before feeding, fish swam between 0.71 and 1.4 body lengths s^{-1} ($BL s^{-1}$) and the routine metabolic rate (RMR) was $366 \pm 32.5 \text{ mg kg}^{-1} \text{ h}^{-1}$ (mean \pm s.e.m.). For all trials, \dot{M}_{O_2} was elevated post feeding, presumably as a result of specific dynamic action (SDA). Swimming velocity was also elevated post feeding for periods similar to that of \dot{M}_{O_2} (between 20–45 h, longest for the largest rations). Post feeding swimming velocity increased to between 0.87–2.6 $BL s^{-1}$ and was also dependent on ration consumed. It is suggested that the purpose of increased post-feeding swimming velocity was to increase ventilation volume as a response to the enhanced metabolic demand associated with SDA. Peak post-prandial \dot{M}_{O_2} increased

linearly with ration size to a maximum of $1290 \text{ mg kg}^{-1} \text{ h}^{-1}$, corresponding to 2.8 times the RMR. When converted to its energy equivalent, total magnitude of SDA was linearly correlated with ration size to a maximum of $192 \text{ kJ kg}^{-1} \text{ h}^{-1}$, and as a proportion of gross energy ingested (SDA coefficient), it averaged $35 \pm 2.2\%$. These results demonstrate that, although the factorial increase of SDA in SBT is similar to that of other fish species, the absolute energetic cost of SDA is much higher. These results support the contention that tuna are energy speculators, gambling high rates of energy expenditure for potentially higher rates of energy returns. The ration that southern bluefin tuna require to equal the combined metabolic costs of SDA and RMR is estimated in this study to be 3.5% M_b of Australian sardines per day.

Key words: tuna, specific dynamic action, heat increment of feeding, oxygen consumption, energetics, Southern bluefin tuna, *Thunnus maccoyii*.

Introduction

Tunas are highly specialized marine predators that are widely distributed throughout the world's tropical and temperate oceans. In this vast habitat, they have evolved numerous unique anatomical, biochemical and physiological adaptations that have been instrumental to their success (Brill, 1996; Bushnell and Jones, 1994; Graham and Dickson, 2004). Of particular interest are adaptations in the areas of metabolism and energetics. Tunas are known to have standard metabolic rates (SMR, the rate when theoretically at complete rest) and metabolic scopes that greatly exceed those of most other well studied fish species (Korsmeyer and Dewar, 2001). These elevated metabolic states allow tuna to achieve physiological feats, including rapid digestion and quick recovery from oxygen debt, that enable them to take advantage of the ocean's patchy prey distribution. However, this metabolic amplification

comes at an energetic cost, which has led some authors to describe tuna as 'energy speculators', animals that gamble high rates of energy expenditure on potential higher rates of energy return (Brill, 1987; Korsmeyer et al., 1996).

Our understanding of tuna energetics lags far behind that of smaller species such as salmonids. Tuna's size and difficulty of handling has meant only a small number of metabolic measurements have been possible. The majority of research on tuna metabolism has focused on evaluation of the SMR or quantification of swimming costs (Brill, 1979; Brill, 1987; Dewar and Graham, 1994; Gooding et al., 1981; Graham and Laurs, 1982; Graham et al., 1989; Sepulveda and Dickson, 2000). The metabolic cost of specific dynamic action (SDA) has yet to be examined in any tuna species.

Specific dynamic action (often referred to as apparent specific dynamic action, calorogenic effect or heat increment of

feeding) refers to the total energy cost involved with ingestion, digestion, absorption and assimilation of a meal. In fish, SDA is a substantial component of total bioenergetics, representing between 5 and 20% of gross ingested energy (Beamish, 1974; Carter and Brafield, 1992; Chakraborty et al., 1992; Fu et al., 2005c; Muir and Niimi, 1972; Peck et al., 2002). However none of these studies have examined marine pelagic fish. Specific dynamic action has been hypothesized to be a significant component of metabolism of tuna, because of their high rates of food consumption and digestion (Korsmeyer and Dewar, 2001). Furthermore, it is hypothesized that rapidly growing fish, such as tuna, should show the greatest post-prandial increase in metabolic rate (Brill, 1996; Jobling, 1981). This theory is based on the consensus that a large proportion of the energetic cost of SDA is related to metabolic work responsible for growth, i.e. protein synthesis and turnover (Brown and Cameron, 1991a; Brown and Cameron, 1991b; Jobling, 1981; Lyndon et al., 1992).

This study uses a large, sea-based, metabolic chamber to overcome some of the logistical difficulties with working with large, pelagic fish (Fitzgibbon et al., 2006). The spacious, low-stress environment of this respirometer supports voluntary feeding, allowing this study to make the first recording of SDA of a tuna species, southern bluefin tuna *Thunnus maccoyii* (SBT), ingesting Australian sardine *Sardinops neopilchardus*, an important food component in the diets of both wild and aquaculture SBT.

Materials and methods

Experimental animals

Southern bluefin tuna *Thunnus maccoyii* (Castelnau 1872) (SBT) were purse-seine netted in the Great Australian Bight, most likely from the same wild school, in early January 2005. They were transferred to a sea-cage and slowly towed approximately 200 nautical miles back to the marine farms in the waters off Port Lincoln, South Australia. Soon after arrival, twelve juvenile SBT were sourced from the Tuna Boats Owners Association of South Australia and transferred into a 12 m diameter, 8 m deep sea-cage, moored in a small bay at the south end of Boston Island. Details of transfers and maintenance were as described (Fitzgibbon et al., 2006). Fish were fed Australian sardine *Sardinops neopilchardus* (Table 1) and allowed 2 months to recover from the tow and transfer, and to become accustomed to the sea-cage environment.

Mesocosm respirometer

The mesocosm respirometer was a large, flexible, plastic cylinder, 12 m × 2.5 m (diameter × depth) manufactured predominantly from polypropylene (Stevens Geomembranes R-PP 45, Holyoke, MA, USA; 1.14 mm thick and reinforced with polyester), thermal bonded by Fabtech SA Pty. Ltd. (Adelaide, Australia) (Fig. 1A). Further to the basic cylinder, the mesocosm had a wave break wall that extended 1 m above water level and a sock-like access port (2 m diameter, 2 m high) positioned in the roof (Fig. 1B). Access into the mesocosm was

Table 1. Nutritional content of the Australian sardine *Sardinops neopilchardus*

Feed component	Content
Protein	20.2%
Fat	1.7%
Ash	3.2%
Dry matter	27.4%
Moisture	72.6%
Energy	5.6 mJ kg ⁻¹

Proximal analysis conducted by Western Food Laboratories (Enfield, NSW, Australia). Feed component presented as % wet mass. Energy value calculated on the basis of 23.6 and 39.5 kJ g⁻¹ of protein and lipid (Suarez et al., 1995).

only possible through this access port, which could be pinched shut to completely seal the system. Five 1 m diameter clear polyvinyl chloride (0.75 mm) windows allowed entry of natural light, and capped polythene tank fittings allowed sealable access for experimental equipment and manual sampling. Once deployed into a 12 m diameter sea cage the mesocosm was pump filled with seawater. Initially, it was filled to capacity (approximately 400 000 l) to reduce the likelihood of confinement stress; however, in subsequent experiments, water volume was reduced to 350 000 l as the initial volume was found to be slightly in excess of what was required to maximize available space within the respirometer.

Fish were introduced into the mesocosm from the adjacent holding sea-cage by use of a baited, barb-less hook as described

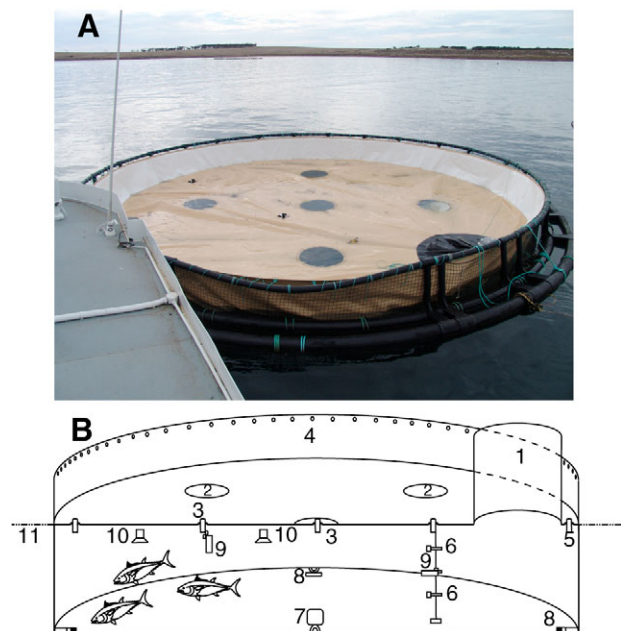


Fig. 1. (A) The mesocosm respirometer. (B) Diagram showing 1 entrance port, 2 windows, 3 sample ports, 4 wave break wall, 5 cable entrance ports, 6 oxygen probes, 7 float, 8 lead weights, 9 video cameras, 10 lights and 11 water level.

(Fitzgibbon et al., 2006) or, in the case of fish being hook-shy, by crowding the fish in a net and a skin-diver securing them by hand and passing them across the soft, wet, slipway into the respirometer. After introduction, any air bubbles that had collected on the internal surface (from scuba-diver expiration or oxygen injection) were rolled out of the access port, before the mesocosm was sealed. Oxygen consumption rates (\dot{M}_{O_2}) were determined by measuring the drop in mesocosm internal dissolved oxygen (DO) level over time. Mesocosm mixing was monitored by manual recordings of DO at the beginning and end of each experimental trial through screw cap access ports in the ceiling at nine positions within the respirometer (3, 6 and 9 m from the port access side and at three depths: 0.25, 1.25 and 2.25 m). Coefficient of variation between manual DO recordings from the nine sample positions did not exceed 2.6% for any trial, indicating that the mesocosm remained well mixed at all times.

Background respiration and photosynthesis of planktonic organisms in the water column and on the respirometer surface was measured in trials immediately before and after each experiment. Background respiration was generally found to be small; however, it was dependent on time of day (respiration rate would flatten during the day due to photosynthesis). All \dot{M}_{O_2} recordings were adjusted for background respiration according to the pertinent time of day. The oxygen holding capabilities of the mesocosm was found to be excellent, with a further two trials conducted to measure the rate of oxygen diffusion through the respirometer material. For these trials, the respirometer DO was reduced to either 1.90 or 2.26 mg l⁻¹ by injecting microbubbles of pure nitrogen with a gas diffuser (Aqua & Co[®] Force 7, BOC Gases, NSW, Australia) and then removing the collected bubbles before the mesocosm was sealed and oxygen monitored for more than 20 h. Subsequent oxygen diffusion across the respirometer wall was found to be very low, representing an oxygen gradient of just 0.0042 mg⁻¹ h⁻¹ per mg l⁻¹ DO between the respirometer and the external environment. This rate of diffusion was nevertheless used to adjust all trial DO recordings according to the pertinent oxygen gradient. Dissolved ammonia concentrations were also monitored by daily analyses of water samples before, during and after each trial, and they never exceeded 0.6 mg l⁻¹.

Experimental protocol

The mesocosm was installed into the marine farm pontoon for 49 days between March and May 2005, when four trials were conducted. For each trial, three fish (10±0.4 kg, mean ± s.e.m.; Table 2) were transferred from the holding sea-cage into the respirometer in the late afternoon. The fish were left overnight to become accustomed to the respirometer environment. To verify whether this time was sufficient for acclimation, \dot{M}_{O_2} was recorded during the acclimation period for one trial. In this trial, \dot{M}_{O_2} was elevated immediately after introduction, but had plateaued within 7 h and remained steady for the subsequent 18 h (Fig. 2). This indicates that overnight was a sufficient period for acclimation.

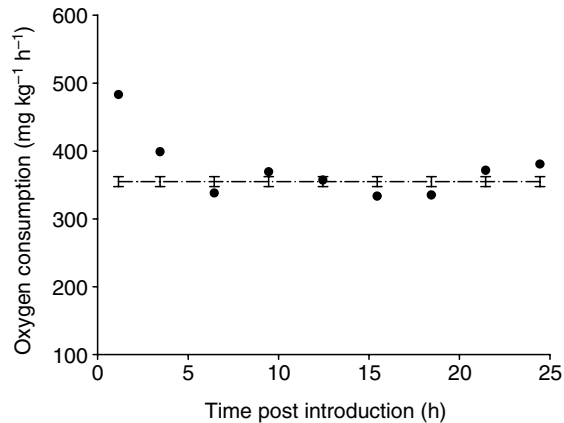


Fig. 2. Oxygen consumption rates (\dot{M}_{O_2}) of three SBT after introduction into the mesocosm respirometer, showing the plateau in \dot{M}_{O_2} within 7 h after transfer and subsequently calculated mean routine metabolic rate [RMR, broken line; values are means ± s.e.m. of measurements (3 h periods)].

Measurement of the routine metabolic rate (RMR) was begun the morning following introduction. The respirometer was sealed and \dot{M}_{O_2} was monitored for 16–24 h. Routine metabolic rate was calculated as the mean, post-acclimation \dot{M}_{O_2} over this period (Fig. 2).

The following morning the mesocosm was re-opened and dissolved oxygen returned to approximately 100% saturation by pure oxygen injected with the diffuser. The fish were then left for roughly 1 h to recover from this disturbance before they were offered Australian sardines through the entrance port. All tuna consumed sardines during all attempts at feeding within the respirometer. Attempts were made to differentiate rations consumed by individual fish from both the surface and by a diver observing from within the mesocosm. However these attempts proved largely unsuccessful as it was not always possible to differentiate individual fish from the surface and fish would often fail to ingest in the presence of a diver. After feeding, a diver collected any uneaten sardines, and this mass was subtracted from the known mass of bait offered to establish total consumption. Following feeding, the respirometer was sealed and \dot{M}_{O_2} monitored for the subsequent 40 h or more (except for one trial when logging failed after 26 h).

Dissolved oxygen and water temperature measurement

Two Hach[®] Luminescent Dissolved Oxygen (LDO[™]) meters (HQ10; Loveland, CO, USA) permanently installed at a depth of 1 and 2 m, respectively, both 3 m from the wall, logged mesocosm DO and water temperature. Meters were calibrated according to the manufacturer's instructions at the start of the trials and calibration checked following the completion of all trials. Meters recorded DO (to 0.01 mg l⁻¹ resolution) that was automatically compensated for water temperature and salinity set at 35‰. Oxygen meters were set to log DO every 5 or 15 min, depending on the trial-logging interval required (24 or 48 h, respectively). All DO recordings were broken up into 3 h blocks according to time of day

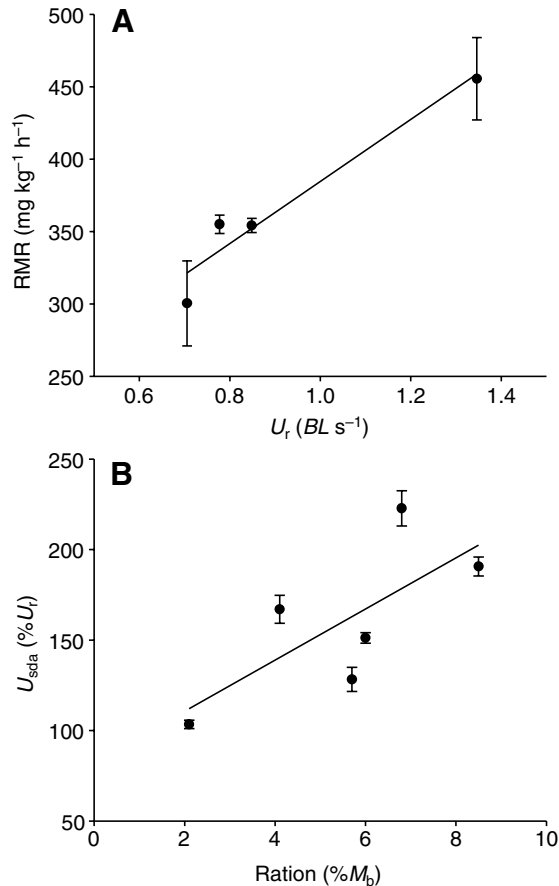


Fig. 3. (A) The relationship between the routine swimming velocity (U_r , $BL\ s^{-1}$) and the routine metabolic rate (RMR) of southern bluefin tuna with fitted linear regression ($y=219x-166$, $R^2=0.94$). Values shown are means \pm s.e.m. ($N=5-9$). (B) The relationship between ration consumed ($\%M_b$) and the factorial increase swimming velocity recorded during the SDA period ($\%U_r$) with fitted linear regression ($y=14.1x+82.5$, $R^2=0.53$). Values are means \pm s.e.m. ($N=5-15$).

(starting at midnight) and linear regressions were fitted to the change in DO ($mg\ l^{-1}$) representative for that 3 h period. The drop in mesocosm DO was approx. $0.04\ mg\ l^{-1}\ h^{-1}$ during RMR measurement and as great as $0.12\ mg\ l^{-1}\ h^{-1}$ during SDA measurement. The high-resolution stability of these luminescent meters meant that the linear regression coefficient of determination generally remained between $R^2=0.96-0.99$ over each 3 h period. \dot{M}_{O_2} calculations were adjusted for the mean background respiration rate (mean of pre- and post-SDA trial background recording) recorded for the respective time of day (3 h block) and oxygen diffusion through the respirometer walls. A similar DO meter was used to make daily recording of the DO in the external environment, which remained between 7.1 and $7.4\ mg\ l^{-1}$.

Swimming velocity analysis

Fish behaviour was monitored (both day and night) using a permanently installed video system (SciElex Pty. Ltd., Hobart, TAS, Australia) that consisted of two 0.05 lux black and white

underwater video cameras and two 6 W white LED lights (housed within resin) (Fig. 1). The system was programmable through a central controller and power supply unit that were secured to the sea-cage. The cameras were programmed to record for 4 min every 90 min (first by the horizontal camera then immediately by the vertical camera) and data stored on an ARCHOSTM pocket video recorder (AV400, Greenwood Village, CO, USA). The lights were programmed to turn on at dusk and remain on until dawn, using a Moeller Easy timer (412-DA-RC, Bonn, Germany). The system was powered by a single 32 Ah, 12 V battery that was exchanged daily.

Video recordings were viewed in the VirtualDub video editing program (1.5.10, Avery Lee). Suitable records were defined as those containing a fish that was swimming perpendicularly to the camera and at least one frame in which body length (BL) could be measured for scaling. This sequence was imported into Video Point[®] software (Version 2.5, Lenox SoftworksTM) where swimming velocity was analysed by tracking movement across the field. Tuna BL was used to calibrate the image scale, accounting for variable distances between the fish and the camera. Any camera movement was corrected for by referring to a stable point within the respirometer on a frame-by-frame basis.

Data analysis

Swimming velocity data were collated within the same 3 h time periods as DO. For each 3 h period, 4–7 video footage segments were analysed for swimming velocity and the mean taken as representative for that period (a total of 448 footage segments were analysed). Due to poor quality footage, four suitable footage segments were not available for some 3 h periods. Video records after 24 h in trial 6 were lost due to video failure.

Mean swimming velocity recordings made during the RMR measurement are subsequently referred to as the routine swimming velocity (U_r) and velocity measurements made post feeding as the specific dynamic action swimming velocity (U_{sda}). U_{sda} duration is the time that post-feeding swimming velocity remained one standard error (s.e.) above U_r . The effect of meal size on metabolic rate was quantified by the following parameters: SDA peak (maximum post-prandial \dot{M}_{O_2}), SDA factorial scope (SDA peak divided by RMR), SDA duration (duration that post-prandial \dot{M}_{O_2} remained greater than 1 s.e. above the RMR), SDA magnitude (total oxygen consumed above the RMR within the SDA duration period) and SDA coefficient (SDA magnitude as a percentage of gross ingested energy). Conversion from oxygen consumed to the energy equivalent was calculated assuming $14.32\ J$ energy expended per $mg\ O_2$ consumed (Beamish and Trippel, 1990).

Results

During the RMR measurement, three of the four groups of fish swam slowly and consistently between approximately 0.7 and $0.8\ BL\ s^{-1}$, the other group swam considerably faster at around $1.4\ BL\ s^{-1}$ (U_r ; Table 2). The fish that swam the fastest

Table 2. Southern bluefin tuna parameters

	Trial						Mean (N=4 or 6)
	1	2	3	4	1	2	
M_b (kg)	9.4±1.6	9.9±0.9	11±1.3	11±1.4			10±0.4
BL (cm)	81±5	83±2	88±3	86±2			84±1.6
T (°C)	19.7–20.1	20.1–20.3	19.1–19.7	18.2–18.5			19.3±0.4
U_r ($BL\ s^{-1}$)	0.71	1.4	0.78	0.83			0.92±0.15
RMR ($mg\ kg^{-1}\ h^{-1}$)	300	456	355	354			366±32.5
Feed trials	1	1	2	1	2	1	
Ration ($\%M_b$)	5.7	6.0	8.5	2.1	6.8	4.1	5.5±0.9
IE (mJ)	8.96	10.0	14.1	3.70	12.1	7.73	9.48±1.48
U_{sda} ($BL\ s^{-1}$)	0.87	2.0	2.6	0.80	1.7	1.4	1.6±0.9
U_{sda} duration (h)	26	38	45+	20	45+	24+	33±4.5
Peak ($mg\ kg^{-1}\ h^{-1}$)	728	1240	1290	469	840	669	872±133
Factorial scope	2.4	2.7	2.8	1.3	2.3	1.9	2.2±0.23
Duration (h)	24	23	42	27	45+	25	31±4.0
Magnitude ($kJ\ kg^{-1}$)	99.2	130	192	30.7	148	74.9	112±23.2
Coefficient (%)	31	38	40	26	39	33	35±2.2

M_b , body mass; BL , body length; T , water temperature; U_r , routine swimming velocity; RMR, calculated routine metabolic rate; IE, total ingested energy; U_{sda} , mean swimming velocity during the SDA period; U_{sda} duration, duration of elevated post-prandial swimming velocity. Values are means ± s.e.m. for the three fish used in each trial.

also consumed the most oxygen, with a strong linear relationship ($R^2=0.94$) between swimming velocity and RMR (Fig. 3A). The evaluated RMR, taking into account background respiration and diffusion, ranged between 300 and 456 $mg\ kg^{-1}\ h^{-1}$, corresponding to a mean of 366±32.5 ($N=4$). This is slightly less than the previously reported RMR of SBT (460 $mg\ kg^{-1}\ h^{-1}$) (Fitzgibbon et al., 2006). The discrepancy is likely due to individual variability in voluntary swimming speeds and the longer acclimation period used in the present study (16+ h versus 6 h).

Six feeding events of rations between 2.1 and 8.5% M_b Australian sardines were recorded (two of the experimental groups were fed twice, the other two experimental groups fed only once) (Table 2). On all occasions, swimming velocity increased post feeding. The duration before swimming velocity returned to pre-feeding levels (U_r) appeared to increase with ration size, from 20 h for the smallest ration to longer than the 45 h measurement period for the greatest two rations. Increase in swimming velocity recorded during the SDA period (U_{sda}) was linearly related to ration size ($R^2=0.53$) (Fig. 3B).

In all trials, \dot{M}_{O_2} was elevated above the RMR post-feeding; however, the nature of this elevation was highly dependent on ration size and experiment (Fig. 4). Maximum post-prandial \dot{M}_{O_2} (SDA peak) increased linearly with ration size ($R^2=0.71$) (Fig. 5A). At the greatest ration consumed (8.5% M_b), SDA peak was 1 290 $mg\ kg^{-1}\ h^{-1}$, corresponding to 2.8× RMR, whilst with the smallest ration (2.2% M_b), SDA peak was 469 $mg\ kg^{-1}\ h^{-1}$, or just 1.3× RMR (Table 2). The duration of SDA ranged between 23 and 45 h and was poorly correlated with ration size ($R^2=0.38$) (Fig. 5B). At the four lowest rations, SDA duration did not appear to be affected by ration size; however, above a ration of 6% M_b , SDA duration was greatly

elevated. The magnitude of SDA ranged between 30.7 and 191 $kJ\ kg^{-1}$ (Table 2) and was strongly linearly correlated with ration size ($R^2=0.98$) (Fig. 5C). SDA coefficient averaged 35±2.2% ($N=6$) (Table 2).

Discussion

Effect of meal size on SDA

The pattern of SDA in fish is characterized by a rapid increase in \dot{M}_{O_2} after feeding before gradually falling back to the resting level (Jobling, 1981). The pattern of SDA response appears to be no different for SBT. The factorial scope and duration of SDA is comparable to those of many fish species examined (Chakraborty et al., 1992; Fu et al., 2005a; Fu et al., 2005b; Hunt von Herbing and White, 2002; Jobling, 1981; Lyndon et al., 1992; Peck et al., 2002). Also like most fish species, peak, duration and magnitude of SDA appear to be directly related to ration size (Carter and Brafield, 1992; Chakraborty et al., 1992; Fu et al., 2006; Fu et al., 2005c; Jobling and Davis, 1980; Muir and Niimi, 1972). However, the energetic cost of SDA is approximately double (SDA coefficient=35%) that recorded in other teleost species (generally between 5 and 20%). It appears that although the factorial pattern (peak and duration) of SDA of SBT is consistent with other fish, the absolute metabolic cost of SDA is much higher.

High metabolic cost of SDA

A complete understanding of the physiological basis of SDA remains unclear; however, much of its effect is attributed to the metabolic cost of growth. That is, the post-prandial influx of amino acids stimulates rapid synthesis and turnover of tissue proteins resulting in much of the increase in metabolic rate

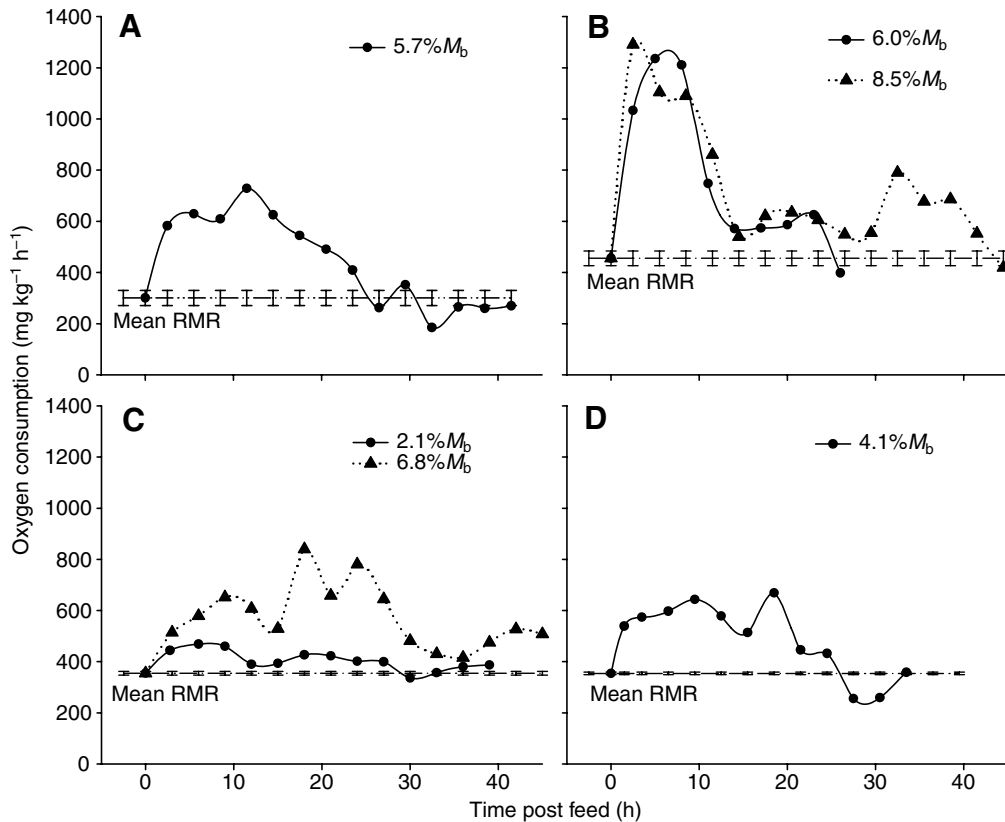


Fig. 4. Post feeding oxygen consumption rate for southern bluefin tuna for the six feeding events recorded of ration size between 2.1 and 8.5% body mass ($\%M_b$) in the four mesocosm respirometer experiments (A–D). Broken line represents the calculated routine metabolic rate (RMR).

known as SDA (Brown and Cameron, 1991a; Brown and Cameron, 1991b; Jobling, 1981; Lyndon et al., 1992). In fish, both protein synthesis and degradation rates have been shown to rise linearly with growth rate (Houlihan et al., 1988), and therefore are likely to contribute more to the metabolic cost of SDA in fast growing species. The growth rates of tuna, like other large pelagic fishes, are known to be high (Brill, 1996; Glencross et al., 2002; Sainsbury et al., 1997; Uchiyama and Struhsaker, 1980). Furthermore, the SBT examined in the present study, although large in comparison to typical specimens examined, were in fact juveniles (Collette and Nauen, 1983; Schaefer, 2001). Juvenile fish have been shown to divert a proportionately high amount of available metabolic scope to support SDA to meet the demands of their fast growth rates (Hunt von Herbing and White, 2002). Evidence to support that SDA is mostly a post-absorptive effect is the probable discrepancy between SDA duration and food gut passage time. The recorded duration of SDA (25–45 h) is far greater than the likely gut evacuation time, which in tuna has been shown to be greatly accelerated (~10–12 h) (Magnuson, 1969; Olson and Boggs, 1986). This suggests that high protein turnover and synthesis rates associated with fast growth rates of juvenile SBT are likely to elevate the metabolic cost of SDA. Unfortunately, there is no information on the cost of SDA in other fast growing pelagic fishes for comparison.

It is possible that the poor low energy value of the Australian

sardines ingested may have contributed to the high SDA coefficient recorded. The nutritional balance of the diet can affect SDA, particularly the protein level and its balance with non-protein energy sources. Deamination of ingested amino acids is considered to be a significant proportion of SDA in carnivorous fish (Beamish and Trippel, 1990; Cho and Kaushik, 1990). Diets with excess amounts of protein or insufficient non-protein energy sources (i.e. fat or digestible carbohydrates) can elevate the energy expenditure of SDA as a result of increased deamination of amino acids (Beamish and Trippel, 1990; Chakraborty et al., 1992; Jobling and Davis, 1980; LeGrow and Beamish, 1986; Peres and Oliva-Teles, 2001). When represented in terms of the digestible protein (P, g) and digestible energy (E, mJ), the P:E ratio of the Australian sardines fed in the present study (34 g mJ^{-1} , assuming 90% and 85% digestible energy and protein, respectively) is considerably greater than that of diets thought to be optimal in aquaculture of salmonid species ($\text{P:E}=20 \text{ g mJ}^{-1}$) (Cho and Kaushik, 1990). It is likely that this extreme protein to energy ratio would have resulted in high levels of amino acid deamination contributing the high SDA coefficient recorded in the present study. However, this nutritional profile is typical for Australian sardines caught in Southern Australian waters (Ellis and Rough, 2005) and as the Australian sardine is an important wild-fish food source (Kemps et al., 1999), this high SDA is biologically relevant.

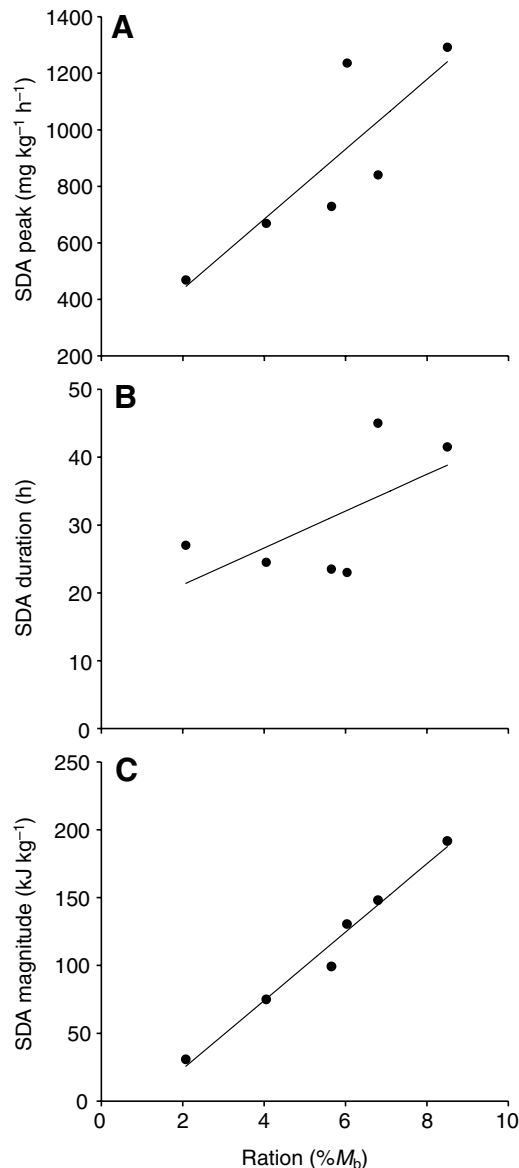


Fig. 5. Relationship between southern bluefin tuna ration size (% M_b) and (A) specific dynamic action (SDA) peak with fitted regression ($y=124x+190$, $R^2=0.71$), (B) SDA duration ($y=2.7x+15.8$, $R^2=0.38$) and (C) SDA magnitude ($y=25.2x+26.7$, $R^2=0.98$), for the six feeding events recorded in the mesocosm respirometer.

Elevated energy expenditure associated with post-prandial visceral warming may also contribute to SDA. Like other bluefin tuna, SBT elevate their visceral temperature which is characterized by the rapid increase following feeding, before slowly cooling to a basal temperature of 2°C above ambient water temperature up to 60 h post feeding (Gunn et al., 2001). The primary purpose of visceral warming is thought to be to accelerate digestion (Stevens and McLeese, 1984). The source of heat is hypothesized to be a result of aerobic metabolism associated with SDA, which is retained by counter-current exchange in retia mirabilia that thermally isolate the stomach, caecum, intestines and spleen (Carey et al., 1984). The liver,

however, is on the cold side of the rete and thus does not contribute to visceral warming. This is surprising, as the liver is considered to have the highest rates of protein synthesis of teleost tissues (Carter and Houlihan, 2001) and thus would be an obvious source of SDA-associated heat production. Protein synthesis rates in the livers of juvenile Atlantic cod have been shown to increase rapidly after feeding, and after 6 h they account for 31% of whole body protein synthesis compared to just 9% for the stomach (Lyndon et al., 1992). This suggests that only a small fraction of SDA contributes to visceral warming (related to gastrointestinal work and absorption), leaving potential for the involvement of another mechanism. Gunn et al. provided support for this (Gunn et al., 2001) by finding that, for a given ration, the magnitude of SBT visceral warming was much greater in winter than in summer. They suggested that SBT possess a compensatory acclimation mechanism to provide increased digestive efficiency at low ambient temperatures, possibly facilitated by increased aerobic metabolism and/or the heat conservation (through changes in the activity of the visceral rete). Thus, it appears that visceral warming may not simply be the accumulation of heat by-product of SDA, but may be an energy-consuming mechanism to maintain optimal digestive rates.

The observed increase in swimming velocity after feeding would have contributed to the measured metabolic cost of SDA. Fish on average swam 1.7 times faster after feeding (1.6 compared to 0.92 BL s^{-1}). Based on the relationship between \dot{M}_{O_2} and swimming velocity described for 2.2 kg yellowfin tuna *Thunnus albacares* (Dewar and Graham, 1994), an increase in swimming velocity from 0.92 to 1.6 BL s^{-1} would increase metabolic rate from 409 to $585 \text{ mg kg}^{-1} \text{ h}^{-1}$. A potential explanation for faster swimming is to increase ventilation volume as a response to the enhanced metabolic demand associated with SDA. This theory is supported by the fact that the fish that consumed the most also swam the fastest (Fig. 3B), and for most of the feeds examined, the duration of elevated swimming velocity post feeding (U_{sda} duration) is similar to the duration of SDA. However, the pattern of post-feeding swimming velocity was more difficult to distinguish than that of SDA, as for the two greatest rations it failed to return to pre-feeding levels. At present the reason for this discrepancy between swimming velocity and SDA is unknown; however, it may be due to measurement error caused by individual variation in swimming speed due to unequal ration consumption, or diurnal swimming cycles (fish appeared to swim faster at dusk and dawn). More intensive examination of the effects of feeding on the effect of individual tuna swimming velocity over longer experimental period is required to verify the metabolic cost of faster post-prandial swimming.

SDA and metabolic scope

Consistent with some fish species, SBT peak post-prandial \dot{M}_{O_2} increased with ration size (Chakraborty et al., 1992; Muir and Niimi, 1972); however for other species, SDA peak reaches a maximum and plateaus with increased ingestion (Beamish,

1974; Fu et al., 2005c). In the latter, SDA peak has a species-specific maximum that limits the proportion of available metabolic scope devoted to SDA and allows other metabolic activities to occur simultaneously (Beamish, 1974). It is possible that SBT reach this plateau at a ration size greater than that examined in the present study ($8.5\%M_b$). However, this appears to be unlikely as anecdotal evidence from tuna farm managers indicates that $8.5\%M_b$ is close to the maximum feed intake that SBT accept in a single meal. According to cardiorespiratory models, the factorial scope of skipjack (*Katsuwonus pelamis*) and yellowfin tuna is approximately 8–9 times the SMR (Brill and Bushnell, 1991; Korsmeyer and Dewar, 2001). If a similar factorial scope of 7 times the RMR is assumed for SBT (less than that predicted above as the comparison is based on a low RMR not the SMR), it corresponds to $2560 \text{ mg kg}^{-1} \text{ h}^{-1}$, which is similar to the maximum-recorded \dot{M}_{O_2} of a tuna species, $2500 \text{ mg kg}^{-1} \text{ h}^{-1}$ (Gooding et al., 1981). The maximum recorded post-prandial metabolic rate ($1300 \text{ mg kg}^{-1} \text{ h}^{-1}$) is approximately 50% of this predicted metabolic scope, suggesting that even during the peak of SDA at the greatest ration recorded, the SBT examined would still have had considerable metabolic scope available to perform other tasks (i.e. oxygen debt recovery and locomotory costs beyond the requirement for hydrostatic equilibrium and ventilation). This supports the theory that the main benefit of high aerobic scope in tunas is to simultaneously support multiple metabolic functions needed to sustain their high performance requirements (Brill and Bushnell, 1991; Korsmeyer et al., 1996).

Energetic consequence of a high metabolic cost of SDA

To estimate minimum daily energetic cost of feeding SBT, we have plotted the total energy expenditure as a percentage of ingested energy for the six feeding trials (calculated as the total oxygen consumption the 24 h post feeding) (Fig. 6). The break-even point (feed ration at which energy expenditure was equal to ingested energy) is approximately a ration of $3.5\%M_b \text{ day}^{-1}$. However, if SBT are ultimately to grow and reproduce, their minimum daily ration of Australian sardines needs to be greater than this, as some ingested energy is indigestible and further energy is lost in the form of urine, gill excretion and surface losses. Furthermore, the calculated energetic cost is likely to be a minimum, as activity was restricted. With wild fish, the cost of activity is likely to be much greater due to the activity requirement of predation and competition.

Several bioenergetic models for tuna species have been described (Kitchell et al., 1978; Korsmeyer et al., 1996). These show that tuna are 'energy speculators', gambling high rates of energy expenditure for potentially higher rates of energy returns. The work presented here agrees with this conclusion; however, it shows that one aspect of tuna energetics, the metabolic costs of SDA, may have been considerably underestimated. Previous models have estimated the cost of SDA to be only 15% of the ingested energy (Kitchell et al., 1978; Korsmeyer et al., 1996). For SBT consuming the

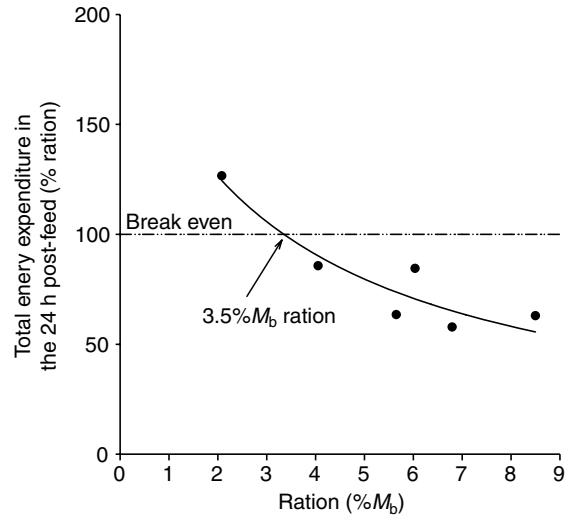


Fig. 6. Relationship between southern bluefin tuna ration size and total energy consumption (calculated as the total oxygen consumption the 24 h after feeding as a percentage of ingested energy for the six feeding events recorded in the mesocosm respirometer). The broken line represents the theoretical point that the amount of energy used by the fish's metabolic processes equals the amount of ingested energy.

predominant natural food source in Australia's southern oceans, 35% of the ingested energy is lost in the SDA process. This finding further exemplifies the risk that tuna take in balancing performance with efficiency and highlights the importance of oceanic prey species communities to these valuable fish.

List of abbreviations

BL	body length
DO	dissolved oxygen
E	digestible energy
\dot{M}_{O_2}	rate of oxygen consumption
P	digestible protein
RMR	routine metabolic rate
SBT	southern bluefin tuna
SDA	specific dynamic action
T	time
U_r	routine swimming velocity
U_{sda}	specific dynamic action swimming velocity

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