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Swimming performance studies on the eastern Pacific bonito *Sarda chiliensis*, a close relative of the tunas (family Scombridae)

I. Energetics

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Summary

A large swim tunnel respirometer was used to quantify the swimming energetics of the eastern Pacific bonito *Sarda chiliensis* (tribe Sardini) (45–50 cm fork length, *FL*) at speeds between 50 and 120 cm s^{-1} and at 18±2°C. The bonito rate of oxygen uptake ($\dot{V}_{O_2}$)–speed function is U-shaped with a minimum $\dot{V}_{O_2}$ at 60 cm s^{-1}, an exponential increase in $\dot{V}_{O_2}$ with increased speed, and an elevated increase in $\dot{V}_{O_2}$ at 50 cm s^{-1} where bonito swimming is unstable. The onset of unstable swimming occurs at speeds predicted by calculation of the minimum speed for bonito hydrostatic equilibrium (1.2 *FL* s^{-1}). The optimum swimming speed (U_{opt}) for the bonito at 18±2°C is approximately 70 cm s^{-1} (1.4 *FL* s^{-1}) and the gross cost of transport at U_{opt} is 0.27 J N^{-1} m^{-1}. The mean standard metabolic rate (SMR), determined by extrapolating swimming $\dot{V}_{O_2}$ to zero speed, is 107±22 mg O_2 kg^{-1} h^{-1}. Plasma lactate determinations at different phases of the experiment showed that capture and handling increased anaerobic metabolism, but plasma lactate concentration returned to pre-experiment levels over the course of the swimming tests. When adjustments are made for differences in temperature, bonito net swimming costs are similar to those of similar-sized yellowfin tuna *Thunnus albacares* (tribe Thunnini), but the bonito has a significantly lower SMR. Because bonitos are the sister group to tunas, this finding suggests that the elevated SMR of the tunas is an autapomorphic trait of the Thunnini.

Key words: energetics, locomotion, swimming, Scombridae, eastern Pacific bonito, *Sarda chiliensis*, standard metabolic rate, cost of transport, tuna.

Introduction

Fishes in the family Scombridae such as the mackerels (tribe Scombrini), bonitos (Sardini) and tunas (Thunnini) exemplify structural design features for maximizing swimming performance (Lighthill, 1969; Webb, 1975; Magnuson, 1978; Nauen and Lauder, 2000; Donley and Dickson, 2000). Tunas, which are the most derived scombrids, possess two additional locomotor-enhancing functions. The first of these is the capacity for regional endothermy, which elevates muscle power (Carey and Teal, 1966; Carey et al., 1971; Graham, 1973; Johnston and Brill, 1984; Altringham and Block, 1997; Graham and Dickson, 2001). The second is the use of the thunniform swimming mode, which reduces drag by minimizing lateral body undulations while generating thrust with rapid oscillations of the high-aspect-ratio caudal fin (Fierstine and Walters, 1968; Lighthill, 1970; Webb, 1975; Lindsey, 1978; Altringham and Shadwick, 2001).

The functional and structural bases for tuna endothermy and thunniform swimming reside in the tunas' myotomal architecture. Red myotomal muscle (RM, the slow-twitch aerobic fibers that power sustained swimming) occurs both more anterior in the body and closer to the vertebral column in tunas than in other fishes (Kishinouye, 1923; Fierstine and Walters, 1968; Graham et al., 1983). Tuna RM position has been hypothesized to have influenced thunniform locomotion through effects on body shape (Magnuson, 1978; Graham and Dickson, 2000) and on the mechanical linkage between myotomes and the caudal fin (Westneat et al., 1993; Shadwick et al., 1998; Ellerby et al., 2000; Graham and Dickson, 2000). In addition, shifts in the pattern of RM vascular supply may have established the basis for counter-current heat transfer and for the origin of endothermy (Graham and Dickson, 2000, 2001).

Although a unique RM position and regional endothermy occur exclusively in the tunas, the sequence of evolutionary changes that took place from the less-derived mackerels and bonitos to the tunas remains unclear. Therefore, testing or

distinguishing among hypotheses about the acquisition sequence of these features requires phylogenetically appropriate structural and functional comparisons with non-tuna scombrids (Magnuson, 1973; Graham, 1975; Collette and Chao, 1975; Collette, 1978; Block et al., 1993; Graham and Dickson, 2000, 2001).

Several works have compared the swimming performance of mackerels to that of tunas. In contrast to the thunniform swimming mode of tunas, both chub (*Scomber japonicus*) and Atlantic (*Scomber scombrus*) mackerels use the carangiform swimming mode (Videler and Hess, 1984; Donley and Dickson, 2000). Although the chub mackerel is not endothermic, rapid swimming does transiently elevate both RM and white muscle temperatures (Roberts and Graham, 1979). Finally, and despite similar costs of locomotion, the standard metabolic rate (SMR, the minimum metabolic rate required for maintenance functions; Videler, 1993) of the chub mackerel is lower than that of the tunas (Sepulveda and Dickson, 2000; Shadwick and Steffensen, 2000).

Although mackerel–tuna comparisons identify key differences between the two groups, most investigators regard the bonitos, which are the tuna sister group (Collette, 1978; Block et al., 1993), as more appropriate for evolutionary comparisons (Block and Finnerty, 1994; Altringham and Block, 1997; Ellerby et al., 2000; Graham and Dickson, 2000). Relative to mackerels, bonitos have many morphological specializations (i.e. body shape, gill surface area, growth rate and maximum size) that are more like those of tunas (Gray, 1954; Campbell and Collins, 1975; Collette, 1978). Bonito RM is also in a more medial position than in the mackerels (Kishinouye, 1923; Graham et al., 1983; Ellerby et al., 2000; Graham and Dickson, 2000), and both bonito myotomal structure and the arrangement of the anterior and posterior oblique tendons (which transmit force from the myotomal musculature to the caudal propeller) are more similar to those of tunas (Ellerby et al., 2000; Westneat et al., 1993; Westneat and Wainwright, 2001; K. A. Dickson and J. B. Graham, unpublished). However, bonitos do not have the anterior RM position found in tunas and they are not endothermic (Carey et al., 1971; Graham, 1975; Graham et al., 1983; Altringham and Block, 1997; Graham and Dickson, 2000, 2001).

While the importance of additional studies with bonitos to increasing our understanding of the swimming adaptations of tunas has long been recognized (Godsil, 1954; Graham, 1975; Block and Finnerty, 1994; Altringham and Block, 1997; Ellerby et al., 2000; Graham and Dickson, 2001), access to live specimens by laboratories capable of conducting physiological studies with them has been rare (Altringham and Block, 1997; Ellerby et al., 2000). The availability of the eastern Pacific bonito *Sarda chiliensis* in southern California coastal waters in the summer of 2000 provided the opportunity to study the swimming energetics and kinematics of this species using the same water tunnel respirometer that had been used for the tuna energetics and kinematics studies reported by Dewar and Graham (1994a,b). This paper reports on bonito swimming energetics, and the companion paper (Dowis et al., 2003) describes bonito swimming kinematics.

Previous work on bonito energetics includes indirect $\dot{V}_{O_2}$ estimates derived from mouth gape and swimming distance (Mendo and Pauly, 1988) and estimates of routine metabolic rate (RMR, which includes both spontaneous movements and locomotion; Beamish, 1978) made for bonito swimming inside of a small annular respirometer, without speed control (Freund, 1999). The objectives of the present study were to quantify bonito swimming energetics and obtain swimming–$\dot{V}_{O_2}$ data over a range of controlled speeds. We also wanted to compare bonito swimming to that of its sister group, the tunas, by contrasting the relationship between $\dot{V}_{O_2}$ and swimming speed in similar-sized fish to estimate the cost of transport and SMR. This approach has provided new insight into two important questions about scombrid physiology. (1) How do the costs of locomotion compare for tunas and bonitos? (2) Is the high SMR of the tunas a unique tuna trait or a synapomorphy of the tribes Sardini and Thunnini?

Materials and methods

Fish collection and maintenance

Eastern Pacific bonito *Sarda chiliensis* Cuvier 1832 (size range: 30–40 cm fork length *FL*, mass 500–1000 g) were caught in waters off La Jolla, California, in July and August of 2000 and transported to the laboratory at Scripps Institution of Oceanography (SIO) in a 378 liter cylindrical tank containing oxygenated seawater. Fish were captured using barbless hooks and transferred untouched into the transport tank. In the laboratory, bonito were transferred, without touching, to an 8 m diameter, 1.2 m deep, above-ground, plastic-lined holding tank supplied with continuously flowing aerated seawater (18±2°C). Fish were held in this tank over the course of the study (90–150 days). They were conditioned to feed with live guppies (Scientific Hatcheries, Huntington Beach, CA, USA) and, once feeding, were fed daily to satiation (about 5–10% body mass) using a mixture of chopped fish and squid.

The respirometer

The variable-speed water-tunnel respirometer used in this study has been described previously (Graham et al., 1990; Dewar and Graham, 1994a; Graham et al., 1994; Bernal et al., 2001). It consists of a 2.3 m×6.3 m (length×width) oval of 46 cm-diameter polyvinylchloride pipe with an in-series diffuser-contraction section and a 100 cm×51 cm×42 cm (length×width×height) working section. It has a total volume of 3000 liters and is powered by a 40 hp variable-speed electric motor with a fixed, low-pitch propeller. Initial flow analyses (Graham et al., 1990) using attached threads, observations of particle motion and dye streaming all confirmed a uniform speed and laminar flow field in the center and first half of the working section, which is where swimming fish spend most of their time (see below).

Experimental protocol

Care was taken not to touch the bonito during all steps involved in capture and transfer to the water tunnel. Prior to all experiments, food was withheld from the entire tank for 24 h. The experimental bonito was obtained by fishing with a baited, barbless hook. The hooked fish was immediately placed in the cylindrical transport tank containing oxygenated seawater and the manufacturer's recommended dose of Fritzyme®, a mucus coat protecting agent. We found that the presence of other fish in the transfer tank minimized the introduced bonito's swimming speed and the frequency of its collisions with the tank wall. Standard procedure therefore was to place between one and five 'companion fish' (either chub mackerel *Scomber japonicus*, or topsmelt *Atherinops affinis*) in the tank prior to introducing the experimental bonito.

After 15 min the bonito and the water around it were scooped up in a soft plastic bucket liner and transferred into the working section of the respirometer. We found that the transferred bonito could better orient to the flow and had fewer erratic movements and bursts if a 'companion fish' was also present in the working section at the time of introduction. Both chub mackerel and topsmelt, which swim well in water tunnels (Sepulveda and Dickson, 2000; C. Sepulveda, personal observation) were used as 'working-section companions'. The companion fish was removed after about 60 min, once the bonito had begun to swim steadily. Covering the working section with a dark cloth and placing a light at its front end helped to keep the bonito swimming in the center of the channel. A mirror positioned at 45° over the working section facilitated remote observation of the fish for the duration of the study.

The bonito was then given a 4 h period of slow, steady swimming to allow its recovery from capture and tunnel placement stress. Previous scombrid respirometry studies have noted a marked change in fish behavior and $\dot{V}_{O_2}$ after about 2 h in the working section (Dewar and Graham, 1994a; Sepulveda and Dickson, 2000). During recovery the bonito swam slowly (about 60 cm s^{-1}) while fresh seawater flowed through the tunnel to maintain temperature and ambient O_2 levels.

Following the recovery period, water inflow to the tunnel was stopped and the system was sealed. Measurements of bonito $\dot{V}_{O_2}$ were then made at different swimming speeds by recording water-tunnel O_2 declination rate over a 30–60 min period of steady swimming. Tunnel water speeds were determined by calibration with a flow meter (model 2035, General Oceanics Inc., FL, USA). The respirometer-water O_2 level was monitored with a polarographic O_2 electrode (Yellow Springs Instrument, OH, USA) connected to a model 52 meter. For each bonito energetics study, ProComm data acquisition software was used to record both water speed and O_2 concentration.

During a given experiment, the respirometer water temperature was maintained within ±1°C of the bonito holding tank, which was supplied with a continuous flow of fresh seawater and subject to subtle environmental fluctuations in temperature (i.e. solar heating, seasonal fluctuation). Collectively for all tests, the experimental temperature was 18±2°C. Respirometer water O_2 concentration was maintained at or above 80% saturation. When fish respiration reduced chamber O_2 levels to near the 80% saturation limit, the system was re-oxygenated by seawater flow and application of a gentle stream of bubbles from a compressed O_2 cylinder.

$\dot{V}_{O_2}$ measurements were made on bonito swimming between 50 and 120 cm s^{-1}. Tests of each fish began by swimming it at the lowest speed it could maintain (50–60 cm s^{-1}) for 30–60 min while O_2 declination was measured. Following this determination, speed was increased by 10 cm s^{-1} and $\dot{V}_{O_2}$ again measured. This protocol was repeated until the bonito could no longer swim steadily or maintain position. Most studies terminated at this point. However, in two cases, replicate $\dot{V}_{O_2}$ measurements were repeated at a lower speeds. Video records of the bonito swimming at the different test speeds were then made for a kinematics analysis (Dowis et al., 2003).

After each individual swimming test, the bonito was removed and the empty respirometer was resealed to measure the background bacterial respiration rate and instrumental drift. Throughout the background measurements, the respirometer motor was circulating the water at approximately 50 cm s^{-1} and the $\dot{V}_{O_2}$ was recorded for approximately 3–6 h. The mean background $\dot{V}_{O_2}$ value for all experiments was 62±2.3 mg O_2 h^{-1} or 6–14% of the maximum measured oxygen consumption rate; the percentage was greatest at lowest speeds. All reported bonito $\dot{V}_{O_2}$ data are background-corrected. After each experiment, the water tunnel was bleached and cleaned with fresh water.

Plasma lactate

Bonito plasma lactate levels were measured to provide an indication of the level of anaerobic metabolic stress associated with three different phases of the respirometry study: (1) pre-experiment, just after capture from the holding tank, (2) at the end of the 15 min period in the transfer tank, (3) at the end of all swimming tests. Phases 1 and 2 used bonito that, although not used in the respirometer, were handled in exactly the same way as were the respirometer fish. Bonito taken directly from the respirometer following the completion of all swimming studies were used for phase 3 measurements.

Blood samples were taken by quickly grasping the bonito behind the operculum, and holding it firmly while removing approximately 2 ml of blood *via* cardiac puncture with a 20-gauge needle attached to a 3 ml syringe. Both the needle and syringe had been flushed with heparinized saline, which also filled the dead space. Plasma obtained by immediately centrifuging the blood (5 min at 3000 ***g***) was stored at –80°C. Lactate assays were performed spectrophotometrically using a Sigma Diagnostics kit (Procedure 735). This method did not employ a deproteination step and may thus have indicated slightly higher lactate levels than actually occurred. The tests do nevertheless provide a relative index for the change in plasma lactate concentrations at the different experimental phases.

Results

Swimming performance

Swimming $\dot{V}_{O_2}$ data were obtained for 12 bonito ranging in body size from 0.98 to 1.49 kg (45-50 cm *FL*) (Fig. 1, Table 1). Swimming speeds ranged from 50 to 120 cm s^{-1}, with all of the fish studied swimming at two or more test speeds, and eight fish swimming at four or more speeds. The best performing fish was bonito 10, which swam from 60 to 120 cm s^{-1}. Replicate $\dot{V}_{O_2}$ tests were performed for two individuals, bonitos 3 and 7, to validate the repeatability of the $\dot{V}_{O_2}$ measurements. The first $\dot{V}_{O_2}$ measurement for bonito 3 was 275 mg O_2 kg^{-1} h^{-1} at 60 cm s^{-1}. After swimming at two higher speeds (70 and 90 cm s^{-1}) for 2 h, the $\dot{V}_{O_2}$ of this fish remeasured at 60 cm s^{-1} was 250 mg O_2 kg^{-1} h^{-1}. The initial $\dot{V}_{O_2}$ of bonito 7 at 50 cm s^{-1} was 259 mg O_2 kg^{-1} h^{-1}; after swimming for 1 h at 60 cm s^{-1}, its $\dot{V}_{O_2}$ at 50 cm s^{-1} was 243 mg O_2 kg^{-1} h^{-1}.

Energetics

Covariance analysis (ANCOVA; Minitab version 12) indicated a significant ($P<0.05$) positive relationship between swimming speed and $\dot{V}_{O_2}$, but no effect of either body mass or *FL* on swimming $\dot{V}_{O_2}$. Absence of a body size effect allowed pooling of data for individual bonito and facilitated comparisons with $\dot{V}_{O_2}$ values obtained for tuna (Dewar and Graham, 1994a).

Fig. 1 shows the expected exponential increase in $\dot{V}_{O_2}$ with increasing speed for each bonito (Videler, 1993; Webb, 1998), but also indicates a trend for bonito $\dot{V}_{O_2}$ to level off or even increase at 50–60 cm s^{-1}. In fact, five of the six bonito for which swimming $\dot{V}_{O_2}$ data were obtained at 50 cm s^{-1} actually had a lower $\dot{V}_{O_2}$ at 60 cm s^{-1}. The tendency for bonito $\dot{V}_{O_2}$ to remain higher than expected at slower speeds is evident in the combined $\dot{V}_{O_2}$-speed relationship for all bonito at each test speed (Fig. 2). This curve is U-shaped; the mean $\dot{V}_{O_2}$ at 50 cm s^{-1} is higher than the $\dot{V}_{O_2}$ at 60 cm s^{-1}, and the value at 60 cm s^{-1} is only slightly less than the rate at 70 cm s^{-1}. Two additional features of bonito low-speed swimming are indicated in Table 1. First, nine of the 12 fish had an elevated $\dot{V}_{O_2}$ at the lowest speed tested (either 50 or 60 cm s^{-1}) than at the next higher test speed. Second, records for these same fish at the time of study all noted erratic swimming (i.e. bursting, lateral movements and rapid fluttering of the pectoral fins) at these lower speeds.

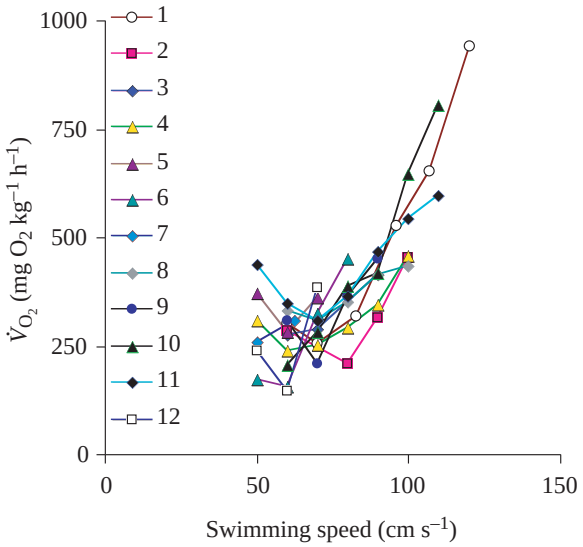

Fig. 1. Relationships between $\dot{V}_{O_2}$ and swimming speed for 12 bonito (44–50 cm *FL*, 0.98–1.49 kg) swimming at 18±2°C. Fish numbers are the same as those in Table 1.

Table 1. *Body size, swimming speed range, rate of oxygen uptake regression equations and low-speed observations for the 12 bonito studied*

Fish number	*FL* (cm)	Mass (g)	Speed range (cm s^{-1})	Regression equation for $\dot{V}_{O_2}$ (exponential fit)	*r*	Slow speed observations: Elevated $\dot{V}_{O_2}$*	Slow speed observations: Erratic swimming
1	45.0	1130	60–120	$y=66.0e^{0.0214x}$	0.94	+	+
2	46.5	1180	60–100	$y=123e^{0.011x}$	0.59	+	+
3	49.0	1430	60–90	$y=0.90e^{0.0168x}$	0.67	–	–
4	45.5	1270	50–100	$y=155e^{0.0091x}$	0.72	+	+
5	44.5	1021	50–70	ND	–	+	+
6	46.5	1150	50–80	$y=3.99e^{0.0361x}$	0.92	+	+
7	46.0	1110	50–60	ND	–	–	–
8	50.0	1490	60–100	$y=188e^{0.0083x}$	0.90	+	+
9	49.5	1280	60–90	$y=0.90e^{0.0168x}$	0.67	+	+
10	46.0	1060	60–110	$y=41.3e^{0.027x}$	0.97	–	–
11	47.5	1190	50–110	$y=225e^{0.008x}$	0.70	+	+
12	45.0	980	50–70	ND		+	+

FL, fork length; $\dot{V}_{O_2}$, rate of oxygen uptake.
*Elevated $\dot{V}_{O_2}$: the $\dot{V}_{O_2}$ at the slowest speed was not the lowest value recorded for that fish. For details, see text.
ND, Equation and *r*-value were not determined for individuals swimming at fewer than 3 different speeds.

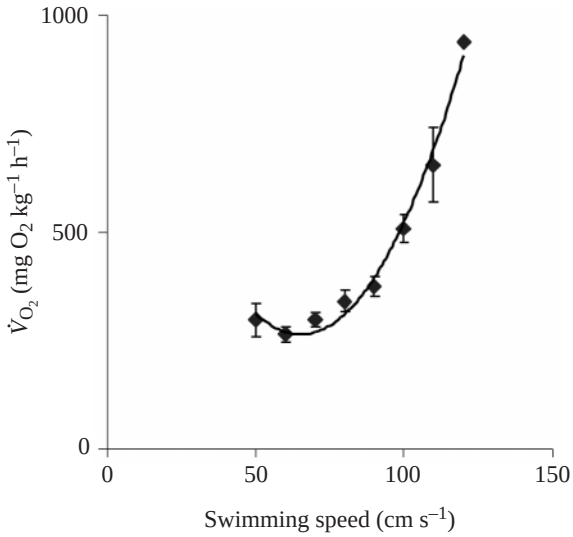

Fig. 2. U-shaped curve obtained by plotting the mean combined $\dot{V}_{O_2}$ (means ± S.E.M.) for all bonitos (N=12) at each test speed.

A higher than expected $\dot{V}_{O_2}$ at low swimming speeds affects estimates of both cost of transport (determined from the instantaneous slope of the $\dot{V}_{O_2}$–speed regression) and SMR (estimated by extrapolation of the regression function to zero speed) (Videler, 1993). It was therefore important to quantify the effect of an elevated $\dot{V}_{O_2}$ at low speed by contrasting a semi-logarithmic regression equation for the complete bonito data set with a 'corrected' regression (i.e. calculated after the selective removal of approximately one high-$\dot{V}_{O_2}$, low-speed data point from each fish). The criteria used to justify the selective removal of a high-$\dot{V}_{O_2}$, low-speed data point were: occurrence of a lower $\dot{V}_{O_2}$ at the next highest test speed and the occurrence, in notes made at the time of study, of observations of erratic swimming (Table 1).

Fig. 3 shows the effect of selective data removal: the exponential form of the regression equation for the complete data set is $y=107e^{0.015x}$. The corrected data set regression equation is $y=70e^{0.020x}$. The corrected function has a higher correlation coefficient (r=0.84 *versus* 0.74); however, there is considerable overlap of the 95% confidence intervals of the slope and y-intercept values of the two functions, indicating that they are not significantly different. These two functions do nevertheless demonstrate the marked effect of an elevated $\dot{V}_{O_2}$ at low speed both in lowering the regression equation's slope (from 0.02 to 0.15, a 25% reduction) and increasing its y-intercept, by 53%. Furthermore, because the y-intercept value at zero speed is an estimate of SMR (Videler, 1993), this selective data removal reduces the calculated bonito SMR from 107 to 70 mg O_2 kg^{-1} h^{-1}.

Bonito cost of transport

Although Fig. 3 indicates differences between the complete and corrected bonito swimming speed–$\dot{V}_{O_2}$ regressions, a valid comparison of the bonito data with published tuna energetics data necessitated use of the complete bonito data set because no high-$\dot{V}_{O_2}$, low-speed data points were removed in the tuna study.

To calculate gross cost of transport (GCOT), the mass-specific $\dot{V}_{O_2}$ values were first converted to weight-specific values (by dividing by 9.8 m s^{-2}, the acceleration due to gravity), and these were converted from mg O_2 to Joules (J), using the oxycalorific coefficient of 14.1 J mg^{-1} O_2 (Tucker, 1975; Videler, 1993; Dewar and Graham, 1994a). Then, these values were divided by the speed at which the value was determined, to obtain GCOT in units of J N^{-1} m^{-1}. Because J=N m, this expression of GCOT is dimensionless: (mg O_2 h^{-1} kg^{-1}) (9.8 m s^{-2})$^{-1}$ (14.1 J mg^{-1} O_2) (cm s^{-1})$^{-1}$ (1 h 3600 s^{-1}) (100 cm m^{-1}) (kg m s^{-2} N^{-1}) = J N^{-1} m^{-1}. The net cost of transport (COT_{net}) at each speed was calculated in the same manner, starting with the rate of oxygen consumption above SMR (mass-specific $\dot{V}_{O_2}$ at each speed – SMR).

The graph showing bonito GCOT in relation to speed (Fig. 4A, note speed units are m s^{-1}), has a U-shaped function. The function's minimum defines the optimal swimming speed (U_{opt}, i.e. the speed with the lowest energy cost per unit distance) (Videler and Nolet, 1990; Videler, 1993; Korsmeyer and Dewar, 2001). The U_{opt} of the bonito at both 18°C and

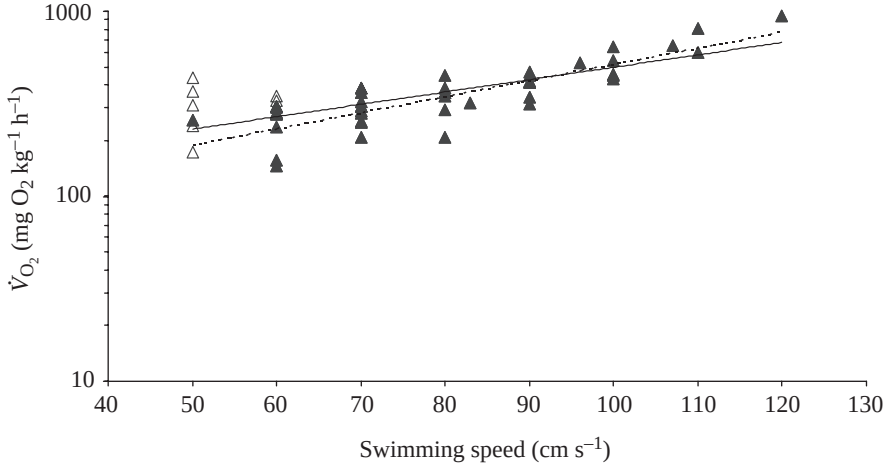

Fig. 3. Semi-logarithmic plots comparing the complete (open triangles, solid line) and corrected (filled triangles, broken line) bonito swimming speed–$\dot{V}_{O_2}$ data sets. [Note: the corrected data set was obtained by the selective removal of 10 elevated-$\dot{V}_{O_2}$, slow-speed data points (see text).] The two data sets are described by the best-fit equations: $y=107e^{0.015x}$, r=0.74, for the complete data set; $y=70e^{0.020x}$, r=0.84, for the corrected data set. Extrapolation of these equations to zero speed estimates bonito SMR as 107±22 mg O_2 kg^{-1} h^{-1} for the complete data set; 70±10 mg O_2 kg^{-1} h^{-1} for the corrected data set.

24°C is approximately 0.7 m s^{-1} (about 1.4 *FL* s^{-1}). The corresponding GCOT at U_{opt} is 0.17 J N^{-1} m^{-1} at 18°C and about 0.27 J N^{-1} m^{-1} at 24°C. Also shown in Fig. 4A are regressions describing bonito COT_{net} at both 18°C and 24°C. These functions are nearly parallel ($y=0.061e^{0.885x}$, $r=0.99$, at 18°C; $y=0.0951e^{0.916x}$, $r=0.99$, at 24°C); the difference in the *y*-intercepts reflects the assumed increase in SMR at 24°C (see below).

Interspecific comparisons

Most tuna respirometry has been done at 24°C. Because we lacked the heating and temperature-control equipment required to acclimate bonito to 24°C, the 18°C bonito $\dot{V}_{O_2}$ data were adjusted to 24°C, assuming a Q_{10} of 2.0 (Brill, 1979, 1987; Dewar and Graham, 1994a), for comparison with tuna data.

Fig. 4B compares the GCOT and COT_{net} values for the bonito and yellowfin tuna at 24°C (data from Dewar and Graham, 1994a). At all speeds compared, the GCOT is higher in the yellowfin tuna than in the bonito. Due to its higher SMR (Korsmeyer and Dewar, 2001), the yellowfin also has a higher U_{opt}, approximately 1 m s^{-1} (2.3 *FL* s^{-1}) *versus* 0.7 m s^{-1} (1.4 *FL* s^{-1}) for the bonito. The GCOT at U_{opt} for the yellowfin tuna is greater than that of the bonito (0.46 J N^{-1} m^{-1} *versus* 0.27 J N^{-1} m^{-1}). The COT_{net} functions for the bonito ($y=0.0951e^{0.916x}$, $r=0.99$) and yellowfin tuna ($y=0.0375e^{2.07x}$, $r=0.98$) differ, with the yellowfin having both a greater slope and a lower intercept. However, because the 95% confidence intervals of these parameters overlap, the two functions are not significantly different.

The bonito standard metabolic rate (SMR), as determined by the complete data set (Fig. 3), does not differ significantly (i.e. there is overlap in the 95% confidence intervals) from that of similar sized teleosts (Fig. 5), the yellowtail (*Seriola quinqueradiata*) at 20°C (Yamamoto et al., 1981) or the salmon (*Oncorhynchus nerka*) at 20°C (Brett and Glass, 1973). However, when adjusted for ambient temperature differences, the bonito SMR (161±33 mg O_2 kg^{-1} h^{-1}) is significantly lower ($P<0.05$, *t*-test) than that of similar sized yellowfin, skipjack and kawakawa *Euthynnus affinis* tunas (Brill, 1979, 1987; Dewar and Graham, 1994a) and dolphinfish *Coryphaena hippurus* (Benetti et al., 1995).

Plasma lactate concentrations

Bonito plasma lactate levels were determined for three phases of this respirometry study: just after capture from the holding tank, after 15 min in the round tank with companion fish, and after the swimming tests. The lactate concentration measured in the post-transfer period (2.84±0.88 mmol l^{-1}, $N=4$) was much greater than the pre-experiment (baseline-

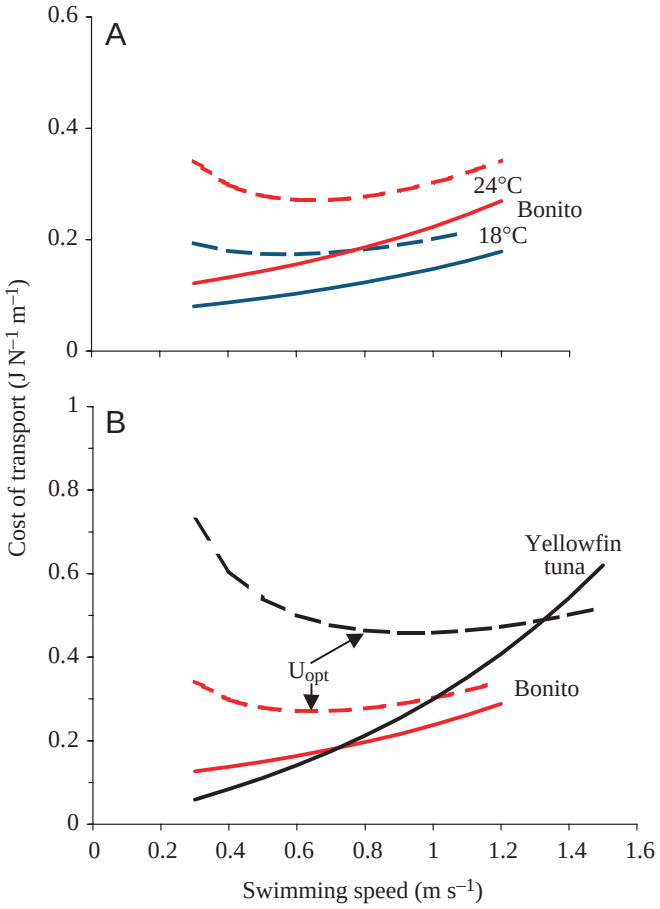

Fig. 4. (A) The gross cost of transport (GCOT, broken lines) and net cost of transport COT_{net}, solid lines) estimates for bonito swimming at 18°C (blue) and 24°C (red). [Note: 24°C values are estimated from 18°C values, based on a Q_{10} of 2.0 (see text).] (B) Comparison of the GCOT (broken lines) and COT_{net} (solid lines) values predicted for the bonito (red) at 24°C with estimates for similar sized yellowfin tuna (black) at 24±1°C (Dewar and Graham, 1994a).

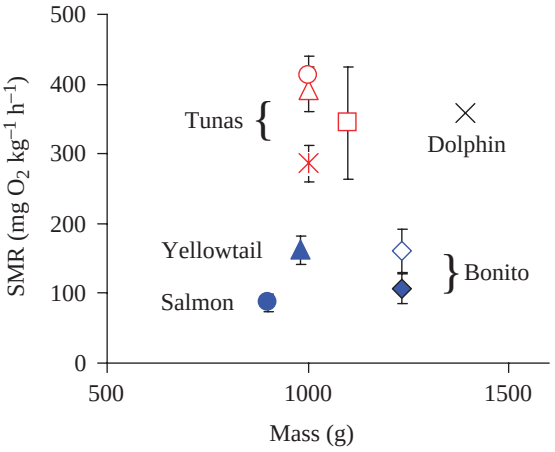

Fig. 5. Comparison of bonito mass-specific standard metabolic rate (SMR) at 18°C and 24°C with values published for other comparably sized species at similar test temperatures: yellowtail *Seriola quinqueradiata* (filled triangle) (20°C; Yamamoto et al., 1981), salmon *Oncorhynchus nerka* (filled circle) (20°C; Brett and Glass, 1973), skipjack *Katsuwonus pelamis* (open circle) (25°C; Brill, 1979), yellowfin *Thunnus albacares* (asterisk) and kawakawa *Euthynnus affinis* (open triangle) tunas (25°C; Brill, 1987), yellowfin tuna (open square) (24±1°C; Dewar and Graham, 1994a) and dolphinfish *Coryphaena hippurus* (cross) (Benetti et al., 1995).

control) lactate concentration (0.11±0.03 mmol l^{-1}, N=2) and significantly higher (two sample t-test, $P<0.05$) than the post-swimming experiment levels (0.26±0.08 mmol l^{-1}, N=4).

Discussion

This study quantifies the swimming energetics of the eastern Pacific bonito at nearly constant temperature and over a range of sustained speeds and provides the first comparative metabolic performance data for a species in the tuna sister group, tribe Sardini. We found that the bonito COT_{net} is similar to that of both tunas and other active teleosts, including another scombrid, the chub mackerel (*Scomber japonicus*, tribe Scombrini). The SMR of the bonito was also found to be similar to values in similar sized yellowtail and salmon, but was significantly lower than that of size-matched yellowfin, skipjack and kawakawa tunas and dolphinfish (Fig. 5). Although we recognize the need for bonito and tuna comparisons at the same experimental temperature, this study offers strong evidence that the elevated SMR of tunas, and not their locomotory costs, distinguishes the tunas from other scombrids and most other pelagic, high performance fishes.

Validation of the bonito $\dot{V}_{O_2}$–speed relationship

Both capture and handling stress have the potential to increase fish metabolic intensity to the point of elevating muscle and plasma lactate levels, followed by a period of elevated aerobic metabolism required for the reconversion of lactate to glycogen (Milligan and Girard, 1993; Milligan, 1996). Validation of the bonito swimming $\dot{V}_{O_2}$ data therefore required confirmation that handling and confinement in the respirometer working section did not result in an excessive build-up of lactate. Our findings that bonito plasma lactate levels were elevated during the handling phases of the experiments, but then fell to low levels during the swimming tests, indicate that the metabolic costs of lactate reconversion were not a significant component of the bonito swimming-$\dot{V}_{O_2}$ determinations.

Unstable swimming

Bonito $\dot{V}_{O_2}$ was determined over speeds ranging from 50 to 120 cm s^{-1}. Although the exponential rise in $\dot{V}_{O_2}$ occurring with incremental speed increases above 60 cm s^{-1} is entirely consistent with theory (Videler, 1993; Webb, 1998), Fig. 2 shows that the mean $\dot{V}_{O_2}$ for bonito is minimal at 60 cm s^{-1} and elevated at 50 cm s^{-1}. Because erratic fin fluttering and unsteady swimming were documented for slow-swimming bonito (Table 1), we attribute the increase in mean $\dot{V}_{O_2}$ at speeds of 50 cm s^{-1} (and, to some extent, 60 cm s^{-1}) to the metabolic costs associated with the additional movements required for low-speed stability. This interpretation is consistent with findings for other fishes at low speeds (He and Wardle, 1986; Lucas et al., 1993; Webb, 1998; Freund, 1999; Sepulveda and Dickson, 2000), as well as for other animals (Withers, 1992; Schmidt-Nielsen, 1993).

Most scombrids, including bonitos, are negatively buoyant and must swim continuously, both for hydrodynamic lift (Magnuson, 1973) and ram ventilation (Roberts, 1975). Magnuson (1973) used comparative morphometric and body density data to estimate the minimum speeds required for bonitos and tunas to maintain hydrostatic equilibrium. Application of the Magnuson (1973) minimum speed equation to bonito (45–55 cm *FL*) in this study yields a minimum speed of approximately 1.2 *FL* s^{-1} or about 54–66 cm s^{-1}, which corresponds to the range where unsteady motion and increased swimming costs occurred for the bonito in this study (Fig. 2).

Unstable swimming and COT and SMR estimates

Comparison of the complete $\dot{V}_{O_2}$–speed data set to one modified by the selective removal of the ten high-$\dot{V}_{O_2}$, low-speed measurements (Fig. 3) documents how unsteady swimming artificially increases the SMR estimate and lowers the estimated swimming cost (regression parameters of the $\dot{V}_{O_2}$–speed relationship). In the case of the bonito, this data manipulation was warranted because of our direct observations of unsteady swimming at low speeds (Table 1) and the known correspondence between unsteady swimming and the bonito's minimum speed requirements for hydrostatic equilibrium (Magnuson, 1973, 1978). While this correction did not significantly change the parameters of either regression function (i.e. there is overlap in the 95% confidence intervals), it did improve the correlation coefficient for the $\dot{V}_{O_2}$–speed function. Although the selected data set appeared to be more meaningful biologically, comparisons with data for other species, for which selective removal was not done, required that we operate with the complete data set.

Comparisons of $\dot{V}_{O_2}$ in bonito

Two previous studies provide swimming $\dot{V}_{O_2}$ estimates for the eastern Pacific bonito. Mendo and Pauly (1988) used the observational swimming speed data of Magnuson and Prescott (1966) to estimate the routine metabolic rate (RMR) [defined by Beamish (1978) as the combination of normal and spontaneous movements] for a 2.5 kg, 57 cm *FL* bonito swimming in a large aquarium at 22°C. By combining mean swimming speed (1.4 *FL* s^{-1}) with the estimated volume of water traversing the gills (based on mouth aperture or gape), and assuming the extraction of 50% of the O_2 in the water contacting the gills, these workers arrived at an estimated RMR of 160 000 cal day^{-1}, or 800 mg O_2 kg^{-1} h^{-1}. This value is three times the $\dot{V}_{O_2}$ that we measured for bonito swimming at 1.4 *FL* s^{-1} (260 mg O_2 kg^{-1} h^{-1}) and doubtlessly reflects the numerous assumptions underlying the Mendo and Pauly (1988) $\dot{V}_{O_2}$ estimate.

Freund (1999) reported similar RMR values for bonito and skipjack tuna swimming in an annular respirometer at 20±1°C. However, speed was not controlled in that study and unsteady swimming was noted for both species. The mean RMR estimated for the bonito was 427 mg O_2 kg^{-1} h^{-1}, and a speed estimate for one bonito was 50 cm s^{-1} (Freund, 1999). Although bonito size and experimental temperature were similar in that study to ours, it is difficult to compare the two.

Inspection of Fig. 2 shows that 50 cm s^{-1} is too slow for stable swimming in bonito of the size studied, and this may account for the 1.4-fold higher $\dot{V}_{O_2}$ measured by Freund (1999).

Bonito and tuna comparisons

Swimming efficiency

Although much of our understanding of tuna morphology and physiology suggests that they should swim more efficiently than other fishes, no study, including this work with the eastern Pacific bonito, has successfully documented this difference (Sepulveda and Dickson, 2000; Korsmeyer and Dewar, 2001). This is paradoxical because tuna specializations, including a high degree of body streamlining, a unique RM position, tendon arrangement, thunniform swimming mode and endothermy, have all been hypothesized to augment aerobic swimming performance and presumably swimming efficiency (Carey and Teal, 1966; Fierstine and Walters, 1968; Graham, 1975; Johnston and Brill, 1984; Westneat et al., 1993; Altringham and Block, 1997; Graham and Dickson, 2000, 2001; Donley and Dickson, 2000; Ellerby et al., 2000; Altringham and Shadwick, 2001; Dowis et al., 2003).

Studies of tuna swimming efficiency, however, have of necessity been carried out on juvenile or sub-adult fishes in swimming chambers (Gooding et al., 1981; Graham and Laurs, 1982; Graham et al., 1989; Dewar and Graham, 1994a; Freund, 1999; Sepulveda and Dickson, 2000; Donley and Dickson, 2000). In the case of water tunnels, it may be that the requirement to maintain position by matching swimming thrust production to water flow speed obscures the utility of structural and physiological specializations for swimming that, in a more natural setting, increase swimming efficiency. A free-swimming tuna, for example, has options for turning, gliding and changing depth, as well as responding behaviorally to physical features in the environment, such as density gradients and thermal fronts. In addition, schooling may augment swimming efficiency (Weihs, 1973). Magnuson's finding (Magnuson, 1973) of allometric changes that lower the minimum speed requirements of larger tunas further suggests that increased size, in combination with swimming specializations, increases swimming efficiency in larger tunas.

Standard metabolic rates

Extrapolation of the Fig. 3 regressions to zero speed yields SMR estimates for the bonito that are comparable to those of the salmon (Brett and Glass, 1973) and yellowtail (Yamamoto et al., 1981), but significantly lower than both similar-sized yellowfin and skipjack tunas swimming in the same respirometer system (Dewar and Graham, 1994a) and spinally blocked (paralyzed) yellowfin, skipjack and kawakawa tunas (Brill, 1979, 1987) and dolphinfish (Benetti et al., 1995) (Fig. 5). The dolphinfish is the only fish species shown to have an SMR comparable to that of the tunas (Benetti et al., 1995). Although it lacks an elevated tissue temperature, the dolphinfish is a highly active species with several specializations (i.e. rapid growth rate, high heart rate) related to its high-energy-demand, pelagic existence (Brill, 1996). Similarity between the bonito SMR and that of the chub mackerel (Shadwick and Steffensen, 2000) suggests that, among the scombrids thus far studied, the tunas are unique in having a high SMR.

The basis for the tuna's elevated SMR has been the topic of considerable discussion (Brill, 1979, 1987, 1996; Gooding et al., 1981; Dewar and Graham, 1994a; Brill et al., 2001; Sepulveda and Dickson, 2000; Korsmeyer and Dewar, 2001; Graham and Dickson, 2001). First, an elevated SMR is consistent with higher maintenance costs associated with the tunas' relatively large gills and heart and with the elevated metabolic requirements of the tunas' warm muscle and other tissues. In addition, there may be functional costs requiring a high SMR, such as the osmoregulatory load imposed by a larger gill surface area (Brill, 1987, 1996; Benetti et al., 1995; Brill et al., 2001). Tunas also have the added costs associated with the aerobic requirements of a larger and thicker-walled ventricle that has both a high cardiac output and a high systolic pressure (Graham et al., 1983; Brill and Bushnell, 1991, 2001; Bushnell and Jones, 1994; Graham and Dickson, 2000). Added to these may be a higher aerobic cost associated with the more aerobic white muscle of tunas. As in other fishes, white muscle accounts for the greatest percentage of body mass, and tuna white muscle has a greater aerobic capacity than in other species (as indicated by the high activity of the aerobic enzyme, citrate synthase) (Dickson, 1995, 1996; Korsmeyer and Dewar, 2001). Finally, there are the additional metabolic costs for processes such as gastric evacuation, somatic and gonadal growth rates, and lactate processing, which all appear to be augmented in tunas relative to other scombrids and other pelagic teleosts (Magnuson, 1969; Schaefer, 1984; Perry et al., 1985; Weber et al., 1985; Hunter et al., 1986; Arthur et al., 1992; Bushnell and Jones, 1994; Brill, 1996; Korsmeyer and Dewar, 2001). The high SMR of tunas therefore appears important in enabling them to sustain high energy production rates required by the combinations of endothermy and a high aerobic scope for activity (Priede, 1985; Bushnell and Jones, 1994; Brill, 1996; Brill et al., 2001; Bushnell and Brill, 2001; Korsmeyer and Dewar, 2001).

Conclusions

The objectives of this study were to obtain swimming energetics data for the eastern Pacific bonito in the same respirometer that has been used to study tunas, and to compare bonito and tuna locomotor costs and SMR. Because the bonito is in the scombrid tribe Sardini, which is the sister group of the tunas (tribe Thunnini), comparisons of tuna–bonito swimming performance have the potential to delineate the pattern of character acquisition leading to tuna locomotor specializations, including endothermy. Although our swimming performance comparisons necessitated a temperature adjustment (from 18°C to 24°C) of the bonito swimming–$\dot{V}_{O_2}$ data, the resulting net cost of transport (COT_{net}) estimate for the bonito significantly overlaps with that of the yellowfin tuna and thus indicates comparable swimming costs over the range of speeds tested.

On the other hand, the finding of a lower SMR in both the

bonito and the chub mackerel relative to tunas implies that, in tuna, elevated SMR is an apomorphy linked to this group's numerous structures and functions requiring high metabolic maintenance. It may be that studies on the more basal species of tunas, for example, the slender tuna, *Allothunnus fallai*, will elucidate the linkages between SMR, aerobic function and endothermy. *Allothunnus* has less RM than other tunas and some of the circulatory modifications required for endothermy, but whether or not it is endothermic is not presently known (Graham and Dickson, 2000).

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