Mar Biol
DOI 10.1007/s00227-007-0757-2

RESEARCH ARTICLE

Aerobic metabolic rates of swimming juvenile mako sharks, *Isurus oxyrinchus*

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Received: 14 February 2007 / Accepted: 19 June 2007
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Abstract The shortfin mako shark, *Isurus oxyrinchus*, is a highly streamlined epipelagic predator that has several anatomical and physiological specializations hypothesized to increase aerobic swimming performance. A large swim-tunnel respirometer was used to measure oxygen consumption (MO_2) in juvenile mako sharks (swimming under controlled temperature and flow conditions) to test the hypothesis that the mako shark has an elevated maintenance metabolism when compared to other sharks of similar size swimming at the same water temperature. Specimen collections were conducted off the coast of southern California, USA (32.94°N and 117.37°W) in 2001-2002 at sea-surface temperatures of 16.0–21.0°C. Swimming MO_2 and tail beat frequency (TBF) were measured for nine mako sharks [77–107 cm in total length (TL) and 4.4 to 9.5 kg body mass] at speeds from 28 to 54 cm s^{-1} (0.27–0.65 TL s^{-1}) and water temperatures of 16.5–19.5°C. Standard metabolic rate (SMR) was estimated from the extrapolation to 0-velocity of the linear regression through the $LogMO_2$ and swimming speed data. The estimated LogSMR (±SE) for the pooled data was 2.0937 ± 0.058 or 124 mg O_2 kg^{-1} h^{-1}. The routine metabolic rate (RMR) calculated from seventeen MO_2 measurements from all specimens, at all test speeds was (mean ± SE) 344 ± 22 mg O_2 $kg^{-1}h^{-1}$ at 0.44 ± 0.03 TL s^{-1}. The maximum metabolic rate (MMR) measured for any one shark in this study was 541 mg O_2 $kg^{-1}h^{-1}$ at 54 cm s^{-1} (0.65 TL s^{-1}). The mean (±SE) TBF for 39 observations of steady swimming at all test speeds was 1.00 ± 0.01 Hz, which agrees with field observations of 1.03 ± 0.03 Hz in four undisturbed free-swimming mako sharks observed during the same time period. These findings suggest that the estimate of SMR for juvenile makos is comparable to that recorded for other similar-sized, ram-ventilating shark species (when corrected for differences in experimental temperature). However, the mako RMR and MMR are apparently among the highest measured for any shark species.

Communicated by J.P. Grassle.

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Introduction

Sharks of the family Lamnidae possess several anatomical and physiological adaptations for a heightened aerobic swimming performance (Carey et al. 1971, 1985; Graham et al. 1990; Bernal et al. 2001a, b, 2003, 2005; Donley et al. 2004). Recent studies have focused on the evolutionary convergence between lamnid sharks and tunas (Thunnini, Teleostei), detailing the high degree to which these two groups are specialized for continuous swimming (Bernal et al. 2001b, 2003; Donley et al. 2004). The tuna-lamnid convergent features are based upon several characteristics related to aerobic locomotor performance. Among these characteristics are the ability to elevate red myotomal muscle (RM) temperatures above the ambient seawater temperature (regional endothermy), and a metabolic rate that exceeds that of other ectothermic species (Carey and Teal 1969; Carey et al. 1971, 1985; Graham et al. 1990; Bernal et al. 2001b; Carlson et al. 2004).

Although recent studies have highlighted the cardiovascular, biochemical, and musculotendinous specializations of the mako shark (*Isurus oxyrinchus*, family Lamnidae; Bernal et al. 2003; Donley et al. 2004; Gemballa et al. 2006), few investigations have focused on the swimming metabolism of this species. Stillwell and Kohler (1982) first estimated daily ration for the mako shark by using data obtained from gut contents, prey caloric information, and the energetics data from spiny dogfish (*Squalus acanthias*) by Brett and Blackburn (1978). Although useful for understanding mako ecology and trophodynamics, these approximations are confounded by several uncertainties (i.e., actual metabolic rate, ambient temperature, feeding frequency, diet composition). Graham et al. (1990) performed the first ship-board swim tunnel studies on the mako shark and measured the swimming oxygen consumption (MO_2) for an 82 cm juvenile mako shark. This study found that that the mako metabolic rates [i.e., the combined average routine metabolic rate for all speeds tested (RMR) and the measured maximum metabolic rate (MMR)] exceeded those recorded for other similar-sized shark species (when corrected for differences in experimental temperature). Because the Graham et al. (1990) study represents the only swimming MO_2 data available for any lamnid species, it has been routinely used as the benchmark to compare regionally endothermic sharks to other elasmobranchs (Bernal et al. 2001a, b; Carlson et al. 2004; Dickson and Graham 2004). From these comparisons, it has been proposed that regionally endothermic sharks (i.e., lamnids) have higher maintenance costs (standard metabolic rate, SMR) than do ectothermic species (Carlson et al. 1999, 2004; Bernal et al. 2001b; Dickson and Graham 2004). Collectively, the proposed basis for the elevated metabolic rates include regional endothermy (i.e., RM, visceral, and cranial temperature elevation) as well as the maintenance costs associated with the specialized cardiovascular and respiratory physiology of these sharks (i.e., high gill surface areas, large heart, elevated hematocrit, and hemoglobin concentrations, high capillary density, high myoglobin concentration) (reviewed by Bernal et al. 2001b).

This study further quantifies the swimming energetics of the mako shark and tests the hypothesis that the mako has an overall elevated metabolic rate when compared to other comparably sized shark species. Here we report on the swimming MO_2, an estimate of SMR, RMR, MMR, and tail beat frequency (TBF) for sharks swimming in a large swim-tunnel respirometer under controlled conditions.

Methods

All the experiments were performed under the guidelines of the Institutional Animal Care and Use Committee, of the University of California, San Diego (protocol S0008).

Sample collection

Juvenile mako sharks, *I. oxyrinchus*, were captured in the coastal waters off Southern California (in the vicinity of 32.94°N and 117.37°W) during summer months (2001–2002) at sea surface temperatures of 16.0–21.0°C. The juvenile makos were transported to Scripps Institution of Oceanography (SIO) using methods described by Bernal et al. (2001a). Briefly, nine mako sharks ranging in size from 77 to 107 cm in total length (TL) (4.4–9.5 kg body mass, Table 1) were chummed to within 1 m of a small vessel, hooked, and immediately dip-netted into a 90-l transport tank outfitted with a submersible recirculating pump. In the tank, each shark was restrained by securing the anterior half of the body to the chamber while the caudal fin moved unimpeded. The head and mouth were placed inside a large plastic funnel that directed a high volume, low-pressure water flow from a submersible pump (Rule Industries 360 gph, MA, USA) directly into the shark's mouth providing sufficient flow for respiration. The seawater in the transport tank was periodically (every 10 min) changed to ensure adequate oxygenation during transport. Upon reaching the laboratory, the shark was quickly transferred to a large "Brett-type" swim tunnel respirometer (described below). The overall transport time, from capture at sea to immersion in the swim tunnel, ranged from 30 to 90 min depending on the distance traveled.

Swim tunnel respirometer

The swim-tunnel respirometer used in this study [described previously by Graham et al. (1990); Dewar and Graham (1994); Bernal et al. (2001a); Sepulveda et al. (2003)] had a working section of 200 cm × 51 cm × 42 cm (length × width × height) and a total volume of 3,000 l. The tunnel was powered by a 40-hp, variable-speed electric motor and had a maximum water velocity of 2 m s^{-1}. Graham et al. (1990) confirmed both a uniform speed and laminar flow field in the center and anterior section of the working section of the respirometer, which is where the juvenile makos swam during the MO_2 experiments.

Experimental protocol

Each mako shark specimen was introduced to the working section of the respirometer and observed at several introductory swimming speeds (approximately 0.3–0.5*U*, where

Table 1 Oxygen consumption rate (MO_2) for nine juvenile mako sharks swimming in a swim tunnel respirometer

Mass (kg)	FL (cm)	TL (cm)	T_{exp} (°C)	U (TL s^{-1})	Trials	MO_2 (mg O_2 kg^{-1} h^{-1})	Duration (min)
4.4	70	77	18.0	0.37	3	281 ± 10	370
				0.40	1	307	
				0.45	2	306 (266, 345) range	
				0.53	1	354	
4.6	73	80	18.5	0.45	3	385 ± 2	450
5.3	74	82	17.8	0.34	3	290 ± 15	450
5.9	74	84	16.5	0.38	9	288 ± 19	720
				0.50	1	361	
				0.56	1	397	
				0.60	1	445	
4.9	75	83	19.5	0.43	4	385 ± 11	540
				0.52	1	466	
				0.65	1	541	
4.9	80	88	18.0	0.34 ± 0.01	4	358 ± 23	480
7.1	85	93	19.3	0.40	3	294 ± 19	450
8.2	95	104	18.6	0.28	4	204 ± 2	480
9.5	98	107	19.2	0.30	3	186 ± 25	450
Mean(±SE)	18.3 ± 0.25	0.44 ± 0.02				344 ± 22	

Shark mass, *FL* fork length, *TL* total length, T_{exp} experimental temperature, U relative swim speed, trials at each U, MO_2 (mean ± SE) at each U and duration of each experiment

U = TL s^{-1}) to determine the velocity that provided the most stable performance (i.e., steady swimming off the bottom and avoiding contact with the side walls). The shark was then left alone to swim for an initial 240-min recovery period under a continuous inflow of filtered seawater (mean ± SE: 18.3 ± 0.25°C, range 16.5–19.5°C) with O_2 levels above 80% saturation. For all sharks, a cloth was draped over the side and top view ports of the working section to minimize outside disturbance, and a light was placed near the anterior end of the working section to keep the fish swimming in the center.

Following the recovery period, the seawater inflow was stopped and the system was sealed for the respirometry trials. Respirometry experiments were initiated at the same speed as the recovery period and the rate of MO_2 was measured for 30–60 min of steady swimming. After a successful respirometry run, efforts were made to slowly increase water velocity by increments of 5 cm s^{-1} for subsequent speed trials. If the shark resisted the change in water speed by drifting to the rear of the working section, or by struggling and switching to the use of burst and glide locomotion, the water speed was returned to the original velocity and the shark was left undisturbed for a short period (15–30 min). Once steady swimming was re-established, additional efforts to increase water velocity were made; for all the experiments, several hours were spent trying to gradually increase water speed. Because all sharks used in this study were also used in biochemical and cardiovascular investigations that immediately followed these experiments, care was taken not to induce undue stress (Bernal et al. 2001a). Therefore, the respirometry experiments were terminated once it was evident that the test specimen would not readily complete additional speed trials.

All respirometry experiments were performed so that seawater O_2 levels in the tunnel were never <80% saturation. After each MO_2 measurement, the seawater inflow to the respirometer was re-opened for re-oxygenation of the system. Once sufficiently oxygenated, the tunnel was re-sealed for the subsequent respirometry trial. When possible, replicate MO_2 measurements were made for each test speed. Background MO_2 measurements (i.e., bacterial respiration) were conducted at the completion of each respirometry experiment by removing the shark from the working section, re-sealing the swim tunnel and recording the change in oxygen concentration for a 480 min period.

MO_2 and speed determination

Mako shark MO_2 (mg O_2 kg^{-1} h^{-1}) was measured by recording the decline in water O_2 concentration over time as the shark swam at a designated speed (Sepulveda et al. 2003). A calibrated polarographic O_2 electrode and meter (Model 52, Yellow Springs Instrument, OH, USA) were interfaced with a data acquisition system and a laptop computer for real-time monitoring of experimental temperature and O_2 content. Post experiment, the background MO_2 was subtracted from the total O_2 consumption for each swimming speed trial to obtain the background-corrected shark MO_2. The shark swimming speed was determined from the relationship between the tunnel motor's RPM (which was continuously recorded) and water velocity determined with a flow meter (General Oceanics Inc., FL, USA, model 2035). To minimize wall effects on swimming velocity and MO_2, only speed trials in which the shark was in the center of the working section were used (Webb 1993). Corrections for solid blocking effects were not performed because, in all cases, the cross-sectional area of the swimming shark occupied <9.7% of the working section of the respirometer (Webb 1971).

Because mako sharks are obligate ram-ventilators and never stop swimming, the SMR was estimated as the MO_2 at "0 velocity" or the *y*-axis intercept of the linear relationship (ANOVA regression; Sokal and Rohlf 1998) through the $LogMO_2$ and swim speed data. The RMR was defined as the mean oxygen consumption rate for all specimens at all swimming speeds, a value that allowed for comparison with other energetics studies (Graham et al. 1990; Carlson et al. 1999), and the MMR was taken as the highest measured MO_2 for any shark at any swim speed (Graham et al. 1990). The effects of body size and temperature on MO_2 were evaluated using multiple regression analysis (Minitab version 12). Statistical significance was established at $\alpha = 0.05$.

For comparison with literature values, metabolic rates were temperature-adjusted using a thermal rate coefficient value (Q_{10}) of 2 (Brett and Groves 1979). All comparisons with previous work were performed using the MO_2 data derived from the relationship between $LogMO_2$ and relative swim speed, U (TL s^{-1}).

Tail beat frequency

The tail beat frequency was quantified for mako sharks during all swimming MO_2 trials as well as in the field. The observations from the controlled experiments were made using a mirror mounted at a 45° angle on top of the respirometer working section. The tail beats were counted with a stopwatch during periods of steady swimming at a constant water velocity. For comparison with the captive mako studies, field observations of TBF were also made on four wild, similar-sized mako sharks (TL estimated from a small boat was 95–105 cm). The field measurements were taken during a calm sea state from an approximate distance of 5 m with a digital stopwatch as the sharks were finning at the sea surface. The field TBF measurements were derived from fish that were not manipulated or attracted to the vessel in any way (i.e., chum or other attractants).

Results

Swimming MO_2 was measured at a mean (±SE) water temperature of 18.3 ± 0.25°C for nine juvenile mako sharks

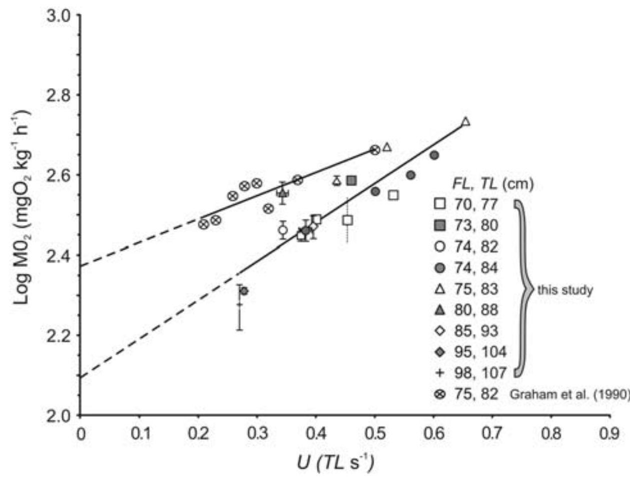

Fig. 1 Swimming oxygen consumption (MO_2) plotted versus relative swim speed, U (TL s^{-1}), for nine *Isurus oxyrinchus* (shortfin mako) (4.4–9.5 kg body mass) at 18.3 ± 0.25°C (this study) and for a 3.9 kg mako at 16–20°C (*circled times*, Graham et al. 1990). Regression lines are derived from the relationship between $LogMO_2$ and U. Present study (*lower line*): $LogMO_2 = 2.0937(\pm 0.06) + 0.97(\pm 0.13)U$ ($r^2 = 0.89$, $P < 0.001$); 3.9 kg mako shark from Graham et al. (1990) (*upper line*): $LogMO_2 = 2.3716(\pm 0.03) + 0.58(\pm 0.12)U$ ($r^2 = 0.87$, $P = 0.003$); where ± are SE. Extrapolation to 0 velocity (i.e., SMR estimate) is shown in *hatched lines*. All plotted values are mean ± SE, except for *open square* at 0.45U which is ± range

ranging in size from 77 to 107 cm TL (4.4–9.5 kg body mass) (Table 1; Fig. 1). Swimming speed ranged from 28 to 54 cm s^{-1} (0.27–0.65U) with four sharks swimming steadily at more than one speed. Two mako specimens swam at four different test velocities [mako no 4 (77 cm TL) at 0.37, 0.40, 0.45, and 0.53U and mako no 9 (84 cm TL) at 0.38, 0.50, 0.56, and 0.60U]. In most cases at least two MO_2 measurements were recorded at each test speed (Fig. 1, Table 1).

Regression analysis indicated a significant positive relationship ($P < 0.001$) between swimming speed and MO_2 and the absence of a significant ($P = 0.16$) effect of body size. Because of the small sample size, and the narrow range of swimming speeds for each shark, the mako MO_2 data were pooled to estimate both SMR (Fig. 1) and RMR (Table 1).

The relationship between MO_2 and relative swim speed (U) was: $LogMO_2 = 2.0937$ $(\pm 0.06) + 0.97(\pm 0.13)U$ ($n = 17$, $r = 0.89$, $P < 0.0001$), where ± intervals are SE. The SMR (±SE) was estimated to be 2.0937 ± 0.058 or 124 mg O_2 kg^{-1} $h^{-1}$and the mean (±SE) RMR was 344 ± 22 mg O_2 $kg^{-1}h^{-1}$ at a mean swim speed of 0.44 ± 0.02 U. The maximum swimming MO_2 measured (541 mg O_2 $kg^{-1}h^{-1}$) was for mako no 3 (83 cm TL) at 0.65U (54 cm s^{-1}) (Table 1, Fig. 1).

The mean (±SE) TBF for all 39 observations was 1.00 ± 0.01 Hz and ranged from 0.92 to 1.15 Hz (Fig. 2).

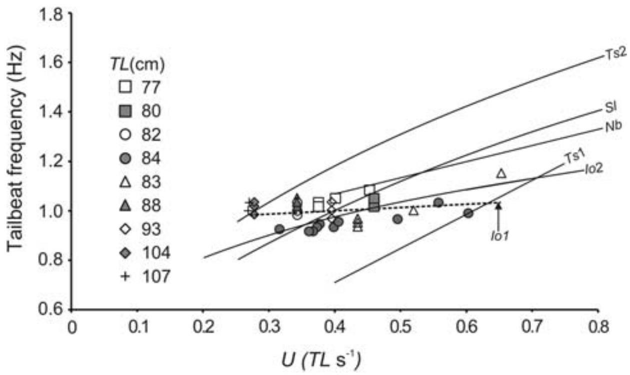

Fig. 2 Shark tail-beat frequency (TBF) in relation to relative swim speed, U (TL s^{-1}) for: *Io*1 (*dotted lines*) *Isurus oxyrinchus* (shortfin mako): $n = 9$, TBF $= 0.94 + 0.14U$ (this study); *Io*2 (*I. oxyrinchus*): $n = 1$; TL $= 82$ cm, TBF $= 1.24U^{0.26}$ (adapted from Graham et al. 1990); *Ts1* (*Triakis semifasciata*, leopard shark): $n = 12$, TL $= 83$–114 (TL derived from body mass using Smith 1984), TBF $= 0.16 + 1.37U$ (adapted from Scharold et al. 1989); *Nb* (*Negaprion brevirostris*, lemon shark): $n = 1$; TL $= 70$ cm, TBF $= 1.5U^{0.48}$ (adapted from Graham et al. 1990); *Sl* (*Sphyrna lewini*, scalloped hammerhead): $n = 12$; TL = 52–60 cm, TBF $= 0.8 + 0.65U$ (adapted from Lowe 1996); *Ts*2 (*T. semifasciata*): $n = 5$; TL $= 60$–90 cm, TBF $= 1.79U^{0.45}$ (adapted from Graham et al. 1990)

There was no significant relationship ($n = 39$, $P = 0.13$) between TBF and U (Fig. 2). The TBF of the makos in this study was not significantly different (T-test; $df = 41$, $P = 0.32$) from that recorded for similar-sized, free-swimming makos ($n = 4$, 1.03 ± 0.03 Hz) observed while finning at the surface during the same experimental period (C. Sepulveda observations).

Discussion

This study was performed to quantify the aerobic metabolic expenditure of the mako shark swimming under controlled conditions. Our findings indicate that when corrected for differences in experimental temperature, mako RMR, and MMR are among the highest recorded for any pelagic shark species. However, the estimate of SMR in this study (124 mg O_2 kg^{-1} h^{-1}) was much lower than that previously estimated for this species (235–240 mg O_2 kg^{-1} h^{-1}) (Bernal et al. 2001b; Carlson et al. 2004; Dickson and Graham 2004).

Mako SMR was estimated by extrapolating the relationship between LogMO_2 and relative swim speed to 0 velocity (Fig. 1). This method has been validated by comparing size-matched MO_2 estimates from immobilized (spinally blocked) sharks and teleosts to values derived from the extrapolation method (Brill 1987; Dewar and Graham 1994; Hove and Moss 1997; Carlson and Parsons 2003; Dowd et al. 2006). Although extrapolation is widely used for estimating SMR in continuously swimming fishes, recent studies on obligate ram-ventilating teleosts have shown that experimental protocol may influence the estimate of SMR (Webb 2002; Sepulveda et al. 2003). This can be the case if the sharks are forced to swim at low speeds below the minimum velocity required for hydrostatic equilibrium, as the cost of locomotion generally increases at these low speeds (Magnuson 1973; Webb 2002; Sepulveda et al. 2003). Therefore, the lowest test velocity for each mako shark in this study was based on the individual specimen's swimming performance (i.e., the minimum speed the shark would swim without changing its angle with reference to the floor of the working section or erratically moving from side to side) (He and Wardle 1986; Sepulveda et al. 2003). This protocol minimized the selective removal of elevated MO_2 measurements at the lower swimming speeds and provided data only from test velocities at which there was steady swimming.

Graham et al. (1990) documented the swimming performance over 41 h for one juvenile mako shark swimming in the same water tunnel that was used in the present study. When the regression through the Graham et al. (1990) data is extrapolated to 0 velocity, the SMR estimate is approximately twofold higher than that of the present study (240 mg O_2 kg^{-1} h^{-1}; Fig. 1). Although these calculations were not performed by Graham et al. (1990), the extrapolated SMR from that shark has been used to compare the mako to other shark species (Bernal et al. 2001b; Carlson et al. 2004; Dickson and Graham 2004). It is possible that specific differences in the experimental protocol between the present study and the Graham et al. (1990) work are largely responsible for the observed differences in SMR. The Graham et al. (1990) study used a more conventional approach for recording the swimming MO_2, in which the test shark was forced to swim throughout a range of swimming speeds (from 0.2 to 0.5 U). These swim speeds included velocities below the minimum velocity for which steady swimming was observed in the present study. It is possible that the slowest speeds for the 82 cm TL mako studied by Graham et al. (1990) were either at, or below the minimum velocity required to maintain hydrostatic equilibrium (Magnuson 1973). This may have caused an increased MO_2 at the lowest test velocities, subsequently providing a reduced slope and increased y intercept of the swimming speed versus MO_2 regression. Moreover, when the mako MO_2 values from Graham et al. (1990) (Fig. 1) are compared with the values for the nine makos in this study, the only values that are strikingly different are those from the lowest speeds.

Most of the metabolic data available for obligate ram-ventilating sharks come from experimental temperatures of 21–28°C, higher than in the present study (18.3 ± 0.25°C, range 16.5–19.5°C). When compared at their respective experimental temperatures, the SMRs of the more-tropical

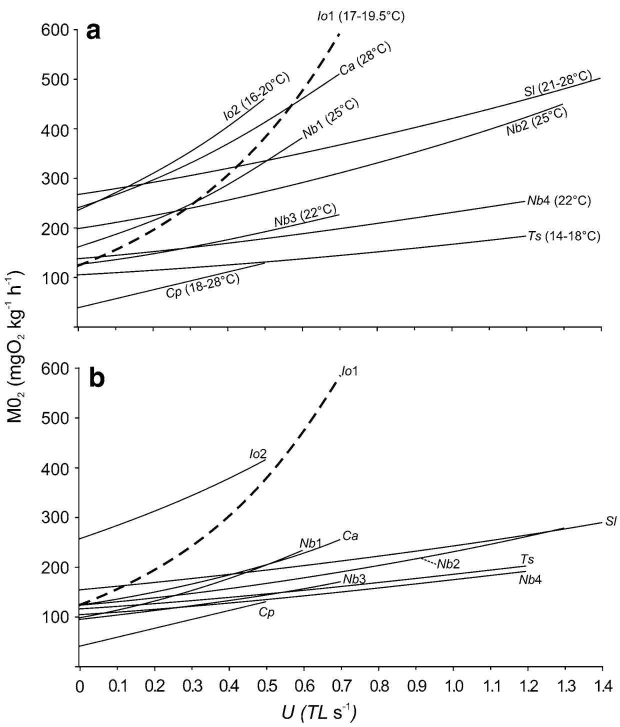

Fig. 3 Measured oxygen consumption plotted versus relative swim speed, *U* (TL) s^{-1} for sharks at **a** respective experimental temperatures and **b** corrected to 18°C. *Io*1 (*Isurus oxyrinchus*, shortfin mako) *n* = 9 (this study); *Io*2 (*I. oxyrinchus*) *n* = 1, 3.2 kg (adapted from Graham et al. 1990); *Ca* (*Carcharhinus acronotus*, blacknose shark) *n* = 8, 0.4–3.5 kg (adapted from Carlson et al. 1999); *Nb*1 (*Negaprion brevirostris*, lemon shark) *n* = 7, 0.8–1.3 kg (adapted from Scharold and Gruber 1991); *Sl* (*Sphyrna lewini*, scalloped hammerhead) *n* = 17, 0.5–0.9 kg (adapted from Lowe 2001, uncorrected raw data); *Nb*2 (*N. brevirostris*) combined data for *n* = 1, 1.65 kg (adapted from Graham et al. 1990) and *n* = 7, 0.8–1.3 kg (adapted from Scharold and Gruber 1991); *Nb*3 (*N. brevirostris*) *n* = 13, 0.8–1.3 kg (adapted from Bushnell et al. 1989); *Nb*4 (*N. brevirostris*) combined data for *n* = 1, 1.65 kg (adapted from Graham et al. 1990) and *n* = 13, 0.8–1.3 kg (adapted from Bushnell et al. 1989); *Ts* (*Triakis semifasciata*, leopard shark) *n* = 5, 2.2–5.8 kg (adapted from Scharold et al. 1989); *Cp* (*Carcharhinus plumbeus*, sandbar shark) *n* = 16, 1.0–10.3 kg (adapted from Dowd et al. 2006; 6.8 kg)

species appear to be higher than those in the present study (Fig. 3a). However, after temperature adjustment (Q_{10} of 2; Brett and Groves 1979), inter-specific comparisons indicate little difference in the extrapolated estimate of SMR (Fig. 3b). This finding is unlike comparisons between endothermic and ectothermic teleosts, which show tunas to have an elevated (2–5 times higher) SMR when compared to similar-sized ectothermic species (Brill 1987; Dewar and Graham 1994; Sepulveda and Dickson 2000; Sepulveda et al. 2003).

It is not clear why tunas have an elevated SMR and makos do not. One plausible explanation may be associated with the energetic costs of osmoregulation. Tunas, like other marine teleosts, are hypo-osmotic relative to their environment and therefore must expend energy to maintain ion balance (Foskett et al. 1983). Sharks use a different osmoregulatory strategy (i.e., urea and trimethylamine oxide are used to maintain a slightly hyperosmotic body fluid composition relative to seawater), which may result in a lower overall metabolic expenditure (Pang et al. 1977).

Although this study recorded replicate MO_2 measurements for most sharks, the inability of the makos to swim over a large range of aerobic swim speeds, (i.e., no shark swam in excess of 0.65 *U*) limited the MO_2 dataset. This limited aerobic range proves problematic for the estimation of parameters commonly used for inter-specific comparisons of swimming performance (i.e., cost of transport, optimum swimming speed, MMR, and SMR) (Videler and Nolet 1990; Webb 1998). The RMR in this study was the most useful for comparing swimming metabolism of the mako to other active shark species, especially because the test velocities were based on performance and likely did not induce stressful and energetically costly behaviors (e.g., tilting, side to side movement, fluttering) (He and Wardle 1986; Webb 2002).

The only known RMR value for the mako shark (369 ± 11 mg O_2 $kg^{-1}h^{-1}$; Graham et al. 1990) does not differ significantly (*T*-test, $df = 51$, $P = 0.25$) from the present study (344 ± 22 mg O_2 $kg^{-1}h^{-1}$; estimated from the 17 speed trials, see Table 1). Because Graham et al. (1990) included lower test speeds in their study, their mean swimming speed in the RMR estimates (0.30 ± 0.01 *U*) was significantly lower (*T*-test, $P < 0.05$) than in the present study (0.44 ± 0.02 *U*).

Temperature adjustment of the mako MO_2 data (Q_{10} of 2; Brett and Groves, 1979) was performed to match the experimental temperatures of the previous studies on similar-sized sharks. These comparisons resulted, consistently, in a higher RMR for the mako shark when compared to other obligate ram-ventilating sharks (reviewed by Carlson et al. 2004). For example, the temperature-adjusted mako RMR is 2.5 times higher than that of similar-sized blacknose sharks (*Carcharhinus acronotus*) at 28°C (Carlson et al. 1999), 3.4 times that of lemon sharks (*Negaprion brevirostris*) at 25°C (Scharold and Gruber 1991), and 2.9 times that of leopard sharks (*Triakis semifasciata*) swimming at 16.8°C (Scharold et al. 1989).

Differences in the experimental protocol often make comparisons of MMR difficult, however, the methods used in this study are similar to those used by Graham et al. (1990) and yielded similar results (MMR present study, 541 mg O_2 $kg^{-1}h^{-1}$, MMR previous study, 507 mg O_2 $kg^{-1}h^{-1}$). Recent work on comparably sized Pacific bluefin tuna (*Thunnus orientalis*) used respirometry to estimate metabolic costs of swimming fish and found a mean MMR of 498 ± 55 mg O_2 $kg^{-1}h^{-1}$ (with the single highest MO_2 measurement ~590 mg O_2 $kg^{-1}h^{-1}$), a value similar to that found in the mako (Blank et al. 2007). This finding further supports studies on convergent features of tunas and lamnid sharks and highlights their cardiovascular similarities (reviewed by Bernal et al. 2001a, b; Donley et al. 2004). Although the mako MMR is comparable to that of the bluefin tuna (Blank et al. 2007), when compared to other shark species (at the same experimental temperature), it represents one of the highest values for any elasmobranch (Carlson et al. 2004). The high mako MMR is probably a result of its specialized cardiovascular and swimming muscle physiology (e.g., large gill surface area, relatively larger heart mass, increased muscle capillary density and myoglobin concentration, RM endothermy) (Carey et al. 1985; Emery 1986; Emery and Szczepanski 1986; Lai et al. 1997; Bernal et al. 2001b). The high MMR may also reflect a heightened aerobic scope and, although not demonstrated in our swimming studies, a greater aerobic scope could enhance other aerobic physiological processes such as digestion, somatic growth, and the processing of metabolic end-products of anaerobic metabolism (Brill 1996).

Although the mako is well known for its fusiform body, use of the thunniform mode of body caudal fin propulsion (Donley et al. 2004), elevated RM temperatures, and long distance migratory capabilities, the present study did not show the mako aerobic performance to be greatly beyond that of other sharks. These findings corroborate Graham et al. (1990) as well as the previous in vivo mako studies that show makos do not exceed $0.6U$ under controlled conditions (Bernal et al. 2001a; Donley 2004; Donley et al. 2004). Thus far, captive mako sharks swimming in a water tunnel do not exhibit faster sustained swimming speeds than other sharks. Further, as proposed by Graham et al. (1990), the data from this study and those available for other shark species suggest that, in general, sharks have a lower aerobic performance capacity in a water tunnel than pelagic teleosts such as tunas and bonitos (Dewar and Graham 1994; Sepulveda et al. 2003; Blank et al. 2007)]. This may be due to the lower relative amount of RM found in the sharks studied to date (2–3% of body mass; Bernal et al. 2003; Sepulveda et al. 2005) when compared to active teleosts with RM quantities of 4–13% body mass (Graham et al. 1983; Bernal et al. 2003).

Because the relative amount of RM is not widely different among the obligate ram-ventilating sharks studied to date (Bernal et al. 2003; Sepulveda et al. 2005), the higher RMR and MMR in the mako cannot be attributed solely to differences in RM amounts. Elevated metabolic rates are, however, most likely associated with other physiological specializations that allow elevated rates of oxygen uptake (e.g., increased gill surface area, elevated hematocrit, and hemoglobin concentrations) and delivery to the aerobic tissues (e.g., high capillary density, high myoglobin concentration) along with the concomitant thermal effects of RM and visceral endothermy (reviewed by Bernal et al. 2001b).

The mean TBF of the makos in the swim tunnel was not significantly different from that of wild, free-swimming individuals (from 1.0 to 1.1 Hz). In addition, both Graham et al. (1990) and Donley et al. (2004) found the mako to have a a similar TBF range while swimming under controlled conditions. Collectively, our field observations, swimming tunnel studies, and recent *in-vivo* work show mako aerobic performance (i.e., TBF) to be limited to around 1 Hz, a TBF considerably less than that reported for other pelagic sharks and teleosts (Bainbridge 1958; Webb 1993).

Our objective was to increase our understanding of aerobic performance in the mako shark and to test the hypothesis that the mako has an elevated metabolic rate relative to other active sharks. The SMR for the mako is lower than that previously reported (Bernal et al. 2001b; Carlson et al. 2004; Dickson and Graham 2004), however, when corrected for differences in experimental temperature the mako RMR and MMR are among the highest recorded for any pelagic shark. Given the experimental protocol, which did not force the sharks to swim at high speeds, it is likely that our measurements of MMR underestimate those values attained in the wild. Although we did not document exceptional aerobic swimming performance for the mako, our estimate of 'performance' and the methods currently available to study captive makos may be inadequate. Further, for pelagic sharks, burst activity and the ability to repay the oxygen debt associated with anaerobic metabolism may ultimately outweigh the advantages of attaining high aerobic swim speeds.

Acknowledgments We thank the following agencies for their direct and indirect support of this work, the National Science Foundation (IOB-0077502, IOB-0091987), California Sea Grant (R/F-85PD; R/F-193), Darryl Lewis and the William H. and Mattie Wattis Harris Foundation, the Scripps Institution of Oceanography Director's Office, Tom Pfleger, and the George T. Pfleger Foundation. We would like to thank J. Valdez for logistical support and the following individuals who assisted, in one form or another, with this project: Jeanine Donley, Doug Syme, Robert Shadwick, Richard Rosenblatt, John Steinitz, Hawkins Dowis, Corey Chan, Nick Wegner, Dan Cartamil, Heather Lee, Scootch Aalbers, Phil Zerofski, Nicholas Sepulveda, Thomas Fullam, Victoria Wintrode, Ashley Knight, Jennifer Nusban, and the vertebrate collection at SIO (H.J. Walker and Cindy Klepadlo). This work is in memory of G. Bernal and F. Ledet, you will be missed.

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