



The effects of temperature and swimming speed on the metabolic rate of the nurse shark (*Ginglymostoma cirratum*, Bonaterre)



Nicholas M. Whitney^{a,*}, Karissa O. Lear^a, Leo Chan Gaskins^a, Adrian C. Gleiss^b

^a Behavioral Ecology and Physiology Program, Mote Marine Laboratory, 1600 Ken Thompson Parkway, Sarasota, FL 34236, USA

^b Centre for Fish and Fisheries Research, Murdoch University, 90 South Street, WA 6150, Australia

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ABSTRACT

Sharks and other top predators have a substantial impact on their ecosystems through trophically mediated effects, and understanding the scope of this impact is essential to forming an accurate picture of energy flow within an ecosystem. One of the most important factors to consider when assessing a predator's impact on their ecosystem is metabolic rate, which is dependent on a number of environmental factors including temperature, as well as underlying physiological and anatomical characteristics. Here the standard (SMR) and routine metabolic rates (RMR) and swimming dynamics of the nurse shark (*Ginglymostoma cirratum*, Bonaterre) were assessed using a static respirometer over two experimental temperatures (23 and 30 °C). The metabolic rates measured here represent the lowest reported for any shark species to date. Mean (\pm SD) SMRs at 23 °C and 30 °C were 36 ± 8 and 60 ± 17 mg O₂ kg⁻¹ h⁻¹, and mean RMRs were 95 ± 15 and 138 ± 21 mg O₂ kg⁻¹ h⁻¹, respectively. The Q_{10} for SMR was 2.42 between 23 and 30 °C. Minimum cost of transport (COT_{min}) at 23 °C was 68 mg O₂ kg⁻¹ km⁻¹, where swimming speed was 0.33 BL s⁻¹. The COT_{min} increased to 81 mg O₂ kg⁻¹ km⁻¹ at 30 °C, where swimming speed was 0.44 BL s⁻¹. The proportional cost of activity, or the cost of activity relative to SMR, was greater compared to other elasmobranchs, and nearly twice that of most ram ventilating shark species. These results highlight the sedentary nature of nurse sharks and suggest that they are energetically suited for a minimally active lifestyle.

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1. Introduction

As apex predators, sharks can have a substantial impact on the structure of their ecosystems through top-down control and behaviorally mediated effects on prey species (Dill et al., 2003; Heithaus et al., 2008; Polovina et al., 2009). Knowing a predator's metabolic rate is crucial to understanding their ecosystem impact, as metabolism accounts for the largest portion of an organism's daily energy expenditure, and thus metabolic demands are directly proportional to consumption rates and foraging needs. There are a number of factors that have been demonstrated to affect metabolic rate and need to be taken into account when predicting the energetic impacts of these predators. These include environmental factors such as temperature, salinity, dissolved oxygen levels, and time of day, as well as physical factors such as body size and body temperature (reviewed by Bernal et al., 2012; Carlson et al., 2004, Lowe and Goldman, 2001).

There is also a large amount of interspecific variation in metabolic rates that cannot be explained by these factors alone, and is likely driven by the ecology of these species (Clarke and Johnston, 1999; Glazier, 2005; Killen et al., 2010; Seibel and Drazen, 2007). For example, sharks that are obligate ram-ventilators (Roberts, 1978) typically have much higher metabolic rates than sharks that can utilize buccal pumping respiration (Carlson et al., 2004), possibly because ram-ventilators have a larger gill surface area that requires more energy for ionoregulation (Brill, 1996; Stevens, 1972). Additionally, the routine metabolic rate measured for mako sharks (*Isurus oxyrinchus*) is two to four times higher than the metabolic rates of most other ram-ventilating species after temperature corrections are applied, likely due to their specialized physiology (including regional endothermy), allowing for an increased metabolic scope and high swimming performance (Lowe and Goldman, 2001; Sepulveda et al., 2007; Watanabe et al., 2015). These kinds of differences suggest that there is variation in metabolic rate stemming from inherent physiological differences between these organisms arising from diversity in ecological demands. For example, variation in metabolic rate related to taxonomic group has been demonstrated for teleosts (Clarke and Johnston, 1999). Additionally, differences in lifestyle have been correlated to variation in metabolic rate in a variety of teleost fishes, with more active pelagic lifestyles correlating

Abbreviations: SMR, standard metabolic rate; RMR, routing metabolic rate; COA_r, total cost of activity; COA_p, proportional cost of activity; COT, cost of transport; COT_{min}, minimum cost of transport.

* Corresponding author.

E-mail address: nwhitney@mote.org (N.M. Whitney).

to higher metabolic rates compared to benthic or bathyal species that are less active, and do not rely on bursts of activity or endurance for foraging (Killen et al., 2010). High metabolic rates and an increased aerobic scope have also been demonstrated for 'high-performance' fish including lamnid sharks and tunas, linked to their pelagic lifestyle and high aerobic demands (Bernal et al., 2009; Brill, 1996). Generally, however, ecology as a driver of metabolic rate and swimming performance has not been examined across elasmobranch taxa with widespread energetic strategies, and most studies have only examined correlations between lifestyle and standard, or resting, metabolic rates. Correlating ecology with routine, or swimming, metabolism may provide a more complete and accurate picture of the daily energy requirements of these animals.

Respirometry has become the standard methodology in studies measuring metabolic rate (Clark et al., 2013). Previous studies have provided metabolic rate estimates for some cool water, inactive species such as dogfish (*Scyliorhinus stellaris*, *Squalus acanthias*) and leopard sharks (*Triakis semifasciata*), as well as some active warm water species including lemon (*Negaprion brevirostris*), bonnethead (*Sphyrna tiburo*), mako (*I. oxyrinchus*), blacknose (*Carcharhinus acronotus*), sandbar (*Carcharhinus plumbeus*), and scalloped hammerhead sharks (*Sphyrna lewini*) (reviewed by Bernal et al., 2012; Carlson et al., 2004). The number of large-bodied elasmobranch species examined has been limited, however, due to the logistical difficulties and expense involved in building and maintaining respirometers large enough to study most species of sharks or rays (Payne et al., 2015).

Here the standard and routine metabolic rates and swimming activity of the nurse shark, (*Ginglymostoma cirratum*, Bonaterre), were measured in a static respirometer under two experimental temperatures (23 and 30 °C). Nurse sharks are one of the most common species of shark in Florida and the Caribbean. They are benthic, sedentary sharks that inhabit shallow tropical waters on both sides of the Atlantic and are capable of resting on the bottom while buccal pumping to breathe (Castro, 2000), representing an ecological niche (a sedentary, warm-water animal) that has not yet been examined in studies of shark metabolism. Additionally, few previous studies have directly assessed the effects of temperature on metabolism in sharks (Clarke and Johnston, 1999; Di Santo and Bennett, 2011; Dowd et al., 2006; Lowe, 2001; Miklos et al., 2003; Tullis and Baillie, 2005), and particularly how temperature affects cost of transport and swimming speeds. Results are compared with metabolic rates measured in other studies to determine how nurse shark energetics relate to those of other elasmobranchs, and how these may reflect the ecology of the species.

2. Materials and methods

2.1. Capture and maintenance

Juvenile nurse sharks (n = 8; Table 1) were captured by rod and reel from the Florida Keys and transported to Mote Marine Laboratory in

Sarasota, FL. They were held in net pens within a 151,400 L tank for the duration of the experiments. Sharks were fed a diet consisting mainly of herring, squid, and shrimp every other day, but were fasted for at least 72 h prior to experimentation in order to achieve a post-absorptive state. Respirometry trials were run in two temperature groupings representing the low (21–24 °C, mean 23 °C) and high (28–31 °C, mean 30 °C) ends of the temperature range nurse sharks are likely to encounter naturally. Sharks were acclimated to experimental temperatures for at least two weeks prior to experimentation.

2.2. Respirometry

Trials were conducted in a circular, closed respirometer constructed from a modified 2800 L fiberglass holding tank (diameter 245 cm), filled to a volume of 2494 L, and sealed using a lid constructed from a PVC frame with translucent plastic sheeting stretched across it (Dowd et al., 2006). Dissolved oxygen (DO) levels were measured using a handheld YSI (model Pro 2030, Yellow Springs, OH). In order to ensure even water mixing in the respirometer and create water flow past the YSI probe for accurate DO measurements, a pump was set up in the center of the tank facing into a T-shaped pipe made of PVC which housed the YSI probe. This system pumped water from the outer part of the tank vertically past the YSI, providing enough water movement to mix water throughout the static system without creating a current for the sharks to swim against. In order to protect the pump and YSI from the sharks and to encourage them to swim around the perimeter of the tank, this pump system was enclosed in a circular cage made of PVC and rigid plastic mesh (diameter 110 cm).

Sharks were moved into the respirometer tank at least 12 h in advance of the start of the trial to allow them to acclimate to the system and recover from handling stress. Nurse sharks tended to rest during the day and were active at night, so trials were run in both of these time periods in order to encompass a full range of activity. Day trials (between around 8:00 and 17:00) were run under constant light conditions, while night trials (between around 18:00 and 2:00) were run under constant dark conditions. During acclimation periods and non-trial periods, sharks were maintained under a 12 h light:dark cycle. The respirometer tank remained connected to a flow-through system during the acclimation process to maintain oxygen levels and water chemistries, and was isolated and converted into a closed system just prior to the start of trials.

At the beginning of trials, the respirometer lid was installed and the tank was surrounded by a curtain so the shark would not be disturbed by observers. The trials were monitored remotely using a live digital video feed. DO was recorded every 5 min and shark behavior was monitored constantly throughout the trials. Swimming speed was measured three times during every 5 min period by recording the amount of time the shark took to complete a full lap around the respirometer. Sharks tended to swim consistently around the outer perimeter of the tank with their body centered about 20 cm inside the edge of the tank, and

Table 1

Shark information for the eight individuals used in respirometry trials. Metabolic rates are reported in mg O₂ kg⁻¹ h⁻¹. Mass and total length (TL) ranges are reported for the entire study period, encompassing 9 months. Some sharks did not show both consistent swimming and resting behavior during a set of trials, thus average SMR and RMR values are not available for all sharks in both temperature groupings.

Shark ID	Mass range (kg)	TL range (cm)	Cold temp trials (21–24 °C)			Warm temp trials (28–30 °C)		
			Number of trials run	SMR mean ± SD	RMR mean ± SD	Number of trials run	SMR mean ± SD	RMR mean ± SD
1	9.7–10	119–122	2	–	75 ± 7	6	74	120 ± 12
2	7.6–9.6	109–118	5	36 ± 8	91 ± 12	8	47 ± 2	160 ± 56
3	10.4–10.9	124–126	2	–	97 ± 4	6	–	155 ± 5
4	7.8–8.1	108–112	2	–	95 ± 8	7	56 ± 15	–
5	5.6–7.8	101–112	7	40 ± 9	126 ± 1	6	82 ± 38	–
6	11.2–12.4	130–132	2	21	99 ± 4	8	57 ± 8	134 ± 15
7	5.0–6.4	91–101	8	33 ± 7	–	4	–	–
8	8.4–9.7	107–116	7	37 ± 8	94 ± 15	8	60 ± 10	134 ± 18
All sharks	5.0–12.4	91–132	35	36 ± 8	95 ± 15	53	60 ± 17	138 ± 21

thus lap length was calculated as the circumference of a circle with radius 20 cm less than the outer edge of the respirometer. Although shark swimming speed was not controlled, sharks tended to maintain a relatively constant speed within measurement intervals. Trials were run until the DO reached 80% saturation. Each shark was run at least twice during the day and twice at night for each temperature grouping (Table 1). To assess background respiration levels, oxygen degradation was measured in a blank respirometer for 4 h at each temperature level.

Additionally, as part of a separate study, sharks during most trials (26 of 35 cold water trials, and all warm water trials) were equipped with acceleration data loggers weighing approximately 23 g, attached to their first dorsal fin. These tags represent less than 0.005% of the body weight of these sharks, and were not observed to alter behavior or significantly affect metabolic rate (*t*-test between SMR of tagged and untagged sharks in cold water trials *df* = 17, *t* = 2.11, *P* = 0.31).

2.3. Data analysis

Periods of the trials where sharks displayed consistent behavior for at least 20 min were used for metabolic rate determination. Oxygen consumption rate (VO_2 , $\text{mg O}_2 \text{ kg}^{-1} \text{ h}^{-1}$) was calculated using the equation:

$$\text{VO}_2 = \frac{(S-b)(60 \text{ min})(V)}{(W)}$$

where *S* is the slope of the oxygen degradation curve, *b* is the slope of the background respiration curve, *V* is the volume of the respirometer in liters, and *W* is the weight of the shark in kg. The volume of the shark (~10 L) was considered to be negligible relative to the respirometer volume (2494 l), representing an error of <0.5%, and was thus not incorporated into our model.

Swimming speed was calculated for each period of consistent activity by averaging swimming speeds recorded during the entire active period. Measured VO_2 values were pooled across all trials by swimming speed and least squares linear regressions conducted to examine the relationship between VO_2 and swimming speed for each temperature group. These relationships were compared with an analysis of covariance using R version 3.1.2 (R Foundation for Statistical Computing, Vienna, Austria).

Cost of transport (COT; $\text{mg O}_2 \text{ kg}^{-1} \text{ km}^{-1}$), an estimate of the energy required to travel per unit distance at a specific speed, was calculated by dividing VO_2 by swimming speed (km h^{-1}). These COT values were also pooled by swimming speed across all trials for each temperature group, and the data fit by least squares with polynomial regressions to determine the swimming speed with the lowest COT for nurse sharks at each temperature. Standard metabolic rate (SMR), or the metabolic rate of a postabsorptive fish at rest (Carlson et al., 2004), was calculated by averaging the metabolic rate values for all periods of inactivity for each temperature group. Overall routine metabolic rate (RMR), the metabolic rate of a postabsorptive fish during volitional activity (Carlson et al., 2004), is generally calculated by averaging the metabolic rate over all levels of activity, which for nurse sharks would include both active and inactive periods. Instead, RMR here was calculated as the average metabolic rate only during periods of active swimming, and does not include metabolic rate data from periods of rest. The total cost of activity (COA_T), representing the amount of additional energy required for movement, was calculated as the difference between routine and standard metabolic rates. The proportional cost of activity (COA_P), showing the proportional increase in energy needed to switch between resting and active states relative to SMR, was calculated by dividing COA_T by SMR.

Metabolic rate has been shown to correlate with body size in several past studies (Payne et al., 2015; Parsons, 1990; Sims, 1996, 2000). Therefore metabolic rates determined here were corrected for body size to 1 kg using a scaling exponent of 0.86 (Sims, 2000) for the sake

of comparison with other studies. Additionally, a Q_{10} of 2.3 was used to correct the VO_2 values reported in other studies to 23 °C to facilitate interspecific comparisons.

3. Results

A total of 35 cold temperature trials (23 ± 0.9 °C mean \pm SD) and 53 warm temperature trials (30 ± 0.3 °C mean \pm SD) were run with eight nurse sharks (Table 1). Cold temperature trials lasted an average of 5.6 ± 1.8 h, and warm temperature trials averaged 3.3 ± 1.1 h. The SMRs measured during day and night were compared to determine whether time of day affected metabolic rate. There were no significant differences between night and day standard VO_2 rates at either 23 or 30 °C (*t*-test *df* = 8, *t* = 2.31, *P* = 0.34 at 23 °C and *df* = 28, *t* = 2.05, *P* = 0.41 at 30 °C), therefore all resting intervals and active intervals regardless of time of day were combined for further analyses.

Standard and routine metabolic rates are presented in Table 1. Swimming speeds, COA, and COT values are reported in Table 2. Metabolic rates, COT, and swimming speeds were greater in higher temperatures, while COA_T and COA_P were lower.

Oxygen consumption rates in both temperature groups increased with swimming speed at a similar rate (ANCOVA interaction effect *F* = 0.147, *df* = 1, *P* = 0.71). Linear regressions of pooled VO_2 data against swimming speed in BL s^{-1} (*U*) produced the relationship $\log \text{VO}_2 = 1.003 U + 1.63$ ($r^2 = 0.93$) at 23 °C, and $\log \text{VO}_2 = 1.003 U + 1.766$ ($r^2 = 0.89$) at 30 °C (Fig. 1). The differences in standard VO_2 levels between the two temperatures groupings resulted in a Q_{10} of 2.42 for nurse sharks between 23 and 30 °C.

Cost of transport showed a parabolic relationship with swimming speed. The highest COT values in both temperature groups correlated with the slowest swimming speeds. Fitting a parabolic curve to COT pooled by swimming speed determined a minimum cost of transport (COT_{\min}) at 0.33 BL s^{-1} at 23 °C and 0.44 BL s^{-1} at 30 °C (Fig. 2), where COT was 68 and 81 $\text{mg O}_2 \text{ kg}^{-1} \text{ km}^{-1}$, respectively (Table 2).

4. Discussion

4.1. Metabolic rate

The metabolic rates of nurse sharks are lower than those reported for any other shark species, after correcting for differences in body mass and temperature (Table 3). Moreover, the routine nurse shark metabolic rates are lower than the standard metabolic rates of most other sharks estimated in previous studies. The relationship between metabolic rate and swimming speed is generally similar to that of other species, increasing exponentially as swimming speed increases (Fig. 3), however the slope of this relationship in nurse sharks appears greater than that of other species studied. This suggests that the low oxygen consumption rates found in this study stem from nurse sharks having a low SMR, which is typical of relatively inactive elasmobranchs compared with ram-ventilating species (reviewed by Bernal et al., 2012; Carlson et al., 2004).

Although nurse sharks were expected to have a lower metabolic rate than active ram-ventilating species, their metabolic rates were also substantially lower compared to cooler-water inactive species such as the spotted dogfish and the leopard shark. The low RMR calculated in this study is partially due to the nurse sharks' slower swimming speeds, as the maximum swimming speed of nurse sharks here was 0.45 BL s^{-1} , whereas sharks in most other studies swam up to at least 0.7 BL s^{-1} . In fact, relationships describing the increase in metabolic rate with swimming speed show that at higher swimming speeds nurse sharks would theoretically surpass previous measurements of lemon and leopard shark metabolic rate, after correcting for temperature (see Fig. 3). Since the swimming speeds observed here represent the volitional activity of nurse sharks and appear to include the speed at which COT is

Table 2
Comparison of swimming behavior and efficiency between the two temperature groupings.

Temperature grouping	Swimming speed range (BL s ⁻¹)	Mean swimming speed (BL s ⁻¹)	Swimming speed at COT _{min} (BL s ⁻¹)	COT _{min} (mg O ₂ kg ⁻¹ km ⁻¹)	COA _T (mg O ₂ kg ⁻¹ km ⁻¹)	COA _P (% of SMR)
21–24 °C	0.23–0.38	0.30 ± .044	0.33	68	59	162%
28–30 °C	0.25–0.45	0.36 ± .064	0.44	81	43	129%

minimized, these higher swimming speeds are unlikely to be utilized in the wild except perhaps during burst swimming.

The low metabolic rates observed in this study cannot be attributed to the size of the study animals. Most previous metabolic rate studies with sharks have used animals approximately 1–2 kg in size (see Table 3), while the animals used here ranged in size from 5.0–12.4 kg. When corrected for mass using a scaling exponent of 0.86 (Sims, 2000) however, the SMR and RMR were still substantially lower than in previous studies, at 48 and 129 mg O₂ kg⁻¹ h⁻¹, respectively, at 23 °C, and thus body size of the test animals is not responsible for the majority of the difference in metabolic rate between nurse sharks and other sharks. It is also worth noting that differences in experimental conditions and methods between studies, including the type of respirometer used, experimental temperatures, swimming speeds, and methods of data compilation, can greatly impact metabolic rate estimates, and these comparisons among different studies should be interpreted with caution (Carlson et al., 2004).

4.2. Temperature effects

Overall metabolic rate increased significantly with the rise in temperature, however, temperature differences did not affect the relationship between swimming speed and VO₂, which maintained a similar slope regardless. The increase in oxygen consumption between 23 and 30 °C produced a calculated Q₁₀ of 2.42. This fits within the assumed Q₁₀ range of 2–3 proposed for fish (and elasmobranchs) in general (Brett and Groves, 1979), as well as calculated Q₁₀ values for a number of shark species (Table 4). This suggests that nurse sharks have a temperature sensitivity typical of most elasmobranchs, however, it does show a substantial difference in metabolic rate between the temperatures that nurse sharks encounter seasonally. The SMR of nurse sharks increased by 66% between 23 and 30 °C, and using the calculated Q₁₀ of 2.42, the metabolic rate would more than double between 20 and 30 °C (from 28 to 60 mg O₂ kg⁻¹ h⁻¹), a conservative temperature range for these sharks given their seasonal and geographic distribution (Castro, 2000).

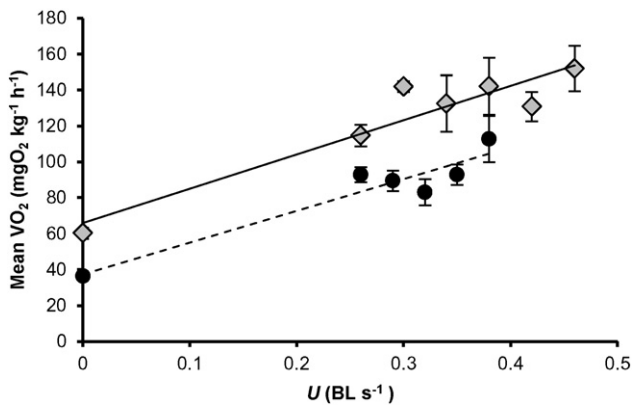


Fig. 1. Pooled VO₂ against swim speed (*U*) at temperatures around 23 °C (black circles) and 30 °C (gray diamonds). Linear regressions produced relationships of log VO₂ = 1.003 *U* + 1.63 (*r*² = 0.93) at 23 °C, and log VO₂ = 1.003 *U* + 1.766 (*r*² = 0.89) at 30 °C. Error bars show ± standard error.

4.3. Cost of transport

Cost of transport in nurse sharks followed trends seen in previous studies, where COT is greatest at the slowest swimming speeds and declines until it reaches a minimum at the most energy efficient swimming speed, before increasing at higher swimming speeds (Videler and Nolet, 1990). Similar to the overall metabolic rate of nurse sharks, both COT_{min} (68 mg O₂ kg⁻¹ h⁻¹ at 23 °C and 81 mg O₂ kg⁻¹ h⁻¹ at 30 °C) and the swimming speed at COT_{min} (0.33 BL s⁻¹ and 0.44 BL s⁻¹ respectively) are much lower than those found for other species of sharks. Carlson et al. (1999) determined a COT_{min} for blacknose sharks of 277–316 mg O₂ kg⁻¹ km⁻¹ at 0.54–0.84 BL s⁻¹ (28 °C), and Lowe (2001) found a COT_{min} of 102 mg O₂ kg⁻¹ km⁻¹ (26 °C) at 0.8 BL s⁻¹ for scalloped hammerhead sharks (26 °C). The swimming speed at COT_{min} determined here for nurse sharks is also outside of the predicted range of optimal swimming speeds theorized by Weihs (1977) based on swimming observations of carcharhinid sharks at 26 °C. The lower nurse shark values are likely tied to the general level of inactivity typical of nurse sharks and their less-streamlined body shape and near anguilliform swimming kinematics compared to more carangiform and thunniform highly streamlined ram-ventilating sharks (Thomson and Simanek, 1977).

The effect of temperature on swimming speed at COT_{min} has not yet been studied in sharks, although the shift observed here has been reported in teleosts. Previous teleost studies have shown that swimming speed at COT_{min} typically shows a bell-curve relationship with temperature: COT_{min} increases up to the optimum temperature and then plateaus or decreases as temperature approaches the thermal tolerance of the fish (Claireaux et al., 2006; Lee et al., 2003; Myrick and Cech, 2000). The COT_{min} for nurse sharks increased by 33% between 23 and 30 °C, which is comparable to percent increases seen in teleosts over similar temperature ranges (Claireaux et al., 2006). The increase in swimming speed of COT_{min} at higher water temperatures in teleosts has been attributed mainly to the increase in metabolic scope and

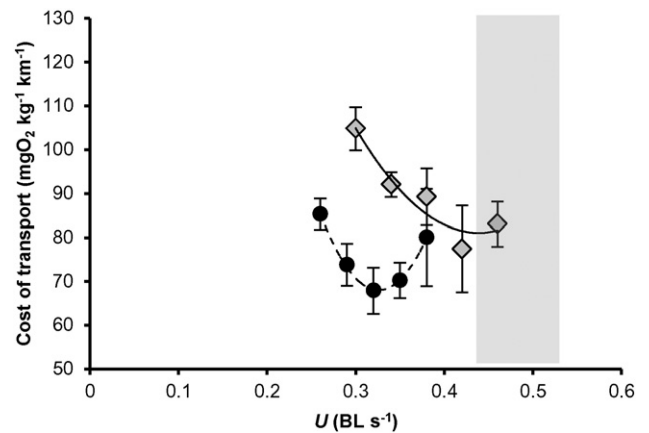


Fig. 2. Cost of transport as a function of swim speed at temperatures near 23 °C (black circles) and 30 °C (gray diamonds). Polynomial regressions describe the relationships COT = 4041.7 *U*² – 2633.7 *U* + 497.09 at 23 °C (*r*² = 0.998), and COT = 1237.3 *U*² – 1085.8 *U* + 319.28 at 30 °C (*r*² = 0.917). The shaded area shows the range of theorized optimal swimming speeds suggested by Weihs (1977) for sharks 93–132 cm TL. Error bars show ± standard error.

Table 3

A comparison of standard and active VO_2 estimates among elasmobranch species. Only species with both an SMR and RMR reported are included. SMR and RMR values were taken from the same study for all species except for bonnethead sharks, where the SMR is reported in Carlson and Parsons (2003), and the RMR in Carlson and Parsons (2001). Estimates were temperature corrected to 23 °C using a Q_{10} of 2.3. Reported standard VO_2 values denoted by * show values obtained by extrapolating power performance curves to zero, and † denotes standard metabolic rates measured through spinal blocked sharks. All other standard VO_2 values were directly measured under normal behavior. All metabolic rates are reported in $\text{mg O}_2 \text{ kg}^{-1} \text{ h}^{-1}$.

Species (n)	Experimental temp (°C)	Animal size (kg)	Reported SMR	SMR at 23 °C	Reported RMR	RMR at 23 °C	COA_T at 23 °C	COA_P at 23 °C	Study
<i>Isurus oxyrinchus</i> (9)	18.3	4.4–9.5	124*	188	344	522	158	43.3%	Sepulveda et al. (2007)
<i>Carcharhinus acronotus</i> (10)	28	0.45–3.51	240*	158	395	261	102	64.6%	Carlson et al. (1999)
<i>Sphyrna lewini</i> (17)	26	0.5–0.93	189*	147	275	214	67	45.5%	Lowe (2001)
<i>Scyliorhinus stellaris</i> (8)	18.3	2.0–2.9	94	139	165	244	105	75.5%	Piiper et al. (1977)
<i>Myliobatus aquila</i> (5)	10	0.15–2.18	44	131	58	172	41	31.5%	Du Preez et al. (1988)
<i>Negaprion brevirostris</i> (7)	25	1.11–1.61	153	130	240	203	74	56.9%	Scharold and Gruber (1991)
<i>Rhinobatos annulatus</i> (10)	15	0.04–2.0	61	119	73	141	23	19.0%	Du Preez et al. (1988)
<i>Triakis semifasciata</i> (18)	22	0.15–5.18	105	114	167	182	67	59.0%	Graham et al. (1990)
<i>Sphyrna tiburo</i> (8/17)	28/26	1.0–1.2	173†	114	235	183	97	50.8%	Carlson and Parsons (2001, 2003)
<i>Carcharhinus plumbeus</i> (16)	24	1.0–10.4	120†	110	213	196	86	77.5%	Dowd et al. (2006)
<i>Squalus acanthias</i> (8)	10	1.52–2.40	32	95	88	192	97	103.1%	Brett and Blackburn (1978)
<i>Raja erinacea</i> (7)	10	0.41–0.71	20	59	48	143	84	141.5%	Hove and Moss (1997)
<i>Ginglymostoma cirratum</i> (8)	23	5.0–12.4	36	36	95	95	59	161.8%	Present study

muscle power generated in higher temperatures, and the delayed recruitment of white muscle fibers compared to colder water activity (Claireaux et al., 2006; Day and Butler, 2005; Randall and Brauner, 1991; Zeng et al., 2009), all factors that would also account for increased swimming speed in elasmobranchs at high temperatures.

While the SMR, RMR, and COT of nurse sharks are low overall, these sharks present the highest proportional COA_P when compared to past studies of elasmobranchs (Table 3). This COA_P is nearly twice that of the lemon shark and some ram-ventilating species (Table 2), suggesting that nurse sharks incur a much higher relative metabolic cost of activity in switching from rest to movement compared to other more active elasmobranchs. This is demonstrated by the difference in the slopes of the power performance curves (swimming speed vs. $\log(\text{VO}_2)$) between nurse sharks and other species. The slopes of most power performance curves for sharks lie between 0.2 and 0.4, with the largest power-performance slope reported for the mako shark at 0.97 (Sepulveda et al., 2007), although the power-performance slope extrapolated from Graham et al. (1990) for mako sharks is 0.51. The nurse shark power performance slope reported here is greater than that of the mako

shark, at 1.003, and three to five folds larger than the slopes for most other sharks. The slope of the power-performance curve is indicative of the increase in hydrodynamic drag the animal has to overcome in relation to increasing speeds. Less streamlined fish would be expected to have steeper slopes, and the nurse shark, with its blunt head and near anguilliform swimming due to its long upper lobe of the caudal fin, appears to fit this general description (Blake, 2004). This finding also emphasizes the extreme increase in energy expenditure that must be associated with the highly active mating period known for this species (Carrier et al., 1994; Pratt and Carrier, 2001; Whitney et al., 2010). It has to be noted here that the steep slope of the power performance curve does not necessarily translate into high cost of transport, as shown for eels, which have surprisingly low cost of transport (van Ginneken et al., 2005). Equally, the low SMR of nurse sharks would reduce COT considerably, albeit at lower speeds as shown here.

4.4. Conclusions

These results indicate that metabolic rates, optimum and routine swimming speeds, and COT for nurse sharks are all substantially lower than those measured for other species of sharks to date, while their COA_P is higher. These parameters highlight the nurse shark's sedentary life strategy, and show a correlation between their ecology and metabolic rate. The low energy requirements and high cost of activity optimize minimal activity as an energetic advantage, enabling these sharks to spend the majority of their time resting and little time foraging. Nurse sharks appear to utilize this low energy lifestyle very efficiently. Previous studies have linked high metabolic rates with increased growth rates and reproductive output in tunas and other pelagic teleosts (Brill and Busnell, 1991; Brill, 1996; Bernal et al., 2009), and

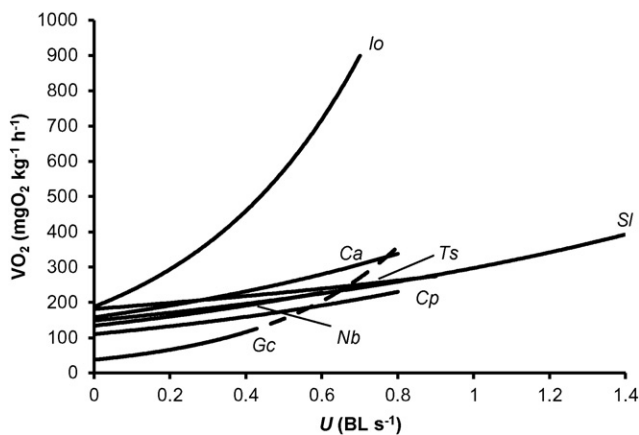


Fig. 3. Relationships between VO_2 and swim speed (U) compared among seven shark species, all temperature corrected to 23 °C using a Q_{10} of 2.3. Data from *I. oxyrinchus* (*Io*) is from Sepulveda et al. (2007) ($n = 9$, 18 °C), *C. acronotus* (*Ca*) is adapted from Carlson et al. (1999) ($n = 8$, 28 °C), *T. semifasciata* (*Ts*) is from Scharold et al. (1989) ($n = 5$, 15 °C), *N. brevirostris* (*Nb*) is from Scharold and Gruber (1991) ($n = 7$, 25 °C), *S. lewini* (*Sl*) is adapted from Lowe (2001) ($n = 17$, 26 °C), *C. plumbeus* (*Cp*) is adapted from Dowd et al. (2006) ($n = 16$, 24 °C), and *G. cirratum* (*Gc*) is from the current study ($n = 8$, 23 °C). The solid lines show the range of swimming speeds observed during the studies, while the dashed portion of the *G. cirratum* line indicates the theoretical metabolic rate of *G. cirratum* at increased swimming speeds.

Table 4

A comparison of Q_{10} values calculated in past shark metabolic rate studies. The Q_{10} calculated in the present study for nurse sharks generally fits well within the Q_{10} values suggested by most past studies, although it is substantially higher than that proposed for scalloped hammerheads by Lowe (2001).

Species	Temperature range (°C)	Calculated Q_{10} of SMR	Source
<i>T. semifasciata</i>	12–24	2.51	Miklos et al. (2003)
<i>C. plumbeus</i>	24–28	2.5	Dowd et al. (2006)
<i>Chiloscyllium plagiosum</i>	15–30	2.7	Tullis and Baillie (2005)
<i>S. tiburo</i>	20–30	2.34	Carlson and Parsons (1999)
<i>S. lewini</i>	21–29	1.34	Lowe (2001)
<i>G. cirratum</i>	23–30	2.42	Present study

thus conversely the low metabolic rates of nurse sharks might be expected to result in slow growth rates and low reproductive potential. Despite their low metabolism, however, nurse sharks have been shown to have similar growth rates to other shark species with higher metabolism (Carrier and Luer, 1990), and have relatively high fecundity as well (Castro, 2000). Future studies can use this metabolic rate information to assess the impact that nurse sharks have on their ecosystem, and compare this impact with that of other predators. While nurse sharks are often one of the most prevalent sharks in tropical and subtropical ecosystems (Castro, 2000), other less-common shark species with higher metabolic costs may have a greater overall energetic impact on these ecosystems.

Additionally, the substantial differences between the two temperature groupings, not only in metabolic rate but also in swimming speed and activity levels, suggest that nurse sharks' metabolic impact on their ecosystem changes drastically during the year. This emphasizes the importance of considering temperature and seasonality when making predictions about ecosystem impacts of apex predators, and the need to consider behavioral effects as well as metabolic effects resulting from environmental changes in temperature.

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