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

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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 (±SD) SMRs at 23 °C and 30 °C were 36 ± 8 and 60 ± 17 mg O_2 kg^{-1} h^{-1}, and mean RMRs were 95 ± 15 and 138 ± 21 mg O_2 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 O_2 kg^{-1} km^{-1}, where swimming speed was 0.33 BL s^{-1}. The COT_{min} increased to 81 mg O_2 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.

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

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

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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 O_2 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 ±
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**