

The metabolic rate of an active, tropical elasmobranch, the lemon shark (*Negaprion brevirostris*)

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Abstract. The oxygen consumption of an active tropical elasmobranch, the lemon shark (*Negaprion brevirostris*), was measured at different swimming speeds in an annular respirometer. The resulting power-performance curve had a slope of 0.36 which is similar to that of moderately active teleosts. The standard metabolic rate of this elasmobranch ($95 \text{ ml O}_2 \cdot \text{kg}^{-1} \cdot \text{h}^{-1}$) was higher than that of other sharks, whereas the routine metabolic rate ($110 \text{ ml O}_2 \cdot \text{kg}^{-1} \cdot \text{h}^{-1}$) was less than that of other elasmobranchs previously studied. Active metabolic rate ($226 \text{ ml O}_2 \cdot \text{kg}^{-1} \cdot \text{h}^{-1}$), measured in one individual, was the highest for any elasmobranch measured to date. The cost of living of the tropical water lemon shark was calculated to be approximately 2.5 times greater than that of a temperate water shark, but not as high as a salmonid. It is possible that previous generalizations on the poor aerobic performance of sharks are based on data from the less active, temperate water sharks, and are misleading since the metabolic rate of this more active species compares well with active teleosts.

Key words: Elasmobranch – Metabolism – Activity

Introduction

Although the popular image of the shark is of a large active carnivore, oxygen consumption studies of elasmobranchs suggest that the metabolic

rate of sharks is on a par with the most sluggish teleosts (Brett and Blackburn 1978). There are several reasons, however, for suspecting that this generalization may be inaccurate.

Firstly, published studies have concentrated on the relatively inactive, temperate water sharks, such as the spotted dogfish shark *Scyliorhinus canicula*, and the larger spotted dogfish *S. stellaris* (Piiper and Schumann 1967; Hughes and Umezawa 1968). Activity in the larger spotted dogfish during the day, for instance, consisted of resting on the bottom, and only swimming an average of 7 min per h (Metcalf and Butler 1984). At night, activity increased, but only to a maximum of 25 min per h.

Secondly, in comparison to what is known for teleosts, the information on metabolic rates of sharks is meagre. The literature contains many in-depth reviews of metabolic rate, exploring such diverse topics as standard, routine, and active metabolism, cost of transport, environmental effects and physiological energetics in teleosts (Fry 1971; Beamish 1978; Jones and Randall 1978; Brett and Groves 1979; Tytler and Calow 1985), yet very little is reported for elasmobranchs.

Finally, the only two measures of active metabolism in sharks in the literature are for the spiny dogfish, *Squalus acanthias* (Brett and Blackburn, 1978), and the leopard shark, *Triakis semifasciata* (Scharold et al. 1989). Unfortunately, the spiny dogfish shark deteriorates rapidly in captivity (Martini 1978), which may account for its poor swimming performance reported in the study.

There is clearly a need for measurement of metabolic rates on more active shark species. The lemon shark (*Negaprion brevirostris*) is an ideal

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subject for this kind of study. It is an active, tropical carnivore, which can be held in captivity and in good physiological condition for periods exceeding 3 years (Gruber and Keyes 1981). In light of the general availability of healthy, active animals, it was the purpose of this study to determine the metabolic rate of the lemon shark at different activity levels, in order to construct a power-performance curve for this species.

Materials and methods

Juvenile lemon sharks 1–2 years old, 0.8–1.3 kg weight, and 54–64 cm total length were captured in the Florida Keys, and transported in oxygenated bags to facilities at the Rosenstiel School of Marine and Atmospheric Science. At the laboratory, they were held in one of several 10,000 l recirculating holding aquaria (22°C, 31‰ salinity), and fed pieces of blue runner (*Caranx chrysos*) daily, and Vigram (Squibb) multivitamin supplements weekly. All animals used in the experiment were kept on a 12 h light/dark cycle and maintained in this manner for at least 1 month before being used in an experiment. The reader is referred to Gruber and Keyes (1981) for a description of the maintenance techniques.

The 80 l flow-through annular chamber (78 cm outer diameter, 35 cm inner diameter, 21 cm height) was constructed of plexiglass and is described in more detail by Nixon and Gruber (1988). Water for the respirometer was pumped from the shark's home aquarium to a 1000 l, well-aerated, holding tank 2 m above the chamber. The water level inside the reservoir was maintained by a large overflow standpipe which allowed air-saturated water to be delivered to the respirometer, via a gravity flow system, at a constant and predictable rate. Dye tests confirmed that the water in the respirometer remained well mixed regardless of whether or not the shark was swimming.

The partial pressure of oxygen (PO₂) of the inflowing and outflowing water was determined by subsampling the water stream with a Radiometer E-5046 oxygen electrode mounted in a thermostatted Radiometer D-616 flow-through cuvette, connected to a Radiometer PHM 72/MkII oxygen analyser and Fischer Recordall strip chart recorder. An infrared beam, passing from the hollow center of the chamber to a receiver mounted on the outside wall, was used to monitor shark activity. Upon passage through the beam, a signal pulse was generated and registered on a chart recorder.

Sharks were fasted for 3 days before being placed in the chamber, and were acclimated in the chamber for at least 24 h before oxygen consumption ($\dot{V}O_2$) and activity measurements were begun. The PO₂ and flow rate of water to the chamber were measured continuously for 15 min at the onset of the experiment, and for 10 min every 1.25 h thereafter. A respirometry experiment generally lasted 48–72 hours utilizing a 12 h light/dark cycle. The oxygen probe calibration was checked every 2 h with air-saturated water and recalibrated if necessary. Upon completion of the experiment, the animal's weight and length were recorded.

Oxygen consumption (ml O₂·kg⁻¹·h⁻¹) was calculated using the formula:

$$\dot{V}O_2 = ((PO_{2(in)} - PO_{2(out)}) \times \dot{V}/\dot{V}_{H_2O} \times \alpha_{O_2}) \times BW^{-1}$$

where PO_{2(in)} and PO_{2(out)} (mm Hg) = partial pressure of oxygen in the inflow and outflow water stream, respectively; \dot{V}_{H_2O} (l·h⁻¹) = flow rate of water through the respirometer α (ml O₂·l H₂O⁻¹·mm Hg⁻¹) = solubility of oxygen in water at

the experimental temperature and salinity, and BW (kg) = body weight of the experimental animal. Swimming speed (cm·s⁻¹) was calculated by dividing the circumference of the swimming channel, measured at a distance 5 cm to the inside of the outermost wall (the preferred swimming path) by the lap time.

In order to analyse the data, respirometry runs were summarized by calculating the oxygen consumption and the associated swimming speed, in body lengths per s (BL·s⁻¹), at 1 min intervals. As there was no way to control the animals' swimming speed, we were obliged to measure $\dot{V}O_2$ at whatever speeds the sharks chose to swim. This was problematic in instances where sharks would not maintain constant (± 0.025 BL·s⁻¹) swimming speeds for long periods. Fortunately this was not usually the case, as most sharks seemed to settle quickly into a preferred swimming speed. In order to insure the $\dot{V}O_{2s}$ were representative of the specific swimming speeds at which they were recorded, data analysis was performed only on measurements made on sharks judged to be in a steady state swimming mode. In our experiments, this meant that the swimming speed must have been maintained at a constant rate for at least 20 min. Oxygen consumption and swimming speeds measured for the first and last 5 min of the steady state swimming period were excluded, and the remaining data points used to calculate mean $\dot{V}O_2$ at the particular swimming speed. In general, sharks swam in one direction in the chamber for about 45 min before turning around and swimming in the opposite direction. Lap times that were obviously too short due to changes in direction, were excluded from swimming speed calculations.

In order to construct the power-performance curve, results from 13 animals were pooled and divided into discrete intervals according to swimming speeds; 0.02 BL·s⁻¹ (resting on the bottom with occasional laps), 0.05–0.14 BL·s⁻¹; 0.15–0.24 BL·s⁻¹; and so on to 0.65–0.74 BL·s⁻¹. Mean oxygen consumption and swimming speeds of each interval were calculated and used for the linear regression.

All values given in the text are mean \pm standard error.

Results and discussion

A least squares linear regression of mean $\dot{V}O_2$ on swimming speed (Fig. 1) yielded the equation:

$$\log \dot{V}O_2 = 0.36 U + 1.945$$

$$r^2 = 0.89$$

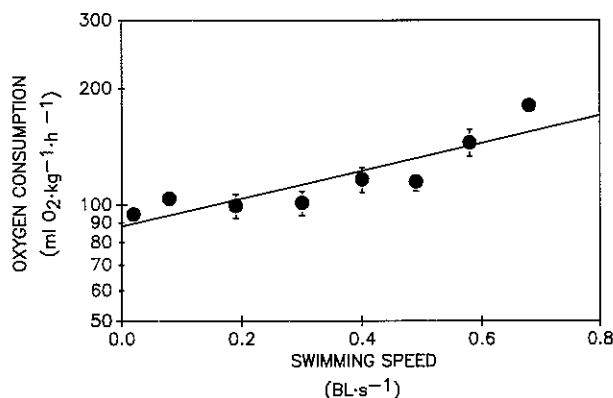


Fig. 1. A power-performance curve estimated from measurements of metabolic rate and swimming speed in 13 juvenile lemon sharks. Points represent means \pm standard error

Where $\dot{V}O_2$ = oxygen consumption ($\text{ml O}_2 \cdot \text{kg}^{-1} \cdot \text{h}^{-1}$), U = speed ($\text{BL} \cdot \text{s}^{-1}$). The slope, which describes the rate at which $\dot{V}O_2$ increases with swimming speed, is similar to that determined for rainbow trout, *Salmo gairdneri* (Webb 1971), and sockeye salmon, *Oncorhynchus nerka* (Brett 1972).

As $\dot{V}O_2$ varies with activity, metabolic rates reported in the literature have been divided into categories based on the associated activity state. The three of interest in this study are standard, routine, and active metabolic rates. The oxygen consumption of an animal in its least active state is termed standard metabolic rate, and is defined as the minimum oxygen consumption of a thermally acclimated organism in a post-absorptive state (Brett and Groves 1979). In instances where activity is not quantified, routine metabolic rate is taken to be the average oxygen consumption associated with spontaneous activity (Brett 1972). Lastly, the maximum rate of oxygen consumption measured at the maximum sustained speed is termed active metabolic rate (Brett and Groves 1979).

The standard metabolic rate of a lemon shark is $94.6 \pm 4.3 \text{ ml O}_2 \cdot \text{kg}^{-1} \cdot \text{h}^{-1}$. Activity during this period consisted of 10–15 min of resting behaviour (lying on the bottom), punctuated by one or

two slow laps, and was represented in Fig. 1 as a swimming speed of $0.02 \text{ BL} \cdot \text{s}^{-1}$. Standard metabolic rates in teleosts vary widely ($20\text{--}330 \text{ ml O}_2 \cdot \text{kg}^{-1} \cdot \text{h}^{-1}$, Altman and Dittmer 1974) due to differences in species, temperature, and experimental methods. It appears however, that the standard metabolic rate recorded for the lemon shark is comparable to that reported for a moderately active predaceous teleost such as the large mouth bass (*Micropterus salmoides*) at a similar water temperature ($84 \text{ ml O}_2 \cdot \text{kg}^{-1} \cdot \text{h}^{-1}$ at 20°C , Beamish 1970).

Compared to other elasmobranchs, the lemon shark's standard metabolic rate is the highest reported to date (Table 1). However, because of temperature effects on metabolism, the wide range of reported experimental temperatures makes it difficult to determine whether the lemon shark's higher metabolic rate was due to higher ambient temperature or to an inherently higher metabolic rate. Therefore, we have compensated for the different experimental temperatures by applying a Q_{10} of 2.2 (Brett and Blackburn 1978), and standardizing all the metabolic rates to a temperature of 22°C (Table 1). Even after this treatment of $\dot{V}O_{2s}$, the lemon shark's standard metabolic rate remains at the upper end of the range of data reported in previous studies.

Table 1. Summary of standard and routine metabolic rates reported in the literature for several species of elasmobranchs. Oxygen consumption values are reported at the experimental temperature as well as recalculated for a temperature of 22°C by applying a Q_{10} of 2.2

Species	Experimental temperature ($^\circ \text{C}$)	Metabolic Rate ($\text{ml O}_2 \cdot \text{kg}^{-1} \cdot \text{h}^{-1}$)				References
		Standard		Routine		
		Reported	Recalculated to 22°C	Reported	Recalculated to 22°C	
<i>Hemiscyllium plagiosum</i>	23	48	44	—	—	Chan and Wong (1977)
<i>Negaprion brevirostris</i>	23	—	—	132–158	122–147	Nixon and Gruber (1988)
<i>Scyliorhinus stellaris</i>	14	—	—	150	281	Raffy (1932) ^a
<i>S. stellaris</i>	17	41	60	—	—	Piiper and Schumann (1967)
<i>S. stellaris</i>	18	36	50	—	—	Randall et al. (1976)
<i>S. stellaris</i>	18.5	62	82	—	—	Bounhiol (1905) ^a
<i>S. stellaris</i>	19	77	97	122	155	Piiper et al. (1977)
<i>S. canicula</i>	13	53	112	—	—	Hughes and Umezawa (1968)
<i>S. canicula</i>	13	—	—	117	237	Buytendijk (1910) ^a
<i>S. canicula</i>	13	—	—	73	147	Buytendijk (1910) ^a
<i>S. canicula</i>	15	51	88	—	—	Short et al. (1979)
<i>Squalus acanthias</i>	10	24	61	36	92	Brett and Blackburn (1978)
<i>S. acanthias</i>	11	43	101	—	—	Lenfant and Johansen (1966)
<i>S. acanthias</i>	13	39	79	—	—	Pritchard et al. (1958)
<i>S. suckleyi</i>	10	31	79	—	—	Hawson and Johansen (1970)
<i>Triakis semifasciata</i>	16	68	109	—	—	Scharold et al. (1989)
<i>Negaprion brevirostris</i>	22	95	95	110	110	present study

^a from Winberg (1956)

In this study, routine metabolic rate was calculated as the grand mean of all metabolic rates measured, regardless of activity. It is useful for comparative purposes, however, to be able to distinguish what the activity pattern was during the routine metabolic rate measurement. In our experiments, lemon sharks swimming in the respirometer were quite active, as some animals swam for 3–5 h without resting on the bottom. More typically, however, sharks would swim at 0.3–0.4 BL·s⁻¹ for approximately 30 min, settle on the bottom for 3–7 min, and then resume swimming. The fact that they were in the comparatively small respirometer did not seem to be a factor in this behaviour, as similar swimming patterns were seen in the larger holding aquaria, as well as in the field (Gruber et al. 1988). In view of the high activity level, it was surprising that the mean routine metabolic rate of the lemon shark (109.7 ml O₂·kg⁻¹·h⁻¹) was less than most of the original and temperature-standardized values for *Scyliorhinus stellaris* and *S. canicula* (147–281 ml O₂·kg⁻¹·h⁻¹, Table 1), elasmobranchs that spend the majority of their time resting on the bottom (Metcalf and Butler 1984; Piiper et al. 1977).

If the cost of locomotion in these other elasmobranchs is high, it may be that the small amount of swimming activity associated with routine metabolism is enough to drive their metabolic rate far above their standard metabolic rate. Unfortunately, in the studies reporting metabolic rates in sharks, none have derived power-performance curves, and few report the swimming speeds associated with the $\dot{V}O_2$ measurements. Piiper et al. (1977) however, found $\dot{V}O_2$ in the larger spotted dogfish (*Scyliorhinus stellaris*), at 17°C, increased from 0.049 mmol·min⁻¹·kg⁻¹ (70 ml O₂·kg⁻¹·h⁻¹) to 0.086 mmol·min⁻¹·kg⁻¹ (123 ml O₂·kg⁻¹·h⁻¹) when dogfish went from resting to swimming at 0.27 BL·s⁻¹. Swimming for 10 min at moderate speeds by these animals was enough to generate an oxygen debt. The contrast to lemon sharks is marked, as they were seen to swim at 0.4 BL·s⁻¹ for hours with little increase in $\dot{V}O_2$ above their resting rate.

It may be that lemon sharks, with their more active life style, have evolved physiological mechanisms which make them more efficient swimmers when compared to the other species of shark studied to date. One adaptation which will reduce the metabolic cost of swimming is their ability to ram-ventilate. When swimming at their normal cruising speed of about 0.4 BL·s⁻¹, lemon sharks cease actively pumping water over their gills and, instead, rely on their forward motion to generate

the ventilatory water flow. This alone could result in a metabolic savings of 10%–15% (Roberts 1978).

The maximum sustained (1 h) swimming speed recorded in an individual lemon shark was 0.63 ± 0.08 BL·s⁻¹ during which $\dot{V}O_2$ averaged 225.6 ± 16.2 ml O₂·kg⁻¹·h⁻¹. Attempts by Brett and Blackburn (1978) to determine active metabolic rate in the spiny dogfish were not completely successful as the authors failed in getting the sharks to swim in a consistent manner in their respirometer. As a result, they were forced to extrapolate active metabolic rates from oxygen debts in sharks maximally stimulated to exhaustion in 15 min by using electric shock, bright lights and/or ringing bells. The swimming speeds associated with the $\dot{V}O_2$ measurements were not reported. Considering the extreme measures used to induce maximal oxygen consumptions, it is noteworthy that the value they calculated (72.6 ml O₂·kg⁻¹·h⁻¹ at 10°C or 187 ml O₂·kg⁻¹·h⁻¹ at 22°C) was lower than the maximal $\dot{V}O_2$ measured in this study. Scharold et al. (1989) measured active metabolism in the leopard shark swimming at 0.9 BL·s⁻¹ in a tunnel respirometer, and found it to be 124.0 ml O₂·kg⁻¹·h⁻¹ at 16°C (199 ml O₂·kg⁻¹·h⁻¹ at 22°C). Therefore, although the active metabolism of the lemon shark is higher than previous reports in elasmobranchs, when compared to teleosts it is similar to that of the moderately active largemouth bass (*Micropterus salmoides*), whose $\dot{V}O_2$ at 20°C was reported by Beamish (1970) as 325 mg O₂·kg⁻¹·h⁻¹ (244 ml O₂·kg⁻¹·h⁻¹).

Not only are metabolic rates useful in estimating swimming costs, they can also be used, in a bioenergetics context, to estimate the energy requirements or cost of living of a species. By utilizing the $\dot{V}O_2$ measurements from this study, along with an oxycaloric equivalent of 5.0 cal·ml O₂⁻¹ (Brett and Groves 1979), a 1 kg shark is predicted to have an energy expenditure between 11.4 kcal·day⁻¹ (standard) and 14.0 kcal·day⁻¹ (cruising speed-0.4 BL·s⁻¹). Increasing the energy requirement by 27% to account for energy loss of ingested food due to excretion (Brett and Groves 1979), will increase the range to 14.4–17.8 kcal·day⁻¹. The favoured prey item of lemon sharks, the blue runner (*Caranx chrysos*), has been shown to have the caloric equivalent of 1.25 kcal·g⁻¹ wet weight (Cortes 1987). A 1 kg lemon shark must therefore consume between 11.5 and 14.2 g of blue runner per day to meet basic metabolic needs. Adding 25% to cover the energy costs of normal events such as attack and

feeding (Brett and Blackburn 1978), indicates a food consumption rate of 5.3–6.5 times body weight over a year. This derived food consumption estimate agrees well with actual measurements from laboratory studies by Gruber (1984), who found 1 kg captive lemon sharks needed $16.5 \text{ g} \cdot \text{day}^{-1}$ of blue runner to maintain body weight. This represents a prey consumption rate equivalent to 6.0 times body weight over a year.

The cost of living of a lemon shark is substantially higher than that of the temperate water spiny dogfish (*Squalus acanthias*). Brett and Blackburn (1978) estimated a 2 kg spiny dogfish at 10°C must consume only twice its body weight per year to meet routine demand. In contrast, a salmon's requirement is 6–8 times its body weight at 10°C (Brett and Blackburn 1978).

It is apparent from this study that elasmobranchs are capable of metabolic rates higher than previously supposed. As Brett and Blackburn (1978) pointed out, shark species chosen for previous studies were selected for ease of handling and resistance to the stress of surgical manipulation. It is hoped that the current availability of sophisticated aquarium techniques, as well as field telemetry systems, will pave the way for laboratory and field research that will move away from the sluggish species of sharks, and instead, concentrate on the more active elasmobranchs.

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