Metabolism, Energetic Demand, and Endothermy

Article · March 2004

DOI: 10.1201/9780203491317.ch7

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Metabolism, Energetic Demand, and Endothermy

John K. Carlson, Kenneth J. Goldman, and Christopher G. Lowe

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7.1 Introduction

Despite the ecological significance of elasmobranchs as top-level predators in most marine ecosystems (Cortés, 1999), information on their energetics and metabolism is meager. Metabolism is an important component of an organism's daily energy budget and may account for its greatest, yet most variable proportion (Lowe, 2001). It was hypothesized that sharks had lower metabolic rates than comparable teleosts because most of the original work on the metabolic rate of sharks focused on relatively inactive,

cooler-water sharks such as spotted dogfish, *Scyliorhinus canicula* (Piiper and Schumann, 1967; Metcalf and Butler, 1984) and spiny dogfish, *Squalus acanthias* (Brett and Blackburn, 1978). Over time, better techniques have evolved that allow study of more active elasmobranch species that were typically considered difficult to work with in captivity. These advances in technology have expanded our knowledge of ecology, activity level, morphology, cellular physiology, and kinematics of elasmobranchs that exhibit a wide range of lifestyles, indicating that elasmobranchs have metabolic rates comparable to teleost fishes of similar size and lifestyle.

Elasmobranchs vary in their ability to pump water over their gills through buccal pumping. Variation in this ability is directly linked to variability in metabolism and lifestyle. For example, elasmobranchs in Orders Heterodontiformes and Rajiiformes are relatively less active and demersal, and oxygenate their gills via buccal pumping. However, more active pelagic species such as those found in Orders Myliobatiformes and Carcharhiniformes (Families Carcharhinidae and Sphyrnidae) utilize ram ventilation, which allows the organism to ventilate its gills by holding the mouth open while swimming (Brown and Muir, 1970). A shift to this mode occurs when swimming velocity reaches a rate at which flow volume is adequate to supply respiratory needs. Among other species of elasmobranchs particularly lamnid, carcharhinid, and sphyrnid sharks, branchiostegal systems are reduced and thus inadequate to force water over the gills when forward movement has slowed or movement has ceased. These sharks are termed obligate ram ventilators because they must maintain constant forward movement for respiration (Roberts, 1978). Like tunas and mackerels, these sharks possess morphological, behavioral, and physiological adaptations for continuous activity (Parsons, 1990). Active swimming not only furnishes adequate gill ventilation, but also generates lift, needed because these species lack a means of buoyancy regulation (Weihs, 1981). However, the requirement for continuous activity results in an increased metabolic cost. While many carcharhiniform sharks have specializations for continuous swimming, lamniform sharks also swim continuously, and several members of this group possess additional characteristics linked to their evolution of endothermy, which may further increase energetic requirements.

The goal of this chapter is to provide an overview of current knowledge on metabolism and energetic requirements of elasmobranchs. In this chapter, we (1) discuss methods used to estimate metabolic rate in elasmobranchs; (2) compare and contrast energetic requirements for elasmobranchs within and among taxa, and document factors that affect these requirements; and (3) discuss potential techniques to stimulate future research and to further our understanding of elasmobranch energetics.

7.2 Methods of Metabolic Rate Estimation

7.2.1 Respirometry

Because oxygen is needed for maximal aerobic conversion of foodstuffs to energy, measuring oxygen consumption rate (mg O_2 kg^{-1} h^{-1}), also known as indirect calorimetry, has become the standard in determination of aerobic metabolism in postabsorptive (i.e., metabolic rate excluding energy devoted to digestion and assimilation) elasmobranchs. Oxygen consumption (VO_2) is typically measured using an oxygen electrode to quantify reduction in dissolved oxygen in water as the animal respires. The amount of oxygen consumed over time can be used to calculate the metabolic rate. Several types of respirometers have been used to measure VO_2 of elasmobranchs. Closed respirometers are common and are simple to use: they require a single O_2 electrode to measure the decrease in O_2 as water is continuously recirculated in a sealed chamber. Open respirometers are a bit more sophisticated and require the use of two O_2 probes to measure the difference in O_2 concentrations before water enters a fish-holding chamber and after water leaves the chamber. A further review of respirometers and their advantages and disadvantages can be found in Cech (1990). With elasmobranchs, both design and complexity in respirometers have varied depending on the study and the component of metabolism of interest.

7.2.1.1 Annular/Circular Respirometers — Because of their relatively simple construction and low costs, many of the estimates of metabolism for elasmobranchs have been obtained using open (Du Preez et al., 1988; Bushnell et al., 1989; Howe, 1990) or closed annular and circular respirometers

(Parsons, 1990; Sims et al., 1993; Carlson et al., 1999). These types of respirometers permit elasmobranchs to swim freely in a circular pattern or to rest on the bottom, and both types allow for estimation of routine (RMR; the metabolic rate of a postabsorptive fish under volitional activity) or standard (SMR; the metabolic rate of a postabsorptive fish completely at rest) metabolic rate. Although annular respirometers are easy to build and simple to operate, there are trade-offs in making them large enough so elasmobranchs can swim freely, but sufficiently small in volume to provide adequate O_2 measurement resolution. Bosclair and Tang (1993) indicated that there is an associated energetic cost of turning and accelerating with swimming in a circular respirometer. However, Boggs (1984) tested a theoretical model devised by Weihs (1981) to correct for fish swimming in a circular path and concluded that there was no substantial bias in determination of metabolic rate made in circular tanks, at least for skipjack tuna, *Katsuwonus pelamis*. Because tunas and sharks (excluding lamnids) differ in their swimming kinematics, it has not been fully resolved whether Boggs' (1984) study is applicable to sharks.

Some problems can arise in closed, static systems as a result of lack of water mixing. This problem can be overcome if a species studied swims continuously, which causes water mixing (Parsons, 1990; Carlson et al., 1999). Because an elasmobranch is permitted to swim voluntarily, direct continuous observation or motion sensors are required to determine when the fish is active or inactive in order to calculate SMR. Annular respirometers are acceptable for determining SMR or RMR, but they may not be sufficient for quantifying costs of swimming because, in most cases, the elasmobranch will not maintain a steady swimming speed over a long enough period of time.

7.2.1.2 Swim Tunnel Respirometers — A number of studies have used closed swim tunnel respirometers (Figure 7.1) to obtain more accurate measures of metabolic rate. Swim tunnels are analogous to treadmills, wherein water is moved through the holding chamber, and the fish or elasmobranch swims in place against the on-flowing current (Brett, 1964). Because swimming velocity is controlled over a range of water speeds, oxygen consumption rates can be more precisely measured for a given level of activity and are typically used to measure active metabolic rate (total cost of standard metabolic rate and activity). In the late 1980s, Graham and colleagues at Scripps Oceanographic Institution in San Diego, CA developed a large "Brett-type" seagoing swim tunnel respirometer that could accommodate larger sharks (Graham et al., 1990). As part of their work, metabolic rates and swimming performance studies have been determined for leopard, *Triakis semifasciata* (Scharold et al., 1989), lemon, *Negaprion brevirostris*, and shortfin mako sharks, *Isurus oxyrinchus* (Graham et al., 1990).

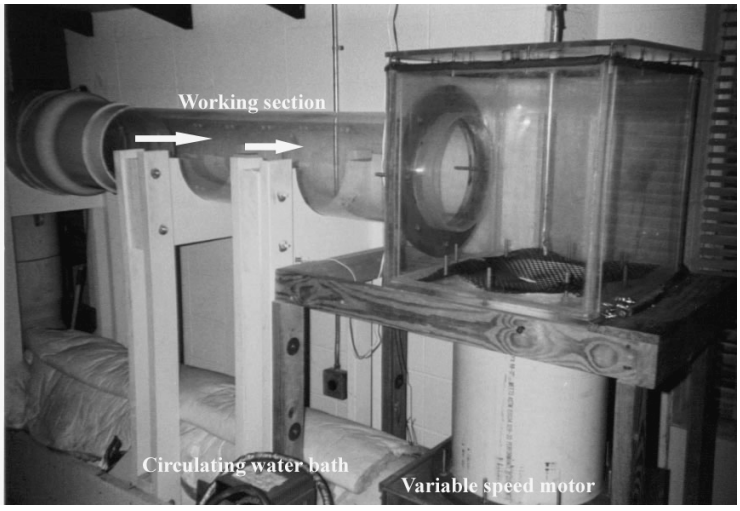

FIGURE 7.1 A "Brett"-type recirculating swim tunnel respirometer. The working section of the water tunnel houses the shark during experimentation and arrows indicate flow direction. Flow filters (not seen) within the tunnel promote rectilinear flow. A heating/cooling circulating water bath pumps heated or cooled water to regulate swim tunnel temperature. The water tunnel is currently housed at the Department of Biology, University of Mississippi, Oxford.

Recently, a smaller version of the "Brett-type" swim tunnel was constructed and used for estimation of swimming performance, kinematics, and metabolism of juvenile scalloped hammerhead sharks, *Sphyrna lewini* (Lowe, 1996, 2001).

Although swim tunnel respirometers may be better for some species (e.g., ram ventilators), their use requires the ability to induce the fish to swim, and the associated stress of being confined can result in increased metabolic expenditures. Brett and Blackburn (1978) attempted to measure swimming performance and metabolism of spiny dogfish in a swim tunnel originally developed for work on sockeye salmon, *Oncorhynchus nerka*. However, spiny dogfish placed in the swim tunnel would not swim continuously, so the authors estimated metabolism using a closed annular respirometer where the shark was permitted to swim freely. Lowe (1996) demonstrated that scalloped hammerhead sharks swimming at similar velocities in a pond beat their tails up to 21% slower than those in a swimming tunnel, which suggests sharks expend more energy while swimming in the tunnel (Lowe, 1996). However, Lowe (2001) developed an adjusted oxygen consumption rate for sharks swimming in a respirometer using a power–performance relationship of tailbeat frequency and relative swimming speed.

The use of respirometry to determine metabolic rates in elasmobranchs has not been without complications. As with any fish, confinement in a respirometer may stress the animal and affect estimates of metabolism. It is difficult to design respirometers that can accommodate the entire size range of a species or allow the animal to move about as it would in the wild because of their size and the associated scaling effect of mass on metabolic rate (Schmidt-Nielsen, 1984). The process of capturing, holding, and transporting sharks to the laboratory for experimentation can also prove to be difficult. Nevertheless, respirometry techniques offer the best means of quantifying metabolic expenditure of ectothermic fishes.

7.2.2 Biotelemetry

Much of what is known about the physiological ecology of many elasmobranchs has come from laboratory studies, because of logistical difficulties in studying marine fishes in their natural environment (e.g., Bushnell et al., 1989; Scharold et al., 1989; Carlson, 1998; Lowe, 1998). Controlled laboratory studies have shown how some elasmobranchs respond to changes in their environment, although there can be problems in extrapolating results from laboratory studies to free-swimming animals in the field or to other unstudied species (Lowe et al., 1998; Lowe and Goldman, 2001). Conversely, large size and high mobility of many elasmobranchs make controlled laboratory studies extremely difficult, and these animals can only be studied in the field. Thus, comparative laboratory and field studies are essential.

The ongoing evolution of acoustic telemetry techniques continues to enhance our ability to gather physiological data from captive and free-swimming elasmobranchs (see Lowe and Goldman, 2001, for a thorough review). A variety of sensors have been used to telemeter data on physiological parameters that are linked to metabolic rate, such as muscle temperature (Carey et al., 1982), heart rate (Scharold et al., 1989; Scharold and Gruber, 1991), swimming speed (Sundström and Gruber, 1998; Parsons and Carlson, 1998), and tailbeat frequency (Lowe et al., 1998; Lowe, 2002). As discussed below, several of these studies have used biotelemetry in combination with respirometry to gauge whether a particular physiological parameter could serve as an accurate estimator (or indicator) of metabolic rate for elasmobranchs in the field.

7.2.2.1 Muscle Temperature Telemetry — Telemetering fish muscle temperature involves placing a rigid thermistor deep into the internal epaxial red muscle then measuring changes in muscle temperature as the transmitter pulse rate changes (Carey and Lawson, 1973; Carey and Robison, 1981). Carey and colleagues (1982) designed a multitransmitter package consisting of an epaxial muscle thermistor, an ambient water thermistor, and depth-sensing transmitters that could be harpooned into the dorsal musculature of a shark. Each transmitter operated at a different frequency so data could be telemetered simultaneously, thus allowing for direct water and body temperature comparisons as the shark swam at different depths.

Carey et al. (1982) found that a large white shark, *Carcharodon carcharias*, tracked in the northwest Atlantic exhibited a 3 to 5°C elevation in muscle temperature over ambient water temperature. This

TABLE 7.1

Summary of Standard Metabolic Rates (VO_2) for a Variety of Elasmobranch Species

Species	Temp. (°C)	Mass (kg)	N	Methods	Metabolic rate (mg O_2 kg^{-1} h^{-1})	Ref.
Isurus oxyrinchus	16–20	3.9	1	Swimming closed	240*	Graham et al. (1990)
Carcharhinus acronotus	28	0.5–0.8	10	Circular closed	239*	Carlson et al. (1999)
Sphyrna lewini	21–28	0.5–0.9	17	Swimming closed	189*	Lowe (2001)
Sphyrna lewini	22–29	0.6–1.2	5	Biotelemetry	170	Lowe (2002)
Sphyrna tiburo	28	1.0	8	Open flow-through	168	Carlson and Parsons (2003)
Sphyrna tiburo	25	0.8–1.4	12	Circular closed	156*	Carlson (1998)
Negaprion brevirostris	25	1.6	7	Annular closed	153*	Scharold and Gruber (1991)
Ginglymostoma cirratum	23	1.3–4.0	5	Flow-through	106	Fournier (1996)
Negaprion brevirostris	22	0.8–1.3	13	Annular closed	95	Bushnell et al. (1989)
Scyliorhinus stellaris	25	2.5	12	Circular flow-through	92	Piiper et al. (1977)
Triakis semifasciata	14–18	2.2–5.8	5	Swimming closed	91.7*	Scharold et al. (1989)
Carcharodon carcharias	15	~943	1	Biotelemetry	60	Carey et al. (1982)
Cetorhinus maximus	—	~1000	—	Modeling	62–91	Sims (2000)
Scyliorhinus canicula	15	1.0	33	Circular closed	38.2	Sims (1996)
Squalus acanthias	10	2.0	6	Circular closed	32.4	Brett and Blackburn (1978)
Squalus suckleyi	10	2.2–4.3	9	Flow-through	31.0	Hanson and Johansen (1970)
Dasyatis americana	20	0.3	6	Flow-through	164	Fournier (1996)
Rhinobatus annulatus	15	1.0	10	Circular flow-through	61	Du Preez et al (1988)
Myliobatus californica	14	5.0	6	Circular flow-through	50	Hopkins and Cech (1994)
Myliobatus aquila	10	1.1–2.1	5	Flow-through	44.4	Du Preez et al (1988)
Dasayatis violacea	20	10.7	9	Circular flow-through	39.1	Ezcurra (2001)
Raja erinacea	10	0.5	6	Circular flow-through	20	Hove and Moss (1997)

Note: Standard metabolic rates estimated through extrapolation to zero velocity are indicated by an asterisk. Methods indicates the type of respirometer used to measure metabolic rate except *Carcharodon carcharias* and *Sphyrna lewini* (Lowe, 2002) VO_2 estimates obtained from biotelemetry field experiments and *Cetorhinus maximus* VO_2 estimate obtained from models.

shark showed a distinct preference for swimming in the thermocline, which is not uncommon behavior for endothermic fishes (Carey et al., 1971, 1981; Carey and Robison, 1981; Holland et al., 1990; Holts and Bedford, 1993; Block et al., 1998; Brill et al., 1999). Because of what Carey et al. (1982) termed, "the shark's fortuitous movements from cold to warm water," they were able to estimate its rate of metabolism from the rate of change in its muscle temperature. Their estimated metabolic rate for an approximately 943-kg white shark was 60 mg O_2 kg^{-1} h^{-1} (Table 7.1). Carey et al. (1982) lacked no savvy when putting their calculation into appropriate terms stating, "Our metabolic rate for the white shark is about three times higher than that estimated for a one ton spiny dogfish at 20°C after the latter had been adjusted for temperature and scaled for size." While they indicated their procedure overestimated the shark's metabolic rate, Carey et al. (1982) did not "pretend to great accuracy" in their calculation but thought it better than extrapolating from smaller specimens of other species, which is almost certainly true. Although this method of determining metabolism is applicable only to endothermic fishes (Carey et al., 1982), it still may not yield results. For example, Tricas and McCosker (1984) tracked a white shark off South Australia that also exhibited a similar 3 to 5°C elevation in muscle temperature over ambient temperature. However, in this study no thermocline was present and water temperature did not vary over the time of the track; hence metabolic rate could not be examined.

7.2.2.2 Heart Rate Telemetry — The first applications of heart rate telemetry for estimating metabolic rates of elasmobranchs were tested on leopard and lemon sharks (Scharold et al., 1989; Scharold and Gruber, 1991). In these studies, sharks instrumented with electrocardiogram (EKG) acoustic transmitters were observed in respirometers to determine relationships between heart rate and VO_2. Scharold et al. (1989) exercised instrumented leopard sharks in a swim tunnel respirometer over a range of aerobic swimming speeds, and the authors found that heart rate increased at a significantly linear rate

with increased swimming speed; however, heart rate varied considerably with increases in VO_2 (r^2 = 0.38). As a result, heart rate was found to account for only 32% of the rise in VO_2. Similar results were obtained from juvenile lemon sharks observed swimming voluntarily in an annular respirometer (Scharold and Gruber, 1991). Heart rates of lemon sharks increased at a significant linear rate with increases in swimming speed, but also varied considerably with increases in VO_2 (r^2 = 0.35). Heart rate only accounted for an 18% rise in VO_2 for the lemon shark.

Both Scharold et al. (1989) and Scharold and Gruber (1991) concluded that heart rate makes a relatively small percentage contribution to changes in VO_2 and that cardiac output is likely facilitated by increases in stroke volume and/or arteriovenous oxygen differences with increased activity. As a result, heart rate was not considered to be an adequate indicator of metabolic rate for these two species, and no field experiments were conducted. These findings were supported by those of Lai et al. (1989), who measured changes in heart rate and stroke volume of resting and swimming leopard sharks in a swim tunnel and found that these sharks modulated stroke volume more than heart rates. Based on similarities in heart structure, it has been suggested that other ectothermic elasmobranch species may also exhibit this cardiac response (Emery, 1985; Farrell, 1991; Tota and Gattusa, 1996). However, this may not be true for endothermic elasmobranchs. Recent studies of cardiac physiology in shortfin mako shark indicate that their hearts resemble those of birds and mammals and these sharks may modulate heart rate more than stroke volume (Lai et al., 1997). Heart rate alone thus may provide an adequate field indicator of metabolic rate for some taxa.

7.2.2.3 Swimming Speed Telemetry — A number of studies have used speed-sensing transmitters to measure swimming speeds and energy consumption of elasmobranchs in the field (Gruber et al., 1988; Carey and Scharold, 1990; Parsons and Carlson, 1998; Sundström and Gruber, 1998). In the early 1980s Gruber and colleagues were able to systematically quantify all components of the energy budget of lemon sharks in the laboratory, albeit focusing on smaller individuals (Gruber, 1984). As part of this effort, Bushnell et al. (1989) determined the relationship between swimming speed and oxygen consumption rate for juvenile lemon sharks in an annular respirometer. Gruber et al. (1988) attached speed-sensing acoustic transmitters to two mature lemon sharks (178 and 210 cm TL, or total length) and made direct measurements of swimming speeds. Later, Sundström and Gruber (1998) tracked three immature lemon sharks (154 to 188 cm TL) using similar speed-sensing transmitters. Using VO_2-swimming speed data from Bushnell et al. (1989), they were able to estimate the metabolic rates of the tracked lemon sharks based on measured swimming speeds. These data allowed Sundström and Gruber (1998) to construct the first field-derived energy budget for an elasmobranch and to bridge a key research gap between laboratory-based data and field measurements of free-swimming sharks.

Although these studies on lemon sharks have developed the most detailed description of a shark energy budget to date, these data are only from larger sharks tracked in the field. Smaller sharks can be studied in respirometers but cannot be tracked using the speed-sensing transmitters because of the current large size of the transmitter package. Conversely, large sharks can be tracked in the field but not studied in respirometers due to restrictions on respirometer size (Graham et al., 1990). Extrapolating metabolic rate data from juvenile sharks to adult sharks remains problematic, requiring mass-specific corrections to account for differences in size between sharks studied in the laboratory and those tracked in the field.

Parsons and Carlson (1998) used speed-sensing (propeller style) acoustic transmitters to quantify swimming speeds of bonnethead sharks, *Sphyrna tiburo*, under normoxic and hypoxic conditions in an artificial lagoon. The authors also compared VO_2 of sharks at different swimming speeds and under different oxygen concentrations in a circular respirometer. Bonnethead sharks swam significantly faster and increased their mouth gape in hypoxic conditions compared with normoxic conditions. As a result, sharks experienced higher VO_2 in hypoxic conditions, which the authors attributed to the increased swimming speeds. Parsons and Carlson (1998) concluded that speed-sensing transmitters provided a more accurate measure of activity than measuring the distance it took for a shark to swim between two points. These authors also noted that differences in swimming speeds between sharks *in situ* and those measured in the respirometer may be attributable to the added stress of handling and confinement. Speed-sensing transmitters undoubtedly increase the accuracy of measuring swimming speeds of elasmobranchs in the field (Parsons and Carlson, 1998; Sundström and Gruber, 1998). Much like using heart rate, use

of swimming speed to quantify metabolism of free-swimming elasmobranchs in the field requires laboratory calibration and thereby limits the use of this technique.

7.2.2.4 Tailbeat Frequency Telemetry — Tailbeat frequency (TBF) has also been used as a correlate of energy consumption. Laboratory studies have shown that most fishes increase TBF in proportion to increases in swimming speed, while some species modulate their tailbeat amplitude or propulsive wavelength in addition to TBF to increase forward thrust (e.g., Bainbridge, 1958; Hunter and Zweifel, 1971; Dewar and Graham, 1994; Lowe, 1996). TBF, therefore, provides a reliable indicator of activity and exertion, although detailed laboratory calibrations are required to determine these relationships as well as energy expenditures of fishes in the field (Stasko and Horrall, 1976; Briggs and Post, 1997; Lowe et al., 1998).

A variety of sensors have been developed to measure TBF in fishes. The most common method uses electromyogram electrodes placed in the epaxial swimming muscle to monitor rhythmic body flexing. However, another type of tailbeat sensor developed uses a simple magnetized pivoting vane, which passes over a reed switch on the caudal peduncle with every lateral sweep of the tail (Lowe et al., 1998).

The first study to use acoustic tailbeat telemetry to quantify energy expenditure of an elasmobranch was conducted by Lowe (2002). Five scalloped hammerhead shark pups instrumented with tailbeat transmitters were tracked for periods up to 50 h continuously, while TBF was recorded from every successive tailbeat and averaged over 15-min periods. These data and previously determined laboratory relationships of VO_2 were used to determine swimming speeds and VO_2 rates over the course of the track. Tracks indicated that these sharks have higher metabolic requirements than those estimated for other species of tropical elasmobranchs and that they swim relatively faster than other species studied. Because of the direct coupling of laboratory and field experiments on the same size sharks, Lowe (1998) likely represents the most accurate estimates of field-based energy consumption for an elasmobranch to date.

Several physiological correlates (e.g., heart rate) do not initially appear to be good indicators for accessing actual metabolic rate; however, their relationships to metabolic rate require further investigation, and while these correlates may or may not provide good indicators of metabolism, they may provide good physiological correlates to other environmental stressors. Additionally, these types of studies have permitted investigation of increased drag and O_2 consumption on animals carrying transmitter packages (Scharold and Gruber, 1991; Lowe, 1998, 2002). Such studies will greatly assist researchers in examining energetic effects of external transmitters on elasmobranch fishes, and estimates of metabolic rates for animals carrying transmitters in the field.

Although each of the bioenergetics studies to date has provided valuable information on physiological correlates of elasmobranch metabolism, it is still very difficult to compare metabolic rates among species because of differences in experimental technique, size of animals used, and water temperature. Although the use of telemetry has certain logistic difficulties and limitations, bioenergetics of near-shore elasmobranchs could be determined by using these methods in direct comparisons between laboratory and field. Use of the latest technologies, such as acoustic transponders, underwater listening stations, and satellite telemetry, along with improvements in captive animal husbandry, will eventually allow study of bioenergetics in more active and pelagic species.

7.3 Estimates and Comparisons of Metabolic Rate

7.3.1 Standard Metabolic Rate

SMR is the metabolic rate of a postabsorptive fish completely at rest (Fry, 1957). SMR can be measured directly for animals that rest or estimated indirectly for species that are obligate ram ventilators. Because obligate ram ventilators such as lamnid and sphyrnid sharks swim continuously, standard metabolism has been estimated by extrapolation to zero velocity based on the oxygen consumption–swimming speed relationship. However, estimating standard VO_2 by extrapolating to zero activity is potentially problematic. This method may bias estimates due to extrapolating beyond the measured swimming speed range and could be overestimated if the swimming speed and VO_2 functions were elevated or the regression

slope was reduced as a result of inefficient swimming at low swimming speeds (Brett, 1964). The use of paralyzed fish has proved to be useful to validate extrapolated standard metabolic rates. Standard metabolic rates determined by extrapolation for yellowfin, *Thunnus albacares,* and skipjack tunas by Dewar and Graham (1994) were similar to that reported by Brill (1987) for paralyzed tunas. Carlson and Parsons (2003) measured a standard VO_2 of 168 mg O_2 kg^{-1} h^{-1} for paralyzed bonnethead sharks, which was close to extrapolation values of 156 mg O_2 kg^{-1} h^{-1}. The few SMRs available for sharks show a wide variation, ranging from 31.0 mg O_2 kg^{-1} h^{-1} for 2.2 to 4.3 kg Pacific dogfish sharks, *Scyliorhinus suckleyi,* at 10˚C to 240 mg O_2 kg^{-1} h^{-1} for a 3.9 kg shortfin mako shark at 16 to 20˚C (Table 7.1).

Ectothermic tropical and subtropical sharks appear to have standard metabolic rates similar to active ectothermic teleosts of comparable lifestyles. Metabolic rates for sharks 0.5 to 1.5 kg in body mass at temperatures from 22 to 28°C range from 95 mg O_2 kg^{-1} h^{-1} for lemon sharks (Bushnell et al., 1989) to 189 mg O_2 kg^{-1} h^{-1} for scalloped hammerhead sharks at 26°C (Lowe, 2001). In general, species that are obligate ram ventilators and swim continuously have the highest measure of metabolism. Lower estimates of VO_2 are generally found for cooler-water (10 to 20°C), less-active species such as leopard shark (91.7 mg O_2 kg^{-1} h^{-1}; Scharold et al., 1989), spotted dogfish (38.2 mg O_2 kg^{-1} h^{-1}; Sims, 1996), and spiny dogfish (32.4 mg O_2 kg^{-1} h^{-1}; Brett and Blackburn, 1978). The highest SMR determined for an ectothermic obligate ram-ventilating shark was for 0.5 kg blacknose sharks, *Carcharhinus acronotus*, at 28°C (239 mg O_2 kg^{-1} h^{-1}; Carlson et al., 1999), although this measure may be slightly higher than expected due to few data points at slow swimming speeds. Comparably sized moderately active teleosts have SMR ranging from 125 mg O_2 kg^{-1} h^{-1} for 0.9 kg largemouth bass (*Micropterus salmoides*; Beamish, 1970) to 158 mg O_2 kg^{-1} h^{-1} for 1.6 kg smallmouth buffalofish (*Ictiobus bubalus*; Adams and Parsons, 1998) at 25 to 27°C. The high SMR found for more-active fishes was hypothesized to reflect increased gill surface areas and associated osmoregulatory costs (Brill, 1996). However, recent measures of Na^+-K^+-ATPase activity in the gills of skipjack and yellowfin tuna (species that possess some of the highest estimates of SMR; Brill, 1996), estimated the costs of osmoregulation to be at most 9 to 13% of standard metabolic rate (Brill et al., 2001). Thus, the reasons for elevated SMR in tunas remain unexplained. Because osmoregulatory costs of more-active elasmobranchs have not been estimated, it cannot be determined if the higher SMR found for more-active sharks is due to osmoregulation or other metabolic processes.

Standard metabolic rates of skates and rays are similar to those determined for similar-sized, cooler-water, less-active sharks. At temperatures from 10 to 15°C, metabolic rates ranged from 20 to 61 mg O_2 kg^{-1} h^{-1} (Table 7.1). Although metabolic rates are in general low, bat rays, *Myliobatus californica*, have a high temperature sensitivity (Q_{10} or the increase in a rate caused by a 10°C increase in temperature; Schmidt-Nielsen, 1983), which is reflected in their VO_2 (see Section 7.6.1). Standard metabolic rate in bat rays increased from about 50 to 170 mg O_2 kg^{-1} h^{-1} over a temperature range of 14 to 20°C (Hopkins and Cech, 1994). Thus, bat rays exposed to thermally heterogeneous environments have marked changes in energetic requirements. To accommodate this, it is thought that bat rays behaviorally thermoregulate by moving to cooler water to reduce energetic demands and moving to warmer water to exploit increases in metabolism for feeding (Matern et al., 2000).

Standard metabolic rates have been measured for embryonic sharks and skates. Diez and Davenport (1987) measured the VO_2 of unencapsulated 3.0 g embryonic spotted dogfish, *Scyliorhinus canicula*, which consumed 0.087 ml O_2 g^{-1} h^{-1}. These rates were slightly higher than those measured from encapsulated 5 to 7 g little skates, *Raja erinacea*, which exhibited average SMR of 0.032 ml O_2 g^{-1} h^{-1} (Leonard et al., 1999).

7.3.2 Maximum Metabolic Rate

Sharks that are more active have higher maximum metabolic rates (MMR) when contrasted to sharks that are more sedentary. Even when standardizing for temperature effects (Q_{10} = 2.0), MMR were about 1.5 to 2.3 times greater for active species. At 25°C, a 2.0 kg spiny dogfish consumed a maximum of 250 mg O_2 kg^{-1} h^{-1} (Brett and Blackburn, 1978) compared to 620 mg O_2 kg^{-1} h^{-1} for a 1.6 kg lemon shark (Graham et al., 1990). Scalloped hammerhead sharks swimming at 1.0 body length per second (bl s^{-1}) consumed up to 500 mg O_2 kg^{-1} h^{-1} at 26°C (Lowe, 2001), while Scharold et al. (1989) measured metabolic rates to 384 mg O_2 kg^{-1} h^{-1} for less-active leopard sharks swimming at 0.9 bl s^{-1}.

7.3.3 Specific Dynamic Action

Specific dynamic action (SDA) refers to the energetic costs associated with digestion and assimilation (Jobling, 1981). Among teleosts, specific dynamic action can account for 15 to 20% of ingested energy and is generally measured by the increase in metabolic rate following feeding (Brett and Groves, 1979).

Although few estimates have been made in elasmobranchs, results suggest that costs of digestion are similar to those found for teleosts. Du Preez et al. (1988) reported energy losses with feeding of 17.3% for guitarfish, *Rhinobatus annulatus*, and 12.9% for bullray, *Myliobatus aquila*, although variables such as prefeeding levels, period of starvation, and activity levels were not controlled or similar between species. Based on controlled feeding studies of lesser spotted dogfish, specific dynamic action was estimated at 6.0 to 12.5% for juvenile and adult dogfish, respectively (Sims and Davies, 1994). The results suggest that juvenile sharks have reduced energy costs in terms of digestion and assimilation despite higher levels of food consumption. Sims and Davies (1994) hypothesized this relationship was due more to efficient conservation of metabolic energy (which could then be used for growth) rather than a reduced rate of biosynthesis.

7.3.4 Anaerobic Metabolism

Anaerobic metabolism is powered by white muscle, which comprises the majority of muscle in ectothermic elasmobranchs. White muscle is the primary muscle used during burst swimming, and some sharks appear to have high burst swimming capacities. Telemetry data on blue sharks, *Prionace glauca*, indicate that they are capable of short duration bursts up to 2 m s^{-1} (Carey and Scharold, 1990). There are descriptions of blacktip, *Carcharhinus limbatus*, and spinner sharks, *C. brevipinna*, leaping and spinning on their body axes above the water surface, which requires considerable exertion to propel themselves out of the water (Castro, 1996; Carlson, pers. obs.).

In general, elasmobranchs and teleosts with similar activity levels have comparable levels of anaerobic metabolism. By using biochemical indices, low levels of citrate synthase (an index of aerobic capacity) and lactate dehydrogenase (an index of anaerobic capacity) in white mytomal muscle were reported for benthic skates and rays, similar to those of demersal teleosts (Dickson et al., 1993). Intermediate levels of citrate synthase and lactate dehydrogenase were similar among moderately active teleosts and elasmobranchs. The greatest capacity for anaerobic metabolism was observed for shortfin mako shark, which, along with tunas, have significantly greater white muscle citrate synthase and lactate dehydrogenase levels and buffering capacities than ectothermic fishes (Dickson et al., 1993). Shortfin mako sharks also have higher white muscle activities of creatine phosphokinase (an index of ATP production rate during burst swimming) than active ectothermic sharks and teleosts, which allows for redox balance to be retained during anaerobiosis (Dickson, 1996; Bernal et al., 2001a).

7.4 Energetic Costs of Swimming

7.4.1 Swimming Efficiency

The relationship between relative swimming speed (bl s^{-1}) and metabolic rate (log transformed mg O_2 kg^{-1} h^{-1}) is similar among comparable size ectothermic sharks (Figure 7.2). The slope of the relationships ranges from 0.27 for blacknose shark (Carlson et al., 1999) to 0.36 for lemon shark (Bushnell et al., 1989). These relationships indicate that the energy required to move a given amount of mass per measure of distance is the same. Although kinematic variables such as TBF and amplitude, and propulsive wavelength may vary among sharks and over swimming speeds, the similarity in rate of change in metabolic rate with swimming speed may be attributable to morphological adaptations for drag reduction that all of these species share. For example, leopard, lemon, and juvenile scalloped hammerhead sharks have similar TBF at a given speed; however, yellowfin tuna have significantly lower TBF at a given speed (Figure 7.3A). In general, TBF increases at about the same rate for each species. While it may appear the tuna is more efficient due to lower TBF at speed, these sharks have a lower cost per tailbeat (Figure 7.3B). This higher cost of propulsion for the tuna is likely attributable to higher SMR. Lemon,

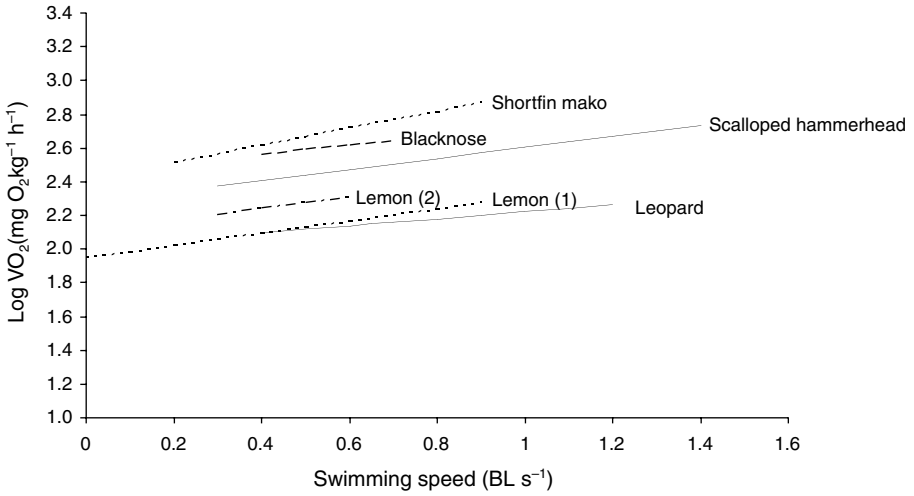

FIGURE 7.2 The relationship of swimming speed and log-transformed metabolic rate of shortfin mako shark (Graham et al., 1990), blacknose shark (Carlson et al., 1999), scalloped hammerhead shark (Lowe, 2001), lemon shark, and leopard shark (Scharold et al., 1989). Relationships are shown over speeds at which data were collected. Lemon (1) refers to data collected by Bushnell et al. (1989) and Lemon (2) for data collected by Scharold and Gruber (1991). Estimates for scalloped hammerhead, blacknose, and lemon shark (2) were collected at 25 to 28°C while shortfin mako, leopard, and lemon (1) were collected between 16 and 22°C.

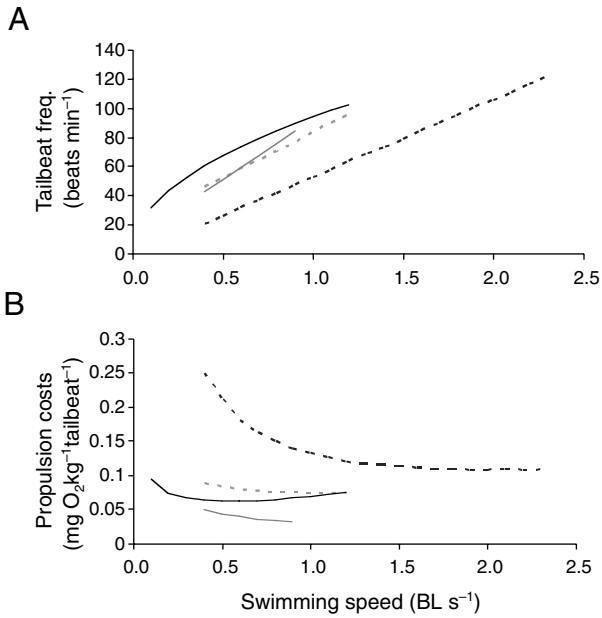

FIGURE 7.3 (A) Relationship between TBF (beats min^{-1}) over a range of swimming speeds (l s^{-1}) for scalloped hammerhead sharks (dashed gray line) (0.5 kg at 26°C; Lowe, 1996), lemon sharks (solid black line) (1.2 kg at 22°C; Graham et al., 1990), leopard sharks (solid gray line) (2 to 5 kg at 16°C; Scharold et al., 1989), and yellowfin tuna (dashed black line) (2 kg at 24°C; Dewar and Graham, 1994). (B) Relationship between propulsion cost (mg O_2 kg^{-1} tailbeat^{-1}) over a range of swimming speeds (l s^{-1}) for the same species.

blacknose, and scalloped hammerhead sharks are characterized by a high aspect ratio caudal fin, high values of dorsal thrust angle, and a moderate heterocercal angle in the tail. The body is fusiform and moderately deep with very large pectoral fins. Sharks with these characters are considered a Group 2 body form (Thompson and Simanek, 1977). Although most swimming speed and metabolic rate relationships have been determined for this body form of shark, it is likely that sharks with less fusiform body, low tail, and dorsal fin insertion more posterior (Groups 3 and 4; Thompson and Simanek, 1977) will have higher energetic costs with increasing swimming speed.

Interestingly, the relationship of relative swimming speed to metabolic rate for shortfin mako shark demonstrates a greater rate of increase of metabolic rate with swimming speed (Graham et al., 1990), suggesting less efficient swimming. This contrasts to the hypothesis that shortfin mako shark energetic capacities and swimming performance approach those of tuna. However, this relationship is based on one individual over limited speeds. Based on other physiological and morphological evidence (Bernal et al., 2001a; Section 7.5), it is likely that shortfin mako sharks (and lamnid sharks overall) possess swimming efficiencies close to tunas.

7.4.2 Critical Swimming Speed and Sustainable Swimming

Critical swimming speed, an index of aerobically sustainable swimming capacity, has been determined only for leopard, lemon (Graham et al., 1990), and scalloped hammerhead sharks (Lowe, 1996). Critical swimming speeds were found to be comparable (~0.9 to 1.7 bl s^{-1}) for sharks of similar lengths (50 to 70 cm total length). The similarity in critical swimming speed among these three species is surprising given leopard sharks have a body design more adapted for a sedentary, demersal life, whereas lemon and scalloped hammerhead sharks have body designs adapted for cruising (Thompson and Simanek, 1977). For scalloped hammerhead sharks, one possible explanation for low critical swimming speeds is the effects of the swimming tunnel (see Section 7.2.1.2) on estimates of critical swimming speed (Lowe, 1996). However, Dickson et al. (1993) found no significant differences in red muscle citrate synthase levels between blue and leopard shark, suggesting similar aerobic capacities despite differences in body design and ecology.

Although ectothermic elasmobranchs lack large quantities of red muscle for sustained swimming, evidence suggests that white muscle contributes to intermediate-speed sustained swimming. Moreover, the division of labor among red and white muscle may be more interchangeable for elasmobranchs. A study on endurance training in leopard sharks found increases in citrate synthase, lactate dehydrogenase, and muscle fiber diameter, suggesting that white muscle can be used for sustained swimming (Gruber and Dickson, 1997).

7.4.3 Cost of Transport

The overall impact of swimming and energy costs (maintenance, SDA, and locomotion) is expressed as the total cost of transport (cal g^{-1} km^{-1}; Schmidt-Nielsen, 1972). Total cost of transport examines use of all energy available. Within a species, larger sharks have a lower cost of transport than smaller sharks (Figure 7.4). For example, Parsons (1990) determined the total cost of transport for a 0.9 kg bonnethead was 1.21 cal g^{-1} km^{-1}, whereas an 8.0 kg bonnethead would expend only 0.4 cal g^{-1} km^{-1}, when swimming at their theoretical optimal velocities (Weihs, 1977). Total cost of transport generally decreases with mass by an exponent of about 0.3 (Schmidt-Nielsen, 1984). It is worth noting that, despite differences in body shape and swimming mode, the total energetic cost of transport appears to be similar across a variety of teleost species (Schmidt-Nielsen, 1984). This relationship indicates that it is more efficient for a large shark to transport 1 kg of body mass over a given distance than it is for a small shark. Among endotherms, this is likely because the mass-specific metabolic rate of a large animal is lower than that of a smaller animal due to lower surface-to-volume ratios for larger animals (Schmidt-Neilsen, 1984). The relationship in sharks and bony fishes could be because larger sharks have higher optimal swimming speeds, presumably attainable due to their increased stride length (Videler and Nolet, 1990).

Total cost of transport demonstrates a U-shaped relationship when plotted against swimming speed. Total costs of transport are initially high, because swimming speed (U) is too slow to overcome inertial

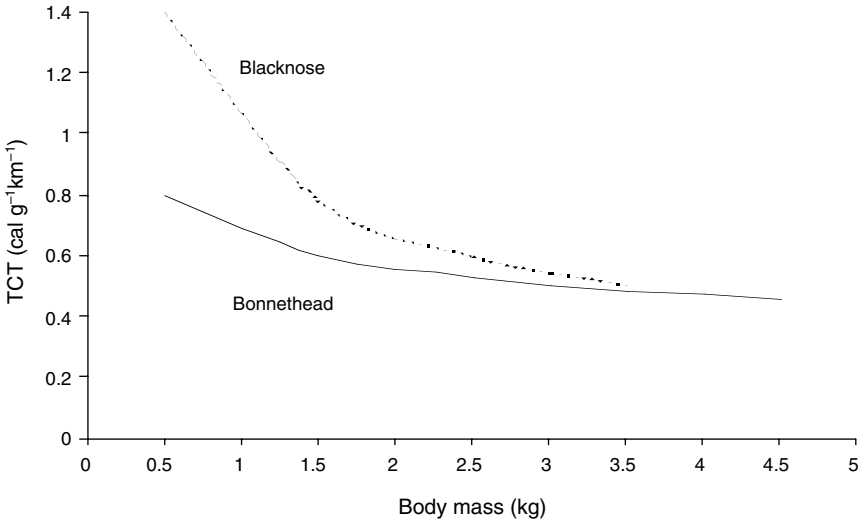

FIGURE 7.4 The effect of total cost of transport and body mass for bonnethead and blacknose shark. (Data are from Parsons, 1990, and Carlson et al., 1999.)

drag. As U increases, a fish overcomes inertial drag and minimizes friction drag. However, as U exceeds this threshold, friction drag will substantially increase (at the rate of $U^{2.5–2.8}$) and result in an increased swimming cost (Videler and Nolet, 1990). This trend has been shown for a variety of species including blacknose shark (Carlson et al., 1999), sockeye salmon (Brett, 1963), white crappie, *Pomoxis annularis* (Parsons and Sylvester, 1992), and yellowfin tuna (Dewar and Graham, 1994). At similar swimming speeds, total cost of transport is generally higher for more active sharks, likely due to the influence of higher standard metabolic rates.

When comparing only costs of swimming, the net cost of transport (the difference between standard and active metabolic rates) is the preferred variable. Some sharks have been shown to demonstrate higher energetic costs at slower swimming speeds. Lowe (2001) proposed the higher net cost of transport for hammerhead sharks at slower speeds could be due to increased drag created by the wing-shaped head of the hammerhead shark, which forces the sharks to swim at suboptimal velocities; whereas at intermediate speeds the shape of the head could increase hydrostatic lift, thereby decreasing energetic costs. Gruber and Dickson (1997) found higher energetic costs when forcing leopard sharks to swim at slower speeds but could not discern whether these costs were due to the respirometer (see Section 7.2.1.2) or to inefficient swimming at slower speeds. Lowe (2002) found that laboratory measures of optimal swimming speed (speed at the lowest net cost of transport; 0.75 bl s^{-1}) were similar to typical swimming speeds of free-ranging sharks (0.81 bl s^{-1}) in their natural environment. At optimal swimming speed, juvenile sharks swimming at 0.8 bl s^{-1} would only be operating at 25% of their metabolic scope. This scope was very similar to that estimated for lemon sharks even though they exhibited an optimal swimming speed of 0.4 bl s^{-1} (Bushnell et al., 1989).

7.5 Endothermy

7.5.1 Background

The steady-state body temperature of most fishes is similar to ambient water temperature as a result of the linkage between aerobic heat production and heat loss via the gills and body surface (Brill et al., 1994). However, lamnid sharks have the capacity to conserve metabolic heat via vascular countercurrent heat exchangers (*retia mirabilia*), thereby maintaining a steady-state body temperature that is elevated

over ambient water temperature (Carey et al., 1981, 1985; Goldman, 1997; Bernal et al., 2001a; Goldman et al., in press). *Retia* in lamnid sharks are located in the cranium near the eyes (orbital *retia*), in locomotor musculature (lateral cutaneous *retia*), and the viscera (suprahepatic *rete*). *Lamna* spp. possess an additional visceral *rete* (kidney *rete*). Lamnids have developed a distinct anterior and medial red muscle position, in conjunction with evolution of *retia* and elevated body temperatures, with the red muscle internalized and lying close to the spine instead of near the body wall as in ectothermic fishes (Carey et al., 1985; Bernal et al., 2001a).

The average body core temperature of lamnid sharks ranges between 22 and 26.6°C, depending on species (Lowe and Goldman, 2001). The maximum reported elevation of body temperature over ambient water temperature is 8.0°C for shortfin mako sharks (Carey et al., 1981), 14.3°C for white sharks (Goldman, 1997), and 21.2°C for salmon sharks, *L. ditropis* (Goldman, 2002; Goldman et al., in press). Lamnid sharks not only possess elevated body temperatures, but also regulate body temperature via physiological means (i.e., regulate heat balance by altering their whole-body thermal rate coefficient, *k*), at least in mako and salmon sharks (Bernal et al., 2001b; Goldman, 2002; Goldman et al., in press).

Several other elasmobranch species have been shown to possess *retia*. Alopiid sharks (threshers) not only possess *retia*, but also have anterior-medial red muscle placement similar to lamnids, a lateral circulation pattern to the red muscle, and exhibit evidence of endothermy (Carey et al., 1971; Bone and Chubb, 1983; Bernal, pers. comm.; Goldman, unpubl. data). Three species of myliobatoid rays possess *retia* (Alexander, 1995, 1996); however, no temperature measurements have been obtained from these species, so their body temperatures and thermoregulatory abilities (if any) are still unknown.

7.5.2 Indirect Calorimetry: Endotherms vs. Ectotherms

Because lamnid sharks are endotherms, they should have higher SMRs than ectothermic sharks, as endothermy increases the total aerobic capacity of an organism. To date, the only lamnid metabolic data to support this hypothesis comes from a single 3.9 kg mako shark with an SMR of 240 mg O_2 kg^{-1} h^{-1} at 16 to 20°C (Graham et al., 1990). However, this value was extrapolated to zero swimming speed, which may not be the most representative metabolic rate estimate for an obligate ram ventilator, whose swimming speed is never zero. Even with the difficulties of controlling for water temperature, animal weight, respirometer type, and swimming speed, comparisons of routine metabolic rates (RMR) would be more meaningful when examining obligate ram ventilators. Additionally, comparing obligate ram ventilators to other obligate ram ventilators would be more meaningful than extrapolating their RMR to zero for comparison to non-obligate ram ventilating species (e.g., lemon sharks). Aside from the shortfin mako shark, the only other obligate ram ventilating sharks for which VO_2 data exist are for two ectothermic species; bonnethead (Parsons, 1990) and blacknose sharks (Carlson et al., 1999). Both studies tested sharks of similar sizes (up to 4.7 kg for bonnethead and 3.5 kg for blacknose sharks) to the 3.9 kg shortfin mako shark tested by Graham et al. (1990).

Routine metabolic rate of the endothermic shortfin mako shark swimming at 24.6 cm s^{-1} was 262 mg O_2 kg^{-1} h^{-1} in 16°C water and 507 mg O_2 kg^{-1} h^{-1} in 20°C water (Graham et al., 1990). Mean RMR over the course of the 36 h experiment (mean swimming speed = 24.6 cm s^{-1}) was 369 mg O_2 kg^{-1} h^{-1}. In contrast, mean RMR for a 3.5 kg ectothermic blacknose was lower (278.5 mg O_2 kg^{-1} h^{-1}) than for the shortfin mako even though the blacknose swam in considerably warmer water (28°C) and at a faster mean swimming speed (31.4 cm s^{-1}; Carlson et al., 1999). Parsons (1990) studied RMR of bonnethead sharks ranging in size from 0.095 to 4.7 kg. Using his equation to estimate VO_2, a 3.9 kg bonnethead, at 25°C, would have a VO_2 of 195.5 mg O_2 kg^{-1} h^{-1}. As with the blacknose shark, the estimated RMR of this ectothermic obligate ram ventilator was less than that of the endothermic shortfin mako. Had water temperatures been the same in all studies, the mako's RMR would be even higher at 28°C or, oppositely, bonnethead RMR would be lower at 16 to 20°C. Although no direct comparisons for weight, swimming speed, temperature, and respirometer type can be made between endothermic and ectothermic elasmobranchs, it appears that endothermic sharks possess higher metabolic rates than ectothermic sharks under similar conditions.

7.5.3 Indirect Evidence of Higher Metabolic Rates in Endothermic Sharks

Along with the evolution of *retia* and endothermy, lamnid sharks possess several characteristics indicating they have high aerobic and anaerobic capacities, and higher metabolic rates than ectothermic sharks. These features show a remarkable evolutionary convergence with endothermic tunas and reflect specializations related to efficient, high-performance swimming and an active lifestyle (see Bernal et al., 2001a, for thorough review).

In addition to red muscle that is internalized with anterior-medial placement, lamnid sharks also show a partial separation (shear) between adjacent red and white muscle, making red muscle free to contract relative to white muscle during slow-speed swimming (Carey et al., 1985; Bernal et al., 2001a). Ectothermic elasmobranchs do not possess this feature; their white muscle appears to contribute to intermediate-speed sustainable swimming, as it is connected to externalized red muscle (and skin). It has been predicted that this "muscle shear" characteristic in lamnids, along with the distinct red muscle position in the body cavity, may decrease energy output requirements and enhance swimming performance by allowing the red muscle to transfer power directly to the caudal peduncle and caudal fin (Bernal et al., 2001a).

High-performance swimming adaptations in lamnid sharks include features that enhance uptake (large gill-surface area) and delivery of a large amount of O_2 to the red muscle, including large heart, and blood hemoglobin and hematocrit levels similar to those of birds and mammals (Emery, 1985, 1986; Emery and Szczepanski, 1986; Oikawa and Kanda, 1997; Tota et al., 1983; Tota, 1999; Bernal, pers. comm.). Elevated red and white muscle temperatures speed the contraction–relaxation cycle and increase muscle power output, which may result in faster cruising speeds (Johnston and Brill, 1984; Dickson et al., 1993; Altringham and Block, 1997; Bernal, pers. comm.).

Lamnid sharks also have been shown to possess modified biochemical characteristics in white myotomal muscle and heart ventricle that enhance greater aerobic and anaerobic metabolic capacities (Dickson et al., 1993; Bernal et al., 2001a; Bernal, pers. comm.). Compared with other active sharks, shortfin mako possesses higher white muscle activities of citrate synthase, lactate dehydrogenase, and creatine phosphokinase (Dickson et al., 1993; Bernal et al., 2001a; Bernal, pers. comm.). Thus, lamnid sharks appear to have high aerobic and anaerobic scopes and a high capacity for anaerobic ATP production during burst swimming. Although no modifications of biochemical characteristics have been found in red muscle, at *in vivo* temperatures both the shortfin mako shark and salmon shark have been estimated to increase red muscle enzyme activities by 48 and 123%, respectively (Bernal et al., 2003).

Elasmobranchs and teleosts deal with similar acid loads in the blood during and after periods of high exertion, but elasmobranchs have a lower capacity to buffer acid at the site of production and differ from teleosts in their tolerance to blood acidification (Dickson et al., 1993). Wells and Davies (1985) found that hemoglobin-O_2 binding and blood O_2-carrying capacity in the shortfin mako shark were not significantly affected by a large drop in blood pH that occurred after periods of high activity. The higher hemoglobin content of blood and the ability to uptake and deliver more oxygen to muscle may reduce oxygen debt, or decrease the amount of time necessary to offset the oxygen debt after periods of sustained burst swimming (Dickson et al., 1993; Bernal et al., 2001a).

Stable tissue temperatures would conserve metabolic function during ambient temperature changes. The thermal buffer created by metabolic heat retention may reduce the impact of ambient temperature fluctuations on metabolic rates of young (small) lamnid sharks, and the buffer may eliminate any effects on larger individuals because they possess greater thermal inertia (Bernal et al., 2001a; Goldman et al., in press). This thermal buffer likely permits lamnids to exploit cool and boreal waters.

7.6 Environmental Effects on Metabolism

7.6.1 Temperature

Ambient temperature is a key variable and plays a major role in controlling metabolic rates of ectothermic elasmobranchs, whereas fluctuations in ambient temperature may have a reduced or no impact on the

metabolic rates of endothermic sharks. Metabolic rate typically increases by a Q_{10} of 2 to 3 for every 10°C rise in temperature, although this rate varies among species (Brett and Groves, 1979; Schmidt-Nielsen, 1983). Du Preez et al. (1988) reported a Q_{10} response of 2.27 between 15 and 25°C for guitarfish whereas the Q_{10} response for bullray was 1.87 between 10 and 25°C. Hopkins and Cech (1994) determined a Q_{10} of 6.8 for bat rays over a temperature range of 14 to 20°C. Among sharks, bonnetheads were found to have a Q_{10} of 2.34 at 20 to 30°C (Carlson and Parsons, 1999), while scalloped hammerhead sharks have a Q_{10} of 1.34 at 21 to 29°C (Lowe, 2001). These trends suggest interspecific differences in Q_{10} among elasmobranchs, but length of acclimation (e.g., acute or seasonal) at each experimental temperature may result in an increased or decreased sensitivity to metabolic rate. For example, Hopkins and Cech (1994) determined a Q_{10} for bat rays exposed to acute changes in temperature, while Carlson and Parsons (1999) and Lowe (2001) measured changes in oxygen consumption rate sensitivity to seasonally acclimatized sharks.

As pointed out by Brett (1971), most ectothermic fishes are thermal conformers and generally inhabit an optimal temperature range between upper and lower lethal temperatures. The optimal temperature range is thought to be where physiological rates (e.g., metabolism, growth, digestion) would be optimized to enhance fitness. Recent studies using telemetry suggest that elasmobranchs found in thermally heterogeneous environments will feed in warmer waters and rest in cooler waters. Matern et al. (2000) proposed that bat rays took advantage of their elevated metabolism by feeding in warmer waters then moving to cooler waters to lower metabolism (i.e., energetic demands) and possibly gastric evacuation rate while maintaining assimilation efficiency. Although this behavioral thermoregulation hypothesis has only been proposed for bat rays, the possibility exists that other species exhibiting diel movements may be taking advantage of thermally heterogeneous environments. For example, blue sharks displayed daily vertical dives from the surface to depths of 250 m and experienced water temperature changes of 7 to 9°C (Carey and Scharold, 1990).

7.6.2 Salinity

Most species of elasmobranchs are found in marine environments and likely would not encounter radical changes in salinity. However, bull shark, *Carcharhinus leucas* (Snelson et al., 1984), and several species of rays (Schwartz, 1995; Meloni et al., 2002) are found in brackish waters. Despite the hypothesis that elasmobranchs are osmoconformers (using solutes to maintain osmolarity) studies on Atlantic stingray, *Dasyatis sabina*, suggest osmoregulatory energy costs associated with decreases in salinity (Janech and Piermarini, 1997; Janech et al., 1998; Piermarini and Evans, 2000).

Increasing osmoregulatory costs could raise SMR (Brett and Groves, 1979). Evidence for this was provided by Meloni et al. (2002) for 0.4 to 1.7 kg bat rays exposed to various levels of salinity: SMR increased from 12.6 mg O_2 h^{-1} at 33 and 36‰ to 24.1 mg O_2 h^{-1} at 15 and 25‰.

7.6.3 Dissolved Oxygen

Oxygen levels throughout marine environments vary in relation to depth, productivity, time of day, and other factors. Sharks have been captured in areas with decreased dissolved oxygen levels suggesting sharks encounter and deal with areas of low dissolved oxygen (Grace and Henwood, 1998; Carlson and Parsons, 2001). Metabolic responses of elasmobranchs to oxygen depletion differ among species depending on behavior and physiology. Metabolic rate and activity were found to decrease in response to low dissolved oxygen in spotted dogfish and Florida smoothhound, *Mustelus norrisi*, species that increase buccal pumping rate to augment the flow of water over the gills (Metcalf and Butler, 1984; Carlson and Parsons, 2001). Reduction in activity during hypoxic exposure is thought to reduce energy expenditure, as a considerable amount of energy may be used for swimming. Energy saved may then be dedicated to additional respiratory needs such as increased buccal pumping rate.

The behavioral response to hypoxia for obligate ram-ventilating sharks is to increase swimming speed and metabolism (Parsons and Carlson, 1998; Carlson and Parsons, 2001). The increase in metabolism has not been determined to be independent of or dependent on hypoxia, but increased swimming speed as a mechanism for regulating respiration would appear to be metabolically costly and would seem to

increase the problem of obtaining sufficient oxygen to meet increased swimming speed. Increased swimming speed could be a flight response as determined for tunas (Bushnell and Brill, 1991). However, Parsons and Carlson (1998) suggested that because sharks have reduced metabolic demands with respect to tunas, increased swimming speed and gape may be energetically similar to other mechanisms for oxygen regulation such as increased buccal pumping rates found in non-obligate ram-ventilator species.

7.6.4 Time of Day

Elasmobranchs exhibit changes in diurnal activity patterns. Higher activity levels at night have been reported for horn, *Heterodontus francisci,* and swell sharks, *Cephaloscylium ventriosum* (Nelson and Johnson, 1970) and for lemon shark (Gruber et al., 1988) *in situ,* suggesting these animals are nocturnal. Lesser spotted dogfish (Sims et al., 1993), bonnethead (Parsons and Carlson, 1998), and little skate (Hove and Moss, 1997) increased swimming at night or under dark conditions. Lowe (2002) found that juvenile scalloped hammerhead sharks significantly increased their swimming speed at night and thus incurred a higher metabolic cost. Nixon and Gruber (1988), Sims et al. (1993), and Hove and Moss (1997) measured increases in metabolic rate coinciding with increased activity. Although activity was not measured, Du Preez et al. (1988) also found nocturnal peaks in routine oxygen consumption rates for guitarfish and bull ray. In these studies, elasmobranchs were exposed to various cycles of light and dark that suggest activity is controlled by an exogenous circadian rhythm influenced by light. Further, experiments conducted on blacknose shark, bonnethead shark, and Florida smoothhound under constant light found no predictable changes in swimming speed and oxygen consumption rate with time of day (Carlson and Parsons, 2001).

Increases in activity and metabolism are likely influenced by stimulation of the pineal organ, which causes the secretion of melatonin and, in fishes, melatonin influences almost all body processes including locomotion, skin color, and reproductive cycle (Bonga, 1993). Sharks possess a pigment-free patch of skin over the epiphysis in the chondrocranium, which could allow for light transmission. Gruber et al. (1975) noted an area of reduced opacity in the top of the chondrocraniums in lemon and bull sharks and in smooth dogfish.

7.7 Conclusions and Future Directions

Most studies on elasmobranch metabolism have been concerned with the juvenile stage and with species confined to coastal areas. Little or no research on adult or pelagic species has been performed despite evidence that metabolism varies by species, size, and life stage. Estimates of metabolism for a variety of ecologically diverse species are becoming increasingly important because bioenergetics have applications to population and ecosystem modeling (Kitchell et al., 2002; Lowe, 2002; Schindler et al., 2002).

Despite the obvious problems of the large size of sharks and construction of a respirometer large enough to accommodate these highly active species, new techniques need to be developed to obtain estimates of metabolism. In lieu of constructing very large water tunnels, mathematical models show promise. Using independent estimates of lower threshold prey densities, Sims (2000) developed a threshold foraging behavior model for estimation of metabolic rate in basking sharks, *Cetorhinus maximus*. The "best estimates" of RMR from Sims' threshold model were 62 to 91 mg O_2 kg^{-1} h^{-1} for a 1000 kg basking shark, which agreed fairly well with his shark and fish VO_2–mass scaling relationships. However, the large number of estimators used in Sims' (2000) threshold model also creates a large uncertainty in his estimates. Nevertheless, the continuing development of models may lead to a viable way of estimating metabolic rates of large sharks in the field and to subsequent comparisons of large endothermic and ectothermic species.

Because elasmobranchs are considered to be iso-osmotic to seawater and the resulting water flux rate would be predicted to be negligible, Parsons and Carlson (unpubl. data) proposed to use the doubly labeled water method (Nagy, 1987) to estimate field metabolic rates in sharks. Unfortunately, bonnetheads exposed to two levels of salinity (30 and 25‰) experienced high levels of water flux. Sharks injected

with tritiated water had no detectable levels of the isotope within the blood after 30 min from injection. These results suggest that this method may be appropriate only when salinity remains high (≥35‰).

The increasing sophistication and technology associated with biotelemetry likely hold the most promise for determining metabolism of these larger species (Lowe and Goldman, 2001). Biotelemetry may be particularly useful for species that are large and difficult to maintain in captivity. In addition, there is a great need for bridging the gap between laboratory and field studies. Development of new physiological sensors and transponding systems may greatly facilitate collection of energetics data for elasmobranch species. Elasmobranch models may also provide the best insight into our understanding of free-ranging fish physiology, because these animals are large enough to carry integrated transmitter packages capable of recording environmental data simultaneously.

Many of the comparisons that we have made among and within taxa are limited. Variability in experimental temperature, mass effects, and experimental design and apparatus make comparisons difficult. To provide a better picture of the energetics and metabolic capacities of sharks, comparisons among taxa must be performed using similarly sized animals that control for temperature under identical experimental protocols. Graham et al. (1990) examined relationships in three species of sharks varying in body form, activity level, and physiology using the same protocols and revealed many of the trends reported herein.

Much remains to be learned about the energetics of elasmobranchs. It is evident that species adapted for continuous activity possess higher energetic capacities, but the details of the swimming performance and its relation to aerobic and anaerobic capacities remain to be quantified. Obtaining large sample sizes will always prove difficult with these animals. Improvements in experimentation techniques, capture, and husbandry of elasmobranchs will aid in elucidating energetic relationships.

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