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Energetics, Metabolism, and Endothermy in Sharks and Rays

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7.1 Energetics

During the last several decades, studies on the aerobic metabolism of elasmobranchs have relied on the use of indirect calorimetry centered on small, generally sedentary species that acclimate well to the tight enclosures of a respirometer chamber and those that are easily maintained in captivity for long periods of time. By contrast, work on larger and obligate ram ventilating species has lagged far behind and typically features a paucity of measurements usually conducted over short durations of time on a few selected species. More recently, field-based empirical models have been used to estimate the metabolic requirements of species too large to work with in the laboratory. The original view of the energetic demands in sharks and rays was that they typically possessed lower metabolic rates relative to similar sized teleosts; however, this view is beginning to change as new data emerge on the metabolism of several large, actively swimming species. Nonetheless, several general important factors need to be considered when attempting to compare the energetic demands between elasmobranchs and teleosts and among elasmobranchs.

7.1.1 Size

Most studies have access to sharks and rays that are of similar sizes, and the lack of a large span of body mass precludes investigation of mass-specific scaling effects; however, mass-specific estimates over a relatively wide range of sizes have been possible for several species.
with small maximum sizes. For example, Parsons (1990) determined routine metabolic rates for bonnetheads, *Sphyrna tiburo*, ranging in body mass \( M \) from 0.9 to 4.7 kg and found that the mass-specific oxygen consumption rate \( (\text{VO}_2 \text{ in mg O}_2 \text{ kg}^{-1} \text{ hr}^{-1}) \) scaled with \( M^{0.86} \) and was described by \( \text{VO}_2 = 68.9 + (177.8 M) \). Work on lesser spotted dogfish, *Scyliorhinus canicula*, reported a mass-specific \( \text{VO}_2 \) relationship of \( \text{VO}_2 = 0.104 M^{0.855} \) (Sims, 1996). Generally, larger sharks have a lower mass-specific metabolic rate than smaller sharks, and this relationship is similar for rays. For example, Neer et al. (2006) estimated almost a sixfold decrease in \( \text{VO}_2 \) for cownose rays, *Rhinoptera bonasus*, ranging in body mass from 2.2 to 8.3 kg (332.8 and 55.9 mg O\(_2\) kg\(^{-1}\) hr\(^{-1}\), respectively). Interspecifically, Sims (2000) reviewed metabolic data for seven species of sharks ranging from 0.35 to 3.5 kg and developed a mass-specific metabolic rate relationship in which the overall routine oxygen consumption rate increased with \( M^{0.86} \), a very similar mass-specific exponent found for bonnethead (Parsons, 1990) and lesser spotted dogfish (Sims, 1996). By comparison, Clarke and Johnston (1999) determined that the mass-specific scaling exponent for 69 teleost species was \( M^{0.80} \), which suggests that even when comparing across diverse taxa with a body mass differing by several orders of magnitude, the physical laws that govern gas diffusion during oxygen uptake, transport, and delivery appear to result in a fairly well-conserved mass-specific scaling of \( \text{VO}_2 \) in fish. Nonetheless, it remains important to increase our understanding of how body mass may affect the metabolic rates of sharks and rays that can range in body mass by up to three or four orders of magnitude and have a wide range of levels of swimming activity. Caution should be taken, however, when applying mass-scaling corrections to compare the metabolic rates between species that are widely different in size, such as a 0.1-kg swell shark, *Cephaloscyllium ventriosum*, and a 10-kg shortfin mako shark, *Isurus oxyrinchus* (Figure 7.1).

### 7.1.2 Temperature

Most studies use a limited range of ambient temperatures and hence exclude the incorporation of the thermal effects on metabolism. Ambient temperature is a key variable and plays a major role in controlling the metabolic rate of ectothermic fishes. In general, the metabolic rate of ectothermic elasmobranchs is directly correlated with temperature, and, for example, metabolic rates will increase between two and three times for every 10°C elevation in ambient temperature (see Section 7.1.6). Thus, temperature will play a major role in the energetic demands of sharks and rays that undergo diurnal or seasonal changes in thermal habitat as a result of their horizontal (i.e., geographic) or vertical (i.e., depth) movement patterns. On the other hand, several species of sharks are capable of regional endothermy, and these unique physiological specializations may result in a different thermal effect on metabolic rate (see Section 7.3). It is important to consider the validity of any correction for the thermal effects on metabolic rate between species that have widely different temperature preferences. For example, the adjustment of the metabolic rate of a coldwater shark (which normally inhabits 5°C) to match that of a tropical species (which normally inhabits 25°C) should take into consideration the potential presence of coldwater adaptations, temperature tolerance, and the thermal limits of each species (Clarke, 1991) (Figure 7.1).

### 7.1.3 Acclimation

The logistical problems of housing captive elasmobranchs for extended periods of time under controlled laboratory conditions (e.g., temperatures, light levels) have resulted in the majority of work focusing on small, relatively inactive and docile elasmobranchs that readily adapt to captivity. For these reasons, there are few studies on larger and obligate ram ventilating species, which can only be studied for short periods of time (hours, days, or weeks) in a captive setting. This lack of proper acclimation may lead to an inaccurate estimation of their energetic requirements, because it is not possible to measure the metabolic rates of sharks that have been fully acclimated to the experimental apparatus (Clarke, 1991). This scenario has been readily observed in recent studies on tunas in which specimens that were acclimated to both the laboratory and respirometer for longer periods of time had significantly lower metabolic rates than those measured in previous studies with shorter acclimation times (e.g., Blank et al., 2007; Dewar et al., 1994). Still not much is known about longer term issues around acclimatization in elasmobranchs.

### 7.1.4 Experimental Apparatus

The mechanical design by which metabolic rates are measured in fishes may also affect their energetic demands (Steffensen, 1989). Lowe (2001), for example, indicated that juvenile scalloped hammerhead sharks, *Sphyraena lewini*, exhibited poorer swimming performance and entrainment when forced to swim in a flume than while swimming freely in a pond, particularly at lower swimming velocities. Therefore, the actual respirometer chamber may impede optimal swimming performance in sharks and rays, and the current measured values of swimming energetics may include data under non-steady and turbulent conditions that do not truly represent the noncaptive (i.e., free-swimming) energetic demands. Despite the presence of potential inter- and intraspecific differences that may or may not be attributed to size effects, thermal effects, or the experimental
techniques used, our body of knowledge on the energetics of sharks and rays has grown considerably during the last 30 years.

7.1.5 Metabolic Rates

In elasmobranchs, VO$_2$ is generally regarded as the standard in determination of aerobic metabolism in a post-absorptive state (i.e., metabolic rate excluding energy devoted to digestion and assimilation). Although some work on sharks has attempted to correlate heart rate, muscle temperature, and food consumption, or an estimate thereof, to metabolic rate (Sims, 2000; Stillwell and Kohler, 1982; reviewed in Carlson et al., 2004), quantifying a reduction in the dissolved oxygen in the water as a function of time during which the animal respires (i.e., respirometry) is the most common method used. Carlson et al. (2004) gave an overview of the types of respirometers used to measure VO$_2$ in elasmobranchs, the problems and benefits of each type, and details on how these systems range from simple closed respirometers to more complex swimming chambers or flumes. We do not repeat this review here.

Although it is very difficult to compare metabolic rates among species because of differences in experimental technique, size of animals used, and water temperature (Figure 7.1; see Sections 7.1.1 to 7.1.4), it is still useful to qualitatively examine trends in metabolism in an attempt to provide an overview of energetic requirements of elasmobranchs. The most common metabolic estimates used to compare the energetic demands of resting or swimming elasmobranchs are standard metabolic rate (SMR), the metabolic rate of a fish at rest (Brill, 1987); routine metabolic rate (RMR) (Fry, 1971); and maximum metabolic rate (MMR), the maximum measured metabolic rate (Korsmeyer and Dewar, 2001).

7.1.5.1 Sharks

As reported in Carlson et al. (2004), SMRs vary greatly among species (Table 7.1, Figure 7.1). In general, species that are obligate ram ventilators and swim continuously have the highest measures of metabolism. Even when correcting for temperature differences (i.e., Q$_{10}$ = 2), lower estimates of VO$_2$ are generally found for less active species (Figure 7.1). For example, a temperature-corrected

<table>
<thead>
<tr>
<th>Species</th>
<th>Temperature (°C)</th>
<th>Average Mass (kg)</th>
<th>N</th>
<th>Methods$^a$</th>
<th>VO$_2$ (mg O$_2$ kg$^{-1}$ hr$^{-1}$)</th>
<th>Ref.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Isurus oxyrinchus</td>
<td>18–20</td>
<td>3.9</td>
<td>1</td>
<td>Swimming closed</td>
<td>240$^b$</td>
<td>Graham et al. (1990)</td>
</tr>
<tr>
<td>Carcharhinus acronotus</td>
<td>28</td>
<td>0.5</td>
<td>10</td>
<td>Circular closed</td>
<td>239$^b$</td>
<td>Carlson et al. (1999)</td>
</tr>
<tr>
<td>Sphyraena lewini</td>
<td>26</td>
<td>0.5–0.9</td>
<td>17</td>
<td>Swimming closed</td>
<td>189$^b$</td>
<td>Lowe (2002)</td>
</tr>
<tr>
<td>Sphyraena tiburo</td>
<td>28</td>
<td>1.0</td>
<td>8</td>
<td>Flow-through</td>
<td>168$^b$</td>
<td>Carlson and Parsons (2003)</td>
</tr>
<tr>
<td>Negaprion brevirostris</td>
<td>25</td>
<td>1.6</td>
<td>7</td>
<td>Annular closed</td>
<td>153$^b$</td>
<td>Scharold and Gruber (1991)</td>
</tr>
<tr>
<td>Isurus oxyrinchus</td>
<td>16–21</td>
<td>4.4–9.5</td>
<td>—</td>
<td>Swimming closed</td>
<td>124$^b$</td>
<td>Sepulveda et al. (2007a)</td>
</tr>
<tr>
<td>Carcharhinus plumbeus</td>
<td>24</td>
<td>1.0</td>
<td>—</td>
<td>Annular closed</td>
<td>120$^b$</td>
<td>Dowd et al. (2006)</td>
</tr>
<tr>
<td>Ginglymostoma cirratum</td>
<td>23</td>
<td>1.3–4.0</td>
<td>5</td>
<td>Flow-through</td>
<td>106$^b$</td>
<td>Fournier (1996)</td>
</tr>
<tr>
<td>Negaprion brevirostris</td>
<td>22</td>
<td>0.8–1.3</td>
<td>13</td>
<td>Annular closed</td>
<td>95$^b$</td>
<td>Bushnell et al. (1989)</td>
</tr>
<tr>
<td>Scyliorhinus stellaris</td>
<td>25</td>
<td>2.5</td>
<td>12</td>
<td>Circular flow-through</td>
<td>92$^b$</td>
<td>Piiper et al. (1977)</td>
</tr>
<tr>
<td>Triakis semifasciata</td>
<td>14–18</td>
<td>2.2–5.8</td>
<td>5</td>
<td>Swimming closed</td>
<td>91.7$^b$</td>
<td>Scharold et al. (1989)</td>
</tr>
<tr>
<td>Chiloscyllium plagiosum</td>
<td>24.5</td>
<td>0.19</td>
<td>13</td>
<td>Circular closed</td>
<td>91.2$^b$</td>
<td>Tullis and Baillie (2005)</td>
</tr>
<tr>
<td>Cephaloscyllium ventriosum</td>
<td>16</td>
<td>0.1–0.2</td>
<td>4</td>
<td>Circular closed</td>
<td>44.3$^b$</td>
<td>Ferry-Graham and Gibb (2001)</td>
</tr>
<tr>
<td>Scyliorhinus canicula</td>
<td>15</td>
<td>1.0</td>
<td>33</td>
<td>Circular closed</td>
<td>38.2$^b$</td>
<td>Sims (1996)</td>
</tr>
<tr>
<td>Squalus acanthias</td>
<td>10</td>
<td>2.0</td>
<td>6</td>
<td>Circular closed</td>
<td>32.4$^b$</td>
<td>Brett and Blackburn (1978)</td>
</tr>
<tr>
<td>Squalus sucklei</td>
<td>10</td>
<td>2.2–4.3</td>
<td>—</td>
<td>Flow-through</td>
<td>31.0$^b$</td>
<td>Hanson and Johansen (1970)</td>
</tr>
<tr>
<td>Rhinoptera bonasus</td>
<td>22–25</td>
<td>2.2</td>
<td>19</td>
<td>Flow-through</td>
<td>332.7$^b$</td>
<td>Neer et al. (2006)</td>
</tr>
<tr>
<td>Myliobatus californica</td>
<td>14</td>
<td>5.0</td>
<td>6</td>
<td>Circular flow-through</td>
<td>50</td>
<td>Hopkins and Cech (1994)</td>
</tr>
<tr>
<td>Rhinobatos annulatus</td>
<td>15</td>
<td>1.0</td>
<td>10</td>
<td>Circular flow-through</td>
<td>61</td>
<td>DuPreez et al. (1988)</td>
</tr>
<tr>
<td>Dasypatis americana</td>
<td>20</td>
<td>0.3</td>
<td>6</td>
<td>Flow-through</td>
<td>164$^b$</td>
<td>Fournier (1996)</td>
</tr>
<tr>
<td>Raja erinacea</td>
<td>10</td>
<td>0.5</td>
<td>6</td>
<td>Circular flow-through</td>
<td>20</td>
<td>Hove and Moss (1997)</td>
</tr>
<tr>
<td>Myliobatis aquila</td>
<td>10</td>
<td>1.1–2.1</td>
<td>5</td>
<td>Flow-through</td>
<td>44.4$^b$</td>
<td>DuPreez et al. (1988)</td>
</tr>
<tr>
<td>Dasypatis violacea</td>
<td>20</td>
<td>10.7</td>
<td>9</td>
<td>Circular flow-through</td>
<td>39.1$^b$</td>
<td>Ezcurra (2001)</td>
</tr>
</tbody>
</table>


$^a$ Methods indicate the type of respirometer used to measure metabolic rate.

$^b$ Values of standard metabolic rate were estimated through extrapolation to zero velocity.
comparison (i.e., at 25°C) between the relatively sedentary lesser spotted dogfish and the more active scalloped hammerhead reveals that the SMR of the former is less than 40% of that of the latter (i.e., 76.4 vs. 189 mg O$_2$ kg$^{-1}$ hr$^{-1}$) (Lowe, 2002; Sims, 1996). Nonetheless, the SMRs for sharks appear to encompass a continuum similar to that of teleosts with a comparable level of swimming activity. The mostly benthic dogfish (Family Squalidae) and catsharks (Family Scyliorhinidae) have metabolic rates that are analogous to some coldwater teleosts such as cod, Gadus morhua (78.2 mg O$_2$ kg$^{-1}$ hr$^{-1}$ at 15°C) (Schurmann and Steffensen, 1997), while comparably sized largemouth bass, Micropterus salmoides, a more active teleost, has SMR values (110 to 190 mg O$_2$ kg$^{-1}$ hr$^{-1}$).
kg\(^{-1}\) hr\(^{-1}\) at 25 to 28°C (Beamish, 1970) that are similar to those of more active sharks (i.e., bonnethead and sandbar shark, *Carcharhinus plumbeus*) (Carlson and Parsons, 2003; Dowd et al., 2006). Therefore, it should be expected that the most actively swimming pelagic shark species such as lamnids (e.g., shortfin mako) would possess SMRs analogous to those of the highly active teleosts (e.g., tunas), which have remarkable similarities in morphology and physiology (Bernal et al., 2001a). Work on a swimming mako by Graham et al. (1990) showed that the SMR was ~240 mg O\(_2\) kg\(^{-1}\) hr\(^{-1}\) at ~16°C, a value comparable to that of similarly sized yellowfin tuna, *Thunnus albacares* (253 to 257 mg O\(_2\) kg\(^{-1}\) hr\(^{-1}\) at 25°C) (Dewar and Graham, 1994). A more recent study on swimming makos by Sepulveda et al. (2007a) reported a SMR of 124 mg O\(_2\) kg\(^{-1}\) hr\(^{-1}\) at 18°C that, although more than twofold lower than previously reported, matches more recent estimates of SMR in Pacific bluefin tuna, *Thunnus orientalis*, and yellowfin tuna (120 and 91 mg O\(_2\) kg\(^{-1}\) hr\(^{-1}\) at 20°C, respectively) (Blank et al., 2007), suggesting that the physiological capabilities of mako sharks are comparable to those of tunas.

It has been suggested that comparing SMRs between species that are obligate ram ventilators and those that have the capability to stop swimming and adequately ventilate their gills via buccal pumping could lead to erroneous results (Carlson et al., 2004; Dowd et al., 2006; Sepulveda et al., 2007a). In general, for species that never stop swimming, SMRs can be determined either by extrapolation to zero velocity based on the oxygen consumption–swimming speed relationship or by measuring SMR on immobilized fish. Although validation of SMRs on spinally blocked sharks indicates that this can be an appropriate technique (Carlson and Parsons, 2003; Dowd et al., 2006), the zero-velocity extrapolation method could potentially lead to an overestimated SMR if the swimming speed and VO\(_2\) functions were elevated or if the regression slope was affected by inefficient swimming at low swimming speeds (Brett, 1964), a likely scenario found by Sepulveda et al. (2007a) for shortfin makos (Figure 7.2).

Several reviews have extrapolated the swimming speed–VO\(_2\) relationship data from the Graham et al. (1990) study on a single shortfin mako and determined a SMR of ~240 mg O\(_2\) kg\(^{-1}\) hr\(^{-1}\) at 18°C that, although more than twofold lower than previously reported, matches more recent estimates of SMR in Pacific bluefin tuna, *Thunnus orientalis*, and yellowfin tuna (120 and 91 mg O\(_2\) kg\(^{-1}\) hr\(^{-1}\) at 20°C, respectively) (Blank et al., 2007), suggesting that the physiological capabilities of mako sharks are comparable to those of tunas.

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speed–VO₂ relationship is to be used to estimate SMRs, then the VO₂ should only be collected at the minimum speeds the shark swims where there are no apparent changes in swimming angle and there are no erratic side-to-side movements during the experimental trials.

Carlson et al. (2004) noted that for most sharks the average slopes of the power–performance curves (i.e., swim speed vs. VO₂) ranged between 0.27 and 0.36 and were similar among ectothermic species, which all share comparable morphological adaptations for drag reduction. Since that review, only two additional studies have examined the relationship of swimming and VO₂. A study on juvenile sandbar sharks by Dowd et al. (2006) reported that the slope of the power–performance curve was about 0.38, a value that is within the range of other carcharhinid sharks that possess similar body morphology (Figure 7.3). Sepulveda et al. (2007a), however, found the slope of the swimming speed–VO₂ relationship for juvenile shortfin makos to be 0.92 (i.e., more than double that of sandbar sharks) (Figure 7.3). This higher cost of propulsion for the shortfin mako is surprising given that the swimming performance of this lamnid is hypothesized to approach that of tunas (Bernal et al., 2001a; Gemballa et al., 2006), in which the slope of the power–performance curves is around 0.33 (Blank et al., 2007). Unlike tunas, however, makos lack a swim bladder, have large pectoral fins that do not retract into grooves along the body (i.e., increasing frictional drag), and may have a more inefficient mechanism of force transmission between the swimming muscles and the caudal fin. Taken together, all of

**FIGURE 7.3**

Oxygen consumption (VO₂) as a function of relative swim speed, U (BL s⁻¹) for sharks. (A) Data at experimental temperatures, and (B) data corrected to 20°C (using Q₁₀ = 2). Hatched lines indicate an extrapolation to zero swim speed. Labels: a, Isurus oxyrinchus (n = 9); b, I. oxyrinchus (n = 1); c, Carcharhinus acronotus (n = 8); d, Negaprion brevirostris (n = 7); e, Sphyra lewini (n = 17); f, combined data for N. brevirostris (n = 1); and (n = 7); g, N. brevirostris (n = 13); h, combined data for N. brevirostris (n = 1)² and (n = 13); i, Triakis semifasciata (n = 5); j, Carcharhinus plumbeus (n = 16) (calculated at 5 kg). Sources: ¹Sepulveda et al. (2007a); ²Graham et al. (1990); ³Carlson et al. (1999); ⁴Scharold and Gruber (1991); ⁵Lowe (2001); ⁶Bushnell et al. (1989); ⁷Scharold et al. (1989); ⁸Dowd et al. (2006).
these marked differences may result in makos having an elevated cost of swimming relative to tunas. Moreover, the finding that the slope of the power–performance curves was also higher for makos when compared to other sharks suggests that makos may not have evolved the capacity to have a lower cost of transport but rather the capacity for a higher maximum metabolic rate and a large aerobic scope. Recent work by Ezcurra et al. (2012a) suggests that the other lamnids may also have a potential higher cost of locomotion and an elevated metabolic rate; for example, the routine VO$_2$ of juvenile (22.6 to 36.2 kg) white sharks, Carcharodon carcharias, being transported in a large 11,356-L tank (15 to 18°C) was 246 ± 13 mg O$_2$ kg$^{-1}$ hr$^{-1}$. When corrected for body mass (mass-specific scaling for lamnids, 458.5 × $M^{0.79}$) (Ezcurra et al., 2012a), this would yield a value similar to that of the RMR in mako sharks (Sepulveda et al., 2007a).

The logistical and technical difficulties surrounding the current methods used to estimate the MMRs in sharks most likely lead to underestimated their total aerobic capacity by not being able to truly measure their MMR and instead measuring values that are limited by experimental conditions (e.g., maximum swim tunnel water velocities, adverse behavioral modification due to confined swimming). In addition, these methods undoubtedly lead to MMR values that not only account for the swimming-related energy expenditures (the target value) but also reflect the simultaneous occurrence of other important aerobic processes that occur during the experimental trial (i.e., recovery from stress, repayment of oxygen debt after anaerobic activity, digestion and assimilation) (Blank et al., 2007; Steffensen, 1989). Nonetheless, these values offer an estimate of the total aerobic capacity of the shark, at least under experimental conditions. In general, sharks that are more active have higher MMRs when compared to sharks that are more sedentary. These differences remain even when adjusting for any temperature effects ($Q_{10} = 2.0$), with the MMRs of active species being from 1.5 to 2.3 times greater than those of more sedentary ones (Figure 7.3).

A comparison at 25°C of a 2.0-kg spiny dogfish, Squalus acanthias, and 1.6-kg lemon shark, Negaprion brevirostris, shows that the former consumed a maximum of 250 mg O$_2$ kg$^{-1}$ hr$^{-1}$ (Brett and Blackburn, 1978), compared to 620 mg O$_2$ kg$^{-1}$ hr$^{-1}$ for the latter (Graham et al., 1990). In addition, at 26°C, scalloped hammerhead sharks swimming at 1.0 body length per second (BL s$^{-1}$) consumed up to 500 mg O$_2$ kg$^{-1}$ hr$^{-1}$ (Lowe, 2001), while the less active leopard shark swimming at a comparable 0.9 BL s$^{-1}$ had a MMR of 334 mg O$_2$ kg$^{-1}$ hr$^{-1}$ (Scharold et al., 1989). More recent respirometry data show that the MMR in juvenile makos (MMR = 541 mg O$_2$ kg$^{-1}$ hr$^{-1}$, $n$ = 9, 4.5 to 9.5 kg at 18°C) exceeded that reported for all other comparably sized elasmobranchs (Carlson et al., 2004; Graham et al., 1990; Sepulveda et al., 2007a), with mako MMRs being similar to those estimated for some tuna species (Blank et al., 2007). The observed MMR for the makos is probably the result of their specialized cardiovascular and swimming muscle physiology (e.g., large gill surface area, relatively larger heart mass, increased muscle capillary density, high hemoglobin and myoglobin concentrations, which allow for an elevated rate of oxygen uptake and delivery) (Bernal et al. 2001a, 2003a; Emery, 1985; Wegner et al., 2010).

While SMR provides a basis for comparing physiological capabilities for basal activities, the question remains whether it is appropriate to use this value for fish that must swim continuously to maintain hydrostatic equilibrium and ventilate their gills and therefore never stop moving. In this case, a more biologically relevant value than either SMR or MMR is the aerobic scope, defined as the difference between MMR and SMR (Priede, 1985). This new estimate represents the potential capacity a shark may have to handle multiple simultaneous aerobic demands (e.g., continuous swimming, recovering from oxygen debt, somatic growth, digestion and assimilation) (Brill, 1996; Bushnell et al., 1989; Korsmeyer et al., 1996; Lowe, 2001; Priede, 1985). For typical carcharhinid sharks, the metabolic cost of swimming (i.e., aerobic scope × SMR$^{-1}$) ranges from about 1.4 to 1.8 times the SMR. The swimming cost ratio is 1.4 for scalloped hammerhead sharks (Lowe, 2001), 1.5 for lemon sharks (Brett and Blackburn, 1978), 1.6 for both bonnethead and sandbar sharks (Dowd et al., 2006; Parsons, 1990), and 1.7 for blacknose sharks (Carlson et al., 1999). Not surprisingly, shortfin mako data show that they have the highest costs of swimming (2.7) (Sepulveda et al., 2007a) (Figure 7.3).

The heightened aerobic scope in continuously swimming pelagic predators most probably reflects their ecological ecology, which revolves around their large-scale seasonal migrations and the need to capture fast-moving prey and its physiological consequences (e.g., rapid recovery from burst activity and rapid digestion), and potentially high rates of somatic and gonadal growth (Brill, 1996; Graham and Dickson, 2004; Korsmeyer et al., 1996; Lowe, 2001; Natanson et al., 2006; reviewed by Bushnell and Jones, 1994). Ezcurra et al. (2012b) estimated growth, daily ration, and a simplified energy budget for young-of-the-year white sharks held in captivity. They found that the daily ration for four young-of-the-year white sharks held in Monterey Bay Aquarium and fed a high-caloric diet peaked at 3.5% body mass per day, yielding a mean growth rate of 71.6 ± 8.2 kg yr$^{-1}$. Based on these captive growth rates and VO$_2$ measurements, they estimated that young-of-the-year white sharks fed a high-caloric diet expended 46 ± 2.9% of their consumed energy on metabolic costs. This is 35% higher than estimates of metabolic costs for juvenile scalloped hammerhead sharks (metabolic costs = ~30%) kept in captivity and fed high-caloric diets (Lowe, 2002).
7.1.5.2 Rays

In general, myliobatoids have similar autecologies in that they are specialized for active swimming (McEachran, 1990), and experiments indicate that SMRs are similar among batoid species. For example, at 20°C, the SMRs of cownose rays, *Rhinoptera bonasus* (0.5 to 4.8 kg), and similarly sized pelagic stingrays, *Dasyatis violacea* (5 kg), were very similar (104.3 and 101.7 mg O$_2$ kg$^{-1}$ hr$^{-1}$, respectively) (Ezcurra, 2001; Neer et al., 2006). At colder temperatures, the SMRs of both bull rays, *Myliobatis australis* (77.0 mg O$_2$ kg$^{-1}$ hr$^{-1}$ at 10°C, 5 kg), and bat rays, *Myliobatis californica* (90 mg O$_2$ kg$^{-1}$ hr$^{-1}$ at 16°C, 4.3 to 6.8 kg), were also similar (DuPreez et al., 1988; Hopkins and Cech, 1994, respectively) (Figure 7.1).

7.1.6 Temperature Effects

In general, temperature has a profound and positive effect on metabolic rate (Figures 7.1 and 7.3). The increase in oxygen consumption rate caused by a $10^\circ$C increase in temperature ($Q_{10}$) (Schmidt-Nielsen, 1983) typically falls between 2 and 3 for elasmobranchs; however, variability does occur in $Q_{10}$, primarily related to the acclimation procedure of the experimental animals. For elasmobranchs exposed to rapid temperature changes, $Q_{10}$ values are generally higher. For bat rays (8 to 26°C) (Hopkins and Cech, 1994), leopard sharks (*Triakis semiferata*) (10 to 26°C) (Miklos et al., 2003), and sandbar sharks (18 to 28°C) (Dowd et al., 2006), $Q_{10}$ values were 3.0, 2.5, and 2.9, respectively. In seasonally acclimated elasmobranchs (19 to 28°C), $Q_{10}$ values were 2.3 in both cownose rays (Neer et al., 2006) and bonnetheads (Carlson and Parsons, 1999), whereas juvenile scalloped hammerhead sharks had a $Q_{10}$ of 1.3 (21 to 29°C) (Lowe, 2001). For animals that were acclimated in the laboratory for longer periods of time (e.g., weeks), $Q_{10}$ values were 1.9 for bull ray and 2.3 for guitarfish, *Rhinobatos annulatus* (10 to 25°C) (DuPreez et al., 1988). Although it is unclear why ectothermic elasmobranchs vary so much in their degrees of metabolic temperature sensitivity, this aspect of their physiological ecology may greatly influence their behavior and use of differing thermal environments (see Section 7.1.8). Although some data exist on how temperature affects swimming VO$_2$, in lamnid sharks, any prediction of the thermal effects on metabolic rate will be inherently complicated by their ability to retain metabolic heat and alter whole-body heat balance (see Section 7.3). Lamnids are known to undergo seasonal migrations to higher latitudes and exhibit rapid and repeated diurnal sojourns to deeper (i.e., colder) waters (Domeier and Nasby-Lucas, 2008; Jorgensen et al., 2009; Weng et al., 2005). Despite the fact that lamnids frequent colder waters, their ability to warm swimming muscles will alter contractile function and, to a certain degree, may lead to a decreased thermal effect on swimming metabolism, as has been shown for some tunas (Carey and Teal, 1966; Dewar et al., 1994; Dizon and Brill, 1979).

7.1.7 Muscle Metabolic Biochemistry

In addition to the direct measurement of VO$_2$, the capacity for aerobic metabolism can be assessed through the quantification of key tissue-specific biochemical indices (Dickson et al., 1993). Because continuous swimming is powered by red muscle (RM), the aerobic potential of this tissue plays a major role in whole-body metabolism; thus, it is possible to use the metabolic biochemical capacity of the RM as a proxy for the aerobic swimming potential in sharks. Most studies have generally focused on the activity of the enzyme citrate synthase (CS), which catalyzes the first step of the Krebs citric acid cycle and correlates with tissue mitochondrial density. Work on elasmobranchs has shown that when the RM metabolic enzyme activities are compared at the same temperature (e.g., 20°C), there is no marked difference among species, suggesting that the capacity for ATP production in elasmobranchs is similar regardless of the level of swimming activity. However, because lamnid sharks are capable of endothermy and the RM is warm (see Section 7.3), their enzyme activities at *in vivo* temperatures are higher than those of ectothermic sharks at 20°C. This thermal effect may significantly increase the RM CS activity of, for example, mako and salmon sharks by 48% and 123%, respectively, when the warmer *in vivo* temperatures are considered, relative to what it would be at ambient temperature (Bernal et al., 2003b). Nonetheless, the potential benefit of an increased aerobic capacity resulting from endothermy requires an increased supply of both O$_2$ and aerobic fuels to the RM, and lamnids have cardiorespiratory specializations that increase the uptake of O$_2$ at the gills and its delivery to the RM (Bernal et al., 2001a, 2003a; Wegner et al., 2010).

7.1.8 Metabolic Rates in the Field

Controlled laboratory studies provide a general basis of elasmobranch metabolism, but the question still remains as to whether those estimates determined in the laboratory are analogous to metabolic rates in the field. Similarly, the large size and high mobility of many elasmobranchs make controlled laboratory studies extremely difficult and field estimates the only practical approach.

Advances in telemetry continue to permit researchers to gather physiological data from captive and free-swimming elasmobranchs (for thorough reviews, see Lowe and Bray, 2006; Lowe and Goldman, 2001), but few studies have bridged the gap between laboratory- and field-based estimates. Sundström and Gruber (1998)
used a speed-sensing transmitter on juvenile lemon sharks in the field and correlated that data with a VO\textsubscript{2} relationship obtained in the laboratory to estimate field metabolic rates. Parsons and Carlson (1998) used speed-sensing acoustic transmitters to quantify in situ swimming speeds of bonnetheads and correlated those with VO\textsubscript{2} measured in the laboratory under different oxygen concentrations. Using a custom-made tail-beat transmitter, Lowe et al. (1998) calibrated tail-beat frequency in relation to speed and oxygen consumption which allowed for estimates of field metabolic rates by tracking free-ranging sharks with these transmitters. As noted by Lowe (2002), however, using tail-beat frequency alone as a measure of activity may be too simplistic because it does not represent acceleration and deceleration and cannot account for any alteration of tail-beat amplitude and thus reduces accuracy of field metabolic rate estimates.

A new technique to determine the locomotor activity of organisms uses accelerometers (Tanaka et al., 2001; Wilson and McMahon, 2006; Yoda et al., 2001). These sensors measure the cyclic changes in lateral position of the body that can vary with activity level and behavior. Recently, overall dynamic body acceleration has shown promise as a proxy of energy expenditure in vertebrates (Wilson and McMahon, 2006) due to the connection between acceleration and work (Gleiss et al., 2010), with some studies showing that overall dynamic body acceleration is closely correlated with oxygen consumption in a number of taxa (Halsey et al., 2009; Wilson and McMahon, 2006), including sharks (Gleiss et al., 2010). Although integrating respirometry and accelerometry technology has the capability to further bridge the gap between laboratory- and field-based metabolic measurements, it is very important that care be taken to control for the costs of carrying accelerometry data-logging packages or transmitters on smaller animals. Lowe (2002) measured the energetic costs of juvenile hammerhead sharks carrying tail-beat transmitters and found that instrumented sharks had costs of transport 25 to 35% higher than those without transmitters, a similar scenario observed between instrumented and control (non-instrumented) leopard sharks (Scharold et al., 1989).

### 7.1.9 Anaerobic Metabolism

Unlike aerobic metabolism, which is powered by the RM and can be estimated using swimming VO\textsubscript{2} measurements, there are no simple in vivo laboratory-based techniques to determine the capacity for anaerobic metabolism in swimming sharks. Anaerobic metabolism, which is powered by white muscles (WM), which comprise the majority of myotomal muscle in elasmobranchs, is the major metabolic pathway used during burst swimming, and there are currently no swim tunnels that can subject sharks to controlled and repeated bouts of burst swimming. Thus, most data on the in vivo burst swimming capacities in sharks come from field-based observations; for example, telemetry data on mako sharks show that during a rapid ascent they are capable of short-duration bursts swimming at speed in excess of 12 ms\textsuperscript{-1} (C. Sepulveda, pers. comm.). There are also numerous observations of blacktip (Carcharhinus limbatus), spinner sharks (Carcharhinus brevipinna), common thresher (Alopias vulpinus), and white sharks leaping and spinning on their body axes above the water surface, which requires considerable exertion to propel themselves out of the water (Castro, 1996; J. Carlson, pers. obs.).

A closer look at the WM metabolic capacities does reveal some differences among sharks, however. In general, elasmobranchs with similar levels of swimming activity have comparable levels of WM anaerobic metabolism (Dickson et al., 1993); for example, several key biochemical metabolic indices in WM showed that both lactate dehydrogenase (an index of anaerobic capacity) and citrate synthase (an index of the capacity to recover from anaerobic activity) were low in benthic skates and rays (Bernal et al., 2003b; Dickson et al., 1993). By contrast, the greatest capacity for anaerobic metabolism was observed for shortfin mako shark, which have significantly greater WM citrate synthase and lactate dehydrogenase levels and proton-buffering capacities than ectothermic sharks (Bernal et al., 2003b; Dickson et al., 1993). Shortfin mako sharks also have higher WM activities of creatine phosphokinase (an index of adenosine triphosphate production rate during burst swimming) than active ectothermic sharks and teleosts, which allows for redox balance to be retained during anaerobiosis (Bernal et al., 2001a, 2003b; Dickson, 1996). Although not measured to date, it is believed that mako sharks, in a manner similar to tunas, are also able to return blood and muscle lactate levels to pre-exercise more quickly than other sharks (Arthur et al., 1992). This is a consequence of the apparent capacity that the lamnid cardiorespiratory system may have to deliver oxygen and metabolic substrates at rates far above those needed at routine activity levels (Brill and Bushnell, 1991), which taken together appear to be a direct result of the selective pressures in the pelagic environment where food resources are aggregated but widely scattered and where no refuge exists for animals to hide and recover from a bout of strenuous activity (Brill, 1996; Dickson, 1995).

There are, however, some interesting cardiorespiratory differences between young mako and white sharks. Although all lamnids are thought to be obligate ram ventilators, their apparent ability to uptake and deliver oxygen to the working tissues during periods of inactivity (no swimming) vary markedly. Anecdotal observations on mako sharks suggest that, when the sharks are not
7.2 Behavioral Thermoregulation of Ectothermic Elasmobranchs

The evolution of acoustic and satellite telemetry technology has also significantly increased the number of studies on movements and habitat use of elasmobranchs (Lowe and Bray, 2006; Lowe and Goldman, 2001). An increasing number of these studies have found evidence of behavioral thermoregulation in ectothermic sharks and rays, which occurs when animals selectively move between thermal environments to achieve some potential energetic benefit. It has been hypothesized that these energetic benefits may influence growth, digestion and assimilation, and reproduction (e.g., Akerman et al., 2000; Campos et al., 2009; Di Santo and Bennett, 2011; Espinoza et al., 2011; Jirik, 2009; Klimley et al., 2005; Sims et al., 2006; Vaudo and Lowe, 2006; Weng et al., 2007). Although it is easy to demonstrate that animals use some thermal environments more than others, it can be very challenging to quantify the actual energetic benefits related to their unique and dynamic thermal preferences.

7.2.1 Foraging and Digestion

One behavioral thermoregulatory benefit for elasmobranchs may come from foraging in warm waters but returning to cooler waters to rest, particularly for species that are highly temperature sensitive (i.e., high $Q_{10}$). This scenario (hunting in warm water and resting in cooler water) is evident in, for example, California bat rays, *Myliobatis californica*, which forage in shallow warmer water during high tide but move to deeper, cooler water during low tides (Matern et al., 2000). In addition, bat rays have been shown to have a very high metabolic $Q_{10}$ of 6.8 (Hopkins and Cech, 1994; Matern et al., 2000), which may translate into significant energetic savings when resting in cooler water after a foraging event. By contrast, the sympatric leopard sharks, which also move into the warmer tidal flats during high tide, have a significantly lower metabolic $Q_{10}$ of 2.5 (Miklos et al., 2003); thus, this behavior will not result in a similar degree of energetic savings when compared to bat rays.

Work on male *Scyliorhinus canicula* also found foraging-related diel movement patterns into shallower, warmer waters at night with daytime retreats back to cooler, deeper waters (Sims et al., 2006). Even though the thermal effects on metabolic rate in this species are rather typical for ectothermic fishes ($Q_{10} = 2.16$) (Davenport and Sayer, 1993), a bioenergetic model for this species estimated that this feeding-related diel movement pattern could result in a 4% reduction in overall energetic costs (Sims et al., 2006). It is thus not surprising that similar cost-saving diel movement patterns were observed in laboratory shuttle box experiments on this species (Sims et al., 2006).

It has been hypothesized that by moving to different temperature conditions some elasmobranchs may ultimately alter the rates of digestion, thereby allowing them to maximize their energetic uptake while decreasing their energetic expenditures, such as for small-spotted catsharks (Sims et al., 1996) and bat rays (Miklos et al., 2003). Wallman and Bennett (2006) used laboratory experiments to demonstrate that the eurythermal Atlantic stingray, *Dasyatis sabina*, moved to cooler environments after feeding but returned to warmer environments when foraging. Di Santo and Bennett (2011) also used laboratory experiments to compare rates of digestion between *D. sabina* and the stenothermal whitespotted bamboo shark, *Chiloscyllium plagiosum*. They found that *D. sabina* would digest food more slowly when exposed to cooler conditions, whereas there was no significant change in rate of passage in *C. plagiosum* over the temperature range; therefore, it was concluded that *D. sabina* would benefit more by moving between different thermal environments to maximize their energy uptake depending on their prandial state. These laboratory experiments provide evidence correlating the level of metabolism in elasmobranchs to behaviorally mediated thermal preferences and movement patterns; such evidence can be used to gain knowledge on lesser well known species for which little is understood of their metabolic demands or temperature sensitivities. Endothermy may contribute to rapid digestion of prey in lamnid sharks because the stomach is located not only centrally to the body core but also directly above the suprahepatic rete and below the lateral cutaneous rete (see Section 7.3) (Carey et al., 1981; Goldman, 1997).
7.2.2 Reproduction

Another possible explanation for behavioral thermoregulation can be seen in species that show sexual segregation and where one gender, particularly mature females, tend to aggregate in warmer environments. It is hypothesized that these mature female elasmobranchs may receive some energetic benefit that enhances embryo development which may lead to shorter gestation periods when exposed to warmer environments during pregnancy (Economakis and Lobel, 1998; Hight and Lowe, 2007; Jirik, 2009). Economakis and Lobel (1998) documented that, after the mating season, gray reef sharks, *Carcharhinus amblyrhynchos*, showed sexual segregation, with numerous mature females aggregating in warm shallow lagoons, and they hypothesized that females stayed in this warmer habitat for a reproductive benefit.

Hight and Lowe (2007) followed the movement patterns and monitored internal body temperatures of aggregating mature female leopard sharks during their breeding season (summer to fall) and found that females moved into the warmest environments throughout the day but dispersed to cooler waters to forage at night. Moreover, during the daytime periods, the core body temperature of the female leopard sharks increased and even remained elevated until late evening. In a similar manner, pregnant round stingrays, *Urobatis halleri*, were found to aggregate in shallow warm embayments in southern California (Mull et al., 2008) and remained in these areas until late summer or early fall, after which time they were observed to leave just prior to parturition in October (Jirik, 2009). (Pregnancy and embryo development over the season were characterized for aggregating females using non-invasive field ultrasoundography.) By contrast, no males and few juvenile females were observed in these warm areas over the course of the season, suggesting that pregnant females may be using these warmer areas to increase embryo development under the warmer thermal conditions. In addition, evidence of an increased rate of embryo development in warmer waters has been documented in captive pregnant Atlantic stingrays. A series of thermal preference tests by Wallman and Bennett (2006) found that pregnant Atlantic stingrays selected warmer conditions more than non-pregnant females and that by being in water 1°C warmer could reduce gestation by 2 weeks. Lamnids may also achieve shorter gestation periods, not through behavioral means but by keeping their viscera (and hence reproductive system) warm (Goldman, 2002). This may be particularly true for porbeagle, *Lamna nasus*, and salmon sharks, *Lamna ditropis*, which possess a kidney (or renal) rete not found in the other lamnids.

It is important to consider that for several coastal temperate ectothermic elasmobranchs potential access to stratified thermal habitats may be important during embryo development, and the recent anthropogenic-related changes on coastal habitats (e.g., freshwater influx limitations, degradation of estuarine habitats, thermal effluent from once-through cooling systems) may enhance or degrade the quality of the habitat, thereby altering the potential growth rates or reproductive output of some species (Hoisington and Lowe, 2005; Vaudo and Lowe, 2006).

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7.3 Endothermy

In most fishes, the body temperature closely matches that of ambient water temperature because all metabolically produced heat is rapidly lost to the water either by convective transfer via the blood at the gills or by thermal conduction across the body surface (Brill et al., 1994); however, several fishes have evolved the capacity to maintain their body core and other regions of the body at a warmer temperature relative to the water they are swimming in (Bernal et al., 2001a; Block and Finnerty, 1994; Carey and Teal, 1966, 1969a,b; Carey et al., 1971). In sharks, this form of endothermy has been documented in the aerobic swimming muscles (in all lamnids and one alopiid), in the eyes and brains (in all lamnids and suspected in one alopiid), and viscera (in all lamnids and suspected in one alopiid) (Anderson and Goldman, 2001; Bernal and Sepulveda, 2005; Bernal et al., 2001a; Carey and Teal, 1969a; Carey et al., 1971, 1985; Fudge and Stevens, 1996; Goldman et al., 2004; Patterson et al., 2011). The presence of endothermy in these sharks does not appear to be the result of specialized thermogenic tissues but rather the ability to retain the metabolic heat generated by the continuous activity of the aerobic swimming muscles during sustained locomotion as well as by digestion and assimilation (Block and Carey, 1985; Carey and Teal, 1969a; Carey et al., 1981, 1985; Wolf et al., 1988). Retia also occur in the head region of myliobatid rays (Alexander, 1995, 1996); however, no temperature data are available for those species.

7.3.1 Myotomal Muscle Endothermy

In sharks, the locomotor musculature is comprised primarily of red (RM) and white (WM) myotomal muscle fiber types, which not only are morphologically different but are also spatially segregated in the body (Bone, 1988; Johnston, 1981; Rome et al., 1988). The aerobic RM fibers are myoglobin rich and are used
during continuous swimming, whereas the anaerobic WM fibers are myoglobin deficient and used during short-duration burst swimming (e.g., catching prey or predator avoidance) (Bone, 1988; Johnston, 1981). The RM in most sharks is located directly beneath the skin (i.e., laterally) along the length of the body; however, in lamnid sharks and the common thresher shark, the RM is located closer to the vertebral column (i.e., medially) and is predominantly distributed more anteriorly along the body (Bernal et al., 2001a; Carey and Teal, 1969a; Carey et al., 1971, 1985; Sepulveda et al., 2005) (Figures 7.4 and 7.6).
The most common systemic vascular layout in sharks is associated with non-endothermic (i.e., ectothermic) species (e.g., spiny dogfish) with a lateral RM position and is generally described as a central circulation, where the two major systemic vessels (i.e., dorsal aorta and post-cardinal vein) run ventral to the vertebral column and give rise to afferent arteries that radiate to, and efferent veins that return blood from, the myotomal muscles (reviewed by Patterson et al., 2011). The second vascular layout (i.e., lateral circulation pattern) in sharks is present in species with a medial RM position that are capable of RM endothermy, where two large vessels branch from either the efferent branchials or the dorsal aorta to form lateral arteries (one on each side of the body) that run directly beneath the skin along the length of the body. Although these sharks may also have a dorsal aorta, it is generally reduced in size (or may even be absent), as, in a manner similar to tunas, they rely mainly on the lateral arteries for systemic blood supply (Figure 7.4) (Carey and Teal, 1969a; Carey et al., 1971; Kishinouye, 1923; reviewed by Bernal et al., 2001a). The major systemic venous return in these sharks is also through enlarged lateral veins that run subcutaneously (very close to the lateral arteries) en route back to the heart. The lateral vessel arrangement in sharks with lateral circulation varies from a single artery and vein (i.e., shortfin mako, white shark, salmon shark, common thresher) to an artery and two veins (i.e., porbeagle shark; see Burne, 1923). In addition, the origin of the lateral arteries also differs between lamnids (from the dorsal root of the fourth efferent branchial arch with vascular connections to all arches) (Burne, 1923; Carey and Teal, 1969a) and the common thresher shark (i.e., arising from the dorsal aorta) (Patterson et al., 2011) (Figure 7.4). Nonetheless, in all sharks with a medial RM position, the arterial flow to the myotomal musculature from the lateral arteries is through smaller, thin-walled arteries that branch inward toward the RM, while venous return from the RM is through small thin-walled veins that run outward until joining the lateral veins. This unique blood flow to and from the medially positioned RM forms a network of juxtaposed vessels (retia) that do not allow for the diffusion of dissolved gases but readily allow the transfer of heat (Carey and Gibson, 1983; Carey and Lawson, 1973). This vascular anatomy effectively acts as a countercurrent heat-exchanging system that allows for thermal transfer between the cool arterial blood entering the RM and the warm venous blood leaving the RM (Carey, 1973; Carey and Teal, 1969a,b; Carey et al., 1971) and thus provides the basis for RM endothermy (Bernal et al., 2001a; Brill et al., 1994; Carey, 1973; Graham, 1983).

Endothermic sharks do show some species-specific differences in both the number of vessel rows comprising the lateral retia and whether they form contiguous blocks of blood vessels or are separated by WM fibers into smaller vascular bands. The common thresher sharks appear to only have one or two lateral rete arterial rows, while among lamnids makos have the lowest number (e.g., longfin mako, Isurus paucus, has 4 to 6; shortfin mako has 20), followed by the white shark (20 to 30), porbeagle (42 to 46), and salmon shark (60 to 69) (Bone and Chubb, 1983; Carey et al., 1985). The retia in the white shark, porbeagle, and salmon shark form vascular bands (2 to 10+ vessels) separated from one another by WM fibers, while in the shortfin mako all the vessels in the lateral retia form a dense band extending from the lateral vessels to the RM, without intervening WM fibers (Carey et al., 1985). By contrast, the longfin mako and the common thresher shark have a very simple artery–vein–artery arrangement (Bone and Chubb, 1983; Carey et al., 1985). Taken together, retia size and complexity appear to provide different degrees of heat retention in sharks, with those having the largest and most intricate retia being able to maintain the highest relative RM temperatures and penetrate the coldest waters (Figure 7.5A).

Historically, the degree to which sharks can elevate RM temperatures was typically measured by inserting a temperature probe (thermocouples or thermistors) into freshly caught fish; the resulting temperatures were plotted in relation to the sea surface temperature (SST) to indicate the thermal excess ($T_X = T_{RM} - SST$) (Anderson and Goldman, 2001; Bernal and Sepulveda, 2005; Bernal et al., 2001a; Carey and Teal, 1969a; Carey et al., 1971, 1985; Goldman et al., 2004; Patterson et al., 2011). In general, the RM $T_X$ of ectothermic sharks (i.e., lateral RM position) is small or may even be negative (i.e., RM temperature below SST) (Figure 7.5A). By contrast, sharks capable of RM endothermy have a large $T_X$ (i.e., $T_X$ of up to 17.5°C), and species having a broad latitudinal or depth distribution show that $T_X$ is largest in cold waters and smallest in warmer waters (Figure 7.5) (Bernal et al., 2001a, 2009; Carey et al., 1971, 1985). In addition, the RM $T_X$ from probed endothermic sharks ranges from 4 to 12°C (up to 17.5°C in salmon sharks) above SST, but stressed and moribund specimens generally have a lower or even negligible $T_X$ relative to live free-swimming sharks (Anderson and Goldman, 2001; Block and Carey, 1985; Carey and Teal, 1969a; Carey et al. 1985; Smith and Rhodes, 1983; D. Bernal and K.J. Goldman, pers. obs.) (Figure 7.5).

How warm do sharks have to be to be considered endothermic? A review of the thermal data available for endothermic and ectothermic fishes by Dickson (1994) proposed that a temperature elevation of at least 2.7°C above ambient be the benchmark for determining whether a species is capable of RM endothermy. Based on this criterion, the in vivo temperature measurements...
of all lamnid sharks and the common thresher shark indicate their capacity for RM endothermy. By contrast, TX data for other sharks suggest they are not capable of RM endothermy (Figure 7.5). Recent work on pelagic (Alopias pelagicus) and bigeye (Alopias superciliosus) threshers found that all myotomal muscles (i.e., RM and WM) were colder than SST (i.e., negative $T_X$) (Figure 7.5A) and showed a marked decrease in temperature from the exterior (lateral RM) toward the WM near the vertebrae (Figure 7.6); this temperature closely matched the ambient temperature at the depth of capture (Figure 7.5B). By contrast, the thermal data collected for lamnids and the common thresher shark indicated that the warmest in vivo RM temperature measurements were

![Figure 7.5](image_url)
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all greater than the SST; the transverse thermal gradient reflected the coolest temperatures proximal to the skin (body periphery), while the warmest measurements were in the vicinity of the medial RM (i.e., near the vertebrae) (Figure 7.6). Further, when compared to the temperatures at the depth of capture, lamnids and the common thresher RM showed a pronounced \( T_x \) (Figure 7.5B) (Bernal and Sepulveda, 2005; Patterson et al., 2011).

Previous work on bigeye thresher sharks by Carey et al. (1971) reported that two specimens had a positive \( T_x \) but that study also mentioned that these specimens were captured in waters where a marked thermal inversion was present (SST = 12.7°C, 30 m = 22°C) and that it was not possible to determine the precise depth at which the sharks were swimming prior to capture. Therefore, it is possible that, if those bigeye thresher sharks were swimming within the cold inversion layer prior to capture, their muscle temperatures would be warmer than the SST. The different result from bigeye threshers (Figure 7.5A) illustrates the inherent types of problems with relying solely on SST as a benchmark for determining the presence of RM endothermy and make it clear that future work not only must consider the thermal stratification of the water column but should also establish the depth at which the sharks were swimming prior to capture.

In general, water temperature in the upper 500 m of the ocean changes with depth (i.e., temperature decreases with increasing depth), and unless a fish swims at a continuous depth for a prolonged period of time it will be subject to changes in water temperatures that will inevitably alter heat balance (i.e., RM \( T_x \)). Thus, the ideal benchmark for determining the capacity for endothermy should be the degree to which tissue temperature is elevated relative to the ambient temperature at which the fish was swimming prior to capture. Accordingly, it becomes apparent that the RM temperature of ectothermic sharks closely matches that of the water at depth, and, by contrast, the RM temperatures for lamnids and the common thresher are not only consistently warmer than the SST (Figure 7.5A) but are both markedly warmer than ambient (Figure 7.5B) and the adjacent WM (Figure 7.6). However, the full extent to which the sharks are capable of RM endothermy still

FIGURE 7.6
Thermal profiles inwards from the skin in (A) pelagic thresher (ectotherm) and (B) salmon shark (endotherm). The thermal data are superimposed on a half-transverse section taken at mid-body showing the position of the red muscle (RM) and heat-exchanging rete (only in part B). SST, sea surface temperature. Temperature probes were inserted along the x-axis following the arrow. (From Patterson, J. et al., J. Morphol., 272(11), 1353–1364, 2011. With permission.)
remains unresolved, as it requires simultaneous measurements of (1) RM temperature, (2) ambient temperature at which the shark was swimming, (3) the duration of time spent at depth, and (4) an index of the level of swimming activity (i.e., metabolic heat production).

Because RM endothermy relies on the retention of metabolically produced heat during sustained, aerobic swimming, the swimming activity level of a shark prior to sampling can influence the degree to which the shark elevates its RM temperature. Therefore, any reduction in swimming activity due to an interaction with fishing gear that leads to exhaustion could act to reduce RM $T_X$ when the shark is sampled boatside (Bernal and Sepulveda, 2005; Carey et al., 1985; Goldman et al., 2004). For this reason, thermal studies on sharks routinely select for specimens that were actively swimming when landed; however, a better assessment of the capacity for RM endothermy in sharks comes from acoustic telemetry determinations of tissue temperatures in free-swimming sharks (Figure 7.7) and from laboratory-based work on sharks swimming in a water tunnel. In combination, these thermal data show that lamnids have the capacity to alter thermal balance in response to changes in ambient temperature and offer evidence of physiological thermoregulation (Bernal et al., 2001b; Carey and Lawson, 1973). Specifically, when makos were exposed to changes in the ambient water temperature while swimming at a constant speed, the magnitude

![Acoustic telemetry tag with external thermistor used to measure internal muscle temperature](image1)

![Acoustic telemetry tag used to measure depth and ambient water temperature](image2)

![Acoustic telemetry tag with extended thermistor inserted into the internal muscle](image3)

**Figure 7.7**
(See color insert.) (A) Close-up of the dorsal fin area of a 140-kg salmon shark (*Lamna ditropis*) showing the acoustic telemetry tag with an external thermistor and a real-time reading of red muscle temperature (i.e., 26.0°C) using a temperature probe. (B) Final tag placement with the extended thermistor inserted ~15 cm into the internal muscle. (Photographs courtesy of Kenneth J. Goldman.) (C) An example of vertical movement patterns of a salmon shark (shown in part B) in the Gulf of Alaska showing 9 hours of depth, ambient temperature, and internal muscle temperature recorded during an ~15.5-hour acoustic telemetry track (no data available between 14:00 and 14:40). Notice the degree to which the internal muscle temperature remains elevated relative to that of ambient water temperature, particularly during the dive between 15:00 and 16:30. (Data from K.J. Goldman, unpublished.)

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and direction of changes in $T_x$ indicated their ability to modulate rates of heat retention and heat loss (presumably by altering blood-flow rate and retial heat-transfer efficiency) (Block and Carey, 1985; Brill et al., 1994; Carey and Teal, 1969a, b; Carey et al., 1982; Dewar et al., 1994; Graham, 1983).

### 7.3.2 RM Endothermy and Movement Patterns

Several hypotheses have been proposed on the selective advantages of RM endothermy in fishes (Block and Finnerty, 1994; Carey et al., 1985; Dickson and Graham, 2004). One hypothesis that has received much attention and support is that of thermal niche expansion, in which the increased thermal capacity of fishes with RM endothermy may allow them to exploit the additional food resources found in cooler waters at both a greater depth and at higher latitudes (Bernal et al., 2001a). Although this scenario applies to lamnids, in which the capacity for RM endothermy appears to be linked to latitudinal distribution and thermal tolerance, it does not appear to explain the different thermal distributions of the alopoids (see below) nor does it help explain how several pelagic carcharhinids (e.g., blue shark, *Prionace glauca*) (Carey and Scharold, 1990) have the capacity to undergo prolonged dives into cooler waters.

Recent studies documenting the movement patterns and distribution of all three thresher species show that, although there may be overlap in their distributions, the ectothermic bigeye thresher routinely dives to greater depths, the endothermic common thresher enters higher latitudes, and the ectothermic pelagic thresher remains most of the time in tropical waters (Cartamil et al., 2010, 2011; Heberer et al., 2010; Liu et al., 1999; Nakano et al., 2003; Weng and Block, 2004; D. Bernal, J. Martinez, and G. Skomal, unpublished). In addition, tracking and tagging data have shown that the bigeye thresher has the greatest thermal tolerance and is able to penetrate cold ambient temperatures ($6$ to $10°C$) for extended periods of time ($6$ to $8$ hours) (Nakano et al., 2003; Weng and Block, 2004). This ability of the bigeye thresher to routinely penetrate cold temperatures for prolonged periods of time will inevitably lead to a low RM $T_x$. Recent findings have shown that in lamnids and common thresher sharks a decrease in temperature has a dramatic detrimental effect on the RM if it cools slightly below its *in vivo* operating temperature (Bernal et al., 2005; Donley et al., 2007; J. Donley, C. Sepulveda, and D. Bernal, unpublished), so the fact that bigeye threshers are able to tolerate such cold temperatures for an extended period of time during their dives is perplexing. If, for example, the RM temperature of salmon sharks, which commonly inhabit water cooler than $10°C$ and as cold as $2°C$ (Weng et al. 2005), falls below $20°C$ then this tissue stops producing positive work (Bernal et al., 2005). In addition, a similar, but less pronounced, muscle performance deterioration has been documented for the RM of mako sharks if cooled below $15°C$ (Donley et al., 2007), even though this species repeatedly dives below the thermocline to water temperatures cooler than $13°C$ (Holts and Bedford, 1993; Sepulveda et al., 2004). By contrast, these thermal effects are not as prominent for other sharks that are not capable of RM endothermy (e.g., leopard shark) in which muscle function is still possible, albeit much slower (i.e., lower cycle frequencies) at cooler temperatures (below $15°C$) (Donley et al., 2007). Thus, unlike the bigeye thresher, regional RM endothermy enables both lamnids and the common thresher to maintain their RM temperatures within a narrow range even when subject to cool ambient conditions and, therefore, may decrease any thermal-induced loss of muscle function when in deeper (colder) waters. The fact still remains that the bigeye thresher, a species that lacks RM endothermy, routinely experiences cold temperatures and somehow maintains adequate muscle performance over a much greater thermal range than the other two thresher species.

Other pelagic sharks, however, that are not capable of RM endothermy share the vertical (i.e., temperature–depth) and horizontal (latitude) distribution of lamnids and the common thresher shark. For example, blue sharks inhabit similar water temperatures and spend extensive periods below the thermocline (Carey and Scharold, 1990). Upon closer examination of the vertical movement data for blue sharks, lamnids, and the common thresher, there appears to be a small difference in the lower limit of water temperature that these sharks routinely penetrate, but a striking difference becomes apparent in both the frequency and duration at which these species undergo their vertical oscillations. Acoustic telemetry data for a blue shark showed that an approximately 150-minute incursion from the relatively warm surface waters ($26°C$) down to depths below the thermocline ($9°C$) resulted in a decrease in deep WM (i.e., body core) temperature from about $21$ to $14°C$ (Carey and Scharold, 1990). If the shark remained at this depth for an additional 300 minutes, its WM (i.e., body core) temperature would ultimately decrease until reaching thermal equilibrium with ambient (Bernal et al., 2009). By contrast, if a mako shark underwent the exact same vertical dive pattern, its physiological ability to alter rates of heat gain and heat loss (Bernal et al., 2001b) would provide it with an overall warmer RM operating temperature throughout the majority of vertical excursions (Bernal et al., 2009). This outcome becomes even more pronounced if these sharks undergo repeated vertical movements with brief periods of basking at the surface (Holts and Bedford, 1993; Sepulveda et al., 2004) (Figure 7.8). In this scenario, the body temperature of the blue sharks would decline progressively with each descent, while the mako
shark would maintain a more stable and warmer RM operating temperature (Bernal et al. 2009). Thus, RM endothermy may, therefore, not provide an overall larger tolerance to colder surface water, but rather it may provide the ability to make frequent sojourns into cooler water (Neill et al., 1976). On the other hand, fishes with RM endothermy may also be able to inhabit very cold, highly productive, subpolar waters (e.g., 2 to 10°C) for prolonged periods of time (i.e., numerous months), while maintaining an almost constant RM temperature 20°C or more above ambient (Goldman et al., 2004) as long as there is an ample supply of metabolic heat (i.e., aerobic swimming) to maintain RM endothermy (Figure 7.7).

7.3.3 Eye and Brain Endothermy

Whereas the eye and brain temperatures of most sharks are in thermal equilibrium with ambient water, lamnid sharks are able to elevate the temperatures of these organs through the strategic placement of heat-exchanging retia and other modifications of the vascular supply to these tissues (Anderson and Goldman, 2001; Bernal et al., 2001a; Block and Carey, 1985; Wolf et al., 1988). Unlike specialized teleosts (i.e., billfish, swordfish, tuna, and opah) (Block, 1986, 1987; Carey, 1982; Runcie et al., 2009; Sepulveda et al., 2007b) where vascular and ocular muscle specializations have been reported as the main brain-heat-producing mechanisms, lamnid sharks have a specialized vessel that transports warm venous blood from the RM to the brain and eyes. This unique vein is embedded deep within the RM and proceeds toward the head, where it joins the myelonal vein prior to entering a vascular plexus in the meningeal membrane that covers the brain. Thus, warm blood arriving from the RM drains through the posterior cerebral veins into a large sinus within the orbital cavity (i.e., the orbital sinus) (Wolf et al. 1988) and effectively elevates the temperature of the brain from 3°C above SST in mako (Block and Carey, 1985) to as much as 9.5°C above mean SST in salmon sharks (Anderson and Goldman, 2001; Bernal et al., unpublished).

The general arterial blood supply to the eyes and brain in sharks, including lamnids, is through the efferent hyoidean and pseudobranchial arteries, which
deliver oxygenated blood that is at thermal equilibrium with ambient (due to their origin at the gills). However, in lamnids these arteries coil extensively and run anteriomedially and enter the orbital sinus (which is filled with warm venous blood arriving from the RM vein), in which the hyoidean artery branches into many smaller vessels to form a rete (Alexander, 1998; Block and Carey, 1985). In all lamnids, the pseudobranchial artery coils profusely within the sinus, and both its diameter and wall thickness decrease significantly, forming a true pseudobranchial rete in the salmon and porbeagle sharks but not in the mako and white shark (Alexander, 1998; Tubbesing and Block, 2000). Nonetheless, the arteries exiting the orbital sinus perfuse the eye and extraocular muscles with warmed arterial blood that in mako elevates the temperature of the eye 2.8°C above SST (Alexander, 1998; Block and Carey, 1985) and in salmon shark as much as 12.9°C above SST (Anderson and Goldman, 2001; D. Bernal and J. Graham, unpublished). In addition, the eyes receive warm blood from a tributary of the cerebral arteries, which send warmed blood to the brain after passing through the orbital sinus (Alexander, 1998; Block and Carey, 1985). Although the bigeye thresher shark has also been suspected of having cranial endothermy (Block and Finnerty, 1994; Carey, 1982; Weng and Block, 2004), no temperature data are available. Additionally, two species of myliobatoid rays possess cranial retia (Alexander, 1996); however, no temperature measurements have been obtained from these species, so their body temperatures and thermoregulatory abilities (if any) remain unknown.

Some workers have suggested that, in lamnids, the extraocular eye muscles may play a role in producing metabolic heat that aids in brain and eye endothermy (Alexander, 1998; Wolf et al., 1988). Indeed, relative to other sharks, lamnids have more than twice the relative extraocular eye muscle mass (comprising 50 to 60% of the total eye weight), and the extraocular eye muscles are a darker red color, suggesting high levels of aerobic metabolism (Alexander, 1998; Block and Carey, 1985; Wolf et al., 1988). Recent morphological and histological examinations of the six extraocular muscles of the shortfin mako shark and other lamnids indicate that they lack the structural specializations for thermogenesis found in the specialized ocular muscle heater tissues of certain teleosts (Block, 1986, 1987; Carey, 1982; Runcie et al. 2009; Sepulveda et al., 2007b; Dickson, pers. comm.). However, preliminary evidence found that all six extraocular muscles are larger as a percentage of total eye mass in *Iurus oxyrinchus* than in *Prionace glauca*, and the specific activity of CS in the medial rectus extraocular muscles of the shortfin mako is significantly higher than that of the ectothermic blue shark (K. Dickson, pers. comm.). Thus, it is possible that contraction of all six extraocular muscles generates heat for cranial endothermy in *I. oxyrinchus*, with muscle mass contributing more than CS activity to interspecific differences in heat production capacity.

In fishes, warming of the brain and eye region has been shown to enhance physiological processes such as synaptic transmission, postsynaptic integration, conduction, and, in the eye, temporal resolution (Friedlander et al., 1976; Fritsches et al., 2005; Konishi and Hickman, 1964; Montgomery and Macdonald, 1990; van den Burg et al., 2005). Recent work on swordfish (*Xiphias gladius*) shows that the flicker fusion frequency of the eye is extremely temperature sensitive (thermal coefficient, $Q_{10}$ of 5.1) and that warming the retina significantly improves temporal resolution (Fritsches et al., 2005). Thus, warming the retina likely enhances the swordfish’s ability to detect and capture fast-moving prey at low temperatures and in dimly lit waters (Block, 1986; Fritsches et al., 2005). The convergence of cranial endothermy among billfishes, tunas, and lamnids sharks suggests a strong selection for this trait among pelagic predators that need to conserve sensory and integrative functions while in the cooler and darker deep water (Alexander, 1998; Block, 1991; Block and Carey, 1985; Linthicum and Carey, 1972; Sepulveda et al., 2007b; Wolf et al. 1988).

### 7.3.4 Visceral Endothermy and Homeothermy

The capacity to elevate and maintain visceral temperatures above ambient is present in all lamnid sharks and has been suspected in the common thresher shark (Bernal et al., 2001a; Carey et al., 1985; Fudge and Stevens, 1996; Goldman, 1997; Goldman et al., 2004; Sepulveda et al., 2004); however, the structural specializations in lamnids and the common thresher differ significantly. In general, blood delivery to the viscera of sharks is through the coelaic artery, but in lamnids the visceral circulation relies mainly on the delivery of arterial blood via greatly enlarged pericardial arteries that arise from the ventral region of the third and fourth efferent branchial arteries (Burne, 1923; Carey et al., 1981). These arteries extend posteriorly and branch repeatedly to form the suprahepatic rete, which is completely enclosed within a venous sinus. Before exiting this venous sinus, the arterial vessels of the rete coalesce to form a large vessel that sends warm blood to the viscera. Thus, unlike in eothermic sharks, the principal flow of blood to and from the viscera (stomach, liver, spiral valve) in lamnids is through the suprahepatic rete. It has been suggested that visceral thermal balance may be altered by changing blood flow to evade the suprahepatic rete (Carey et al., 1981) by: (1) delivering arterial blood via the dorsal aorta to the relatively reduced celiac, spermatic, and lineogastric arteries, which flow into the viscera; or (2) bypassing the venous return through the suprahepatic...
rete into the sinus via a large central channel that bypasses the suprahepatic rete and empties directly into the sinus venosus (Burne, 1923; Carey et al., 1981; K. Goldman and D. Bernal, pers. obs.). Carey et al. (1981) described the presence of smooth and circular muscle within the walls of this venous vessel and suggested that this passage may be opened or closed in order to regulate (up to 20% of) returning blood flow through or around the rete. The blood delivery to the viscera of thresher sharks appears to be considerably different from lamnids based on a very brief description of visceral retia from a common thresher shark (Eschricht and Müller, 1835, in Fudge and Stevens, 1996). Eschricht and Müller (1835) described a number of retia, including a single rete along the portal vein to several others associated with the stomach wall and spiral valve. Although these retia appear to be different from those observed in tunas and porbeagle sharks (Burne, 1923), there is still a need to undergo a detailed description of visceral retia in sharks so the differences between alopriid and lamnid sharks can be clearly addressed.

Although lamnids and the common thresher differ in the location and complexity of the retia that enable visceral heat conservation, both groups appear to utilize heat produced from digestion (catabolism) to maintain elevated gut temperatures. For example, probed lamnid visceral temperatures (stomach, liver, spiral valve) range from 4 to 14°C above mean SST (Anderson and Goldman, 2001; D. Bernal and C. Sepulveda, unpublished), and the spiral valve, which digests and assimilates food arriving from the stomach and has a large size and surface area, is among the warmest organs or tissues and thus may be a main source of visceral heat production (Anderson and Goldman, 2001; D. Bernal, unpublished). In salmon and porbeagle sharks, the spiral valve and surrounding area may be assisted in staying warm due to proximity to the kidney or renal rete (Burne, 1923; K.J. Goldman and D. Bernal, pers. obs.); however, the role that this and other organs (e.g., the liver) play in lamnid visceral heat production is unknown. Temperature measurements show that the $T_x$ within the renal rete ranges from 8 to 11.4°C (Anderson and Goldman, 2001; D. Bernal and J. Graham, unpublished), suggesting a highly effective heat-conserving function. Unfortunately, there are no visceral temperature data for any thresher shark species, leaving a gap in our knowledge of that group's ability to elevate and potentially thermoregulate body core temperature.

Whereas white sharks possess a slightly higher absolute mean body temperature than other lamnids, the maximum relative stomach temperature elevation over ambient is 8°C for shortfin mako sharks (Carey et al., 1981), 14.3°C for white sharks (Goldman, 1997), and 21.2°C for salmon sharks (Goldman et al., 2004). Stomach temperature is a good indicator and proxy for body core temperature due to its central location in the viscera and its proximity to the suprahepatic and lateral cutaneous retia (Goldman, 1997; Goldman et al., 2004). Thermal data obtained via acoustic telemetry from mako, white, and salmon sharks show that stomach temperature remains elevated over ambient, is uniform within a very narrow range, and appears to be independent of changes in ambient temperature (Carey et al., 1981; Goldman, 1997; Goldman et al., 2004; McCosker, 1987; Sepulveda et al., 2004) (Figure 79). All stomach and body core temperature data from adult lamnid sharks obtained to date support the homeothermy hypothesis of Lowe and Goldman (2001). Adult lamnids appear to essentially function as homeotherms, in a way analogous to mammals, through a combination of thermal inertia and physiological thermoregulation. Additionally, the presence of elevated visceral temperatures has been considered to be a potential mechanism for enhancing the rate of digestion and assimilation (Carey, 1981; Goldman, 1997; Stevens and McLeese, 1984) and may also be a significant contributor to the warming of the body core, which may allow these fishes to penetrate and inhabit cool waters (reviewed by Dickson and Graham, 2004).

### 7.3.5 Endothermy and Blood-Oxygen Binding

In all sharks, the temperature of the blood leaving the gills and entering the systemic circulation is in thermal equilibrium with ambient conditions; however, in lamnids, as this cool blood approaches the RM it passes through the retia, where it is rapidly warmed by heat transfer from the venous blood returning from the warm RM. Efficient countercurrent heat exchange within the rete minimizes heat loss from the RM; however, changes in the temperature of the blood have the potential of altering the partial pressure of oxygen (PO$_2$) and affecting diffusion (Carey et al., 1971, 1985). For example, in sharks the warming of arterial (oxygen-rich) blood is expected to lower the affinity of hemoglobin (Hb) for oxygen, driving bound O$_2$ off Hb and into the plasma and increasing arterial blood PO$_2$ (reviewed by Bernal et al., 2009). Thus, because the rete arteries in lamnids and the common thresher shark are in close proximity to the oxygen-poor veins, a diffusion gradient would form and an arterial to venous short circuit for oxygen diffusion could potentially result in decreased O$_2$ delivery to the RM. Moreover, an acute change in the temperature of the blood modifies Hb quaternary structure (Rossi-Fanelli and Antonini, 1960), and, in addition to O$_2$ binding, this could also affect CO$_2$ transport and acid–base regulation (Nikinmaa and Salama, 1998). It is possible that in lamnids the presence of elevated hematocrit, hemoglobin, and myoglobin (equivalent to those of birds and mammals) (Emery, 1985) may play a role in buffering against the potential detrimental effects of a decreased blood-oxygen affinity by warming of the blood.
Recent work on blue and mako sharks subjected their blood to rapid temperature changes under PO$_2$ and PCO$_2$ conditions that mimicked blood passing through the rete. For blue sharks, the arterial blood-oxygen equilibrium curves showed the expected thermally induced right-shift (O$_2$ affinity decrease), while mako shark blood-oxygen equilibrium curves were hardly affected by this rapid warming (D. Bernal, J. Graham, and J. Cech, unpublished). This apparent temperature insensitivity decreases the potential for trans-retial oxygen diffusion and ensures the efficient delivery of oxygen to the aerobic RM and other tissues. These results for whole mako blood are similar to findings for both tunas and other lamnids in which neither crystallized Hb nor whole blood preparations showed expected loss of oxygen affinity with an increase in temperature (Andersen et al., 1973; Brill and Bushnell, 1991; Cech et al., 1994; Larsen et al., 2004; Rossi-Fanelli and Antonini, 1960; Sharp, 1975). Thus, the presence of a low thermal effect on oxygen binding in some tunas and lamnids reflects their convergence for endothermy and the need to prevent premature oxygen dissociation within the rete.

Future studies of the blood-oxygen binding properties in the tropically distributed longfin mako, coldwater salmon, and porbeagle sharks, as well as the three thresher species, may demonstrate the importance of changes in ambient temperature and RM $T_{X}$ on blood-oxygen affinity. For example, the longfin mako and pelagic thresher are distributed in tropical environments and, to some extent, appear to have either a small RM $T_{X}$ or none at all (Carey et al., 1985) (Figure 7.5). Therefore, thermal sensitivity in the blood-oxygen binding properties of these species is predicted. In contrast, salmon, porbeagle, and common thresher sharks penetrate cold waters, and in some species a large RM $T_{X}$ (Figure 7.5) is necessary to maintain proper RM function (Bernal et al., 2005). Thus, for those species an adequate delivery of O$_2$ to the warm RM may require thermally insensitive blood-oxygen binding properties.

**Figure 7.9**

Stomach ($T_s$) and water temperature obtained by acoustic telemetry in three species of free-swimming lamnid sharks. Juvenile shortfin mako (male and female) tracks from Sepulveda et al. (2004) ranged from 6.8 to 45.4 consecutive hours, whereas tracks from Carey et al. (1981) were separated by size with the juvenile (136-cm) mako tracked for just over 5 hours and the adult (240 cm) mako tracked continuously for over 4 days. White shark (male and female) tracks ranged from 5.3 to 7.3 non-consecutive hours (data were accumulated over 7- to 10-day periods) on individuals estimated to be between 370 and 490 cm (Goldman, 1997). Salmon shark tracks ranged from 3.8 to 20.7 consecutive hours on females (Goldman et al., 2004). Mean ambient water temperatures are from the swimming depth (or mean swimming depth, $T_w$) of all shark studies except Sepulveda et al. (2004), which used sea surface temperature (SST). Data for this figure were summarized from text and figures in the above cited papers.
7.4 Summary

Considerable progress has been made since Carlson et al. (2004) on elucidating the energetic requirements of elasmobranchs. Trends in standard metabolic rates still follow the continuum analogous to teleost fishes in that cooler water species have lower metabolic demands with respective to more active tropical species. Research using a suite of techniques from biochemical assays to archival satellite tracking has revealed that lamnid sharks possess the highest metabolic capacities, which may enable this group of sharks to exploit a variety of niches from deepwater habitats to subarctic seas (e.g., Weng et al., 2005). Still, issues remain with regard to laboratory testing, especially of larger individuals, and correlation of these estimates with valid determinations in the field. Further work should also focus on quantifying the energetic tradeoffs of behavioral and physiological thermoregulation, and greater attention should be given to studying the thermal effects on elasmobranch energetics, especially in ectothermic species that experience large changes in temperature (seasonally and diurnally) and those capable of endothermy. In addition, little is known about the effects of scaling on metabolic rates in elasmobranchs, which span a wide range of body mass and include some of the largest fishes in the ocean; future work should combine laboratory and field experiments and incorporate energetic modeling. There also is a need to quantify how endothermy may vary across size and age classes in lamnid and alopaid sharks and the degree to which free-swimming sharks can remain warm and have the capacity to thermoregulate.

Acknowledgments

We thank J. Valdez, T. Tazo, S. Adams, and T. Reposado for their unwavering logistical support. We are indebted to Jeff Carrier for being so patient and flexible with our multiple deadlines. Most importantly, we thank our wives, children, and pets for being so understanding about the time we had to dedicate to this piece of work. This work is dedicated to J.B Graham (grandpa). For some of us, not enough can be said to describe the significant impact he has had on our work and in our lives.

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