Oxygen Consumption Rate of Young-of-the-Year White Sharks, *Carcharodon carcharias*, during Transport to the Monterey Bay Aquarium

**Juan M. Ezcurra**
Monterey Bay Aquarium

**Christopher G. Lowe**
California State University, Long Beach

**Henry F. Mollet**
Monterey Bay Aquarium and Moss Landing Marine Laboratories

**Lara A. Ferry**
Arizona State University

**John B. O’Sullivan**
Monterey Bay Aquarium

**ABSTRACT**

In 2002, the Monterey Bay Aquarium (MBA) started a project to display young-of-the-year (YOY) White Sharks (*Carcharodon carcharias*) in the 3.8-million-L Outer Bay exhibit and to conduct field research on the movement patterns of this highly active predator in the Southern California Bight. A pelagic fish transport tank used to bring YOY White Sharks to the MBA between 2004 and 2009 allowed the first direct measurements of oxygen consumption rates (MO₂) of free-swimming White Sharks during transport, ranging in duration between 5 and 7.5 h. We obtained MO₂ data during five transports of four individual White Sharks [137–157 cm of total length (TL) and 22.6–36.2 kg of body mass] at water temperatures ranging from 15.2 to 17.9°C. The mass-specific MO₂ calculated from 16 measurements for the four sharks was 246 ± 13 mg O₂ kg⁻¹ h⁻¹ (mean ± SE), which is...
among the highest reported for any shark species. Total MO$_2$ values of White Sharks from our study were pooled with the routine metabolic rate of the Shortfin Mako Shark to estimate the mass-scaling relationship for lamnid sharks, which is described by the allometric equation $MR = 458.5 \times M^{0.79}$.

**INTRODUCTION**

The White Shark is a large, highly active predator that is known to undergo long-distance migrations that can span thousands of kilometers (Boustany et al., 2002; Bonfil et al., 2005; Bruce et al., 2006; Weng et al., 2007a; Domeier and Nasby-Lucas, 2008; Jorgensen et al., 2010; Chapters 11, 12, 13, 16, and 21, this book). It is a member of the family Lamnidae and is a regional endotherm using vascular, countercurrent heat exchangers (*retia mirabilia*) to maintain elevated tissue temperatures (Carey and Teal, 1969; Carey et al., 1981, 1982, 1985; Block and Carey, 1985; Goldman et al., 1996; Goldman, 1997; Bernal et al., 2001b, 2005). Elevated tissue temperatures and increased activity levels in this species have lead researchers to theorize that White Sharks have high metabolic demands (Lowe and Goldman, 2001; Carlson et al., 2004). Because of the difficulty of obtaining live specimens and their high mobility and large size, field or laboratory studies on the metabolic rate of the White Shark have not been conducted. However, the capture of small White Sharks has enabled measurements comparable to those obtained for another lamnid, the Shortfin Mako (*Isurus oxyrinchus*) (Graham et al., 1990; Bernal et al., 2001b; Sepulveda et al., 2007).

In 2002, the MBA initiated a field project to study young-of-the-year (YOY) White Sharks in the Southern California Bight and took steps toward placing a live specimen on public display. Studies using pop-up satellite archival tags of YOY White Sharks that were incidentally captured by commercial fishers have allowed researchers to gain a better understanding of the migratory patterns and thermal niche of these juvenile sharks (Dewar et al., 2004; Weng et al., 2007b). Since 2004, access to these YOY White Sharks has allowed the MBA to place four sharks on public display in the 3.8-million-L Outer Bay exhibit, which houses a community of pelagic fishes, including the Yellowfin (*Thunnus albacares*) and Bluefin (*Thunnus orientalis*) tunas. The opportunity to handle live YOY White Sharks allowed staff at the MBA to record oxygen consumption rates during transport of this species, which has not been previously maintained successfully in aquaria (Chapter 1, this book). This chapter presents an estimate of the mass-specific metabolic rate as determined from oxygen consumption rates (MO$_2$) of four YOY sharks. The objective was to determine the allometric equation that describes the increase in metabolic rate with increasing body mass of the White Shark and the closely related Shortfin Mako Shark (*I. oxyrinchus*) to allow comparison between these lamnid sharks and other pelagic species.

**MATERIALS AND METHODS**

Oxygen consumption rate data (MO$_2$) were obtained for four YOY White Sharks during transport from a 40-m-diameter ocean pen anchored in the Southern California Bight to the MBA between September 14, 2004 and August 26, 2009. These sharks ranged in size from 137 to 157 cm of TL and 22.6 to 36.2 kg of body mass (Table 2.1) and were held from 10 to 25 d in the ocean pen to allow their recovery from capture stress and begin feeding prior to transport. Sharks scheduled for transport were not fed for at least 24 h prior to their being netted from the ocean pen, placed unrestrained in a 250-L vinyl shark box containing oxygenated seawater (~125% saturation) at 16°C, and equipped with a recirculating submersible pump (4164 lph; Rule Industries, Gloucester, MA), which provided ventilation during the 30–90-min. transport via boat to the shore (15–30 km). Each shark was then transferred to an 11,356-L pelagic fish transport tank (Figure 2.1) mounted on the trailer of a commercial tractor for the drive to the MBA (524 km). Upon placement in the transport tank, the sharks were able to swim unimpeded, and at times they would rest on the bottom of the tank for periods of 30–90 sec during the approximately 6-h trip to Monterey. One individual, shark
Table 2.1  White-Shark Total Length (cm), Mass (kg), Mean Temperature (°C), and Oxygen Consumption Rate (MO2) as Calculated for Each Individual Run during the Transports of Four Sharks to the Monterey Bay Aquarium and One Shark Transported from the Aquarium to Santa Barbara, CA to Be Released (#08-01 on September 7, 2008)

<table>
<thead>
<tr>
<th>White Shark Number</th>
<th>Transport Destination Date: Run</th>
<th>Shark Total Length (cm)/Mass (kg)</th>
<th>MO2 (mg O2 kg⁻¹ h⁻¹)</th>
<th>Mean Temperature (°C)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>To MBA</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>04-01</td>
<td>September 14, 2004: #1</td>
<td>141/28.0</td>
<td>348.0</td>
<td>15.5 ± 0.02</td>
</tr>
<tr>
<td>04-01</td>
<td>September 14, 2004: #2</td>
<td>141/28.0</td>
<td>226.3</td>
<td>16.5 ± 0.01</td>
</tr>
<tr>
<td>07-01</td>
<td>August 28, 2007: #1</td>
<td>143/30.6</td>
<td>267.2</td>
<td>17.1 ± 0.01</td>
</tr>
<tr>
<td>07-01</td>
<td>August 28, 2007: #2</td>
<td>143/30.6</td>
<td>202.6</td>
<td>18.3 ± 0.01</td>
</tr>
<tr>
<td></td>
<td>To MBA</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>08-01</td>
<td>August 27, 2008: #1</td>
<td>137/25.2</td>
<td>370.4</td>
<td>16.6 ± 0.01</td>
</tr>
<tr>
<td>08-01</td>
<td>August 27, 2008: #2</td>
<td>137/25.2</td>
<td>256.9</td>
<td>17.1 ± 0.01</td>
</tr>
<tr>
<td>08-01</td>
<td>August 27, 2008: #3</td>
<td>137/25.2</td>
<td>267.7</td>
<td>17.5 ± 0.01</td>
</tr>
<tr>
<td>08-01</td>
<td>August 27, 2008: #4</td>
<td>137/25.2</td>
<td>281.2</td>
<td>17.8 ± 0.01</td>
</tr>
<tr>
<td></td>
<td>To MBA</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>08-01</td>
<td>September 7, 2008: #1</td>
<td>137/22.6</td>
<td>189.9</td>
<td>16.8 ± 0.01</td>
</tr>
<tr>
<td>08-01</td>
<td>September 7, 2008: #2</td>
<td>137/22.6</td>
<td>223.1</td>
<td>17.2 ± 0.01</td>
</tr>
<tr>
<td>08-01</td>
<td>September 7, 2008: #3</td>
<td>137/22.6</td>
<td>235.2</td>
<td>17.4 ± 0.01</td>
</tr>
<tr>
<td>08-01</td>
<td>September 7, 2008: #4</td>
<td>137/22.6</td>
<td>189.9</td>
<td>17.5 ± 0.01</td>
</tr>
<tr>
<td></td>
<td>To MBA</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>09-01</td>
<td>August 26, 2009: #1</td>
<td>157/36.2</td>
<td>247.0</td>
<td>16.8 ± 0.02</td>
</tr>
<tr>
<td>09-01</td>
<td>August 26, 2009: #2</td>
<td>157/36.2</td>
<td>226.2</td>
<td>17.0 ± 0.01</td>
</tr>
<tr>
<td>09-01</td>
<td>August 26, 2009: #3</td>
<td>157/36.2</td>
<td>198.0</td>
<td>17.5 ± 0.02</td>
</tr>
<tr>
<td>09-01</td>
<td>August 26, 2009: #4</td>
<td>157/36.2</td>
<td>215.0</td>
<td>17.6 ± 0.01</td>
</tr>
</tbody>
</table>

Figure 2.1  Young-of-the-year White Shark swimming in the pelagic fish transport tank (volume, 11,356 L) during transport to the Monterey Bay Aquarium for public display. (Courtesy of Randy Wilder, Monterey Bay Aquarium.)
During transport, oxygen levels in the transport tank were maintained between 8 and 11 mg L$^{-1}$ by delivering pure oxygen from an oxygen cylinder and regulator through flexible airline tubing to Venturi injectors in the filtration piping (Figure 2.2). Water flow in the chamber was driven through a filter loop by a ¾ HP pool pump (Hayward Industries, Inc., Elizabeth, NJ) operated during transport. The transport tank could not be shut with an airtight seal because of the presence of baffles, which were used to reduce motion at the surface of the water. Water temperature, pH, and oxygen concentration data were logged with a YSI Model 556 Multi Probe system that sampled water off the main filtration loop. Transport water pH declined (maximum decrease was 0.4 units pH) because of the production of CO$_2$ by the shark during transport; however, the pH remained above 7.4 because of the large water volume in the transport tank.

Total MO$_2$ values for each shark were calculated from the rate of decline in oxygen concentration of the transport water during periods when oxygen was not added to the system. Linear regression was used to calculate the rates of total oxygen decline, which were corrected by subtracting estimates of background oxygen depletion obtained prior to each transport. Background oxygen depletion could not be measured at the end of the transports because the water was drained from the tank to remove the shark. Total MO$_2$ was calculated as Total MO$_2$ = −slope ((mg O$_2$ L$^{-1}$) min.$^{-1}$) × water volume (11,356 L) × 60 min. h$^{-1}$. Each shark was measured and weighed using an Intercomp model CS 1500 hanging scale prior to being placed on display, and shark #08-01 was reweighed prior to transport for release. At the time of release, all of the sharks were tagged with pop-up archival satellite tags according to the methods used by Weng et al. (2007b). The satellite tagging results demonstrated that the sharks survived at least 30–180 d following release.

RESULTS

Water temperature and pH did not change significantly during the transports. Surface water temperature at the ocean pen was approximately 20°C (±1°C), and upon capture all sharks were
transferred to the 250-L shark box, which contained water at a temperature of 16°C. Water temperature in the pelagic fish transport tank ranged from 15.2 to 17.9°C (mean ± SE = 17.1 ± 0.3°C) during transports. Slight temperature increases (1.03 ± 0.12°C) occurred during individual transports (Table 2.1). Linear regressions of time and oxygen concentration, made during specific periods when oxygen was not being injected into the transport tank, showed a significant negative relationship (p < 0.0001; Figure 2.2).

In most cases, the trend for the mass-specific MO$_2$ values was to decline with time. Background oxygen decline versus time without the shark in the transport tank yielded values of 1.5–69.3 mg O$_2$ h$^{-1}$, which were subtracted from each result to yield adjusted total MO$_2$ values for each run. The mass-specific MO$_2$ values for the four sharks ranged between 189.9 and 370.4 mg O$_2$ kg$^{-1}$ h$^{-1}$ (Table 2.1). The mean mass-specific MO$_2$ values for each shark were very similar, ranging from 221.5 ± 10.3 to 287.2 ± 60.8 mg O$_2$ kg$^{-1}$ h$^{-1}$, and the mean for all four sharks was 246.5 ± 13.1 mg O$_2$ kg$^{-1}$ h$^{-1}$.

The routine metabolic rate (RMR) for the Shortfin Mako Shark (Sepulveda et al., 2007) and the total MO$_2$ of the White Shark were combined and plotted as a function of body mass to calculate the allometric equation ($MR = a \times M^b$), which describes the increase in metabolic rate with increasing body mass and the mass-scaling coefficient (b) for lamnid sharks. For comparison of lamnid sharks with other elasmobranchs and endothermic teleosts, the metabolic rates for other species of elasmobranchs were temperature adjusted to 17°C using a $Q_{10}$ of 2.3 (Carlson et al., 2004) and then analyzed in the same manner described above.

**DISCUSSION**

Because measurement of metabolic rate was secondary to the husbandry and display of White Sharks, the metabolic data reported in this study were obtained during the transport of specimens from the field to the MBA. This approach, while limited, has added to our understanding of the metabolic rate for lamnid sharks. The ratio of White Shark mass to water volume (2.0–3.2 $\times$ 10$^{-3}$ kg L$^{-1}$) of our transport tank is almost identical to that of the Shortfin Mako Sharks studied in a swim tunnel respirometer (1.5–3.2 $\times$ 10$^{-3}$ kg L$^{-1}$) used by Graham et al. (1990) and Sepulveda et al. (2007). However, the inability of our system to be closed with an airtight seal was a drawback to our method, as necessitated by the transports. It is possible that the unsealed surface of the tank allowed oxygen to be lost to the surrounding environment; therefore, to account for this loss, our background oxygen decline was measured at the highest oxygen differential between the water (~120% saturation) and atmosphere prior to the sharks being placed into the tank. This oxygen loss from the system, in addition to variation in background respiration, may have contributed to some of the variability in oxygen consumption rates of the sharks. Alternatively, it is possible that the background oxygen decline measured is an underestimate of background respiration because it was measured at the beginning of the transports. The good fit between time and oxygen decline during the respiration runs to a linear model ($r^2$ values greater than 0.96) suggests that no oxygen was entering the water system via leaks in the plumbing during the respirometry runs. Swimming of the White Sharks was erratic at times and less efficient than straight-line swimming because of the amount of turning necessitated by the confines of the transport tank (Weihs, 1981). At times, the sharks would stall and rest on the bottom of the tank for brief periods; however, rough estimates of approximate swimming speed fall within the range of swimming speeds for juvenile Shortfin Mako Sharks studied by Graham et al. (1990) and Sepulveda et al. (2007). Although swimming speed could not be controlled, our study provides the only oxygen consumption rates for YOY White Sharks obtained by direct measurement to date.
Despite the limitations of this study, the oxygen consumption rate reported for YOY White Sharks appears to fit well with the RMR reported for the Shortfin Mako Shark, which are among the highest reported for any pelagic shark (Graham et al., 1990; Sepulveda et al., 2007). The mean mass-specific VO₂ from this study (246 ± 13 mg O₂ kg⁻¹ h⁻¹) is lower than the values reported by Graham et al. (1990) and Sepulveda et al. (2007) for the Shortfin Mako at similar experimental temperatures (369 ± 11 and 344 ± 22 mg O₂ kg⁻¹ h⁻¹), as would be expected for White Sharks that were four to five times greater in body mass. To account for these differences in body mass, metabolic rate data (mg O₂ h⁻¹) for the Shortfin Mako (Sepulveda et al., 2007) and White Sharks (this study) were pooled to estimate the scaling relationship for lamnid sharks described by the allometric equation \( M \text{RMR} = 458.5 \times M^{0.79} \) (Figure 2.3). The mass-scaling coefficient, \( b \), for lamnid is very similar to the range of \( b \) values (mean = 0.8) reported for other elasmobranch and teleost species to date (Parsons, 1990; Ezcurra, 2001; Korsmeyer and Dewar, 2001; Dowd et al., 2006). The similarity in oxygen consumption rates in these two closely related species are very similar. An elevated metabolic rate for both of these endothermic, lamnid sharks would be expected based on their high activity level and capacity for high-performance swimming (Bernal et al., 2001a; Donley et al., 2004). In addition, endothermy increases the efficiency of the aerobic, red muscles used in continuous swimming (Bernal et al., 2001) and is theorized to provide a selective advantage for these species during “bounce diving” forays into cool waters during vertical oscillatory swimming patterns associated with prey search (Dewar, 2004; Sepulveda et al., 2004; Weng et al., 2007b).

Lamnid sharks have metabolic rates that are much higher than those of ectothermic, pelagic sharks and more similar to those of endothermic tunas (Figure 2.3). The experimental temperature

![Figure 2.3](image-url)
in our study (17°C) was generally lower than the temperatures in other metabolic studies, which necessitated temperature adjustment of RMR reported for other sharks (Q₁₀ of 2.3; Carlson et al., 2004). In addition, the body mass of the White Sharks (22.6–36.2 kg) was 2–30 times greater than that of sharks in other metabolic studies (Bushnell et al., 1989; Carlson et al., 1999; Lowe, 2001; Dowd et al., 2006). However, when differences in temperature and body mass are taken into account, the RMR for lamnids is approximately five times greater than the RMR for species of ectothermic, obligatory ram-ventilating sharks (Figure 2.3). Although they are more divergent taxonomically, the metabolic rate for lamnid sharks is closer to that of Bluefin and Yellowfin Tuna at minimal swimming speeds (0.65–1.0 body lengths s⁻¹) at similar experimental temperatures (Fitzgibbon et al., 2006; Blank et al., 2007; Figure 2.3). The convergent evolution of high-performance swimming and endothermy in the lamnid sharks and tunas has resulted in specialized morphology and physiology (streamlined body shape; internalized aerobic, red muscle capable of retaining metabolic heat; elevated enzyme activities associated with aerobic and anaerobic metabolism in white muscle; large gill surface area; low blood-water barrier thickness; and a circulatory system with a high-oxygen delivery capacity to the tissues) in these distant groups (Dickson et al., 1993; Bernal et al., 2001a; Korsmeyer and Dewar, 2001; Donley et al., 2004; Sepulveda et al., 2007; Wegner et al., 2010). Until now, comparisons of metabolic rate and swimming kinematics between these two groups have been limited, because studies focusing on lamnids have been restricted to the Shortfin Mako Shark (Graham et al., 1990; Bernal et al., 2001b; Donley et al., 2004; Sepulveda et al., 2007). By using methods developed to transport highly active, ram-ventilating tunas (Farwell, 2001), we have been able to report the first direct measurement of oxygen consumption rates of YOY White Sharks. Continued implementation of these methods could lead to further studies of White Shark metabolic rates and swimming kinematics under laboratory conditions to advance our understanding of energetics in lamnid sharks.

ACKNOWLEDGMENTS

Many thanks go to a very talented and diverse group of people who have made this study possible, including the crew of the F/V Barbara H, Randy Hamilton, Dr. Mike Murray, Chuck Winkler, Chuck Farwell, Joe Welsh, Bobby Bettancourt, and the staff of the husbandry and applied research departments at the MBA. Thanks also to Ellen Freund, Dan Cartamil, Nick Wegner, Jeffrey Graham, and an anonymous reviewer for their helpful comments and suggestions for this manuscript. J. M. E. especially thanks his family for their understanding and support during his absences while working in the field.

REFERENCES


