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

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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 (MO_2) of free-swimming White Sharks during transport, ranging in duration between 5 and 7.5 h. We obtained MO_2 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 MO_2 calculated from 16 measurements for the four sharks was 246 ± 13 mg O_2 kg^{-1} h^{-1} (mean ± SE), which is

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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 oxyrhinchus*) (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 16ºC, 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 (MO$_2$) 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)

White Shark Number	Transport Destination Date: Run	Shark Total Length (cm)/ Mass (kg)	MO$_2$ (mg O$_2$ kg^{-1} h^{-1})	Mean Temperature (°C)
		To MBA		
04-01	September 14, 2004: #1	141/28.0	348.0	15.5 ± 0.02
04-01	September 14, 2004: #2	141/28.0	226.3	16.5 ± 0.01
07-01	August 28, 2007: #1	143/30.6	267.2	17.1 ± 0.01
07-01	August 28, 2007: #2	143/30.6	202.6	18.3 ± 0.01
		To MBA		
08-01	August 27, 2008: #1	137/25.2	370.4	16.6 ± 0.01
08-01	August 27, 2008: #2	137/25.2	256.9	17.1 ± 0.01
08-01	August 27, 2008: #3	137/25.2	267.7	17.5 ± 0.01
08-01	August 27, 2008: #4	137/25.2	281.2	17.8 ± 0.01
		To Release Site		
08-01	September 7, 2008: #1	137/22.6	189.9	16.8 ± 0.01
08-01	September 7, 2008: #2	137/22.6	223.1	17.2 ± 0.01
08-01	September 7, 2008: #3	137/22.6	235.2	17.4 ± 0.01
08-01	September 7, 2008: #4	137/22.6	189.9	17.5 ± 0.01
		To MBA		
09-01	August 26, 2009: #1	157/36.2	247.0	16.8 ± 0.02
09-01	August 26, 2009: #2	157/36.2	226.2	17.0 ± 0.01
09-01	August 26, 2009: #3	157/36.2	198.0	17.5 ± 0.02
09-01	August 26, 2009: #4	157/36.2	215.0	17.6 ± 0.01
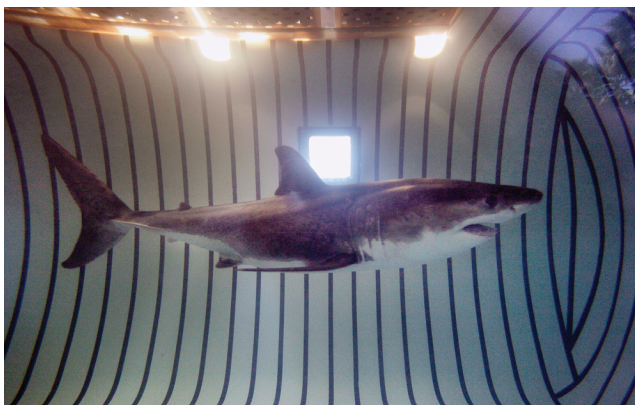
Figure 2.1 Young-of-the-year White Shark swimming in the pelagic fish transport tank (volume, 11,356 L) during transport to the Monterey Bay Aquarium for public display. (Courtesy of Randy Wilder, Monterey Bay Aquarium.)
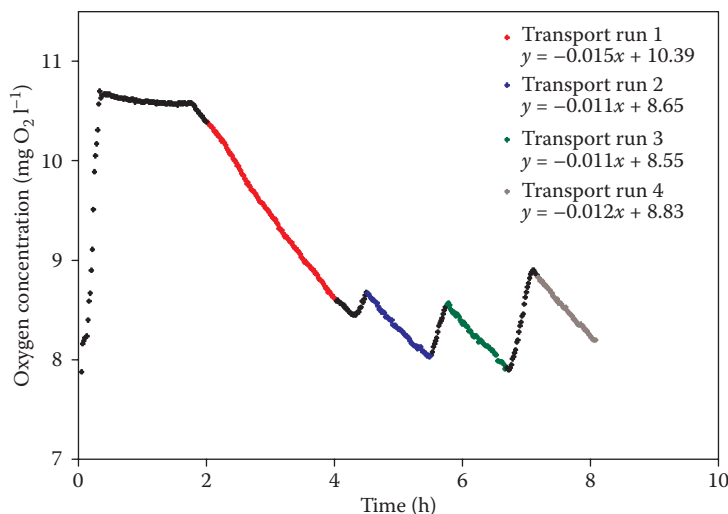
Figure 2.2   The seawater dissolved oxygen concentration (mg O_2 L^{-1}) profile in the 11,356-L transport tank during the transport of a 25.2-kg female White Shark (#08-01) to the Monterey Bay Aquarium from Southern California on August 27, 2008. Oxygen consumption rates (MO_2) for the White Shark were determined by using linear regression analysis of oxygen concentration (mg O_2 L^{-1}) versus time (minutes) for each of the four periods (depicted in color) when oxygen was not injected into the transport tank.

#08-01, was also transported back to Southern California for release on September 7, 2008 because of inconsistent feeding while on display.

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 20ºC (±1ºC), and upon capture all sharks were

transferred to the 250-L shark box, which contained water at a temperature of 16ºC. Water temperature in the pelagic fish transport tank ranged from 15.2 to 17.9ºC (mean ± SE = 17.1 ± 0.3ºC) during transports. Slight temperature increases (1.03 ± 0.12ºC) 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 17ºC 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 × 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 × 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 swimming speed from video of sharks #08-01 and #09-01 taken immediately after introduction to the transport tank ranged from approximately 58 to 81 cm s^{-1} or 0.4 to 0.5 TL s^{-1}. These 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 MO_2 from this study (246 ± 13 mg O_2 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 O_2 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 O_2 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 $MR = 458.5 \times M^{0.79}$ (Figure 2.3). The mass-scaling coefficient, b, for lamnids 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 the mass-scaling coefficient from our study to those reported for other species suggests that 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., 2005) 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
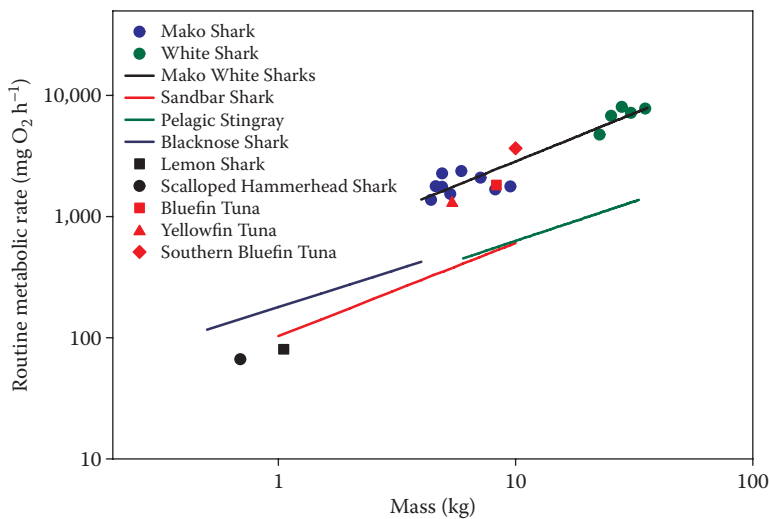
Figure 2.3 RMR (mg O_2 h^{-1}) of lamnid sharks (Shortfin Mako Shark, *I. oxyrinchus*, Sepulveda et al., 2007; White Shark, *C. carcharias*, present study) in relation to mass (kilograms) compared with other active pelagic sharks and tunas. The lines are for RMR calculated over a range of mass with the allometric equation RMR = aM^b. The line describing the RMR in relation to mass for lamnid sharks is 458.5 $M^{0.79}$, from log (a) = 2.66 ± 0.08 (SE) and slope (b) = 0.79 ± 0.08 (SE). Lemon Shark (*Negaprion brevirostris*, Bushnell et al., 1989), Scalloped Hammerhead Shark (*Sphyrna lewini*, Lowe, 2001), Pelagic Stingray (*Dasyatis violacea*, Ezcurra, 2001, RMR = 140.1 $M^{0.65}$), Blacknose Shark (*Carcharhinus acronotus*, Carlson et al., 1999, RMR = 446.8 $M^{0.62}$), and Sandbar Shark (*Carcharhinus plumbeus*, Dowd et al., 2006, RMR = 102.7 $M^{0.77}$) were temperature-adjusted to 17°C by using a Q_{10} of 2.3 (Carlson et al., 2004). Metabolic rates for Yellowfin and Bluefin Tuna (*T. albacares* and *T. orientalis*, Blank et al., 2007 at 20°C) and Southern Bluefin Tuna (*Thunnus maccoyii*, Fitzgibbon et al., 2006 at 19°C) were for tunas swimming at swimming speeds of 0.65–1.0 body lengths s^{-1}.

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 (Q_{10} 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

REFERENCES

Bernal, D., K. A. Dickson, R. E. Shadwick, J. B. Graham. 2001a. Analysis of the evolutionary convergence for high performance swimming in lamnid sharks and tunas. *Comp Biochem Physiol* 129A: 695–726.

Bernal, D., J. M. Donley, R. E. Shadwick, D. A. Syme. 2005. Mammal-like muscles power swimming in a cold-water shark. *Nature* 437: 1349–1357.

Bernal, D., C. A. Sepulveda, J. B. Graham. 2001b. Water-tunnel studies of heat balance in swimming mako sharks. *J Exp Biol* 204: 4043–4054.

Blank, J. M., C. J. Farwell, J. M. Morrissette, R. J. Schallert, B. A. Block. 2007. Influence of swimming speed on metabolic rates of juvenile Pacific bluefin tuna and yellowfin tuna. *Physiol Biochem Zool* 80: 167–177.

Block, B. A., F. G. Carey. 1985. Warm brain and eye temperatures in sharks. *Comp Biochem Physiol* 156B: 229–236.

Bonfil, R., M. Meyer, M. C. Scholl, R. Johnson, S. O'Brien, H. Oosthuizen, S. Swanson, D. Kotze, M. Paterson. 2005. Transoceanic migration, spatial dynamics, and population linkages of white sharks. *Science* 310: 100–103.

Boustany, A. M., S. F. Davis, P. Pyle, S. D. Anderson, B. J. Le Boeuf, B. A. Block. 2002. Satellite tagging: Expanded niche for white sharks. *Nature* 415: 35–36.

Bruce, B. D., J. D. Stevens, H. Malcolm. 2006. Movements and swimming behaviour of white sharks (*Carcharodon carcharias*) in Australian waters. *Mar Biol* 150: 161–172.

Bushnell, P. G., P. L. Lutz, S. H. Gruber. 1989. The metabolic rate of an active, tropical elasmobranch, the lemon shark (*Negaprion brevirostris*). *J Exp Biol* 48: 279–283.

Carey, F. G., J. G. Casey, H. L. Pratt, D. Urquhart, J. E. McCosker. 1985. Temperature, heat production and heat exchange in lamnid sharks. *Mem S Calif Acad Sci* 9: 92–108.

Carey, F. G., J. W. Kanwisher, O. Brazier, G. Gabrielson, J. G. Casey, H. L. Pratt, Jr. 1982. Temperature and activities of a white shark, *Carcharodon carcharias*. *Copeia* 1982: 254–260.

Carey, F. G., J. M. Teal. 1969. Mako and porbeagle: Warm bodied sharks. *Comp Biochem Physiol* 28A: 199–204.

Carey, F. G., J. M. Teal, J. W. Kanwisher. 1981. The visceral temperatures of mackerel sharks (lamnidae). *Physiol Zool* 54: 334–344.

Carlson, J. K., J. K. Goldman, C. G. Lowe. 2004. Metabolism, energetic demand, and endothermy. In: J. C. Carrier, J. A. Musick, M. R. Heithaus (eds.), *Biology of sharks and their relatives* (pp. 203–224). Boca Raton, FL: CRC Press Inc.

Carlson, J. K., C. L. Palmer, G. H. Parsons. 1999. Oxygen consumption rate and swimming efficiency of the blacknose shark, *Carcharhinus acronotus*. *Copeia* 1999: 34–39.

Dewar, H., M. Domeier, N. Nasby-Lucas. 2004. Insights into young of the year white sharks (*Carcharodon carcharias*) behavior in the Southern California Bight. *Environ Biol Fishes* 70: 133–143.

Dickson, K. A., M. O. Gregorio, S. J. Gruber, K. L. Loefler, M. Tran, C., Terrrel. 1993. Biochemical indices of aerobic and anaerobic capacity in muscle tissues of California elasmobranch fishes differing in typical activity level. *Mar Biol* 117: 185–193.

Domeier, M. L., N. Nasby-Lucas. 2008. Migration patterns of white sharks *Carcharodon carcharias* tagged at Guadalupe Island, Mexico, and identification of an eastern Pacific shared foraging area. *Mar Ecol Prog Series* 370: 221–237.

Donley, J. M., C. A. Sepulveda, P. Konstantinidis, S. Gemballa, R. E. Shadwick. 2004. Convergent evolution in mechanical design of lamnid sharks and tunas. *Nature* 429: 61–65.

Dowd, W. W, R. W. Brill, P. G. Bushnell, J. A. Musick. 2006. Standard and routine metabolic rates of juvenile sandbar sharks (*Carcharhinus plumbeus*), including the effects of body mass and acute temperature change. *Fish Bull* 1104: 323–331.

Ezcurra, J. M. 2001. The mass-specific routine metabolic rate of captive pelagic stingrays, *Dasyatis violacea*, with comments on energetics. MS thesis, Moss Landing Marine Laboratory, California State University, Stanislaus.

Farwell, C. J. 2001. Tunas in captivity. In: B. A. Block, E. D. Stevens (eds.), *Tunas: Physiology, Ecology and Evolution* (pp. 391–412). San Diego, CA: Academic Press.

Fitzgibbon, Q. P., R. S. Seymour, D. Ellis, J. Buchanan. 2006. The energetic consequence of specific dynamic action in southern bluefin tuna *Thunnus maccoyii*. *J Exp Biol* 210: 290–298.

Goldman, K. J. 1997. Regulation of body temperatures in the white shark, *Carcharodon carcharias. J Comp Physiol Biochem* 167: 423–429.

Goldman, K. J., S. D. Anderson, J. E. McCosker, A. P. Klimley. 1996. Temperature, swimming, depth, and movements of a white shark at the South Farallon Islands, California. In: A. P. Klimley, D. G. Ainley (eds.), *Great white sharks: The biology of Carcharodon carcharias* (pp. 111–120). San Diego, CA: Academic Press.

Graham, J. B., H. Dewar, N. C. Lai, W. R. Lowell, S. M. Arce. 1990. Aspects of shark swimming performance determined using a large water tunnel. *J Exp Biol* 151: 175–192.

Jorgensen, S. J., C. A. Reeb, T. K. Chapple, S. Anderson, C. Perle, S. R. Van Sommeran, C. Fritz-Cope, A. C. Brown, A. P. Klimley, B. A. Block. 2010. Philopatry and migration of Pacific white sharks. *Proc R Soc B Biol Sci* 277: 679–688.

Korsmeyer, K. E., H. Dewar, 2001. Tuna metabolism and energetics. In: B. A. Block, E. D. Stevens (eds.), *Tunas: Physiology, ecology and evolution* (pp. 35–78). San Diego, CA: Academic Press.

Lowe, C. G. 2001. Metabolic rates of juvenile scalloped hammerhead sharks (*Sphyrna lewini*). *Mar Biol* 139: 447–453.

Lowe, C. G., K. J. Goldman. 2001. Physiological telemetry of elasmobranchs: Bridging the gap. *Environ Biol Fishes* 60: 251–256.

Parsons, G. R. 1990. Metabolism and swimming efficiency of the bonnethead shark, *Sphyrna tiburo*. *Mar Biol* 104: 363–367.

Sepulveda, C. A., J. B. Graham, D. Bernal. 2007. Aerobic metabolic rates of swimming juvenile mako sharks, *Isurus oxyrinchus*. *Mar Biol* 152: 1087–1094.

Sepulveda, C. A., S. Kohin, C. Chan, R. Vetter, J. B. Graham. 2004. Movement patterns, depth preferences, and stomach temperatures of free-swimming juvenile mako sharks, *Isurus oxyrinchus*, in the Southern California Bight. *Mar Biol* 145: 191–199.

Wegner, N. C., C. A. Sepulveda, K. R. Olson, K. A. Hyndman, J. B. Graham. 2010. Functional morphology of the gills of the shortfin mako, *Isurus oxyrinchus*, a Lamnid shark. *J Morphol* 27: 937–948.

Weihs, D. 1981. Effects of swimming path curvature on the energetics of fish motion. *Fish Bull* 79: 171–176.

Weng, K. C., A. M. Boustany, P. Pyle, S. D. Anderson, A. Brown, B. A. Block. 2007a. Migration and habitat of White Sharks (*Carcharodon carcharias*) in the eastern Pacific Ocean. *Mar Biol* 152: 877–894.

Weng, K. C., J. B. O'Sullivan, C. G. Lowe, C. E. Winkler, H. Dewar, B. A. Block. 2007b Movements, behavior and habitat preferences of juvenile white sharks *Carcharodon carcharias* in the eastern Pacific. *Mar Ecol Prog Ser* 338: 211–224.