Abstract—Standard and routine metabolic rates (SMRs and RMRs, respectively) of juvenile sandbar sharks (*Carcharhinus plumbeus*) were measured over a range of body sizes (n=34) and temperatures normally associated with western Atlantic coastal nursery areas. The mean SMR Q_{10} (increase in metabolic rate with temperature) was 2.9 ±0.2. Heart rate decreased with increasing body mass but increased with temperature at a Q_{10} of 1.8–2.2. Self-paired measures of SMR and RMR were obtained for 15 individuals. Routine metabolic rate averaged 1.8 ±0.1 times the SMR and was not correlated with body mass. Assuming the maximum metabolic rate of sandbar sharks is 1.8–2.75 times the SMR (as is observed in other elasmobranch species), sandbar sharks are using between 34% and 100% of their metabolic scope just to sustain their routine continuous activity. This limitation may help to explain their slow individual and population growth rates, as well as the slow recoveries from overfishing of many shark stocks worldwide.

Standard and routine metabolic rates of juvenile sandbar sharks (*Carcharhinus plumbeus*), including the effects of body mass and acute temperature change*

W. Wesley Dowd[1]

Richard W. Brill[2]

Peter G. Bushnell[3]

John A. Musick[1]

[1] Department of Fisheries Science
Virginia Institute of Marine Science
1208 Greate Road, P.O. Box 1346
Gloucester Point, Virginia 23062
Present address (for W. W. Dowd): Department of Wildlife, Fish and Conservation Biology
University of California Davis
One Shields Avenue,
Davis, California 95616

E-mail address (for W. W. Dowd): wwdowd@ucdavis.edu

[2] Virignia Cooperative Marine Education and Research Program
Virginia Institute of Marine Science
1208 Greate Road, P.O. Box 1346
Gloucester Point, Virginia 23062

[3] Department of Biological Sciences
Indiana University South Bend
1700 Mishawaka Avenue
South Bend, Indiana 46634

Shark populations continue to suffer from overfishing throughout the Northwest Atlantic and worldwide (Baum et al., 2003). The sandbar shark (*Carcharhinus plumbeus*) can serve as a model for overfished coastal shark species, many of which share ecological and ecophysiological characteristics. After the rapid expansion of the Atlantic coastal commercial shark fishery in the mid-1980s, sandbar shark numbers declined 66% by 1991 (Musick et al., 1993; Sminkey and Musick, 1995). Like many of their K-selected relatives, sandbar sharks grow slowly and mature after a minimum of 13–15 years (Casey and Natanson, 1992; Sminkey and Musick, 1995). Demographic models of these species predict very slow rates of population increase even in the absence of fishing pressure, and elasticity analyses of these models demonstrate that the juvenile stage is the most critical life history stage (Sminkey and Musick, 1996; Cortes, 1999; Brewster-Geisz and Miller, 2000). It is necessary, therefore, to understand the actual and potential contributions of various juvenile nursery areas to recovery of the Northwest Atlantic sandbar shark population and to recovery of other coastal shark stocks (Branstetter, 1990).

Bioenergetics models can be used to assess the impacts and requirements of juvenile sharks as apex predators. Metabolic rate is the largest and most variable component of the energy budget for active fish species, and it is critical that it be determined accurately in order to construct realistic bioenergetics models (Ney, 1993). Systematic metabolic rate data for elasmobranchs are only rarely available, and previous models of sandbar shark bioenergetics have relied upon metabolic rate data from unrelated species (Medved et al., 1988; Stillwell and Kohler, 1993).

The lower Chesapeake Bay, Mid-Atlantic Bight, and adjacent coastal lagoon systems serve as the primary summer nurseries for sandbar sharks in the Northwest Atlantic (Musick et al., 1993). Juvenile sandbar sharks return for four to ten years to these nursery grounds, where they enjoy the benefits of generally high food availability and limited exposure to large shark predators (Musick and Colvocoresses, 1986; Grubbs et al., in press). Juvenile sandbar sharks in the nurseries are exposed to seasonal water temperature variations, as well as shorter time-scale fluctuations associated with their vertical movements and day to day variation. The minimum seasonal temperatures (≈15°C) occur in mid or late May, whereas the maximum temperatures (≈28°C) are reached in surface waters in July and August (Merson and Pratt, 2001). Throughout the day, sandbar sharks perform frequent vertical excursions and thus experience surface and bottom water temperatures that can differ by up to 5°C (Grubbs, 2001). Similarly, in Virginia's Eastern Shore lagoons, juvenile sandbar sharks venture onto broad, warm tidal flats at high tide and return to deeper, cooler channels as the tide recedes (Conrath[1]).

To improve bioenergetics models and to define critical habitat and the current suitability of nursery areas more accurately, standard (SMR) and routine metabolic rates (RMR) of juvenile sandbar sharks were measured over a relevant range of body masses (≈1 to 10 kg) and temperatures (18–28°C) (Merson and Pratt, 2001). This is the first direct measurement of SMR, and the first comparison of paired SMR and RMR, in a continuously active carcharhiniform species.

Materials and methods

All experiments were conducted at the Virginia Institute of Marine Science Eastern Shore Laboratory from June through September 2002. Sandbar sharks (57–124 cm total length; 1.025–10.355 kg) were captured by using hook and line from the surrounding tidal lagoon system and maintained in shoreside tanks (temperature 22–29°C, salinity 34–36‰). Individuals were fasted for at least 48 hours prior to use in an experiment to reduce any confounding effects of specific dynamic action (Medved, 1985).

Standard metabolic rates

Because sandbar sharks are continuously active obligate ram ventilators, SMR measurements were obtained from chemically immobilized and artificially ventilated animals maintained in flow-through, sealed box respirometers (Brill, 1979, 1987; Leonard et al., 1999). Respirometers were constructed of 0.85 cm thick acrylic, sized to accommodate the fish being studied, and cov-

ered with black plastic to minimize visual disturbance. Aerated and filtered seawater from a constant pressure head tank passed through the mouth and over the gills of the sharks, was mixed in the chamber by a small recirculating pump, and exited the respirometer by a hose mounted at the top. Water leaving the respirometer was collected, re-aerated, and mixed with a small amount of fresh filtered seawater to help maintain a constant temperature. Turnover rate for the system was 20–30%/hour (Steffensen, 1989).

Sharks were netted, injected with 0.4–1.8 mg/kg of the neuromuscular blocking agent pancuronium bromide through the caudal vein, and returned to the holding tank until they were unable to swim (typically 1–2 min). They were then placed supine on a moist towel and ventilated with aerated seawater while electrocardiogram (EKG) wire leads were inserted subcutaneously over the pectoral girdle to monitor heart rate. Individuals were also given an intramuscular injection (0.2–1.2 mg/kg) of steroid anesthetic Saffan® (alphaxalone and alphadolone; Pitman-Moore, Uxbridge, UK) (Oswald, 1978). Two 20-gauge hypodermic needles were inserted into the dorsal musculature and used to administer supplementary doses of pancuronium bromide and Saffan® whenever any slight tail movement was observed.

The partial pressure of oxygen (PO_2, mm Hg) in the seawater was measured with a polarographic oxygen electrode (Radiometer A/S, Copenhagen, Denmark) mounted in a water-jacketed cuvette (maintained at the experimental temperature) and connected to a digital oxygen meter (Cameron Instruments Company, Port Aransas, TX). All equipment was calibrated to manufacturer's specifications. Oxygen level in the inflow water was measured hourly, and outflow water was otherwise monitored continuously. Water temperature, PO_2, and heart rate were recorded every 10 seconds with a computerized data acquisition system (Daqbook 120 with a DBK52 thermocouple expansion card; Iotech, Inc., Cleveland, OH). The inflow ventilation volume (V_g, L/min) was adjusted to keep oxygen extraction between 10% and 20%. Measured PO_2 values were converted to oxygen content (mg O_2/L) following Richards (1965) and Dejours (1975). Standard metabolic rate (mg O_2/h) was calculated by using the Fick principle (Steffensen, 1989). Because the effects of pancuronium bromide were not reversible, at the end of each experiment individuals were euthanized with a massive overdose of sodium pentobarbital injected into the caudal vein. Sex was then determined and they were weighed to the nearest five grams and measured (precaudal and total lengths).

Standard metabolic rate data for each individual were plotted against time and averaged over all hours (range 1–7 hours) after the outflowing PO_2 stabilized. Standard metabolic rate measurements were obtained at 24 ±1°C on 33 of the 34 animals. In addition, 18 animals were exposed to acute temperature changes (to 18 ±1°C or 28 ±1°C, or to both). Temperature change rates averaged 4.5 ±0.6°C per hour and 6.4 ±1.1°C per hour for cooling and heating, respectively, although these were not statistically different ($t = -1.46$, df=36, P=0.15). Data

collection was not resumed until at least one hour after the chamber had equilibrated to the new temperature (Steffensen, 1989). In order to minimize any systematic errors, the direction of temperature change was not always the same. To quantify the effects of acute temperature changes on SMR and heart rate, Q_{10} values were calculated over the temperature ranges 18–24°C, 24–28°C, and 18–28°C by following the methods of Schmidt-Nielsen (1997).
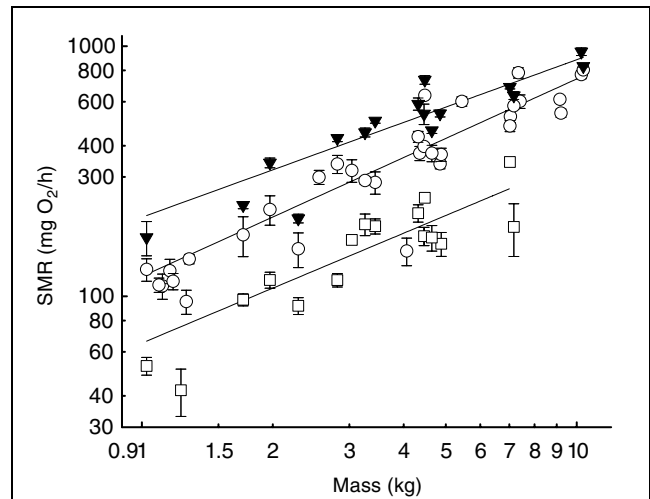
Routine metabolic rates

An annular respirometer (1250 L; diameter 167 cm) was used to measure RMR (Bushnell et al., 1989; Parsons, 1990; Carlson et al., 1999). A cage (diameter 61 cm) was placed in the center to force the sharks to swim around the perimeter of the tank. Water temperature was controlled during an experiment at 24–26°C by adjusting room temperature.

Sharks were transferred to the respirometer and allowed to recover for 30–90 minutes. The tank was sealed and data recording continued until oxygen content was reduced by 15% (≈two hours). The tank water was then re-oxygenated before the next measurement by pumping the seawater through a membrane oxygenator (Medtronics, Inc., Minneapolis, MN) (Steffensen et al., 1984). A complete RMR experiment consisted of one to five iterations of this process.

Oxygen concentration (mg O_2/L) was measured with a YSI 57 oxygen meter by using a YSI 5739 polarographic electrode oxygen-temperature probe (Yellow Spring Instruments, Yellow Spring, OH). Water temperature and oxygen content were recorded at 20-second intervals with a computerized data acquisition system (model PCA-14, Dianachart, Inc., Oak Ridge, NJ). Routine metabolic rates (mg O_2/h) were calculated from the rate of decline in dissolved oxygen (mg O_2/(L×min)) and the volume of the respirometer (Steffensen, 1989). Swimming speeds (in body lengths per second, BL/s) were determined every 15–30 minutes by averaging the time required for the shark to complete three to six laps. To account for the increased costs of swimming in a circular path, recorded RMRs were corrected to straight line estimates (RMR_{sl}) by following the method of Weihs (1981).

Statistical analysis

Routine and standard metabolic rate data at each temperature were fitted to the allometric equation $MR = a \times M^b$ by using nonlinear, iterative Gauss-Newton regression (Brill, 1979, 1987). This technique provides more accurate estimates of the parameters than log-transformed linear regression (Glass, 1969). The likelihood ratio test statistic was used to test for differences in the allometric exponents (b) among temperatures and between SMR and RMR at 24–26°C. Analysis of covariance (ANCOVA) of log-transformed metabolic rate (with log-transformed mass as covariate) was also used to test the equivalence of the exponents (b) in the untransformed allometric equations. Differences in SMR

Figure 1

Standard metabolic rates (mg O_2/hr) of juvenile sandbar sharks (*Carcharhinus plumbeus*) as determined by flow-through box respirometry at 18°C (□), 24°C (○), and 28°C (▼). Lines show best-fit allometric equations at each temperature. Error bars indicate ±1 standard error.

and heart rate among temperatures were evaluated by using ANCOVA. Analysis of covariance with mass as covariate was used to test for differences in mean SMR Q10's and heart rate Q10's among the three temperature ranges. The relationship between the RMR-to-SMR ratio and body mass was assessed with linear least squares regression. Statistical analyses were performed in Statistica 6.1 (StatSoft, Inc., Tulsa, OK) and SAS, version 8.0 (The SAS Institute, Inc., Cary, NC), with $P<0.05$ taken as the limit for significance. All values reported are means ± standard error of the mean.

Results

Standard metabolic rates

Standard metabolic rate increased with body mass (range 1.025–10.355 kg) at all three temperatures (ANCOVA, logmass, $F_{1,59}=265.04$, $P< 0.001$) (Fig. 1). The best-fitting allometric equations relating SMR (mg O_2/h) to body mass (M, kg) were

$$18°C: SMR = 65 (\pm15) \times M^{0.73 (\pm0.14)} \qquad n=16, r^2=0.71 \qquad (1)$$

$$24°C: SMR = 120 (\pm17) \times M^{0.79 (\pm0.08)} \qquad n=33, r^2=0.84 \qquad (2)$$

$$28°C: SMR = 207 (\pm28) \times M^{0.63 (\pm0.07)}. \qquad n=16, r^2=0.87 \qquad (3)$$

Standard metabolic rate increased with temperature for each individual and overall (ANCOVA, temperature,

$F_{2,59}$=20.99, P<0.001). However, the allometric exponents (b) at each temperature were not significantly different (likelihood ratio test, χ^2_2=3.2, P=0.20; ANCOVA, logmass×temperature interaction, $F_{2,59}$=0.81, P=0.45).

The mean SMR Q_{10}'s were 3.2 ±0.4 for 18–24°C (n=14), 2.5 ±0.2 for 24–28°C (n=16), and 2.9 ±0.2 for 18–28°C (n=13). There was no overall effect of body
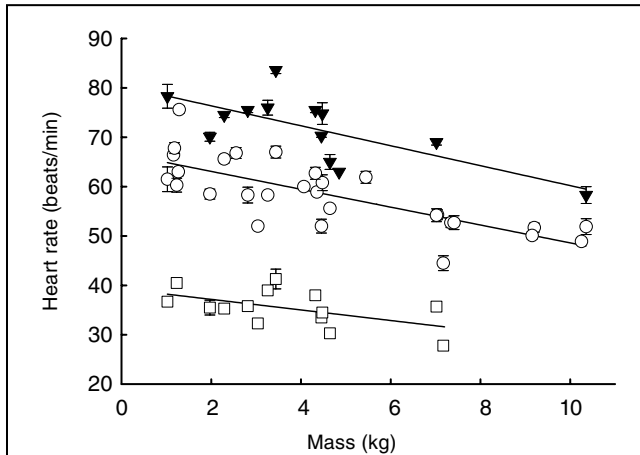
Figure 2

Heart rates (beats/min) of juvenile sandbar sharks (*Carcharhinus plumbeus*) (treated with pancuronium bromide) measured during standard metabolic rate experiments at 18°C (□), 24°C (○), and 28°C (▼). Solid lines represent best-fit linear regressions at each temperature as a function of body mass. Error bars indicate ±1 standard error.
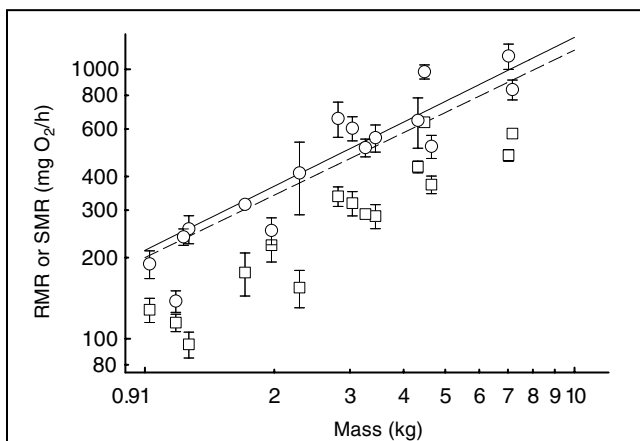
Figure 3

Paired routine (RMR, ○) and standard metabolic rates (SMR, □) (mg O_2/h) of 15 juvenile sandbar sharks (*Carcharhinus plumbeus*) at 24–26°C. Error bars indicate ±1 standard error. The solid line depicts the best-fitting allometric equation with the fish swimming in a curved path in an annular respirometer: RMR = 213 (±38) $M^{0.79(\pm0.11)}$. The dashed line represents the best-fit allometric equation using the corrected straight-line swimming (RMR_{sl}) estimates: RMR_{sl} = 200 (±33) $M^{0.77}$.

mass on SMR Q_{10}'s (increases in metabolic rate with temperature) (ANCOVA, mass, $F_{1,36}$=0.04, P=0.84), but there was a significant negative correlation between mass and SMR Q_{10} for 24–28°C (P=0.014, r^2=0.36; slope=–0.20 ±0.07). The temperature range did not affect mean SMR Q_{10} (ANCOVA, range, $F_{2,36}$=1.37, P=0.27). The data sets were therefore pooled and the overall mean Q_{10} was 2.9 ±0.2 (n=43).

Heart rates

Heart rate was negatively correlated with body mass at all temperatures (ANCOVA, mass, $F_{1,50}$=29.99, P<0.001) (Fig. 2). The relationships between heart rate and body mass at each of the three temperatures were

$$18°C:\ Heart\ rate = 39.3\ (\pm2.0) - 1.07\ (\pm0.49) \times M \qquad n=14,\ P=0.05,\ r^2=0.29 \qquad (4)$$

$$24°C:\ Heart\ rate = 66.7\ (\pm1.6) - 1.81\ (\pm0.30) \times M \qquad n=29,\ P<0.001,\ r^2=0.58 \qquad (5)$$

$$28°C:\ Heart\ rate = 80.4\ (\pm2.9) - 2.02\ (\pm0.61) \times M. \qquad n=13,\ P=0.01,\ r^2=0.50 \qquad (6)$$

Heart rate increased with temperature for each individual and overall (ANCOVA, temperature, $F_{2,50}$=64.21, P<0.001) (Fig. 2). However, the influence of body mass on heart rate did not vary among temperatures (ANCOVA, mass×temperature interaction, $F_{2,50}$=0.69, P=0.51).

The mean Q_{10}s for heart rate were 2.2 ±0.05 for 18–24°C (n=14), 1.8 ±0.04 for 24–28°C (n=12), and 2.1 ±0.03 for 18–28°C (n=11). Heart rate Q_{10} was not correlated with body mass (ANCOVA, mass, $F_{1,31}$=0.95, P=0.34). However, an overall significant effect of temperature range on heart rate Q_{10} was observed (ANCOVA, range, $F_{2,31}$= 4.68, P=0.02). 18–24°C and 18–28°C were significantly different from 24–28°C (P<0.001), but not from each other (P=0.08, Tukey unequal n HSD test).

Routine metabolic rates

Routine metabolic rate increased with increasing body mass (Fig. 3). The best-fitting allometric equation relating RMR (mg O_2/h) to mass (range 1.025–7.170 kg) was

$$RMR = 213\ (\pm38) \times M^{0.79\ (\pm0.11)}.\quad n=16\ (53\ trials), \qquad (7)$$
$$r^2=0.82$$

The estimated additional costs of swimming in a curved path versus a straight line increased with body mass (range 0.8–19.9%; Fig. 3). With the straight-line swimming (RMR_{sl}) estimates, the allometric equation for RMR became:

$$RMR_{sl} = 200\ (\pm33) \times M^{0.77\ (\pm0.11)}.\quad n=16,\ r^2=0.83 \qquad (8)$$

Although the acclimation periods in the annular respirometer were relatively short, it has been shown that

sandbar sharks recover rapidly from angling stress (6–10 h; Spargo et al.[2]). There was no evidence of systematic decreases in RMR (relating to recovery from handling stress) during individual RMR experiments, which averaged 16.2 ±2.0 hours in length. Using only the final trial for each individual, we fitted RMR to the allometric equation:

$$RMR = 203\ (\pm35) \times M^{0.76\ (\pm0.12)}. \qquad n = 16,\ r^2 = 0.78 \qquad (9)$$

Routine (average ±SEM) swimming speeds decreased with increasing body size according to the exponential equation speed (bl/s)$= 3.54\ TL^{-0.43}$ ($r^2 = 0.18$) (Fig. 4). In most cases the animal maintained a swimming speed and direction along the outer wall of the chamber for 5–20 minutes before turning around. Because each shark swam at a relatively constant speed, the effect of swimming speed on metabolic rate could not be determined.
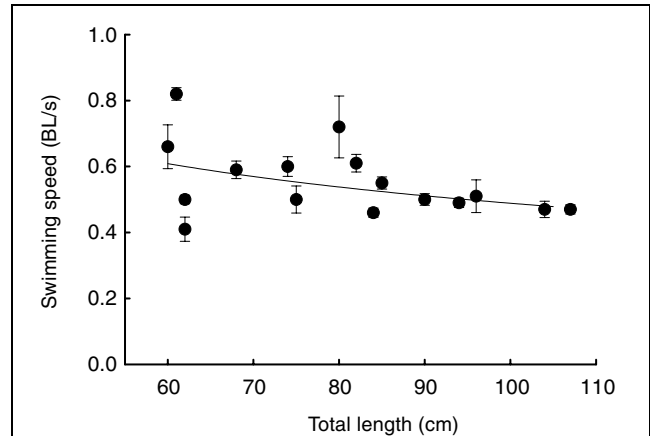
Paired standard and routine metabolic rates

Paired SMR and RMR measurements were obtained for 15 sharks (1.025–7.170 kg) (Fig. 3). The mean ratio of RMR to SMR at 24°C was 1.8 ±0.1. The mean ratio of RMR$_{sl}$ to SMR was 1.6 ±0.1. There was no significant correlation between body mass and the ratio of RMR to SMR ($P = 0.93$, $r^2 < 0.01$). The allometric exponents for RMR and SMR at 24°C were also not significantly different (likelihood ratio test, $\chi_1^2 = 0.002$, $P = 0.96$; ANCOVA, logmass×type interaction, $F_{1,45} = 0.33$, $P = 0.57$).

Discussion

Effects of body mass and temperature on SMR and RMR

This study presents the first direct measures of SMR and expands the size range over which SMR and RMR have been reported for continuously active shark species (Fig. 5). Sandbar shark metabolic rate, like that of a wide variety of species, increases with increasing body mass according to the allometric equation $MR = aM^b$, with a b of ~0.71–0.79 (Schmidt-Nielsen, 1997). The effects of body mass on SMR, RMR, and RMR$_{sl}$ (b in Eqs. 1–3 and 7–9) in sandbar sharks were similar to published values for other elasmobranchs (e.g., Pritchard et al., 1958; DuPreez et al., 1988; Sims, 1996). The temperature independence of b, previously reported for the lesser sandshark (*Rhinobatos annulatus*) and the bullray (*Myliobatus aquila*) (DuPreez et al., 1988), was evident overall in sandbar sharks. However, there was a significant effect of mass on SMR Q_{10} for the 24–28°C

[2] Spargo, A. L., N. Kohler, G. Skomal, and R. Goodwin. 2001. The physiological effects of angling on post-release survivorship in juvenile sandbar sharks (*Carcharhinus plumbeus*). (Abstract.) American Elasmobranch Society 17th Annual Meeting, State College, PA. Website:http://www.flmnh.ufl.edu/fish/organizations/aes/abst2001d.htm [accessed on 26 September 2005.]

Figure 4

Mean (±1 SE) voluntary swimming speeds of sandbar sharks (*Carcharhinus plumbeus*) during RMR experiments. The solid line represents the best-fit equation: *speed* (*BL*/s) = 3.54×(*total length*)$^{-0.43}$.
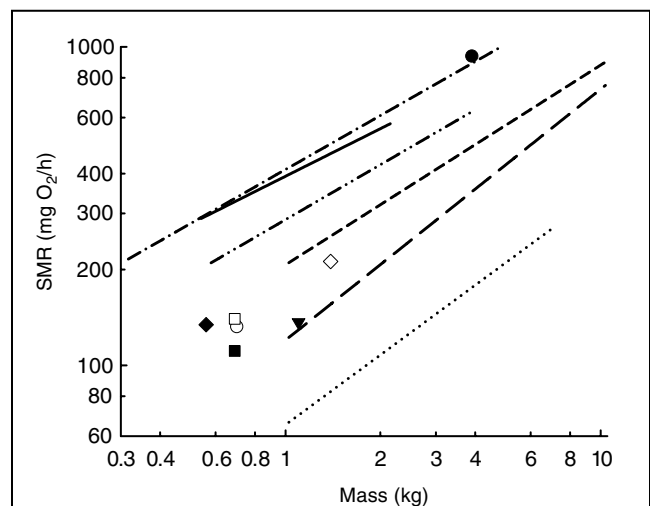
Figure 5

Standard metabolic rates of active elasmobranch species and tunas as a function of body mass: *Isurus oxyrinchus* 18°C (●, Graham et al., 1990); *Sphyrna lewini* 21°C (■), 26°C (○), and 29°C (□) (Lowe, 2001); *Negaprion brevirostris* 22–25°C (▼, Bushnell et al., 1989) and 25°C (◇, Scharold and Gruber, 1991); *Carcharhinus acronotus* 28°C (♦, Carlson et al., 1999); *C. plumbeus* 18°C (·······), 24°C (— — —), and 28°C (– – –) (present study); kawakawa (*Euthynnus affinis*) 25°C (———, Brill, 1987); yellowfin tuna (*Thunnus albacares*) 25°C (– ·· –, Brill, 1987); skipjack tuna (*Katsuwonus pelamis*) 23.5–25.5°C (– · –, Brill, 1979). Lines are best-fit allometric equations at the stated experimental temperatures.

range. These two findings appear to contradict each other, but the 24–28°C pattern may be influenced by small sample sizes at larger body masses (only 2 sharks >7.5 kg).

The effects of acute temperature change on SMR were consistent with published values for other elasmobranchs ($Q_{10} \approx 2-3$; e.g., DuPreez et al., 1988; Carlson and Parsons, 1999; Miklos et al., 2003). The Q_{10} for the SMR in elasmobranchs has also been reported to vary with the temperature ranges assessed (Butler and Taylor, 1975; Hopkins and Cech, 1994), but this was not the case for sandbar sharks. It is important to note the distinction between acute temperature changes and seasonal acclimatization when reporting Q_{10} values (Schmidt-Nielsen, 1997). In the present study, sandbar sharks were exposed to rapid temperature changes that mirrored short-term temperature fluctuations experienced in the wild (SMR $Q_{10}=2.9 \pm 0.2$). In seasonally acclimatized bonnethead sharks (*Sphyrna tiburo*), the effect of seasonal temperature change on metabolic rate was lower ($Q_{10}=2.29-2.39$; Carlson and Parsons, 1999).

Cost of activity and routine energy expenditure

The SMR is never realized in fish that must swim continuously to maintain hydrostatic equilibrium or to ventilate their gills. Measurement of SMR and RMR in active species nevertheless allows insight into the division of metabolic costs between swimming and maintenance processes. For example, the average metabolic rate of juvenile scalloped hammerhead sharks (*Sphyrna lewini*) in the wild was 1.4 times the estimated SMR (Lowe, 2002). In sandbar sharks, the RMR to SMR ratio (1.8 ± 0.1) and RMR_{sl} to SMR ratio (1.6 ± 0.1) were similar to those observed and estimated for several elasmobranch species (e.g., 1.5, Brett and Blackburn, 1978; 1.4, Nixon and Gruber, 1988; 1.7, Carlson et al., 1999). In other words, SMR comprises 56–63% of total metabolic rate at routine activity levels. Because the allometric exponents for RMR and SMR were not different at 24°C, we conclude that the RMR-to-SMR ratio (and, therefore, cost of activity) is also size independent, at least over the size range of sandbar sharks tested.

Our metabolic rate data span the size and temperature ranges relevant to the summer populations of juvenile sandbar sharks in Chesapeake Bay and other western Atlantic nursery areas (Grubbs et al., in press; Merson and Pratt, 2001). Bioenergetics models require estimates of field activity and corresponding energetic costs (Lowe, 2002). The swimming speeds of sandbar sharks in the annular respirometer (mean 0.55 ± 0.03 bl/s) were well within the range of activity levels observed in nature (Grubbs, 2001). After the application of an oxycalorific coefficient of 13.6 J/(mg O_2) (Elliott and Davison, 1975), the RMR and RMR_{sl} for a 1-kg sandbar shark at 24°C represent energy expenditures of 69.7 and 63.4 kJ/day, respectively. These values are comparable to those for the lemon shark (*Negaprion brevirostris*, 67.7 kJ/day; Nixon and Gruber, 1988), *S. tiburo* (80.2 kJ/day; Parsons, 1990), and *S. lewini* (96 kJ/day at ~28°C; Lowe, 2002) . The Q_{10} values for SMR obtained between 18° and 28°C demonstrate that juvenile sandbar shark metabolic demands change significantly as ambient temperature changes, both on short time scales and over the course of the summer stay in the nursery areas.

Heart rates

Heart rate decreased with increasing body mass but increased with temperature (Fig. 2), as it does for other ectothermic species (Schmidt-Nielsen, 1997). Heart rates of juvenile sandbar sharks were comparable to heart rates of two other shark species while swimming (Scharold et al., 1989; Scharold and Gruber, 1991), although the sandbar shark data should be interpreted with caution. Pancuronium bromide has been shown to exhibit vagolytic activity in mammals (Melnikov et al., 1999), but to our knowledge its effect on shark heart rates is unknown and would depend on the resting vagal tone. In the dogfish (*Scyliorhinus canicula*), resting vagal tone increased with temperature between 7°C and 17°C (Taylor et al., 1977). The resting vagal tone and resulting elevation in heart rate after treatment with pancuronium bromide could be significant in sandbar sharks, especially at the higher temperatures. If so, Figure 2 may reflect the effect of temperature and body mass on intrinsic heart rate.

Measuring SMR of immobilized sharks

Standard metabolic rate is defined as the oxygen consumption of a postabsorptive-stage fish at rest, and it is considered the minimum metabolic cost of organismal maintenance (Brett and Groves, 1979). Two methods are commonly used to determine SMR. In the first, the slope of a power-performance curve relating the logarithm of oxygen consumption rate to relative swimming speed is extrapolated back to zero activity (e.g., Lowe, 2001). However, extrapolation does not take into account physiological differences between active and quiescent fish, specifically the induction of anaerobic metabolism during high-velocity swimming, and may misrepresent SMR (Brett and Groves, 1979; Cech, 1990). Further, swimming kinematics can be significantly altered in a swim flume, leading to overestimates of SMR (Lowe, 1996, 2001). The second option for measuring SMR is to confine the fish in a sealed or flow-through respirometer (e.g., Brill, 1987; Hopkins and Cech, 1994). This process works well for sedentary species, but active fish will struggle in such situations, requiring the use of paralytic and sedative agents, as well as artificial ventilation.

Several studies have confirmed, however, that the two methods yield identical results (SMRs and allometric exponents) in various fish species (e.g., yellowfin tuna [*Thunnus albacares*]; kawakawa [*Euthynnus affinis*]; skipjack tuna [*Katsuwonus pelamis*]; rainbow trout [*Onchorynchus mykiss*]; American shad [*Alosa sapidissima*]; aholehole [*Kuhlia sandvicensis*] [Brill, 1979, 1987; Dewar and Graham, 1994; Leonard et al., 1999]). Moreover, treatment with anaesthetics has been shown to have no effect on the SMR of little skate *(Raja erinacea*; Hove and Moss, 1997) or nursehound (*Scyliorhinus stellaris*; Baumgarten-Schumann and Piiper, 1968).

Because sandbar sharks are continuously active, we chose to measure SMR in immobilized and artificially ventilated animals in flow-through respirometers. As a check of this technique, a two-point power-performance curve was constructed by using the logarithms of self-paired SMR and RMR and the mean swimming speed of the animal in the annular respirometer. The average slope for 15 sharks (0.38 ±0.04) at 24–26°C was similar to the slopes of power-performance curves for four other ectothermic shark species (0.2, Scharold et al., 1989; 0.34, Scharold and Gruber, 1991; 0.38, Carlson et al., 1999; 0.32, Lowe, 2001), and we interpret these data as additional evidence that the technique provides acceptable results. This approach, moreover, avoids the expense and difficulties of developing a swimming tunnel large enough to accommodate juvenile sandbar sharks and may well be generally applicable for generating power performance curves in other continuously active fish species.

Elasmobranch metabolic rates and the cost of growth

The published SMRs of active elasmobranchs are well below those of high-energy demand teleosts (e.g., the endothermic tunas; Korsmeyer et al., 1996), with the exception of the endothermic mako shark (*Isurus oxyrinchus*) (Graham et al., 1990) (Fig. 5). Brill (1987, 1996) proposed that the high SMRs of tunas are an unavoidable consequence of their morphological, biochemical, and physiological adaptations for extremely high maximum aerobic metabolic rates, specifically that their large gill surface areas have led to high osmoregulatory costs (but see Brill et al., 2001). Most elasmobranchs, including the sandbar shark, have less than one third the gill surface area of a similar-size tuna (Muir and Hughes, 1969; Emery and Szcepanski, 1986). These modest mass-specific gill surface areas and corresponding low rates of oxygen delivery in ectothermic sharks likely dictate slow asymptotic growth rates (Pauly, 1981), in contrast to those of tunas, whose cardiovascular systems are adapted for meeting multiple metabolic demands (including growth) (Bushnell and Brill, 1991; Korsmeyer et al., 1996; Brill and Bushnell, 2001).

Significant levels of specific dynamic action (SDA, the elevation in metabolic rate in conjunction with protein synthesis after a meal [Brown and Cameron, 1991]) can probably not be met by the cardio-respiratory systems of elasmobranchs, particularly in continuously active species such as the sandbar shark, while they sustain routine activity levels. The oxygen consumption rate following a meal can exceed 2–3 times the SMR (DuPreez et al., 1988; Sims and Davies, 1994; Ferry-Graham and Gibb, 2001), whereas the RMR of sandbar sharks was 1.6–1.8 times SMR. Assuming that the maximum metabolic rate is 1.8 to 2.75 times the SMR (Scharold et al., 1989; Lowe, 2001), we determined that sandbar sharks are using between 34% and 100% of their metabolic scope just to sustain routine activity levels.

Given these limitations, sandbar sharks and other active elasmobranchs probably make tradeoffs among metabolic demands at the expense of SDA or growth to remain within their available metabolic scope, or they may adjust their behavior to seek cooler waters during digestion (Matern et al., 2000). Because rapid incorporation of ingested amino acids into body proteins is not possible, many elasmobranchs may have to reduce the rate of digestion or integrate SDA over a longer period (or do both). For example, estimated daily rations for several elasmobranch species average 1–2% of body weight per day (e.g., Bush and Holland, 2002; Dowd et al., 2006), compared to 4% or more in fast growing teleosts (e.g., Olson and Boggs, 1986). Not surprisingly, sandbar sharks in the Northwest Atlantic mature only after 13–15 years and grow less than 10 cm per year during that time (Sminkey and Musick, 1995). Growth rates for many other large, active elasmobranch species are also slow (Branstetter, 1990). Future research might well focus on exploring the relationship between SDA, active metabolic rates, and metabolic scopes of slow growing, continuously active sharks.

Acknowledgments

Literature cited

Baum, J. K., R. A. Myers, D. G. Kehler, B. Worm, S. J. Harley, and P. A. Doherty.
    2003. Collapse and conservation of shark populations in the Northwest Atlantic. Science 299:389–392.
Baumgarten-Schumann, D., and J. Piiper.
    1968. Gas exchange in the gills of resting unanesthetized dogfish (*Scyliorhinus stellaris*). Resp. Physiol. 5:317–325.
Branstetter, S.
    1990. Early life-history implications of selected carcharhinoid and lamnoid sharks of the Northwest Atlantic. *In* Elasmobranchs as living resources: advances in the biology, ecology, systematics, and status of the fisheries (H. L. Pratt Jr, S. H. Gruber, and T. Taniuchi, eds.), p. 17–28. NOAA Technical Report NMFS 90.
Brett, J. R., and J. M. Blackburn.
    1978. Metabolic rate and energy expenditure of the spiny dogfish, *Squalus acanthias*. J. Fish. Res. Board Can. 35:816–821.
Brett, J. R., and T. D. D. Groves.
    1979. Physiological energetics. *In* Fish physiology

(W. S. Hoar, D. J. Randall, and J. R. Brett, eds.), p. 279–352. Academic Press, New York, NY.

Brewster-Geisz, K. K., and T. J. Miller.
　2000. Management of the sandbar shark, *Carcharhinus plumbeus*: implications of a stage-based model. Fish. Bull. 98:236–249.

Brill, R. W.
　1979. The effect of body size on the standard metabolic rate of skipjack tuna, *Katsuwonus pelamis*. Fish. Bull. 77:494–498.
　1987. On the standard metabolic rates of tropical tunas, including the effect of body size and acute temperature change. Fish. Bull. 85:25–35.
　1996. Selective advantages conferred by the high performance physiology of tunas, billfishes, and dolphin fish. Comp. Biochem. Phys. A. 113:3–15.

Brill, R. W., and P. G. Bushnell.
　2001. The cardiovascular system of tunas. *In* Tuna—physiology, ecology and evolution (B. A. Block and E. D. Stevens, eds.), p. 79–120. Academic Press, San Diego, CA.

Brill, R., Y. Swimmer, C. Taxboel, K. Cousins, and T. Lowe.
　2001. Gill and intestinal Na⁺-K⁺ ATPase activity, and estimated maximal osmoregulatory costs, in three high-energy-demand teleosts: yellowfin tuna (*Thunnus albacares*), skipjack tuna (*Katsuwonus pelamis*), and dolphin fish (*Coryphaena hippurus*). Mar. Biol. 138:935–944.

Brown, C. R., and J. N. Cameron.
　1991. The relationship between specific dynamic action (SDA) and protein synthesis rates in the channel catfish. Physiol. Zool. 64:298–301.

Bush, A., and K. Holland.
　2002. Food limitation in a nursery area: estimates of daily ration in juvenile scalloped hammerheads, *Sphyrna lewini* (Griffith and Smith, 1834) in Kane'ohe Bay, O'ahu, Hawai'i. J. Exp. Mar. Biol. Ecol. 278:157–178.

Bushnell, P. G., and R. W. Brill.
　1991. Responses of swimming skipjack (*Katsuwonus pelamis*) and yellowfin (*Thunnus albacares*) tunas to acute hypoxia, and a model of their cardiovascular function. Physiol. Zool. 64:787–811.

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

Butler, P. J., and E. W. Taylor.
　1975. The effect of progressive hypoxia on respiration in the dogfish (*Scyliorhinus canicula*) at different seasonal temperatures. J. Exp. Biol. 63:117–130.

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

Carlson, J. K., and G. R. Parsons.
　1999. Seasonal differences in routine oxygen consumption rates of the bonnethead shark. J. Fish Biol. 55:876–879.

Casey, J. G., and L. J. Natanson.
　1992. Revised estimates of age and growth of the sandbar shark (*Carcharhinus plumbeus*) from the Western North Atlantic. Can. J. Fish. Aquat. Sci. 49:1474–1477.

Cech, J. J., Jr.
　1990. Respirometry. *In* Methods for fish biology (C. B. Schreck and P. B. Moyle, eds.), p. 535–556. Am. Fish. Soc., Bethesda, MD.

Cortes, E.
　1999. A stochastic stage-based population model of the sandbar shark in the Western North Atlantic. *In* Life in the slow lane: ecology and conservation of long-lived marine animals (J. A. Musick, ed.), p. 115–136. Am. Fish. Soc. Symp. 23, Bethesda, MD.

Dejours, P.
　1975. Principles of comparative respiratory physiology, 253 p. Elsevier, New York, NY.

Dewar, H., and J. B. Graham.
　1994. Studies of tropical tuna swimming performance in a large water tunnel. I. Energetics. J. Exp. Biol. 192:13–31.

Dowd, W. W., R. W. Brill, P. G. Bushnell, and J. A. Musick.
　2006. Estimating consumption rates for juvenile sandbar sharks (*Carcharhinus plumbeus*) in Chesapeake Bay, Virginia, using a bioenergetics model. Fish. Bull. 104:332–342.

DuPreez, H. H., A. McLachlan, and J. F. K. Marais.
　1988. Oxygen consumption of two nearshore marine elasmobranchs, *Rhinobatus annulatus* (Muller and Henle, 1841) and *Myliobatus aquila* (Linnaeus, 1758). Comp. Biochem. Physiol. 89A:283–294.

Elliott, J. M., and W. Davison.
　1975. Energy equivalents of oxygen consumption in animal energetics. Oecologia 19:195–201.

Emery, S. H., and A. Szcepanski.
　1986. Gill dimensions in pelagic elasmobranch fishes. Biol. Bull. 171:441–449.

Ferry-Graham, L. A., and A. C. Gibb.
　2001. A comparison of fasting and post-feeding metabolic rates in a sedentary shark *Cephaloscyllium ventriosum*. Copeia 2001:1108–1113.

Glass, N. R.
　1969. Discussion of calculation of power function with special reference to respiratory metabolism in fish. J. Fish. Res. Board Can. 26:2643–2650.

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

Grubbs, R. D.
　2001. Nursery delineation, habitat utilization, movements, and migration of juvenile *Carcharhinus plumbeus* in Chesapeake Bay, Virginia, USA. Ph. D. diss., 223 p. College of William and Mary, Gloucester Point, VA.

Grubbs, R. D., J. A. Musick, C. L. Conrath, and J. G. Romine.
　In press. Long-term movements, migration, and temporal delineation of a summer nursery for juvenile sandbar sharks in the Chesapeake Bay region. *In* Shark nursery grounds of the Gulf of Mexico and the East Coast waters of the United States (C. T. McCandless, N. E. Kohler, and H. L. Pratt Jr., eds.). Am. Fish. Soc. Symp., Bethesda, MD.

Hopkins, T. E., and J. J. Cech Jr.
　1994. Effect of temperature on oxygen consumption of the bat ray, *Myliobatis californica* (Chondrichthyes, Myliobatididae). Copeia 1994:529–532.

Hove, J. R., and S. A. Moss.
　1997. Effect of MS-222 on response to light and rate of metabolism of the little skate *Raja erinacea*. Mar. Biol. 128:579–583.

Korsmeyer, K. E., H. Dewar, N C. Lai, and J. B. Graham.
　1996. The aerobic capacity of tunas: Adaptation for

multiple metabolic demands. Comp. Biochem. Physiol. 113A:17–24.

Leonard, J. B., J. F. Norieka, B. Kynard, and S. D. McCormick.
    1999. Metabolic rates in an anadromous clupeid, the American shad (*Alosa sapidissima*). J. Comp. Physiol. 169B:287–295.

Lowe, C. G.
    1996. Kinematics and critical swimming speed of juvenile scalloped hammerhead sharks. J. Exp. Biol. 199:2605–2610.
    2001. Metabolic rates of juvenile scalloped hammerhead sharks (*Sphyrna lewini*). Mar. Biol. 139:447–453.
    2002. Bioenergetics of free-ranging juvenile scalloped hammerhead sharks (*Sphyrna lewini*) in Kane'ohe Bay, O'ahu, HI. J. Exp. Mar. Biol. Ecol. 278:141–156.

Matern, S. A., J. J. Cech Jr, and T. E. Hopkins.
    2000. Diel movements of bat rays, *Myliobatis californica*, in Tomales Bay, California: evidence for behavioral thermoregulation? Environ. Biol. Fish. 58:173–182.

Medved, R. J.
    1985. Gastric evacuation in the sandbar shark, *Carcharhinus plumbeus*. J. Fish Biol. 26:239–253.

Medved, R. J., C. E. Stillwell and J. G. Casey.
    1988. The rate of food consumption of young sandbar sharks (*Carcharhinus plumbeus*) in Chincoteague Bay, Virginia. Copeia 1988:956–963.

Melnikov, A. L., K. Y. Malakhov, K. G. Helgesen, and D. A. Lathrop.
    1999. Cardiac effects of non-depolarizing neuromuscular blocking agents pancuronium, vecuronium, and rocuronium in isolated rat atria. Gen. Pharmacol. 33:313–317.

Merson, R. R., and H. L. Pratt Jr.
    2001. Distribution, movements and growth of young sandbar sharks, *Carcharhinus plumbeus*, in the nursery grounds of Delaware Bay. Environ. Biol. Fish. 61:13–24.

Miklos, P., S. M. Katzman, and J. J. Cech Jr.
    2003. Effect of temperature on oxygen consumption of the leopard shark, *Triakis semifasciata* (Chondrichthyes Triakidae). Environ. Biol. Fish. 66:15–18.

Muir, B. S., and G. M. Hughes.
    1969. Gill dimensions for three species of tunny. J. Exp. Biol. 51:271–285.

Musick, J. A., S. Branstetter, and J. A. Colvocoresses.
    1993. Trends in shark abundance from 1974 to 1991 for the Chesapeake Bight region of the U.S. Mid-Atlantic coast. *In* Conservation biology of elasmobranchs (S. Branstetter, ed.), p. 1–18. NOAA Technical Report, NMFS 115.

Musick, J. A., and J. A. Colvocoresses.
    1986. Seasonal recruitment of subtropical sharks in Chesapeake Bight, USA. *In* Workshop on recruitment in tropical coastal demersal communities (A. Yanez-Arancibia and D. Pauly, eds.), p. 301–311. FAO/UNESCO, Campeche, Mexico.

Ney, J. J.
    1993. Bioenergetics modeling today: growing pains on the cutting edge. Trans. Am. Fish. Soc. 122:736–748.

Nixon, A. J., and S. H. Gruber.
    1988. Diel metabolic and activity patterns of the lemon shark (*Negaprion brevirostris*). J. Exp. Zool. 248:1–6.

Olson, R. J., and C. H. Boggs.
    1986. Apex predation by yellowfin tuna (*Thunnus albacares*): independent estimates from gastric evacuation and stomach contents, bioenergetics, and cesium concentrations. Can. J. Fish. Aquat. Sci. 43:1760–1775.

Oswald, R. L.
    1978. Injection anesthesia for experimental studies in fish. Comp. Biochem. Phys. 60C:19–26.

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

Pauly, D.
    1981. The relationships between gill surface area and growth performance in fish: a generalization of von Bertalanffy's theory of growth. Meeresforschung 28:251–282.

Pritchard, A. W., E. Florey, and A. W. Martin.
    1958. Relationship between metabolic rate and body size in an elasmobranch (*Squalus suckleyi* [*S. acanthias*]) and in a teleost *(Ophiodon elongatus)*. J. Mar. Res. 17:403–411.

Richards, F. A.
    1965. Dissolved gases other than carbon dioxide. *In* Chemical cceanography (J. P. Riley and G. Skirrow, eds.), p. 197–224. Academic Press, New York, NY.

Scharold, J., and S. H. Gruber
    1991. Telemetered heart rate as a measure of metabolic rate in the lemon shark, *Negaprion brevirostris*. Copeia 1991:942–953.

Scharold, J., N. C. Lai, W. R. Lowell, and J. B. Graham.
    1989. Metabolic rate, heart rate, and tailbeat frequency during sustained swimming in the leopard shark *Triakis semifasciata*. J. Exp. Biol. 48:223–230.

Schmidt-Nielsen, K.
    1997. Animal physiology: adaptation and environment, 607 p. Cambridge Univ. Press, New York, NY.

Sims, D. W.
    1996. The effect of body size on the standard metabolic rate of the lesser spotted dogfish. J. Fish Biol. 48:542–544.

Sims, D. W., and S. J. Davies.
    1994. Does specific dynamic action (SDA) regulate return of appetite in the lesser spotted dogfish, *Scyliorhinus canicula*? J. Fish Biol. 45:341–348.

Sminkey, T. R., and J. A. Musick.
    1995. Age and growth of the sandbar shark, *Carcharhinus plumbeus*, before and after population depletion. Copeia 1995:871–883.
    1996. Demographic analysis of the sandbar shark, *Carcharhinus plumbeus*, in the western North Atlantic. Fish. Bull. 94:341–347.

Steffensen, J. F.
    1989. Some errors in respirometry of aquatic breathers: How to avoid and correct for them. Fish Physiol. Biochem. 6:49–59.

Steffensen, J. F., K. Johansen, and P. G. Bushnell.
    1984. An automated swimming respirometer. Comp. Biochem. Physiol. 79A:437–440.

Stillwell, C. E., and Kohler, N. E.
    1993. Food habits of the sandbar shark *Carcharhinus plumbeus* off the U.S. northeast coast, with estimates of daily ration. Fish. Bull. 91:138–150.

Taylor, E. W., S. Short, P. J. Butler.
    1977. The role of the cardiac vagus and the response of a dogfish *Scyliorhinus canicula* to hypoxia. J. Exp. Biol. 70:57–75.

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