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Metabolic Rates and Bioenergetics of Juvenile Sandbar Sharks (Carcharhinus plumbeus)

W. Wesley Dowd

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METABOLIC RATES AND BIOENERGETICS OF JUVENILE SANDBAR SHARKS (CARCHARHINUS PLUMBEUS)

A Thesis

Presented to

The Faculty of the School of Marine Science

The College of William and Mary in Virginia

In Partial Fulfillment

Of the Requirements for the Degree of

Master of Science

by

W. Wesley Dowd

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APPROVAL SHEET

This thesis is submitted in partial fulfillment of the requirements for the degree of

Master of Science

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Approved, May 2003

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ABSTRACT

The lower Chesapeake Bay and adjacent coastal waters serve as the primary summer nursery areas for juvenile sandbar sharks (*Carcharhinus plumbeus*) in the Northwest Atlantic Ocean. The large population of juvenile sandbar sharks in this ecosystem benefits from increased food availability that fuels rapid growth and from limited exposure to large shark predators. Juvenile growth and survival is the most critical life history stage for sandbar sharks, and juvenile nursery grounds will continue to play an important role in the slow recovery of this stock from severe population declines due to overfishing. The goal of this study was to assess the possible impacts of juvenile sandbar sharks as apex predators on the lower Chesapeake Bay ecosystem and to evaluate the energetic benefits of using this nursery. The bioenergetics model was used as a tool to predict energy consumption rates of individual sandbar sharks based on their energetic demands: metabolism, growth, and loss of waste.

Metabolic rate is the largest and most variable component of the energy budget, particularly for species such as the sandbar shark that must swim continuously to ventilate their gills. The standard (basal) and routine metabolic rates of juvenile sandbar sharks were measured in two laboratory respirometry systems, using oxygen consumption rate as a proxy for metabolic rate. These data span the entire range of body sizes and water temperatures characteristic of the Chesapeake Bay population. Standard metabolic rates of sandbar sharks were similar to values obtained for related shark species by extrapolation of power-performance curves. The effects of body size and temperature on standard metabolic rate were similar to previous results for elasmobranchs and teleost fishes. In fifteen sharks, routine metabolic rate while swimming averaged 1.8 times the standard metabolic rate when the sharks were immobilized. Data obtained from the literature support the theory that limited gill surface areas and narrow metabolic scopes of many elasmobranchs help to explain their slow growth rates, since growth has the lowest rank of the multiple metabolic demands placed on the oxygen delivery system.

These new metabolic rate data were then combined with other species-specific data to construct a bioenergetics model for juvenile sandbar sharks for the time they spend in Chesapeake Bay each summer. This model predicted higher daily rations than previous estimates for this species that were based on simple bioenergetics models or stomach contents and gastric evacuation rate models. However, the predicted rations agree with reconstructed meal sizes of juvenile sandbar sharks and are comparable to those of ecologically similar shark species. When extrapolated from individuals to the population level, the model predicted a negligible effect of predation by juvenile sandbar sharks on the lower Chesapeake Bay ecosystem; the consumption rate of juvenile sandbar sharks pales in comparison to other carnivorous fishes and to humans, the true apex predators in the system.
METABOLIC RATES AND BIOENERGETICS OF JUVENILE SANDBAR SHARKS (*CARCHARHINUS PLUMBATUS*)
CHAPTER 1:
Paired Standard and Routine Metabolic Rates of Juvenile Sandbar Sharks (*Carcharhinus plumbeus*), Including the Effects of Body Mass and Seasonal Temperature Range
INTRODUCTION

The lower Chesapeake Bay and adjacent coastal waters serve as the primary summer nursery areas for juvenile sandbar sharks (*Carcharhinus plumbeus*) in the Northwest Atlantic Ocean (Musick et al. 1993). Sandbar sharks enter the system in early summer and then emigrate in early October to waters off the coast of Cape Hatteras, North Carolina (Musick and Colvocoresses 1986, Grubbs 2001). Juvenile sandbar sharks occupy an apex position in the Chesapeake Bay food web due to their relatively large size and mobility, feeding on commercially important species such as blue crabs (*Callinectes sapidus*) and menhaden (*Brevoortia tyrannus*) (Medved and Marshall 1981, Medved et al. 1985, Stillwell and Kohler 1993, Ellis 2003). The abundant fish and invertebrate fauna of the Chesapeake Bay system provides sufficient prey to fuel up to 75% of the annual growth in approximately four months each summer (Sminkey and Musick 1995). In order to sustain these growth rates, juvenile sandbar sharks in the Chesapeake Bay nursery must consume a significant surplus of energy beyond that required to carry out their daily activity and to maintain physiological functions.

Sandbar sharks are obligate ram-ventilators and must swim constantly to pass oxygenated water over their gills (W. Dowd, personal observation) and to maintain hydrodynamic lift via the large pectoral fins and the heterocercal caudal fin (Alexander 1965, Pelster 1997, Wilga and Lauder 2002). Juvenile sandbar sharks are relatively fast, active predators, covering large activity spaces and the entire water column (Medved and Marshall 1983, Grubbs 2001). These characteristics, combined with the relatively warm
water temperatures typical in the lower Chesapeake Bay in summer, would be predicted to elevate the metabolic demands of sandbar sharks, but metabolic rate has never been measured in this species. Metabolic rate is the largest and most variable component of the energy budget for active fish species (Kerr 1982, Boisclair and Leggett 1989). Sensitivity analyses have demonstrated the need for accurate metabolic rate data in constructing bioenergetics models (Kitchell et al. 1977, Bartell et al. 1986, Essington in review). Previous attempts to model the energetic demands of sandbar sharks relied upon metabolic rate estimates from an unrelated species (Medved et al. 1988, Stillwell and Kohler 1993), but this practice of borrowing parameters is usually unjustified (Ney 1993).

The metabolic rate of all organisms scales with both temperature and body size (Schmidt-Nielsen 1997). The effect of body size on metabolic rate is defined by the exponent \( b \) in the allometric equation \( MR = a \cdot M^b \), where \( MR \) is metabolic rate and \( M \) is body mass. The allometric exponent \( b \) is typically around 0.8 for metabolism in fishes (Glass 1969, Fry 1971, Brett and Groves 1979, Sims 1996). The effect of temperature on metabolic rate is reported as a \( Q_{10} \) value, which represents the relative change in metabolic rate due to a 10°C increase in temperature. \( Q_{10} \) usually lies between 2 and 3 in fishes (Fry 1971, Brett and Groves 1979), but it has been shown to depend on the size range and temperature range tested in some elasmobranch species (DuPreez et al. 1988, Hopkins and Cech 1994). Only a few studies have explored the size-metabolic rate relationship at more than one temperature or over large ranges in body mass (e.g. Pritchard et al. 1958, DuPreez et al. 1988, Hopkins and Cech 1994, Sims 1996); fewer
still have explored these metabolic rate relationships in large, active elasmobranch species (e.g. Bushnell et al. 1989, Carlson et al. 1999, Lowe 2001).

The primary objective of this study was to obtain detailed data on the metabolic rates of juvenile sandbar sharks over the size range that inhabits the lower Chesapeake Bay nursery grounds in summer and over the range of water temperatures experienced during that time. The summer population of juvenile sandbar sharks in Chesapeake Bay is composed almost entirely of animals less than 100 cm precaudal length (PCL) (Musick et al. 1993, Grubbs 2001), and neonates average approximately 47 cm PCL. Juvenile sandbar sharks have been landed in Chesapeake Bay at surface temperatures ranging from 15-29°C (Virginia Institute of Marine Science (VIMS) Longline Survey, unpublished data). Water temperatures in Chesapeake Bay oscillate seasonally; the lower range corresponds to early summer and autumn, and the highest temperatures occur in the surface waters in July and August. In addition, the lower Chesapeake Bay is characterized by a thermocline that is reinforced by the stratification of less dense freshwater from the tributaries flowing over higher density seawater from the Atlantic Ocean. The temperature of surface and bottom waters can differ by up to 5-6°C (VIMS Longline Survey, unpublished data). These temperature changes have implications for physiological energetics. In particular, the metabolic costs of sandbar sharks could change dramatically both over the course of the summer and over shorter time scales due to diel activity patterns and depth distributions relative to the thermocline. Tracking studies demonstrate that juvenile sandbar sharks in Chesapeake Bay perform frequent vertical excursions that cover much of the water column in a few minutes (Grubbs 2001), which would correlate with changes in ambient water temperature as they cross the
thermocline. Similarly, preliminary tracking data from Virginia’s Eastern Shore lagoons suggests that juvenile sandbar sharks in that system may venture onto broad tidal flats at high tide and return to deeper channels as the tide recedes (C. Conrath, personal communication). Temperature is elevated on these shallow flats relative to the deeper channels, which are flushed regularly with cooler bottom waters from the Atlantic Ocean through the inlets.

No technology exists for directly determining the metabolic rates of fishes in the wild. Since aerobic processes account for the bulk of metabolism in most situations, metabolic rate in fishes is determined by measuring the decline of dissolved oxygen content in a closed or flow-through laboratory respirometry system (indirect calorimetry) and calculating the metabolic rate in milligrams of oxygen consumed per hour (mg O$_2$·hr$^{-1}$) (Fry 1971, Brett and Groves 1979). Oxygen consumption is then converted to energy consumption (metabolic rate) using an oxycalorific coefficient, which represents the average energy yield per gram of oxygen consumed in cellular metabolism (Elliott and Davison 1975). The animals are usually starved for several hours to a few days prior to the experiment to guarantee complete gastric evacuation and to minimize the confounding effects of specific dynamic action (cost of digestion and protein assimilation; Brown and Cameron 1991a,b) on metabolic rate measurements. Three aerobic metabolic rates of fishes are distinguished in the literature, each obtained by different means: standard metabolic rate, routine metabolic rate, and maximum metabolic rate. Measures of maximum aerobic metabolic rate are difficult to obtain because the fish must be forced to sustain high swimming speeds in a Brett-type swim tunnel (e.g. Brett 1965, Gruber and Dickson 1997, Lowe 2001) or stimulated to vigorous activity in an
annular chamber (Brett and Blackburn 1978). The first option is logistically difficult (Graham et al. 1990), particularly for large species such as the sandbar shark, and the second may introduce other stress-related errors into the measurements. Standard metabolic rate (SMR) applies to a post-absorptive, thermally acclimated organism at rest, and may be considered the minimum metabolic rate for organismal maintenance (Fry 1971, Brett and Groves 1979). Two methods have been reported for determining SMR, one indirect and one direct. In the first, a power-performance curve relating the logarithm of oxygen consumption rate to relative swimming speed is constructed from data obtained in a swim tunnel or annular respirometer. SMR is then estimated by extrapolating the slope of the curve back to zero activity (Bushnell et al. 1989, Carlson et al. 1999, Leonard et al. 1999, 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 (Cech 1990), and may misrepresent SMR. Further, the swimming kinematics of juvenile scalloped hammerhead sharks (*Sphyrna lewini*) were significantly altered in a swim flume compared to the wild, perhaps affecting swimming performance and leading to overestimates of SMR (Lowe 1996, 2001).

The second option for measuring SMR is to confine the fish in a flow-through box respirometer and measure the decrease in oxygen concentration between the inflow and outflow water streams (Pritchard et al. 1958, Brill 1987, Hopkins and Cech 1994, Ferry-Graham and Gibb 2001). This process works well for sedentary, quiescent animals, but obligate ram-ventilators will struggle in such situations and present a unique problem. Brill (1987) directly measured the SMR of two species of obligate ram-ventilating tunas
(yellowfin, *Thunnus albacares*, and kawakawa, *Euthynnus affinis*) and two freshwater species (aholehole, *Kuhlia sandvicensis*, and rainbow trout, *Salmo gairdnerii*) by paralyzing them with the neuromuscular blocking agent gallamine triethiodide (Flaxedil™) and artificially ventilating them in a box respirometer. The SMR results for the two freshwater species were consistent with published values from extrapolation of power-performance curves and led to the conclusion that direct measurement of SMR in paralyzed fish gave reasonable results. Subsequent research generated extrapolated SMR values indistinguishable from those measured in paralyzed fish for *T. albacares*, *E. affinis*, and skipjack tuna (*Katsuwonus pelamis*, Brill 1979) (Dewar and Graham 1994). Similar techniques led to the same conclusion for adult American shad (*Alosa sapidissima*) (Leonard et al. 1999). The box respirometry method also allows for easy monitoring of other physiological variables such as heart rate and muscle temperature (Brill 1987) and for easy sampling by way of cannulae or catheters.

Routine metabolic rate (RMR) is the mean metabolic rate observed in an organism performing random physical activity over a given period (Fry 1971, Parsons 1990, Carlson et al. 1999). RMR is frequently measured in a relatively large, closed system known as an annular respirometer. The fish determines its own activity level and swimming speed (Bushnell et al. 1989, Carlson et al. 1999, Freund 1999). These systems are useful for obtaining a grand mean of metabolic rate over a given time period at a mean activity level. More detailed analyses of the relationship between transient activity levels and oxygen consumption are more difficult and less common in the literature (e.g. Bushnell et al. 1989, Carlson et al. 1999), due to unknown lags between the activity and detectable changes in the slope of the decline of dissolved oxygen concentration or due to
the fish assuming a narrow range of swimming speeds. A number of studies have reported RMR values that are approximately 1.5-3 times the basal or standard metabolic rate (Piiper et al. 1977, Brett and Blackburn 1978, Hove and Moss 1997, Duffy 1999, Lowe 2002). This increase in metabolic rate over SMR is primarily due to the costs of powering the swimming muscles during routine activity (Fry 1971). Weihs (1981) also used theoretical hydrodynamic arguments to develop a correction factor to account for the increased metabolic costs of continuous turning in an annular chamber relative to straightforward swimming, but this correction is rarely applied in practice (e.g. Scharold and Gruber 1991).

Both the routine and standard metabolic rates of juvenile sandbar sharks were determined over an order of magnitude range of body mass. Routine metabolic rate was measured in an annular respirometer at 24-26°C and in 3 cases also at 28°C. Standard metabolic rate was determined in a modified flow-through box respirometer system at 18°C, 24°C, and 28°C, on sharks immobilized with the neuromuscular blocking agent pancuronium bromide. Metabolic rates were determined for 15 sandbar sharks in both systems at 24°C, allowing direct comparison of SMR to RMR in individual sharks. The relationships between body mass and $Q_{10}$ and between temperature and the allometric exponent $b$ for sandbar shark SMR are also reported. This is the first direct measurement of SMR and the first comparison of paired SMR and RMR in individual sharks for an obligate ram-ventilating carcharhiniform species. These data will be useful in bioenergetics models to assess the energetic state and the ecosystem level function of these apex predators in the Chesapeake Bay summer nursery area.
MATERIALS AND METHODS

Shark Capture and Maintenance:

All experiments were conducted at the Virginia Institute of Marine Science Eastern Shore Laboratory in Wachapreague, VA, from June through September 2002. Juvenile sandbar sharks were captured with recreational hook and line fishing gear aboard small research vessels in the surrounding tidal lagoon system near Wachapreague Inlet. Hooks were cut to minimize the trauma to the shark during their removal. Sandbar sharks were transported to holding facilities in aerated seawater tanks. The sharks were maintained in a 14,000-gallon, aerated, recirculating seawater tank prior to experiments. Very small sharks were maintained in separate 800-gallon flow-through tanks to prevent cannibalism. Individual sharks were kept from 3 days to more than 6 weeks prior to being used in metabolic rate experiments. Food was presented every 1 to 3 days during that time. Individual sharks were moved to separate 800-gallon flow-through tanks and starved for several days prior to metabolic rate experiments. Temperatures in the holding facilities ranged from 21.6-28.9°C and salinity ranged from 34-36‰.

Routine Metabolic Rate:

An annular respirometer chamber (see Bushnell et al. 1989, Parsons 1990, Carlson et al. 1999) was constructed for routine metabolic rate measurements from a 1,250 L, round polyethylene tank (diameter 167 cm) (Figure 1). The lid was constructed of an 8 mil clear plastic sheet attached to a circular polyvinylchloride (PVC) pipe frame
Figure 1. The routine metabolic rate (RMR) annular respirometer setup. The large chamber houses the swimming shark, and the cage (c) forces the sharks to swim laps around the perimeter so that swimming speed can be quantified. During reoxygenation of the chamber, seawater is pumped to the blood oxygenator (b), where O₂ is added from the oxygen cylinder. The dissolved oxygen meter (d) output and water temperature are recorded by the computer at 20s intervals. For more details, see text.
that was wrapped in foam pipe insulation. The entire lid was removable to allow the shark to be placed in the chamber. To test the gas permeability of the lid, nitrogen gas was bubbled into the chamber to lower the dissolved oxygen (DO) content to 4.3 mg L\(^{-1}\), and the chamber was sealed for 3 hours with no detectable change in DO during that time. A circular, rubber-coated, wire-mesh cage (diameter 61 cm) was placed in the center of the chamber to force the sharks to swim around the perimeter of the tank. The mesh allowed the water in the chamber to mix more efficiently, and the swimming motion of the shark was assumed to be sufficient to thoroughly mix the chamber.

In order to reoxygenate the chamber between runs, a submersible pump inside the cage drew seawater from inside the respirometer and passed it through a small diameter PVC pipe and out of the chamber. From there seawater passed into a Harvey™ blood oxygenator cylinder, which was connected to an oxygen gas tank. The seawater passed through the blood oxygenator, where the large surface area increased the dissolution rate of oxygen without introducing bubbles, and then returned to the respirometry chamber through another hose. This system allowed quick reoxygenation (15-30 minutes) of the chamber without removing the lid and disturbing the shark. The oxygen tank valve was closed and the pump turned off when a new run began.

Prior to a routine metabolic rate trial, sandbar sharks were starved in the holding tanks from 2-6 days to allow for gastric evacuation and to eliminate any confounding effects of specific dynamic action on metabolic rate measurements. Gastric evacuation in this species ranges from 70 to 92 hours (Medved 1985). The annular respirometer was filled with sand-filtered seawater, and the shark was then transferred to the chamber by dip net. Each shark was allowed to acclimate in the chamber for 30-90 minutes before the
lid was sealed and any bubbles removed. The lights in the room were on during respirometry runs; most runs occurred between 09:00 and 24:00.

Dissolved oxygen concentration (mg O$_2$·L$^{-1}$) was measured with a Clark-type, polarographic electrode oxygen-temperature probe (YSI 5739, Yellow Spring Instruments), placed in the bottom of the annular respirometer, equipped with a battery-operated stirrer, and attached to a YSI 57 dissolved oxygen meter. The oxygen meter was calibrated in air-saturated seawater each morning prior to starting respirometry trials. The analog output from the oxygen meter was run to an analog to digital (A/D) personal computer data acquisition system (Dianachart, Inc., model PCA-14). A thermocouple was also connected to the A/D system to record water temperature in the chamber (°C). The respirometer was filled with seawater at ambient temperature, and room temperature was modified to maintain the seawater temperature at approximately 24-26°C during the trials. During three trials in mid-August, when water temperatures reach their peak in the Eastern Shore lagoons, sufficient data was collected at 28°C to allow routine metabolic rate determinations at this temperature. A data acquisition software program (INSTATREND™ Professional, Dianachart, Inc.) displayed temperature and dissolved oxygen charts and recorded both values and a time stamp at 20-second intervals throughout the trial for later analysis.

Dissolved oxygen content at the commencement of a run averaged 5.83±0.07 mg O$_2$·L$^{-1}$. Each run continued until the DO in the chamber had been reduced by 14.5±0.8%, after which the oxygen tank and submersible pump were turned on and the DO increased. Run times varied from 0.17 to 7.12 hours (mean 2.30±0.16 hours) depending on the size of the shark and the percent decline. At no time did the oxygen content fall below 4.45
mg O₂·L⁻¹. This process was repeated from 1 to 5 times for each shark. The total time in
the chamber for each experiment ranged from 4.6-34.8 hours.

Swimming speed was determined every 15-30 minutes during the run by
measuring the time required for the shark to pass a mark on the outside of the chamber
for 1-6 laps. It was possible to observe the shark’s shadow through the chamber wall for
these determinations, thus minimizing visual disturbance to the animal. This time was
converted to a swimming speed in body lengths per second (U, l·s⁻¹) using the following
equation:

\[
U = \frac{\text{laps} \cdot \text{circumference}}{\text{time} \cdot TL}
\]

TL is the total length of the shark (cm), and the swimming path circumference was
assumed to be a constant 463 cm. All of the sharks swam primarily along the outer wall
of the chamber near the middle of the water column. They maintained a slight but
unquantified inward yaw in their orientation. Sharks typically established a swimming
speed and direction and maintained that behavior for 5-20 minutes before turning around.
Periodically the sharks would swim quick laps near the surface of the chamber, but this
behavior was transient and did not appear to significantly affect the RMR measurements.
Swimming speed measurements were not intended to be an exact measure of behavior
and thus were not subject to rigorous statistical analysis. They merely served as an
estimate of the activity state of the shark while in the chamber.

The data were analyzed by run within each trial (Figure 2), with each run assigned
a RMR value and a mean swimming speed. The oxygen content measurements of each
run were regressed against the cumulative minute timing of the measurement to
determine the slope of the decline over the course of a run. In all cases these regressions
Figure 2. Sample routine metabolic rate experiment dataset. In this case, the experiment consisted of 4 consecutive runs at approximately 24-25°C, depicted by the negatively sloping segments of the dissolved oxygen concentration plot. Routine metabolic rate (mg O₂ consumed per hour) was calculated by multiplying the slope of each decline by the volume of the respirometer and then by 60 minutes. The period from 09:00 until 10:15 represents the initial acclimation period.
Dissolved oxygen (mg $\text{O}_2\text{L}^{-1}$)

Seawater temperature (°C)

Time of Day
were highly significant and very consistent ($R^2>0.98$). The metabolic rate in mg O$_2$·hr$^{-1}$
for each run was calculated by multiplying this slope (mg O$_2$·L$^{-1}$·min$^{-1}$) by the volume of
the chamber in liters ($V_R$) and then by 60 minutes (Steffensen 1989):

$$RMR = \text{Slope} \cdot V_R \cdot 60$$

Swimming speed measures were compared to predicted swimming speeds based
on Weihs’ (1977) equation:

$$U_0 = 0.503 \cdot \text{PCL}^{0.43}$$

This equation predicts swimming speed in meters per second (m·s$^{-1}$) based on PCL (m),
assuming that a free-swimming fish will assume the speed that minimizes its energetic
cost of transport per unit distance. This is predicted to occur at roughly 2 times the
were converted to PCL based on length-length regressions of data from the VIMS Shark
Longline Survey database:

$$\text{PCL} = 0.7502 \cdot \text{TL} - 0.8539 \quad (N=4,362, R^2=0.99)$$

These predicted swimming speeds were then converted to body lengths per second. The
relationship between swimming speed and metabolic rate was not tested since the sharks
typically maintained a relatively constant speed throughout the experiments.

To correct for the increased costs of swimming in a circular path, straight-line
routine swimming costs were estimated using the correction factor for banking fish
developed by Weihs (1981, equation 18):

$$\frac{\dot{V}O_{2T}}{\dot{V}O_{2S}} = 1 + \frac{D_o}{D_x} \left[ \left( \frac{\rho_f + \lambda \rho_w}{\rho_f - \rho_w} \cdot \frac{U^2}{gR} \right)^2 + 1 \right] \left( \frac{b_s}{b_i} \right)^2 - 1$$
The left side of the equation represents the ratio of metabolic rate (oxygen consumption) while swimming in a path with radius $R$ to metabolic rate while swimming in a straight line, assuming a constant speed $U$ (cm·s$^{-1}$). The derivation of this equation is outlined in Weihs (1981), and several parameters were borrowed from published literature values for other species. $D_t$ is the total hydrodynamic drag, and $D_i$ is the induced drag in straight-line swimming. The ratio of $D_i$ to $D_t$ was assumed to be 0.3 (Weihs 1981, derived for skipjack tuna from data in Magnuson 1978). $\rho_f$ and $\rho_w$ are the density of the fish and of seawater, respectively. The longitudinal added mass coefficient $\lambda$ is related to the volume of water dragged along with the swimming shark, and was assumed to be 0.2 (Webb 1975). $b_s$ and $b_t$ are the pectoral fin spans in straight-line swimming and banking, respectively. Due to the rigid nature of sandbar shark pectoral fins, the ratio of $b_s$ to $b_t$ was assumed to be 1 in all cases. Gravitational acceleration $g$ is 981 cm·s$^{-2}$.

The seawater was not treated with an ultraviolet sterilizer. Blank trials were performed to correct for the rate of background microbial respiration in the respirometer. For these trials the seawater was oxygenated, the respirometer lid sealed, and oxygen content monitored for 2-10 hours. Background respiration rates were insignificant in the first 24 hours after placing the shark in the respirometer, and were still minor compared to the metabolic rate of the shark after 24 hours. 56 of the 60 runs used in data analyses took place in the first 22 hours after adding the shark to the chamber.

*Standard Metabolic Rate:*

Standard metabolic rate was measured in a flow-through box respirometer system similar in design to that of Brill (1987) (Figure 3). Raw seawater was passed through a series of sand-filters and cartridge filters before entering the system. Seawater was
Figure 3. Laboratory flow-through respirometer setup for measuring standard metabolic rate (SMR). Seawater is pumped to the head tank (h), which provides a steady ventilation volume to the shark in the chamber (c) via the incurrent seawater hose (i). Outflow seawater oxygen content is measured by the oxygen electrode (e) from the outflow seawater line (o) and compared to the inflow oxygen content to determine metabolic rate. For more details, see text.
pumped into a 110 L reservoir, which was constantly and vigorously aerated to maintain its oxygen saturation. From the reservoir, seawater was pumped to a head tank, the overflow from which flowed back into the reservoir. Seawater flowed from the head tank at a constant pressure to the front of the respirometer box. All seawater entering the box passed through a hose inserted into the mouth of the shark. Fluorescein dye tests demonstrated that it was safe to assume that all flow through the hose passed through the opercular slits. A small, recirculating pump mounted near the rear of the chamber was used to ensure thorough mixing of the water and thus satisfy one of the major assumptions of the flow-through technique (Steffensen 1989). Upon exiting the chamber, the seawater passed back into the reservoir to be aerated.

Three respirometer boxes were constructed of 3/8” acrylic to accommodate the size range of animals studied: 76.2 cm long x 29.8 cm wide x 20.0 cm high (45.4 L); 101.6 cm x 40.0 cm x 26.0 cm (105.6 L); 127.0 cm x 50.2 cm x 33.0 cm (210.4 L). The large dorsal and pectoral fins of the sandbar sharks necessitated these large box volumes in order to minimize discomfort for the animals. The respirometer lids were held in place with a number of stainless steel bolts, and a rubber gasket prevented air or water leaks under the lid.

Temperature was maintained at the desired level ±1°C using a chiller and freshwater heat exchanger on the inflow seawater line, a flow-through chiller on the head tank line, and a number of submersible heaters in the reservoir and head tank. The limited capacity of the chillers made the use of the reservoir necessary. The chillers could not keep up with the required flow rates of raw seawater in a strict flow-through system. Also, the dissolved oxygen content of the ambient water surrounding the Wachapreague
facility changes over tidal and diel time scales, which would have introduced additional lags and uncertainty into the measurements. The system recycled a portion of the seawater that passed out of the chamber. This exhalant water mixed with the incoming raw seawater, and the excess overflowed the reservoir and was lost. The estimated turnover rate was on the order of 20-30% per hour of the total system volume (Kraul et al. 1985).

Sandbar sharks were starved from 2-7 days (4.1±0.2 days) prior to SMR experiments to ensure full gastric evacuation. The morning of an experiment, the flow-through system was started and the chillers turned on to establish the initial temperature for the experiment, usually 24°C. The shark was removed from its holding tank (or the RMR chamber if paired RMR values were obtained the day before) with a dip net, and 0.41-1.78 mg·kg⁻¹ (0.84±0.06 mg·kg⁻¹) of the neuromuscular blocking agent pancuronium bromide was injected into the caudal vein. The shark was then returned to the holding tank until it was unable to swim. The pancuronium bromide quickly immobilized the animals, usually after only 1-2 minutes.

The shark was then transported to the laboratory and placed supine on a moist towel suspended across the respirometry box. The incurrent seawater hose was placed in the shark’s mouth, supplying adequate flow of water over the gills. To help minimize the impact of circulating catecholamines and other physiological responses to handling stress (Wells and Davie 1985, Gerwick et al. 1999, Manire et al. 2001), each shark was then injected intramuscularly with 0.22-1.17 mg·kg⁻¹ of the steroid anesthetic combination alphaxalone/alphadolone (Saffan™, Glaxo-Vet). Electrocardiogram (EKG) wire leads were inserted subcutaneously just ventral to the pelvic girdle in order to monitor the
shark’s heart rate during the experiment. These leads were sutured into place and sealed with adhesive. The shark was then placed upright on the bottom of the flow-through chamber with the incurrent seawater hose positioned midway into the oral chamber. Two Velcro™ straps gently held the shark in place in the chamber. Two 20-gauge hypodermic needles were attached to polyethylene tubing and inserted into the dorsal musculature. This tubing passed out of the chamber and was used to periodically administer controlled intramuscular doses of pancuronium bromide and Saffan™ throughout the experiment. Pancuronium bromide doses were administered only when the shark showed repeated tail movements; some minimal tail twitching was observed in most sharks. Finally, the box lid was positioned and all air bubbles were removed before it was sealed. A black plastic cover was placed over the front end of the chamber and the lighting reduced in the room to minimize visual disturbance to the shark. The entire process from the initial pancuronium bromide injection to sealing the respirometer lasted from 20-60 minutes (mean 33±2 minutes).

The ventilation volume ($V_g$, L·min⁻¹) over the gills was controlled by a valve below the head tank and was adjusted to keep oxygen extraction between 10 and 20% in most trials. $V_g$ was determined every hour by measuring the time required for the outflow seawater from the chamber to fill a 2L graduated cylinder.

The partial pressure of oxygen in the seawater ($pO_2$, mm Hg) was measured using a Radiometer™ blood oxygen electrode mounted in a water-jacketed cuvette, maintained at the experimental temperature, and connected to a Cameron™ digital oxygen meter. A peristaltic roller pump moved either incurrent or excurrent seawater through oxygen-impermeable Tygon™ tubing and past the electrode at a steady rate. The tubing was
usually connected to a needle in the excurrent water hose, but every hour the tubing was transferred to a needle in the incurrent water hose to determine the inflow pO₂. This incurrent pO₂ was assumed to stay constant over the course of the hour and usually changed by less than 0.03% between successive determinations. The oxygen meter was also recalibrated in air-saturated seawater at the experimental temperature every hour. The first 5-10 minutes of data after each calibration were excluded from analyses while the dissolved oxygen probe reading asymptoted on the outflow seawater line.

The analog output of the oxygen meter, a thermocouple mounted in the chamber, and the EKG leads were connected to an A/D laptop computer system running the DASYLab™ (DASYTEC, National Instruments) data acquisition software package and sampling at 100 Hz. The EKG signal passed through a differential amplifier (DAM-50, World Precision Instruments) and electronic filter (Humbug™, Quest Scientific) before reaching the A/D system. Heart rate in beats per minute (bpm) was calculated by measuring the time change (Δt, s) between QRS peaks in the EKG signal:

\[ HR = \left( \frac{1}{\Delta t} \right) \cdot 60 \]

Heart rate was recorded every hour during recalibration.

The standard metabolic rate (mg O₂·hr⁻¹) was determined using the Fick principle (Steffensen 1989):

\[ SMR = \left( [O_2]_{in} - [O_2]_{out} \right) \cdot \dot{V} \cdot g \cdot 60 \text{ min} \]

\([O_2]_{in}\) and \([O_2]_{out}\) represent the dissolved oxygen concentration (mg O₂·L⁻¹) prior to entering and after leaving the chamber, respectively. The measured pO₂ was converted to mg O₂·L⁻¹ using the following equations. At the beginning of each run, the barometric
pressure (bp, mm Hg), salinity, and ventilation volume were determined and set in the DASYLab™ layout. These values were used to calculate the metabolic rate as described below. The oxygen solubility (mL·L⁻¹) of seawater at the current salinity (S) and temperature (T_sw) were determined following Richards (1965):

\[ O_2\text{sat} = (9.9096 - 0.2759 \cdot T_{sw} + 0.005398 \cdot T_{sw}^2 - 0.00004527 \cdot T_{sw}^3 \\
- (0.05896 - 0.00179 \cdot T_{sw} + 0.00002618 \cdot T_{sw}^2) \cdot S) \]

This oxygen solubility was then converted to mg O₂·L⁻¹ (Dejours 1975):

\[ [O_2\text{sat}] = O_2\text{sat} \cdot \left( \frac{32}{(T_{sw} + 273) \cdot 22.4} \right) \]

At the same time, the pO₂ at saturation at the current T_sw was determined. An interpolation table was used to determine vapor pressure (vp) at the current T_sw (Dejours 1975). This value was then used to calculate pO₂sat, where 0.2095 represents the mole fraction of oxygen gas in air (Pilson 1998):

\[ pO_2\text{sat} = (bp - vp) \cdot 0.2095 \]

Finally, the measured outflow and hourly inflow pO₂ values were converted to mg O₂·L⁻¹ using the results of the previous two equations:

\[ [O_2]_{\text{measured}} = \frac{pO_2\text{measured}}{pO_2\text{sat}} \cdot [O_2]_{\text{sat}} \]

Every 10 seconds, all of the values over that 10-second interval were averaged and added to a data file containing the following columns: time, T_sw, pO₂, \( \dot{V}_g \), metabolic rate (mg O₂·hr⁻¹), bp, salinity, and [O₂]_in.
Sandbar shark SMR measurements were obtained at 24°C in all trials; approximately half were also run at 18°C and/or 28°C. Due to the limitations of the temperature control system, the first experimental temperature and the subsequent order of the temperature changes were chosen based on the temperature of the raw seawater at the start of each experiment. The necessary changes in experimental seawater temperature were achieved by adjusting the chiller and heater thermostats in the system and by altering the flow rate of raw, warm seawater into the system. The system usually heated up more rapidly than it cooled. Temperature change rates averaged 4.5±0.6°C per hour for cooling and 6.4±1.1°C per hour for heating. Each fish was allowed an initial acclimation period of 43 to 843 minutes at each experimental temperature before the data were used in analyses. This acclimation period began when the seawater temperature reached within 1°C of the target temperature. Lag adjustment periods were defined as the time required for equilibration of the system after the last change in ventilation volume or after seawater temperature first reached within 1°C of the target temperature. These values ranged from 38-145 minutes for 99% re-equilibration of the system (Niimi 1978, Steffensen 1989). In all but 7 runs the acclimation times exceeded the 99% lag adjustment periods; acclimation times for these 7 runs exceeded the 95% lag adjustment period and were included in data analyses.

SMR measurements for each trial were plotted against time and averaged over all hours (range 1-7 hours) of consistent data for each temperature. If there was an obvious slope change in the pO2 signal during an hour, that hour was excluded from the analysis. Calibration difficulties with the oxygen electrode occurred on several days, and some values had to be dropped from the analysis. The total time each shark spent in the
respirometer ranged from 7.2-62.5 hours, depending on the number of temperature changes and the behavior of the oxygen electrode. At the end of each experiment, the shark was measured for total and precaudal length, sexed, and weighed to the nearest 5 grams wet weight.

To determine the effects of temperature changes on both SMR and heart rate, the $Q_{10}$ values were calculated for the appropriate temperature ranges of 18-24°C, 24-28°C, and 18-28°C (Schmidt-Nielsen 1997):

$$\log Q_{10} = \left( \log R_2 - \log R_1 \right) \cdot \frac{10}{T_{SW_2} - T_{SW_1}}$$

$R_2$ and $R_1$ correspond to the rates at the higher and lower temperatures, $T_{SW_2}$ and $T_{SW_1}$, respectively. $Q_{10}$ values were calculated for all relevant temperature change ranges, both those that were explicitly tested and those that could be determined from the SMR results at non-consecutive experimental temperatures.

Blank trials were conducted on two occasions to assess the rate of background respiration. The system was set up in the same manner as when sharks were present and run for several hours. A third control data set was obtained when a shark struggled off of the incurrent seawater hose and died overnight near the end of an experiment; the system was run for an hour with the shark still present. Each of these tests indicated background respiration rates not significantly different from zero.
Statistical Analyses:

Routine and standard metabolic rate data at each temperature were fitted to the allometric equation \( \text{MR} = a \cdot M^b \). The allometric exponents and allometric constants were estimated using a non-linear, iterative Gauss-Newton regression technique on non-transformed data (\textit{sensu} Brill 1979, 1987). A number of previous studies have fit metabolic rate data to the allometric equation using a double logarithmic plot with linear least squares regression (e.g. Pritchard et al. 1958, DuPreez et al. 1988, Sims 1996), but the Gauss-Newton technique provides better estimates of model parameters when the assumptions of log-linear regression cannot be met (Zar 1968, Glass 1969). The resulting \( R^2 \) statistic is based on the agreement of the observed and predicted values. The likelihood ratio test statistic was used to test for differences in the allometric exponents among temperatures and between SMR and RMR at 24-26°C (Freund and Walpole 1987, Morita 2001). This statistic approximates to a chi-squared distribution with degrees of freedom (d.f.) equal to the difference in the number of parameters between the full and reduced models (i.e. unequal vs. equal exponents).

One-way analysis of variance (ANOVA) followed by a Bonferroni \textit{post hoc} multiple comparison test were used to detect differences in mean heart rate \( Q_{10S} \) and SMR \( Q_{10S} \) among the three temperature ranges assessed and to determine which ranges were different, respectively. The relationships of HR \( Q_{10} \), SMR \( Q_{10} \), the RMR to SMR ratio, the HR \( Q_{10} \) to SMR \( Q_{10} \) ratio, and heart rate to body mass were each assessed with linear least squares regression.

The alpha value was \( p<0.05 \) for all statistical analyses. Statistical analyses were performed in SYSTAT© Version 8.0 (SPSS Inc., 1998) and SAS© Version 8.0 (SAS
Institute, Inc., 1999). All values given are means and standard error of the mean (mean±S.E.), except for SMR and RMR values. Due to the high sampling frequency and large sample sizes, the variation in SMR and RMR was represented as means and standard deviations (mean±S.D.).
RESULTS

A total of 34 juvenile sandbar sharks were used in routine metabolic rate and/or standard metabolic rate experiments (Table 1).

Routine Metabolic Rate:

Routine metabolic rates were measured for 16 sharks (60-107 cm TL; 1.025-7.170 kg) at 24-26°C (53 runs) and in 3 sharks at 28°C (7 runs) in the annular respirometer (Table 1). The best-fitting allometric equations at 24-26°C were:

Using all runs:

\[ R_{MR} = 213.2 \pm 22.4 \cdot M^{0.757 \pm 0.067} \quad R^2 = 0.77 \]

Using averages for each shark:

\[ R_{MR} = 212.9 \pm 38.0 \cdot M^{0.793 \pm 0.114} \quad R^2 = 0.82 \]

RMR is in mg O₂·hr⁻¹ and M is body mass in kilograms. The values in parentheses are the standard errors of the parameters. The allometric exponents determined by the two methods were not significantly different (likelihood ratio test, 1 d.f., \( p_{27,0.084} = 0.772 \)).

The estimated additional costs of swimming in a curved path versus a straight line ranged from 0.8-19.9% (7.7±1.1%). Using the corrected straight-line RMR estimates and averages for each shark, the allometric equation at 24-26°C took the form:

\[ R_{MR} = 199.6 \pm 32.8 \cdot M^{0.775 \pm 0.106} \quad R^2 = 0.83 \]

Sandbar sharks in the annular respirometer exhibited a fairly limited range of voluntary swimming speeds. The observed speeds correlated well with the theoretical
Table 1. Summary of standard metabolic rate (SMR), routine metabolic rate (RMR), and heart rate data for 34 juvenile sandbar sharks used in respirometry experiments. Missing values were either not tested or were unavailable due to equipment failures. Values for SMR and RMR are means±S.D. All other values are means±S.E.
predictions of Weihs (1977), although the fitted relationship predicted speeds slightly higher than the Weihs equation (Figure 4):

\[ U_0 = 0.572 \cdot \text{PCL}^{0.512} \]

\( U_0 \) is swimming speed in m·s\(^{-1}\) and PCL is in meters in this equation.

**Standard Metabolic Rate:**

Standard metabolic rates were measured for 34 sharks (57-124 cm TL; 1.025-10.355 kg). SMR was measured at 24°C for 33 of these sharks, at 28°C for 16 sharks, and at 18°C for 16 sharks (Table 1). The best-fitting allometric equations were:

\[
\begin{align*}
18°C: \quad \text{SMR} & = 65.1 (\pm14.7) \cdot M^{0.728 (\pm0.145)} & R^2 & = 0.71 \\
24°C: \quad \text{SMR} & = 120.0 (\pm17.3) \cdot M^{0.788 (\pm0.076)} & R^2 & = 0.84 \\
28°C: \quad \text{SMR} & = 206.9 (\pm27.6) \cdot M^{0.627 (\pm0.072)} & R^2 & = 0.87
\end{align*}
\]

SMR is in mg O\(_2\)·hr\(^{-1}\) and M is body mass in kilograms. The allometric constants (\(a\) in \(\text{SMR} = a \cdot M^b\)) were significantly different at all three temperatures based on their 95% likelihood confidence intervals. The allometric exponents (\(b\)) at each temperature were not significantly different (likelihood ratio test, 2 d.f., p\(\chi^2,3,2=0.202\), common \(b\) of 0.713).

The thermal history of the animal during the course of the experiment did not affect the observed SMR (Figure 5). The duration of the fasting period before the experiment also did not affect the SMR measurements, suggesting that any residual SDA effects were minimized.

**\( SMR_{Q_{10}} \):**

The effect of acute temperature change on standard metabolic rate (SMR \(Q_{10}\)) was determined in a total of 18 sharks (Table 1). Calculated SMR \(Q_{10}\)s from nonconsecutive temperature exposures were consistent with those from explicitly performed temperature
Figure 4. Relation of observed swimming speeds of juvenile sandbar sharks in the annular respirometer to the predicted swimming speeds of Weihs (1977) ($U_0 = 0.503 \cdot \text{PCL}^{0.43}$, dashed line). The solid line is the best fit to the sandbar shark swimming speed data ($U_0 = 0.572 \cdot \text{PCL}^{0.512}$). These equations predict swimming speed in m·s$^{-1}$ based on precaudal length in meters. Values here were converted to total lengths (TL) per second (l·s$^{-1}$). Error bars are ± 1 S.E.
Figure 5. Standard metabolic rates of juvenile sandbar sharks at a) 28°C, b) 24°C, and c) 18°C, determined by flow-through box respirometry. Different symbols represent different thermal histories of animals during the course of the experiment, i.e. the last experimental temperature prior to changing to the temperature of interest. No change indicates that the experimental temperature was the first temperature tested during the experiment. Solid lines are the best-fit allometric equations at each temperature. Error bars are ± 1 S.E.
a) 28°C

b) 24°C
c) 18°C
changes (Figure 6). The mean SMR $Q_{10}$ for 18-24°C was 3.53±0.44 (N=15). Excluding the one outlier ($Q_{10}$=7.47, Studentized residual=4.01), the mean was 3.24±0.37. The mean SMR $Q_{10}$s were 2.54±0.23 for 24-28°C (N=16) and 2.93±0.17 for 18-28°C (N=13). One-way ANOVA revealed no significant difference among the mean SMR $Q_{10}$s over each of the three temperature change ranges (F=2.682, p=0.080; F=1.813, p=0.176 excluding outlier). The overall mean SMR $Q_{10}$ was 2.99±0.19 (N=44, 2.89±0.16 if drop outlier). There was no significant correlation between body mass and SMR $Q_{10}$s for 18-24°C (p=0.384, p=0.625 if exclude outlier) or 18-28°C (p=0.752). There was a significant negative correlation between mass and SMR $Q_{10}$ for 24-28°C (p=0.014, slope= -0.198±0.070, $R^2=0.36$).

Heart Rate:

Heart rate data were obtained for 14, 29, and 13 sandbar sharks at 18°C, 24°C, and 28°C, respectively (Table 1). The relationship between heart rate and body mass at each of the three temperatures was determined using linear least-squares regression (Figure 7):

18°C: $HR = 39.3 \, (±2.0) - 1.07 \, (±0.49) \cdot M$

N=14, p=0.049, $R^2=0.29$

24°C: $HR = 66.7 \, (±1.6) - 1.81 \, (±0.30) \cdot M$

N=29, p<0.0005, $R^2=0.58$

28°C: $HR = 80.4 \, (±2.9) - 2.02 \, (±0.61) \cdot M$

N=13, p=0.007, $R^2=0.50$

Heart rate decreased with increases in body mass at all temperatures, and the slope of this decrease did not vary among temperatures (likelihood ratio test, 2 d.f., $p_{X^2,1.54}=0.463$). Heart rates of individual sharks increased with increasing water temperature in all cases.
Figure 6. Standard metabolic rate (SMR) $Q_{10}$s for juvenile sandbar sharks from a) 18-24°C, b) 24-28°C, and c) 18-28°C. Different symbols represent the direction of change over which the temperature was adjusted. Calculated values were not tested explicitly by measuring SMR at consecutive temperatures but were calculated from standard metabolic rate data in Table 1.
a) 18-24°C

b) 24-28°C

c) 18-28°C

SMR Q₁₀

Mass (kg)
Figure 7. Heart rates of juvenile sandbar sharks plotted against body mass at each of the experimental temperatures during standard metabolic rate experiments. Heart rate increased with increasing temperature for all sharks. Solid lines are best-fit linear regression models (see text). Error bars are ± 1 S.E.
Heart Rate $Q_{10}$:

The effect of acute temperature change on heart rate ($HR\ Q_{10}$) was determined in a total of 15 sharks (Table 1). As for SMR, all applicable $HR\ Q_{10}$s were calculated for each animal, regardless of which temperatures were measured consecutively. Calculated $HR\ Q_{10}$s from nonconsecutive temperature exposures were consistent with those from explicitly performed temperature changes (Figure 8). $HR\ Q_{10}$s averaged 2.22±0.05 for 18-24°C ($N=14$), 1.77±0.04 for 24-28°C ($N=12$), and 2.07±0.03 for 18-28°C ($N=11$). One-way ANOVA revealed significant differences among the mean $HR\ Q_{10}$s over the three temperature ranges ($F=28.718$, $p<0.0005$). The Bonferroni post hoc test showed that the mean $HR\ Q_{10}$ values for 18-24°C and 18-28°C were significantly different from the mean $HR\ Q_{10}$ for 24-28°C ($p<0.0005$) but not from each other ($p=0.062$). There was no significant correlation between body mass and $HR\ Q_{10}$s for 18-24°C ($p=0.972$), 24-28°C ($p=0.298$), or 18-28°C ($p=0.225$).

Heart rate $Q_{10}$s were less than SMR $Q_{10}$s in 29 of 36 cases (Figure 9). The ratio of heart rate $Q_{10}$ to SMR $Q_{10}$ averaged 0.75±0.08 for 18-24°C ($N=13$), 0.80±0.08 for 24-28°C ($N=12$), and 0.75±0.04 for 18-28°C ($N=11$). One-way ANOVA revealed no significant difference among the three temperature ranges ($F=0.139$, $p=0.871$). There was no significant correlation between the $Q_{10}$ ratio and mass for 18-24°C ($p=0.819$) or 18-28°C ($p=0.085$). There was a significant positive correlation between the $Q_{10}$ ratio and mass for 24-28°C ($p=0.030$, slope=0.072±0.028, $R^2=0.39$), which appeared to be driven by one data point (Figure 9b).
Figure 8. Sandbar shark heart rate $Q_{10}$ values for a) 18-24°C, b) 24-28°C, and c) 18-28°C. Different symbols represent the direction of change over which the temperature was adjusted. Calculated values were not tested explicitly by measuring heart rate at consecutive temperatures but were calculated from data in Table 1.
a) 18-24°C

b) 24-28°C

c) 18-28°C
Figure 9. The ratio of heart rate $Q_{10}$ to SMR $Q_{10}$ for all instances in which both values were determined for juvenile sandbar sharks in the flow-through respirometer for a) 18-24°C, b) 24-28°C, and c) 18-28°C. Values less than one indicate compensatory increases in stroke volume or arterio-venous oxygen difference to compensate for increased oxygen demands at higher temperatures.
a) 18-24°C

b) 24-28°C

c) 18-28°C
Paired RMR and SMR:

Paired RMR and SMR measurements were obtained for 15 sandbar sharks (1.025-7.170 kg) (Table 1). The ratio of mean RMR at 24-26°C to mean SMR at 24°C varied from 1.13-2.68 (1.78±0.12). At 28°C, this ratio equaled 1.58±0.13 (N=3). When corrected for the cost of swimming in a curved path, this ratio equaled 1.62±0.11 at 24-26°C and 1.47±0.13 at 28°C. There was no significant correlation between body mass and the ratio of RMR to SMR when tested with linear regression on uncorrected (p=0.926) or corrected data (p=0.955). The allometric exponents for RMR and SMR at 24°C were also not significantly different (likelihood ratio test, 1 d.f., $p_{0.002}=0.964$).
DISCUSSION

_Sandbar Shark Ecology and Energetics:

The metabolic rate data presented herein span the vast majority of the size and
temperature ranges relevant to the summer population of juvenile sandbar sharks in
Chesapeake Bay. Bioenergetics analyses require estimates of field activity and the
corresponding metabolic rate. Several studies have attempted to estimate field metabolic
rate by relating telemetric measures to corresponding laboratory oxygen consumption
rates, with varying success: examples include telemetered heart rate (Armstrong et al.
1989, Scharold et al. 1989, Scharold and Gruber 1991), swimming speed (Sundström and
Gruber 1998), electromyograms (Briggs and Post 1997), and tailbeat frequency (Lowe
2001, 2002). The validity of such extrapolations is often questioned, but it represents the
best available option at this time (Lowe and Goldman 2001). Another, much simpler
method for estimating field metabolic rate is to assume a constant activity multiplier of
the standard metabolic rate (sensu Winberg 1960, e.g. Kitchell et al. 1977, Schindler et al.
2002). Assuming that the ratio of RMR to SMR reported here represents a reasonable
approximation of an activity multiplier for the sandbar shark during routine field
behavior, and applying an oxycalorific coefficient of 13.59 J·mg O₂⁻¹ (Elliott and Davison
1975), RMR accounts for between 63.4 and 69.7 kJ per day of energy utilization for a 1
kg sandbar shark at 24°C. This value is comparable to values for the lemon shark
*(Negaprion brevirostris*, 67.7 kJ·day⁻¹, Nixon and Gruber 1988) and the bonnethead
(Sphyrna tiburo, 80.2 kJ-day⁻¹, Parsons 1990). The Q₁₀ values for SMR obtained between 18 and 28°C suggest that juvenile sandbar shark metabolic demands and energetic requirements are significantly affected by ambient temperature changes, both on short time scales and over the course of the summer stay in the nursery areas.

Juvenile sandbar sharks are found in high concentrations in summer both in coastal lagoon nurseries and in estuaries such as Chesapeake Bay. The experiments presented here were conducted at Virginia’s Eastern Shore, where salinities are near full-strength seawater. Meanwhile, sandbar sharks in the Chesapeake Bay nursery area have been captured at salinities down to 20‰ (Grubbs 2001). In addition to changes in ambient temperature, juvenile sandbar sharks in Chesapeake Bay experience fluctuations in the osmotic strength of their environment both as they move across the thermocline and during horizontal movements between high salinity waters near the mouth of the Bay and lower-salinity areas farther inland. These salinity fluctuations may significantly affect the metabolic rates of these animals by increasing their osmoregulatory costs. Changes in salinity are known to dramatically influence the metabolic rates of some teleosts (e.g. Nordlie and Leffler 1975, Furspan et al. 1984). In elasmobranchs, decreasing the salinity from 34‰ to 25‰ or 15‰ doubled the SMR of the bat ray (Myliobatis californica, Meloni et al. 2002), while the lip-shark (Hemiscyllium plagiosum) exhibited no change in oxygen consumption rate after dilution from 33‰ to 15‰ (Chan and Wong 1977). The physiological response of sandbar sharks to salinity changes represents a necessary and interesting line of exploration.

The relatively high temperatures, and possibly the low salinities, of the Chesapeake Bay nursery elevate the energetic requirements of juvenile sandbar sharks.
Thus, nursery utilization carries associated costs that are presumably outweighed by the benefits of increased food availability (Musick et al. 1986, Dauer 1997) and reduced vulnerability to predation (Musick et al. 1993). Similar benefits are associated with the evolution of nursery utilization in a number of slow-growing elasmobranchs (Branstetter 1990).

**RMR and SMR:**

In obligate ram-ventilators, the SMR state is probably never realized in nature since the fish must swim continuously (Korsmeyer and Dewar 2001). However, measurement of SMR and RMR in these species allows insight into the division of metabolic costs between swimming and maintenance processes. For example, the average metabolic rate in field-tracked juvenile *S. lewini* was 1.45 times the estimated SMR (Lowe 2002). Self-paired samples of SMR and RMR were obtained for 15 individual sandbar sharks swimming at voluntary speeds, allowing estimation of the additional costs of routine swimming beyond SMR. The observed ratio of RMR to SMR (1.78± 0.12) is similar to that published for a variety of teleost and elasmobranch species (Figure 14c). When corrected for the increased cost of transport while swimming in the curved annular respirometer, this ratio equaled 1.62±0.11 for straight-line swimming. The corrected values are an approximation only, since several parameters in the correction factor equation were borrowed from other species. It appears that SMR comprises approximately 50-60% of RMR in the sandbar shark. The allometric exponent for RMR was also not significantly different from that for SMR at 24°C. This agrees with the observed consistent relationship between RMR and SMR over the size range of animals tested.
As in several earlier studies (Howe 1990, Parsons 1990, Carlson et al. 1999), voluntary routine swimming speeds in the annular respirometer generally agreed with the theoretical predictions of Weihs (1977). Contrary to some previous studies (Metcalf and Butler 1984, Carlson and Parsons 2001), there was no evidence of increased swimming speeds with declines in ambient dissolved oxygen concentrations in the annular respirometer over the course of a run. Dissolved oxygen concentrations in the annular chamber never fell below 4.45 mg O₂·L⁻¹, and most runs were stopped at higher oxygen concentrations.

The metabolic rate data for sandbar sharks exhibit a high degree of variability (Figure 5), presumably due to individual physiological differences among the sharks used. Such variability is typical of metabolic rate experiments, but the relatively large sample sizes used allowed for accurate determination of the regression parameters. The effect of body size on SMR and RMR, as expressed by the allometric exponent \( b \), was not statistically distinguishable at the three experimental temperatures for juvenile sandbar sharks. Similarly, the allometric exponents for RMR and SMR were consistent at three temperatures for the lesser sandshark (Rhinobatos annulatus) and at four temperatures for the bullray (Myliobatus aquila) (DuPreez et al. 1988). The allometric exponents for sandbar sharks were similar to published values for other elasmobranchs (Table 2) and numerous teleost species (Glass 1969, Brett and Groves 1979).

Effects of Temperature Changes:

The effects of acute temperature changes on SMR were consistent with published values for other elasmobranch species (Table 3) and were relatively constant over the range of temperatures tested. \( Q_{10} \) values have been reported from 1.34 (Lowe 2001) to
Table 2. Summary of published values for the allometric exponent $b$ ($\text{MR}=a\cdot M^b$) for elasmobranch species. Values are mean ± 1 S.E. Sample size (N) is number of animals used with the number of trials in parentheses. $b$ is for standard metabolic rate (SMR) unless otherwise noted. AMR and RMR are active and routine metabolic rates, respectively.

<table>
<thead>
<tr>
<th>Species</th>
<th>Mass range (kg)</th>
<th>N</th>
<th>T (C)</th>
<th>$b$</th>
<th>Citation</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Myliobatis californica</em></td>
<td>0.41-1.72</td>
<td>7</td>
<td>12-14.5</td>
<td>0.68</td>
<td>Meloni et al. 2002</td>
</tr>
<tr>
<td><em>Scyliorhinus retifer</em></td>
<td>0.1001-0.3784</td>
<td>13 (17)</td>
<td>10</td>
<td>0.51±0.179</td>
<td>Duffy 1999</td>
</tr>
<tr>
<td><em>Scyliorhinus canicula</em></td>
<td>0.003-0.929</td>
<td>33 (40)</td>
<td>15</td>
<td>0.655</td>
<td>Sims 1996</td>
</tr>
<tr>
<td><em>Sphyra tiburo</em></td>
<td>0.095-4.65</td>
<td>3</td>
<td>25</td>
<td>0.59 (RMR)</td>
<td>Parsons 1990</td>
</tr>
<tr>
<td><em>Rhinobatos annulatus</em></td>
<td>0.025-2.244</td>
<td>10</td>
<td>20</td>
<td>0.74 (AMR) 0.82 (RMR) 0.84 (SMR)</td>
<td>DuPreez et al. 1988</td>
</tr>
<tr>
<td><em>Myliobatus aquala</em></td>
<td>0.157-2.390</td>
<td>5</td>
<td>20</td>
<td>0.75 (AMR, RMR) 0.76 (SMR)</td>
<td>DuPreez et al. 1988</td>
</tr>
<tr>
<td><em>Squalus acanthias</em></td>
<td>0.102-8.970</td>
<td>38</td>
<td>13</td>
<td>0.74 (0.77)$^b$</td>
<td>Pritchard et al. 1958</td>
</tr>
<tr>
<td><em>Carcharhinus plumbeus</em></td>
<td>1.025-7.170</td>
<td>16</td>
<td>16</td>
<td>0.728±0.145</td>
<td>present study</td>
</tr>
<tr>
<td></td>
<td>1.025-10.355</td>
<td>33</td>
<td>24</td>
<td>0.788±0.079</td>
<td>present study</td>
</tr>
<tr>
<td></td>
<td>1.025-10.355</td>
<td>16</td>
<td>26</td>
<td>0.627±0.072</td>
<td>present study</td>
</tr>
<tr>
<td></td>
<td>1.025-7.170</td>
<td>16</td>
<td>24-26</td>
<td>0.793±0.114 (RMR)</td>
<td>present study</td>
</tr>
</tbody>
</table>

$^a$ Reported as *S. suckleyi*.

$^b$ The allometric exponent for *S. acanthias* in parentheses was recalculated using all raw data in Pritchard et al. (1958).
Table 3. Summary of published $Q_{10}$ values for elasmobranchs. Acclimation time refers to the number of hours allowed after a temperature change before measurements of metabolic rate began. Temperature ranges are in degrees Celsius.

<table>
<thead>
<tr>
<th>Species</th>
<th>Temp Range</th>
<th>Acc. time</th>
<th>$Q_{10}$</th>
<th>Citation</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Triakis semifasciata</em></td>
<td>12-24</td>
<td>12</td>
<td>2.51</td>
<td>Miklos et al., in review</td>
</tr>
<tr>
<td></td>
<td>12-14</td>
<td>12</td>
<td>2.73</td>
<td></td>
</tr>
<tr>
<td></td>
<td>14-20</td>
<td>12</td>
<td>2.5</td>
<td></td>
</tr>
<tr>
<td></td>
<td>20-24</td>
<td>12</td>
<td>2.3</td>
<td></td>
</tr>
<tr>
<td><em>Sphyrna lewini</em></td>
<td>21-29</td>
<td></td>
<td>1.34</td>
<td>Lowe 2001</td>
</tr>
<tr>
<td><em>Sphyrna tiburo</em></td>
<td>20.0-29.6</td>
<td>12</td>
<td>2.34</td>
<td>Carlson and Parsons 1999</td>
</tr>
<tr>
<td></td>
<td>20.0-25.3</td>
<td>12</td>
<td>2.39</td>
<td></td>
</tr>
<tr>
<td></td>
<td>25.3-29.6</td>
<td>12</td>
<td>2.29</td>
<td></td>
</tr>
<tr>
<td><em>Myliobatis californica</em></td>
<td>8-26</td>
<td>12</td>
<td>3</td>
<td>Hopkins and Cech 1994</td>
</tr>
<tr>
<td></td>
<td>8-14</td>
<td>12</td>
<td>2.23</td>
<td></td>
</tr>
<tr>
<td></td>
<td>14-20</td>
<td>12</td>
<td>6.81</td>
<td></td>
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<td></td>
<td>20-26</td>
<td>12</td>
<td>1.85</td>
<td></td>
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<tr>
<td><em>Myliobatus aquila</em></td>
<td>10-15, 15-20, 20-25, 10-25</td>
<td>12</td>
<td>1.87 (1.54-2.18)$^b$</td>
<td>DuPreez et al. 1988</td>
</tr>
<tr>
<td><em>Rhinobatos annulatus</em></td>
<td>15-20, 20-25, 15-25</td>
<td>12</td>
<td>2.27 (1.96-2.69)$^b$</td>
<td>DuPreez et al. 1988</td>
</tr>
<tr>
<td><em>Scyliorhinus canicula</em></td>
<td>7-17</td>
<td></td>
<td>2.1</td>
<td>Butler and Taylor 1975</td>
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<td></td>
<td>7-12</td>
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<td>2.64</td>
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<td></td>
<td>12-17</td>
<td></td>
<td>3.11</td>
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<tr>
<td><em>Carcharhinus plumbeus</em></td>
<td>18-24</td>
<td>0.75-14</td>
<td>3.53±0.44$^c$</td>
<td>present study</td>
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<td></td>
<td>24-28</td>
<td>0.75-14</td>
<td>2.54±0.23</td>
<td></td>
</tr>
<tr>
<td></td>
<td>18-28</td>
<td>0.75-14</td>
<td>2.93±0.17</td>
<td></td>
</tr>
</tbody>
</table>

$^a$ *S. tiburo* $Q_{10}$s are seasonal between autumn and summer, autumn and spring, and spring and summer, respectively.

$^b$ Mean with range in parentheses. Smaller animals were more sensitive to temperature changes (i.e. higher $Q_{10}$s).

$^c$ 3.24±0.37 when drop one outlier.
6.81 (Hopkins and Cech 1994) for elasmobranchs. There was no obvious explanation for the SMR Q\textsubscript{10} outlier (e.g. acclimation period, obvious stress). Several studies have shown that Q\textsubscript{10} varies for an individual elasmobranch species depending on the particular temperature range assessed (DuPreez et al. 1988, Hopkins and Cech 1994, Carlson and Parsons 1999, Miklos et al. in review). This was not the case for the sandbar sharks as a group. However, in the individual sharks for which all three temperature range Q\textsubscript{10}s were available (N=13) SMR Q\textsubscript{10} from 18-28°C was always intermediate to the other two values; SMR Q\textsubscript{10} from 18-24°C was the highest value in half of these animals and the lowest in the other half. Q\textsubscript{10} for routine oxygen consumption rate decreased with an increase in body mass for R. annulatus and M. aquila (DuPreez et al. 1988); however, there was no control for activity in that study and the Q\textsubscript{10}s were calculated from best-fit regression lines at each temperature rather than temperature changes on individual animals. SMR Q\textsubscript{10} appeared to decline with increasing body mass in sandbar sharks for 24-28°C, but these results should be interpreted with caution due to small sample sizes at the larger end of the body mass scale that drive the regression fit (Figure 6b). Further, the allometric exponents at each of the three experimental temperatures were not significantly different, suggesting that temperature effects are consistent over all body sizes. Interactions between body mass and metabolic responses to temperature change may occur, but the results presented herein do not support this conclusion.

It is important to note the distinction between acclimation and acclimatization when reporting Q\textsubscript{10} values. Acclimation is the short-term physiological adjustment to environmental changes, whereas acclimatization usually refers to predictable adaptive changes over seasonal time scales (Fry 1971). The process of acclimatization can work to
reduce the seasonal Q_{10} by altering the biochemical state of the organism in order to maintain a relatively stable metabolic pattern (Fry 1971, Schmidt-Nielsen 1997). The sandbar sharks in this study were exposed to acute temperature changes that should mirror short-term temperature fluctuations experienced in the wild, and they were allowed short acclimation times at each temperature. It is interesting that the seasonal Q_{10}s reported for RMR of *S. tiburo* (Q_{10}=2.29-2.39, Carlson and Parsons 1999) were lower than the mean Q_{10}s reported here. More work is needed to clarify the adjustments in metabolic physiology of elasmobranchs in response to seasonal temperature fluctuations.

The heart rate Q_{10}s were less than the SMR Q_{10}s in almost all individual cases and for the overall means, suggesting compensatory changes in stroke volume or arterio-venous blood oxygen difference to meet the elevated oxygen demands at increased temperatures. These variables were not measured, but modification of stroke volume is a typical elasmobranch response to elevated metabolic demand during exercise (Tota 1999) and may be the underlying mechanism in sandbar sharks.

*Measuring SMR of Paralyzed Sharks:*

The technique of measuring metabolic rate on paralyzed animals ensures that the necessary conditions are met for measurement of SMR in continuously active species. This method has been validated in other species by comparison with extrapolation of power-performance curves to zero velocity (Brill 1987, Leonard et al. 1999). This was not an objective of the annular respirometry portion of the present study, and insufficient swimming speed data were collected to test the relationship between activity level and metabolic rate for individual or grouped animals. A simple calculation, using the
logarithms of SMR and RMR and the mean swimming speed from the annular chamber, was performed to estimate the slope of a hypothetical power-performance curve. The resulting slopes averaged 0.38±0.04 for 15 sharks at 24-26°C and 0.37±0.06 for 3 sharks at 28°C. These values are similar to slopes of power-performance curves for other sharks (Table 4) and are cautiously interpreted as additional evidence that the method used to measure SMR provides reasonable results.

The heart rate data suggest that all of the sandbar sharks were healthy during the standard metabolic rate experiments. Heart rates of juvenile sandbar sharks were comparable to those of other free-swimming shark species (Scharold et al. 1989, Scharold and Gruber 1991). These data should be interpreted with caution, however, since pancuronium bromide exhibits vagolytic activity (Fitzal et al. 1983, Husby et al. 1996, Melnikov et al. 1999, Mycek et al. 2000), blocking the parasympathetic muscarinic acetylcholine receptors of the cardiac branch of the sharks’ vagus nerve (Tota 1999). The resulting percent elevation in heart rate is unknown, but the heart rate values are probably reasonable for free-swimming sharks.

Confinement and handling of the sharks were unavoidable due to the nature of this study. Stress effects should not have significantly affected the standard metabolic rate measurements, particularly after the initial acclimation period in the respirometer. Following exhaustive exercise during hook and line capture, blood metabolites and gases return to normal levels within 6-10 hours for this species (Spargo et al. 2001). The transient stress experienced by the sharks during handling was likely not nearly as severe as exhaustive capture stress and was presumably counteracted by the administration of the anesthetic Saffan™. Saffan™ was chosen for its minimal cardiovascular effects and
Table 4. Power-performance curves for elasmobranch species, relating the logarithm of oxygen consumption to swimming speed in body lengths per second (U, l·s⁻¹). logVO₂=a + b·U.

<table>
<thead>
<tr>
<th>Species</th>
<th>T (°C)</th>
<th>Size range (kg)</th>
<th>a</th>
<th>b</th>
<th>Citation</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sphyrna lewini</td>
<td>26</td>
<td>0.506-0.927</td>
<td>0.324</td>
<td></td>
<td>Lowe 2001</td>
</tr>
<tr>
<td>Negaprion brevirostris</td>
<td>22</td>
<td>0.8-1.3</td>
<td>1.945</td>
<td>0.36</td>
<td>Bushnell et al. 1989</td>
</tr>
<tr>
<td>Carcharhinus acronotus</td>
<td>27</td>
<td>0.45-0.85</td>
<td>2.38</td>
<td>0.377</td>
<td>Carlson et al. 1999</td>
</tr>
<tr>
<td>Isurus oxyrinchus</td>
<td>18</td>
<td>3.9</td>
<td>2.36</td>
<td>0.595</td>
<td>Graham et al. 1990</td>
</tr>
<tr>
<td>Triakis semifasciata</td>
<td>14-18</td>
<td>2.2-5.8</td>
<td>2.2</td>
<td>0.2</td>
<td>Scharold et al. 1989</td>
</tr>
<tr>
<td>Negaprion brevirostris</td>
<td>25</td>
<td>1.11-1.61</td>
<td>2.1</td>
<td>0.344</td>
<td>Scharold and Gruber 1991</td>
</tr>
<tr>
<td>Carcharhinus plumbeus</td>
<td>24-26</td>
<td>1.025-7.170</td>
<td>0.38±0.04</td>
<td></td>
<td>present study</td>
</tr>
</tbody>
</table>

\(^a\) C. plumbeus slopes were calculated from metabolic rates determined at zero and average routine swimming speed (SMR and RMR).
ease of administration (Oswald 1978). Treatment with anesthetics reportedly had no
effect on the SMR of little skate (Raja erinacea, Hove and Moss 1997) or spiny dogfish
(Squalus acanthias, Pritchard et al. 1958). Similarly, the nursehound (Scyliorhinus
stellaris) exhibited similar SMRs under and without anesthesia (Piiper and Schumann

The sandbar sharks in this study were immobilized with the neuromuscular
blocking agent pancuronium bromide, which competitively binds with the nicotinic
acetylcholine receptors at the neuromuscular junction. It was anticipated that the
pancuronium bromide blockade would be reversible by administration of the
acetylcholine esterase inhibitor neostigmine (Hildebrand and Howitt 1984, Goldhill et al.
1988, Mycek et al. 2000). At the end of four of the first experiments, intravenous
injections of neostigmine and atropine were administered to antagonize the pancuronium
bromide and to reverse the neuromuscular blockade (Mycek et al. 2000). This treatment
appeared to work temporarily, and the sharks restarted slow swimming. However, usually
after less than 30 minutes the sharks were unable to continue swimming and settled onto
the bottom of the recovery tank. Repeated and increased doses of neostigmine proved
unsuccessful in restoring swimming capacity in these sharks, though they maintained
struggle responses. Several attempts to artificially ventilate the sharks overnight to allow
recovery also proved futile, as the sharks were able to twitch off of the seawater hose
overnight but were unable to resume swimming. Consequently, most sharks were
euthanized with an overdose of sodium pentobarbital (390 mg·mL⁻¹), administered
intravenously via the caudal vein. Eight sharks were euthanized in ice before the sodium
pentobarbital was obtained, one was euthanized with an intravenous overdose of
Saffan™, and one shark died overnight in the SMR chamber after it came off the
incurrent seawater hose. Persistent muscle weakness after prolonged treatment with
pancuronium bromide has been described in clinical applications in humans (O’Connor
and Russell 1988, Barohn et al. 1994); this was the likely phenomenon in the sandbar
sharks here. Future attempts to identify reversible methods and/or minimal effective
doses for neuromuscular blockade in elasmobranchs will allow increased sample sizes for
physiological experiments while minimizing the unnecessary destruction of experimental
subjects. Early attempts to immobilize sandbar sharks and smooth dogfish (Mustelus
canis) using gallamine triethiodide (Flaxedil™) proved unsuccessful, possibly due to
differences between these sharks and other fishes in the higher order structure of the
acetylcholine receptors at the neuromuscular junction.

**Elasmobranch Metabolic Rates:**

Several studies have reviewed various aspects of elasmobranch metabolic rates
reporting metabolic rate values for 22 species were reviewed in an attempt to summarize
the current knowledge of elasmobranch metabolic rate. Many of these studies utilized
smaller, more tractable species such as S. acanthias, but recent studies have addressed
larger, more active species. Elasmobranch standard metabolic rates reported in the
literature range from 13 mg O₂ per kilogram of body weight per hour (mg O₂·kg⁻¹·hr⁻¹)
for the bat ray at 13°C (Myliobatis californica, Meloni et al. 2002) to 240 mg O₂·kg⁻¹·hr⁻¹
for C. acronotus at 28°C (Carlson et al. 1999). Differences in experimental design and
analysis make comparisons among the studies difficult, but several observations can be
gleaned from the available data in the literature. The obvious observation is that the data
are still limited in scope, particularly for larger, more active species such as sandbar sharks. The data presented herein for juvenile sandbar sharks are the first direct measures of standard metabolic rate for a continuously active, obligate ram-ventilating elasmobranch species. This study also expands the body mass range over which SMR and RMR have been reported for continuously active shark species.

The available SMR data were adjusted to an intermediate temperature (20°C) using a $Q_{10}$ of 2.3 (Brett and Groves 1979) (Figure 10). These data exhibit a high degree of variability, with no obvious differences between highly active and more sedentary species. Adjusting metabolic rate data outside the normal thermal tolerance of a particular species is probably not justified, so the data were also pooled into three narrower temperature ranges (Figure 11). The SMR of the sandbar shark falls in the middle of the distribution for each of these temperature ranges, but again differences in experimental protocols make interpretation difficult. There are no obvious patterns between active, obligate ram-ventilating species and more sedentary species. Similar plots were developed for RMR, and again the sandbar shark falls in the middle of the existing scatter of data points (Figure 12).

The SMR of juvenile sandbar sharks is lower than those of similar sized tunas and the shortfin mako shark (*Isurus oxyrinchus*), but it lies in reasonable agreement with the few published values for ecologically similar shark species at similar temperatures determined by extrapolation of power-performance curves (Figure 13). Brill (1987, 1996) proposed that the high SMRs of tunas were a physiologically unavoidable consequence of their structural adaptations for extremely high sustainable aerobic metabolic rates, specifically that large gill surface areas led to high osmoregulatory costs. The estimated
Figure 10. Standard metabolic rates of 19 species of elasmobranchs adjusted to 20°C using a $Q_{10}$ of 2.3 (Brett and Groves 1979). The solid line is the regression for sandbar sharks adjusted to 20°C. The three open white symbols represent obligate ram-ventilating species. Cited in Brett and Blackburn 1978.
Carcharhinus acronotus (Carlson et al. 1999)
Cephaloscyllium ventriosum (Ferry-Graham and Gibb 2001)
Hemiscyllium ocellatum (Rahayu et al. 2002)
Hemiscyllium plagiosum (Chan and Wong 1977)
Isurus oxyrinchus (Graham et al. 1990)
Myliobatis californica (Hopkins and Cech 1994, Meloni et al. 2002)
Myliobatis aquila (DuPreez et al. 1988)
Raja erinacea (Hove and Moss 1997)
Raja tay decad (Bouhisot 1985)
Rhinobatos annularis (DuPreez et al. 1988)
Sphyraena lewini (Lowe 2001)
Squalus acanthias (Pritchard et al. 1958, Lenfant and Johansen 1966, Brett and Blackburn 1978)
Triakis semifasciata (Scharidt et al. 1989, Miklos et al. in review)

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**Mass (kg)**

![Graph showing relationship between mass and some parameters for various species of elasmobranchs.](image)
Figure 11. Standard metabolic rates of elasmobranch species from the literature, divided into a) 16-20°C, b) 23-25°C, and c) 26-29°C. Solid lines are the best-fit allometric equations for juvenile sandbar sharks at 18, 24, and 28°C.
**a) 16-20°C**

- Cephaloscyllium ventriosum (Ferry-Graham and Gibb 2001)
- Isurus oxyrinchus (Graham et al. 1990)
- Myliobatis californica (Hopkins and Cech 1994)
- Myliobatus aquila (DuPreez et al. 1988)
- Rhinobatos annulatus (DuPreez et al. 1988)
- Scyliorhinus canicula (Butler and Taylor 1975)
- Torpedo marmorata (Hughes 1978)
- Triakis semifasciata (Miklos et al. in review)

- Carcharhinus plumbeus (present study)

**b) 23-25°C**

- Hemiscyllium ocellatum (Routley et al. 2002)
- Hemiscyllium plagiourum (Chan and Wong 1977)
- Myliobatus aquila (DuPreez et al. 1968)
- Negaprion brevirostris (Gruber 1984, Nixon and Gruber 1988, Scharold and Gruber 1991)
- Rhinobatos annulatus (DuPreez et al. 1988)
- Triakis semifasciata (Miklos et al. in review)

- Carcharhinus plumbeus (present study)

**c) 26-29°C**

- Myliobatis californica (Hopkins and Cech 1994)
- Sphyrna lewini 26°C (Lowe 2001)
- Carcharhinus azorensis (Carlson et al. 1999)
- Sphyrna lewini 29°C (Lowe 2001)

- Carcharhinus plumbeus (present study)
Figure 12. Routine metabolic rates of elasmobranch species from the literature, divided into a) 16-20°C, b) 23-25°C, and c) 26-29°C. The solid line in b) is the best-fit allometric equation for juvenile sandbar sharks in the annular respirometer at 24-26°C. Note the difference in vertical axis scales.
a) 16-20°C

- Isurus oxyrinchus (Graham et al. 1990)
- Myliobatus aquila (DuPreez et al. 1988)
- Rhinobatos annulatus (DuPreez et al. 1988)
- Scyliorhinus stellaris (Piiper et al. 1977)
- Sphyrna tiburo (Parsons and Carlson 1998, Carlson and Parsons 1999)
- Triakis semifasciata (Gruber and Dickson 1997)

b) 23-25°C

- Myliobatus aquila (DuPreez et al. 1988)
- Negaprion brevirostris (Gruber 1984, Nixon and Gruber 1988, Scharold and Gruber 1991)
- Rhinobatos annulatus (DuPreez et al. 1988)
- Sphyrna tiburo (Carlson and Parsons 1999, 2001)
- Triakis semifasciata (Gruber and Dickson 1997)

Carcharhinus plumbeus (present study)

RMR (mg O₂·kg⁻¹·hr⁻¹)

Mass (kg)

c) 26-29°C

- Carcharhinus acronotus (Carlson et al. 1999)
- Mustelus norris (Carlson and Parsons 2001)
- Sphyrna lewini (Howe 1990, Lowe et al. 1998, Lowe 2001)
- Sphyrna tiburo (Carlson and Parsons 1999, 2001)
- Carcharhinus plumbeus (present study)

RMR (mg O₂·kg⁻¹·hr⁻¹)

Mass (kg)
Figure 13. Standard metabolic rates of active elasmobranch species and tunas. Lines are best-fit allometric equations at the stated experimental temperatures.
**Graphical Representation**

- **SMR (mg O₂ hr⁻¹)** vs **Mass (kg)**

- Key:
  - • *Isurus oxyrinchus* 18°C (Graham et al. 1990)
  - ○ *Sphyra lewini* 26°C (Lowe 2001)
  - ▼ *Negaprion brevirostris* 22-25°C (Bushnell et al. 1989)
  - ▽ *Negaprion brevirostris* 25°C (Scharold and Gruber 1991)
  - ■ *Sphyra lewini* 21°C (Lowe 2001)
  - □ *Sphyra lewini* 29°C (Lowe 2001)
  - ♦ *C. acronotus* 28°C (Carlson et al. 1999)
  - ——— *C. plumbeus* 28°C (present study)
  - ——— *C. plumbeus* 24°C (present study)
  - ——— *C. plumbeus* 18°C (present study)
  - ——— Kawakawa (*Euthynnus affinis*) 25°C (Brill 1987)
  - ——— Yellowfin (*Thunnus albacares*) 25°C (Brill 1987)
  - ——— Skipjack (*Katsuwonus pelamis*) 23.5-25.5°C (Brill 1979)
gill surface area of the skipjack tuna is approximately 13 cm² per gram of body mass (Muir and Hughes 1969, Roberts 1975). In contrast, the sandbar shark has approximately 2-4 cm² of gill filament surface area per gram of body mass, and other ectothermic shark species have similarly low gill surface areas (Emery and Szczepanski 1986, Hata 1993). Elasmobranchs retain urea and maintain their blood slightly hyperosmotic to seawater, and their plasma concentrations are significantly different from their environment (Shuttleworth 1988, Karnaky 1997). Consequently, elasmobranchs face significant influxes of water and ions across the gills, leading Carlson et al. (1999) to suggest a similar osmoregulatory cost argument to explain high SMRs for obligate ram-ventilating sharks. However, as demonstrated above, the SMRs of continuously active elasmobranchs are not consistently higher than their less active elasmobranch relatives when adjusted to a common temperature of 20°C. The major exception among elasmobranchs studied to date is the mako shark, an active, regionally endothermic pelagic predator with similar gill surface areas (10cm² per gram body mass, Emery and Szczepanski 1986) to those of tunas. The estimated SMR of a 3.9kg mako shark is comparable to, and possibly greater than, that of tunas of the same size (Figure 13).

One consequence of large gill surface areas and the corresponding suite of high-performance physiological characteristics that has received significant attention with respect to the physiological energetics of tunas is the concept of adaptation for multiple metabolic demands (Bushnell and Brill 1991, Brill 1996, Korsmeyer et al. 1996, Brill and Bushnell 2001, Korsmeyer and Dewar 2001). Tunas, and certain other teleosts, are capable of maximum aerobic metabolic rates (MMR) approximately 6-10 times the SMR (Brett and Groves 1979, Korsmeyer and Dewar 2001). This ratio defines the fish’s
available metabolic scope (Fry 1971, Hochachka and Somero 2002). The high sustainable oxygen delivery rates of tunas allow them to maintain activity metabolism (swimming) while also carrying out other metabolic tasks: standard metabolism, rapid oxygen debt repayment after anaerobic swimming bursts and buildup of lactate, and rapid growth (specific dynamic action, SDA). SDA alone can elevate metabolic rate several-fold; this elevation in metabolic rate represents the energetic costs of protein synthesis after a meal (Brown and Cameron 1991a,b). Due to their high maximum metabolic rates, tunas can sustain significant activity levels even during the SDA period.

In many other species SDA occupies a large portion of the available metabolic scope. For the 4 relatively inactive species of elasmobranchs in which SDA has been measured, the oxygen consumption rate during the SDA period can exceed 2-3 times the SMR (Figure 14a). Meanwhile, the limited data available suggest relatively narrow metabolic scopes for elasmobranchs; active metabolic rate (AMR) averages 2.08±0.14 times the estimated SMR for 10 elasmobranch species (Figure 14b). It should be noted, however, that only two studies report the true MMR at the critical swimming speed for an elasmobranch species (MMR/SMR of 1.82 for Triakis semifasciata, Scharold et al. 1989; MMR/SMR of ~2.75 for S. lewini, Lowe 2001). The other studies reported the maximum observed metabolic rate and should be interpreted with some caution and hopefully provoke further research into the subject. Regardless, these AMR data, in conjunction with the relatively modest mass-specific gill surface areas of ectothermic sharks, suggest that metabolic scope for many elasmobranchs is somewhat narrower than that of tunas. Consequently, many elasmobranchs probably face more stringent restrictions on their
Figure 14. Relationships of a) metabolic rate during specific dynamic action (SDA), b) active metabolic rate, and c) routine metabolic rate, to standard metabolic rate for several species of elasmobranchs. ¹SDA reported as the metabolic rate average during the 24 hours after feeding divided by routine metabolic rate during that same period, with no control for activity. ²SDA reported as the peak metabolic rate after feeding. ³Higher values for S. retifer were never realized; these values represent predicted RMR at 100% activity level (Duffy 1999). ⁴Values were predicted from allometric equations for a mass of 0.5 kg (DuPreez et al. 1988). ⁵T. semifasciata and S. lewini are the only species in b) for which the true maximum sustainable metabolic rate was determined (sensu Brett 1964). Note the differences in the scales of the horizontal and vertical axes.
metabolic expenditures and must make tradeoffs among metabolic demands, including SDA (growth).

SDA presents a particularly difficult problem for obligate ram-ventilating species such as the sandbar shark, which must continue to swim during the SDA period. The reported routine metabolic rates for 11 elasmobranch species average 1.58±0.09 times the SMR (Figure 14c), and the sandbar sharks in this study maintained RMR levels approximately 1.6-1.8 times SMR. Assuming ratios of maximum metabolic rate to SMR of 2-3 as seen in other elasmobranch species, sandbar sharks are using roughly 90-50% percent of their metabolic scope simply to sustain routine activity levels, with only limited potential to increase oxygen delivery to fuel growth. Pauly (1981) suggested that the supply of oxygen to the tissues, which is correlated with respiratory surface area and cardiac output (Coulson et al. 1977), limits the growth rates of fishes. Growth rates for many large elasmobranch species are exceptionally slow (Musick 1999); 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). The ratio of gill surface area to body mass predicted slow asymptotic growth rates very similar to those observed in several large shark species, including the sandbar shark (Hata 1993). Since rapid incorporation of ingested amino acids into body proteins is not possible, slow-growing elasmobranchs may reduce the rate of digestion while integrating SDA over a longer time period and/or reduce ingestion rates. For example, sandbar shark gastric evacuation at 22-30°C requires 70-92 hours (Medved 1985), and estimated daily rations for a number of sharks average 1-2 percent of body weight per day (Medved et al. 1988, Cortes and Gruber 1990, Stillwell and Kohler 1993, Sundström and Gruber 1998, Bush and Holland 2002),
compared to 4% or more in many fast-growing teleosts (e.g. Olson and Boggs 1986, Hartman and Brandt 1995). Future research should focus on determining the SDA effect and the maximum aerobic metabolic rates of slow-growing, obligate ram-ventilating elasmobranchs.
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CHAPTER 2:
Summer Nursery Ground Bioenergetics of Juvenile Sandbar Sharks
(Carcharhinus plumbeus) in Chesapeake Bay, Virginia
INTRODUCTION

The lower Chesapeake Bay, Mid-Atlantic Bight, and adjacent coastal lagoon systems serve as the primary summer nursery areas for the Northwest Atlantic Ocean sandbar shark (*Carcharhinus plumbeus*) population (Medved and Marshall 1981, Musick et al. 1993, Merson 1999, Grubbs 2001). Pregnant females enter the Chesapeake Bay and other estuaries along the Atlantic coast in May and June to pup and then return to deeper waters on the continental shelf for the remainder of the summer (Springer 1960, Musick and Colvocoresses 1986). Neonate and juvenile sandbar sharks remain in the nursery grounds until water temperatures and day length begin to decline in autumn, when they migrate south and east of Cape Hatteras, North Carolina, to overwinter in the warmer waters adjacent to the Gulf Stream (Musick and Colvocoresses 1986, Grubbs 2001, Merson and Pratt 2001). Juvenile sandbar sharks return to the estuarine nursery grounds in early summer, coincident with the increase in water temperature above 16-18°C, for the first 4 to 10 summers of life (Musick and Colvocoresses 1986, Sminkey and Musick 1995, Grubbs 2001).

Sandbar sharks are the most abundant large coastal sharks in the Mid-Atlantic Bight (Musick et al. 1993), and along with blacktip sharks (*C. limbatus*) they dominate the catch in the biannual Atlantic coastal commercial shark fishery (Cortes 1999a, 2000). After the rapid expansion of this fishery in the mid 1980s, catch rates in the fishery-independent Virginia Institute of Marine Science (VIMS) Longline Survey indicated that
the sandbar shark population in Virginia’s coastal waters had declined by approximately 66% by 1991 (Musick et al. 1993, Sminkey and Musick 1995). Meanwhile, survey catch per unit of effort (CPUE) in the lower Chesapeake Bay, the core nursery area for juvenile sandbar sharks, remained relatively stable (Musick et al. 1993). Recent increases in CPUE in the lower Chesapeake Bay and adjacent coastal waters may indicate the early stages of a recovery, but similar increases are not yet evident for subadult and adult sandbar sharks (VIMS Longline Survey unpublished data). Coast-wide, the sandbar shark population remains below optimum yield levels due to continued heavy fishing pressure (U.S. Department of Commerce 2003).

The neonate and juvenile nursery grounds are vital to the life history and potential recovery of the Northwest Atlantic sandbar shark stock (Branstetter 1990, Hoff and Musick 1990). Sandbar sharks, like many of their K-selected relatives, grow slowly and mature after at least 13-15 years (Casey et al. 1985, Casey and Natanson 1992, Sminkey and Musick 1995). Demographic models predict very slow rates of population increase even in the absence of fishing pressure, and elasticity analyses of these models demonstrate that juvenile survivorship is the most significant stage of the life history (Sminkey and Musick 1996, Cortes 1999b, Brewster-Geisz and Miller 2000). Genetic evidence indicates that the Northwest Atlantic and Gulf of Mexico sandbar shark populations comprise one interbreeding genetic unit (Heist et al. 1995, Heist and Gold 1999). Meanwhile, tagging data suggest that juvenile sandbar sharks return to natal nursery areas in Chesapeake Bay and Delaware Bay for at least 1 to 3 years (Grubbs 2001, Merson and Pratt 2001), although the temporal and ontogenetic consistency of this pattern remains undetermined (Casey and Kohler 1990). If natal homing does occur, as
these tagging data suggest, then management of particular juvenile nursery areas could
play a significant role in the population’s recovery. Regardless, it is necessary to
understand the contributions of individual nursery areas to the production of the sandbar
shark stock.

Nursery Area Hypothesis:

Juvenile sandbar sharks are not unique among sharks in their use of coastal
nursery areas (Springer 1967, Clarke 1971, Van der Elst 1979, Branstetter 1990, Holland
tropical and subtropical latitudes, such as the lemon shark (Negaprion brevirostris),
utilize nursery areas throughout the year (Morissey and Gruber 1993a,b). At temperate
latitudes subtropical species, including sandbar sharks, tend to leave their coastal and
estuarine summer nurseries in autumn, coincident with the emigration of most of the
ichthyofauna (Cowan and Birdsong 1985, Musick et al. 1986, Grubbs 2001, Merson and
Pratt 2001). The nursery utilization pattern can also vary within a species for
geographically distinct populations. For example, some neonate and juvenile scalloped
hammerhead sharks (Sphyrna lewini) in Hawaii utilize Kāne'iohe Bay as a nursery year-
round (Clarke 1971, Lowe 2002), while S. lewini in the Northwest Atlantic Ocean must
incorporate seasonal migrations between northern and southern nursery areas into their
life-history strategy due to seasonal temperature extremes (Branstetter 1990, Castro
1993).

Two benefits are often associated with the use of nursery areas by juvenile sharks,
leading to the formulation of the shark nursery hypothesis. First, nurseries serve as a
refuge for juvenile sharks since large sharks, their primary predators, are usually rare in
these areas (Branstetter 1990, Holland et al. 1993, Musick et al. 1993). Nurseries also tend to be shallower and can provide more cover than the open pelagic realm (Castro 1993, Morrissey and Gruber 1993a,b, Merson and Pratt 2001, Heupel and Simpfendorfer 2002). Potential predators of juvenile sandbar sharks include larger sandbar sharks as well as the other large coastal sharks that are occasional to rare visitors to the lower Chesapeake Bay (e.g. bull sharks (*C. leucas*), smooth hammerhead sharks (*Sphyrna zygaena*), and dusky sharks (*C. obscurus*)) (Murdy et al. 1997). In particular, large sandtiger sharks (*Carcharias taurus*) are known to prey on juvenile sandbar sharks during their seasonal migrations along the coast and near the mouth of Chesapeake Bay (Murdy et al. 1997). Two to three-meter *C. taurus* are frequently captured in the lower Bay and adjacent waters while attempting to prey on hooked juvenile sandbar sharks (VIMS Longline Survey unpublished data). Historically, the density of these predators in the lower Chesapeake Bay appears very low (Musick et al. 1993, Murdy et al. 1997), and the dramatic decline in large coastal shark abundance after the onset of commercial fishing (Musick et al. 1993) helps to explain the stability of the sandbar shark nursery population (Sminkey and Musick 1996). In addition, the apparent ability of juvenile sandbar sharks to tolerate salinities down to 20% or less in Chesapeake Bay (Grubbs 2001) may help to isolate them from larger sharks that prefer higher salinities or are incapable of osmoregulating under such conditions.

The nursery hypothesis also proposes that individual sharks gain an energetic advantage in the nursery grounds, usually as a result of increased availability of appropriately sized food, which leads to high growth rates (Gruber 1984, Castro 1987). Recent results appear to contradict this generally accepted explanation for juvenile
nursery utilization, suggesting that both aspects of the nursery hypothesis need not be met in all cases. Juvenile *S. lewini*, an apex predator in Kāne'ohe Bay, Hawaii, lose weight and suffer high mortality rates from starvation in this nursery area (Bush and Holland 2002, Lowe 2002). Like a number of carcharhiniform species, *S. lewini* are obligate ram-ventilators and must swim constantly to pass oxygenated water over their gills, which leads to high daily metabolic expenditures (Lowe 2001, 2002). The low energetic content and small size of the primary food source in the nursery (snapping shrimp, *Alpheus malabaricus*) might be insufficient to meet the high metabolic demands of these juvenile sharks, especially during the warm summer months (Bush and Holland 2002, Lowe 2002). These findings can be reconciled by consideration of other aspects of the life history and ecology of the species. *S. lewini* have larger litters (30-40 pups per litter) than sandbar sharks (6-10 pups per litter), such that higher mortality rates in the nursery may be mitigated by a larger year class (Branstetter 1990). Further, heavy predation pressure outside of Kāne'ohe Bay by large tiger sharks (*Galeocerdo cuvier*) and adult conspecifics (Clarke 1971) might have driven selection for use of the inshore nursery despite the energetic consequences.

The productive Chesapeake Bay waters host an abundant, diverse catalog of fishes and benthic invertebrates that serve as potential food for young sandbar sharks (Musick et al. 1986, Dauer 1997, Murdy et al. 1997). Like *S. lewini*, sandbar sharks are active obligate ram-ventilators, but juvenile sandbar sharks appear to consume sufficient prey in the Chesapeake Bay nursery grounds to satisfy their energetic demands. Annual growth of juvenile sandbar sharks occurs in two distinct phases: one period of rapid growth in the summer nursery grounds during which the sharks achieve ~75% of their
annual growth in length, followed by a period of little somatic growth during the winter (Sminkey and Musick 1995).

**The Bioenergetics Model:**

Sandbar sharks occupy an apex position in the coastal food web (Cortes 1999c), preying upon a number of commercially important species (Medved and Marshall 1981, Medved et al. 1985, Stillwell and Kohler 1993, Ellis 2003). Even neonate sandbar sharks, which are approximately 47-50 cm precaudal length (PCL) at birth (Springer 1960, Sminkey and Musick 1995, VIMS Longline Survey unpublished data), immediately enter the Chesapeake Bay food web at a high trophic level due to their size and mobility. Despite their abundance and position at the apex of many coastal and pelagic food webs, few studies have quantified the energetic demands of elasmobranchs as predators (Gruber 1984, DuPreez et al. 1990, Sundström and Gruber 1998, Lowe 2002, Schindler et al. 2002).

The bioenergetics model is often used to estimate consumption rates or energetic demands of fishes (e.g. Olson and Boggs 1986, Helminen et al. 1990, Hartman and Brandt 1995b, Hansson et al. 1996). This model relies on the first law of thermodynamics- the law of conservation of energy- to balance an organism’s energy inputs (consumption) with its energy outputs (total metabolism (respiration), growth, and loss of wastes) (Winberg 1960):

\[ C = R + G + W \]  

*(Equation 1)*

If any three of these quantities can be measured or predicted, the fourth can be determined by difference. This basic model is often refined to include subcomponents of the three energetic outputs (e.g. Schindler et al. 2002):
\[ C = SMR + AMR + SDA + G + U + F \]  
(Equation 2)

These include the basal or standard metabolic rate (SMR), energy expenditure beyond SMR due to routine activity (activity metabolism, AMR), the cost of digestive processes and protein synthesis for growth (Brown and Cameron 1991a,b) (specific dynamic action, SDA), the energy stored in changes in biomass (growth, G), and waste losses to excretions (U) and feces (F). G may also be subdivided into somatic and reproductive growth outputs. Each quantity is expressed in the same standardized energetic rate units (e.g. Joules (J) per gram of body mass per day). Laboratory values for metabolic rates are converted to energy units based on an oxycalorific coefficient, which represents the average energy yield per gram of oxygen consumed in cellular metabolism. In elasmobranchs, the oxycalorific coefficient most frequently used is 3.25 calories or 13.59 J per milligram of oxygen (mg O\textsubscript{2}) consumed (Brett and Blackburn 1978, Sundström and Gruber 1998, Lowe 2002), though it can vary with the relative proportions of fat, carbohydrate, and protein catabolyzed (Elliott and Davison 1975).

In most cases, 6 of the 7 parameters in Equation 2 are used to solve for either growth or consumption. The bioenergetics model is generally more useful for predicting consumption rates when growth rates are known than the inverse situation (Bartell et al. 1986). Since most physiological processes are temperature and size-dependent, it is theoretically possible to simulate in situ consumption rates using data on water temperature, diet composition, and estimates of metabolic rate. The bioenergetics model has been applied to numerous fishery management questions, among them the impacts of predators on prey populations (Olson and Boggs 1986, Hansson et al. 1996, Cartwright et al. 1998), population dynamics (Duffy 1998), management of freshwater recreational fish
stocking (Baldwin et al. 2000), predicting climate change effects on organismal ecology (Van Winkle et al. 1997), and the ecological consequences of varying life history strategies in apex predator species exposed to heavy fishing pressure (Schindler et al. 2002).

Development of bioenergetics models often outpaces acquisition of the necessary data for a particular species (Ney 1993). Bioenergetics models have been criticized for extrapolation of laboratory data far beyond the experimental conditions reported in the literature and for unjustified borrowing of data from other phylogenetically or ecologically unrelated species (Ney 1993, Sundström and Gruber 1998). In particular, metabolic rate is the largest and most variable component of the energy budget for any active fish species (Kerr 1982, Boisclair and Leggett 1989). This parameter is often borrowed (e.g. Schindler et al. 2002), but sensitivity analyses have demonstrated the need for accurate metabolic rate data, including the allometric and thermal scaling of metabolism, in constructing bioenergetics models (Kitchell et al. 1977, Bartell et al. 1986, Essington in review).

**Bioenergetics of Juvenile Sandbar Sharks:**

Previous efforts to model the energetic requirements of sandbar sharks suffered from a lack of species-specific data. Stillwell and Kohler (1993) constructed a simple bioenergetics model for a 1.7 kg juvenile sandbar shark and estimated daily ration as 1.49 percent of body weight (%BW) per day. Medved et al. (1988) attempted a similar bioenergetics analysis and arrived at a daily ration of 1.32 %BW per day. However, each of these models incorporated metabolic rate data from the spiny dogfish (*Squalus*
acanthias, Brett and Blackburn 1978), an unrelated species that inhabits much cooler waters than the sandbar shark.

The sandbar shark provides a unique opportunity for a reassessment of the bioenergetics of active elasmobranch species, since it is one of the few large elasmobranchs for which many of the species-specific data are now available. The objective of this study was to construct a bioenergetics model for juvenile sandbar sharks solely for the time spent in their Chesapeake Bay summer nursery grounds. Model parameters were derived from available data in the literature and from archived VIMS Longline Survey data. The model incorporates the seasonal nature of growth, utilizes historical temperature data from lower Chesapeake Bay, and includes newly acquired data on the metabolic rate of this species (Dowd et al. in prep). This model is used to predict consumption rates by each age-class and to make quantitative predictions of the ecosystem impacts of juvenile sandbar sharks as predators in the lower Chesapeake Bay system. Assumptions of the model are tested by error analyses using Monte Carlo simulations, acknowledging continued uncertainty in some model parameters. The limitations of the model are discussed in relation to the available data and future studies are proposed that could resolve these limitations.
MATERIALS AND METHODS

Study Area and Nursery Habitat Utilization:

The lower Chesapeake Bay is extremely spatially heterogeneous in terms of its depth and benthic habitat characteristics (Wright et al. 1987). Overall, it is fairly shallow (<10 m), except for several deep (>30 m) shipping channels along its eastern and southern portion. Visibility is limited (Secchi depths ~1.8 m) due to relatively high turbidity. In an analysis of VIMS Longline Survey catch rates from Chesapeake Bay, CPUE of juvenile sandbar sharks was strongly correlated with salinity (>20.5%) and was somewhat less dependent on water depth (>5.5 m) and dissolved oxygen concentration (>5.35 mg O₂·L⁻¹) (Grubbs 2001). An area on the order of 500-1,000 km² of the lower, eastern Chesapeake Bay meets these requirements on average and forms the core sandbar shark nursery area (Figure 1). This area supports a seasonal population of approximately 10,000 individuals (Sminkey 1994), composed almost entirely of sandbar sharks less than 90 cm PCL (Musick et al. 1993) (Figure 2).

Springer (1967) proposed that limited nursery areas could impose density-dependent controls on shark populations. The negative correlation between annual survival rate and the initial population size of juvenile *N. brevirostris* in Bimini, Bahamas, was consistent with density-dependent control of mortality (Gruber et al. 2001), but results from this subtropical nursery cannot be extrapolated to the temperate

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1 Chesapeake Bay Program Water Quality Database. http://www.chesapeakebay.net/data/index.htm
Figure 1. The core sandbar shark nursery area in the lower Chesapeake Bay (dark region) (adapted from Grubbs 2001)). K and M represent the VIMS Longline Survey standard stations at Kiptopeke State Park and Middle Ground Shoal, respectively.
Figure 2. Length-frequency of all sandbar sharks captured by the VIMS Longline Survey in Chesapeake Bay waters since 1974 (N=2,185). Shaded bars represent the frequency for each 5 cm length bin, and the solid line is the cumulative frequency distribution. The cumulative distribution demonstrates that the vast majority of sandbar sharks in Chesapeake Bay are less than 90 cm precaudal length (PCL).
nurseries of sandbar sharks. Like many temperate estuarine systems, the lower Chesapeake Bay is highly dynamic in terms of its salinity, dissolved oxygen, and temperature profiles, over interannual, seasonal, and shorter time scales. The suitable sandbar shark nursery area in Chesapeake Bay defined using the environmental parameters described above could change by as much as 75% between years due to climatic fluctuations that drive the salinity regime of the Bay (Grubbs 2001). The impacts of such fluctuations on the distribution and abundance of juvenile sandbar sharks within the nursery are not known. The severe summer declines in dissolved oxygen concentration in the bottom waters of Chesapeake Bay typically occur in the deep paleochannels north of the core nursery area, and would therefore only influence the extent of the sandbar shark nursery in very dry years when isohalines shift north in the Bay or when the anoxic conditions are particularly severe and extensive (Grubbs 2001).

Juvenile sandbar sharks move nomadically within the nursery area, covering large activity spaces (>110 km²) and the entire water column (Medved and Marshall 1983, Grubbs 2001). Sandbar sharks tracked using sonic telemetry tended to maintain deeper swimming depths during the day (12.8±5.01 m) than at night (8.46±2.30 m) (Grubbs 2001). Similarly, CPUE of sandbar sharks on recreational fishing gear at midwater and near-surface depths was higher during the night than during the day in Chincoteague Bay (Medved and Marshall 1981). Activity spaces were often centered on one of three deep channels in the lower Chesapeake Bay during the day and expanded at night (Grubbs 2001). This apparent diel pattern might be an adaptation for nighttime foraging near the

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surface or in shallow waters near tidal creeks (Grubbs 2001); although juvenile sandbar sharks do not feed exclusively at night, and a number of their dominant prey items are benthic fishes and invertebrates (Medved et al. 1985, Stillwell and Kohler 1993, Ellis 2003). This behavior may also play a role in predator avoidance. Juvenile *S. lewini* in Kāne‘ohe Bay, Hawaii, had expanded activity spaces at night relative to daylight hours, presumably due to daytime refuging (Holland et al. 1993). Juvenile sandbar sharks also performed a series of vertical excursions throughout a track, often moving 10 m or more through the water column in the ten minutes between telemetry fixes (Grubbs 2001). These excursions may further enhance the three-dimensional search for patchy pelagic prey.

*Bioenergetics Model Scope and Outputs:*

This sandbar shark bioenergetics model was constructed solely for the period from immigration to the lower Chesapeake Bay summer nursery through emigration in autumn. The beginning and end dates for the simulation were chosen as May 15 and September 30 based on historical catch data from the VIMS Longline Survey. The model used a daily time step, consistent with the division of growth and metabolism to daily rates and the determination of daily ration. Model inputs of growth, metabolic rate, and waste losses were used to predict energetic requirements (daily energy ration, Joules) using a modified bioenergetics model:

\[ C = RMR + SDA + G + F + U \]  
(Equation 3)

The derivations of the five energy output parameters are described below. In turn, these energetic requirements were combined with estimates of the composition and energetic content of the diet to estimate rates of food consumption (daily ration) and predatory
impact of individual sharks over the course of the summer for each age-class. Finally, these individual estimates were merged with estimates of population size and age structure to estimate the overall predatory demand of juvenile sandbar sharks in the Chesapeake Bay nursery area.

**Summary of Existing Data and Bioenergetics Model Parameters:**

The bioenergetics model is only as reliable as the parameters used to construct it. Many of these parameters were available for juvenile sandbar sharks, as outlined below. Some parameters of the bioenergetics model still have not been determined for sandbar sharks, but reasonable estimates were available from related species.

1. **Growth Rates:**

   The growth rates of juvenile sandbar sharks have been documented both before and after the onset of the commercial fishery in the 1980s and the resulting population decline (Sminkey and Musick 1995). The annual periodicity of the growth rings used to age sandbar sharks has been validated for juvenile age-classes (Casey et al. 1985, Branstetter 1987). The growth rates of certain younger age-classes of juvenile sandbar sharks in Chesapeake Bay increased slightly between 1980-1981 and 1991-1992, possibly due to density-dependent compensation (Sminkey and Musick 1995). The von Bertalanffy equation was used to predict annual growth rates for these two periods to assess the consequences of this change from an energetic perspective (Sminkey and Musick 1995):

   \[
   L_t = L_\infty \cdot \left(1 - e^{-K(a-t_0)}\right)
   \]  

   \[(Equation\ 4)\]

   - 1980-1981  \(L_\infty = 199\) cm, \(K = 0.057\), \(t_0 = -4.9\) years
   - 1991-1992  \(L_\infty = 164\) cm, \(K = 0.089\), \(t_0 = -3.8\) years
The bioenergetics model treats average individuals within each of six age-classes present in the lower Bay, back calculated as size at age 0-5 (Musick et al. 1993, Sminkey 1994). The predicted sizes from Equation 4 were assumed to represent the PCL of sharks of age \( a \) upon immigration in May or birth for young-of-the-year (age 0). The total seasonal growth in the nursery grounds \( (G_{NG}) \) for each age-class was calculated and used to determine the PCL at emigration \( (L_E) \):

\[
L_E = L_a + G_{NG} = L_a + p \cdot (L_{a+1} - L_a)
\]  

(Equation 5)

\( p \) is the proportion of annual growth in PCL that occurs in the Chesapeake Bay nursery and \( L_a \) is PCL at age \( a \) predicted from Equation 4.

As a baseline estimate, 75% of the annual growth in PCL was assumed to occur in the Chesapeake Bay nursery area each summer (Sminkey and Musick 1995). Tag-return validation of the purported seasonal growth rates in the nursery has been difficult to obtain. Very few of the sharks tagged by the VIMS Longline Survey have been reported recaptured, probably due to underreporting by the commercial sector (Grubbs 2001), and reliable measures of length upon recapture are rarer still. One tagged juvenile (TL 67 cm at tagging) was recaptured by VIMS scientists 0.5 km from the tagging location in September 1998 in the coastal lagoon nursery area of Virginia’s Eastern Shore after 44 days at liberty; it had grown 3 cm in total length. In comparison, another juvenile of similar size (TL 66 cm) was tagged in Chesapeake Bay in September 1995 and recaptured by VIMS scientists 9.5 km away during the subsequent immigration period. This shark was at liberty for 225 days and grew 3.5 cm in that time. One sandbar shark that was tagged and recaptured by NMFS scientists in the same summer grew 3 cm in FL (48-51 cm FL) over 62 days at liberty between mid-July and mid-September (Casey et al.
In Delaware Bay, two same-summer recaptures grew 3 cm FL (45 cm FL at tagging) and 1 cm FL (no size given) in 40 and 47 days at liberty, respectively (Merson and Pratt 2001). All of these tag-return results roughly agree with the proposed seasonal growth pattern.

Weight increases with length according to the equation $W = L^b$. Two equations have been published relating weight to length for sandbar sharks, where fork length (FL) is in centimeters and weight is in grams:

$$W = 0.0123 \cdot FL^{2.9577} \quad \text{(Medved et al. 1988)} \quad \text{(Equation 6)}$$

$$W = 0.0109 \cdot FL^{3.0124} \quad \text{(Kohler et al. 1995)} \quad \text{(Equation 7)}$$

Lengths were converted between PCL and FL using a regression obtained from historical VIMS data:

$$FL = 1.0791 \cdot PCL + 2.78 \quad \text{(N = 4,385, } R^2 = 0.99) \quad \text{(Equation 8)}$$

A third length-weight equation was fit to historical data obtained over 20 years by the VIMS Longline Survey (44 cm < PCL < 167 cm). These measurements were recorded at least to the nearest pound, and most were reported to the nearest quarter pound. The best fit for all the data was:

$$W = 0.00422 \cdot PCL^{3.289} \quad \text{(N = 533)} \quad \text{(Equation 9)}$$

Equations 6, 7, and 9 group all sharks, regardless of the time of year they were captured. A number of fish species experience seasonal fluctuations in their condition index due to variations in the availability and quality of food (e.g. Castro et al. 1999, Henderson et al. 2000). To test for this phenomenon in sandbar sharks from Chesapeake Bay, the VIMS data were fit to two seasonal length-weight equations using the PROC NLP procedure in SAS© Version 8.0 (SAS Institute, Inc., 1999), one for the immigration
period in May and June and another for the emigration period in September and early October. These seasonal models were significantly different from the grouped VIMS equation (likelihood ratio test, 2 d.f., $p_{37.36} < 0.0005$). The best fitting seasonal equations were:

- **Spring:** $W = 0.00268 \cdot PCL^{3.382}$ (N = 245)  
  (Equation 10a)

- **Fall:** $W = 0.00846 \cdot PCL^{3.144}$ (N = 288)  
  (Equation 10b)

These equations predict that juvenile sandbar sharks grow proportionately faster in weight than in length over the course of the summer in Chesapeake Bay.

Specific growth rate (grams per gram of body weight per day) has been shown to vary with temperature (e.g. Huuskonen et al. 1998), dissolved oxygen levels, energy intake, or food quality for other species (see Brett and Groves 1979). There was no evidence supporting the choice of one of these growth patterns for sandbar sharks. Therefore, daily growth rates ($G_D$) in grams per day were calculated by assuming that the weight of the shark increased by a constant proportion ($x$) in each of the $n$ days of the simulation:

$$M_E - M_I = \sum_{D=1}^{n} G_D = \sum_{D=1}^{n} x \cdot M_D$$  
(Equation 11)

$M_D$ is the weight of the shark at the beginning of day $D$. The weight of the shark at the first ($M_I$ for $L_I$) and last ($M_E$ for $L_E$) day of the simulated nursery season was determined using the four length-weight equations. Proportional daily growth was represented by a linear first order difference equation with a constant coefficient (Brown and Rothery 1993):

$$M_E = x^n M_I$$  
(Equation 12)
Fitted values for $x$ in Equation 12 were on the order of 0.1-0.5 percent increases in weight per day.

The energetic conversion factor relating growth in weight to increase in energy content was estimated from other shark species, since no data of this type exist for sandbar sharks. Energetic content values for juvenile *N. brevirostris* and 4 juvenile *S. lewini* (one outlier excluded) have been reported as 5.4 kilojoules per gram (kJ·g$^{-1}$) and 5.36±0.20 kJ·g$^{-1}$, respectively (Cortes and Gruber 1990, Lowe 2002). This value (5400 J·g$^{-1}$) was assumed to be reasonable for sandbar sharks. The one outlier *S. lewini* had an energetic content of 8.83 kJ·g$^{-1}$ (Lowe 2002), which exceeds that for oily fish such as Atlantic menhaden (~6.7 kJ·g$^{-1}$, Thayer et al. 1973). Growth outputs to reproductive products were assumed to be negligible since all of the age-classes in the model are at least 8-10 years from the age at maturity (Casey et al. 1985, Sminkey and Musick 1995).

2. Metabolic Rate:

The weakest link in previous sandbar shark bioenergetics models was unreliable estimates of metabolic rates (Medved et al. 1988, Stillwell and Kohler 1993). Recent laboratory metabolic rate studies of carcharhiniform sharks revealed relatively high oxygen consumption rates for obligate ram-ventilating species (Carlson et al. 1999, Lowe 2001), which would suggest higher energetic requirements for sandbar sharks as well. Reliable estimates of field activity levels and the corresponding metabolic rates are also needed to validate the extrapolation of laboratory metabolic rates to fishes in the wild (Diana 1983, Boisclair and Leggett 1989).
2.1 Laboratory Metabolic Rates of Juvenile Sandbar Sharks:

The allometric (size-dependent) and thermal influences on standard metabolic rate in juvenile sandbar sharks were recently determined in a laboratory respirometry system over the entire size range (1-10 kg) characteristic of the Chesapeake Bay nursery areas and at 18, 24, and 28°C (Dowd et al. in prep). For 33 sharks at 24°C, the best fitting allometric equation for SMR was:

\[ SMR_{24} = 120.0 (\pm 17.3) \cdot M^{0.788 (\pm 0.076)} \]  

(Equation 13)

*M* is weight in kilograms and SMR is mg O₂ consumed per hour. The values in parentheses are the standard errors of the allometric intercept and the allometric exponent estimates, respectively.

The relationship of routine metabolic rate (RMR)- the average oxygen consumption rate of a free-swimming shark- to standard metabolic rate was also determined for sharks swimming in an annular respirometer (Dowd et al. in prep). In the 15 sandbar sharks for which self-paired SMR and RMR measurements were obtained, the ratio of RMR to SMR averaged 1.78±0.12 for the raw data and 1.62±0.11 when corrected for the costs of swimming in the circular annular respirometer (sensu Weihs 1981). For three sharks the RMR to SMR ratio was also measured at 28°C and was not significantly different from that at 24°C.

2.2 Extrapolation From Laboratory to Field Metabolic Rate:

Several techniques have been attempted to estimate the field metabolic rates (RMR = SMR + AMR) of fishes from a combination of field and laboratory data (Armstrong et al. 1989, Scharold et al. 1989, Scharold and Gruber 1991, Briggs and Post 1997, Sundström and Gruber 1998, Lowe 2002). In one method that has been applied to
sharks, instantaneous in situ swimming speed measurements are converted to metabolic rate based on power-performance curves, constructed from laboratory data, that relate the logarithm of oxygen consumption rate to the relative swimming speed (body lengths per second, l·s⁻¹) (Bushnell et al. 1989, Scharold et al. 1989, Graham et al. 1990, Scharold and Gruber 1991, Lowe 2001). For example, the estimated field metabolic rates of three subadult *N. brevirostris* equipped with speed-sensing transmitters for tracks of 18.5-62 hours were approximately 1.3 times the standard metabolic rate for this species (Bushnell et al. 1989, Sundström and Gruber 1998). In another study, tail-beat frequency (TBF) transmitters were attached to five juvenile *S. lewini* (54-65 cm TL, 0.59-1.22 kg), and field TBF was translated to metabolic rate based on swimming flume experiments. The routine field metabolic rate was corrected for the 25-34% increase in cost of transport for instrumented relative to uninstrumented sharks and averaged 1.45±0.08 times SMR over tracks of 20-57 hours (Lowe 2002). The routine swimming speed (0.85±0.13 l·s⁻¹) was in the energetically optimal range for this species (Lowe 2001, 2002).

Another, much simpler method for estimating field metabolic rate is to assume a constant activity multiplier (Winberg 1960). A number of studies have assumed that routine field metabolic rate equals between 1.2 and 3 times the standard metabolic rate (e.g. Kitchell et al. 1977, Hansson et al. 1996, Schindler et al. 2002). In addition, a theoretical hydrodynamic model predicting swimming speeds based on length assumed that fish maintain the routine speed that minimizes energy expenditure per unit distance traveled, which was predicted to occur at roughly two times the standard metabolic rate (Weihs 1977). Voluntary swimming speeds of juvenile bonnethead sharks (*Sphyrna tiburo*) in a laboratory annular respirometer approached the predicted values (Parsons
1990), as did those for blacknose sharks (C. acronotus, Carlson et al. 1999) and N. brevirostris (Bushnell et al. 1989), although the routine metabolic expenditures in these studies were not exactly twice the estimated SMR. The optimal swimming speed—the speed correlated with the minimum total cost of transport—for C. acronotus in an annular chamber agreed with the predicted value (Carlson et al. 1999). These relationships found in the laboratory do not preclude different behavior patterns in the wild, but N. brevirostris in holding facilities maintained similar speeds to sharks swimming in an annular respirometer (Bushnell 1982). Similarly, the instantaneous swimming speeds of S. tiburo in large enclosures (~0.38 l s⁻¹) agreed with the predicted values (Parsons and Carlson 1998). The average in situ swimming speeds for three subadult N. brevirostris were 4.8, 6.6, and 21.8% above the predicted swimming speeds (Sundström and Gruber 1998).

2.3 Field Behavior of Juvenile Sandbar Sharks:

Only one study has reported the instantaneous swimming speed for a sandbar shark, and that for one adult animal (210 cm total length) in captivity (Weihs et al. 1981). Three studies have reported the mean rate of movement (ROM) of juvenile sandbar sharks in the wild as determined by telemetry methods (Huish and Benedict 1977, Medved and Marshall 1983, Grubbs 2001) (Figure 3a). In general, these ROM data agree with the predicted values from Weihs (1977). However, these telemetry studies estimated mean ROM by converting consecutive “fixes” of a shark’s position to distance traveled and dividing by the time interval. It is problematic to convert ROM from telemetry

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3 Huish and Benedict (1977) published their results under the species name for the dusky shark (Carcharhinus obscurus), but Grubbs (2001) noted that the size of the animals tracked was smaller than size at birth for C. obscurus. Misidentification of these two closely-related species is common.
Figure 3. Swimming speeds (body lengths per second, l·s⁻¹) of juvenile sandbar sharks versus total length (TL). a) Mean rate of movement (ROM) of juvenile sandbar sharks determined using a variety of tracking and telemetry techniques with varying times between location ‘fixes’. The solid line is the predicted optimal swimming speed (Weihs 1977). b) Mean swimming speeds (±S.E.) of 16 juvenile sandbar sharks in a laboratory annular respirometer (Dowd et al. in prep). The dashed line is the predicted swimming speed from Weihs (1977).
a)

![Graph showing Mean ROM vs TL (cm)]

- Medved and Marshall 1983 (float 10 min)
- Medved and Marshall 1983 (float 15 min)
- Grubbs 2001 (telemetry 10 min)
- Medved and Marshall 1983 (telemetry 15 min)
- Weihs et al. 1981 (enclosure)
- Huish and Benedict 1977 (telemetry 15 min)

b)

![Graph showing Swimming speed vs TL (cm)]
studies to instantaneous swimming speeds, primarily because sharks do not swim in
straight lines between telemetry fixes (reviewed by Sundström et al. 2001). For example,
the ROM determined for *N. brevirostris* using telemetry fixes at 15-minute intervals
underestimated routine swimming speed by approximately half (Gruber et al. 1988).
Instantaneous swimming speeds for 7 large juvenile *N. brevirostris* averaged 1.67±1.2
times the ROM determined from telemetry fixes at 5-minute intervals (Sundström et al.
2001). The average instantaneous swimming speeds measured using TBF telemetry of 5
juvenile *S. lewini* (54-65 cm TL, 0.83±0.11 l·s⁻¹, Lowe 2002) were approximately 1.8-2.9
times the mean ROM (38-64 cm TL, 0.18 m per second or 0.47-0.28 l·s⁻¹) determined for
the same species using 15-minute interval telemetry fixes (Holland et al. 1993, Lowe et
al. 1998). There is no reliable means of converting the sandbar shark field ROM
measures to actual instantaneous swimming speed measures, and borrowing a correction
factor from another species is unjustified. Adjusting the ROM measures for juvenile
sandbar sharks in the wild (Figure 3a) with a conservative correction factor of 1.5 would
yield inconclusive results. A number of the ROM measures would approach the predicted
values, while several others would be significantly higher than measures of instantaneous
swimming speed observed for juvenile sandbar sharks in the annular respirometer (Dowd
et al. in prep) (Figure 3b).

Sandbar sharks appear to spend a large portion of their time moving with the
dominant tidal current direction (Huish and Benedict 1977, Medved and Marshall 1981,
Grubbs 2001, C. Conrath personal communication). This behavior might reduce the
metabolic activity costs for these obligate ram-ventilators by reducing the necessary
swimming effort (Medved and Marshall 1981). However, sandbar sharks are negatively
buoyant, requiring forward relative movement to generate lift via the large pectoral fins and the heterocercal caudal fin (Alexander 1965, Pelster 1997, Wilga and Lauder 2002). Juvenile sandbar sharks in Chesapeake Bay also make frequent and large vertical movements through the water column and do not strictly move in line with the tidal current direction (Grubbs 2001). Periodic vertical movements may represent another cost-minimizing strategy wherein sharks ascend and then “coast” downward (Weihs 1973), but more data are needed including field measures of TBF coincident with these vertical movements to determine whether coasting occurs. Juvenile sandbar sharks in a 14,000 gallon holding facility ~2 m deep maintained relatively constant TBF and did not demonstrate coasting behavior (W. Dowd, personal observation). Large juvenile sandbar sharks observed in an aquarium setting also never coasted (J. A. Musick, personal communication).

2.4 Constant Activity Multiplier for Juvenile Sandbar Sharks:

In the absence of field data supporting an alternative method, the raw ratio of RMR to SMR derived in the laboratory (1.78 ± 0.12, Dowd et al. in prep) was used as a constant activity multiplier (ACT) to estimate the field metabolic rates (RMR in Equation 3) of juvenile sandbar sharks. The raw RMR to SMR ratio was assumed to be more reliable than that corrected for the cost of swimming in a curved path, since parameters for the correction were borrowed from other species (Dowd et al. in prep). The ratio of RMR to SMR was assumed to remain constant for all age-classes and over all temperatures, which appears to be a reasonable assumption (Dowd et al. in prep).

As in other obligate ram-ventilating sharks, the routine swimming speeds of juvenile sandbar sharks in an annular respirometer were consistent with the predicted
optimal swimming speeds using Weihs’ equation (Dowd et al. in prep) (Figure 3b), and the ACT value used here is within the range usually assumed for fishes. This ratio of RMR to SMR is similar to, but greater than, the field estimates described above for *S. lewini* (1.45) and *N. brevirostris* (1.3). These differences could be due to several factors. The sandbar shark is the only species for which SMR was measured directly under controlled conditions. Extrapolation of power-performance curves to zero activity in the other species could have yielded inaccurate estimates of SMR (Cech 1990, Lowe 2001). Further, the power-performance curve for *N. brevirostris* was determined for ~1 kg juveniles (Bushnell et al. 1989) and extrapolated to subadults (20-34 kg) using an average allometric exponent of 0.86 from the literature (Sundström and Gruber 1998). Changes in swimming efficiency, kinematics, or drag could also cause the slope of the power-performance curve to change ontogenetically (Webb 1977). Or there may simply be physiological differences among these three species.

2.5 Effects of Temperature on Metabolic Rate:

Juvenile sandbar sharks have been captured in the Chesapeake Bay nursery at surface temperatures ranging from 17-29°C and bottom temperatures ranging from 15-29°C (VIMS Longline Survey unpublished data). Further, the lower Chesapeake Bay exhibits a thermocline, with surface to bottom temperature differences of up to 5-6°C in July and August (VIMS Longline Survey unpublished data). The vertical excursions of sandbar sharks appear to cross this boundary repeatedly throughout the day (Grubbs 2001).
Historical surface and bottom water temperature data were obtained from the Chesapeake Bay Program’s (CBP) Water Quality Database\(^4\) for seven monitoring stations within the sandbar shark’s core Chesapeake Bay nursery area for the period of the simulation (May-September) for 1996-2002. Temperature measurements were averaged over all stations for each day of the simulation and over all years to minimize the influence of spatial and temporal patterns in the data. Water temperatures for simulation days that were not represented in the CBP data set were estimated using linear interpolation between nearest neighbors. Tracking data suggest that sandbar sharks spend roughly equal amounts of time above and below the thermocline (Grubbs 2001). Consequently, the surface and bottom temperature readings were averaged to obtain a mean temperature experienced by each shark on each day of the simulation in an average year. The simulation temperatures ranged from 16.8-27.9°C over the summer nursery season (mean 23.0±0.2°C) (Figure 4).

Dowd et al. (in prep) measured the effects of temperature changes on SMR (Q\(_{10}\)) for juvenile sandbar sharks between 18 and 28°C for animals from 1-10 kg in body weight:

\[
\begin{align*}
Q_{10} \text{ 18-24°C: } & 3.24\pm0.37 \ (N=14) \quad ^5 \\
Q_{10} \text{ 24-28°C: } & 2.54\pm0.23 \ (N=16) \\
Q_{10} \text{ 18-28°C: } & 2.94\pm0.17 \ (N=13)
\end{align*}
\]

Q\(_{10}\)s were consistent over the size range tested, and the overall mean Q\(_{10}\) was 2.89±0.16 (N=43).

\(^4\) http://www.chesapeakebay.net/data/index.htm

\(^5\) One outlier value was excluded in determining this average (Dowd et al. in prep).
Figure 4. Historical lower Chesapeake Bay water temperature data used in the sandbar shark bioenergetics model simulations plotted against the simulation day. Values are the mean of surface and bottom temperatures from seven Chesapeake Bay Program water quality monitoring stations within the core sandbar shark nursery area. Unreported values were estimated using linear interpolation between the nearest neighbors. Simulation day 0 is May 15, and day 138 is September 30.
For each day of the simulation, the Q_{10}S from either 18-24°C or 24-28°C were used to adjust the predicted SMR at 24°C (from Equation 13) to the simulated daily temperature (T) depending on whether T was above or below 24°C (equation adapted from Schmidt-Nielsen 1997):

\[
SMR_T = 10^{\left( \log{SMR_{24}} + \log{Q_{10}} \cdot \frac{(T-24)}{10} \right)}
\]  
(Equation 14)

The SMR Q_{10}S were assumed to remain constant over the course of the summer stay in the Chesapeake Bay nursery grounds, which appears to be a reasonable assumption (DuPreez et al. 1988, Hopkins and Cech 1994, Carlson and Parsons 1999). The SMR at the daily temperature was then multiplied by the activity multiplier and by 24 hours to obtain the daily metabolic expenditure in mg O_2 per day:

\[
RMR_D = SMR_T \cdot ACT \cdot 24
\]  
(Equation 15)

Finally, this value was converted to daily metabolic energy utilization using the oxycaloric coefficient 13.59 J per mg O_2 (Elliott and Davison 1975, Brett and Blackburn 1978, Sundström and Gruber 1998, Lowe 2002).

3. SDA:

Specific dynamic action as an input to a bioenergetics model is somewhat problematic to physiologists. SDA primarily represents the cost of incorporation of digested amino acids into new proteins (Jobling 1983, Brown and Cameron 1991a,b). Therefore, SDA would be predicted to vary with growth rate or the protein content of ingested food (Tandler and Beamish 1979, Carter and Brafield 1992, Ross et al. 1992), but most bioenergetics models set SDA as a constant fraction of consumed energy (Hewett and Johnson 1992).
The proportion of consumed energy devoted to SDA has not been determined for sandbar sharks. SDA has only been measured in a few elasmobranch species and is typically a small fraction of consumed energy (Table 1). Similarly, SDA averages 12-16% of consumed energy for carnivorous and omnivorous teleosts (Brett and Groves 1979). Previous models have estimated SDA as 10% of consumed energy for elasmobranchs (e.g. Schindler et al. 2002). As an initial estimate, SDA was assumed to expend 10% of consumed energy for juvenile sandbar sharks.

4. Waste Losses:

Waste losses (W) in feces (F) and excretions (U) are similarly little known, primarily due to difficulties in measuring excretory products and gathering feces in the aquatic environment (Wetherbee and Gruber 1993). Absorption efficiency (1-W) in carnivorous teleosts is routinely 0.8-0.9 and depends on experimental conditions of meal size, energy content, and experimental temperature (Beamish 1972, Elliott 1976, Kitchell et al. 1977, Brett and Groves 1979). Estimated fecal waste losses for chain dogfish (Scyliorhinus retifer) were 4.8-6.2% of consumed energy (Duffy 1999). Juvenile N. brevirostris fed at five ration levels of an experimental diet formulation exhibited absorption efficiencies ranging from 61.9-83.1% of consumed energy (F=38.1-16.9%) (Wetherbee and Gruber 1993), but the ration levels were all below the maintenance ration determined for this species (Cortes and Gruber 1994). Brett and Groves (1979) stated that “variability is least for the excretion fraction” of the diet, which averaged 7% of ingested energy for a number of fishes. A generally accepted value for total waste loss to excretion and fecal waste for carnivorous fishes and elasmobranchs is 27±3% of consumed energy (C) (Brett and Groves 1979, Sundström and Gruber 1998, Lowe 2002, Schindler et al.)
Table 1. Specific dynamic action (SDA) estimates for elasmobranch species as a percentage of ingested energy (%C). Mean ± S.E. (range in parentheses). Rations are meal sizes expressed as a percentage of body weight (%BW). Duration is the number of hours the SDA effect appeared to persist. Most studies show one or more peaks in SDA (oxygen consumption) during the first few hours after feeding followed by a gradual decline to pre-feeding metabolic rates. SDA was estimated by integrating the area between pre-feeding metabolic rate and the oxygen consumption rate after feeding. DuPreez et al. (1988) only measured the SDA effect for 24 hours.

<table>
<thead>
<tr>
<th>Species</th>
<th>N</th>
<th>SDA (%C)</th>
<th>Ration (%BW)</th>
<th>Duration</th>
<th>T (°C)</th>
<th>Citation</th>
</tr>
</thead>
<tbody>
<tr>
<td>Scyliorhinus canicula (juvenile)</td>
<td>4</td>
<td>6.01 ± 1.58</td>
<td>7.25 ± 0.23 (squid)</td>
<td>45</td>
<td>15</td>
<td>Sims and Davies 1994</td>
</tr>
<tr>
<td>Scyliorhinus canicula (adult)</td>
<td>4</td>
<td>12.52 ± 1.95</td>
<td>6.52 ± 0.73 (squid)</td>
<td>84</td>
<td>15</td>
<td>Sims and Davies 1994</td>
</tr>
<tr>
<td>Scyliorhinus retifer</td>
<td>5</td>
<td>12.7</td>
<td>1.5 - 1.8 (squid)</td>
<td>129</td>
<td>10</td>
<td>Duffy 1999</td>
</tr>
<tr>
<td>Scyliorhinus retifer</td>
<td>8</td>
<td>13.3</td>
<td>0.9 - 1.8 (fish)</td>
<td>146</td>
<td>10</td>
<td>Duffy 1999</td>
</tr>
<tr>
<td>Cephaloscyllium ventriosum</td>
<td>4</td>
<td>5 - 17</td>
<td>4.2 - 5.9</td>
<td>12</td>
<td>16</td>
<td>Ferry-Graham and Gibb 2001</td>
</tr>
<tr>
<td>Rhinobatos annulatus</td>
<td>12</td>
<td>17.3 ± 12.3 (4.2-32.9)</td>
<td>4 - 6 (24)</td>
<td>20</td>
<td>DuPreez et al. 1988</td>
<td></td>
</tr>
<tr>
<td>Myliobatus aquila</td>
<td>5</td>
<td>12.9 ± 4.4 (5.8-21.8)</td>
<td>4 - 8 (24)</td>
<td>20</td>
<td>DuPreez et al. 1988</td>
<td></td>
</tr>
</tbody>
</table>
105

2002). This value was assumed here for the sandbar shark, divided into U (0.07°C) and F
(0.2°C).

*Model Calculations:*

For each daily time step of the model, RMR and G were calculated as described
above. These were input to the following equation to solve for daily consumption in
Joules, where SDA, U, and F are fractions of consumption:

\[
C_D = \frac{RMR_D + G_D}{1 - SDA - U - F}
\]  

(Equation 16)

The daily consumption estimates were summed over all days to determine total energy
consumption for an individual of each age-class during the entire stay in the Chesapeake
Bay nursery:

\[
C_{SUMMER} = \sum_{D=1}^{n} C_D
\]

(Equation 17)

Mean daily energy ration (DRkJ, kJ·d⁻¹) was calculated by dividing \( C_{SUMMER} \) by 1000 and
then by the \( n \) days of the simulation. The daily energy ration was also expressed as a
percentage of the average total energy content (\( \%J_{tot} \)) of the shark for each day:

\[
DR_{\%J} = \frac{C_D}{\left( \frac{M_D + M_{D+1}}{2} \cdot 5400 \right)}
\]

(Equation 18)

This value was also averaged over the \( n \) days of the simulation for each age-class.

Finally, the daily gross conversion efficiency (\( K_I \)) was calculated:

\[
K_{I_D} = \frac{G_D \cdot 5400}{C_D}
\]

(Equation 19)
Gross conversion efficiency, the amount of consumed energy that is devoted to growth, has been reported between 5 and 12% for adult *C. leucas* fed to satiation in captivity (Schmid and Murru 1994) and between –64.0 and 25.2% for juvenile *N. brevirostris* fed daily rations of 0.60-2.73 %BW per day (Cortes and Gruber 1994). \( K_f \) for *N. brevirostris* in the wild was estimated between 9.5 and 13.0% based on their observed growth rates (Cortes and Gruber 1994). These values should be similar to those for sandbar sharks and were used as a general test of the model outputs.

*Parameter Uncertainty: Error Analyses and Monte Carlo Simulations:*

Assessing uncertainty in input parameters is one of the heuristic benefits of constructing bioenergetics models (Kitchell et al. 1977). Several assumptions of this model warranted formal analysis. For example, since SDA, excretion (U), and feces (F) were modeled as constant percentages of consumption, the initial choices of these values had a direct effect on the predicted consumption rates. Further, a number of the input parameter estimates were measured with some uncertainty. Consequently, the sandbar shark bioenergetics model was run in two forms. Static models were run using the initial parameter estimates to determine point estimates of consumption.

A stochastic, Monte Carlo simulation routine (Crystal Ball© 2000 Academic Edition v5.2.2, Decisioneering, Inc.) was then used to assess uncertainty in the model parameters using error analysis (Bartell et al. 1986). In this procedure, variables are assigned to probability distributions, and the simulation randomly draws values from each of these distributions for each Monte Carlo iteration. Error analysis is particularly useful for evaluating model sensitivity to parameters that enter the model in a non-linear fashion (Bartell et al. 1986), such as the allometric exponent and allometric constant in
the SMR equation and the $Q_{10}$s. These parameters, as well as ACT, were assigned normal distributions using the means and standard errors described above. The parameters for SDA, F, and U were assigned triangular distributions, with the initial estimates described above as the most likely values. The ranges assigned to these parameters were 6-17% C (Table 1), 17-38% C (Wetherbee and Gruber 1993), and 5-8% C (Brett and Groves 1979, Duffy 1999), respectively. The percentage of annual growth that occurs in the summer months as well as the von Bertalanffy growth equation parameters were assigned normal distributions with coefficients of variation of 10% (Bartell et al. 1986). The results of 2000 Monte Carlo iterations for each age-class were used to build distributions for the consumption estimates that were compared to the results of the static models. The twelve bioenergetics model parameters were ranked in importance by their relative contribution to the variance of these stochastic model outputs (Bartell et al. 1986).

Individual Prey Consumption Estimates:

Juvenile sandbar sharks appear to forage opportunistically in the nursery grounds, consuming crustaceans such as blue crabs (*Callinectes sapidus*) and mantis shrimp (*Squilla empusa*), teleost fishes including Atlantic menhaden (*Brevoortia tyrannus*) and summer flounder (*Paralichthys dentatus*), and skates and other smaller elasmobranchs (Medved and Marshall 1981, Medved et al. 1985, Stillwell and Kohler 1993, Ellis 2003). Previous bioenergetics models for sandbar sharks estimated the energetic content of the diet based on the assumption that one or two prey species were dominant over all size classes (Medved et al. 1988, Stillwell and Kohler 1993). Recent data detail the ontogenetic and temporal patterns of juvenile sandbar shark diet composition, reported as the percent index of relative importance (%IRI) for each prey species, in Chesapeake Bay
and the surrounding waters (Ellis 2003). %IRI is considered to have less bias than other diet indices (Cortes 1997). For the bioenergetics model, the prey species were grouped into four categories for each age-class: teleost fishes, molluscs (e.g. squids, *Loligo* spp.), crustaceans (primarily *C. sapidus* and *S. empusa*), and elasmobranchs (primarily skates, *Raja* spp.) (Figure 5). Diet composition was assumed to remain constant during the simulation period. The average energetic content (J·g⁻¹ wet weight) of each prey type was set at 5050 J·g⁻¹, 4390 J·g⁻¹, 4810 J·g⁻¹, and 5400 J·g⁻¹, respectively (Thayer et al. 1973). These energy content values and the proportion of each prey type in the diet were used to convert daily energy ration (kJ·d⁻¹) to daily ration (%BW·d⁻¹) for each day of the simulation for each age-class of shark. These values were averaged over all simulation days to arrive at an average daily ration for each age-class over the entire summer. The daily ration estimates were also summed over the entire nursery season to estimate the total seasonal prey consumption by individuals of each age-class.

**Population Consumption Estimates:**

Reliable estimates of the total population size and the age structure are needed in order to extrapolate from an individual-based bioenergetics model to population and ecosystem level impacts. The historical trends in the relative abundance and size-class composition of the Chesapeake Bay summer sandbar shark population are well documented (Musick et al. 1993, VIMS Longline Survey unpublished data). Virtual population analysis (VPA) using CPUE data from the standard VIMS Longline Survey gear for 1989-1993 produced an unrealistic age-structure in which the age 2 and age 3 cohorts were as abundant as the age 0 and age 1 cohorts (Sminkey 1994) (see Figure 7). This predicted age structure was a function of recruitment of juvenile sharks to the
Figure 5. Ontogenetic variation in diet composition for juvenile sandbar sharks ages 0-5 used to predict daily rations in the bioenergetics model. Data were reported as percent index of relative importance for each prey type (Ellis 2003).
longline gear used; the standard VIMS gear selects for larger animals (VIMS Longline Survey unpublished data). Since 1997, monofilament puppy hooks have been used to target younger age-classes in the VIMS survey. To achieve better estimates of the true population structure, the catch rates for these monofilament puppy hooks were compared with those for the standard VIMS gear on all occasions when both gears were fished simultaneously at the two lower Chesapeake Bay standard sampling stations (Kiptopeke State Park and Middle Ground Shoal, Figure 1) (N=25 longline sets). The mean CPUEs were similar for ages 3-5, but they were significantly higher on the monofilament gear for ages 0, 1, and 2 (Figure 6). The mean monofilament catch rates of ages 0-2 were indexed against the mean monofilament catch rates of age 3 sharks. Assuming that catchability remained constant between the early and late 1990s, this index was used to adjust the VPA cohort sizes for the younger age-classes (Figure 7).

No direct estimates exist for the rate of juvenile sandbar shark natural mortality in the nursery areas. Generalized equations relating mortality to growth parameters or environmental conditions (Pauly 1980, Hoenig 1983, Peterson and Wroblewski 1984, Chen and Watanabe 1989) predict instantaneous mortality rates (M) on the order of 0.1-0.25 (Cortes 1999b). In all likelihood, the mortality of young sandbar sharks varies with age, with younger, smaller animals being more susceptible to predation. Estimates of young-of-the-year mortality in juvenile *N. brevirostris* in Bimini, Bahamas (Manire and Gruber 1993), and young-of-the-year blacktip sharks (*Carcharhinus limbatus*) in Terra Ceia Bay, Florida (Heupel and Simpfendorfer 2002), ranged from 44-61% per year and 61-91% per summer, respectively. Heupel and Simpfendorfer (2002) hypothesized that the first 3 to 4 months of life in the nursery were critical for *C. limbatus* to learn to
Figure 6. Comparison of survey catch per unit of effort (CPUE) of juvenile sandbar sharks using monofilament puppy hooks (mono) and the standard VIMS Longline Survey gear (steel) at Kiptopeke State Park (K) and Middle Ground Shoal (M) in the Chesapeake Bay nursery. Data presented are means±S.E. for all stations at which both gears were fished simultaneously since 1997.
Survey CPUE (sharks hooks' hours' *1000)

- K mono
- O M mono
- ▼ K steel
- △ M steel

![Graph showing survey CPUE with different symbols for different types of hooks and steel. The x-axis represents age class, and the y-axis represents survey CPUE in sharks hooks hours *1000.](image-url)
Figure 7. Juvenile sandbar shark estimated cohort sizes and total population size in the lower Chesapeake Bay nursery area during the summer. Black bars are mean±S.E. of virtual population analysis estimates for 1989-1993 (Sminkey 1994), and gray bars are revised estimates using indices developed from the catch rate data in Figure 6.
Estimated Cohort Size

16000
14000
12000
10000
8000
6000
4000
2000

Sm inkey (1994)

Indexed cohort

Age Class

Estimated Cohort Size

0 1 2 3 4 5 TOTAL

Sminkey (1994)
Indexed cohort
capture prey and to avoid predators. Both of these estimates are probably significantly higher than the mortality experienced by juvenile sandbar sharks in Chesapeake Bay, particularly in light of the near absence of large coastal shark predators in the nursery (Musick et al. 1993).

The available data imply that juvenile sandbar sharks remain in the Chesapeake Bay nursery for the duration of the summer. Seventeen tagged juvenile sandbar sharks have been recaptured in the same summer within 0-37 kilometers of the tagging location in Chesapeake Bay after 4-82 days at liberty (Grubbs 2001). Similarly, 38 juvenile sandbar sharks were recaptured in Delaware Bay at an average distance of 10 km from the tagging location after an average of 18 days at liberty (Merson and Pratt 2001). In addition, survey data show fairly constant average abundance indices of juvenile sandbar sharks at the Kiptopeke State Park and Middle Ground Shoal stations between immigration in May and emigration in October (Grubbs 2001, VIMS Longline Survey unpublished data). There is a decline in the mean semimonthly CPUE at these two stations after a peak in late July (Grubbs 2001), but whether this is caused by emigration, mortality, some combination of these, or other unexplained variance in the data set is unknown. The longline sampling gear used to establish these abundance indices produces variable results (Musick et al. 1993), and strong interannual variations are present in the data. This decline in CPUE later in the summer may represent dispersal of juvenile sharks within the nursery area (Grubbs 2001); a similar mechanism of dispersal of juveniles from the core nursery areas has been proposed for Delaware Bay (Merson and Pratt 2001). Further, none of ten sharks tracked using ultrasonic telemetry were observed to leave Chesapeake Bay over tracks of 10-50 hours (Grubbs 2001). Two tracks in
Chincoteague Bay, Virginia were cut short when the sandbar sharks left this coastal lagoon nursery (Medved and Marshall 1983), but the activity spaces of juvenile sandbar sharks probably exceed the relatively small area of Chincoteague Bay. More data are needed over longer duration tracks or using underwater acoustic dataloggers (see Simpfendorfer et al. 2002) to definitively determine whether juvenile sandbar sharks repeatedly enter and exit the nursery areas.

The present model assumes negligible mortality and zero emigration of juvenile sharks during their stay in the Chesapeake Bay nursery. Consequently, the mean revised cohort sizes (Figure 7) were assumed to remain constant throughout the simulation period.
RESULTS

Length-Weight Relationships:

Preliminary runs of the model demonstrated that the three grouped length-weight relationships (Equations 6, 7, and 9) gave very similar results, especially after age 0 (Figure 8). Meanwhile, the seasonal length-weight relationship derived from VIMS data (Equation 10) yielded significantly higher consumption rates (Figure 8), since sharks in the fall were heavier than same-sized animals in the spring. The VIMS seasonal length-weight equation predicted total energy consumptions of 325-342% of the total energy content of an age 0 shark during the 4.5 month stay in the Chesapeake Bay nursery area. This quantity declined to 193-199% for age 5 sharks. The corresponding values using the three grouped length-weight relationships were 293-309% and 182-186%, respectively.

Only the grouped (Equation 9) and seasonal (Equation 10a,b) relationships derived from the VIMS data were used as inputs to further model runs, since these data were collected from the population of interest.


The minor differences in predicted growth rates between the 1980-1981 and 1991-1992 periods (Sminkey and Musick 1995) had little effect on the consumption estimates from the bioenergetics model (Figure 8). All other things being equal, including temperature, the model predicted slightly increased conversion efficiency in 1991-1992 relative to 1980-1981, and this difference decreased as age increased (Figure 9). The
Figure 8. Daily energy rations of juvenile sandbar sharks predicted with the bioenergetics model, expressed as a percentage of the total energetic content of the shark on the simulation day (%J_{tot}). Daily energy rations were predicted from the static model using each of the four length-weight equations in the text (Medved et al. 1988, Kohler et al. 1995, VIMS grouped, and VIMS seasonal) and both sets of von Bertalanffy growth parameters (1980-1981 and 1991-1992, Sminkey and Musick 1995). Error bars are ± 1 S.E.
Figure 9. Gross conversion efficiency ($K_1 = \text{growth/consumption}$) for age 0-5 sandbar sharks determined using the static model, the 1980-1981 and 1991-1992 von Bertalanffy growth parameters, and the two VIMS length-weight regressions (seasonal and grouped). Values are means ±S.E.
Mean Gross Conversion Efficiency ($K_1$)

- 1991-1992 VIMS seasonal
- 1991-1992 VIMS grouped
- 1980-1981 VIMS seasonal
- 1980-1981 VIMS grouped

Age Class

Mean Gross Conversion Efficiency ($K_1$)

0.00 0.05 0.10 0.15 0.20 0.25

0 1 2 3 4 5
reasons for the observed difference in growth rates are unknown. The remainder of this discussion will focus on results using the 1991-1992 von Bertalanffy parameters.

Metabolic Rate vs. Growth:

The relative significance of growth in the overall energy budget (gross conversion efficiency) declined quickly with age from 14-21% of consumed energy for age 0 sharks, reaching roughly 10-14% of consumed energy by age 5 (Figure 9). Since growth plus routine metabolism comprised a constant proportion of the total energy budget in the static model, the proportion of consumption devoted to metabolism increased over the same age range. Metabolism for age 0 sandbar sharks accounted for 42-49% of ingested energy, increasing to 50-53% of the energy budget for age 5 juveniles.

To emphasize the relative insignificance of growth in the overall energy budget, maintenance energy rations (daily consumption when growth is set to 0) were calculated for each age-class using the 1991-1992 von Bertalanffy growth parameters (Figure 10). The mean daily energy ration for maintenance averaged 78% of the ration when growth was included.

Daily Energy Ration and Total Energy Consumption:

The static models predicted average daily energy rations declining from roughly 2.5% (210 kJ per day) to 1.4% (870 kJ per day) of the total energetic content of the shark between age 0 and age 5 (Figure 8). The significant influence of routine metabolism on consumption estimates was readily apparent. Since metabolism scales with water temperature according to the $Q_{10}$ (Equation 14), daily energy ration estimates tracked very closely with the simulated water temperatures (Figure 11).
Figure 10. Daily maintenance energy ration (ration when growth is set to 0) for juvenile sandbar sharks compared with daily energy ration, assuming the 1991-1992 von Bertalanffy growth parameters.
Daily Energy Ration (%Jtot d⁻¹)

- Maintenance
- 1991-1992 VIMS seasonal

Age Class

Daily Energy Ration (%Jtot d⁻¹)

0.0 0.5 1.0 1.5 2.0 2.5 3.0

0 1 2 3 4 5
Figure 11. Example of the strong correlation between daily energy ration and the simulated daily temperature, driven primarily by the effect of temperature changes on metabolic rate ($Q_{10}$). This example is for a 3 year-old sandbar shark using the 1991-1992 grouped length-weight model.
Total seasonal energy consumption by individual sharks during the stay in the Chesapeake Bay nursery area increased from ~29,000 kJ for young-of-the-year sharks to ~120,000 kJ for age 5 animals in the static models using the VIMS grouped length-weight equation. Results were similar, but 10±1% higher, for the VIMS seasonal length-weight equations (Figure 12).

Monte Carlo Simulations and Error Analysis:

The Monte Carlo simulations predicted seasonal energy consumption rates 14-17% higher than those derived for the static models, with wide standard deviations around the means (Figure 12). This elevation was primarily due to the fact that SDA and fecal waste (F) were allowed to comprise larger proportions of the diet than in the static model runs.

The results of the error analyses were consistent for the two VIMS length-weight equations. The relative contributions of each of the input parameters to the variance of the model predictions from the 1991-1992 VIMS seasonal length-weight model showed similar patterns for all age-classes (Figure 13). The von Bertalanffy parameters (Equation 4) predicting size at age consistently had high ranks, as did those describing the allometric scaling of standard metabolism (Equation 13). Fortunately, these parameters are among the best known for juvenile sandbar sharks, and the initial estimates used are considered reliable. The contributions of uncertainty in excretion (U) and the Q_{10} values were negligible for all age-classes. Not surprisingly, those parameters that compete directly with growth for the limited energy consumption (e.g. metabolism, F, and SDA) had negative influences on the gross conversion efficiency and positive effects on total consumption (Figure 13). Variability in the proportion of annual growth in the
Figure 12. Total seasonal energy consumption estimates (kilojoules per summer) predicted from the bioenergetics model for age 0-5 sandbar sharks. Values are presented for the 1991-1992 von Bertalanffy growth parameters using the VIMS grouped and VIMS seasonal length-weight equations. The results of the Monte Carlo simulations are also presented for the VIMS seasonal length-weight equation for both the full and reduced versions (see text for details). Error bars are ± 1 S.D. for the Monte Carlo estimates.
Seasonal energy consumption (kJ per summer)

- VIMS grouped
- VIMS seasonal
- VIMS seasonal full Monte Carlo
- VIMS seasonal reduced Monte Carlo

Age class

Seasonal energy consumption (kJ per summer)
Figure 13. Error analysis results for the full Monte Carlo simulation model for ages 0-5 using the 1991-1992 von Bertalanffy growth parameters and the VIMS seasonal length-weight equation. The horizontal axis is the percentage contribution of the variable of interest to the variance in three of the model predictions: daily energy ration ($\%J_{tot \cdot d^{-1}}$), total seasonal energy consumption (J per summer), and gross conversion efficiency ($K_i$). Positive values indicate that an increase in the parameter yields an increase in the model output, and negative values indicate that an increase in the parameter yields a decrease in the model output.
Chesapeake Bay nursery area (ρ) exhibited a strong positive influence on conversion efficiency, but again this parameter’s initial estimate of 0.75 was assumed to be relatively robust (Sminkey and Musick 1995).

In a second series of Monte Carlo simulations, the allometric parameters for standard metabolic rate and the von Bertalanffy growth parameters were held constant, assuming that the initial parameter estimates were valid. The consumption estimates output by the model did not change significantly, but the standard deviations about the estimates were substantially reduced (Figure 12). The error analysis of this reduced model scenario revealed similar patterns to the full model (Figure 14). Uncertainty in the fecal waste parameter accounted for approximately 60% of the variance in the reduced model outputs, suggesting that F should be investigated in sandbar sharks to refine the bioenergetics model with species-specific data.

*Individual and Cohort Predation Estimates:*

Incorporation of the diet composition data into the 1991 VIMS grouped length-weight model yielded daily ration estimates ranging from 2.50 %BW per day for young-of-the-year to 1.43 %BW per day for an age 5 juvenile (Figure 15). Using the VIMS seasonal length-weight relationships, the daily ration estimates ranged from 2.76 to 1.53 %BW per day (Figure 15). The total seasonal consumption in the Chesapeake Bay nursery simulation using the VIMS grouped length-weight equation varied from 6,017 grams (345 %BW) to 23,716 grams (198 %BW) for age 0 and age 5 sharks, respectively.
Figure 14. Error analysis results for the reduced Monte Carlo simulation model for ages 0-5 using the 1991-1992 von Bertalanffy growth parameters and the VIMS seasonal length-weight equation. Initial parameter estimates for the von Bertalanffy growth equation (Equation 4) and the standard metabolic rate equation (Equation 13) were held constant in this run. The horizontal axis is the percentage contribution of the variable of interest to the variance in three of the model predictions: daily energy ration ($%J_{tot} d^{-1}$), total seasonal energy consumption (J per summer), and gross conversion efficiency ($K_t$). Positive values indicate that an increase in the parameter yields an increase in the model output, and negative values indicate that an increase in the parameter yields a decrease in the model output.
Figure 15. Mean daily rations (±S.E.) over the simulated summer nursery season for age 0 to age 5 juvenile sandbar sharks, expressed as a percentage of body weight (%BW) per day. Results are presented for both the VIMS grouped and VIMS seasonal length-weight models using the 1991-1992 von Bertalanffy growth parameters.
Daily ration (%BW d⁻¹)

Age class

VIMS seasonal
VIMS grouped
Extrapolating these values to the population level, age-0 sandbar sharks in Chesapeake Bay would consume 26,343 kg of prey each summer, while the age-5 cohort would consume 4,463 kg (Figure 16). The total estimated population of sandbar sharks in Chesapeake Bay in any given summer (~11,500 sharks) was predicted to consume 122,933 kg of prey items (Figure 16).
Figure 16. Seasonal sandbar shark cohort prey consumption estimates (kg per summer) from the static model for each of the four prey categories. Line and scatter plot represents the mean (±S.E.) number of sharks of each age class in the lower Chesapeake Bay (from Figure 7).
Seasonal cohort consumption (kg per summer)

- Teleostei
- Mollusca
- Crustacea
- Elasmobranchii

Estimated cohort size (Mean±S.E.)

Age Class

Seasonal cohort consumption (kg per summer)
DISCUSSION

Comparison with Previous Results:

The daily rations for juvenile sandbar sharks determined using the bioenergetics model were higher than previous estimates (Medved et al. 1988, Stillwell and Kohler 1993). This difference can be explained primarily by the incorporation of species-specific metabolic rate data into the new bioenergetics model. The metabolic rates of the active, obligate ram-ventilating sandbar sharks are higher than the estimates for *S. acanthias* that were used in previous models (Dowd et al. in prep). In addition, the two earlier models estimated daily ration at a mean temperature over an entire year, whereas the present model focused only on the period spent in the summer nursery in Chesapeake Bay. Test runs of the bioenergetics model were used to predict daily rations in the winter nursery, assuming constant diet composition, 25% of annual growth occurs in the winter nursery (Sminkey and Musick 1995), and an average water temperature of 14°C (Springer 1960). These runs predicted daily rations less than half (<1 %BW per day) of those estimated for the summer nursery season. More data are needed on the biology of sandbar sharks in the winter nursery grounds in order to develop an accurate year-round bioenergetics model.

The bioenergetics model, when properly parameterized, provides a useful “demand-side” alternative for estimating energy consumption rates that can be compared with other methods. For example, the estimated daily rations for juvenile *S. lewini* from a simple bioenergetics model generally agreed with those derived from gastric evacuation
models for this species (Bush and Holland 2002, Lowe 2002). Gastric evacuation models developed by Elliott and Persson (1978) and Diana (1979) predicted juvenile sandbar shark daily rations of 0.93 %BW per day and 1.07 %BW per day, respectively (Medved et al. 1988). These results are less than half of the estimated daily rations from the bioenergetics model herein. However, the diet data violated the assumption of continuous feeding in the Elliott and Persson model and probably violated the assumption that time between meals exceeds digestion time for the Diana model (Medved et al. 1988) (reviewed by Cortes 1997).

The daily rations from the bioenergetics model can also be compared to values estimated from data on meal size and meal frequency. The stomach contents of juvenile sandbar sharks averaged 0.96±0.06 %BW, 1.2 %BW, and less than 1 %BW in three diet studies (Medved et al. 1985, Stillwell and Kohler 1993, Ellis 2003, respectively), but these mean values underestimate the actual meal sizes. One shark had a meal of 10.3 %BW, and maximum stomach capacity was estimated as 13 %BW (Medved et al. 1985). The average reconstructed meal size using stage of digestion estimates was 4.23±0.31 %BW for juvenile sandbar sharks in Chincoteague Bay feeding on crustaceans and teleosts (Medved et al. 1988). Further, previous studies have demonstrated both a lengthy period of gastric evacuation for sandbar sharks (70-92 hours, Medved 1985) as well as a high proportion of sharks with empty stomachs (17.9%-20.0%) or containing a single food item at a late stage of digestion (21.5%) (Medved and Marshall 1981, Medved et al. 1985, Ellis 2003). Assuming a period of 48-72 hours between meals based on these results (Medved et al. 1985), the reconstructed meal size corresponds to daily
consumption rates of 2.12-1.41 %BW per day. The upper end of this range agrees in general with the bioenergetics model predictions herein (Figure 15).

The daily ration estimates from the sandbar shark bioenergetics model are similar to those for other active shark species. For example, the estimated daily ration for a 1 kg *N. brevirostris* was 2.62 %BW (Gruber 1984), and the estimated daily ration of a 0.76 kg *S. lewini* at 26°C was 2.9-3.9% BW (Lowe 2002). These estimates are slightly higher than the mean daily ration of a young-of-the-year sandbar shark, which may be due to differences in physiology or environmental conditions. It should be noted that the daily rations reported above for sandbar sharks are averaged over the entire simulated nursery season, during which temperature fluctuated by 10°C. Predicted daily rations in mid-summer were often higher than 3.0 %BW (Figure 17).

*Parameter Uncertainty:*

Most of the parameters for the sandbar shark bioenergetics model were developed from species-specific data, avoiding typical shortcomings of this approach (Ney 1993). Error analyses indicated that the constant proportions of consumed energy assigned to SDA and fecal waste had high ranks with respect to their influence on model outputs. Parameters with the highest sensitivities are those that deserve future research attention and clarification (Kitchell et al. 1977). For example, the gastric evacuation rate of the sandbar shark is very slow (70-92 hours for a meal of ~1% BW at 25°C, Medved 1985); what effects this slow rate has on the magnitude of the SDA or waste parameters are unknown.

The bioenergetics model was also sensitive to parameters that determined metabolic rate, since routine metabolism represents a significant fraction of the energy
Figure 17. Estimated daily ration plotted against the simulation day for a young of the year sandbar shark using the 1991-1992 von Bertalanffy equation parameters and the VIMS grouped length-weight equation.
budget for juvenile sandbar sharks. These results reinforce the need for species-specific metabolic rate data when constructing bioenergetics models (Kitchell et al. 1977, Bartell et al. 1986, Essington in review). The sandbar shark standard metabolic rate parameters were based on relatively large sample sizes (N=33, Dowd et al. in prep), and the method used to measure standard metabolic rate has been validated in other species (Brill 1987, Leonard et al. 1999). SMR may or may not increase in Chesapeake Bay as osmoregulatory costs increase at the relatively low salinities of this habitat (Chan and Wong 1977, Meloni et al. 2002). Future studies are planned to test the effects of salinity changes on the metabolic rate of juvenile sandbar sharks. The potential also exists for confounding factors, such as movement with dominant tidal currents or burst swimming followed by oxygen debt repayment, to influence routine metabolic rates (specifically via the constant activity multiplier, ACT) in the wild. Activity metabolism has a significant effect on consumption estimates derived from bioenergetics models (Kerr 1982, Boisclair and Leggett 1989). As noted above, tracking studies that documented tailbeat frequency or some other correlate of swimming behavior would be useful in addressing some of these potential problems.

In addition, the present model accounted for the seasonal pattern of sandbar shark growth (Sminkey and Musick 1995). The growth period in the Chesapeake Bay nursery was assumed to begin in mid-May and last through September. The annual growth bands in vertebral centra used to age sandbar sharks are presumably the manifestation of differences in cartilaginous mineralization during the two growth phases (Cailliet et al. 1983, Casey et al. 1985). Marginal increment analysis of the annuli in sandbar shark vertebrae suggested that the period of rapid summer growth might begin later in the year
(Sminkey and Musick 1995), though the timing of formation of the annulus is debated (Casey et al. 1985). Thus, the mean daily rations predicted with the bioenergetics model are conservative estimates for the time spent in the summer nursery. Less than 75% of the estimated annual growth of sharks classified as young-of-the-year occurred between July and September in Delaware Bay (Merson and Pratt 2001). This finding was based on sharks that were not aged (40-60 cm FL), perhaps biasing the growth estimate. These results may also indicate nursery-specific growth rates (see Wass 1973), information which could be critical to fishery managers. Differences in the length of the summer nursery season, the availability and quality of food, or the temperature regime would have physiological energetic implications for local nursery populations of sandbar sharks that could be addressed using the bioenergetics model approach developed here and adapted with site-specific data.

Since the specific timing and pattern of growth is unknown for juvenile sandbar sharks, daily growth was estimated as a constant proportional increase in weight per day. More detailed growth data would be useful, but are difficult to obtain. The choice of a length-weight relationship also affected the bioenergetics model predictions. The VIMS seasonal length-weight model yielded significantly higher consumption rates than the VIMS grouped model. Assuming that 75% of annual growth in PCL occurs in the Chesapeake Bay nursery, juvenile sandbar sharks add anywhere from 18-100% of their initial body weight during the summer nursery season, depending on the age of the animal and the length-weight model used. Some form of seasonal fluctuation of condition index is likely for juvenile sandbar sharks in the productive Chesapeake Bay waters, but the exact form of this model is not known.
In addition to changes in condition index, numerous studies indicate fluctuations of average energetic content in teleost fishes as a result of seasonal spawning or migratory patterns (e.g. Diana 1983, Helminen et al. 1990, Hartman and Brandt 1995a, Jonsson et al. 1997, Hendry and Berg 1999, Henderson et al. 2000). In the only elasmobranch example, the average energetic content and the ratio of liver weight to body weight (hepatosomatic index, HSI) of juvenile Atlantic sharpnose sharks (Rhizoprionodon terraenovae) in a northern Gulf of Mexico nursery area were high upon immigration, decreased in the nursery area during summer, and then increased again prior to emigration (Hoffmayer 2003). Meanwhile, biochemical indices of enzyme activity for ketone-body catabolism and ketogenesis in the red and cardiac muscle tissue of several shark species, including R. terraenovae and sandbar sharks, suggested that ketones derived from liver lipid stores could fuel a large fraction of their aerobic metabolism (Watson and Dickson 2001). Sharks have large, fatty livers (HSI ~12.4% for sandbar sharks, Oguri 1990), representing a significant energy store for times between meals or when food is scarce (Rossouw 1987, Watson and Dickson 2001). These liver lipids may also be used to fuel the long seasonal migrations between summer and winter nursery grounds, although data are needed to test this hypothesis. Collectively, these findings suggest that surplus energy in juvenile R. terraenovae is devoted to somatic growth in length or muscle mass during most of the summer stay in the nursery grounds, followed by a buildup of high energy-density lipid reserves in the liver in preparation for the fall emigration. Anecdotal evidence, from sharks primarily captured in June and July, supports a similar pattern in juvenile sandbar sharks. Stillwell and Kohler (1993) noted “large cream-colored livers that floated slightly above the surface when placed in
seawater” in neonates. In contrast, older juveniles had livers that were “reduced in size, varied in color from tan to gray-green, and sank slowly or floated just beneath the water surface”.

Data documenting fluctuations in the HSI and energetic content of sandbar sharks over the course of the summer will help to refine the bioenergetics model. However, assuming that the energetic content of sandbar sharks is similar to the other species studied, these fluctuations will not significantly affect the consumption estimates. Error analysis of a run of the full Monte Carlo sandbar shark bioenergetics model, with energy content assigned a coefficient of variation of 10%, ranked this parameter 8th – 10th in importance out of the 13 model inputs. Further, runs of the static sandbar shark bioenergetics model that assumed either a 10% or 20% difference between the maximum and minimum energy content (average 5400 J·g⁻¹) over the summer predicted consumption levels indistinguishable from those in the baseline model formulation.

One of the implicit assumptions of the bioenergetics model is that all energy is derived from food. Since juvenile sandbar sharks in the Chesapeake Bay nursery appear to grow steadily and rapidly (Sminkey and Musick 1995), the assumption that the vast majority of energy is derived from food and not from energy reserves is probably justified. The large proportion of empty stomachs (~20%) noted above does not take into account meals at later stages of digestion in other parts of the digestive tract (Holmgren and Nilsson 1999). In contrast, little is known of the feeding habits of sandbar sharks during their seasonal migrations or in the winter nursery. At these times stored energy may play a greater role in the energy budget.
Ecosystem Interactions:

Ongoing efforts to create Chesapeake Bay-wide trophic models for eventual use in ecosystem-based management efforts will require knowledge of the trophic relationships between apex predators, including sandbar sharks, and other commercially important stocks. The top-down consequences of changes in the population size, mortality rates, or age structure of apex predators have been both documented and modeled; the possible, and frequently unforeseen, outcomes include “release” of lower trophic levels and shifts to alternative stable ecosystem states (Estes et al. 1998, Fogarty and Murawski 1998, Stevens et al. 2000, Kitchell et al. 2002, Schindler et al. 2002). Ecosystem models have predicted both significant (Stevens et al. 2000) and negligible (Kitchell et al. 2002) top-down effects of changes in shark biomass on ecosystem structure, depending primarily on the trophic complexity of the system.

The results presented herein downplay the top-down role of sandbar sharks in the trophic economy of the lower Chesapeake Bay. Juvenile sandbar sharks were predicted to consume ~120,000 kg of prey in an average summer in the nursery. In comparison, the annual prey consumption rates by bluefish (*Pomatomus saltatrix*), striped bass (*Morone saxatilis*), and weakfish (*Cynoscion regalis*), the dominant teleost piscivores in Chesapeake Bay, were roughly estimated as 27,000,000 kg, 10,000,000 kg, and 5,000,000 kg, respectively (Hartman and Brandt 1995b). The seasonal consumption by juvenile sandbar sharks also pales in comparison with fisheries landings. For example, the Chesapeake Bay sandbar shark population was predicted to consume roughly 74,000 kg of crustaceans per summer, while the commercial fishery has landed an average of
12,900,000 kg of blue crabs in each of the past three years. Similarly, the total predicted consumption of Teleostei by juvenile sandbar sharks equals 0.01 percent of the annual Atlantic menhaden landings in Virginia.

Bottom-up effects on sharks as apex predators are also possible if lower trophic levels are overfished, but the apparent opportunistic foraging strategy of sandbar sharks probably reduces their vulnerability to declines of specific prey species (Stevens et al. 2000). However, if current fisheries landings in Chesapeake Bay are not sustainable, the dietary overlap between the dominant piscivorous teleost species and sandbar sharks (Hartman and Brandt 1995c, Ellis 2003) could lead to significant competition among these apex predators for limited prey.

Ecosystem-level consequences affecting apex shark species are more likely in more oligotrophic systems with simpler food webs (Stevens et al. 2000). For example, the shift of Kāne'ohe Bay to a more oligotrophic productivity pattern after the cessation of sewage dumping may have reduced the forage base for juvenile S. lewini in that nursery (Bush and Holland 2002). This example serves as a compelling, though somewhat ironic, demonstration of the potential influence of human activities on shark populations. Semi-enclosed, coastal shark nursery areas such as Chesapeake Bay are particularly vulnerable to anthropogenic influences that drive overall ecosystem health.

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Conclusions:

The bioenergetics model for juvenile sandbar sharks has been updated using a number of recent species-specific data. This improved model predicts higher consumption rates than earlier bioenergetics estimates, but the daily ration estimates generally agree with reconstructed meal sizes from stomach contents data. Further research will help to refine the model; the model is easily adaptable to new data as it becomes available. The results presented herein will be useful for larger ongoing efforts to build ecosystem-wide trophic models for the lower Chesapeake Bay.

As the Northwest Atlantic sandbar shark population slowly recovers from overfishing, juvenile sharks play a significant role in that recovery. The contributions of the summer nursery grounds of the lower Chesapeake Bay and adjacent waters to juvenile growth and survival via both aspects of the nursery area hypothesis are critical. Meanwhile, the slow growth rate and low consumption rate of these long-lived elasmobranchs in a complex trophic system suggest a limited ecosystem role for sandbar sharks in Chesapeake Bay. The predictions of this bioenergetics model have implications for the ecosystem effects of rebuilding strategies for sandbar shark stocks as well as the other elasmobranch stocks that have declined throughout the Northwest Atlantic Ocean (Musick et al. 1993, Baum et al. 2003). This study adds to the growing literature supporting the conclusion that the effects of anthropogenic activities- fisheries and otherwise- on shark populations greatly outweigh the effects of these populations on their ecosystems (Stevens et al. 2000, Kitchell et al. 2002).
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