Estimating consumption rates of juvenile sandbar sharks (*Carcharhinus plumbeus*) in Chesapeake Bay, Virginia, using a bioenergetics model*

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Abstract—Using a bioenergetics model, we estimated daily ration and seasonal prey consumption rates for six age classes of juvenile sandbar sharks (*Carcharhinus plumbeus*) in the lower Chesapeake Bay summer nursery area. The model, incorporating habitat and species-specific data on growth rates, metabolic rate, diet composition, water temperature (range 16.8–27.9°C), and population structure, predicted mean daily rations between 2.17 ±0.03 (age-0) and 1.30 ±0.02 (age-5) % body mass/day. These daily rations are higher than earlier predictions for sandbar sharks but are comparable to those for ecologically similar shark species. The total nursery population of sandbar sharks was predicted to consume ~124,000 kg of prey during their 4.5 month stay in the Chesapeake Bay nursery. The predicted consumption rates support the conclusion that juvenile sandbar sharks exert a lesser top-down effect on the Chesapeake Bay ecosystem than do teleost piscivores and humans.

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 (Musick et al., 1993). Sandbar sharks are the most abundant large coastal sharks in the Mid-Atlantic Bight (Musick et al., 1993) and an important part of the commercial shark catch. After the rapid expansion of the fishery in the mid 1980s, the sandbar shark population in Virginia's coastal ocean waters declined by approximately 66% by 1991 (Musick et al., 1993). Meanwhile, catch rates in the lower Chesapeake Bay, the core nursery area for juvenile sandbar sharks, remained relatively stable (Musick et al., 1993). Because juvenile sandbar sharks return to the coastal or estuarine nursery grounds for the first four to six summers of life (Sminkey and Musick, 1995; Grubbs et al., in press), these nursery grounds are vital to the life history and potential recovery of the Northwest Atlantic sandbar shark stock (Branstetter, 1990; Hoff and Musick, 1990; Sminkey and Musick, 1996; Cortes, 1999).

Despite the abundance and position of elasmobranchs at the apex of many coastal and pelagic food webs, their energetic demands and the role of elasmobranchs as predators have rarely been quantified (Gruber, 1985; DuPreez et al., 1990; Sundström and Gruber, 1998; Lowe, 2002; Schindler et al., 2002). In the Chesapeake Bay, sandbar sharks occupy an apex position in the food web, preying upon

Table 1

Parameters, distributions, and values used in error analyses of the sandbar shark (*Carcharhinus plumbeus*) bioenergetics model. See text for parameter definitions. For parameters with triangular distributions, the initial estimates described in the text were assumed to be the most likely values.

Parameter	Distribution type	Mean or most likely value	SE or range	Source
$SMRa$	Normal	120.0	17.3	Dowd et al. (2006)
$SMRb$	Normal	0.788	0.076	Dowd et al. (2006)
Q_{10}	Normal	2.89	0.16	Dowd et al. (2006)
ACT	Normal	1.62	0.11	Dowd et al. (2006)
SDA	Triangular	0.10C	0.06–0.17C	DuPreez et al. (1988), Sims and Davies (1994), Duffy (1999), Ferry-Graham and Gibb (2001)
L_∞	Normal	164 cm	16.4[1]	Sminkey and Musick (1995)
t_0	Normal	−3.8 yr	0.38[1]	Sminkey and Musick (1995)
K	Normal	0.089	0.0089[1]	Sminkey and Musick (1995)
p	Normal	0.75	0.075[1]	Sminkey and Musick (1995)
F	Triangular	0.20C	0.17–0.38C	Wetherbee and Gruber (1993)
U	Triangular	0.07C	0.05–0.08C	Brett and Groves (1979), Duffy (1999)

[1] SE was assigned by the authors to yield a coefficient of variation of 10% (*sensu* Bartell et al., 1986)

a number of commercially important species such as menhaden (*Brevoortia tyrannus*), blue crabs (*Callinectes sapidus*), striped bass (*Morone saxatilis*), and bluefish (*Pomatomus saltatrix*) (Medved and Marshall, 1981; Medved et al., 1985; Stillwell and Kohler, 1993; Ellis, 2003). Interestingly, previous 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 and the incidence of omnivory (Bascompte et al., 2005).

Because the sandbar shark is one of the few species for which many of the necessary modeling parameters have been measured, it serves as an excellent system for assessing the bioenergetics and ecosystem role of large coastal elasmobranchs. This article has the following objectives:

1 to construct a realistic bioenergetics model for juvenile sandbar sharks in the Chesapeake Bay summer nursery grounds. Because previous sandbar shark models have suffered from a lack of species-specific data (Medved et al., 1988; Stillwell and Kohler, 1993), we have incorporated updated species-specific and habitat-specific data.
2 to use the model to assess the role of juvenile sandbar sharks as predators in the Chesapeake Bay to aid ecosystem modelers and fishery management efforts.
3 to test the sensitivity of the model to uncertainty in parameter estimates using error analysis to identify future research priorities (Kitchell et al., 1977).

Materials and methods

Study area and nursery habitat

The core sandbar shark nursery area (~500–1000 km²; Grubbs and Musick, in press) in the lower, eastern Chesapeake Bay supports a seasonal population of ~10,000 individuals (Sminkey, 1994), composed almost entirely of sandbar sharks <90 cm precaudal length (PCL) (Musick et al., 1993; VIMS[1]). Juvenile sandbar sharks move actively throughout the nursery area, covering large activity spaces (>110 km²) and the entire water column, as shown in telemetry studies (Medved and Marshall, 1983; Grubbs, 2001).

Sandbar sharks in the nursery area are exposed to both long-term and short-term changes in water temperatures. Juvenile sandbar sharks inhabit Chesapeake Bay at seasonal temperatures ranging from 15 to 29°C (VIMS[1]). During the months of July and August, a seasonal thermocline also develops in the lower Chesapeake Bay, which sandbar sharks will cross repeatedly throughout the day (Grubbs, 2001). The magnitude of the temperature gradient from top to bottom is typically 5–6°C (VIMS[1], Chesapeake Bay Program[2]).

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[1] VIMS (Virginia Institute of Marine Science) Shark Ecology Program Longline Survey. 1973–2003. Unpubl. data (as a Microsoft Excel file). [Available from J. A. Musick. 1208 Greate Road, Gloucester Point, VA 23062-1346.]

[2] Chesapeake Bay Program Water Quality Database. Website: http://www.chesapeakebay.net/data/index.htm [accessed on March 2003.]

Bioenergetics model

Rates of anabolism, catabolism, and waste losses (Table 1) were used to construct a bioenergetics model that predicted daily energy consumption (C_D, in joules per day, J/d):

$$C_D = RMR_D + SDA + G_D + F + U. \quad (1)$$

The model used a daily time step, consistent with the determination of daily energy ration. Due to the reporting of the daily routine metabolic rate (RMR_D), specific dynamic action (SDA), fecal losses (F), and excretions (U) as fractions of consumption (see below), we rearranged Equation 1 and solved for C_D to yield the model:

$$C_D = \frac{RMR_D + G_D}{(1 - SDA - U - F)}. \quad (2)$$

We set the immigration and emigration dates for the simulation as May 15 and September 30, respectively (VIMS[1]).

We used the model to estimate daily energy ration for average individuals within each of six age-classes using the Chesapeake Bay nursery (Musick et al., 1993). In turn, we combined energetic requirements with diet composition data 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.

Model parameters

Routine metabolic rate (RMR) Like a number of carcharhiniform species, sandbar sharks are continuously active, which leads to high daily metabolic expenditures (e.g., Carlson et al., 1999). As a result, metabolic rate is the largest and most variable component of the energy budget for these active fish (Kerr, 1982; Boisclair and Leggett, 1989). Unfortunately, because of a paucity of available data, metabolic rate parameters are often borrowed from other species (e.g., Schindler et al., 2002). Sensitivity analyses have shown that accurate metabolic rate data are needed to construct realistic bioenergetics models (Kitchell et al., 1977; Bartell et al., 1986).

The allometric (size-dependent) influence on standard metabolic rate (SMR) in juvenile sandbar sharks was recently determined over the entire size range (42–92 cm PCL, 1–10 kg) characteristic of the Chesapeake Bay nursery area in flow-through respirometers for sharks treated with a neuromuscular blocker (Dowd et al., 2006). The best fitting allometric equation for SMR ($SMR = a \times M^b$) for 33 sharks at 24°C was

$$SMR_{24} = 120.0 \, (\pm17.3) M^{0.788 \, (\pm0.076)}, \quad (3)$$

where M = mass in kilograms; and
SMR = mgO$_2$ consumed per hour.

The values in parentheses are the standard errors of the allometric intercept and the allometric exponent estimates (hereafter $SMRa$ and $SMRb$, respectively).

Dowd et al. (2006) also determined the routine metabolic rate (the average oxygen consumption rate of a swimming shark) for 15 individual sandbar sharks at 24°C in an annular respirometer (diameter 1.67 m). The ratio of routine metabolic rate to SMR, corrected for the cost of swimming in a curved path in the respirometer (Weihs, 1981), averaged 1.62 ±0.11 (Dowd et al., 2006). This ratio was used in the model as a constant activity multiplier (ACT) to estimate field metabolic rate (*sensu* Winberg, 1960; Kitchell et al., 1977; Schindler et al., 2002). The ACT used is similar to those derived from field data for subadult *Negaprion brevirostris* (1.3; Sundström and Gruber, 1998) and juvenile *Sphyrna lewini* (1.45; Lowe, 2002). The sandbar shark ACT was assumed to remain constant for all age classes and over all temperatures (Dowd et al., 2006).

The effects of acute temperature changes (quantified as Q_{10}) on SMR for juvenile sandbar sharks (mass 1—10 kg) between 18° and 28°C have also been measured (Dowd et al., 2006). The overall mean Q_{10} (the relative increase in metabolic rate with temperature, scaled to a 10° temperature range) was 2.89 ±0.16 (n=43), was consistent over the size range of sharks tested, and was statistically indistinguishable among three treatments (18–24°C, 24–28°C, and 18–28°C). We assumed that the SMR Q_{10} remained constant throughout the simulation period.

For each day of the simulation, the Q_{10} was used to adjust the predicted SMR from Equation 3 to the simulated daily temperature (T) (equation adapted from Schmidt-Nielsen, 1997):

$$SMR_T = 10^{\left(\log SMR_{24} + \log Q_{10} \cdot \frac{(T-24)}{10} \right)}. \quad (4)$$

SMR_T was then multiplied by the ACT and by 24 hours to obtain the daily metabolic expenditure in mgO$_2$/day. Finally, this value was converted to daily metabolic energy utilization (RMR_D) by using the oxycalorific coefficient 13.59 J/mgO$_2$ (Elliott and Davison, 1975).

Specific dynamic action (SDA) Specific dynamic action represents the energetic cost of incorporation of digested amino acids into new proteins (Brown and Cameron, 1991). Although SDA varies with growth rate, or the protein content of ingested food (e.g., Ross et al., 1992), most bioenergetics models set SDA as a constant fraction of consumed energy (e.g., Hewett and Johnson, 1992). Fortunately, although SDA has been measured in only a few elasmobranch species, it is typically a relatively small fraction of consumed energy (DuPreez et al., 1988; Sims and Davies, 1994; Duffy, 1999; Ferry-Graham and Gibb, 2001). As an initial estimate, we assumed SDA to be 10% of consumed energy (Schindler et al., 2002).

Growth (*G*) Growth (*G*) is the change in energy stored in biomass and can be subdivided into somatic and reproductive growth outputs. We assumed the latter to be negligible because all the age classes in the sandbar shark bioenergetics model are at least 8 years from the age at maturity (Casey et al., 1985; Sminkey and Musick, 1995).

We employed a von Bertalanffy growth equation (Sminkey and Musick, 1995), based on a validated aging technique for sandbar sharks (Branstetter, 1987), to represent the precaudal length (PCL) of sharks of age *y* (*y* = 0–5 **yr**) upon immigration (or birth) on May 15:

$$L_{yI} = L_\infty \left(1 - e^{-K(y-t_0)}\right) \tag{5}$$

where L_∞ = 164 cm;
K = 0.089; and
t_0 = –3.8 years.

The PCL at emigration (L_{yE}) was determined by

$$L_{yE} = L_{yI} + p\left(L_{yI+1} - L_{yI}\right). \tag{6}$$

where *p* = the proportion of annual growth in PCL that occurs in the Chesapeake Bay nursery.

Analysis of vertebral rings indicates that annual growth of juvenile sandbar sharks occurs in two distinct phases: one period of rapid growth in the summer nurseries during which the sharks achieve roughly 75% of their annual growth in length, followed by a period of reduced somatic growth during the winter (Sminkey and Musick, 1995). Therefore, we assumed a *p* of 0.75 as an initial estimate. Limited tag-return data support this seasonal growth pattern. One juvenile (67 cm total length [TL] at tagging) was recaptured 0.5 km from the tagging location within the summer nursery in September 1998 by VIMS scientists; it had grown 3 cm TL after 44 days at liberty. Similarly, a juvenile sandbar shark of similar size that had been tagged and recaptured by NMFS scientists grew 3 cm in fork length (FL) (48–51 cm FL) over 62 days at liberty between mid-July and mid-September (Casey et al., 1985). In Delaware Bay, two sandbar sharks recaptured during the same summer grew 3 cm FL (45 cm flat tagging and 1 cm FL) (no size given) in 40 and 47 days at liberty, respectively (Merson and Pratt, 2001). In comparison, another juvenile (66 cm TL) was tagged in Chesapeake Bay in September 1995 and recaptured by VIMS scientists during the subsequent immigration period. This shark was at liberty for 225 days and grew only 3.5 cm TL during that time.

Both Medved et al. (1988) and Kohler et al. (1995) published equations relating mass to length for sandbar sharks. Because preliminary runs of the model demonstrated that these length-mass relationships yielded very similar results, we used the equation produced by Kohler et al. (1995) because it was derived from a larger number of individuals:

$$M = 0.0109\, FL^{3.0124}. \tag{7}$$

Fork length (FL) is in centimeters and mass (M) is in grams. Lengths were converted from PCL to FL and *vice versa* by using the regression (VIMS[1]):

$$FL = 1.0791\, PCL + 2.78. \quad (n = 4385;\ r^2 = 0.99) \tag{8}$$

Specific growth rate (grams added per gram of body mass per day) was modeled by assuming that the mass of the shark increased by a constant proportion (*x*) in each of the *n* days of the simulation:

$$M_E - M_I = \sum_{D=1}^{n} x \times M_D. \tag{9}$$

M_D is the mass of the shark at the beginning of day *D*. No data exist to support an alternative pattern (e.g., growth varying with temperature or dissolved oxygen levels).

The mass of the shark on the first and last day (M_I and M_E, respectively) of the simulated nursery season was determined by using Equations 5–8. Fitted values for *x* in Equation 9 were on the order of 0.1–0.5% increases in mass per day. We used these values to calculate daily growth increments in grams per day and then multiplied by 5400 J/g of body mass (Cortes and Gruber, 1990; Lowe, 2002) to determine the daily increase in energy content.

Waste loss in feces (*F*) and excretions (*U*) A generally accepted value for total waste loss to excretions and fecal waste for carnivorous fishes and elasmobranchs is 27 ±3% of consumed energy (*C*) (Brett and Groves, 1979; e.g., Sundström and Gruber, 1998; Lowe, 2002; Schindler et al., 2002). This value was assumed for the sandbar shark in the present study, divided into *F* = 0.20C and *U* = 0.07C. Juvenile *N. brevirostris* have fecal waste losses between 38.1% and 16.9% (Wetherbee and Gruber, 1993), and excretory losses average 7% of ingested energy for a number of teleosts (Brett and Groves, 1979).

Water temperature data Surface and bottom water temperatures were obtained from the Chesapeake Bay Program's water quality database[2] for seven monitoring stations within the core sandbar shark nursery area in Chesapeake Bay for 1996–2002. Temperature measurements were averaged over all stations and over all years for each day of the simulation. The surface and bottom temperature readings were also averaged to obtain a mean water temperature for each day of the simulation in an average year. The simulated temperatures ranged from 16.8° to 27.9°C over the summer nursery season (mean 23.0° ±0.2°C).

Diet composition data Recent data detail the ontogenetic patterns of juvenile sandbar shark diet composition in and around Chesapeake Bay for sharks captured with longline and gillnet gears (Ellis, 2003). Diet data are represented by the index of relative importance. Index of relative importance combines the frequency, weight, and number of each prey type and is considered to have

Table 2

Diet composition data for juvenile sandbar sharks (*Carcharhinus plumbeus*) used to estimate daily rations and seasonal prey consumption. Prey species were grouped into four categories for each age class. Diet data, adapted from Ellis (2003), are expressed as index of relative importance. The average energetic content (J/g wet mass) of each prey type was calculated from data in Thayer et al. (1973).

Category	Representative species	Ages 0–1	Ages 2–3	Ages 4–5	Energy density (J/g)
Teleostei	Atlantic menhaden (*Brevoortia tyrannus*) Summer flounder (*Paralichthys dentatus*)	0.146	0.292	0.463	5050
Mollusca	Squids (*Loligo* spp.)	0.007	0.004	0.023	4390
Crustacea	Blue crab (*Callinectes sapidus*) Mantis shrimp (*Squilla empusa*)	0.847	0.672	0.421	4810
Elasmobranchii	primarily skates (*Raja* spp.)	—	0.031	0.094	5400

Table 3

Cohort sizes and estimated mean seasonal prey consumption in the lower Chesapeake Bay for each age class in the sandbar shark (*Carcharhinus plumbeus*) bioenergetics model. Cohort sizes are mean ±SE.

Age class	Initial cohort size[1]	Indexed cohort size[2]	Seasonal prey consumption (kg)[3]				
			Teleostei	Mollusca	Crustacea	Elasmobranchii	Total
0	2545 ±216	4377 ±1074	4236	207	24,667	—	29,110
1	2122 ±284	2626 ±645	3634	178	21,157	—	24,969
2	2083 ±398	1837±451	6684	100	15,385	716	22,885
3	1698 ±417	1698 ±417	7757	115	17,855	831	26,558
4	900 ±184	900 ±184	7754	380	7053	1575	16,762
5	188 ±40	188 ±40	1900	93	1728	386	4,107
Total	9537 ±313	11,627 ±2483	31,965	1073	87,844	3,508	124,391

[1] Estimates are from Sminkey (1994).

[2] We retained the initial cohort size estimates for ages 3–5.

[3] Estimated by using mean indexed cohort size.

less bias than other diet indices (Cortes, 1997). For the present study, prey species were grouped into four categories for each age class of shark: teleost fishes, mollusks, crustaceans, and elasmobranchs (Table 2). The proportion of each prey type in the diet and the mean energy content values for each category (calculated from data in Thayer et al., 1973) were used to convert daily energy ration (kJ/d) to daily ration (percent body mass per day, %BM/d). Diet composition was assumed to remain constant during the simulation period. The average daily ration and total seasonal prey consumption were calculated for individuals of each age class.

Population estimates The relative abundance and size-class composition of the seasonal nursery population were estimated from catch per unit of effort (CPUE) data (Musick et al., 1993; VIMS[1]). Sminkey (1994) used virtual population analysis to estimate the sandbar shark cohort sizes in the Chesapeake Bay nursery from the VIMS Shark Longline Survey data, using the standard Mustad™ 9/0 J hooks between 1989 and 1993 (Table 3).

However, the standard hooks select for larger animals, yielding underestimates of abundance for ages 0–2 years. Therefore, we indexed the VIMS CPUE data for ages 0–2, using smaller Mustad™ 12/0 circle hooks against the CPUE for larger hooks for 25 longline sets between 1997 and 2002 when both gears were fished simultaneously at the two lower Chesapeake Bay survey stations. We then used this index to produce a more realistic population age structure (Table 3). The mean adjusted nursery population size was 11,627 ±2483 individuals.

For simplicity, we assumed negligible mortality and zero emigration of juvenile sharks during the simulation period. Consequently, the revised cohort sizes were held constant throughout the simulation period. Low natural mortality rates would be expected for these sharks, particularly in light of the near absence of large coastal shark predators in the nursery (Musick et al., 1993). Tracking, tagging, and survey data all indicate that juvenile sandbar sharks remain within the nursery throughout the summer (Grubbs et al., in press; Merson and Pratt, 2001).

Model calculations

For each daily time step of the model and for each age class, RMR_D and G_D were calculated as described above. These estimates were used to solve for daily consumption in joules in Equation 2, where *SDA, U,* and *F* are the fractions of consumption described above. These daily energy consumption estimates were summed to determine total energy consumption for an average individual of each age class during the entire stay in the Chesapeake Bay nursery. Mean daily energy ration (DER) was calculated in kJ/d. The daily energy ration was also expressed as a percentage of the average total energy content (%DER) for each day:

$$\%DER = 100 \cdot \frac{C_D}{\left(\dfrac{M_D + M_{D+1}}{2} \cdot 5400\right)} \cdot \qquad (10)$$

Finally, gross conversion efficiency (K_I), the fraction of consumed energy that is devoted to growth, was calculated for each day:

$$K_{1_D} = \frac{G_D}{C_D} \cdot \qquad (11)$$

This value was used as a general test of the model outputs.

Error analysis

Static models were run by using the initial parameter estimates described above to determine point estimates of consumption. *SDA* and energy losses in *U* and *F* were modeled as constant fractions of consumption. The initial choices of these values, therefore, had a direct effect on the predicted consumption rates. Further, a number of the model parameters were measured with some uncertainty. A stochastic, Monte Carlo simulation routine (Crystal Ball© 2000 Academic Edition, vers. 5.2.2, Decisioneering, Inc., Denver, CO) was used to assess this uncertainty with error analysis (Bartell et al., 1986). Error analysis is particularly useful for evaluating model sensitivity to parameters that enter the model in a nonlinear fashion (Bartell et al., 1986), such as the SMR allometric exponent (SMRb) and allometric constant (SMRa) and the Q_{10}. The simulation randomly drew values from probability distributions for each model parameter (Table 1) for each of the 2000 Monte Carlo iterations. The model parameters were ranked in importance by their relative contribution to the variance of the stochastic model outputs (Bartell et al., 1986).

Results

Consumption rates

The model predicted mean daily energy rations (DER) increasing from 233 ±5 kJ/d (%DER=1.95 ±0.03%) for young-of-the-year to 784 ±16 kJ/d (%DER=1.20

Table 4

Gross conversion efficiency (K_I), daily energy ration (DER), daily ration (DR), and total seasonal prey consumption (C_{tot}) for individuals of each age-class of the sandbar shark (*Carcharhinus plumbeus*) in the bioenergetics model. DER and DR were averaged over the 138 days of the simulation (mean ±SE).

Age class	K_I	DER (kJ/d)	DR (%BM/d)	C_{tot} (kg)
0	0.16	233 ±5	2.17 ±0.03	6.6
1	0.15	333 ±7	1.89 ±0.03	9.5
2	0.13	442 ±9	1.67 ±0.03	12.5
3	0.12	555 ±11	1.52 ±0.03	15.6
4	0.11	669 ±14	1.39 ±0.02	18.6
5	0.10	784 ±16	1.30 ±0.02	21.8

±0.02%) for an age-5 juvenile. These values correspond to prey consumption rates of 2.17 ±0.03%BM/d and 1.30 ±0.02%BM/d, respectively (Table 4). The predicted daily rations for a given age class over the course of the simulation period fluctuated with temperature because of the thermal influence on metabolic rate.

During the 4.5-month stay in the Chesapeake Bay nursery area, the static model predicted total energy consumption of 269% of the total energy content for an age-0 shark (~32,000 kJ), declining to 165% (~108,000 kJ) for age-5 sharks. When merged with diet composition data, the model predicted that an age-0 shark would consume 6.6 kg (300% average BM) of prey per summer, and an age-5 juvenile would consume 21.8 kg (180% average BM). Therefore, the total sandbar shark population would consume 124,400 kg of prey over the course of the summer in the Chesapeake Bay nursery area (Table 3).

The average K_I declined quickly with age from 16.3 ±0.3% of consumed energy for age-0 sharks to 10.0 ±0.2% of consumed energy by age five. Because 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 with age. Metabolism for age-0 sandbar sharks accounted for roughly 46% of ingested energy, increasing to 53% of the energy budget for age-5 juveniles. When growth was set to zero, we calculated the maintenance rations to be 63–80% of the rations when growth was included.

Error analysis

The relative contributions of each of the input parameters to the variance of the model outputs exhibited similar patterns for all age classes (Fig. 1). The von Bertalanffy parameters predicting size at age (L_∞, K) had consistently high ranks for their contribution to model variance, as did those describing the allometric scaling of standard metabolic rate (*SMRa, SMRb*). *F* also contributed significantly to the variance of the model outputs for all age classes (Fig. 1). The contributions
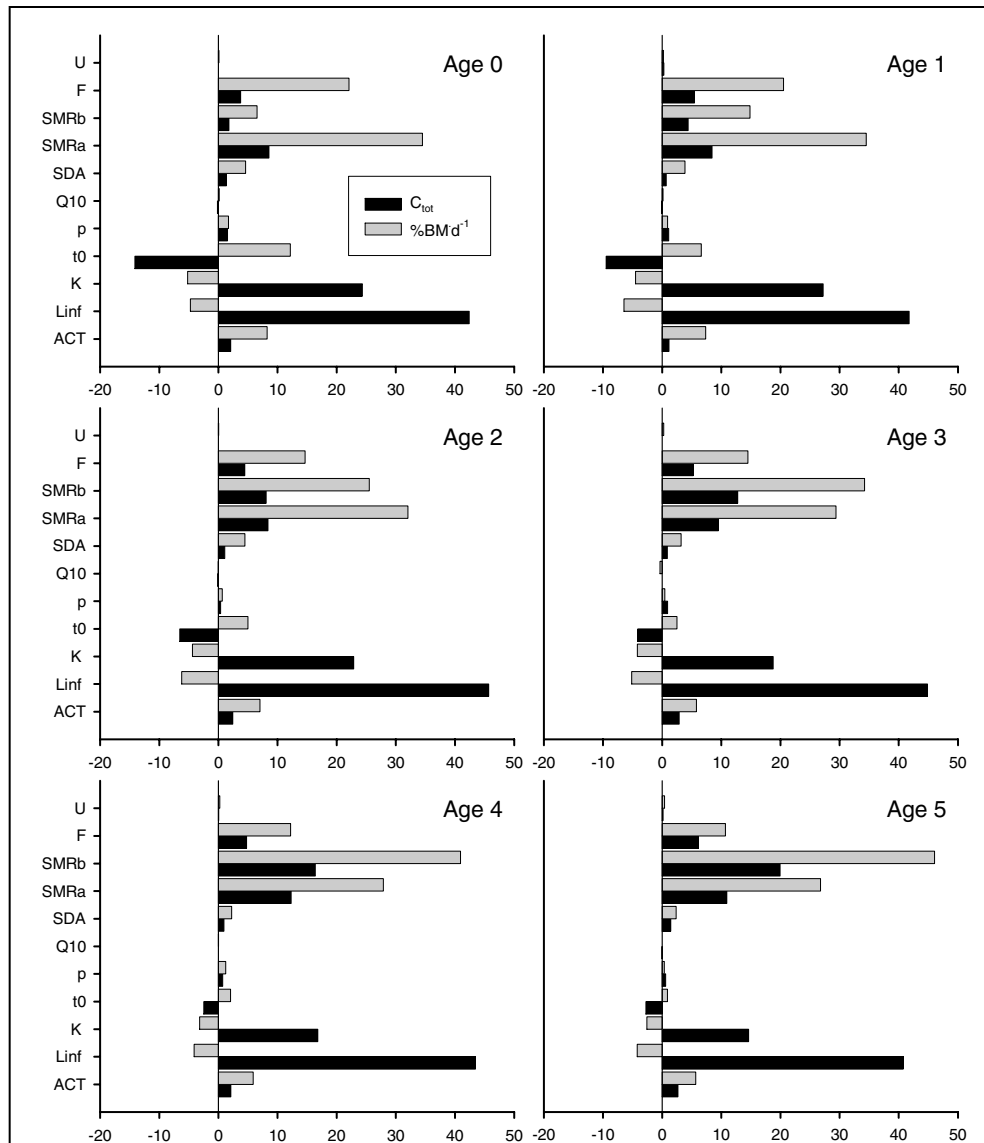
Figure 1

Results of the error analyses for the sandbar shark (*Carcharhinus plumbeus*) bioenergetics model for ages 0–5 years, using the eleven parameters and distributions from Table 1 in 2000 Monte Carlo simulations. The horizontal axis is the percentage contribution of the variable of interest to the variance in two model predictions: total seasonal prey consumption in kg (C_{tot}, black bars) and mean daily ration (%BM/d, grey bars). Positive values indicate that an increase in the parameter yields an increase in the model output, and negative values indicate the opposite. See text for definitions of parameter abbreviations along the *y* axix.

of uncertainty in U, p, and Q_{10} were negligible for all age classes.

The Monte Carlo simulations predicted mean seasonal energy consumption rates 11–15% higher than those derived by using the static model. This elevation was primarily due to the fact that SDA and fecal waste (F) were allowed to comprise larger proportions of consumption than in the static model runs.

Discussion

Comparison with previous results

The mean daily rations for age-0 juvenile sandbar sharks predicted from our bioenergetics model (2.17 %BM/d, average M=2.2 kg) were higher than those previously reported (1.32 %BM/d, *M*=1.9 kg, Medved et al., 1988;

1.49%BM/d, M=1.7 kg, Stillwell and Kohler, 1993). This difference was partly due to the incorporation of species-specific routine metabolic rate data into our model, which were 8–15% higher than values from the spiny dogfish (*Squalus acanthias*) used in earlier models. Earlier models also estimated daily ration at a mean temperature over the entire year, whereas our model incorporated seasonal temperature shifts and the resulting effects on metabolic rate using the Q_{10}. Test runs of our model were used to predict daily rations over the winter, assuming that the diet composition was the same, 25% of annual growth occurred in the winter (Sminkey and Musick, 1995), and average water temperature was 14°C (Springer, 1960). These model runs predicted daily rations less than half (<1%BM/d) of those estimated for the summer nursery season. More data, however, are needed on the biology of sandbar sharks in the winter nursery grounds in order to develop an accurate year-round bioenergetics model.

Sandbar shark daily consumption rates have also been estimated by using meal size and frequency, as well as gastric evacuation rates. Our model's predicted consumption rates (1.30–2.17 %BM/d) support estimates based on meal size and frequency. The reconstructed meal size for juvenile sandbar sharks in Chincoteague Bay, based on stage of digestion estimates, was 4.23 ±0.31% BM (Medved et al., 1988). Given the sandbar shark's 70–92 hour gastric evacuation rate (Medved, 1985), as well as the high proportion of sharks landed with empty stomachs (17.9–20.0%) (Medved and Marshall, 1981; Medved et al., 1985; Stillwell and Kohler, 1993; Ellis, 2003), it seems likely that 48–72 hours pass between significant feeding events (Medved et al., 1985). Therefore, the reconstructed meal sizes correspond to daily consumption rates of 2.12–1.41% BM/d. In contrast, gastric evacuation models predicted juvenile sandbar shark daily rations (0.93% BM/d to 1.07% BMd; Medved et al., 1988) lower than our bioenergetics model. However, the data probably violated the gastric evacuation models' assumptions of continuous feeding and that time between meals exceeds digestion time (reviewed by Cortes, 1997).

The estimated sandbar shark daily rations are comparable to those for other active shark species. For example, the estimated daily rations for a 1-kg *N. brevirostris* and a 0.76-kg *S. lewini* were 2.62% BM/d and 2.9–3.9% BM/d, respectively (Gruber, 1985; Lowe, 2002). The sandbar shark daily rations were averaged over the entire simulated nursery season, during which temperature fluctuated by 10°C. Predicted daily rations in mid-summer were frequently higher than 3.0% BM/d.

The predicted mean gross conversion efficiency from our model (0.10–0.16) was similar to estimates for bull sharks (*Carcharhinus leucas*) fed to satiation in captivity (0.05–0.12, Schmid and Murru, 1994) and for juvenile lemon sharks (*N. brevirostris*) in the wild (0.10–0.13, Cortes and Gruber, 1994).

Parameter uncertainty

The largest potential sources of error in the model were L_∞, K, *SMRa*, and *SMRb* (Fig. 1). Fortunately, the von Bertalanffy growth parameters (L_∞, K) and the SMR allometric scaling parameters (*SMRa* and *SMRb*) are among the best known for juvenile sandbar sharks, and the initial estimates used are considered reliable. Metabolic rate may also be impacted by osmoregulatory costs incurred by penetrating the less saline regions (~20–25 ppt) of the Chesapeake Bay nursery area (Chan and Wong, 1977; Meloni et al., 2002). Future studies should investigate this possibility. Other confounding factors which will alter metabolic rate estimates associated with routine swimming behavior include movement of the animals with dominant tidal currents or burst swimming followed by oxygen debt repayments (or both factors) (e.g., Kerr, 1982; Boisclair and Leggett, 1989). Although these factors may affect ACT estimates, field tracking data from juvenile sandbar sharks indicate that mean rates of movement (converted to body lengths per second, BL/s) in the wild (0.23 BL/s, Huish and Benedict[3]; 0.46 BL/s, Medved and Marshall, 1983; 0.59 BL/s, Grubbs, 2001) are comparable with laboratory swimming speeds used to estimate the ACT (mean 0.55 BL/s; Dowd et al, 2006).

The effects of temperature on metabolism were not important in the error analyses, but two points merit consideration. Seasonal (e.g., winter vs. summer) metabolic rate Q_{10} may be lower than Q_{10} in response to acute temperature changes (Carlson and Parsons, 1999); future studies should address this possibility in sandbar sharks. The averaging of surface and bottom water temperatures in the model potentially obfuscated short-term changes in metabolic rate caused by sharks crossing the thermocline. Energetic implications of such short-term movements could be investigated with more detailed spatial models, but such an approach lies outside the scope of the present study.

Uncertainty in the fecal waste parameter accounted for a large portion of the variance in the stochastic model outputs, indicating that F should be investigated in sandbar sharks to refine the bioenergetics model. The effects of the slow gastric evacuation rate of the sandbar shark on the magnitude of the waste and SDA parameters are unknown.

One of the implicit assumptions of our model is that all energy spent is derived from food. Because 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. However, little is known about the feeding habits of sandbar sharks during their seasonal migrations or during their time in the winter nursery. At these times stored energy may play a greater role in the energy budget. Seasonal changes in energy content occur in Atlantic sharpnose sharks (*Rhizoprionodon*

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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 the size at birth for *C. obscurus*. Misidentification of the congeneric sandbar and dusky sharks is common.

*terraenova*e) (Hoffmayer, 2003); if such changes occur in sandbar sharks, these fluctuations could also affect the model's consumption estimates.

Ecosystem interactions

Our results downplay the top-down role of sandbar sharks in the trophic economy of the lower Chesapeake Bay. The model results presented above predict that juvenile sandbar sharks consume ~120,000 kg of prey in an average summer in the nursery. In comparison, the estimated annual prey consumption rates of the dominant teleost piscivores (bluefish, *P. saltatrix*; striped bass, *M. saxatilis*; and weakfish, *Cynoscion regalis*) in Chesapeake Bay were 27,000,000 kg, 10,000,000 kg, and 5,000,000 kg, respectively (Hartman and Brandt, 1995a). Moreover, the seasonal consumption of prey species by juvenile sandbar sharks is insignificant compared to fisheries landings. The total predicted consumption of Crustacea and Teleostei by juvenile sandbar sharks equals only 0.57% and 0.01% of the annual commercial landings of blue crabs (*C. sapidus*) and Atlantic menhaden (*B. tyrannus*) in Virginia, respectively (U.S. Department of Commerce[4]).

Bottom-up effects on sharks as apex predators are possible if lower trophic levels are overfished, but the apparent opportunistic foraging strategy of sandbar sharks (Medved and Marshall, 1981; Medved et al., 1985; Stillwell and Kohler, 1993; Ellis, 2003) probably reduces their vulnerability to declines of specific prey species (Stevens et al., 2000). However, if current fishery landings in Chesapeake Bay are not sustainable, the dietary overlap between the dominant piscivorous teleost species (Hartman and Brandt, 1995b) and sandbar sharks could lead to competition among these predators for limited prey.

Conclusions

An updated sandbar shark bioenergetics model predicts higher consumption rates than earlier bioenergetics estimates, but the daily ration estimates generally agree with reconstructed meal sizes from stomach contents data. Our results will be useful for ongoing efforts to build ecosystem-wide trophic models for the lower Chesapeake Bay.

As the sandbar shark population slowly recovers from overfishing, the contributions of the summer nursery grounds of the lower Chesapeake Bay to juvenile growth and survival will remain critical. Meanwhile, the slow growth rate and low consumption rate of these long-lived elasmobranchs in a complex trophic system may indicate a limited top-down ecosystem role for sandbar sharks in Chesapeake Bay. Our results support the

conclusion that the effects of anthropogenic activities—fisheries and other activities—on shark populations often greatly outweigh the effects of these populations on their ecosystems (Stevens et al., 2000; Bush and Holland, 2002; Kitchell et al., 2002; Baum et al., 2003; Bascompte et al., 2005).

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