## CHAPTER 1

# Captive Feeding and Growth of Young-of-the-Year White Sharks, *Carcharodon carcharias*, at the Monterey Bay Aquarium

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## ABSTRACT

The Monterey Bay Aquarium developed a program with the support of colleagues from Stanford University, California State University Long Beach, and the Southern California Marine Institute to display young-of-the-year (YOY) White Sharks (*Carcharodon carcharias*), culminating in the display of five White Sharks in the 3.8-million-L Outer Bay exhibit between 2004 and 2009. The Outer Bay exhibit displays a variety of pelagic fishes, including Yellowfin Tuna (*Thunnus albacares*), Dolphinfish (*Coryphaena hippurus*), and Scalloped Hammerhead Sharks (*Sphyrna lewini*) and is maintained at 20ºC. Four of the White Sharks fed consistently while on display (70–198 d), eating mostly King Salmon (*Onchorhynchus tshawytscha*), Pacific Mackerel (*Scomber japonica*), and Sablefish (*Anoplopoma fimbria*) at a mean (±SE) daily ration of 747 ± 46 g or 1.62 ± 0.15% body

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mass $d^{-1}$ (% BM $d^{-1}$). One shark did not feed regularly and was released after 11 d. Daily ration peaked between 3.1 and 3.5% BM $d^{-1}$, which is among the highest reported for any shark species. The captive White Sharks grew in mass at a rate of 71.6 ± 8.2 kg yrs.$^{-1}$, yielding a mean gross conversion efficiency of 27.1 ± 3.8%. They grew at a mean rate of 64.9 ± 8.5 cm yrs.$^{-1}$, approximately twice the growth rate estimated from a von Bertalanffy growth function for White Sharks (Cailliet et al., 1985). A simplified bioenergetics model was used to determine parameter estimates for consumption, growth, and metabolism. This model assumed that 27% of energy intake was lost to waste, and it suggested that a mean 26.8 ± 2.9% of energy intake was invested into somatic growth, and 46.2 ± 2.9% of energy was consumed by metabolism. YOY White Sharks showed high growth capacity at optimal conditions in captivity; however, the energetic demands of White Sharks in the wild remain unknown.

## INTRODUCTION

Although the White Shark, *Carcharodon carcharias*, is the focus of much interest from both the research community and the public, the display and study of a living specimen have been difficult to achieve. Many studies have focused on predatory behavior (e.g., Anderson et al., 1996; Long et al., 1996; Klimley et al., 1996, 2001), reproductive biology (Pratt, 1996; Uchida et al., 1996; Francis, 1996; Saidi et al., 2005; Chapter 30, this book), age and growth (Cailliet et al., 1985), and more recently on migration patterns of adult White Sharks (e.g., Boustany et al., 2002; Bonfil et al., 2005; Bruce et al., 2006; Domeier and Nasby-Lucas, 2008; Chapters 11, 13, 16, and 21, this book). Very little is known about neonates and juveniles of this species. However, satellite archival tag technology has recently been used to study the swimming behavior and thermal niche of young-of-the-year (YOY) and juvenile White Sharks, which were bycatch of commercial fisheries in the Southern California Bight (Dewar et al., 2004; Weng et al., 2007; Chapters 14 and 16, this book). This information on juvenile White Sharks has enabled the Monterey Bay Aquarium (MBA) to conduct a program to continue the study of juvenile White Sharks in the wild (Chapters 14 and 15, this book) and to place living specimens on display to the public.

Historically, the long-term display of a living White Shark has been attempted by many public aquariums with little success because of the difficulty in acquiring healthy specimens and the challenges in transport (Hewitt, 1984; http://homepage.mac.com/mollet/Cc/Cc_captive.html); however, since 2004 the MBA has displayed five juvenile White Sharks. The White Shark is a top-level predator that has cosmopolitan distribution in temperate and tropical seas (Compagno, 1984). These sharks can attain large size (Mollet et al., 1996) and are active swimmers that undergo large-scale geographic migrations (Boustany et al., 2002; Bonfil et al., 2005; Bruce et al., 2006; Domeier and Nasby-Lucas, 2008; Chapters 11, 13, 16, and 21, this book). These factors make acquisition and display of this species difficult. With this in mind, the program undertaken by the MBA to display a White Shark was a multiyear, incremental approach to study the behavior and movements of YOY White Sharks in the Southern California Bight and to display a specimen in the 3.8-million-L Outer Bay exhibit (OBE) (Figure 1.1). We report the captive feeding and growth and the energy budgets of YOY White Sharks displayed at the Monterey Bay Aquarium.

## MATERIALS AND METHODS

The YOY White Sharks were captured in the Southern California Bight between August 2004 and August 2009 with the intent to place them on public display at the MBA. The YOY White Sharks, ranging in size from 137 to 164 cm total length (TL) and 25.2 to 47.0 kg body mass, were either bycatch of the commercial gillnet fishery or targeted catch by the MBA collecting staff. The

**Figure 1.1** A YOY White Shark on public display in the 3.8-million-L Outer Bay exhibit at the Monterey Bay Aquarium. (Courtesy of Randy Wilder, Monterey Bay Aquarium.)

sharks were transported in water tanks on the fishing vessels to a 40-m diameter by 11-m deep ocean pen anchored off Malibu, California to allow them to recover from capture stress and begin feeding (Figure 1.2). Upon introduction to the pen, some sharks were tagged with a pop-off archival satellite tag (PSAT) to record their swimming behavior with respect to depth and water temperature. During the period that the sharks were in the pen (10–25 d), MBA husbandry department staff made observations on the condition of the sharks and offered fresh fish—Pacific Mackerel (*Scomber japonicus*), White Croaker (*Genyonemus lineatus*), Bonito (*Sarda chiliensis*), and King Salmon (*Oncorhynchus tshawytscha*)—to stimulate feeding.

The YOY White Sharks were transported to the MBA after they were determined to be healthy and feeding regularly in the pen. Food was generally withheld from the sharks 24 h prior to

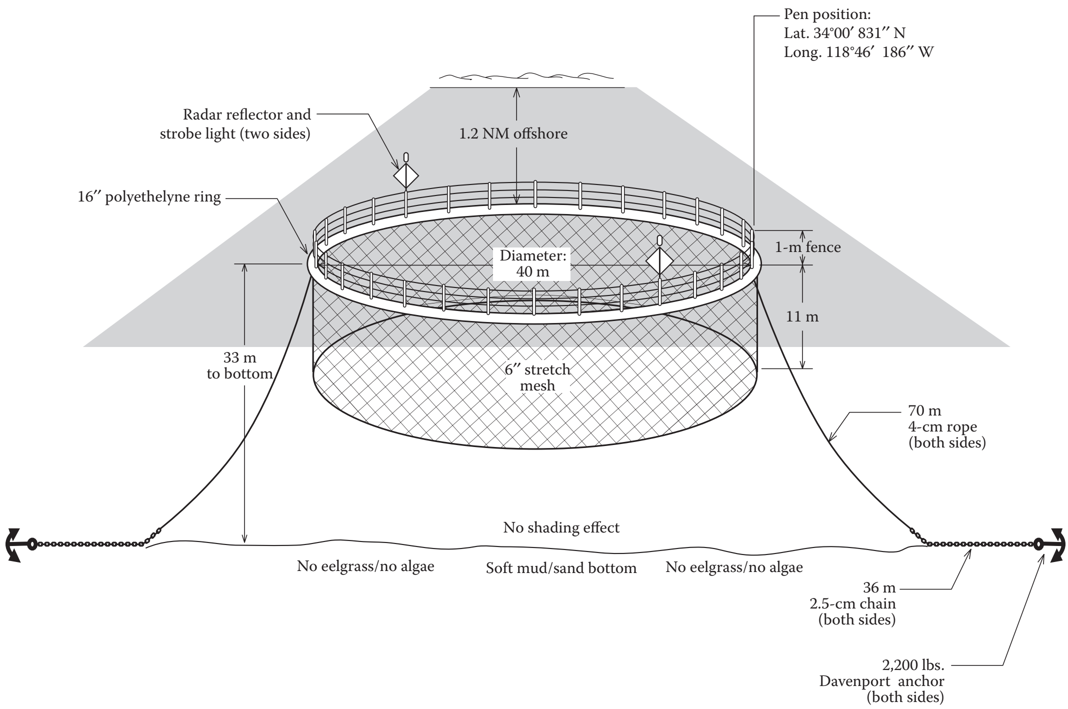


**Figure 1.2** The ocean net pen (40 m diameter × 11 m depth) used to hold YOY White Sharks after capture in the Southern California Bight. The sharks were allowed to recover from capture stress and begin feeding prior to transport to the Monterey Bay Aquarium for public display. (Courtesy of John O'Sullivan, Monterey Bay Aquarium.)

transport, except in 2006 when the shark was fed within approximately 6 h prior to transport. The sharks were netted out of the ocean pen and placed unrestrained in a 250-L vinyl shark box with oxygenated seawater (~125% saturation) at 16ºC, with a recirculating submersible pump (4164 lph; Rule Industries, MA) to ventilate the sharks during the 30–90-min. transport via boat to the shore. The sharks were then transferred to an 11,356-L pelagic fish transport tank mounted on the trailer of a commercial tractor for the approximately 6 h duration transport to the MBA (Chapter 2, this book). Upon arrival at the MBA, except for shark #06-01, the sharks were weighed and measured (measurement was taken over the curve of the body for most animals but straight length for sharks #07-01, 08-01, and 9-01) and placed on public display in the 3.8-million-L Outer Bay exhibit. Shark #06-01 was measured over the body curve in the field on August 17, 2006.

While on display, the YOY White Sharks were offered food daily. Food items were individually weighed, tethered with cotton string to attach them to the feeding pole, and fed to the shark. This method reduced the potential of the shark biting the feeding stick or of other tank inhabitants taking food items offered to the White Sharks. If a food item was shredded and dropped, then an estimate of the weight of the food ingested was made. The mean daily ration for each week was calculated as wet weight (g) and as % BM $d^{-1}$ for each 7-d period that the sharks were on display. Food items fed to the White Shark were also sent for caloric analysis at NP Analytical Laboratories (St. Louis, MO). The energy equivalent of total food consumption was determined by the feeding rate (% BM $d^{-1}$), energy content of food type, and total duration in captivity. In addition, two dead YOY White Sharks (whole fish) that were bycatch of the commercial fishery were sent to NP Analytical Laboratories for caloric analysis to determine the energy content of White Shark tissue.

Conversion from total length over the curve of the body to straight length for the sharks was done via linear regression analysis. Straight total length and mass for the YOY White Sharks were log-transformed and plotted, allowing a linear regression analysis to determine the intercept and slope, which were used to calculate mass with the back-transformed allometric equation Mass = $a\mathrm{TL}^b$, where log ($a$) is the intercept and $b$ is the slope. Feeding data were recorded and calculated as the mean daily feeding ration for each week, both as wet weight (g) and % BM $d^{-1}$. Feeding and growth data were analyzed using Microsoft Office Excel 2003 and graphed using Sigma Plot 9.0.

Simplified energy budgets were created by using food consumption data ($C$) and calculated gain in mass ($G$) by using assumptions regarding energy loss to waste ($W$) and by solving for metabolic costs ($M$) and were described by the formula $C = G + M + W$. The total number of calories from food ingested by each shark while in captivity was used to calculate consumption ($C$). The energy invested into somatic growth ($G$) was calculated as the gain in mass converted to energetic equivalent by multiplying the mass by the caloric content of YOY White Shark tissue. Energy loss to waste such as feces and urine ($W$) was estimated to be 27% of consumption (Wetherbee and Gruber, 1993; Wetherbee and Cortes, 2004). Metabolic costs were solved as consumption minus energy loss and energy invested into growth ($M = C - (G + W)$).

## RESULTS

### Feeding Ration

After transport to the MBA, most YOY White Sharks fed within 7 d and continued feeding regularly; however, individual behavior influenced feeding in the OBE, which contained many other larger fishes. Shark #06-01 did not feed for 7 d, presumably because of being fed at the ocean pen until the day of transport. Feeding for this shark was initiated after a live California Skate (*Raja inornata*) offered as food was wounded by one of the Galapagos Sharks (*Carcharhinus galapagensis*) in the OBE. Feeding was also difficult to initiate with shark #09-01 because it swam at the bottom of the OBE for the first month in captivity. Fresh, dead Pacific Mackerel was used to initiate feeding; however, at first this shark was intimidated by the Galapagos and Scalloped Hammerhead Sharks in the exhibit. This was most likely the cause for the slower feeding rate initially for this shark. Larger Bluefin Tuna (*Thunnus orientalis*), Yellowfin Tuna (*T. albacares*), and Common Dorado (*C. hippurus*), ranging in body mass from approximately 40 to 140 kg, also posed significant challenges because of their aggressive competition for food. Feeding the relatively small YOY White Sharks in this setting necessitated surface feedings to reduce the potential of collisions with other fishes and to accurately record feeding amounts. However, within 1 month, the YOY White Sharks became the most aggressive animals in the OBE and at times would charge the other fishes if they came close to the feeding station. Sharks #04-01 and 09-01 began to chase and attack other sharks prior to release; however, feedings on other fishes were not observed by staff or recorded by cameras monitoring the OBE. The White Sharks did not feed on tunas that were fatally wounded by collisions with the exhibit window and were consumed by the other sharks. Unrecorded feedings would not have been significant enough to change the feeding rates reported in this study.

Four of the five YOY White Sharks fed within 1 d to 1 week of introduction into the OBE and fed consistently while on display, ranging from 70 to 198 d. Three sharks (#04-01, #06-01, and #07-01) showed a strong feeding preference for King Salmon (*O. tshawytscha*), which comprised 80.9–96.6% of the diet as wet weight (Table 1.1). One shark (#09-01) ate primarily Pacific Mackerel (*Scomber japonicus*; 99.1% of the diet as wet weight). Shark #04-01 had the widest diet range in addition to salmon, consisting of 13.6% whole Pacific Mackerel, 4.1% whole Albacore (*Thunnus alalunga*), and 1.4% whole Bonito (*Sarda chiliensis*). Shark #06-01 also fed on Sablefish (*A. fimbria*), comprising 14.9% of the diet as wet weight, along with a variety of other food items comprising less than 2% of the total diet. Sharks #07-01 and #09-01 had the narrowest diet range, with the

**Table 1.1** **Diet of Four Captive YOY White Sharks while on Display in the Outer Bay Exhibit at the Monterey Bay Aquarium from September 14, 2004 until November 4, 2009**

| Food Type | Shark #04-01 | Shark #06-01 | Shark #07-01 | Shark #09-01 |
|---|---|---|---|---|
| King Salmon (*Onchorynchus tshawytscha*) | 80.9% | 83.1% | 96.6% | 0.9% |
| Pacific Mackerel (*Scomber japonicus*) | 13.6% | 0.3% | 0.9% | 99.1% |
| Sablefish (*Anoplopoma fimbria*) | 0% | 14.9% | 2.5% | 0% |
| Albacore (*Thunnus alalunga*) | 4.1% | 0.8% | 0% | 0% |
| Pacific Bonito (*Sarda chiliensis*) | 1.4% | 0.2% | 0% | 0% |
| Mahi-Mahi (*Coryphaena hippurus*) | 0% | 0.1% | 0% | 0% |
| California Skate (*Raja inornata*) | 0% | 0.6% | 0% | 0% |

Food types are indicated as percentages of the diet on a wet-weight basis.

preferred food item comprising 96.6–99.1% of the diet as wet weight (King Salmon and Pacific Mackerel, respectively).

The YOY White Shark displayed in 2008 fed only once during the 11 d it was on display and was released because of concern regarding its health. This shark was feeding in the ocean pen, and upon arrival at the MBA, it navigated the OBE very well; however, this shark only fed once on approximately 400 g of salmon. While it was on display, the shark lost 2.6 kg of mass from its original body mass of 25.2 kg, or 10.3% of its body mass. Body mass loss because of starvation can be used to estimate a maintenance ration of 0.94% BM $d^{-1}$ for YOY White Sharks, which is equivalent to 405 kcal $d^{-1}$. This shark was transported back to the Southern California Bight, where it was tagged with a PSAT and released. Data from the PSAT showed that this shark survived for at least 30 d after release, at which time the PSAT separated from the shark and began reporting data of the shark's movements.

Mean daily ration for each week as wet weight (g) showed an oscillating pattern with feeding peaks and troughs that generally diminished over the time the four sharks were on display (Figure 1.3). Mean daily ration for each week ranged from a low of 0 g for the first week of shark #06-01 to a high of 1718.6 g, also for shark #06-01 (Figure 1.3). The grand mean daily ration for all four sharks was 747 ± 46 g $d^{-1}$. A period of approximately 3–8 weeks corresponded to a single cycle of feeding peak and decline, with larger differences in feeding peaks and troughs tending toward longer cycles as seen with shark #06-01. Observations showed that total evacuation time after the first feeding (on salmon fillet) for shark #04-01 was approximately 36 h. After 15–23 weeks in captivity, there was a large decrease in the oscillations in feeding ration for sharks #04-01, 06-01, and 07-01. Shark #09-01 was released after approximately 10 weeks because of predatory behavior in the exhibit and did not follow the general feeding pattern of the other sharks.

The mean daily ration for each week as % BM $d^{-1}$ for three of the four White Sharks (#04-01, #06-01, and #07-01) showed a significant decreasing trend over the period that they were on display (Figure 1.4). Mean daily ration for each week for the three sharks ranged between a low of 0.2% BM $d^{-1}$ once the sharks began to feed to a high of 3.5% BM $d^{-1}$. The decreasing trend in mean daily ration as % BM $d^{-1}$ was similar for all three sharks, and the slopes for the linear regressions were statistically significant ($p < 0.0013$). Mean daily rations during the time on display for sharks #04-01, #06-01, and #07-01 were 1.68 ± 0.11, 1.32 ± 0.10, and 1.46 ± 0.10% BM $d^{-1}$, respectively.

White shark #09-01 had a different swimming and feeding pattern, spending most of the time near the bottom of the exhibit, which made feeding attempts much more difficult because of

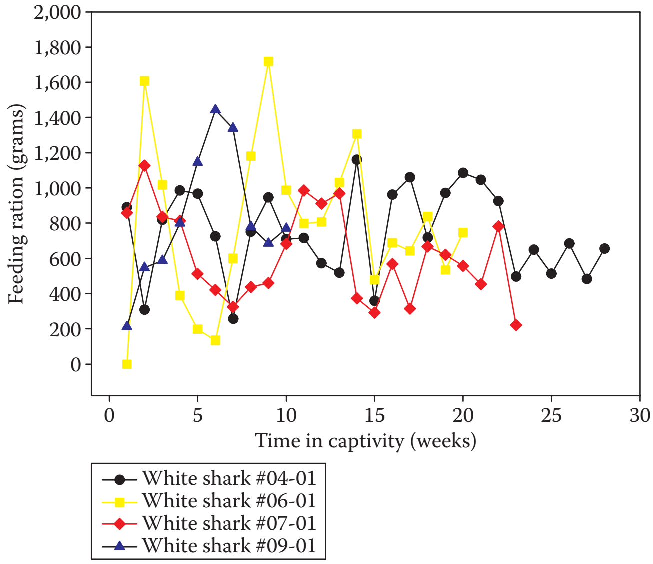


**Figure 1.3** Feeding ration as wet weight of food (grams) for four captive YOY White Sharks displayed at the MBA from September 14, 2004 until November 4, 2009.

competition from the other fishes. The feeding pattern for shark #09-01 showed a slowly increasing mean daily ration for each week until reaching a peak (3.5% BM $d^{-1}$) at week 6 and then decreasing until release at week 10 on display. Mean daily ration for shark #09-01 was somewhat higher than for the three other sharks at 2.03 ± 0.16% BM $d^{-1}$. The grand mean daily ration for each week for all four sharks was 1.62 ± 0.15% BM $d^{-1}$.

The energy equivalent of food consumption showed a general pattern of highest total consumption and mean daily consumption for the entire time on display (kcal $d^{-1}$) for YOY White Sharks

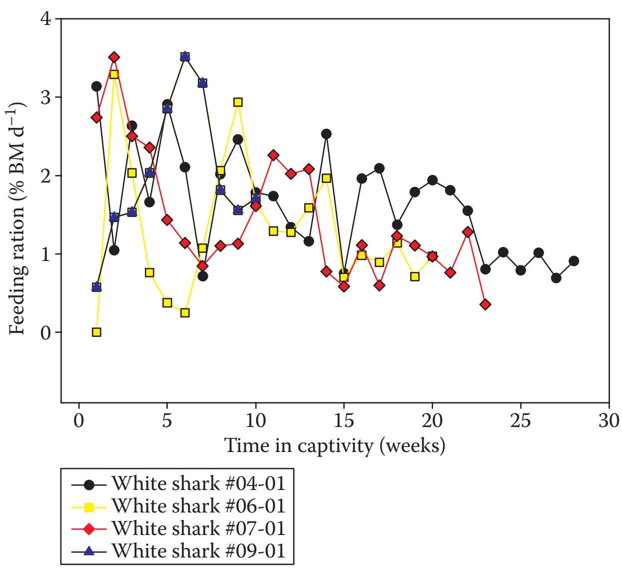


**Figure 1.4** Feeding ration as % BM $d^{-1}$ for four captive YOY White Sharks displayed at the MBA from September 14, 2004 until November 4, 2009.

**Table 1.2 Total Length and Body Mass upon Introduction to the Outer Bay Exhibit and upon Release of Five Captive YOY White Sharks Displayed at the Monterey Bay Aquarium**

| White Shark Number | Duration in Captivity (d) | Initial/Final Total Length (m) | Initial/ Final Body Mass (kg) | Growth in Length (cm yrs.$^{-1}$) | Growth in Mass (kg yrs.$^{-1}$) | $K_1$ Wet Weight (%) | $K_1$ Energetic Equivalent (%) |
|---|---|---|---|---|---|---|---|
| #04-01 | 198 | 1.41/1.84 | 28.0/73.4 | 80.8 | 83.7 | 30.9 | 29.7 |
| #06-01 | 138 | 1.64/1.87 | 47.0/77.6 | 56.3 | 80.9 | 28.2 | 26.1 |
| #07-01 | 161 | 1.43/1.76 | 30.6 /63.6 | 76.2 | 74.8 | 33.3 | 31.4 |
| #08-01 | 11 | 1.37/1.37 | 25.2/22.6 | 0 | –86.3 | — | — |
| #09-01 | 70 | 1.57/1.66 | 36.2/45.4 | 45.2 | 48.0 | 16.0 | 24.3 |

The table notes the total length (meters) and body mass (kilograms) upon introduction to the Outer Bay exhibit and upon release of five captive YOY White Sharks displayed at the Monterey Bay Aquarium. Duration in captivity (d), growth in total length (cm yrs.$^{-1}$) and body mass (kg yrs.$^{-1}$), and gross conversion efficiency ($K_1$) on a wet-weight and energetic-equivalent basis are also listed. Dashes for gross conversion efficiency of White Shark #08-01 indicate weight loss (–86.3 kg yrs.$^{-1}$) rather than growth.

#04-01, #06-01, and #07-01, and lowest for shark #09-01. Sharks #04-01, #06-01, and #07-01 fed at a relatively high rate (1.32–1.68% BM d$^{-1}$) on energetically dense foods (energy content: Black Cod > King Salmon > Albacore > Pacific Mackerel) (Table 1.1). Mean daily food consumption for the entire time in captivity was greatest for the sharks #04-01 and #06-01 and decreased for sharks #07-01 and 09-01; mean daily food consumption values were 1329.9 ± 72.5, 1470.2 ± 106.6, 1119.5 ± 71.4, and 940.3 ± 85.2 kcal d$^{-1}$, respectively. Shark #09-01 fed at a higher rate (2.03% BM d$^{-1}$) but on energetically less dense Pacific Mackerel because of a feeding preference, and this shark was on display (70 d) less than half the time as the other sharks (Table 1.2).

Predatory behavior was observed in two of the five YOY White Sharks while on display in the OBE. During the final 5 weeks on display, shark #04-01 fatally attacked two Soupfin Sharks (*Galeorhinus galeus*), consuming the caudal fin and caudal peduncle of one of the Soupfin Sharks. However, this feeding was not included in this study because the estimated weight of this meal was less than 1 kg and amounted to less than 1% of the diet on a wet-weight basis. This shark was also observed chasing Scalloped Hammerhead Sharks and Galapagos Sharks prior to being released. White shark #09-01 was also observed chasing Scalloped Hammerhead Sharks and attacked a male Galapagos Shark, which prompted MBA staff to release this shark. No other predatory behavior of White Sharks was observed by MBA staff or verified by security cameras mounted in the exhibit that recorded constantly to a digital video recorder.

## Captive Growth

The YOY White Sharks on display in the OBE grew in length at twice the calculated growth for YOY White Sharks in the wild. Shark #04-01 was on display the longest (198 d) and grew at the fastest rate (80.8 cm yrs.$^{-1}$; Table 1.2). Both sharks #06-01 and 07-01 were held for a shorter durations (138 and 161 d, respectively) and grew at slightly slower rates (56.3 and 77.1 cm yrs.$^{-1}$, respectively). Shark #09-01 was on display only 70 d and grew at the slowest rate (45.2 cm yrs.$^{-1}$). Mean growth for all four sharks was 64.9 ± 8.5 cm yrs.$^{-1}$, which is almost twice the calculated first-year growth rate for White Sharks in the wild (35 cm yrs.$^{-1}$; Cailliet et al., 1985).

Growth in body mass followed the expected general pattern of highest growth for the sharks that had the highest total food consumption (kcal d$^{-1}$) while on display. Shark #04-01 had the highest annual growth in mass (83.7 kg yrs.$^{-1}$) and had the highest total food consumption (261,979 kcal), followed by shark #06-01 (80.9 kg yrs.$^{-1}$ and 201,410 kcal). Shark #07-01 grew at a slightly slower rate (74.8 kg yrs.$^{-1}$ and 180,232 kcal), and shark #09-01 grew most slowly and consumed the lowest amount of calories while on display (48.0 kg yrs.$^{-1}$ and 64,882 kcal). Mean

**Table 1.3** **Simplified Energy Budgets of Four Captive YOY White Sharks at the Monterey Bay Aquarium**

| White Shark Number | Consumption (*C*) (kcal) | Growth (*G*) (kcal) | Metabolism (*M*) (kcal) | Energy Budget $C = G + M + W$ |
|---|---|---|---|---|
| #04-01 | 261,980 | 77,861 | 113,384 | 100 = 29.7 + 43.3 + 27 |
| #06-01 | 201,411 | 52,479 | 94,551 | 100 = 26.1 + 46.9 + 27 |
| #07-01 | 180,232 | 56,595 | 74,974 | 100 = 31.4 + 41.6 + 27 |
| #09-01 | 64,883 | 15,778 | 31,586 | 100 = 24.3 + 48.7 + 27 |
| | | | | **Mean:** 100 = 27.9 + 45.1 + 27 |

The table shows the simplified energy budgets of four captive YOY White Sharks at the Monterey Bay Aquarium as described by the equation $C = G + M + W$, where $C$ = consumption, $G$ = energy investment into somatic growth, $M$ = metabolic costs, and $W$ = energy loss to waste, which is set at 27% of $C$. $C$ is based on the energetic equivalent (kcal) of total feedings for each shark, $G$ is based on growth in mass for each shark converted to energetic equivalent (kcal) by using the conversion factor of 1,715 kcal $kg^{-1}$ as determined from caloric analysis of two YOY White Sharks. $M$ was determined by solving the simplified energy budget equation.

growth in mass for all four sharks was 71.6 ± 8.2 kg $yrs.^{-1}$ Gross conversion efficiency ($K_1$) on a wet-weight basis was lowest for shark #09-01 (16.0%) and much higher for sharks #04-01, #06-01, and #07-01 (30.9, 28.2, and 33.3%, respectively; Table 1.3). Mean $K_1$ on a wet-weight basis for all four sharks was 27.1 ± 3.8%. $K_1$ on an energy-equivalent basis was slightly lower than $K_1$ on a wet-weight basis but showed high agreement to the general pattern of $K_1$ for all four sharks. The largest difference between the two $K_1$ values (8%) was for shark #09-01. This shark had a higher $K_1$ (24.3%) on an energy-equivalent basis because of the lower caloric value of its primary food item, Pacific Mackerel.

Mass in relation to TL was very similar for sharks #04-01, #06-01, and #07-01 and was described by the allometric equation $M = a\mathrm{TL}^b$. Sharks #04-01, #06-01, and #07-01 had very similar $a$ and $b$ values ($a$ = 8.34, 7.37, and 8.42, respectively; and $b$ = 3.55, 3.74, and 3.47, respectively). However, growth was much lower for shark #09-01, and the $a$ and $b$ values for the allometric equation describing total length and mass were somewhat different ($a$ = 5.25 and $b$ = 4.26).

### Energy Budgets

Simplified energy budgets for the YOY White Sharks showed a general pattern of the greatest energy expenditure from metabolic costs ($M$) and large energy investment into somatic growth ($G$) while the sharks were on display (Table 1.3). Energy loss to waste ($W$) was held constant (27% of $C$), and the amount of energy invested into metabolic costs as a proportion of $C$ ranged from 41.6 to 48.7% of $C$. The mean consumption rate for all four White Sharks was 1215.0 ± 116.5 kcal $d^{-1}$. The energetic content of the two YOY White Sharks was determined to be 1.715 kcal $g^{-1}$ of tissue. This value was multiplied by the gain in body mass for each shark while they were on display to determine the energy investment into $G$, which ranged between 24.3 and 29.7% of $C$. A mean energy budget for all four sharks while in captivity was described by the following equation:

$$C = G + M + W{:}100 = 27.9\% \ (\pm 1.6) + 45.1\% \ (\pm 1.6) + 27\% \qquad (1.1)$$

## DISCUSSION

The peak in mean daily ration recorded for the White Sharks in this study were similar to those reported for active pelagic sharks (Salini et al., 1999; Bush and Holland, 2002) but were slightly lower than the daily ration calculated for the Shortfin Mako Shark (*Isurus oxyrinchus*; Wood et al., 2009). Daily rations reported for juveniles of three species of carcharhinid sharks (2.9–3.44% BM $d^{-1}$ for *Carcharhinus dussumieri*, *C. tilstoni*, and *Negaprion acutidens*; Salini et al., 1999) were similar to the initial peaks in mean daily ration of YOY White Sharks in our study (3.1–3.5% BM $d^{-1}$). However, the feeding experiments done by Salini et al. (1999) were of very short duration (10 d) and therefore do not give any indication of the range in daily ration over time in captivity for these species. The highest daily ration calculated for an ectothermic, obligate ram-ventilating shark is for the Scalloped Hammerhead Shark (3.54% BM $d^{-1}$; Bush and Holland, 2002), which is also similar to the peak in mean daily ration in our study. The peak in mean daily ration of the White Sharks in our study is lower than the daily ration calculated for the Shortfin Mako Shark (4.6% BM $d^{-1}$; Wood et al., 2009); however, the daily ration in that study was estimated by calculating the energetic needs of the Shortfin Mako Shark and then calculating the amount of food needed to satisfy those energetic needs. The dominant food item in the diet of Shortfin Mako Sharks in the northeast Atlantic ocean as determined by gut content analysis is Bluefish (*Pomatomus saltatrix*), which is 63% lower in energy content (4,800 kJ $kg^{-1}$) compared with the preferred food for White Sharks in our study, King Salmon (7,536 kJ $kg^{-1}$). If the main prey item of Shortfin Mako Sharks had been more energetically dense, then the estimate of daily ration for the Shortfin Mako Shark would have been lower. Indeed, shark #09-01 fed on the least energetically dense food item (99% Pacific Mackerel by weight, 4,312 kJ $kg^{-1}$), and of all the White Sharks in our study, it fed at the highest daily ration for the entire period it was on display (mean = 2.03% BM $d^{-1}$).

Captive growth of the YOY White Sharks in our study support the assertion by Van Dykhuizen and Mollet (1992) that captive growth may be higher than growth in the wild by factors of two to three. We report a mean growth rate of captive YOY White Sharks ($64.9 \pm 8.5$ cm $yrs.^{-1}$) that is twice the first-year growth calculated from a von Bertalanffy growth function for this species (35 cm $yrs.^{-1}$; Cailliet et al., 1985). In addition, a YOY White Shark tagged and released as part of MBA's field research program in Southern California was recaptured 405 d later, yielding a growth rate of 33.4 cm $yrs.^{-1}$ (C. G. Lowe, personal observation). This observed growth rate is in close agreement with the growth rate for a YOY White Shark calculated using the von Bertalanffy growth function from Cailliet et al. (1985), and it further supports that our captive growth rate is approximately twice that of growth in the wild. We also report a mean growth rate in mass ($71.6 \pm 8.2$ kg $yrs.^{-1}$) that is up to three times greater than the calculated rate (23 kg $yrs.^{-1}$) for first-year growth using the von Bertalanffy growth function (Cailliet et al., 1985) and allometric equations for TL and mass for White Sharks from Mollet and Cailliet (1996). Growth of sharks in captivity can be variable and depends on a variety of factors, with feeding ration thought to be a main determinant (Taylor and Wisner, 1989). In addition, lamnid sharks in the wild have high growth rates in the first year of life (39 cm $yrs.^{-1}$ for Shortfin Mako Sharks in New Zealand waters; Bishop et al., 2006), and a diet of energy-rich salmonids has been correlated with faster growth in lamnid sharks (Goldman and Musick, 2003). Many studies of growth in captivity report faster growth for species such as the Sandbar Shark (*Carcharhinus plumbeus*), Bull Shark (*Carcharhinus leucas*), Lemon Shark (*Negaprion brevirostris*), and Scalloped Hammerhead Shark (reviewed in Mohan et al., 2004); however, studies on the Sevengill Shark (*Notorynchus cepedianus*; Van Dykhuizen and Mollet, 1992) and the Sand Tiger Shark (*Carcharias taurus*; Govender et al., 1991) have reported growth in captivity that may be similar to growth in the wild. For this reason, caution should be used when citing growth rates in captivity. However, these captive growth studies can add to our understanding of the biology of elasmobranchs that are difficult to acquire or need large enclosures for a captive environment, such as the White Shark (Mollet et al., 2002; Cailliet and Goldman, 2004; Mohan et al., 2004).

Mean gross conversion efficiency ($K_1$) on a wet-weight basis for captive YOY White Sharks ($27.1\% \pm 3.8$) was similar to reported values for sharks in the first year of life. Van Dykhuizen and Mollet (1992) reported $K_1$ values of 25–40% for captive Sevengill Sharks (*Notorynchus cepedianus*) in the first year of life. $K_1$ values of 10–25% have also been reported for other elasmobranchs and teleosts (Wetherbee and Cortes, 2004). In addition, we report $K_1$ as energetic equivalents, which show very good agreement with $K_1$ on a wet-weight basis for three of the four captive White Sharks (#04-01, #06-01, and #07-01). The largest difference in $K_1$ values (wet weight versus energetic equivalents) was for shark #09-01, which fed almost entirely on Pacific Mackerel, which was lower in caloric value to the main food item of the other sharks, King Salmon. $K_1$ values also decrease with increasing age and are affected by the level of consumption (Wetherbee and Cortes, 2004). Endothermy in lamnid sharks has been theorized to speed up digestive processes, shortening the time for gastric evacuation and enhancing food intake (Cortes and Gruber, 1990: Carlson et al., 2004). Total evacuation time (36 h) observed for White Sharks in this study is faster than the values reported for gastric evacuation for ectothermic sharks (Wetherbee and Cortes, 2004), and peak daily feeding ration and $K_1$ are among some of the highest reported for any shark species to date.

The simplified energy budgets constructed for captive YOY White Sharks at the MBA reflect a high investment into somatic growth (mean ± SE = 27.9% ± 1.6). The energetic content of YOY White Shark tissue as determined by caloric analysis yielded a value (7.18 kJ $g^{-1}$) that is slightly higher than those reported to date for the Lemon Shark (5.41 kJ $g^{-1}$; Cortes and Gruber, 1990), the Scalloped Hammerhead Shark (6.07 kJ $g^{-1}$; Lowe, 2002), or the Shortfin Mako Shark (5.56 kJ $g^{-1}$; Wood et al., 2009). These differences in energy content of shark tissue may be the result of interspecific differences in the relative abundance of tissues with different caloric content (i.e., liver mass). Another possibility is that the differences are due to the methods used to determine energy content, which is why we chose to send whole specimens to be homogenized and sampled. Investment into somatic growth as high as 24.3–31.4% of consumption are most likely the result of higher growth rates caused by the high growth capacity of YOY sharks compared with mature animals, such as the Bull Shark studied in captivity ($G$ = 7%; Schmid and Murru, 1994). Higher growth rates and potentially lower metabolic costs because of captive conditions are also presumably the cause for greater investment into $G$.

The largest and most variable component of an energy budget is the energy invested into metabolic costs (Lowe, 2002), which ranged for White Sharks from 41.6 to 48.7% of $C$ (mean ± SE = 45.1% ± 1.6). The shark that did not feed (#08-01) incurred a body mass loss that was 0.94% BM $d^{-1}$; this is equivalent to 405 kcal $d^{-1}$, or 33% of the mean consumption for all sharks (1215 kcal $d^{-1}$). This estimate of metabolic costs is similar to our estimate from the energy budget, especially when taking into account the added energy consumption because of specific dynamic action for the feeding sharks. Our estimate of metabolic costs for White Sharks in this study is also quite similar to the metabolic costs (44.9% of $C$) reported from an energy budget for captive Pelagic Stingrays (*Dasyatis violacea*; Ezcurra, 2001). However, caution should be used when comparing the metabolic costs determined from an energetics model derived for captive elasmobranchs with those reported from the more common indirect calorimetry method because of the many differences between the two methods. Schmid and Murru (1994) also reported lower estimates of $M$ for the Bull Shark from a bioenergetics approach compared with reported metabolic rates for carcharhinid sharks derived from the method of indirect calorimetry.

Our estimates of metabolic costs in a captive setting may be useful as a starting point toward better understanding of the energetic demands of YOY White Sharks in the wild. Migratory patterns of YOY White Sharks in the wild include large-scale horizontal (thousands of kilometers) and vertical movements (hundreds of meters) (Dewar et al., 2004; Weng et al., 2007), which would be much more energetically costly than the activity levels of captive White Sharks. A bioenergetics study of wild White Sharks similar to the one reported for another lamnid shark, the Shortfin Mako (Wood et al., 2009), may now be possible. Energy investment into growth may be estimated with existing information on growth in the wild (Cailliet et al., 1985), and determining the metabolic costs for YOY White Sharks in the wild is now possible because of technological advances in the field of physiological telemetry (Lowe and Goldman, 2001). This step is crucial to a better understanding of daily ration and energetic demands of this top-level predator.

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