Aust. J. Mar. Freshwater Res., 1992, **43**, 297–318

Growth, Age Estimation and Feeding of Captive Sevengill Sharks, *Notorynchus cepedianus*, at the Monterey Bay Aquarium

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Abstract

Five methods, all based on the von Bertalanffy growth function (VBGF) model, were used with captive sevengills to characterize growth and to estimate both age and age at sexual maturity. Fabens' method (M1) gave a high $k = 0{\cdot}25 \pm 0{\cdot}04$ year^{-1} and a low $L_\infty = 202 \pm 13$ cm and $W_\infty = 41 \pm 11$ kg. Determination of the third VBGF parameter, L_0 or W_0, requires age to be known.

Reported estimates of size at birth were used to estimate ages of individual sharks. For the 'individual VBGF fit' method (M2), the age axis was fixed by using size at birth. For the 'derivative' method (M3), a growth rate was calculated from observed size when the sharks were received and size at birth. The results of either method confirmed that two sharks were first-year class and three sharks were second-year class when they were received. Both M2 and M3 required the use of a combination of total length (TL) and weight data via the 'TL-scaled cube root weight' method (M4) to obtain adequate statistics for individual sharks.

The 'exponential regression' method (M5) was used to predict the sizes and ages of larger and older sharks. Age at sexual maturity for males was estimated by using $L_\infty = 225$–250 cm and $k = 0{\cdot}174$ to $0{\cdot}132$ year^{-1}, which gave 4·3 to 5 years, in good agreement with the age estimated from clasper-length measurements from a single male. Age at sexual maturity for females was estimated by using $L_\infty = 275$–300 cm and $k = 0{\cdot}107$ to $0{\cdot}090$ year^{-1}, which gave 11–21 years.

Feeding habits have been monitored for captive sevengill sharks since 1985. Pups consumed up to 2% of their body weight (BW) per day, juveniles about 0·6% BW day^{-1}, and adults about 0·2% BW day^{-1}. Food consumption and, more importantly, total efficiency changed with age. The observed large food consumption and the observed high total efficiency of pups could be substantiated on the basis of a theoretical calculation of food intake based on von Bertalanffy growth. Adult sevengills showed a 'feast or famine' feeding pattern that followed a cycle of 5–7 days and that may have been influenced by water temperature and previous meal size.

We conclude that growth rates in captivity and in the field are similar, based on the available growth data and feeding behaviour of sevengills in captivity and in the field.

Introduction

Because of the recent increased interest in elasmobranchs as commercial resources, researchers have realized the need for life-history information to formulate management programmes. In addition to field studies, research performed on elasmobranchs under controlled conditions can help to provide such information.

Several investigators have contributed work on the age, growth and feeding of captive elasmobranchs (Wass 1973; Medved 1985; Branstetter 1987; Wetherbee *et al.* 1987; Taylor and Wisner 1989; Carrier and Luer 1990; Cortes and Gruber 1990; Natanson and Cailliet 1990; Schmid *et al.* 1990; West and Carter 1990). These studies serve as comparisons to field data in addition to providing fundamental information for the successful husbandry of captive elasmobranchs.

0067-1940/92/010297$10.00

Ebert (1986, 1989*a*, 1989*b*) has investigated the life-history characteristics of the sevengill shark, *Notorynchus cepedianus*, off California, Namibia and South Africa. Sevengills are found predominantly in shallow temperate to warm temperate waters throughout the South Atlantic, Pacific and Indian Oceans. They are most abundant where the water temperature is between 12 and 18°C in areas with upwelling and high productivity. In the eastern North Pacific, sevengills range from south-eastern Alaska to the Gulf of California but are sporadic south of San Francisco Bay.

Little is known about the age, growth and age at sexual maturity of sevengill sharks. Elasmobranchs have been aged from growth zones in vertebral centra by several methods (Cailliet *et al.* 1983, 1986). However, Ebert (1989*a*) reported that none of the methods involving vertebrae was successful because sevengill sharks do not have well calcified vertebrae. Tag–recapture experiments in Humboldt Bay (1978) and South Africa (1985–89) had a very low success rate and produced a single nonzero growth-rate data point from a juvenile of unknown sex (Ebert, personal communication). Ebert (1989*b*) found that male sevengills with total lengths of more than 153 cm were sexually mature and that females with total lengths between 218 and 244 cm were considered to be entering their first breeding season, but the corresponding ages were unknown.

Sevengills in northern California were reported to feed both on cartilaginous fishes, predominantly bat rays, *Myliobatis californica*, and brown smoothhounds, *Mustelus henlei*, and on bony fishes (Ebert 1989*a*). Ebert (personal communication) observed a 'feast or famine' type of feeding pattern in the field that peaked every 10–14 days for adults. Rupp (1984) observed that captive sevengills at the Point Defiance Aquarium and Zoo were selective feeders and that they followed a feeding cycle of 3–5 days.

No studies of growth, age determination and daily ration have been published for sevengills. We have kept sevengills alive in the Monterey Bay Habitats Exhibit of the Monterey Bay Aquarium since 1984. In an attempt to add to knowledge about the sevengill shark, the present study was designed to investigate the growth and feeding of captive sevengill sharks.

Materials and Methods

Collection and Transport of Captives

The Steinhart Aquarium donated three juveniles (J1–J3) in October 1985 and two pups (J4 and J5) in September 1987, all collected from San Francisco Bay. Adult sevengills were collected by hook and line in Humboldt Bay in northern California and transported by truck to the Monterey Bay Aquarium. Four adult males (A1–A4) were selected as subjects for the study. Adult male A1 was collected in 1984 and was part of the study through 1990; the other adult males were collected in 1985 but were released in 1986. Detailed descriptions of the capture and transport of sevengill sharks are given by Rupp (1984).

Environment of Captives

Sevengill sharks were housed in a 1·25 ML semi-open system with a modified hourglass shape. The tank was 27·5 m long, 12·2 m wide, and from 4·2 to 5·2 m deep. Several artificial rocky reefs lined the walls and the bottom of the exhibit. The Monterey Bay Habitats Exhibit (MBHE) is a multi-species exhibit representing the local fish fauna of Monterey Bay.

Filtered and unfiltered sea water from Monterey Bay was pumped into the exhibit, with a turnover time of approximately 90 min. Water temperature in the MBHE was measured on a weekly basis, and monthly means were calculated. A photoperiod of 12–14 h light and 12–10 h dark was maintained throughout the study period.

Growth Measurements

Length and weight measurements were taken for the three juveniles (two female, one male) beginning in October 1985 and for the two pups (both female) beginning in September 1987, continuing through 1990. Quarterly measurements were initially planned, but unfortunately sampling did not always follow this schedule. Length and weight were recorded for the adult males when received and prior to release.

Sharks were removed from the MBHE into a holding tank where total length (TL), precaudal length (PCL), predorsal length (PDL) and girth (G) at the pectoral axil (Castro 1983, p. 4) were measured to the nearest centimetre. The inner clasper length (CL) was measured on the single juvenile male shark. Sharks were then moved onto a stretcher and weighed on a suspended spring scale to the nearest 0·5 kg. The stretcher weight was subtracted from the total to determine the actual shark weight (W).

The TL, PCL and PDL measurements were taken 'on the contour' and are not the more standard 'straight line' measurements that would have required anaesthesia. We are not aware of any attempts to correlate these two types of length measurements for other sharks. For the sevengill shark, the conversion factor is 0·961 and was the same for trunk and tail (unpublished data). In this paper, we use the contour measurements and convert reported straight-line measurements if required for comparison purposes.

Morphological Calculations

A linear regression was used to fit the PDL–TL and PCL–TL data. A power regression was used to fit the W–TL data ($y = \ln W$, $x = \ln TL$). They were calculated by using the geometrical-mean (GM) regression given by Ricker (1975). A functional regression line is more suitable than an ordinary regression line because either variable can be selected as the independent variable since the relative accuracy in measuring the variables is about the same for all variable-pairs listed (Ricker 1973). The GM regressions were calculated from the ordinary regression results obtained by the MGLH module of SYSTAT (Wilkinson 1988*a*), using the following formulae: slope $b(\mathrm{GM}) = b(\mathrm{MGLH})/R$, intercept $a(\mathrm{GM}) = \bar{y} - b(\mathrm{GM})\bar{x}$. The results of the ordinary regression as obtained by SYGRAPH (Wilkinson 1988*b*) were plotted, and the results of the GM regression were included as text in the figure (SYGRAPH does not provide for plotting of the GM regression and the associated confidence band). For comparison purposes, a power curve was fitted to the data for one male and four female sharks separately.

Growth Analysis

Length and weight were plotted against time (t, years) for young and adult sevengill sharks. Although adult sevengills were included in this plot, the growth analysis addresses only the young sevengills. In all, 53 data points (providing 48 measurements of length-based growth rate and 48 measurements of weight-based growth rate) were collected over a period of 1771 days (about 5 years) and 1073 days (about 3 years) for juveniles J1–J3 and pups J4 and J5, respectively.

A total of five methods, all based on the von Bertalanffy model, were used to analyse the data. The first method, named 'M1, (standard) Fabens' method', was used for the initial growth analysis, with the von Bertalanffy growth function (VBGF) being expressed in the form (Fabens 1965) $L(t) = L_\infty(1 - be^{-kt}) = L_\infty - (L_\infty - L_0)e^{-kt}$, $b = (L_\infty - L_0)/L_\infty = e^{kt_0}$. Only two of the three parameters (L_∞ and k) can be calculated if just growth data (analogous to tag–recapture data) are available. The calculation of the third parameter (L_0) requires a known age. The VBGF using L_0 (y-axis intercept) rather than t_0 (x-axis intercept) is proposed to be more suitable for sharks that are born with a well defined length (L_0). If needed for comparison purposes, t_0 can be calculated from the other parameters. Initial VBGF fits were carried out by using the FABGROW module of FSAS (Saila *et al.* 1988). However, this program does not calculate the asymptotic standard error of the fitting parameters. Thus, the von Bertalanffy calculations were continued by using the NONLIN module of SYSTAT (Wilkinson 1988*a*). This is a more general program suitable for any nonlinear model, and Fabens' equation was used as the fitting equation.

Age Determination

A complete analysis of the growth data required an age estimate for the juvenile sharks. Two graphical methods were developed to determine the age of an individual shark (at the time it was received), based on the growth data taken during captivity after the shark was received. In one method, named 'M2, individual VBGF method', the VBGF obtained from the growth data (using Fabens' method) was fixed with respect to the age axis ($=x$-axis), using the estimated birth TL = 35–45 cm (Ebert 1989*b*). The intersection of the VBGF with the line defined by the observed TL of the shark when received yields the age at that time.

The other method, named 'M3, (individual) derivative method', is based on a plot of instantaneous growth rate (= slope = derivative) versus length; i.e. $L'(L) = dL/dt = kL_\infty - kL$. As the best approximation to this growth-rate plot, the observed (annualized) growth rates were plotted at $L_{\mathrm{average}} =$

$(L_{initial} + L_{final})/2$. The shorter the period between growth measurements (corresponding to 'at-large times'), the better the approximation. If the length at birth is known, an additional growth rate can be calculated by $(L_{when\ received} - L_0)$/assumed age and plotted at $L_{average} = (L_{when\ received} + L_0)/2$. A comparison of this calculated growth rate with the regression line obtained from the data collected after the shark was received allows determination of the shark's age. The calculated growth rate will fall on the regression line once the assumed age agrees with the 'true' age. The ordinary regression was used instead of a GM regression because the error associated with the difference of two TL measurements is much larger than the error associated with the sum of two TL measurements.

Combination of Length and Scaled Cube-root-weight Data

The age determinations described above require individual growth curves rather than an average growth curve because individual sharks of the same length can represent several year classes (Ricker 1975). For individual sharks, the number of TL data was insufficient to yield statistically significant values of VBGF parameters at the 95% confidence interval. To improve the statistics, TL and scaled cube-root-weight (CRW) data from an individual shark were combined for the purpose of calculating VBGF parameters. To scale the CRW data, the mean TL/CRW ratio was used. The fourth method, an ancillary method used in age determination, was named 'M4, TL-scaled CRW method'. Ebert (1989*b*) reported updated birth weights of 0·2–0·3 kg for sevengills. We used the range 0·140–0·323 kg in order to have a birth-size data set consistent with the calculated W versus TL GM power regression. The above description of Methods M2 and M3 was simplified by stating just the L_0 range, but in fact an average of L_0 range and scaled CRW_0 range was used. This method is justified because the differential equation used by von Bertalanffy was based on W, but the method has limitations because TL instead of PCL was used as the length parameter (unpublished data).

Exponential Regression and Age at Sexual Maturity

The fifth method, named 'M5, exponential regression method', allowed determination of age at sexual maturity. A VBGF in the form $y(t) = L_\infty - L(t) = (L_\infty - L_0)e^{-kt}$ is suitable for an exponential regression of $L_\infty - L(t)$ on t (i.e. estimated age). This requires L_∞ to be known or to be treated as an input parameter. The results of the regression are slope $= k$ and y-axis intercept $= \ln(L_\infty - L_0)$. L_0 can then be calculated from the latter expression by using the chosen value for L_∞. The results of exponential regression for different values of L_∞ can be shown on the same plot, for illustrative purposes, if we plot length versus age rather than $\ln[L_\infty - L(t)]$ versus age.

Selecting appropriate values for L_∞ (ideally by using observed average maximum TL values) guarantees a good fit for large TL and W values (often a region without experimental data) and allows extrapolation into this region. We used $L_\infty = 225$–250 cm for males and $L_\infty = 275$–300 cm for females to determine age at sexual maturity for sevengills. Because TL estimates at sexual maturity were based on straight-line measurements (Ebert 1989*a*, 1989*b*) and our TL measurements were contour measurements, Ebert's TL estimates were converted to a range to allow for this. For the actual graphical determination, it was more convenient to use an inverted M5 VBGF; i.e. age = age (TL) instead of the usual TL = TL (age).

Feeding

Sharks were offered a diet consisting of salmon, *Oncorhynchus* sp.; Pacific mackerel, *Scomber japonicus*; rockfish, *Sebastes*; and herring, *Clupea pallasii*. Food items were supplemented with multivitamins and weighed to the nearest 10 g. Sharks were fed twice a week for the majority of the study except for a 2-year period from June 1986 to May 1988, when they were fed once a week. Sharks were offered food by using 3-m-long bamboo poles fitted with an attachment clip at the end. Once a sevengill removed food from the pole, that individual was observed to determine if the food item was consumed.

Food intake was recorded for each individual and converted to percentage of body weight per day (% BW day^{-1}). Body weight was determined by linear extrapolation between W measurements. Mean values of annual food consumption, with standard deviations, were calculated for six sharks (one adult male, three juveniles and two pups) from October 1985 to December 1990.

Monthly averages of food intake (% BW day^{-1}) were plotted versus estimated age of the shark. A distance-weighted, least-squares-smoothing curve was drawn to sort out trends in the data (Wilkinson 1988*b*). The smoothing curve was compared with the calculated food intake (based on the von Bertalanffy growth model, using appropriate values for L_∞, L_0 and k) and with appropriate efficiency values by

the formula $I = [(dW/dt)/W](100/365)(1/E_{pg}) + \varkappa(100/365)(1/E_{pm})$, where I is the food intake (% BW day^{-1}), $(dW/dt)/W$ is the fractional growth rate (year^{-1}) based on the von Bertalanffy model, 100/365 is the time fraction (% year day^{-1}), $\varkappa(=3k)$ is the catabolic constant (tissue breakdown) (year^{-1}) of the von Bertalanffy model, E_{pg} is the partial growth efficiency ($=G/(I-M)$, where G is the growth, I is the food intake, and M is the maintenance ration; Warren and Davis 1967), and E_{pm} is the partial maintenance efficiency ($=L_p/I_p$, where L_p is the tissue loss prevented and I_p is the part of the ration preventing the loss; Warren and Davis 1967).

This formula is based on the concept that total food intake must be the sum of food converted to growth and food required for maintenance (to prevent tissue breakdown), with each term then being divided by the corresponding efficiency factor. The assumptions are that the caloric values of all of the food items are equal and that the MBHE temperature is constant. Total food intake as a function of age is readily calculated if we also assume that partial growth efficiency (E_{pg}) and partial maintenance efficiency (E_{pm}) are age-independent. The formula was used only to explore the anticipated food intake of a shark pup immediately after birth (near age 0). Therefore, we forced the theoretical curves to agree with the observed food intake for large values of t by setting the second term, $\varkappa/E_{pm}$, equal to the observed food intake of 0·2% BW day^{-1} for adult males. The first term, $(dW/dt)/(WE_{pg})$, was calculated by using $W_\infty = 180$ kg, $W_0 = 0{\cdot}323$ kg, $k = 0{\cdot}1$–$0{\cdot}4$ year^{-1}, and a variable E_{pg} between 0·1 and 0·4.

We were cautious to distinguish between observed cumulative total efficiency (yielding an approximate measure of total efficiency, E_T) and the not-directly-observable partial growth efficiency (E_{pg}) in the formula for food intake versus age based on the von Bertalanffy model. In general, we have $E_{pg} = G/(I-M) > E_T = G/I$, but for pups we can assume that $E_{pg} \approx E_T$ because the observed food intake for the pups was a factor of 10 or more larger than the amount required for maintenance of adults (most of the food intake for pups is assumed to be used for growth).

The experimentally observable total (or gross) efficiency was calculated by using $E_T = G/I$ (Warren and Davis 1967), where G is the growth (kg) and I is the food intake (kg). Cumulative total efficiencies were calculated because the observed total efficiencies for short durations between growth measurements were erratic but indicated a definite trend toward smaller values. The cumulative total efficiency represents an integrated value of observed total efficiency for the short duration between weight measurements.

Daily food intake (kg) for one adult male and two juveniles during 1989 was plotted to determine if a temporal feeding pattern occurred. Food intake (% BW day^{-1}) for 1985–90 was compared with mean monthly MBHE temperatures to explore a potential correlation between food consumption and temperature.

Results

Morphology

The regression analysis indicated that the morphometrics were all positively and significantly related according to the following equations (numbers in parentheses are standard errors, n indicates number of data points):

$$(1)\ \text{PDL (cm)} = -11{\cdot}7(1{\cdot}6) + 0{\cdot}576(0{\cdot}012)\ \text{TL (cm)}\ (n = 25,\ r^2 = 0{\cdot}996),$$
$$(2)\ \text{PCL (cm)} = -7{\cdot}0(1{\cdot}4) + 0{\cdot}718(0{\cdot}010)\ \text{TL (cm)}\ (n = 25,\ r^2 = 0{\cdot}995),$$
$$(3)\ \ln W = -13{\cdot}9(0{\cdot}3) + 3{\cdot}33(0{\cdot}06)\ \ln \text{TL}\ (n = 53,\ r^2 = 0{\cdot}983),$$

yielding $W = 8{\cdot}74.10^{-7}$ (kg cm^{-3}) TL$^{3{\cdot}33}$]. The result for the single male did not differ significantly from the result for the females:

$$(3,\ \text{m})\ \ln W = -12{\cdot}6(0{\cdot}6) + 3{\cdot}12(0{\cdot}12)\ \ln \text{TL}\ (n = 13,\ r^2 = 0{\cdot}983),$$
$$(3,\ \text{f})\ \ln W = -13{\cdot}8(0{\cdot}3) + 3{\cdot}38(0{\cdot}07)\ \ln \text{TL}\ (n = 40,\ r^2 = 0{\cdot}983).$$

The data range extended from TL = 65 cm, W = 1 kg (J5, f) to TL = 188 cm, W = 28·9 kg (J2, m) or TL = 184 cm, W = 33·4 kg (J1, f) (Fig. 1). The mean TL/CRW ratio was $60{\cdot}873 \pm 2{\cdot}507$ cm kg$^{-0{\cdot}333}$.

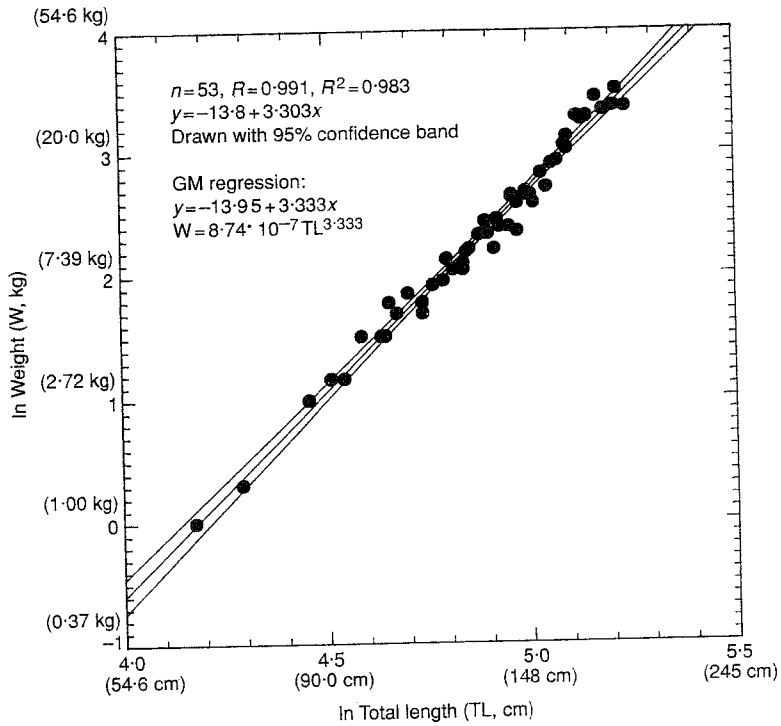


Fig. 1. Log–log plot of weight versus total length for five juvenile sevengill sharks (*Notorynchus cepedianus*). The lines are the ordinary regression (y on x) with 95% confidence limits as calculated and drawn by SYGRAPH. The GM functional regression was calculated separately. n, Number of data points.

Growth

TL growth of sevengills was consistent with pups having maximum growth rates (e.g. 38 cm year^{-1} for J4 at age 1 year) and growing at a faster rate than did juveniles, and with male adults showing zero growth rates (Fig. 2, bottom). W growth of sevengills was consistent with pups growing at a slightly slower rate than did juveniles, and with male adults showing very slow growth rates (Fig. 2, top). The W growth rates were consistent with the anticipated maximum at a juvenile age (e.g. 16 kg year^{-1}) for J1 at age 6 years, 10 kg year^{-1} for J3 at age 5 years, 12 kg year^{-1} for J2 at age 2·5 years). J3 grew much more slowly than did the other juveniles, perhaps because it was a 'runt in the litter', and it was 'overtaken' by one of the pups (J4). Growth for the only male (J2) was similar to that for the females (except J3).

The mean growth rates of five juvenile sevengills (mean age about 3·5 years) were 18·8 ± 11·5 cm year^{-1} and 4·3 ± 3·4 kg year^{-1}, indicative of fast and variable growth rates (Table 1). The mean individual TL growth rates for pups J4 and J5 were, as expected, slightly larger than the ones for juveniles J1–J3 (Table 1). The mean individual W growth rates for the pups were, as expected, slightly less than the ones for the juveniles (except J3) (Table 1). The mean sizes of the pups at an age of about 5 months and of the juveniles at an age of about 18 months were 69·0 ± 5·7 cm, 1·2 ± 0·3 kg and 101 ± 17 cm, 4·7 ± 2·2 kg, respectively.

The VBGF fit (M1, Fabens' method) to TL and W data for pups and juveniles gave low values of L_∞ and W_∞ (compared with observed maximum TL and W values) and relatively high values of k, regardless of whether TL or W was used: $L_\infty = 202 \pm 13$ cm, $k = 0{\cdot}26 \pm$

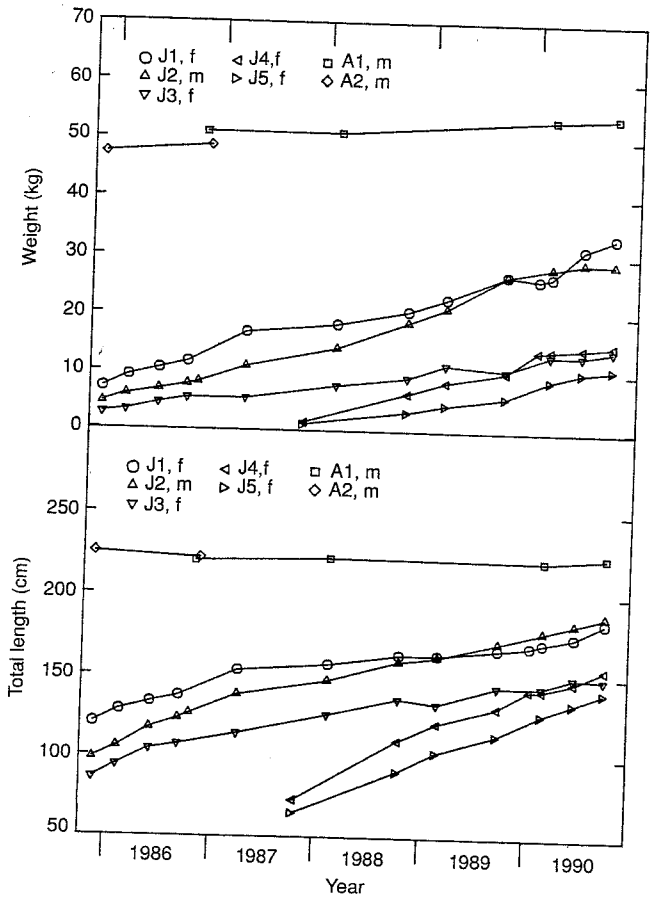


Fig. 2. Growth of captive sevengill sharks at the Monterey Bay Aquarium. J1–J3, juveniles; J4 and J5, pups; A1 and A2, adults; m, male; f, female.

0·04 year^{-1}; $W_\infty = 40·5$ (31–52) kg, $k = 0·25 \pm 0·06$ year^{-1} (Table 2, top). Using these results, we calculated, for comparison purposes with field growth data, (1) first-year TL growth of 37 ± 7 (30–45) cm, (2) TL and W growth rates at age 1 year of 32 ± 7 (25–40) cm year^{-1} and 1·5–3·5 kg year^{-1}, respectively, and (3) TL growth rates of 8–11 and 6·4–9·0 cm year^{-1} at TL = 165·5 and 172·2 cm, respectively. Combining TL and W data (using M1 aided by M4) yielded almost identical results (Table 2, top).

The VBGF fit to female-only data yielded even lower values of L_∞ and W_∞ and correspondingly higher values of k: $L_\infty = 189 \pm 12$ cm, $k = 0·30 \pm 0·05$ year^{-1}; $W_\infty = 33$ (24–43) kg, $k = 0·29 \pm 0·07$ year^{-1}. Combining TL and W data yielded almost identical results (Table 2, centre). The von Bertalanffy parameters for the only male were not all statistically significant at the 95% confidence interval. Combining TL and W data yielded almost identical and very reasonable values of L_∞ and W_∞ (compared with observed maximum TL and W values) and now a statistically significant value of k: $L_\infty = 239 \pm 31$ cm, $W_\infty = 61$ (40–88) kg, $k = 0·20 \pm 0·07$ year^{-1} (Table 2, bottom). Asymptotic standard errors and 95% confidence limits for L_∞ and W_∞ are given for all calculations in Table 2.

Age Determination

Both age-determination methods (M2 and M3) applied to pups and juveniles produced similar results. The individual VBGF method (M2) gave the following age estimates for the juvenile sevengills when they were received: J4 = 6 months, J5 = 7 months, J1 = 21 months,

Table 1. Initial and final total lengths (TL), weights (W), estimated ages, and mean growth rates of five juvenile sevengill sharks
f, Female, m, male; *n*, number of data points

Shark No.	Date	TL (cm)	W (kg)	Est. age (years)
J1, f	24.x.85	120	7·0	1·5
J2, m	24.x.85	98	4·5	1·5
J3, f	24.x.85	86	2·7	1·5
J4, f	22.ix.87	73	1·4	0·42
J5, f	22.ix.87	65	1·0	0·42
J1	30.viii.90	184	33·4	6·4
J2	30.viii.90	188	28·9	6·4
J3	30.viii.90	149	14·1	6·4
J4	30.viii.90	155	15·0	3·4
J5	30.viii.90	141	10·9	3·4

Shark No. (*n*)	Period (years)	TL growth (cm year^{-1})	W growth (kg year^{-1})
J1 (12)	4·86	15·1 ± 10·8	5·8 ± 5·5
J2 (12)	4·86	20·9 ± 9·0	4·6 ± 2·7
J3 (11)	4·86	13·4 ± 13·6	2·6 ± 2·5
J4 (7)	2·94	23·7 ± 13·0	4·4 ± 3·8
J5 (6)	2·94	26·1 ± 5·0	3·7 ± 1·9
All (48)	3·5 ± 1·6 (mean age)	18·8 ± 11·5	4·3 ± 3·4

J2 = 22 months, J3 = 17 months. Only one plot is presented here (Fig. 3). The derivative method (M3) yielded the following most probable ages: 5 months rather than 17 months for J4 and J5 (first-year class when received) and 18 months rather than 6 or 30 months for J1–J3 (second-year class when received). Only one plot is shown here (Fig. 4).

Exponential Regression and Age at Sexual Maturity

The exponential regression method (M5) gave a variety of curves that fitted the TL growth data fairly well, irrespective of the L_∞ value chosen, but that produced a high L_0 value (Fig. 5). This method gave, as expected, an identical value of k (0·254 ± 0·021 year^{-1}) as was obtained with Fabens' method (M1) if the best-fit M1 value of L_∞ = 202·1 cm was used as the input parameter (Fig. 5 gives the results for L_∞ = 200 cm). Using L_∞ = 225–250 cm (the most likely mean maximum TL range for a male sevengill) gave k = 0·174 to 0·132 year^{-1} (lower, but not significantly different from, the M1 result of k = 0·22 ± 0·11) and large L_0 = 71·7–76·3 cm (t_0 = −2·21 to −2·76 years). Using L_∞ = 275–300 cm (the most likely mean maximum TL range for a female sevengill) gave k = 0·107 to 0·090 year^{-1} (significantly lower than the M1 result of k = 0·295 ± 0·052) and large L_0 = 78·7–80·1 cm (t_0 = −3·15 to −3·45 years). The table of results for all L_∞ input values considered (200–325 cm in steps of 25 cm) is included with Fig. 5.

Fig. 6 shows a range of ages and weights at sexual maturity based on Method 5 (i.e. a range of M5 VBGF fits) and the W versus TL power regression from the sexual-maturity TL range. Ebert (1989*a*) estimated that a sexually mature male was at least 153 cm long and weighed 13·5 kg and that a sexually mature female was about 250 cm long and weighed in excess of 91 kg. On the basis of more recent egg maturation data, Ebert (1989*b*) suspects that females enter their first breeding season between 218 and 244 cm TL. For males,

Table 2. von Bertalanffy growth parameters for sevengill sharks
Parameters are given first for all five juveniles combined and then separately for the four females and the one male. For each group, the parameters using TL and W data are given first separately and then combined. For this combination, scaling factor = mean TL/CRW = 60·873 ± 2·507 cm kg^{-3} (n = 53). a.s.e., Asymptotic standard error; <95%>, 95% confidence limits; n, number of data points; SCRW, scaled cube root weight

Data type	$k \pm$ a.s.e. (year^{-1})	$L_\infty \pm$ a.s.e. (cm)	W_∞ (a.s.e. band) (kg)	<95%> for L_∞ or W_∞
		All sharks		
TL (n=48)	0·258±0·043	202·1±12·5		177–227 cm
W[A] (n=48)	0·249±0·055		40·5 (31–52)	23–66 kg
Average	0·254			
TL/SCRW (n=96)	0·254±0·035	205·6±10·8	38·8 (32–45)	184–227 cm 28–52 kg
		Females only		
TL (n=36)	0·295±0·052 (t=5·67)	189±12		165–214 cm
W[A] (n=36)	0·286±0·069 (t=4·13)		32·8 (24–43)	17–55 kg
Average	0·291			
TL/SCRW (n=72)	0·290±0·047 (t=6·19)	192±12	31·3 (26–37·5)	169–215 cm 21–44 kg
		Males only		
TL (n=12)	0·22±0·11 (t=1·95[B])	229±41		137–320 cm
W[A] (n=12)	0·18±0·10 (t=1·75[B])		69 (32–126)	8·4–233 kg
Average	0·20			
TL/SCRW (n=24)	0·196±0·067 (t=2·90)	239±31	61 (40–88)	175–304 cm 24–124 kg

[A] By way of cube root weight. [B] Not significant.

we used TL = 153–160 cm (153/0·961; i.e. creating a range by converting from straight-line TL to contour TL; see Materials and Methods) and obtained a sexual-maturity age of 4·3–5·0 years and a sexual-maturity weight of 17–19 kg. For females, we used TL = 218–254 cm (244/0·961; i.e. expanding the range to allow for our contour TL) and obtained a sexual-maturity age of 11·0–20·9 years and a sexual-maturity weight of 54–91 kg.

Feeding

The mean annual food consumption for the five pups and juveniles was larger than that for the adult male (Table 3). The two pups, J4 and J5, ingested more than 1·0% BW day^{-1} in 1988 before decreasing to about 0·40% BW day^{-1} in 1990. The juvenile sevengills, J1–J3, averaged 0·96–0·54% BW day^{-1} in 1985–86 before decreasing to 0·67–0·3% BW day^{-1} in 1989–90. The peak values in 1988 did not follow this pattern. J2, the male that reached maturity in early 1989 while in captivity, consumed considerably less compared with female J1, which showed signs of accelerated food intake in 1989–90. The adult male consumed a low of 0·14% BW day^{-1} in 1985 and a high of 0·3% BW day^{-1} in 1988. The overall 5-year mean for the adult male was 0·21% BW day^{-1}.

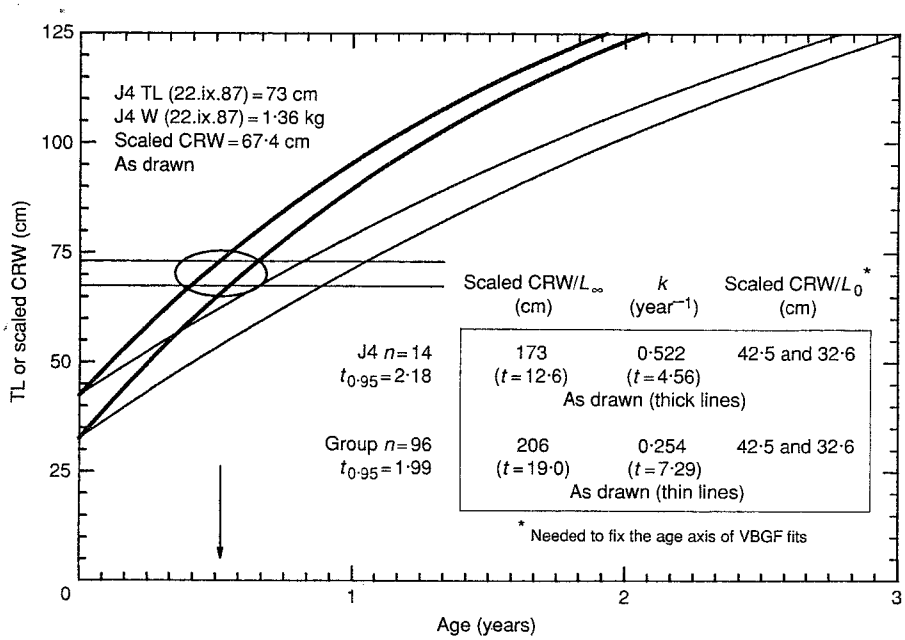


Fig. 3. Graphical method of determining the age of juvenile sevengill sharks by the individual VBGF method (M2). The VBGFs for each individual were used to determine age from the known birth TL and W. The VBGF parameters L_∞ and k were determined by using TL and scaled CRW data combined by Fabens' method (M1) and fixing the time axis from the average of TL_0 and scaled CRW_0. Scaling factor = mean TL/CRW = 60·873 cm kg^{-3}. J4, female pup; n, number of data points.

The pronounced decrease in food consumption during the initial 5 years of a sevengill's life becomes more apparent when plotted against age (Fig. 7). The pups showed a more than 10-fold higher food consumption of between 2·0 and 0·5% BW day^{-1} compared with that of adults A1, A2 and A4 of between 0·3 and 0·2% BW day^{-1}.

Cumulative total efficiency for the pups and juveniles decreased sharply with age (Table 4). Pups J4 and J5 and juveniles J1–J3 had cumulative total efficiencies of 40–25% at age 1–3 years. By age 5–6 years, the cumulative total efficiency dropped by a factor of about three to 15–10%. The changes in total efficiency rather than cumulative total efficiency were even more pronounced but also were more erratic.

The results of theoretical calculations of food intake versus age for fixed W_0 and fixed $\varkappa/E_{pg}$ were as follows (two of many calculations carried out, for $k = 0{\cdot}1$ and $0{\cdot}4$ $year^{-1}$, are shown in Fig. 7): (1) Large food-intake values of more than 2% were to be expected near $t = 0$. (2) The theoretical curves were relatively insensitive to changes in the parameter k as a variable in the model. (3) The theoretical curves were surprisingly insensitive to changes in the parameter W_∞. For example, using $W_\infty = 80$ kg (which is appropriate for males) instead of the value used in Fig. 7 ($W_\infty = 180$ kg is appropriate for females) reduced the food intake by merely 10% at age 1 year. (4) The theoretical curves were, however, very sensitive to the partial growth efficiency, E_{pg}, the third parameter considered as a variable in the model. A value of approximately 0·3 (0·1 produced about three times larger food-intake values at young ages) was required to bring the curve near the observed food-intake values.

Sevengills followed a 'feast or famine' feeding mode. Adult male A1 showed a pattern of high consumption followed by low food intake for several feedings before peaking again

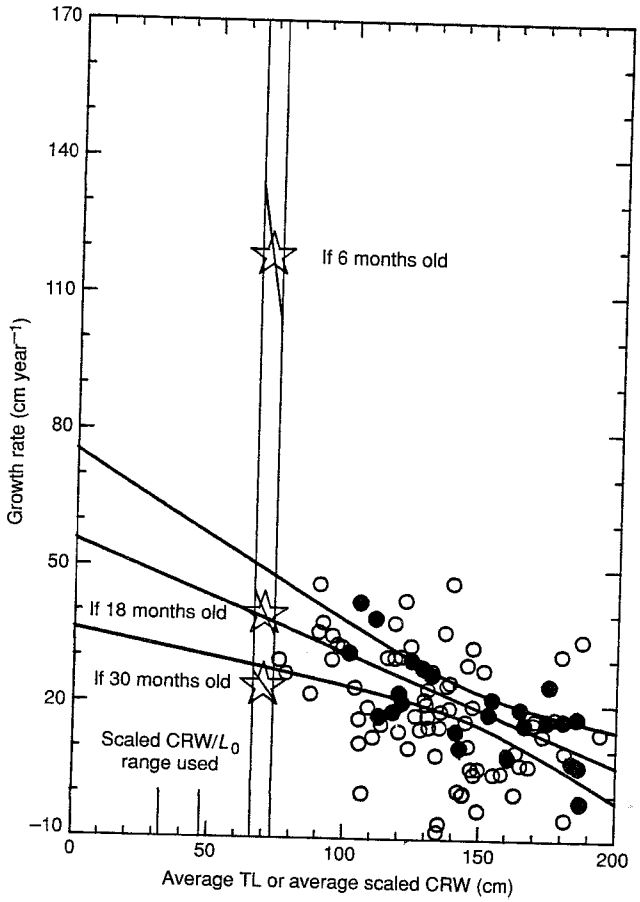
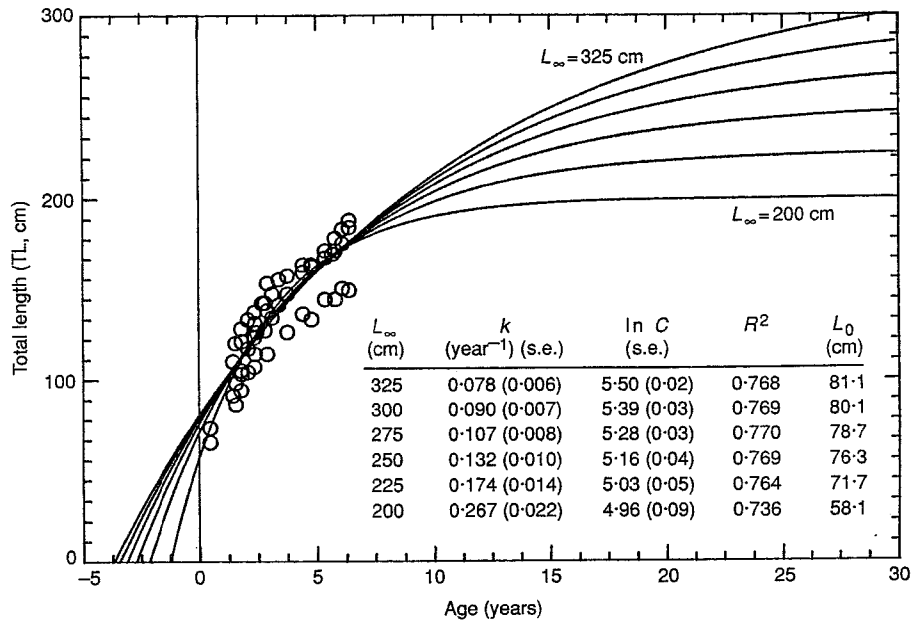


Fig. 4. Graphical method of determining the age of juvenile sevengill sharks by the derivative method (M3). TL and scaled CRW data from an individual shark (●) were combined to determine the linear regression ($y = 55 \cdot 6 + 0 \cdot 25x$) and the 95% confidence limits. The growth-rate data for the other sharks are shown for comparison (○), but the regression from all data ($y = 46 \cdot 1 + 0 \cdot 20x$) is not drawn. Stars indicate the calculated first growth rate (actually a range) based on TL and scaled CRW when received and at birth, using assumed ages of 6, 18 and 30 months. Juvenile male J2, when received on 24 October 1985, was 98 cm long and weighed 4·5 kg (scaled CRW = 100·5 cm).

(Fig. 8). Qualitatively, the pattern appears to follow a cycle of 5–7 days. The juvenile sevengills had fewer feedings with zero consumption, but they, too, consumed less following a large peak in feeding (Fig. 8).

The anticipated effect of water temperature on food consumption is difficult to demonstrate due to minor seasonal fluctuations in temperature. Temperatures generally ranged from 12 to 14°C in the MBHE. In general, temperatures in Monterey Bay follow a seasonal pattern that is observed in the aquarium as well. Spring and summer are periods of upwelling, resulting in colder water temperatures, whereas autumn and winter typically are influenced by warm-water coastal and oceanic water movements. In the (northern) autumn of 1987, however, the temperature in Monterey Bay was unusually high, with a



L_∞ (cm)	k (year^{-1}) (s.e.)	ln C (s.e.)	R^2	L_0 (cm)
325	0·078 (0·006)	5·50 (0·02)	0·768	81·1
300	0·090 (0·007)	5·39 (0·03)	0·769	80·1
275	0·107 (0·008)	5·28 (0·03)	0·770	78·7
250	0·132 (0·010)	5·16 (0·04)	0·769	76·3
225	0·174 (0·014)	5·03 (0·05)	0·764	71·7
200	0·267 (0·022)	4·96 (0·09)	0·736	58·1

Fig. 5. Exponential regression of total length on estimated age. TL and estimated age data for juvenile sevengill sharks were fitted to the von Bertalanffy growth curve in the form $L_\infty - L(t) = (L_\infty - L_0)e^{-kt}$, with $y(t)$ = constant e^{-kt}. L_∞ was treated as an input parameter ranging from 200 to 325 cm in steps of 25 cm. s.e., Standard error. $C = L_\infty - L_0$.

corresponding high temperature in the MBHE of nearly 17°C. Another temperature peak occurred in late 1988. Coincidentally, an observed broad peak of higher food consumption for juveniles J1–J3 occurred during this interval of increased temperatures. Adult sevengill A1 also showed a slight increase in food intake during this time.

Discussion

Morphology

Linear regressions fitted the PDL–TL and PCL–TL data well. A power regression ($L_1 = aL_2^b$) may be preferable from a theoretical viewpoint (Ricker 1979) to demonstrate the accelerated growth in the trunk region compared with that in the tail region (allometric growth).

It is strongly suggested that PCL of forklength (FL) rather than TL should be used to analyse the growth of sharks. Wass (1973) used PCL for a growth analysis of sandbar sharks and observed that PCL can be measured more accurately. For sevengills, the power regression for the W–TL data is characterized by $b = 3 \cdot 33$, showing that growth is not isometric if TL is used as the length parameter. The use of PCL gave an isometric relationship ($b = 3 \cdot 00$; unpublished data), an indication that PCL is the more fundamental length parameter. Medved *et al.* (1988) obtained $b = 2 \cdot 96$ by using FL data for sandbar sharks, *Carcharhinus plumbeus*. By approximating a sevengill's shape as a prolate spheroid (the shape of an American football), we obtained excellent agreement between observed and calculated weight (using the measured PCL and the calculated half-axis ratio—found to be reasonably constant—from the observed PCL and girth; unpublished data). This is additional support for our suggestion that PCL is the fundamental length parameter in the case of sevengill sharks.

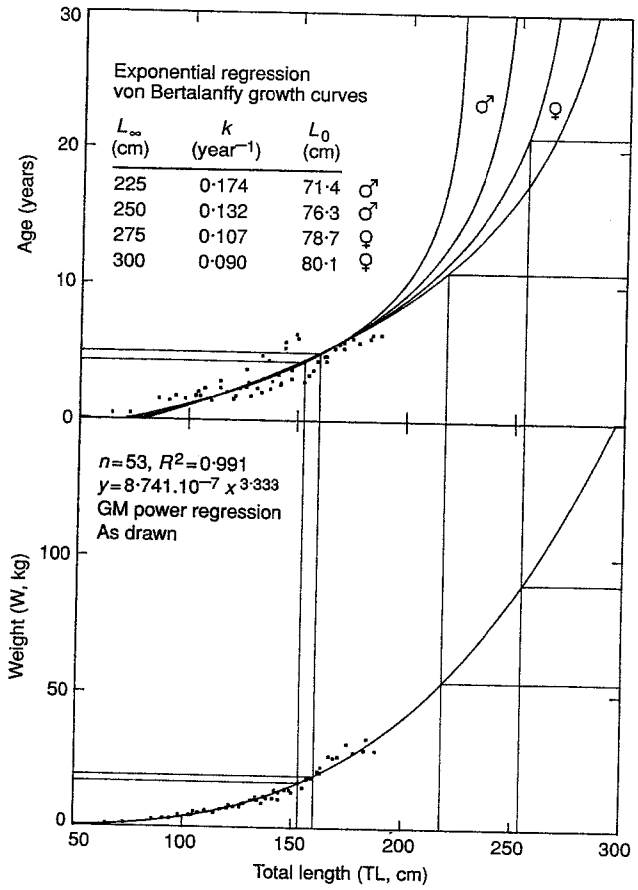


Fig. 6. Age and weight versus total length for sevengill sharks. The M5 VBGF-fitting curves and the W versus TL power regression based on data from five juveniles were used to estimate ages and weights at sexual maturity on the basis of the length requirement estimated by Ebert (1989*a*, 1989*b*). *n*, Number of data points.

Table 3. Mean annual food consumption (% BW day^{-1} ± s.d.) for sevengill sharks
Means were calculated from 12 monthly averages unless otherwise indicated. A1, adult male estimated to be 13–19 years old in October 1985; J1–J3, juveniles (J1 and J3 female, J2 male) estimated to be 18 months old in October 1985; J4 and J5, pups estimated to be 5 months old in September 1987

Year	A1	J1	J2	J3	J4	J5
1985[A]	0·14±0·07	0·76±0·09	0·86±0·14	0·96±0·33	–	–
1986	0·15±0·09	0·53±0·20	0·54±0·25	0·56±0·39	–	–
1987	0·19±0·07	0·49±0·18	0·59±0·20	0·70±0·39	1·48[B]	1·33[B]
1988	0·30±0·11	0·81±0·12	0·71±0·17	0·81±0·21	1·04±0·26	1·05±0·44
1989	0·23±0·09	0·65±0·10	0·42±0·11	0·38±0·11	0·60±0·16	0·66±0·22
1990	0·19±0·09	0·67±0·09	0·30±0·08	0·33±0·13	0·40±0·14	0·44±0·13
1985–90	0·21±0·10	0·64±0·19	0·55±0·23	0·58±0·34	0·70±0·35	0·73±0·44

[A] Calculated from three monthly averages. [B] December average.

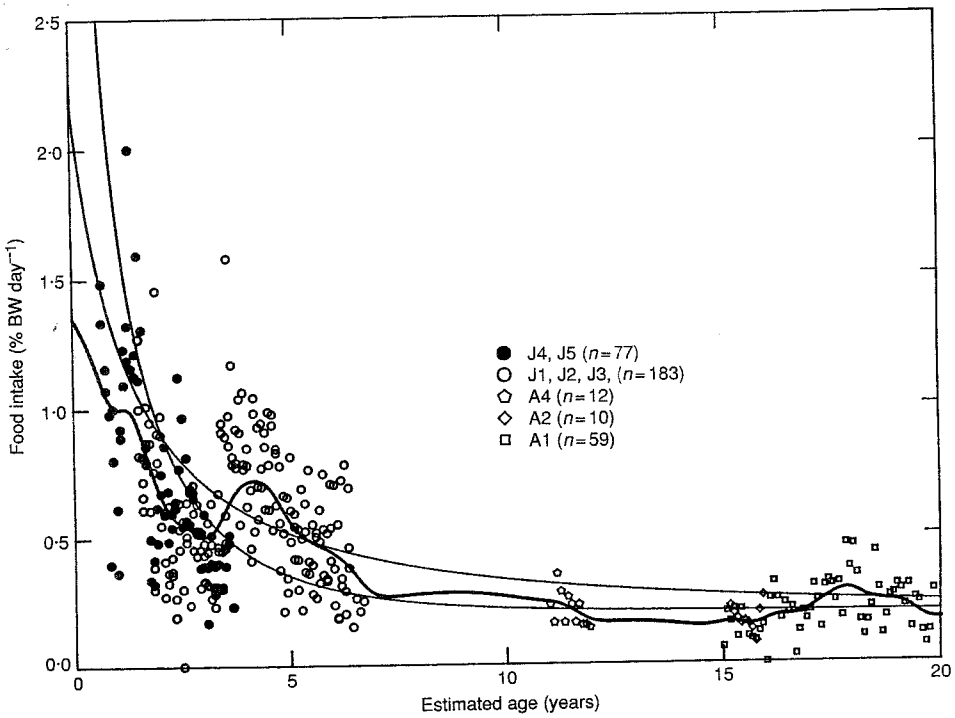


Fig. 7. Food intake versus estimated age for sevengill sharks. Time ranges: December 1987 to December 1990 (pups J4 and J5), October 1985 to August 1990 (juveniles J1 and J2 and adult A1), October 1985 to December 1990 (juvenile J3), October 1985 to September 1986 (adult A4), and December 1985 to September 1986 (adult A2). The thick line is a distance-weighted, least-squares-smoothing curve through all data points ($n = 341$). The thin lines are theoretical curves based on the VBGF ($W_\infty = 180$ kg, $W_0 = 0{\cdot}323$ kg, $k = 0{\cdot}1$ and $0{\cdot}4$ year^{-1}), assuming an age-independent partial growth efficiency of 0·3 and an age-independent maintenance constant of 0·2% BW day^{-1}.

Table 4. Cumulative total efficiencies (E_T) for sevengill sharks
E_T = weight gain (kg)/food consumed (kg). n.d., No data

Period	J1	J2	J3	J4	J5
24.x.85					
to 6.v.86	2·1/5·2=0·40	1·4/3·6=0·39	0·5/2·3=0·22		
to 7.v.86	0·30	0·27	0·38		
to 13.viii.86	0·31	0·31	0·36		
to 4.iii.87	0·37	0·33	0·23		
to 13.i.88	0·34	0·22	0·21		
to 14.ix.88	0·20	0·20	0·16	5·0/14·3=0·35	2·2/7·2=0·31
				(22.ix.87–14.ix.88)	
to 25.i.89	0·14	0·19	0·17	0·30	0·29
to 23.viii.89	0·13	0·20	0·13	0·26	0·26
to 26.i.90	0·11	0·19	0·16	0·27	0·28
to 16.v.90	0·12	0·18	0·15	0·24	0·29
to 39.viii.90	0·12	0·17	0·15	0·22	0·26
to 5.xii.90	n.d.	n.d.	0·14	0·24	0·29
Totals (kg):					
Weight gain	26·4	24·4	11·4	16·1	12·4
Amount fed	225·8	145·5	80·6	65·9	42·7

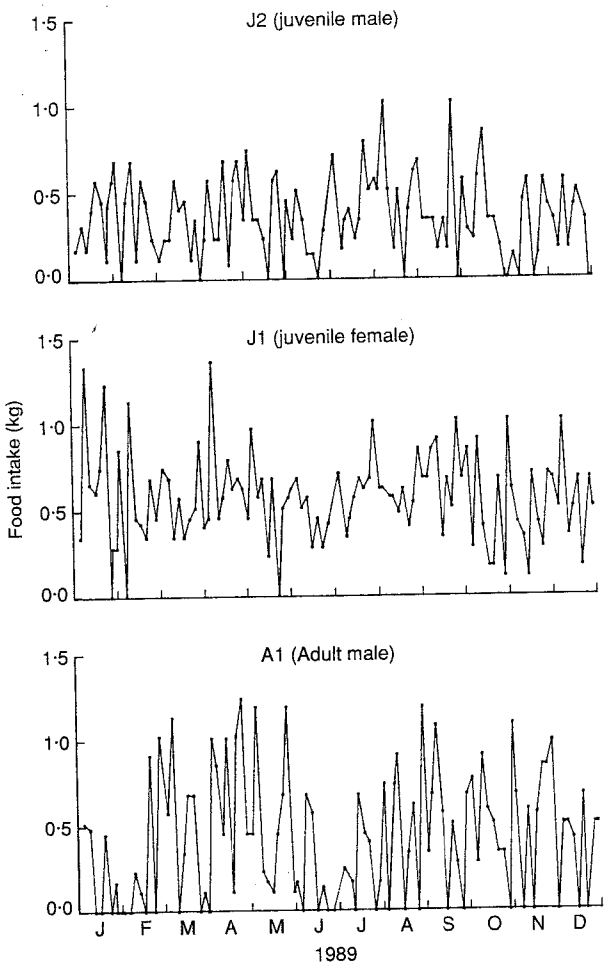


Fig. 8. Food intake versus feedings ($n = 104$) for three sevengill sharks in 1989.

The results from juvenile sharks in captivity are in good agreement with the preliminary GM power regression obtained by Ebert (personal communication) for 524 male and female sevengill sharks collected worldwide (W in kg, TL in cm): $\ln W = -14{\cdot}03(0{\cdot}07) + 3{\cdot}315(0{\cdot}015) \ln TL$ ($n = 524$, $r^2 = 0{\cdot}989$). Ebert (personal communication) observed no significant differences for the W–TL power regression between male and female sevengills. Accordingly, no difference was anticipated for males and females in captivity and none was observed.

Growth

Growth is best discussed with the help of a growth model rather than growth rates, especially if long times are involved or there is no reference to age. The calculated values for L_∞ (202 cm) and W_∞ (41 kg) are considerably lower than the observed values for the largest females (TL = 296 cm, W = 170 kg and TL = 290·7 cm, W > 182 kg) and even the largest male (TL = 242 cm, W = 65·9 kg) (Ebert 1989*b*). On the basis of the wide 95% confidence limits for L_∞ (177–227 cm) and W_∞ (23–66 kg), it is evident that the VBGF model is not adequate to represent the growth of female sevengills but is possibly adequate to represent the growth of male sevengills. Knight (1968) pointed to the danger of predicting maximum sizes from juvenile data by means of the von Bertalanffy model. Chien and

Condrey (1987) showed that Fabens' method systematically overestimates k and underestimates L_∞ in the VBGF model. However, their worst-case scenario gives a relative difference of 'only' 24% for k and a 'mere' 3·65% for L_∞.

On the basis of limited growth data for males, we obtained different VBGF parameters for the two sexes (statistically different at the 70% confidence interval but not at the 95% confidence interval). This result is not surprising because different VBGF parameters for males and females have been observed for many elasmobranchs such as the gray smoothhound, *Mustelus californicus* (Yudin and Cailliet 1990), the sandbar shark (Wass 1973; Casey *et al.* 1985), and possibly the leopard shark, *Triakis semifasciata* (Kusher *et al.* 1992). Because of the large difference in reported maximum size for male and female sevengills (50 cm for TL, 100 kg for W), different VBGF parameters would be expected. The comparison suggests that the growth curves for male and female sevengills in captivity are different and that the VBGF model is adequate for male sevengills but not for female sevengills.

Growth in Captivity versus Growth in the Field

We conclude that, on the basis of the available data, the growth rates of sevengills in captivity and in the field are similar. The limited field data available allow a preliminary and conservative estimate of growth in the field to be compared with growth in captivity. Ebert (1989*a*) observed that pups with a TL of 54–70 cm and with recently healed umbilical scars were caught at shark derbies in September. First-year growth in the field can be estimated on the basis of an observed late-spring birth TL of 35–45 cm. Growth in the 4–5 months following birth is 19–25 cm, or 45–60 cm year^{-1}. This is larger than the first-year growth of 30–45 cm calculated from the VBGF for captive sevengills 5 months to 6 years old.

Ebert's (1989*b*, and personal communication) tag–recapture experiment yielded growth data for only two juvenile sevengills (TL_{tag} = 159 and 163 cm, calculated from the PCL). The TL growth rates were 13·8 cm year^{-1} (at large for 359 days) and 0 cm year^{-1} (at large for 538 days), respectively, compared with calculated growth rates of 8–13 cm year^{-1} (or even less – 6·4–9·0 cm year^{-1} – if we convert to contour TL) based on the von Bertalanffy parameters from five juveniles in captivity. Large individual growth variations in the field were observed for other sharks, and this included data from tag–recapture experiments (reviewed in Kusher *et al.* 1992).

It is proposed that 'population' field growth rates at age 1 year (average age of the two pups and three juveniles when they were captured) can be estimated from the observed mean sizes of the sharks in this study (belonging to different age classes) at the time of capture. This gave 30 cm year^{-1} and 3·2 kg year^{-1}, compared with calculated growth rates of 25–40 cm year^{-1} and 1·5–3·5 kg year^{-1} based on VBGF parameters determined from the observed growth in captivity after capture.

Growth-rate differences in captive and wild environments of up to a factor of two to three only are plausible. Taylor and Wisner (1989) demonstrated that juvenile blacktip sharks (*Carcharhinus melanopterus*) in various aquaria grew twice as fast on twice the ration. Young lemon sharks (*Negaprion brevirostris*) could not be induced to feed voluntarily beyond two times the maintenance ration of about 250 kJ kg^{-1} day^{-1} (Wetherbee *et al.* 1990). Unless lemon sharks in the field are close to starvation, with resulting very small growth rates, growth-rate differences between captive and wild lemon sharks of more than two to three are unlikely. The often quoted factors of nine and ten for lemon sharks and grey reef sharks (*C. amblyrhynchos*), respectively (Gruber and Stout 1983), could not be substantiated. Analysis of the data given by Wass (1971) for grey reef sharks supports a factor of three. The short-term growth study on captive lemon sharks (Gruber and Stout 1983) supports a factor of two.

Laboratory studies often report faster growth of young sharks. This has been interpreted to indicate that growth in captivity is generally faster than growth in the field (Gruber and Stout 1983; Natanson and Cailliet 1990). However, this is basically due to younger sharks growing faster than older ones (Carrier and Luer 1990). Growth data can be misinterpreted if growth rates are compared without strict attention to age. Misinterpretations are less likely if one characterizes von Bertalanffy growth by using the approach of Fabens (1965), who distinguishes between growth rates and k values. The constant k has units of time^{-1}, but it has often bean misnamed as a growth-rate constant and perceived as a unitless quantity, as a slope or rate of growth. Fabens (1965) clearly stated that ln $2/k$ represents a 'half-life'; i.e. at age ln $2/k$ a shark is half-way between L_0 and L_∞, and at age $5/k$ (about seven half-lives) the shark is within less than 1% of its asymptotic size, L_∞. The slope of the VBGF (=instantaneous growth rate), with units of length/time or weight/time (both quantities are age-dependent!), can be calculated in explicit form from the VBGF. The L growth rate is a maximum at birth and decreases exponentially with age. The W growth rate is zero at birth, reaches a maximum (when $W = 8/27\ W_\infty$), and then decreases exponentially. Experimentally measured growth rates are indeed integrated rather than instantaneous. However, they have similar properties for sufficiently small times of integration (say less than 1 year), and integrated growth rates (e.g. first-year growth, annual growth at average age x) can also be calculated from the VBGF.

Holden's (1974) method allowed easy calculation of k values from observed L_∞ and L_0 values and the estimated gestation time, $-t_0$. This cannot be recommended if k is then misinterpreted as a growth rate. Sharks have a well defined L_0, which can be used to replace t_0 as the third VBGF parameter. This eliminates the questionable assumption that growth during the embryonic stage can serve as a model for post-partum growth (Pratt and Casey 1990).

Age Determination

The results of two age determination methods applied to five juveniles (J1–J5) confirmed the original age estimates. It should be pointed out that J1 and J2 exhibited relatively rapid growth rates from the time they were received until the time they were released on 30 August 1990, whereas J3 exhibited much slower growth rates, perhaps characteristic of a 'runt of the litter'. J4 'overtook' J3 in spring 1990, and J5 is expected to become longer and heavier than J3 by spring 1991. These observations underline the importance of using individual growth curves for age determination. The Gulland equation—$L_{\text{increment}}$ (cm) = $(1 - e^{-kT})(L_\infty - L_{\text{initial}})$, T = at-large time (Gulland 1983)—might be considered to have been more suitable than the M3 (derivative) method for the age determination because it is an equation for an integrated growth rate. This was explored and yielded similar results. The M3 method is an approximation because experimentally observable growth rates are not instantaneous. The Gulland method was an approximation in the case of our sevengill data because the times between measurements (at-large time) were unequal (between 37 and 358 days).

The need for individual VBGFs led to the use of combined TL and W data in the the TL-scaled CRW method (M4) to improve the statistics of the results. This amounts to claiming that TL and W data from one shark is equivalent to TL data from two sharks, which is questionable. Because it is justifiable to calculate k values from TL and W data separately and then to average the results, we assumed that this combination method must improve the statistics. However, a rigorous justification was beyond our statistical expertise.

Age at Sexual Maturity

The exponential regression method (M5) is a step in the determination of sexual maturity. The parameters of the VBGF fit using Fabens' method (M1) could not be used to predict growth rates or sizes at age that were much larger than the range of observed data because

the best-fit L_∞ and W_∞ were unreasonably low, especially in the case of female sevengills. This does not mean that one can not apply the von Bertalanffy model—using a different fitting method to obtain different parameter values—to the adult age range. It amounts to considering two age ranges and applying the same growth model to each region separately. A growth model covering the complete range would be preferable, but calculations using other growth functions were not successful. However, to calculate the age of male sexual maturity, one could have used the M1 method instead of the M5 method because male sexual maturity was reached within the range of our growth data and because one VBGF appeared to represent male sevengill growth satisfactorily.

The M5 method uses a fixed value of L_∞, which provides a better fit in the adult region. Unreasonably large L_0 (or t_0) values are of no concern because the results are not expected to provide a good fit for small ages. The method is not very sensitive and was used primarily to estimate age at sexual maturity. The standard methods used to fit the VBGF are equally unsatisfactory considering the reported large standard errors because of small numbers of growth data (Cailliet *et al.* 1990; Tonaka *et al.* 1990). According to Cerrato (1990), our 48 growth-rate data points would be more than adequate for a two-parameter linear model. If we interpret Cerrato (1990) correctly, sample sizes in excess of 300 would be required to produce parameter values with adequately small asymptotic standard errors for the three-parameter nonlinear von Bertalanffy model.

The predicted age range for male sexual maturity of 4·3 to 5·0 years based on TL = 153–160 cm agrees with our observation that J2 reached sexual maturity while in captivity (TL = 98–188 cm). The clasper length increased from 7·0 to 11·0 cm between 13 January 1988 and 26 January 1990 (Table 5), and J2 reached sexual maturity between the ages of 3·7 and 5·8 years. An intermediate clasper-length measurement would have been required to pinpoint more accurately the increase in clasper length associated with sexual maturity. On the basis of the corresponding TL and W data, sexual maturity was probably reached before the age of 4·8 years. Thus, it can be said that the predicted and observed sexual-maturity ages for this male are in good agreement.

Table 5. Clasper length and estimated age for one male sevengill shark

n.m., Not measured

Date	TL (cm)	W (kg)	Clasper length (cm)	Est. age (years)
24.x.85	98	4·5	n.m.	1·5
13.viii.86	123	7·7	7·0	–
4.iii.87	138	10·9	7·0	–
13.i.88	147	14·1	7·0	3·7
25.i.89	162	21·1	n.m.	4·8
26.i.90	178	28·2	11·0	5·8
16.v.90	183	29·1	11·0	–

The predicted age range for female sexual maturity (11–21 years) is large and at least 6 years older than the sexual-maturity estimate for male sevengills. Different sexual-maturity ages for male and female elasmobranchs, and often older female sexual-maturity ages (more than 10 years), were listed for several elasmobranchs by Pratt and Casey (1990). The large range of 10 years arises because we assume continuous development on the basis of the von Bertalanffy model for the period of female maturation. A growth discontinuity during this period is a possibility, which would explain why a single VBGF is not adequate to describe the growth of female sevengills. Although this growth study covered a 5-year period, this was insufficient to completely characterize the growth of female sevengills.

The calculated weight for males at sexual maturity (17–19 kg) is 26–41% larger than the weight of 13·5 kg observed by Ebert (1986). The upper limit of the calculated weight range for females at sexual maturity (54–91 kg) agrees with the weight of more than 91 kg suggested by Ebert (1989*a*) for a 250 cm TL female.

Feeding

It is evident from our study that adult male sevengills require very little food in captivity to meet their daily metabolic requirements. Brett and Blackburn (1978), using metabolic requirement rates, estimated that the food consumption of the smaller spiny dogfish, *Squalus acanthias*, was 0·4% BW day^{-1} at 10°C. Schmid *et al.* (1990) reported food consumption values for four tropical shark species maintained in a 2·5 ML closed system at a constant temperature of 25°C. Adult sand tiger sharks, *Carcharias taurus*, which are similar in size and behaviour to sevengills, consumed amounts (0·28% BW day^{-1}) that were similar to those eaten by adult sevengills.

It is important to be aware of the ages of sharks when comparing food consumption values for sharks in captivity and in the field. The observed food intake for the sevengill pups (up to 2% BW day^{-1}) was about 10 times as large as that for the adults (0·2% BW day^{-1}). A theoretical calculation of expected food intake (based on the VBGF) confirmed that food intake is high near birth. Similar results have been noted for captive bull shark pups, *Carcharhinus leucas* (Schmid *et al.* 1990), lemon shark pups, *Negaprion brevirostris* (Cortes and Gruber 1990), and young sandbar sharks, *Carcharhinus plumbeus* (Medved *et al.* 1988).

Age appeared to be the most important factor determining the food intake of sevengills. Other factors such as feeding cycles, previous meal size, rates of digestion, gastric evacuation and water temperature are expected to affect food consumption in sharks. We observed adult sevengills exhibiting a 'feast or famine' feeding pattern over an interval of 5–7 days. Rupp (1984) observed a cycle of 3–5 days for captive sevengills held at 10°C. Longval *et al.* (1982) found a 4-day feeding cycle for several captive juvenile lemon sharks, and they mentioned that hunger and satiation play a role in a shark's food intake behaviour. We found that adult and juvenile sevengills consumed less food following a large meal.

Although we were not able to determine rates of digestion, they certainly play an important role in the determination of feeding cycles. Medved (1985) and Wass (1973) reported that sandbar sharks have total evacuation times of 3–4 days, and Jones and Green (1977) found that dogfish took approximately 5 days to digest a meal of herring at 10°C. Wetherbee *et al.* (1987) found that juvenile lemon sharks take 68–82 h to completely evacuate the digestive tract. It appears that our estimate of a feeding cycle of 5–7 days is in agreement with gastric evacuation times for sharks, although more thorough studies are needed on large temperate species.

Water temperature was considered as a possible factor affecting food consumption by both juvenile and adult sevengills. In most captive situations, large pelagic species are housed in large aquaria with a constant temperature regime. The water temperature in the MBHE fluctuates with the temperature in Monterey Bay. We believe the elevated temperatures recorded in late 1987 and late 1988 coincided with increased food consumption.

Temperature fluctuation also plays an important role in rates of digestion and evacuation, as has been shown for many bony fishes (Elliott and Persson 1978). Additional work is required in this area to elucidate further the role of temperature, food type, and other variables affecting the digestion and gastric evacuation of elasmobranchs.

Ricker (1979) reviewed the growth–ration relationship and concluded that no simple relationship exists. We accept this conclusion and have used the derived five-parameter (k, W_0, W_∞, E_{pg} and E_{pm}) relationship based on von Bertalanffy growth merely to calculate the expected food intake for pups near age 0. The observed large total or gross efficiency for the pups was surprising, and we considered that it may be due to unrecorded food

intake during regular daily feeding at the MBHE. Such unrecorded food intake was observed, but we believe that it was acceptably small once a pup reached a TL of 70–80 cm. At this size, the pups were higher in the water column and were more accessible for pole feeding. The theoretical calculations confirmed the large total (gross) efficiency, and we believe that the observed results are genuine.

Acknowledgments

We are grateful to the Steinhart Aquarium (CAS), which donated the juvenile sevengills used in this study. G. Cailliet (MLML) introduced us to the analysis of shark growth data and helped with critical comments as the work progressed. We appreciate the comments and suggestions offered by referees to improve the manuscript. J. Watanabe, R. Phillips, N. Allen and D. Anderson of the MBA Research Division and J. Scharold of CSUF provided computer support and contributed helpful suggestions. We thank D. Ebert for his invaluable information and observations on sevengill sharks. We also thank K. Kopp for editing the figures. We are grateful to the Husbandry Department of the Monterey Bay Aquarium (D. Powell, C. Farwell, S. Nygren, M. Ferguson and aquarists), in particular R. Gary and P. Ferrante, for their support of this study and their help with the collection of growth and feeding data.

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Manuscript received 28 February 1991; revised and accepted 16 September 1991