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ORIGINAL PAPER

Age and growth of the sandbar shark, *Carcharhinus plumbeus*, in Hawaiian waters through vertebral analysis

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Abstract Age and growth estimates were determined for the sandbar shark, *Carcharhinus plumbeus*, from Oahu, Hawaii in the central Pacific Ocean. Age estimates were obtained through vertebral centra analysis of 187 sharks. We verified our age estimates through marginal increment analysis of centra and oxytetracycline marking methods of at liberty sandbar sharks. Sizes of sampled sharks ranged from 46 to 147 cm pre-caudal length. Four growth models were fitted to length-at-age data; two forms of the von Bertalanffy growth model, the Gompertz growth model, and a logistic growth model. Males and females exhibited statistically significant differences in growth, indicating that females grow slower and attain larger sizes than males. Growth parameter estimates revealed slower growth rates than previously estimated (based on captive specimens) for Hawaiian sandbar sharks. The von Bertalanffy growth model using empirical length-at-birth provided the best biological and statistical fit to the data. This model gave parameter estimates of $L_\infty = 138.5$ cm PCL and $k = 0.12$ year^{-1} for males and $L_\infty = 152.8$ cm PCL, $k = 0.10$ year^{-1} for females. Male and female sandbar sharks mature at approximately 8 and 10 years of age, respectively.

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Introduction

The sandbar shark, *Carcharhinus plumbeus*, is a common large-coastal shark that inhabits temperate and subtropical waters world-wide and attains lengths greater than two meters (Bigelow and Schroeder 1948; Compagno 1984). In Hawaiian waters, sandbar sharks most frequently occur between depths of 10 and 50 m (Wass 1973). The species is not commercially important in the central Pacific, which provides a unique opportunity to examine age and growth of a late maturing carcharhiniform shark that has not been greatly affected by fishing mortality.

Male and female sandbar sharks in Hawaiian waters have historically been shown to reach maximum sizes of 132 and 146 cm pre-caudal length (PCL), respectively (Wass 1973). The sandbar shark is viviparous via yolk-sac placenta, giving birth to well-developed live young following a gestation period of approximately 9–12 months (Springer 1960; Clark and von Schmidt 1965; Wass 1973; Lawler 1976). In Hawaiian waters, pups are approximately 47 cm PCL at birth and litter sizes average 5.5 pups per litter (Wass 1973). Wass (1973) estimated maturity to occur at 110 cm PCL for males and at 115 cm PCL for females.

The age and growth of the sandbar shark off Hawaii has been previously investigated. However, dissimilarities in some parameter estimates such as growth rates and age-at-maturity exist. Using data from captive sharks, Wass (1973) reported very fast growth rates ($k = 0.4015$ year^{-1} for males, $k = 0.3745$ year^{-1} for females) and indicated that sandbar sharks in Hawaii reached maturity at 3 years of age. Conversely, growth rate estimates obtained from tooth replacement calculations suggested maturity occurred at 13 years of age. The discrepancy between the two methods may be due to the use of captive animals, which may not be indicative of growth rates in the Hawaiian wild population. Furthermore, the results based on tooth replacement rates are comparable to other sandbar shark populations around the world. For example, sandbar sharks in the Northwest Atlantic Ocean attain maturity between 12 and 15 years of age (Casey et al. 1985; Sminkey and Musick 1996). Additionally, Joung et al. (2004) estimated age-at-maturity to be between 7.5 and 8.2 years of age for females and 8.2 years of age for males for sandbar sharks in Taiwanese waters. Given the variability in growth estimates calculated by Wass (1973), we used vertebral centra from wild sandbar sharks to re-estimate growth-rates in the Hawaiian population.

Materials and methods

Sample collection and preparation

We collected sandbar sharks using demersal longlines outside of Kaneohe Bay, Hawaii at depths between 70 and 100 m (Fig. 1). Longlines were set perpendicular to the shoreline and baited with sardines, *Sardinops sagax*, chub mackerel, *Scomber japonicus*, yellowfin tuna, *Thunnus albacares*, skipjack tuna, *Katsuwonus pelamis*, barracuda, *Sphyraena barracuda*, and mahi-mahi, *Coryphaena hippurus*. Gangions consisted of a stainless-steel snap-clip attached to 3 m of monofilament followed by a 1-m stainless-steel leader that was attached to a circle hook. We used two sizes of gangions. Smaller gangions included 250 kg monofilament, 1.6 mm stainless-steel leaders, and 14/0 galvanized circle hooks, whereas large gangions included 410 kg monofilament, 2.2 mm stainless-steel leaders, and 18/0 stainless-steel circle hooks. Hooks were allowed to fish for 3 h before being retrieved. Captured sharks were landed, measured, and euthanized if needed for samples. At least five male and female sharks within each 5 cm size class between 45 cm PCL and 150 cm PCL were euthanized and vertebral samples were removed from below the first dorsal fin. Once the required vertebral samples had been collected, subsequently caught sharks were injected with oxytetracycline (OTC, 25 mg kg body weight^{-1}), tagged with Hallprint dart tags, and released for age-validation purposes.

Vertebral samples were frozen after collection. We cleaned the thawed vertebrae of excess tissue and stored five centra from each specimen in 75% ETOH. Using a Beuhler Isomet rotary diamond saw, we sectioned vertebral centra sagitally through the focus of the centrum. Sections were then dried for 24 h. Once dry, samples were mounted on a microscope slide via mounting medium. Samples were polished using a Metaserv 2000 grinder polisher until light was readily transmitted through the samples and rings were distinguishable using a dissection microscope. Vertebrae of sharks that were recaptured and sacrificed were examined under ultraviolet light for OTC marks.

Maturity

We determined maturity of males and females using macroscopic methods. Male sharks were classified as mature if claspers were deemed fully calcified (i.e. hard) and could be rotated forward (Clark and von Schmidt 1965; Driggers et al. 2004). Females were classified as mature if they were pregnant or had enlarged oviducal glands and well developed uteri (Castro 1993).

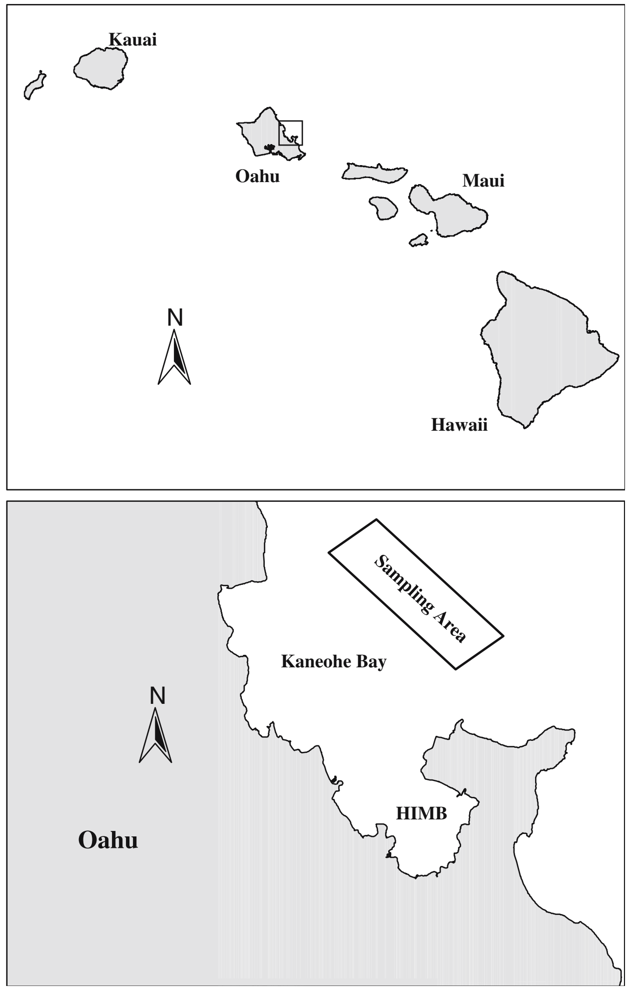


Fig. 1 Sampling area on the windward coast of Oahu. All sharks used for age and growth were captured within the rectangle noted as sampling area

Age assignment and validation

The rings or annuli counted for age estimates were defined as a band pair consisting of an opaque zone combined with a wider translucent zone in the intermedialia, which continued on to the corpus calcareum (Casey et al. 1985; Sminkey and Musick 1995). The birthmark was determined as the first band that intersected the inflection of the corpus calcareum. If annuli were not readily distinguishable, samples were stained with a 0.01% crystal violet solution to enhance readability.

Mounted vertebral sections were examined for age using a dissecting microscope and the Optimas video imaging system. The principal author and another reader conducted multiple blind readings of all vertebrae. Once all vertebrae were read, Hoenig's (1995) and Evans and Hoenig's (1998) tests of symmetry were conducted to test the hypothesis that age estimates between readers did not differ significantly and were due to random error.

Age estimates for vertebrae that were not consistent between readers were reexamined by both readers until a consensus was reached. The consensus estimate was used in the final analysis. If a consensus age estimate could not be reached the sample was removed from the study (Cailliet and Goldman 2004).

A relative marginal increment analysis was conducted to determine periodicity of ring formation (Branstetter and Musick 1994; Natanson et al. 1995; Goldman and Musick 2006). The Marginal Increment Ratio (MIR) is defined as:

$$\mathrm{MIR} = (\mathrm{VR} - R_n)/(R_n - R_{n-1}),$$

where VR = centrum radius, R_n = distance from the focus to the last complete narrow band, and R_{n-1} = the distance to the penultimate complete narrow band. All measurements were made along the corpus calcareum using an Optimas imaging system. We plotted monthly mean MIR values to determine the periodicity of band pair formation and tested for statistically significant differences for all months and seasons via one-way analysis of variance. Young-of-the-year sharks were not used in MIR analyses as they have no fully formed rings. We used centrum radius measurements to estimate the relationship between radius and precaudal length.

Growth models

Following Carlson and Baremore (2005), we fit four growth models to length-at-age data for male and female sharks. Two forms of the von Bertalanffy growth model were fit to the data (von Bertalanffy 1938; Beverton and Holt 1957; Cailliet et al. this issue). The first form, a three-parameter von Bertalanffy model (VB) incorporating the theoretical age-at-zero (t_0) term is described as:

$$L_t = L_\infty(1 - \mathrm{e}^{-k(t-t_0)}),$$

where t_0 = age or time when length theoretically equals zero. The second form of the model (VB2) used the length-at-birth intercept rather than a theoretical age at zero length and is described as:

$$L_t = L_\infty - (L_\infty - L_0)\mathrm{e}^{-kt},$$

where L_t = length at time t, L_∞ = theoretical asymptotic length, k = coefficient of growth, and L_0 = mean length-at-birth (47 cm PCL). Length-at-birth was estimated from observed at-term embryos and free-swimming young-of-the-year during this study as well as previously reported data by Wass (1973). A modified version of the Gompertz growth model (Ricker 1975) was also fitted to the data:

$$L_t = L_0(\mathrm{e}^{G(1-\mathrm{e}(kt))}),$$

where $G = \ln(L_\infty/L_0)$ (vonBertalanffy 1938). These lengths were determined from empirical data from this study and confirmed by Wass (1973). Finally, a logistic model (Ricker 1975) was fitted to the data:

$$L_t = L_\infty/(1 + \mathrm{e}^{-k(t-t_0)}).$$

All model parameters were estimated using the Marquardt least-squares nonlinear (NLIN) procedure in SAS statistical software (SAS V.9, SAS Institute, Inc). Growth parameter estimates for males and females were compared for statistically significant differences following the methods of Bernard (1981), Quinn and Deriso (1999), and Wang and Milton (2000) with a generalized T^2-statistic:

$$T^2 = (\beta_1 - \beta_2)' V^{-1} (\beta_1 - \beta_2),$$

where β_1 and β_2 are vectors of growth-model parameter estimates, V is the variance–covariance matrix of

$$[\beta_1 - \beta_2] : \beta_1 - \beta_2 = \begin{bmatrix} L_{\infty(1)} - L_{\infty(2)} \\ k_{(1)} - k_{(2)} \\ t_{0(1)} - t_{0(2)} \end{bmatrix}.$$

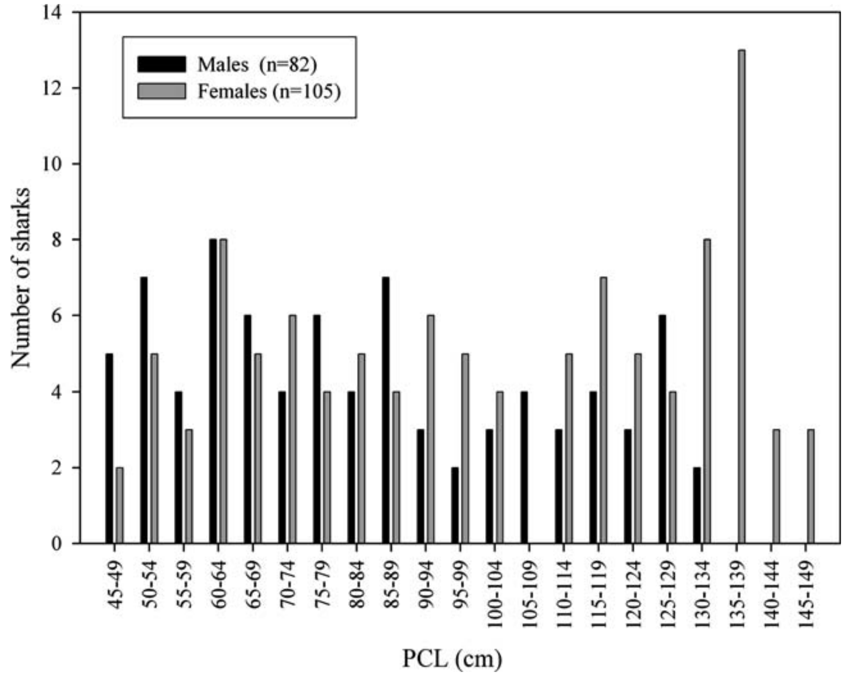
The coefficient of determination (r^2), residual mean square error (MSE), Akaike's Information criteria (AIC) (Akaike 1973), and standard deviation of the residuals were used as measures of goodness-of-fit for all models. A Shapiro–Wilks test and a normal probability plot of the residuals were used to test for normality, excessive skew or excessive kurtosis using the univariate procedure in SAS statistical software (SAS V.9, SAS Institute, Inc).

Results

Sample collection

We captured a total of 320 sandbar sharks as a part of this study. Vertebral samples were obtained from 194 sharks (Fig. 2) while the remainder of sharks were measured, tagged, injected with OTC and released. Size ranges for females and males captured were 46–147 cm PCL

Fig. 2 Size frequency of sandbar sharks used for age and growth in this study



and 46–132 cm PCL, respectively. Sharks were captured in all months except March.

Vertebral radius and length analysis

The relationship between vertebral radius and shark length (PCL = 12.0VR + 8.12) significantly correlated ($n = 148$, $r^2 = 0.97$, Fig. 2). No significant difference between males and females was found ($Z = 0.109$, $P = 0.55$), thus vertebral radius measurements were combined to estimate the regression.

MIR analysis

For combined sexes, MIR analysis suggests a single growth band pair is formed annually with the narrow opaque band being formed in winter months. Marginal increment ratios increased from spring to winter (Figs. 3, 4). Differences in monthly marginal increment ratios were not significant between all months in which samples were collected, (ANOVA, $n = 120$, $F = 0.64$, df = 8, $P = 0.74$, Fig. 4). The periodicity of band formation was also supported from one recaptured shark. This shark measured 60 cm PCL at its release on 26 June 2004 and 62 cm PCL at its recapture on 20 January 2005. An OTC stained opaque growth band was present at the very margin of the centra, suggesting ring formation had recently begun during the winter months.

Age estimation

After our initial readings, we reached consensus age estimates for 187 (105 females, 82 males) samples. Consensus could not be reached for seven samples which were removed from all analyses. Agreement between blind readings of readers was reached 43.1% of the time. Reader agreement was 71.2% within one band and 84.3% within two bands. We could not reject the hypothesis of symmetry between ages assigned by both readers ($X^2 = 38.64$, df = 39, $P = 0.488$, Hoenig 1995) indicating that differences between readers were due to random error.

Growth models

We found significant differences between male and female von Bertalanffy growth-model parameters, when using the form of the model that incorporated the theoretical age at zero length ($T^2 = 8.48 > T_0^2 = 8.11$, $P < 0.05$). Therefore, all models were subsequently fitted to male

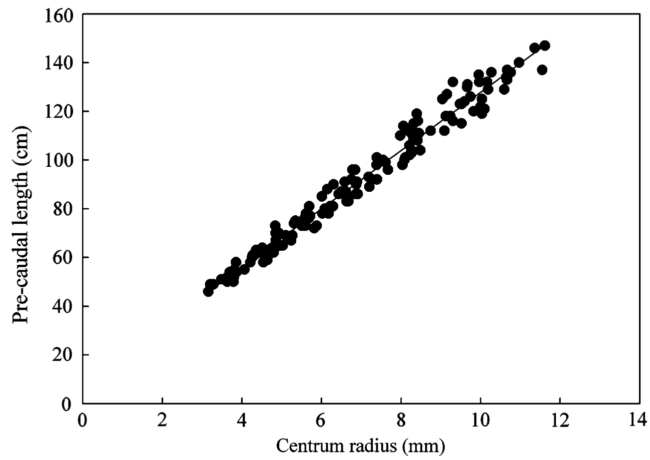


Fig. 3 Regression of pre-caudal length and centrum radius ($r^2 = 0.97$, $n = 148$) for males and females combined

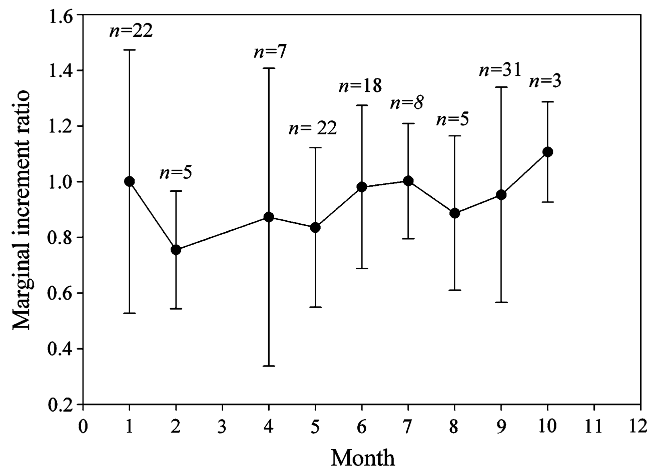


Fig. 4 Mean marginal increment ratio monthly values and standard deviation of the monthly means for both sexes combined

and female length-at-age data for each sex separately.

All growth models fitted to observed length-at-age data were significant ($P < 0.0001$, Table 1, Figs. 5, 6). Coefficients of determination were all greater than 0.94. The residuals of all models were normally distributed and no excessive skew or kurtosis was detected.

Table 1 Estimates of model parameters and goodness of fit statistics for models fitted to length-at-age data for male and female sandbar sharks.

	Model	L_∞ (cm PCL)	k (year^{-1})	t_0	L_0 (cm PCL)	AIC	r^2	MSE	SD of residuals
Males	VB	151.1(± 16.3)	0.09(± 0.03)	–5.01(± 1.02)	na	2639	0.951	33.75	5.74
	VB2	138.5(± 9.7)	0.12(± 0.02)	na	47	3381	0.994	42.74	6.31
	Gompertz	130.4(± 6.6)	0.19(± 0.03)	na	47	3780	0.993	47.8	6.58
	Logistic	134.3(± 7.5)	0.19(± 0.03)	1.98(± 0.66)	na	2740	0.995	35.05	5.85
Females	VB	164.9 (± 14.9)	0.08(± 0.02)	–5.26(± 1.08)	na	5307	0.943	51.97	7.14
	VB2	152.8(± 8.8)	0.10(± 0.02)	na	47	6406	0.994	62.16	7.72
	Gompertz	143.5(± 5.6)	0.17(± 0.02)	na	47	6976	0.995	67.69	7.98
	Logistic	146.4(± 6.4)	0.17(± 0.02)	2.66(± 0.61)	na	5278	0.995	51.69	7.12

All length values are for pre-caudal length (PCL) in cm. Values in parentheses are 95% confidence intervals. (VB = von Bertalanffy three-parameter model with t_0 term, VB2 = von Bertalanffy two-parameter model with empirical length-at-birth (L_0), L_0 = average measured length-at-birth used in VB2 and Gompertz growth models only, AIC = Aikake's Information Criteria, MSE = Mean Square Error, SD = standard deviation, na = not applicable)

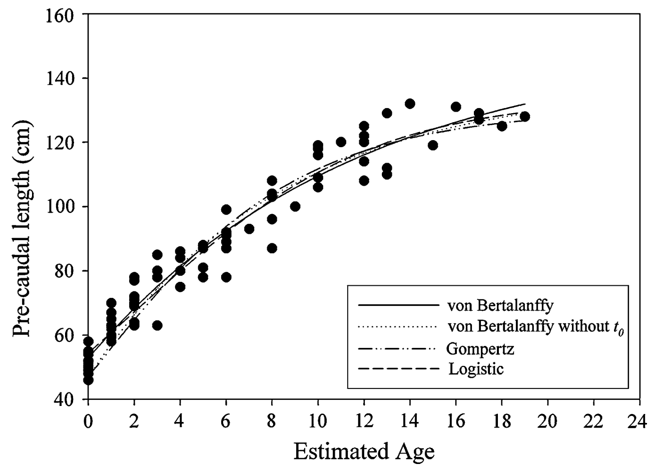


Fig. 5 Length-at-age estimates and growth models fitted to data for male sandbar sharks (n = 81)

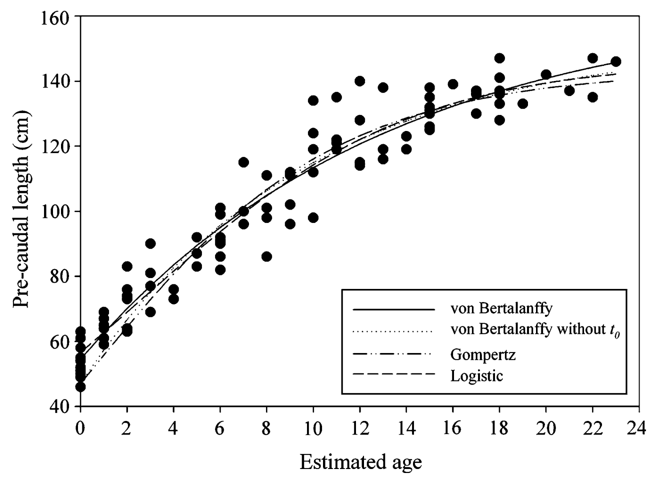


Fig. 6 Length-at-age data and fit of growth models to the data for female sandbar sharks (n = 105)

The von Bertalanffy growth model that included the theoretical t_0 term provided the best statistical fit to the observed size-at-age data for male sandbar sharks. This model had the lowest residual mean square error (MSE), and the lowest AIC values (Table 1). The von Bertalanffy growth model that included the theoretical t_0 term and the logistic model provided the best statistical fits to the observed size-at-age data for female sandbar sharks. These models had the lowest AIC and MSE values, respectively.

The three-parameter von Bertalanffy model produced the highest estimates for asymptotic maximum length for both males (151.1 cm PCL) and females (164.9 cm PCL, Table 1). The Gompertz model produced the lowest estimates for asymptotic length for males (130.4 cm PCL) and females (143.5 cm PCL). Observed maximum lengths for males (132 cm PCL) and females (147 cm PCL) fell within the 95% confidence intervals of all models. The three-parameter von Bertalanffy model produced the lowest estimates of the growth coefficient (k) for males (0.09 year^{-1}) and females (0.08 year^{-1}). The Gompertz and logistic models produced the highest estimates of the growth coefficient for males (0.19 year^{-1}) and females (0.17 year^{-1}).

Six sharks were recaptured over the time period of this study. Time at liberty ranged from 7 to 526 days. Lengths of recaptured sharks ranged from 60 to 77 cm PCL at release. The average growth rate was 6.97 cm year^{-1} for the five sharks that were at liberty for more than 100 days. This value agreed with growth rates for sharks in this size range estimated from vertebral analyses.

Mean length-at-age estimates determined from the three-parameter von Bertalanffy model differed between males and females (Table 2). Females were generally larger at a given age and attained older ages than males. Males attained maturity between 100 and 110 cm PCL and females attained maturity between 110 and 120 cm PCL. These sizes correspond to 8 and 10 years of age for males and females, respectively, as determined by the two-parameter von Bertalanffy model. Maximum observed age was 19 years for male and 23 years for females.

Discussion

Wass (1973) estimated maturity to occur at 3 years of age and produced k estimates of 0.4015 year^{-1} for males and 0.3745 year^{-1} for females by observing the growth rates of captive sharks. Wass also estimated maturity to occur at 10.2 and 13.1 years of age for males and females, respectively, using tooth replacement methodology and hypothesized the true value for the wild population to lie somewhere between the estimates from both methods used in his study. Using vertebral analyses, our estimated ages-at-maturity determined from the two-parameter von Bertalanffy models were 8 and 10 years of age for males and females, respectively, and produced k estimates of 0.12 and 0.10 year^{-1} for males and females, respectively.

Although all models fit the data well; statistically, the three-parameter von Bertalanffy model described the male size-at-age data better than the other three models. This model overestimated observed maximum size, but observed maximum size fell within the confidence intervals for this model. Size at birth was also overestimated by this model (47 cm PCL observed vs. 52 cm PCL predicted). The overestimate of size-at-birth could be due to the lack of newborns sampled during this study. The smallest male sampled was 46 cm PCL and only two females under 50 cm PCL were sampled. Despite the statistical ranking of the two-parameter von Bertalanffy model amongst the other models we feel the two-parameter von Bertalanffy growth model should be used

Table 2 Mean size at age for male and female sandbar sharks

	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
Females																								
PCL (cm)	53.5	63.9	72	79.6	74.5	88.5	90.9	103.7	99	105.3	117.4	124.3	124.3	124.3	121.7	131.1	139.0	135.0	137.0	133.0	142.0	137.0	141.0	146.0
SD	5.3	3.4	6.1	7.6	2.1	4.4	6.5	10.0	10.3	7.6	13.5	7.3	12.3	11.9	2.3	4.3	na	3.4	6	na	na	na	8.5	na
n	11	8	11	5	2	4	8	3	4	4	5	4	4	3	3	8	1	4	7	1	1	1	2	1
Males																								
PCL (cm)	50.9	63.4	70.3	76.5	81.3	83.5	89.3	93	99.6	100	114	120	118	117	132	119	131	128	125	128				
SD	3.12	3.52	5.05	9.47	4.86	4.8	6.89	na	8.26	na	5.77	na	6.8	10.4	na	na	na	1.41	na	na				
n	14	12	9	4	4	4	6	1	5	1	5	1	5	3	1	1	1	2	1	1				

All lengths are PCL (cm), SD = standard deviation, and na = not applicable when describing growth of the male sandbar shark in Hawaii. This model provided a biologically realistic fit to the observed data. Predicted maximum asymptotic length agreed closely to observed data (132 cm PCL observed and 138.5 cm PCL predicted, Table 1) and it incorporated observed size at birth.

All models fit the female size-at-age data well. Statistically, the logistic and three-parameter von Bertalanffy models fit the data better than the other models. The asymptotic length estimate from the logistic model agreed with observed maximum size (147 cm PCL). The logistic model overestimated the size-at-birth (47 cm PCL observed vs. 56 cm predicted). The three-parameter von Bertalanffy model overestimated asymptotic length and size-at-birth. As with the male data, we feel the two-parameter von Bertalanffy growth model provided a more biologically realistic fit to the female data and should be employed when describing the growth of the female sandbar shark in Hawaii.

The Gompertz models fit the data well for both sexes, but underestimated the maximum asymptotic length. This inherently increased the rate at which asymptotic length was approached and, therefore, these models provided the highest growth coefficients. The logistic models for both males and females provided high growth coefficient values due to the overestimation of the size-at-birth and estimate of asymptotic maximum size. The combination of these factors effectively increased the rate at which asymptotic length was approached.

The three-parameter von Bertalanffy growth model overestimated both size-at-birth and asymptotic maximum length for both sexes. Both estimates were unrealistic and caused the estimated growth coefficients to be the lowest amongst all models.

Given the variability of growth rates within and between populations it is imperative to conduct rigorous examination of all possible methods to describe length-at-age data. As illustrated in this study, models fitted to size-at-age data can produce variable estimates of growth parameters. In this study, the growth coefficient estimates ranged from 0.09–0.19 year^{-1} for males to 0.08–0.17 year^{-1} for females between all models. Growth coefficients are often used in demographic analyses for stock assessment purposes. Researchers must consider statistical results and observed biological data when determining which model provides the best fit to the data. Often the two viewpoints do not agree, as in this study. Although the three-parameter von Bertalanffy model, which is often the only model used to describe the growth of fishes, provided the best statistical fit to these data, it produced unrealistic asymptotic lengths and sizes-at-birth. Thus, we suggest the use of the growth parameters estimated by the two-parameter von Bertalanffy model.

Age and growth of sandbar sharks in Hawaii differ from other populations that have been studied. Growth coefficients in Hawaii (K = 0.09–0.19 year^{-1} for males and 0.08–0.17 year^{-1} for females) are much higher than those reported for the northwest Atlantic Ocean (k = 0.057 year^{-1}, combined sexes, Sminkey and Musick 1995). Hawaiian sandbar sharks obtain smaller maximum sizes (132 cm PCL for males and 147 cm PCL for females, observed) and reach maturity earlier (8 years for males and 10 years for females) than those in the northwest Atlantic (172 cm PCL, observed and 15 years at maturity, sexes combined). Sandbar sharks in Taiwanese waters also reach larger maximum sizes (209 cm TL for males and 219 cm TL for females, observed—Joung et al. 2004) than those in Hawaii (179 cm TL for males and 196 cm TL for females, observed). Joung et al. (2004) estimated the growth coefficient for sandbar sharks in Taiwanese waters to be k = 0.17 year^{-1} for both sexes combined and the onset of maturity to occur at 8 years of age for both sexes. The youngest sharks sampled in the Taiwanese study were 4 years-of-age which led to estimates of length-at-birth (80.8–85.8 cm TL) that were much larger than observed (60–65 cm TL) for this population. Therefore, the estimated growth coefficients may have been overestimated by the use of the three-parameter von Bertalanffy model, which incorporated the t_0 parameter, and the age-at-maturity underestimated. It is likely that the life history parameters of the Taiwanese population are intermediate between the Hawaiian and northwest Atlantic populations.

Vertebrae from larger sharks were more difficult to read due to decreased band pair widths near the margin of the vertebrae. This contributed to the increased variability in age estimates between readers as shark size increased. This also contributed to discrepancies in mean size-at-age estimates for older ages of male and female sandbar sharks (Table 2). The low sample sizes for older male sharks also contributed to these discrepancies. Although there were difficulties in assigning age estimates to specimens, the oldest sharks estimated blind consensus was 22 years for females and 12 years for males.

Our ageing methodology was supported via OTC mark recapture, but tagging and OTC validation has only been shown for one at liberty shark under 78 cm PCL. A more robust tag recapture data set is needed to obtain empirical data on the growth rates of sandbar sharks in Hawaii and to investigate the long-term movements of sharks in Hawaii. During the period of the study seven tagged sharks were recaptured. Time at liberty ranged from 7 to 526 days. Growth of these sharks during time at liberty supported our growth models for sharks between 60 and 83 cm PCL. All recaptured sharks were under 100 cm PCL and thus do not offer any support of our models for maturing or mature sandbar sharks in Hawaii.

The age and growth estimates for this population of sandbar sharks in Hawaii supports the generalization that sharks are slow growing and have low reproductive output. Currently, a legal fishery does not exist for this population. Should a fishery open, caution in management of the fishery should be exercised. The life history parameters of this population, as with other populations of slow growing, late maturing and low fecundity fishes, render it extremely vulnerable to overfishing even at low levels of fishing effort (Musick 1999).

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