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Age and growth of the bonnethead shark, *Sphyrna tiburo*, from northwest Florida, with comments on clinal variation

John K. Carlson[1,2] & Glenn R. Parsons[2]
[1] *Southeast Fisheries Science Center, National Marine Fisheries Service, NOAA, 3500 Delwood Beach Road, Panama City, FL 32408, U.S.A.*
[2] *Biology Department, University of Mississippi, University, MS 38677, U.S.A.*

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Synopsis

Age and growth rates of the bonnethead shark, *Sphyrna tiburo*, from northwest Florida were estimated from vertebrae collected between October 1992 and October 1995. The von Bertalanffy growth equation was fit to male and female vertebral age data. Initial growth was rapid (≈ 200 mm TL) for both sexes from age 0–1. At age 2 growth slowed for males but continued for females. Similar to many species of sharks, females grew slower than males (K = 0.28 and K = 0.69, respectively) but attained a larger maximum size (L_∞ = 1226 and L_∞ = 897). Maximum age was estimated in males and females to be 8+ and 12+ years, respectively. Growth of young-of-year sharks was 21 to 30 mm TL per month determined by three different methods. A comparison of age and growth estimates from populations at more southerly latitudes suggest that clinal variation in total length may be evident among bonnethead sharks in the Gulf of Mexico with females reaching larger sizes in northern areas as compared to south Florida.

Introduction

The bonnethead, *Sphyrna tiburo*, is a small species of shark, common in shallow coastal waters and estuaries of the Gulf of Mexico and southwest Atlantic Ocean, and reaches a maximum size of about 150 cm (Compagno 1984). Bonnethead sharks are classified as a small coastal species in the fishery management plan for sharks of the Atlantic Ocean, and are not currently considered to be overfished (National Marine Fisheries Service[1]).

[1] National Marine Fisheries Service. 1993. Fishery management plan for sharks of the Atlantic Ocean. U.S. Department of Commerce, National Oceanic Atmospheric Administration, National Marine Fisheries Service, Silver Spring. 167 pp.

Previous studies on bonnethead sharks documented differences in size and reproductive parameters from different areas. Parsons (1993a,b) found the average and maximum size of adult females, and size at birth, to be greater in a northern population of bonnethead sharks along the western coast of Florida. From these studies it was not clear whether differences could be attributed to population differences or due to latitudinal gradients.

Some shark populations exhibit geographic variation in growth and size. Blacktip sharks, (*Carcharhinus limbatus*), from the western Gulf of Mexico are thought to be smaller than those in the eastern Gulf of Mexico (Baughman & Springer 1950). Juvenile tiger sharks *Galeocerdo cuvieri* from the Gulf of Mexico had faster growth rates than those from

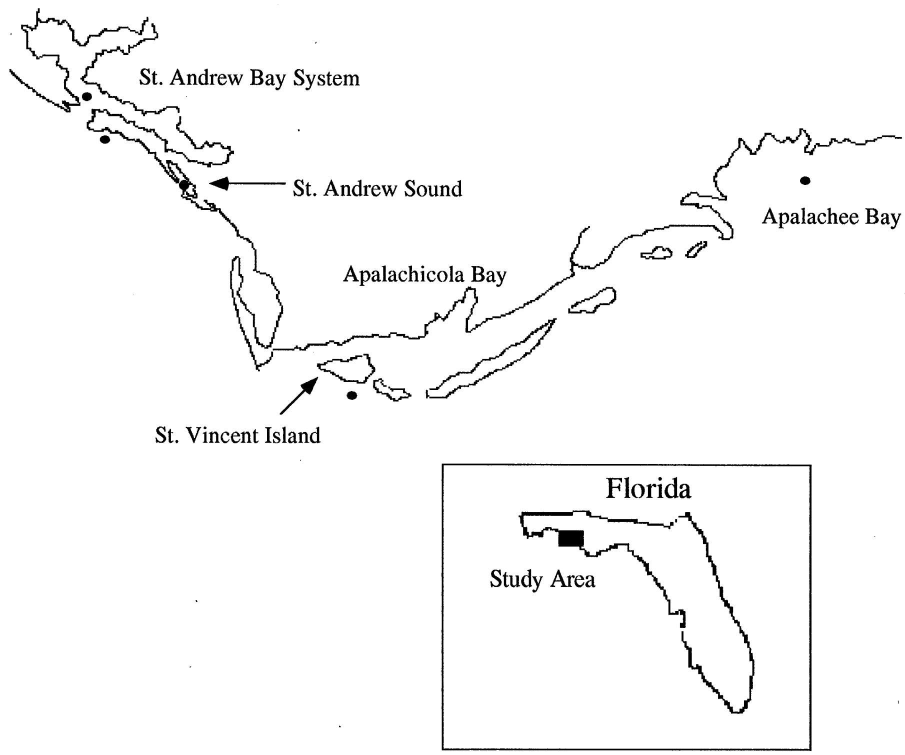

Figure 1. Map of study area in northwest Florida near latitude 30°00′ N and longitude 85°35′ W illustrating the five major stations (●) where bonnethead sharks were captured during 1992–1995.

the Atlantic Ocean off Virginia (Branstetter et al. 1987). If latitudinal gradients in size and growth exist, it is important to recognize them so that natural and potential anthropogenic affects can be discriminated. If sharks in a particular region show a smaller size structure than from other regions, the pattern may be explained by changes in mortality and growth affected in turn by possible factors such as fishing mortality. But if adverse changes occur, we may not be able to detect them unless we understand the natural influence of environmental factors (e.g. temperature, food limitations) across the geographic range where these sharks are common.

In this report for bonnethead sharks from northwest Florida, our objectives were to provide estimates of: (1) age and growth using the vertebral ring method; (2) early growth using both monthly length-frequency analysis on sharks held in captivity, and (3) a comparison in size and growth of bonnethead sharks from northwest Florida with sharks in more southern parts of Florida.

Methods

Bonnethead sharks were captured from northwest Florida using 90–330 m long gill nets with stretch mesh sizes of 5.0–20.0 cm between October 1992 and October 1995 (Figure 1). Sharks were caught during all times of the day, sexed, and measured (total length, TL) to the nearest mm. Sharks in poor condition were sacrificed for vertebrae, and those in good condition were tagged with a multi-recapture dart tag (Hueter & Manire[2]) and released.

[2] Hueter, R.E. & C.A. Manire. 1994. By-catch and catch-release mortality of small sharks and associated fishes in the estuarine nursery grounds of Tampa Bay and Charlotte Harbor. NOAA NMFS/MARFIN Program, Proj. Rep. NA17FF0378-01. 183 pp.

Vertebral sections were sampled anterior to the first dorsal fin, stored on ice, and then frozen. Vertebrae were prepared for ageing by removing excess tissue and soaking for 30 min in a solution of 5% sodium hypochlorite. Each vertebra was washed with water for 30 min following cleaning, and stored in 95% ethyl alcohol. Each vertebra was read by accentuating the rings with a soft lead pencil passed across the face of the centra (Parsons 1983). The rings were counted using a dissecting microscope and the centrum diameter measured. Ring counts were made independently by two readers. If the readers counts could not agree, the sample was eliminated from the analysis. A previous validation study (Parsons 1993a) indicated that with the exception of a ring formed at birth, rings form annually beginning with the first winter; we assigned ages to rings based on those findings.

Growth for male and female sharks was expressed using the von Bertalanffy growth equation (von Bertalanffy 1938) fitted to observed lengths at age using Marquardt least squares nonlinear regression. The equation is stated as:

$$L_t = L_\infty (1\text{-}\exp^{(-k(t-to))}),$$

where L_t =length at age t in years, L_∞ =maximum theoretical length, K = the growth coefficient and t_o = theoretical age at zero length. Longevity was approximated at the age at which L_∞ is reached and age at maturity was determined by comparing size at maturity information.

To determine monthly growth, as estimated according to the ‘Petersen’ method (Macdonald 1987), length data from juvenile bonnethead sharks (< 700 mm) were taken from the same stretch mesh (8.9 cm) gill nets to reduce size selectivity. The resulting length-frequency distributions were grouped into 10 mm length intervals and examined visually for polymodality and modal size progression. Monthly growth rate was determined by following the progression of the mode for three months.

Early growth were also obtained for 11 young-of-year sharks held in captivity. Sharks were transported to the laboratory by boat and acclimated for one week in a 20 x 15 x 1.5 m fenced area adjacent to the laboratory. After the acclimation period, we seined the pen, tagged the sharks with a Dalton rototag inserted in the dorsal fin, recorded TL, and released the sharks back to the pen. Sharks were held for up to 84 days from May through September and were fed to satiation every other day on a diet of squid or fish. Temperature, salinity, and dissolved oxygen levels fluctuated with environmental conditions present in the bay. Growth was estimated based on

Table 1. A comparison of life history parameters for male and female bonnethead sharks from northwest Florida, Tampa Bay, and Florida Bay. All lengths are expressed in mm TL. Values are ±95% confidence intervals and designated as (M) for male and (F) for female.

Parameter	NW Florida (This study)	Tampa Bay (Parsons 1993a)	Florida Bay (Parsons 1993a)
Theoretical maximum size (L_∞)	897 ± 51.1 (M)	888 ± 82.9 (M)	815 ± 80.9 (M)
	1226 ± 153.7 (F)	1150 ± 67.6 (F)	1033 ± 83.3 (F)
Growth coefficient (K)	0.69 ± 0.20 (M)	0.58 ± 0.27 (M)	0.53 ± 0.25 (M)
	0.28 ± 0.10 (F)	0.34 ± 0.09 (F)	0.37 ± 0.12 (F)
Theoretical age (yr) at zero length (t_o)	−0.04 ± 0.27 (M)	−0.77 ± 0.54 (M)	−0.64 ± 0.54 (M)
	−0.79 ± 0.43 (F)	−1.1 ± 0.43 (F)	−0.60 ± 0.40 (F)
Observed maximum size	1086 ± 18.7 (M)	890 ± 16.7 (M)	820 ± 18.8 (M)
	1241 ± 14.5 (F)	1160 ± 15.1 (F)	1037 ± 15.2 (F)
Observed average size	816 ± 18.7 (M)	823 ± 16.7 (M)	780 ± 18.8 (M)
	984 ± 20.1 (F)	1003 ± 15.1 (F)	909 ± 15.2 (F)
Age at maturity (years)	2.0 (M)	2.0 (M)	2.0 (M)
	2.4 (F)	2.2 (F)	2.3 (F)
Length of oldest animal	925 (M)	879 (M)	747 (M)
	1095 (F)	1110 (F)	992 (F)

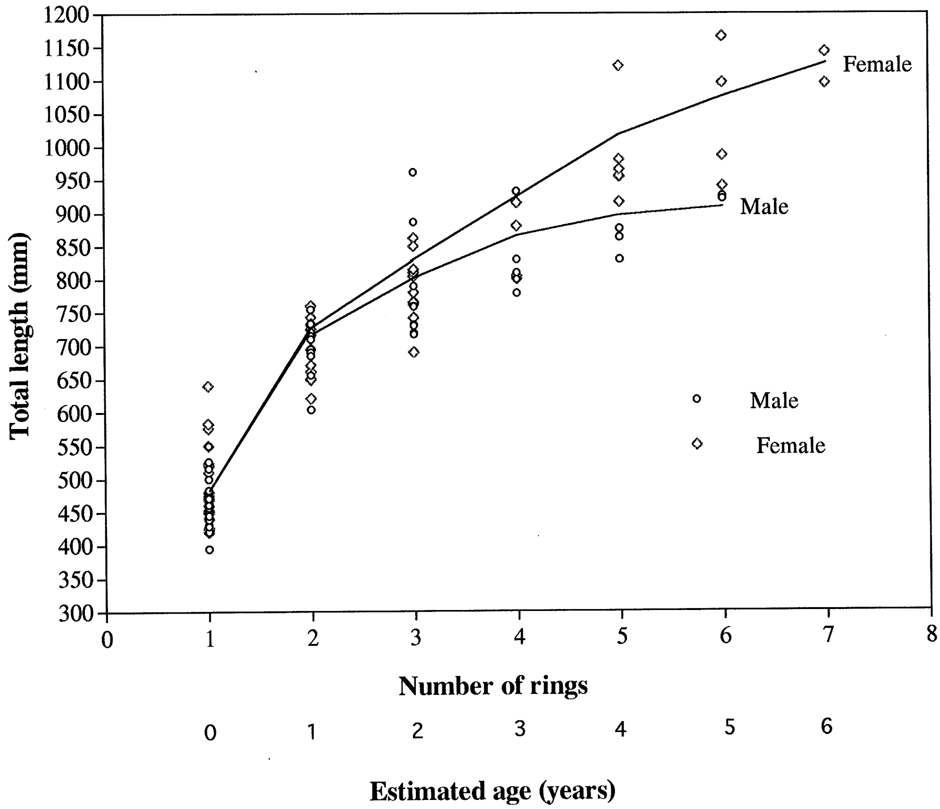

Figure 2. Von Bertalanffy growth equation fitted to observed length at age data for male (n = 50, r^2 = 0.92) and female (n = 65, r^2 = 0.93) bonnethead sharks captured in northwest Florida.

the difference between initial and final tagging length for sharks removed after 30 days and after 84 days.

Von Bertalanffy estimates and observed sizes of bonnethead sharks in northwest Florida were compared to those animals from Tampa Bay and Florida Bay (Parsons 1993a) to determine if there was latitudinal variation in growth and size. Growth models were compared by examining predicted size at age and for overlap in 95% confidence intervals. Additional statistical comparison of growth models using Hotelling's T^2 test (Bernard 1981) was also utilized. The differences in the observed size distribution between adult shark populations was tested using analysis of variance with post hoc comparison and regression of total length on latitude.

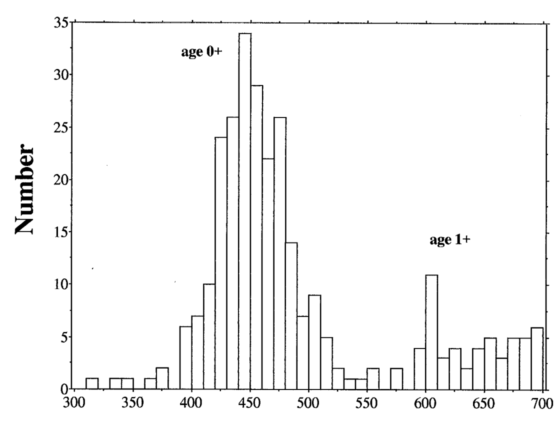

Figure 3. Length-frequency distribution of male and female bonnethead sharks (n = 286) caught in 8.9 cm stretch mesh gill nets in 1994 grouped into 10 mm intervals (e.g. 450–459 mm). Sharks caught above 700 mm were not included. The mean size of sharks was 450 mm (± 34.4) for age 0+ and 640 mm (± 37.1) for age 1+.

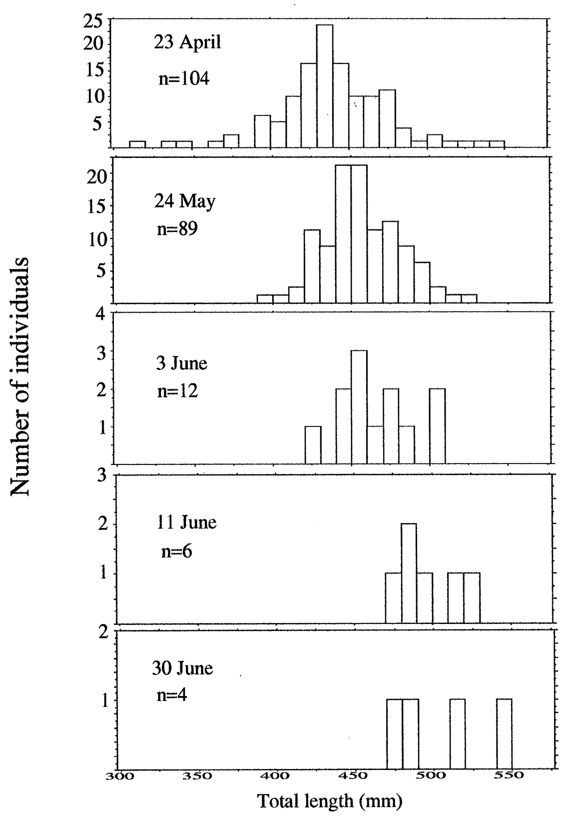

Figure 4. A length frequency distribution of young-of-year (age 0+) bonnethead sharks (range 310–550 mm TL; n = 215) based on date of capture (23 April–30 June 1994) and mesh size (8.9 cm). A line was fit through modes over time to estimate growth rate.

Results

Vertebral age and growth determination

Rings were readily recognizable which made counts straightforward. Agreement between independently determined ring counts was high with 90% matching exactly and 99% within one ring. In addition, vertebrae were collected only during summer months which allowed for less confusion that a ring has been deposited. We were able to assign ages to sharks possessing up to 6 (age 5, males) and 7 rings (age 6, females) within this population.

The von Bertalanffy growth model was fit to sex specific length at age data for 50 males (395–961 mm TL) and 65 females (420–1165 mm TL) (Table 1). Average growth was similar between sexes

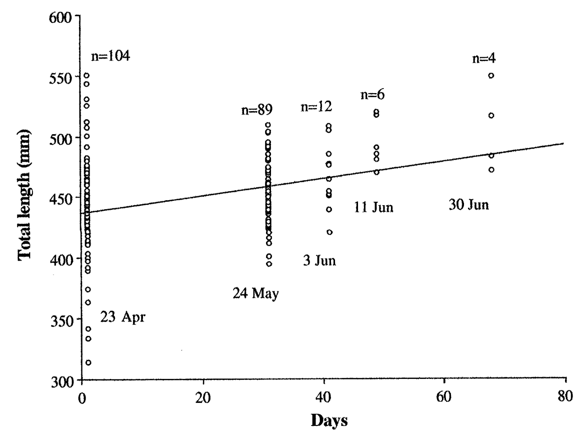

Figure 5. Growth of young-of-year bonnethead sharks (range 310–550 mm TL; n = 215) with a line fitted ($p < 0.05$, $r^2 = 0.13$) through lengths at days of capture. Data are taken for sharks captured in stretch mesh (8.9 cm) gillnets.

from age 0 to age 1, about 200 mm per year (Figure 2). Thereafter, males grew about 100 mm to age 2, 50 mm to age 3 and grew little after age 4. Females grew about 130 mm to age 2, 100 mm to age 3, 80 mm to age 4, 60 mm to age 5, and 40 mm to age 6.

Females had a lower growth coefficient (K = 0.28) than males (K = 0.69) but attained a larger maximum size and higher age of maturity and longevity (Table 1). Theoretical maximum size was 1226 mm for females and 897 mm for males. Preliminary reproductive data (Carlson unpublished data) suggests sharks mature at about 2.0 and 2.4 years for males and females, respectively. Longevity was approximated at age 12+ years for females and 8+ years for males.

Early growth rates

Growth of young-of-year bonnethead sharks were made by observing progressions in lengths of catches made from 23 April through 30 June 1994. We assumed that sharks smaller than about 550 mm were age 0+ and those above this were age 1+ based on examination of length data where the frequencies between the modal groups were lowest (Figure 3).

Length distributions of age 0+ sharks generally showed modal progression, and growth was estimated to be about 30 mm per month through dates of capture (Figure 4). Modal length was 435 mm on 23 April 1994 and increased to a mean of about 510 mm on 30 June 1994. A line was fit through the observed modes or means to determine growth (mode: 435, 23 Apr; 450, 24 May; 455, 3 Jun; 485 mm, 11 Jun; mean: 505 mm, 30 Jun); a mean length was used to replace the mode for 30 June because a distinct mode did not occur. Because sample sizes were small (n = 6 and 4) for the last 2 sampling periods, a regression model was fit to individual lengths through date of capture to corroborate modal growth (Figure 5). Linear regression provided the best fit to observed lengths ($r^2 = 0.13$, $p < 0.05$) and estimated growth at ≈ 21 (± 3.6) mm per month.

Young-of-year sharks held in captivity grew rapidly, on average 24.5 mm (± 4.9) per month (Table 2). The mean size of 11 sharks initially placed in the pen during May was 470 mm (± 27.9). The mean size increased to 490 mm (± 33.4) after 30 days and to 544 mm (±27.8) after 84 days.

Size comparisons

Length at age data for male shark populations in northwest Florida, Tampa Bay, and Florida Bay produced similar von Bertalanffy growth curves (Table 1). Predicted mean lengths were smallest in Florida Bay but 95% confidence intervals overlapped in all but two ages (Figure 6).However, using statistical methods outlined by Bernard (1981) that combines all von Bertalanffy parameters, statistical differences were found between male sharks from northwest Florida and Tampa Bay ($p < 0.05$); northwest Florida and Florida Bay ($p < 0.05$) and Tampa Bay and Florida Bay ($p < 0.05$).

Female growth curves appeared to be different between Florida Bay and Tampa Bay and Florida Bay and northwest Florida. Mean lengths were smallest in Florida Bay and 95% confidence intervals overlapped in only ages 0–3. However, growth curves did not appear to be different between northwest Florida and Tampa Bay with most ages overlapping in confidence intervals. Similar to males, Bernard's (1981) method found statistical differences in female sharks from northwest Florida and Tampa Bay ($p < 0.05$); northwest Florida and Florida Bay ($p < 0.05$) and Tampa Bay and Florida Bay ($p < 0.05$).

Comparisons of bonnethead sharks captured from Florida Bay, Tampa Bay (Parsons 1993 a,b) and northwest Florida showed latitudinal variation in size of adult female sharks along the western coast of Florida. Sizes of adult females significantly increased with latitude ($p < 0.05$, $F = 14.43$, df = 179) (Figure 7). Analysis of variance testing the effect of latitude on mean total length of adult females revealed a significant difference between populations ($p < 0.05$, $F = 21.12$, df = 179). However, Tukey mean separation procedure (Zar 1984) found the average size of females were not statistically different between northwest Florida and Tampa Bay ($p \geq 0.05$; mean size at NW Florida = 984 mm and Tampa

Table 2. Growth rates of bonnethead sharks held in captivity.

Initial total length (mm)	Recapture total length (mm)	Days elapsed	Increase in total length (mm)	Growth rate (per 30 days) (mm)
496	525	30	29	29.0
456	473	30	17	17.0
495	526	30	31	31.0
455	475	30	20	20.0
435	452	30	17	17.8
515	581	84	66	23.5
463	539	84	76	27.1
483	551	84	68	24.2
485	546	84	61	21.7
421	496	84	75	26.7
468	555	84	87	31.0

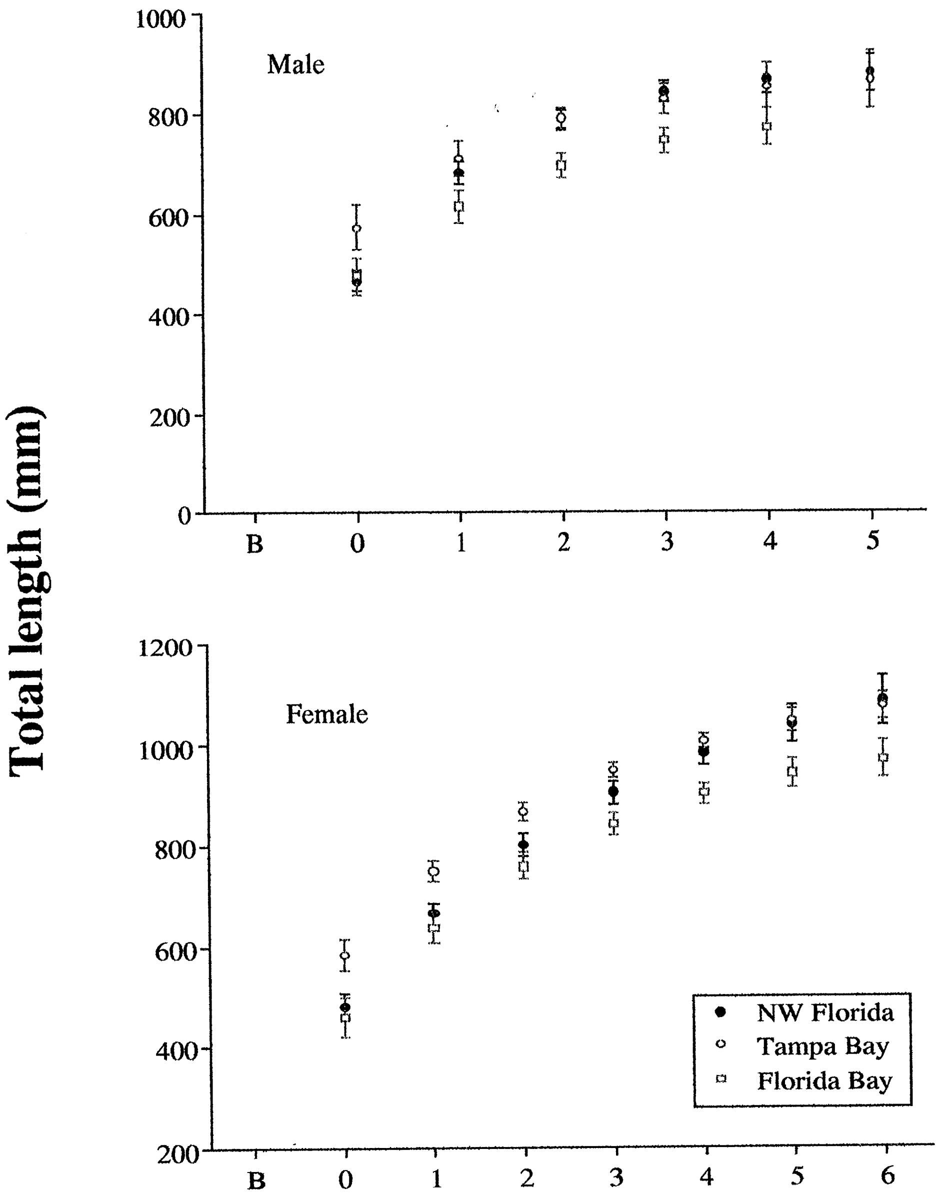

Figure 6. Growth curves for male and female bonnethead sharks from northwest Florida (this study), Tampa Bay and Florida Bay (Parsons 1993a). Mean size at age was estimated from the von Bertalanffy model. The vertical bars are 95% confidence intervals.

Bay = 1003) but were significantly different between Florida Bay and Tampa Bay ($p < 0.05$) and Florida Bay and northwest Florida ($p < 0.05$). Tampa Bay and Florida Bay were also found to be statistically different ($p < 0.05$). Adult male bonnethead sharks were of similar size ($p \geq 0.05$, $F = 3.30$, df = 81) along the western coast of Florida (Figure 6).

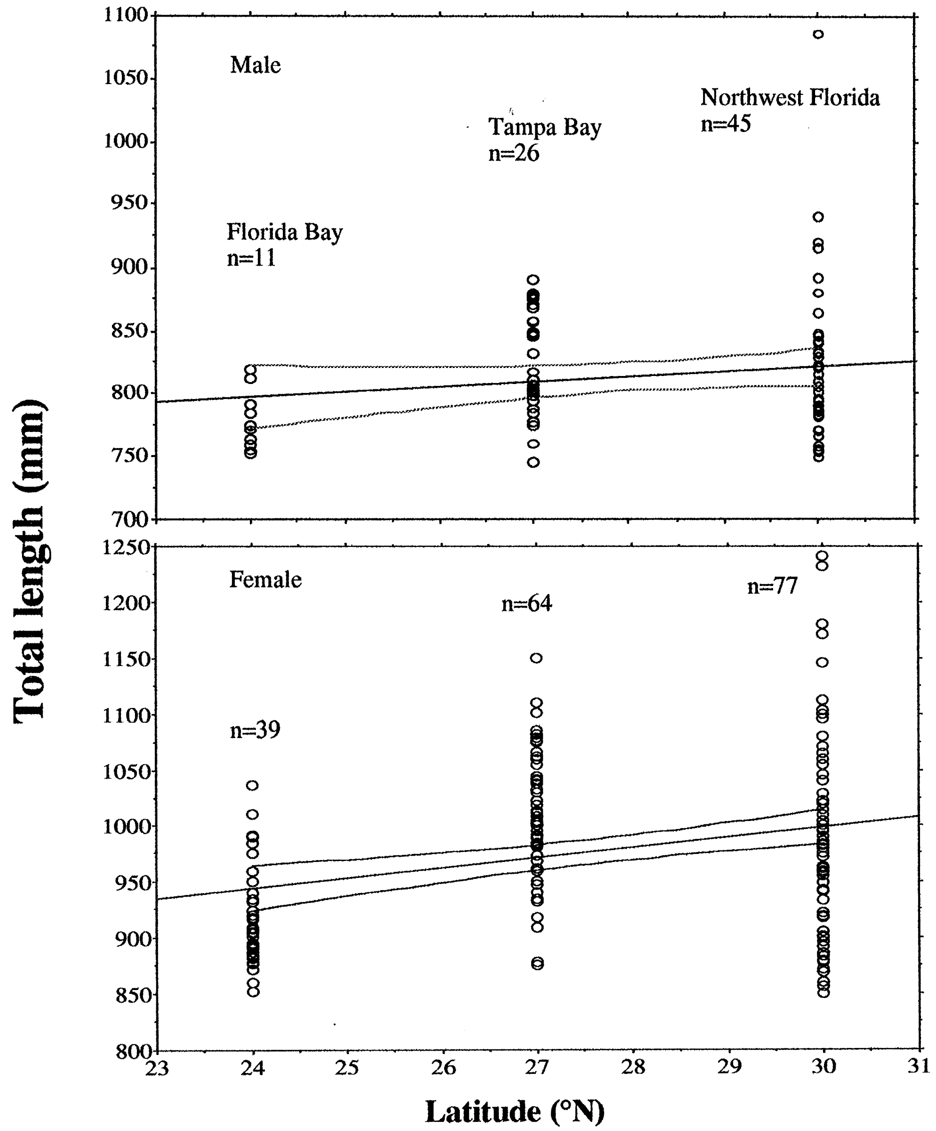

Figure 7. The relationship between total length of adult bonnethead sharks with geographic latitude. Lines surrounding the regression are 95% confidence intervals of the mean. A significant relationship ($p < 0.05$) was found with females among areas but not with males ($p \geq 0.05$).

Discussion

Age and growth estimates

The vertebral method provided valid growth data of this population of bonnethead sharks from northwest Florida. The estimates are verified by the size at age growth rates obtained through length frequency analysis. The use of length frequency analysis has been successfully used to verify growth curves in other studies (Calliet 1990, Simpfendorfer 1993). However, the use of length frequency information for verification was limited to age 0 sharks due to overlap of age groups beyond age 1. Furthermore, the von Bertalanffy growth equation for sharks in northwest Florida was fit to validated ring deposition information of bonnethead sharks from Parsons (1993a).

Observed size information from sharks captured shows similarity to the estimate of L_∞ calculated from the von Bertalanffy growth equation. The theoretical maximum size of males and females was estimated at 897 and 1224 mm TL, respectively. Modal groups of bonnetheads 1200–1250 mm (female) and 850–900 mm (male) were caught during this study thereby confirming the accuracy of asymptotic total lengths. Confirmation of growth parameters using this method has been used by Pratt & Casey (1983) on shortfin mako shark, *Isurus oxyrinchus*; Killam & Parsons (1989) on blacktip sharks, *C. limbatus*; Kusher et al. (1992) on leopard sharks, *Triakis semifasciata*; and Simpfendorfer (1993) on Australian sharpnose sharks, *Rhizoprionodon taylori*.

Female bonnethead sharks had a larger theoretical maximum size and age (1226 mm, 12+ years) than males (897 mm, 8+ years). Moreover, growth rates to maturity were similar for both sexes but growth slowed considerably for males, thereafter. The higher maximum size in females is due to continued growth of females after maturation and a older maximum age. Female sharks usually grow larger than males requiring separate growth analysis (Thorson & Lacy 1982, Parsons 1985, Pratt & Casey 1983, Casey et al. 1985, Killam & Parsons 1989, Kusher et al. 1992, Parsons 1993a, Simpfendorfer 1993) because construction of a single curve for both sexes would underestimate growth for females.

The growth coefficients (K = 0.28 and 0.69 for males and females, respectively) estimated for this population of bonnethead sharks were typical of values found in other small sharks of temperate waters. Parsons (1993a) found growth coefficients of 0.58 and 0.34 for male and female bonnethead sharks, respectively, from Tampa Bay, Florida. Atlantic sharpnose sharks, *Rhizoprionodon terraenovae*, from the northern Gulf of Mexico have growth coefficients between 0.36 and 0.53. (Parsons 1985, Branstetter 1987). However, most larger shark species, such as the dusky shark, *C. obscurus*, have much slower growth rates (K = 0.03), a later age at maturity (19–21 years) and higher maximum age (33 years) (Natanson et al. 1995). Consequently, the rapid growth rates in smaller species found in warmer waters appear to be a function of their early age of maturity, usually 2–3 years, and being relatively short lived (up to 12 years).

Early growth rates

The length frequency method has been used to estimate growth in other shark species. Pratt & Casey (1983) determined growth for three age classes of mako shark using similar methods. Killam & Parsons (1989) assessed growth of juvenile blacktip shark by following modes for 12 months. Kusher et al. (1992) produced growth rates by using size mode analysis of leopard sharks. Although modes were identified subjectively and estimating growth using these methods can be problematic (Macdonald 1987), there was little overlap among bonnethead shark cohorts and growth was estimated only for young-of-year sharks when there is less variation in size at age and growth is similar.

Early growth estimated using 3 methods: following modal length progression over time, using regression on length-frequency and from tagged sharks held in captivity, was similar from 21–30 mm per month. The grand mean of these is 24.5 ± 4.5 mm per month and shows considerable similarity to a captive growth rate from young-of-year sharks of 27 mm per month by Parsons (1993a).

The rapid growth of young-of-year bonnethead sharks is similar to early growth determined for other small coastal species. Young-of-year Atlantic sharpnose sharks *R. terranovae* grew at a rate of up to 50 mm per month during summer, but slowed during winter (Parsons 1985, Branstetter 1987). Australian sharpnose sharks (*R. taylori*) from north Queensland, Australia grew 315 mm from age 0 to age 1 (Simpfendorfer 1993). However, this relatively high growth rate is an attribute of juvenile growth and decreases considerably once maturation has occurred.

Size variation among areas

Increasing size with latitude for the bonnethead shark has been suggested to occur along the western coast of Florida from Florida Bay to Tampa Bay (Parsons 1993a,b) and our results support this conclusion. Parsons (1993a) found maximum and mean size of female sharks to be larger in more northern areas along the western coast of Florida. The results from this study on bonnethead sharks from northwest Florida extends the clinal range, and thus supports the contention of increasing size with latitude.

Growth plasticity has been suggested to be caused by differences in environmental conditions among areas. Bonnethead sharks continuously exposed to warmer temperatures may have elevated standard metabolism than those from cooler waters (Parsons 1993b). This additional energy expenditure may limit energetic investment in reproductive and somatic growth. Water temperatures are slightly cooler along the northern Gulf of Mexico (Galtsoff 1954) but whether variation in environmental conditions caused differences in size among areas is still unresolved. A study of the influence of temperature on energy budgets for sharks in northwest Florida would test this hypothesis.

Statistical analysis of the von Bertalanffy growth equation gave contradictory results on differences in growth between these populations. The mean size at age data produced similar growth curves and the overlap of confidence intervals between some ages would tend to indicate similar growth rates between populations. Yet, results from Bernard's (1981) multivariate analysis suggest growth is not similar between populations. However, this method (Bernard 1981) combines von Bertalanffy parameter values and analyzes them simultaneously which may give statistical differences which are not real.

Movement patterns of adult bonnethead sharks may also confuse size differences between Tampa Bay and northwest Florida. Although larger sharks were found in northwest Florida, the average size of adult females was not significantly different between Tampa Bay and northwest Florida. This may suggest mixing of individuals between Tampa Bay and northwest Florida. On 21 June 1995, a female bonnethead shark (850 mm TL) that was tagged in northwest Florida was recovered about 180 miles to the south near Cedar Key (C.A. Manire personal communication) which demonstrates that at least some mixing occurs between these two areas.

Although this study was inconclusive in measuring distinct clinal characteristics in size, female bonnethead sharks show a tendency to be larger at a later age at more northern latitudes. In order to clarify whether a distinct cline is evident, research is needed especially in the energy budgets and reproductive biology of bonnethead sharks from northwest Florida. Size at birth, fecundity, and energetics may be different in bonnethead sharks from northwest Florida compared to Tampa and Florida Bay (Parsons 1993b). Moreover, the effect that environmental parameters, such as temperature and food availability, have in shaping life history characteristics should additionally be clarified.

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