SUMMARY PAPER

# Shark Ageing Methods and Age Estimation of Scalloped Hammerhead, *Sphyrna lewini*, and Dusky, *Carcharhinus obscurus*, Sharks Based on Vertebral Ring Counts

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## INTRODUCTION

Ageing of bony fishes, which began as early as 1759 (Hederström 1959), has often been accomplished by counting growth rings on a variety of skeletal structures such as scales, spines, otoliths, head bones, or vertebrae (Menon 1950; Chuganova 1963; Bagenal 1974). Conversely, elasmobranchs are difficult to age as they possess few hard skeletal structures. I review shark ageing methods and present data on scalloped hammerhead, *Sphyrna lewini*, and dusky, *Carcharhinus obscurus*, sharks, captured in North Carolina, where, with remarks on 10 other species, age was estimated based on counts of vertebral rings stained with silver nitrate.

## PREVIOUS SHARK AGEING METHODS

Many early attempts to age sharks were conducted by investigators noting size differences for aquarium or experimentally held specimens (Hisaw and Abramowitz 1937; Clark 1963). Other studies assessed length frequency data to separate year classes of tag-recaptured individuals as a means to estimate age (Templeman 1944; Olsen 1954; Aasen 1963; Ketchen 1975; Davies and Joubert 1967; Kato and Carvallo 1967; Wass 1973; Stevens 1975; Grant et al. 1979). Although the accuracy of age interpretations obtained from length frequency histograms has been increased by plotting the data on probability paper (Cassie 1954), or by using computers (Hasselblad 1966), early age estimates of sharks was still an arduous procedure that lacked a direct ageing method, such as ring counts on skeletal hardparts.

Recently Forrester et al. (1972) and Childs et al. (1973) used mercury accumulations in vertebrae to estimate age in elasmobranchs. However, Forrester's et al. (1972) mercury level-length frequency estimates were substantially less than those predicted by Bonham et al. (1949) who studied the same species but used length-frequency analysis. Childs' et al. (1973) mercury level data were likewise inadequate when applied to pup or small-sized sharks (Ketchen 1975).

Tooth replacement of upper and lower teeth in sharks, which are continuously renewed from posterior to anterior, can be related to body growth (James 1953; Strasburg 1963; Applegate 1965; Moss 1967). For example, knowing tooth replacement rate, Moss (1972) estimated maximum body size and age of maturity for the lemon shark, *Negaprion brevirostris*. Other shark ageing methods utilized fin spines (Kaganovskaia 1933; Holden and Meadows 1962; Ketchen 1975), and vertebral ring counts (Ridewood 1921; Aasen 1963; Parker and Stott 1965; LaMarca 1966; Holden 1974; Stevens 1975).

Most previous shark ageing techniques were unvalidated since growth rings in spines or vertebrae, i.e., of spiny dogfish, *Squalus acanthias* (Holden and Meadows 1962), basking shark, *Cetorhinus maximus* (Parker and Stott 1965), and porbeagle, *Lamna nasus* (Aasen 1963), had not been substantiated as annual events. Parker and Stott (1965) examined unstained vertebrae of the basking shark and suggested that two rings were formed annually based on a correlation of a hypothetical asymptote growth curve calculated from size frequency data. However, this information has been criticized by Pauly (1978). Stevens (1975), Holden and Vince (1973), Cailliet, Martin, Harvey, Kusher, and Welden (1983); Cailliet, Martin, Kusher, Wolf, and Welden (1983); Casey et al. (1983); Gruber and Stout (1983); and Pratt and Casey (1983) also counted, often under reflected light, the circuli in the centra of vertebrae and thereby estimated age. Although LaMarca (1966), studying the sand tiger, *Odontaspis taurus*, established that vertebral rings were present, he did not know if these rings were actually calcified or just "a peculiar tinctorial property of the centra." Several vertebrae were decalcified by LaMarca (1966) in 5% nitric acid for 18 h before staining. Instead of being stained, these vertebrae were completely colorless. This suggested that the stained areas were areas of concentrated $Ca^{++}$. Calcified vertebral rings have also been reported and related to age for: Porbeagle (Stevens 1975); basking shark (Ridewood 1921; Parker and Stott 1965; Springer and Gilbert 1976); eiraku shark, *Galeorhinus japonicus*, (Tanaka et al. 1978); blue shark (Stevens 1975); sandbar shark, *Carcharhinus plumbeus*, (Springer 1960; Wass 1973; Casey et al. 1983); and other species. Ridewood (1921) suggested ring calcification may be a response to physiological demands of the cartilage.

Holden and Vince (1973), using tetracycline as an internal tag, were the first to validate elasmobranch vertebrae ageing methods by establishing that opaque and translucent zones were formed annually in the skate, *Raja clavata*, and could be used as a means to count rings as age markers. Gruber and Stout (1983) also used tetracycline in age studies of the lemon shark. Urist (1961), employing X-radiography, determined that the various densities within shark vertebrae were associated

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with $Ca^{++}$ and $P^{2}$ depositions. Jones and Geen (1977), using radiography on the spiny dogfish, also noted that vertebral rings contained high levels of $Ca^{++}$ and slightly lower levels of $P^{2}$. Others that used X-ray methods to age sharks were Ishiyama (1952), Aasen (1963), Applegate (1967), Cailliet, Martin, Harvey, Kusher, and Welden (1983), and Cailliet, Martin, Kusher, Wolf, and Welden (1983), yet the main problem that remained was determining the time of growth band formation.

Others, such as Bass et al. (1975), Cailliet, Martin, Harvey, Kusher, and Welden (1983), Cailliet, Martin, Kusher, Wolf, and Welden (1983), and Casey et al. (1983), have tried to determine a shark's age by calculating or estimating maximum size by employing growth model procedures of Walford (1946), Beverton and Holt (1957), or von Bertalanffy (1957). Subsequent ages were then determined after applying known length data to these models. Holden (1974) suggested that the von Bertalanffy growth curve could be constructed on the basis of embryonic growth rate data and thereby estimate age at maturity for several species of dogfish, (*Mustelus* spp.). Holden (1977), Tanaka and Mizue (1979), and Francis (1981) carried this procedure further in their studies of *Mustelus* spp.

Several stains have been used by others to enhance ring patterns in elasmobranch vertebrae (Gruber and Stout 1983). Haskell (1949), Stevens (1975), and Johnson (1979) proposed silver nitrate or crystal violet staining methods as a means to enhance ring definition. De Crosta (1981), Thorson and Lacy (1982), Cailliet, Martin, Harvey, Kusher, and Welden (1983), Cailliet, Martin, Kusher, Wolf, and Weldon (1983), and Pratt and Casey (1983), have also applied the silver nitrate stain technique to a variety of sharks from California, Hawaii, Nicaragua, and the northeast United States.

## DEFINITIONS

The following definitions of terms apply throughout this paper. For more detailed definitions see the Glossary.

Ring: A mark or zone on the vertebrae which may be (but not necessarily) formed once each year (analogous to annulus, see Glossary).

Marginal increment: That distance or growth from the last ring to the outermost edge of the vertebra.

Vertebral radius: That distance from the focus to the outer margin of the vertebra.

## SCALLOPED HAMMERHEAD AND DUSKY SHARKS

Supposedly, some of the obstacles that stood in the way of determining the age of sharks were overcome following the work of LaMarca (1966) and Stevens (1975) who studied the concentric rings on the inner concave faces of shark vertebrae. Yet, questions still remained on how the vertebrae should be prepared, "How long should they be exposed to the stain, could the time of growth band formation be determined, and what modifications were necessary to the stain methods for best results?" Some of these questions were addressed by studying the age of the scalloped hammerhead and dusky sharks.

## METHODS

Twelve of the 36 species of sharks known to occur in North Carolina waters (Schwartz 1979) were captured from April through November, between 1968 and 1981, in the Atlantic Ocean 1-3.5 km south of Shackleford Banks and 4-6.5 km east of Beaufort Inlet, N.C. All sharks were caught on unanchored 4.8 km longlines of 7.6 mm braided nylon which were fished in depths of 9-14 m. Drop lines of No. 2 chain, 1.8 m long, were snapped onto the mainline at either 9.1 or 13.7 m intervals, depending on desirability of the line to be fished high or low in the water column. Hooks were No. 9 tuna hooks. Orange plastic floats were attached to the mainline every 10 hooks to help suspend the line and keep it off the substrate. Two sets of 100 or 200 hooks per set were made daily, one east-west, the other north-south, to note capture with depth and tide.

Bait was whole fresh fish. Soak time of the line varied between 2 h for spring and fall sets to 1 h during June-September sets, when waters were the warmest. Live sharks were tagged and released. Sharks that had died fighting the line or were near death were measured (fork length), sexed, embryos removed from females, and vertebrae excised directly beneath the first dorsal fin.

### Vertebral Preparation

Excised vertebrae were cleaned of excess muscle, cartilage, and either frozen or air dried under ordinary incandescent 60-W lamps for several days before storage. These "fresh" vertebrae were compared with long-term dried specimens in relation to their reliability and use in ageing, density of stain retention, and ring enhancement once stained. Both fresh and dried vertebrae proved equally receptive to staining and usable for ageing. Although no shark vertebrae that had been preserved in Formalin[2] or alcohol were used as part of this study, vertebrae shat had been preserved in Formalin and stored in 70% isopropyl alcohol for as long as 3 mo were acceptable for age determination, as they exhibited distinct rings upon staining. However, I do not recommend Formalin-preserved vertebral samples since Formalin acts as a decalcifying agent (Lillie 1954), which may etch the vertebrae and render the rings less distinct or poorly stained.

Freshly excised vertebrae were separated with a sharp knife by cutting the junction separating two adjacent vertebral centra. Vertebrae of small specimens were readily separated by simply bending the vertebral column until the juncture broke apart. Dried vertebrae were often more difficult to separate, especially from extremely large sharks, and usually necessitated careful cutting between the disks with a saw until bending or rupture separation occurred.

Vertebral fascia was removed by soaking the vertebrae in 5.25% sodium hypochlorite for approximately 1 h (Johnson 1979). Soak duration depended on size of vertebrae and how much fascia material was removed before soaking. Other methods for removing vertebral fascia connective tissue were: Soaking the vertebrae for 24 h in 0.2% sodium hydroxide and then carefully removing the connective tissue with forceps (LaMarca 1966), or soaking the vertebrae in 10 ml of 0.7% pepsin in 0.2% HCl with incubation at 39.4 °C for 24 h. Soaking the vertebrae in sodium hypochlorite was adopted as the easiest method, as it saved time and was the cheapest way to prepare the vertebrae before staining.

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Once cleaned, several staining methods, such as alizarin red S and anise oil, were also tried. However, only two were considered of value in enhancing growth rings: Staining with silver nitrate (Stevens 1975) and crystal violet (Johnson 1979). In general, the crystal violet method was used only when doubt, as revealed by the silver nitrate stain, existed in distinguishing growth rings. Modifications of stain time or procedure, in relation to shark fork length, for the silver nitrate and crystal violet methods are tabulated in Tables 1 and 2. Each stained vertebra was examined by two observers and when agreement as to number of rings or marginal increment distance did not correspond, the vertebra was not used in further age determination.

**Table 1.—Silver nitrate and crystal violet staining procedures for vertebrae of 12 species of sharks.**

Blacknose shark, *Carcharhinus acronotus*
Blacknose shark vertebrae were prepared as noted in the text. However, vertebrae should be left in the silver nitrate stain for approximately 0.5 min longer than the standard indicated time. While staining, regardless of shark size, the vertebrae should be checked every 30 s for the desired intensity of stain. Immersion staining time, depending on vertebra size, in crystal violet, which worked well, is noted in Table 2.

Blacktip shark, *Carcharhinus limbatus*
Blacktip shark vertebrae, as in the blacknose shark, had to be stained approximately 0.5 min longer in silver nitrate for best definition. The crystal violet procedure seemed to work better than the silver nitrate method for this species.

Bull shark, *Carcharhinus leucas*
Increase stain time in silver nitrate by 0.5-1 min for vertebrae of sharks larger than 2,000 mm FL. Crystal violet stain time follows that stated in Table 2.

Dusky shark, *Carcharhinus obscurus*
Of all the sharks tested, growth rings on dusky shark vertebrae were hardest to stain. Fresh vertebrae worked best, while dried vertebrae had to be immersed in the silver nitrate approximately 1-1.5 min longer than usual to pick up the stain. See Table 2 for immersion time depending on shark size.

Lemon shark, *Negaprion brevirostris*
Increase stain time in silver nitrate by 1 min for sharks larger than 2,000 mm FL as extremely large vertebrae stain slowly. Follow crystal violet stain intervals noted in Table 2.

Sand tiger shark, *Odontaspis (Eugomphodus) taurus*
Increase stain time in silver nitrate 0.5 min longer than in Table 2. Follow crystal violet stain intervals in Table 2 for large lemon sharks.

Sharpnose shark, *Rhizoprionodon terraenovae*
A change from the standard procedure is necessary because of the structure of the sharpnose vertebrae. The concave face of the sharpnose shark vertebra is deep and possesses a small hole in the middle which permits the stain to run through instead of being retained on the face. The entire vertebra must therefore be completely immersed in the silver nitrate or crystal violet stains. Failure to retain the stain on the concave face of the vertebra may jeopardize staining the first growth band.

No changes were necessary in either the silver nitrate or crystal violet methods noted in the text for the following:
Great hammerhead, *Sphyrna mokarran*
Sandbar shark, *Carcharhinus plumbeus*
Scalloped hammerhead, *Sphyrna lewini*
Silky shark, *Carcharhinus falciformis*
Spinner shark, *Carcharhinus brevipinna*

**Table 2.—Suggested duration (minutes) of immersion of shark vertebrae in silver nitrate or crystal violet stain, according to fork length of shark.**

| Silver nitrate | | Crystal violet | |
|---|---|---|---|
| Time (min) | Fork length (mm) | Time (min) | Fork length (mm) |
| 1 | -600 | 10 | -700 |
| 1.25 | 700-900 | 12 | 700-1,000 |
| 1.50 | 900-1,000 | 15 | 1,000-1,500+ |
| 2 | 1,000-1,200 | | |
| 3 | 1,500-2,590+ | | |

## Silver Nitrate Stain Method

The silver nitrate method can be used for vertebral faces that have been thoroughly cleaned and repeatedly washed for at least 5 min in distilled water after cleaning. This can be achieved by using a series of five jars with a 1 min transfer rinse in each. The 1% stain should be stored in a dark bottle and away from light when not used to prevent deterioration. Contrary to Stevens (1975), who fully immersed the vertebrae in the stain, each vertebra was positioned with one concave face uppermost. The concave vertebral face of each species examined, except for those of the Atlantic sharpnose shark, *Rhizoprionodon terraenovae*, was filled to the brim with a 1% silver nitrate solution. A 2-3 ml overfill was often necessary to insure staining the extreme edge of exceptionally large vertebrae. Filling only one concave face instead of immersing the entire vertebrae conserves staining solution and permits a tidier and just as reliable operation. Sharpnose shark vertebrae have to be completely immersed in the stain since a large hole occupies the center of the vertebra, thereby permitting the stain to run out, instead of being retained as in other shark vertebrae.

The centrum should be exposed to the stain for 1-3 min, depending on size of vertebra (Table 2), and illuminated for 2 min with a 4-W UV lamp. Overstaining can easily occur, so it is advisable to check the centrum every 30 s to note the intensity of staining. While destaining with sodium thiosulfate or Kodak Farmers reducer is possible, neither method was used. Following staining, the vertebra is rinsed in distilled water and transferred to a 5% solution of sodium thiosulfate for 2 min. Stained vertebrae can be stored dry or in 70% isopropyl alcohol (Stevens 1975) once the thiosulfate has been rinsed off with distilled water.

## Crystal Violet Stain Method

The crystal violet stain method consisted of cleaning the vertebra, then soaking it in 0.01% solution of crystal violet. Johnson (1979) suggested a soak time of 0.2 to 4.0 h, depending on vertebra size for teleosts. Shorter stain intervals of 10-15 min were used in this study (Table 2), with best ring definition attained if the vertebra was first overstained and then destained in 50% isopropyl alcohol, until the desired intensity of the growth rings was achieved. Destaining requires only 1 min, at most, for best results.

## Reading Vertebrae

Vertebrae were measured with the centrum lying flat on the microscope stage with a calibrated ocular micrometer in a Bausch & Lomb dissecting scope under 0.7 × magnification and with overhead illumination on a dark background. Growth rings appeared as opaque and translucent zones (see Glossary). Distances from the core to and between each visible stained ring and from the core to the outer edge of the centrum were measured with the interface of the centrum at an angle to the field of view. Growth rings were best discernible immediately following staining. Immersion in water or glycerol did not increase ring intensity appreciably.

To gain insight into when growth rings were formed, vertebrae were grouped by month of capture. Size of growth rings was measured, noting when large or small incremental variations occurred between rings, especially near the edge of the centrum.

The relationship between vertebral radius and fork length was determined for scalloped hammerheads and dusky sharks using linear regression, rather than a curvilinear relationship often used for other fishes (Rounsefell and Everhart 1953). This was expressed by the formula $y = a + bX$ where $X$ was vertebral radius (in millimeters) and $y$ was shark fork length. Substitution of the measurement distance from core to each growth ring, for each species, into the linear relationship formula permitted back calculations of length for each estimated age observed. All statistical inferences were made with a significance level of $\alpha = 0.05$.

In this report, I concentrate on the age and growth of the scalloped hammerhead and dusky sharks, as those species were the most abundant of the 12 species captured. Growth and back-calculation estimates for most of the other 10 sharks studied will await adequate samples of vertebrae and are outside the scope of this study.

## RESULTS AND DISCUSSION

Even though criteria used to estimate age and growth were first established by studying teleost fish scales (Van Oosten 1929), the same criteria can be adapted to estimate a shark's age and growth. These criteria (Jolley 1977; Brothers 1983; Smith 1983) can be summarized as follows: 1) The ageing structure must develop early in life and remain constant in number and identity, 2) growth of the structure must be proportional to growth of the fish, 3) growth rings must be formed at approximately the same time each year, and 4) theoretical lengths or weights back calculated from various growth rings must have positive correlations with empirical data.

Criterion 1 was easily met as the vertebral column of sharks develops early in life. The relationship of proportional vertebral growth to growth of fish was noted by plotting fork length against vertebral radius. These data exhibited a linear (range for all species, $r$ = 0.91-0.97, and for scalloped hammerhead and dusky sharks, Fig. 1) rather than a curvilinear relationship. Preliminary attempts to resolve Criterion 3 by examining the marginal growth ring on vertebrae suggested that hammerhead shark vertebral growth rings are formed annually, whereas

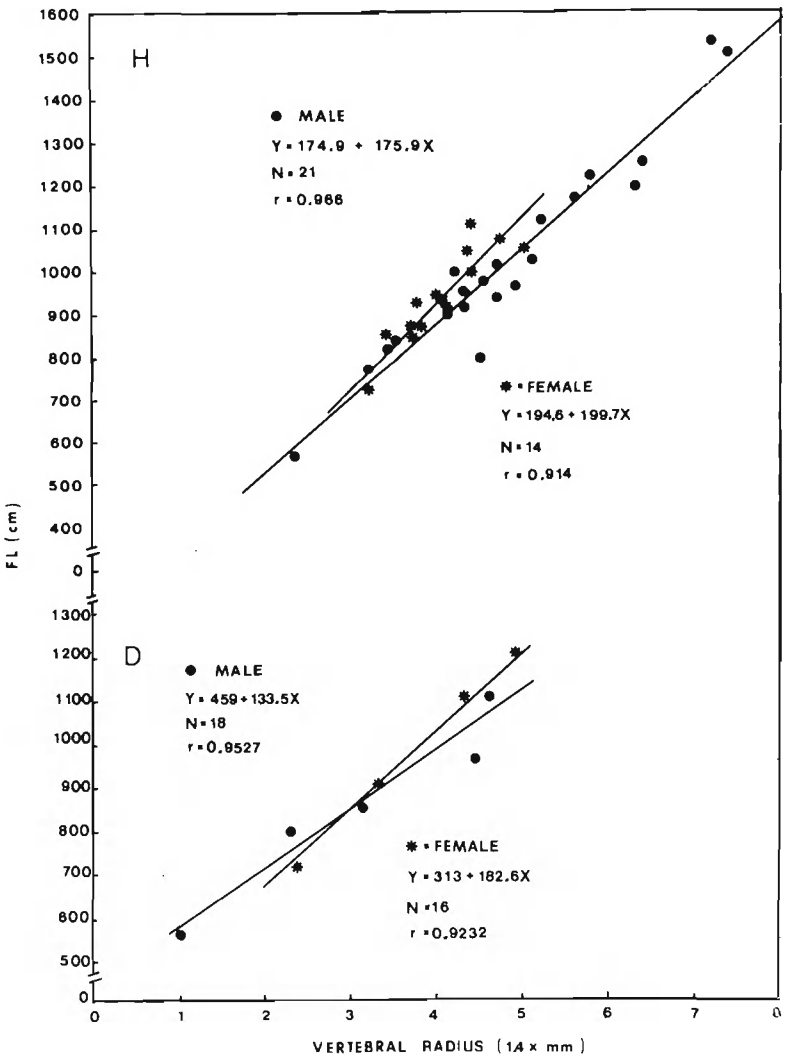


Figure 1.—Relationship between fork length (cm) and vertebral radius (mm) for male and female scalloped hammerhead (H, top) and dusky sharks (D, bottom).

those for the dusky shark may be formed one or more times a year. Casey's et al. (1983) observations of false checks and other rings in vertebrae of sandbar sharks may explain the trend observed for dusky sharks. However, more definitive results for both species awaits adequate samples of the full size range of each sex. Slight differences between back calculations of the theoretical shark length and actual fork lengths suggested a Dahl-Lee effect (discussed later).

## Scalloped Hammerhead

Scalloped hammerhead sharks appear in North Carolina inshore waters, near Shackleford Banks, from May to October, and occasionally remain until November. Peak abundance occurs from July to mid-August. There was a significant linear relationship between fork length and vertebral radius for male ($N$ = 21) and female ($N$ = 14) hammerhead sharks (Fig. 1, $r$ = 0.96 and 0.91 for males and females, respectively). These relationships were expressed by the linear regressions: Males $y$ = 175.9 + 174.9 $X$, and females $y$ = 124.6 + 199.7 $X$. Maximum age for males was estimated to be 8 yr, while females appeared to be at least 5 yr old.

Back calculations of fork length at estimated age produced relatively close agreement with observed data for the female scalloped hammerhead data (Fig. 2), while back calculations for males were usually smaller than the actual observed measurements (Fig. 2, Table 3). In such cases, small overall sample sizes may explain the disagreement noted.

While Bass et al. (1975) calculated that the maximum size for male hammerhead sharks should be 2,950 mm TL, Clarke (1971) reported a 3,090 mm TL female from Hawaii. Gilbert (1967) speculated that the maximum length for scalloped hammerhead shark was probably between 3,700 and 4,000 mm TL. Gudger (1947) cited a 4,560 cm TL (15 ft), an unlikely size, hammerhead shark from Australia. Our largest specimen was a mature male scalloped hammerhead shark of 1,560 mm FL;

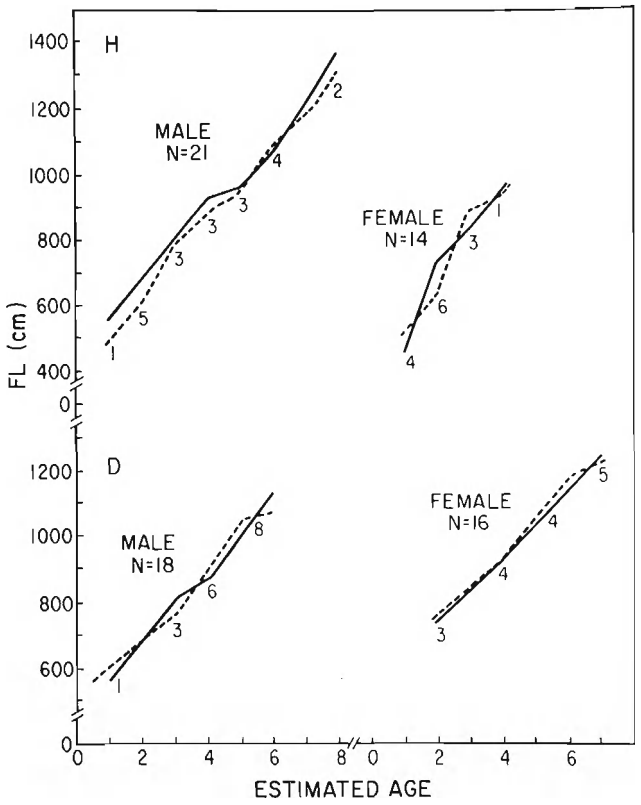


**Figure 2.—Actual (solid line) and back-calculated (dashed line) fork lengths for male and female scalloped hammerhead (H, top) and dusky sharks (D, bottom). Numbers refer to sample size.**

**Table 3.—Back-calculated fork lengths (mm) for male and female scalloped hammerhead sharks.**

| Estimated age | $N$ | Fork length at vertebral ring 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 |
|---|---|---|---|---|---|---|---|---|---|
| | | | | Male | | | | | |
| 1 | 1 | 495.7 | | | | | | | |
| 2 | 5 | 495.5 | 621.8 | | | | | | |
| 3 | 3 | 501.2 | 667.8 | 783.6 | | | | | |
| 4 | 3 | 499.5 | 631.9 | 762.3 | 894.2 | | | | |
| 5 | 3 | 498.5 | 634.5 | 779.1 | 916.1 | 976.5 | | | |
| 6 | 4 | 505.3 | 636.5 | 800.9 | 898.2 | 974.6 | 1,073.6 | | |
| 7 | — | — | — | — | — | — | — | — | |
| 8 | 2 | 508.2 | 621.9 | 814.4 | 910.8 | 997.9 | 1,085.4 | 1,172.8 | 1,242.8 |
| $\bar{x}$ FL | | 500.4 | 635.1 | 787.2 | 903.8 | 980.4 | 1,077.5 | 1,172.8 | 1,242.8 |
| | | | | Female | | | | | |
| 1 | — | — | | | | | | | |
| 2 | 4 | 466.9 | 636.7 | | | | | | |
| 3 | 6 | 454.1 | 609.8 | 773.6 | | | | | |
| 4 | 3 | 424.2 | 583.9 | 748.7 | 933.4 | | | | |
| 5 | 1 | 384.2 | 563.9 | 743.7 | 943.4 | 1,043.2 | | | |
| $\bar{x}$ FL | | 446.4 | 608.7 | 763.1 | 935.9 | 1,043.2 | | | |

otherwise, most of the scalloped hammerhead sharks examined were immature.

### Dusky Shark

Dusky sharks appear in the Shackleford Banks inshore waters in early May and remain until late October. Peak abundance occurs in May-early June and again in early September. During July and August they apparently move north or south along the Atlantic coast, as they are usually replaced by other carcharhinids. Similar north-south movements along southeastern Natal have been reported by Bass et al. (1973).

The vertebral radius to fork length relationships for 18 male and 16 female dusky sharks, like those for hammerhead sharks, also exhibited a significant linear relationship (Fig. 1, $r = 0.99$ male, 0.92 female). These relationships are expressed by the formulas: Males $y = 459.0 + 133.5\,X$, and females $y = 313.0 + 182.6\,X$. Males attained a maximum fork length of 1,120 mm by estimated age 6, while female maximum lengths were 1,215 mm at estimated age 7.

Back calculations of fork length at estimated age for dusky sharks agreed with observed data for both sexes, except that the largest male and female fork lengths were slightly underestimated by the regressions (Fig. 2, Table 4). These results suggested a possible Dahl-Lee effect among the specimens studied. Again, small sample sizes may also account for these differences.

Springer (1960) recorded 3,400 mm TL male and 3,650 mm TL female dusky sharks in the western Atlantic, while those in the Indian Ocean attained total lengths of 3,240 mm for males and 2,570 mm for females (Bass et al. 1973).

Too few vertebrae were available for 10 other species of sharks to adequately estimate age by the silver nitrate method or to permit regression analyses or back calculations at this time. Also, little can be reliably said regarding month of growth ring formation for those 10 species. Estimated ages from the largest sized vertebra and maximum fork length (mm), by species, were: Blacknose shark, *C. acronotus*, 7 yr (male maximum 1,340 mm, female 1,195 mm); spinner shark, *C. brevipinna*, 7 yr (male 1,640 mm, female 1,571 mm); silky shark, *C. falciformis*, 5 yr (male 1,052 mm, female 1,055 mm); bull shark, *C. leucas*, 10 yr (male 2,460 mm); sandbar shark, *C. plumbeus*, 5 yr (male 1,000 mm, female 1,130 mm); lemon shark, *Negaprion brevirostris*, 14+ yr (female 2,421 mm); sand tiger, *Odontaspis taurus*, 8+ yr (male 2,161 mm); Atlantic sharpnose, *Rhizoprionodon terraenovae*, 6 yr (male 890 mm, female 895 mm); and great hammerhead, *Sphyrna mokarran*, 14+ yr (male 3,660 mm). The male sandbar shark age-growth data agree well with that noted by Casey et al. (1983), whereas their females were estimated to be age 7 at 1,100 mm FL. Gruber and Stout (1983) noted that von Bertalanffy growth estimates of a 310 cm TL lemon shark would be at least 9 yr old. While they gave no formula for converting total length to fork length, a specimen of about 290 cm FL would either be a faster growing shark, or the von Bertalanffy growth model overestimates growth. Gruber and Stout (1983) believed the latter is true. Thorson and Lacy's (1982) largest male bull shark (201 cm TL) exhibited 10 vertebral rings. Bull sharks examined in this study were near the maximum total length reported by Schwartz (1959, 1960), yet would be 5 or more years younger than those determined by Thorson and Lacy. These discrepancies suggest more work is needed.

**Table 4.—Back-calculated fork lengths (mm) for male and female dusky sharks.**

| Estimated age | N | Fork length at vertebral ring 1 | 2 | 3 | 4 | 5 | 6 | 7 |
|---|---|---|---|---|---|---|---|---|
| Male | | | | | | | | |
| 1 | 1 | * 592.5 | | | | | | |
| 2 | — | — | — | | | | | |
| 3 | 3 | 619.2 | 712.7 | 819.5 | | | | |
| 4 | 6 | 504.9 | 712.7 | 766.1 | 872.9 | | | |
| 5 | — | — | — | — | — | — | | |
| 6 | 8 | 632.6 | 712.7 | 766.1 | 952.9 | 1,006.4 | 1,073.1 | |
| $\bar{x}$ FL | | 585.5 | 712.7 | 775.5 | 918.6 | 1,006.4 | 1,073.1 | |
| Female | | | | | | | | |
| 1 | — | — | | | | | | |
| 2 | 3 | 586.9 | 732.9 | | | | | |
| 3 | — | — | — | — | | | | |
| 4 | 4 | 568.6 | 696.5 | 787.8 | 915.6 | | | |
| 5 | — | — | — | — | — | — | | |
| 6 | 4 | 550.4 | 659.9 | 806.0 | 998.6 | 1,061.7 | 1,152.9 | |
| 7 | 5 | 568.6 | 659.9 | 824.3 | 952.1 | 1,061.7 | 1,134.7 | 1,207.7 |
| $\bar{x}$ FL | | 567.5 | 682.7 | 807.4 | 954.4 | 1,061.7 | 1,142.9 | 1,207.7 |


## ACKNOWLEDGMENTS

Numerous graduate students assisted, during the many years of longlining, in obtaining and preparing the various shark vertebrae studied. Institute staff deserving special thanks: R. Avent helped with preparations of hammerhead shark data; Captain O. Lewis, Mate J. Purifoy, W. Link, and G. Safrit were most helpful in assuring the success of each shark trip. P. Fisher, G. Morina, and B. Bright typed the manuscript.


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