

## The determinants of sexual segregation in the scalloped hammerhead shark, *Sphyrna lewini*

A. Peter Klimley

Marine Biology Research Division (A-002), Scripps Institution of Oceanography, University of California, San Diego, La Jolla, CA 92093, U.S.A.

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### Synopsis

Female scalloped hammerhead sharks move offshore at a smaller size than do males to form schools composed primarily of intermediate size female sharks. This movement results in smaller females feeding more on pelagic prey than do males and with greater predatory success. It is contended that this change in habitat causes females to grow more rapidly to reproductive size. Intermediate size females grow at a more rapid rate than males. Female scalloped hammerhead sharks mature at a size larger than males. For many elasmobranch species, females: (1) occupy a different habitat, (2) grow more rapidly prior to maturity and continue growth following maturation, (3) feed on different prey with increased feeding success, and (4) reproduce at a size larger than males. It is suggested that female segregation increases fitness, resulting in more rapid growth for the former sex. The females reach maturity at the larger size necessary to support embryonic young, yet similar age to males, matching the female reproductive lifetime to that of males.

### Introduction

A general characteristic of elasmobranch populations is segregation of the sexes. Such separation has been inferred from unequal numbers of each sex in catches for many species of sharks such as *Carcharodon carcharias* (Bass et al. 1975, Klimley 1982, 1985), *Carcharhinus plumbeus* (Springer 1960), *Galeus arae* (Bullis 1967), *Galeorhinus zygoterus* (Ripley 1946), *Galeorhinus australis* (Olsen 1954), *Negaprion brevirostris* (Springer 1950), *Prionace glauca* (Nakano 1985), and *Sphyrna lewini* (Clarke 1971). However, shark investigators generally have not attempted to explain this disequilibrium. Only Springer (1967) described shark populations as being divided at times into social units of subadults of both sexes, sexually mature males, and mature females, and speculated

that such separation might be based on different swimming capabilities, dietary preferences, or absence of aggression between similar size sharks. Munoz-Chapuli (1984) has suggested the offshore distribution of adults and inshore distribution of juveniles reduce intraspecific predation. In this paper, I present evidence that female *Sphyrna lewini* in the Gulf of California: (1) segregate from males, moving offshore prior to them, (2) feed at this time on a greater proportion of pelagic species, and with more success, and (3) grow more rapidly than males. I contend that these behavioral strategies are adaptive because the body size required for female gestation of embryonic young is greater than that for male production of spermatozoa for ovum fertilization. Evidence is provided that females mature at a larger size than males. By the former growing faster, members of both sexes

reach maturity at a similar age, allowing reproductive activities to occur over similar periods in their lifetimes. I then cite examples from the literature that this life history pattern occurs, at least in part, in many other elasmobranchs.

## Methods

The size, sex, reproductive state, and stomach contents were recorded for scalloped hammerhead sharks captured from May to October 1978–1981 in the Gulf of California by fishermen in the proximity of Juncalito (25° 48' N, 111° 18' W), Isla Paredito (24° 53' N, 110° 35' W), and San Jose del Cabo (23° 03' N, 109° 39' W). Sharks were caught on bottom long lines or gill nets. The fishing gear used is described in Applegate et al. (1979).

The significance of prey items in the diet of the scalloped hammerhead shark was determined using the Index of Relative Importance (IRI) of Pinkas (1971):

$$\text{IRI} = (\text{N} + \text{V})\text{F},$$

where N is the numerical percentage of prey items, V the volumetric percentage, and F that of stomachs containing such items. Stomach content mass was weighed for a comparison between female and male food intake.

The size range over which females mature was determined from maximum diameter measurements of individual ova in the manner of Pratt (1979). He found large ova together with small ova at the onset of maturity, indicative of at least one previous generation of egg production. The size at which males reach maturity was determined from an increase in clasper length in relation to overall length. This was used by Aasen (1961), McLaughlin & O'Gower (1971), and Jensen (1976) to identify the onset of maturity in *Prionace glauca*, *Heterodontus portusjacksoni*, and *Carcharhinus leucas*, respectively. Clasper length was measured from the axil of the right pelvic fin to the tip of the clasper. Lengths were converted to a fraction of the longest clasper length in the sample for comparison to mouth width, a non-reproductive character. These fractional values were then plotted as a func-

tion of total length (TL). A sudden increase in clasper length (as evidenced by an increased slope over intermediate sizes) in the absence of a similar increase in mouth width would indicate maturation. The concurrent presence of spermatophores in sharks of this size would corroborate their having reached maturity as found by Pratt (1979) for *Prionace glauca*. The ampulla ductus deferens was dissected away from the kidney at its thickest part, cut cross-sectionally, and squeezed so that the seminal fluid with its spermatophores would flow onto a slide. The slide was then immersed briefly in Bouin's fixative to preserve the sample and stained with methylene blue prior to examination under a compound microscope.

Total lengths (TL) of free-swimming sharks were measured stereophotographically from May to August 1980 and 1981 in the Gulf of California at two islands, Las Animas (24° 57' N, 110° 16' W) and Cerralvo (24° 21' N, 110° 20' W), and at two seamounts, El Bajo Espiritu Santo (24° 46' N, 109° 26' W) and El Bajo Gorda (22° 59' N, 109° 29' W). I have described the stereophotographic sampling, measurements, and calculations for determining TL elsewhere (Klimley & Brown 1983).

## Results

### *Sexual separation by depth*

Capture data indicate that female scalloped hammerhead sharks migrate offshore at a smaller size than males. Capture depths for sharks of each sex are presented as a function of TL in Figure 1. From the scatterplots it is evident that small females are captured more frequently than similar size males in deeper water. For the sake of comparison, the median capture depth is given above the center mark for each size class. Females in the 100 cm TL class, from 74 to 125 cm, were captured at a median depth of 50 m whereas males in the same class were caught at a median depth of 25 m. This difference was statistically significant (Mann-Whitney test,  $p = 0.0064$ ). Although female and male capture depth medians for the 150 cm size class, from 126 to 175 cm, 120 and 70 m respectively, appeared quite

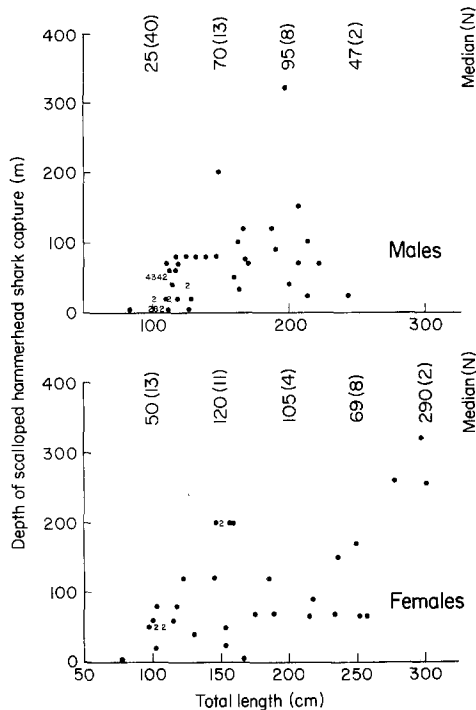


Fig. 1. Capture depths of male (above) and female (below) scalloped hammerhead sharks from the Gulf of California as a function of their total lengths. Above scattergrams are given median capture depths and sample size in 50 cm size classes with center marks given on the lower abscissa.

different, they did not differ significantly (Mann Whitney test,  $p = 0.094$ ). The median capture depths in the next two larger size classes were more similar. From this data I infer that more females than males move offshore in the 74 to 125 cm TL range.

The difference between the sizes at which females and males move offshore is evident from the different distributions of TL for free-swimming sharks of both sexes, stereophotographically measured at offshore sites where local depths often exceeded 400 m, with the size distributions for females and males, measured directly following capture in shallower water (Fig. 2). Length frequencies are expressed as percent of the total number of sharks in each sample to facilitate between-sample comparison. Equal percentages of female and male scalloped hammerhead sharks were captured in the 80 cm class. Correlated with the increasing percentages of free-swimming female scalloped ham-

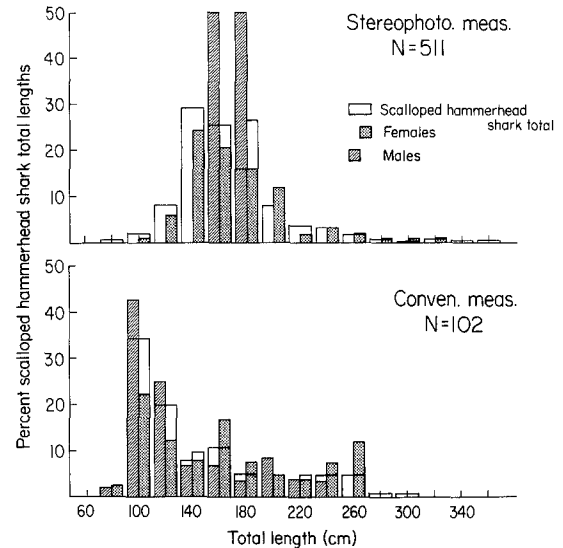


Fig. 2. Percentages of lengths in different classes of scalloped hammerhead sharks either measured by stereocamera in offshore schools (top) or by tape measure (bottom) from catches by fishermen in the Gulf of California. Cross-hatched bars are male, stippled bars female, and clear bars pooled frequencies.

merhead sharks in the classes 100 through 140 cm observed offshore are decreasing percentages in the same classes of captured females inshore. As indicated in Figure 1, females within this size range move into deeper water, and, as is evident from Figure 2, are observed in offshore schools.

#### Dietary divergence

This movement of female scalloped hammerhead sharks offshore at an earlier age than males results in their having different diets. To illustrate this, prey species, grouped according to habitat, are presented in pie-shaped diagrams for both sexes (Fig. 3). In order to detect ontogenetic divergence, the diet is further separated for sharks  $\leq$  and  $>160$  cm. This division was chosen because males did not appear in offshore schools until within this size class while females in the 100 cm class were seen in the schools (see Fig. 2). As might be expected from their early offshore movement, females  $\leq 160$  cm fed on a higher percentage of pelagic prey than did males of similar sizes. Mesopelagic prey formed 27.5% and epipelagic prey

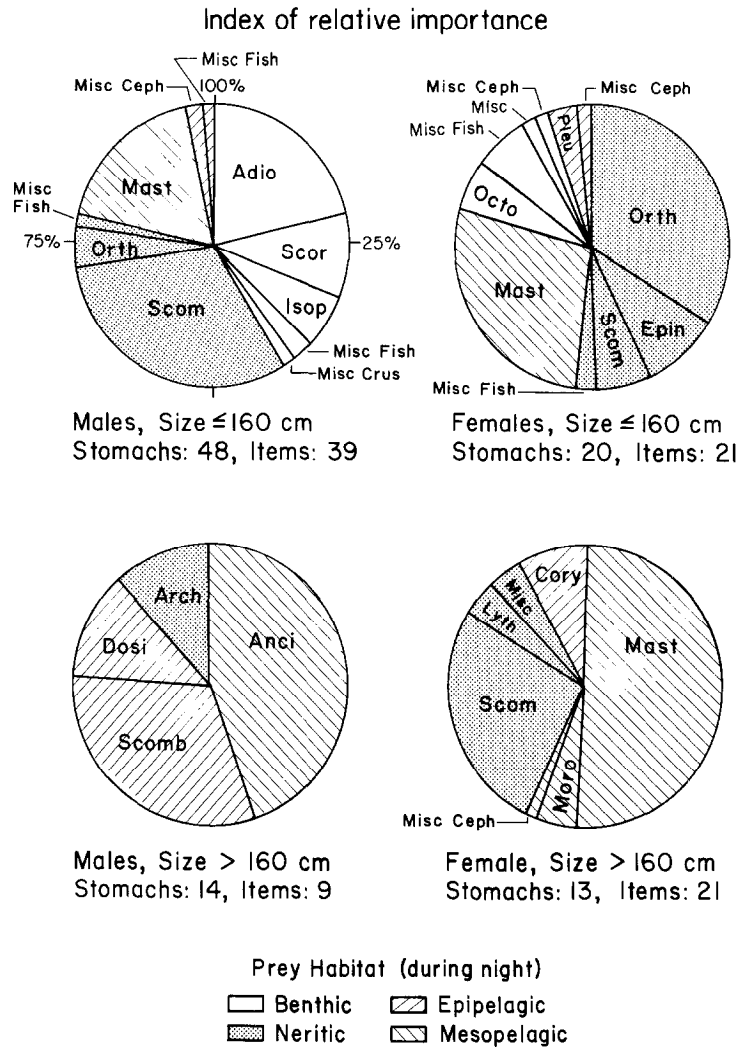


Fig. 3. Relative importance of prey species for male and female scalloped hammerhead sharks  $\leq$  and  $>160$  cm. Adio = *Adioryx suborbitalis*, Scor = *Scorpaena sonorae*, Isop = Isopoda, Scom = *Scomber japonicus*, Orth = *Orthopristis inornatus*, Mast = *Mastigoteuthis* sp., Epin = *Epinephalus* sp., Octo = *Octopus* sp., Pleu = *Pleuroncodes planipes*, Anci = *Ancistrocheirus leseuri*, Scomb = *Scomberomorus sierra*, Dosi = *Dosidicus gigas*, Anch = *Anchoa* sp., Moro = *Moroteuthis robustus*, Lyth = *Lythrulon flaviguttatum*, and Cory = *Coryphaena hippurus*.

5.5% of the female total IRI while such prey formed only 18.1% and 3.6% of the male total IRI. Furthermore, the diet of the females consisted of only 15.1% benthic prey in comparison to 40.9% of the IRI of male sharks. Males and females  $>160$  cm fed on neritic and pelagic prey.

In addition, the early offshore movement of females increasing may result in an increase in their predatory success while similar size males, which remaining inshore, do not increase their success. Feeding success is quantified for both sexes by

plotting each individual shark's stomach contents as a function of its total length (Fig. 4). Content mass is plotted on a logarithmic scale to emphasize small differences. These are important because items remaining in the stomachs are often small hard parts such as cephalopod beaks and teleost skeletal remains, and a small mass difference may constitute a large difference in the number of cephalopod beak pairs in any two stomachs. For the purpose of identifying size related differences between the sexes, linear curves (based on the least

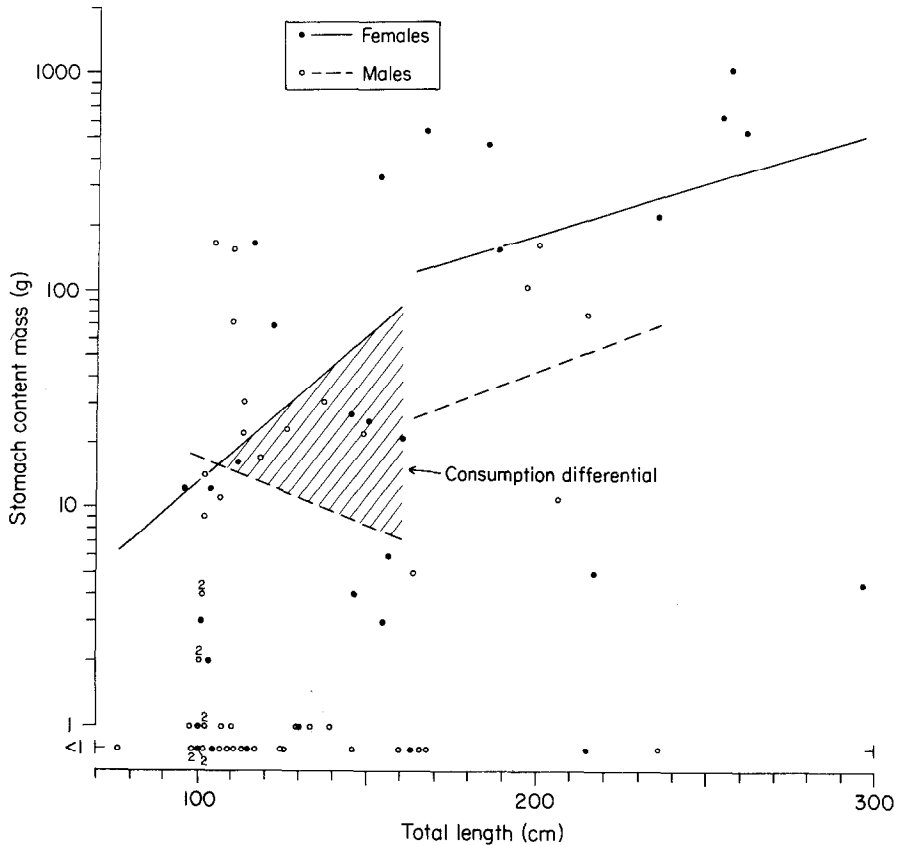


Fig. 4. Scattergram of female (solid circles) and male (clear circles) stomach content mass as a function of total length. Lines (based on the least squares criterion) have been drawn for females (solid) and males (dashed)  $\leq$  and  $>160$  cm, the size at which males were observed to enter offshore schools. Because the difference between the slopes for male and female sharks  $\leq 160$  cm is significant, the area between the slopes has been cross hatched to indicate a surplus of food consumed by the females.

squares criterion) are drawn for both sexes  $\leq$  and  $>160$  cm (following the convention of Fig. 3). These curves are only rough estimates of average food consumption. Feeding success of females  $\leq 160$  cm is greater than that of males. The slope for females is significantly greater than that for the male's (analysis of covariance,  $p < 0.05$ ). Furthermore, while the regression slope for female stomach contents is greater than 0 at a marginally significant level ( $t$ -test,  $p = 0.05$ ), the slope for males does not differ significantly from 0 ( $t$ -test,  $p > 0.50$ ). Females  $> 160$  cm might appear to be more successful feeders than males, having larger stomach content masses. Because of the absence of overlap on the ordinate of the female and male stomach mass curves, their elevations were not compared using an analysis of covariance, but the

two samples were compared using the  $t$ -test. Female masses did not differ from the male masses, the difference being only marginally insignificant ( $t$ -test,  $p = 0.06$ ). The slopes did not differ significantly from 0 either for the former ( $t$ -test,  $p > 0.10$ ) or the latter sex ( $t$ -test,  $p > 0.25$ ).

The area between the stomach content mass curves of females and males  $\leq 160$  cm TL (see cross hatched area on Fig. 4) may constitute an energy surplus that results in more rapid growth rate in females. The surplus occurs over the size range when females are offshore and males inshore.

#### *Growth differential*

Although growth was not measured for scalloped hammerhead sharks in the Gulf of California,

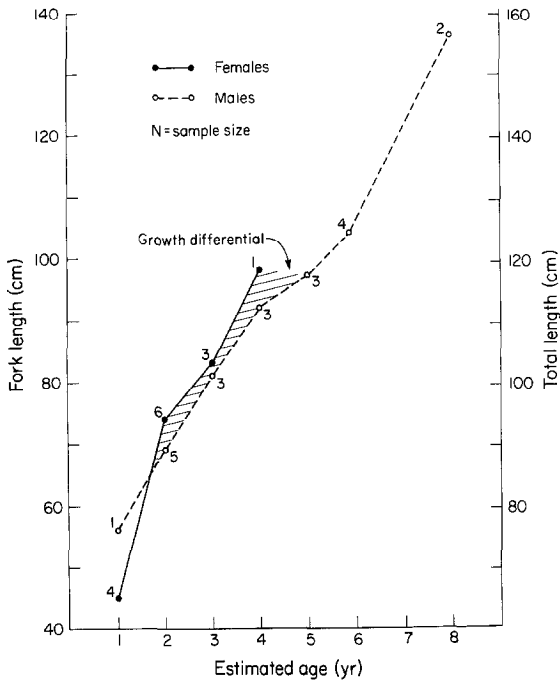


Fig. 5. Growth curves, based on vertebral ring counts, for female (solid) and male (dashed lines) scalloped hammerhead sharks caught in Atlantic Ocean off North Carolina. The figure is redrawn from Figure 2, p. 171 in Schwartz (1983). Numbers refer to sample size. Note growth differential (cross hatched area between curves) as females grow at a more rapid rate than males.

Schwartz (1983) published growth curves, based on vertebral ring counts, for females and males caught off the coast of North Carolina (Fig. 5). Schwartz (1983) used the dimension of fork length (FL), the distance from the snout to the union of the upper and lower caudal fin lobes, rather than TL. I have added a second ordinate to the right with TL to allow comparison of the sizes in this figure to those in other figures in which TL was used. The TL axis was calibrated in relation to the FL axis by: (1) measuring both TL and FL from drawings of the lateral aspects of the species in Bigelow & Schroeder (1948) and Bass et al. (1975), (2) calculating fractions of FL to TL, and (3) averaging the two resulting fractions. The resulting fraction was 0.79. The axis for TL was then adjusted so that a FL of 79 cm equaled a TL of 100 cm. Although it is possible that the morphometric relationship on which the calibration is based may change as size of the

shark changes, it is believed that such a change will be minimal and not affect my conclusions greatly. Furthermore, the two drawings were based on sharks with lengths, 67 cm TL in the former and 88 cm TL in the latter case, centered in the range of lengths for which age estimates were determined.

Between the ages of 3 and 4 years females grow at a more rapid rate than males in the Atlantic off the coast of North Carolina. The slope of the female growth curve in Figure 6 between ages 3 and 4 years is greater than the slopes for male growth between either 3 and 4 or 4 and 5 years. At 3 years an average female with a TL of 103 cm is only 2 cm larger than a male of comparable age. However, an average female at an age of 4 years has a TL of 119 cm, and she is 6 cm larger than a male at the same age and actually larger than a male of 5 years. Females in the 100 cm TL class (see Fig. 2) first appear within offshore schools in the Gulf of California. An offshore movement of females similar to that in the Gulf of California may occur off North Carolina resulting in the growth differential. Unfortunately, female age estimates for sizes greater than 118 cm were not present in the data of Schwartz.

More rapid growth prior to maturity by females than males occurs in other sexually segregating shark species such as *Mustelus canis* (Moss 1972), *Carcharhinus plumbeus* (= *milberti*) (Wass 1973), and *Galeorhinus japonicus* (Tanaka et al. 1978). However, in other species females grow at the same rate as males such as in *Squalus acanthias* (Jensen 1965), *Lamna nasus* (Aasen 1963), *Isurus oxyrinchus* (Pratt & Casey 1979), and *Galeorhinus australis* (Grant et al. 1979). Females in these species, however, continue to grow after they reach maturity while male growth decreases. This results in females reaching a larger maximum size than males.

Why should female sharks move to a seamount or offshore island, increasing their growth rate, while males do not? The cost of such a movement might be high. At a size of 100 cm a female might increase the risk of predation. At these locations I have encountered large groups of adult *Carcharhinus limbatus* and *Carcharhinus falciformis* in addition to the scalloped hammerhead shark. I also

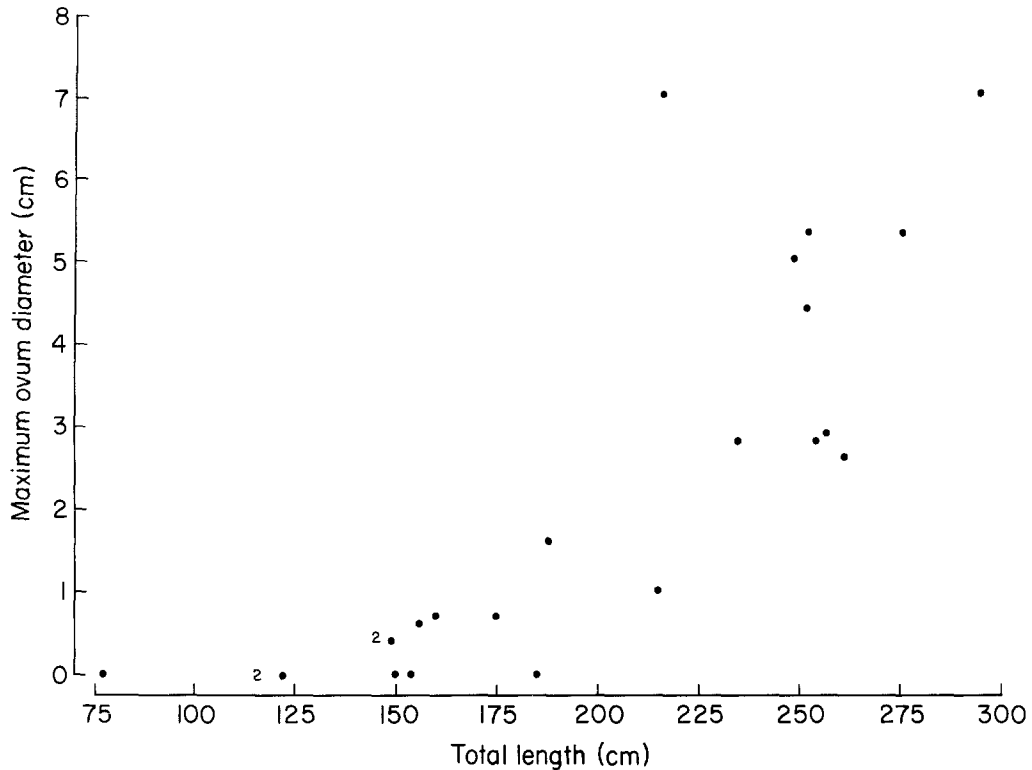


Fig. 6. Scattergram of maximum ovum diameter as a function of total length.

have observed or am aware others either encountering or capturing members of other large shark species such as *Carcharhinus leucas*, *Carcharhinus obscurus*, *Carcharodon carcharias*, and *Galeocerdo cuvieri* at such locations. Perhaps, adults of these species might occasionally prey on small scalloped hammerhead sharks. What is the benefit to such a movement and concurrent accelerated growth? The answer to this question may lie in the requirement that female body size be larger than male body size to accommodate developing young during the gestation period. Increased body size would not only provide more body cavity space for the female's ova or embryos, but also more muscle and a larger liver for energy storage, later to be allocated to reproduction. The male's reproductive system produces only spermatozoa for fertilization of female's ova. If females moved offshore to an environment with greater abundance of prey, they would grow more rapidly to a reproductively active size. They then would be capable of reproducing at

the same age as males, matching the reproductively active period of their life with that of males. Offshore seamounts and islands are ideal refugia from which predators can make movements both into the neritic and pelagic environments to capture prey. Males in the same size range might not migrate offshore because the benefit of rapid growth might not exceed the cost of higher risk of mortality due to predation.

Supporting the assertion that greater growth increases reproductive success in females and not males is continued growth of the former upon reaching maturity and absence of such growth in the latter. Female increase in size results in greater fecundity. Production by male of additional spermatozoa for insemination of another female requires little more body space or energy reserves while the development by a female of another embryo may require substantial body space and energy reserves. Indeed, a positive correlation in the number of embryos or juveniles born with female

size has been found in *Galeorhinus australis* (Olsen 1954), *Squalus acanthias* (Jensen 1965), *Carcharhinus leucas* (Thorsen and Lacy 1982), and *Prionace glauca* (Nakano 1985).

### Bimaturism

Does the scalloped hammerhead shark exhibit bimaturism, and if so, does the female become reproductively mature at a larger size than the male? Maximum ovum size, plotted as a function of TL, is shown in Figure 6. The smallest TL of a female scalloped hammerhead shark with large ova was 217 cm. This TL is slightly smaller than that which other investigators have found. Clarke (1971) judged a 214 cm female scalloped hammerhead shark to be immature, but 294 and 304 cm females to be mature, based upon the presence of embryos or a flaccid uterus indicative of recent parturition. Bass et al. (1975) found a 212 cm female to be virgin (but possibly mature) and a 307 cm female to be mature based on the presence of distinct ova and the expansion of the uterus into loose sacs.

At what size do male hammerheads become mature? Clasper lengths and mouth widths, converted to percents of their maxima, are plotted together as a function of TL (Fig. 7). Standardized mouth width (squares) increases at a constant rate. There is a strong linear relationship between mouth width and TL of the shark ( $r = 0.93$ ). Standardized clasper length (circles), on the other hand, are smaller than such mouth widths for small TLs. Such clasper lengths increase at a constant rate until the sharks reach a TL of 163 cm, increasing more rapidly to 170 cm before resuming to increase at the prior rate. This sudden enlargement is also indicated by large standard residuals (which would be 0 if the lengths were to lie directly on the regression line) and a weaker relationship between standardized clasper length and TL ( $r = 0.81$ ). Spermatophores (triangles) were present in the ampulla ductus deferens of male sharks with TLs equal or greater than 163 cm. Based on these two indices, the minimum TL at which males reach maturity is 163 cm (all males 218 cm and larger were mature). This size for the onset of maturity is similar to that

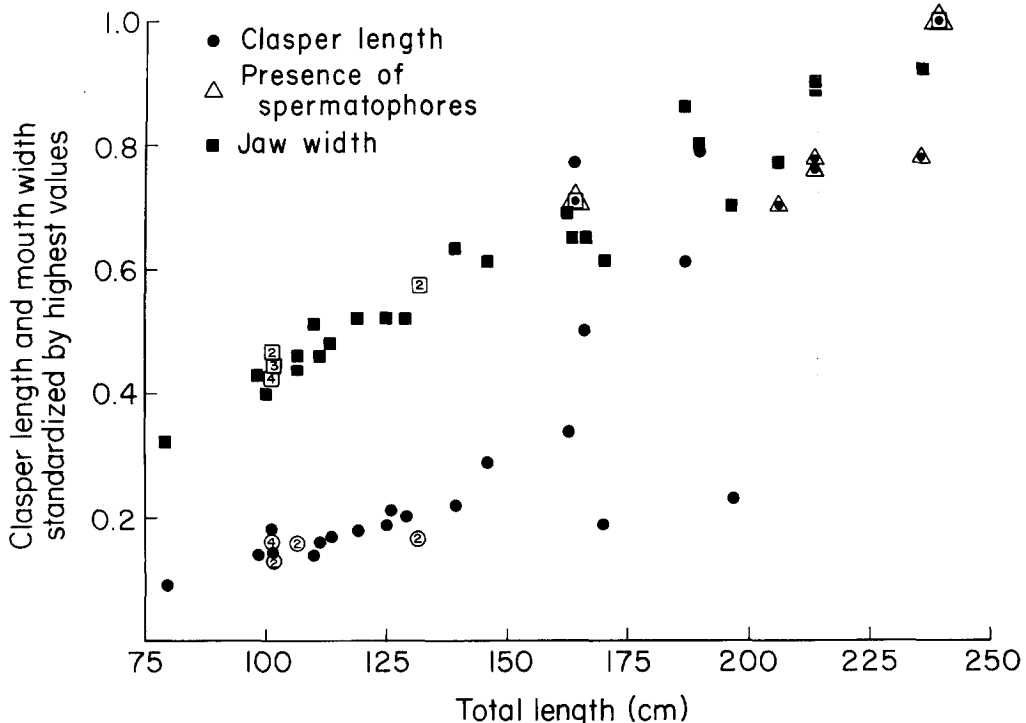


Fig. 7. Scattergram of clasper length (circles) and mouth width (squares) standardized by the division by their highest values a function of total length. Presence of spermatophores indicated by triangles.



found by other investigators. Clark & von Schmidt (1965) examined four male scalloped hammerhead sharks for their state of reproductive maturity. A 152 cm male was immature while three others, ranging from 177 to 209 cm, were judged mature. Bass et al. (1975) found that males matured over a range of from 140 to 165 cm.

## Discussion

### *Ecological determinants of sexual segregation*

It is argued that the offshore movement of female *Sphyrna lewini* prior to that of males is followed by increased feeding. The females grow at a more rapid rate to the size of reproductive maturity. Supporting this is that females: (1) <160 cm TL are caught in deeper water than males, (2) 105 to 120 cm TL are observed in offshore schools while males appear first at sizes from 150 to 165 cm, (3)  $\leq 160$  cm TL forage on more neritic and pelagic prey than similar size males, (4) 77 to 160 cm TL have statistically significantly larger stomach content masses than males of the same sizes, (5) at intermediate sizes grow more rapidly than males in the Atlantic off North Carolina, and (6) mature at a larger size than males (217 cm for the former versus 163 cm TL for the latter). This pattern also occurs in many other elasmobranch species. I present in Table 1 such data, extracted from studies of the feeding ecology, growth, and reproduction of selected shark species.

Let us examine *Squalus acanthias* as an example. This species has been studied by numerous investigators, most of its general biology thus being well known. Unfortunately, the studies were often carried out in different geographical areas. Females of an intermediate size appear to segregate from males. For instance, Kaganovskaya (1937) found such females to be pelagic and males to be neritic. Prior to maturity females grew slightly faster than males (Kaganovskaya 1937), and upon reaching maturity females continued to grow while male growth diminished (Sato 1935). This resulted in females growing to a larger size than males (Ford 1921, Sato 1935, Kaganovskaya 1937, Bonham et al.

1949, Jones & Geen 1977a). Females became mature at a greater size than males (Ford 1921, Hickling 1930, Sato 1935, Kaganovskaya 1937, Bonham et al. 1949, Jones & Geen 1977a). In perhaps the most detailed dietary analysis of a shark species to date, Jones & Geen (1977b) separated intermediate size females that were almost mature into a distinct group, the subadult females. These had higher seasonal consumption rates than adult males, exhibiting possibly greater growth at this time (see Table 2, Jones & Geen 1977b). The consumption rate of adult females was even greater than that of subadult females. Furthermore, the diet composition of subadult females differed slightly from adult males, leading Jones & Geen to infer that adult males preferred the neritic habitat to females. Although information on the general biology of the other species is less complete, parts of this general pattern are evident.

Of particular relevance to this argument would be those species which differ substantially in their life history traits from the before-mentioned pattern. For instance, Pratt & Casey (1983) found similar growth rates in females and males of *Isurus oxyrinchus* based on back-calculated lengths. In this species one would then expect females not to segregate from males. Indeed, Stillwell & Kohler (1982) found both sexes of this species to be caught with equal frequency in the two sampled areas. In addition, the investigators found no differences in the relative prey amounts consumed by females and males in the different forage categories and in stomach content volumes. However, Pratt & Casey (1983) observed that females matured at a greater size than males and grew to a larger size.

Another test of this hypothesis is to examine oviparous species of sharks to see if they have different life history traits as the majority of ovoviviparous or viviparous species. Possibly the energetic demand (and related size constraint) to females is less for the former reproductive mode than the latter. If such were the case, one would expect less of a difference in the size of maturation between females and males, less geographic segregation by the sexes, and small differences in the diets and growth of females and males of oviparous species. Indeed, these predictions appear correct.

Table 1. Life history data from the scientific literature for some species of elasmobranchs. TL = total length; FL = fork length, and PL = precaudal length. Note often in species where females occupy a different habitat than males, females: (1) feed on different prey, (2) grow more rapidly, (3) grow to a larger size, and (4) must grow to a larger size than males to reproduce.

Species	Reproduction	Author(s)	Segregation by sex	Dietary divergence	Growth rate	Maximum size, cm		Size of matur., cm		Fecundity increase with size
						Females	Males	Females	Males	
Heterodontidae <i>Heterodontus portus jacksoni</i>	oviparous	McLaughlin & O'Gower (1971)	mature FF in shallower water than MM		FF>	MM	70	70-95		
Squalidae <i>Squalus acanthias</i>	ovoviviparous	Ford (1921)	'shoals' of mature females, medium-sized mature males, immat. females		110 TL	83 TL	70-80 TL	59-60 TL	increase in ovarian eggs, embryos	
		Hickling (1930)	'male(s) ... in shallower water than females'				70-80 TL	62 TL		
		Kaganovskaya (1933)	'bottom nets (caught) ... males, drift pelagic nets ... chiefly mature females'							
		Kaganovskaya (1937)								
		Sato (1935)								
		Bonham et al. (1949)								
		Jones & Geen (1977a)								
		Jones & Green (1977b)	pelagic; FF more common neritic; MM more common	FF feed more, and on different prey	prior to matur. F> M rate after matur., F> M rate		130 TL	78.5 TL	72 TL	
							124 TL	92 TL	72 TL	
							130 TL	93.5 TL	78.5 TL	
Lamnidae <i>Lamna nasus</i>	ovoviviparous	Aasen (1963)	'sexes ... move in separate concentrations'				256 TL	266 TL		
		Pratt & Casey (1979)	FF and MM 'represented almost equally in both areas'	No differences in forage categories and volumes	F = M rate (based on equal TLs) F similar to M rate		328 FL	260 FL	180 FL	
		Stillwell & Kohler (1982)								
		Stevens (1983)					280 TL	195 TL		
Scyliorhinidae <i>Scyliorhinus canicula</i>	oviparous	Ford (1921)	FF = MM late spring and autumn, FF> summer, FF< winter				70 TL	57-60 TL	57-60 TL	

Table 1. (Continued).

Species	Reproduction	Author(s)	Segregation by sex	Dietary divergence	Growth rate	Maximum size, cm		Size of matur., cm		Fecundity increase with size
						Females	Males	Females	Males	
<i>Scyliorhinus canicula</i>	oviparous	Capape (1974)		Adult MM > FF feeding success						
cont.		Capape (1977)	Adult FF = MM during all months					40-45 TL	40 TL	increase in eggs with size
Carcharhinidae										
<i>Carcharhinus acronotus</i>	viviparous	Schwartz (1984)			M > F at very small size	154 TL	164 TL		110 TL	
<i>Carcharhinus plumbeus</i> = <i>milberti</i>	viviparous	Springer (1960)	FF 'in deeper... water' than MM		F > M rate prior to maturity F = M rate	146 PL	132 PL	140 PL	138 PL	no increase in embryos
		Wass (1973)	1F:2M					115 PL	110 PL	embryo no. vs PL, regr. sig. 0.05 level
		Casey et al. (1983)						153 FL	153 FL	
<i>Galeorhinus australis</i>	ovoviviparous	Olson (1954)	school by sex			174	155	135	120	embryo no. vs length, regr. sig. at 0.01 level
		Grant et al. (1979)			M slightly > F rate					
<i>Galeorhinus japonicus</i>	ovoviviparous	Tanaka et al. (1978)			prior to matur.	118 TL	104 TL	83 TL	82 TL	
<i>Galeorhinus zygoterus</i>	ovoviviparous	Ripley (1946)	FF inshore, MM offshore	FF feed on different prey	F > M rate	195 TL	185 TL	150 TL	135 TL	increase in embryos with size
<i>Mastelus canis</i>	viviparous	Moss (1972)			prior to matur.	146 TL	109 TL	82 TL	77 TL	
<i>Prionace glauca</i>	viviparous	Pratt (1979)	immat. 6F:1M mat. 5F:1M		F > M rate			185 FL	183 FL	
		Nakano (1985)	FF 'to shore... northward', MM 'offshore... southward'						147 TL	increase in size of litter with female size
Sphyrnidae										
<i>Sphyrna lewini</i>	viviparous	Schwartz (1983) Author	FF move offshore, prior to MM	FF feed on more, and different prey	prior to matur. F > M rate	296 TL	244 TL	217 TL	163 TL	

Ford (1921) found that both female and male *Scyliorhinus canicula* in the North Atlantic mature over the same size range (see Table 1). In the Mediterranean female *S. canicula* mature over a range encompassing that over which males mature (Capape 1977). The absence of bimaturation in this oviparous species is accompanied as predicted by a weaker tendency to segregate by sex. Although Ford (1921) noted different numbers of females and males were caught in the North Atlantic in summer and winter, similar numbers were captured in late spring and autumn. Capape (1977) found little difference in the number of female and male *S. canicula* caught during the different months of the year in the Mediterranean (see Fig. 3). The decrease in sexual segregation is accompanied by a similarity in the diets of females and males. Capape (1977) found both sexes to feed on similar prey. He found little difference in the percentage of stomachs containing prey between females and males during the summer, although slightly higher percentages of male stomachs contained prey during the rest of the year. Although growth data are not available for this species, Ford (1921) found no difference between the maximum sizes reached by females and males, a characteristic uncommon in viviparous-ovoviviparous species. In another study of an oviparous species, *Heterodontus portusjacksoni*, McLaughlin & O'Gower (1971) also found males and females to mature at roughly the same length, and this would be predicted from the observed absence of segregation in immatures of the species.

### Conclusions

Female scalloped hammerhead sharks move offshore at a smaller size than do males to form schools composed primarily of intermediate size female sharks. This movement causes small females to feed on more pelagic prey than the same size males and with greater predatory success. It is argued that this movement results in females growing more rapidly than males to maturity. Greater growth allows for egg production and gestation at that age at which males first produce spermatazoa. Females thus synchronize their lifetime period of reproductive activity to that of males. Female scal-

loped hammerhead sharks do, indeed, become mature at a size larger than males. Repeated, in part, in many elasmobranchs species is the pattern of females: (1) segregating from males, (2) growing more rapidly prior to maturity and continuing to grow past maturation, (3) feeding on different prey with increased feeding success, and (4) not reproducing until reaching a size greater than males.

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### References cited

- Aasen, O. 1961. Some observations on the biology of the porbeagle shark, *Lamna nasus*, Bonnaterre. Int. Council. Explor. Sea, C.M. 109: 1-7.
- Aasen, O. 1963. Length and growth of the porbeagle (*Lamna nasus*, Bonnaterre) in the North West Atlantic. Fiskeridirektoratets Skrifter, Serie Havundersokelser 13: 20-37.
- Applegate, S.P., L. Espinosa, L.B. Menchaca & F. Sotelo. 1979. Tiburones Mexicanos. Fideocom. Ives. Educ. Pesq. Techn. Mar., Mexico. 146 pp.
- Bass, A.J., J.D. D'Aubrey & N. Kistnasamy. 1975. Sharks of the east coast of southern Africa. III. The families Carcharhinidae (excluding *Mustelus* and *Carcharhinus*) and Sphyrnidae. Invest. Rep. No. 38, Oceanographic Research Institute, Cape Town. 100 pp.
- Bigelow, H.B. & W.C. Schroeder. 1948. Fishes of the Western North Atlantic, Part 1: Sharks. Sears Foundation for Marine Research, New Haven. 576 pp.
- Bonham, K., F.B. Sandford, W. Clegg & G.C. Bucher. 1949.

- Biological and vitamin A studies of dogfish landed in the State of Washington (*Squalus suckleyi*). State of Wash. Dep. Fish., Biol. Rep. 49A: 83–114.
- Bullis, Jr., H.R. 1967. Depth segregation and distribution of sex-maturity groups in the marbled catshark, *Galeus arae*. pp. 141–148. In: P.W. Gilbert (ed.) Sharks, Skates, and Rays, Johns Hopkins Press, Baltimore.
- Capape, C. 1974. Contribution à la biologie des *Scyliorhinidae* des côtes Tunisiennes. II-*Scyliorhinus cannicula* Linne, 1758: régime alimentaire. Ann. Inst. Michel Pacha 7: 13–29.
- Capape, C. 1977. Contribution à la biologie des *Scyliorhinidae* des côtes Tunisiennes. I. *Scyliorhinus cannicula* (Linne 1758). Répartition géographique et bathymétrique, sexualité, reproduction, fécondité. Bull. Off. natn. Pech. Tunisie 1: 83–101.
- Casey, J.G., H.L. Pratt, Jr. & C.E. Stillwell. 1983. Age and growth in sandbar shark, *Carcharhinus plumbeus*. pp. 189–191. In: E.D. Prince & L.M. Pulos (ed.) Proceedings of the International Workshop on Age Determination of Oceanic Pelagic Fishes: Tunas, Billfishes, and Sharks, NOAA Tech. Rep. NMFS 8, U.S. Dept. of Commerce.
- Clark, E. & K. von Schmidt. 1965. Sharks of the Central Gulf Coast of Florida. Bull. Mar. Sci. 15: 13–83.
- Clarke, T.A. 1971. The ecology of the scalloped hammerhead shark, *Sphyrna lewini*. Pacif. Sci. 25: 133–144.
- Ford, E. 1921. A contribution to our knowledge of the life-histories of the dogfishes landed at Plymouth. Journ. Mar. Biol. Ass., Ser. B, 12: 468–505.
- Grant, C.J., R.L. Sandland & A.M. Olsen. 1979. Estimation of growth, mortality and yield per recruit of the Australian school shark, *Galeorhinus australis* (Macleay), from tag recoveries. Aust. J. Mar. Freshw. Res. 30: 625–637.
- Hickling, C.F. 1930. A contribution towards the life-history of the spur-dog. J. Mar. Biol. Ass. U.K., Series B, 16: 529–576.
- Jensen, A.C. 1965. Life history of the spiny dogfish. U.S. Fish. Bull. 65: 527–554.
- Jensen, N.H. 1976. Reproduction of the bull shark, *Carcharhinus leucas*, in the Lake Nicaragua-Rio San Juan system. pp. 539–559. In: T.B. Thorson (ed.) Investigations of the Ichthyofauna of Nicaragua Lakes, University of Nebraska, Lincoln.
- Jones, B.C. & G.H. Geen. 1977a. Reproduction and embryonic development of spiny dogfish (*Squalus acanthias*) in the Strait of Georgia, British Columbia. J. Fish. Res. Board Can. 34: 1286–1292.
- Jones, B.C. & G.H. Geen. 1977b. Food and feeding of spiny dogfish (*Squalus acanthias*) in British Columbia waters. J. Fish. Res. Board Can. 34: 2067–2078.
- Kaganovskaya, S. 1933. A method of determining the age and the composition of catches of the spiny dogfish (*Squalus acanthias* L.). Vestn. Dalnevost. Filiala Akad. Nauk SSSR (Vladivostok) 13: 139–141. (In Russian).
- Kaganovskaya, S. 1937. Contribution to the biology of the spiny shark, *Squalus acanthias* L. Izv. Tikhook. Nauchn.-Issledovatel. Inst. Morsk. Rybn Khoz. Okeanogr. 10: 105–115. (In Russian).
- Klimley, A.P. 1985. The areal distribution and autoecology of the white shark, *Carcharodon carcharias*, off the West Coast of North America. Memoirs, South. Cal. Acad. Sci. 9: 15–40.
- Klimley, A.P. 1982. Social organization of schools of the scalloped hammerhead, *Sphyrna lewini* (Griffith and Smith), in the Gulf of California. Doctoral Dissertation, University of California, San Diego. 341 pp.
- Klimley, A.P. & S.T. Brown. 1983. Stereophotography for the field biologist: measurement of lengths and three-dimensional positions of free-swimming sharks. Mar. Biol. (Berl.) 74: 175–185.
- McLaughlin, R.H. & A.K. O’Gower. 1971. Life history and underwater studies of a heterodont shark. Ecol. Monogr. 4: 271–289.
- Moss, S.A. 1972. Tooth replacement and body growth rates in smooth dogfish, *Mustelus canis* (Mitchell). Copeia 1972: 808–811.
- Munoz-Chapuli, R. 1984. Ethologie de la reproduction chez quelques requins de l’Atlantique Nord-est. Cybium 8: 1–14.
- Nakano, H. 1985. Distribution and biological characteristics of the blue shark in the Central Pacific Ocean. Report of Japanese Group for Elasmobranch Studies 19: 9–20.
- Olsen, A.M. 1954. The biology, migration, and growth rate of the school shark, *Galeorhinus australis* (MacLeay) (Carcharhinidae) in southeastern Australian waters. Aust. J. Mar. Freshw. Res. 5: 353–410.
- Pinkas, L. 1971. Food habits study. Calif. Fish Game 152: 5–10.
- Pratt, Jr., H.L. 1979. Reproduction in the blue shark, *Prionace glauca*. U.S. Fish. Bull. 77: 445–470.
- Pratt, H.L. Jr. & J.G. Casey. 1983. Age and growth of the shortfin mako, *Isurus oxyrinchus*, using four methods. Can. J. Fish. Aquat. Sci. 40: 1944–1957.
- Ripley, W.E. 1946. The soupfin shark and the fishery. Calif. Fish Game 64: 7–37.
- Sato, S. 1935. A note on the Pacific dog-fish (*Squalus suckleyi* Girard) in the coastal waters of Hokkaido, Japan. J. Fac. Sci., Ser. 6, Zool. 4: 127–141.
- Schwartz, F.J. 1984. Occurrence, abundance, and biology of the blacknose shark, *Carcharhinus acronotus* in North Carolina. Northeast Gulf. Sci. 7: 29–47.
- Schwartz, F.J. 1983. Shark ageing methods and age estimation of scalloped hammerhead, *Sphyrna lewini*, and dusky, *Carcharhinus obscurus*, sharks based on vertebral ring counts. pp. 167–174. In: E.D. Prince & L.M. Pulos (ed.) Proceedings of the International Workshop on Age Determination of Oceanic Pelagic Fishes: Tunas, Billfishes, and Sharks, NOAA Tech. Rep. NMFS 8, U.S. Dept. of Commerce.
- Springer, S. 1967. Social organization of shark populations. pp. 149–174. In: P.W. Gilbert, R.F. Mathewson & D.P. Rall (ed.) Sharks, Skates and Rays, Johns Hopkins Press, Baltimore.
- Springer, S. 1960. Natural history of the sandbar shark, *Eulamia milberti*. U.S. Fish. Bull. 61: 1–37.
- Springer, S. 1950. Natural history notes on the lemon shark, *Negaprion brevirostris*. Tex. J. Sci. 1950: 349–359.
- Stevens, J.D. 1983. Observations on reproduction in the short-

- fin mako *Isurus oxyrinchus*. Copeia 1983: 126-130.
- Stillwell, C.E. & N.E. Kohler. 1982. Food, feeding habits, and estimates of daily ration of the shortfin mako (*Isurus oxyrinchus*) in the northwest Atlantic. Can. J. Fish. Aquat. Sci. 39: 407-414.
- Tanaka, S., C.T. Chen & K. Mizue. 1978. Studies on sharks XVI, Age and growth of eiraku shark *Galeorhinus japonicus* (Muller and Henle). Bull. Faculty Fish. Nagasaki Univ. 45: 19-28.
- Thorson, T.B. & E.J. Lacy, Jr. 1982. Age, growth rate and longevity of *Carcharhinus leucas* estimated from tagging and vertebral rings. Copeia 1982: 110-116.
- Wass, R.C. 1973. Size, growth, and reproduction of the sandbar shark, *Carcharhinus milberti*, in Hawaii. Pac. Sci. 24: 305-318.

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