UNITED STATES DEPARTMENT OF THE INTERIOR • Fred A. Seaton, *Secretary*

FISH AND WILDLIFE SERVICE • Arnie J. Suomela, *Commissioner*

NATURAL HISTORY OF THE SANDBAR SHARK *EULAMIA MILBERTI*

By STEWART SPRINGER

FISHERY BULLETIN 178

From Fishery Bulletin of the Fish and Wildlife Service

VOLUME 61

PUBLISHED BY U.S. FISH AND WILDLIFE SERVICE • WASHINGTON • 1960

PRINTED BY U.S. GOVERNMENT PRINTING OFFICE, WASHINGTON, D.C.

For sale by the Superintendent of Documents, U.S. Government Printing Office, Washington 25, D.C.
Price 35 cents

The series, Fishery Bulletin of the Fish and Wildlife Service, is cataloged as follows:

U. S. *Fish and Wildlife Service.*
Fishery bulletin. v. 1–
Washington, U. S. Govt. Print. Off., 1881–19

v. in illus., maps (part fold.) 23–28 cm.

Some vols. issued in the congressional series as Senate or House documents.
Bulletins composing v 47– also numbered 1–
Title varies: v. 1–49, Bulletin.
Vols. 1–49 issued by Bureau of Fisheries (called Fish Commission, v. 1–23)

1. Fisheries—U. S. 2. Fish-culture—U. S. I. Title.

SH11.A25 639.206173 9—35239*

Library of Congress [59r55b1]

CONTENTS

ABSTRACT

Populations of sandbar sharks of the eastern and western parts of the Atlantic Ocean are defined and general problems of nomenclature, the ecology of large carcharhinid sharks, and field recognition of sandbar sharks are discussed.

A more-detailed account of observations on *Eulamia milberti*, restricted to the population of the western North Atlantic, is given, outlining distribution of adults and young, migrations, development, and behavior, based on observations from the commercial shark fishery which operated from centers in the Southeastern States from 1935 to 1950 and supplemented by data from research vessels operating after 1950.

Comparisons with other species in the area, lists of large species of sharks taken at certain times off Salerno, Florida; Bimini, Bahamas; the mouth of the Mississippi River, Louisiana; and the Caribbean coast of Nicaragua-Costa Rica, as well as discussions of interspecies competition, are included.

NATURAL HISTORY OF THE SANDBAR SHARK, *EULAMIA MILBERTI*

By Stewart Springer, *Fishery Methods and Equipment Specialist*
Bureau of Commercial Fisheries

This account of the sandbar shark, *Eulamia milberti* (Müller and Henle), is an attempt to bring together all the significant information on one kind of common and moderately large shark. Sharks have been studied because they are occasionally dangerous to man, often a nuisance to fishermen and, in the past at least, have been valuable as a source for food, leather, vitamin A, fish meal, and some specialty products. A rather comprehensive body of knowledge exists about some of the smaller species, such as the comparatively valuable soupfin shark of the coast of North America (Ripley, 1946) and the school shark of Australia (Olsen, 1954), both species of *Galeorhinus*, and the common spiny dogfish, *Squalus* (Ford, 1921; Hickling, 1930; Templeman, 1944). Information on the natural history of the larger species is fragmentary. This is to be expected, because large species not only are difficult to catch and handle, but also are far-ranging and require observation over a wide geographical area.

The sharks, together with their relatives, the skates, rays, and chimaeroids, form a class of vertebrates that is sharply set off from the classes which contain the fishes, amphibians, reptiles, birds, and mammals. The sharks and other members of the class Chondrichthyes have cartilaginous skeletons, and while elements of the shark skeleton may become calcified, no true bone is formed. This is the basis for the definition that is generally used to distinguish the Chondrichthyes from the higher vertebrates. But there are other differences in the chemistry and physiology that are very likely of great importance but are little understood. The evolutionary connections of the modern sharks and their allies with other modern vertebrates are obscure and of great antiquity.

Sharks occupy a place in nature at the top of the food chain. As predators they compete with man, but it is by no means established that their predatory activities are always harmful. They are a nuisance or are harmful to fishermen chiefly because of the damage they do to nets or to fish that have been caught on setlines. In some localities, in England and Australia, for example, sharks are utilized and are consequently of some value. In the United States, landings at present are of no great importance.

Sharks may be dangerous to man through attacks on swimmers and survivors of marine disasters, but *Eulamia milberti* is not a species implicated in well-documented records of attacks. There may be several reasons for this. *E. milberti* ordinarily stays away from beaches and does not often feed at the surface. It usually seeks small prey. During the summer, when the female sandbar sharks come inshore near the heavily populated centers from New York southward along the Atlantic coast to give birth to their young, it is not their habit to seek food. The large males do not come inshore. So the sandbar shark, while large enough to be dangerous and perhaps the most common of the larger sharks in shore waters southward from New York, is isolated by its habits from encounters with man. Nevertheless, the sandbar shark is potentially dangerous to man and might become a more serious danger with minor shifts in the environmental situation.

The most annoying aspect of my work with sharks, prior to the publication in 1948 of the first volume of Fishes of the Western North Atlantic on sharks by Dr. Henry B. Bigelow and William C. Schroeder, was that many western Atlantic sharks could not be identified with confidence because of a scattered literature of varying quality. It is appropriate that I acknowledge the importance of this excellent general work to me, because without it and without the encourage-

Note.—Approved for publication, October 27, 1958. Fishery Bulletin 178.

ment of its authors, I would not have attempted preparation of this report. Dr. Richard H. Backus of the Woods Hole Oceanographic Institution, Dr. Giles W. Mead of the U.S. Fish and Wildlife Service, and Dr. Leonard P. Schultz of the U.S. National Museum made many helpful suggestions during the preparation of this report. Captain B. W. Winkler was especially helpful in keeping fishing logs and measurements of about 1,300 large sharks he took off the Bahama Banks and off Nicaragua. Records obtained while I was employed by the Shark Industries Division of the Borden Company and while I was aboard the exploratory fishing vessel *Oregon* of the Fish and Wildlife Service comprise the basic data used here. Special assistance was given me also by the Lerner Marine Laboratory of the American Museum of Natural History, by permitting 2 months of field study at Bimini, Bahamas, in the summer of 1948. In all my work with sharks, I have been given the most generous help by my associates in commercial shark fishing and aboard exploratory fishing vessels.

NOMENCLATURE

This report is not intended to settle problems of nomenclature and taxonomy, but to be useful it is necessary to name the sharks under discussion and to define the names used. My choice of a name for the sandbar shark is *Eulamia milberti* (Müller and Henle) 1841. Use of *Eulamia* follows my partial revision of the carcharhinids (Springer, 1950). For the specific name *milberti* I follow Bigelow and Schroeder (1948) who note that, if it is finally proved that the Mediterranean form is identical with the American, the name *plumbeus* Nardo 1827, must be used for the combined species in place of *milberti*.

I disagree, however, with Fowler (1936), with the preceding statement by Bigelow and Schroeder, and with Tortonese (1951, 1956) that Nardo's description is valid. The description by Nardo would apply to almost any carcharhinid and the specific mention of the rounded snout [1] would apply better to some other carcharhinids than to the sandbar shark. Because there is no type and because Nardo's description would apply to almost any carcharhinid if applied liberally but to none if applied strictly, I regard *Squalus plumbeus* as a *nomen nudem*.

I am also unable to accept Nardo's description as specifically applicable to the sandbar shark based on the argument that the sandbar shark is the most common large carcharhinid of the Adriatic.

A most extraordinary snarl has developed over the years in the determination of the scientific name to be applied to the sandbar shark. The origin of this complication probably lies in the peculiarities of the distribution of species of carcharhinid sharks along the Atlantic coast of the United States. Mistakes in identification of specimens have been frequent, probably because the descriptive accounts of the early authors were very brief and did not select truly diagnostic features for emphasis. Systematists had too few specimens and too little data on distribution to note that segregation of the sexes and segregation of the adults and young characterized these sharks at some seasons.

In the latitudes from New York to Chesapeake Bay at depths within easy reach of collectors or fishermen, two common large carcharhinid sharks occur, the sandbar shark, *E. milberti* (Müller and Henle), and the bull shark, *Carcharhinus leucas* (Müller and Henle). The sandbar shark is represented in this area by adult females and by the young of both sexes, but rarely by adult males in the observable elements of the population. The bull shark is represented usually by adult males, but females and young are also present sporadically.[2]

The ranges of the sandbar shark and the bull shark will be discussed later as well as the apparent competition between these species. An effect of the occurrence of the two species to-

[1] The total description and diagnosis of *Squalus plumbeus* by Nardo, 1827, p. 35, is as follows: "Speciei secundae convenit exacte *Squal. Glaucus*. Bloc. si color exciperetur et forma rostri quae in exemplari nostro rotunda est."

[2] Large male *Carcharhinus leucas* were reported from the Chesapeake Bay area by Schwartz (1958); one was taken from the Patuxent River in 1957 and another at Flag Pond in the summer of 1958. This is apparently the first published report of the species from Chesapeake Bay. Specimens of large sharks came to the attention of Edgar H. Hollis, of the Maryland Department of Tidewater Fisheries in 1957, because Chesapeake fishermen regarded them as rarities. Photographs of the specimens sent me by Mr. Hollis were sufficient to permit identification as *C. leucas*. Nichols (1918) and Nichols and Breder (1927) reported *C. leucàs* from the south shore of Long Island, noting that these specimens were large males. Attention is called to this parenthetically because the appearance of adult males at the periphery or in the cooler parts of ranges of carcharhinid sharks is frequent.

gether, however, has been to foster confusion in the nomenclature. There appears to have been a tacit assumption by some naturalists that sexual dimorphism accounted for differences in sandbar sharks and bull sharks despite recognition of the existence of both species.

Superficially, the sandbar shark and the bull shark resemble one another but, as will be shown later, sandbar sharks can easily and positively be separated from bull sharks on the basis of several anatomical characteristics. Identification of specimens from the Middle Atlantic States, particularly the Atlantic coast from Cape Cod to Chesapeake Bay, presents an added difficulty because of the several very similar offshore species which may be caught occasionally, but probably rarely in inshore waters: *Eulamia obscura* (Le Sueur), *E. falciformis* (Müller and Henle), *E. floridana* (Bigelow, Schroeder, and Springer), and *E. altima* Springer. Recent unpublished records of the occurrence of *E. milberti* young and of the occurrence of *Carcharhinus leucas* adults are rather numerous, and following publication of the first volume of Fishes of the Western North Atlantic (Bigelow and Schroeder, 1948) there appears to be little confusion of the two species.

Belaboring the point that descriptive accounts of carcharhinids must be detailed and selective to have any meaning seems necessary to affect the intrenched misconceptions about *E. milberti* that can be derived from the literature. Fowler's (1936) description of *E. plumbeus* (*plumbeus*=*milberti*), which was based on American Middle States examples, although in a report on West African marine fishes, is not unique in confusing *E. milberti* with another species,[3] but it is detailed enough to be especially vulnerable to criticism. More elements of his description fit the bull shark, *Carcharhinus leucas*, than *E. milberti*, but additional confusion is introduced by the probability that juvenile and adult characteristics of both species are mixed. There is no selection of diagnostically useful characteristics for emphasis. The result is a plausible literary synthesis that is a hazard to one attempting to fit a real shark to a position in zoological classification.

POPULATIONS OF *EULAMIA MILBERTI*

Sandbar sharks, *Eulamia milberti*, occur in portions of the temperate and tropical Atlantic, the Caribbean, the Gulf of Mexico, and the Mediterranean. Our data in this study primarily cover the population inhabiting the western North Atlantic, the Gulf of Mexico, and the eastern Caribbean. Later, the normal movements and distribution of this population will be discussed. We need first to consider the relationships of the various populations. In addition to the population of the western North Atlantic two others may be roughly defined. One occurs along the coast of South America from Trinidad eastward and southward. The other is found along the west coast of Africa and is presumed to be continuous with the stock entering the Mediterranean.

The population occurring on the coast of South America appears to be a minor one. The species has been reported and figured by Ribiero (1923) from the coast of Brazil.

While engaged in commercial shark fishing in April and May 1949, I made shipboard examinations (Springer, 1949) of a series of sandbar sharks from the north and east coasts of Trinidad and identified them in error as *E. plumbeus*. I now believe that differences between the Trinidad specimens and typical *milberti* from the Atlantic coast of the United States are insufficient to warrant recognition of separate species, and that the conservative course, pending accumulation of new data, is to look upon the various Atlantic sandbar sharks as representing a single species. At the Trinidad locations, adult males and females as well as young of all sizes from 4 feet upward were taken on single setlines. Although commercial shark fishing was carried on throughout 1949 from the coast of French Guiana westward to the Gulf of Venezuela, sandbar sharks were reported only from the north and east coasts of Trinidad and chiefly from depths of 5 to 20 fathoms near Galera Point.

There are no records of sandbar sharks from the West Indies north of Trinidad except from the north coast of Cuba and from the western part of the Bahama Banks. This is not, of

[3] Garman's illustration of *Carcharhinus platyodon* (1913, pl. 3, figs. 4 and 6) appears to be very well drawn from a specimen of *Eulamia milberti*. Bigelow and Schroeder (1948) note that Garman's illustration is mislabeled. The accompanying illustration of the teeth in Garman's plate 3, figure 5, appears to have been drawn from the teeth of *platyodon*. *Carcharhinus platyodon* (Poey) is a synonym of *C. leucas* (Müller and Henle).

course, conclusive evidence of their absence from a region so poorly known ichthyologically as the West Indies. Nevertheless, all of the evidence points to a discontinuous distribution with no regular contact between the population known from Cape Cod to Costa Rica and the South American population known from Trinidad and the east coast of South America south of the Amazon.

In connection with possible future work with the sandbar sharks, it should be noted that the *E. milberti* from Trinidad were taken in eddies of the very strong, westerly current flowing between Trinidad and Tobago; and that recruitment for this stock could take place in part by transport by the Equatorial Current of the growing young to Trinidad from shore waters of the African coast.

The stock of *Eulamia milberti* in the eastern Atlantic is known from scattered records from the Mediterranean and the west coast of North Africa as summarized by Tortonese (1956). These records cover a long period of time and although critically reviewed by Tortonese and unquestionably accurate, they give little basis for an estimate of the abundance of the sandbar shark in relation to the abundance of other large species of the area. For our purposes here, that is, to estimate the relative importance and abundance in comparison with other large sharks of the area, reports by Cadenat (1950, 1957) on *E. milberti* and other species from the coast of Senegal are quite informative. Cadenat has been able to make observations on fresh material from a fishery taking relatively large numbers of the larger species of sharks. His reports suggest that the stock of *E. milberti* off northwest Africa is a strong one.

The list of species of large sharks reported by Cadenat is quite similar to lists of large sharks from the southeastern coast of the United States. The endemic species of both areas are the smaller sharks.

Precisely the same factors of prevailing wind and surface currents that make the southern crossing from the North African coast to Trinidad easier for man when it is from east to west may be expected to operate for sharks. Similarly, for a more northerly crossing, the one from west to east is more easily followed. The postulate that such contacts as exist between the stocks of the western Atlantic and the stock of the eastern Atlantic result from exchanges following this general clockwise circulation is a reasonable one. No actual evidence of regular contacts between the three stocks exists, however, and there is substantial reason for the belief that movements of individual sharks from one stock to another are relatively infrequent occurrences.

Knowledge of the distribution of large sharks in oceanic situations at considerable distance from land was extremely meager until very recently when data from oceanographic vessels and exploratory fishing vessels became available. The most comprehensive study covers sharks of the Central Pacific (Strasburg, 1958) in which data showing patterns of distribution of some of the larger species is given. Before the appearance of that study and of a less comprehensive account of Atlantic pelagic sharks (Backus et al., 1956), questions of shark distribution seaward of the continental shelves were unanswerable.

Now, while it is known that neritic species of large sharks are capable of moving over great distances of open ocean, there is increasing evidence that they rarely do.

ECOLOGICAL AND SYSTEMATIC RELATIONSHIPS OF THE GENUS *EULAMIA*

The genus *Eulamia* may be divided into two groups on the basis of the structure and arrangement of the dermal denticles. The group to which *E. milberti* belongs is characterized by nonimbricate denticles as contrasted with the other group which has denticles with overlapping edges or points. The *milberti* group includes comparatively few species. Probably *Eulamia dussumieri* (Müller and Henle) and *E. japonicus* (Schlegel) of the western Pacific belong here. In the Atlantic, the group is represented by a deep-water species, *Eulamia altima* Springer, which is quite different from *milberti*, not only in its morphology but in its habitat. Aside from *E. altima*, the only Atlantic representative of the genus *Eulamia* (or any carcharhinid genus) with widely spaced, nonimbricate denticles is *Eulamia milberti*, the sandbar shark.

E. milberti has the shoalest range and occupies the most inshore habitat of any of the 5 or 6 species of *Eulamia* of the Atlantic coast of North

America. Although *milberti* may be in competition with other species of *Eulamia* for food in some parts of its range, it does not compete with other species of *Eulamia* for nursery grounds.

Of the other carcharhinids of the northwestern Atlantic, the genera *Prionace* and *Pterolamiops* are pelagic surface dwellers; *Hypoprion* is confined to waters generally deeper than 100 fathoms near shelves or banks; *Negaprion*, *Apriondon*, *Scoliodon*, and *Carcharhinus* are shallow water sharks that spend at least some part of their lives in shallow lagoons, river mouths, or estuaries, and venture into deeper water rarely except for transitory movements; the species of *Eulamia* are sharks of the continental shelves, oceanic banks, and island terraces, although some species extend their ranges well inshore and also for considerable distances beyond the limits of the Continental Shelf. The only other western North Atlantic carcharhinid genus, *Galeocerdo*, is represented by a single species in subtropical and tropical waters out to depths of at least 200 fathoms. It does not exhibit the specialized schooling habits of the other carcharhinids, shows no strong migratory tendencies, and is less restricted in habitat choice than the others. There seems to be a tendency to greater variation in the number of young produced as well as a greater number per litter in *Galeocerdo* and *Prionance* and possibly also in *Pterolamiops* than in other northwestern Atlantic carcharhinids. Insofar as is known, there are no very important differences in the general outlines of the life history patterns of *Negaprion*, *Aprionodon*, *Scoliodon*, *Carcharhinus*, and *Eulamia*, although there appear to be many differences in detail.

Barriers which may restrict the movements of the larger sharks including *Eulamia milberti* are not readily apparent. Occasional captures of sharks outside areas of normal concentration of the species prove that they can and do wander. The remarkable thing is that large sharks tend to remain within definable habitats and geographical ranges.

Since species of *Eulamia* are, in general, less dependent on land masses than *Carcharhinus* and extend their activities regularly to surface waters of the open ocean beyond the Continental Shelf, it would not be surprising to find that some species have a very wide distribution in temperate and tropical seas. *Eulamia floridana* (Bigelow, Schroeder, and Springer) may be an example of such a distribution (see Strasburg, 1958). Those species of *Eulamia*, such as *milberti*, which are tied to shallow-water habitats are presumably subject to a greater degree of isolation.

SPECIMENS EXAMINED

Specimens, records, and field observations for this report have been assembled over a period of about 25 years during which time I have examined several thousand sandbar sharks. Available records of the commercial shark fishery cover more than 100,000 adult *Eulamia milberti*. About half of these sharks were measured at the point of landing. Earlier records of the stations included specimens of *Eulamia altima* and *Eulamia floridana* under the heading sandbar sharks. Since I visited most of the stations frequently, and during part of the period between 1935 and 1950 supervised recording procedures, I saw relatively large numbers of sandbar sharks. Specimens which appeared unusual to station employees were retained when practicable for my inspection. Most of my observations were made along the coasts of southern Florida. Adequate numbers of specimens for some purposes have been examined from the eastern and northern parts of the Gulf of Mexico, the Atlantic coast of the United States south of Cape Cod, and from the Caribbean coast of Nicaragua and Costa Rica. The available material in several museum collections in the United States was studied, but this consisted chiefly of preserved embryos or very young sharks and dried jaws.

The collection of data in the shark fishery suffered from interruptions and was assembled to aid an industrial operation rather than for a biological study. The difficulty in handling specimens, averaging nearly 7 feet in length as adults with an average weight of about 135 pounds, has made it necessary to select different series or samples for different objectives: one sample for length-weight relations; another for tooth counts, and so on.

I was unable to find spirit-preserved specimens of eastern Atlantic or Mediterranean origin referable to either *E. plumbeus* or *E. milberti* during a hasty examination of catalogs and specimens at the Museum d'Historie Naturelle in Paris or in the British Museum of Natural History, although specimens from the western Atlantic were present. Tortonese noted (1938) that there are two specimens in the Musee di Trieste collected in 1869 and 1871 and, after examination of specimens labeled *milberti* from the western Atlantic in the Museum at Paris and the British Museum, he indicated (in 1951) that he regards *milberti* as a synonym of *plumbeus*.

FIELD RECOGNITION

Eulamia milberti is commonplace in appearance. It has neither unusual color markings nor spectacular structural features. The length of the shark at maturity, 7 feet, makes the species too large for the biological collector and too small to interest the journalist. It is necessary to search for distinguishing features (fig. 1). The opportunity for comparison of series under ordinary circumstances is negligible, and almost all identifications of the larger sharks are necessarily made in the field. The suggestion that many of the presently recognized species of carcharhinid sharks are not in fact separable from one another but should be regarded as unidentifiable parts of a species complex has been advanced in speculative conversation by some of my friends who are ichthyologists. This view may easily develop from unsatisfactory attempts to make identifications with methods which are quite adequate and successful in application to teleosts but fall short when applied to sharks, and particularly to carcharhinid sharks. *E. milberti*, in waters off the United States, is readily defined and problems concerning it are not complicated by the existence of geographic or environmental races or subspecies, insofar as the available evidence shows. This is apparently not true of some of the other carcharhinids where separate populations may be defined on the basis of morphological differences shown in the analysis of adequate sėries from different areas.

The keys and descriptions given by Bigelow and Schroeder (1948) are adequate for the identification of the carcharhinid sharks of the western North Atlantic excepting *Eulamia altima*, which was described (Springer, 1950) after publication of this work. Nevertheless, identifications need to be made carefully because of the general structural similarity of the species which look alike on superficial examination. Sharks of the genus *Eulamia* in the *falciformis-springeri* group are

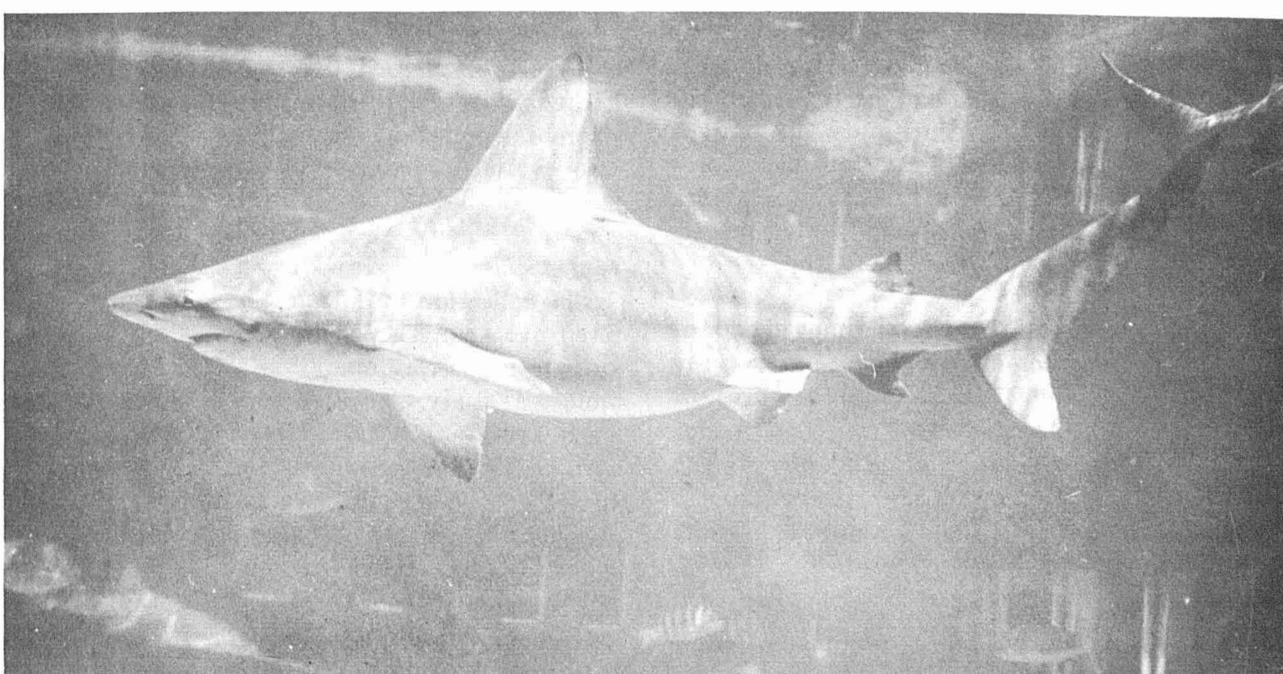

FIGURE 1.—*Eulamia milberti* in an exhibition tank. The high, triangular first dorsal fin, nonfalcate pectoral fins, and relatively high second dorsal and anal fins, nearly equal to one another in area, are characteristic of the species. (Photograph courtesy of Marine Studios, Marineland, St. Augustine, Fla.)

not well known and possibly are incompletely defined. Minor differences between Atlantic and Gulf of Mexico populations of *E. obscura* need further study. There is no difficulty, however, in distinguishing *E. milberti* from these species or from other species of sharks ordinarily found within its geographical range.

The importance of determining the presence or absence of a middorsal ridge (a low ridge in the skin extending for all or a part of the distance between the first and second dorsal fins) for the identification of carcharhinid sharks cannot be overemphasized. This minor structural feature is certainly nonadaptive and its usefulness as an indicator of probable relationships should be great (see Springer, 1950: p. 1, and Backus, Springer, and Arnold, 1956: p. 180, for discussion). The first mention of this characteristic in published work was by Nichols and Breder (1927), but correct identifications of the common large ground sharks of the east coast of the United States were made by Nichols and by Radcliffe independently before 1916.

In one of the more valuable papers on sharks, Radcliffe (1916) made the first general use of the structure of the dermal denticles to show differences in western North Atlantic carcharhinid species; and his illustrations show clearly the distinctive denticle type and arrangement which sets *E. milberti* off from other carcharhinids within its range, except for the newly described *E. altima*. Both *E. milberti* and *E. altima* differ from all other North American carcharhinid sharks in having nonimbricate denticles without strongly projecting points; however, the denticles of *E. altima* are much smaller than those of *E. milberti.*

Commercial shark fishermen at Salerno and Key West, Fla., recognized *altima* as distinct from the sandbar shark and called it the bignose shark or Knopp's shark before it received a scientific name. The diagnosis given with the original description of *E. altima* (Springer, 1950) should be adequate for the determination of specimens of all sizes. All of the known examples of *E. altima* have been taken at depths of 50 to 150 fathoms off Salerno, Florida, in the Straits of Florida, in the northeastern Gulf of Mexico, and in the Dragon's Mouth between Trinidad and Venezuela. Its vertical range overlaps that of the shallower water *E. milberti* in the Straits of Florida area and extends well into the nighttime range of the night shark, *Hypoprion signatus* Poey. The geographical range of *E. altima* may be quite extensive, but it is unknown because comparatively little fishing has been carried out at the depths where this species might be expected to occur. Such fishing as has been done in midwater and just beyond the edges of the Continental Shelf by commercial shark fishermen indicates that the species is relatively common.

Probably many more *E. altima* would have been taken by the commercial fishery were it not for the fact that in the Florida-Caribbean region the liver oil of *altima* is characteristically lower in vitamin-A content than is that of any of the other species of *Eulamia* or of *Hypoprion* in that area.

In a large measure, the confusion in the nomenclature of the larger American carcharhinids that existed before the publication of the 1948 work by Bigelow and Schroeder would undoubtedly have been avoided if descriptive literature had included information on the presence or absence of the middorsal ridge. A fine replica of a shark, which in the light of the better descriptions now available can easily be identified as *Carcharhinus leucas* (Müller and Henle), a species without a middorsal ridge, is shown in an illustration in an informative article (Rockwell, 1916: p. 161) under the caption *Carcharhinus obscurus* (*Eulamia obscura*), a species with a middorsal ridge. Determination of the presence or absence of the ridge is sometimes difficult, particularly for museum specimens or for specimens that have been exposed to the sun for a long period. Although identifications can be made without reference to the ridge, they are likely to be difficult and use of all of the available differentiating characteristics is desirable.

The confusion of the sandbar shark with the bull shark extends to the Pacific. References have frequently been made to the sandbar shark, *Eulamia milberti*, as occurring on the Pacific coast of Panama. There is no evidence of this and the species probably is not found there. Garman's (1913) synonymy of *milberti* included *Eulamia nicaraguensis* Gill and Bransford, the fresh-water bull shark. The two bull sharks, *nicaraguensis* and *leucas* are so similar to one another that their separation is doubtful. There is a Pacific species so similar to *nicaraguensis* and *leucas* that commercial shark fishermen who fished on both coasts claimed they were unable to distinguish one from the other except by area of capture. I do not know the scientific name for the form if it has a name, but whatever the species, it is like *nicaraguensis* or *leucas* and not like *milberti*. Meek and Hildebrand seemingly had difficulties with this one in Fishes of Panama (1923), wherein they discuss a Pacific species *Carcharhinus azureus* (Gilbert and Starks) as a synonym of *milberti*. But Meek and Hildebrand did not see a specimen from the area which they themselves could identify as *milberti* and the significant sentence in their treatment states—

We certainly must regard the present arrangement as tentative only, for more specimens must be compared before the true affinities of the specimens from the opposite coasts can be established.

A paper by Rosenblatt and Baldwin (1958) on some of the carcharhinids of the eastern Pacific presents for the first time information on the presence or absence of the middorsal ridge in Pacific species. This is an important contribution and includes more comprehensive descriptions than have hitherto been available for sharks of the eastern tropical Pacific. These authors find the separation of *Eulamia* from *Carcharhinus* unacceptable for Pacific species. In support of this an unfortunate choice of illustrative argument is used. They say *C. altima*, for example, has a definite dermal ridge but teeth which are as narrow as those of any member of the smooth-backed group (Springer, 1950). This is an error. The teeth of *altima* in the upper jaw are similar in general shape to the teeth of the other species of *Eulamia*. These authors logically call attention to the ill-assorted group left in the genus *Carcharhinus* by my 1950 revision, mentioning *leucas* and *velox* as examples. I am in complete agreement with this but find no cogent argument for the elimination of *Eulamia*, since the species of *Eulamia* as restricted are remarkably similar to one another in all of their morphological features. The sharks allied to the genus *Carcharhinus* are far too widespread and numerous and there is far too little known about them for an adequate study of the entire group. Additional revisions of the group are needed.

Differences between adults of *E. altima* and *milberti* are quite apparent in field examination when the two are seen side by side. The snout of *altima* is longer and notably thicker dorsoventrally. Furthermore, the first dorsal fin in *E. altima* looks quite different because it is not quite so far forward as in *E. milberti* and is neither so erect nor so high. The high and erect dorsal fin of *E. milberti* in a forward position (fig. 2) is a reliable and adequate character for field recognition of adults in the water, if the size of the shark is taken into consideration.

Gill (1862) based his classification of the carcharhinid sharks almost entirely on the structure of the teeth. His arrangement of genera was not satisfactory and it is apparent that short descriptions of shark teeth are inadequate and lead to confusion even though the number and form of the teeth show comparatively little variation within species and are of considerable diagnostic value. The persistence of essentially similar shape and structure in the successively larger teeth appearing in some carcharhinid sharks as they grow has been fairly well established by observation. In *E. milberti*, at least, this appears to be true, although this is neither universal among sharks nor adequately demonstrated for many species.

To obtain some verification of the extent of variation in the number of tooth rows in carcharhinid sharks, I took advantage of a situation requiring the preparation of several hundred clean, dry shark jaws for a commercial order. I carefully identified the sharks and tagged the jaws of a series of 110 *E. milberti* together with all other sharks appearing at the same time on the dock at Salerno, Fla. All of the *milberti* and most of the other sharks were adults; sex was not noted. After the jaws were cleaned I counted and recorded the number of tooth rows (table 1). To the extent that this sample represents the population of *milberti*, the counts of rows of teeth indicate that variation is small in that species.

The shape and the relative position of the fins in carcharhinid sharks are reasonably useful characteristics for identification. Small differences in the size of fins or even in their positions, however, are of comparatively little value because of differential growth and the diverse trends this

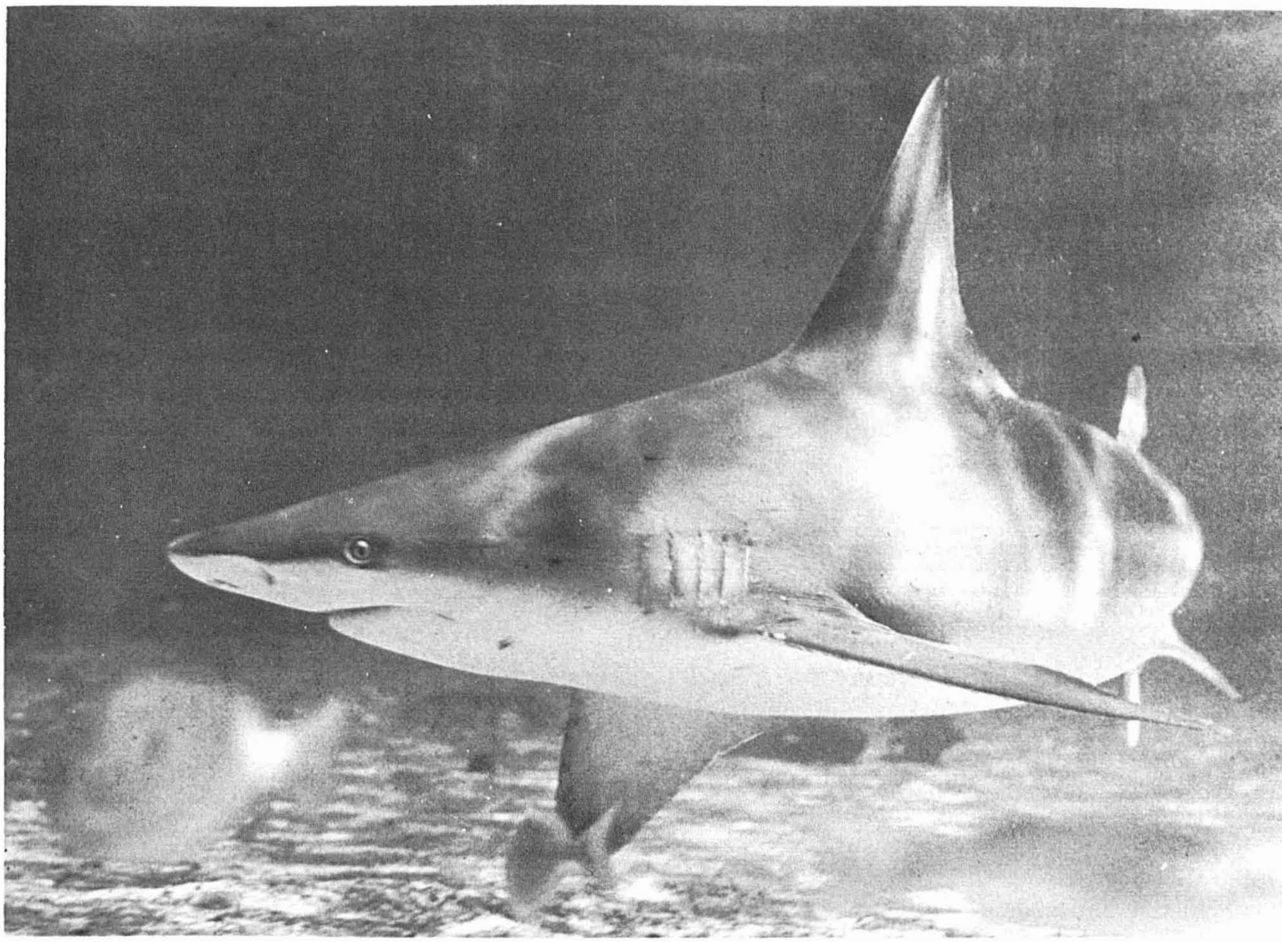

FIGURE 2.—*Eulamia milberti* turning in front of the camera at Marineland, Fla. Note that the pectoral fins are quite broad at their bases, relatively pointed and not strongly concave on their trailing edges. With the exception of the caudal fin, all fins function as rudders or stabilizers and cannot be used independently for locomotion The pectorals provide lift to offset the lift of the asymmetrical caudal since without a forward lift the shark would tend to somersault. The large stiff fins in forward positions reduce the ability of this species to roll and twist but may be expected to increase the precision of its forward swoops at creatures on the sea bottom. (Photograph courtesy of Marine Studios, Marineland, Fla.)

growth may take in different species. Data to show adequately the differential growth in carcharhinids are lacking. But one example will suffice to show how unreliable proportional measurements can be for comparisons between species in which specimens of different sizes and ages are involved, and in which the growth patterns of the species being compared are unknown. In three examples of young *E. milberti*, 685, 680, and 635 mm. long, from the vicinity of Woods Hole, Mass., the lengths of pectoral fins (measured on their outer margins or leading edges) are 16.2, 15.9, and 15.0 percent of the total length of the sharks. In three adult *milberti* from off Englewood, Fla., 2,210, 2,070, and 2,240 mm. long, the pectoral fin lengths are 21.3, 21.5, and 21.0 percent of the total length. Let us compare these proportions with measurements of pectoral fin lengths of the whitetip shark, *Pterolamiops longimanus* (Poey). A late-embryo whitetip 530 mm. long, taken 135 miles off New Smyrna, Fla., has a pectoral fin length 22.6 percent of the total length; a young whitetip 1,020 mm. long, taken off Tampico, Mexico, has a pectoral fin 25.5 percent of the total length; and an adult whitetip, 2.310 mm. long, from the central Caribbean, has a pectoral fin 22.0 percent of the total length. The figures indicate a proportionately longer

TABLE 1.—*Tooth-row counts in carcharhinid sharks taken off Salerno, Fla., summer of 1947*

Species	Number of specimens having toothrow counts [1] of—																
	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37
Eulamia milberti (110 specimens):																	
Upper jaw								3	37	55	11	4					
Lower jaw							12	20	44	30	3	1					
E. floridana (48 specimens):																	
Upper jaw											1	29	11	3	1	3	
Lower jaw										1	6	13	23	4	1		
E. obscura (39 specimens):																	
Upper jaw									3	15	12	7	2				
Lower jaw							1	3	15	10	8	1	1				
Carcharhinus leucas (24 specimens):																	
Upper jaw					2	5	15	1	1								
Lower					18	3	3										
C. limbatus (31 specimens):																	
Upper jaw									1	0	4	14	11	0	1		
Lower jaw									1	25	5						
C. maculipinnis (13 specimens):																	
Upper jaw												1	1	2	4	3	2
Lower jaw											2	1	9	1			
Galeocerdo cuvier (21 specimens):																	
Upper jaw	4	3	12	2													
Lower jaw	1	2	13	2	3												
Negaprion brevirostris (8 specimens):																	
Upper jaw										1	1	6					
Lower jaw									5	1	2						

[1] All counts made from cleaned jaws from which all membranous sheathing had been removed to permit accurate counts whether or not teeth of the functional row were missing.

pectoral fin in adults than in young for *E. milberti*, but an entirely different condition in *P. longimanus*.

The sandbar sharks available to me were remarkably uniform in general appearance and in those features that I could measure, count, or compare. In an attempt to learn something from morphometrics, a considerable number of *milberti* and other species were measured carefully and in detail. However, the principal value that I derived from this excessively laborious task was in the deliberate examination of specimens enforced by measurement of detail and in the notes made to accompany the measurements. The exercise served also to impress upon me the difficulties attending attempts to get adequate series to show growth patterns among some of the species of large sharks which are not only migratory but probably short lived.

A characteristic of great importance for field recognition of specimens of carcharhinid sharks is the total length of the specimen considered in connection with its sex and maturity (fig. 3). The mammalogists and ornithologists have long considered total length important in identification because mammals and birds have determinate growth patterns. As will be shown later, *E. milberti* has growth characteristics which result in adults of predictable size. Furthermore, the size range of adults within the known segments of the population falls within limits which are narrow enough to facilitate field identification by process of elimination. Thus, an adult *Eulamia* more than 92 inches in total length is probably not *milberti*, and adult males less than 70 inches or adult females less than 72 inches in total length are unknown.

DISTRIBUTION OF *EULAMIA MILBERTI*

General nature of distribution

The distribution of *Eulamia milberti* is difficult to treat adequately because, even though further discussions will be limited to the population of the western North Atlantic, the distribution patterns are extremely complex. The adults segregate by sex and to some degree have different vertical ranges. The nursery areas occupied by the very young sharks are free of adults except when the females come inshore to give birth to their young.

The migratory patterns of young and adults differ greatly. Finally there is a well-defined principal range occupied by at least nine-tenths of the western North Atlantic population and an accessory range of uncertain importance. It is quite possible that the population occupying the accessory range is not self-sustaining and exists only because there is continuous but quite acci-

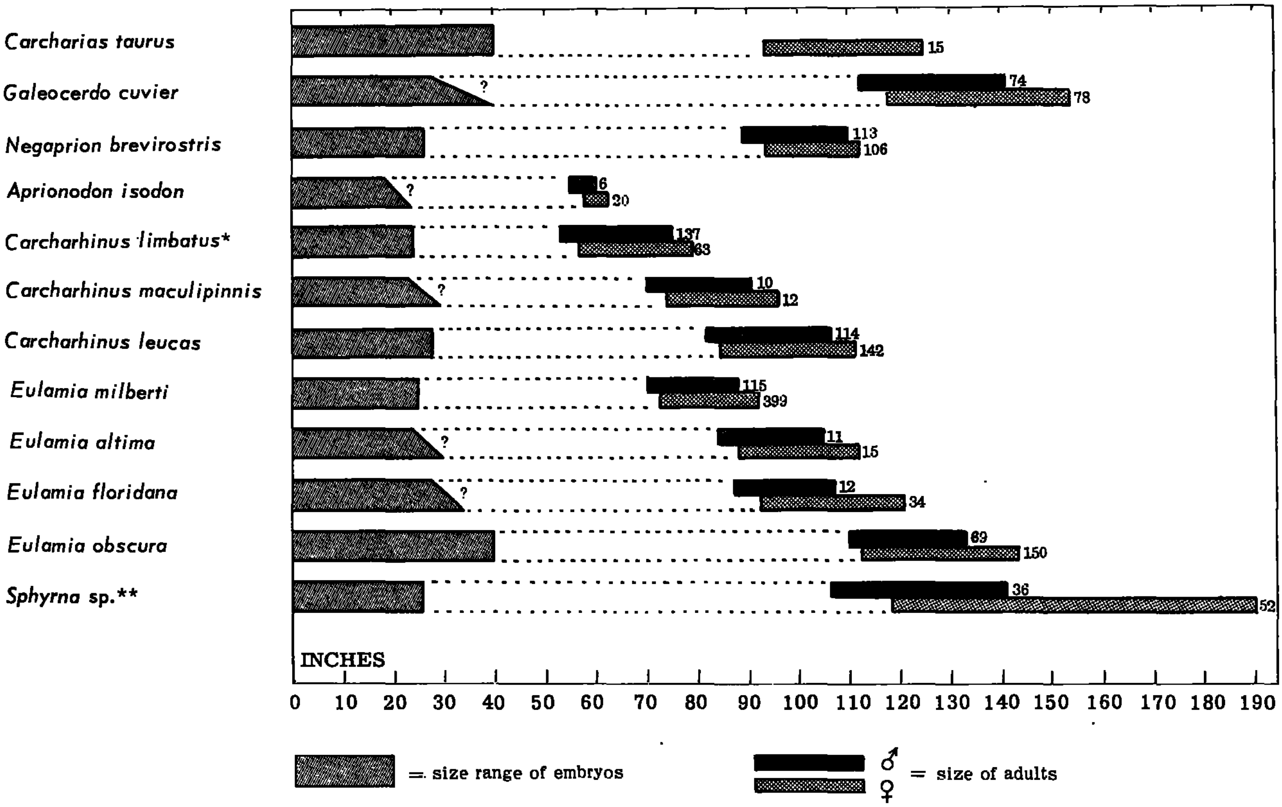

FIGURE 3.—Comparative sizes of adults and young of common large sharks found within the geographical range of *E. milberti*. The figures at the right indicate the number of specimens in the sample used to determine size range. The size ranges for embryos are estimates based on maximum observed lengths of embryos and minimun lengths of free-swimming young observed in Florida collections. (* Size range in Florida-Antillean specimens. Western Gulf of Mexico and Central American coast specimens are smaller and produce smaller young. The western stock may prove to be distinct and if so should take the name *Carcharhinus natator* Meek and Hildebrand. ** The great hammerhead of the West Indian region, following Bigelow and Schroeder (1948). The nomenclature is now unsettled. The name *Sphyrna tudes* is not available for the great hammerhead and probably should be replaced by *Sphyrna mokarran* (Rüppell).)

dental recruitment from the principal population. Within the expected vertical and geographical range of the species are some areas which appear to be avoided. It is well to mention again that the sandbar shark, like other large sharks, is not prevented by well-defined barriers from wandering out of its normal range.

The limits of distribution are therefore not sharply defined. Following the traditional pattern in descriptions of distribution it may be said that the sandbar shark, as represented by the western North Atlantic population, is common in summer off the Atlantic coast from Cape Cod to West Palm Beach, Fla., and in winter from the coast of the Carolinas around the tip of Florida to the gulf coast of Florida as far north as Tarpon Springs. It occurs uncommonly in the western part of the Gulf of Mexico and along the continental shores southward to Costa Rica. It is a casual visitor on the northern coast of Cuba and the western edges of the Bahama Banks. Its vertical range is from the shoreline out to 135 fathoms. It enters bay mouths but is not found in fresh waters.

The principal source of information on the distribution of the sandbar shark comes from the commercial shark fishery. Atlantic coast shark fishermen used bottom setlines more often than any other gear. Each unit of gear consisted of a main line of chain or wire rope a half-mile or more in length. This was set on the bottom, anchored at both ends with the anchors rigged with buoys so that the lines could be retrieved. Short, branch lines made of chain, each with a baited hook, were spaced at intervals of 20 to 40 feet along the central part of the main line. The typical unit had 100 hooks. Floating lines and anchored gill nets were also used occasionally in the fishery.

Positive information from the shark fishery on the distribution of *E. milberti* is quite voluminous and detailed. Systems of payments to fishermen required detailed records involving identification and measurement of all sharks landed by vessels of the principal fishing company. Altogether, records of landings of more than 100,000 *milberti* during a period of 15 years have been examined.

Information on the absence of *E. milberti* from specific areas has been difficult to assemble, but here also the records of the shark fishery supply most of the data. The species was first reported in the Florida area from correctly identified specimens after the commercial shark fishery began (Springer, 1938), so the earlier scientific literature has been useless in the establishment of the range of the species in the Florida area southward. Offshore records, from areas where water depths are more than 500 fathoms, are exclusively from catches made on tuna longlines used by the exploratory fishing vessel *Oregon* (for descriptions of this gear see Bullis, 1955, and Captiva, 1955). Some information on the distribution of the young was obtained from otter-trawl catches made by the exploratory fishing vessel *Delaware* off the coast of North Carolina. Additional scattered records were picked up from accidental catches made by commercial and sport fishermen who used various types of gear, from catches made by collectors fishing for aquarium specimens, and from biologists who captured specimens incidental to other collecting activities.

The area of greatest uncertainty is in the offshore and midwater range. Recent marine exploration has shown that substantial populations of large sharks, fishes, and invertebrates live in subsurface waters beyond the Continental Shelf where they have escaped the attention of naturalists. On June 11, 1954, the first *E. milberti* known from waters beyond the Continental Shelf was taken on a tuna longline hook at USFWS *Oregon* station 1099, 85 miles off the coast of Texas where the depth was approximately 600 fathoms. Since the hook was set to fish at about 30 fathoms, this shark, an adult male, was cruising in midwater. Throughout the second half of 1954, all of 1955, and the first part of 1956, longline fishing was carried on in the offshore waters of the Gulf of Mexico by the M/V *Oregon* and a few commercial vessels. Large numbers of sharks were taken, chiefly species known to be partly or entirely pelagic. No additional *milberti* were taken until early February 1955, when a commercial vessel caught two adult females about 50 miles off the northern edge of the Campeche Bank where depths were estimated to be more than 1,000 fathoms. These sharks were caught on longlines with hooks fishing not more than 50 fathoms deep. These three captures, outside the principal range, appear to have little significance in the general picture of the distribution of *Eulamia milberti*.

Factors affecting distribution

It may be assumed that water temperature and salinity are important in limiting the distribution of the sandbar shark and that there are other factors clearly influencing the movements and distribution of the species. The reaction of sandbar sharks to ocean currents, the availability of food, the relation between the growth rate or the reproductive pattern and the migratory movements, all appear to be important in forcing the species into a particular range. No data are available, however, to show the relative strengths of these conditions as determinants of the range of the sandbar shark.

The facts, from superficial examination at least, do not support the thesis that competition with other species is a powerful influence in the selection of a particular range. Young *Eulamia milberti*, for example, apparently cannot long survive where large *Carcharhinus leucas* in proportion to *milberti* are relatively abundant. The presence of large numbers of large *C. leucas* in the vicinity of the mouth of the Mississippi River seemingly does not deter gravid female *milberti* from moving into the area to give birth to young.

Whatever the particular reason or reasons may be, the general absence of young *milberti* in the Gulf of Mexico shows that conditions are unfavorable for them. Circumstantial evidence suggests that interspecies competition is responsible, because large *C. leucas* eat young *milberti.*

No explanation is apparent for the common occurrence of *E. milberti* along the continental shores and its absence from most of the West Indian shallow waters except that the species seems to have preferences for certain types of bottom. *E. milberti* is ordinarily not common in areas of coral reefs or where the bottom is rough. Since it is chiefly a bottom-dwelling species, it is not surprising that it would exhibit preference for one type of bottom over another. In its migratory passages around the southern tip of Florida and the Florida Keys, however, there appears to be active avoidance of the fringing reef. Here the migrating adults leave the relatively shallow areas they inhabit on both the east and west coasts of Florida and temporarily enter and feed in much deeper water.

Nursery grounds and distribution of young

The principal nursery grounds of the western North Atlantic population of *Eulamia milberti* lie in relatively shallow water along the Atlantic coast of the United States from Long Island to Cape Canaveral, Fla. This range may be extended slightly at its northern end to the south side of Cape Cod in favorable years but the southern limit is more definitely fixed. Not one young *milberti* has been taken south of Cape Canaveral, around the tip of Florida, or in the eastern Gulf of Mexico. On the east coast of Florida, south of Cape Canaveral, a few sexually immature *milberti* of almost adult size have been taken; but in this area adult *milberti* are common. A great quantity and variety of fishing effort has been concentrated south of Cape Canaveral on the Florida coast. The total absence of young *milberti* here is remarkable in view of the somewhat indefinite range limits of the adults.

A secondary nursery range apparently lies in the northwestern part of the Gulf of Mexico. It is indicated only by the capture of a few females with near full-term embryos near the mouth of the Mississippi River, the capture of a large *milberti* with nearly full-term embryos off the Texas coast (Henry Hildebrand, 1954), and a specimen 747 mm. (nearly 30 inches) from the Texas coast (Bigelow and Schroeder, 1948).

552508 O—60——3

It is probable that gravid females wandering away from the principal range of the species give birth to young along the Mexican and Central American coast, but no records of the capture of young in this area have been found. Shark fishing on a small scale has been carried out over most of this area and catches have been examined at various points from the mouth of the Rio Grande River to Costa Rica; but excepting the Gulf of Campeche, no young *milberti* appeared.

The female *Eulamia milberti*, which move into the principal nursery areas to give birth to their young, do not remain there long and do not feed actively while there. This may explain the scarcity of records of captures of adult *E. milberti* along the Atlantic coast. Great South Bay, Long Island, is one of the nursery areas of *E. milberti* and accounts of the appearance of females in the bay and birth of the young are given by Thorne (1916). Additional mention of the appearance of *E. milberti* in the Great South Bay area is made by Nichols (1918), who notes that the interesting fact about them is that the adults of the two sexes of the same species are almost never taken together near Long Island. Here the adult females are *E. milberti* and the adult males are *Carcharhinus leucas.*

Records of young sharks from Chesapeake Bay show that *E. milberti* gives birth to young in the bay in summer. William Massmann, of the Virginia Fisheries Laboratory, has kindly given me (in correspondence) records of *E. milberti* from the lower Chesapeake Bay. He says—

> Although young of this species are probably the most abundant shark in the Bay in summer, I would not say that it is numerous. * * * It is commonly caught by anglers and probably rather generally distributed in the lower Bay. I have not seen an adult in the Bay or any individual more than three and a half feet long.

After a comparatively brief period in shallow water or in the mouths of bays, perhaps at the beginning of cool weather, young *milberti* appear to move offshore. The only area from which young *milberti* are known in the winter season lies off the coasts of the Carolinas at depths out to 75 fathoms.

Distribution off Atlantic coast of the United States and in eastern Gulf of Mexico

The northern limit of the range of the sandbar shark is easily established. There are no reliable records of its capture from the Gulf of Maine (Bigelow and Schroeder, 1953), but south of Cape Cod it has been taken frequently but irregularly at Woods Hole, Mass. Numerous records of the species along the Atlantic coast of the United States are summarized by Bigelow and Schroeder (1948). Sandbar sharks may be said to be common in summer along the Atlantic coast of the United States from Long Island to the tip of Florida and in winter along the waters of the Continental Shelf off the Carolinas southward to the southern tip of Florida, in water of moderate depths in the Florida Straits and along the west coast of Florida northward to Tarpon Springs or the Middle Grounds (the rough bottom area south of Cape San Blas, Fla.). This area is the principal known range, but the species has also been taken in small numbers from the northern and western Gulf of Mexico, the western borders of the Bahama Bank, the northern coast of Cuba, and the Caribbean coast of Nicaragua and northern Costa Rica (fig. 4).

The hypothesis is advanced here that the sandbar sharks of the eastern and southern sides of the Gulf Stream in the Straits of Florida are casual visitors to those areas and that the stock of the northern and western parts of the Gulf of Mexico is a breeding stock which is not self-sustaining, but is recruited in part from migratory adults moving to the northern and western parts of the Gulf by mistake or through error in orientation and navigation during the regular winter migration of the principal stock.

The sandbar shark has been taken from the shallows along beaches out to a depth of about 135 fathoms. The young have been taken most often in shallow waters to depths of about 5 to 25 fathoms in summer, but in winter they move offshore to warmer water and depths as great as 75 fathoms off the Carolina coast.

The sandbar shark is known only from the shallower part of the Continental Shelf in the warmer months in the extreme northern part of its range. Probably the adults are more common off beaches than in major bays or inlets. Hildebrand and Schroeder (1928) found the species rather rare in Chesapeake Bay although more common than any other shark except the spiny dogfish. Radcliffe (1916) states that the species appears to be rare in the Beaufort, North Carolina, region. However, it was regarded as common in bays on the ocean side of Long Island from mid-June to mid-September, by Nichols and Breder (1927).

The apparent scarcity of adult *E. milberti* noted by Hildebrand and Schroeder and by Radcliffe is easily explained. It is possible that *E. milberti* enters the mouths of bays to give birth to young more frequently than records suggest. Female *Carcharhinus leucas* and *Negaprion brevirostris* move inshore and stop feeding for a short period at the time of the birth of their young, and immediately after the young are born the females move into comparatively deeper water. This may be a common habit among carcharhinids and certainly a very useful one to provide for survival of the species. The Long Island records are to a large extent based on harpooned specimens, and adult females should probably not be expected to be easily available to capture on baited hooks in areas where the young are born.

The best fishing depth for adult *E. milberti* from the Carolinas south to Miami was found by the commercial shark fishermen to be 15 to 30 fathoms. On this stretch of coast it was rarely if ever taken beyond 50 fathoms on bottom setlines and made up less than 5 percent of the catch on floatlines set beyond the 100-fathom curve.

Southward from Miami, *milberti* was rare among the keys, in Hawk Channel, or along the shallower portions of the reefs south of the Florida Keys. In the winter, a few appeared in catches made in the Northwest Ship Channel but, in general, these waters were left to other species. The sandbar sharks, however, were the commonest sharks on the bottom beyond the fringing reef out to depths of 50 fathoms and made up substantial portions of catches out to 100 fathoms. They were appreciably more numerous in catches off the lower keys where currents were not so strong. Northward from the keys along the west Florida coast as far as Tampa, *E. milberti* was found to be most abundant in depths of less than 30 fathoms.

Shark-fishing vessels operated out of Salerno, Fla., almost every day that weather permitted

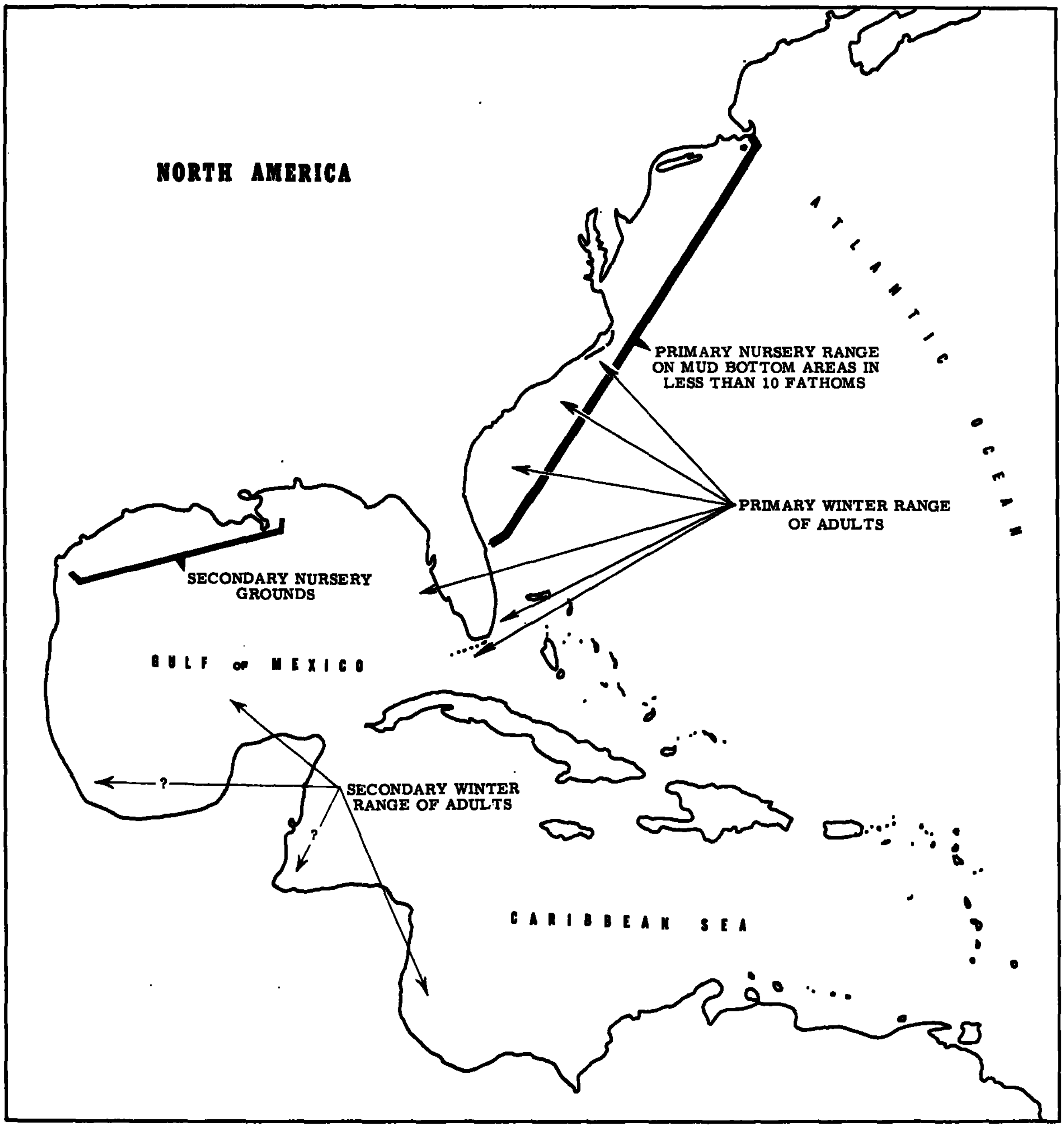

FIGURE 4.—Geographical distribution of the western North Atlantic population of the sandbar shark, *Eulamia milberti*.

from 1936 to 1950, except for parts of 1939 and 1940 when activities were suspended due to overproduction. These vessels landed their catches daily at Salerno where the sharks were identified, measured, and recorded. Catches included in the Salerno landings were made from Bethel Shoal, north of Fort Pierce, Fla., to the offings of Jupiter Light. Some details of these landings, showing catch per unit of effort, were reported in an earlier publication (Springer, 1951). These data show that at Salerno the highest average rate of catch of *E. milberti* occurred annually in the month of February and the lowest average rate of catch in September. These data concern only adult *milberti* and the comparatively few sexually immature *milberti* of adult size occurring with the adults.

On the west coast of Florida, shark-fishing vessels caught no *E. milberti* at all from May through November and reported their largest catches from January through March in each of several years for which data are available.

At Key West, Fla., high catch rates were obtained for *milberti* from deepwater sets made in the winter and early spring but catches at other seasons were poor.

High catch rates of adult *E. milberti* were obtained by shark-fishing vessels off the Carolinas in September, and from 1946 to 1949 one or two of the more able shark-fishing vessels followed the fishing for adult *milberti* southward, arriving off Salerno in January or February.

Scouting by shark-fishing vessels showed that some adult *milberti* were present in each month of the year along the Atlantic coast between the latitudes of Charleston, South Carolina, and Miami, Florida. Although *E. milberti* was the principal species sought in this area, other species contributed variously to the value of the total catch. Table 2 shows the comparative availability of large sharks to the kinds of fishing gear employed in the Salerno area in the late spring.

Distribution in Bahamas and West Indies

E. milberti is common only on the western side of the Gulf Stream. On the eastern side of the stream, it is replaced by *E. falciformis* as the common inshore *Eulamia*. The wandering of *milberti* into the Antillean area may be quite limited. There are no records of *milberti* eastward through the West Indies nor from the southern shores of Cuba. A shark fishing operation on the eastern part of the Bahama Bank in the period from 1947 to 1949 did not take *milberti*.

E. falciformis was reported by Evermann and Marsh (1902) from Puerto Rico; by Beebe and Tee Van (1928) from Port-au-Prince Bay, Haiti; by Nichols (1929) from Puerto Rico; and by Backus (1957) from open sea situations east of the Gulf Stream. None of these authors noted the presence of *E. milberti*.

Frank Mather III has told me in correspondence of the capture of *E. falciformis* and *E. floridana* from the vicinity of St. Croix and St. Thomas in the Virgin Islands. Mather's fishing operations covered the depth range in which *E. milberti* would be expected if its geographical range extends through the West Indies and if the absence of *milberti* follows the usual pattern in the West Indies.

TABLE 2.—*Sharks taken by commercial fishing vessels in the Salerno-Fort Pierce area (Bethel Shoal to Jupiter Light) and landed at Salerno, Fla., in May and June 1945–46*

[1 to 3 vessels; only sharks with hide length of 55 in. or more included; fishing depths from 18 to 40 fathoms]

Species	Number of sharks	
	1945	1946
Eulamia milberti (Müller and Henle), sandbar shark	1,515	987
Sphyrna sp.,[1] hammerheads	323	268
Eulamia obscura (LeSueur), dusky shark	269	94
Eulamia floridana (Bigelow, Schroeder, and Springer), silky shark	220	191
Galeocerdo cuvier (LeSueur), tiger shark	68	64
Carcharhinus leucas (Müller and Henle), bull shark	61	41
Negaprion brevirostris (Poey), lemon shark	20	19
Carcharhinus sp.,[2] blacktips	3	16
Ginglymostoma cirratum (Gmelin), nurse shark	2	6
Carcharodon carcharias (Linnaeus), great white shark	2	5
Isurus oxyrinchus Rafinesque, mako	0	2
Unidentified	120	2

[1] 3 species; station records do not distinguish kind.
[2] 2 species; station records do not distinguish kind.

That the Gulf Stream is not itself a barrier to *E. milberti* is apparent from the occasional captures along the Bahama Banks and off the northern coast of Cuba. It is possible that large numbers of migratory sharks may wander away from normal migratory routes at times when unusual conditions prevail. Certainly a few *milberti* cross the stream.

From May 18, 1948, to July 8, 1948, I undertook a program of experimental shark fishing along the western edge of the Bahama Bank from Riding Rock northward. Fishing operations were carried out from a base at the Lerner Marine Laboratory of the American Museum of Natural History at Bimini, using a fishing vessel and gear provided by the Shark Industries Division of the Borden Co. Fishing was carried on chiefly by bottom setlines at depths from 10 to 200 fathoms, but some floating lines were used to assure collection of as wide a variety of sharks as possible. Sets included some made at various levels along the extremely precipitous slope of the bank, which drops off abruptly from about 20 fathoms down to the floor of the Gulf Stream channel where depths are more than 150 fathoms.

During the entire fishing period along the Bahama Banks only 14 *E. milberti* were caught in the lot of 447 sharks. Of the total, 197 were reef sharks, *Eulamia springeri* (Bigelow and Schroeder).

TABLE 3.—*Sharks taken in exploratory fishing from the* Dusky *along edges of northwestern Bahama Banks, May 18 to July 8, 1948*

Species	Number of sharks taken in—	
	Bimini area (20–200 fathoms)	Walker Key (10–100 fathoms)
Eulamia springeri (Bigelow and Schroeder), reef shark	10	187
Galeocerdo cuvier (LeSueur), tiger shark	60	13
Eulamia obscura (LeSueur), dusky shark	46	5
Negaprion brevirostris (Poey), lemon shark	2	18
Eulamia altima Springer, bignose shark	17	2
Fulamia floridana (Bigelow, Schroeder, and Springer), silky shark	15	0
Eulamia milberti (Müller and Henle), sandbar shark	10	4
Hypoprion signatus Poey, night shark	12	2
Scoliodon terra-novae (Richardson), sharpnose shark	11	3
Ginglymostoma cirratum (Gmelin), nurse shark	2	3
Sphyrna lewini Griffith, southern hammerhead	5	2
Heranchus sp. (not *H. griseus*), little cowshark	3	0
Carcharhinus limbatus (Müller and Henle),[1] little blacktip	3	1
Sphyrna sp.,[2] great hammerhead	1	2
Carcharhinus leucas (Müller and Henle), bull shark	0	3
Mustelus canis (Mitchill), common smooth dogshark	1	0
Pterolamiops longimanus (Poey), whitetip	1	0
Carcharhinus maculipinnis (Poey), big blacktip	0	1
Carcharhinus acronotus (Poey), blacknose shark	1	0
Eulamia sp., undetermined	1	0

[1] Antillean form.
[2] Nomenclatorial status of this species not determined.

During the same season of the year in which the exploratory fishing was done, a great number of sharks were landed across the Gulf Stream at Salerno, Fla., about 80 miles from the northern end of our Bahama fishing area. But more than half of them were *E. milberti*, and no *E. falciformis* was landed. Results of the Bahama fishing are summarized in table 3, which shows catches made in two areas off the Bahama Banks. For purposes of camparison, catches made in the Salerno–Fort Pierce area in May and June 1945 and 1946 are shown in table 2. The two fishing operations are not exactly comparable, of course, not only because they were carried on in different years but because the Bahama fishing was essentially exploratory while the Salerno–Fort Pierce fishing was a part of a continuing commercial operation concentrated in limited depths and locations. Exploratory fishing with sets scattered in different depths and locations off Salerno would presumably produce a few *E. springeri* because there are normally a few to be found along inshore reefs adjacent to the St. Lucie Inlet at Salerno. This is a poor fishing spot, however, so the commercial vessels rarely caught *springeri*.

Distribution in western Gulf of Mexico and western Caribbean

Positive knowledge of the distribution of *Eulamia milberti* in the western part of the Gulf of Mexico and along the Caribbean coast of Central America is based on records of 8 gravid females off the Mississippi River delta, 1 gravid female and 1 young male from the coast of Texas, 1 adult male and 2 adult females from the south-central part of the Gulf of Mexico over deep water, and 51 adults from the Caribbean coast of Nicaragua and Costa Rica.

From the mouth of the Mississippi River eastward and southward around the Gulf to the vicinity of Tarpon Springs on the Florida west coast, *milberti* appears to be absent or at least rare from inshore waters out to 30 fathoms. No catches were reported by shark fishermen and no specimens were seen. I should note that while employed in the shark fishery, seasonal shark-fishing stations were maintained at various times at all of the fishing ports of any consequence from the mouth of the Mississippi River around the tip of Florida to the Carolinas. I visited all of these stations frequently and sometimes participated in fishing operations. The presence of *milberti* in appreciable quantity would almost certainly have been noted in catches from the stations at Panama City and Carrabelle, Fla., had specimens been taken.

It is not possible to present a meaningful account of the sandbar shark, *Eulamia milberti*, without frequent reference to the bull shark, *Carcharhinus leucas*, and its fresh-water representative, *Carcharhinus nicaraguensis* (Gill and Bransford). The sandbar shark has been confused with the bull shark because of the peculiar manner in which their ranges overlap. In addition, bull sharks appear to be the most important of the predators on young sandbar sharks and the primary factor that prevents *E. milberti* from extending its nursery range into otherwise suitable areas in tropical seas.

As has already been noted, bull sharks are found along the Atlantic coast as far north as Long Island but increase in numbers somewhat in the latitude of Salerno, Fla., where, as noted in table 2, they were sixth in number of large sharks landed by the shark fishery. The abundance of bull sharks at various locations in the Gulf of Mexico varies seasonally, but from the vicinity of Apalachicola, Fla., westward along the northern coast of the Gulf of Mexico and southward along the coasts of Central and South America as far at least as French Guiana, bull sharks form the major part of catches of large sharks made by shallow-water setlines in some seasons. Table 4 shows the comparative frequence of capture of large sharks during a test-fishing period off the mouth of the Mississippi River.

TABLE 4.—*Large sharks taken from the* Joe Leckich *on bottom lines set in 5 to 35 fathoms off the mouth of the Mississippi River, June 25 to July 29, 1947*

Species [1]	Number of sharks	Average weight of liver (lb.)
Carcharhinus leucas (Müller and Henle), bull shark	275	38
Eulamia obscura (LeSueur), dusky shark	83	53
Galeocerdo cuvier (LeSueur), tiger shark	56	129
Carcharhinus limbatus (Müller and Henle), little blacktip [2]	47	3
Sphyrna sp., great hammerhead	9	49
Carcharhinus maculipinnis, big blacktip	8	13
Eulamia milberti (Müller and Henle), sandbar shark	8	14
Carcharias taurus Rafinesque, sand shark	7	26
Negaprion brevirostris (Poey), lemon shark	4	20
Sphyrna lewini Griffith, southern hammerhead	3	12
Eulamia floridana (Bigelow, Schroeder, and Springer), silky shark	1	16
Eulamia springeri (Bigelow and Schroeder)	1	4

[1] Also taken but not recorded because of small size: several *Scoliodon terra-novae* (Richardson), *Carcharhinus porosus* Ranzani, and *Mustelus canis* (Mitchill), and one young *Ginglymostoma cirratum* (Gmelin).
[2] Continental form—typical of western Gulf of Mexico.

The eight *E. milberti* were adult females and five of them were gravid. Since *milberti* has liver oil of comparatively higher potency than the oil from other species in the area, a special effort was made to catch them in subsequent, larger scale fishing efforts. Nevertheless, catches of *milberti* were not made later during 1947 and commercial fishermen operating in the area reported sandbar sharks absent in 1948 and 1949. The few records of *E. milberti* from offshore Gulf waters would not be important except that they serve to show the species can move into and across deep areas of the ocean. Off the Atlantic States there has been comparatively little longline fishing beyond the Continental Shelf and there are no records of *milberti* from deep water. There are, however, records of catches of *Eulamia falciformis* (Müller and Henle) and *E. obscura* from longline sets made by the exploratory fishing vessel *Delaware* beyond the limits of the Continental Shelf off the Middle Atlantic States. These two species are also reported by Backus (1957) from the Atlantic beyond Continental Shelf limits.

A lot of 51 adult sandbar sharks was taken by Captain B. W. Winkler from off the Caribbean coast of Nicaragua and Costa Rica. This group included all of the sandbar sharks in a collection of 854 sharks of all species which Captain Winkler measured and recorded for me from September through December, 1948. The most interesting feature of this collection of *E. milberti* was that it was made up of approximately equal numbers of adult males and females (26 males and 25 females).

The shark fauna of the area as represented by Captain Winkler's collections included a large number of species that are predatory on sharks of the size of young *E. milberti.* The following sharks were taken:

Species:	*Number*
Carcharhinus,[1] chottos or bull sharks	421
Galeocerdo cuvier (LeSueur), tiger shark	85
Eulamia obscura (LeSueur), dusky shark	76
Eulamia floridana (Bigelow, Schroeder, and Springer), silky shark	70
Carcharhinus limbatus (Müller and Henle),[2] little blacktip	54
Eulamia milberti (Müller and Henle), sandbar shark	51
Sphyrna sp. (not determined), hammerhead shark	27
Eulamia sp.,[3] reef sharks	25
Scoliodon sp., sharpnose shark	15
Hexanchus sp.,[4] cow sharks	13
Ginglymostoma cirratum (Gmelin), nurse shark	3
Eulamia altima Springer, bignose shark	2
Negaprion brevirostris (Poey), lemon shark	1
Undetermined [5]	4

[1] Either *C. leucas* (Müller and Henle) or *C. nicaraguensis* (Gill and Bransford) or both.
[2] Continental form.
[3] Probably *E. springeri* (Bigelow and Schroeder) or *E. falciformis* (Müller and Henle).
[4] Includes two species.
[5] Possibly a small species of *Galeorhinus*.

A few days' fishing with bottom longlines along the outer edge of the Continental Shelf off northern Nicaragua and on Serrana and Seranilla Banks in February 1949 failed to produce *E. milberti* or any adult sharks, but moderate numbers of young *E. floridana* were taken.

As a grader and buyer, I examined several lots of dried shark fins said to have been taken off the coasts of Colombia and Venezuela. *E. milberti* fins were not noticed although it is possible that a few might have been overlooked. The fins of *E. milberti* adults (pectorals, first dorsal, and lower caudal lobe) are more desirable for commercial purposes than the fins of some other species because they are thicker and have a relatively large proportion of the material used for shark-fin soup. Shark fishermen with whom I talked and who would recognize *milberti* also reported the absence of the species from their catches made off Colombia and Venezuela. Thus, evidence for the occurrence of *E. milberti* in the southwestern Caribbean, while not very satisfactory, is negative.

MIGRATION

It is probable that the migrations of *E. milberti* are of two kinds. One is simply the gradual withdrawal of the sharks from waters that become too cold or too warm—a movement that is accompanied by normal feeding activities and is characteristic of immature sharks. The other is a movement, generally, over a greater distance that may or may not be induced by temperature changes. The general patterns of the major movements of adult sandbar sharks suggest that ocean currents greatly influence the direction and extent of the movements.

It is necessary to consider the migratory movements of the adult male, the adult female, and the immature *Eulamia milberti* separately. We may look upon the Atlantic coast from the vicinity of Charleston, South Carolina, to the northern part of Florida as the core of distribution of the principal stock of the western North Atlantic population because it is only in this area that all three groups are known to be found. This may mean merely that in this area there is overlapping distribution. We know that the adult females go as far north as Long Island to give birth to young in summer and in some years even farther, to the vicinity of Cape Cod. There are no data to show whether the adult males or nongravid females move northward into the portion of the species' range lying north of the Carolinas. All that is known of the distribution of the young is that the young are born in water of moderate salinity from Cape Canaveral to Cape Cod and that some of them move in winter into the comparatively warmer offshore water found at depths of 50 to 75 fathoms on the Carolina coast. Until the young sharks reach adult size they do not take part in the long southern migration characteristic of adults or move south of Cape Canaveral. One capture of a lot of nearly 200 young off North Carolina indicates that the young occur in schools of both sexes and of mixed sizes.

Migratory movements of adult *E. milberti* south of Cape Canaveral are more clearly outlined from the data available from the shark fishery. The annual southward movement appears to be coincidental with the beginning of cooler weather and to be accelerated by cold snaps.

A very much larger number of adult female sandbar sharks were taken than adult males by the Florida shark fishermen. This and the tendency to segregation by sex, will be discussed later in connection with reproduction. But it should be pointed out here that no adult males are recorded from inshore nursery grounds and probably occur there but rarely. In the Florida shark fishery, adult males of most species brought more money than adult females and were particularly sought by fishermen. The fishermen were convinced by observation that adult males of most species including *milberti* were usually in deeper and cooler water than the females, that they usually preceded the females in migration, and that they usually were to be found in more compact aggregations so that fishing was best where males could be found. Such figures as are available bear this out. A rationale for this condition is suggested by the thermal sensitivity (decreased fertility with application of heat) of the male germ plasm among vertebrates in general (see Cowles, 1945).

The sandbar shark is properly considered a "ground shark" and is rarely to be seen from the surface except when it comes into shallow water. An exception to this occurs off Salerno immediately following periods of especially cold winter weather north of that area. At such times, when weather and water surface conditions permitted observations from a boat, large schools of *milberti* were to be seen headed south, swimming at about 3 to 5 knots 5 to 10 feet below the surface, but where water depths were about 20 fathoms or more. Shark fishermen have told me, and my own experience bears this out, that it is useless to try to follow these sharks or to try to divert them by chumming or by setting lines ahead of them. The appearance of southbound schools at Salerno was generally accepted as a harbinger of better fishing a few days later.

The southbound migratory movements of *E. milberti* at Salerno were inshore and within the southbound eddy of the Gulf Stream; northbound movements were not observed. It is suggested that these movements were either offshore movements or slower movements of more diffuse aggregations. Northbound movements offshore would be aided by the Gulf Stream. An hypothesis which may be more convenient than significant is that *E. milberti* tends to follow currents in migration and if the currents are strong does not go against them. Of course, sharks would not make appreciable headway against the current at the surface near the axis of the Gulf Stream without vigorous and persistent effort. The sandbar shark does appear to take advantage of eddies or countercurrents and the fishing plans of some of the more successful shark fishermen were based on an assumption that the shark's seasonal movements would follow the currents available at the time.

The distance traveled by various segments of the population probably does not extend from one end of the geographical range of the species to the other. From the southern end of the nursery range of the principal stock at Cape Canaveral, a seasonal gradient of availability was shown by catch per unit-of-effort data. This availability decreased in summer southward and around the tip of Florida to the west coast of Florida where the species was completely absent from summer catches. Thus, the minimum migratory travel of the part of the stock reaching the vicinity of Tampa would be approximately 600 miles. Catches of *E. milberti* throughout the area beyond the southern end of the nursery range reach their highest peak in midwinter. Catch per unit-of-effort data previously published (Springer, 1951) show the catch of *E. milberti* at Salerno, Florida, as decreasing from 4.8 fish per 100 hooks for February to a low of 1.1 per 100 hooks for September. A cold upwelling over the narrow Continental Shelf immediately north of Jupiter Light usually occurs in June or July. It is probably of brief duration but annually stuns great quantities of fish, although the sharks are not affected. This phenomenon coincides with spectacularly good shark fishing and possibly also with considerable mating activity on the part of *E. milberti*. This may give some bias to Salerno catch per unit-of-effort figures for early summer.

REPRODUCTION

Courtship and mating

I have seen neither the courtship nor mating of *Eulamia milberti*. The general pattern may be constructed, however, from fragments of information and from inferences based on the few facts known about related large sharks. The comparative morphology of the secondary sexual apparatus of male sharks has been given comprehensive discussion by Leigh-Sharpe in 11 papers. The functions ascribed by Leigh-Sharpe in three of these papers (1920, 1921, and 1924) to the various parts of the apparatus in carcharhinid sharks are in general accord with my observations on *Galeocerdo*, the tiger shark. The courtship patterns in *Galeocerdo*, *Eulamia milberti*, and other large carcharhinids probably do not differ greatly.

A brief outline of the mechanics of fertilization in the carcharhinid sharks is included here to orient the reader in following some of the inferences made in later discussion of differential death rates in the sexes. Carcharhinid sharks are born alive and fertilization is internal. Paired intromittent organs of the male known as claspers are supported by cartilages. Immediately following the rapid enlargement of the testes, which occurs at maturity, layers of calcification appear at the surface on the principal clasper cartilages. At this time the claspers become semirigid except at the basal area of attachment of the claspers to the base of the pelvic fin adjacent to the cloaca. The tip of each clasper, however, is expandible. When expanded, the cartilages of the tip are transverse to the main axis of the clasper and open as the ribs of a fan. The expanded tips are thought to serve both to hold the oviducts of the female open and to prevent withdrawal of the claspers because of the rigid cartilages in a transverse position. The very large clasper siphons are a distinguishing and peculiar feature of the apparatus in male carcharhinids. These siphons are a pair of separate sacs lying just under the skin of the belly on either side of the midline and extending from the pelvic to the pectoral areas. They function as reservoirs for the sea water used to flush the male sex cells from the bases of the claspers into the oviducts of the female during mating. The siphons may hold a large amount of sea water, as much as 2 gallons in *Galeocerdo*. The siphons do not ordinarily contain the sea water which is presumed to enter the siphons during the period immediately preceding mating.

During the mating season the area at the bases of the claspers of the larger carcharhinids exhibit extraordinary vascular congestion. Characteristically, in male *Galeocerdo*, a mass of very soft spongy tissue appears around the cloaca. This is present to a lesser degree in the smaller carcharhinids such as *E. milberti*. Unusual congestion, edema, and subdermal hemorrhage at the base of the claspers are evidences of courtship activity on the part of the male.

Large sharks are not highly maneuverable and cannot swim backward, so it is necessary for the claspers to rotate and point forward during mating. Since the muscle system in the typical carcharhinid clasper seemed functionally inadequate or feeble, I carried out an experiment which incidentally revealed the probable method by which the clasper siphons are filled with sea water. I obtained an adult male *Carcharhinus limbatus* about 5 feet long and evidently in mating condition. The choice of species was dictated by circumstances, one of which was the fact that a 5-foot shark was as large as I could manage. By injecting a considerable quantity of an isotonic solution into the caudal vein, I was able to induce the claspers to assume the normal mating position. This action caused the claspers to revolve inward and forward. As the claspers moved into a forward pointing position, a funnel, formed by a membrane supported by rods of cartilage, opened at the base of each clasper. The mouth of the funnel was also directed forward and the constricted end led into the siphon. The caudal vein was plugged experimentally to hold the claspers and funnel in position and the shark was moved forward as rapidly as possible through the water. This caused the clasper siphons to fill with water. Application of additional pressure to the caudal vein resulted in complete expansion of the fanlike tip of each clasper.

The course of courtship and mating in all of the larger carcharhinids including *E. milberti* probably follows the pattern in which the male persistently follows and occasionally bites the female on the back until she swims upside down. Both claspers probably function at the same time, one entering each oviduct of the female by way of the lateral opening from the cloaca. The contact of the two sharks may be presumed to force the sperm-ladened sea water from the siphons into the oviducts.

The mating pattern has been given in some detail to emphasize the point that mating is very complicated in carcharhinids, and that the mechanical difficulties are compounded among the larger species by their greater weight and lesser maneuverability.

Time of mating

The approximate period of the mating season is established by the appearance of males with enlarged testes and also with some evidence of vascular congestion of the pelvic-fin area and by the appearance of females with eggs of full size in the ovaries (about 1 to 1¼ inches in diameter in *E. milberti*). In the vicinity of Salerno, Fla., mating of *E. milberti* evidently takes place in the spring or early summer. Males appear commonly in inshore catches after the first of February but remain segregated for some time. Catches of both sexes indicating mixed schools are more frequently made in April and May than in other months. After May, male *E. milberti* are relatively scarce in Salerno catches. Among carcharhinids, the males may stop eating during the courtship period. This is an inference drawn partly from the general reduction of catches of males on baited hooks during mating seasons, partly from the observed smaller size of the livers of males immediately following the mating season, and partly from observations on the mating activity of *Galeocerdo*.

Fertilized eggs and the smallest detectable embryos were observed first in Salerno catches from the first part of July to the first part of August. The time of mating can be established with more precision, however, by observation of the time of appearance of the fresh courtship scars on the females. Scars, tooth marks, and small open wounds produced by shark teeth are commonly found on adult female carcharhinids and are generally restricted to the dorsal surfaces between the two dorsal fins. These are never present on males or immature females and are obviously produced during courtship. Scars or wounds are not always present on gravid females or at least are not always detectable but were found on about half the gravid *E. milberti* taken at Salerno. The coexistence of old and completely healed scars with fresh scars on some females is one bit of evidence that female *E. milberti* produce more than one litter of pups in a lifetime.

All available evidence points to the month of June as the time of maximum mating activity of *E. milberti* in southeastern Florida waters. It has already been pointed out that males were rarely taken during the month of June when mating activity is assumed to be at a peak. There is some evidence from catches that the males were present in substantial numbers at that time. From 3 to 5 percent of the catches of the better fishermen at Salerno, who kept their hooks very sharp, were snagged sharks; that is, the sharks were caught by hooks in the fins or tails or occasionally in other parts of the body but not in the mouth. More males were caught in this way during June than were hooked by mouth.

Development of the embryo

In *E. milberti*, as in other carcharhinids, it is presumed that fertilization occurs after the large egg leaves the single functional ovary. It is also presumed that fertilization occurs before the egg has been moved through a shell gland. Shell glands are located near the anterior end of each of the two functional oviducts. In passing through the shell-gland area of an oviduct, a single egg is enveloped by a diaphanous tubelike shell capable of great expansion to accommodate the growth of the embryo to a very large size. The nutrient material from the egg yolk is sufficient only to provide for early growth of the embryo and to supplement nutrient materials necessary for intermediate growth. The means by which nourishment is supplied to the growing embryos probably varies in different species of carcharhinids, but in species of *Eulamia*, three principal methods appear to be involved. In addition to that supplied by the yolk some absorption of nutrient material from fluids in the oviducts may be assumed to take place. This would appear to be necessary to provide sufficient material to carry the embryo to a length of about 12 inches at which length the pseudoplacenta is formed from the yolk sac.

My observations on the embryology of the sandbar shark are limited to general notes on the external appearance of the eggs and embryos at several stages during development.

The spherical, unfertilized eggs in the single functional ovary reach a diameter of 1 to 1¼ inches. In winter and early spring, large numbers of adult females not carrying embryos were found to have developing eggs ½ to ¾ inch in diameter in the ovaries. In a few instances, females taken in July and August were found with eggs of maximum size in the ovaries as well as fertilized eggs in the oviducts. In the greatest disparity of development noted, there were two large yellow eggs remaining in the functional ovary while embryos in the oviducts ranged from less than 6 mm. to 10 mm. in length.

A female *milberti*, 6 feet 7 inches long collected off Salerno on July 2, 1948, in 25 fathoms, was typical of a series taken in early July of that year. This female contained 10 egg cases, 5 in each oviduct; no large eggs remained in the functional ovary. Each stringlike egg case was about 120 centimeters long, with thin membranous, amber-colored, transparent walls. A single yolk was contained in one expanded oval section of each egg case. The expanded section, approximately 6 cm. long, was located about 10 to 12 cm. from one end of the egg case. This section also contained a clear fluid in each of 8 of the egg cases that had developing embryos 9 to 13 mm. long. The remaining 2 egg cases, one anteriorly in each oviduct, contained milky fluid and there was no evidence of fertilization nor development of the single egg yolk contained in each. The section of the egg case occupied by the embryo, spherical yolk, and clear fluid was held in shape by two longitudinal folds and by folded constrictions of the egg-case membrane at either end. The egg case could, however, be unfolded and expanded with relatively light internal pressure.

The egg case surrounds the embryo until birth and unfolds or stretches to accommodate the developing embryo. When the embryo reaches full term the pseudoplacental mass extends outside of the eggshell membrane, but my notes do not indicate at what point the pseudoplacenta functions outside of the shell membrane. The amount of clear fluid within the shell increases as the embryo grows. It is present at the time the embryo reaches the approximate size at which the young are born—24 inches in the Florida area. External gills were noted on embryos up to about 4 inches but were absent on 4¼- to 5-inch embryos. Some yolk was found remaining in the pseudoplacental apparatus in embryos that had reached a size of 12 inches, but yolk material was entirely absent from the well-developed, yolk-sac placental apparatus of embryos 15 inches long. As the embryo grows, the yolk or attachment of the pseudoplacenta lengthens. In *E. milberti* and in other western North Atlantic *Eulamia* the yolk stalk has no structural embellishments at any stage in its development insofar as I have been able to discover. Structures of this kind occur in some species of hammerhead, *Sphyrna*, but differ in the various species. When embryonic *E. milberti* are near full term the stalk (pseudoplacental attachment) is easily broken at the point of attachment to the embryo. The scar of this attachment remains clearly visible until the young shark has attained an inch or more of postnatal growth.

Normally the large eggs in the ovary of *E. milberti* are bright yellow; but white eggs, suggesting some pathological condition, were found a few times in the fall. White eggs were noticed less frequently in *E. milberti*, however, than in *Eulamia obscura*, *Carcharhinus leucas*, or *Sphyrna* sp. In these last three species, white eggs were noticed in exceptionally large sharks (*E. obscura* and *Sphryna* sp.) and deformed sharks (*leucas*). No excessively large deformed or obviously diseased *milberti* were seen in examinations of many hundreds of adult females. Dead embryos were noted occasionally but not frequently in *E. milberti* and these were generally 10 to 15 inches long, that is, at about the size at which the egg yolk would be completely absorbed. The dead embryos sometimes appeared to be dehydrated but there was no noticeable putrefactive decomposition.

Number of young in litter

In an earlier publication (Springer, 1940), I reported the collection of 13 litters of *Eulamia milberti* pups from Englewood, Fla. In this lot 59 were males and 63 were females. Another series of 28 litters from the west coast of Florida had 130 males and 130 females. A third series of 24 litters from the east coast of Florida included 116 males and 112 females. The number of embryos in each litter varied from 1 to 14 but the modal number was 10 and the average number was 9.

The available data do not show an increase in the number of young with increased size of the mother as reported for some other genera (Backus et al., 1956). In *Eulamia milberti*, however, the size range of adult females is not great and such a correlation, if it exists, would be difficult to demonstrate.

Species of *Eulamia* taken in the Florida region other than *milberti* all frequently carry 10 embryos to full term. The average number of embryos to the litter for these other species is less than 9, which is the average litter number for *E. milberti*. All of the other Florida species of *Eulamia* are somewhat larger than *milberti* and the largest species, *Eulamia obscura*, has the smallest average number of embryos to the litter. In *E. obscura*, pups were often found only in one of the oviducts. This suggests the possibility that fertilization was effected only through one oviduct. Various other observations on the location and numbers of embryos in *E. obscura* and other Florida *Eulamia* lead to the conclusion that the normal maximum [usual] number of young in each species is 10 plus or minus 2, but that actual numbers are progressively smaller the larger the mother.

Length of young at birth

Consideration of all of the available data places the time of birth from March to early August and the size at birth from 17 to 25 inches. The length at birth of 24 inches seems, however, to be the best estimate for the young born in northern Florida waters. Smaller young and a somewhat later birth date may be characteristic of the part of the population in cooler waters. An estimate of the gestation period based on southern Florida specimens is 9 months with limits of the estimate 8 to 12 months. Some variation might reasonably be expected to result from differences in water temperature during development.

TABLE 5.—*Embryos of* Eulamia milberti, *by size group and month, from females collected off the southeast coast of Florida between Fort Pierce and Tortugas, 1946–49*

Average litter length	Number of litters											
	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June
1 inch and under	5	7										
2 inches		5										
3 inches		4										
4 inches		6										
5 inches		1		1								
6 inches		1										
7 inches												
8 inches			2	2								
9 inches				1								
10 inches				1								
11 inches				1								
12 inches			1		1							
13 inches								1				
14 inches					2					3		
15 inches					2			1		27		
16 inches					1		1	1		11		
17 inches						6	1					
18 inches						7	4	1				
19 inches						4	6	3	1			
20 inches						3	1					
21 inches										1		
22 inches										5		
23 inches									1	1	4	
24 inches									1		5	1

Table 5 shows the length distribution by months of embryos of *E. milberti* from off southeastern Florida. It is possible that some of the variation in length of embryos near full term is due to inclusion in the sample of measurements from females of widely differing geographical origin, for example northern Florida and Chesapeake Bay.

At Salerno, Fla., 5- to 10-mm. sandbar shark embryos were found commonly in July and August but no large embryos were seen during these months. In June only a few among the large numbers of adult female *E. milberti* landed at the Salerno dock contained embryos and the few that were found were 24 inches long. Since no free-swimming young were taken at Salerno or around southern Florida, estimation of the size at birth in this area depends entirely on determination of the maximum length of embryos. Records of young *E. milberti* from Cape Canaveral, about 60 miles north of Salerno, northward are common. Twenty-four-inch embryos from south Florida were found to be most common in May but substantial numbers were seen in April, and one set of 24-inch embryos was taken from a female collected off Marquesas Island in the Lower Florida Keys in March. Eight adult female sandbar sharks were taken on July 2, near the mouth of the Mississippi River. Of these, five contained 24-inch embryos and one had 25-inch embryos. Two had evidently given birth to young just before they were caught.

Hildebrand and Schroeder (1928) report six *E. milberti* in their collection from Chesapeake Bay 17¾ to 25½ inches long. Presumably these were not embryos. Records furnished by William H. Massmann (in correspondence) for young Chesapeake Bay *milberti* include specimens from 21¾ to 28 inches that were taken in 10 collections from June 7 to October 7. Massmann's series is not large enough to establish progressively larger size with later dates.

Some young *E. milberti* may be born prematurely at lengths of less than 20 inches either because of crowding, in large litters, or extraordinary activity on the part of the mother. Captures of very small young in otter trawls, for example, might result from the entry of the mother into the net followed by a successful struggle to escape. This could bring about premature birth of one or more young which might be left in the net.

Nichols and Breder (1927) note that females carrying young were taken in Great South Bay, Long Island, from June 22 to August 5. Also they state, when released the young were about 22 inches long and weighed 2½ pounds. One of about 3 feet seen in Sandy Hook Bay as early as June 9 may have been of the preceding year. In September 1924, five young ranged from 24⅞ to 26 inches in total length. Bigelow and Schroeder (1948) summarized the indications of size at birth from various Atlantic coast records north of Florida in approximately the same way. It is reasonable to expect that *E. milberti* at birth may be somewhat smaller in the northern part of its range than in the southern part and that the growth rate in cooler waters is slower.

Abnormal embryos

In the late spring of 1942 I collected at Salerno, Fla., a series of *Eulamia milberti* embryos of both sexes and near full term which were apparently perfect except for having the eyes on the lower side of the snout, almost in contact with one another and just posterior to the nostrils, and having no trace of an opening in the skin for the mouth, although the jaw cartilages were apparently normal. The specimens were preserved in formalin but dried out during the following years and were discarded. Again in 1946 similar embryos were collected, and about half a barrel were preserved; but all were lost in a hurricane which destroyed a dock building.

No abnormal young were found in the relatively large series of litters examined in 1948 and I had no later opportunity to see substantial numbers of *E. milberti* embryos. All litter mates exhibited the same abnormal condition and were remarkably uniform structurally. A very rough estimate of the frequency of occurrence is one set of abnormal young in 500 to 1,000 sets of apparently normal pups.

SEX RATIOS

It was the general observation that landings of adult *Eulamia milberti* at Salerno were in the ratio of 5 females to 1 male. A similar sex ratio was estimated for Salerno landings of *E. obscura* and for Bahama landings of adult *E. springeri*. A disproportionately large number of female *E. floridana* were landed at Salerno but the records do not furnish an adequate basis for an estimate. An insufficient number of *E. altima* or *E. springeri* were recorded for estimate. Murphy and Nichols (1916) say that the commonest large sharks in the waters about New York are the ground sharks *(Carcharhinus)*, and also that males of these fishes are rarely seen but toward midsummer many of the females enter our bays where they give birth to their young. They further state that the commonest ground shark is *Carcharhinus milberti*. The only record suggesting equality in the number of adults of the sexes of *E. milberti* is Captain Winkler's record of the capture of 26 males and 25 females off the Caribbean coasts of Nicaragua and Costa Rica in the fall.

Data on the sex ratio in young *E. milberti* is limited to a series of 203 young from 26 to 50 inches long collected by otter trawl in February 1958 off North Carolina. There were 91 males and 112 females in this collection.

Florida shark fishery records of carcharhinids other than those of the genus *Eulamia* show local segregation by sex and size but in no other carcharhinid nor in the hammerheads is there any clear indication from available records from Florida of great imbalance in the sex ratios of adults.

The unavailability of male *milberti* to baited hooks during the mating season may explain in part the smaller number of males in the landings. However, because Florida commercial shark fishing after 1946 was carried on out to depths greater than the maximum known depth range of the species, and because the males brought the fishermen a higher price than the females, it is certain that there was no intentional selection of females. The fishermen believed that the schools of males, if found, were easier to catch in large numbers. Females were far more abundant than males in the deeper water catches made off the Florida Keys in the late fall and early spring, and a much greater abundance of females characterized the winter catches on the west coast of Florida.

It has already been shown that approximately equal numbers of male and female *milberti* are born. The evidence that there are substantially more females than males in the adult population is very strong, if our information adequately covers the geographical range of the species. Although it is quite possible that segments of the adult population have been entirely overlooked in the offshore and midwater depths in the northern part of its range, the shortage of males in the population around southern Florida is remarkable.

There is some indirect evidence also of a shortage of males in the breeding population. If the females bear pups in alternate years, 50 percent of the adult females would be expected to be gravid in winter. I have previously reported (Springer, 1940) that only about 17 percent of the adult females taken in winter off Englewood, on the west coast of Florida, were gravid. I saw large numbers of *E. milberti* in 1942 and again from 1946 through 1949 at Salerno, and my notes include several estimates of the proportion of gravid to nongravid adult females seen on the dock. For the late-winter and early spring periods, it was estimated that substantially less than a third of the females were carrying pups. In my sample of 399 adult females taken for length-frequency data, approximately 18 percent were gravid.

Three interesting, if theoretical, explanations are suggested to account for the apparent differences in the number of males and females in *milberti* and in other *Eulamia*.

The mating pattern appears to be particularly dangerous to the males, since mating occurs when the females are in a feeding cycle while the males are not. That is, during courtship males may nip or slash to some extent but do not take large bites. The females have no such inhibitions except at the time the young are born, and fatal accidents to males may be frequent during courtship. However, if this explanation is to be acceptable, some further speculation is needed to suggest why *Galeocerdo* with a similar mating pattern is not represented in the adult population by a preponderance of females.

Geiser (1924) summarized a variety of reports on the higher death rate for males in some mammals, fishes, and invertebrates, and suggests that there is a genetic basis for this in certain cases where the possession of two sex chromosomes by the females * * * ensures a greater longevity of the female by "canceling out" possible mutations in the x-chromosome, especially associated lethals, while in the male there is no such "canceling out."

The third explanation is that the males occupy wider geographical and vertical ranges than the females, remain in the cooler parts of the ranges, and exhibit a greater tendency to wander than the females. Thus, greater numbers of males than females are lost to the breeding population by wandering and death in unfavorable environments.

Whatever the explanation for the unequal sex ratio, the smaller number of males is not a sufficient handicap to prevent *E. milberti* from being one of the commoner sharks.

GROWTH AND SIZE AT MATURITY

In Florida catches, adult male *Eulamia milberti* average 4.2 inches shorter than the average adult female and weigh 32 pounds less than the average nongravid adult female. The smaller size of the adult male is characteristic of all of the western North Atlantic carcharhinids although the size of males and females at birth is approximately the same. For about 20 years I maintained a close watch on landings of one or more commercial vessels and saw no *milberti* females longer than 92 inches and no males longer than 89 inches among the thousands that were examined.

The smallest sexually mature male in the material examined was 71 inches and the smallest sexually mature female was 72 inches in total length. Sexual maturity in the male is easily and positively determined because enlargement of the testes to functional size is immediately followed by the appearance of a ring of calcium at the surface of the major clasper cartilage. This ring is easily seen in cross section but since its effect is to stiffen the segments of the clasper, sectioning is unnecessary for positive determinations. Determination of sexual maturity in female specimens where the specimens were nongravid or had no courtship scars was made by examination of the ovary and the oviducts. The females were regarded as sexually immature if none of the eggs in the ovary had begun to increase in size and if the oviducts were smaller in diameter than is characteristic of the fully contracted oviducts in females following parturition. It may be noted in table 6 that, while at least 2 female *milberti* were mature at a length of 72 inches, 5 immature females of greater length were collected. Obviously the length at which the females may become sexually mature varies more than 4 inches.

The left skew of the length-frequency polygons shown in figure 5 may be the result of any of several variables including the length at which maturity is reached.

A total of 513 adult sandbar sharks was selected from southeastern Florida catches for measurement of total length and for comparison of

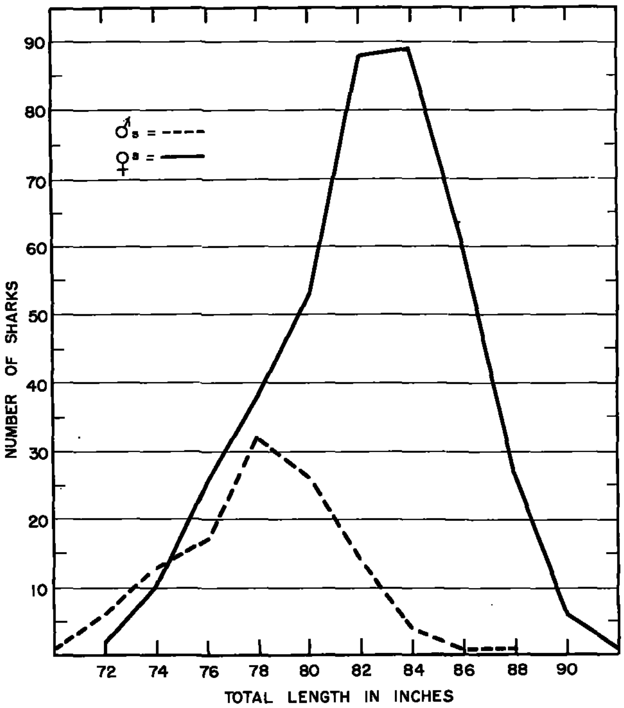

Figure 5.—Length-frequency polygons for adult male and female *Eulamia milberti* from southern Florida.

length frequency with the length frequencies of 76 sharks from off Fort Myers on the west coast of Florida and of 51 sharks from the Caribbean coast of southern Nicaragua and northern Costa Rica (table 6). To reduce bias, all sharks of all species in any catch were measured and recorded or none were recorded. Selection was affected by the scarcity of males. The comparatively large sample of fall females at Salerno had to be measured to get any catches that included males which rarely appeared there at that season. In the sample taken from the lower east coast of Florida, 10 sharks, 5 males and 5 females, were found to be immature. These immature sharks were excluded from the calculations of mean lengths of adults, but the sizes together with the dates of capture are given in footnotes to table 6, which shows the mean length of the sample lots.

By its migratory movements and its restriction to limited nursery areas, the North American population of *E. milberti* appears to be subject to constant mixing. It does not seem reasonable to expect a rigid segregation by area of origin of those *milberti* mating off southern Florida. This may be one factor in the apparent homogeneity of the population.

In some of the other carcharhinids, environmental or racial factors appear to affect the size at which the species becomes mature. For example, the average size of the bull shark, *Carcharhinus leucas*, from the vicinity of Trinidad is appreciably less than the average size of adults of the same species from the Gulf of Mexico. Important differences in the size at maturity as well as the size at birth separate the Texas and southern Florida populations of the little black-

Table 6.—*Mean length, number measured, and length range of adult* Eulamia milberti, *by sex, area, and season of collection*

[Lengths in inches; length range in samples in parentheses]

Area	January-March		April-June		July-September		October-December		Combined data	
	Number in sample	Mean length	Number in sample	Mean length	Number in sample	Mean length	Number in sample	Mean length	Number in sample	Mean length
Males:										
Southeastern Florida [1]	69	78.1 (71-89)	36	78.4 (72-86)	5	78.8 (76-82)	5	78.8 (73-82)	114	78.7 (71-89)
Southwestern Florida (from 2 schools)	29	79.0 (73-84)								
Nicaragua-Costa Rica					16	79.9 (72-89)	10	75.0 (71-84)	26	78.4 (71-89)
Females:										
Southeastern Florida [2]	111	82.8 (72-91)	63	82.9 (76-92)	64	83.0 (74-91)	161	82.9 (73-90)	399	82.9 (72-92)
Gravid [3]									71	83.2 (73-88)
Gravid (from 1 school)							59	82.8 (75-88)		
Nongravid (from 1 school)							48	83.8 (75-87)		
Southwestern Florida: Nongravid	47	83.3 (72-90)								
Nicaragua-Costa Rica: Nongravid					7	82.6 (78-88)	18	83.9 (76-90)	25	83.5 (76-90)

[1] 5 immature males were collected with this sample but excluded from tabulation and from calculations of mean length: 1 specimen 64 inches long collected in March, 2 specimens each 66 inches long collected in August, 1 specimen 59 inches long collected in October, and 1 specimen 68 inches long collected in November.

[2] 5 immature females were collected with this sample but excluded from tabulation and from calculation of mean lengths: 1 specimen 72 inches long collected in January, 1 specimen 76 inches long collected in April, 1 specimen 73 inches long collected in July, and 2 specimens collected in October of which 1 was 75 inches long and the other 76 inches.

[3] From preceding collections.

tip shark, *Carcharhinus limbatus*, but whether different species, subspecies, or races are involved remains to be determined.

In the last week of February 1958, I was able to get evidence that the edge of the Continental Shelf off the Carolinas is indeed an important wintering ground for immature *milberti*. A series of 25 tows with a modified Number 41 otter trawl made by the Bureau of Commercial Fisheries exploratory vessel *Delaware* while I was aboard took 203 immature *milberti* between the offings of Cape Hatteras and Cape Lookout. In one tow in 52 fathoms, 197 *milberti* from 27 to 43 inches long were taken and in three other tows at depths of about 50 fathoms 4 *milberti* were picked up. Tows made at other depths from 20 to 250 fathoms failed to catch *milberti*. The water temperature at the bottom at this time was about 64° F. in 50 fathoms, but temperatures were appreciably cooler, about 57° F., in both 30 fathoms and 80 fathoms.

It is suggested that the 197 young *milberti* taken in February 1958, were young of the year, born in the summer or early fall of 1957, and that their average length of 34 inches represented growth from birth of about 12 inches in approximately 7 months. However, if it is correct that all of these young were born in 1957, some may have grown as little as 5 inches and some more than 20 inches. Such an irregular growth pattern would help to explain some other facts of the *milberti* life history, for example, the seasonal differences in the vitamin-A potency of adults taken by the shark fishery.

In January and February 1945, I obtained two boatloads of sharks from O. E. Holley, an expert shark fisherman at Fort Myers, Fla. Of the 133 sharks brought in, 73 were adult *E. milberti* and none of the female *E. milberti* were gravid. The 27 males in the sample ranged from 74 to 84 inches in total length (average, 79 inches) and weighed from 94 to 130 pounds (average, 113.7 pounds). The 46 females ranged from 72 to 90 inches in length (average, 82.3 inches) and weighed from 102 to 184 pounds (average, 145.1 pounds). The specimens were weighed and measured about 36 hours after capture and the stomachs of all of the sharks were empty or nearly empty. Weight among sharks of the same length varied considerably. Thus, three 78-inch males weighed 94, 115, and 122 pounds, while eight 83-inch females weighed 122, 127, 141, 142, 146, 148, 161, and 162 pounds, and six 78-inch females weighed 102, 136, 147, 147, 154, and 164 pounds. Weights of livers, other viscera, fins, and eviscerated carcasses were obtained, but unfortunately when these weights were recorded they were tied in solely with the total weight of each shark. Analysis of the figures gives some indication that liver weights in female *E. milberti* contributed disproportionately to total weights. Livers of males weighed from 7 to 14 pounds and livers of females from 7.25 to 31 pounds. The average weight of 40 livers from females was 18.5 pounds.

It would be convenient and would fit most of the facts to assume that the growth of *Eulamia milberti* is very rapid, but there is merely presumptive evidence for this. It is by no means the only view that could be reasonably advanced and it would be especially weak for *milberti* for which the immature part of the population is not well known. Nevertheless, on the basis of little real evidence I suggest that it is probable that growth from birth to maturity takes about 2 years, occasionally 1 year, rarely 3 years.

The length uniformity indicated in table 3 for both male and female adult *milberti* from different seasons would be expected from a species with determinate growth. Predictable adult size in relatively narrow ranges also characterizes other species of *Eulamia*, *Negaprion*, and perhaps *Carcharhinus*. On the other hand, it is presumed that some individuals of *Prionace* and *Pterolamiops* continue growing after maturity to reach abnormally large sizes. Records of *Galeocerdo* more than 14 feet long are not uncommon in the literature and some of these records apparently are reliable and I accept them as such. Nevertheless, I have seen more than a thousand large *Galeocerdo* from the Florida–West Indian region and have measured all of the exceptionally large ones that I have seen. None were found to exceed 14 feet in total length. Great increase beyond the usual adult size has been noted, however, for *Sphyrna* sp., the great hammerhead. In my sample of 52 adult females, 5 were much larger than would be expected. If, as indicated by my sample, the usual size for adult female great hammerheads is 10 to 12 feet, the attainment of approximately 15 feet by 10 percent of the lot precludes description of the growth as determinate, at least for the great hammerhead. One individual, measured but not included in the sample, was 18 feet long. Although the continuation of growth after maturity as a peculiarity of the female apparently does not obtain in *E. milberti*, it is evidently the pattern in some species of *Sphyrna*, in *Pterolamiops*, and occasionally in *Galeocerdo*.

FOOD AND FEEDING HABITS

Examination of stomachs of *Eulamia milberti* as a source of information on the food of the species has been disappointing. Comparison of the feeding habits of *E. milberti* with the feeding habits of other carcharhinid species of the Florida region, however, has proved to be more illuminating. Various bits of evidence show that *E. milberti* is a discriminating feeder; that it is a bottom feeder; that it feeds on small bottom fish and invertebrates rather than the larger ones; that it prefers fresh fish to stale or decomposed fish; that it prefers fish to porpoise meat or to the flesh of domestic animals; and that its feeding is remarkably successful in comparison with some of its larger carcharhinid relatives.

A very large proportion of the sharks in commercial landings were found to have empty stomachs. An obvious explanation for this is that most of the sharks were examined after the passage of several hours when small and readily digestible meals would presumably have been completely hydrolized. Observations and examinations of stomachs of sharks of many species has led me to the opinion that the larger species find food less often than the small ones, and that through no choice of their own, large sharks have empty stomachs more often than not.

In the stomachs of *Eulamia milberti* a few fish remains, usually not identifiable as to species, cephalopods, and crustacean remains were found from time to time. Goatfishes (Mullidae), snake eels (Ophichthyidae), sea robins (Triglidae), and cusk eels (Ophidiidae), were among the types most commonly found. A collection of 167 *milberti*, all with fish, octopus, or crabs in their stomachs was reported in an earlier publication (Springer, 1946). There were unusual circumstances about this catch, however, which suggest that the large amount of food in the stomachs resulted from the sharks being taken in an area of localized upwelling that had stunned large numbers of fish and bottom invertebrates. Very few instances were noted in which shark remains were found in *milberti* stomachs and no evidence was found that *milberti* commonly fed on large turtles, porpoises, birds, ships' garbage, or surface material recognized by the inclusion of Sargassum weed or typical surface-dwelling forms.

Some indication of the probable food preferences of *E. milberti* can be found in the experiences of commercial fishermen. It was demonstrated to the satisfaction of Florida shark fishermen that there were somewhat different requirements for bait depending on what species was sought. It was also found that the increased cost of very fresh bait, or bait frozen when fresh, was fully justified by the improved catches. All of the carcharhinid species of the Florida area, even those frequently feeding on garbage, apparently prefer fresh bait. The bait most universally accepted by all species was fresh fish and *E. milberti* rarely was taken on any other bait. Some species, notably *Eulamia obscura* and *Galeocerdo*, took cut porpoise readily, and one species, *Carcharhinus leucas*, occasionally preferred pieces of fresh shark. Cut bait was found to be very much better than the entire fish of any species. Probably the diffusion of juices from cut bait was greater than from fish in the round.

In the Salerno, Fla., area the best catches were obtained by sets made in the late afternoon with pickup of the lines starting the following morning as soon as there was sufficient light to locate the buoys. The freshness of the bait may have had some bearing on the apparent better fishing at dusk and during the early part of the night. Catches made during the early morning and throughout the day were not infrequent, however, and it seems probable that the early part of the night is merely a period of increased feeding activity for *Eulamia milberti*.

It is the common habit of many species of sharks, including *Eulamia milberti*, to nudge or hit objects with their noses. I am convinced that they do this to test the object for juices. The edible qualities of the object are thus determined by the shark through sensory crypts which are widely dispersed over the skin of the head and body. These organs, which perform a function corresponding to taste, have been described in detail by Budker (1938). Under ordinary circumstances the testing procedure is routine for objects which are not moving or which are not part of a series of similar-appearing objects, one of which has already proved edible. The procedure may be omitted if there is competition for food.

It seems improbable that the sensory crypts of the head function in any other way than as gustatory organs. To find suitable food or to find an area having food in it, *Eulamia milberti* as well as many other species depends on olfactory organs. Experiments by Parker and Sheldon (1913) with *Mustelus canis* probably outline the general pattern of behavior of the cacharhinids in their search for food.

Carcharhinid sharks in general are opportunists in feeding and necessarily so. Without special techniques, developed in some species but not to my knowledge in *Eulamia milberti*, sharks are relatively ineffective at catching uninjured fish in open water or even at finding such slow-moving objects as crabs. The shark's ability to exist on a regimen of feast and famine, imposed by its ineptness in catching food at will, is probably made possible through its unique digestive and fat-storage organs. A general outline of the processes of digestion and fat storage by sharks is beyond the scope of this report. It is pertinent to point out that their digestion is rapid and thorough, and that the shark's liver with its high percentage of oil is a good index of its metabolic well-being. The larger, fatter livers are found in sharks in good condition while small livers with little oil are frequently found in sharks having severe injuries, sharks in obviously poor condition, or in the males at the end of the mating season.

The liver of adult *E. milberti* typically represents between 10 and 15 percent of the animal's total weight, rarely more than 18 percent and rarely less than 6 percent. The proportional weight of the liver in adult *E. milberti* males is lower than in females, but the liver weight of the species is remarkably uniform in comparison with larger species of carcharhinids within its geographical range. This is strong evidence that *E. milberti* is successful in getting an adequate supply of food regularly. *Galeocerdo cuvier*, *Carcharhinus leucas*, and *Eulamia obscura*, all species more than twice as heavy as *milberti*, frequently have livers 25 percent or more of the total weight of the fish. On the other hand, they often have very small livers, as low as 3 percent of the total weight. The inference is reasonable that the larger species have greater difficulties finding food, or more precisely, may have to wait longer between meals. This inference from liver weight also is consistent with the observation that the foods of the larger species are frequently of a less digestible type and may be taken as a kind of desperation measure and certainly not as a first choice. *Galeocerdo*, for example, frequently fills its stomach with large horseshoe crabs, huge horse conchs complete with shell, or even old shoes and tin cans.

Because of commercial interest in the vitamin-A content of shark-liver oils that existed for a number of years, a large amount of data is to be found in the literature on the subject. Also available to me are data on the oil and vitamin-A content of livers of *E. milberti* taken at Salerno. Some determinations for Salerno species were given in an earlier publication (Springer and French, 1944). Better methods of estimation of the vitamin-A concentration in liver oils came into general use later, but these did not appreciably alter the general trends observed.

The tendency in each species to an increase in the vitamin-A concentration, or potency, of the liver oil with the increase in size of that species has been noted by many workers (Pugsley, 1939; Brocklesby, 1941; Templeman, 1944; Ripley and Bolomey, 1946, et cetera). The liver-oil vitamin-A potency varies considerably. Each species and locality produces sharks having potencies that are approximately predictable. Characteristically, in most species the males produce oil of somewhat higher vitamin-A potency than that of the females, but they often have less oil in their livers.

An hypothesis which has general support is again advanced here that within a given species and locality, the total amount of vitamin A in the liver of a shark is roughly proportional to the age of the shark. Thus, the older the shark the greater is the total amount of vitamin A in its liver. The rate of increase in vitamin A may rise sharply as the shark becomes sexually mature but this does not affect the general trend in the total amount of vitamin A stored. Fluctuations in the amounts of oil stored in the liver may normally accompany such events as young bearing, mating, and periods of poor feeding, and these fluctuations apparently affect potency, but the total amount of vitamin A is subject to fluctuation to a lesser degree. It has been shown for *Galeorhinus zyopterus* of the Pacific coast (Ripley and Bolomey, 1946) that the total amount of vitamin A in the largest males and largest females does not greatly differ.

Livers of *Squalus suckleyi* of the Pacific coast have a higher average vitamin-A potency than livers of *Squalus acanthias* of the Atlantic. The two species are morphologically so similar that taxonomists have had doubts about their separation. Concerning the differences in liver oil potency, Templeman (1944) has the following comment:

> **Whether the greater length of the mature *Squalus sucklii* reflects a greater age or a greater growth rate than those of *Squalus acanthias* is not known, but this greater size is possibly partly responsible for the higher vitamin-A value of its liver oil.**

The greater vitamin-A content of shark livers does not always occur in the larger individuals in a given species. For example, my own measurements and assays show that *C. leucas* off the mouth of the Mississippi River average appreciably longer and heavier than *C. leucas* taken off the mouth of the Orinoco River; but the liver-oil potency of the species from the vicinity of the Mississippi River mouth is extremely low, while that of the *C. leucas* from the vicinity of the Orinoco is high. These differences are quite great and reasonably constant. Adult male *C. leucas* from the Orinoco area have liver-oil potencies above 50,000 I.U./gm. (international units per gram uncorrected for irrelevant absorption), while adult males from the Mississippi area generally have liver-oil potencies of 1,000 to 5,000 I.U./gm. Variation in liver-oil potency by area is perhaps greater in *C. leucas* than in most shark species of the northwestern Atlantic, but the variation is appreciable in all species.

A rough classification by regions of part of the northwestern Atlantic on the basis of shark-liver vitamin-A potency from data assembled by the shark fishery is as follows:

Extremely low potencies—Gulf of Mexico; low potencies—northern Bahamas and shallow-water areas of the West Indies; intermediate potencies—Carolina coast, east coast of Florida, and coast of Cuba; high potencies—southern Caribbean, coast of Costa Rica to the Guiana coasts. To a limited extent this classification is useful to trace probable origins of elements of migratory stocks. Potency differences among liver oils taken from single adult specimens of *Eulamia milberti* were in the range from about 2,500 to 25,000 I.U./gm. One exception was noted in that one assay (the only one available) on mixed *E. milberti* livers from the coast of Nicaragua–Costa Rica was substantially higher, about 38,000 I.U./gm.

If *E. milberti* from the coast of Nicaragua–Costa Rica returned regularly to the species' Atlantic population center from Florida northward, some among the hundreds of livers of *milberti* taken at Salerno, and assayed separately should have had potencies greater than 38,000 I.U./gm. None had such a high potency.

The average potency of oil from livers of *Eulamia milberti* was found to be substantially lower from the southwest coast of Florida than from the southeast coast although the extremes in individual potencies were about the same. Since both stocks have a common origin from the Atlantic coast north of Cape Canaveral we might assume that the difference in averages results from either the lower age of the adult *milberti* reaching the west coast of Florida or a lower rate of vitamin-A accumulation due to the period spent in the Gulf of Mexico, or from both of these.

The liver-oil potency of the eight adult female *E. milberti* from the mouth of the Mississippi River was higher and the total vitamin A from these sharks was about the amount to be expected from similar sharks taken on the east coast of Florida. This potency would be expected only if these sharks originate outside of the Gulf of Mexico.

To the extent that data on vitamin-A potency determinations have any validity for the determination of age or the areas of origin of migratory stocks, they support the general conclusions that *E. milberti* does not live to a great age and that those individuals migrating a great distance to the coast of Nicaragua–Costa Rica do not return.

ABUNDANCE

The inshore range of the sandbar shark has made this species readily available to the shark fishery. This was particularly noticeable at Salerno, where the range is restricted by a narrowing of the Continental Shelf and where special conditions of current and temperature tend to produce a narrow path inshore for the southbound migrants. Approximately 58 percent of the sharks landed by the fishery at Salerno between 1938 and 1946 were sandbar sharks. Although present throughout the year, they were comparatively more frequent in Salerno catches from December through July as shown by records of the catch per unit of effort (Springer, 1951). Except for winter fishing on the southwest coast of Florida which produced a few hundred *E. milberti* each winter, few sandbar sharks were taken in the Gulf of Mexico.

It is estimated that during the period 1935 to 1950 from 5,000 to 15,000 sandbar sharks were taken yearly from the entire range of the fishery and that these were nearly all adults with an average weight of about 130 pounds. The yearly catch might be estimated, therefore, as between 650,000 and 1,950,000 pounds, a small quantity compared with yearly landings by the commercial fishery of many species of bony fishes. During the years that the shark fishery operated, it was prosecuted vigorously, and, although there was no evidence that fishing pressure reduced the stock of sandbar sharks, it was found that the catch per unit of effort was reduced by concentrating too much gear in one area. Efforts to expand production were successful chiefly by extension of the area of fishing into the ranges of other species of sharks. A fluctuation in abundance with a low in every third year was found in the catch per unit of effort at Salerno (Springer, 1951).

Although data are lacking to support such a contention except observations at sea, it is estimated that several other species of *Eulamia*, particularly *E. floridana*, occur in substantially greater species-mass around Florida than does *E. milberti*, chiefly because of the greater area of their habitats.

It is generally recognized that marine animal populations are unstable and are subject to remarkable changes in total numbers and occasional shifts in geographical range. Such changes may, of course, occur in the Atlantic population of *E. milberti.*

A concentration of *E. milberti* appeared for a few days in the late spring or early summer of 1935 off Dog Keys Pass on the coast of Mississippi. These sharks were not only out of their normal range but behaved in a way that is not normal for *milberti* or perhaps for any shark. They struck at anything thrown into the water, fought one another over pieces of charcoal, fought so vigorously that some were killed and eaten by others of the school. Sharks frequently follow shrimp boats such as we were using at the time, and churn the surface of the water after scrap fish thrown overboard; but the intensity of this attack by out-of-range *milberti* was much stronger than any shark action I have seen since.

Although no great fluctuations were noted in the general abundance of *E. milberti* during the period from 1935 to 1950, its competitor, the bull shark *C. leucas*, appeared once to go through a major but temporary shift in abundance. In 1937 so many bull sharks were caught off Salerno that catches exceeded the demand. The company buying shark livers and oil was forced to delay payments to fishermen for a period of several months. This was not merely a matter of economic adjustment to be settled by a reduction in price but the supply of tanks and drums for storage of liver oil was exhausted and a court injunction was finally issued to stop all shark landings because shark carcasses were accumulating along the shores. This was the only known appearance of bull sharks in large numbers on the east coast of Florida. It seems likely that persistence of great numbers of bull sharks, especially north of Cape Canaveral, would have adversely affected the population of *E. milberti.*

ENEMIES

The principal predators on sharks are other sharks of larger size. Wherever concentrations of mixed sizes occur predation by the larger sharks on the smaller ones is normal. The concentration of sharks occurring near the mouth of the Mississippi River in the summer months may be as great as anywhere in the world. Some idea of the predation that may occur is furnished by the results of one line of 180 shark hooks set on the night of July 22, 1947, off Pass a l'Outre, La. This line caught 68 large sharks, whole and undamaged, but 40 of the hooks had only the heads of large sharks and 12 more had only the heads of small sharks. Almost all of the larger sharks on the line contained small sharks or pieces of large ones. One tiger shark, *Galeocerdo*, had swallowed a medium-sized bull shark which in turn had a major portion of a somewhat smaller blacktip in its stomach. The blacktip, however, had driven the head of a *Mustelus canis* about 4 feet long up the leader so it would be reasonable to assume that the large tiger shark was the fourth shark to be taken in that one night on one hook. The bottom conditions, depths, and temperatures where this line was set appeared to be similar to conditions on *milberti* nursery grounds but predation would presumably eliminate young *milberti* in the area.

Full-grown sandbar sharks probably are rarely subject to successful shark attack by other species. The tiger shark (*Galeocerdo*), dusky shark (*Eulamia obscura*), and bull shark (*Carcharhinus leucas*), have all been found occasionally with pieces of full-grown sandbar shark in their stomachs, but the sandbar sharks may have been on shark lines when attacked. Perhaps none of these species are able to catch adult sandbar sharks under ordinary circumstances. Great white sharks, *Carcharodon carcharias*, have been found with adult *milberti* in their stomachs and it is probable that the great white shark could catch them. The white shark is not common enough, however, to be an important factor in predation. At Salerno, captures were about 27 great white sharks per 100,000 of all species.

All carcharhinids more than 6 feet long may occasionally eat young *E. milberti*, but circumstances of seasonal and geographical distribution keep most species from preying on them. There are two notable exceptions: the tiger shark and the bull shark. These sharks feed on young sharks or on small species regularly, and both may be found at times within the known range of young *milberti*.

Tiger sharks, perhaps for reasons of poor speed and maneuverability associated with their smaller and lighter weight fins, catch young sharks less frequently than do bull sharks. Furthermore, tiger sharks are primarily nocturnal in forays into inshore waters and at such times newborn or small sharks retreat to shoaler water. On the other hand, bull sharks are not exclusively nocturnal and they are more frequent in relatively shallow water. Stomach contents show that they are regularly predatory on small species such as *Carcharhinus acronotus*, *C. porosus*, *Scoliodon terra-novae*, and *Aprionodon isodon*. The bull shark also is the only species in the range of *E. milberti* with a preference for shark as a bait.

There is strong circumstantial evidence, derived from an examination of the geographical ranges and nursery-ground preferences of the various species of *Eulamia*, that the bull shark is the most important predator on young sharks and actually restricts the distribution of *milberti*. The life history of the bull shark is similar to that of species of *Eulamia*, but the bull shark is always found in shallow water and its nursery grounds are in bays or estuaries, even in brackish and fresh water. The nursery range of the bull shark is shoaler and less saline than the nursery range of *milberti*, but adult bull sharks inhabit the depth and salinity range normal to nursery grounds of *milberti*. Young bull sharks remain in estuarine waters during the early growing season, and since the females do not eat at the time the young are born and generally move out of the very shallow water immediately after the birth of the young, the young bull sharks are protected to some degree from predation by the large members of their own species.

Bull sharks occur from Long Island southward and are migratory but their centers of abundance are in the Gulf of Mexico and southward, particularly near the mouths of large rivers. Along the Atlantic coast north of Florida, bull sharks are not common, but may be subject in this area to great fluctuation in abundance. Bull sharks are extremely common around the mouths of the Mississippi and Orinoco Rivers and between these points along the inshore Continental Shelf. There is practically no information about their occurrence in the West Indies.

No *Eulamia* except *milberti* is known to have nursery grounds within the geographical and habitat range of the bull shark. The nursery ranges of *E. altima* and *E. obscura* are well offshore in deeper water, *E. floridana* nursery grounds are on offshore banks where bull sharks do not go, and bull sharks are uncommon at least, or normally absent around reefs which are nursery grounds for *springeri*. The suggestion is advanced here that predation by the bull shark is the chief reason, and perhaps the only reason, for the scarcity of *E. milberti* in the Gulf of Mexico and southward in continental waters. The comparatively few bull sharks of the Atlantic coast may be presumed to act as a check on the numbers of young *E. milberti*, but without disastrous effects for that species.

Some interesting complications are associated with predation of large sharks upon smaller ones. Evidently all carcharhinid sharks will eat other sharks sometimes if not regularly. However, it is a shark fisherman's axiom that sharks left on the line to spoil will burn out the fishing grounds and make it necessary to move away 5 miles or so to continue fishing. A rationale has been partly outlined in an earlier publication (Springer, 1954) covering experiments with *Mustelus* in tanks. Feeding of *Mustelus* was entirely inhibited in the presence of shark flesh that had been allowed to stand at room temperature for 4 days.

Presumably sharks have no difficulty digesting shark flesh provided it is fresh. Although sharks appear to be able to digest the partially decomposed flesh of other vertebrates, their digestive processes are slowed or stopped completely when they swallow large quantities of decomposing sharks or rays.

The flesh of sharks becomes strongly alkaline during decomposition. The continuous liberation of ammonia through action of enzymes produced during the course of ordinary putrefactive decomposition on the urea that normally occurs in sharks (see Smith, 1936), seems effectively to block, or at least to greatly retard, digestion. The proteolytic enzymes of the shark's stomach are most active in an acid medium (Sprissler, 1942). In my examinations of juices of shark stomachs in the field, estimates were made of the hydrogen-ion concentration, as shown by indicator solutions. Juices from shark stomachs that contained large amounts of shark flesh in obviously decomposing condition were found to be substantially above pH 8.0, whereas juices from shark stomachs containing fish, turtles, birds, or small amounts of fresh shark were estimated at pH 4.0 or below. It is not clear whether excessively large meals of decomposed shark flesh produce any result more serious than delayed digestion.

I have not seen evidence that internal parasites ever greatly damage *Eulamia milberti*. Roundworms in the stomach, roundworms and adult tapeworms in the scroll-type intestine, and copepods on the gills and external surfaces were commonly seen. In comparison with other large Florida sharks, *milberti* seemed to be the least troubled by parasites. Occasionally, sharks taken from lines apparently set in areas of extraordinary abundance of a small isopod were found to have a large proportion of the viscera eaten away by swarms of the isopods, which had entered the body cavity by way of the soft parts around the anus. It has been assumed that these isopods attack successfully only after the sharks die on the lines or at least have been restricted in movement. Similar isopods attack living small fishes and man (Springer, 1957) and it seems quite possible that they may also attack living sharks. If they successfully attack living sharks they may be one of the principal enemies of sharks in temperate and tropical waters of shallow and moderate depth. I have seen evidence of their work on shark catches made off South Carolina, Florida, Louisiana, Cuba, and southern California.

SUMMARY

The overlapping geographical and habitat ranges and superficial resemblance of *Eulamia milberti*, the sandbar shark, and *Carcharhinus leucas*, the bull shark, have led to some confusion and a tangled nomenclature. The recognition of *milberti* of Müller and Henle as the species name for the sandbar shark is based on the opinion that *plumbeus* of Nardo is a *nomen nudem*.

The sandbar shark differs from the bull shark in the structure and spacing of the dermal denticles, in having a ridge in the skin of the back between the first and second dorsal fins, and in

the smaller size and less robust body form. The sandbar shark swimming in the open sea or in an exhibition tank may be distinguished readily from the bull shark because of its comparatively more erect and higher first dorsal fin placed slightly further forward, its somewhat larger eye, its somewhat longer snout, and its generally less robust body form.

Although the sandbar shark inhabits both the eastern and western parts of the Atlantic, this report concerns only one population of the species centered along the southeastern coast of the United States.

Species of the genus *Eulamia* usually are sharks of the continental shelves, oceanic banks, and island terraces throughout their life cycles in contrast to most species of *Carcharhinus*, which are typically shallow-water forms having their nursery grounds in brackish or fresh-water estuaries, river mouths, or along continental beaches, or in island lagoons. *Eulamia milberti* occupies the shoalest habitat range of the 5 or 6 species of *Eulamia* of the Atlantic coast of North America and enters estuaries to some extent to give birth to its young. Its habitat preference may thus be said to be intermediate between that typical of *Eulamia* and that typical of *Carcharhinus*.

The sandbar shark is clearly separable from all other species within its geographical range and exhibits little variation in form and in tooth count.

The sandbar shark, *Eulamia milberti*, is found in waters of suitable depth, southward from Cape Cod along the Atlantic coast. It occurs in the Gulf of Mexico and along the Caribbean coast of Central America to Costa Rica. It occurs casually off the northern coast of Cuba and along the western edges of the Bahama Bank, but principal elements of the population are confined to the western side of the Gulf Stream. Sandbar sharks occur as bottom dwellers out to depths of 100 fathoms (extreme record 135 fathoms) and may occasionally move out in midwater to oceanic situations. The principal part of the range of adults, away from the nursery grounds, has been shown by commercial catches to be in depths of 10 to 30 fathoms.

The sandbar shark populations of the northern and western parts of the Gulf of Mexico and the Caribbean coast of Central America are small and are probably not self-sustaining without recruitment from the main population by migratory wandering or failure of such orientation mechanisms as the species may possess.

The primary nursery range lies in shallow coastal waters of less than 20 fathoms from Cape Cod, Mass., to Cape Canaveral, Fla.; and a secondary nursery range lies in the Gulf of Mexico west of Mobile Bay and north of the 28th parallel. Newborn sandbar sharks are not known outside the general geographical limits of the nursery ranges, but the young sharks move offshore to deeper (and warmer) water during the winter.

The species is migratory with annual movements of some segments of the population extending at least 600 miles. Sandbar sharks in migratory passage around the southern tip of Florida hold to depths of 50 fathoms or more in apparent avoidance of coral reef areas. Their vertical distribution in the southern part of the species' geographical range, however, is somewhat deeper than in the northern part, suggesting thermal influence in the selection of habitat.

There is reason to believe that female sandbar sharks are inhibited from feeding at the time of birth of the young and for a short time thereafter. Nursery grounds are away from the normal range of the males thus giving additional protection to newborn young. Feeding appears to be inhibited in male sandbar sharks during periods of active courtship.

Young of nearly uniform size, numbering from 1 to 14 in each litter, are born in early summer (probably also in late spring) off northern Florida. The average number in a litter is 9 and the modal number 10. The gestation period is from 8 to 12 months' duration, with 9 months estimated in the latitude of northern Florida. Both oviducts are functional, a single embryo develops in each shell membrane, and a pseudoplacenta with a simple stalk (yolk-sac attachment) forms.

Length at birth is approximately 24 to 25 inches in the latitude of northern Florida but may be less in higher latitudes. Young born in the vicinity of Long Island, N. Y., have been reported to be 22 to 23 inches long at birth, and even smaller young have been reported from Chesapeake Bay.

Although approximately equal numbers of males and females are born, catches indicate a much larger proportion of adult females than adult males except off the coast of Nicaragua.

Females produce young no oftener than every other year, but since only about 18 percent of the adult females taken in the fishery were found to be gravid, this apparent low productivity may be the result of the low proportion of males in the adult population.

In samples from Florida, adult males are from 71 to 89 inches in total length and adult females from 72 to 92 inches. Average weights of adults in samples from southern Florida are for males, 114 pounds, and for nongravid females, 145 pounds.

The mean length and length-frequency distribution (size range) by sex in catches believed to have been made from single large schools closely approximated the mean length and size range by sex of all adults of the species from southern Florida. No appreciable difference was noted in mean lengths and size ranges of adults in samples taken at various seasons on the east coast of Florida, the west coast of Florida, and the Caribbean coast of Nicaragua and Costa Rica except the constant difference of about 4.2 inches between average lengths of adult males and adult females. Differences in the average lengths of gravid and nongravid females were small.

The rate of growth is not known. Indirect evidence indicates that it may be very rapid until sexual maturity is reached, after which little growth occurs.

The sandbar shark feeds chiefly on small bottom-dwelling fishes, mollusks, and crustaceans. It rarely swallows indigestible materials. Uniformly plump livers suggest that *milberti* has little difficulty in meeting its requirements for food.

From commercial catches it is estimated that the population is small in species mass as compared with many teleosts.

The only important predators on sharks are other sharks and not necessarily sharks of other species. Full-grown sandbar sharks, unless injured or caught on a shark line, appear rarely to be eaten by other sharks. Young sandbar sharks are especially vulnerable to attack by large sharks, particularly by bull sharks, but also to a lesser extent by tiger sharks, dusky sharks, and full-grown sharks of their own species.

LITERATURE CITED

BACKUS, RICHARD H.
1957. Notes on western North Atlantic sharks. Copeia, No. 3, pp. 246–248.

BACKUS, RICHARD H., STEWART SPRINGER, and EDGAR L. ARNOLD, JR.
1956. A contribution to the natural history of the white-tip shark, *Pterolamiops longimanus* (Poey). Deep-Sea Research, vol. 3, pp. 178–188.

BEEBE, WILLIAM, and JOHN TEEVAN.
1928. The fishes of Port au Prince Bay, Haiti. Zoologica, vol. 10, No. 1, pp. 1–279.

BIGELOW, HENRY B., and WILLIAM C. SCHROEDER.
1948. Sharks. *In* Fishes of the western North Atlantic. Memoir No. 1, Sears Foundation Marine Research, pt. 1, pp. 59–576.
1953. Fishes of the Gulf of Maine. U.S. Fish and Wildlife Service, Fishery Bulletin 74, vol. 53, pp. 1–577.

BROCKLESBY, H. N.
1941. The chemistry and technology of marine animal oils with particular reference to those of Canada. Fisheries Research Board of Canada, Bull. 59, pp. 1–442.

BUDKER, PAUL.
1938. Les cryptes sensorielles et les denticules cutanés des Plagiostomes. Annales de l'Institut Océanographique, vol. 18, pp. 207–288, pl. 1.

BULLIS, HARVEY R., JR.
1955. Preliminary report on exploratory longline fishing for tuna in the Gulf of Mexico and the Caribbean Sea. Commercial Fisheries Review, vol. 17, No. 10, pp. 1–15.

CADENAT, JOHN.
1950. Rapport sur les Sélaciens des côtes du Sénégal et plus spécialement sur les Requins. Bulletin de l'Institut français d'Afrique noire, vol. 12, pp. 944–975.
1957. Notes d'ichtyologie ouest-africaine. XVII Biologie. Régime alimentaire. Bulletin de l'Institut français d'Afrique noire, vol. 19, ser. A, No. 1, pp. 274–294.

CAPTIVA, FRANCIS J.
1955. Longline gear used in yellowfin tuna exploration. Commercial Fisheries Review, vol. 17, No. 10, pp. 16–20.

COWLES, RAYMOND B.
1945. Temperature induced sterility and evolution. Science, vol. 101, No. 2618, pp. 221–222.

EVERMANN, BARTON W., and MILLARD C. MARSH.
1902. The fishes of Puerto Rico. Bulletin of the U.S. Fish Commission, vol. 20 (1900), pt. 1, pp. 51–350, pls. 1–51.

FORD, E.
1921. A contribution to our knowledge of the life histories of dogfishes landed at Plymouth. Journal of the Marine Biological Association of the United Kingdom, New Series, vol. 12, No. 3, pp. 468–505.

FOWLER, HENRY W.
1936. The marine fishes of west Africa. Bull. American Museum National History, vol. 70, pt. 1, pp. 1–605.

GARMAN, SAMUEL.
1913. The Plagiostomia (sharks, skates, and rays). Memoir Museum Comparative Zoology, vol. 36, pp. 1–518, pl. 1–77.

GEISER, SAMUEL WOOD.
1924. Differential death-rate of the sexes among animals, with a suggested explanation. Washington University Studies, Science Series, vol. 12, No. 1, pp. 73–96.

GILL, THEODORE N.
1862. Analytical synopsis of the order Squali. Annals Lyceum Natural History, New York, vol. 7, pp. 367–408.

HICKLING, C. F.
1930. A contribution towards the life-history of the spur-dog. Journal of the Marine Biological Association of the United Kingdom, new series, vol. 16, No. 2, pp. 529–576.

HILDEBRAND, HENRY H.
1954. Shrimp (*Penaeus aztecus* Ives) grounds in the western Gulf of Mexico. Publication of the Institute of Marine Science University of Texas, vol. 3, No. 2, pp. 233–366.

HILDEBRAND, SAMUEL F., and WILLIAM C. SCHROEDER.
1928. Fishes of Chesapeake Bay. Bulletin of the U.S. Bureau of Fisheries, vol. 43, pt. 1, pp. 1–366.

LEIGH-SHARPE, W. HAROLD.
1920. The comparative morphology of the secondary sexual characters of elasmobranch fishes. Memoir I. Journal of Morphology, vol. 34, No. 2, pp. 245–265.
1921. *Idem*, Memoir II. *Ibid.*, vol. 35, No. 2, pp. 359–380.
1924. *Idem*, Memoir VI. *Ibid.*, vol. 39, No. 2, pp. 553–566.

MEEK, SETH E., and SAMUEL F. HILDEBRAND.
1923. The marine fishes of Panama. Field Museum Natural History Publication No. 215, Zoological Series, vol. 15, pt. 1, pp. 1–330.

MÜLLER, JOHANNES, and F. G. J. HENLE.
1841. Systematische beschreibung der plagiostomen. Berlin, pp. 3–200, pls. 1–60.

MURPHY, ROBERT CUSHMAN, and JOHN TREADWELL NICHOLS.
1916. The shark situation in the waters about New York. Brooklyn Museum Science Quarterly, vol. 3, No. 4, pp. 145–160.

NARDO, G. D.
1827. Prodromus Observationum et disquisitionum Adriaticae Ichthyologiae. Giornale fisica, chimica, storia naturale, medicina ed arti, vol. 10, pp. 22–40. Pavia (1827).

NICHOLS, JOHN TREADWELL.
1918. Ground sharks of Florida and elsewhere. [Abstract.] Copeia, No. 53, p. 13.
1929. The fishes of Puerto Rico and the Virgin Islands. New York Academy of Science Survey, vol. 10, Pt. 2, pp. 161–295.

NICHOLS, JOHN TREADWELL, and CHARLES M. BREDER, JR.
1927. The marine fishes of New York and southern New England. Zoologica, vol. 9, No. 1, pp. 1–192.

OLSEN, A. M.
1954. The biology, migration, and growth rate of the school shark, *Galeorhinus australis* (Macleay) (Carcharhanidae) in south-eastern Australian waters. Australian Journal of Marine and Freshwater Research, vol. 5, No. 3, pp. 353–410.

PARKER, G. H., and R. E. SHELDON.
1913. The sense of smell in fishes. Bulletin of the U.S. Bureau of Fisheries, vol. 32, Doc. No. 775. pp. 35–46.

PUGSLEY, L. I.
1939. Factors influencing the vitamin A and D potency of grayfish liver oil, *Squalus sucklii* (Girard). Journal of the Fisheries Research Board of Canada, vol. 4, No. 5, pp. 405–408.

RADCLIFFE, LEWIS.
1916. The sharks and rays of Beaufort, North Carolina. Bulletin of the U.S. Bureau of Fisheries, vol. 34, Doc. No. 882, pp. 241–284, pls. 38–49.

RIBIERO, ALIPIO DE MIRANDA.
1923. Fauna Braziliense, Peixes, vol. 2.

RIPLEY, WILLIAM ELLIS.
1946. The soupfin shark and the fishery. California Division of Fish and Game, Fish Bulletin 64, pp. 6–37.

RIPLEY, WILLIAM ELLIS, and RENE A. BOLOMEY.
1946. The relation of the biology of the soupfin shark to the liver yield of vitamin A. California Division of Fish and Game, Fish Bulletin 64, pp. 39–72.

ROCKWELL, ROBERT H.
1916. Long Island sharks for the Museum. Brooklyn Museum Quarterly, vol. 3, No. 4, pp. 160–167.

ROSENBLATT, RICHARD H., and WAYNE J. BALDWIN.
1958. A review of the eastern Pacific sharks of the genus *Carcharhinus*, with a redescription of *C. malapoensis* (Fowler) and California records of *C. remotus* (Dumeril). California Fish and Game, vol. 44, No. 2, pp. 137–159.

SCHWARTZ, F. J.
1958. The cub shark, *Carcharhinus leucas*, taken at Flag Pond, Chesapeake Bay, Maryland. Maryland Tidewater News, vol. 14, No. 4, pp. 14 and 16.

SMITH, HOMER W.
1936. The retention and physiological role of urea in Elasmobranchii. Biological Reviews, vol. 11, pp. 49–81.
SPRINGER, STEWART.
1938. Notes on the sharks of Florida. Proceedings of the Florida Academy of Science, vol. 3, pp. 9–41.
1940. The sex ratio and seasonal distribution of some Florida sharks. Copeia, No. 3, pp. 188–194.
1946. A collection of fishes from the stomachs of sharks taken off Salerno, Florida. Copeia, No. 3, pp. 174–175.
1949. An outline for a Trinidad shark fishery. Proceedings of the Gulf and Caribbean Fisheries Institute, 2d annual session, pp. 17–26.
1950. A revision of North American sharks allied to the genus *Carcharhinus*. American Museum Novitates, No. 1451, pp. 1–13.
1951. The effect of the availability of sharks on a shark fishery. Proceedings of the Gulf and Caribbean Fisheries Institute, 4th annual session, pp. 140–145.
1954. Laboratory experiments with shark repellents. Proceedings of the Gulf and Caribbean Fisheries Institute, 7th annual session, pp. 159–163.
1957. Some observations on the behavior of schools of fishes in the Gulf of Mexico and adjacent waters. Ecology, vol. 38, No. 1, pp. 166–171.
SPRINGER, STEWART, and PRICE M. FRENCH.
1944. Vitamin A in shark liver oils. Industrial and Engineering Chemistry, vol. 36, p. 190.
SPRISSLER, G. PAUL.
1942. An investigation of the proteinase of the gastric mucosa of shark. Catholic University of America, Contributions from Biological Laboratory, No. 42, pp. 1–52.
STRASBURG, DONALD W.
1958. Distribution, abundance, and habits of pelagic sharks in the Central Pacific Ocean. U.S. Fish and Wildlife Service, Fishery Bulletin 138, vol. 58, pp. 335–361.
TEMPLEMAN, WILFRED.
1944. The life-history of the spiny dogfish (*Squalus acanthias*) and the vitamin A values of dogfish liver oil. Newfoundland Department of Natural Resources Research Bulletin No. 15 (Fisheries), pp. 1–102.
THORNE, EDWIN.
1916. Occurrence of ground sharks, *Carcharhinus*, in Great South Bay. Copeia, No. 35, pp. 71–96.
TORTONESE, ENRICO.
1938. Revisione degli Squali del Museo Civico di Milano. Atti della Società Italiana di Scienze Naturali, vol. 77, pp. 283–318.
1951. Studi sui Plagiostomi V, Ulteriori considerazioni sulle specie Mediterranee dei generi *Sphyrna* e *Carcharhinus*. Doriana, Supplemento agli Annali del Museo Civico di Storia Naturale "G. Doria", vol. 1, No. 20, pp. 1–8.
1956. Fauna d'Italia, vol. 2, Leptocardia, Ciclostomata, Selachii. Edizioni Calderini, Bologna, pp. 1–332.

O

U.S. GOVERNMENT PRINTING OFFICE: 1960 O - 552508