# LIFE HISTORY OF THE SPINY DOGFISH 

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#### Abstract

The spiny dogfish, a small shark, is a costly nuisance to commercial fishermen off both coasts of the United States. Data on the species' life history were gathered from the literature and from original studies and assembled in one report as a basis for possible future management. The species reaches a maximum length of $100-124 \mathrm{~cm}$. and a maximum weight of $7-10 \mathrm{~kg}$. The females are slightly larger than the males. Dogfish are known to migrate in large schools and, occasionally, to travel long distances. Tagging studies suggest they move offshore in the winter and inshore in the summer. They are opportunistic feeders with a diet list that includes fishes and crustaceans. Age determinations from interpretation of spine markings indicate the dogfish are long lived with some individuals living for

20 or 30 years. The species is ovoviviparous and mating takes place in the cold months. After a nearly 2 -year gestation period, a female gives birth to 3-11 pups, each about 25 cm . long. Natural mortality rate apparently is low, and the species has few natural enemies. In 1944 more than 40 million pounds of spiny dogfish were landed as a source of vitamin A. Today about 2 million pounds are landed. In the United States the species has limited value as an industrial fish and even less value as a food fish. It is edible, however, and is valued as food in some European nations. Management of the spiny dogfish off North America is indicated to reduce the damage it causes to more valuable commercial fisheries.


The spiny dogfish Squalus acanthias L., a small shark of the family Squalidae, has been one of the most intensively studied fishes, but one in which extensive knowledge is lacking. The species is studied by college students in zoology, ichthyology, comparative anatomy, and vertebrate taxonomy and is a favorite experimental animal for physiological studies including pharmacological toxicity tests. Few comprehensive biological studies of this fish have been made, however, except for Ford's (1921) study at Plymouth, England, Templeman's (1044) study in Newfoundland, and the studies made by Bonham, Sanford, Clegg, and Bucher (1949) in the State of Washington. In general, most of the published reports represent isolated observations or extremely specific studies. As a result, we know, for example, the function of the rectal gland of the spiny dogfish (Burger

[^0]and Hess, 1960), but we do not know the wintering grounds of the species; we know the mechanism controlling movements of the spiral intestine (Sawyer, 1933), but we do not know the relationship between the groups of dogfish in any one area.

This paper is an attempt to organize and summarize the available information, to which I have added additional original data from recent studies of the spiny dogfish in the Northwest Atlantic. This report is undoubtedly incomplete, but will serve as a starting point for other studies and help the researcher who is not completely familiar with the literature to interpret future observations.

As a convenient method of handling the information, the various phases of the life history of the fish are taken up in turn. Because the species is distributed throughout the Northern Hemisphere (Bigelow and Schroeder, 1948), I have reviewed reports from both the Atlantic and Pa eific Oceuns. Some consideration has been given,
as well, to the role of the spiny dogfish in the commercial fishery.

Much of the information reported here is of interest solely because it adds to man's fund of knowledge about the species; however, some of the information has more concrete implications for our commercial fishermen. This latter consideration has been aptly summed up by Bigelow and Schroeder (1948), who state:
"From a practical aspect the spiny dog in the Western Atlantic is chiefly important because it is undoubtedly more destructive to gear and interferes more with fishing operations than does any other fish-shark or teleost."

## DESCRIPTION

The spiny dogfish is typically sharklike in appearance (fig. 1). In Western Atlantic waters it
grows to a length of about $50-90 \mathrm{~cm}$. and weighs $3.5-4.9 \mathrm{~kg}$., with a maximum of about 100 cm . and $7.3-9.8 \mathrm{~kg}$. The females are slightly larger than the males (Bigelow and Schroeder, 1953). In the Pacific Ocean, off the west coast of the United States, the males reach a maximum of about 100 cm . and 3.9 kg ., while the females reach a maximum of about 124 cm . and 9.8 kg . (Bonham et al., 1949).

The upper part of the fish is slate colored, sometimes tinged with brown, with irregular rows of small white spots on each side. The white spots are generally typical of younger fish and may be lacking on older individuals. A distinguishing feature of this shark is the presence of two sharp spines, one anterior to each dorsal fin, the rear spine longer than the front spine. Halstead (1959) reports that a venom gland is located on


Figure 1.-The spiny dogfish, squalus acanthias.
the upper posterior part of each spine. He cites no case histories of injuries, however. The spines presumably are used in defense and are capable of inflicting a painful wound.

Spiny dogfish frequently are confused with the smooth dogfish, Mustelus canis (Mitchill), a member of the family Triakidae, although examination of the two species will clearly separate them. The smooth dogfish, as the name implies, lacks the sharp dorsal spines. It is a lighter color than the spiny, although it has great ability to change color to match its surroundings. Above a white sandy bottom it usually is a translucent, pearly shade; over a dark bottom it will have a darker color. Individuals, in general, tend to be larger than spiny dogfish; smooth dogfish are $59-137 \mathrm{~cm}$. long with a few attaining 152 cm . in length. Food of the smooth dogfish is mostly large Crustacea, especially lobsters and crabs, although it also eats small fish such as menhaden and tautog. It is a coastal, warm water species that ranges in the Western Atlantic from Uruguay and southern Brazil to Cape Cod. It is one of the sharks that develops a placental attachment between the embryos and the mother; thus it is truly viviparous. The smooth dogfish is of little concern to commercial fishermen.

## DISTRIBUTION

Distribution of the spiny dogfish has been, until recently, somewhat obscured by the question of its specific identity. Many ichthyologists held that there were two distinct species, S. aconthias in the North Atlantic Ocean and S. suchleyi in the North Pacific Ocean. Bigelow and Schroeder (1948) noted that although it. was not entirely clear how the two species were related, they had not obviously differentiated themselves specifically during the period since their ranges had become discontinuous. The prevailing opinion today is that. the two populations represent but a single species, S. acanthias, which occurs in both the Atlantic and Pacific Oceans (American Fisheries Society, 1960). Briefly, the distribution may be expressed as both sides of the North Atlantic, chiefly in temperate and subaretie latitudes, and also on both sides of the North Pacific, in similar latitudes (fig. 2), with close allies in corresponding latitudes in the Southern Hemisphere. The species is of minor economic importance in the Southeast Atlantic, off the West Coast of Africa, but fairly important in

Mediterranean Atlantic waters. ${ }^{-}$It occurs chiefly in continental, as contrasted with oceanic, waters, anywhere between the surface and the bottom down to 165-185 meters (Bigelow and Schroeder, 1948 ) and has been found as deep as 290 meters ( see table 1).


Figure 2.-Distribution of the spiny dogfish in the Northern Hemisphere.

The distribution in the Northeast Atlantic is described in detail by Bigelow and Schroeder (1948) as follows: off France, north to Ireland, Scotland, southern Scandinavia, the English Chamel, and the North Sea, from there eastward to the Kattegat. The spiny dogfish rarely enters the Baltic Sea. It is plentiful around the Orkney Islands, the Faroes, and south and east of Iceland (but less to the north and west), and is found off Norway to the Murman coast. It is also generally distributed in the Mediterranean Sea and the Black Sea.
In the Northwest Atlantic the spiny dogfish is found in coastal waters from Cape Lookont, N.C., northward around Nova Scotia, along both the northern and southern shores of the Gulf of St. Lawrence, past the Strait of Belle Isle to southeast

[^1]Labrador (Bigelow and Schroeder, 1048). It is common northward along the coasts of Newfoundland. There is no record of its occurring along the coast north of Hamilton Inlet. Offshore it occurs in season on Nantucket Shoals, Georges Bank, Browns Bank, the Nova Scotian banks, and the Newfoundland banks. It was also recorded on the west coast of Greenland to Sukkertoppen and Holsteinborg. Hansen (1949) reports that dogfish were formerly a rarity around Greenland, but in the 1930's some were caught in several places on the southwest coast and in the autumn of 1947, around Sukkertoppen.

Irocal observations of spiny dogfish, and their seasonal occurrence, are reported by Perley (1852), Stafford (1912), Cox (1921), and Jeffers (1932). Each of these authors noted that the appearance of dogfish usually indicater an end of commercial fishing for food fishes.

Table 1.-Water temperature and dogfish catches of 100 or more by otter trawl from research vessels in the Northwest Allantic from Nova Scolia to the offing of New York, 1948-59

| Date | Depth | Bottom temperature | Catch of dogfish |
| :---: | :---: | :---: | :---: |
|  | Mfelers | ${ }^{\circ} \mathrm{C}$ | Number |
| Feb. 3, 1956 | 180 | 9.4 | 428 |
| Apr. 22.1950 | 152 | 11.7 | 367 |
| Apr. 23, 1850 | 110 | 7.2 | 100 |
| Apr. 26,1950 | 219 | 7.8 | 103 |
| Da. | 219 | 7.2 | 224 |
| May 1, 1950 | 189 | 8.9 | 372 |
| Do. | 183 |  | 1. 200 |
| Do. | 177 | 8.9 | 475 |
| Do. | 201 | 8.9 | $\underline{99}$ |
| May 2, 1950 | 110 | 4.4 | 490 |
| May 13, 1950 | 91 | 11.1 | 1,476 |
| Do.. | 91 | 11.1 | 15: |
| Do. | 82 | 11.1 | 150 |
| Do. | 81 | 5.0 | 610 |
| May 14, 1950 | 83 | 7.2 | 253 |
| May 15, 1950 | 142 | 11.1 | 110 |
| May 16, 1950 | 113 | 7.8 | 120 |
| Do. | 85 | 6.7 | 140 |
| May 17, 1950 | 76 | 5.6 | 156 |
| June 14, 1855 | 103 | 6. 1 | 110 |
| Weighted average | 134 | 8.3 |  |
| July 29, 1949 | 67 | 10.6 | 3, 637 |
| Aug. 1, 1950 | 85 | 7.8 | 294 |
| $\mathrm{DO}^{\text {D }}$ | 85 | 8.3 | 455 |
| Aug. 2, 1950 | 94 | 8.9 | 146 |
| Aug. 5, 1950 | 293 | 6.1 | 234 |
| Aug. 4, 1948 | 58 | 6. 7 | 123 |
| Aug 5 5, 1948 | 33 | 13.3 | 131 |
| Do. | 40 | 11.7 | 210 |
| Oet. 8, 1958. | 204 | 7.8 | 900 |
| Oct. 9, 1958. | 222 | 7.8 | 122 |
| Oet. 16. 1948. | 24 | 12.2 | 374 |
| Oct. 17, 1948 | 37 | 8.3 | 101 |
| Oct. 20, 1959 | 55 | 11.1 | 1,051) |
| Get. 30, 1949 | 74 | 15.6 | 24x |
| Do.- | 76 | 13.3 | 100 |
| Do. | 60 | 14.4 | 283 |
| ${ }^{\text {Do }}$ | 55 | 15.6 | 115 |
| Oct. 31, 1948 | 61 | 15.0 | 1.561 |
| Nov. 5, 1948. | 61 | 14.4 | 187 |
| Nov. 17, 1956. | 56 | 13.3 | 160 |
| Dec, 3, 1948-- | 56 85 | 16.7 | 211 |
|  |  |  |  |
| Weighted average | 85 | 11.4 |  |

In the Pacific Ocean, Bigelow and Schroeder (1948) report that the spiny dogfish is found on ". . . both sides of the Northern Pacific south to California, Japan, Northern China and the Hawaian Islands."

## MIGRATIONS

The spiny dogfish is a gregarious fish and occurs in sehools containing large numbers of individuals. Usually the schools are composed of: (1) very large, mature females; (3) medium-sized individuals, all mature males or all immature females; or (3) small immature individuals of both sexes in about equal numbers (Bigelow and Schroeder, 1953). Hickling (1930), in his studies of spiny dogfish collected off the southern coast of Ireland, noted a relation between the size of the individuals in the schools and the depth of water. Fish of both sexes, from 30 to 45 cm . long, were caught in 55 m ., while larger fish of both sexes, from 50 to 89 cm . long, were caught in depths of 164 to 183 m . In general, male dogfish were found in shallower water than females of the same size. The exception to this, however, was for the large pregnant females that were found migrating into shallower water to bear their young.

The appearance of dogfish in our northeastern coastal waters is a rather sudden event. One day, in a given area, there will be fine cod and haddock fishing; the next day there will be nothing but dogfish. They appear as early on Georges Bank (March-April) as they do along New Jersey (March) (Bigelow and Schroeder, 1953). Dogfish are spring and autumn transients only in the southern part of their range, from New York to North Carolina, and in the Cape Cod area they are mostly transients, moving to the north in the spring and to the south in the autumn.

In Newfoundland waters they first begin to appear in June, off the southern end of the island (Templeman, 1044). The largest fish-mature and probably pregnant females-appear first. The mature males appear in the late autumn. As the season progresses, dogfish appear farther northward along the coast and are off Labrador by September. In general, dogfish are plentiful around Newfoundland from June through November or December.

The nature of the dogfish's seasonal migrationcoastal north-south, offishore-onshore, or a combi-
nation of the two-is not clearly understood. Part of the problem is the mystery of where the dogfish spends it winters. Bigelow and Welsh (1925) stated, "The winter home of the Gulf of Maine dogfish is still to be learned." They examined the evidence, including the presence of the adults in deep water in Long Island Sound in midsummer, the almost simultaneous appearance of the fish all along the coast north of North Carolina in the spring, and the capture of dogfish by the Albatross, February 1020 , in 164 to 365 m . along the continental edge off Chincoteague, Va., and off Delaware Bay, and concluded that this ". . . argues for an on-and-off rather than a long-shore migration, with the deep water off the continental slope as their winter home."

More recent evidence of the presence of dogtish in deep water during the winter has been accumulated from observations of dogfish off the Middle Atlantic and New England States (Bigelow and Schroeder, 1936, 1948, 1953). In January 1961, spiny dogfish were taken in an otter trawl by the Bureau of Commercial Fisheries research vessel Delaware in $15 S$ to 183 m . along the edge of the Continental Shelf 80 miles south of Martha's Vineyard.

At times, however, dogfish may come into shallow water in the winter. Collins (1883) quotes an item in the newspaper "Cape Ann Advertiser" dated February 10, 1882: "Immense schools of dogfish, extending as far as the eye can reach, have appeared off Portsmouth, an unusual sight in winter."

The accumulated wealth of evidence suggests that temperature governs the seasonal movements of the spiny dogfish. Bigelow and Schroeder (1048) note that dogfish do not appear along the east coast until the water warms to $6^{\circ} \mathrm{C}$. and disappear when the water temperature rises to about $15^{\circ} \mathrm{C}$. The preferred range of temperature on the offshore wintering grounds seems to be $6^{\circ}$ to $11^{\circ} \mathrm{C}$.

Survey data (table 1) collected during 1949-59 by the Bureau of Commercial Fisheries Biological Laboratory at Woods Hole indicate dogfish in the Northwest Atlantic prefer bottom water temperatures between $7.2^{\circ}$ and $12.8^{\circ} \mathrm{C}$. (average, $9.8^{\circ}$ ). The average temperature at which 100 or more dogfish per haul were caught during the period

January-June was $8.3^{\circ} \mathrm{C}$.; for the period TulyDecember, $11.4^{\circ} \mathrm{C}$.

The survey data also tend to support Bigelow and Schroeder's statement that this species winters in relatively deep water, moving into shoaler water in summer and fall. The average depth at which 100 or more dogfish were caught during the period Jaiuary-June is found to be significantly different from the corresponding depth for the period July-December ( 134 and 85 m ., respectively).

In Alaska waters incidental catches of spiny dogfish are reported by Hanavan and Tanonaka (1959) during experimental gill netting for salmon. The dogfish were caught in the Bering Sea and in the Gulf of Alaska during July and August when the surface water temperatures ranged from $7^{\circ}$ to $13.3^{\circ} \mathrm{C}$.

In waters oft Jopan, Sato (1935) reports an interesting diurnal migration of spiny dogfish. He recorded the body temperatures of dogfich caught. in the daytime and at night, on a fishing ground in depths of 110 to 128 m . Thirty dogfish caught. at night in a surface drift gill net had body temperatures of from $9.5^{\circ}$ to $11.2^{\circ} \mathrm{C}$. The surface water temperature at the time was quite similar, from $9^{\circ}$ to $12.2^{\circ} \mathrm{C}$. In contrast, 28 dogfish caught during the day on a longline on the bottom had body temperatures of from $3.5^{\circ}$ to $5.5^{\circ} \mathrm{C}$. Unfortunately Sato does not report the water temperature on the bottom. It seems reasonable to assume, however, that the bottom water temperature was within the range of the body temperature of the fish caught on the bottom and that the dogfish were rising to or near the surface at night and descending to the bottom during the day.

In early August 1961, during a cruise of the Bureau of Commercial Fisheries research vessel Delaware, dogfish were frequently observed at or near the surface on many of the inshore Gulf of Maine fishing grounds (Robert L. Edwards, personal communication). The water temperatures at the surface were normal for the season (around $15.6^{\circ} \mathrm{C}$.), but at the bottom they were abnormally cold ( $2.8^{\circ}$ to $3.9^{\circ} \mathrm{C}$. at 73 m .). Few dogfish were taken in the otter trawl at this time.

Edwards (personal communication) observed the dogfish appeared at the surface itself late at night and early in the morning. One morning in Ipswich Bay they were observed to be harrying small schools of euphausiids-as many as six to
eight fish circling each school. The numbers of fish that could be seen at this time were in the thousands. During the day the dogfish retreated to depths of 3 to 5 fathoms. Several hundred were handlined from this depth for tagging and for examining the embryos in the preguant females. In the late afternoon, occasional fish were again observed at the surface. South of Cape Cod, the dogfish were taken again a few fathoms below the surface. They appeared whenever the otter trawl was hauled in and unwanted fish were discarded.

Edwards, Livingstone, and Hamer (1962) studied the distribution of fishes across the Continental Shelf from Nantucket Shoals to Cape Hatteras. Their results indicate that male spiny dogfish are usually found in cooler water than the females.

Little is known of the salinity preferences of the spiny dogfish. Bigelow and Schroeder (1948), however, note a record of a spiny dogfish that entered a river in Denmark. In their opinion the water was undoubtedly brackish at least near the bottom, rather than fresh, since both cod and Mertuccius were also present in the river at the same time. Spiny dogfish captured off British Columbia and studied in the laboratory, were able to live for more than 1 hour in distilled water and for nearly 2 hours in tap water (Quigley, 192Sa). The author concludes, "Since the dogfish continued to breathe for an average of 113 minutes in tap water and remained active during most of this time, they probably could escape from a fresh water stream even if they were to swim into it above tide water level."

## TAGGING STUDIES

Spiny dogfish have been tagged over most of their range by biologists interested in making precise determinations of the migration routes of this fish, and also in learning something of the nature of the clogfish populations. Tag returns from most of the experiments have been at a lower rate than for tagging experiments with commercially valuable fishes: in most fisheries the dogfish is either a nuisance to be avoided or, at best, is retained as a very minor part of the catch. Although many tagged dogfish are undoubtedly recaptured, most are discarded at sea without having their tags noticed; consequently, few tags are recovered. Tagging returns suggest that the dog-
fish is long lived, for several fish were at liberty for 10 years. Some individual fish migrated long distances.
In a British experiment in November and December 1957,75 spiny dogfish were tagged with a yellow plastie tab attached with a braided nylon loop (Beverton, Gulland, and Margetts, 1959). The fish were tagged incidentally during a whiting tagging experiment in the northwest part of the Irish Sea. At the time of the report, after i months at liberty, only two tagged dogfish were returned despite the fact that originally the dogfish appeared particularly robust and little atfected by capture or tagging. No information was given as to the place of recapture of the tagged fish.

One thousand spiny dogfish were tagged near the Shetland Islands, north of Scotland, in November 1958 (Aasen, 1960). The mark used was a yellow slip of polyethylene film with printed text rolled up as a cylinder and attached to the fish with a stainless steel bridle in front of the first dorsal fin. After $21 / 2$ months at liberty, 12 tagged fish ( 1.2 percent) were recaptured, most of them near the west coast of Norway. After 2 years at liberty, 10.8 percent of the dogfish had been recaptured. The returns from this experiment, combined with returns from nearly 3,000 dogfish tagged in later experiments, yielded a combined return rate of 6 percent. Aasen (1962) concluded, "It is obvious that most of the fish migrate towards the Norwegian coast in winter and return to the grounds northwest of the British Isles in summer."

Holden (1962) tagged 27 S dogfish in the Irish Sea during 1957-59, and 15 ( 5.4 percent) were recaptured. Most of the winter recaptures came from the southern part of the Irish Sea, while the summer and autumn recaptures came from Scotland, as far north as the Shetland Islands. Presumably the dogfish wintered in the Irish Sea and migrated to mingle with the Norwegian dogfish north of Scotland in the summer.

Nearly 10,000 dogfish were tagged in the waters off British Columbia and Washington in the 1940 's, and 655 ( 6.7 percent) were recovered (Holland, 1957). In general, the tag returns demonstrated a southward, coastal migration in the autumn and winter and a northward migration in the spring and summer. Several long-distance recaptures were reported from the constal migrations but the
one outstanding offshore, long-distance migration that was reported was when a dogfish that had been tagged off Willapa Bay, Wash., in 1944 was recaptured near the northern end of Honshu Island, Japan, in 1950. This is a straight line distance of 4,700 miles, but the author concluded that the fish probably followed a great circle route at aceustomed depths along the coastal shelf. Longrevity of the spiny dogfish is suggested by the above example, a fish at liberty 7 years, and two other fish tagged in the same experiment, which were at liberty 8 years and 10 years, respectively.

Dogfish tagging experiments in the Northwest Atlantic have been reported by Templeman (1954, 1958) for the Newfoundland-Grand Bank area and by Jensen (1961) for the Gulf of Maine-Georges Bank and Browns Bank areas (fig. 8). In the Newfoundland experiment, 279 females were tagged near St. John's in July 1942, and, as of September 1949,14 fish ( 5 percent.) were recaptured. Many of the tagged fish were caught in the local area and the Maritimes, but two were caught off Gloucester, Mass. (one in 1942 and one in
1943), a distance of 900 miles, and one was canght off Cape Henry, Va., in 1947, a distance of 1,300 miles. The last return was from the Strait of Canso, Nova Scotil, in 1949. Templeman noted (1054), ". . . most of the tagged fish were mature. females carrying young and the recaptures show a southward late fall movement of some at least of these large pregnant females, with presumably a compensating northward movement in the spring and early summer." In an earlier report (1944) he suggested that the dogtish migrate rapidly and for long distances in the upper layers of the water.

While the tag returns reported by Templeman indicated a coastwise migration, he did report an astonishing offshore migration from a later tagging experiment (Templeman, 1958). A fish that had been tagged on the southwestern slope of the Grand Bank in June 194 was recaptured in Faxa Bay, Iceland, in Angust 1957. The straight line distance between the tagging area and the point. of recapture is over 1,300 nautical miles.

Returns of dogfish tagged in the Gulf of Maine area have done little to confirm either a north-


Figure 3.-Results of dogish tagging in the Northwest Atlantic.
south or inshore-offshore migration pattern (.Tensen, 1961). In these experiments, 155 dogfish were tagged near Cape Anin, Mass., in July 1956; and 50 were tagged on Browns Bank in October 1957. To date, nine tags have been returned ( 5.8 percent). eight from the 1056 experiment and one from the 105 - experiment. Most of the tagged fish were recaptured relatively close to the areas in which they had been released; six were caught less than 50 miles from the tagging area; one, 73 miles away; and another, 140 miles away. One, however, at liberty nearly 5 years, was recaptured 200 miles away, on the eastern edge of Georges Bank. In general, the recaptures suggest that spiny dogfish return to the same general area at about the same time of year and the same fish probably school together for long periods of time.

An interesting recapture was made recently of a dogfish tagged in a later series of experiments carried out aboard the Delaware. The fish was 1 of 143 caught on handlines in 15 m . of water, July 29, 1961. It was tagged and released 3 miles off Halibut Point, Cape Ann. Mass., and was recaptured by a commercial otter trawler in 119 m . on December 30, 1961, in the vicinity of the Hudson Canyon. The fish had moved about 250 miles in 23 weeks and was caught south and offshore of the tagging area. This recovery adds further evidence to support the hypothesis that some of the dogfish that spend the summer in the inner Gulf of Maine migrate south and oftshore to spend the winter.

Table 2 grives the tagging and recapture information for 17 spiny dogfish tagged by personnel of the Bureau of Commercial Fisheries Biological Laboratory at Woods Hole. The 17 represent the returns from a total of 844 dogfish tagged in 1956, 1957, 1960, and 1961.

## SEROLOGIGAL STUDIES

An approach to the identification of spiny dogfish subpopulations, by blood typing techniques, was made by Sindermann and Mairs (1961). The authors proposed a two-antigen blood group system. They found that individual dogish collected in the Gulf of Maine were of blood types $S_{1}, S_{\text {. }}$. $\mathbf{S}_{1} \mathbf{S}_{2}$, or $\mathbf{S}_{0}$. Blood groups of pregnant females and their unborn pups were compatible, ". . . with a simple genetic hypothesis of three alleles, $\mathbf{S}^{1}, \mathrm{~S}^{2}$, and $\mathrm{S}^{0}$, controlling the system." Continua-
tion of the work, complemented with tagging and other population studies, will make it possible to determine the existence of reproductively isolated subpopulations of spiny dogfish. In addition serological techniques may clarify the relationship between the various Squalus species and groups throughout the world.

Table 2.—Returns of tagged spiny dogjish

| Date and locality of- |  | Time at liberty | Distance |
| :---: | :---: | :---: | :---: |
| Tagging | Recapture |  |  |
| July 7, 195h, Boon Island, <br> Maine ( $43^{\circ} 05^{\prime}$ N.-70 ${ }^{\circ}{ }^{\circ} 8^{\prime}$ <br> W.). $\qquad$ <br> Do $\qquad$ | July 22, 1057, Cape Ann, Mass. (42 $2^{\circ} 44^{\prime}$ N. $-70^{\circ} 19^{\prime}$ W.). <br> July 29. 1959. Cape Elizabeth. Miaine ( $43^{\prime 2} 8^{\prime}$ N.$70^{\circ} 12^{\prime} \mathrm{W}$.). <br> July 21, 19fi, Cape Elizabeth. Maine ( $43^{\circ} 27^{\prime}$ N.- | Weekz54 | ${ }^{\text {Mill }}{ }_{22}$ |
|  |  |  |  |
|  |  |  | 20 |
|  |  | 159 |  |
|  |  | 210 | 25 |
| Do------------------ |  |  |  |
| July 8. 1956. Cape Ann. <br> Mass. $\left(42^{\circ} 48^{\prime} \mathrm{N} .-70^{\circ} 15^{\prime}\right.$ W.). | Nov. 15, 1956, Cape Elizareth, Maine ( $43^{\circ}{ }^{\circ} 28^{\prime}$ N.$70^{\circ} 10^{\prime}$ W. . | 18 | 40 |
|  |  |  |  |
|  | Mar. 2, 1957, Cape Ann. Mass. (42"38' N. $7 \mathbf{2 0}^{\circ} 17^{\prime}$ W.) | 34 | 10 |
|  |  |  |  |
|  | May 22. 1957, Chatham, Mass. ( $41^{\circ} 40^{\prime} \mathrm{N} .-69^{\circ} 42^{\prime}$ W.). | 45 | 73 |
|  |  |  |  |
| Do------------------ | July 16, 1959, Cape Elizabeth. Maine ( $42^{\circ} 28^{\prime}$ N.$70^{\circ} 10^{\prime} \mathrm{W}$.). | 157 | 40 |
|  |  |  |  |
| Do. | May 15, 1061, Georges Bank ( $41^{\circ} 33^{\prime}$ N. $-86^{\circ} 35^{\prime}$ W.). | 248 | 185 |
|  |  |  |  |
| Do. | Sept. 4, 1961. Port Mouton Harbour, Nova Scotia ( $43^{\circ} 57^{\prime} \mathrm{N}-64^{\circ} 38^{\prime} \mathrm{W}$ ). | 974 | 280 |
|  |  |  |  |
|  | July 12, 1958. Chance Harhour. New Brunswick ( $44^{\circ} 55^{\prime} \mathrm{N} .-66^{\circ} 21^{\prime} \mathrm{W}$.). | 39 | 140 |
| Oct. 14, 1957. Browns Bank ( $42^{\circ} 36^{\prime}$ N. $-65^{\circ} 46^{\prime}$ W.). |  |  |  |
|  |  |  |  |
| July 8, 1960. Stellwagen Bank (42 ${ }^{\prime} 13^{\prime}$ N.-70 $0^{\circ} 17^{\prime}$ W.). | June 13. 1961, Buzzards Bay. Mass. $\left(41^{\circ} 32^{\prime} \mathrm{N}\right.$.$70^{\circ} 40^{\prime}$ W.). | 49 | 45 |
|  |  |  |  |
| May 26,1061 , Woods Hole. Mass. ( $41^{\circ} 31^{\prime}$ N. $-70^{\circ} 40^{\prime}$ Wo | June 11, 1961, Buzzards <br> Bay, Mass. ( $41^{\circ} 36^{\prime}$ N.$70^{\circ} \mathrm{E} 0^{\prime}$ W.). <br> June 15, 1962, Montauk Point, N. Y. $140^{\circ} 54^{\prime}$ N.$71^{\circ} 39^{\prime} \mathrm{W}$.). | 3 | 9 |
|  |  |  |  |
|  |  |  |  |
|  |  | 63 | 64 |
|  |  |  |  |
| June 13. 19is. Stellwagen Bank ( $42^{\circ} 25^{\prime} \mathrm{N},-70^{\circ} \mathrm{O} 1^{\prime}$ W.). | Aug. 22, 1962. Cape Ann. Mass. ( $42^{\prime} 46^{\prime} \mathrm{N},-70^{\prime} 39^{\prime}$ W.). | 62 | 24 |
|  |  |  |  |
|  |  |  |  |
| July 22. 1961. Cape Ann; Mass. $\left(42^{\circ} 44^{\prime}\right.$ N. $-70^{\circ} 30^{\prime}$ W.). Do | Dee. 30. 1961. Hudson Canyon. ( $39^{\circ} 41^{\prime}$ N.-72 $2^{\circ} 12^{\prime}$ W.). <br> Aug. 24. 1962. Seguin Island, Maine ( $43^{\circ} 38^{\prime}$ N. $-69^{\circ} 37^{\prime}$ W.). | 23 | 250 |
|  |  |  |  |
|  |  |  |  |
|  |  | 57 | 71 |
|  |  |  |  |
| July 26, 1961, Cape Ann, Mass. (42" $46^{\prime}$ N. $-70^{\circ} 41^{\prime}$ W.). | Sept. 5, 1961, Portsmouth,$\begin{aligned} & \text { N.H. ( } 43^{\circ} 01^{\prime}{ }^{\text {N. }}-70^{\circ} 41^{\prime \prime} \\ & \text { W.). } \\ & \text {, } \end{aligned}$ | 6 | -15 |
|  |  |  |  |

## FOOD HABITS

Several studies of the stomach contents of spiny dogfish from many parts of the Northern Hemisphere have shown that it is primarily a fish enter but will also feed on invertebrates, both swimming and bottom-dwelling forms. In many areas, clupeoids are important in the diet of the dogfish, but it undoubtedly feeds on whatever species it can capture.
In the Pacific Ocean three important studies of dogfish feeding habits have been made. One such
study was conducted to determine the amount of predation, if any, by dogfish on salmon smolts as they descended the Fraser River, British Columbia (Chatwin and Forrester, 1953). In the river mouth, 849 dogfish were examined and 20 ( 8 percent.) had empty stomachs. Of those that contained food, 100 percent contained eulachon (a smelt, Thaleichthys pacificus), or traces of it, 5 percent contained sand lance, Ammodytes. and 19 percent contained invertebrates, including shrimp, crabs, small crustaceans, squid, and octopus. A large number ( 91 percent) contained sticks and leaves, no doubt ingested accidentally with the food items. Outside the river mouth, the dogfish diet was much the same: 91 percent eulachon, 29 percent invertebrates, and 5 percent sticks and leaves. Miscellaneous food items included a honeybee and polychaete worms. On the basis of their findings the authors concluded the spiny dogfish was an opportunistic feeder.
Another study in the same general area was made by Bonham (1954) who examined more than 1,100 spiny dogfish stomachs, of which nearly 60 percent contained food. He found more than 77 different food items; fish constituted two-thirds of the diet. The three most common food items were ratfish, Hy ydrolagus colliei, (20 percent) ; herring, Clapea harengus pallasii, (18 percent) ; and krill, Euphausiidae, ( 9 percent). The only evidence of cannibalism was the finding of a $230-\mathrm{mm}$ (newborn?) dogfish pup in the stomach of a large pregnant female. Bonham concluded, "Large and small dogfish eat much the sume kind of food, with the exception of very small dogfish in whose diet worms and other mud-inhabiting organisms appear prominently."
Sato's (1035) studies of the spiny dogfish in the water around Japan indicate that clupeoids are important in the diet in this area as they are in other parts of the world. He examined the stomach contents of 128 dogfish collected in gill and set nets in June and July. Sixty stomachs contained fish; 48 contained sardines, Sardinops salua melanosticta; and 12 contained other fishes, including herring, clupeal harengus pallasii, salmon Oncorthynchass keta, and cod, Gadus macrocephalus. Invertebrates were found in 21 stomachs.

In waters north of Japan, around Sakhalin, food items found in the stomachs of spiny dogfish were noted by Kaganovskạia (1937). The items
were listed simply as herring, iwashi (sardine), cod, octopus, crab, squid, and sea cucumbers.

Food habits of the dogfish in the North Atlantic are quite similar to those of the dogfish in the Pacific. From waters around the British Isles, Ford (1921) reported food items from 143 spiny dogfish with recognizable stomach contents. Fishes were found in 137 stomachs and included herring and pilchard ( 67 percent), mackerel (19 percent), and gadids (4 percent). Six stomachs contained crustacea, and three had mollusks. The stomachs were collected at a time when the clupeoids and mackerel were abundant and thus readily available to the dogfish.

In the Northwest Atlantic, around Newfoundland, capelin, Mallotus villosus, are important in the diet of the spiny dogfish. Templeman (1944) made a casual examination of 94 dogfish stomachs collected in July 1942 and found all of them contained capelin. During this month the capelin were plentiful on the inshore grounds and the dogfish appeared to be feeding almost exclusively on them. He notes, "Some of the stomachs were full of capelin, one containing 13 capelin, 1 of 7 cm . and 12 from 14 to 19 cm . long."

From August to November, Templeman (1944) made a detailed analysis of 1,171 dogfish stomachs of which 665 were empty, 367 contained only the bait used to capture them, and 139 contained food. In the stomachs that contained food, about 60 percent contained fishes, about 45 percent contained Crustacea, about 8 percent contained coelenterates, and a few contained mollusks, polychaetes, - algae, and miscellaneous items. The recognizable fishes were herring ( 14 percent), capelin ( 5 percent), and cod ( 5 percent).

In the Gulf of Maine, spiny dogfish feed on a wide variety of species and at one time or another prey on practically all species smaller than themselves. They are regarded as the chief enemy of the cod, and also feed on mackerel, haddock, herring, squid, worms, shrimps, and crabs. They are one of the few fishes that eat ctenophores (Bigelow and Schroeder, 1953)

My own observations of spiny dogfish stomach contents have revealed a curious condition in which the stomachs were distended with a clear watery fluid. Casual observations of 50 dogfish stomachs collected during a cruise of the research vessel Delnware in June 1961 on Stellwagen Bank re-
vealed fish remains in only three stomachs. Five stomachs contained about 4 ounces of a light-gray, custardlike material, evidently food well advanced in digestion. Most of the stomachs, however, were filled with clear fluid; only a few stomachs were empty and flaceid.

Fifty stomachs examined at Pt. Judith, R.I., in July 1959, contained mostly amphipods (Leptocheirus) and occasional fish remains.

In July 1961, John M. Hoberman found silver hake (Mcrluccius bilinearis) in the stomachs of dogfish collected in Ipswich Bay during a cruise of the Delawire. Silver hake were aboudant in the area at the time.

Fishes and rock crabs (Cancer) were the principal food items of 33 spiny dogfish collected in June 1963 off Block Island, R.I. The dogfish were examined aboard the research vessel Albutross IV. Sisty percent contained fish, 33 percent contained rock crabs, and 7 percent contained squid. Recognizable food items included squirrel hake, Urophycis ohuss: silver hake; winter flounder, Pseudopleuronectes amerioanus; and sculpin, Myoxocephatus sp.

It is evident spiny dogfish have no food preferences, but eat nearly anything that moves. It is evident too, they are opportunistic feeders, preying on whatever species are abundant and available. Their catholic food habits probably contribute greatly to the species' biological success.

## AGE AND GROWTH

The traditional techniques used in fishery biology for age determination are not, unfortunately, applicable to the spiny dogfish. The dogfish does not have scales suitable for examination, and being a cartilaginous fish, it has no true bones in which visible growth zones are formed. Dogfish otoliths, undike the ealcareous otoliths of the telensts, are simply aggregations of sand particles loosely joined in a gelatinous substance, and thus offer no opportunity for detection of growth zones.

A possible solution to the problem of determining the age of the dogfish is presented in an obscure Russian paper (Kiaganovskaia, 1933) read in English translation. Briefly, the paper notes that the dorsal spines of the dogfish are marked with ammulations apparently related to growth periodicity (fig. 4). The Russian biologist had collected the dogfish from the waters around

Sakhalin. At first she examined the vertebrae, but the barely noticeable rings in them became even less visible after treatment. Cross sections of the teeth and of the dorsal spines were examined, but without success. The teeth showed no zones, and the spines were found to have an internal cavity along their entire length. The enamel conting of the spines, however, had markings, ". . . which doubtless represent annual deposits."


Figune 4.-Photograph of a dogtish spine showing the annulations.

The makeup of the spine is quite similar to the makeup of a mammalian tooth. Daniel (1984) describes the structure of the spine as follows:

For almost half its length the spine is buried in the integument. 'The buried part is designated as the root or base and the exposed portion the crown or spine proper . . .
. . . The spine contains a large central cavity which when in place fits over a cartilage of the fin skeleton. The walls of the spine are made of dentine which in the crown consists of a double laver. The more superficial liayer is bounded anteriorly and laterally by a laver of enamel, but enamel does not extend over the posterior groove which fits up against the basal cartilage of the tin skeletom. A more or less compact layer of pigment . . . separates the enamel . . . in front from the layer of dentine.

Kiganovskaia (1933) did not try to validate the spine markings as year marks although she noted that the spines of fish less than 1 year old were light gray in color and had no markings. She examined a sample of rear dorsal spines (the posterior spines are more clearly marked than the interior spines) from 210 dogfish, $380-1,180 \mathrm{~mm}$. in length, and reported their ages as $2-25$ years.

Her data were presented in a table which I have incorporated into a growth curve (fig. 5). It seems reasonable to consider the spiny dogfish a long-lived species in view of the evidence of tagged dogfish at liberty for up to 10 years.


Figure b.-Two growth rates for the spiny dogtish, based on interpretation of spine markings.

Using the Russian method, Bonham et al. (1949) examined the spines from 215 dogfish collected in State of Washington waters. The fish were 34-127 em. long and $1-99$ years old, and although there is variation in the Washington data, the trend is similar to that in the Russian paper. To prepare the spines for reading, Bonham (personal communication) removed them by slicing down along the bases of the spines into the back of the dogfish and freeing the spines from the skin or muscle. The spines were not treated; and low magnification (5X) or none at all was used in actual examination.

Only about 90 percent of the spines ( 915 out of 1,100 ) had markings that were sufficiently distinct to be readable without appreciable disagreement by different observers (Bonham, personal communication). In the report (Bonham et al., 1949) the authors cautioned, "It must be understood that rejection of unclear or doubtful spines would probably eliminate from consideration most of the old dogfish, whose spines usually are broken, badly eroded, and have the annulations closely crowded near the bases of the spines."

A recent study by Holden and Meadows (1962) supports the hypothesis of annual zone formation
in dogfish spines. The authors examined the spines from dogfish landed by trawlers that fished the grounds around the north and west coasts of Scotland. A total of 317 males ( $41.3-82.5 \mathrm{~cm}$. long) and 445 females ( $39.6-97.5 \mathrm{~cm}$. long) were examined. The ages determined were $1-19$ years for males and $1-21$ years for females. The rate of growth for both sexes was about the same up to the time of sexual maturity (at an age of about 9 years). After the fish became mature, the females grew faster than the males.

Comparisons between dogfish growth calculated from spine readings or length frequencies, and growth observed in tagged dogfish indicate that the growth of the tagged individuals is often half, or less, of the calculated values. Bonham et al. (1949) report that on the basis of a study of eggs and embryos, the suggested rate of growth is 7 cm . in 9 years or about 3.5 cm . per year. The rate calculated from spine readings is 3.1 cm . per year, and from length frequencies 3.3 cm . per year, but from tagging studies the rate is only 1.4 cm . per year.

In the above example, the spine readings were from fish $40-100 \mathrm{~cm}$. long ( $0.5-21$ years, indicated age). An examination of Kaganovskaia's (1933) data for fish of similar lengths and indicated ages suggests a growth of 3.5 cm . per year. Templeman (1944) calculated ". . . approximately $11 / 2$ cm . as the average growth per year for all mature females and 1.6 cm . for the first mature year . . ." However, a tagged dogfish at liberty for 10 years grew only about 8.1 cm . in that time (Templeman, 1958 ), but he concludes the fish was in worse condition when recaptured than when tagged, hence the poor growth rate. Kauffiman (1955) reports the growth of two tagged spiny dogfish from the Pacific Coast as 14 cm . after $81 / 2$ years at liberty ( $2.3 \mathrm{~cm} . /$ year). A dogfish tagged in British Columbia waters and at liberty almost 8 years grew 5\% inches (Fisheries Research Board of (anada, 1950 ), or about 14.1 cm . ( $1.8 \mathrm{~cm} . /$ year). My own experience with the growth of tagged dogfish is limited to one specimen at liberty nearly 1 year during which time it grew only 0.7 cm .

At the present time there is no way to resolve the differences reported for the annual growth of the spiny dogfish. No doubt it is a long-lived species, attaining a maximum age of $25-30$ years. The lengthy time interval between tagging and recapture, up to 10 years for certain individuals, is
perhaps the strongest evidence supporting the reported age determination studies.

## LENGTH-WEIGHT RELATION

As with many fishes, female spiny dogfish grow longer and heavier than the males. Templeman (1944) reported that the immature females are slightly hearier than the males at all sizes. Mature and pregnant females are significantly heavier than either mature males or immature females. He presents a length-weight graph and lists the following lengths and average weights for dogfish from the Newfoundland area:

| Length |  | Weight |  |
| :---: | :---: | :---: | :---: |
|  |  | Males | Mature females |
| Cm. |  | Pounds | Pounds |
| ¢0.-- |  |  | 3.8 |
| 75 |  | 3.3 4.5 | 5.1 |
| $9{ }^{3}$ |  |  | 8.4 |

Pugsley (1939) reported that Pacific dogfish females tend to be heavier per unit of length than males. He includes a length-weight graph that shows this relation for males, females, and pregnant females.

Some length-weight data were collected from 210 dogfish at Point . Tudith, R.I., as part of a study of the Southern New England industrial fishery. These data (sexes combined) were used to calculate the length-weight relation presented in table 3.

Table 3.-Length-weight relation for spiny dogfish, sexcs combined, Point Judith, R.I., October 1955

| Lengt.h | Weight | Length | Weight |
| :---: | :---: | :---: | :---: |
| 2. Cm. | 0. | Cm. | G. 90 |
| 31 | 75 90 | 64.---- | 1, 0,50 |
| 34 | 110 | 70 | 1, 200 |
| 37. | 140 | 73. | 1,370 |
| 40. | 180 | 76..- | 1,550 |
| 43. | 230 | 79. | 1.780 |
| 46. | 310 | 82 | 2. 000 |
| 49. | 390 | 85. | 3. 250 |
| 52 | 470 | 88. | 2. 560 |
| 55. | 570 | 91 | 2.850 |
| 58. | 680 | 94 | 3,200 |
| 61... | 790 |  |  |

## POPULATION STATUS

The total population of the spiny dogfish is not known, although there is no doubt that it is relatively abundant and may be subject to long-term fluctuations in abundance. In the spring of 1846 they were so numerous around Gay Head, Mass.,
that 600 were caught on hooks in 1 day by the crew of a single boat (Storer, 1867).

Collins (1884) relates an eyewitness report from a fisherman who observed a school of mackerel at the surface of Wood Island, Maine, that was being harried by an immense school of dogfish in August 1880. The fishermin estimated there were about " 100 barrels of dogfish" in the school. The dogfish surrounded the mackerel ". . . in such a manner as to inclose the mackerel on all sides and underneath, completely preventing their escape." Many of the mackerel were seen with their tails bitten off and with wounds in their flanks.

Cod as well as mackerel suffered from the attacks of the dogfish. Earll (1880) considered the dogfish to be the principal enemy of the cod and reported that adult cod in the market were seen to have teeth marks and spine wounds in their flesh, a result of attacks by dogfish. "The arrival of a school of dogfish in any locality," Earll noted, "is the signal for all other species to leave; and in this way the work of the fisherman is often suddenly terminated."

Bowers (1906) reported grod groundfishing in Boston Bay in July and August 1903, but in 1904 ". . . homed dogfish [were] present in such great numbers that it was impossible to catch anything else."

Dogfish were much more numerous in Massachusetts Bay during the last quarter of the 19th Century and during the early 1900's than they had been previously, although in the Woods Hole region they were more plentiful before 1887 than they have been at any time since (Bigelow and Schroeder, 1953). These authors felt that perhaps the period 1904-05 marked a peak in the cycle of dogfish abundance.

It may be, however, that the population of dogfish does not fluctuate greatly but that in their seasonal migrations the main body of fish may visit one area this year and other areas next year. Our lack of knowledge about the nature of the population(s) makes it difficult to come to any firm conclusion regarding the absolute or relative numbers of fish involved.

As a result of his early studies of the dogfish around Newfoundland, Templeman (1944) said, "It is obvious . . . that dogfish migrate rapidly and for long distances, and since they swim chiefly in the upper layers of water there are no hinder-
ances to migration such as the contours of the bottom offer to haddock and cod. Thus, it is quite possible that the dogfish stocks on the whole eastern coast of North Americun mingle sufficiently to constitute a single population."

He modified this somewhat later (1954) after analyzing his tag return data. "The distant recaptures are also numerous enough, considering the small number tagged, and occur in enough different years to show that even if there is not indeed a single population, there is at least a widespread intermingling of the populations of adult female Squalus acumthics on the Atlantic Coast of North America."

Explomatory cruise data indicate that, rather than being distributed relatively homogeneously over large areas, dogfish congregate in dense, localized schools. Thus, high concentrations of dogfish at a given time and locality provide no accurate indication of their overall abundance, as they may be exceedingly scarce a few miles distant. Large hauls of dogfish tend to be grouped within a period of a few days, as the vessel fishes the same general area during tho interval. Similarly, consecntive tows at different depths may produce no dogfish at one depth but numerous dogfish at only slightly greater depths (table 4).

There is evidence that dogfish may vary in availability, or abundance, from year to year as well as from place to place. Data were analyzed from survey cruises of the research vessels Albatross III and Delaware (table 5). The relative abmudance of dogfish, expressed as catch per 30 -minute tow, was high in 1948, 1949, and 1950. Abundance declined markedly in 1955 and 1956 but was moderately high in 1958 . In 1959, abundance of spiny dogfish declined once more, but during 1960-62 it reached a high level nearly on a par with the peak in 1949. The changes in abundance are also reflected in the commercial catch of dogfish (see figs. 8 and 9). No explanation exists for this apparent periodicity in abundance.

## POPULATION DYNAMICS

The dynamics of the spiny dogfish population would be difficult to study now to any fine degree because much of the necessary information is lacking or is imperfectly known. Perhaps the greatest gap in our understanding of the species is a knowledge of the nature of the population itself.

Table 4.-Dogfish catches on Albatross III Cruise 126, by depth, temperature, and sex along Middle Atlantic Coast, January-February 1959


Table 5.-Spiny dogfish catch on annual survey cruises, all seasons, all grounds from Nova Scotia to Hudson Canyon, 1945-62

| Year | Total tows | Tows with dogfish | Total caught | Catoh per tow |
| :---: | :---: | :---: | :---: | :---: |
|  | Number | Number | Number | Number |
| 1948. | 233 |  | 4, 551 |  |
| 1949 | 115 | 21 | 3,755 | 33 |
| 1950 | 339 | 173 | 10,333 | 31 |
| 1955 | 279 | 64 | 672 | $2+$ |
| 1956 | 93 | 40 | 727 | 8 |
| 1958 | 159 | 63 | 1,923 | 12 |
| 1959 | 212 | 38 | 1,106 | $5+$ |
| 1960 | 117 | 41 | 2, 636 | 22 |
| 1961 | 161 | 42 | 3,799 | 23 |
| 1962 | 138 | 37 | 3,444 | 25 |

The basic plus and minus factors of natality and mortality lack adequate quantitative investigation. There have been some studies, however, of certain phases in the reproductive cycle, and these are discussed below.

## REPRODUCTION

Spiny dogfish are ovoviviparous. The eggs in the female are fertilized internally by means of the
male's claspers, and the young are born alive. The period of fetal development is lengthy, perhaps up to 2 years. The number of young produced at each delivery by a female dogfish is small.

## Sex Ratio

During development in the females, and presumably at birth, the sex ratio of the pups is very nearly 1:1. Ford (1921) collected 2,700 embryos at the fish market in Plymouth, England, and found 1,377 were males and 1,343 were females. Templeman (1044) counted 983 males and 931 female embryos in the uteri of 492 females collected in July-November 1942, off St. John's, Newfoundland. For dogfish in the Pacific, Bonham et al. (1949) report, "Males and females occur in equal numbers among the embryos." Aasen (1964b) examined the pups in a sample of 41 females collected in November 1958 about 100 miles west of the Orkney Islands. There were 126 males and 130 females. Our observations for dogfish in the Gulf of Maine agree with those from other waters. In July-August 1961 on a cruise of the Delaware in Ipswich Bay, 234 female dogfish were examined. Fifty-three contained pups, of which 155 were males and 140 were females.

From the time of birth to the time of attaining sexual maturity, the young dogfish tend to school together, but the mature adults tend to school by sex. Ford (1921) classified the schools, or shoals, as follows: (1) Shoals of large fish consisting exclusively of females, the majority in the pregnant condition; (2) shoals of medium-sized fish exclusively males in the mature condition; (3) shoals of medium-sized fish of which the majority were immature females; and (4) shoals of immature fish in which the males and females were equal in number.

Sex-size segregated schools are also reported by Hickling (1930) around Ireland, Templeman (1944) off Newfoundland, and Bigelow and Schroeder (1953) in the Gulf of Maine. In the eastern Pacific, however, Quigley (1928b) observed that the schools contained both sexes, and the data listed by Bonham (1954) for the same general area support this statement, although in individual catches the percentage of males varied as much as from 35 to 76 percent. In the western Pacific, however, Kaganovskaia (1933) observed the schools of dogfish to be segregated by sex, size, age, and depth. She notes, ". . . the shore-set nets caught mainly
immature sharks from 4 to 8 years of age, the bot-tom-set nets older fish, from 10 to 18 years, mainly males-(July-October) ; the drift pelagic netschiefly mature females." Thus, her observations agree in general with those reported from other parts of the world. I suspect that the dogfish in the eastern Pacific also school by sex despite the reports to the contrary by Quigley (1928b) and the data presented by Bonham (1954).

On the basis of the reports from areas that include the known range of the spiny dogfish, it is difficult, therefore, to determine the sex ratio of the adults because of the manner in which they school.

## Size at Sexual Maturity

Sexual maturity in male dogfish is attained at a smaller size than in females, and reported studies indicate that the larger the maximum size of fish in a population, the larger the size at maturity. Table 6 lists the data extracted from reports that specifically mention average size at first maturity for the spiny dogfish.

Table 6.-Maximum size and size at first maturity of spiny dogfish from several areas

| Author | Locality | Stze of males |  | Size of females |  |
| :---: | :---: | :---: | :---: | :---: | :---: |
|  |  | $\underset{\text { rity }}{\text { Matu- }}$ | Maximum | $\begin{gathered} \text { Matu- } \\ \text { rity } \end{gathered}$ | Maximum |
| Ford (1921) ---------- | Plymouth, England. <br> Irish Sea <br> Sakhalin | Cm. 59-80$\qquad$ | Cm. 83 | $\underset{70-\mathrm{SO}}{\mathrm{Cm}}$ | Cm. 110 |
| Hickling (1930).-- |  |  |  | 70-80 |  |
| Kaganovskaia |  |  |  | 100 | ${ }^{1} 124$ |
| Templeman (1944).-- | Newfoundland Washington | 6072 | $\begin{array}{r} 86 \\ 100 \end{array}$ | 74 | 101 |
| Bonliam et al. (1949)- |  |  |  | 92 | 124 |

${ }^{1}$ Sex not specified, probably a female.
Because of the age determination problem discussed earlier, it is difficult to assign an age value to the time of first maturity. Templeman (1944), however, suggests that, ". . . it takes the average female dogfish 9 or 10 years from the fertilized egg or 7 or 8 years after birth to reach sexual maturity." Based on the spine readings of Bonham et al. (1949), the data indicate 11 years for males and 19 to 20 years for females as the age of first maturity for spiny dogfish in waters off Washington. Kaganovskaia (1937) did not discover mature females less than 19 years old or less than $1,000 \mathrm{~mm}$. long. It seems incredible that dogfish mature at such a late age, but a critical examination of the evidence offers support for Bonham's data and Kaganovskaia's statement.

The reported sizes of spiny dogfish at time of first maturity are about 7 O percent (range 68-80 percent.) of the reported maximum sizes for the species. This is in general agreement with similar data reported by Bigelow and Schroeder (1953) for nine species of sharks from the Gulf of Maine where the sizes at first maturity are about 62 percent (range $52-75$ percent) of the maximum sizes. If we assume (1) that the maximum age (sexes combined) of the spiny dogfish is 25 to 30 years, (2) that we can equate length with age, and (3) that the largest individuals are females, then the age at first maturity of the females is about 72 percent of the maximum or about 18 to 21 years.

## Mating

Although there are no recorded observations of the actual mating of spiny dogfish and no conclusive data to confirm the senson of year when it takes place, the evidence presented by most authorities suggests that mating takes place during months when the water temperatures are low. Ford (1921) found newly formed embryos at Plymouth during November to May. Templeman (1944) concludes that the eggs are fertilized and pass into the uteri in February and March, but more generally in March. He cautions, however, that his lack of information about the spring temperatures when the eggs are developing may vary the dates a month in either direction. An examination of dogfish captured in the Woods Hole area suggests that ovulation probably occurs in February or March (Hisaw and Albert, 1947) and perhaps we can infer that mating and fertilization of the eggs take place soon after. Bigelow and Schroeder (1948) believe that in the Atlantic Ocean, nating probably takes place shortly after the young are born, although no definite information is available.

Reports on mating of the spiny dogfish in the Pacific Ocean tend to be contradictory, but in general support the hypothesis that mating takes place in the cold months, as in the Atlantic Ocean. Quigley (1928b) examined slightly over 200 dogfish collected in June, July, and August and found embryos that ranged in size from the smallest to those with the umbilical scar completely healed and apparently ready for birth. These observations suggested that ". . . in the vicinity of Nanaimo, Squalus sucklii breeds at all times of the year." We know now, of course, that what she had seen
were the two broods of young that are typical of the species. Hart ( 1942 ) on the other hand, reporting the work of Lucus, concluded that breeding takes place during the winter and that, ". . . fertilization by the male takes place soon after the birth of the young . . ." Bonham et al. (1949) admitted that the season at which mature dogfish mate is not known, but regards as a popular misconception the belief that dogfish breed and bear young at all times of the year. Sato (1935) concluded, without much firm basis for the statement, that dogfish breed throughout the year around Hokkaido.

## Fecundity

As might be expected for a live-bearer, the number of young produced per female spiny dogfish is small and the period of development within the mother is long, lasting nearly 2 years. The eggs are large and contain a great deal of yolk and have been well described by Templeman (1944). Following fertilization, and during early development of the fetus, the eggs (figs. 6 and 7 ) are contained in a horny capsule ("candle") that later breaks down leaving the embryos free in the enlarged part of the oviduct (termed the "uterus"). There is no placental attachment (Bigelow and Schroeder, 1953) as with some other species of sharks, but additional material (at. least water) is obtained from the uterine wall (Templeman, 1944). The reported number of pups per female probably should be considered a minimal figure. The observations were made of fish caught by otter trawls or other fishing gear and examined on board the vessel or in the market. I have seen pups that were apparently near term prematurely delivered when the females were landed on the deck of our research vessel. It seems reasonable to assume that this also happened in the studies reported in the literature. Fortunately, the number of premature pups was never very great so that the reported data may be accepted with a fair degree of confidence.

The greatest number of pups per female was reported by Kaganovskaia (1937) who recorded 5 to 19 , with an average of 11 , for the spiny dogfish near Sakhalin. The least number of pups per female was reported by Templeman (1944) who recorded 1 to 7 , with an average of 4 , for the dogfish near Newfoundland. Ford (1921) reported 1 to 11, mostly 2 to 4, from England, while from the


Figure 6.-Spiny dogfish egg collected July 1961 in Ipswich Bay. Note the embryo, probably about 4 months old.

West Coast of North America, Quigley (1928b) reported 3 to 11 (average 7), Clemens and Wilby (1961) reported 3 to 14, and Bonham et al. (1949) reported 2 to 17 , mostly 7 to 8 . Female spiny dogfish collected about 100 miles west of the Orkney Islands contained 2 to 13 pups, with an average of 6.2 pups per female (Aasen, 1964b).

In the Gulf of Maine, Bigelow and Schroeder (1953) state that the number of pups per female may be as many as 8 to 11 , or as few as 2 , but mostly 4 to 6 . Data collected in July-August 1961, in the inner Gulf of Maine (Ipswich Bay), show the females may contain from 1 to 11 pups, mostly 4 to 7 .

To examine the relation between the size of pregnant female and the size and number of pups (fetuses) per female, I grouped the data by length of females by $3-\mathrm{cm}$. groups (table 7). In addition to the data for fetuses, the measurements and numbers of embryos are also included.

Table 7.-Fecundity of spiny dogfish examined aboard R/V Delaware, 1961

| Length | $\begin{aligned} & \text { Females } \\ & \text { with } \\ & \text { embryos } \end{aligned}$ | Embryos |  | $\begin{aligned} & \text { Females } \\ & \text { with } \\ & \text { fetuses } \end{aligned}$ | Fetuses |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  |  | Average per female | Average length |  | Average per female | Average length |
| 60. Cm. | Number | Number 5. 0 | Mm. ${ }_{4}$ | Number | Number | Mm. |
| 75 | 1 | 5.0 | 5 |  |  |  |
| 78 | 1 | 3.0 | 5 | 2 | 4.5 | 154 |
| 81. |  |  |  | 2 | 6.0 | 190 |
| 84. | 2 | 4.5 | 3 | 6 | 4.7 | 186 |
| 87. | 6 | 4.5 | 9 | 6 | 3.7 | 194 |
|  | 4 | 4.2 | 12 | 14 | 5.6 | 197 |
|  | 4 | 6.2 | 7 | 9 | 5.6 | 194 |
| 96. | 1 | 9.0 | 6 | 5 | 7.2 | 197 |
| 99. |  |  |  | 8 | 7.9 | 205 |
|  | 1 | 3.0 | 20 | 1 | 8.0 | 220 |

The data suggest that the larger females tend to have slightly more and slightly larger pups than the smaller females. This, in general, agrees with the reports from other parts of the range of the spiny dogfish. A comparison between the aver-


Figure 7.-Microphotograph of the embryo shown in Figure 6. Actual size of embryo is 19 mm .
age number of embryos per female and the average number of fetuses per female seems to indicate there is very little loss (mortality?) between the two stages of development. The size of the young dogfish at the time of birth is $20-30 \mathrm{~cm}$., regardless of the part of the world from which the observations are reported (table 8).

Table 8.-Size of dogfish at birth

| Author | Locality | Reported size of dogfish pups |
| :---: | :---: | :---: |
| Ford (1921) | Plymouth, England. | ${ }_{25-31 .}^{C m} .$ |
| Hickling (1930) | Irish Sea | About 26. |
| Kaganovskaia (1933, 1937) | Sakhalin. | Average 24 |
| Templeman (1944) --. | Newfoundland...- | 24-31. |
| Hisaw and Albert (1947) -...-- | Woods Hole, Mass | 25-30. |
| Bigelow and Schroeder (1918)- Bonham, et al. | Gulf of Maine..... | Avera |
| Aasen (1964b) .-..... | Orkney Islands... | A verage 26. |

## Process of Birth

There are two recent instances of spiny dogfish giving birth to young in tanks at the Bureau's Woods Hole aquarium. In one instance, I suspect the female aborted rather than having a normal, full-term delivery.

The first dogfish was caught with hook and line October 19, 1962, in water about 27 m . deep. The
surface water temperature was $14.2^{\circ} \mathrm{C}$. The fish was placed in the aquarium the same day, in water of the same temperature, and apparently adjusted well to the tank conditions. On November 22, 1962, during the night, she gave birth to three pups that measured $20.0,20.3$, and 20.7 cm . None of the pups had any evidence of the yolk sac except for a small scar on the ventral surface between the pectoral fins where the yolk sac had been attached. Presumably the yolk had been resorbed and the pups were fully developed. The water temperature in the tank at the time was $8.4^{\circ}$ C. The pups did not survive, although the mother continued to live for several weeks until she was sacrificed.

The second dogfish was collected in a fish trap and placed in the aquarium on July 24,1963 . The next day the aquarium attendant observed the delivery of two pups. The female was resting motionless at a slight incline on a pile of rocks in the tank. Two pups were delivered simultaneously, head first, in rhythmical movements that suggested uterine contractions during mammalian birth. Delivery of the two pups took about 10 minutes. The female also delivered four more pups, but the aquarium attendant had been called
away and could not observe the delivery. An hour later, about 2 cm . of the caudal fin of a pup could be seen protruding from the female's vent. This pup was not delivered, and the female died later in the day. The average length of the pups was 21 cm ., and each had a yolk sac attached. Although their size suggests the pups were nearly full term, presence of the yolk sac indicates they were still developing. Presumably the female aborted, perhaps from the shock of capture and handling or perhaps from the water temperature. The surface water temperature in the trap was $19.5^{\circ} \mathrm{C}$. and the tank temperature was the same. This is well above the temperature where the species is commonly found.

When the female was examined, post mortem, the partially delivered pup was found to be held by one dorsal spine in the anterior part of the female's left uterus. The dogfish pup is morphologically suited to head presentation in birth. No doubt the caudal presentation noted here was accidental; the rearward sloping dorsal spinessmall as they are-deter smooth, tail-first movement out of the uterus. It is not known if partial delivery occurs among dogfish in the sea, and none has been observed aboard our research vessels.

## Season of Birth

The gestation period of dogfish is nearly 2 years, although the authorities differ in the exact number of months involved. Birth generally occurs in the cold months of the year. Ford's (1921) extensive studies at. Plymouth led him to conclude that gestation occupies $21-25$ months, with the fetuses ready for birth from August to December. Hickling (1930) confirmed Ford's findings. Templeman (1044) suggested a gestation period of almost 24 months with birth between January and May. Assen's (1964b) data suggest that in the offing of the Orkney Islands, dogfish pups are ready for birth in late November or soon after.

A somewhat shorter gestation period for dogfish captured in the vicinity of Woods Hole is reported by Hisaw and Albert (1945) who state, "The gestation period apparently covers about 20 to 32 months and a female gives birth every other year." The pups, they note, are bom in the late fall, somewhere south of Woods Hole. Bigelow and Schroeder (1953) report a gestation period of 18 to 2.2 months with birth probably taking place on the offshore wintering grounds, although some
may be born in the spring and summer. Latham (1921) confirmed that some may be born in the summer when he reported many young dogfish only a few hours old that were caught in a fish trap in Long Island Sound in August.

In the Pacific the gestation period is 2 years with birth taking place during the winter (Hart, 1942), more specifically in November and December (Bonham et al., 1949).

An individual female produces young only in alternate years (Hart, 1942; Hisaw and Albert, 1947; Bonham et al., 1949; Clemens and Wilby, 1961). The data presented by Ford (1921), Hickling (1930), and Templeman (1944) confirm the broods-in-alternate-years conclusions of the workers cited above.

## MORTALITY

The spiny dogfish has few enemies and is cannibalistic only to a very small degree. Thus, except for disease, there is little to act as a deterrent to the buildup of dogfish populations, and this no doubt is one of the prime reasons for the vast numbers of dogfish reported in one area or another. The predators of the spiny dogfish are mostly the large sharks and large bony fishes. In table 9, I have listed the predators as reported in Bigelow and Schroeder (1953) and noted certain appropriate remarks. It should be stressed that in all but two of the instances the prey is specifically identified as the spiny dogfish. The remaining two instances were simply listed as "dogfish" and possibly may be the smooth dogfish.

Table 9.-Predators of the spiny dogfish

| Predator | Remarks |
| :---: | :---: |
| Mackerel shark (Lamno nasus).-.-- | Known to prey on spiny dogitsh in the eastern Atlantic; probably Gulf of Maine also. |
| Maneater (Carcharodon carcharias) - | One spiny dogfish, evidently torn off a line trawl. |
| Tiger shark (Galcocerdo cupier).....- | Dogfish (species ?) from one captured in Woods Hole. |
| Blue shark (Prionace glauca) | Preys on spiny dogfish in northern waters. |
| Barndoor skate (Raja laenis) Laricetfish (Alepisaurus feror) | Spiny dogish from Woods Fole records. |
| Laricetfish (-Alepisaurus feror) ------ | Small spiny dogish eaten by Block Island specimen. |
| Tuna (Thunnus thynnus) | Swallowed whole dogfish (species ?) weighing 8 pounds |
| Tilefish (Lopholatilus. | One contained two spiny dogfish. |
| Goosefish (Lophius americanus)..-- | One contained a spiny dogfish 1 foot long and the vertebral columns of 6 others. |

Marine mammals apparently are not a threat to the dogfish. In a study of the food habits of seals (Fisher and Mackenzie, 1955), dogfish remains
were found in the stomach of a grey seal (Halichoerus grypus) but constituted only 1 percent of the volume of the stomach contents. Killer whales (Grampus orca) may feed on dogfish, but probably only when other food is unavailable. One killer whale was seen, "Scavenging round longlining vessel, eating dogfish." in the Strait of Belle Isle, July 1953 (Sergeant and Fisher, 1957). No doubt the relatively large size, spines, and tough, scabrous skin of the dogfish are effective deterrents to predation.

## UTILIZATION OF THE SPINY DOGFISH

The dogfish is not completely valueless or useless. It has some slight value, in limited quantity, in the United States, and it has greater value in some parts of the world where it is sought as a food fish. The greatest value of the dogfish in North American waters is as an industrial fish for processing into oil and meal, and at one time it was under intense exploitation for its liver as a source of natural vitamin $A$ (fig. 8).

The Bureau of Commerical Fisheries collects and publishes yearly summaries ${ }^{3}$ of U.S. fisheries by regions. In this paper, data collected from the Puget Sound, Middle Atlantic, and New England regions are discussed. The data given in table 10, and shown in figures 8 and 9 , are taken from various sections of the statistical reports.

Table 10.—Catch of grayfish ${ }^{1}$ at principal regions, 1915-61

| Year | New England States |  | Middle Atlantic States |  | Puget Sound, Wash. |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | Catch | Value | Catch | Value | Catch | Value |
| 191 | Pounds | Dollars | Pounds | Dollars | Pounds <br> 7,093,996 | $\begin{aligned} & \text { Dollars } \\ & 15,959 \end{aligned}$ |
| 1919 | 63, 667 | 184 |  |  |  |  |
| 1923 |  |  |  |  | 6,359 53,400 | 72 |
| 1924 | 21,950 | 367 |  |  | 97,005 | 247 |
| 1925 |  |  |  |  | 41,549 | 88 |
| 1926 |  |  | 6,755 | 347 | 290, 395 | 1,459 |
| 1928 | 206, 309 | 3, 312 |  |  | 89,707 3,203 | 449 16 |
| 1929 | 213, 306 | 2, 829 | 38, 605 | 552 | 286, 419 | 1,060 |
| 1930 | 93, 196 | 3,049 | 12, 690 | 267 | 371, 180 | 1,309 |
| 1931 | 44,330 | 454 | 4,796 | 90 | 778, 560 | 2,335 |
| 1932. | 27,049 | 374 | 8,140 | 81 |  |  |
| 1933 | 13, 428 | 151 | 6,739 | 135 |  |  |
| 1935 | 35, 300 | 733 | 115, 500 | 2,053 | 277, 500 | 527 |
| 1936 |  |  |  |  | 330, 700 | 764 |
| 1937 | 31,600 | 578 | 57,700 | 545 | 1,620,100 | 14,360 |
| 1938. | 46,200 | 1,111 | 100, 200 | 1,021 | 578, 100 | 4, 173 |
| 1939. | 85,700 575,500 | 1,124 | $\begin{aligned} & 47,800 \\ & 51,8 \mathrm{~m} \end{aligned}$ | + 478 | $\begin{aligned} & 2,365,200 \\ & 3.341 .100 \end{aligned}$ | 17,738 |
| 1940 - | 575,500 575,500 | 19,426 19,426 | 51, 51,800 | 1, 1,009 | $23,341,100$ $23,532,300$ | 36, 751, 204 |

See footnotes at end of table.

[^2]Table 10.-Catch of grayfish ${ }^{1}$ at principal regions, 1915-61-Continued

| Year | New England States |  | Middle Atlantic States |  | Puget Sound, Wash. |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | Catch | Value | Catch | Value | Catch | Value |
|  | Pounds | Dollars | Pounds 127, 300 | Dollars 3, 802 | Pounds 16. 932,400 | Dollars 668.863 |
| 1943 | 89,700 | 1.637 | 47,300 | 1,959 | 22, 021.500 | 1,243,858 |
| 1944 | 53,300 | 1,446 | 6,600 | 200 | 39, 513, 700 | 2, 094,217 |
| 1945 | 31, 100 | 565 | 31,000 | 1,211 | 22, 149, 100 | 1,063, 149 |
| 1946 | 107, 600 | 2,472 | 54,200 | 3, 327 | 20, 991,800 | 1, 366, 513 |
| 1947. | 24,000 | 455 | 21, 200 | 1,046 | 14,984,800 | 954, 535 |
| 1948. | 55, 100 | 775 | 3. 000 | 150 | 12,302,700 | 711, 125 |
| 1949 | 625, 200 | 5,718 | 55, 500 | 2,163 | 10,587, 000 | 447, 828 |
| 1950 | 111, 200 | 1, 171 | 37, 200 | 1,829 | 1, 914,600 | 33, 197 |
| 1951 | 39, 600 | 539 | 63,700 | 3, 051 | 2,412, 900 | 58,750 |
| 1953. | 11, 200 | 254 | 42, 700 | 1,857 | 2, 981, 400 | 47,535 |
| 1953 | 9,000 | <500 | 65, 000 | 3,000 | 2,225,600 | 17,669 |
| 1954 | 2,000 | < 500 | 61.000 | 3,000 | 2, 008,800 | 19, 931 |
| 1955. | 7,000 | <500 | 88, 000 | 3, 000 | 1, 935, 300 | 14, 029 |
| 1956 | 486, 000 | 4,000 | 60, 000 | 2,000 | 1, 526, 400 | 12.808 |
| 1957. | 1,287, 000 | 10,000 | 55, 000 | 2,000 | 1, 860,900 | 33, 390 |
| 1958 | 893, 000 | 8,000 | 50, 000 | 1,000 | 4, 233, 100 | 26, 675 |
| 1959 | 763,000 | 6.000 | 71,000 | 3,000 | 3,091,900 | 28, 189 |
| 1960 | 1,006,000 | 7. 000 | 52,000 | 2,000 | 1,378, 400 | 6,931 |
| 1961 | 970,000 | 6,000 | 70,000 | 3,000 | 790,700 | 3,953 |

${ }^{1}$ Grayish is the market name for dogfish.
2 No survey on east coast. Data reported were those collected in 1940.


Fioure 8.-Dogfish catch from Puget Sound, Wash., 1915-61.

The fishery for dogfish on the west coast of the United States has been studied by Alverson and Stansby (1963), who discussed the technological developments in the use of dogfish and some methods for control of the extensive populations. They reviewed the fishery and its effects on the abundance of the dogfish and recommended that an economic use be developed for the dogfish and that research be instituted to determine the biological effects of control of the species.

The possible uses of dogfish are the subject of an extensive review by Osterhang (1961), who included a bibliography of 166 references on the subject. The first part of the review discusses the significance of the urea content of dogfish flesh. The second part discusses possible uses including animal feeds, particularly for ruminants that are able to utilize urea in their diets.

The fishery for dogfish on the east coast of the United States was never as intensive, nor did it ever reach the heights reported for the fishery on the west coast. However, from time to time the east coast fishery was active for oil, guano, meal, and human food (fig. 9). Details of the fishery are outlined below.


Figure 9.-Dogfish catch from the New England and Middle Atlantic States, 1910-61.

## INDUSTRIAL USES

One of the earliest mentions of an industrial use for dogfish was made by Perley (1S52), who reported on the species in the Gulf of St. Lawrence. He noted that the skins were used by cabinet makers to polish hardwood, the livers were used for oil, and the carcasses were dried and fed
as a winter food supplement to cattle. Pigs in particular were said to thrive on this diet.

## Reduction for Oil and Meal

A fishery for dogfish existed around Provincetown, Mass., during the late 19th century and was prosecuted with handlines baited with silver hake (Storer, 1867). The fishery took place in September through November when the dogfish appeared in the area during their seasonal migration. Only the livers were wanted for their oilone thousand livers yielded one barrel of oiland the oil was sold to tanners and curriers for preparing and treating leather.

In other places, the whole dogfish was used for reduction, especially when more desirable species such as menhaden were less abundant. A menhaden reduction plant in East Boothbay, Maine, processed dogfish for oil and guano (Gallup, 1883). The fishermen were paid $\$ 1$ per 100 fish, but it was suggested that the Federal government pay a subsidy to encourage greater fishing effort. Spiny dogfish was the principal species used for oil and guano when a guano factory was established at Woods Hole (Smith, 1898), but a scarcity of the species in the season of 1897 , and the general irregularity of their supply, caused the factory to turn to menhaden for raw material.

Many early writers tried to stimulate utilization of the dogfish by citing the different ways the fish could be used. I. Field (1907) mentions that dogfish oil (liver oil?) was used for illumination in some areas and that on Cape Cod the carcasses were dried and used for fuel. G. Field (1912) reports that on Cape Breton Island dogfish were dried on fences and fed to horses as a diet supplement and the well-yolked eggs were used experimentally as a substitute for ${ }^{4}$ hen's eggs to tan leather.

Barraclough (1953) cites interesting historical information about the early uses and developments of dogfish oils in and around the coastal areas of British Columbia. The local Indians processed the livers and used the oil obtained for dressing skins and hides. Later, as lumbering operations began in the area, the oils were used to lubricate skidways on logging roads. The oil was used extensively for lubrication and illumination in sawmills, coal mines, and coastal lighthouses. Most of the oil was processed in small home-type operations, but in 1876 the first large commercial
factory was established for oil production. It is worth noting here that during the time of World War I (1916-18) almost the entire catch of dogfish from British Columbia was exported as "grayfish" to the U.S. fresh fish market.

## Extraction of Vitamin A

No doulst the greatest industrial use of the dogfish took place about $1037-47$ when the species was fished intensively in Puget Sound and surrounding waters. Their rich, oily livers were in demand as a valuable source of natural vitamin A. The livers contain $50-75$ percent oil, and the vitamin A content of the oil is 5,000 to 30,000 U.S. Pharmacopeia (U.S.P.) units per gram (Harrisom and Samson, 1942).

The first extraction of vitamin A from shark liver oil was begun on a commercial scale about 1936-37, and the dogfish fishery was underway in Puget Sound in 1937-38 (Harrison and Samson, 1942). The fishery was on a small scale until about 1940 , then, with the entry of the United States in World War II and the loss of foreign sources of vitamin A from cod liver oil, the fishery increased in intensity. In 1940 the average price paid to the fishermen for the livers was 5.7 cents per pound, but by 1943 the average price was 46 cents per pound and tit one point reached a high of 54 cents (Bonham et al., 1949). The intensity of the fishery undoubtedly had a marked eftect on the size of the dogfish population. Barraclough (1953) reports a decline in availability of the species in Hecate Strait beginning in 1944.

Dogfish liver oil has high vitamin A potency. Bonham et al. (1949) note that oil rendered commercially from livers of dogfish taken in the waters in and around Washington varies from 5,000 to 25,000 U.S.P. units of vitamin A per gram. The vitamin values increase several hundred percent when the fish attain sexual maturity, and the content is greater in winter than in other seasons. In contrast, Templeman's (1944) laboratory extractions of vitamin A from Cauadian dogfish liver oil ranged from 300 to 19,700 U.S.P. units per gram with an average value for immature females of 1,183 units, for mature males of 1,662 units, and for mature females of 2,780 units. (For purposes of comparison, pharmaceutical cod liver oil must contain not less than 850 U.S.P. units of vitamin A per gram (Bailey, 1952).) Hirao, Yamada, and Kikuchi (1959) report vita-
min A values of spiny dogfish flesh from 329 to 5,220 U.S.P. units per 100 grams of flesh. Liver oil from the same fish contained from 2,080 to 38,800 U.S.P. units of vitamin A per gram.

Following the end of World War II, two major events occurred that had a devastating effect on the west coast fishery for dogfish. First, foreign sources of vitamin-rich fish oils again became available, and second, vitamin A was synthesized in 1947. Soon after this the dogfish fishery collapsed except for relatively small volumes landed for reduction and an extremely limited food market.

During World War II the Canadian government became interested in the east coast dogfish liver oils and their vitamin content, but the prices paid to the fishermen were too low to develop a fishery (Templeman, 1044).

Oils obtained from dogfish are of value today chiefly as raw materials for other industrial processes. The liver oil is sulfurized and used as a rubber extender, and the body oils are used in the tanning of leather (Bailey, 1952).

## New England Industrial Fishery

The late 1940's saw the beginning of a new kind of fishery in New England-the so-called trash or industrial fishery-in which nonfood species, including spiny dogfish, were landed in great quantities for reduction to meal and oil. Sayles (1951) marks 1948 as the start of the trash fishery at southern New England ports with the processed meal destined for use as supplements in hog and poultry feeds.

The amount of dogfish used was small at the start of the industry. For example, the species composition of a sample from one boat that landed at New Bedford in October 1949 included only 1 dogfish in the sample of 536 fishes (Snow, 1950 ), but by $1956,259,000$ pounds of spiny dogfish were landed by the industrial fleet at New Bedford (Edwards and Lux, 1958). The dogfish represented 1 percent of the total industrial landings and were caught off No Mans Land, mostly in November and December.

In 1957 the Southern New England industrial landings of spiny dogfish were slightly more than 5 million pounds ( 3 percent of the total), with most of them landed at Point Judith, R.I. (Edwards, 1958a). There were two peaks in the landings of dogfish, one in the spring and one in
the fall, no doubt representing periods when they were locally abundant during their migrations. The industrial fishery fleet at Gloucester caught quantities of dogfish off Cape Ann, Mass., on Stellwagen Bank, and off Nauset, Mass., although the volume landed represented only from 1.5 to 3 percent of the total pounds landed (Edwards, 1958b).

Reduction plants do not like to process large amounts of spiny dogfish because they yield only meal, with very Jittle oil, and there are serious mechanical problems involved in handling the species. The rough skin of the dogfish causes these fish to jam conveyor belts, and to pack in bins and chutes. The collagen in the carcasses clogs screens (Tarr, 1958). Tarr also states that the dogfish result in a poor yield of meal compared to other fishes.

Change in the design of processing machinery is suggested as one way to overcome the problems in handling dogfish carcasses. For example, installation of grinders designed specifically for dogfish may solve the jamming problem, but further technological research is needed before dogfish carcasses can profitably be used (Alverson and Stansby, 1963).

The rapidly expanding pet-food industry has been suggested as a potential user of great quantities of dogfish. Jones (1959) reports that on the Pacific coast the estimated potential annual production of dogfish for dog and cat food is on the order of 60 to 80 million pounds.

## FOOD USES

A vast protein food resource is wasted each year in the United States because only infinitely small amounts of spiny dogfish are used for human food. Under present economic conditions, however, and because of prejudice toward eating shark flesh, it probably would be most unprofitable to fish and market dogfish for human food.

The repugnance (and perhaps fear) that most people feel towards sharks in particular does not help to make dogfish popular as a food fish. The very name "dogfish" connotes something not suitable for humans. Efforts to disguise the species under a euphemism have included simply not mentioning what it was. Thus, Field (1907) reports it was served as "fish" on two occasions in the Marine Biological Laboratory (Woods Hole)
mess hall and enthusiastically accepted by the unsuspecting diners. It has been served experimentally in hotels and listed on the menu as "Japanese halibut." In England, dogfish are gutted, skinned, beheaded, and marketed as "flake" and "rock salmon" and are widely used as one of the ingredients in the popular carryout dish, fish-andchips.
In the United States during World War I, a great effort was made to popularize a number of relatively unesploited fishes to increase their acceptance by the consumer and thus relieve the war-induced meat shortage. Spiny dogfish was one such fish, and it was dubbed "grayfish," the name by which it is marketed today. A 14-ounce can of grayfish sold retail for 10 cents, and a Government circular (U.S. Bureau of Fisheries, 1916) was published in which 17 different recipes for preparing grayfish were listed.

Canned grayfish did not prove to be a practical solution to the problem of dogfish utilization. Corrosion of the cans, caused by changes in the chemistry of the meat, and the offensive ammonia smell that developed caused the buying public to reject the product. The flesh of dogfish, as with other elasmobranchs, contains large amounts of urea, which rapidly decomposes to form ammonia (Mavor, 1921). Fresh and frozen dogfish tissue contain about the same amounts of urea (0.91.5 percent.), and hydrolysis, with the subsequent release of ammonia, occurs in the frozen flesh (Benson, 1924). Moyer, Southcott, Baker, and Tarr (1959) tested several methods of storing fresh dogfish flesh for periods up to 21 days. The storage included in ice and in refrigerated sea water, with and without added antibiotics (chlorotetracycline). They concluded, ". . . dogfish, when stored under nearly ideal conditions, : ppear to spoil no more rapidly than most other sea fish." It seems obvious though that dogfish is best eaten when very fresh.

The keeping quality of dressed dogfish was further studied by Southeott, Moyer, Baker, and Tarr (1960). The fish were stored in individual polyethylene bags at $0^{\circ}, 5^{\circ}$, and $10^{\circ} \mathrm{C}$., with a control lot unbagged in crushed ice. The experiment lasted 21 days. Each day two fillets were cut from a single fish from each treatment and used for bacteriological and chemical determinations. The authors found that, "Less ammonia and
trimethylamine were produced in iced fish samples than in bagged fish samples at $0^{\circ} \mathrm{C}$., although bacterial counts in the two treatments were comparable." They suspected, however, that the melt water from the ice leached some of the chemical products from the flesh. Bacterial and chemical values rose rapidly at. $5^{\circ} \mathrm{C}$. and $10^{\circ} \mathrm{C}$., and these treatments were ended at 17 days and 8 days, respectively. In general, pronounced ammonia odors were noted in only a ferw samples, and these were "strongly masked" by putrid odors.

Dogfish flesh is quite palatable and may be prepared in a variety of ways. My family and I have eaten fried dogfish fillets and enjoyed the meal. The fillets are easily cut from the fish and easily skinned. The meat is bone-free and white and has a flaky consistency and firmness similar to haddock fillets. The flavor is mild, and the frying produced no odors other than would be expected with any fish.

Dogfish fillets were prepared in several different ways and eaten by a test panel at the University of Washington in 1959 (Liston, 1960). The steamed fillets were rated very good and brined and smoked dogfish was well accepted. In a comparison between fishsticks made with dogfish and two brands of fishsticks bought in a retail store, those made with dogfish were rated as first or second preference by all panel members.

Dogfish is popular in Europe today as a food fish, not only in England but also in Continental Europe. In 1960, 25,600 metric tons, worth nearly 11 million kroner ( 1 krone is about. (U.S.) 14 cents), were landed by Norwegian fishermen and shipped to England (Food and Agriculture Organization of the United Nations, 1961). It is marketed both in steak and fillet form.

A small but steady market for dogfish (listed as grayfish) exists in New York's Fulton Fish Market where it has an ex-vessel value of 3-4 cents per pound but has gone as high as $8-10$ cents per pound.* The fish are mostly incidental to otter trawl catches of other food fishes. The dogfish are gutted, skinned, and cut into small pieces, and sold at retail mostly to buyers of southern European extraction (Italians, Portuguese, Greeks), Chinese, and Negroes. Some retailers

[^3]fry the pieces to order for "fish and chips." (Farther south on the Atlantic coast, in the Chesapeake States, the species sold as grayfish is the smooth dogfish.)

## MANAGEMENT OF THE SPECIES

The problem of the spiny dogfish as a pest of the commercial fishermen has led to a search for some method to control the species and at least reduce their numbers to the point where they would no longer constitute a problem. Many ideas have been advanced-some quite fancifulincluding the usual solution to such pest problems, the payment of bounties for their capture. Unfortunately, most of the schemes suffer from a lack of, or incomplete, knowledge of the life history and habits of the dogfish.

Some of the earlier control methods proposed were based on methods used to control terrestrial pests. Atkins (1904) recounts a few suggestions offered by the public as to how the dogfish problem might be handled. Among these are the following: (1) Attach streamers, bells, chains, etc. to hundreds of dogfish and release them to frighten off the school (like belling a rat in a pack) ; (2) inoculate some of the dogfish with a fatal disease organism, such as had been done with rabbits in Austrialia; (3) dynamite the dogfish schools when they appear; (4) employ Government boats and men to capture the dogfish, until the plague is reduced; (5) pay a bounty to fishermen for capturing the dogfish; and (6) use long seines of strong cord, 41,000 yards or more in length, and surround the schools as is done with the schools of sharks in India.

The best control method, however, would be greater utilization of the dogfish, particularly as human food. Or, as Atkins stated it: let the public ". . . apply their teeth and eat the dogfish up."

Increased use of the species, particularly industrial utilization, carried out over a period of years, would undoubtedly reduce the numbers and keep them at a relatively low level. There is evidence that short-term programs designed to reduce the dogfish population, particularly if carried out in local areas, are not successful. Templeman (1944) notes, "In Placentia Bay alone during the 1938 attempt to reduce dogfish numbers, about 10,391 ,000 pounds of dogfish were caught or approx-
imately 2 or 3 million fish without any apparent diminution of the supply."

The results of increased exploitation of the North European oceanic stock of dogfish are discussed by Aasen (1961, 1963, 1964a, 1964b). In the period 1957-62, the Norwegian catch of dogfish increased by 50 percent. Returns from dogfish tagged in 1958-60 indicated an annual fishing mortality rate of 7 percent and an annual natural mortality rate of 20 percent.
During the 1961-62 fishing season, there was an annual mortality rate of 38 percent. (Aasen did not separate fishing and natural mortality.) And he reported (1964a) an average total instantaneous mortality rate of 72 percent in the years 1960-63. He interpreted the high figure as a "danger signal." A measure of catch per unit of effort for the period 1957-63 ". . . shows a heavily declining stock [of spiny dogfish]."
The evidence presented by Aasen in his several papers, and by Barraclough (1953), shows that long-term exploitation of the dogfish can produce a real reduction in their numbers. Thus, increased fishing effort on the dogfish off the United States could bring about some marked changes in the size of the population. It is not unreasonable to suspect that future fishery biologists might be called on for studies to save declining dogfish stocks in North American coastal waters.

If increased use of the dogfish is not feasible, either for food or industrial purposes, some other method of control should be investigated. A rather unique method-the sterile-male technique-has been used successfully to control the screwworm, an insect pest of cattle, and may prove of some value in the case of the spiny dogfish. The method is described by Knipling (1959) and, briefly, involves sterilizing laboratory-reared male screwworms through the use of gamma irradiation. The treated males are released in the area of infestation in the ratio of 5 to 10 times the number of normal males. Females that mate with the sterile males lay infertile eggs, thus reproduction is greatly reduced. The treatment has been successful in eliminating the pest on the island of Curacao and controlling it in Florida. Knipling states that this control method is based on the following biological principle: "The introduction of sexually sterile but otherwise sexually vigorous males, and to a lesser extent females, into the
natural population of an animal species will have greater influence in reducing the biotic potential of the population than elimination of the same number of individuals from the same population by destruction or removal." The sterilization could be done either by irradiation or with chemicals.

It would be difficult at the present time to try to evaluate on a theoretical basis the sterile-male technique applied to the spiny dogfish problem. We lack some very necessary knowledge of the life history of the species. For example: (1) How many dogfish need to be sterilized to effect control (that, is, how many dogfish are present in the total population), (2) how many times in its lifespan will a dogfish mate (screwworms mate once), and (3) does one male dogfish mate with more than one female in a given season?

The low fecundity of the spiny dogfish and the long period of gestation are factors very much in the favor of any control method that might be applied. But mere control is not a very satisfying solution to the problem of dogfish abundance. From a conservation standpoint it would be more desirable, of course, to find a use for what is very obviously a rich potential resource. It is possible that in future years, when additional sources of animal protein are needed for human food, we may see development of an active fishery for the species. Such a development would then remove the dogfish from the pest classification.

## SUMMARY

The spiny dogfish, Squalus acanthias, is a small shark of the family Squalidae. It is extremely abundant locally and seasonally and has proved to be a costly nuisance to commercial fishermen in the United States.

It grows to a maximum length of $100-124 \mathrm{~cm}$. and a maximum weight of $7.3-9.8 \mathrm{~kg}$. The females usually are slightly larger than the males. Two sharp spines, one anterior to each dorsal fin, are the features that give the species its common name and serve to separate it readily from the smooth dogfish, Mustelus camis.

Although the spiny dogfish is distributed in many parts of the world, this report deals mostly with the groups found in the Northwest Atlantic. Pertinent information, however, is reported from studies of the species made in other areas.

The spiny dogfish usually is found in large schools composed of: (1) large, mature females; (2) medium-size-fish, either mature males or immature females; or (3) small, immature fish of both sexes in about equal numbers. The schools may spend considerable time in an area and then move rapidly from one area to another.

In the Northwest Atlantic they move from the southern part of their range, off North Carolina to New York, northward with the advance of the spring season. It is suspected they spend the winter offshore in deep water. In addition to the seasonal migrations, spiny dogfish take part in a daily migration, rising to or near the surface during the night and returning to the bottom during the day.
Tagging studies have had low rates of return compared with tagging studies of commercially valuable fishes. But the returns have shown that the spiny dogfish is capable of long-distance migra-tions-one individual travelled 4,700 miles-and is long-lived since several tagged fish were at liberty 7 to 10 years. In the New England area, the recaptures suggest that spiny dogfish school together for long periods of time and return to the same general area at about the same time of year.

Food habits studies show that spiny dogfish are primarily fish eaters but also feed on invertebrates, both swimming and bottom-dwelling forms. Clupeoids, smelts, and chimeroids were the fishes found most frequently in dogfish stomachs. They also feed on shrimp, crabs, and squids and are one of the few fishes that eat ctenophores. In general, they are considered opportunistic feeders, preying on whatever is abundant and readily available to them.

Age and growth studies based on interpretation of annulations on the dorsal spines suggest the spiny dogfish is long-lived with some individuals attaining ages of 20 to 30 years. Based on the spine readings, the growth rate is about $31 / 2 \mathrm{~cm}$. per year. Growth of tagged dogfish, however, is less, usually about $11 / 2 \mathrm{~cm}$. per year. At a given length, female dogfish are slightly heavier than male dogfish; mature and pregnant females are the heaviest and longest individuals.

It is difficult to make any, analyses of the dynamics of dogfish populations because so much of the basic life history information is lacking. More is
known about the natality of the species than about the mortality.

The spiny dogfish is ovoviviparous. Sex ratio of the developing fetuses is very nearly $1: 1$, and presumably the young are born in the same ratio. Sex ratio of the older fish varies with the sexual maturity of the individuals; in general they tend to group themselves by sex. Sexual maturity is attained by males at $80-100 \mathrm{~cm}$. in length and by females at $100-124 \mathrm{~cm}$.

Mating takes place during the cold months, probably on the wintering grounds, and the young are born after a 2 -year development. The number of young born per female varies with location. In the Pacific it averages about 11 in the western part and about 7 in the eastern part. In the Atlantic it averages about 4 in the western part and about 3 in the eastern part. At the time of birth the young dogfish are about $20-30 \mathrm{~cm}$. long.

The natural mortality of the adults apparently is low. In the Western Atlantic their principal predators are the large sharks and large bony fishes. Records of cannibalism are rare, and there are few records of marine mammals feeding on spiny dogfish. Fishing mortality, however, takes a relatively high toll.

In the United States the spiny dogfish has been exploited mostly as an industrial fish for reduction to meal and oil. Immediately preceding and during World War II, the groups on the west coast were heavily exploited for their livers, an important source of natural vitamin A. At the peak of the fishery, in 1944, more than 40 million pounds of dogfish were taken from Puget Sound. The fishery collapsed when vitamin A was synthesized in 1947, and today about 2 million pounds are landed yearly. Most dogfish are caught with otter trawls or gill nets.

There is a small and relatively steady market in the United States for dogfish as human food. Technological problems, however, have prevented it from becoming more than just locally popular. Fresh dogfish fillets have a flavor and texture somewhat resembling those of haddock. It is a popular food fish in parts of Europe.

Management of the species is indicated to reduce the damage it causes to more valuable commercial fisheries. Finding an economically attractive use for the dogfish would be the most worthwhile management method. Lacking this,
perhaps some form of biological control must be instituted. However, more detailed information is needed about the life history and biology of the spiny dogfish before any management plan can be drawn up.

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