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SYNOPSIS OF BIOLOGICAL DATA ON THE ATLANTIC MENHADEN,

Brevoortia tyrannus

UNITED STATES DEPARTMENT OF THE INTERIOR
U.S. FISH AND WILDLIFE SERVICE
BUREAU OF COMMERCIAL FISHERIES

Circular 320

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By

JOHN W. REINTJES

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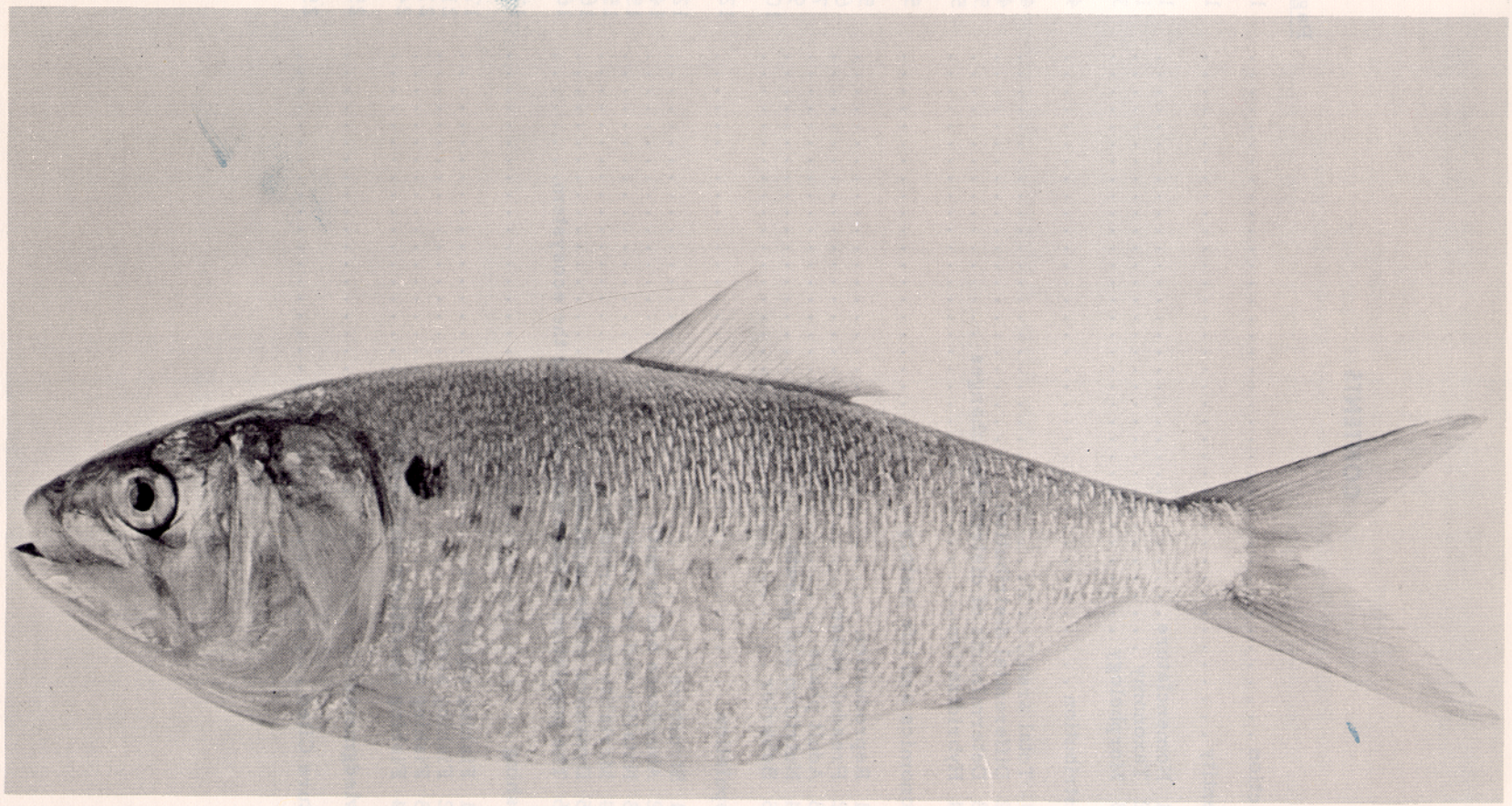

Adult Atlantic menhaden, Brevoortia tyrannus, 25 cm. fork length.

Synopsis of Biological Data on the Atlantic Menhaden, *Brevoortia tyrannus*

By

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ABSTRACT

This review of the biology of Atlantic menhaden includes taxonomy, morphology, distribution, reproduction, life history, growth, behavior, and abundance. Also included are: data on the size, age, and sex composition of the commercial catch; estimates of relative abundance; and a description of fishing methods and equipment.

INTRODUCTION

BCF (Bureau of Commercial Fisheries) has assigned the preparation of synopses on various economically important species to a number of its laboratories. Most of these synopses will be published in the U.S. Fish and Wildlife Service Circular series[1] and will follow the format presented by H. Rosa, Jr. (1965). Rosa is in the Biology Branch, Fisheries Division, Food and Agriculture Organization of the United Nations.

1 IDENTITY

1.1 Nomenclature

1.11 Valid name

Brevoortia tyrannus (Latrobe) 1802.

1.12 Synonymy

Clupea tyrannus Latrobe, 1802.

Clupea menhaden Mitchill, 1814.

Clupea neglecta Rafinesque, 1818.

Alosa menhaden: De Kay, 1842.

Clupea carolinensis Gronovius, 1854.

Brevoortia menhaden: Gill, 1861.

Brevoortia tyrannus: Goode, 1878c.

1.2 Taxonomy

1.21 Affinities

Classification follows Berg (1947) and more recently Greenwood, Rosen, Weitzman, and Myers (1966). Taxa higher than superorder are not included.

Superorder	Clupeomorpha
Order	Clupeiformes
Suborder	Clupeoidei
Family	Clupeidae
Subfamily	Alosinae
Genus	*Brevoortia*
Species	*Brevoortia tyrannus*

Latrobe (1802) did not describe the fish he named *Clupea tyrannus* but published a figure of a fish, without a dorsal fin, that resembles the menhaden. He also described a parasitic isopod, *Olencira praegustator*, known only from *Brevoortia*, which is further evidence that he was dealing with the Atlantic menhaden. The type locality was Chesapeake Bay. There is no reason to question the availability of the name *tyrannus* (Hildebrand, 1948).

[1] One synopsis (MacGregor 1966) has appeared in the U.S. Fish and Wildlife Service Special Scientific Report--Fisheries series.

Genus Brevoortia, proposed by Gill (1861), is distinguished from other Clupeidae by a large head, absence of teeth, pectinated scales, and the location of the dorsal fin over the interval between the pelvic and anal fins. Brevoortia menhaden, a junior synonym of B. tyrannus, is the genotype designated by Gill. The generic description by Hildebrand (1964: 342) follows:

> "Body oblong, compressed. Bony scutes present, the median line of chest and abdomen with a sharp edge. Scales adherent, the exposed part much deeper than long, the margin serrate or pectinate in adults; a series of modified scales present next to median line on back in front of dorsal fin. Cheek deeper than long. Mouth large. Maxillary extending to or beyond middle of eye. Upper jaw with a distinct median notch. Lower jaw included in the upper one, not projecting, its upper margin (within mouth) nearly straight. Teeth wanting in adults. Lower limb of first gill arch with an obtuse angle. Gill rakers long and numerous, increasing in number with age, those on upper limb of first arch extending downward and over those on upper part of lower limb. Dorsal with 17-22 rays, the last one not greatly produced; its origin about equidistant between rim of snout and base of caudal. Anal with 17-25 rays, the last one a little enlarged. Pelvic small, with 7 rays. Vertebrae about 42-50. Intestine very long. Peritoneum black."

Other important generic characters are the cephalic sensory canals, pharyngeal accessory organ, gill rakers, and muscular pyloric stomach or gizzard (Gunter and Demoran, 1961; Monod, 1961).

There are six valid species of Brevoortia in the western Atlantic Ocean, four along the coast of North America and two along South America. Breifly the geographical range for each species is as follows:

Brevoortia tyrannus (Latrobe), 1802 - Atlantic menhaden - Nova Scotia, Canada to West Palm Beach, Fla.

Brevoortia smithi Hildebrand, 1941 - yellowfin menhaden - Cape Lookout, N.C. to the Mississippi River Delta, La.

Brevoortia patronus Goode, 1878 - Gulf menhaden - Cape Sable, Fla. to Veracruz, Mexico.

Brevoortia gunteri Hildebrand, 1948 - finescale menhaden - Mississippi River Delta, La. to Campeche, Mexico.

Brevoortia aurea (Agassiz), 1829 - lacha or savelha - Salvador, Brazil to Rio de la Plata, Argentina.

Brevoortia pectinata (Jenyns), 1842 - lacha or savelha - Rio Grande, Brazil to Bahia Blanca, Argentina.

The two South American species are imperfectly known and may represent geographic variants of a single species.

One other species, Brevoortia brevicaudata Goode, 1878, was described from a collection made at Noank, Conn. in 1874. No specimens have been reported since, and in my opinion the type specimens are aberrant forms of B. tyrannus.

Two species of menhadenlike fishes, Ethmidium maculatum (Valenciennes), 1847, and E. chilcae Hildebrand, 1946, found off the coasts of Chile and Peru, were placed in the genus Brevoortia by deBuen (1958). Although these two species are similar to menhaden in some respects, they warrant generic distinction. Ethmidium has a single row of scutes from the nape to the origin of the dorsal fin, whereas Brevoortia has a double row of scales but no scutes.

Another menhadenlike fish, Ethmalosa fimbriata (Bowdich), 1825, from the west coast of Africa was identified as B. tyrannus by Fowler (1936). Ethmalosa shows many similarities to Brevoortia and could belong to the same subfamily but according to Monod (1961) is generically distinct. He lists the arrangement of the branchiospinal filter, the number of branchiostegals, the complexity of the pharyngeal pouches, and the structure of the intestine as significant differences.

Annotated bibliographies have been published on the taxonomy, distribution, life history, biology, and fishery of the American menhadens (Reintjes, Christmas, and Collins, 1960) and on menhadenlike fishes of the world (Reintjes, 1964a).

1.22 Taxonomic status

The taxonomic status of the American menhaden was reviewed by Hildebrand (1948, 1964). He wrote the manuscripts about the same time, but the latter one was not published until 16 years later. An emendation of Hildebrand (1964) was prepared by Berry (1964). The confluent ranges of several species of Brevoortia in Florida and the intergradation of morphological characters have prompted questions about species identity (Reintjes, 1960, 1964b).

1.23 Subspecies

Subspecies were indicated in early descriptions as Brevoortia tyrannus brevicaudata, Brevoortia tyrannus patronus, and Brevoortia tyrannus tyrannus (Goode, 1878a, 1878b, 1879; Jordan and Evermann, 1896; and Jordan, Evermann, and Clark, 1930). Breder (1948) briefly described the distribution of Brevoortia tyrannus on the basis of what he believed to be its subspecies: B. tyrannus brevicaudata, B. tyrannus patronus, and B. tyrannus tyrannus. Recent publications do not consider subspecies to exist.

1.24 Standard common name, vernacular names.

Atlantic menhaden is the common name given B. tyrannus by American Fisheries Society (1960).

Goode (1878b, 1879) reported at least 30 vernacular names. The names now in general use are alewife, bunker, fatback, menhaden, mossbunker, pogy, and shad.

1.3 Morphology

1.31 External morphology

Hildebrand (1948, 1964) published reviews and descriptions of menhadens including a key that will identify many individuals to species, and Dahlberg (1966) prepared a key to the four species and two hybrids of North American menhaden. The keys will not work for all specimens because of intergrading characters, pigment variations, body measurements that vary with physical condition, age, and stage of sexual maturity, and meristics that vary from year to year or between localities. Nevertheless, the keys serve as a guide to species identity and can be used with reasonable success when supported by descriptions, photographs or drawings, and locality of capture.

The following description of an adult Brevoortia tyrannus is based on the classical descriptions by Gill (1861), Jordan and Evermann (1896), Regan (1917), and Hildebrand (1948):

> Body elliptical, compressed, deepest anteriorly, tapering posteriorly. Head very large; cheeks deeper than long. Mouth large, the lower jaw fitting into a notch in the upper, no teeth; gill rakers very long and numerous, densely set, filling the mouth and throat with a basketlike sieve. Scales deeper than long, closely imbricated, adherent, and with the exposed edges pectinated. Two rows of modified scales forming a crest along midline of body from nape to origin of dorsal fin. Axillary scales at base of pectoral and ventral fins. Adipose eyelid present. Fins small, pectorals not reaching ventrals, dorsal origin about even with insertion of ventrals, anal origin behind base of dorsal. Bluish above and sides silvery with a reddish or brassy luster, fins tinged with pale yellow or buff and edged with black, a conspicuous scapular spot usually followed by two irregular rows of secondary spots or blotches along the sides. Omnivorous with a well-developed pair of epibranchial organs to concentrate plankton. Utilizes phytoplankton including diatoms with muscular gizzard like stomach and a long coiled alimentary tract. The following meristics are usually encountered: dorsal fin rays 19-20; pectoral fin rays 16-17; pelvic fin rays 7; anal fin rays 20-22; caudal rays 10 + 9 = 19 principal with 8 dorsal and 7 ventral secondary or procurrent rays; oblique scale rows 45-52; predorsal scales 33-39; preventral scutes 19-21; postventral scutes 11-13; gillrakers on lower limb of first arch 100-150, increase with age; vertebrae 47-49, including hypurals. Depth of body 2-2/3 to 3, length of head 3-1/4, and depth of head 2-1/2, all in standard length; upper jaw 2-1/2, pectoral fin 1-3/4, and pelvic fin 3-1/2, all in head length. The preceding proportions are for average adults and may vary greatly with size and condition of fish.

Hildebrand (1948) conjectured that each section of the Atlantic coast has its own population or race. June (1958) concluded from a study of the meristic characters of juveniles that at least two subpopulations occur, one north and one south of Long Island, N.Y., and Sutherland (1963) examined juveniles of four successive year classes--1956-59 with the same conclusions. June (1965) further supported the hypothesis by reporting significant differences in vertebral counts for maturing or nearly ripe adults of different spawning populations.

1.32 Cytomorphology

No data available.

1.33 Protein specificity

In a serological comparison of five Atlantic clupeids, Sindermann (1961) and Mairs and Sindermann (1962) found a greater affinity of Atlantic menhaden with American shad, Alosa sapidissima, than with three other species of Alosa: alewife, A. pseudoharengus; blueback herring, A. aestivalis; and hickory shad, A. mediocris. The Alosa species, however, showed greater affinities with each other than with Atlantic menhaden.

2 DISTRIBUTION

2.1 Total area

The Atlantic menhaden is a euryhaline species that occurs in the Atlantic Ocean and inland tidal waters along the eastern coast of the United States and Canada. The species has been reported from Nova Scotia to southern Florida (Hildebrand, 1948, 1964; Reintjes, 1960, 1964b).

Juveniles and adults occupy bays, sounds, and estuaries to the uppermost limits of brackish water. In the ocean they generally are confined to, or at least closely associated with, the waters overlying the Continental Shelf and never have been observed far from land. Gusev (1964) reported a catch of menhaden by a Soviet trawler about 130 km. south of Cape Cod--about the maximum distance from land that schools have been sighted by scouting aircraft, and farther offshore than the seaward limit of American purse seine operations.

2.2 Differential distribution

2.21 Spawn, larvae, and juveniles

The Atlantic menhaden spawns principally at sea and in the larger sounds and bays from May to October in the northern part of its range and from October to April in the southern part (Hildebrand, 1964; Mansueti and Hardy, 1967). Eggs have been collected in Nantucket Sound and Buzzards Bay from May to October (Kuntz and Radcliffe, 1917; Marak and Colton, 1961; Marak, Colton, and Foster, 1962), in Narragansett Bay from May through August and again in October (Herman, 1963), and in Long Island Sound from May to October (Perlmutter, 1939; Wheatland, 1956; Richards, 1959). Perlmutter obtained thousands of eggs during May and June in Peconic Bay and Gardiners Bay off eastern Long Island and near Cold Spring Harbor on the western end. He also collected a few eggs on July 21 and October 14. There are only a few published reports of menhaden eggs from the region south of Long Island. Pearson (1941) reported eggs from lower Chesapeake Bay in late summer, and Reintjes (1961) collected some off North Carolina in December and February and off Florida in January and February. In addition, BCF (Bureau of Commercial Fisheries) personnel aboard the Bureau of Sport Fisheries and Wildlife R/V Dolphin discovered a concentration of Atlantic menhaden eggs in December 1966 off the coast of North Carolina (see 3.16).

Larvae move into estuaries where they soon transform into juveniles and usually remain from 6 to 8 months before returning to sea. The movement into estuaries reaches a peak in late winter and early spring. Whether it represents passive drifting or active swimming or a combination of the two is not known. All estuaries from Cape Cod, Mass., to Cape Kennedy, Fla., the major part of the species' range, are used as nurseries (Pacheco and Grant, 1965; Reintjes and Pacheco, 1966).

Most juveniles remain in the estuaries until September or October. Movement from the estuaries occurs earliest in the North Atlantic States and progressively later to the south. This exodus is not complete in some years; some menhaden overwinter in all of the major estuaries from Chesapeake Bay to Florida. Frank Schwartz, biologist at the Chesapeake Biological Laboratory, Solomons, Md., reported young menhaden in the Patuxent River, Md., during January and February 1965, and BCF personnel have also collected juvenile menhaden in Bath Creek, N.C., in February. In late February 1966, BCF biologists observed hundreds of thousands of juveniles in Core Sound, N.C., and from September 1966 until May 1967, gill nets set overnight every 2 weeks in the Neuse River, N.C., never failed to take juvenile and adult menhaden, in numbers ranging from a hundred to several thousand.

2.22 Adults

The distribution of adult menhaden in the ocean and in the larger bays and sounds is characterized by marked seasonal movements. Surface schools appear when the coastal waters warm in April and May. Schools move slowly northward as the water warms. They appear first in the coastal waters of Florida, Georgia, and the Carolinas, then in the offing of Chesapeake and Delaware Bays, and subsequently along New Jersey and Long Island by June or July. The most northern excursion usually occurs during August to the Gulf of Maine and into the Bay of Fundy, although the abundance north of Cape Cod has varied greatly during the past century. Published records show that menhaden were abundant in Maine in 1870-78 (Goode, 1879; Goode and Clark, 1887), 1894, 1898, 1903, and 1922 (Bigelow and Welsh, 1925), and 1949-59 (June and Reintjes, 1959, 1960; June 1961a, 1961b). A southward migration along the coast begins in early autumn. From Cape Hatteras the movement appears to be offshore as well as southward. This movement continues until the surface schools disappear from the coastal waters near Cape Fear, N.C., in late December or early January (Roithmayr, 1963). Menhaden occur annually at points between Cape Cod and northern Florida with striking seasonal regularity.

2.3 Determinants of distribution changes

The appearance of schools and the apparent seasonal movements along the Atlantic coast accompany changes in water temperature. Goode (1879) observed that the preferred temperature for adult menhaden is 15° to 20° C. and that movement of menhaden schools past a given coastal point in the spring and in the autumn coincided with the seasonal shift of the 10° C. isotherm.

Salinity does not seem to restrict the distribution of menhaden during most of their life cycle. Juveniles and adults tolerate salinities of less than 1 to as high as 36 p.p.t. (parts per thousand). Eggs and early larvae usually are in salinities greater than 25 p.p.t., but Wheatland (1956), Richards (1959), and Herman (1963) found eggs and small larvae in Long Island Sound and Narragansett Bay in salinities as low as 18 p.p.t.

Among other factors that undoubtedly influence the distribution of menhaden during some stage in their life history are food, predators, currents, and pollution, but no data are available.

2.4 Hybridization

2.41 Hybrids

Interspecific hybridization apparently occurs along the coast of Florida where the range of the Atlantic menhaden overlaps with that of the yellowfin menhaden, B. smithi. Menhaden with intermediate characters occur near Cape Kennedy, Fla., where both species are known to spawn in autumn and winter (Reintjes, 1960). Dahlberg[2] concluded that B. smithi hybridizes with B. tyrannus on the east coast of Florida as well as with B. patronus, the Gulf menhaden, on the west coast. I have reexamined specimens from both localities and concur with him.

Hettler (1968) obtained hybrid larvae by fertilizing eggs of yellowfin menhaden with sperm of Gulf menhaden and of hybrid fish that appeared intermediate between the two species. The larvae died from lack of food after the yolks were absorbed.

The suspected hybrids of Atlantic menhaden and yellowfin menhaden are intermediate in appearance to the parent species. The meristic characters that show the greater divergence are anal rays, predorsal scales, ventral scutes, and vertebrae. The hybrids were all males, a condition common among the hybrids of other fishes.

[2] Unpublished Ph.D. thesis "A systematic review of the North American species of menhaden, genus Brevoortia," by Michael Daniel Dahlberg, Tulane University, New Orleans, La. (1966), 161 pp.

2.42 Influence of hybridization

Hybrids of Atlantic and yellowfin menhaden do not seem to appear in the landings except near Cape Kennedy, Fla. BCF personnel have been unable to find hybrids in the menhaden landings at Fernandina Beach, Fla., in North Carolina, or northward along the Atlantic coast. Because hybrids have come to our attention only recently, their significance to the menhaden populations during the past cannot be evaluated. Hybrids now occur commonly in the gill net catches near Cape Kennedy, Fla., where they often account for half of the landings.

3 BIONOMICS AND LIFE HISTORY

3.1 Reproduction

3.11 Sexuality

Atlantic menhaden are heterosexual. They possess no accessory reproductive organs, and there is no way to distinguish the sexes externally. Functional hermaphroditism is unknown. Occasionally an individual with a single maturing testis and a single maturing ovary is found in menhaden landings. Whether such fish produce sperm or ova capable of developing into living embryos is not known.

3.12 Maturity

Higham and Nicholson (1964) determined when females become sexually mature. A few individuals mature at age 1 (180-280 mm. fork length); more than four-fifths at age 2 (195-320 mm.), and all, at age 3 (over 200 mm.).

McHugh, Oglesby, and Pacheco (1959) reported that males matured at the same age and size as females.

3.13 Mating

Mating in the literal sense is not known to occur nor is there parental care of eggs or larvae.

3.14 Fertilization

Fertilization is external.

3.15 Gonads

Higham and Nicholson (1964) estimated Atlantic menhaden fecundity by projecting counts of all ova 0.35 mm. or more in diameter from weighed samples of ovaries in each of 38 specimens (203-345 mm. fork length). Estimates ranged from 38,000 to 631,000 ova per fish. They speculated that

ova continue to mature and are released periodically. From their examination of males they concluded that testes mature concurrently with the ovaries of fish of similar size. Testes were not weighed, nor were maturing sperm measured or counted.

3.16 Spawning

In their study of ovary development, Higham and Nicholson (1964) concluded that menhaden spawn in every month of the year but not in all localities each month. Spawning occurs in New York and New England from May to October; in the Middle Atlantic States in March, April, September, and October; and in the South Atlantic States from October to March. Much of the spawning apparently takes place along the North Carolina coast from Cape Hatteras south. Biologists of the Bureau of Commercial Fisheries obtained hundreds of thousands of developing eggs during several 10-minute plankton tows in December 1966, in an area less than 8 km. in diameter about 65 km. off New River Inlet, N.C. I concluded, on the basis of the estimated ages of three groups of eggs in different stages of development, that spawning occurred after midnight but before dawn on 3 successive days.

As reported by Goode (1879), Bigelow and Schroeder (1953), and Hildebrand (1948, 1964), spawning, hatching, and early larval development take place in the ocean. Eggs and small larvae occasionally are observed in Long Island Sound, Narragansett Bay, and Chesapeake Bay, but spawning in these localities is believed to make only minor contributions to the stock (see section 2.21).

3.17 Spawn

Fertilized Atlantic menhaden eggs are spherical, 1.3 to 1.9 mm. in diameter, with a thin, transparent, and unsculptured shell. The yolk, 0.9 to 1.2 mm., is light yellow and faintly segmented, has a single oil globule, 0.12 to 0.14 mm., and no pigment spots. Usually a wide perivitelline space occupies nearly half of the egg diameter in the larger eggs. The eggs are not adhesive. They are buoyant in sea water, and float in loose aggregations near the surface.

Predators of eggs may be assumed to be other plankton, including chaetognaths, fish larvae, mollusks, and salps. Parasitism by ciliates, fungi, and suctorians was observed when the eggs of B. smithi were reared, but these infections may have been induced in the laboratory (Reintjes, 1962).

3.2 Preadult phase

Kuntz and Radcliffe (1917) gave the only account of hatching and early larval development of Atlantic menhaden (fig. 1). They observed that fertilized eggs from the plankton hatched within 48 hours. They also reported that the yolksac is large and that the newly hatched larva, 4.5 mm. long, is primitive--without fins, a functional mouth, or pigmentation.

The yolk is completely absorbed in about 4 days, when the larvae are 5.7 mm. long. Pectoral fins appear, the eyes become pigmented, and the mouth becomes functional. The larvae have caudal and dorsal fins at 9 mm. and a full complement of fin rays at 23 mm. (Ages at these lengths are not known.)

Larvae move into estuaries when they are 10 to 30 mm. long and proceed into the small creeks and tributaries to the upper limits of brackish water (June and Chamberlin, 1959). The rate of development of menhaden larvae has not been determined.

No estimates of survival in nature are available. Low temperatures in some years may destroy most larvae in certain areas. Temperatures below 3° C. for more than 2 days have been observed to kill most larvae held under controlled laboratory conditions, although such mortality depends in large degree on acclimation temperature and rate of thermal change (Lewis, 1965, 1966).

Larvae transform into juveniles in the estuaries when they are about 30 to 35 mm. long. Slender, transparent larva with no scales or ventral scutes metamorphose gradually to a miniature adult with a deep body, large head, scales, scutes, and pigmentation. Collections of juveniles at intervals of 2 or 3 days have indicated increases in mean length of nearly 1 mm. per day, the best estimate of growth available.

Searches for parasites of larval and juvenile menhaden by personnel of Virginia's Institute of Marine Science and BCF have been in progress for several years. In one study, larvae were free of monogenetic trematodes in the spring, but 30 to 50 percent of the juveniles were infested by August (W. J. Hargis and J. S. Sterling, Research Biologists, Virginia Institute of Marine Science, Gloucester Point, Va., Progress Report, March 1961). A copepod, Lernaeenicus radiatus, that frequently occurs on the sides of adults, and an isopod, Olencira praegustator, that often inhabits the buccal cavity, were not found among

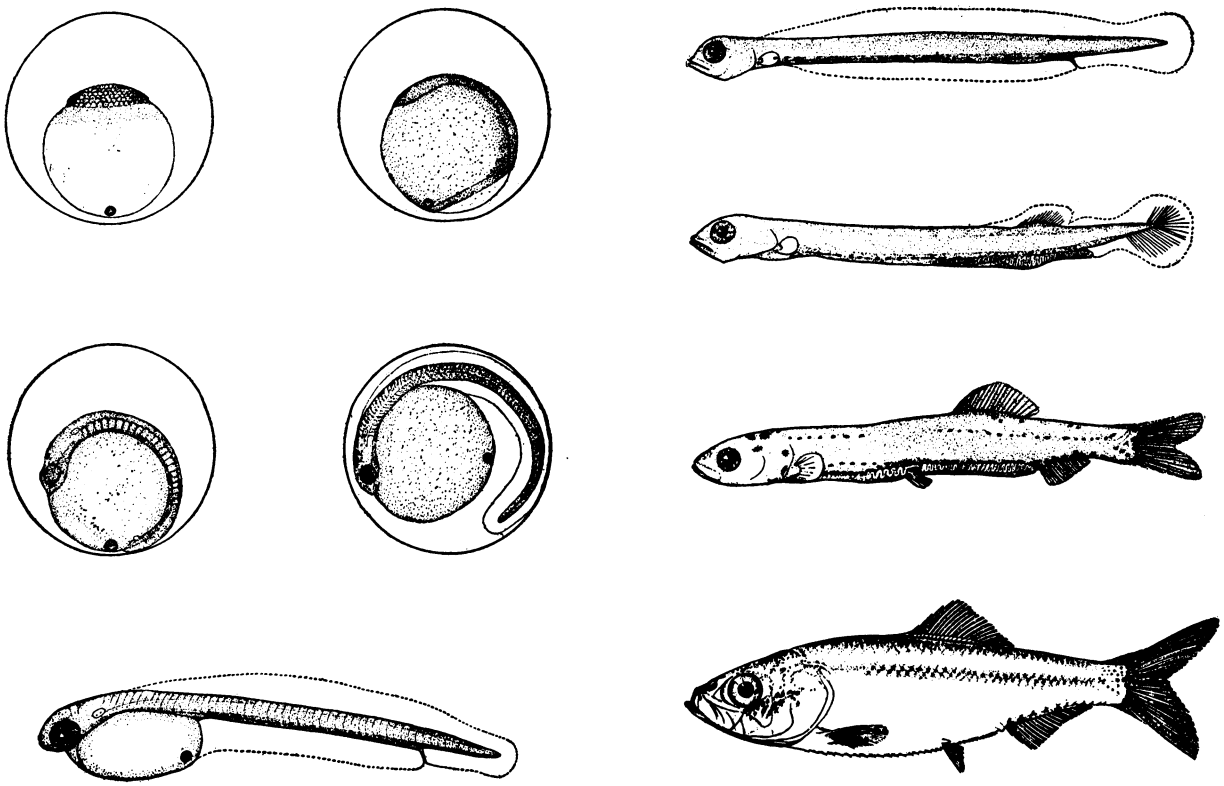

Figure 1.--Atlantic menhaden eggs, 1.6 mm.; yolksac larvae, 4.5 mm.; postlarvae, 5.7, 9, and 23 mm.; and juvenile, 33 mm. (after Kuntz and Radcliffe, 1917).

juveniles until late summer. These preliminary observations indicate that three common parasites of yearling and adult menhaden appear initially on juveniles in the estuary.

Predators include nearly all large carnivorous fishes and sea birds inhabiting the estuaries. Fishes of major importance are the bluefish, Pomatomus saltatrix (Grant, 1962); striped bass, Roccus saxatilis (Hollis, 1952); summer flounder, Paralichthys dentatus (Poole, 1964); and weakfish, Cynoscion regalis (Peck, 1896; Welsh and Breder, 1924). BCF personnel have observed the osprey, Pandion haliaetus, and herring gull, Larus argentatus, feeding on juvenile menhaden.

Larval menhaden feed selectively on individual planktonic animals, mainly crustaceans. This manner of feeding changes to nonselective filtration of plankton as the young menhaden transform into juveniles. Structural modifications associated with feeding during metamorphosis are: (a) loss of maxillary and mandibular serrations, (b) elongation and branching of gill rakers, (c) development of pharyngeal pouches and accessory organs, (d) formation of a muscular pyloric stomach or gizzard, and (e) elongation and coiling of the intestine (June and Carlson[3]).

3.3 Adult phase

3.31 Longevity

Longevity may be surmised by examining large numbers of specimens from menhaden landings. During the period 1952-62, BCF personnel determined age of more than 116,000 menhaden and published the results in the series of reports listed under section 4.11. Six- and 7-year-old fish occurred frequently, 8-, 9-, and 10-year-olds were uncommon, and only one 12-year-old was encountered.

3.32 Hardiness

Little information is available on the tolerance of Atlantic menhaden to marked changes in the environment. Deaths among Atlantic and

[3] Unpublished manuscript "Food and feeding habits of Atlantic menhaden in relation to the metamorphosis from larval to postlarval stages," by Fred C. June and Frank T. Carlson, Bureau of Commercial Fisheries Biological Laboratory, Beaufort, N.C. 28516, 45 pp.

Gulf menhaden have been attributed to low temperature (Gunter, 1941), abruptly changing salinity (Westman and Nigrelli, 1955), high salinity (Simmons, 1957), and toxic dinoflagellates or red tide (Gunter, Williams, Davis, and Smith, 1948). Adults are easily injured during capture and transport. Yearlings up to 150 mm. long have been held in small tanks from 3 to 6 months and in an artificial pond for 18 months at Beaufort, N.C., but holding larger fish has been unsuccessful because of head injuries that cause hemorrhages in the complex sensory canal system around the eyes.

3.33 Competitors

Competitors for food and space are many animals that occupy the same estuaries and coastal waters and feed on the small plants and animals in the plankton community. The more apparent competitors are the herrings, anchovies, mullets, oysters, mussels, barnacles, and tube worms.

3.34 Predators

All large carnivorous sea mammals, fishes, and sea birds are potential predators of menhaden. Whales, dolphins, sharks, tunas, swordfish, Xiphias gladius, bonito, Sarda sarda, pollock, Pollachius virens, hakes, Urophycis spp., striped bass, Roccus saxatilis, weakfish, Cynoscion regalis, tarpon, Megalops atlanticus, and bluefish, Pomatomus saltatrix, were all listed by Goode (1879) as predators. Of these, the bluefish has been singled out as the principal natural enemy of menhaden. Bigelow and Welsh (1925: 123-124) wrote:

> "Whales and porpoises devour them in large numbers; sharks are often seen following the pogy schools; pollock, cod, silver hake, and swordfish all take their toll in the Gulf of Maine, as do weakfish south of Cape Cod. Tuna, or 'horse mackerel', also kill great numbers, but the worst enemy of all is the bluefish, and this is true even in the Gulf of Maine during periods when both bluefish and menhaden are plentiful there... Not only do these pirates devour millions of menhaden each summer but they kill far more than they eat."

Sharks and birds prey regularly on menhaden. Bigelow and Schroeder (1948) reported menhaden in the food of several species of sharks. I examined stomachs of dusky, hammerhead, and silky sharks (Carcharhinus obscurus, Sphyrna zygaena, and C. floridanus) caught off Beaufort, N.C., in November 1961. Twenty-four of the 45 sharks examined contained menhaden. BCF personnel have seen cormorants, Phalacrocorax auritus, gannets, Morus bassanus and Sula leucogastra, and pelicans, Pelecanus occidentalis and P. erythrorhynchos, diving into schools and presumably feeding on menhaden. Arthur (1931) included menhaden among the principal foods of the pelican in Louisiana.

The relation of schooling to predators recently has been considered by several investigators. Brock and Riffenburgh (1960) proposed that schooling or grouping of prey reduces the opportunity for successful attacks by predators. They further hypothesized that when school size exceeds the quantity of fish that a predator can consume at each encounter, the rate of consumption of the prey species by the predator is reduced. Moulton (1963), while studying the effects of sound on menhaden, noted that the species formed a tight mill by crowding together with frenzied swimming when a recording of porpoise calls was played. This type of response may be interpreted as a defense against noisy predators.

3.35 Parasites, diseases, injuries, and abnormalities

A partial list of parasites prepared by Westman and Nigrelli (1955) includes:

Chloromyxum clupeidae - myxosporidian in flesh.

Diclodophora sp. - mongenetic trematode on gills.

Hemiurus appendiculatus - digenetic trematode in stomach.

Podocotyle atomon - digenetic trematode in intestine.

Cryptocotyle lingua - digenetic trematode cercaria in skin.

Pterobothrium heteracanthus - cestode cyst in viscera.

Rhynchobothrium sp. - cestode cyst in viscera.

Bomolochus teres - copepod on gills.

Caligus chelifer - copepod on body surface.

Caligus schistonyx - copepod on body surface.

Lernanthropus brevoortiae - copepod on gills.

Lernaeenicus radiatus - copepod on body surface.

Clavellisa spinosa - copepod on gills.

Several unidentified ascaroid nematodes in viscera.

In addition, the following have been reported:

Eimeria brevoortiana - sporozoan in testes (Hardcastle, 1944),

Clupeocotyle brevoortia - monogenetic trematode on gills (McMahon, 1963).

Mazocraeoides georgei - monogenetic trematode on gills (McMahon, 1963).

Olencira praegustator - isopod in buccal cavity (Latrobe, 1802).

Petromyzon marinus - sea lamprey on body surface (Mansueti, 1962).

Menhaden are resilient to some types of unintentional or purposeful injury. For example, small incisions in the body wall through which ferromagnetic tags are inserted usually heal in 2 or 3 weeks and leave small, scaleless scars (F. T. Carlson, BCF Biological Laboratory, Beaufort, N.C., Quarterly Report, December 1962). Also, when extremities of caudal and pectoral fins are removed for marking fish, they quickly regenerate without causing significant disfigurement or incapacitation.

Several abnormalities have been reported. Sutherland (1963) who used X-ray photographs to study meristic characters of Atlantic menhaden noted abnormal vertebrae in 238 of 17,024 fish. The most frequent abnormality was the fusion of two centra (54 percent). Others included fusion of three or more centra, heavily ossified centra (fused and nonfused), and centra with more than one neural or hemal spine. Musick and Hoff (1968) reported 3 humpbacked specimens in a catch of 338 juvenile Atlantic menhaden. Pugheaded menhaden were reported by Schwartz (1965) and Warlen (1969) from Chesapeake Bay and the Neuse River, N.C.

3.4 Nutrition and growth

3.41 Feeding

Menhaden feed by straining small animals and plants from the water with a sievelike branchial apparatus. This apparatus is composed of gill arches with dermal flaps and long branched gill rakers covered with mucus. Feeding was closely observed by Goode (1879), Peck (1894), and Bigelow and Welsh (1925), who generally agreed that menhaden filter organic matter from the water by swimming with mouths gaped and opercles flared. When a mixture of fish meal and chopped clam meats was added to tanks holding menhaden at the BCF laboratory in Beaufort, N.C., the schooled fish swam rapidly back and forth through the food until it was consumed and then resumed normal swimming. Clark and Clark (1962) observed menhaden 10 to 13 cm. long darting about selecting their prey. Apparently the size and distribution of food organisms determine whether adult menhaden feed by filtration or by selection. No daily or seasonal changes in feeding have been reported in the literature or observed during our studies. Hand and Berner (1959) speculated that cessation of feeding by California sardines in a spawning condition serves to protect their own planktonic eggs and larvae. Whether or not such a phenomenon is true of menhaden is unknown.

3.42 Food

The food of menhaden are the plankters, both plant and animal, that are filtered from the water. Peck (1894) reported that the food of menhaden comprises the smaller plants and animals normally occurring in the fish's habitat. The larger and more active plankters were not found among the stomach contents. He estimated that adult menhaden are capable of filtering 23 to 27 liters of water per minute. Richards (1963) reported that planktonic crustaceans predominated in the stomach contents of 28 juvenile menhaden from Long Island Sound. June and Carlson (see footnote 3) identified diatoms as the principal food of juveniles in Indian River, Del.

3.43 Growth rate

Growth of Atlantic menhaden has been estimated from differences in mean lengths of fish between successive age groups. Rush (1952) developed a growth curve by using data for 34 menhaden ranging from 10 to 37 cm. long and 0 to 6 years old. Westman and Nigrelli (1955) obtained growth rates similar to that of Rush from a much greater number of fish but did not present their data. McHugh, Oglesby, and Pacheco (1959) showed changes in modal fish lengths and weights that reflected growth. These data were used by McHugh (1967) to construct growth curves by length and by weight for menhaden 6 to 34 months old. His data indicate an average increment of 7.5 mm. per month for fish in the Chesapeake Bay area during their first 3 years of life.

Several factors interfere with an accurate estimation of growth. Since spawning may occur in any month, two fish with scales containing the same number of annuli may differ in actual age by nearly a year. For example, menahden caught in July with one scale annulus may be as young as 5 months or as old as 17. Since menhaden school by size, fish with the same number of annuli collected from one locality at about the same time may differ in size owing to one or all the following: (1) difference in growth, (2) difference in actual age, (3) schooling by size, and (4) selective capture. These factors must be considered in any determination of growth from scale marks or size composition.

C. E. Richards, Marine Scientist, Virginia Institute of Marine Science, Gloucester Point, Va. (personal communication February 1968), examined age-length and age-weight data obtained from Atlantic menhaden sampled during the North Carolina fall fishery, 1959-62 (Nicholson and Higham, 1964a, 1964b, 1965, 1966). The fish caught during the fall are not representative of the population in other areas and at other times. Much of the catch is composed of adults that are sexually mature and approaching spawning. Females are heavier than males of the same lengths because the weights of mature ovaries exeed the weights of mature testes. He fitted the von Bertalanffy (1938) growth equation t o the data with an analog computer (Richards, 1968).

Thus for

Males: $L_t = 334 \left[1 - e^{-0.484\,(t + 0.025)} \right]$

$W_t = 724 \left[1 - e^{-0.475t} \right]^3$

females: $L_t = 345 \left[1 - e^{-0.464\,(t + 0.032)} \right]$

$W_t = 817 \left[1 - e^{-0.478t} \right]^3$

Where: L = fork length in millimeters

W = body weight in grams

t = age in years equal to one more than number of annuli. For example, menhaden with one annulus are nearly 2 years old when caught during the fall fishery.

The results of these computations are shown in figure 2. The curves were fitted by inspection.

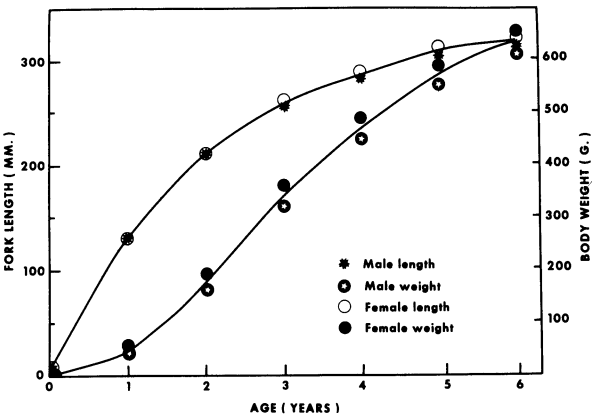

Figure 2.--Calculated growth in fork length and body weight for male and female Atlantic menhaden sampled during the North Carolina fall fishery, 1959-62. (From C. E. Richards, Marine Scientist, Virginia Institute of Marine Science, Gloucester Point, Va., February 1968, personal communication).

3.44 Metabolism

No data available.

3.5 Behavior

3.51 Migration and local movements

Migrations of menhaden along the Atlantic coast were reported by Goode (1879), inferred from the distribution of catches by purse seine vessels (Roithmayr, 1963), and currently are being determined by tagging. Fishery statistics giving the seasonal distribution of surface schools, on which the fishery depends for its production, indicate movements northward in the spring and early summer and southward in the autumn. Hildebrand (1964) believed the more probable migration was inshore and offshore. In 1967 and 1968 menhaden were tagged throughout the purse seine season in each fishing area from New York to Florida. Tag recoveries showed that all movement from each release locality during the spring and summer was northward. In the fall, tagged fish from all localities to the north migrated south and were recovered in North Carolina. At least part of the answer to the question whether migration is north and south along the coast is provided by these tagging results. Whether there is also inshore and offshore migrations has not been determined.

Local or short-term movements in and out of bays and inlets evidently accompany changes in the tides, weather, and season. These movements are watched carefully by airplane pilots scouting fish schools for purse seine fleets from Cape Cod, Mass., to St. Augustine, Fla.

3.52 Schooling

Schooling is an outstanding behavior characteristic of menhaden that seems innate from the late larval stage to old age. Menhaden school by size and the number of fish in a school varies greatly. Purse seine fishing depends wholly on the sighting of surface schools from airplanes or from the carrier vessels. The purse seine is set around the school and, according to the fishermen, usually all or most of the school is captured. If this observation is accurate, the catch per set represents school size.

The mean catch per set differs from area to area as does the mean size of the fish caught. During the period 1955-66, the mean catch per set was 19 metric tons in the North and Middle Atlantic areas, 15 metric tons in Chesapeake Bay and in the South Atlantic areas, and 38 metric tons in the North Carolina fall fishery. If the mean fish weight for each area is used to calculate the number of fish in an average sized school, the numbers range from 50,000 in the North Atlantic area to nearly 200,000 in the North Carolina fall fishery.

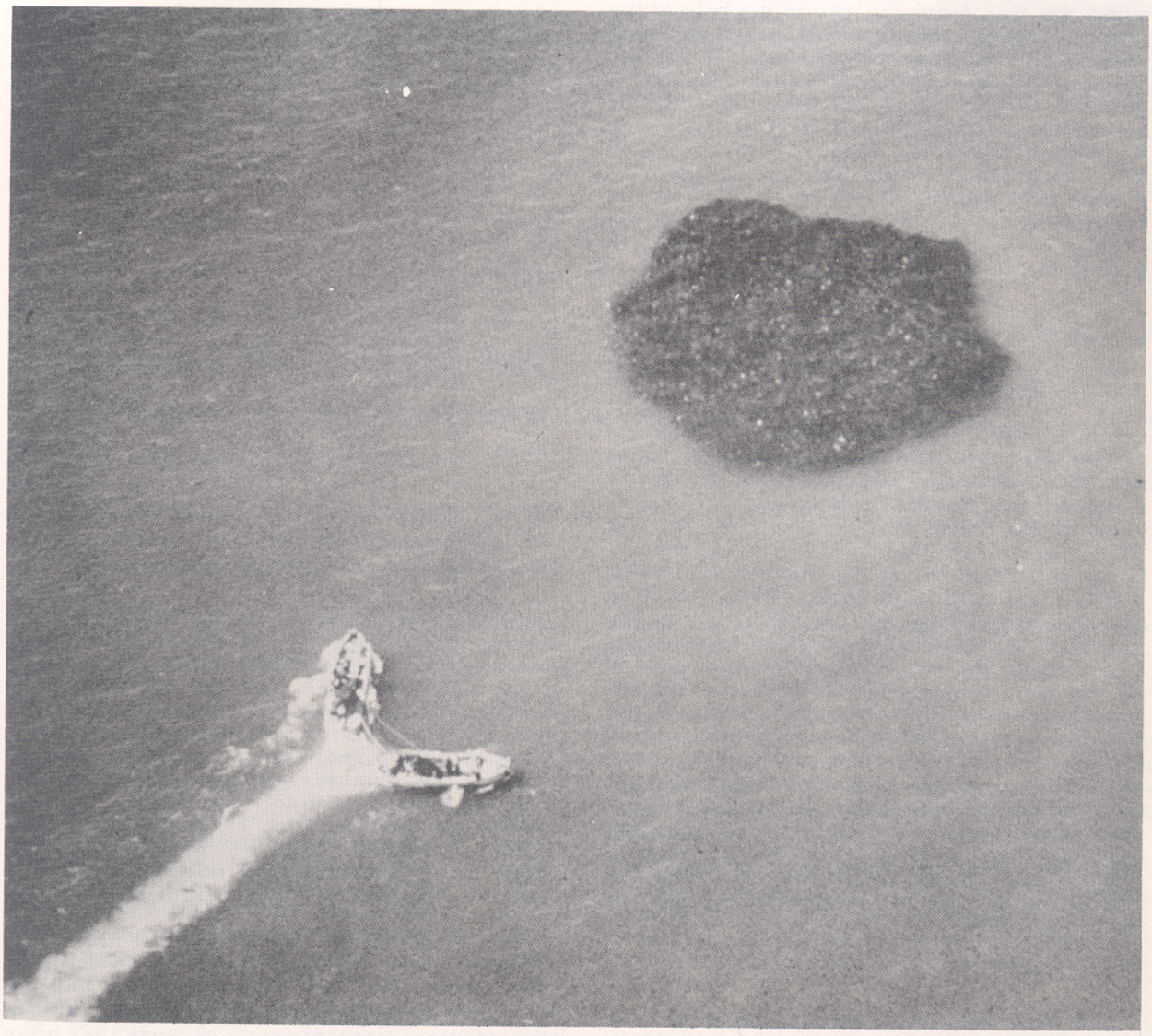

Figure 3.--A 64-metric ton school of Atlantic menhaden. (Photographed by Hall Watters, Standard Products Co., Southport, N.C.).

3.53 Response to stimuli

Few studies have been made of the responses of menhaden to mechanical, chemical, thermal, or optical stimuli. Moulton (1963) reported that menhaden reacted violently to a sound field of from 2 to 20 kilocycles/sec.; the degree of frenzy was inversely related to the sound frequency. In sustained tests, the same fish became accustomed to the sound and behaved less violently. Kreutzer (1959) discussed the behavior of menhaden in a strong electrical field after their confinement in a purse seine. The electrical device was used to concentrate the fish near the intake of the hose used to pump the fish from the net to the hold of the carrier vessel. Smith (1961) reported that schools of menhaden moved along a "curtain" of air bubbles and did not break through it. Several schools were enclosed and held by air-bubble curtains for as long as 10 hours. A charged electrode similar to the one used in concentrating menhaden in the net for pumping (Kreutzer, 1959) was located at one corner of the air-bubble enclosure, but the captive menhaden never ventured near enough to be affected by the electrical field.

4 POPULATION

4.1 Structure

Since 1955, BCF has obtained information on the sex, age, and size composition of the Atlantic menhaden population by regularly sampling the commercial landings. The procedures and results of the sampling through 1962 were presented in a series of reports (June and Reintjes, 1959, 1960; June, 1961a, 1961b; June and Nicholson, 1964; Nicholson and Higham, 1964a, 1964b, 1965, 1966). The procedures essentially consisted of obtaining 20 fish from the last daily set made by each of two or three vessels landing at major Atlantic coast ports. After recording the length, weight, and sex of each fish, personnel removed six scales for age determination. Ages were assessed by counting, under 40 X magnification, the number of annular marks on the scales. The scale method for aging menhaden was used by Rush (1952), Westman and Nigrelli (1955), and McHugh, Oglesby, and Pacheco (1959). Its validity was confirmed by June and Roithmayr (1960).

4.11 Sex ratio

The sex ratio at each age remains essentially the same from area and from year to year. Numbers of males and females are nearly equal until 4 years of age. Among older fish, females outnumber males (table 1). There is no evidence that menhaden segregate by sex.

Table 1.--Sex ratio of Atlantic menhaden by age in samples of landings by purse seiners, 1955-66

Age[1/]	Examined	Ratio
		Male : Female
Years	Number	
0	5,490	1 : 0.98
1	52,498	1 : 1.03
2	66,381	1 : 0.99
3	31,340	1 : 1.08
4	15,609	1 : 1.16
5	8,545	1 : 1.19
6	3,731	1 : 1.36
7	919	1 : 1.90
8-10	239	1 : 1.78
Total	184,752	1 : 1.05

[1/] Age shown is the number of annuli and not annuli plus one as given in figure 2.

4.12 Age composition

The estimated numbers of menhaden of various ages caught with purse seines has changed markedly from year to year (table 2). For example, the numbers of 1-year-old fish increased nearly fivefold from 1958 to 1959 and decreased 14-fold from 1959 to 1960. Among some of the older ages the changes have been even more dramatic. The number of 4-year-olds increased by 22 times from 1961 to 1962.

Year classes of above-average numerical strength were those of 1951, 1953, 1955, 1956, and 1958 (table 2). The catch of young-of-the-year (0-age) fish is not a reliable indicator of year class strength because they often are not available on the fishing grounds and when they are, the fishermen and spotter pilots avoid them. In some years these small fish are taken principally during the North Carolina fall fishery. Their capture depends more on

Table 2.--Age composition of Atlantic menhaden in samples of landings by purse seiners, 1955-66

Year	Weight of landings	Age in years 1/									
		0	1	2	3	4	5	6	7	8-10	Total
	Metric tons	Millions of fish									
1955	641,900	761.0	636.5	1,045.6	265.5	300.4	35.3	9.5	1.8	0.6	3,056.2
1956	712,100	36.4	2,078.5	902.6	318.0	45.2	152.4	28.9	6.7	2.0	3,570.7
1957	606,100	300.8	1,596.5	1,348.3	96.5	70.9	40.4	37.0	4.3	1.2	3,495.9
1958	510,300	106.1	859.5	1,625.1	71.9	17.3	15.9	9.1	4.9	0.4	2,710.2
1959	659,000	11.4	4,032.6	821.9	382.7	33.6	11.7	12.3	4.4	1.7	5,312.3
1960	529,300	72.2	281.0	2,207.9	75.0	101.2	24.6	7.4	2.3	0.6	2,772.2
1961	575,700	0.3	832.4	502.3	1,207.1	19.2	29.8	3.1	0.8	0.2	2,595.2
1962	538,000	51.6	519.8	831.8	221.0	421.9	30.6	24.5	2.8	0.6	2,104.6
1963	346,100	84.6	717.8	640.7	199.7	47.0	53.3	10.3	3.5	0.6	1,757.5
1964	271,700	315.7	704.6	578.4	120.7	18.9	8.3	7.7	1.3	0.3	1,755.9
1965	273,000	127.2	820.5	389.2	102.2	12.6	1.9	1.3	0.6	0.1	1,455.6
1966	219,600	303.8	421.8	412.8	106.1	12.0	0.9	0.1	0.1	--	1,257.6

1/ See footnote Table 1.

weather, economics of the fish meal industry, and other vagaries of fishing than on their abundance. Since 1958 there have been no strong year classes, and the total landings as well as the numbers of fish caught each year have diminished. This decline has occurred in all age groups and has been most striking among fish 4 years old and older.

The relative age composition of landings differs among geographical areas and between years (table 3). During the summer the older and larger fish go farther north than do the 1- and 2-year-olds. A few 0-age fish are caught during the summer in Chesapeake Bay and off the South Atlantic States. Age-1 and age-2 fish constitute about 90 percent of all menhaden taken in those areas. All ages, including young of the year, are caught during the fall off North Carolina.

4.13 Size composition

The length and weight of menhaden within each age group vary greatly between fishing seasons and areas. To exemplify these variations, table 4 gives fork lengths and weights for each age contributing to catches during the North Carolina fall fishery (November-January) in 1962-63. The mean lengths and weights differ markedly between geographical areas (tables 5 and 6). During the summer, the larger fish in each age group, except 0-age, are taken in the most northern part of the fishery.

Temporal variation in size composition relative to coastwise movement of Atlantic menhaden was discussed in section 3.5. No analysis of variation in size with depth, distance offshore, density, or time of day has been attempted.

Menhaden as long as 450 mm. and weighing 1,800 g. have been reported (Goode, 1879). The longest menhaden encountered by BCF personnel during regular sampling of the landings, 374 mm. (fork length), and the heaviest, 1,184 g., were both females. The largest menhaden in the BCF collection at Beaufort,

Table 3.--Relative age composition of Atlantic menhaden by season and area in samples of landings by purse seiners, 1955-66

[Range of annual values is given in parentheses]

Season and area	Number of fish caught	Age in years 1/								
		0	1	2	3	4	5	6	7	8-10
	Millions	Percent								
Summer										
North Atlantic	1,244	-	1 (0-5)	19 (0-54)	31 (15-79)	26 (5-68)	16 (3-54)	6 (1-26)	1 (0-5)	<1 (0-1)
Middle Atlantic	9,445	-	19 (0-59)	55 (18-95)	19 (1-80)	6 (0-42)	1 (0-2)	<1 (0-2)	<1 (0-1)	
Chesapeake Bay	10,943	6 (0-32)	59 (18-91)	31 (9-82)	4 (0-28)	<1 (0-5)	-	-	-	-
South Atlantic	6,875	<1 (0-4)	70 (28-99)	27 (1-68)	3 (0-14)	<1 (0-3)				
Fall										
North Carolina	3,337	46 (0-87)	14 (1-52)	19 (6-36)	12 (1-58)	5 (0-21)	3 (0-3)	1 (0-1)	<1 (0-1)	

1/ See footnote Table 1.

Table 4.--Ranges of length and weight of Atlantic menhaden by age in samples of landings during the North Carolina fall fishery, 1962 1/

Measurement	Age in years 2/							
	0	1	2	3	4	5	6	7
Fork length Mm.	100-149	140-274	225-334	230-324	240-339	275-334	305-339	320-349
Weight G.	10-49	40-339	180-709	270-779	250-789	390-759	540-739	720-819

1/ From Higham and Nicholson, 1965b.

2/ See footnote Table 1.

taken with a gill net in Delaware Bay in 1956, is a female 420 mm. long that weighs 1,490 g. To my knowledge the heaviest specimen is at the Bureau's laboratory in Boothbay Harbor, Maine -- a 7-year-old female that was 418 mm. long and weighed 1,674 g. when taken from a fish trap near Newport, R.I. (Cooper, 1965).

4.2 Abundance and density

Since 1957, BCF has annually estimated the relative abundance of juvenile menhaden in Atlantic coast estuaries. From 1957 to 1961 the estimates of population size were derived from surveys by haul seines and a mark-

Table 5.--Mean fork length of Atlantic menhaden by age, season, and area in samples of landings by purse seiners, 1955-66

[Number of fish in parentheses]

Season and area	Age in years[1/]								
	0	1	2	3	4	5	6	7	8-10
	Mm.	Mm.	Mm.	Mm.	Mm.	Mm.	Mm.	Mm.	Mm.
Summer									
North Atlantic	--	216 (148)	277 (4,048)	295 (7,774)	312 (6,915	321 (5,375)	329 (2,462)	335 (605)	340 (136)
Middle Atlantic	137 (9)	210 (7,695)	250 (31,258)	275 (16,684)	298 (6,866)	310 (2,194)	324 (933)	333 (238)	337 (90)
Chesapeake Bay	151 (3,009)	193 (21,769)	229 (15,130)	249 (2,132)	278 (304)	287 (41)	308 (12)	315 (5)	303 (1)
South Atlantic	136 (138)	161 (19,559)	188 (11,000)	207 (1,729)	214 (201)	259 (8)	--	--	--
Fall									
North Carolina	128 (2,334)	191 (3,327)	265 (4,945)	287 (3,021)	306 (1,323)	320 (927)	324 (324)	333 (71)	334 (12)

[1/] See footnote Table 1.

recapture method. Since 1961 survey procedures have gradually changed and now consist of sampling with a surface trawl pulled by two small boats and censusing schools of juveniles from aircraft. When used concurrently during the period 1962-66, all four methods gave results that were generally in agreement. Surface trawling and aerial sightings were established as the survey methods in 1967 because they were the most adaptable to the variety of conditions encountered, provided the best coverage in the shortest time, and seemed to be the most reliable.

Survey results with 1962 as the base year (table 7) revealed that the relative abundance of juveniles in the estuaries has declined. The trawling index showed an increase in 1963 that was not supported by the aerial index nor by the landings during the years following. At such low relative abundance, there is no assurance that this disagreement is meaningful.

Some indication of the relative sizes of recent year classes can be obtained by accumulating the contribution of each year class to the fishery throughout its life span (table 8). The total contributions from the year classes after 1959 are not shown in the table because some older fish are being caught. If the trend of the past few years continues, the contribution by each age group, 4 years and older, will number less than 0.1 billion fish.

4.3 Natality and recruitment

No data available.

4.4 Mortality and morbidity

BCF has received reports of mass mortalities each year since the beginning of the menhaden research program in 1955. The apparent causes of death included: (a) capture in a net that failed to hold the catch, (b) near-freezing temperatures in estuaries and the lower reaches of tributaries, (c) low dissolved oxygen, and (d) pollution by industrial wastes or agricultural chemicals.

Westman and Nigrelli (1955) observed distressed menhaden in tidewaters of northern New Jersey. These fish showed loss of coordination and balance before death. Postmortem examination revealed exophthalmia and hemorrhages in the gills and brain apparently caused by gas emboli. Their search disclosed no causative microorganism. Similar mortalities

Table 6.--Mean weight of Atlantic menhaden by age, season, and area in samples of landings by purse seiners, 1955-66

[Number of fish in parentheses]

Season and area	Age in years[1/]								
	0	1	2	3	4	5	6	7	8-10
	G.	G.	G.	G.	G.	G.	G.	G.	G.
Summer									
North Atlantic	--	184 (148)	418 (4,047)	504 (7,762)	594 (6,884)	649 (5,355)	704 (2,451)	729 (607)	786 (136)
Middle Atlantic	46 (9)	176 (7,691)	285 (31,242)	405 (16,668)	513 (6,863)	574 (2,193)	663 (932)	703 (237)	729 (90)
Chesapeake Bay	61 (3,006)	131 (21,755)	213 (15,126)	275 (2,131)	381 (304)	403 (41)	461 (12)	529 (5)	522 (1)
South Atlantic	46 (138)	74 (19,463)	115 (10,989)	153 (1,730)	210 (201)	372 (8)	--	--	--
Fall									
North Carolina	38 (2,329)	136 (3,325)	367 (4,935)	471 (3,020)	583 (1,319)	651 (925)	695 (324)	748 (71)	620 (12)

1/ See footnote Table 1.

have been observed in Chesapeake Bay (L. E. Cronin, Director, Chesapeake Biological Laboratory, Solomons, Md., August 1962, personal communication).

There are no published estimates of mortality rates for Atlantic menhaden, but K. A. Henry, Director, BCF Biological Laboratory, Beaufort, N.C. 28516 (personal communication, September 1968), has completed some preliminary estimates of total apparent mortality in 1955-66. The best estimate for instantaneous mortality rate (Ricker, 1958) for the entire population is i = 1.2.

4.5 Dynamics of the population

Only preliminary studies of the population dynamics of Atlantic menhaden have been attempted. Summary tabulations of the results of sampling the commercial landings, 1952-62, were published in a series of reports cited in section 4.1. A review of the landings, fishing effort, mean age by area of capture, and estimates of juvenile abundance was prepared by Henry (1965).

BCF began marking and recapture experiments in 1966. Menhaden are marked with numbered metal tags (3 by 14 by 0.5 mm.) inserted into the abdominal cavity. The tags are ferromagnetic and are recovered by magnets in the fish reduction plants. The general area and approximate date of capture are known because the vessels usually fish less than 60 km. from the plant site and most of the tags are recovered soon after the fish are processed. During 1966, 1967, and 1968 nearly 845,000 Atlantic menhaden were tagged and 118,000 tags were returned. Movements between areas can be shown, and estimates of mortality are being developed. One plant near Beaufort, N.C., is now using a prototype electronic detector that will recover tagged fish as they are unloaded from the vessel. Marked fish so recovered will provide information on growth and on the catch location and date.

4.6 The population in the community and the ecosystem

Characteristics of menhaden that contribute to their position of eminence in the ecosystem and marine community include (1) large populations or biomass, mainly in the shallow

Table 7.--Indices of the relative abundance of juvenile menhaden in Atlantic coast estuaries, 1962-67

Method and area	Year					
	1962	1963	1964	1965	1966	1967
Surface trawling[1/]						
North Atlantic	100	677	17	17	164	47
Middle Atlantic and Chesapeake Bay	100	577	90	8	50	2
South Atlantic	100	105	41	25	46	17
Total Atlantic	100	206	45	22	55	18
Aerial surveying[2/]						
North Atlantic	100	38	24	22	7	8
Middle Atlantic and Chesapeake Bay	100	138	61	15	72	3
South Atlantic	100	38	1	15	7	1
Total Atlantic	100	80	34	16	31	6

1/ Basic information is catch per 5 minutes' trawling.
2/ Basic information is total area of fish schools in square feet per mile.

coastal waters and estuaries, (2) dense, conspicuous schools, (3) feeding on plankton, mainly phytoplankton, to subsist at the lower trophic levels, and (4) use as food by nearly all of the larger fishes, marine mammals, and birds. Although the role of menhaden in the ecosystem has been much discussed, little has been published on menhaden ecology.

5 FISHING

5.1 Fishing equipment

5.11 Gears, 5.12 Vessels, and 5.13 Methods

Atlantic menhaden are caught commercially with purse seines and pound nets; the latter method accounted for less than 4 percent of the total annual landings, 1947-67. Very small quantities, caught incidental to other species in gill nets, otter trawls, and haul seines, are used for bait or are discarded.

Purse seines have been the principal gear for catching menhaden since 1850 when reduction plants were built along the New England coast. The menhaden purse seine is 400 to 600 m. long and 20 to 35 m. deep. It is constructed of nylon or a similar synthetic twine and has meshes ranging from 3 to 6 cm. stretched measure. The net is carried in two purse-seine boats; each boat is about 11 m. long and 3 m. wide, and is equipped with gasoline or diesel engine and a hydraulic seine block (fig. 4).

The menhaden fleet is composed of carrier vessels that are 20 to 60 m. long and have a capacity of 50 to 600 tons. Their design has changed little during the past century. Forward are the wheelhouse, cabins, and galley; amidships is the large hold; and aft are the engine-room and boat davits. The vessels are distinguished by a tall mast topped with a prominent crow's-nest (fig. 5). Until about 1940 vessels were constructed of wood; since then they have been built of steel. The vessels

Table 8.--Contributions of Atlantic menhaden year classes, 1954-64, to landings by purse seiners

Year class	Years in the fishery	Contribution
	Number	Billions of fish
1954	8	1.7
1955	9	4.3
1956	9	3.8
1957	9	2.1
1958	8	7.9
1959	8	1.1
1960[1/]	7	2.0
1961	6	1.3
1962	5	1.5
1963	4	1.3
1964	3	1.6

1/ Total contributions, 1960-64, not available.

are powered with one or two diesel engines of 200 to 1,800 horsepower. From 1946 to the present, the fleet has included a number of converted auxiliary naval vessels, trawlers, and small coastal transports.

Fishing for Atlantic menhaden takes place during daylight, usually within 60 km. of the reduction plants. Vessels make daily trips to the fishing grounds. The vessels carry the purse seine boats in davits to and from the grounds and provide living accommodations for the fishermen. June (1963) described the method of fishing as follows:

"On the fishing grounds, the purse boats are lashed side by side, with half the seine in each boat, and towed behind the carrier. When a school has been selected for capture, the fishing captain and crew enter the purse boats and start out in the direction of the school. The spotter pilot keeps the captain informed of the movements of the school by radio contact and, at the appropriate moment, directs the two boats to separate. The seine is payed out as each boat completes a half circle to enclose the school. As soon as the two purse boats meet, the ends of the purse line are made fast and run through two snatch blocks attached to a heavy, lead weight called a tom. The tom is thrown overboard and closes the seine as it rides to the bottom. After pursing has been completed and the tom retrieved, the wings of the seine are hauled aboard by means of the power-driven blocks mounted in the purse boats. The fish are gradually concentrated in the bunt between the two purse boats. A small skiff, called the striker boat, is sometimes used to support the corkline, particularly when a heavy catch has been made. After the carrier vessel is brought alongside, a flexible suction hose is lowered into the net, and the fish are pumped into the hold. A number of carrier vessels are equipped with an electrical shocking device which attracts and immobilizes the fish around the end of the suction hose. Use of this gear not only increases the efficiency of the pumping operation, but minimizes the loss of large sets in which the fish cannot be raised because of their heavy weight."

Atlantic menhaden are caught in pound nets, principally in Chesapeake Bay and near Long Island, N.Y., and New Jersey. The nets are set for species other than menhaden, but in many localities the catch of menhaden is considered profitable to the fishermen. Menhaden frequently make up the most of the catch and, in spite of their low price per pound, are often first in value.

A pound net is a trapping device or weir made of netting hung on poles. A typical net has the following components: (1) a leader or hedging that usually is perpendicular to the shore, (2) two bays or hearts that concentrate the fish, (3) the funnel, and (4) the head or central impoundment. The net is tended daily by four to six men in a boat 10 m. long. Two men in a small skiff slack off the lines holding the head of the net to the poles whenever the catch is to be removed. The funnel is closed to prevent the escape of any fish, and the floor of the net is raised to concentrate the catch. The fish are then brailed into the boat.

The design and operation of pound nets have changed little since their introduction about 100 years ago. Net design has changed somewhat in recent years; the use of synthetic twines has reduced the number of poles needed. The first engines to power the boats were installed about 50 years ago. A few operators now use power winches for brailing, and some use pumps to set the large poles in deep water.

Historical accounts of the menhaden fishery from its inception in the early 1800's until

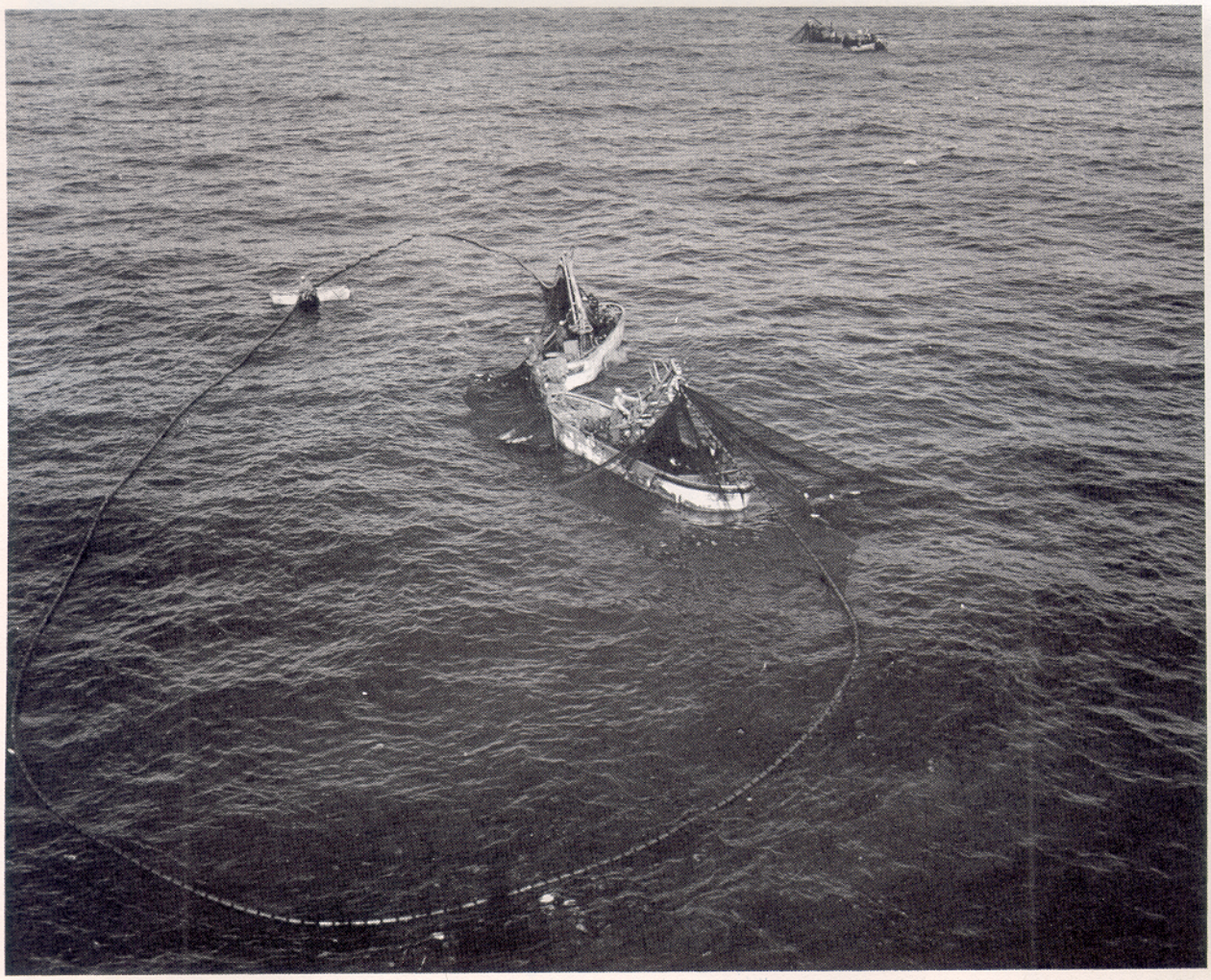

Figure 4.--Purse seine boats using hydraulic blocks to concentrate the catch into the bunt of the net.

1930 were given by Goode (1879), Goode and Clark (1887), Greer (1915), and Harrison (1931). Recent reviews of the fishery by June (1961b), Henry (1965), and Nicholson[4] described the changes that have affected the fishery in the past two decades.

The principal changes in vessels, gear, and methods are summarized in the following chronology:

1930 - Installation of internal combustion engines and power winches in the purse seine boats. By 1935 most of the fleet was so equipped.

1946 - Use of aircraft for spotting menhaden schools and directing purse seine boats. By 1955 the procedure of setting the net by radio communication between the airplane pilot and the purse seine boat personnel was widely established.

1946 - Use of pumps rather than brails to transfer the fish from the net to carrier vessel. By 1955 most vessels were equipped with fish pumps.

1947 - Construction of steel purse seine boats. Some steel boats were used successfully by larger vessels, but many captains returned to wooden boats after mishaps with the heavier boats.

[4] Unpublished manuscript "Changes in catch and effort in the Atlantic menhaden purse seine fishery, 1940-1966" by William R. Nicholson, Bureau of Commercial Fisheries Biological Laboratory, Beaufort, N.C. 28516. 36 pp.

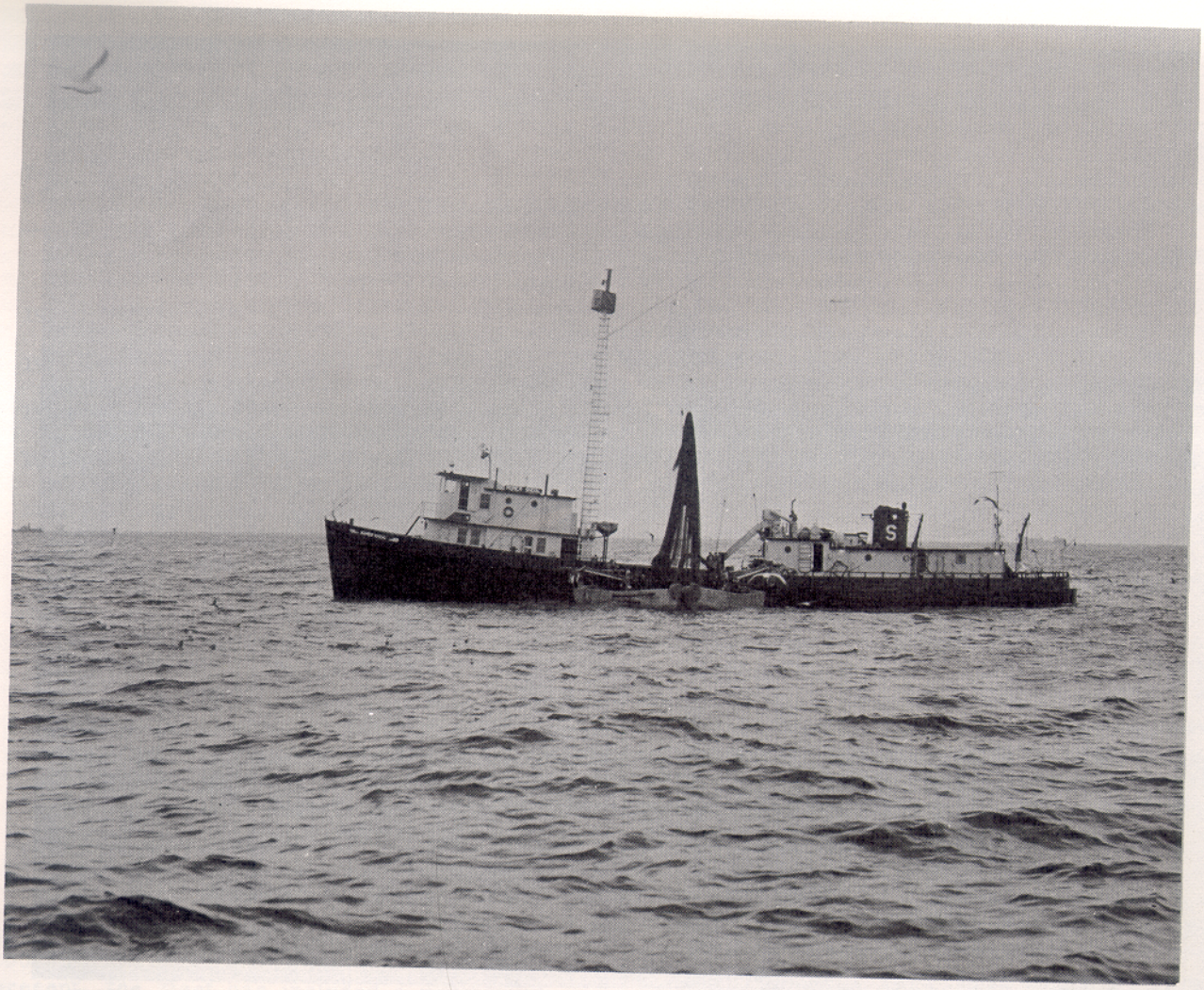

Figure 5.--Menhaden carrier vessel pumping fish into its hold. Two purse seine boats lie alongside with the seine. A powerblock is hauling aboard part of the net.

1954 - Use of nylon or similar synthetic twine in net construction. By 1958 few cotton nets remained in the fishery.

1957 - Attachment of electrical shocking devices to the intake hose of the fish pump. For the pump to work effectively, the fish in the net must be raised to the surface and concentrated. Whether lifting is done manually or mechanically, it is often difficult when the catch is large. A positive electrode was mounted on the intake hose of most vessels in the Middle Atlantic area by 1959. Electric current further concentrated the fish and held them during pumping (Kreutzer, 1959, 1964).

1957 - Installation of hydraulic blocks in purse seine boats. These aids followed shortly after the introduction of synthetic fibers that could withstand greater stress during mechanical hauling.

1958 - Construction of aluminum purse seine boats. These were immediately accepted despite their greater cost.

Many minor changes in the methods and equipment increased the effectiveness of fishing. Some of these were (1) increased power and greater speed of carrier vessels and purse boats, (2) more aircraft for scouting, and better communications for their directing the setting of the nets, (3) improved winches and blocks for handling the boats and the nets, and (4) better electronic navigation equipment.

5.2 Fishing areas

5.21 General geographical distribution

The fishing areas have changed over the years. From 1800 to 1850 fishing generally was limited to the inshore waters of Massachusetts, Rhode Island, Connecticut, and New York and in Chesapeake Bay. Menhaden were used for bait, oil, fertilizer, and to a limited extent for human food. Oil was first produced by allowing the fish to rot in casks. The demand for oil increased, and the process was hastened by cooking. Small factories were started in New England about 1850 when the purse seine was introduced. The introduction of the curb press followed in 1856. These changes increased the demand for fish; fishing shifted from the inland tidal waters to the ocean sounds and larger bays. Immediately after the Civil War, plants were started in southern New Jersey, Virginia, and North Carolina. By 1870 a well-developed fishery was established in the Gulf of Maine, and New England had scores of small plants. The fishery in the Gulf of Maine declined after 1879 and, except for a brief recovery in 1888-89 and in 1898, the industry was not reestablished until 1949 when menhaden again appeared in numbers. During the 1950's the fishery made a brief comeback, but by 1963 menhaden again had nearly disappeared in northern New England.

The Middle Atlantic Bight, including Delaware and Chesapeake Bays and the coast of North Carolina, has supported a sustained fishery since the latter part of the 19th century. Only recently, since 1965, have decreased numbers of menhaden caused the closing of plants and a great reduction in fishing in the region. From information provided by Goode (1879), Greer (1915), Harrison (1931), and recent observations, a summary of geographic distribution of reduction plants for selected years is given in table 9.

Table 9.--Distribution of menhaden reduction plants along the Atlantic coast in selected years, 1875-1967

State	Year					
	ca. 1875	1912	1929	1955	1965	1967
	Number					
Maine	22	1	-	2	-	-
Massachusetts	4	-	-	2	-	-
Rhode Island	13	-	-	1	-	-
Connecticut	5	-	-	1	-	-
New York	26	5	2	1	1	-
New Jersey	5	5	3	3	2	2
Delaware	-	2	3	2	1	-
Virginia	4	19	12	6	7	7
North Carolina	2	12	12	6	7	7
South Carolina	-	-	1	1	-	-
Georgia	-	-	1	-	-	-
Florida	-	1	2	3	2	2
Total	81	45	36	28	20	18

5.22 Geographic range

Atlantic menhaden range from latitude 46° N. to 27° N. along the Atlantic coast of North America, occurring mainly in the shallow waters overlying the Continental Shelf. The areas of greatest abundance are immediately adjacent to the major estuaries. Few have been caught more than 60 km. from land.

5.3 Fishing seasons

5.31 General pattern of season

The fishery for Atlantic menhaden is seasonal and closely related to the vernal warming and autumnal cooling of the coastal waters. Scouting and fishing by the seiner fleet depends upon the appearance of surface schools that are rarely seen before April and usually are last seen, off North Carolina, in late December and early January.

5.32 Dates of beginning, peak, and end of season

The fishing season begins earlier and ends later in the South Atlantic States than in the Middle and North Atlantic States. The earliest and latest landing dates for the purse seiners at each plant location, together with the month or months of peak production in 1952-67, are given in table 10. Pound nets are set in late March or in April after the threat of winter storms and ice is past. April, May, and October are the months of peak production. Nets are usually removed from the poles in November, and are rarely fished in December, January, and February.

Table 10.--Schedule of earliest and latest landing dates, and months of peak production in the purse seine fishery for Atlantic menhaden, 1952-67

Locality	Earliest date	Peak months	Latest date
Portland, Maine	June 18	August	September 13
Gloucester, Mass.	June 3	July-August	October 6
Point Judith, R.I.	May 24	July-August	October 13
Amagansett, N.Y.	May 25	July-August	October 20
Port Monmouth, N.J.	May 18	July-August	October 20
Tuckerton, N.J.	May 21	June-August	October 24
Wildwood, N.J.	May 16	June-September	October 31
Lewes, Del.	May 16	July-September	October 28
Reedville, Va. [1/]	May 25	June-August	November 19
Beaufort, N.C.	April 29	June-July, December	January 31
Southport, N.C.	April 28	June	January 7
Yonges Island, S.C.	May 28	June	October 17
Fernandina Beach, Fla.	March 23	June	December 9

1/ Regulations provide that no menhaden may be caught by purse seines in Chesapeake Bay for the manufacture of fish meal and oil between December 1 and the last Monday in May.

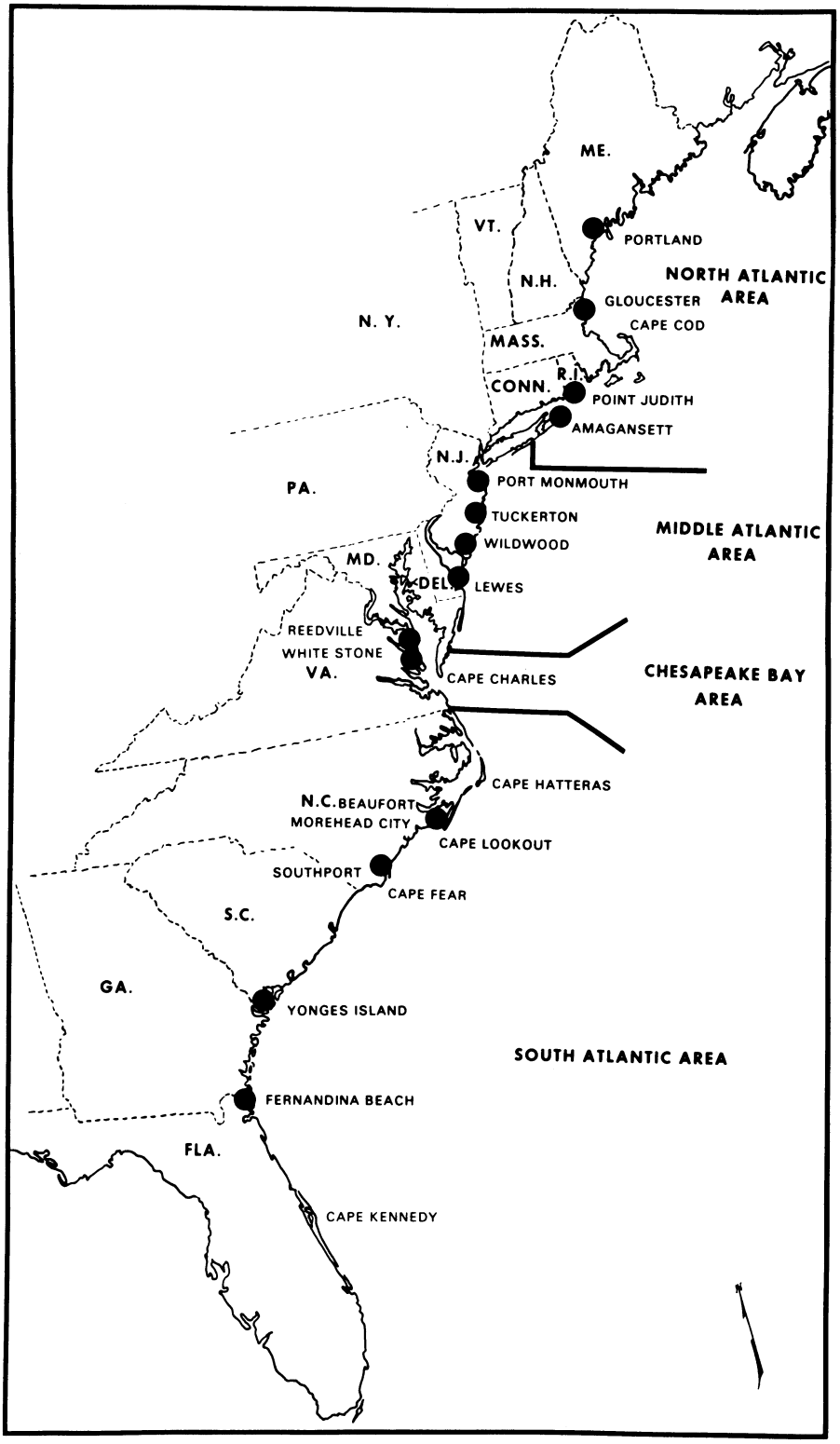

Figure 6.--Locations of reduction plants in 1955 (dots) and the areas for which statistics on catch and biology were compiled.

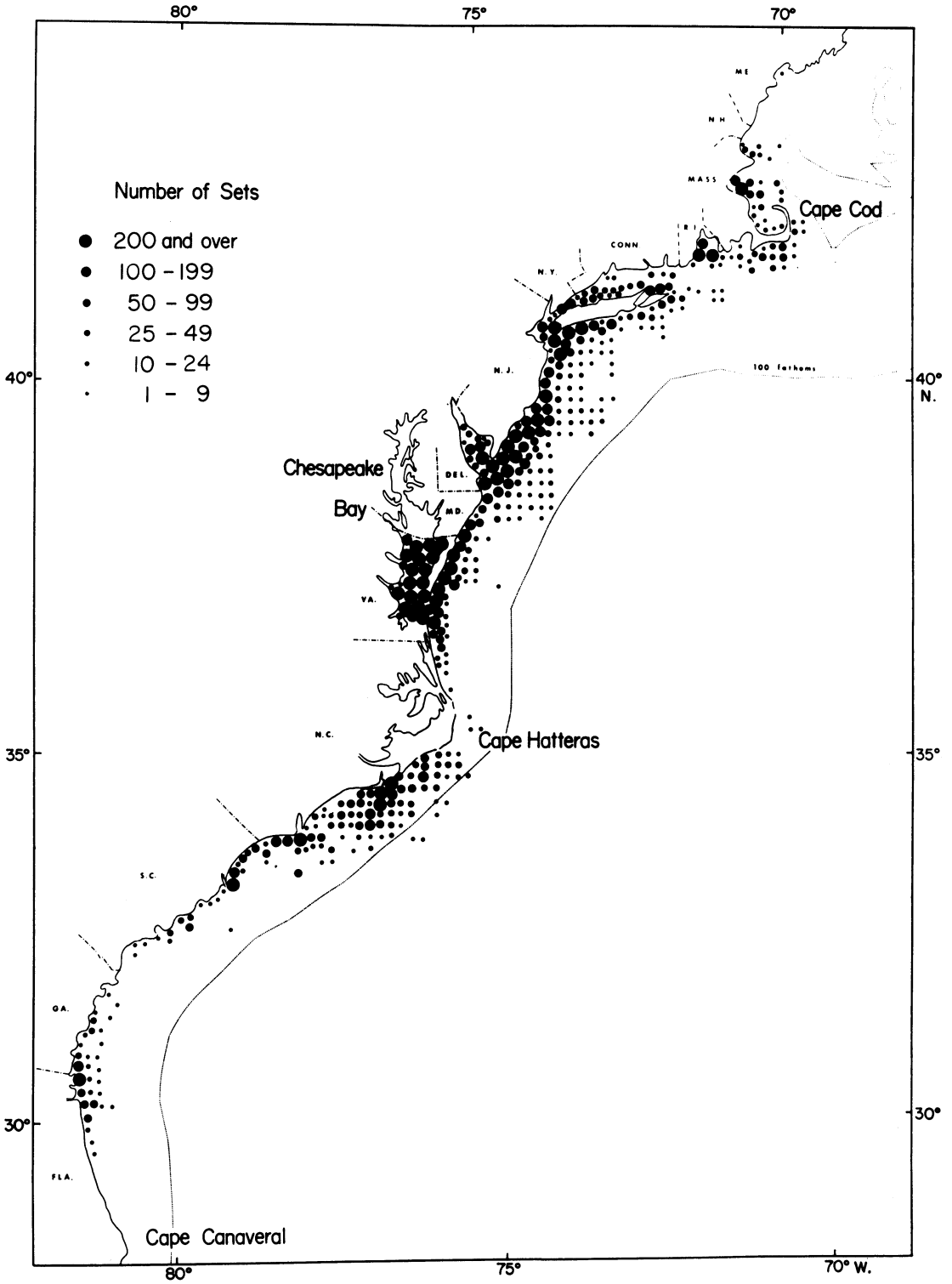

Figure 7.--Distribution of fishing activity during 1959 (after Nicholson and Higham, 1964a).

5.33 Variation in date and duration of season

Annual variation in the beginning and end of the menhaden fishing season depends on weather. Scouting and fishing by purse seiners depend upon visual detection of surface schools. As wind, rain, and fog can impede detection of fish and mobility of vessels, the season may be lengthened or shortened accordingly. The pound net season varies little, but storms may delay the beginning of the season or hasten its end. Since pound netting depends on a variety of fishes, the abundance of menhaden often has little effect on the length of the season.

Regulations affect the fishing season only in Chesapeake Bay. Purse seining is prohibited in Maryland waters; in the Virginia part of the Bay, menhaden may not be caught for the production of fish meal and oil between December 1 and the last Monday in May. Regulations do not effect the seasonal catch of menhaden with pound nets.

5.4 Fishing operations and results

5.41 Effort and intensity

Fishing effort has been compiled for menhaden purse seiners for the period 1940-66. Preliminary attempts to determine a valid measure of effort have involved the number of sets, number of vessel days, number of vessel weeks, and number of vessel months. Changes in fishing methods and equipment over the past 20 years (see section 5.1) have increased efficiency of the vessels so that comparisons of effort between years during this period must be made with caution. A direct comparison of effort in one area, within a season and for different seasons, with that in another area also is difficult because of fish movements, differences in age and size distributions, and changes in abundance. Nevertheless some trends are apparent regardless of the measures of effort that are used. In the North and Middle Atlantic areas of the fishery, effort generally increased after World War II and continued to rise until 1959. Since then effort has declined. In 1966 effort in the Middle Atlantic area was less than one-eighth the mean effort for the 25 preceding years and in the North Atlantic, less than one-half. Effort in Chesapeake Bay remained relatively stable until 1954, but then nearly doubled by 1964. Fishing effort off North Carolina generally has fluctuated widely in the fall without pronounced trends.

Catch per unit of effort has shown definite trends in each of the three areas. In the North and Middle Atlantic areas it rose to very high levels in the 1950's. About 1958 it began to decline, slowly at first, and then drastically after 1962. By 1966 it had declined to about one-tenth the high in the North Atlantic area and about one-fifth the high in the Middle Atlantic. Catch per unit of effort in Chesapeake Bay increased sharply after 1953, remained relatively high through 1962, then began a steady decline in 1963. In the South Atlantic and in the fall off North Carolina, fluctuations were wide, but trends were not pronounced.

5.42 Selectivity

Mesh selectivity is of little consequence in the menhaden fishery. Most purse seines for Atlantic menhaden are constructed of meshes of 65 mm., stretched measure, in the wings of the net and 35 mm. in the bunt. Such nets would permit many fish less than 100 mm. long to escape. Menhaden this small are seldom on the fishing grounds during the summer for they usually are in the shallow tributaries and streams.

Some selectivity is exercised by spotter pilots and fishermen, who avoid setting the nets on juvenile menhaden. Small menhaden can be avoided because the size of menhaden can usually be determined by the shape, size, and color of the school. Reduction plant operators are reluctant to process fish less than 130 mm. long due to the low oil and protein content.

5.43 Catches

Purse seine landings of Atlantic menhaden from 1940 to 1967 show the expansion and development of the fishery after World War II. The fishery experienced a decade (1953-62) of sustained production exceeding 500,000 metric tons annually. In 1963 a decline began that has continued to the present (table 11). Changes in catches in the Middle and North Atlantic areas were responsible for most of the increased production before 1962, as well as for the decline thereafter.

Pound net landings may reflect abundance of Atlantic menhaden in some years but usually show changes in the fishery brought about by the behavior of fishermen and the demand for menhaden. Production by this gear increased during the early 1950's to nearly 20,000 metric tons annually (table 12). Catches were mainly from the Middle Atlantic area (northern New Jersey) until 1957 when landings from Chesapeake Bay exceeded those to the north; landings from the Bay maintained this advantage through 1967.

Table 11.--Landings of Atlantic menhaden by purse seiners, by area and season 1940-67[1/]

Year	Area and season					
	South Atlantic (Summer)	Chesapeake Bay (Summer)	Middle Atlantic (Summer)	North Atlantic (Summer)	North Carolina (Fall)	Total
	Thousands of metric tons					
1940	38.1	35.4	91.2	16.8	36.7	218.2
1941	45.4	60.3	103.9	33.6	34.9	278.1
1942	33.1	21.8	78.0	14.5	20.0	167.4
1943	59.9	42.2	96.6	10.0	28.6	237.3
1944	47.2	32.2	122.5	27.7	28.6	258.2
1945	58.5	34.9	136.5	34.0	31.8	295.7
1946	40.8	57.6	183.7	43.1	37.2	362.4
1947	34.0	81.2	186.0	44.0	32.7	377.9
1948	55.8	68.5	137.4	44.5	40.4	346.6
1949	59.4	62.6	149.7	52.2	39.9	363.8
1950	20.0	63.0	142.9	49.4	21.8	297.1
1951	54.4	56.2	168.3	50.8	31.3	361.0
1952	86.2	45.8	193.2	58.1	26.3	409.6
1953	52.6	78.0	363.3	59.9	39.5	593.3
1954	39.5	126.1	335.7	64.9	41.7	607.9
1955	43.1	132.9	317.5	83.5	64.9	641.9
1956	68.5	93.9	378.3	98.4	73.0	712.1
1957	36.3	126.6	304.4	83.5	55.3	606.1
1958	41.3	151.5	211.4	35.8	70.3	510.3
1959	63.0	196.9	250.8	66.2	82.1	659.0
1960	36.8	108.4	255.8	66.2	62.1	529.3
1961	44.0	128.4	274.9	58.5	69.9	575.7
1962	42.2	155.1	249.9	64.9	25.9	538.0
1963	34.0	103.9	111.6	35.4	61.2	346.1
1964	46.7	133.8	35.4	16.8	39.0	271.7
1965	36.7	126.1	45.8	11.8	52.6	273.0
1966	24.5	115.7	5.9	1.8	71.7	219.6
1967	35.9	91.1	18.9	0	51.2	197.1

1/ Provisional data subject to minor revisions.

Table 12.--Landings of Atlantic menhaden by pound netters, by area, 1942-67

Year	Area			
	North Atlantic	Middle Atlantic	Chesapeake Bay	Total
	Metric tons			
1942	15	5,223	1,177	6,415
1943	28	6,142	1/	1/
1944	13	5,597	2,623	8,233
1945	44	5,250	6,740	12,034
1946	28	1/	4,081	1/
1947	46	6,127	3,324	9,497
1948	474	7,295	4,597	12,366
1949	215	6,056	4,029	10,300
1950	142	4,904	3,599	8,645
1951	28	14,650	3,341	18,019
1952	54	9,267	2,400	11,721
1953	41	22,415	2,564	25,020
1954	98	12,384	5,677	18,159
1955	50	9,940	3,829	13,819
1956	15	17,392	4,759	22,166
1957	15	10,312	12,535	22,862
1958	13	3,182	9,676	12,871
1959	32	7,806	10,522	18,360
1960	12	7,298	9,473	16,783
1961	15	8,144	9,881	18,040
1962	24	10,297	13,837	24,158
1963	9	5,971	14,546	20,526
1964	1	4,092	14,814	18,907
1965	4	3,035	15,917	18,956
1966	5	1,594	8,923	10,522
1967 2/	15	1,235	8,301	9,551

1/ Incomplete records.
2/ Preliminary source: U.S. Fish. Wildl. Serv. Statistical Digests.

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