Made in United States of America
Reprinted from AMERICAN FISHERIES SOCIETY
SPECIAL PUBLICATION NO. 3, 1966
pp. 50–58

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ABSTRACT

Menhaden, genus *Brevoortia*, use estuaries along the Atlantic and Gulf coasts of the United States as nursery areas for more than half of their first year of life. The Atlantic menhaden, *B. tyrannus*, and Gulf menhaden, *B. patronus*, support the largest fishery in North America and observations reported concern mainly these species. Spawning occurs in the Atlantic Ocean and Gulf of Mexico. After hatching and early development the larvae move into estuaries. The time spent in the ocean before entering the estuaries is not known. Larvae move into the tributaries near the upstream limits of saline water. Water temperatures below 3 C deter entry into the estuaries, inhibit movements into the tributaries, and cause mass mortalities. Temperatures below 3 C killed larvae confined in the laboratory at salinities of 24‰ but effects varied somewhat with acclimation temperatures. Larvae and juvenile menhaden were collected in salinities of 1‰ or less along the Atlantic and Gulf coasts of the United States. Along the south Texas coast juveniles survived salinities up to 60‰ but were killed by 80‰. Other physical, chemical, and biological factors affecting young menhaden are mentioned but supporting data are few. Literature citations include most of the publications on the estuarine phase of the menhaden's life history.

INTRODUCTION

Most common commercial and sport fishes of the Atlantic and Gulf States live in estuaries during part of their life cycle. None of these fishes are so widely distributed and abundant as the menhaden, genus *Brevoortia.* Menhaden support the largest commercial fishery in North America and also provide forage for many carnivores. Most, perhaps all estuaries from New England to the Mexican border are utilized by schools of juvenile menhaden. The association of menhaden with estuaries for the greater part of the first year of life appears to be a persistent, if not a necessary, aspect of the life history. References to the occurrence, distribution, and other aspects of the estuarine biology of menhaden not cited in this report are included in annotated bibliographies by Reintjes, Christmas, and Collins (1960) and Reintjes (1964a). Although this report principally concerns the Atlantic menhaden, and to a lesser extent the Gulf menhaden, a brief summary of the distribution of juveniles of additional species of menhaden is given to introduce the problems of menhaden and estuaries.

DISTRIBUTION

Young Atlantic menhaden, *B. tyrannus*, were recorded in Canada by Leim and Day (1959) but their occurrence in waters that far north was unusual. The customary range extends from the Gulf of Maine (Scattergood, 1948; Scattergood, Trefethen, and Coffin, 1951a, 1951b) to central Florida (Goode, 1879; June, 1958; Sutherland, 1963). Juvenile menhaden usually occupy the estuaries between these geographical limits from May to October. Juvenile yellowfin menhaden,[1] *B. smithi*, are limited in distribution from Sapelo Island, Georgia, to Tampa Bay, Florida (Suttkus, 1958; Springer and Woodburn, 1960; Reintjes, 1962, 1964b; Tabb and Manning, 1961, 1962). Young Gulf menhaden,[1] *B. patronus*, occurred in collections from southern Florida to the Mexican border; the principal region of abundance was from Apalachicola, Florida, to Galveston, Texas (Suttkus, 1956; Gunter, 1956; Reid, 1957; Arnold, Wheeler, and Baxter, 1960; Gunter and Christmas, 1960). Distribution of juvenile finescale menhaden, *B. gunteri*, seems to be only from Matagorda, Texas, to the Gulf of Campeche in the western Gulf of Mexico.

[1] Common names of two species of menhaden do not agree with American Fisheries Society (1960). "Yellowfin shad" was proposed by Hildebrand (1919) in the original description of *Brevoortia smithi* from specimens collected at Beaufort, N. C., where "shad" is the vernacular name for menhaden. No distinguishing common name is in use among fishermen in Florida, the only area where it is caught commercially. Therefore, yellowfin menhaden is used for greater conformance to the accepted generic common name. "Largescale menhaden" was proposed as the common name for *Brevoortia patronus*, probably to shorten "largescale Gulf menhaden" used by Hildebrand (1948). The deletion was a poor choice, for "Gulf menhaden" has been used as the common name for nearly a century (Goode, 1879; Jordan and Evermann, 1896).

The areas of principal abundance are limited to Copano Bay, Corpus Christi Bay, and Laguna Madre of Texas and Laguna Madre of Tamaulipas (Gunter, 1945; Hildebrand, 1948, 1955, 1958, 1963; Breuer, 1957; Simmons, 1957; Christmas and Gunter, 1960; Gunter and Christmas, 1960).

SPAWNING AND EARLY DEVELOPMENT

Atlantic menhaden spawn in oceanic waters along the Continental Shelf (Reintjes, 1961), including Long Island Sound (Perlmutter, 1939; Wheatland, 1956; Richards, 1959), Narragansett Bay (Herman, 1963), and the Gulf of Maine (Bigelow and Schroeder, 1953; Marak and Colton, 1961; Marak, Colton, and Foster, 1962). Some spawning apparently occurs every month from May to October off New York and New England, in March and April and again in September and October off the Middle Atlantic States, and from November through March off the South Atlantic States (Higham and Nicholson, 1964). Heaviest spawning apparently is off North Carolina.

Although the depth at which menhaden spawn is not known, eggs and larvae were collected in oblique tows from 70 m to the surface during cruises of the *Theodore N. Gill* (Reintjes, 1961). Personnel of the Institute of Marine Science of Virginia collected eggs and larvae in surface plankton tows in the Atlantic Ocean off the Virginia Capes (Massmann, Norcross, and Joseph, 1961, 1962, and personal communications).

Hatching of eggs and early development of larvae also occur in the ocean. Embryos and yolk-sac larvae from eggs collected in nets near Woods Hole, Massachusetts, were described and sketched by Kuntz and Radcliffe (1917). They concluded that eggs hatched in 2 days at 15 C, and that the yolk was absorbed completely 5 days later. The smaller size of larvae in the ocean than in the estuaries gives further evidence of oceanic spawning (June and Chamberlin, 1959; Reintjes, 1961; Massmann, Norcross, and Joseph, 1961, 1962; Pearcy and Richards, 1962).

MORPHOLOGICAL CHANGES DURING METAMORPHOSIS

Larvae undergo morphological changes when they transform into juveniles. At the time of entry into the estuaries, larvae are slender, transparent, and nearly colorless except for several rows of melanophores. Their fins are partially formed, they have no scales, and their mouths and eyes are large. In contrast, juveniles have deep bodies, well developed fins, ventral scutes, scales, and a large head. Internal changes during metamorphosis mainly concern the method of feeding and the digestive tract: gill rakers elongate and branch to form a basket-like sieve; a complex structure develops in the pharynx, presumably to accumulate the collected plankton; a muscular pyloric stomach or gizzard develops; and the intestinal tract elongates and coils. These changes are normally associated with the change from a selective, particulate-feeding carnivore to a nonselective, filter-feeding omnivore. No description has been published of late larval development or metamorphosis of Atlantic menhaden. Suttkus (1956) described the development and transformation of Gulf menhaden with proportional measurements, photographs, and detailed accounts of fin formation, pigmentation, and other external characters. Generally, the species are similar except for size. Apparently, Gulf menhaden are smaller than Atlantic menhaden at all stages of development from embryo to adult.

TIME OF ENTRY INTO THE ESTUARINE NURSERY AREA, AND SIZE

Larvae enter estuaries from May to October in the New England States (Kuntz and Radcliffe, 1917; Perlmutter, 1939; Warfel and Merriman, 1944; Bigelow and Schroeder, 1953; Wheatland, 1956; Richards, 1959; Herman, 1963); the period is October to June in the Middle Atlantic States (Hildebrand and Schroeder, 1928; Pearson, 1941; Massmann, 1953, 1954; DeSylva, Kalber, and Shuster, 1962); and December to May in the South Atlantic States (Deubler, 1958; Tagatz and Dudley, 1961). Larvae were 14 to 34 mm, fork length, when they entered the estuaries. At Indian River Inlet, Delaware, 1958–61, the earliest time of entry was October 25 and the latest, June 11. The mean monthly catch per haul and range of fork lengths for these Indian River fish are given in Table 1.

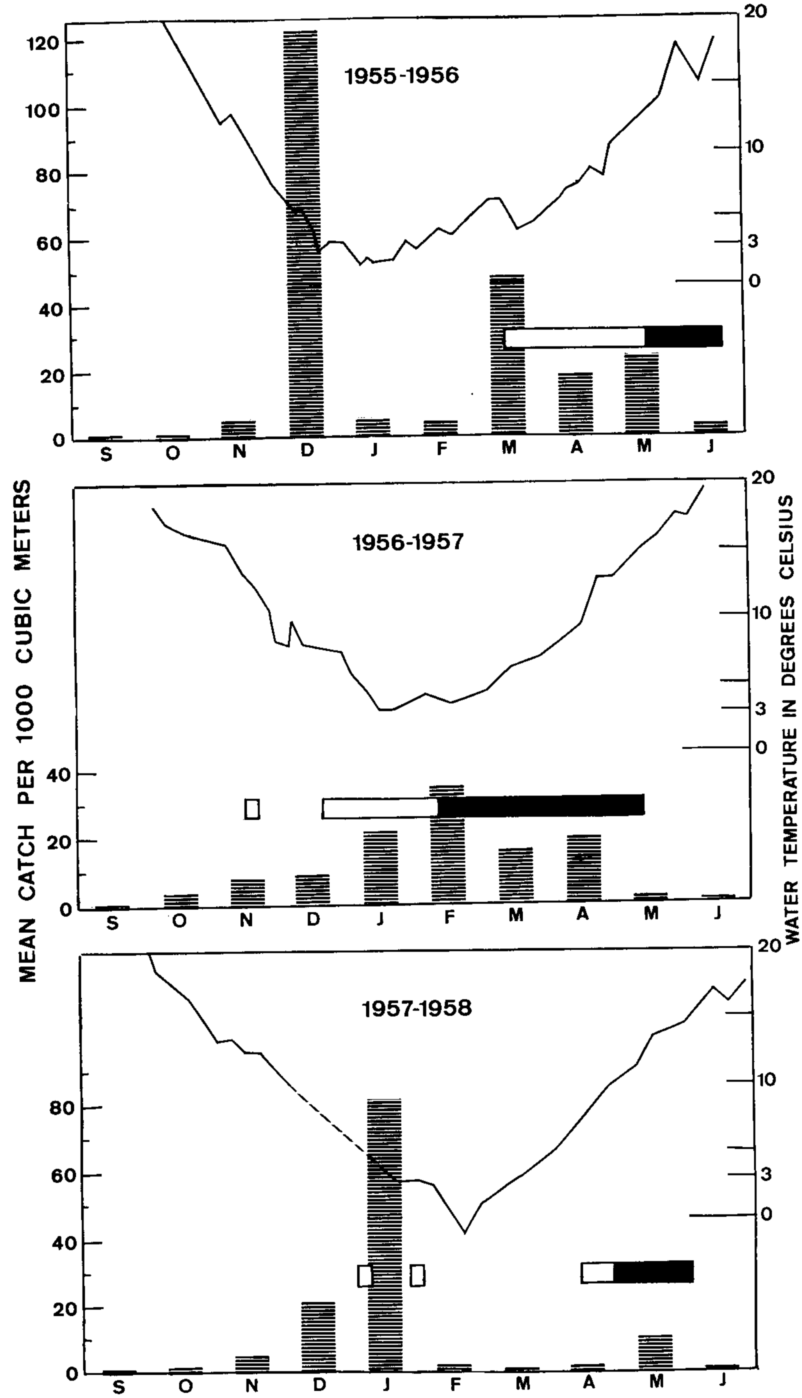

FIGURE 1.—Catches of menhaden larvae and water temperatures in the inlet compared to catches of larvae in a tributary, by month, Indian River, Delaware, 1955–58. The vertical bars represent monthly weighted geometric mean catches of larvae at the inlet during night flood tides. The horizontal bars represent weekly catches at the nursery area (open for 1 to 10 and solid for more than 10). The line graph shows the weekly mean water temperatures at the inlet during flood tides (from Pacheco MS).

EFFECTS OF TEMPERATURE AND SALINITY ON MENHADEN

The combined influence of weather, tides, and river flow can subject estuarine organisms to rapid changes in temperatures and salinities. The effects of temperature and salinity on marine and brackish water animals has been reviewed by Kinne (1963, 1964). He stated (1963, p. 301):

> "Temperature and salinity are two of the most potent physical factors in the life of marine and brackish water organisms. They largely characterize the physico-chemical properties of a given body of water. It has become increasingly evident from numerous papers that both factors should be considered together. There exists a complex correlation between the biological effects of temperature and salinity, the 'temperature-salinity relation' (tsr): temperature can modify the effects of salinity and change (enlarge, narrow, shift) the salinity range of an organism, and salinity can modify the effects of temperature accordingly. . . ."

Although menhaden occur in a wide range of temperatures (0 to 40 C) and salinities (0 to 60‰) the effects of these extremes on survival, metamorphosis, and growth are not well known, and even less is known of the combined effects of temperature and salinity.

Temperature

The collections at Indian River, Delaware, appeared to show a relation of temperature to time of entry into the estuary and, subsequently, to movements and survival within the estuary. The water temperatures, catches of larval menhaden at the inlet and catches at a nursery area nearly 12 miles above the inlet at the base of Millsboro Dam were compared from December to June, 1955–56 and from September to June, 1956–61[2] (Figs. 1 and 2). Comparison of the occurrences of the larvae at the inlet with their subsequent appearances or absences in the tributary nursery area indicate that a water temperature 3 C may be critical. This conclusion is in agreement with June and Chamberlin (1959).

TABLE 1.—*Mean monthly catch per plankton net tow of Atlantic menhaden larvae and range of fork lengths in mm (in parentheses) from Indian River, Delaware, 1958–61*
[From Pacheco]

Month	Year 1958–59	1959–60	1960–61
October	—	4.5 (15–25)	—
November	—	2.2 (15–25)	1.9 (18–26)
December	0.8 (18–25)	156.6 (18–33)	69.3 (21–34)
January	0.5 (25)	428.8 (14–31)	66.0 (21–32)
February	1.0 (24–26)	441.1 (14–31)	—
March	153.6 (17–28)	47.9 (15–32)	0.7 (21–26)
April	34.5 (19–32)	40.8 (17–31)	2.3 (19–33)
May	1.7 (31–40)[1]	6.0 (21–43)[1]	8.6 (23–32)

[1] Menhaden more than 34 mm, fork length, are transforming into juveniles; 4 were taken in May 1959 and 14 in May 1960.

On the basis of these field observations, the effects of different low temperatures on larval Atlantic menhaden for various initial or acclimation temperatures were tested in the laboratory (Lewis, 1965). Larvae were acclimated at five temperatures from 7.0 to 20.0 C and were exposed to temperatures from 0.0 to 6.0 C at half-degree intervals. Salinities were held at 24‰ during the tests. The results are briefly, as follows:

> If the test temperature reached 3 C or less, 50 per cent of the larvae died within 1½ days.
> If the acclimation temperature was 10 C or warmer, a greater number died at 3 C and 50 per cent were killed at 4.5 C.
> Cooling to 1.5 C for less than 12 hours was tolerated by most of the larvae if the acclimation temperatures were below 15 C.

These results indicated that larval menhaden can suffer mass mortalities when water temperatures fall below 3 C for several days or chill rapidly to 4.5 C.

Salinity

Young and adult menhaden tolerate a wide range of salinities, from the fresh water of coastal rivers to high-salinity lagoons (Hildebrand, 1948; Reid, 1955; Gunter, 1956; Breuer, 1957; Simmons, 1957; Gunter and Christmas, 1960). Atlantic menhaden larvae migrate from the ocean where the salinities range from 33 to 36‰ into tributaries near

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[2] Catches of postlarval Atlantic menhaden, *Brevoortia tyrannus*, at Indian River, Delaware. Unpublished manuscript by Anthony L. Pacheco.

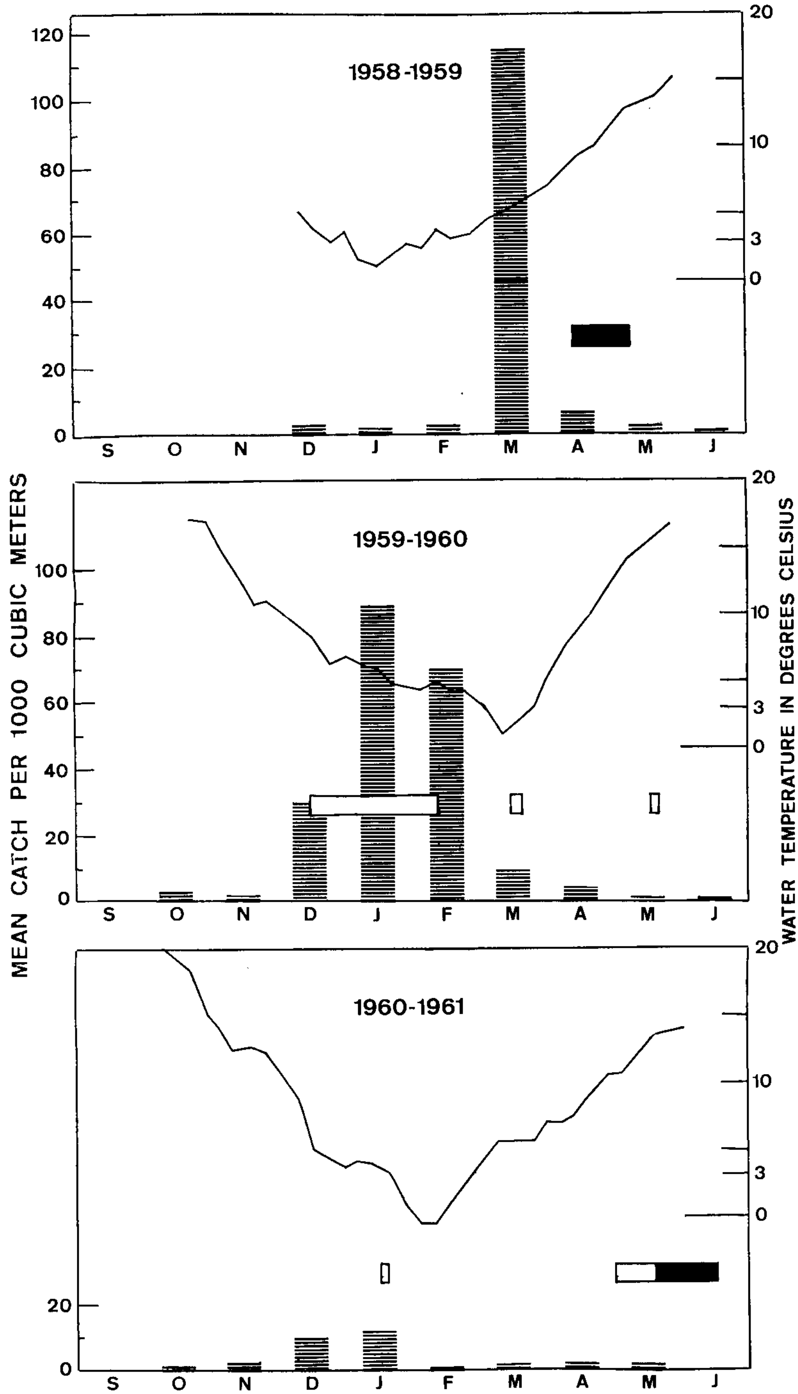

FIGURE 2.—Catches of menhaden larvae and water temperatures in the inlet compared to catches of larvae in a tributary, by month, Indian River, Delaware, 1958–61. The vertical bars represent monthly weighted geometric mean catches of larvae at the inlet during night flood tides. The horizontal bars represent weekly catches at the nursery area (open for 1 to 10 and solid for more than 10). The line graph shows the weekly mean water temperatures at the inlet during flood tides (from Pacheco MS).

the boundary of fresh and salt water where the salinity falls to 1‰ or less (Massmann, Ladd, and McCutcheon, 1954; June and Chamberlin, 1959; Pacheco and Grant, 1965). This tolerance was demonstrated when juvenile menhaden became landlocked in a freshwater reservoir in South Carolina and survived several years to grow to a large size; they gave no evidence of reproduction, however (R. L. Stevens, personal communication).

Mass movements of larvae from the ocean to estuaries for subsequent transformation and growth led to the speculation that lower salinities were required for metamorphosis (June and Chamberlin, 1959). No transforming menhaden were encountered at sea, but larvae undergoing metamorphosis were in tributaries of lower salinities. In 1962 and 1964 however, larvae kept in the laboratory at Beaufort, N. C., completed metamorphosis in salinities at 25 to 40‰. These results indicated that low salinities may not be essential for transformation as was previously thought. Dissection and X-ray examination of the juveniles showed none of the deformities that appeared in the earlier attempt to hold larvae in the laboratory at normal ocean salinities (June and Chamberlin, ibid.).

Observations of menhaden in hypersaline estuaries are limited to the Laguna Madre of Texas where both *B. patronus* and *B. gunteri* were regularly taken in salinities from 20 to 60‰, but rarely above (Simmons, 1957). Simmons also reported mass mortalities, apparently due to salinities of 80‰ or greater. Salinities exceeding 36‰ are rare in Atlantic coast estuaries, and we have no observations or reports of tolerances to high salinity by Atlantic menhaden.

OTHER FACTORS AFFECTING MENHADEN

Many other factors in the environment in addition to temperature and salinity undoubtedly affect the behavior and well-being of menhaden. Some physical factors are light, tides, waves, currents, and turbidity. Light is needed for food production and vision. Tides, waves, currents, and turbidity can influence the suitability of the habitat, as well as the distribution of fish and their feeding. Some of the chemical factors are oxygen, carbon dioxide, hydrogen sulfide, hydrogen-ion concentration, inorganic salts, and organic compounds. Mass mortalities of menhaden have been attributed to oxygen depletion but the suspicion was not confirmed. Generally, no published information is available concerning the effects of physical and chemical factors on Atlantic menhaden.

Food is probably the principal biological factor affecting the well-being of menhaden in an estuary. Zooplankton is the principal food of larval menhaden. During metamorphosis their feeding changes from selective predation upon individual animals to indiscriminant filter-feeding, and their food becomes predominantly diatoms and dinoflagellates with some smaller zooplankters.[3] Their complex branchial filtering apparatus seems capable of retaining nannoplankton, including bacteria. A description of this structure by Monod (1961) supports this view. Peck (1894), who described the food and feeding of juvenile and adult Atlantic menhaden, concluded that their planktonic food had the same species composition as the natural plankton except for the larger and more agile organisms. According to Darnell (1958, 1961), juvenile Gulf menhaden feed on phytoplankton, small crustaceans, and detritus and do some grazing directly upon *Anabaena*, a dense floating scum in Lake Pontchartrain, Louisiana. Menhaden may feed on the bottom as is shown by the presence of detritus, sand, mud, clay, and benthic diatoms (Peck, 1894; Anderson, Jonas, and Odum, 1958).

Crowding sufficient to produce intense competition for space or for food and dissolved oxygen either among menhaden or with other species may restrict populations significantly in the limited nursery areas of many estuaries. Menhaden school from the time of entry into the estuary as larvae, and school size varies with fish size, turbidity, turbulence, and other factors, including predation. The number of schools in an estuary apparently is determined by the suitability of the estuary and by the year-class abundance.

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[3] Food and feeding habits of Atlantic menhaden in relation to the metamorphosis from larval to post-larval stages. Unpublished manuscript by Fred C. June and Frank T. Carlson, U. S. Fish and Wildlife Service, Bureau of Commercial Fisheries Biological Laboratory, Beaufort, N. C.

Juvenile menhaden are preyed upon by many marine carnivores. Some authors (Goode, 1879; Ellison, 1951; Bigelow and Schroeder, 1953) were impressed by the importance of young menhaden as a food for other fishes, but the effects of predation upon the menhaden populations are not known. The principal carnivores reported are bluefish, *Pomatomus saltatrix* (Goode, 1879; Hildebrand and Schroeder, 1928; Ellison, 1951; Bigelow and Schroeder, 1953; Grant, 1962), striped bass, *Roccus saxatilis* (Merriman, 1937; Hollis, 1952), bluefin tuna, *Thunnus thynnus* (Crane, 1936), and sharks (Field, 1907; Bigelow and Schroeder, 1953).

Parasites and diseases are among the more obvious biological factors affecting menhaden, but their role is not well known. Adult Atlantic menhaden often are heavily parasitized by copepods on the body surface and gills (Wilson, 1905, 1915, 1917, 1922, 1932), by monogenetic trematodes on the gills (McMahon, 1963), by digenetic trematodes in the intestine (Linton, 1901, 1905, 1940), by isopods in the buccal cavity (Richardson, 1905), and by sporozoans in the testes (Hardcastle, 1944). Apparently infestation originates, or at least the parasites become noticeable, during the estuarine phase of the life history. Westman and Nigrelli (1955) stated, "Parasites, especially those found on the gills, may contribute to an early demise of fish whose resistance has been considerably reduced by abnormal conditions of the environment such as high temperatures, lowered salinity and other chemical and physical factors leading to an 'imbalance' of the biocenose." Hardcastle (1944) found more than 50 per cent of testes infested with a sporozoan. He stated that the extensive infection could cause sterility. That mass mortalities may be attributable to diseases has been suggested by Westman and Nigrelli (1955). They reported, "The annual, heavy mortality of menhaden in the waters adjacent to New York Harbor occurs in late May and June when millions of fish die and litter the beaches. Dying fish, called 'spinners', are characterized by a loss of coordinated movements and exophthalmia of one or both eyes. Hemorrhages, caused by gas emboli, were noted in the capillaries of the gills, eyes, and optic lobes of the brain. The culture tests of the scales, and the feeding of stomachs and intestines to experimental cats, yielded negative results."

Estuaries apparently are an important habitat for young menhaden. The physical, chemical, and biological factors of this environment affect and in some way determine the populations of menhaden. The number and size of Atlantic and Gulf coast estuaries and the suitability for menhaden are of vital importance to the resource.

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