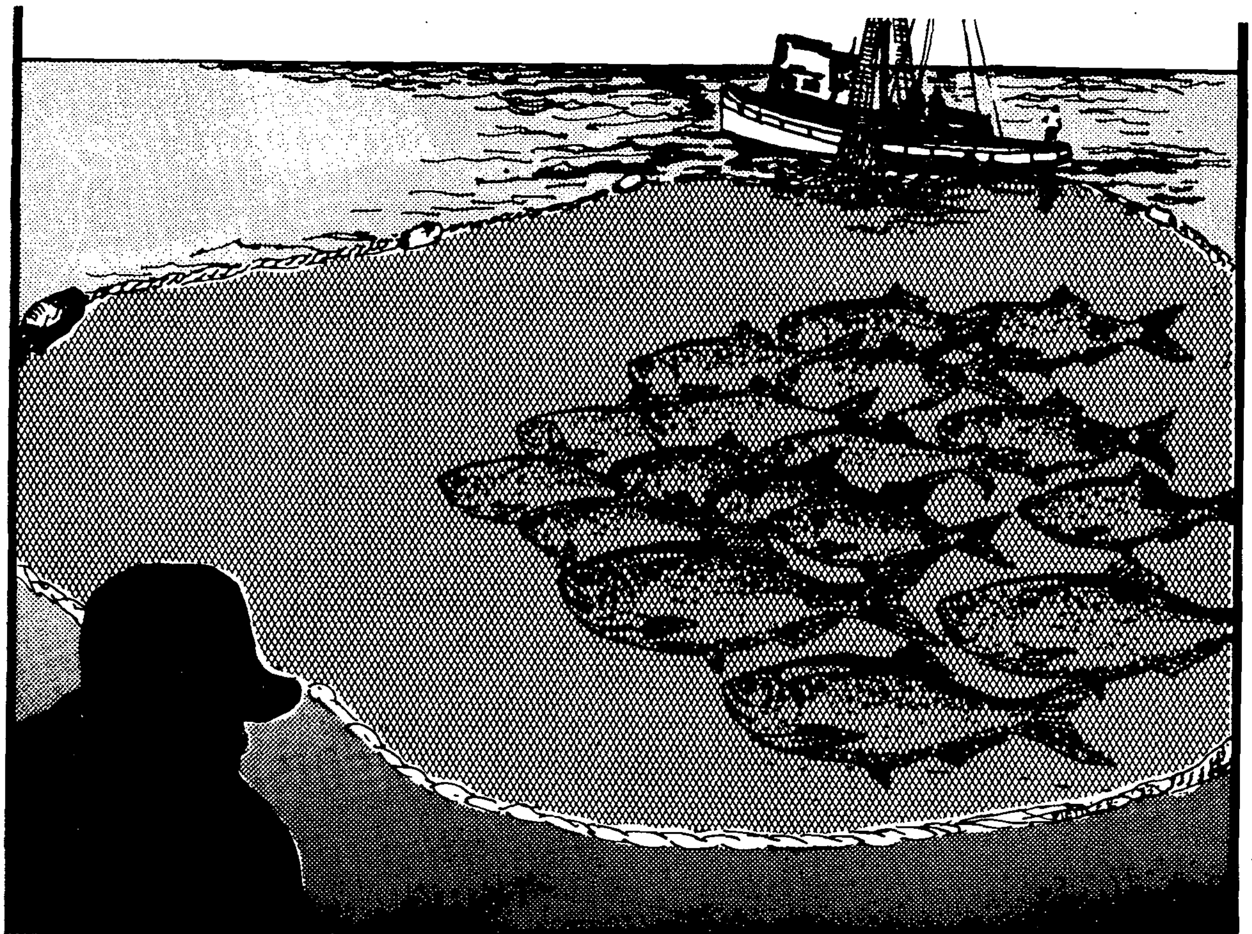

Fish and Wildlife Service

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Coastal Ecology Group
Waterways Experiment Station

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Species Profiles: Life Histories and Environmental Requirements of Coastal Fishes and Invertebrates (Mid-Atlantic)

ATLANTIC MENHADEN

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PREFACE

This species profile is one of a series on coastal aquatic organisms, principally fish, of sport, commercial, or ecological importance. The profiles are designed to provide coastal managers, engineers, and biologists with a brief comprehensive sketch of the biological characteristics and environmental requirements of the species and to describe how populations of the species may be expected to react to environmental changes caused by coastal development. Each profile has sections on taxonomy, life history, ecological role, environmental requirements, and economic importance, if applicable. A three-ring binder is used for this series so that new profiles can be added as they are prepared. This project is jointly planned and financed by the U.S. Army Corps of Engineers and the U.S. Fish and Wildlife Service.

Suggestions or questions regarding this report should be directed to one of the following addresses.

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CONVERSION TABLE

Metric to U.S. Customary

Multiply	By	To Obtain
millimeters (mm)	0.03937	inches
centimeters (cm)	0.3937	inches
meters (m)	3.281	feet
meters (m)	0.5468	fathoms
kilometers (km)	0.6214	statute miles
kilometers (km)	0.5396	nautical miles
square meters (m^2)	10.76	square feet
square kilometers (km^2)	0.3861	square miles
hectares (ha)	2.471	acres
liters (l)	0.2642	gallons
cubic meters (m^3)	35.31	cubic feet
cubic meters (m^3)	0.0008110	acre-feet
milligrams (mg)	0.00003527	ounces
grams (g)	0.03527	ounces
kilograms (kg)	2.205	pounds
metric tons (t)	2205.0	pounds
metric tons (t)	1.102	short tons
kilocalories (kcal)	3.968	British thermal units
Celsius degrees (°C)	1.8(°C) + 32	Fahrenheit degrees

U.S. Customary to Metric

Multiply	By	To Obtain
inches	25.40	millimeters
inches	2.54	centimeters
feet (ft)	0.3048	meters
fathoms	1.829	meters
statute miles (mi)	1.609	kilometers
nautical miles (nmi)	1.852	kilometers
square feet (ft^2)	0.0929	square meters
square miles (mi^2)	2.590	square kilometers
acres	0.4047	hectares
gallons (gal)	3.785	liters
cubic feet (ft^3)	0.02831	cubic meters
acre-feet	1233.0	cubic meters
ounces (oz)	28350.0	milligrams
ounces (oz)	28.35	grams
pounds (lb)	0.4536	kilograms
pounds (lb)	0.00045	metric tons
short tons (ton)	0.9072	metric tons
British thermal units (Btu)	0.2520	kilocalories
Fahrenheit degrees (°F)	0.5556 (°F - 32)	Celsius degrees

CONTENTS

	Page
PREFACE	iii
CONVERSION TABLE	iv
ACKNOWLEDGMENTS	vi
NOMENCLATURE/TAXONOMY/RANGE	1
MORPHOLOGY/IDENTIFICATION AIDS	1
REASON FOR INCLUSION IN SERIES	3
LIFE HISTORY	3
Adult Migration and Spawning	3
Fecundity	4
Eggs and Larvae	4
Juveniles and Adults	6
GROWTH CHARACTERISTICS	7
THE FISHERY	9
History	9
The Catch	9
Management	10
Subpopulations	11
ECOLOGICAL ROLE	12
ENVIRONMENTAL REQUIREMENTS	13
Temperature, Salinity, and Dissolved Oxygen	13
Substrate and System Features	14
Environmental Contaminants	15
Other Factors	15
LITERATURE CITED	17

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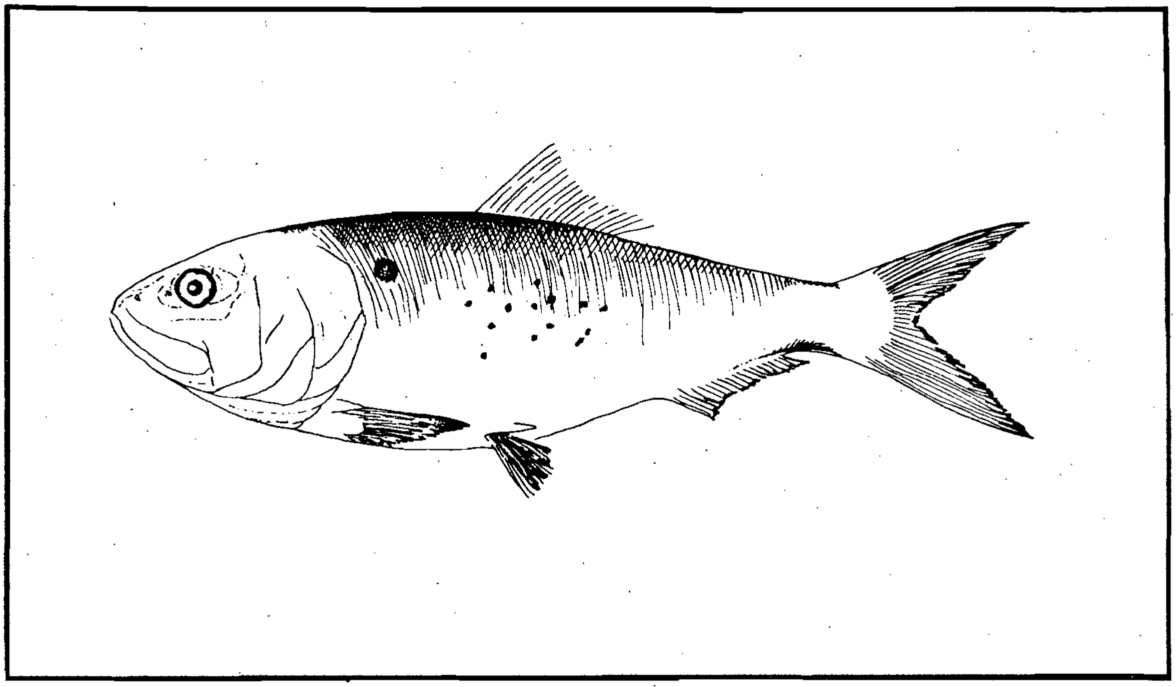

Figure 1. Atlantic menhaden.

ATLANTIC MENHADEN

NOMENCLATURE/TAXONOMY/RANGE

Scientific name: Brevoortia tyrannus (Latrobe)
Preferred common name.........Atlantic menhaden (Robins et al. 1980; Figure 1)
Other common names: pogy, moss-bunker, bunker, fat-back, shad, bug-mouth
Class.....................Osteichthyes
Order.....................Clupeiformes
Family............Clupeidae (herrings)

Geographic range: Temperate coastal waters from Nova Scotia southward to Jupiter Inlet, Florida (Dahlberg 1970). Atlantic menhaden are seasonally abundant in the Mid-Atlantic Region (Figure 2). Concentrations of age 0 fish occur in inshore estuarine waters along the entire Atlantic seaboard.

MORPHOLOGY/IDENTIFICATION AIDS

Branched dorsal rays, 13-18; branched anal rays, 16-22; pectoral rays, 14-18; pelvic rays, 7; gill filaments, 51-66; lateral line scales, 40-50; ventral scutes, 29-34; vertebrae, 44-49. Body oblong and compressed with a thin belly wall; scales large, coarse, with long slender pectinations, strongly overlapping and in regular rows; predorsal scales on either side of median line enlarged; prominent radiating opercular striations; and pelvic fin rounded with innermost and outermost rays about equal in length (Hildebrand 1963; Dahlberg 1970, 1975).

Color in life: green, brown, or blue-gray, darker on dorsal surface. A dark humeral spot may be followed posteriorly by a series of smaller

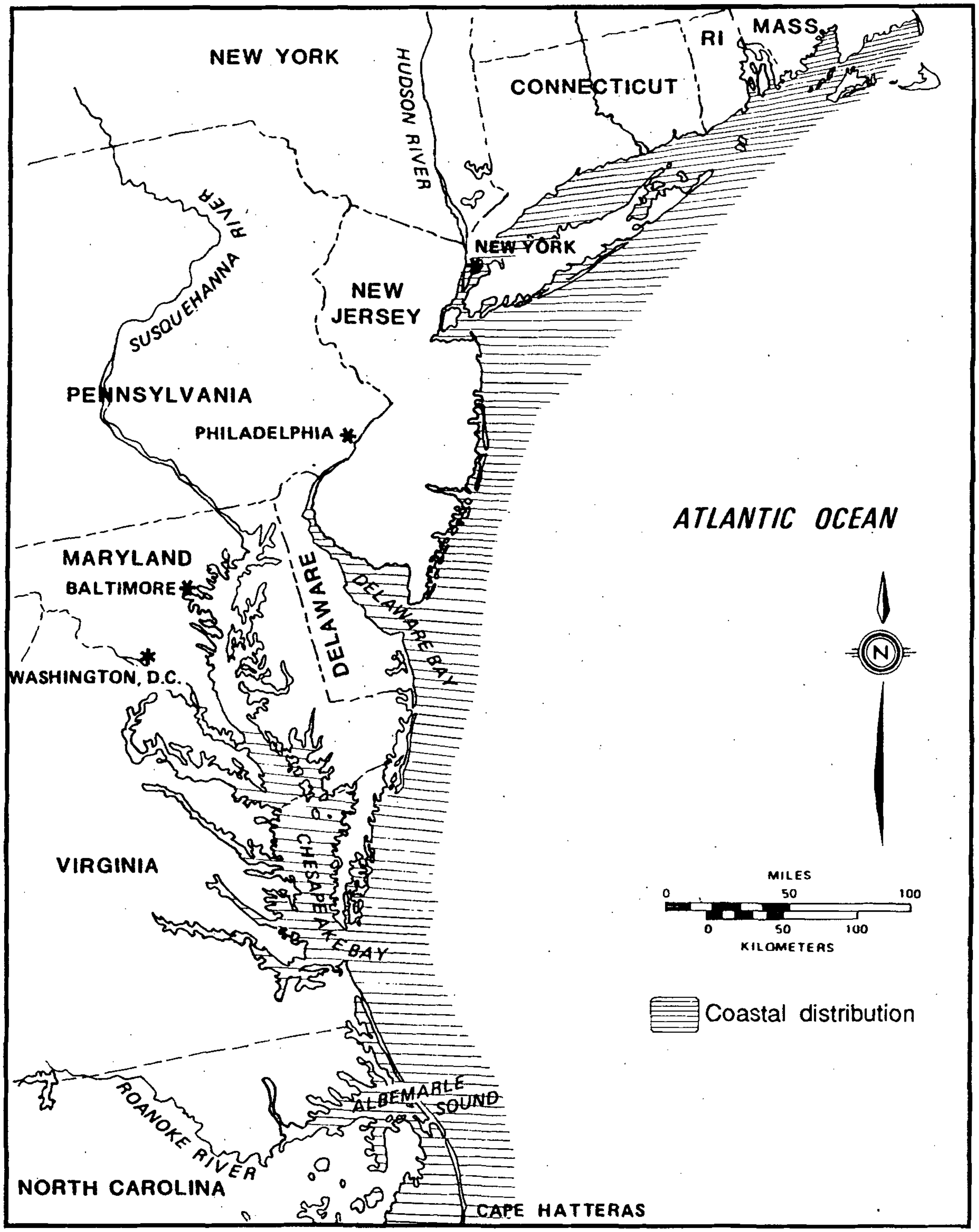

Figure 2. Distribution of the Atlantic menhaden in the Middle Atlantic Region, eastern United States.

spots which can fade readily upon capture. Brevoortia tyrannus can be distinguished from B. smithi (yellowfin menhaden, the only other North American coast species) because B. tyrannus has a frontal groove, larger and coarser scales in regular rows (therefore, lower scale-related counts), pointed (versus rounded) scale pectinations, a row of lateral spots behind the humeral spot, more gill filaments on the ceratobranchial arch, rounded pelvic fins, and opercular striations. The caudal fin of B. smithi is bright yellow, whereas the caudal fin of B. tyrannus is not. Fresh B. tyrannus may have a darker anal fin and more body mucus than does B. smithi. Atlantic menhaden can be distinguished from F_1 hybrid Atlantic menhaden (Brevoortia smithi x B. tyrannus) by its longer frontal groove, lateral spots (absent to few in hybrid), and a rounded ventral fin. Dahlberg (1970, 1975) provided additional measurements and descriptions of qualitative characters. Jones et al. (1978) gave detailed descriptions of Atlantic menhaden developmental stages (egg through adult). Hettler (1984) gave meristic and morphometric descriptions of Atlantic menhaden larvae and juveniles.

REASON FOR INCLUSION IN SERIES

Atlantic menhaden constitute about 25% to 40% of the combined annual landings of Atlantic coast and Gulf of Mexico menhaden species, which collectively comprised the largest commercial fishery by weight and eighth largest in dollar value in 1984 in the United States (NMFS 1985). They are important prey for many other fish species and are seasonally important components of estuarine and shelf fish assemblages. Atlantic menhaden depend on habitats along the entire eastern seaboard and adjacent shelf waters throughout their life cycle and use estuaries as nursery areas. Some spawning occurs in estuarine zones and nearshore shelf waters northward from Chesapeake Bay. Due to the species' great abundance, extensive migration patterns, and importance as a prey species, the Atlantic menhaden influences the conversion and exchange of energy and organic matter within biological systems throughout its range (Peters and Schaaf 1981; Lewis and Peters 1984).

LIFE HISTORY

Terminology used to describe life history stages conforms to that used by Lewis et al. (1972) and Moyle and Cech (1982).

Adult Migration and Spawning

Knowledge of timing and location of spawning has been mainly obtained from collections of adult females that were spent or contained maturing ova (Higham and Nicholson 1964; June 1965; Dahlberg 1970) as well as from collections of eggs and larvae (Reintjes 1961, 1968; Herman 1963; Kendall and Reintjes 1975; Ferraro 1980a,b; Judy and Lewis 1983). Data on movement and population age or size structure have been obtained from distribution of purse-seining effort (Roithmayr 1963); frequencies of lengths, weights, and ages in catches (June and Reintjes 1959; June 1972; Nicholson 1971, 1972); and returns from extensive tagging experiments (Dryfoos et al. 1973; Kroger and Guthrie 1973; Nicholson 1978). Atlantic menhaden undergo extensive north-south seasonal migrations and inshore-offshore movements along the Atlantic seaboard. Schools are composed of fish of similar size and age. Migration patterns are also related to spawning habits, and some spawning occurs every month of the year.

Atlantic menhaden of all ages congregate off North Carolina from

November to March and some spawn there in shelf waters that are 100 to 200 m deep, probably within 70 m of the surface (Reintjes and Pacheco 1966). All eggs of Atlantic menhaden collected by Judy and Lewis (1983) were taken at depths of 10 m or less. The spawning is heaviest off Cape Lookout, North Carolina, from December through February. Adults then move inshore and northward in spring and stratify by age and size along the Atlantic seaboard. Adult menhaden have been collected from estuaries, and some move as far inland as the brackish-freshwater boundary. The oldest and largest fish migrate the farthest, some moving as far north as the Gulf of Maine. Adults that remain in the South Atlantic Region move southward and reach northern Florida by fall. Representatives of all age classes return to the shelf waters of the South Atlantic Region in late fall.

During migration northward in spring, spawning occurs progressively closer inshore; by late spring, some fish spawn within coastal embayments of the North Atlantic Region. There are definite spring and fall spawning peaks in the Middle and North Atlantic Regions, and some spawning occurs during the winter in the shelf waters of the Mid-Atlantic Region. Temporal and spatial segregation of spawning activity provides a mechanism for the existence of races (= subpopulations). Higham and Nicholson (1964) and Schaaf (1979) have speculated that a female may spawn more than once in a season.

Fecundity

Higham and Nicholson (1964) reported values of 38,000 to 631,000 ova per fish, and June (1961a) gave values of 40,000 to 700,000 ova per fish; estimates depend on the size of the fish. Dietrich (1979) reported fecundities of 116,000 to 568,000 ova per fish at age I to age V, respectively (Table 1). Higham and Nicholson (1964) gave the following equation for the estimation of fecundity (F = ova per fish; FL = fork length, mm):

Table 1. Estimated fecundity of Atlantic menhaden at different ages (from Dietrich 1979).

Age	Number of eggs per female (thousands) Mean	Range	N
I	115.8	26.5 - 250.7	21
II	177.4	39.2 - 368.8	34
III	302.8	127.7 - 458.3	33
IV	308.6	142.7 - 514.0	12
V	568.4	---	1

$$\ln F = 7.2227 + 0.0176\ FL$$

$$r^2 = 0.726.$$

Dietrich (1979) gave the following equations (W = wet body weight less weight of ovaries, g; A = age, years; FL = fork length, mm):

$$F = 488\ W$$
$$r^2 = 0.916$$

$$F = 92{,}592\ A$$
$$r^2 = 0.879$$

$$\ln F = 8.6463 + 0.0120\ FL$$
$$r^2 = 0.871.$$

Eggs and Larvae

Eggs of the Atlantic menhaden are pelagic and have been reported to hatch in 2 days at unspecified temperatures (Kuntz and Radcliffe 1917), 2.9 days at 15.5 °C (Ferraro 1980a), and at 2.5 to 2.9 days at an average temperature of 15.5 °C (Hettler 1981).

Survival of laboratory reared Atlantic menhaden embryos to hatching is very low (2% to 45%); 49% to 94% of mortality occurs before blastopore closure (Ferraro 1980a).

Atlantic menhaden larvae begin feeding on individual zooplankters (Reintjes and Pacheco 1966) about 4 days after hatching when the yolk sac is almost absorbed, the eyes are pigmented, and the mouth is functional (Hettler 1981). Larvae in the South Atlantic Region enter estuaries after 1 to 3 months at sea (Reintjes 1961) at fork lengths (FL) of 14 to 34 mm (Reintjes and Pacheco 1966); fish longer than 30 mm FL are then already metamorphosing to the prejuvenile morphology (Lewis et al. 1972). This migration into estuaries occurs from May through October in the North Atlantic Region, October through June in the Mid-Atlantic, and December through May in the South Atlantic Region (Reintjes and Pacheco 1966). As they grow, the larvae probably feed on progressively larger zooplankters (Kjelson et al. 1975).

Young fish move into the shallow portions of estuaries including river shoals and the heads of small tidal creeks (Massmann 1954; Massmann et al. 1954; June and Chamberlin 1959; Pacheco and Grant 1965; Wilkens and Lewis 1971; Lewis et al. 1972; Weinstein 1979; Weinstein et al. 1980; Rozas and Hackney 1984; Rogers et al. 1984). They apparently prefer Spartina, Juncus, and the vegetation typical of fresh tidal marshes and swamps (Taxodium, Typha, Nyssa, Peltandra, Rumex, Sagittaria, Zizania) over vegetated habitats in open water (Adams 1976; Weinstein and Brooks 1983). While in estuaries, Atlantic menhaden grow and metamorphose through a prejuvenile stage into juveniles.

Several studies have reported abundances of young menhaden that were higher in portions of estuaries with the lowest salinity <5 ppt (Lewis et al. 1972; Weinstein 1979; Weinstein et al. 1980). Massmann et al. (1954) reported that the abundance of prejuveniles was higher above than below the brackish-freshwater boundary, and Rogers et al. (1984) showed that this pattern persists during high river discharge. Massmann et al. (1954), Rozas and Hackney (1984), and Rogers et al. (1984) provided evidence that prejuvenile Atlantic menhaden select tidewater areas that are fresh or of low salinity. Only fish of prejuvenile lengths were resident in low salinity river shoals and in intertidal creeks (Lewis et al. 1972). This phenomenon persisted for about 4 months (Rogers et al. 1984).

A "critical period" of survival in young fishes was first defined by Hjort (1914) and discussed for clupeiform fishes by Schumann (1965) and May (1974). Menhaden, like most fishes with high fecundity and little parental care, hatch in an undeveloped state. Such fish typically rely on energy contained in the yolk-sac for 4-5 days after hatching, after which they are sufficiently developed to more efficiently feed on an external food supply (Schumann 1965). Feeding of the youngest Clupea, Engraulis, and Sardinops larvae depends largely on food availability; fish will eat to capacity in the presence of high food concentrations and starve in the absence of high concentrations because they are unable to move about to search for food. A routine search pattern is initiated only after an encounter with or capture of a food particle. Given the heterogeneity in distribution of pelagic plankters and the inability of many clupeiform fishes to cope with low food concentrations, menhaden probably have a critical period of larval survival. Year-class strength may be partly determined during this period. This problem is most likely to occur when larvae are spawned offshore or swept offshore after having been spawned nearshore. Individual larval condition factors (weight-length ratios) increase rapidly when the fish enter an estuary (Lewis and Mann 1971). Metamorphosis is not totally dependent on low salinity; Hettler (1981) reared Atlantic menhaden from eggs to juveniles using water with a high salinity. However, metamorphosis rarely is successful outside the food-rich, low-salinity estuarine zones (Kroger et al. 1974).

No data are available that link survival at yolk sac absorption to year-class strength or that enable quantitative estimates of mortality from predation or starvation (May 1974). Minimum food concentration for inception of feeding activity is not known, and survival curves do not exist for larval Atlantic menhaden. Nelson et al. (1977), however, developed an environment-recruit model in an attempt to explain variation in year-class strength. Since larval menhaden are thought to depend largely on wind-driven (Ekman) transport to reach estuarine nursery grounds (particularly in the Middle and South Atlantic Regions), the model incorporated four variables: (1) the known spawning times and locations; (2) wind vectors specific for year, time, and location; (3) year- and time-specific discharges of major tributary systems; and (4) the minimum sea surface temperature at the mouth of Delaware Bay. A survival index was calculated as the ratio of observed recruitment to the fishery (age I) to that predicted by a Ricker (1954) spawner-recruit (density-dependent) model. The magnitude of the index "should reflect those environmental (density independent) effects which influence survival of menhaden from the time of spawning to the time of recruitment to the fishery at age I" (Nelson et al. 1977). The model explained 84% of the variation in the survival index for the years investigated (1961-71); Ekman transport was the principal component. The correlation has not been statistically significant in recent years (D. Vaughan, National Marine Fisheries Service (NMFS), Beaufort, North Carolina; pers. comm.).

Survival of Atlantic menhaden to age I has been estimated by comparing estimates of population size of age I fish (based on a virtual population analysis that incorporated data from commercial landings) with number of eggs predicted to have been spawned in previous years. Estimates of recruits per million eggs spawned have ranged from 27 to 159 (Nelson et al. 1977) and from 78 to 282 (Dietrich 1979).

Juveniles and Adults

Metamorphosis marks a change in feeding mode from capturing individual zooplankton to filter-feeding (June and Carlson 1971; Durbin and Durbin 1975). This shift is accompanied by a loss of teeth, an increase in the number and complexity of gill rakers, and an increase in the complexity and musculature of the digestive tract (June and Carlson 1971). Prejuveniles are somewhat intermediate in feeding mode (June and Carlson 1971) and body structure (June and Carlson 1971; Lewis et al. 1972).

Juveniles begin congregating in dense schools as they leave shoal areas. Most emigrate from estuaries from August through November (earliest in the North Atlantic Region) at lengths of 55 to 150 mm FL (June 1961a) or 55 to 140 mm total length (TL) (Nicholson 1978). Nicholson stated that most emigrants are 75 to 110 mm TL. As judged by the results of extensive tagging, many age 0 fish migrate southward along the North Carolina coast in late fall and early winter (Nicholson 1978). Fish in the southernmost portion of the South Atlantic Region, however, showed less offshore migration (Dahlberg 1970), and tagging results indicated that juveniles leaving the estuaries of the South Atlantic Region and the North Atlantic Region may not move far north or south during their first year (Nicholson 1978). Larvae entering estuaries late in the season may remain in the estuary one additional year and emigrate at age I. Some juveniles and adults are found in sounds and bays along the South Atlantic Region during mild winters (June 1961a). Fish leaving estuaries along the entire Atlantic seaboard eventually disperse throughout most of the geographic range (Nicholson 1978).

Most Atlantic menhaden reach maturity by the end of their second full year. About 10% were found to be capable of spawning at age I (late in the year), and 90% at age II (Higham and Nicholson 1964). Fish of all ages, however, are found in the migrating schools. Although Atlantic menhaden can live 8 to 10 years (June and Roithmayr 1960), fish older than age IV had been rare in the commercial catch. As stocks rebuild, however, age V and VI fish are becoming more common and may be locally abundant in the North Atlantic and North Carolina fall fishery (Powers 1984).

Adult feeding behavior is affected by food availability (Durbin and Durbin 1975; Durbin et al. 1981). Swimming speed is increased at higher food concentrations, and associated energetic costs rise exponentially. Modeling studies have suggested that Atlantic menhaden maximize growth rate, not efficiency (Durbin and Durbin 1983), and that efficiency of dietary assimilation changes seasonally with the quality of available food. The Atlantic menhaden has behavioral, physiological, and morphological adaptations for an active migratory existence in waters with pronounced seasonal and spatial variation in food abundance. It has large lipid reserves that are seasonally assimilated (Durbin and Durbin 1983), a body shape adapted for continuous swimming, and copious body mucus (Dahlberg 1970).

GROWTH CHARACTERISTICS

Growth rates vary among years and localities throughout the species' range (June and Reintjes 1959, 1960; June 1961b; June and Nicholson 1964; Nicholson and Higham 1964a, 1964b, 1965; Nicholson 1975; Reish et al. 1985). The age of Atlantic menhaden can be determined from annual scale markings (McHugh et al. 1959; June and Roithmayr 1960; Kroger et al. 1974).

Fish of the same age are progressively larger in more northerly fisheries (Nicholson 1978; Reish et al. 1985), but mature at smaller sizes in more southerly areas. Minimum size at maturity was 180 mm FL in the South Atlantic and 210 mm FL in the Middle Atlantic (Higham and Nicholson 1964). There is evidence that growth rates have changed in response to fishing pressure: fish of the same age were larger in the late 1960's and early 1970's than in the late 1950's and early 1960's (Nicholson 1975). Reish et al. (1985) indicated that growth rates do not depend upon fish abundance. Atlantic menhaden in years of high abundance probably are smaller than Atlantic menhaden in years of low abundance because the former were smaller at the time of recruitment, not because of any difference in growth rates after recruitment.

Growth has been shown to be allometric in larval, prejuvenile (Lewis et al. 1972), juvenile (Lewis et al. 1972; Epperly 1981), and adult stages. Reish et al. (1985), however, reported that Atlantic menhaden exhibited growth that was close to isometric, although growth appeared to become allometric with increasing age. Three different "stanzas" of growth in young menhaden were reported by Lewis et al. (1972), with inflection points at 30 and 38 mm TL (70 and 469 mg weight). These points served as the basis for their division of the life history stages. Balon (1984) pointed out that these are functional, not arbitrary, divisions. Lewis et al. (1972) cited an unpublished manuscript that stated that the relationship between length and weight is similar for juveniles and adults. Length-weight conversions can be made using the appropriate equation in Table 2.

Atlantic menhaden growth begins in spring and ends in fall, as the water temperature crosses an approximate 15 °C threshold (Kroger et al. 1974). At Beaufort Inlet, North Carolina, age 0 fish ranged from 40 to 185 mm TL at the end of the growing season, depending on when they were spawned and entered the estuary. Young of the next year class arrived in the spring only 20 to 30 mm TL shorter than the smallest fish of the previous year class. These factors, combined with differences in larval growth rates (Lewis et al. 1972; Kroger et al. 1974) and latitudinal differences in growing season, probably explain the observed differences in sizes of fish of the same "age" within a single year's catch. See Durbin and Durbin (1983) and the section on Life History for discussions of growth in relation to feeding, environment, and body morphology.

Table 2. Weight-length regressions for Atlantic menhaden; $\log_e$ weight = a + b ($\log_e$ length).

Location	Types of measurement units: Weight (wet)	Length (mm)	a	b
White Oak River Estuary, NC[1]				
Larvae (≤ 30 mm TL)	mg	TL	-8.110	3.605
Prejuveniles (30-38 mm TL)	mg	TL	-16.964	6.308
Juveniles (≥ 38 mm TL)	mg	TL	-5.230	3.145
Fall and winter spawners and offspring (Middle, S. Atlantic Regions)[2]	g	SL	-10.884	3.067
North Atlantic spring spawners and offspring[2]	g	SL	-11.240	3.145
Middle Atlantic spawners and offspring[2]	g	SL	-11.037	3.103
South Atlantic spawners and offspring[2]	g	SL	-10.579	2.995
All spawners, for the fishery as a whole[3]	g	SL	-12.075	3.215

[1]Lewis et al. 1972.
[2]Epperly 1981.
[3]Douglas Vaughan, National Marine Fisheries Service, pers. comm.

Atlantic menhaden reach lengths of about 500 mm TL and weights of over 1,500 g at ages of 8 to 10 years. Cooper (1965) collected an 8-year-old that measured 470 mm TL and weighed 1,674 g.

THE FISHERY

History

The Atlantic menhaden fishery was first established in the late 1600's and early 1700's to obtain fish for agricultural fertilizer (Frye 1978). In the early 1800's, an industry was developed to obtain oil from menhaden (Goode 1879; Goode and Clark 1887), and by 1869 there were 90 reduction plants in North Carolina alone (June 1961a). Today this species contributes 25% to 40% of the landings in the largest commercial fishery (by weight, *Brevoortia* species) in the United States. Annual landings for 1979 to 1981 averaged about 400,000 metric tons and $38 million in market value (NMFS 1980, 1981, 1982, 1983, 1984, 1985). Plants that process Atlantic menhaden products currently operate from Maine to Florida. About 96% to 98% of the catch is sold to livestock and cosmetic interests as fishmeal, soluble proteins, and oils; the rest is used in pet food products and as fish bait (NMFS 1980, 1981, 1982, 1983, 1984, 1985). Most of the landings are made with purse seines. Federal efforts to collect data for management of Atlantic menhaden began in 1955 (June 1957).

The Catch

The Atlantic menhaden fishery has two annual phases: a summer and fall fishery from Maine to northern Florida, and an intensive fall and winter fishery off North Carolina between Cape Lookout and New River Inlet (June 1961a; Nicholson 1978). Landings for the entire fishery have recently included primarily age I and II fish. During the summer fishery in the South Atlantic Region, fish caught have been mostly ages I and II except in 1984 when a large number of age 0 fish were caught; the north Florida landings have been composed mostly of age I fish. Concurrently, fish in the Chesapeake Bay area and the southern portion of the Mid-Atlantic Region are also age I and II, although they are longer and heavier on the average. Some fish of ages III and IV are present in an early spring pound-net fishery in Chesapeake Bay. Most of the fish caught in the northern portion of the Mid-Atlantic Region are of ages II and III, the age II fish being larger than those to the south. For the entire Atlantic menhaden fishery, the average percentage of numbers of age I and II fish between 1955 and 1984 was 78.4%; the range was 51.4% (in 1961) to 95.9% (in 1970). Numbers of age 0 fish composed 25% or more of the catch for the entire fishery in 1955, 1966, 1979, 1981, 1983, and 1984 (D. Vaughan, National Marine Fisheries Service; pers. comm.). The north Atlantic fishery operates from mid-June through October and primarily exploits fish of age III or older. The purse seine fishery north of Cape Hatteras is over by late November. Age 0 fish begin to be vulnerable to the fishery during late fall and winter from Chesapeake Bay south. The North Carolina fall fishery is composed of fish of all age classes; age 0 fish have predominated since 1971, except in 1980 and 1982.

Atlantic menhaden stocks were drastically reduced during the 1960's. Annual landings dropped from 671,400 metric tons in 1955 to about 200,000 metric tons per year from 1966 through 1969 (Nelson et al. 1977). As the population size decreased, the age structure also changed. Fish older than age III became scarce and fish older than age IV were practically non-existent even in the North Carolina fall-winter fishery. Many northern processing plants closed down -- especially those in the New England area, where the fishery depended on fish of ages III and IV (Henry 1971; Nicholson 1975). Age I and II fish constituted the bulk of the landings and age 0 became more important (Nicholson 1975). The stocks began to recover in the early 1970's, when age III fish again appeared in North Atlantic catches. The first significant Maine landings (3,100 metric tons) since the 1960's occurred in 1973 (NMFS 1973, 1974, 1975; Nelson et al. 1977). North Atlantic (from Cape Cod, Massachusetts, to Cape Breton, Nova Scotia) landings in 1929-71 correlated strongly with 3-year-lagged local water temperatures and mixing factors for St. Lawrence River inputs (Sutcliffe et al. 1977). These North Atlantic fish, though vulnerable throughout the fishery, may be a unique biological stock. Catches continued to improve into the early 1980's; however, the size of the reproductive stocks (ages III and IV) remained low (Atlantic Menhaden Management Board [AMMB] 1981; NMFS 1983, 1984, 1985). Heavy exploitation results in smaller and fewer fish (June 1972) and higher catchability coefficients (Schaaf 1979). The implications of these phenomena are **not fully understood; however, a recent model showed that pollution stress may greatly reduce first-year survival rate (Schaaf et al. 1987).**

Management

More than 50% of the annual landings of Atlantic menhaden are from within State territorial waters, mostly from the Chesapeake Bay area (R. B. Chapoton, NMFS, Beaufort, North Carolina; pers. comm.). This fact, combined with the migratory nature of the species and the dependence of northern fisheries on escapement of age I and II fish from fisheries in the South Atlantic Region and Chesapeake Bay (Nicholson 1978), makes regulation a compromise situation between the industry and Federal and State agencies; only the states have final regulatory power.

The stocks have generally been unmanaged. Nelson et al. (1977) suggested that the fishery is somewhat self-regulating in that reduced catches bring about reduced effort and plant closures, allowing the stocks to recover. They stress that proper management practices could reduce the chance of repeating the mistakes of the past and prevent a crash in the fishery. In addition, Schaaf (1975) pointed out that "allowing the fishery to be controlled . . . by the economics of free market competition . . . assures that (1) the average profit for the whole industry will be zero . . . and (2) there is no mechanism to provide for protection of the resource, since if either costs go down or value goes up new effort can afford to enter the fishery and eventually may exceed the BBEP [Biological Break-Even Point, a point at which the fishery collapses]." Schaaf (1975) also warned that the level of effort when the fishery collapsed in the 1960's might be maintained during the mid-1970's even if catches dropped to 200,000 metric tons per year because product prices were higher at that time. He urged implementation of a flexible quota system coordinated by the Atlantic States Marine Fisheries Commission (ASMFC) that would allow the stocks to continue to rebuild while effort regulation mechanisms were studied.

The management option endorsed by the ASMFC, Option 7 of the Atlantic Menhaden Advisory Committee, proposed the following closing dates to protect age 0 recruits: the week ending between October 4 and 10 for the North Atlantic, the week ending between October 11 and 17 for the Mid-Atlantic, the week ending between November 8 and 14 for Chesapeake Bay, and the week ending between December 13 and 19 for the South Atlantic. This closure would primarily affect the North Carolina late-fall fishery.

To be effective, the regulation still needs to be implemented in North Carolina; it has been implemented already in six states (Virginia and north). National Marine Fisheries Service personnel have analyzed the effects that Option 7 would have by using data for 1976-82. Increases in yield-per-recruit ranged from 0.4% to >10% and varied with strength of the targeted age 0 year class and the timing of arrival at the North Carolina fall fishery. These estimates may be low because of sampling errors, but would be substantially greater only in years with very abundant age 0 cohorts that arrive at the North Carolina fall fishery after the mid-December closing date (D. Vaughan, pers. comm.). This management strategy is an extension of NMFS recommendations made since the early years of study. The continued existence of the Atlantic menhaden fishery despite heavy exploitation is quite unlike that of other well-studied clupeid stocks (Schaaf 1979), and probably is a product of differences in density-independent phenomena (e.g., reproductive strategy). In spite of the difficulties involved in managing such a complex resource, the prospects of developing a workable management plan are good, primarily due to the capability of the stocks to respond to conservation of age 0 fish (Schaaf 1975). However, the cooperation of affected states is necessary to effectively implement such a plan.

Annual maximum sustained yield (MSY) from historic catch-effort data has been estimated by Schaaf and Huntsman (1972) at 600,000 metric tons and by Schaaf (1975) at 560,000 metric tons. Estimates incorporating the use of a Ricker (1954) spawner-recruit (density-dependent survivorship) model were given as 380,000 metric tons per year by Schaaf and Huntsman (1972) and averaged 419,000 metric tons per year on the basis of known survivorship in 1961-71 (Nelson et al. 1977). The recruit-environment model developed by Nelson et al. (1977) likewise averaged 419,000 metric tons per year (1961-71) and is proposed to offer a way of "fine-tuning" predicted catch on a yearly basis by constantly updating yield estimates. The vulnerability of the Atlantic menhaden fishery to fluctuations in year class strength was first pointed out by June (1961a). It has since been stressed that the maintenance of a healthy stock of spawning-age fish should be a primary concern of management (Schaaf and Huntsman 1972; Schaaf 1975; Nelson et al. 1977; Vaughan 1977). Good stocks of spawning-age fish would bring multiple benefits, including higher reproductive potential (decreasing the effects of years with poor recruitment), decreased vulnerability to weak year classes, and increased weight of landings due to a higher contribution of older fish to the catch. Recent calculations of MSY remain near 450,000 metric tons (D. Vaughan, pers. comm.).

Annual instantaneous natural mortality was estimated at 0.36 (1955-64) by Schaaf and Huntsman (1972) and at 0.42 for the 1955 year class by Nelson et al. (1977). Their respective estimates of annual instantaneous fishing mortality were 0.82 to 2.14 (1955-64) and 0.36 for the 1955 year class. A combination of these data yields total instantaneous mortality estimates ranging from 1.18 to 2.56, which correspond to total annual mortality rates of 69% to 92% (ages I - VI). Reish et al. (1985) estimated annual natural mortality at 0.54 for late juveniles (9-23 months), 0.15 for age I (12-23 months), 0.49 for age II (24-35 months), and 0.52 for age 3+ (36+ months). Except for the age I fish, these estimates were comparable with the annual mortality of 0.52 obtained from mark-recapture data by Dryfoos et al. (1973).

Subpopulations

Because a genetically distinct stock can have its own homogenous vital parameters of recruitment, growth, and mortality (Cushing 1968), identification of the stock (=subpopulations) and stock-specific biological traits is necessary for proper management. Various authors have proposed the existence of two to five Atlantic menhaden subpopulations on the basis of meristic and morphometric comparisons (June 1958, 1965; Sutherland 1963; Higham and Nicholson 1964; June and Nicholson 1964; Dahlberg 1970; Epperly 1981). Dahlberg (1970) reported a distinct subpopulation of Atlantic menhaden south of Cape Canaveral in the vicinity of the Indian River, Florida. Nicholson (1978) stated that the extensive north-south migrations, latitudinal stratification by age and size in the summer, and intermingling of all age classes south of Cape Hatteras in winter preclude the existence of more than one stock. Epperly (1981), however, provided electrophoretic as well as meristic and morphometric data that indicated significant differences between fish spawned in the waters north of Long Island, New York, during the spring and those spawned in the fall and winter in the South and Mid-Atlantic Regions. Other groups -- fall-spawning fish of the Gulf of Maine and spring-spawning fish of the Mid-Atlantic Region -- may also be distinct subpopulations, but this aspect has not been fully investigated. Menhaden species hybridize readily (Turner 1969; Dahlberg 1970), but Atlantic x yellowfin hybrids have been recorded only as far north as Beaufort, North Carolina (Dahlberg 1970). Apparently, hybrids do not occur in the Mid-Atlantic Region.

ECOLOGICAL ROLE

Atlantic menhaden occupy two distinct types of feeding niches during their lifetime. They are size-selective plankton feeders as larvae and filter feeders as juveniles and adults. Data on the food of larvae before they enter the estuary do not exist. After entering the estuary, Atlantic menhaden larvae appear to be extremely selective for prey of certain sizes and species. Larvae from the Newport River Estuary, North Carolina, 26 to 31 mm TL ($\bar{x}$ = 29 mm TL), consumed copepods and copepodites of only four taxa, which composed 99% by numbers and volume of their gut contents (Kjelson et al. 1975). These prey items, ranging from 300 to 1200 µm in length ($\bar{x}$ = 750 µm), were eaten despite an abundance of copepod nauplii, barnacle larvae, and small adult copepods in plankton tows. Larvae that were offered copepods in the laboratory ignored all other food items, including <u>Artemia</u> and <u>Balanus</u> nauplii (June and Carlson 1971). Larval menhaden in the Newport River Estuary, North Carolina, fed primarily during daylight (Kjelson et al. 1975).

Juvenile and adult Atlantic menhaden strain particulates from the water column with a complex set of gill rakers. The rakers can sieve particles down to 7-9 µm in size (Friedland et al. 1984), including zooplankton, larger phytoplankton, and chain-forming diatoms. Biochemical analyses indicated that the gut contents of juveniles vary with prey availability; reliance on zooplankton decreases as the fish move from open waters to marshes (Jeffries 1975). Atlantic menhaden may also be capable of eating epibenthic materials (Edgar and Hoff 1976). Peters and Schaaf (1981) speculated that the annual phytoplankton and phytoplankton-based production in east coast estuaries is not sufficient to support the juvenile Atlantic menhaden population during its residency and that the abundant organic detritus may be eaten. Lewis and Peters (1984) reported that juvenile Atlantic menhaden in North Carolina salt marshes ate primarily detritus.

The roles of Atlantic menhaden in systems function and community dynamics have received little attention. Larvae and juveniles are seasonally important components of estuarine fish assemblages (Tagatz and Dudley 1961; Cain and Dean 1976; Bozeman and Dean 1980). Estimates of the mean daily ration for larvae range from 4.9% (Kjelson et al. 1975) to 20% (Peters and Schaaf 1981) of wet body weight. Assimilation of ingested energy exceeded 80% for plant and animal material (Durbin and Durbin 1981). Because of their tremendous numbers, individual growth rates, and seasonal movements, these fish annually consume and redistribute large amounts of energy and materials, including exchanges between estuarine and shelf waters.

Kjelson et al. (1975) noted that the copepod taxa preferred by larval menhaden and other species decreased from a mean value (2 years) of 81% to 48% of the total zooplankton biomass during the period of larval residence. They speculated that this decrease may be partly explained by larval feeding. Durbin and Durbin (1975) suggested that Atlantic menhaden in coastal waters may also alter the composition of plankton assemblages by grazing on certain size ranges.

Important Atlantic menhaden predators include bluefish (Pomatomus saltatrix), striped bass (Morone saxatilis), bluefin tuna (Thunnus thynnus), and sharks (Reintjes and Pacheco 1966). Atlantic menhaden occurred in 13% of stomachs of sandbar sharks (Carcharhinus plumbeus). About 46% of the menhaden were consumed whole and were 5-10 cm TL. Menhaden consumed in more than one piece or partially consumed were 5-17 cm TL. This prey was the second most frequently consumed type for sandbar sharks (Medved et al. 1984). Because Atlantic menhaden are eaten by predators in several ecosystems, they are a direct pelagic link in the food web between detritus and plankton and top predators.

ENVIRONMENTAL REQUIREMENTS

Temperature, Salinity, and Dissolved Oxygen

Atlantic menhaden occur through a wide range of physicochemical conditions. Several studies have raised questions about limits of tolerance and optimum conditions. June and Chamberlin (1959) and Reintjes and Pacheco (1966) reported that larval menhaden did not enter estuarine waters at temperatures below 3 °C. Many studies have noted an affinity of young menhaden for low salinity waters (see the Life History section). Wilkens and Lewis (1971) speculated that larval menhaden require low salinity water to metamorphose properly, and Lewis (1966) found that although larvae metamorphosed in salinities of 15 to 40 ppt, one-third of the juveniles developed slightly crooked vertebral columns. However, larvae held in the laboratory at 25 to 40 ppt metamorphosed completely with no abnormalities (Reintjes and Pacheco 1966; Hettler 1981); and larvae trapped in a natural cove at Beaufort, North Carolina, transformed into juveniles at 24 to 36 ppt (Kroger et al. 1974).

Salinity affects temperature tolerance, activity, metabolism, and growth. Low salinities decreased survival at temperatures below 5 °C, and survival was poor at 6 °C in freshwater (Lewis 1966). The effect of salinity on upper temperature tolerance was not significant (Lewis and Hettler 1968). Larvae that Hettler (1976) reared at 5 to 10 ppt exhibited significantly higher activity levels, metabolic rates, and growth rates than those reared at 28 to 34 ppt. Lewis (1966) also noted slower growth at high salinities. Subtle physiological adaptations to low salinity may be an evolutionary response to larvae "seeking" the food-rich estuarine environment. Rogers et al. (1984) noted that pre-juveniles of many fishes, including those of Brevoortia species, entered estuarine habitats during seasonal peaks of freshwater influx when the area of low-salinity and fresh tidal water was greatest.

An important management consideration is that, during the evolution of the Atlantic menhaden, estuarine zones received freshwater from contiguous wetlands and riverine systems. However, channelization, diking of river courses, ditching and draining of marginal wetlands, and urbanization have reduced the freshwater retention capacities of coastal wetlands. Furthermore, extensive filling of estuarine marshlands has diminished the area receiving runoff in many locations. In combination, these changes cause rapid discharge of high volumes of freshwater during brief periods and reduced amounts of freshwater at other times. High inflows, particularly those that occur in early spring after the arrival of prejuvenile menhaden, can expose fish to extreme fluctuations of temperature, turbidity, and other environmental conditions. Although the effects of altered freshwater flow regimes on Atlantic menhaden are not known, effects on other estuarine-dependent, offshore-spawned fishes range from disappearance (Rogers et al. 1984) to death (Nordlie et al. 1982). These effects are also mediated by temperature (Nordlie 1976).

Salinities of 10 to 30 ppt did not affect developing embryos, though temperature did (Ferraro 1980a). Mortality of embryos was complete at temperatures less than 7 °C and was significantly higher at 10 °C than at 15, 20, and 25 °C. Time to hatching was significantly shorter at each progressively higher temperature. Surface temperature in the spawning areas of the South Atlantic Region during the months of highest egg capture were generally 12 to 20 °C (Walford and Wicklund 1968). The lowest temperatures at which Atlantic menhaden eggs and larvae were collected in the North Atlantic Region were between 10 and 13 °C (Ferraro 1980a). The temperature range for the Middle Atlantic Region was 0 to 25 °C, but most eggs and larvae were collected at 16 to 19 °C (Kendall and Reintjes 1975).

The limits of larval temperature tolerance are also affected by acclimation time. Survival above 30 °C (Lewis and Hettler 1968) and below 5 °C (Lewis 1965) was progressively extended by acclimation temperatures closer to test values, suggesting that rapid changes to extreme temperatures are more likely to be lethal than prolonged exposure to slowly changing values. Winter shutdown of power plant operations may result in rapid temperature decreases near the effluent discharge area. Mortality of juvenile Atlantic menhaden to a temperature decrease of 10 °C (from 15 to 5 °C) was less at rates of decrease of 6.7 °C/h or lower than at faster rates. Winter menhaden kills can be minimized by reducing the rate of decrease as the power plant discharge is shut down (Burton et al. 1979).

Hettler and Colby (1979) demonstrated that photoperiod at least partly explains variation in resistance to heat stress. Median lethal time increased linearly with photoperiod at 34 °C. They also speculated that it may be important to other types of physiological stress. Lewis and Hettler (1968) observed increased survival of juveniles at 35.5 °C with increased dissolved oxygen (DO) saturation. Burton et al. (1980) reported a mean lethal DO concentration of 0.4 mg/l, but warned against interpretation of this value as "safe," in view of the interactive nature of environmental factors. Westman and Nigrelli (1955) observed mass mortalities from gas embolism only in areas with highly variable salinity and organic pollution sufficiently severe to make shellfish unfit for human consumption. Lewis and Hettler (1968) observed decreased survival at high temperatures by fish affected by gill parasites. The interaction of environmental factors must be considered when one defines healthy ranges for an organism.

Substrate and System Features

The association of the Atlantic menhaden with estuarine and nearshore systems during all phases of its life cycle is well documented. It is evident that young menhaden require these food-rich waters to survive and grow, and the fishery is concentrated near major estuarine systems (June 1961a). Filling of estuarine wetlands, in addition to exacerbating extremes in environmental conditions, has physically limited the nursery habitat available to Atlantic menhaden and other estuarine-dependent species. The relative importance, however, of different habitat types (i.e., sounds, channels, marshes) and salinity regimes has received little detailed attention.

Environmental Contaminants

In a study of chlorinated hydrocarbon residues in menhaden fishery products from the Atlantic and Gulf of Mexico, Stout et al. (1981) showed that overall levels have decreased since the late 1960's, although significant differences between years for levels of polychlorinated biphenyls (PCB's) in the South Atlantic Region and for dieldrin in the Middle Atlantic Region could not be demonstrated. There was also a general lack of significant differences between areas within years, although this may have been due to the sampling regime. They speculated that PCB levels have remained somewhat high because of leakage from sources established prior to regulation and continued allowance of limited specialty uses. Menhaden oil products carry the highest concentrations of such non-polar compounds and some samples contained levels in excess of United States Food and Drug Administration temporary tolerances, as of 1977. Warlen et al. (1977) demonstrated that ^{14}C-DDT uptake by Atlantic menhaden is dose-dependent, with an assimilation value between 17% and 27%. Application of their model to field data suggested that uptake was by way of plankton and detritus. Little information exists about the toxicity of contaminants to Atlantic menhaden.

Other Factors

The seasonal depth distribution of Atlantic menhaden is tied to migration patterns. Some fish occur year-round in depths of 1 to 200 m (3 to 656 ft). The role of turbidity in Atlantic menhaden biology apparently has not been studied. Blaber and Blaber (1980) proposed that gradients of turbidity, nutrients, and salinity could provide cues that enable fry to locate estuarine nursery areas along the Australian coast. The "seeking" of turbid zones is probably related to differential mortality linked to food supply and predation (Blaber and Blaber 1980; Norcross and Shaw 1984).

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16. Abstract (Limit: 200 words)
Species profiles are literature summaries of the life history, distribution, and environmental requirements of coastal fishes and invertebrates. Profiles are prepared to assist with environmental impact assessment. The Atlantic menhaden (Brevoortia tyrannus) is an important commercial fish along the Atlantic coast. In the South Atlantic Region, Atlantic menhaden spawn during winter in continental shelf waters. Adults then move inshore and northward in spring; some move into estuaries as far as the brackish-freshwater boundary. Atlantic menhaden larvae in the South Atlantic Region enter estuaries after 1 to 3 months at sea. Young fish move into the shallow regions of estuaries and seem to prefer vegetated marsh habitats. Atlantic menhaden are size-selective plankton feeders as larvae, and filter feeders as juveniles and adults. Due to their large population size, individual growth rates, and seasonal movements, Atlantic menhaden annually consume and redistribute large amounts of energy and materials. They are also important prey for large game fishes such as bluefish (Pomatomus saltatrix), striped bass (Morone saxatilis), and bluefin tuna (Thunnus thynnus). The Atlantic menhaden is associated with estuarine and nearshore systems during all phases of its life cycle. Young menhaden require these food-rich habitats to survive and grow. Destruction of estuarine wetlands has decreased nursery habitat available to Atlantic menhaden and other estuarine-dependent species.

17. Document Analysis a. Descriptors
Estuaries
Fishes
Growth
Feeding habits

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