Population Biology and Life History of the North American Menhadens, *Brevoortia* spp.

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ABSTRACT—Four recognized species of menhaden, Brevoortia *spp., occur in North American marine waters: Atlantic menhaden,* B. tyrannus*; Gulf menhaden,* B. patronus*; yellowfin menhaden,* B. smithi*; and finescale menhaden,* B. gunteri*. Three of the menhaden species are known to form two hybrid types. Members of the genus range from coastal waters of Veracruz, Mex., to Nova Scotia, Can. Atlantic and Gulf menhaden are extremely abundant within their respective ranges and support extensive purse-seine reduction (to fish meal and oil) fisheries. All menhaden species are estuarine dependent through late larval and juvenile stages. Depending on species and location within the range, spawning may occur within bays and sounds to a substantial distance offshore. Menhaden are considered to be filter-feeding, planktivorous omnivores as juveniles and adults. Menhaden eggs, immature developmental stages, and adults are potential prey for a large and diverse number of predators. North American menhadens, including two hybrids, are hosts for the parasitic isopod,* Olencira praegustator*, and the parasitic copepod,* Lernaeenicus radiatus*. Although the data are quite variable, a dome-shaped Ricker function is frequently used to describe the spawner-recruitment relationship for Atlantic and Gulf menhaden. Each of these species is treated as a single stock with respect to exploitation by the purse-seine reduction fishery. Estimates of instantaneous natural (other) mortality rates are 0.45 for Atlantic menhaden and 1.1 for Gulf menhaden.*

Introduction

Menhaden are members of the worldwide family Clupeidae, one of the most important families of fishes both economically (Hildebrand, 1963), and ecologically. Clupeids are characteristically very numerous and form large, dense schools which enhance our ability to harvest them. Many of the species are filter feeders, being either primary consumers, feeding on phytoplankton, or secondary consumers, feeding on zooplankton, or both. Many clupeids are in turn prey for various piscivorous predators through virtually their entire lives. Life history patterns for this family of fishes include species which can complete their entire life cycle in either fresh or marine waters, or are anadromous species, or marine migratory (estuarine dependent) species.

The large-scaled menhadens, the Atlantic menhaden, *Brevoortia tyrannus*, and the Gulf menhaden, *B. patronus*, have received considerable attention in fishery science research due to their large population sizes and resulting economic and ecological importance. The small-scaled menhadens, the yellowfin menhaden, *B. smithi*, and the finescale menhaden, *B. gunteri*, are less numerous and have received far less consideration in the scientific literature. The contrast in relative importance is quite marked. On one extreme, the purse-seine reduction fishery (to fish meal and oil) for Gulf menhaden was the largest U.S. fishery by weight from 1963 through 1988, and Atlantic menhaden purse-seine reduction landings, currently one-third to two-thirds those for Gulf menhaden, were the largest for the U.S. from 1947 to 1962. On the other extreme, finescale menhaden are apparently not directly sought by any recognized fishery, and yellowfin menhaden (and their hybrids) are only harvested by specialized bait fisheries on both coasts of Florida. The following is a general description of the population biology and life history of these four North American menhaden species.

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Geographic Ranges

Reintjes (1969) summarized the geographic ranges for the four menhaden species. Atlantic menhaden are seasonally found from Nova Scotia, Can., to southeastern Florida, near West Palm Beach. Gulf menhaden range from southwestern Florida, near Cape Sable, to Veracruz, Mex. Yellowfin menhaden overlap the ranges of all three other menhaden species and are found from Cape Lookout, N.C., to the Mississippi River Delta. Finescale menhaden overlap the ranges of both the Gulf and yellowfin menhaden, and are found from just east of the Mississippi River Delta (Turner, 1971) to Campeche, Mex.

The numbers of Gulf menhaden relative to numbers of yellowfin menhaden become reduced proceeding southward on the Gulf of Mexico coast of Florida. There appears to be a similar distribution pattern for relative numbers of Atlantic and yellowfin menhaden proceeding southward along the Atlantic coast of Florida. The coastal area between West Palm Beach and Miami, Fla., where menhaden are relatively rare (Dahlberg, 1970), geographically separates the Atlantic menhaden from the Gulf menhaden, as well as apparent eastern and western populations of yellowfin menhaden.

A large amount of hybrid introgression occurs between Atlantic and yellowfin menhaden on the Atlantic coast of Florida, and Gulf and yellowfin menhaden on the Gulf coast of Florida. Areas with pure strains of yellowfin menhaden are yet to be defined. As the relative density of Gulf menhaden decreases proceeding southward, the number of Gulf × yellowfin menhaden (*B. patronus* × *B. smithi*) hybrids increases along with

pure strains of yellowfin. For example, Turner (1969) reported that collections of menhaden from Panama City to Cedar Keys, Fla., consisted of 94% Gulf menhaden and 6% yellowfin menhaden, while samples from farther south, Tampa Bay to Cape Sable, Fla., were 7% Gulf menhaden, 56% yellowfin menhaden, and 37% Gulf × yellowfin hybrids. Hettler (1968) reported on two collections made along the southern Gulf coast of Florida; one near Naples consisted of 17% Gulf menhaden, 9% yellowfin menhaden, and 74% Gulf × yellowfin hybrids, and the other from near Sanibel Island consisted of 5% Gulf menhaden, 54% yellowfin menhaden, and 41% Gulf × yellowfin hybrids. A similar situation apparently exists on the east coast of Florida with the distributions of Atlantic and yellowfin menhaden and the Atlantic × yellowfin hybrids; for example, the menhaden gill-net fishery in Indian River, Fla., is dominated by yellowfin menhaden and the Atlantic × yellowfin hybrids (Dahlberg, 1970).

Table 1.—Distinguishing and comparative characteristics of North American coastal menhadens (modified from Dahlberg, 1970).

	Large-scaled menhaden		Small-scaled menhaden	
Character	*B. tyrannus*	*B. patronus*	*B. smithi*	*B. gunteri*
Frontal groove	Complete	Complete	Absent	Absent
Lateral spots	Usually present above and below the level of shoulder spot	Usually present above and below the level of shoulder spot	Absent	Absent
Ventral fin	Middle rays and sometimes inner rays equal in length to outer rays	Inner rays equal to or longer than outer rays	Inner rays about one-half to two-thirds length of fin	Inner rays about one-half to two-thirds length of fin
Scale pectinations [1]	Pointed, length medium or long	Pointed	Rounded tip, shorter	Rounded tip, shorter
Body mucus [2]	Copius	Copius	Sparse	Sparse
Flesh [2]	Soft	Soft	Firm	Firm
Ovarian color	Yellow	Yellow	White	?
Lateral scale rows	43-53 (40-58)	42-48	57-73 (54-80)	65-72 (60-76)
Opercular striations	Prominent (12-31)	Prominent (13-25)	Faint or absent (0-15)	Faint or absent (0-18)
Predorsal scales	35-44 (33-46)	29-37 (28-39)	39-51 (37-56)	40-49 (39-52)
Vertebrae	46-48 (44-49)	44-46 (43-47)	44-45 (43-46)	42-43 (41-43)
Ventral scutes	31-34 (29-34)	29-31 (28-32)	30-32 (29-34)	28-30 (27-31)

[1] Older adults.
[2] Fresh specimens.

Species Characteristics

Menhaden are generically distinguished from other clupeids by their relatively large heads, pectinated scales, absence of teeth (beyond juvenile stages), and by their dorsal fin being over the interval between the pelvic and anal fins (Reintjes, 1969; Hildebrand, 1963). The two large-scaled menhaden species can be separated from the two small-scaled species by a variety of characteristics (Table 1). Fresh specimens can be separated simply by feel, as the large-scaled menhadens have large amounts of body mucus and relatively soft flesh, while the small-scaled species have relatively small quantities of body mucus and their flesh is firm. Additionally, the large-scaled species possess a frontal groove, accessory lateral spots beyond the large shoulder spot, and have larger and fewer scales. The small-scaled menhadens lack the former characteristics and have smaller and more numerous scales. Gulf menhaden have a deeper (more convex) body shape and fewer predorsal scales, vertebrae, and ventral scutes than their Atlantic congener (Table 1, Fig. 1, 2). The yellowfin menhaden can be separated from the finescale menhaden by the yellowfin's greater number of vertebrae and ventral scutes, and relatively smaller

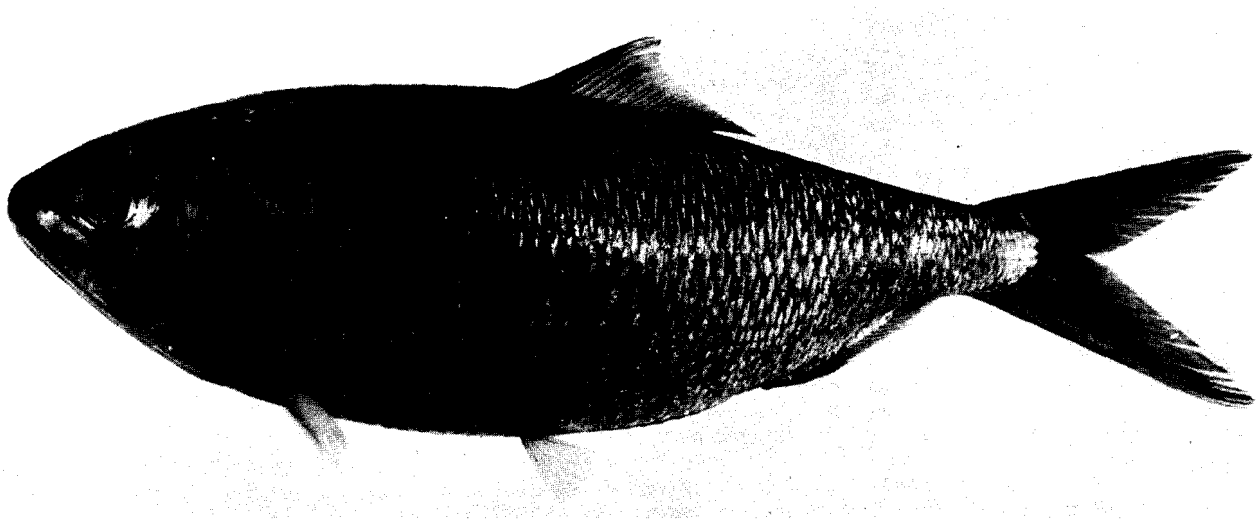

Figure 1.—Adult Atlantic menhaden, 250 mm FL (J. W. Reintjes photo).

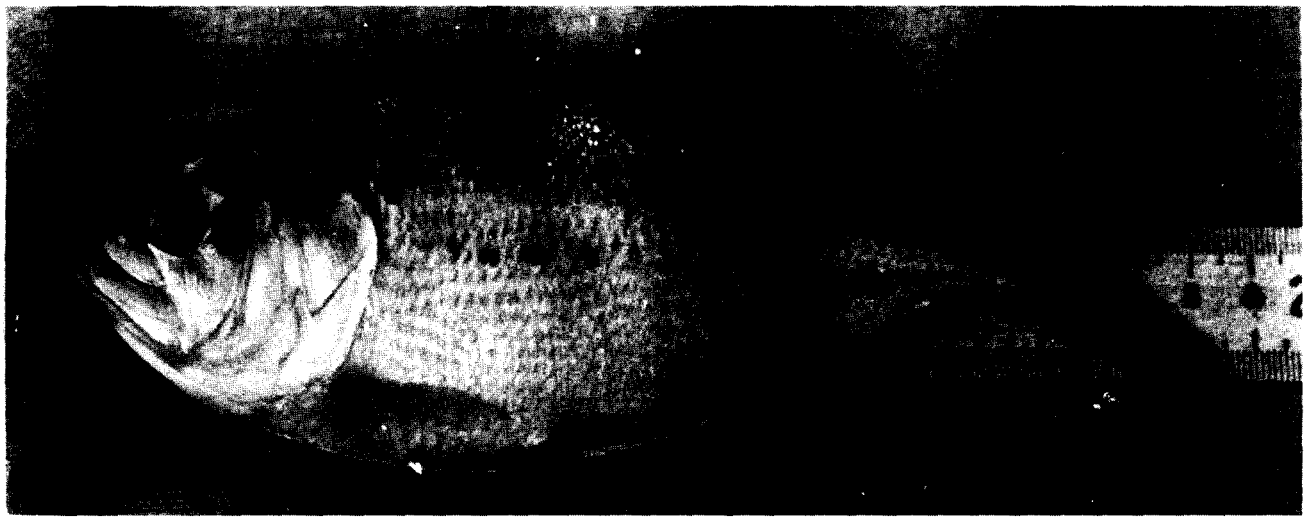

Figure 2.—Adult Gulf menhaden, 167 mm FL (R. B. Chapoton photo).

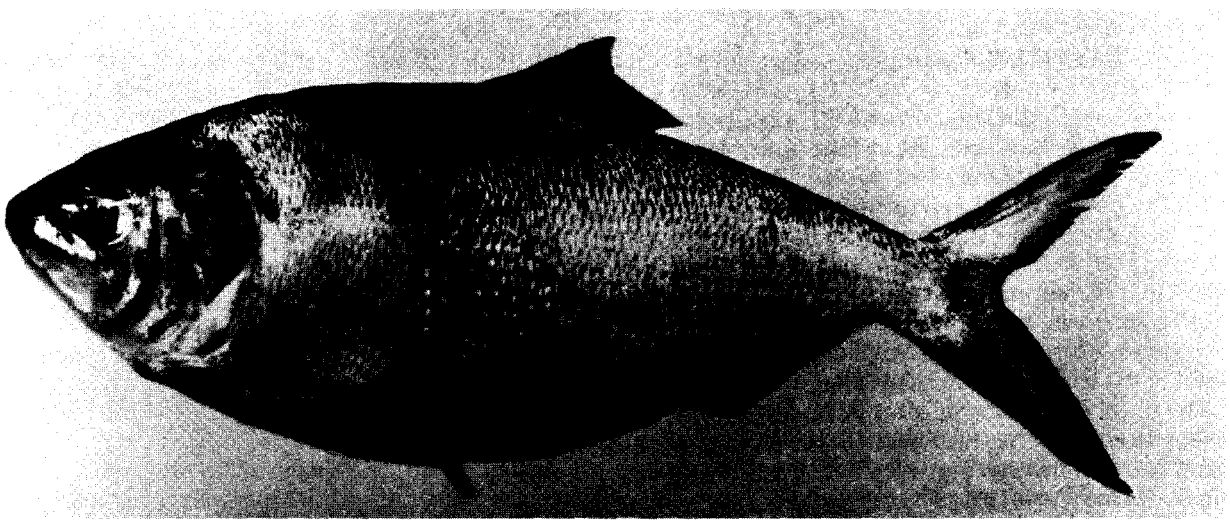

Figure 3.—Adult yellowfin menhaden, 300 mm FL (J. W. Reintjes photo).

head (Table 1, Fig. 3, 4). More detailed descriptions are available from Dahlberg (1970) and Hildebrand (1963). Dahlberg (1970) also provides divergent characteristics between the Atlantic and Gulf populations of yellowfin menhaden.

The morphological and morphometrical appearances of the large-scaled menhaden and yellowfin menhaden hybrids are intermediate to those for the parents (Dahlberg, 1970) (Fig. 5). The presence of a gradient of characteristics between the parental types suggests back-crossing also occurs. Back-crossing with either parental population will be predominantly by male hybrids, as they dominate the hybrid population. A self-sustaining population of hybrids is unlikely due to the preponderance of males. Hettler (1968) found no female hybrids (*B. patronus* × *B. smithi*), while Turner (1969) reported finding 4 females out of 390 hybrids examined. Dahlberg (1970) discovered one female hybrid (*B. tyrannus* × *B. smithi*) from an unknown number of hybrids examined on the Atlantic coast, and found no females among Gulf hybrids.

Hybrids of *B. gunteri* × *B. patronus* (finescale × Gulf menhaden) and *B. gunteri* × *B. smithi* (finescale × yellowfin menhaden) have not been reported. Although the ranges of the three species overlap, yellowfin and finescale menhaden are not abundant in the area of overlap (the Mississippi Delta region). Except for the southeastern Texas coast, finescale menhaden are apparently not abundant in U.S. Gulf coastal waters where Gulf menhaden predominate. Definitive studies on finescale menhaden are lacking.

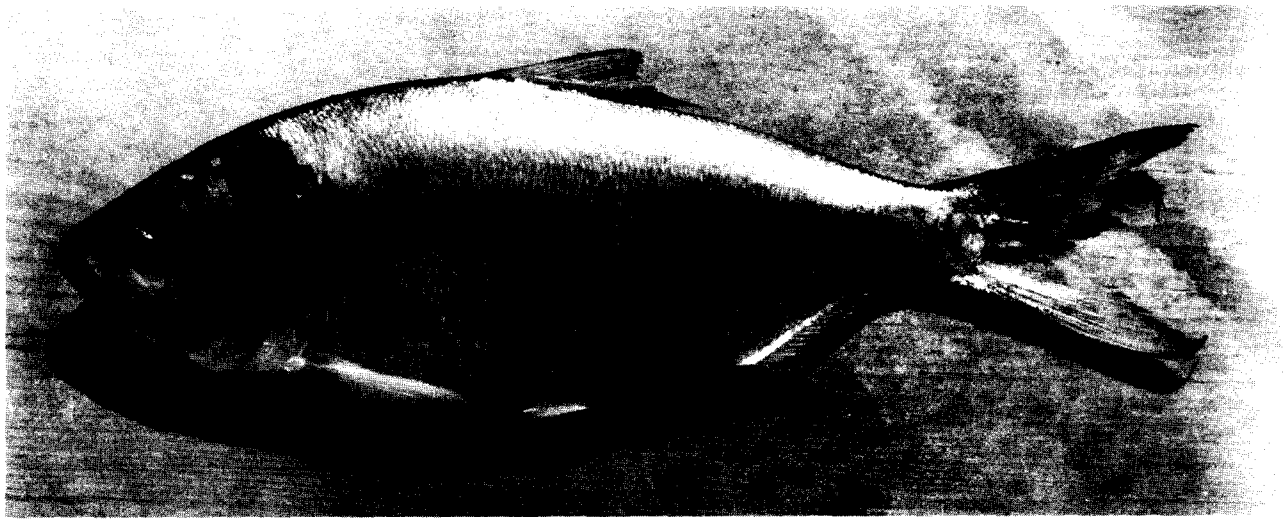

Figure 4.—Adult finescale menhaden, 320 mm FL (R. B. Chapoton photo).

General Life Cycle

Menhaden are estuarine dependent, marine migratory species. Spawning generally occurs during the cooler months in the marine environment, and larvae undergo early growth and development at sea. About 1-2 months later, those larvae that have been transported shoreward enter estuarine bays, sounds, and streams, and metamorphose into juveniles. Menhaden juveniles (young-of-the-year) normally reside in estuarine areas until the following fall or early winter when many migrate into marine waters. Adults generally occur in nearshore oceanic waters and frequently reside in large estuarine systems.

Migratory Behavior and Spawning Season

Atlantic Menhaden

Early hypotheses of the migratory behavior of Atlantic menhaden were based upon observations of schools appearing and disappearing along the U.S. Atlantic coast, and from the examination of the age and size composition of catches among fishing ports along the U.S. Atlantic coast (June and Reintjes, 1959). An analysis of the frequency and distribution of purse-seine sets contributed additional information with respect to the timing of migrations (Roithmayr, 1963). The existing knowledge of migration and distribution was further strengthened by an analysis of the age and length distributions of Atlantic menhaden in the landings (Nicholson, 1971), and finally from results of an internal, ferromagnetic tagging program (Dryfoos et al., 1973; Kroger and Guthrie, 1973; Nicholson, 1978).

During summer, Atlantic menhaden are generally distributed from northern Florida to Maine. The adult population stratifies by age and size, with the older and larger individuals farther northward and the younger and smaller fish in the southern half of the species' range. Although localized movements occur during summer, no major systematic movement occurs until September, when the more northerly portion of the population begins to migrate southward. By December, a significant portion of the adult population that was north of Chesapeake Bay during summer has moved southward to waters off the North Carolina coast. These fish are followed by large numbers of juvenile (young-of-the-year) menhaden, which have recently emigrated from nursery areas farther north. Usually by late January, menhaden schools disappear and schools disperse from nearshore surface waters of North Carolina. During March or early April, schools of adult menhaden reassemble in coastal waters and move rapidly northward. By June, the population is redistributed from Florida to Maine. Even though some Atlantic menhaden migrate north and south along the U.S. Atlantic coast, because the fish distribute themselves on the basis of size and age, the movement actually represents a seasonal expansion and contraction of the Atlantic menhaden's range.

Geotemporal aspects of spawning for this species are closely associated with the migratory behavior of the adults, and some degree of spawning activity is believed to occur during virtually every month of the year. Some fish ripen and some spawning occurs in the more northerly portions of the fishes range as the fish begin moving southward in September. Spawning continues with increasing intensity as the fish move progressively farther southward in October and November. Spawning intensity is believed to peak in waters off the North Carolina coast during winter. Spawning continues, but with decreasing levels of intensity as the fish move northward the following spring and early summer. Supporting evidence for these conclusions was obtained earlier by Higham and Nicholson (1964), subsequently by Kendall and Reintjes (1975), and later by Judy and Lewis (1983). Atlantic menhaden are believed to spawn in oceanic waters over much of the continental shelf, and in bays and sounds in Long

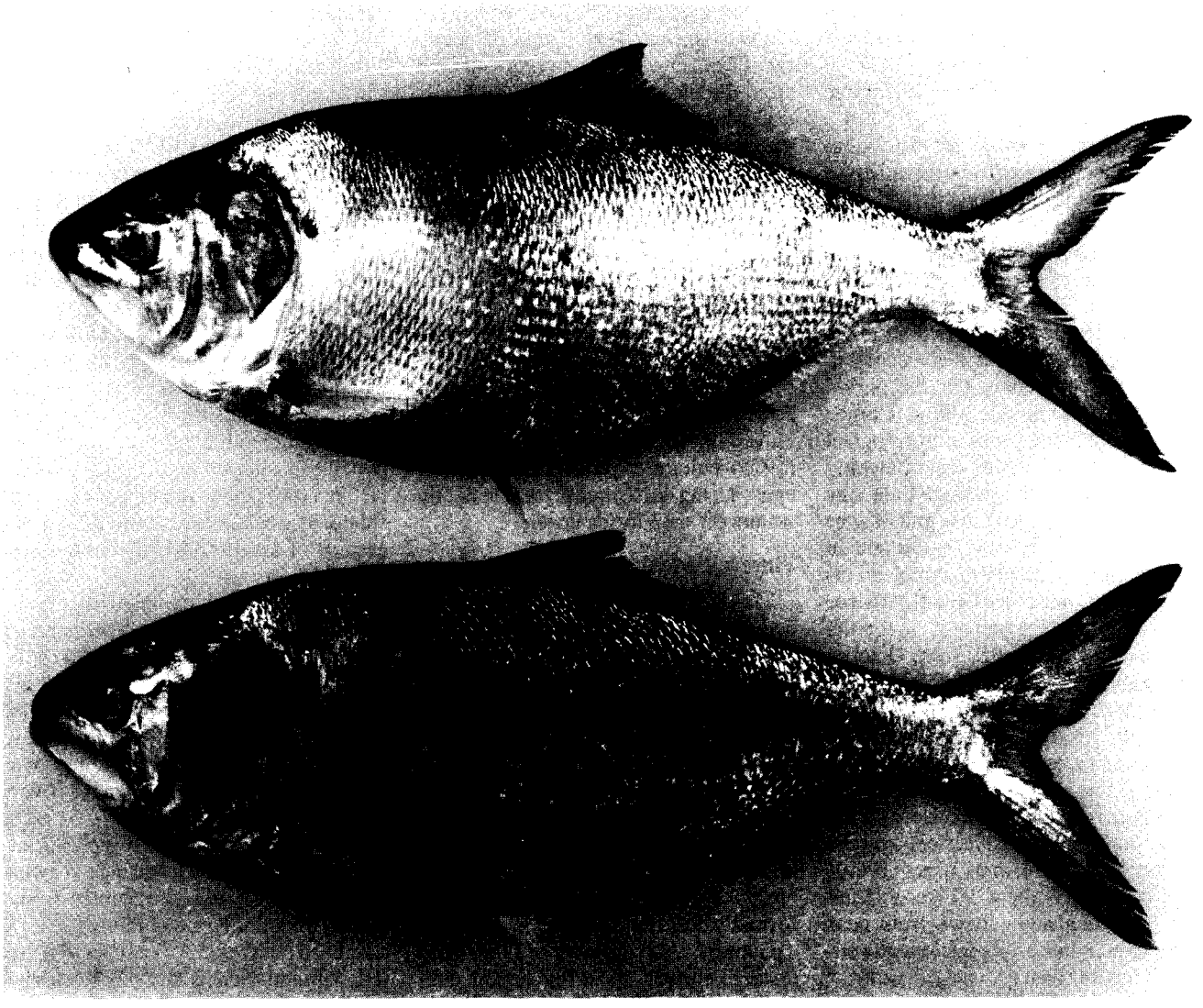

Figure 5.—Adult yellowfin menhaden (upper), 280 mm FL, and Atlantic × yellowfin menhaden hybrid (lower), 285 mm FL (J. W. Reintjes photo).

Island waters and northward (Nelson et al., 1977; Ferraro, 1980b). Evidence for recent spawning activity was based on the presence of menhaden larvae and eggs in plankton samples. Evidence of imminent spawning was also provided by the presence of near-ripe specimens in fish samples obtained from commercial purse-seine landings. However, spawning has not been directly observed in the marine environment, and running-ripe females are rarely captured.

The relative magnitude of temporal spawning activity within and between geographic regions is in part a function of the age/size structure of the spawning population. For example, with the bulk of the spawning stock in recent years consisting of late age-2 fish, relatively less spawning activity would have been expected in the New England and Middle Atlantic areas as compared to the 1950's when a broader and stronger age structure was more extant in the population (Ahrenholz et al., 1987b).

Gulf Menhaden

Gulf menhaden do not exhibit an extensive migratory pattern. During late spring and summer they distribute along the U.S. Gulf coast in nearshore waters. Beginning in October, they move offshore into deeper waters for winter. Roithmayr and Waller (1963) reported that during summer Gulf menhaden occurred in depths of 1-8 fathoms, while during winter months they were found in 4-18 fathoms east and west of the Mississippi Delta, and at 20-48 fathoms in a smaller area east and northeast of the Delta.

Results of tagging studies failed to identify any east-west component of annual migration for Gulf menhaden (Pristas et al., 1976; Kroger and Pristas, 1975); however, multiple-year juvenile

tag-recovery data indicated a tendency for Gulf menhaden from the eastern and western extremes of their range to move toward the center of their range with age (Ahrenholz, 1981).

The spawning season for Gulf menhaden was determined by observations of larvae, gonadal development, and presence of eggs in plankton samples. Spawning has not been directly observed. From observations of the occurrence of larvae in Lake Ponchartrain, La., Suttkus (1956) concluded that spawning probably began in October and ceased in February; he presumed that this period could fluctuate among years. Combs (1969) concluded from a histological examination of ovaries that spawning ranged from October through February or early March. Christmas and Waller (1975), after a literature review and an examination of plankton samples collected from much of the Gulf of Mexico, concluded that spawning "...for the most part..." occurred from October through March. Shaw et al. (1985a) presented arguments and evidence for an even more protracted season.

Spawning areas have been determined by noting the geographic collection sites where Gulf menhaden eggs were taken. Based on their own collections and the work of Fore (1970) and Turner (1969), Christmas and Waller (1975) concluded that Gulf menhaden spawn from near shore to 60 miles offshore along the entire U.S. Gulf coast.

Yellowfin Menhaden

Adult yellowfin do not appear to display any systematic, annual migratory behavior. Dahlberg (1970) referred to them as "...common near shore along both Florida coasts throughout the year." He considered them an inshore or bay form (in contrast to the large-scaled menhadens). Some larger individuals are occasionally found as far north as Cape Lookout, N.C., during summer.

Spawning seasons and some spawning areas have been identified by collecting specimens for artificial spawning and rearing. For the Atlantic coast population, Reintjes (1962) began sampling near Sebastian, Fla., in November. He noted ripening males in December, several ripening females in January, and by February 8 about 25% of females were ready to spawn. Hettler's (1970) specimens from the Atlantic coast were taken from the Indian River, Fla., in February. Dahlberg (1970) concluded that the spawning season for yellowfin menhaden was February and March on both the Atlantic and Gulf coasts of Florida. His conclusion for the Gulf coast was at least in part based on Hettler's (1968) collection just north of Naples during mid-March of two ripe female yellowfin menhaden and Turner's (1969) collection of ripe females during February and March off the southern Gulf coast of Florida. Spawning may occur as early as November, as Houde and Swanson (1975) collected yellowfin menhaden eggs during this month from Atlantic waters off the Florida coast.

Finescale Menhaden

There is no evidence from which to deduce any systematic seasonal migration by the finescale menhaden other than the notation of an apparent seasonal shift of larger finescale menhaden between Texas bays (Gunter, 1945). Like the yellowfin menhaden, the finescale menhaden appears to occur more in estuarine or nearshore areas. Gunter (1945) referred to it as a brackish-water form, as opposed to the more saline Gulf menhaden, although this species was not formally described until 3 years later.

Gunter (1945) discovered a ripe male during February and a ripe female during the latter part of March, and noted that the spawning season was probably from midwinter to early spring. He also observed post-larval finescale menhaden from January to May. Simmons (1957) reported that this species spawned in the upper Laguna Madre of Texas during February. Given these observations, a spawning period of November to March appears realistic. Both Simmons (1957) and Gunter (1945) reported that spawning occurs in inside (estuarine) Texas waters.

Maturation and Fecundity

Gulf menhaden become sexually mature near the end of their second year of life (age 1) (Lewis and Roithmayr, 1981). By comparison, only a small percentage of Atlantic menhaden become sexually mature during their second year of life, while from two-thirds to nearly all are sexually mature by the end of their third year (age 2) (Higham and Nicholson, 1964; Lewis et al., 1987). Female Gulf menhaden about 150 mm FL and larger are generally sexually mature by the spawning season (Lewis and Roithmayr, 1981), while the smallest sexually mature female Atlantic menhaden are at least 180 mm FL (Lewis et al., 1987).

Age and size at maturation data is limited for the small-scaled menhadens. Gunter (1945) observed a ripe female finescale menhaden 150 mm TL, and a ripe male 125 mm TL. The smaller of the two ripe female yellowfin menhaden that Hettler (1968) found was 186 mm FL. No standing stock ova counts for either species of small-scaled menhaden are available.

Atlantic and Gulf menhaden are considered to be multiple (fractional or intermittent) spawners (Higham and Nicholson, 1964; Combs, 1969). As noted by Combs (1969), the fishes' ovaries could not contain all the developing ova if they matured at the same time. Thus, ova mature and are spawned in batches over a protracted spawning season.

The potential number of ova produced by an individual female during a spawning season has been determined (estimated) by counting the standing stock of advanced oocytes in Atlantic menhaden (Higham and Nicholson, 1964; Dietrich, 1979; Lewis et al., 1987) and Gulf menhaden (Suttkus and Sundararaj, 1961; Lewis and Roithmayr, 1981). For this technique to provide a reasonable estimate of true annual fecundity, the number of ova produced during a season must be annually determinate, like that of the multiple spawning Atlantic silverside, *Menidia menidia* (Conover, 1985), as opposed to being annually indeterminate, similar to the multiple spawning northern anchovy, *Engraulis mordax* (Hunter and Macewicz, 1985). While some workers (e.g., Lewis et al., 1987) felt that determinate fecundity is likely for the Atlantic menhaden (and thus likely for the other menhadens), this condition has not been demonstrated, nor has batch fecundity been estimated for any species of menhaden.

Fecundity estimates currently used in spawner-recruitment analyses (when number of potential eggs produced is used as a measure of spawning stock) are derived from the results of Lewis and Roithmayr (1981) for Gulf menhaden (Fig. 6). Fecundity values for the Atlantic menhaden are results of pooled data from Higham and Nicholson (1964), Dietrich (1979), and Lewis et al. (1987) (Fig. 6). These fecundity estimates are useful in stock assessment analyses because they ascribe a measure of relative reproductive value for larger (and older) fish in the population.

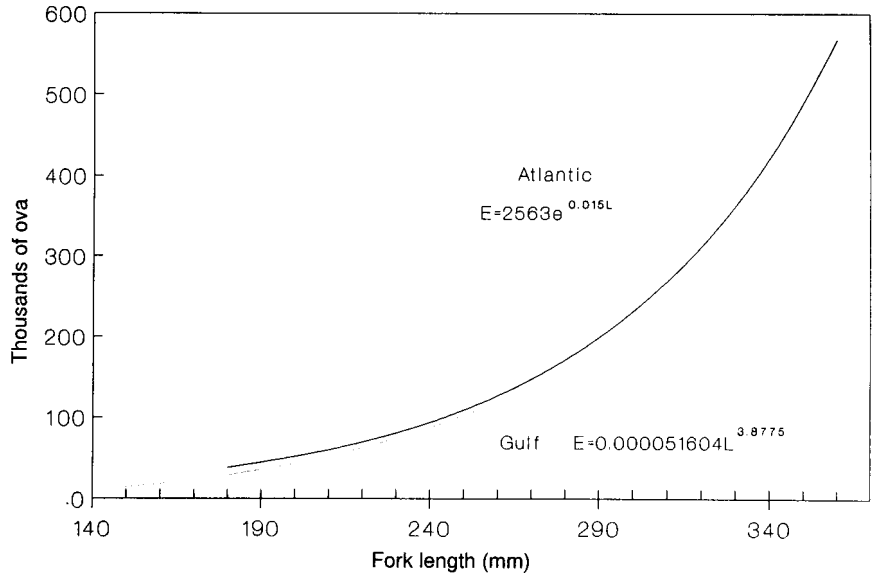

Figure 6.—Potential number of ova (in thousands) as a function of FL for Atlantic menhaden (line) and Gulf menhaden (dashes).

Description and Development of Immature Life Stages

Eggs

A description of the early life history forms of Atlantic menhaden is given by Kuntz and Radcliffe (1917). These authors collected a developmental series of ripe adults through eggs, embryos, larvae, and juveniles during summer from Woods Hole Harbor, Martha's Vineyard, and Nantucket Sound. They described the eggs as spherical in shape, highly transparent with a thin, horny egg membrane and a relatively wide perivitelline space. Each egg contained a single oil globule. Their recorded egg dimensions are summarized in Table 2.

Descriptions of eggs from other species of menhaden followed a number of years later. Reintjes (1962) described yellowfin menhaden eggs obtained on the Atlantic coast of Florida from both planktonic sampling and artificial fertilizations. Hettler (1968) described yellowfin × Gulf menhaden eggs from the Gulf coast of Florida, obtained by artificial cross fertilization. Houde and Fore (1973) described Gulf menhaden eggs from planktonic collections. An additional description of yellowfin menhaden eggs obtained from the Atlantic coast of Florida was given by Houde and Swanson (1975). Hettler (1984) described eggs obtained for laboratory-spawned Atlantic and Gulf menhaden (Table 2). Powell and Phonlor (1986) indicate that Atlantic menhaden eggs tend to be larger than those of Gulf menhaden for a particular set of conditions; however, due to dimensional overlap, menhaden eggs are not distinguishable to species with morphological characteristics (Table 2).

Egg hatching time varies as a function of temperature and species. Kuntz and Radcliffe (1917) reported incubation time for Atlantic menhaden eggs as less than 48 hours. Ferraro (1980a) developed a temperature-dependent empirical equation from which temporal estimates of duration for any stage of embryological development, including hatching, could be obtained. Reintjes (1962) reported hatching times of 46 hours from fertilization for yellowfin menhaden eggs held at temperatures of 18.5° to 19.0°C. Additional data on hatching time obtained from the study reported by Reintjes (1962) are given by Hettler (1968) as 46 hours at 18°C, 34 hours at 21°C, and 26 hours at 26°C. Hettler (1968) further reported that the yellowfin × Gulf menhaden eggs hatched in about 38-39 hours when held at 19.5 to 21.5°C. Hettler (1984) reported Gulf

Table 2.—Comparative characteristics of North American coastal menhaden eggs by species and source.

Species and source	Egg diameter (mm)	Yolk diameter (mm)	Oil globule diameter (mm)	Source of eggs
B. tyrannus				
Kuntz and Radcliffe (1917)	1.4-1.6	0.9	0.12-0.14	Planktonic
Jones et al. (1978)	1.30-1.95	0.90-1.20	0.11-0.17	?
Hettler (1984)	1.54-1.64	0.82-0.95	0.20-0.23	Laboratory reared
B. patronus				
Houde and Fore (1973)	1.04-1.30		0.08-0.20	Planktonic
Hettler (1984)	1.18-1.34[1]	0.95 (0.05)[2]	0.16-0.22[1]	Laboratory reared
B. smithi				
Reintjes (1962)	1.21-1.48	0.77-1.04	0.05-0.18	Planktonic
Reintjes (1962)	1.15-1.30	0.77-0.95	0.07-0.16	Artificially spawned
Houde and Swanson (1975)	1.21-1.34	0.80-1.19	0.12-0.17	Planktonic
B. gunteri	No data			
B. smithi × *B. patronus*				
Hettler (1968)	1.05-1.18	0.98		Artificially spawned

[1] Combined results from two spawning series.
[2] Range for spawning with larger yolks not given, mean and one standard deviation shown; range for spawning with smaller yolks 0.66-0.79 mm.

menhaden eggs hatched in 40-42 hours at 19-20°C.

Larvae

Larval development through the prejuvenile stages are described by Kuntz and Radcliffe (1917) and Lewis et al. (1972) for Atlantic menhaden, by Hettler (1984) for Gulf menhaden, and by Houde and Swanson (1975) for yellowfin menhaden. Additional information on early larval yellowfin menhaden is given by Reintjes (1962) and Hettler (1970).

The size of menhaden larvae at hatching is thought to be a function of egg size (Powell and Phonlor, 1986). Observed sizes at hatching ranged from 2.6 mm to about 3.7 mm SL (Houde and Swanson, 1975; Hettler, 1984; Powell and Phonlor, 1986). The smallest individuals were Gulf menhaden and the largest, Atlantic menhaden, with yellowfin menhaden about midrange.

The larvae are relatively undeveloped upon hatching. The mouth is not formed, the eyes are unpigmented and thus nonfunctional, and the fin rays are undeveloped (Houde and Fore, 1973; Reintjes, 1962). Depending on temperature, larval menhaden begin feeding within 2-6 days. Most of the yolk is absorbed during the prefeeding developmental period, but some may remain after the onset of feeding (Houde and Swanson, 1975). Once the yolk sac is absorbed, the larvae are slender and rodlike.

The subsequent rate of growth for each species depends on temperature and food availability. Hettler (1984) reported that larval Gulf menhaden growth averaged 0.30 mm day^{-1} for the first 90 days of rearing. He also reported that growth of yellowfin menhaden larvae averaged 0.36 mm day^{-1} through 32 days (Hettler, 1970). Houde and Swanson (1975) observed larval yellowfin menhaden growth of 0.45 mm day^{-1} for the first 20 days of rearing, albeit at a higher temperature than Hettler (1970). Additional comparative growth values were obtained by adjusting the exponential expressions given by Powell and Phonlor (1986). Growth for their Atlantic menhaden was about 0.41 mm day^{-1} and for their Gulf menhaden, 0.33 mm day^{-1} for about 18 days of rearing. Warlen (1988) reported an average rate of 0.30 mm day^{-1} over 60 days for ocean-sampled Gulf menhaden larvae.

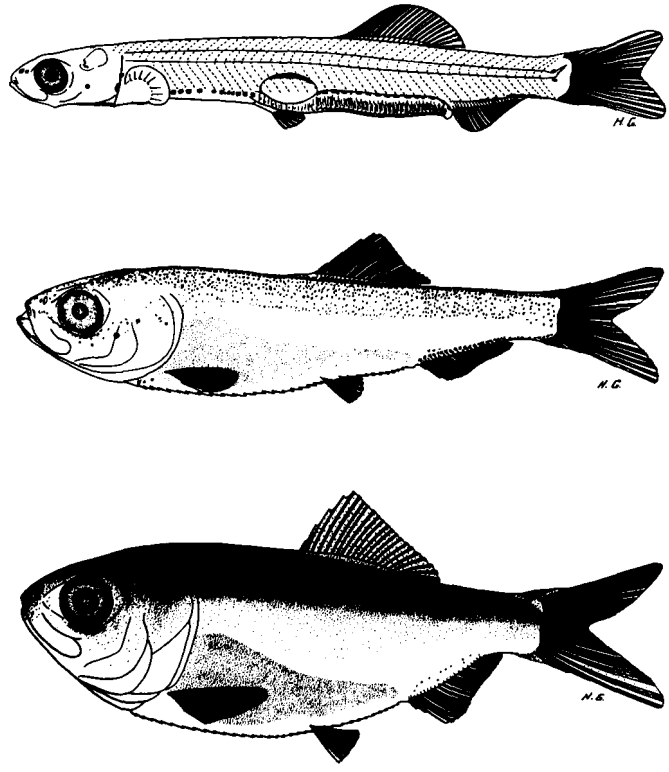

Figure 7.—Illustrations of Atlantic menhaden larva (27 mm TL), prejuvenile (32 mm TL), and juvenile (64 mm TL); upper, middle, and lower, respectively, from Lewis et al. (1972).

Atlantic menhaden larvae ranging from 14 to 34 mm FL (Reintjes and Pacheco, 1966) enter estuarine nursery areas at about 45-60 days of age (Nelson et al., 1977). Larvae are reported as entering estuaries in New England during May through October, in the U.S. Middle Atlantic from October to June, and along the U.S. South Atlantic coast from November to May (Reintjes and Pacheco, 1966; Wilkins and Lewis, 1971).

The length of the oceanic period for larval Gulf menhaden is estimated at 6-10 weeks (Deegan and Thompson, 1987). Estuarine immigration was observed from late October through April, and larvae ranged in size from 10 to 32 mm TL (Fore, 1970; Tagatz and Wilkins, 1973).

Systematic observations of larval immigration for small-scaled menhadens are unavailable. Since some spawning presumably occurs near or in some estuarine areas, oceanic larval transport may not be as critical a life-history event for these species as it is for the large-scaled species.

Juveniles

When menhaden larvae undergo metamorphosis to the juvenile stage, they have all the characteristics of an adult except for sexual maturity (Fig. 7). During transformation (prejuvenile stage), they undergo a substantial increase in relative body depth and weight, while achieving only a slight increase in length. The pronounced difference in relative body proportions is shown graphically for Atlantic menhaden by Lewis et al. (1972), and for Gulf menhaden by Deegan (1986). Length during the prejuvenile period varies between individuals and species, but is between 30 and 40 mm TL for Atlantic menhaden (Lewis et al., 1972; June and Carlson, 1971). Gulf menhaden metamorphose at a slightly smaller size, with complete transformation by 28-30 mm SL (Suttkus, 1956). An even smaller size was reported for yellowfin menhaden (laboratory-reared) by Houde and Swanson

(1975), with the transformation complete between 20 and 23 mm SL. Gunter (1945) observed post-larval finescale menhaden as small as 21 mm TL.

In addition to the more apparent external changes in body shape, significant internal morphological changes occur during metamorphosis as well. Gill rakers increase in number, length, and overall complexity (June and Carlson, 1971). The functional morphology of the resulting elaborate branchial basket is described by Friedland (1985). Intestine length increases dramatically, and a gizzard-like pyloric stomach and pyloric caeca develop (June and Carlson, 1971). These changes are diagnostic and necessary for a lifetime trophic habit of filter-feeding, microphagous planktivory.

Ultimate juvenile size achieved during estuarine residence is a function of favorable growth conditions and absolute age of individual fish. The observed size range of juvenile Atlantic menhaden is quite large (Table 3), and is attributed to the broad geographic and temporal spawning range. Most of a new year class is 10-18 months old on their first designated birthday (by convention, March 1). Hence, some individuals in a year class may be 8 months older than other individuals.

The spawning which initiates a year class begins off the New England coast in September, then proceeds southward to the U.S. Mid-Atlantic and Chesapeake Bay coasts in October and November and subsequently to the oceanic waters off the Carolinas. Spawning resumes as fish move north in early spring and continues into summer. The longest temporal period between spawning origins of a developing year class occurs in the most northern waters and the least in the more southern. Hypothetically, this type of spawning pattern should result in bimodal length-frequency distributions in geographic regions with a detectable hiatus in spawning due to migration, and a single mode in the more southerly reaches of the migratory route. Some supporting evidence for these hypotheses exists. A seasonal bimodality in length frequencies has been observed for young-of-the-year in the Chesapeake Bay area, presumably one mode resulting from spawning during the southern migration and one from spawning during the northern migration (McHugh et al., 1959). Also, preliminary length-frequency analyses of juveniles sampled in South Carolina waters indicate a fair degree of unimodality from that area, presumably from a relatively unbroken spawning period.

Some juvenile length-frequency distributions from northern coastal estuaries of North Carolina appear to have two, and in some cases three, modes. The first of these modes may be attributable to spawning in October or early November by sexually maturing age-2 and some age-3 fish which summered in North Carolina or Virginia waters (Wilkins and Lewis, 1971). The second (and major) mode probably represents progeny from subsequent winter spawning by migratory adults which summered in the U.S. Mid-Atlantic and New England waters. Trimodality in length frequency distributions is sometimes observed and could result from a large portion of the migratory spawners moving even farther south, or from a cessation in spawning by the overwintering fish, or from differential survival of larvae or juveniles in winter.

A substantial variance in mean size of older juveniles exists among years. This can be partly due to density-dependent growth, as size-at-age data was shown to be inversely related to year class size, at least as early as the estuarine growth phase (Reish et al., 1985; Ahrenholz et al., 1989).

A relatively wide range in juvenile size has also been observed for Gulf menhaden (Table 3). Some of the broad range in sizes is expected as a result of their protracted spawning season. There is additional evidence for bimodality in the juvenile population, and hence suggestions of two spawning peaks (Tagatz and Wilkins, 1973). The bulk of a year class is 10-14 months old on their first designated birthday (by convention January 1). Density-dependent growth during the juvenile stage is not prominant, if present at all, and Nelson and Ahrenholz (1986) could find no evidence of density-dependent growth from an examination of fishery landings size-at-age data. However, Guillory and Bejarano (1980) reported evidence for density-dependent growth among mean lengths of juveniles sampled from several estuarine areas and subsequent catch-per-unit-effort (CPUE) data for age-1 fish in the purse-seine reduction fishery.

Much narrower ranges in size were noted for juvenile finescale and yellowfin menhaden (Table 3). This may be due to sampling limitations, as well as from a relatively less protracted spawning season.

Table 3.—Reported ranges in length of juvenile menhaden near the end of estuarine nursery habitation. Numbers in parentheses are approximate conversions from total length to fork length using parameters from Jorgenson and Miller (1968).

Species	Range of FL in mm	Month sampled	Source
B. tyrannus	38-171	September	Kroger et al. (1974)
B. patronus	38-110	October	Unpublished[1]
B. patronus	(78-103)	August	Tagatz and Wilkins (1973)
B. smithi	63-88	August	Unpublished[2]
B. gunteri	(74-94)	"1-year-old"	Gunter (1945)

[1] Range from tagging records over several years; NMFS, SEFC Beaufort Laboratory, Beaufort, N.C.
[2] Range from tagging records, Turnbull Creek, Fla., 1971; NMFS, SEFC Beaufort Laboratory, Beaufort, N.C.

Table 4.—Maximum sizes reported for adult menhaden by species. Values in parentheses are approximate conversions from values reported, for purposes of comparison. Conversions to fork length (FL) used equations from Jorgenson and Miller (1968), while total length (TL) to standard length (SL) and vice versa used combined ratios (two large-scale species' values combined, and two small-scale species' values combined) from ranges in study specimens reported by Hildebrand (1963).

Species	TL mm	FL mm	SL mm	Source
B. tyrannus	500	(419)	(409)	Hildebrand (1963)
B. patronus[1]	265	(223)	(214)	Hildebrand (1963)
B. smithi[1,2]	(341)	(281)	257	Christmas and Gunter (1960)
B. gunteri[3]	(351)	(289)	264	Christmas and Gunter (1960)

[1] Some larger individuals of *B. patronus* and *B. smithi* were reported by Dahlberg (1970). It appears, however, that some of his reported standard lengths may be fork lengths.
[2] Fish on Figure 3 is larger than from this earlier report.
[3] Fish on Figure 4 is larger than from this earlier report.

Age and Growth of Adults

Relative to absolute size, Atlantic menhaden are the largest of the genus, Gulf menhaden are the smallest, with both small-scaled species being of intermediate size (Table 4). Similarly, the Atlantic menhaden is probably the most long lived (10-12 years) and the Gulf menhaden the shortest (5-6 years). The longevity of the small-scaled menhadens

is unknown, but probably is equal to or greater than that for Gulf menhaden, and certainly less than that for Atlantic menhaden.

Size-at-age data, and hence rates of growth in years are only available for large-scaled menhadens. The technique for ageing Atlantic menhaden with scales was developed by June and Roithmayr (1960). Additional validation of the technique was provided by Kroger et al. (1974). Gulf menhaden are aged with scales by criteria developed by Nicholson and Schaaf (1978).

Since the density-dependent growth effect persists for several years in the fishery dependent size-at-age data for the Atlantic menhaden, descriptive growth equations were estimated for each year class (Ahrenholz et al., 1987b). Comparative growth curves for length and weight are given for a relatively large year class (1975) and a small year class (1970) in Figure 8. Only one equation was used to describe adult growth in Gulf menhaden in a stock assessment and population simulation study by Nelson and Ahrenholz (1986) (Fig. 9).

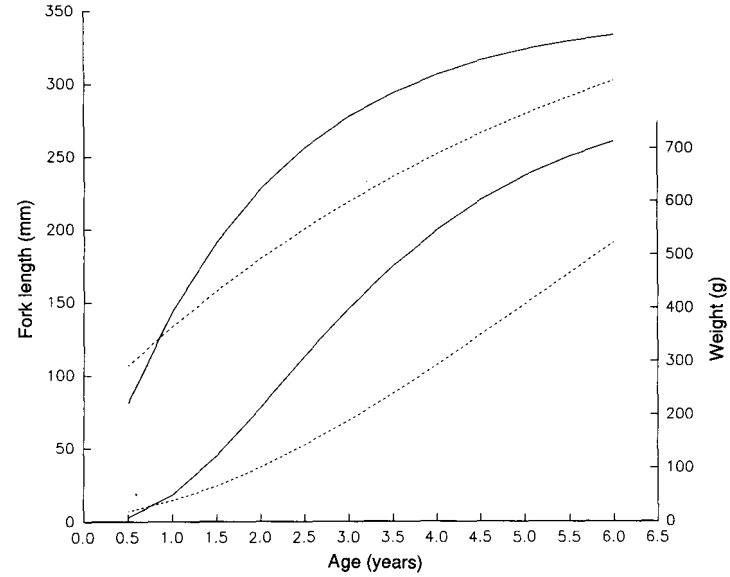

Figure 8.—Comparative fitted von Bertalanffy curves of two dissimilar sized Atlantic menhaden year classes (numbers of fish), 1970 (small year class, solid curves), and 1975 (large year class, dashed curves). Upper curves are fork lengths in millimeters, lower curves are weights in grams, as a function of age in years.

Trophic Relationships

Because the general morphology of menhaden is similar, a high degree of similarity among species with respect to their roles as both predators and prey is assumed. Observations and study results are given here by the particular species upon which they were made, but, in general, parallel conclusions should be possible for the other menhaden species.

Menhaden As Consumers

From the first-feeding larval stage into the prejuvenile stage, Atlantic menhaden selectively sight-feed on individual planktonic organisms (Chipman, 1959; June and Carlson, 1971). Govoni et al. (1983) noted that small Gulf menhaden larvae feed heavily on larger phytoplankton (predominantly dinoflagellates) and some zooplankton. As the larvae grow, phytoplankton become less important in the diet, and (larger) zooplankton, especially copepods (all life stages) become more important. After metamorphosis, filter feeding omnivory becomes the rule. Juveniles consume zooplankton and phytoplankton, but interestingly, some of the phytoplankton they consume are an order of magnitude smaller than the smallest phytoplankton consumed during the larval phase (Chipman, 1959; June and Carlson, 1971). Darnell (1958) found relatively large quantities of phytoplankton along with detritus and some zooplankton in the guts of small juvenile Gulf menhaden.

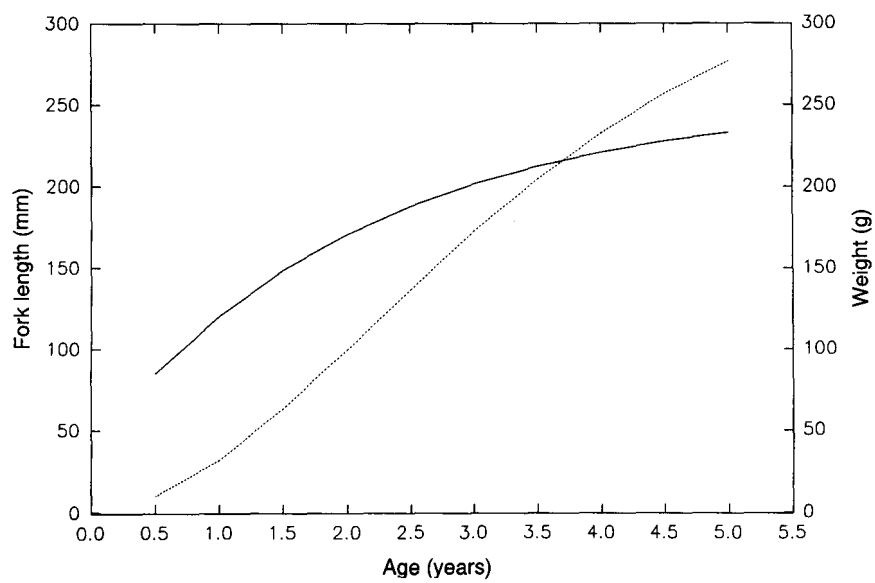

Figure 9.—Fitted von Bertalanffy curves of mean size-at-age for Gulf menhaden, solid curve is fork length in millimeters, dashed curve is weight in grams.

Adult Atlantic menhaden stomach contents examined by Peck (1893) consisted of phytoplankton (especially dinoflagellates and diatoms); zooplankton; greenish, brownish, or yellowish organic "mud" or amorphous matter; and detritus. He also examined stomach contents from juveniles and found the same type of organic material that was in adult fish. Because of the menhaden's elaborate, highly specialized gill-rakers for filter-feeding, Peck (1893) hypothesized that what was in the surface waters could also be found in menhaden stomachs. He further demonstrated this conclusion by pouring sampled seawater through a gauze and white sand filter. This paper emphasized that similarities and differences in the composition of the fishes' diet are due to local variations.

Peck's (1893) hypothesis has been only slightly modified by more recent studies. The relative composition of microorganisms/materials within the fishes' stomachs, as compared to that in the surrounding water, is a function of the menhaden's filtering efficiencies for different sizes and types of organisms. In addition, there is some minimum size threshold, below which the fish is incapable of capturing by filtration, as well as a maximum size, above which the fish will simply avoid (and/or the organism avoids the fish). A knowledge of these maximum and (especially) minimum thresholds is critical for the determination of the ecological role of Atlantic menhaden (Durbin and Durbin, 1975; Friedland et al., 1984). Of major concern is the nanoplankton (2-20 μm by classification of Sieburth et al., 1978), which can be a dominant fraction of the phytoplankton production in estuarine and nearshore systems, especially during summer (see Durbin et al., 1975; McCarthy et al., 1974).

The minimum size threshold for adult menhaden (about 260 mm FL) was determined from feeding experiments to be 13-16 μm (Durbin and Durbin, 1975). Friedland et al. (1984) determined the minimum size threshold for juveniles (about 138 mm FL) to be 7-9 μm. They noted an increase in filtering efficiency for some types of organisms when detritus was present in the water column. Since the minimum threshold appears to be a function of fish size, the abundant 40-90 mm FL juveniles present in estuarine systems during spring and summer, probably take advantage of the predominating primary productivity occurring within the nanoplankton segment of the plankton community.

On the other extreme, Friedland et al. (1984) noted maximum filtration efficiency occurred for objects about 100 μm in diameter for the 138 mm FL juveniles, but did not give an estimate for maximum acceptable prey size. Durbin and Durbin (1975) did not give a prey size for maximum filtration efficiency, but they did note that the maximum acceptable prey size was between 1,200 μm and 10 mm, as prey (copepods) of the smaller size were consumed while those of the larger (adult brine shrimp) were not.

In addition to the living organisms consumed, varying quantities of detritus and/or amorphous material is also injested while filter feeding. While the actual organic source of this material, and the actual magnitude of the energetic contribution it makes, can vary by habitat type and is not well known, evidence of the digestion and subsequent absorption of this material by menhaden is accumulating (Jeffries, 1975; Lewis and Peters, 1984; Peters and Lewis, 1984; Deegan et al., 1990).

Menhaden As Forage

All life history stages of menhaden from egg through adults are potential prey for a large variety of predators. Moreover, the potential exists for menhaden to feed on their own eggs (Nelson et al., 1977), as well as the eggs and larvae of other fishes and invertebrates (Peck, 1893; McHugh, 1967). Larvae and juveniles of a number of piscivorous species of fish potentially prey upon menhaden larvae, depending on their coincidence in space and time, along with compatible body sizes. Many invertebrate predators, especially in oceanic waters, can be expected to prey upon menhaden larvae; notable among this group are the abundant chaetognaths (Clements, 1990). Other potential invertebrate predators include, but are not limited to, squids (mollusks) and ctenophores and jellyfishes (coelenterates).

In estuarine and marine waters of the U.S. Atlantic and Gulf coasts, menhaden juveniles and adults are potential prey for a large number of species and sizes of piscivorous fishes (Sykes and Manooch, 1979). The relative degree of predation will again be a product of the coincidence in space and time of the potential predators and prey, and their relative sizes. For the most part, prey selection among menhaden predators appears to be predominantly opportunistic. However, since menhaden are so widespread and abundant in estuarine and nearshore systems, they are frequently an important component of many fishes' diets during one or more time periods within the year. For example, Atlantic menhaden were reported as an important component of the diet of striped bass, *Morone saxatilis*, in Albemarle Sound, N.C. (Manooch, 1973), but of variable importance to weakfish, *Cynoscion regalis* (Merriner, 1975). Peck (1893) noted that bluefish, *Pomatomus saltatrix*, and bonito, *Sarda sarda*, are major predators of menhaden, and pointed out that the potential breadth of the role of Atlantic menhaden as prey is well demonstrated by its popularity as bait.

Menhaden are thought to be an important forage for piscivorous birds, e.g. brown pelicans, *Pelecanus occidentalis*, and are known to be heavily preyed upon by osprey, *Pandion haliaetus* (Spitzer, 1989) and common loons, *Gavia immer* (Spitzer[1]). Menhaden were also reported as prey for marine mammals (Hildebrand, 1963).

Parasites and Disease

Two common parasites encountered on Atlantic menhaden are the parasitic isopod, *Olencira praegustator*, and the parasitic copepod, *Lernaeenicus radiatus*. The relatively common occurrence of *O. praegustator* in the mouth and throat of *B. tyrannus* is reflected by one of the Atlantic menhaden's early common names, i.e., "bug-fish" (Smith, 1907). Kroger and Guthrie (1972a) noted that the highest rate of infestation of this isopod among juvenile Atlantic

[1] P. R. Spitzer, Univ. Md. System, Cent. Environ. Est. Stud., Horn Point Environ. Lab., P.O. Box 775, Cambridge, MD 21613. Personal commun.

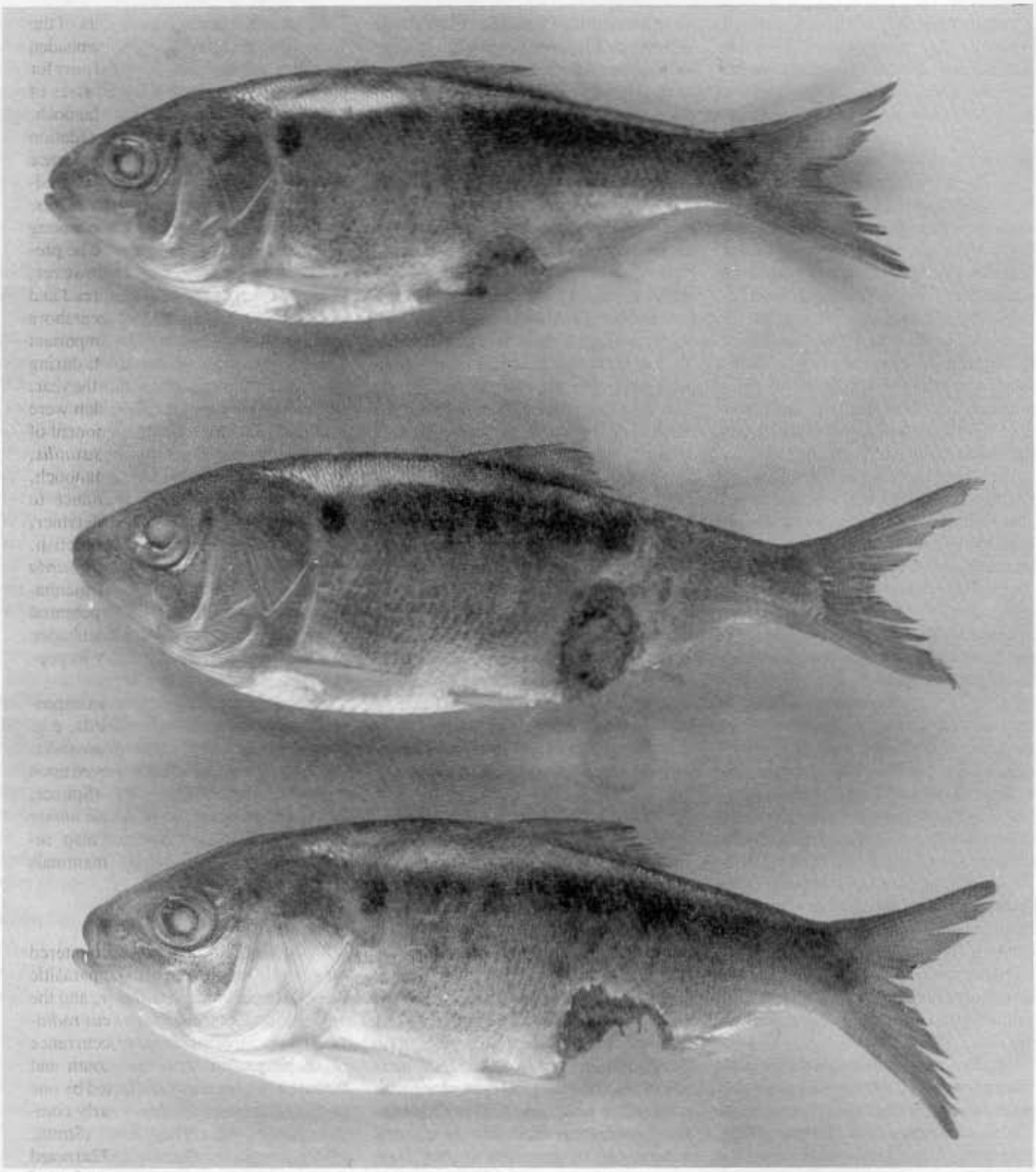

Figure 10.—Ulcerative mycosis lesions on juvenile Atlantic menhaden from Hancock Creek, N.C. (fall of 1986).

menhaden was in estuaries along the mid-portion of the fishes' range, i.e., Virginia through New Jersey.

In addition to Atlantic menhaden, *O. praegustator* has been reported in specimens from the Atlantic and Gulf populations of yellowfin menhaden, as well as Gulf menhaden, and both the hybrids *B. patronus* × *B. smithi* and *B. tyrannus* × *B. smithi* (Dahlberg, 1969; Turner and Roe, 1967). Similarly, the copepod *L. radiatus* has been found on the large-scaled species of menhaden and their hybrids with *B. smithi*, as well as *B. smithi* from the Gulf of Mexico and Atlantic populations (Dahlberg, 1969). Lists of additional parasites of Atlantic menhaden are contained in Westman and Nigrelli (1955), Hildebrand (1963), and Reintjes (1969).

Two major diseases are commonly associated with Atlantic menhaden. Westman and Nigrelli (1955) reported on annual die-offs in the New York area. The dying fish, "spinners" (hence "spinning disease") were characterized as having lost coordinated movements, with one or both eyes protruded, and with hemorrhages in the gills, eyes, and optic lobes of the brain. Similar mortalities have been noted among Atlantic menhaden in Chesapeake Bay (Reintjes, 1969). The cause of these mortalities was undetermined. A virus has subsequently been identified as the agent of this disease, at least in Chesapeake Bay (Stephens et al., 1980).

The second disease, ulcerative mycosis (UM), became prominent in recent years. Atlantic menhaden with deep, crater-like lesions of UM, were observed in collections from the Pamlico River, N.C., during spring 1984 by personnel from the North Carolina Division of Marine Fisheries. Although these lesions occurred on most areas of the body, they were most common in the anal area (Noga et al., 1988) (Fig. 10). Hargis (1985) provided an early description of this disease. Pathological investigations of infected fish revealed the presence of aseptate fungal hyphae of the genera *Aphanomyces* and *Saprolegnia* in the area of the lesions (Dykstra et al., 1986; Noga and Dykstra, 1986). During 1985, Ahrenholz et al. (1987a) found infected juvenile Atlantic menhaden from estuarine systems from Delaware Bay to northern Florida. They suggested that the infected fish captured in South Carolina and Georgia were actually migrants from an area of primary infection farther north. This report also noted fish which had lesions that resembled UM from collections made in New York estuaries in 1982.

Although UM has been detected in various families of estuarine dependent fishes (Sindermann, 1988), it has not been reported from the other three species of North American menhadens. However, Noga et al. (1988) pointed out that what was reported by Kroger and Guthrie (1972b) as wounds attributed to predators on some juvenile Gulf menhaden as caused by predators, appeared similar to UM lesions.

Population Processes

Stock Structure

Considerable debate relative to the stock structure of the Atlantic menhaden population has been expended, and as many as three different stocks have been advanced, primarily on the basis of meristic and morphometric analyses (June, 1958, 1965; Sutherland, 1963; June and Nicholson, 1964; Nicholson, 1972, 1978; Dryfoos et al., 1973; Epperly, 1989). Some evidence for the presence of more than one stock exists; however, the fish reared in different geographic areas and those from different temporal spawning cohorts appear to mix rapidly due to the nature of their movement patterns. Since potentially different spawning groups are currently inseparable in the Atlantic purse-seine reduction fishery, the Atlantic menhaden population is treated as a single exploited stock with respect to that fishery.

In marked contrast to Atlantic menhaden, Gulf menhaden lack any systematic seasonal movement through their range and tend to mix very slowly. Tagging studies revealed that movement across the Mississippi Delta is infrequent, either within or between seasons (Kroger and Pristas, 1975; Pristas et al., 1976). Hence, it has been suggested that the Gulf menhaden population could be treated as two management stocks, even though differences in meristic characteristics (hence potential genetic separation) are insignificant between eastern and western populations (GSMFC, 1988). However, population dynamics analysts treat the Gulf menhaden population as a single biological and managerial stock relative to the purse-seine reduction fishery (Nelson and Ahrenholz, 1986; Vaughan, 1987; GSMFC, 1988).

On the east coast of Florida, the yellowfin menhaden, the extreme southern portion of the Atlantic menhaden population, and their hybrids appear to comprise the "stock" for a menhaden bait fishery. Similarly, on the west coast of Florida, the yellowfin menhaden, the southeastern most portion of the Gulf menhaden population, and their hybrids represent the "stock" for another menhaden bait fishery. Yellowfin menhaden from each coast of Florida are probably genetically separate populations. Dahlberg (1970) gives some meristic comparisons for these potentially distinct populations. Very little is known or speculated relative to genetic mixing within the population of finescale menhaden.

Mortality

Traditionally, losses in numbers of individuals from fish populations (total mortality) are ascribed to either fishing or natural mortality. Analytical procedures used to estimate instantaneous rates of total (Z) and fishing (F) mortality for each of the large-scaled menhaden populations assume constant rates of instantaneous natural mortality (M) among time intervals and estimated rates of fishing for each interval (Nelson and Ahrenholz, 1986; Ahrenholz et al., 1987b; Vaughan, 1987; Vaughan and Smith, 1988). The catch-at-age data does not contain enough information to estimate both M and F simultaneously, as they are additive exponential rates ($Z = F + M$). Thus, the computational procedures have ascribed to F all the variances observed in Z among time intervals, even though true M also probably varied as well, albeit to a lesser degree.

The estimate of M recently used in assessment analyses for Atlantic menhaden is $M = 0.45$. This estimate is a mean of a range of available estimates: Dryfoos et al. (1973) estimated $M = 0.52$

from an analysis of returns of adult-tagged Atlantic menhaden; Reish et al. (1985) estimated $M = 0.50$ for ages 2 and 3 from analyses of tag returns of both adult- and juvenile-tagged fish; Schaaf and Huntsman (1972) estimated $M = 0.37$ from an analysis of catch statistics.

An estimate of $M = 1.1$ has been used in stock assessment analyses for Gulf menhaden (Nelson and Ahrenholz, 1986; Vaughan, 1987; GSMFC, 1988); it represents the mean of six estimates of M ranging from 0.69 to 1.61, obtained from an analysis of mark-recovery data (Ahrenholz, 1981).

Since estimates of M for both Atlantic and Gulf menhaden were obtained from purse-seine reduction landings or tag recoveries from reduction plants, they include "other" losses. In addition to predation and disease, losses due to bycatch in other fisheries, as well as landings for bait are included as losses in M.

No estimates for M are available for either of the two small-scaled menhadens. Values of M are probably intermediate between those for Atlantic and Gulf menhaden.

Recruitment

Tempered by the number of age classes represented in the fisheries, fluctuations in year-class size have naturally contributed to the variability in landings among years (Smith, 1991). Estimates of recruitment into the Gulf menhaden stock at age 1 have varied more than fivefold, while estimates of recruitment into the Atlantic stock at a similar age have fluctuated almost thirteenfold (Vaughan and Merriner, 1991).

The observed uncertainty for menhaden recruitment among years and its ramification for landings have fostered a number of different investigations ranging from those designed to determine if fishing was impacting recruitment to those designed to predict recruitment and/or landings. Additionally, studies were designed to directly sample and estimate prerecruitment abundance.

Factors affecting recruitment are traditionally categorized as density dependent, where the absolute spawning stock size and the size of the subsequent year class are related; or density independent, where the number of recruits to the population are dependent on one or more environmental factors. Removal of adult fish from the population can have a pronounced effect on subsequent recruitment if the stock-recruitment relationship is strong. Results from analyses conducted by Schaaf and Huntsman (1972) revealed a very weak association between the spawning stock size and subsequent recruitment for Atlantic menhaden. Later analyses used potential egg production in place of spawning stock, but did not substantially improve the analytical relationship (Nelson et al., 1977). The data used in both analyses, when plotted as scatter diagrams, did not display any pattern well enough to suggest an appropriate functional model. Of the two theoretical recruitment functions commonly used, Ricker's (1954) equation, which results in a dome-shaped curve, was selected on biological grounds for both of the earlier reports (Schaaf and Huntsman, 1972; Nelson et al., 1977). For example, menhaden may consume their own eggs under certain circumstances, which can contribute to the descending right hand limb of the Ricker curve. Further, four other ocean-spawning clupeids are thought to be represented by a dome-shaped curve (Cushing, 1971). Based on statistical grounds, Reish et al. (1985) preferred the function developed by Beverton and Holt (1957) for simulation purposes.

Nelson and Ahrenholz (1986) found that potential egg production-recruitment scatter plots for Gulf menhaden were dome-shaped. Coupled with biological arguments, they used the Ricker function for both description and subsequent population simulation studies.

Since deterministic, density-dependent spawner-recruitment functions alone would be of little value in predicting subsequent year-class sizes of Atlantic menhaden, Nelson et al. (1977) developed a mixed regulatory factor (both density-dependent and density-independent) model. First, they fitted a density-dependent Ricker function to the potential egg production-recruitment data, then used the deviations from the fitted model to develop a survival index. This index was in turn the dependent variable for a multiple regression analysis with environmental variables which were considered important a priori. Emphasis was placed on Ekman transport, which was thought to be a substantial contributor to oceanic currents which would bring larval Atlantic menhaden from offshore spawning areas to the vicinity of inlets and estuarine nursery areas. The resultant model described the recruitment data for 1955-70 fairly well. Though conceptually sound, this model did not effectively describe the recruitment estimates obtained during the 1970's and early 1980's. Reish et al. (1985) felt that much of the strong statistical correlation obtained by Nelson et al. (1977) for Ekman transport was due to one data point, i.e., the exceptionally large 1958 year class. Additional mixed regulatory factor models were developed by Yoshiyama et al. (1981), who preferred a Ricker function with an environmental parameter (Ekman transport at lat. 35°N., long. 75°W.) in the stock-independent term of the equation.

Checkley et al. (1988) described a process-oriented study relative to spawning, larval transport, and early survival of Atlantic menhaden. They suggested that spawning off the North Carolina coast occurred along the western wall of the Gulf Stream, and that the ultimate survival of larvae was dependent on storm-induced upwelling and buoyancy-driven transport (the result of water and air temperature differentials). They also postulated that events on the order of days rather than months, were critical to spawning and larval transport and development.

Shaw et al. (1985b, 1988) examined onshore transport and subsequent estuarine immigration processes for Gulf menhaden larvae. They hypothesized that larvae spawned in the waters west of the Mississippi Delta moved shoreward in a west-northwesterly direction and subsequently enter more westerly estuaries, rather than estuaries nearer to where spawning actually occurred. These studies may ultimately permit a more refined examination of potential environmental factor influences on larval survival over a reduced temporal and geographic scale.

Two studies which emphasized envi-

ronmental variables and are at least tangentially related to fishery recruitment, were conducted on Gulf menhaden. In the first study, Stone (1976) conducted an extensive, systematic, multiple-regression search of various environmental data. Methodical temporal lags and commercial fishing effort were used as independent variables to detect any potential relationships between these variables and landings of Gulf menhaden. Some of the analyses were conducted using monthly time periods. He thought that environmental factors which influence important life history events (especially factors affecting recruitment) could be detected by the analyses when appropriately temporally matched.

The second study was reported by Guillory et al. (1983), who used first-order linear regressions and stepwise multiple regressions to determine the relationship between a wide variety of environmental factors, both singly and in combination. They examined catch-per-sampling-effort (CPSE) of young-of-the-year Gulf menhaden from otter trawl shrimp abundance surveys in Louisiana estuaries (Guillory and Bejarano, 1980), as well as landings of age-1 Gulf menhaden per-vessel-ton-week of effort (CPUE as reported earlier) by the commercial purse-seine fleet from Louisiana ports. Both the CPSE and CPUE values were used as surrogates for recruitment estimates (year-class strength).

In general terms, Guillory et al. (1983) and Stone (1976) found some strong correlations for the temporally lagged variables such as temperature (air or water), and wind speed and direction, with the CPUE and CPSE values and landings, respectively. Stone's (1976) analyses provide some insight into important environmental variables, but only at a more general level. Recruitment variability is not clearly expressed in purse-seine landings because they are dominated by two age classes. But, predictions of landings, not year-class sizes, were apparently the desired products of Stone's (1976) analyses. In addition, the author stated that potential environmental effects could be masked in the regression models by effort and temporal effects. Finally, the results have to be viewed cautiously because systematic, exploratory regression analyses have a high probability of providing some spurious relationships.

Guillory et al. (1983) treated each year class separately, thus, their models may provide some insight into important environmental factors. As with Stone's (1976) work, however, caution must be exercised in applying the results because there is a strong possibility of spurious correlations resulting from such a large number of exploratory regressions. This is especially true when using the CPSE values, as they are the result of an earlier exploratory series of analyses (Guillory and Bejarano, 1980). Additionally, the predictive accuracy of relationships will depend on how strongly CPUE of age-1 menhaden reflects true year class size.

The NMFS Beaufort Laboratory attempted to obtain prerecruitment estimates of year-class strength by directly sampling juvenile menhaden in estuarine areas a few months prior to their emigration and recruitment into the coastal populations. Some forms of juvenile relative abundance sampling began as early as 1956 on the Atlantic coast (Ahrenholz et al., 1989). Two-boat, surface-trawl surveys were initiated for juvenile Atlantic menhaden in 1962 and for juvenile Gulf menhaden during 1964 (Turner, 1973; Turner et al., 1974). The studies culminated with an extensive two-boat, surface-trawl relative abundance survey on each coast from the early 1970's through 1978. Although density estimates from these surveys appeared to reflect local and regional abundance of menhaden, they did not correlate well with subsequent virtual population analyses estimates of year-class size for either coast (Ahrenholz et al., 1989). Nevertheless, these surveys were invaluable for determining juvenile menhaden distribution patterns in estuaries and aided many life history studies, even though they had limited predictive application.

The limited success of attempts to model or estimate recruitment at relatively young ages may well be due to oversimplification in the models' or sampling programs' designs relative to the complexity of the recruitment patterns. With respect to at least Atlantic menhaden, an accounting must be made of both the geographic and temporal spawning origins of prerecruits. Research along these lines is being conducted.

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