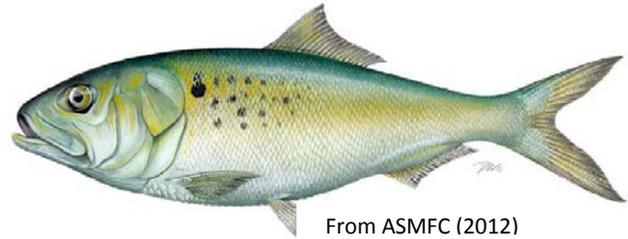


Atlantic Menhaden

Brevoortia tyrannus

Contributor (2014): Joseph C. Ballenger (SCDNR)



From ASMFC (2012)

DESCRIPTION

Atlantic menhaden, a Clupeoid fish of interest to fisheries, is one of the most common forage fish species encountered in South Carolina estuarine and coastal waters. It is estuarine-dependent with juveniles utilizing estuarine nursery areas (Whitehead 1985).

Taxonomy and Basic Description

Atlantic menhaden, *Brevoortia tyrannus* (Latrobe 1802), belong to the herring family, Clupeidae, and are similar in appearance to the alewife and shad. In particular, they belong to the subfamily Alosinae (a.k.a. the shads), which includes 7 genera, 2 of which (*Brevoortia* and *Alosa*) have representatives in the western Atlantic (Whitehead 1985). The genus *Brevoortia* includes a total of 6 species: *B. aurea*, *B. gunteri*, *B. patronus*, *B. pectinata*, *B. smithi*, and *B. tyrannus*. *B. tyrannus* and *B. smithi* (yellowfin menhaden) overlap in distribution off the East coast of the United States, particularly off Florida (Whitehead 1985). In areas of overlap, *B. tyrannus* and *B. smithi* will hybridize, with hybrids being common (Dahlberg 1970).

Atlantic menhaden have a bluish body above with silvery sides possessing a reddish luster and fins tinged with pale yellow and edged in black (ASMFC 1981). They are distinguished from other Clupeidae by a large head, an upper jaw with distinct median notch, no teeth, pectinated scales, the location of the dorsal fin over the interval between the pelvic and anal fins, the pelvic fin with a rounded hind margin, modified pre-dorsal scales, and a compressed body with bony scutes along the belly (ASMFC 1981; Whitehead 1985). Atlantic menhaden possess long gill rakers and a muscular pyloric stomach or gizzard (ASMFC 1981). The lateral line scales above the base of the anal fin and at the base of the tail are much smaller and irregularly spaced (Whitehead 1985). There is a conspicuous black spot behind the gill opening that is usually followed along the flank by a variable number of smaller spots (or blotches) forming up to 6 approximate lines (ASMFC 1981; Whitehead 1985). Atlantic menhaden is readily distinguished from yellowfin menhaden due to the difference in lateral line scale number (40 to 58 (usually 45-

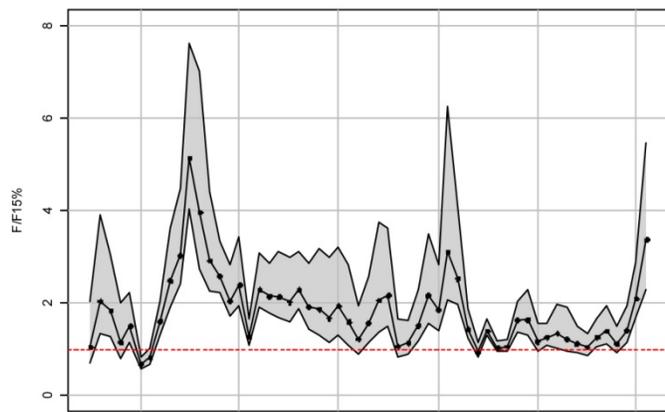


Figure 1: Overfishing stock status determination figure from 2012 update assessment of Atlantic menhaden (Source: ASMFC 2012).

52) versus 54 to 80 (usually 60-70) in *B. tyrannus* and *B. smithi*, respectively) and lack of lines of spots on flank in *B. smithi* (Whitehead 1985). Other *Brevoortia* species do not overlap in range while other clupeids lack the modified pre-dorsal scales (Whitehead 1985).

Status

Currently, the Atlantic menhaden population is managed as a unit stock along the east coast of the United States and managed by the Atlantic States Marine Fisheries Commission. As of the most recent assessment of stock status in 2012, the stock was not considered overfished but overfishing was occurring (ASMFC 2012a). The assessment suggested that overfishing had occurred in almost all of the years used in the assessment (1955-2011; Figure 1) with annual F never falling below target F (Figure 2; ASMFC 2012a). The last extended period when the stock was overfished was from 1964-1970, with the stock being approximately at the target spawning stock biomass (SSB) in recent years (Figure 3; ASMFC 2012a). Despite this status determination, the ASMFC Atlantic menhaden technical committee warns that severe retrospective patterns in F and SSB and a number of other issues cast considerable doubt on the accuracy of the estimates, though they were reasonably confident that the status determinations were likely robust (ASMFC 2012a). In other words, though they felt the ratio of current F to $F_{\text{threshold}}$ is likely greater than 1.0 (overfishing is occurring) and the ratio of current SSB to $SSB_{\text{threshold}}$ is likely greater than 1.0 (the stock is not overfished), the exact magnitude of these ratios could not be determined. In the end, it was recommended by the ASMFC Atlantic menhaden technical committee that the estimates from the 2012 update assessment not be used by the ASMFC Menhaden management board for management. To resolve some of the concerns arising from the 2012 update assessment, an expedited benchmark assessment was begun in 2014 to address data analysis and modeling questions with the intent of better

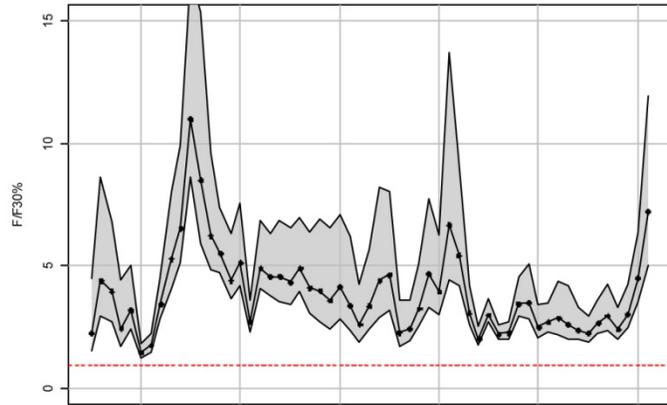


Figure 2: Annual F relative to target F ($F_{30\%}$) figure from 2012 update assessment of Atlantic menhaden (Source: ASMFC 2012).

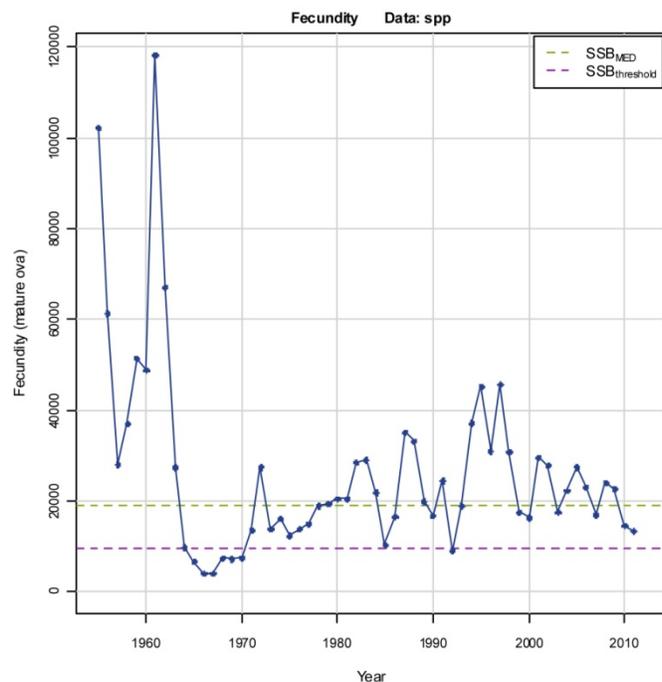


Figure 3: Annual SSB (measured in annual fecundity (mature ova)) relative to the SSB threshold ($SSB_{\text{threshold}}$) and SSB target (SSB_{MED}) from the 2012 update assessment (Source: ASMFC 2012).

parameterizing the uncertainty of the model such that the model output can be used for management decisions.

POPULATION SIZE AND DISTRIBUTION

Atlantic menhaden are distributed from Nova Scotia, Canada, southward to Indian River, Florida (Figure 4). Throughout this range, they are a euryhaline species that occurs in the Atlantic Ocean and inland tidal waters (Hildebrand 1948; Hildebrand 1964; Reintjes 1960; Reintjes 1964). Being euryhaline, juveniles and adults occupy bays, sounds, and estuaries to the uppermost limits of brackish water (ASMFC 1981). In coastal ocean waters, they are generally confined to waters of the Continental Shelf and are never observed far from land (ASMFC 1981). Seaward, the farthest from land that an Atlantic menhaden has been captured was approximately 130 km (81 mi.) south of Cape Cod by a Soviet trawler (Gusev 1964). Historically, this distance from shore is about the maximum distance from land that schools have been sighted by scouting aircraft, and further offshore than the seaward limit of the purse seine fishery (ASMFC 1981).

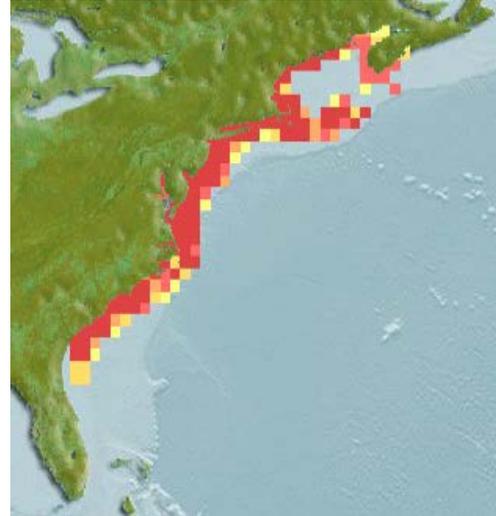


Figure 4: Menhaden distribution map (Source: www.fishbase.org)

Generally, Atlantic menhaden are found inshore during summer months, but at least some move into deeper waters in winter. It is thought this offshore movement during winter months is less pronounced in the southern part of their range (Whitehead 1985). Adults are found in near surface waters (June 1961), most commonly in Continental Shelf water, in greatest abundance immediately adjacent to major estuaries (Jones et al. 1978). Juveniles are generally found in shallower, potentially lower salinity waters, with the smallest size groups being found farthest up river (June and Chamberlain 1959).

All size menhaden are pelagic, forming large and compact schools (Whitehead 1985). The majority of the population appears to be migratory in nature, with northward migrations occurring during the spring/summer and southward migrations occurring during the fall (Figure 5; ASMFC 1981; Whitehead 1985). More specifically, different size/age menhaden appear to undergo

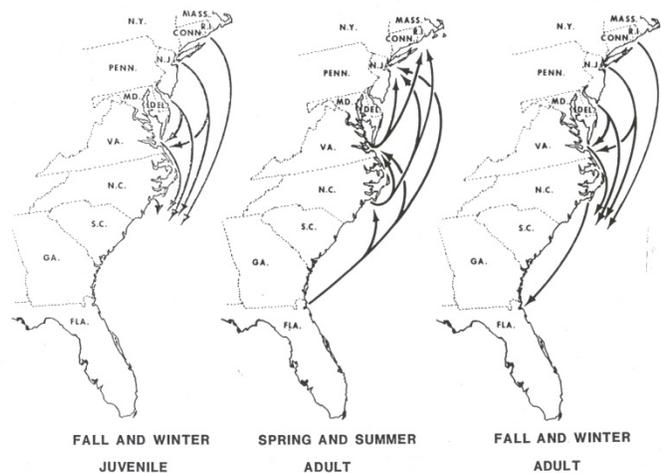


Figure 5: Juvenile and adult migrations of Atlantic menhaden (Source: ASMFC 1981).

migrations of different degrees, with larger/older individuals migrating further distances (Dryfoos et al. 1973; Nicholson 1978). Thus, during the summer, the smaller and younger fish are found in the southern part of the range, while progressively larger and older fish occur in more northerly latitudes (Dryfoos et al. 1973; Nicholson 1978; Whitehead 1985). Menhaden typically school with individuals of a similar size and age in a locality, with schools remaining distinct from those of overlapping sizes and ages in adjacent localities. The net effect is a north-south gradient in size and age becoming established during summer months, with larger and older fish found farther northward (June and Reintjes 1959; McHugh et al. 1959). In the fall, there is once again a southward withdrawal of fish from the summer grounds, with fish congregating in large schools (sometimes covering a surface area of many square kilometers) for the southward migration (ASMFC 1981). These large, migrating schools are last seen off the North Carolina coast in December or January (June 1961; Roithmayr 1963; Reintjes 1969; Nicholson 1971; Nicholson 1972; Dryfoos et al. 1973; Kroger and Guthrie 1973). Kroger and Guthrie (1973) found that juvenile Atlantic menhaden also exhibit a seasonal north-south movement. From tag recoveries, they report that juveniles (age-0's) migrate as far south as Florida in fall and winter, then redistribute northward along the coast by size as age-1 fish during the following spring and summer. Due to the redistribution by size, the smaller age-1 fish tend to remain along the south Atlantic coast.

In South Carolina, juvenile and adult Atlantic menhaden are present in estuaries and coastal ocean waters throughout the year. Unfortunately, there is not an

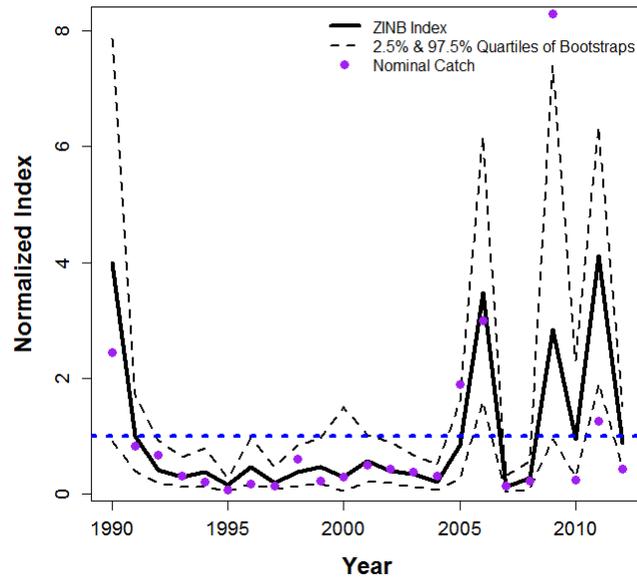


Figure 6: Preliminary zero-inflated negative binomial model of Atlantic menhaden catch in the SEAMAP-SA Coastal Trawl Survey conducted from Cape Hatteras, NC, to Cape Canaveral, FL.

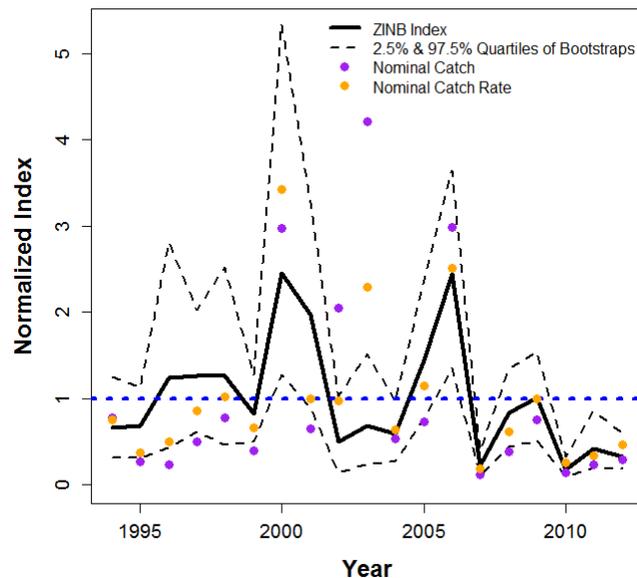


Figure 7: Preliminary zero-inflated negative binomial model of Atlantic menhaden catch in the SCDNR trammel net survey conducted throughout South Carolina in coastal estuaries.

estimate available of their absolute population size off South Carolina. There are three estimates of relative abundance of Atlantic menhaden available via three separate SCDNR fishery-independent surveys: SEAMAP-SA Coastal Trawl Survey, SCDNR Trammel Net Survey, and SCDNR Electrofishing Survey. While none of these surveys were used in the 2012 update assessment of Atlantic menhaden, each is being considered for use as an index of relative abundance of Atlantic menhaden in the ongoing 2014 benchmark stock assessment (Joseph Ballenger, SCDNR, pers. comm.).

Catches of Atlantic menhaden adults in the SEAMAP-SA Coastal Trawl Survey indicates an initial steep downward trend in relative abundance, with low relative abundance through 2004, with a slight, although noisy, increase in relative abundance on average since then (Figure 6). A slightly different pattern is observed regarding the catch of adult Atlantic menhaden in the SCDNR Trammel Net Survey, with catch being relatively stable (although noisy) through 2006, with a decreasing trend since then (Figure 7). A somewhat similar pattern is suggested for the relative abundance of young-of-the-year Atlantic menhaden as calculated based on catches from the SCDNR electrofishing survey (Figure 8). Atlantic menhaden young-of-the-year relative abundance seems to have been slightly decreasing since approximately the mid-2000s.

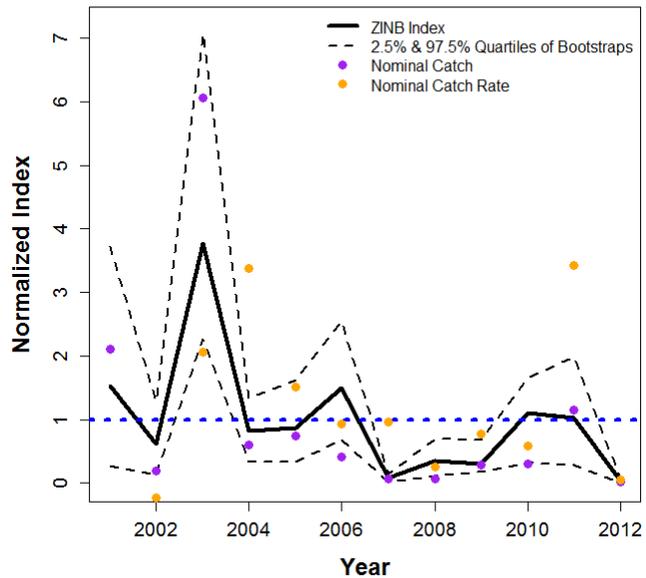


Figure 8: Preliminary zero-inflated negative binomial model of Atlantic menhaden catch in the SCDNR Electrofishing Survey conducted throughout South Carolina in coastal estuaries.

HABITAT AND NATURAL COMMUNITY REQUIREMENTS

Being euryhaline, Atlantic menhaden can tolerate a wide range of salinities. As such, both juveniles and adults can be found in a wide array of nearshore habitats, including bays, sounds, and estuaries to the uppermost limits of brackish water (ASMFC 1981). In general, the smallest size groups are found farthest up river (June and Chamberlain 1959), as attested by the catch of very small young-of-the-year in the SCDNR electrofishing survey. Regardless of size, Atlantic menhaden are pelagic in nature, feeding by filtering phytoplankton and zooplankton (Whitehead 1985; Scott and Scott 1988). As adults they are obligate filter-feeders, while larvae and pre-juvenile fish (smaller than 4.0 cm or 1.6 in. TL) are particulate feeders (Lazzaro 1987; James 1988). In the ecosystems where menhaden are found in South Carolina, they are a significant forage fish for a host of predators, including striped bass, bluefish, spotted seatrout, red drum, and various sharks and rays.

Spawning likely occurs year-round, though there is evidence that the breeding season in specific locals is limited by high water temperatures (Higham and Nicholson 1964; Whitehead 1985). This limits spawning to certain seasons along the entire coast: spawning during the spring (April/May) in New England waters, autumn (October/November) in the mid-Atlantic, and winter (December to March) in the South Atlantic (Whitehead 1985). It is thought that the major spawning season occurs off the Carolinas during December-February (ASMFC 2011), with the majority of ovigerous females being observed in the South Atlantic (Nelson et al. 1977). The temperature, depth, and salinity at presumed spawning locations varies widely depending on latitude and distance from shore (Kendall and Reintjes 1975; Bourne and Govoni 1988; Berrien and Sibunka 1999; Checkley et al. 1999). Reported water temperatures are typically in the range of 55-77°F (13 to 25°C). Spawning generally occurs at depths <33-66 ft. (<10-20 m). Salinity at spawning sites has been reported to be 29-36 ppt at offshore mid-Atlantic sites and 35.8-36.6 ppt at South Atlantic sites. Eggs have been found at 18-28 ppt in Long Island Sound (Wheatland and Lewis 1956) and 10-22 ppt in Chesapeake Bay (Dovel 1971). Post hatching, larvae are pelagic (Massman et al. 1962), probably spending approximately a month in waters over the Continental Shelf (McKenney 1969), prior to entering estuarine waters at about in. 0.39 in. (10 mm) and larger (Reintjes 1969).

In the mid- and south-Atlantic nursery areas, bottom composition is “unconsolidated,” consisting of sand-mud, and organic material which may be important to juvenile consumption (Lewis and Peters 1984; Peters and Schaaf 1991). Juvenile menhaden remain in their estuarine nursery areas throughout the summer. In fall, most juveniles emigrate southward, though some overwinter in the Chesapeake Bay and south-Atlantic region estuaries. Immature adult menhaden are most abundant in inshore and estuarine areas from Chesapeake Bay southward (Nicholson 1978). Older, larger adults are typically found in colder, rockier northerly habitats during summer, while they overwinter off North Carolina and further south (Nicholson 1978). Adults appear to prefer temperatures of about 64°F (18°C) (ASMFC 2011).

CHALLENGES

As menhaden of different life stages use a diverse array of habitats, almost all of the estuarine and nearshore waters along the Atlantic coast from Florida to Nova Scotia serve as an important habitat for some life stage. As such, pollution and habitat degradation of any estuarine and nearshore habitat could be expected to threaten the coastal menhaden population. Such habitat degradation concerns are especially acute in estuarine waters due to the residency of larvae and juveniles in these habitats (ASMFC 2011). An indication of the threat habitat degradation poses to menhaden is the concern that the outbreaks of ulcerative mycosis in the 1980s may have been symptomatic of deteriorating water quality in estuarine waters along the East coast (Ahrenholz et al. 1987). As coastal development increases, we expect estuarine water quality to further deteriorate unless steps are taken to ameliorate their effect on the environment (Cross et al. 1985). Estuarine and coastal habitats have been significantly affected by dredging, filling, coastal construction, energy plant development, pollution, waste disposal, and other human-related

activities (ASMFC 1999a). Other potential threats in coastal waters include the offshore dumping of sewage. High concentrations of DDT have been reported in menhaden due to their feeding on plankton and detritus (Warlen et al. 1977).

An additional challenge to the Atlantic menhaden population is the large-scale fisheries that operate on the population. At present, two large-scale fisheries target Atlantic menhaden: a commercial reduction fishery (Figure 9) and a commercial bait fishery (Figure 10; ASMFC 2012a).

Landings for the reduction fishery rose during the 1940s (from 167,000 t to 376,000 t), peaked during the late 1950s (>600,000 for four of five years), and then declined to low levels during the 1960s (from 576,000 t in 1961 to 162,000 t in 1969). The stock rebuilt some during the 1970s, with landings rising before leveling off in the 1980s (landings varied between 238,000 t in 1986 to 418,000 t in 1983). In the 1990s, landing declined again to a low of 171,200 t in 1999. Since then the commercial reduction fishery landings have leveled off at between 150,000-200,000 t. In contrast, coastwide bait landings of Atlantic menhaden have gradually increased from 1985 (1st year reported) to the present, approaching 60,000 t in 2011. Though landings off the coast of South Carolina have generally been small, due to the migratory nature of the stock, any overharvest of the stock in other regions can have an adverse effect on the sub-population located off the coast of South Carolina.

CONSERVATION ACCOMPLISHMENTS

Atlantic menhaden are currently managed under Amendment 2 to the Interstate Fishery Management Plan (FMP) for Atlantic Menhaden established via the Atlantic States Marine Fisheries Commission (ASMFC; ASMFC 2012b). This amendment, which took effect in December 2012, established a 170,800 MT total allowable catch (TAC) beginning in 2013 that would stay in place until changed. Amendment 2 allocates the TAC on a state-by-state basis based on landings history of the fishery from 2009-2011. As such, when a states quota is met

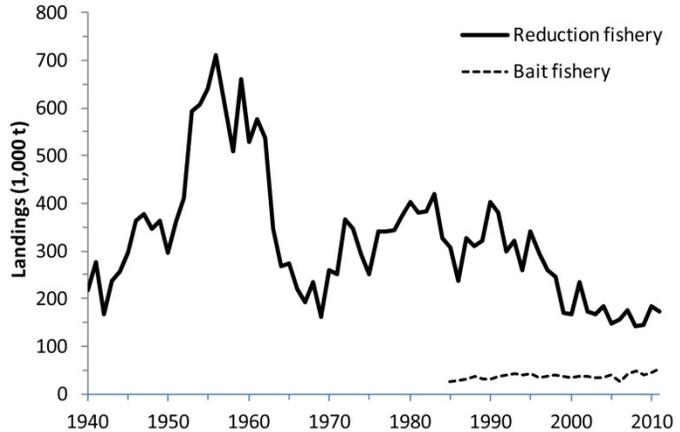


Figure 9: Annual menhaden reduction and bait landings, 1940-2011 (ASMFC 2012).

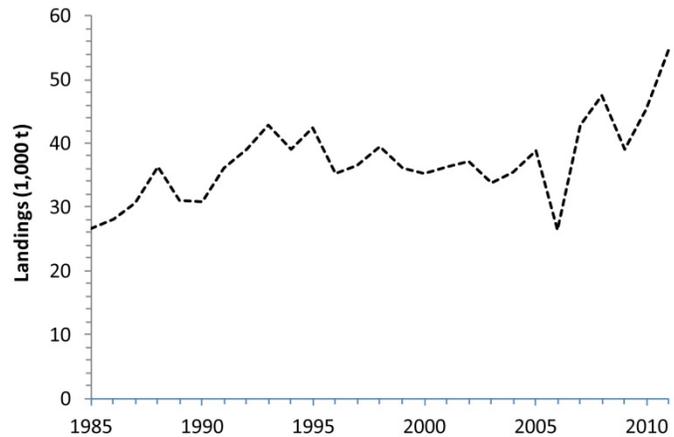


Figure 10: Annual menhaden bait landings, 1985-2011 (ASMFC 2012).

within a year, the state is required to close their fisheries and any overages must be paid back the following year.

Further, the ASMFC Atlantic Menhaden Board continues to place a high priority on advancing the development of ecosystem-based reference points using a multispecies modeling approach. This is because of the realization that Atlantic menhaden constitute a major component of the diet of coastal water piscivores. Ecosystem reference points are expected to address the forage needs of menhaden's predator species. For this project, they have been relying on the use of a multi-species stock assessment model. Fisheries management is expected to move away from individual species assessments to ecosystem-based fishery management. Members of the ASMFC Multispecies Technical Committee and others have worked to develop a multispecies Virtual Population Analysis (MSVPA) model to explore important predator-prey interactions among key ASMFC-managed species, including Atlantic menhaden as the primary forage fish and striped bass, bluefish, and weakfish as predators. The most recent update was in 2012.

CONSERVATION RECOMMENDATIONS

- Continue to evaluate the effects of fishing and management plans on the South Carolina sub-population of Atlantic menhaden.
- Continue the development of ecosystem reference points for Atlantic menhaden management that would account for the role that menhaden plays in coastal ecosystems as a main forage fish for a number of piscivores.
- Initiate studies to investigate the within-year age composition variability of Atlantic menhaden in South Carolina coastal waters.
- Explore the trophic assemblages involving menhaden.
- Monitor trends in Atlantic menhaden young-of-the-year and adult relative abundance by continuing to collect data about this species during ongoing fishery-independent monitoring programs.
- Initiate additional work to understand the local and regional movement patterns of menhaden occurring in South Carolina waters.
- Initiate work to quantify the role that South Atlantic region spawning plays in determining annual recruitment.
- Protect water quality in marine ecosystems by encouraging municipalities to use Best Management Practices (BMPs) to reduce runoff from highways, agricultural fields, and housing developments. Improve BMPs in areas already affected by non-point source pollution.
- Plan development based on sound terrestrial and estuarine ecology that takes into consideration all factors that will affect the long-term health of the estuary ecosystem.
- Identify the origin of non-point source pollution and specific point source pollution and develop a plan of action to mitigate any negative impacts to the affected aquatic systems.

MEASURES OF SUCCESS

The SCDNR fishery-independent programs that annually monitor the relative abundance and length frequency of inshore fish species are already in place to monitor for changes in size distribution and relative abundance as a result of regional management efforts. The measurement of success will be to see an increasing trend in catch of Atlantic menhaden in these surveys.

LITERATURE CITED

- Ahrenholz, D. W., J. F. Guthrie and R. M. Clayton. 1987. Observations of ulcerative mycosis infections in Atlantic menhaden (*Brevoortia tyrannus*). NOAA Tech. Memo. NMFS-SEFSC-196.
- ASMFC. 1981. Fishery Management Plan for Atlantic Menhaden. Fisheries Management Report No. 2 of the Atlantic States Marine Fisheries Commission. 146 p.
- ASMFC. 1999. Terms of Reference & Advisory Report for the Atlantic Menhaden Stock Assessment Peer Review. Atlantic States Marine Fisheries Commission, Stock Assessment Report No. 99-01, 16 p.
- ASMFC. 2011. Atlantic Menhaden Stock Assessment and Review Panel Reports. Stock Assessment Report No. 10-02 of the Atlantic States Marine Fisheries Commission. 326 p.
- ASMFC. 2012a. 2012 Atlantic Menhaden Stock Assessment Update. Atlantic States Marine Fisheries Commission. 228 p.
- ASMFC. 2012b. Amendment 2 to the interstate fishery management plan for Atlantic Menhaden. Atlantic States Marine Fisheries Commission. 114 p.
- Berrien, P. and J. Sibunka. 1999. Distribution patterns of fish eggs in the United States Northeast Continental Shelf ecosystem. U.S. Dep. Commer., NOAA Tech. Rep. NMFS 145, 310 p.
- Bourne, D. W. and J. J. Govoni. 1988. Distribution of fish eggs and larvae and patterns of water circulation in Narragansett Bay, 1972-1973. Am. Fish. Soc. Symp. 3: 132-148.
- Checkley, D. M., Jr., P. B. Ortner, F. E. Werner, L. R. Settle, and S. R. Cummings. 1999. Spawning habitat of the Atlantic menhaden in Onslow Bay, North Carolina. Fish. Oceanogr. 8 (Suppl. 2): 22-36.
- Cross, F. A., D. S. Peters, and W. E. Schaaf. 1985. Implications of waste disposal in coastal waters on fish populations, p. 383-399 *In*: Cardwell, R. D., R. Purdy, and R. C. Bhaner (eds). 35 "Aquatic Toxicology and Hazard Assessment: Seventh Symposium". ASTM STP854. American Society for Testing and Materials, Philadelphia: 383-399.
- Dahlberg, M. D. 1970. Atlantic and Gulf of Mexico menhadens, genus *Brevoortia* (Pisces: Clupeidae). Bull. Fla. State Mus. Biol. Ser. 15(3): 91-162.
- Dovel, W. L. 1971. Fish eggs and larvae of the upper Chesapeake Bay. Univ. Md. Nat. Resourc. Inst., Spec. Rept. 4. 71 p.
- Dryfoos, R. L., R. P. Cheek, and R. L. Kroger. 1973. Preliminary analyses of Atlantic menhaden, *Brevoortia tyrannus*, migrations, population structure, survival and exploitation rates, and availability as indicated from tag returns. Fish. Bull. 71(3): 719-734.
- Gusev, E. E. 1964. Some peculiarities in menhaden morphology – *Brevoortia tyrannus* (Latrobe). [Translated by J. M. Moulton (Mimeo.) 4 p.] Contrib. Comm. Fish. Res. Arctic Basin (Murmansk) 2: 13-16.
- Higham, J. R. and W. R. Nicholson. 1964. Sexual maturation and spawning of the Atlantic

- menhaden. U.S. Fish Wildl. Serv., Fish. Bull. 63(2): 255-271.
- Hildebrand, S. F. 1948. A review of the American menhaden, genus *Brevoortia*, with a description of a new species. *Smithson. Misc. Coll.* 107(18): 1-39.
- Hildebrand, S. F. 1964. Family Clupeidae. P. 257-454 in H. B. Bigelow et al. (eds.) *Fishes of the Western North Atlantic*. Mem. Sears Fdn. Mar. Res., New Haven, (1-3): 1-630.
- James, A. G. 1988. Are clupeid microphagists herbivorous or omnivorous? A review of the diets of some commercially important clupeids. *S. Afr. J. Mar. Sci.* 7: 161-177.
- Jones, P. W., F. D. Martin and J. D. Hardy Jr. 1978. Development of fishes of the Mid-Atlantic Bight. An atlas of eggs, larval and juvenile stages. Vol. 1: Acipenseridae through Ictaluridae. U.S. Fish Wildl. Ser. Biol. Serv. Program FWS/OBS-78/12. 336 p.
- June, F. C. 1961. The menhaden fishery of the United States. U.S. Fish Wildl. Serv., Fish. Leaflet. 521. 13 p.
- June, F. C. and L. Chamberlain. 1959. The role of the estuary in the life history and biology of Atlantic menhaden. *Gulf Caribb. Fish. Inst. Proc.* 1958: 41-45.
- June, F. C. and J. W. Reintjes. 1959. The role of the estuary in the life history and biology of Atlantic menhaden. *Proc. Gulf and Carib. Fish. Inst.* 11: 41-45.
- Kendall, A. W. and J. W. Reintjes. 1975. Geographic and hydrographic distribution of Atlantic menhaden eggs and larvae along the middle Atlantic coast from RV *Dolphi* cruises, 1965-66. *Fish. Bull.* 73: 317-335.
- Kroger, R. L. and J. F. Guthrie. 1973. Migrations of tagged juvenile Atlantic menhaden. *Trans. Amer. Fish. Soc.* 2: 417-422.
- Lazzaro, X. 1987. A review of planktivorous fishes: their evolution, feeding behaviours, selectivities, and impacts. *Hydrobiologia* 146: 97-167.
- Lewis, V. P. and D. S. Peters. 1984. Menhaden – a single step from vascular plant to fishery harvest. *J. Exp. Mar. Biol. Ecol.* 84(1): 95-100.
- Massman, W. H., J. J. Norcross and E. B. Joseph. 1962. Atlantic menhaden larvae in Virginia coastal waters. *Chesapeake Sci.* 3(1): 42-45.
- McHugh, J. L., R. T. Oglesby, and A. L. Pacheco. 1959. Length, weight, and age composition of the menhaden catch in Virginia waters. *Limnol. Oceanogr.* 4: 145-162.
- McKenney, T.W. 1969. Life history of Atlantic menhaden. U.S. Fish Wildl. Serv., Circ. 350. 49 p.
- Nelson, W. R., M. C. Ingham and W. E. Schaff. 1977. Larval transport and year-class strength of Atlantic menhaden, *Brevoortia tyrannus*. *Fish. Bull.* 78(1): 23-41.
- Nicholson, W. R. 1971. Coastal movements of Atlantic menhaden as inferred from changes in age and length distributions. *Trans. Amer. Fish. Soc.* 100(4): 708-716.
- Nicholson, W. R. 1972. Population structure and movements of Atlantic menhaden, *Brevoortia tyrannus*, as inferred from back-calculated length frequencies. *Ches. Sci.* 13(3): 161-174.
- Nicholson, W. R. 1975. Age and size composition of the Atlantic menhaden, *Brevoortia tyrannus*, purse seine catch, 1963-71, with a brief discussion of the fishery. NOAA Tech. Rep. NMFS SSRF-684, 28 p.
- Peters, D. S. and W. E. Schaff. 1991. Empirical model of the trophic basis for fishery yield in coastal waters of the eastern USA. *Trans. Am. Fish. Soc.* 120: 459-473.
- Reintjes, J. W. 1960. Continuous distribution of menhaden along the south Atlantic and Gulf coasts of the United States. *Proc. Gulf. Carib. Fish. Inst.* 12th Annu. Sess., pp. 31-35.
- Reintjes, J. W. 1964. The importance of the occurrence of menhaden in the coastal waters and estuaries of peninsular Florida. *Proc. Gulf Carib. Fish. Inst.* 16th Annu. Sess., pp. 108-

113.

- Reintjes, J. W. 1969. Synopsis of biological data on the Atlantic menhaden *Brevoortia tyrannus*. FAO Fish. Synops. 42 and U.S. Wildl. Serv. Circ. 320. 30 p.
- Roithmayr, C. M. 1963. Distribution of fishing by purse-seine vessels for Atlantic menhaden, 1955-59. U.S. Fish Wildl. Serv. Spec. Sci. Rep. Fish. 434, 22 p.
- Scott, W. B. and M. G. Scott. 1988. Atlantic fishes of Canada. Can. Bull. Fish. Aquat. Sci. 219: 731 p.
- Warlen, S. M. 1994. Spawning time and recruitment dynamics of larval Atlantic menhaden, *Brevoortia tyrannus*, into a North Carolina estuary. Fish. Bull. 92: 420-433.
- Wheatland, E. P. H. and R. M. Lewis. 1956. Abundance and distribution of young Atlantic menhaden, *Brevoortia tyrannus*, in the White Oak River estuary, North Carolina. Fish. Bull. 69: 783-789.
- Whitehead, P. J. 1985. FAO Species Catalogue Volume 7: Clupeoid fishes of the world (suborder Clupeoidei) – An annotated and illustrated catalogue of the herrings, sardines, pilchards, sprats, shads, anchovies and wolf-herrings. FAO Fish. Synop 125 (7/1): 1-303. Rome: FAO.