

4.2 Other Managed Species in the South Atlantic

4.2.1 Atlantic Menhaden

Description and Distribution

Atlantic menhaden are members of the worldwide family Clupeidae, one of the most important families of fishes both economically and ecologically (Ahrenholz 1991). Clupeids are characteristically very numerous and form large, dense schools. 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 life.

Atlantic menhaden are euryhaline species that inhabit nearshore and inland tidal waters from Florida to Nova Scotia, Canada (Ahrenholz 1991). Spawning occurs principally at sea with some activity in bays and sounds in the northern portion of its range. Eggs hatch at sea and the larvae are transported to estuaries by ocean currents where they metamorphose and develop as juveniles. Adults stratify by size during the summer, with older, larger individuals found farther north. During the fall, Atlantic menhaden migrate south and disperse from nearshore surface waters off North Carolina by late January or early February. Schools of adult menhaden reassemble in late March or early April and migrate northward. By June the population is redistributed from Florida to Maine (Ahrenholz 1991).

Atlantic menhaden are abundant in the estuarine and nearshore ocean waters of North America from Nova Scotia to central Florida. They have been taken in commercial quantities from northern Florida to southern Maine. A few individuals have been taken as far north as St. John, New Brunswick, and St. Mary Bay, Nova Scotia. The southern limit seems to be Indian River City, Florida (Hildebrand 1963). Spawning occurs in the ocean, while larvae and juveniles utilize coastal estuaries. 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 (Ahrenholz 1991).

Reproduction

Most Atlantic menhaden reach sexual maturity during their third year of life (late age 2) at lengths of 180 - 230 mm fork length (FL). Spawning occurs year-round throughout much of the species' range, with maximum spawning off the North Carolina coast during late fall and winter. Adults then move inshore and northward in spring and stratify by age and size along the Atlantic coast (Rogers and Van Den Avyle 1989). During this northern migration, spawning occurs progressively closer inshore and by late spring, some spawning occurs within coastal embayments. There are definite spring and fall spawning peaks in the Middle and North Atlantic Regions, with some spawning occurring during the winter in the shelf waters of the Mid-Atlantic Region. Larval menhaden have been collected as far as 64km inland in the Santee River channel and backwater sloughs, South Carolina (Meador 1982), suggesting spawning may occur in inland waters.

Atlantic menhaden are relatively prolific spawners. Predicted fecundities range from 38,000 eggs for a small female (180 mm FL) to 362,000 for a large female (330 mm FL) according to an equation derived by Lewis et al. (1987):

$$\text{Number of eggs} = 2563 * e^{0.015*FL}$$

This equation was derived by fitting an exponential model to length-specific fecundity data for fish collected in 1978, 1979 and 1981, as well as data reported in two earlier studies (Higham and Nicholson 1964; Dietrich 1979) for fish collected during 1956-1959 and in 1970. Fish in all three studies were collected from the North Carolina fall fishery, which harvests fish of all ages.

Analysis of eggs and larvae collected at various locations along the Atlantic coast during 1953-75 (e.g., Judy and Lewis 1983) generally confirmed earlier knowledge of spawning times and locations based on observations of adults with maturing or spent ovaries (e.g., Reintjes and Pacheco 1966). During December-March, most spawning-age fish congregate in offshore waters south of Cape Hatteras.

Maximum spawning probably occurs at this time. Checkley et al. (1988) reported maximum spawning off North Carolina in January 1986 during periods of strong northeast winds in up-welled water near the western edge of the Gulf Stream. Spawning continues at a decreasing rate closer inshore as fish migrate north in late March. By May, most spawning is restricted to coastal waters north of Cape Hatteras.

Spawning reaches a minimum in June, but continues at a low level until September north of Long Island. As mature fish migrate south in October, spawning increases from Long Island to Virginia. The capture of a 138 mm juvenile Atlantic menhaden in an estuary on the Maine coast in October 1990 (T. Creaser, Maine DMR, pers. comm.; as cited in ASMFC 1992) suggests that a limited amount of spawning may occur as far north as the Gulf of Maine. Some ripening female menhaden were offloaded on to the Soviet processing ship near Portland, Maine in August and September 1991 (S. Young, Maine DMR observer on the M/V *Riga*, pers. comm.; as cited in ASMFC 1992). Egg and larval surveys have been restricted to waters south of Cape Cod (Judy and Lewis 1983) and, thus, would not have produced any evidence for spawning in the Gulf of Maine.

Development, growth and movement patterns

Atlantic menhaden produce pelagic eggs about 1.5 mm in diameter which hatch within 2.5-2.9 days at an average temperature of 15.5°C (Hettler 1981). Embryonic development is completed in <36 hr at 20- 25°C, but takes about 200 hr at 10°C (Ferraro 1980). Egg mortalities observed in the laboratory were >90% at 10°C, and 48-92% at 15, 20 and 25°C (Ferraro 1980).

A full morphological description of Atlantic menhaden eggs and larvae was provided by Jones et al. (1978). Hettler (1984) compared Atlantic menhaden (*Brevoortia tyrannus*) larvae with gulf and yellowfin menhaden (*B. patronus* and *B. smithi*) larvae. Atlantic menhaden larvae co-occur with yellowfin menhaden larvae along the east coast of Florida to North Carolina, but not with gulf menhaden.

A fourth species (*B. gunteri*) occurs exclusively in the Gulf of Mexico. Powell and Phonlor (1986) also compared early life history characteristics of Atlantic and gulf menhaden.

Yolk-sac larvae hatched at 3-4 mm standard length (SL) and maintained at 16° and 24°C began to feed at 4.5-5 mm SL (Powell and Phonlor 1986). First feeding was a function of size, not age. Larvae raised at 16°C began feeding after 5 days, while larvae raised at 24°C began feeding after only 2 days. Larvae reached 10.7 mm SL after 21 days at 20°C. Caudal and dorsal fins developed at 9 mm, and all fin rays were developed by 23 mm (Reintjes 1969). The swimbladder and acoustico-lateralis system become functional in larvae measuring approximately 20 mm (Hoss and Blaxter 1982).

Low temperatures (<3°C for >2 days) killed most larvae held in laboratory experiments (Lewis 1965, 1966), although mortality depended on acclimation temperature and the rate of thermal change. Best survival occurred at temperatures >4°C and salinities of 10-20 ppt.

Larvae which hatch offshore are transported shoreward and enter estuaries in the south Atlantic region after 1-3 months at sea (Reintjes 1961) at a size of 14-34 mm FL (Reintjes and Pacheco 1966). Larval migration into estuaries occurs during May-October in the north Atlantic region, October-June in the mid- Atlantic, and December-May in the south Atlantic (Reintjes and Pacheco 1966). Larval condition improved rapidly after fish entered two North Carolina inlets (Lewis and Mann 1971).

Metamorphosis to the juvenile stage occurs at about 38 mm total length (TL) during late April-May in North Carolina estuaries and later in the year farther north. Most larvae entered the White Oak estuary (North Carolina) in March and moved upstream to a fresh water-low salinity zone where they transformed into “pre-juveniles” in late March-April and then into juveniles in late April-May (Wilkins and Lewis 1971). Other studies (Weinstein 1979; Weinstein et al. 1980; Rogers et al. 1984) also show young menhaden are more abundant in shallow, low salinity (< 5 ppt) estuarine zones. Metamorphosis to the “pre-juvenile” stage occurs at lengths >30 mm TL and to the juvenile stage beyond 38 mm TL (Lewis et al. 1972). Metamorphosis is rarely successful outside of the low-salinity estuarine zone (Kroger et al. 1974), although Atlantic menhaden have been successfully reared from eggs to juveniles in high salinity water (Hettler 1981).

The morphological changes that occur at metamorphosis are associated with a change in feeding behavior. Larvae feed on individual zooplankters, whereas juveniles rely more heavily on filter feeding (June and Carlson 1971; Durbin and Durbin 1975). This shift in feeding behavior is associated with a loss of teeth and an increase in the number and complexity of the gill rakers through which sea water is filtered as it passes through the gills. Older larvae (25-32 mm) feed on large copepods, but only rarely on small zooplanktonic organisms (Kjelson et al. 1975). Fish larger than 40 mm FL feed primarily on phytoplankton (June and Carlson 1971), but zooplankton has also been reported as an equally important food source in juvenile Atlantic menhaden (Richards 1963; Jeffries 1975). Juveniles are capable of filtering particles as small as 7-9 microns (Friedland et al. 1984) and, thus, directly utilize the abundant small photosynthetic organisms that are not consumed by most other species of fish. Detritus derived from saltmarsh cordgrass (*Spartina alterniflora*) has also been reported as a primary food source for juveniles in

North Carolina saltmarshes (Lewis and Peters 1984). Based on calculations incorporating feeding rates and population estimates from eight east coast estuaries, Peters and Schaaf (1981) concluded that juveniles must consume more food during estuarine residency than is available from a strictly phytoplankton-based food chain.

Young-of-the-year menhaden congregate in dense schools as they leave shallow, estuarine waters for the ocean, principally during August to November (earliest in the north Atlantic region) at lengths of 75-110 mm TL (Nicholson 1978). Many of these juveniles migrate south along the North Carolina coast as far as Florida in late fall and early winter and then redistribute northward by size as age-1 fish during the following spring and summer (Kroger and Guthrie 1973; Nicholson 1978). Larvae which enter the estuaries late in the season may remain there for an additional year and emigrate to the ocean at age 1.

Age-1 menhaden migrate north and south along the coast over a greater distance than young-of-the-year juveniles (Nicholson 1978). Abundance and distribution of juvenile Atlantic menhaden is monitored by the marine resource agencies of most Atlantic coast states under a variety of estuarine surveys using trawls and seines. According to a survey conducted by AMAC in February 1990, juvenile menhaden have been taken from Massachusetts to Georgia (there is no survey on the Atlantic coast of Florida). Juvenile menhaden were observed in Gulf of Maine estuaries during 1998 and 1999.

Juveniles collected at 2-3 day intervals have shown growth rates of nearly 1 mm/day (Reintjes 1969). Water temperatures $>33^{\circ}\text{C}$ caused death in young-of-the-year and age-1 Atlantic menhaden (Lewis and Hettler 1968), although the time until death depended, in part, on acclimation factors. Sudden exposure to lethal temperatures, for example, caused greater mortality. Juvenile Atlantic menhaden can adjust rapidly to abrupt changes (increase or decrease) in salinity from 3.5 to 35 ppt and vice-versa (Engel et al. 1987). Juveniles raised in low salinity water (5-10 ppt) were more active, ate more, had higher metabolic rates, and grew faster than juveniles raised in high salinity water (28-34‰) (Hettler 1976).

Adult Atlantic menhaden are strictly filter feeders, grazing on planktonic organisms. They can be observed swimming slowly in circles, in tightly packed schools, with their mouths wide open and their opercula (gill flaps) flaring. In lab experiments (Durbin and Durbin 1975), they fed on small adult copepods as well as phytoplankton. Organisms smaller than 13-16 microns (slightly larger than the minimum size reported by Friedland et al. (1984) for juveniles) were not retained in the gills. Menhaden did not feed on large zooplankton (10 mm brine shrimp) in these experiments. The filtering process is purely mechanical; particles are not selected by size (Durbin and Durbin 1975). These experiments showed that the filtering rate depended on mouth size, swimming speed, food particle concentration, and the mechanical efficiency of the gill rakers. The structure of the "branchial basket," the area underneath the opercula where the extremely fine and closely-spaced gill filaments and gill rakers are located, was described in detail by Friedland (1985).

Growth occurs primarily during the warmer months. Fish as old as age 8 were fairly common during the 1950s and early 1960s, but in more recent years, fish older than age 6 have been rare. Older (age-6) fish reach an average length of 330 mm FL and a weight of 630 g, although growth

varies from year to year and is inversely density-dependent. Growth rates appear to be accelerated during the first year when juvenile population size is low and are reduced when juvenile population size is high.

Adults migrate extensively along the entire United States East Coast. Following winter dispersal along the south Atlantic coast, adults begin migrating north in early spring, reaching as far north as the Gulf of Maine in June. Older and larger fish migrate farther than younger, smaller fish. The return southern migration occurs in late fall and early winter.

Stock Structure and Migration

The Atlantic menhaden resource is believed to consist of a single unit stock or population, based on tagging studies (Dryfoos et al. 1973; Nicholson 1978). Adult Atlantic menhaden undergo extensive seasonal migrations north and south along the United States East Coast. Early reports of this migratory behavior were made by Roithmayr (1963) based on the decrease in the number of purse seine sets north of Cape Cod in September. Also, Reintjes (1969) observed the disappearance of fish in October north of Chesapeake Bay and their appearance off the coast of North Carolina in November. Nicholson (1971) examined latitudinal differences in length-frequency distributions of individual age groups at different times of year and described a cyclic north-south movement with the largest and oldest fish proceeding farthest north such that the population stratifies itself by age and size along the coast during summer. A study of length frequencies at the time of first annulus formation on scales (Nicholson 1972) supported the concept of a north-south migratory movement and also indicated that a great deal of mixing of fish from all areas occurs off the North Carolina coast before fish move northward in spring.

Returns of tagged Atlantic menhaden (Dryfoos et al. 1973; Nicholson 1978) have generally confirmed what was already concluded from earlier work and added some important details. Adults begin migrating inshore and north in early spring following the end of the major spawning season off the North Carolina coast during December-February. The oldest and largest fish migrate farthest, reaching the Gulf of Maine in May and June. Adults that remain in the south Atlantic region for the spring and summer migrate south later in the year, reaching northern Florida by fall. Fish begin migrating south from northern areas to the Carolinas in late fall. During November, most of the adult population that summered north of Chesapeake Bay moves south around Cape Hatteras.

Mortality

The Atlantic menhaden population is subject to a high natural mortality rate. There is a somewhat reduced probability of death from natural causes when the population is being harvested. Natural mortality is also higher during the first two years of life than during subsequent years. Ahrenholz et al. (1987a) reported an annual instantaneous natural mortality rate (M) of 0.45 in the absence of fishing; this rate is equivalent to an annual reduction in population numbers of 36%. This rate is quite high compared to other pelagic marine species. Atlantic herring, for example, is characterized by an 18% annual natural mortality rate (Fogarty et al. 1989). During the 1955-1987 period, under exploitation, the annual natural mortality rate for age-1 Atlantic menhaden was 30% and, for ages 2 and older, it was 20% (see Vaughan 1990). Natural mortality removes an estimated 30% of the exploited population at age 1 and 20% each year thereafter.

Menhaden natural mortality is probably due primarily to predation, since the fish are so abundant in coastal waters during the warmer months of the year. All large piscivorous sea mammals, birds, and fish are potential predators on Atlantic menhaden. Menhaden are preyed upon by species such as bluefish, striped bass, king mackerel, Spanish mackerel, pollock, cod, weakfish, silver hake, tunas, swordfish, bonito, tarpon, and a variety of sharks.

Coastal pollution and habitat degradation threaten marine fish species, such as Atlantic menhaden, which spend their first year of life in estuarine waters and the rest of their life in both ocean and estuarine waters.

Other poorly understood sources of natural mortality for Atlantic menhaden are diseases and parasites. A partial list of parasites was given in Reintjes (1969), but there is no information available concerning the extent of parasitism or its possible effect on survival. Ahrenholz et al. (1987b) described the incidence of ulcerative mycosis (UM), a fungal infestation which was observed in menhaden over much of their range in 1984 and 1985 and in a more restricted area in 1986. A large fish kill in Pamlico Sound, North Carolina in November, 1984 was associated with UM, but its primary effect may be to weaken fish, making them more susceptible to other causes of mortality, such as predation, parasites, other diseases, and low dissolved oxygen concentrations. The overall impact of UM on the 1984 and 1985 year classes could not be assessed, but it was not believed to be significant (Ahrenholz et al. 1987b). However, Vaughan et al. (1986b) believed that the mortality effects of a disease or other event must be "truly catastrophic" to be detectable.

Another source of natural mortality for Atlantic menhaden (and many other species) may be "red tide." The term refers to the color of water caused by the rapid multiplication (a "bloom") of single-celled planktonic organisms called dinoflagellates, which produce a toxic compound. The toxin accumulates in the tissues of filter-feeding animals which ingest the dinoflagellate. An outbreak of red tide occurred along the coast of the Carolinas during November, 1987 - April, 1988 when Gulf Stream water containing the dinoflagellates was transported into coastal waters. Menhaden recruitment in Beaufort Inlet during this period was severely reduced (S. Warlen, NMFS, Beaufort N.C., pers. comm.; as cited in ASMFC 1992). A new species of toxic dinoflagellate was identified as the causative agent in a major menhaden kill in the Pamlico River, North Carolina, in May, 1991. Problems with toxic phytoplankton organisms may increase in the future since their appearance has been correlated with increasing nutrient enrichment in estuarine and coastal waters which are subject to increasing organic pollution (Smayda 1989).

An additional source of mortality are fish "kills" which occur when schools of menhaden enter enclosed inshore bodies of water in such large numbers that they consume all available oxygen and suffocate. The mean lethal dissolved oxygen concentration for menhaden has been reported to be 0.4 mg/l (Burton et al. 1980). Bluefish are known to follow (or even chase) schools of menhaden inshore, feeding on them, and may contribute to their mortality by preventing them from leaving an area before the oxygen supply is depleted. Oxygen depletion is accelerated by high water temperatures which increase the metabolic rate of the fish; at the same time, oxygen is less soluble in warm water. Menhaden which die from low oxygen stress can immediately be recognized by the red coloration on their heads caused by bursting blood capillaries. Just before death, the fish can be seen swimming very slowly in a disoriented manner just below the surface of the water. This is a common phenomenon which has been observed throughout the range of the species. Menhaden spotter pilots have reported menhaden "boiling up" from the middle of dense schools, and washing up on the beach, apparently from oxygen depletion within the school. This phenomenon was observed during December, 1979 in the ocean off Atlantic Beach, North Carolina (M. Street, NC DMF, pers. comm.; as cited in ASMFC 1992). Smith (1999a)

reported a similar event off Core Banks, North Carolina, in December 1997. Other species are not nearly as susceptible simply because they do not enter enclosed inshore waters in such large numbers.

Ecological relationships

Menhaden are extremely abundant in nearshore coastal waters because of their ability to directly utilize phytoplankton, which is the basic food resource in aquatic systems. Other species of marine fish are not equipped to filter such small organisms from the water. Consequently, such large populations of other species cannot be supported. Because menhaden are so abundant in nearshore coastal and estuarine waters, they are an important forage fish for a variety of larger piscivorous fishes, birds, and marine mammals. In ecological terms, menhaden occupy a very important link in the coastal marine food chain, transferring planktonic material into animal biomass. As a result of this, menhaden influence the conversion and exchange of energy and organic matter within the coastal ecosystem throughout their range (Peters and Schaaf 1981; Lewis and Peters 1984; Peters and Lewis 1984).

Because menhaden only remove planktonic organisms larger than 13-16 microns (7 microns for juveniles) from the water, the presence of large numbers of fish in a localized area could alter the composition of plankton assemblages (Durbin and Durbin 1975). Peters and Schaaf (1981) estimated that juvenile menhaden consumed 6-9% of the annual phytoplankton production in eight estuaries on the east coast, and up to 100% of the daily production in some instances. A large school of menhaden can also deplete oxygen supplies and increase nutrient levels in the vicinity of the school. Enrichment of coastal waters by large numbers of menhaden can be expected to stimulate phytoplankton production. Oviatt et al. (1972) measured ammonia concentrations (from excretion) inside menhaden schools that were five times higher than ambient levels 4.5 km away. At the same time, chlorophyll values increased by a factor of five over the same distance, indicating the grazing effect of the fish on the phytoplankton standing crop. Oxygen values were not significantly reduced by the fish, but were much more variable inside the schools than outside them.

Also, in a study of energy and nitrogen budgets (Durbin and Durbin 1981), food consumption rates, energy expenditures, and growth efficiency were examined. Results indicated that swimming speed, the duration of the daily feeding period, and the concentration of plankton in the water controlled the energy and nitrogen budgets for this species.

Predator/Prey Relationships

Atlantic menhaden are a major forage species for a wide number of important predatory fish species including, but not limited to, bluefish, striped bass, weakfish, king mackerel, bluefin tuna and sharks (Grant 1962; Reintjes and Pacheco 1966; Manooch 1973; DeVane 1978; Saloman and Naughton 1983; Juanes et al. 1993; Hartman and Brandt 1995a, 1995b). Marine mammals, including whales and porpoises, also have been reported to feed on menhaden (Bigelow and Schroeder 1953). Since Atlantic menhaden are eaten by predators in several ecosystems, they serve as a direct pelagic link in the food web between detritus and plankton and top predators (Rogers and Van Den Avyle 1989).

Ecological Role

Atlantic menhaden occupy two distinct types of feeding niches during their lifetime. They are size selective plankton feeders as larvae and filter feeders as juveniles and adults. Data on the food of larvae before they enter the estuary is currently unavailable. After entering the estuary, menhaden larvae appear to be extremely selective for prey of certain sizes and species. Larvae from the Newport River estuary, North Carolina, ranging in size from 26-31 mm TL (mean = 29 mm TL), consumed copepods and copepodites of only four taxa, which composed 99% by number and volume of their gut contents (Kjelson et al. 1975). These prey items, ranging from 300 to 1200 microns in length (mean = 750 microns), were eaten despite an abundance of copepod nauplii, barnacle larvae, and small adult copepods in plankton tows. Larvae that were offered copepods in the laboratory ignored all other food items, including *Artemia* and *Balanus* nauplii (June and Carlson 1971). Larval menhaden in the Newport River estuary, North Carolina, fed primarily during daylight (Kjelson et al. 1975).

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

The role of Atlantic menhaden in systems function and community dynamics has received little attention. Larvae and juveniles are seasonally important components of estuarine fish assemblages (Tagatz and Dudley 1961; Cain and Dean 1976; Bozeman and Dean 1980). Estimates of the mean daily ration for larvae range from 4.9% (Kjelson et al. 1975) to 20% (Peters and Schaaf 1981) of wet body weight.

Assimilation of ingested energy exceeded 80% for plant and animal material (Durbin and Durbin 1981). Because of their tremendous numbers, individual growth rates, and seasonal movements, these fish annually consume and redistribute large amounts of energy and materials, including exchanges between estuarine and shelf waters. Kjelson et al. (1975) noted that the copepod taxa preferred by larval menhaden and other species decreased from a mean value (2 years) of 81% to 48% of the total zooplankton biomass during the period of larval residence. They speculated that this decrease may be partly explained by larval feeding. Durbin and Durbin (1975) suggested that Atlantic menhaden in coastal waters may also alter the composition of plankton assemblages by grazing on certain size ranges.

Related Species and Hybrids

There are two species of menhaden that occur on the Atlantic coast, the Atlantic menhaden, *Brevoortia tyrannus*, and the yellowfin menhaden, *B. smithi*. Yellowfin menhaden range from Cape Lookout, North Carolina, to the Mississippi River delta (Ahrenholz 1991). The numbers of Atlantic menhaden relative to yellowfin menhaden become reduced proceeding southward along

the Atlantic coast of Florida. A large amount of hybridization occurs between these two species and areas with pure strains of yellowfin menhaden have yet to be defined. As the relative density of Atlantic menhaden decreases as one proceeds southward, the number of Atlantic x yellowfin menhaden hybrids increases along with pure strains of yellowfin menhaden. Historically, the menhaden gill net fishery in Indian River, Florida, was dominated by yellowfin menhaden and the Atlantic x yellowfin menhaden hybrid (Dahlberg 1970). Yellowfin menhaden were traditionally targeted by specialized bait fisheries in Florida but this may have changed due to the net ban implemented by that state in 1995.

Abundance and status of stocks

(Source: ASMFC, 2007 FMP Review)

Status of the coastwide stock is determined based on the terminal year (2005) estimate relative to its corresponding limit (or threshold). Benchmarks have been estimated based on the results of the updated base run. The terminal year estimate of fishing mortality rate (F₂₊) was estimated to be 56% of its limit (and 91% of its target). Correspondingly, the terminal year estimate of population fecundity was estimated at 158% of its fecundity target (and 317% of its limit).

Hence, the coastwide stock is not considered to be overfished, nor is overfishing occurring.

The model used in the assessment (ASMFC 2006) calculates the benchmarks referred to above using the method described in Addendum I of Amendment 1 to the Menhaden FMP. The values used for benchmarks change each assessment as new data are added to the model. For a historical comparison of fishing mortality rate relative to its annually estimated threshold benchmark (F/F_{rep}) and population fecundity relative to its annually estimated target (FEC/FEC_{target}), please see Figure 7.5 of the Stock Assessment Report.

The current coastwide estimate of F is near the lowest of the time series (1955-2005). However, recent recruitment estimates are of concern because they are below the 25th percentile [Table 6.2, ASMFC 2006]. Most of the concern stems from the decline in juveniles seen in Chesapeake Bay as documented by the Virginia and Maryland seine surveys. The Technical Committee has provided research recommendations in the past to better understand poor recruitment in Chesapeake Bay. Several projects are ongoing to address this issue.

The current stock assessment model has several limitations. It cannot provide details on the status of the menhaden stock in geographical areas smaller than coastwide. However, the Stock Assessment Subcommittee is considering how to incorporate a spatial component into the stock assessment prior to the next peer review. In addition, the model is not capable of addressing questions of multispecies interactions. Many ongoing research projects are being conducted and the MSVPA-X is being implemented to provide more information to answer those questions.

4.2.2 Striped Bass

Description and Distribution

(Source: Amendment 6 to the Striped Bass FMP, ASMFC 2003)

The striped bass is a long-lived (at least up to 29 years of age, Merriman 1941; Secor et al. 1995) species which normally spends the majority of its adult life in the coastal estuaries or the ocean,

migrating north and south seasonally, and ascending rivers to spawn in the spring. Mature female striped bass (age 4 and older) produce large quantities of eggs, which are fertilized by mature males (age 2 and older) as they are released into waters of riverine spawning areas. The fertilized eggs drift downstream with currents while developing, eventually hatching into larvae. The larvae and postlarvae begin feeding on microscopic animals during their downstream journey. After their arrival in the nursery areas, located in river deltas and the inland portions of the coastal sounds and estuaries, they mature into juveniles. They typically remain in coastal sound and estuaries for two to four years, and then migrate to the Atlantic Ocean. In the ocean, fish tend to move north during the summer and to the south during the winter. Important wintering grounds for the mixed stocks are located from offshore New Jersey as far south as Cape Hatteras, NC historically including the North Carolina sounds. With warming water temperatures in the spring, the mature adult fish migrate to the riverine spawning areas to complete their life cycle. In general, the Chesapeake Bay spawning areas produce the majority of coastal migratory striped bass.

Atlantic coastal migratory striped bass live along the eastern coast of North America from the St. Lawrence River in Canada to the Roanoke River and other tributaries of Albemarle Sound in North Carolina. Stocks which occupy coastal rivers from the Tar-Pamlico River in North Carolina south to the St. Johns River in Florida are believed primarily endemic and riverine and apparently do not presently undertake extensive Atlantic Ocean migrations as do stocks from the Roanoke River north (Richkus 1990). Striped bass are also naturally found in the Gulf of Mexico from the western coast of Florida to Louisiana (Musick et al. 1997). Striped bass were introduced to the Pacific Coast using transplants from the Atlantic Coast in 1879. Striped bass also were introduced into rivers, lakes, and reservoirs throughout the US, and to foreign countries such as Russia, France and Portugal (Hill 1989).

Reproduction

Spawning

Striped bass spawn in freshwater or nearly freshwater of Atlantic Coast rivers and estuaries. They spawn above the tide in mid-February in Florida but in the St. Lawrence River they spawn in June or July. The bass spawn in turbid areas as far upstream as 320 km from the tidal zone (Hill 1989). The tributaries of the Chesapeake Bay are the primary spawning areas for striped bass, but other major areas include the Hudson River, Delaware Bay and the Roanoke River. Spawning is triggered by increased water temperature (Shepherd 2000). Spawning occurs between 10 and 23 degrees Celsius, but optimal temperature for spawning is between 17 and 19 degrees Celsius. No spawning occurs below 13 degrees Celsius or above 22 degrees Celsius (Bain 1982). Spawning is characterized by brief excursions to the surface by females surrounded by males, accompanied by much splashing. Females release eggs in the water. This is where fertilization occurs (Raney 1952). Striped bass do not eat during spawning but they may eat heavily before and afterward. Spawning occurs in the late afternoon and early evening as well as late evening and early morning.

Development, growth and movement patterns

Eggs and larvae

An egg is only viable for about an hour for fertilization. Following fertilization the fertilized eggs are spherical, non-adhesive, and semi-buoyant and will harden within one to two hours at 18

degrees Celsius (Hill 1989). Eggs need adequate water velocity, from either current or tidal flow, to keep them suspended in the water column. Survival of striped bass eggs is dependent on environmental conditions. A temperature range of 17-19 degrees Celsius is important for egg survival as well as for maintaining appropriate dissolved oxygen

Yolk-sac larvae occur in open water but ultimately form schools and migrate inshore. The fin fold larvae and larger larvae have been collected in mid-channel areas near the bottom. Occurrence of fin fold larvae varied with the time of day and the depth of the river (Hill 1989). Striped bass larvae usually stay in the open surface waters of estuaries.

There are three stages of larval development. These are: yolk-sac larvae, finfold larvae, and post-finfold larvae (Hill 1989). The yolk-sac larvae occur right after hatching and this stage usually lasts for about 3 to 9 days. They are 2.0 to 3.7 mm in length and contain an easily identified yolk-sac. The yolk-sac is the main source of energy for the striped bass during this time. Also during this time, the mouth has not been formed and the eyes are not pigmented (Mansueti 1958). This phase is finished when the yolk-sac is absorbed. The finfold phase lasts for about 11 days and the striped bass reach a length of 12mm. The last phase is the post-finfold larvae which lasts for about 20 to 30 days and the larvae reach a length of 20 mm (Bain 1982).

Survival of the larvae depends on three main factors: temperature, salinity, and dissolved oxygen. The optimal temperature for larvae is 18 to 21 degrees Celsius, but temperatures of 12 to 23 degrees Celsius have been and can be tolerated (Bain 1982). Studies have shown that striped bass larvae do better and have a higher survival rate when they are in low salinity waters rather than freshwater (Setzler et al. 1980). The third factor, dissolved oxygen, is equally critical for larvae as it was for the egg stage. A reduction in the dissolved oxygen level diminishes the chances of survival of the larvae (Turner and Farley 1971). Other factors that also influence the survival of striped bass larvae include turbulence. While at first it is necessary for the larvae to reside in turbulent waters to maintain position, the larvae quickly become motile and then are able to maintain position on their own (Doroshev 1970).

Juveniles

Juvenile striped bass are able to tolerate a wider range in environmental conditions. The habitat requirements for the juvenile fish are much like the habitat required for the adult bass. As the juvenile bass grow, they migrate to nearshore areas and then to higher salinity areas of an estuary (Raney 1952). Juvenile striped bass prefer clean, sandy bottoms but they have been found in gravel beaches, rock bottoms, and soft mud areas. They are usually found in schools of as many as several thousand fish.

However, the location of the schools depends on the age of the fish (Hill 1989).

Striped bass become juveniles at about 30 mm, when the fins are fully developed. At this point they resemble adults. Bluefish, weakfish, and other piscivores prey on striped bass (Buckel et al. 1999; Hartman and Brandt 1995b). The location of the striped bass determines the content of its diet. In the diet of the stock from the York River, where the salinity was higher than other places, the fish fed on mysids. In the James River, where the salinity was lower, the same sized fish fed mostly on insects. This and other evidence showed that there is a relationship between the diet of the stock of striped bass and the salinity of the habitat in which the fish live (Setzler et al. 1980).

Adults

Mature adult striped bass leave the estuaries and migrate along the coast where they have similar temperature and dissolved oxygen requirements as juvenile bass (Bain 1982). Tagging studies indicate that fish from all stocks range widely along the Atlantic Coast, generally remaining in state (0-3 miles) waters but in some areas entering the Exclusive Economic Zone (EEZ; 3-200 miles). Studies are presently underway, using Geographic Information Systems (GIS) analysis, to characterize the habitats used by striped bass when they are in nearshore waters during the summer, fall and winter months. Schools of striped bass which winter off North Carolina use nearshore habitats from the surf zone to beyond the state-EEZ boundary line.

Migration Patterns

Migration of striped bass occurs at juvenile and adult stages. Migratory patterns for all life stages vary by location, but in general juveniles migrate downstream in summer and fall, while adults migrate upriver to spawn in spring, afterwards returning to the ocean and moving north along the coast in summer and fall, and south during the winter (Shepherd 2000).

Juvenile striped bass migration varies by locations. In Virginia, the movement of young bass during their first summer was downstream into waters of higher salinity (Setzler et al. 1980). In the Hudson River, the bass began migrating in July. Migration was documented through an increase in the number of juvenile striped bass caught along the beaches and subsequent decline in the numbers in the channel areas after mid-July. Downstream migration continues through late summer, and by the fall, juveniles start to move offshore into Long Island Sound (Raney 1952).

Juvenile striped bass rarely complete complete coastal migrations, but even though fish that are under the age of two are non-migratory, many do leave their birthplaces when they are two or more years old. From Cape Hatteras, North Carolina, to New England, fish may migrate in groups along the coast. They migrate north in the summer and south in the winter, however, the extent of the migration varies between sexes and populations (Hill 1989). Larger bass, typically the females, tend to migrate farther distances. However, striped bass are not usually found more than 6 to 8 km offshore (Bain, 1982). These coastal migrations are not associated with spawning and usually begin in early spring, but this time period can be prolonged by the migration of bass that are spawning.

Some areas along the coast are used as wintering grounds for adult striped bass. The inshore zones between Cape Henry, Virginia, and Cape Lookout, North Carolina, serve as the wintering grounds for the migratory segment of the Atlantic coast striped bass population (Setzler et al. 1980). There are three groups of fish that are found in nearshore ocean waters of Virginia and North Carolina between the months of November and March, the wintering period. These three groups are bass from Albemarle and Pamlico Sounds, North Carolina, fish from the Chesapeake Bay, and large bass that spend the summer in New Jersey and north (Holland & Yelverton 1973). Based on tagging studies conducted under the auspices of the Southeast Area Monitoring and Assessment Program (SEAMAP) each winter since 1988, striped bass wintering off Virginia and North Carolina range widely up and down the Atlantic Coast, at least as far north as Nova Scotia, and represent all major migratory stocks (U.S. Fish and Wildlife Service and National Marine Fisheries Service, unpublished data).

Ecological relationships

Striped bass larvae feed only on mobile planktonic food. They pass the prey repeatedly in order to aim and rush at the prey successfully. It was found that the first successful feeding of a 9-day-old larvae occurred at concentrations of 15,000 Cyclops nauplii and copepodites per liter. By the 11th and 12th day, when the air bladder of the larvae is filled, the prey concentration may be reduced to 2,000 and 5,000 per liter. By days 40 to 50, the striped bass feed on plankton and epibenthos and by days 50 to 80, the food of the striped bass larvae includes mysid shrimp, gammarid amphipods, and fish up to 20 mm in length (Doroshev 1970).

Abundance and status of stocks

At the 2006 Annual Winter Board Meetings, the Striped Bass Technical Committee submitted a request to the Striped Bass Management Board to bypass the 2006 annual update stock assessment in favor of having more time to prepare new methods and better data for the 2007 benchmark stock assessment. The Board approved this request, such that the most recent data on the status of the stock are derived from the 2005 stock assessment.

The estimate of total abundance for January 1, 2005 from the ADAPT VPA was 65.3 million age-1 and older fish. This estimate is about 1.2 million fish lower than the 2004 abundance but 10% higher than the average stock size for the previous five years. Population estimates were calculated for the first time this year from tag-based F estimates using the catch equation. The 2004 population estimate of age 3+ fish was 48.5 million fish; that is, roughly 8 million fish higher than the 2003 estimate. This estimate is higher than the ADAPT VPA estimate of 39.2 million age 3+ fish at the beginning of 2004. This discrepancy in population estimates between the two approaches increased with older age classes. The tag-based approach estimated the 2004 population of age 7+ fish to be 17.1 million, whereas the ADAPT VPA estimated the age 7+ population to number 9.4 million fish. The abundance of older fish (age 13+) in the stock estimated from the ADAPT VPA increased from 382,000 fish at the beginning of 2003 to 547,000 fish on January 1, 2005.

The female spawning stock biomass for 2004 was estimated (from the VPA) at 54.8 million pounds, which is above the recommended biomass threshold of 30.9 million pounds (13,956 mt) and the target SSB of 38.6 million pounds (17,500 mt). SSB has declined by 9% since 2002 when it peaked at 60.6 million pounds.

Recruitment of the 2004 cohort for all stocks combined is 12.7 million age-1 fish, which is close to the average age-1 recruitment observed since the stocks were declared recovered in 1995.

Based on VPA results, average age 8-11 fishing mortality in 2004 was estimated at $F=0.40$ which is below the Amendment 6 threshold of 0.41 but exceeds the target of 0.30. However, it was the consensus of the Technical Committee members that this was likely an overestimate of the 2004 F given the uncertainty with the terminal year estimate from the VPA and the systematic positive bias observed in the retrospective analysis. The 2003 value of F from the 2005 VPA is 0.29, which is substantially lower than the terminal year F from the 2004 VPA run of 0.62. This is due not only to the addition of another year's worth of data, but to the modified suite of tuning indices used in the 2005 VPA and the inclusion of wave 1 (Jan./Feb.) estimates of

recreational harvest mortality from NC and VA for 1996 – 2004 (see Data and Uncertainty section in Plan Review Document available at www.asmf.org).

The 2004 tag-based estimates of F using stock-specific, model-based estimates of fishing mortality and a constant M of 0.15 were as follows. For fish greater than 28 inches, the coast-wide average F was estimated as 0.29 and specific tagging program values ranged from 0.02 in the New York ocean haul survey (NYOHS) to 0.31 in the Maryland (MD) tagging program. This value was similar to the VPA F weighted by N value for age 7-11 fish of 0.32. For fish greater than 18 inches, the coast-wide average F was estimated as 0.29 and specific tagging program values ranging from 0.06 in the Virginia spawning stock (VARAP) program to 0.68 in the New Jersey Delaware Bay (NJDEL) program. This tag-based F estimate was greater than the VPA F weighted by N value for age 3-11 fish of 0.15.

The 2004 variable M tag-based estimates of F for fish greater than 28 inches indicated the coast-wide average F was 0.14, and specific tagging program values ranged from 0.09 in the VARAP program to 0.26 in the Delaware and Pennsylvania (DE-PA) tagging program. These F estimates were less than the VPA F weight by N, for age 7-11 fish, of 0.32. For fish greater than 18 inches, the coast-wide average was 0.11, and specific tagging program F estimates ranged from 0.05 in three different programs to 0.17 in the MD program. This tag-based F estimate is similar to the VPA F weighted by N value for age 3-11 fish of 0.15. Chesapeake Bay fishing mortality in 2004 was estimated as $F=0.16$ by the direct enumeration study. This F represents mortality during the June 2003 – June 2004 period, so it is not directly comparable to the average, weighted (by N) VPA calendar-year F on age 3-8 striped bass that is equal to 0.12.

4.2.3 Alewife

Description and Distribution

(all information below from draft ASMFC alewife doc)

The alewife, *Alosa pseudoharengus*, is an anadromous, highly migratory, euryhaline, pelagic, schooling species. Both alewife and blueback herring are often referred to as “river herring,” a collective term for these two species, which often school together (Murdy et al. 1997). Although this term is often used generically in commercial harvests and no distinction is made between the two species (ASMFC 1985), landings are reported as alewife (Dixon 1996).

The alewife spends the majority of its life at sea, returning to freshwater river systems along the U.S. Atlantic Coast to spawn. There are also some alewife populations that have been successfully introduced into landlocked freshwater systems, such as the Great Lakes and some of the Finger Lakes of New York (Scott and Crossman 1973), as well as those that have been stocked in man-made reservoirs (Bigelow and Schroeder 2002). Their historical coastal range was South Carolina to Labrador and northeastern Newfoundland (Berry 1964; Winters et al. 1973; Burgess 1978), but more recent surveys indicate that they do not occur in the southern range beyond North Carolina (Rulifson 1982; Rulifson et al. 1994). Alewife from the southernmost range are capable of migrating long distances (over 2000 km) in ocean waters of the Atlantic seaboard and patterns of migration may be similar to those of American shad (Neves 1981). Although alewife and bluebacks co-occur throughout much of their range, alewife are typically more abundant than bluebacks in the northern part of their range (Schmidt et al. 2003).

Several long-term data sets were recently analyzed to determine the current status of alewife in large river systems along the Atlantic Coast, including the Connecticut, Hudson, and Delaware rivers. These analyses suggest that alewife are showing signs of overexploitation in all of these rivers, including reductions in mean age, decreases in percentage of returning spawners, and decreases in abundance. Researchers did note that some runs in the northeastern U.S. and Atlantic Canada have been increasing recently (Schmidt et al. 2003). Alewife appear to be doing well in inland waters, colonizing many freshwater bodies, including all five Great Lakes (Waldman and Limburg 2003). Much of the research regarding specific environmental requirements of alewife, such as temperature, dissolved oxygen, salinity, and pH has been conducted on landlocked populations, not anadromous stocks therefore, data should be interpreted with discretion.

Development, growth and movement patterns

Spawning

Adult alewife populations migration to spawning grounds in freshwater and brackish waters progresses seasonally from south to north, with populations further north returning as the season progresses (and water temperatures increase). Fish typically begin spawning from late February in their southern range and June in their northern range (Neves 1981; Loesch 1987). Neves (1981) suggested that alewife migrate from offshore waters north of Cape Hatteras, encountering the same thermal barrier as American shad, then move south along the coast for fish homing to South Atlantic rivers; northbound pre-spawning adults head north along the coast (Stone and Jessop 1992). They spawn in rivers as far south as North Carolina and as far north as the St. Lawrence River, Canada (Neves 1981). Fish may spawn as late as June in the southern range and through August in their northern range (Marcy 1976a). Spawning is triggered most strongly by a change in the water temperature. Movement upstream may be controlled by water flow, with increased movement occurring during higher flows (Collins 1952; Richkus 1974). Although adult alewife will move upstream at various times, peak migration typically occurs during the day, between dawn and noon, and also from dusk to midnight (Richkus 1974; Rideout 1974; Richkus and Winn 1979). High midday movement is restricted to overcast days, and nocturnal movement occurs when water temperatures are abnormally high (Jones et al. 1978). Males are first to arrive at the mouths of spawning rivers, prior to the arrival of females (Cooper 1961; Tyus 1971; Richkus 1974).

There is strong evidence that suggests that alewife home to their natal rivers to reproduce, but some colonize new areas; they have also been found to reoccupy systems from which they have been extirpated (Havey 1961; Thunberg 1971; Messieh 1977; Loesch 1987). Messieh (1977) found that alewife strayed considerably to adjacent streams in the St. Johns River, Florida, particularly during the prespawning period (late winter, early spring), not during the spawning run. It appears that olfaction is the primary means for homing behavior (Ross and Biagi 1990).

In general, alewife are less selective in choosing their spawning sites than blueback herring. Alewife will select slow-moving sections of rivers or streams to spawn, where the water may be as shallow as 30 cm (Jones et al. 1978). They may enter lakes or ponds, including freshwater coves behind barrier beaches (Smith 1907; Belding 1920; Leim and Scott 1966; Richkus 1974; Bigelow and Schroeder 2002). Alewife often spawn in ponds that form the headwaters of most

coastal streams in New England and Nova Scotia (Loesch 1987). They are typically more abundant than bluebacks in rivers where there are well-developed headwater ponds in New England. In rivers where headwater ponds are absent or poorly-developed, alewife may be most abundant further upstream in headwater reaches, while bluebacks may select the mainstream proper for spawning (Ross and Biagi 1990). In tributaries of the Rappahannock River, Virginia, upstream areas were found to be more important than downstream areas for spawning alewife (O’Connell and Angermeier 1997). Although earlier studies suggested that alewife will ascend further upstream than bluebacks (Hildebrand 1963; Scott and Crossman 1973), Loesch (1987) noted that both species have the ability to ascend rivers far upstream.

Alewife are noted for their greater ability than American shad for navigating suitable fishways (Dominy 1973). In rivers where dams are an impediment, spawning may occur in shore-bank eddies or deep pools (Loesch and Lund 1977). Alewife will generally spawn 3-4 weeks before blueback herring in areas where they co-occur; however, there may be considerable overlap (Loesch 1987) and peak spawning periods may differ by only 2-3 weeks (Jones et al. 1978). In a tributary of the Rappahannock River, Virginia, O’Connell and Angermeier (1997) found that blueback eggs and larvae were more abundant than those of alewife, but alewife used the stream over a longer period of time. They also reported that there was only a 3-day overlap of spawning by alewife and bluebacks. Although it has been suggested that alewife and bluebacks select separate spawning sites in sympatric areas to reduce competition (Loesch 1987), O’Connell and Angermeier (1997) reported that the two species used different spawning habitat. They suggested that there was a temporal, rather than spatial segregation that minimized the competition between the two species.

Alewife may spawn throughout the day, but do so more commonly at night (Graham 1956). One female fish and as many as 25 male fish broadcast their eggs and sperm simultaneously just below the surface of the water or over the substrate (Belding 1920; McKenzie 1959; Cooper 1961). Spawning lasts 2-3 days for each group or “wave” of fish that arrives (Cooper 1961; Kissil 1969; Kissil 1974), with older and larger fish usually spawning first (Belding 1920; Cooper 1961; Libby 1981, 1982). Upon spawning, spent fish return quickly downstream (Bigelow and Schroeder 2002).

Alewife are repeat spawners, with some fish spawning up to seven or eight times in a lifetime (Jessop et al. 1983). It is not clear whether there is a clinal trend from south to north for repeat spawners (more repeat spawners in the north than the south) (Klauda et al. 1991), or there is a general overall value (i.e. 30-40% repeat spawners throughout their range) (Richkus and DiNardo 1984).

Tables 4.2-1 and 4.2-2 present percentages of repeat spawners observed in several areas of the species range and spawning seasons, respectively

Table 4.2-1. Percentages of repeat spawners by area for alewife, *Alosa pseudoharengus*.

State	Percentage of repeat spawners	References
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Nova Scotia	60%	O'Neill 1980
Maryland	30-72%	Weinrich et al. 1987; Howell et al. 1990
York River, Virginia	61%	Joseph and Davis 1965
North Carolina	13.7% (1993); 61% (1995)	Winslow 1995

Table 4.2-2. Reported spawning seasons for alewife, *Alosa pseudoharengus*, by state or region.

State or Region	Reported Spawning Season	References
Bay of Fundy tributaries	late April or early May	Leim and Scott 1996; Dominy 1971, 1973
Gulf of St. Lawrence tributaries	late May or early June	Leim and Scott 1996; Dominy 1971, 1973
Maine	late April to mid-May	Rounsefell and Stringer 1943; Bigelow and Schroeder 1953; Havey 1961; Libby 1981
Massachusetts	early to mid-April	Belding 1920; Bigelow and Schroeder 1953
Mid-Atlantic and southern New England	late March or early April	Cooper 1961; Kissil 1969; Marcy 1969; Smith 1971; Saila et al. 1972; Richkus 1974; Zich 1978; Wang and Kernehan 1979
Chesapeake Bay region	mid-March	Jones et al. 1978; Loesch 1987
North Carolina	late February	Holland and Yelverton 1973; Frankenstein 1976

Adults will typically spend 2 to 4 years at sea before returning to their natal rivers to spawn (Neves 1981). The majority of adults reach sexual maturity at ages-3, 4, or 5, although some adults from North Carolina (Richkus and DiNardo 1984) returned to spawn at age-2 (Jessop et al. 1983). The oldest fish recorded in North Carolina were age-9 (Street et al. 1975; Johnson et al. 1979), and age-10 fish have been caught in New Brunswick (Jessop et al. 1983) and Nova Scotia (O'Neill 1980). Kissil (1974) found that alewife spawning in Bride Lake, Connecticut, spent 3 to 82 days on the spawning grounds, while Cooper (1961) reported that most fish left within 5 days of spawning. Kissil (1974) suggests that alewife might spawn more than once in a season.

Temperature

There is some discrepancy regarding minimum spawning temperatures for alewife. Although running ripe fish of both sexes have been reported at temperatures as low as 4.2°C in the Chesapeake Bay area (Mansueti and Hardy 1967), it is suggested that the minimum temperature at which adults spawn is 10.5°C (Cianci 1965; Loesch and Lund 1977). Marcy (1976a) suggested that the majority of spawning activity in the lower Connecticut River probably occurs at temperatures between 7.0-10.9°C. There does appear to be a broad range of temperatures for spawning in some regions, such as the Chesapeake Bay, where reported ranges are between 10.5-21.6°C (Jones et al. 1978), and 11-19°C in the Patuxent River, Maryland (Mowrer 1982). Cooper (1961) noted that upstream migration ceased in a Rhode Island stream when temperatures

reached 21°C, while Edsall (1970) reported that spawning ceases altogether at 27.8°C. Peak spawning has been reported to occur at 13°C in North Carolina (Tyus 1974) and 14.0-15.5°C in Rhode Island (Jones et al. 1978). Although quantitative data were lacking, Pardue (1983) suggested that the optimum spawning temperature for alewife is 15-20°C, based on available information.

Adults have been collected in temperatures ranging from 5.7-32°C (Marcy 1976b; Jones et al. 1978). Upper incipient lethal temperatures (temperature at which 50% of the population survives) ranged from 23.5-24.0°C for adults that were acclimated at temperatures of 10, 15, and 20°C (Otto et al. 1976). Another study reported upper incipient lethal temperatures of 29.8 and 32.8°C at acclimation temperatures of 16.9 and 24.5°C, respectively (Stanley and Holzer 1961). McCauley and Binkowski (1982) reported an upper incipient lethal temperature of 31-34°C after acclimation at 27°C for a northern population of adults.

The lower incipient lethal temperature range for adults acclimated at 15.0 and 21.0°C is between 6-8°C (Otto et al. 1976). At temperatures below 4.5°C, normal schooling behavior was significantly reduced for adult alewife from Lake Michigan (Colby 1973). No fish survived below 3°C, regardless of acclimation temperature (Otto et al. 1976).

In general, alewife may prefer cooler water, and northern populations may be more cold tolerant than other migratory anadromous fish (Stone and Jessop 1992). Richkus (1974) showed that the response of migrating adults to a particular hourly temperature was determined by its relationship to a changing baseline temperature and not on the basis of its absolute value. Stanley and Colby (1971) found that decreased temperatures (from 16 to 3°C at a rate of 2.5°C per day) reduced adult alewife ability to osmoregulate. Adults were also shown to survive temperature decreases of 10°C, regardless of acclimation temperature, if the temperature did not drop below 3°C (Otto et al. 1976).

Depth

Water depth in spawning habitat may be a mere 6 inches (15.2 cm) deep (Bigelow and Schroeder 1953; Rothschild 1962), or as deep as 10 feet (3 m) (Edsall 1964); however, it is typically less than 1 m (3.3 ft) (Murdy et al. 1997). Adults may utilize deeper water depths in order to avoid high light intensities (Richkus 1974).

Salinity

While it is known that alewife can adjust to a wide range of salinities, experimental evidence is lacking (Klauda et al. 1991). Richkus (1974) found that adults that were transferred from freshwater to saline water (32 ppt) and vice versa experienced zero mortality. Leim (1924) studied the life history of American shad in its northern range and noted that they do not ascend far beyond the tidal influence of the river, yet alewife migrate as far upstream as they can travel. He concluded that alewife may be less dependent on salt water for development. Also, unlike American shad, some populations of alewife have become landlocked and are not dependent on salt water (Scott and Crossman 1973).

Water Velocity/Flow

Increased movement upstream occurs during higher water flows (Collins 1952; Richkus 1974), while spawning typically takes place in quiet, slow-moving waters for spawning alewife (Smith 1907; Belding 1921; Marcy 1976a).

Differential selection of spawning areas has been noted by some researchers. For example, in Connecticut, alewife choose slower moving waters in Bride Lake (Kissil 1974) and Higganum and Mill creeks, while bluebacks select fast-moving waters in the upper Salmon River and Roaring Brook (Loesch and Lund 1977). In other areas where alewife and bluebacks are forced to spawn in the same vicinity due to blocked passage (Loesch 1987), alewife generally spawn along shorebank eddies or deep pools, whereas, bluebacks will typically select the main stream flow for spawning (Loesch and Lund 1977). In North Carolina, they select slow moving streams and oxbows (Street et. al. 2005).

Bottom composition

The spawning habitat of alewife can range from sand, gravel or coarse stone substrates, to submerged vegetation or organic detritus (Edsall 1964; Mansueti and Hardy 1967; Jones et al. 1978). Boger (2002) found that river herring spawning areas along the Rappahannock River, Virginia had substrates that consisted primarily of sand, pebbles, and cobbles (usually associated with higher-gradient streams), while areas with little or no spawning were dominated by organic matter and finer sediments (usually associated with lower-gradient streams and comparatively more agricultural land use).

Pardue (1983) evaluated studies of cover component in spawning areas, suggesting that substrate characteristics and associated vegetation were a measure of the ability of a habitat to provide cover to spawning adults, their eggs, and developing larvae. In high flow areas, there is little accumulation of vegetation and detritus, while in low flow areas, detritus and silt accumulate and vegetation has the opportunity to grow. Based on a review of the literature, Pardue suggested that substrates with 75% silt or other soft material containing detritus and vegetation, and sluggish waters are optimal for alewife.

pH

There are only a few studies of pH sensitivity in alewife (Klauda et al. 1991). Byrne (1988) found that the average pH level was 5.0 in several streams in New Jersey where alewife spawning was known to occur. Since blueback herring did not spawn in these streams, he suggested that early life history stages of alewife were more tolerant to acidic conditions than bluebacks. Laboratory tests found that fish from those streams could successfully spawn at a pH as low as 4.5. In one pH change study, adults tolerated changes up to 0.8 units within a range of pH 6.5-7.3 (Collins 1952). When aluminum pulses were administered in the laboratory, critical conditions for spawning could occur during an acidic pulse between pH 5.5 and 6.2 with concomitant concentrations of total monomeric aluminum ranging from 15-137 µg/L for a pulse duration of 8-96 h (Klauda 1989). Klauda et al.(1991) suggested a range of 5-8.5 as suitable for alewife eggs, but no range was provided for spawning.

Dissolved Oxygen

There is little information regarding sensitivities of various life history stages of alewife to dissolved oxygen (DO) (Klauda et al. 1991). Adults that were exposed to DO ranging from 2.0-

3.0 mg/L for 16 hours in the laboratory experienced a 33% mortality rate (Dorfman and Westman 1970). They were able to withstand DO concentrations as low as 0.5 mg/L for up to five minutes, as long as a minimum of 3.0 mg/L was available, thereafter. Jones et al. (1988) suggested that the minimum DO concentration for adults is 5.0 mg/L.

Egg and Larval Habitat

Eggs may hatch anywhere from 50 to 360 hours, depending on water temperature (Fay et al. 1983), but hatch most often within 80-95 hours (Edsall 1970). Fertilized eggs remain demersal and adhesive for several hours (Mansueti 1956; Jones et al. 1978), after which they become pelagic and are transported downstream (Wang and Kernehan 1979). Marcy (1976a) observed eggs more often nearer the bottom than at the surface in the Connecticut River.

Within 2 to 5 days, the yolk-sac is absorbed and larvae will begin feeding exogenously (Cianci 1965; Jones et al. 1978). Post-yolk-sac larvae are positively phototropic (Odell 1934; Cianci 1965). Dovel (1971) observed larvae near or slightly downstream of presumed spawning areas in the Chesapeake Bay, only where the water was less than 12 ppt salinity (Dovel 1971). Larvae were also found in or close to observed spawning areas in Nova Scotia rivers in relatively shallow water (2 m) over sandy substrate (O'Neill 1980).

Temperature

In general, average time to median hatch varies inversely with temperature. Edsall (1970) reported the following hatch times for alewife eggs taken from Lake Michigan: 2.1 days at 28.9° C, 3.9 days at 20.6° C, and 15 days at 7.2° C. Reported hatch times in saltwater by various researchers are comparable: 2-4 days at 22° C (Belding 1921); 3 days at 23.8-23.9° C and 26.7-26.8° C, and 3-5 days at 20° C (Mansueti and Hardy 1976); and 6 days at 15.5° C (Bigelow and Welsh 1925). Laboratory tests conducted by Kellogg (1982) found that eggs from the Hudson River, New York achieved maximum hatching success at 20.8° C. Edsall (1970) reported some hatching at temperatures as low as 6.9° C for eggs from Lake Michigan (below 11° C caused a high percentage of deformed larvae) and as high as 29.4° C, but optimum hatching occurred between 17.2-21.1° C. Although this was the suggested optimal range, Edsall determined that considerable hatch rates and proper development could occur over a broader range from 10.6° C to 26.7° C. In the upper Chesapeake Bay, alewife eggs were collected where temperatures ranged from 7-14° C and 70% of these eggs were found where temperatures were between 12-14° C (Dovel 1971).

Edsall (1970) correlated egg mortality with incubation temperature. He developed an equation for predicting incubation time for alewife eggs from temperature, which is as follows:

$$t = 6.335 \times 106 (T) - 3.1222$$

where t = time in days

T = incubation temperature in degrees °F

Several investigations have been conducted to determine the effects of temperature on alewife eggs. One study examined the effects of power plants on alewife eggs found that they suffered no significant mortality or abnormal egg development, after being acclimated at 17° C, then exposed to 24.5° C for 6-60 minutes (Schubel and Auld 1972). Koo et al. (1976) determined that

the critical thermal maximum (CTM) for alewife eggs was 35.6°C, acclimated at 20.6°C, with a critical exposure period of 5-10 minutes.

Larval alewife were collected at water temperatures between 4-27°C in the upper Chesapeake Bay although 98% were collected at water temperatures 25° C (Dovel 1971). In laboratory experiments, larvae acclimated at 18.6°C withstood temperatures as high as 33.6°C for one hour (Koo et al. 1976). The upper temperature tolerance limit for yolk-sac larvae from the Hudson River, New York, acclimated at 14-15°C was 31°C (Kellogg 1982); their preferred range when acclimated at 20°C appears to be 23-29°C (Ecological Analysts Inc. 1978; Kellogg 1982).

Although alewife eggs taken from Lake Michigan were able to hatch at temperatures as low as 6.9°C, larvae held at incubation temperatures below 10.6°C had a 69% rate of deformities (Edsall 1970). Dovel (1971) found that growth rates of alewife larvae were much lower in freshwater compared to saltwater (1.0-1.3 ppt) at 26.4°C. He also observed substantial growth increases with small temperature increases above 20.8°C. Average daily weight gain for alewife larvae has been directly correlated to water temperature. The maximum larval growth rate was 0.084 g/day at 29.1°C; net gain in biomass (a function of survival and growth) was highest at 26.4° C (Kellogg 1982).

Based on Kellogg's (1982) observations that the optimum growth temperature (26°C) exceeds peak spawning temperatures by about 10-13°C, he suggested that it is not likely that survival and early development of young alewife would be threatened by rapid warming trends following spawning or by moderate thermal discharges. He further indicated that temperature elevations above normal following spawning and hatching would probably be beneficial to alewife populations.

In their review of the literature, Klauda et al. (1991) provided optimal ranges for both the prolarva and postlarva life stages for alewife. They suggested a suitable range of 8-31°C and 14-28°C, and an optimum range of 15-24°C and 20-26°C, respectively, for these two life stages.

Salinity

Alewife eggs have been collected in the upper Chesapeake Bay in salinities between 0-2 ppt; however, almost 99% of these eggs were collected where the salinity was 0 ppt. Larvae were collected where salinities ranged from 0-8 ppt, but again, most (82%) were collected in freshwater (Dovel 1971). Klauda et al. (1991) suggested that the optimal range for egg development for alewife is 0-2 ppt.

Growth rates of larval alewife were demonstrated to be considerably faster in saltwater (1.0-3.0 ppt) compared to growth in freshwater, at temperatures of 26.4°C (Klauda et al. 1991). Later review by Klauda et al. (1991) suggested that the optimal range for the prolarva life stage was 0-3 ppt and for the postlarva life stage was 0-5 ppt.

Water Velocity/Flow

Sismour (1994) observed a rapid decline in abundance of early preflexion river herring larvae (includes both alewife and blueback herring) in the Pamunkey River, Virginia following high river flow in 1989. He speculated that high flow led to increased turbidity, which reduced prey

visibility, leading to starvation of larvae. O'Connell and Angermeier (1997) found that current velocity (and DO) were the strongest predictors of alewife early egg presence in a Virginia stream. Findings from Rhode Island suggest the importance of river flow to alewife stocks. Drought conditions in the summer of 1981 were strongly suspected of impacting the 1984 year class, which was only half of its expected size (ASMFC 1985). In tributaries of the Chowan system, North Carolina, water flow was related to recruitment of larval river herring (O'Rear 1983).

Bottom composition

As with spawning habitat, Pardue (1983) suggested that egg and larval habitat with substrates with 75% silt or other soft material containing detritus and vegetation was optimal.

pH and aluminum

Klauda et al. (1991) suggest that a range of pH 5.0-8.5 for both the alewife egg and prolarva life stage was preferred. Klauda (1987) suggested that during an acidic pulse between pH 5.5.-6.2 critical conditions associated with > 50% direct mortality could occur. Klauda et al. (Klauda et al. unpublished, cited in Klauda et al. 1991) found that larvae subjected to a single 24-hour, acid-only pulse of pH 4.5 experienced no mortality, while those subjected to a 24-hour single acid pulse and 446 µg/L inorganic monomeric aluminum pulse suffered a 96% mortality rate. A single 12-hour acid-only pulse of 4.0 resulted in 38% mortality.

Dissolved Oxygen

Jones et al. (1988) determined that the minimum DO concentration requirement for eggs and larvae is 5.0 mg/L. O'Connell and Angermeier (1997) found that DO (and current velocity) were the strongest predictors of alewife early egg presence in a Virginia stream.

Suspended solids/turbidity

Alewife eggs subjected to suspended solids concentrations up to 1000 mg/L did not exhibit a reduction in hatching success (Auld and Schubel 1978). Despite these results, high levels of suspended sediment may significantly increase rates of egg infections from naturally occurring fungi, as was witnessed in earlier experiments (Schubel and Wang 1973), which can lead to delayed mortalities (Klauda et al. 1991).

Juveniles

In North Carolina, juveniles may spend the summer in the lower ends of rivers where they were spawned (Street et al. 1975). In the Chesapeake Bay, juveniles can be found in freshwater tributaries in spring and early summer, but may head upstream in the summer when saline waters encroach on their nursery grounds (Warriner et al. 1970). Some juveniles in the Chesapeake Bay remain in brackish water through the summer (Murdy et al. 1997).

Juveniles in the Hudson River usually remain in freshwater tributaries until June (Schmidt et al. 1988). Juvenile alewife were found to be most abundant in inshore areas at night in the Hudson River, compared to inshore abundance of American shad and blueback herring during the day (McFadden et al. 1978; Dey and Baumann 1978). Hudson River juveniles were observed in shallow portions of the upper and middle estuary in late June and early July, where they remained for several weeks before moving offshore as they grew (Schmidt et al. 1988). They

typically spend 3-9 months in their natal rivers before returning to the ocean (Kosa and Mather 2001).

In summer in the Potomac River, juveniles are abundant near surface waters during the day, but shifted to mid-water and bottom depths in September, where they remained until they emigrated in November (Warriner et al. 1970). Juvenile alewife respond negatively to light and follow diel movements similar to blueback herring. There appears to be some separation between the alewife and blueback as they emigrate from nursery grounds in the fall, most notably at night, when alewife can be found more frequently at midwater depths, while bluebacks are found mostly at the surface (Loesch and Kriete 1980). This may reduce interspecific competition for food (Loesch 1987), given that their diets are similar (Davis and Cheek 1966; Burbidge 1974; Weaver 1975).

Once water temperatures begin to drop in the late summer through early winter (depending on geographic area), juveniles start heading downstream, initiating their first phase of seaward migration (Pardue 1983; Loesch 1987). Some researchers found that movement of alewife peaked in the afternoon (Richkus 1975a; Kosa and Mather 2001), while others found that it peaked at night (Stokesbury and Dadswell 1989). Migration downstream is also prompted by changes in water flow, water levels, precipitation, and light intensity (Cooper 1961; Kissil 1974; Richkus 1975a, 1975b; Pardue 1983). Other researchers have suggested that water flow plays little role in providing the migration cue under riverine conditions. Rather, timing is triggered more by water temperature and moon phases that provide dark nights, generally new and quarter moons (O'Leary and Kynard 1986; Stokesbury and Dadswell 1989). Stokesbury and Dadswell (1989) found that alewife remained in the offshore region of the Annapolis estuary, Nova Scotia for almost a month before the correct migration cues triggered emigration. Large juveniles begin moving downstream before smaller juveniles (Schmidt et al. 1988), moving to saline waters before they begin their seaward migration (Loesch 1969; Marcy 1976a; Loesch and Kriete 1980).

Richkus (1975a) observed waves of juveniles leaving following environmental changes but the number of fish leaving was unrelated to the level of magnitude of change. Most fish (60-80%) emigrated during a small percentage (7-8%) of available days. These waves also lasted 2 to 3 days, regardless of the degree of environmental change. Others have also observed the majority (i.e., >80%) of river herring emigrating in waves (Cooper 1961; Huber 1978; Kosa and Mather 2001). Richkus (1975a) also noted that in some instances, high abundances of juveniles may trigger very early (i.e., summer) emigration of large numbers of small juveniles from the nursery area, which is likely a response to a lack of forage. Juvenile migration of alewife is about one month earlier than that of blueback herring (Loesch 1969; Kissil 1974).

Although most juveniles emigrate offshore their first year, some overwinter in the Chesapeake (Hildebrand 1963) and Delaware bays (Smith 1971). Marcy (1969) suggests that many juveniles (age-1+) spend their first winter close to the mouth of their natal river because he found in the lower portion of the Connecticut River in early spring. Some juvenile alewife may remain in deep estuarine waters through the winter (Hildebrand and Schroeder 1928). There is some indication that alewife in northern states may remain in inshore waters for one to two years (Walton 1981). Since juvenile river herring cannot survive water temperatures of 3°C or below

(Otto et al. 1976), they likely do not overwinter in coastal systems where temperatures are below 3°C (Kosa and Mather 2001).

Temperature

Juveniles tolerate a broad range of temperatures. Juvenile alewife have been collected in water temperatures between 4-27°C in the upper Chesapeake Bay. Ninety-eight percent of those were collected at 25°C (Dovel 1971). In the Cape Fear River, North Carolina, juveniles have been collected in seasonally in temperatures ranging from 13.5-29°C (Davis and Cheek 1966). The upper lethal temperature for juvenile alewife is about 30°C (McCauley and Binkowski 1982). Young-of-the-year alewife have critical thermal maxima (CTM) that are 3-6°C higher than adults (Otto et al. 1976).

In Lake Michigan, upper incipient lethal limits, the temperature at which 50% of the population survives, for young-of-the-year alewife acclimated at 10, 20, and 25°C was estimated to be slightly less than 26.5°C, 30.3°C, and 32.1°C, respectively (Otto et al. 1976). A separate study found that juveniles exposed to 35°C waters for 24 hours after acclimation to water at 18.9-20.6°C had a 20% survival rate (Dorfman and Westman 1970). When subjected to decreasing temperatures (15.6-2.8°C) over the course of 15 days, juveniles suffered greater than 90% mortality (Colby 1973).

Pardue (1983) suggests that the overall optimal water temperature for juvenile alewife is 15-20°C. Klauda et al. (1991) suggest a broader range of 10-28°C as suitable. Preferred water temperatures in waters with 4-7 ppt salinity were 17-23°C after acclimation at 15-21°C (Meldrim and Gift 1971; PSEGC 1982). In Lake Michigan, juveniles that were acclimated to ambient inshore water temperatures of 15-18°C preferred waters with temperatures of 25.0°C. Juveniles acclimated at 10°C to 20°C had temperature preferences of 25.0°C and 24.0°C, respectively. This preference declined even further to 21.0°C in November and 19.0°C in December (Otto et al. 1976). Juveniles acclimated to 26°C avoided temperatures $\geq 34^\circ\text{C}$ (PSEGC 1984).

Juveniles exposed to 9°C, following acclimation at 20°C in 5.5 ppt salinity suffered no mortality. However, when the temperature was decreased to 7°C for 96 h, they suffered 27-60% mortality (PSEGC 1984). The lower limit at which juvenile river herring are unable to survive is 3°C or less (Otto et al. 1976).

Depth

Jessop (1990) reported that juvenile alewife were completely absent from near-surface water during daylight hours. No other information was available regarding depth preferences or optima for juvenile alewife.

Salinity

Richkus (1974) reported that juveniles that were transferred from freshwater to saline water (32 ppt), and vice versa, experienced zero mortality. Similar to alewife larvae, juvenile alewife in the upper Chesapeake Bay are found in salinities that range from 0-8 ppt, but most (82%) were collected in freshwater (Dovel 1971). Pardue (1983) suggested that salinities less than or equal to 5 ppt were considered optimal for the juvenile life stage.

Water Velocity/Flow

Water discharge is an important factor influencing variability in relative abundance and emigration of juvenile alewife. Extremely high discharges may adversely affect juvenile emigration, and high or fluctuating discharges may lead to a decrease in the relative abundance of adults and juveniles (Kosa and Mather 2001). Laboratory experiments suggest juvenile alewife avoid water velocities greater than 10 cm/s, especially in narrow channels (Gordon et al. 1992). In large rivers, where greater volumes of water can be transported per unit of time without substantial increases in velocity, the effects of discharge may differ (Kosa and Mather 2001).

Kissil (1974) observed juveniles leaving Lake Bride, Connecticut between June and October and noted especially high migration occurring during times of heavy water flow. These results are consistent with Cooper's (1961) observations that 98 % of juveniles left after periods of heavy rainfall. Huber (1978) also noted that juvenile emigration in the Parker River, Massachusetts was triggered by an increase in water flow. Jessop (1994) found that the juvenile abundance index (JAI) of alewife decreased with mean river discharge during summer. Daily instantaneous mortality increased with mean river discharge from July-August from the Mactaquac Dam headpond on the Saint John River, New Brunswick, Canada.

Bottom composition

Olney and Boehlert (1988) found juvenile alewife among submerged aquatic vegetation (SAV) beds of the lower Chesapeake Bay and suggested that SAV likely confers some level of protection from predation.

pH and aluminum

Kosa and Mather (2001) report that of juvenile river herring abundance peaks at a pH of 8.2 in coastal systems in Massachusetts and suggest that pH appears to contribute to variations in juvenile abundance.

Dissolved Oxygen

Jones et al. (1988) determined that the minimum DO concentration for juveniles is 3.6 mg/L. Dorfman and Westman (1970) reported that at concentrations below 2.0 mg/L, juvenile alewife became stressed. At concentrations as low as 0.5 mg/L, juveniles survived for approximately five minutes in oxygen. In the Cape Fear River system, juveniles preferred waters where DO levels ranged from 2.4-10.0 mg/L (Davis and Cheek 1966).

Subadults

Some young-of-the-year overwinter in deep, high salinity areas of the Chesapeake Bay (Hildebrand and Schroeder 1928). Dovel (1971) reported juvenile populations in the upper Chesapeake Bay that did not emigrate until early spring of their second year. Milstein (1981) found that juveniles overwintered in waters approximately 0.6-7.4 km from the shore of New Jersey, at depths of 2.4-19.2 m, in what is considered an offshore estuary (Cameron and Pritchard, 1963). This area is warmer and has a higher salinity than the cooler, lower salinity river-bay estuarine nurseries where they reside in fall. The majority of fish were present during the month of March, when bottom temperatures ranged from 4.4 to 6.5°C and salinity was between 29.0 and 32.0 ppt. Further south, young alewife have been found overwintering off the North Carolina coast from January to March, concentrated at depths of 20.1-36.6 m (Holland and

Yelverton 1973; Street et al. 1973). Other sources have noted that during their first year in saltwater, juveniles tend to remain near the surface (Bigelow and Schroeder 1953). In Lake Michigan, age-1 fish were usually pelagic, except in spring and fall, where they often occurred on the bottom; age-2 fish were typically found on the bottom (Wells 1968).

Information on the life history of young-of-the-year and adult alewife after they emigrate to the sea is sparse (Klauda et al. 1991). But it is generally accepted that juveniles join the adult population at sea within the first year of their lives and follow a north-south seasonal migration along the Atlantic coast, similar to that of American shad (Neves 1981). Sexual maturity is reached at a minimum of age-2 but may vary regionally. In North Carolina, sexual maturity occurs mostly at age-3. In Connecticut, most males achieve maturity at age-4, and most females at age-5 (Jones et al. 1978).

No adults older than age IX have been captured in North Carolina; however age X fish have been recorded in New Brunswick and Nova Scotia.

Despite a lack of conclusive evidence, it is thought that alewife are similar to other anadromous clupeids in that they may undergo seasonal migrations within preferred isotherms (Fay et al. 1983).

While at sea, alewife are more available to bottom trawling gear during the day, leading researchers to conclude that they follow the diel movement of plankton in the water column and are sensitive to light (Neves 1981). Thus, feeding and vertical migration are likely controlled by light intensity patterns within thermal preference zones (Richkus and Winn 1979; Neves 1981).

During spring, alewife from the Mid-Atlantic Bight move inshore and north of 40° latitude to Nantucket Shoals, Georges Bank, coastal Gulf of Maine, and the inner Bay of Fundy for the summer; commercial catch data indicated that they were most frequent on Georges Bank and south of Nantucket Shoals (Neves 1981; Rulifson et al. 1987). Distribution in the fall is similar to the summer, but they are concentrated along the northwest perimeter of the Gulf of Maine. In the fall, they move offshore and southward to the mid-Atlantic coast, with catches reported between latitude 40° and 43° north, where they remain until early spring (Neves 1981). It is unknown to what extent they overwinter in deepwater off the continental shelf, but they have rarely been found more than 130 km from the coast (Jones et al. 1978).

Canadian spring survey results also reveal river herring distributed along the Scotian Gulf, southern Gulf of Maine, and off southwestern Nova Scotia from the Northeast Channel north to the central Bay of Fundy, and to a lesser degree, along the southern edge of Georges Bank and in the canyon between Banquereau and Sable Island Banks (Stone and Jessop 1992). A large component of the overwintering population on the Scotian Shelf moves inshore during spring to spawn in Canadian waters, but may also include the U.S. Gulf of Maine region. Summer aggregations of river herring in the Bay of Fundy/eastern Gulf of Maine may consist of a mixture of stocks from the entire Atlantic coast, as do similar aggregations of American shad (Dadswell et al. 1987). However, based on commercial offshore catches by foreign fleets in the late 1960's, it is believed that coastal river herring stocks do not mingle to the extent that American shad stocks apparently do, at least during the seasons during which foreign harvests were being made

(ASMFC 1985). They typically migrate in large schools of fish of similar size and may even form mixed schools with other herring species (Bigelow and Schroeder 2002).

Temperature

Alewife were caught offshore from Cape Hatteras to Nova Scotia where surface water temperatures ranged from 2-23°C and bottom water temperatures ranged from 3-17°C; catches were most frequent where the average bottom water temperature was between 4-7°C (Neves 1981). Stone and Jessop (1992) reported a temperature range of 7-11°C for alewife in their northern range off Nova Scotia, the Bay of Fundy, and the Gulf of Maine. They also noted that the presence of a cold (<5°C) intermediate water mass over warmer, deeper waters on the Scotian Shelf (Hatchey 1942), where the largest catches of river herring occurred, may have restricted the extent of vertical migration during the spring. Since few captures were made where bottom temperatures were <5°C during the spring, vertical migration may be confined by a water temperature inversion in this area at this time of the year.

Alewife may prefer, and be better adapted to cooler water than blueback herring (Loesch 1987; Klauda et al. 1991). Northern populations may exhibit more tolerance to cold temperatures (Stone and Jessop 1992). Additionally, antifreeze activity was found in blood serum from an alewife off Nova Scotia, but not for those from Virginia (Duman and DeVries 1974).

Depth

Sixteen years of National Marine Fisheries Service catch data conducted from Cape Hatteras to Nova Scotia (Neves 1981) found that fish offshore were caught most frequently in the 56-110 m zone (sampling was conducted as deep as 200 m). Their position in the water column may be influenced by zooplankton concentrations (Neves 1981), which are at depths <100m in the Gulf of Maine (Bigelow 1926). Stone and Jessop (1992) found that alewife off Nova Scotia, the Bay of Fundy, and the Gulf of Maine were found offshore at mid-depths of 101-183 m in the spring, in shallower nearshore waters at 46-82 m in the summer, and in deeper offshore waters at 119-192 m in the fall. They also found differences in depth distribution, with smaller fish (sexually immature) occurring in shallow regions (<93 m) during spring and fall, while larger fish occurred in deeper areas (≥93 m) in all seasons.

In coastal waters (Neves 1981), juvenile alewife are found deeper in the water column than blueback herring, despite their diets being identical in these locations (Davis and Cheek 1967; Burbidge 1974; Watt and Duerden 1974; Weaver 1975). Jansen and Brandt (1980) reported that a nocturnal depth distribution of adult landlocked alewife differed by size-class, with the smaller fish at shallower depths.

Salinity

As noted above, young-of-the-year alewife have been found overwintering offshore of New Jersey (Milstein 1981), where salinities range from 29.0-32.0 ppt. For sub-adults and non-spawning adults that remain in the open ocean, they will reside in full-strength sea water (33.0 ppt). Since it has been suggested that alewives may follow a north-south seasonal migration along the Atlantic coast, similar to that of American shad (Neves 1981), and prespawning adult American shad may detour into estuaries (Neves and Depres 1979), they may be subject to more brackish waters during migration.

Ecological relationships

Adults

Food

Adults do not feed extensively, or typically not at all, during their upstream spawning run (Bigelow and Schroeder 1953; Colby 1973), but spent fish that have reached brackish waters on their downstream migration will feed voraciously, mostly on mysids (Bigelow and Schroeder 2002). Adults may consume their own eggs during the spawning run (Edsall 1964; Carlander 1969), but it is the juveniles that reportedly feed more actively on them (Bigelow and Schroeder 2002).

Competition and Predation

In freshwater, adults may be preyed upon by osprey, green heron, mink (Colby 1973), lake trout (Royce 1943), Atlantic salmon, striped bass (Scott and Scott 1988), and other fish (Loesch et al. 1987). Erkan (2002) notes that predation of alewives has increased dramatically in Rhode Island rivers in recent years, especially by the double-crested cormorant, which often takes advantage of fish staging near the entrance to fishways. Populations of nesting colonies have increased in size and have expanded into areas in which they have previously not been observed. Predation by otters and herons has also increased, but to a lesser extent (Erkan, Rhode Island DEM, 2003, personal communication).

Eggs and larvae

Food

Once larvae begin feeding exogenously, they select relatively small cladocerans and copepods, adding larger species as they grow (Norden 1968; Nigro and Ney 1982). Alewife larvae are highly selective feeders (Norden 1967), usually favoring cladocerans (mainly *Cyclops* sp. and *Limnocalanus* sp.) and copepods over other food types (Norden 1968; Johnson 1983).

Competition and Predation

Alewife eggs may be consumed by yellow perch, white perch, spottail shiner, as well as other alewife (Edsall 1964; Kissil 1969). Alewife larvae are preyed upon by both vertebrate and invertebrate predators (Colby 1973).

Juveniles

Food

Juvenile alewife are opportunistic feeders and usually favor items that are seasonally available (Gregory et al. 1983). For example, in the Hamilton Reservoir, Rhode Island, juveniles fed primarily on dipteran midges in July and cladocerans in August and September (Vigerstad and Colb 1978). Juveniles either select their prey individually or switch to a non-selective filter-feeding mode, which they do more at night (Janssen 1976). Grabe (1996) found that juvenile alewife fed on chironomids, odonates, amphipods, and other amphipods during the day and early evening hours in the Hudson River. Juveniles have also been observed consuming epiphytic fauna (Grabe 1996), especially at night (Weaver 1975).

Juveniles may also feed extensively on benthic organisms, including ostracods, chironomid larvae, and oligochaete worms (Watt and Duerden 1974). Morsell and Norden (1968) found that

juveniles will consume zooplankton until they reach 12 cm TL, and may then switch to increasing amounts of the more benthic amphipod *Pontoporeia* sp.

The number of zooplankton per liter is assumed to be critical for the survival and growth of juvenile alewife. Pardue (1983) suggested that habitats that contained 100 or more individuals of zooplankton per liter are optimal. Walton (1987) found that juvenile abundance in Damariscotta Lake, Maine was controlled by competition for zooplankton, rather than parental stock abundance and recruitment. It has been suggested that clupeids evolved so as to synchronize the larval stage with the optimal phase of annual plankton production cycles (Blaxter and Hunter 1982). Several researchers (Vigerstad and Colb 1978; O'Neill 1980; Yako 1998) hypothesize that a change in food availability may provide a cue for juvenile anadromous herring to begin emigrating seaward, but no causal link has been established.

Invasive species may threaten food sources for alewife. There is strong evidence that juveniles in the Hudson River have experienced a reduced forage base as a result of zebra mussel colonization (Waldman and Limburg 2003).

Competition and Predation

Juvenile alewife are consumed by American eel, white perch, yellow perch, grass pickerel, largemouth bass, pumpkinseed, shiners, walleye and other fishes, as well as turtles, snakes, birds, and mink (Kissil 1969; Colby 1973; Loesch 1987). In estuarine waters of Maine, juvenile bluefish preyed heavily on alewife (Creaser and Perkins 1994). In Massachusetts rivers, juvenile alewife were an energetically valuable and a key food source for largemouth bass during late summer (Yako et al. 2000).

It is often noted throughout the literature, that alewife and blueback herring co-exist in the same geographic regions, yet interspecific competition is often reduced through several mechanisms. For example, juveniles of both species in the Connecticut River consume or select different sizes of prey (Crecco and Blake 1983). Juvenile alewife in the Minas Basin, Nova Scotia favor larger, more benthic prey (particulate-feeding strategy) than do juvenile bluebacks (filter feeding strategy) (Stone 1985; Stone and Daborn 1987). In the Cape Fear River, North Carolina, juvenile alewife consumed more ostracods, insect eggs, and insect parts than did blueback herring (Davis and Cheek 1966).

Alewife also spawn earlier than bluebacks, thereby giving juvenile alewife a relative size advantage over juvenile bluebacks, allowing them a larger selection of prey (Jessop 1990). Difference in juvenile diel feeding activity further reduces competition. One study noted diurnal feeding by juvenile alewife was bimodal, with peak consumption about one to three hours before sunset and a minor peak occurring about two hours after sunrise (Weaver 1975). Another study found that juvenile blueback herring began to feed actively at dawn, increasing throughout the day and maximizing at dusk, then diminishing from dusk until dawn (Burbidge 1974).

Contaminants

A 24 hour LC₅₀ of 2.25 mg/L for total residual chlorine (TRC) was reported for juveniles exposed for 30 minutes at 10°C (Seegert et al. 1977). Thirty-minute LC₅₀ values for TRC were 2.27 mg/L for juveniles exposed at 10°C, and 0.30 mg/L when fish were exposed at 30°C

(Brooks and Seegert 1978; Seegert and Brooks 1978). Juvenile alewife held at 15°C in 7 ppt salinity exhibited an avoidance response to 0.06 mg/L TRC (PSEGC 1978). Juveniles held at 19-24° C in freshwater exhibited an avoidance response at <0.03 mg/L (Bogardus et al. 1978). Juvenile alewife subjected to 0.48 mg/L total chlorine for 2 hours in freshwater (at 22°C) suffered 100% mortality.

Subadults

Food

At sea, alewife feed largely on particulate zooplankton including euphausiids, calanoid copepods, mysids, hyperiid amphipods, chaetognaths, pteropods, decapod larvae, and salps (Edwards and Bowman 1979; Neves 1981; Vinogradov 1984; Stone and Daborn 1987; Bowman et al. 2000). Alewife also consume small fishes, including Atlantic herring, other alewife, eel, sand lance, and cunner (Bigelow and Schroeder 2002). They feed either by selectively preying on individuals or non-selectively filter-feeding with their gill rakers. Feeding mode depends mostly on prey density, prey size, and water visibility, as well as size of the alewife (Janssen 1976, 1978a, 1978b). In Minas Basin, Bay of Fundy, alewife diets shifted from micro-zooplankton in small fish to mysids and amphipods in larger fish. Feeding intensity also decreased with increasing age of fish (Stone 1985).

Alewife generally follow the diel movement of zooplankton, feeding most actively during the day; nighttime predation is usually restricted to larger zooplankton, which are easier to detect (Janssen 1978b; Janssen and Brandt 1980; Stone and Jessop 1993). In Nova Scotia, alewife feeding peaked at midday during the summer and mid-afternoon during the winter. Alewife were also found to have a higher daily ration in the summer than in the winter (Stone and Jessop 1993). Although direct evidence is lacking, catches of alewife in specific areas along Georges Bank, the perimeter of the Gulf of Maine, and south of Nantucket Shoals may be related to zooplankton abundance (Neves 1981).

Competition and Predation

At sea, schooling fish such as bluefish, weakfish, and striped bass prey upon alewife (Bigelow and Schroeder 1953; Ross 1991). Other fish such as dusky shark, spiny dogfish, Atlantic salmon, goosefish, cod, pollock, and silver hake also prey on alewife (Rountree 1999; Bowman et al. 2000). Of these species, spiny dogfish had the greatest quantity of alewife in their stomachs (Rountree 1999).

Abundance and status of stocks

Factors affecting stock size

At low stock levels, Havey (1973) and Walton (1987) demonstrated a weak relationship between spawning stock and juvenile migrant alewife. Jessop (1990) found a stock recruitment relationship for the spawning stock of river herring and year-class abundance at age 3. Despite these results, most studies have been unable to detect a strong relationship between adult and juvenile abundance of clupeids (Crecco and Savoy 1984; Henderson and Brown 1985; Gibson 1994; Jessop et al. 1994). Researchers have suggested that although year-class is driven mostly by environmental factors (see subsequent sections), if the parent stock size falls below a critical level, the size of the spawning stock may become a factor in determining juvenile abundance (Kosa and Mather 2001).

The 2006 Plan Review of the Shad and River Herring Fishery Management Plan (ASMFC, 2006) states:

While the FMP addresses four species including American shad, hickory shad, alewife, and blueback herring, lack of comprehensive and accurate commercial and recreational fishery data for the latter three species make it difficult to ascertain the status of these stocks. A stock assessment for American shad was completed in 1997 and submitted for peer review in early 1998 based on new information and Management Board recommended terms of reference. The 1998 assessment estimated fishing mortality rates for nine shad stocks and general trends in abundance for 13 shad stocks. The next stock assessment update to be externally peer reviewed is scheduled for 2007.