

Chapter 2

AMERICAN SHAD

(Alosa sapidissima)

Section I. American Shad Description of Habitat

American Shad General Habitat Description and Introduction

American shad (*Alosa sapidissima*) are an anadromous, pelagic, highly migratory, schooling species (Colette and Klein-MacPhee 2002). The historical range of American shad extended from Sand Hill River, Labrador, Newfoundland, to Indian River, Florida, in the western Atlantic Ocean (Lee et al. 1980; Morrow 1980). The present range extends from the St. Lawrence River in Canada to St. Johns River, Florida. In addition, American shad were introduced to the Sacramento River in California, and the Columbia, Snake, and Willamette rivers in Oregon in the late 1800s. Since that time, the species' range in the Pacific Ocean has expanded to Cook Inlet, Alaska, and the Kamchatka Peninsula, Russia, south to Todos Santos Bay, Baja California (Lee et al. 1980; Howe 1981). Attempts to introduce the species in the Gulf of Mexico, Mississippi River drainage, Colorado streams, and the Great Lakes were unsuccessful (Walburg and Nichols 1967; Whitehead 1985). Interestingly, a landlocked population exists in a reservoir of the San Joaquin River on the Pacific coast, but no landlocked populations have been reported along the Atlantic coast (Zydlewski and McCormick 1997a). This document will focus on behaviors of Atlantic populations of anadromous American shad.

American shad spend most of their lives in marine waters, with adults migrating into coastal rivers and tributaries to spawn. On average, American shad spend four to five years at sea, and some individuals from the southernmost range may travel over 20,000 km during this time period (Dadswell et al. 1987). Researchers believe that the historical spawning range of American shad included all accessible rivers and tributaries along the Atlantic coast (MacKenzie et al. 1985). Additionally, rivers, bays, and estuaries associated with spawning reaches are used as nursery areas by American shad (ASMFC 1999).

Over the past 170 years, declines in American shad stocks have been attributed to overfishing, pollution, and habitat loss due to dams, upland development, and other factors (Limburg et al. 2003). Turn of the century catch levels of 30,000 metric tons (Walburg and Nichols 1967) have dropped considerably to a low of 600 metric tons in 1996 (ASMFC 1999). Overfishing contributed to the decline in American shad landings in many East Coast rivers; this decline is seen in harvest records from the 1950s to the 1970s (Talbot 1954; Walburg 1955, 1963; Williams and Bruger 1972; Sholar 1976). Unfortunately, due to habitat loss, American shad stocks have continued to decline in many coastal rivers, including the Hudson River, New York. However, some populations, such as in the Connecticut River, the Pawcatuck River, Rhode Island, and the Santee River, South Carolina, have stabilized or are increasing in numbers (ASMFC 1988; Cooke and Leach 2003).

In 1998, an assessment of American shad confirmed that most stocks were not overfished, however, overall stock abundance was historically low. Researchers concluded that, "the current strategy to restore American shad stocks by improving habitat and fish passage, stocking, and inter-basin transfers will yield much stronger dividends than a strategy of stock restoration based solely on reduction of fishing mortality" (Boreman and Friedland 2003).

Although there is an abundance of literature on adult American shad migration trends, migration physiology, and young-of-the-year ecology, research on American shad habitat

requirements is greatly needed. Much of the information contained in this chapter was derived from fisheries surveys, and research studies on American shad and other fish from the sub-family Alosinae (also referred to as “aloses”).

Part A. American Shad Spawning Habitat

Geographical and temporal patterns of migration

The existing Atlantic coast stocks of American shad have a geographic range that currently extends from the St. Johns River, Florida, to the St. Lawrence River, Canada (see above for historic range). Scientists estimate that this species once ascended at least 130 rivers along the Atlantic coast to spawn, but today fewer than 70 systems have runs (Limburg et al. 2003). Most American shad return to their natal rivers and tributaries to spawn (Fredin 1954; Talbot 1954; Hill 1959; Nichols 1966; Carscadden and Leggett 1975), although on average, 3% stray to non-natal river systems (Mansueti and Kolb 1953; Williams and Daborn 1984; Melvin et al. 1985). In fact, Hendricks et al. (2002) demonstrated that hatchery-reared American shad homed to a specific tributary within the Delaware River system several years after stocking, and also preferred the side of the tributary influenced by the plume of their natal river.

The degree of homing by American shad may depend on the nature of the drainage system. If so, mixing of stocks and consequent straying would more likely occur in large and diversified estuarine systems, such as the Chesapeake Bay, while more precise homing could be expected in systems that have a single large river, such as the Hudson River (Richkus and DiNardo 1984).

Timing	Month	Location	Citation
Begin	December	St. Johns River, FL	Williams and Bruger 1972
Peak	January	St. Johns River, FL	Leggett 1976
Begin	mid-January	GA and SC	Walburg and Nichols 1967; Leggett and Whitney 1972
Begin	mid-February	NC and VA	Walburg and Nichols 1967; Leggett and Whitney 1972
Peak	March	NC and VA	Walburg and Nichols 1967; Leggett and Whitney 1972
Peak	April	Potomac River	Walburg and Nichols 1967; Leggett and Whitney 1972
Peak	early May	Delaware River	Walburg and Nichols 1967; Leggett and Whitney 1972
Range	March-June	Hudson & Connecticut rivers	Walburg and Nichols 1967;

Timing	Month	Location	Citation
			Leggett and Whitney 1972
Range	June-August	Androscoggin River, Maine	Brown and Sleeper 2004
End	July-August	Canadian rivers	MacKenzie et al. 1985; Scott and Scott 1988

Table 2-1. American shad temporal spawning trends along the Atlantic coast of North America

American shad spring spawning migrations begin in the south and move gradually north as the season progresses and water temperatures increase (Table 2-1; Walburg 1960). Spawning runs typically last 2-3 months, but may vary depending on weather conditions (Limburg et al. 2003). The diel timing of migration may not vary greatly from region to region. In the James River, Virginia, spawning adults ascended mostly between 0900 and 1600 hours (Weaver et al. 2003). Arnold (2000) reported similar results in the Lehigh River, Pennsylvania, where American shad passed primarily between 0900 and 1400 hours.

American shad show varied preferences for migration distance upstream depending on the river system. There does not seem to be a minimum distance from brackish waters at which spawning occurs (Leim 1924; Massmann 1952), but upstream and mid-river segments appear to be favored (Massmann 1952; Bilkovic et al. 2002). It is not unusual for American shad to travel 25 to 100 miles upstream to spawn; some populations historically migrated over 300 miles upstream (Stevenson 1899; Walburg and Nichols 1967). In the 18th and 19th centuries, American shad runs were reported as far inland as 451 miles along the Great Pee Dee and Yadkin rivers in North Carolina (Smith 1907) and over 500 miles in the Susquehanna River (Stevenson 1899).

Male American shad arrive at riverine spawning grounds before females (Leim 1924). Females release their eggs close to the water surface to be fertilized by one or several males. Diel patterns of egg release depend upon water turbidity and light intensity. In clear open water, eggs are released and fertilized after sunset (Leim 1924; Whitney 1961), with peak spawning around midnight (Massmann 1952; Miller et al. 1971; 1975). In turbid waters (or on overcast days; Miller et al. 1982), eggs are released and fertilized during the day (Chittenden 1976a). For example, in the Pamunkey River, Virginia, spawning has been observed throughout the day, which may be due to relatively turbid waters damping light intensity (Massmann 1952). These findings support the hypothesis of Miller et al. (1982) that daily spawning is regulated by light intensity.

Another interesting aspect of American shad migration is the regional difference in spawning periodicity. American shad that spawn north of Cape Hatteras are iteroparous (repeat spawners), while almost all American shad spawning south of Cape Hatteras are semelparous (die after one spawning season). This may be due to the fact that south of North Carolina the physiological limits of American shad are stretched during long oceanic migrations; higher southern water temperatures may also have an effect (Leggett 1969). Moreover, Leggett and Carscadden (1978) suggest that southern stocks produce more eggs per unit of body weight than northern populations to compensate for not spawning repeatedly.

Location	% of repeat spawners	Citations
Neuse River, NC	3	Leggett and Carscadden 1978
York River, VA	24	Leggett and Carscadden 1978
Connecticut River	63	Leggett and Carscadden 1978
Saint John River, Canada	73	Colette and Klein-MacPhee 2002

Table 2-2. Percentage of repeat spawners for American shad along the Atlantic coast of North America

Studies show the percentage of iteroparous adult American shad increases northward along the Atlantic coast (Table 2-2). However, the percentage of repeat spawners may fluctuate over time within the same river due to pollution, fishing pressure, land-use change, or other factors (Limburg et al. 2003). Furthermore, almost 59% of American shad in the St. Lawrence River did not spawn every year following the onset of maturation, skipping one or more seasons (Provost 1987). Additionally, some fish spawn up to five times before they die (Carscadden and Leggett 1975).

Members of this species exhibit asynchronous ovarian development and batch spawning. In addition, American shad spawn repeatedly as they move upriver (Glebe and Leggett 1981a), which some researchers think may be a function of their high fecundity (Colette and Klein-MacPhee 2002). Estimates of egg production for the York River, Virginia, are 20,000 to 70,000 eggs per kg somatic weight spawned every four days (Olney et al. 2001).

However, some researchers believe that fecundity in American shad may be indeterminate, and that previous annual or lifetime fecundity estimates may not be accurate (Olney et al. 2001). Researchers examining batch fecundity of semelparous American shad in the St. Johns River, Florida, and iteroparous individuals in the York and Connecticut rivers in Virginia and Connecticut, respectively, found no statistically significant differences in batch fecundity among the populations. Until spawning frequency, duration, and batch size throughout the spawning season are known, lifetime fecundity for various stocks cannot be determined and previous methods to determine fecundity throughout the coastal range will be inadequate (Olney and McBride 2003). Nevertheless, the habitat productivity potential estimate used in Maine is 2.3 shad per 100 square yards of water surface area (Brown and Sleeper 2004).

It is interesting to note that Olney et al. (2001) found that approximately 70 percent of post-spawning American shad females leaving the York River had only partially spent ovaries, which suggests that the maximum reproduction level of most females in the river system each year is not achieved. Researchers hypothesize that these females utilize partially spent ovaries by reabsorbing unspawned, yoked oocytes to supplement somatic energy sources as they return to the ocean. These fish likely have a greater potential for surviving multiple spawning events than individuals that are fully spent and have no such energy reserves (Olney et al. 2001). Even with energy reserves, spent adults are usually very emaciated and return to sea soon after spawning (Chittenden 1976b), sometimes feeding before reaching saltwater (Atkins 1887).

Layzer (1974) found that American shad selected discrete spawning sites in the Connecticut River and remained there for most of the season despite the large area available for spawning. Sometimes spawners forego areas with highly suitable habitats that are further downstream, suggesting that there are other variables that influence habitat choice (Bilkovic 2000). Ross et al. (1993) suggest that choice of spawning habitat may be unrelated to physical variables, but rather may reflect a selective pressure such as fewer egg predators in selected habitats.

Spawning and the saltwater interface

Adult American shad may spend two to three days in estuarine waters prior to upriver migration (Dodson et al. 1972; Leggett 1976). Leim (1924) observed spawning by American shad in brackish waters, but other researchers believe that spawning occurs only in freshwater (Massman 1952; MacKenzie et al. 1985). Spawning typically occurs in tidal and non-tidal freshwater regions of rivers and tributaries (Chittenden 1976a). While in the Hudson River, American shad ascend beyond the saltwater interface and go as far upstream as they can travel (Schmidt et al. 1988), eggs are typically deposited slightly above the range of tide in the Shubenacadie River, Canada (Leim 1924). In many rivers, adult spawners historically migrated beyond tidal freshwater areas, but they can no longer reach these areas due to dam blockages (Mansueti and Kolb 1953).

Interestingly, American shad tolerate a wide range of salinities during early developmental stages (Chittenden 1969) and adult years (Dodson et al. 1972), even though their eggs are normally deposited in freshwater (Weiss-Glanz 1986). Additionally, Limburg and Ross (1995) concluded that a preference for upriver spawning sites may be genetically fixed, but its advantage or significance was not related to salt intolerance of eggs and larvae.

Leggett and O'Boyle (1976) conducted an experiment to see if American shad require a period of acclimation to freshwater. The researchers determined that fish transferred from seawater to freshwater, with a 6°C temperature increase over a 2.5-hour period, experienced physiologic stress and a 54% mortality rate five hours later. Furthermore, adults did not survive transfers from saltwater (27 ppt) to freshwater with a 14°C temperature increase. Mortality rates varied from 0 to 40% for transfers from waters with salinities ranging from 13 to 25 ppt to freshwater and temperature increases up to 6°C. However, adult American shad may be better adapted to transfers from freshwater to saltwater. They tolerated transfers from freshwater to 24 ppt and temperature increases of up to 9°C (Leggett and O'Boyle 1976).

Spawning substrate associations

Spawning often occurs far upstream or in river channels dominated by flats of sand, silt, muck, gravel, or boulders (Mansueti and Kolb 1953; Walburg 1960; Walburg and Nichols 1967; Leggett 1976; Jones et al. 1978). The importance of substrate type to American shad spawning behavior is still debated. Bilkovic et al. (2002) concluded that substrate type was not predictive of spawning and nursery habitat in two Virginia rivers that were surveyed. Similarly, Krauthamer and Richkus (1987) do not consider substrate type to be an important factor at the spawning site since eggs are released into the water column.

However, eggs are semi-buoyant and may eventually sink to the bottom. Thus, areas predominated by sand and gravel may enhance survival because there is sufficient water velocity to remove particles and prevent suffocation if eggs settle to the bottom (Walburg and Nichols 1967). Furthermore, Layzer (1974) noted that survival rates of shad eggs were highest where gravel and rubble substrates were present. Likewise, Hightower and Sparks (2003) hypothesize that larger substrates are important for American shad reproduction, based on observations of spawning in the Roanoke River, North Carolina. Other researchers have also observed American shad spawning primarily over sandy bottoms free of mud and silt (Williams and Bruger 1972).

Spawning depth associations

Depth is not considered a critical habitat parameter for American shad in spawning habitat (Weiss-Glanz et al. 1986), although Witherell and Kynard (1990) observed adult American shad in the lower half of the water column during the upstream migration. Once they reach preferred spawning areas, adults have been found at river depths ranging from 0.45 to 10 m (Mansueti and Kolb 1953; Walburg and Nichols 1967). However, depths less than 4 m are generally considered ideal (Bilkovic 2000).

Ross et al. (1993) observed that the greatest level of spawning occurred where the water depth was less than 1 m in the Delaware River. Other studies suggest that adults select river areas that are less than 10 ft deep (3.3 m) or have broad flats (Mansueti and Kolb 1953; Leggett 1976; Kuzmeskus 1977). Adults may reside in slow, deep pools during the day, and in the evening move to shallower water where riffle-pools may be present to spawn (Chittenden 1969; Layzer 1974). During the spawning event, females and males can be found close to the surface for the release and fertilization of eggs (Medcof 1957).

Stier and Crance (1985) suggest that for all life history stages, including spawning, egg incubation, larvae, and juveniles, the optimum depth range is between 1.5 and 6.1 m. Depths less than 0.46 m (for spawning adults, larvae, and juveniles) and 0.15 m (for egg incubation), and depths greater than 15.24 (for all life history stages) are considered unsuitable (Stier and Crance 1985). However, recent studies on optimal habitat for spawning events have found that these areas may be defined more narrowly than indicated by studies focused primarily on egg collection. For example, sites deeper than 2 m in the Neuse River, North Carolina, were used less extensively than expected for spawning based on depth availability within the spawning grounds and over the entire river (Beasley and Hightower 2000; Bowman and Hightower 2001).

Spawning water temperature

Activity	Temperature (°C)	Location	Citation
Migration	5 - 23	Throughout range	Walburg and Nichols 1967
Migration (peak)	8.6 - 19.9 (16 - 19)	North Carolina	Leggett and Whitney 1972
Peak migration	16.5 - 21.5	Southern rivers	Leggett 1976
Spawning	8 - 26	Throughout range	Walburg and Nichols 1967;

Activity	Temperature (°C)	Location	Citation
			Stier and Crance 1985
Optimum spawning	14 - 20	Throughout range	Stier and Crance 1985
Optimum spawning	14 – 24.5	Throughout range	Ross et al. 1993

Table 2-3. American shad migration and spawning temperatures for the Atlantic coast

Spawning for American shad may occur across a broad range of temperatures (Table 2-3). Water temperature is the primary factor that triggers spawning, but photoperiod, water flow and velocity, and turbidity also exert some influence (Leggett and Whitney 1972). Based on the temperature range reported by Leggett and Whitney (1972), Parker (1990) suggests that pre-spawning adults tolerate higher temperatures as they undergo physiological changes and become sexually ripe.

Most spawning occurs in waters with temperatures between 12-21°C (Walburg and Nichols 1967; Leggett and Whitney 1972). Generally, water temperatures below 12°C cause total or partial cessation of spawning (Leim 1924). However, Jones et al. (1978) reported American shad moving into natal rivers when water temperatures were 4° C or lower. Additionally, Marcy (1976) found that peak spawning temperatures varied from year to year. For example, peak spawning temperatures in the Connecticut River were 22°C and 14.8°C in 1968 and 1969, respectively (Marcy 1976).

Other factors, such as the pace of gonadal and egg development may also be related to water temperature. Mansueti and Kolb (1953) found that shad ovaries developed more slowly at 12.8°C than at 20 to 25°C. In theory, eggs may develop slowly at first then mature rapidly with higher temperatures (DBC 1980).

Spawning dissolved oxygen associations

American shad require well-oxygenated waters in all habitats throughout their life history (MacKenzie et al. 1985). Jessop (1975) found that migrating adults require minimum dissolved oxygen (DO) levels between 4 and 5 mg/L in the headwaters of the Saint John River, New Brunswick. Dissolved oxygen levels below 3.5 mg/L have been shown to have sub-lethal effects on American shad (Chittenden 1973a); levels less than 3.0 mg/L completely inhibit upstream migration in the Delaware River (Miller et al. 1982). Additionally, dissolved oxygen levels less than 2.0 mg/L cause a high incidence of mortality (Tagatz 1961; Chittenden 1969), and below 0.6 mg/L cause 100% mortality (Chittenden 1969). Although minimum daily dissolved oxygen concentrations of 2.5 to 3.0 mg/L should be sufficient to allow American shad to migrate through polluted areas, Chittenden (1973a) recommends that suitable spawning areas have a minimum of 4.0 mg/L. Miller et al. (1982) propose even higher minimum concentrations, suggesting that anything below 5.0 mg/L should be considered potentially hazardous to adult and juvenile American shad.

Spawning water velocity/flow

Water velocity (m/sec) is an important parameter for determining American shad spawning habitat (Stier and Crance 1985). Walburg (1960) found that spawning and egg incubation most often occurred where water velocity was 0.3 to 0.9 m/s. In support, Stier and Crance (1985) suggested that this was the optimum range for spawning areas. Ross et al. (1993) observed that American shad spawning activity was highest in areas where water velocity ranged from 0.0 to 0.7 m/s; this suggested that there was no lower suitability limit during this stage and that the upper limit should be modified. However, Bilkovic (2000) determined that the optimum water velocity range for eggs and larvae was 0.3 to 0.7 m/s, and hypothesized that some minimum velocity was required. A minimum velocity is needed in order to prevent siltation and ensure that conditions conducive to spawning and egg incubation occur (Williams and Bruger 1972; Bilkovic 2000).

Appropriate water velocity at the entrance of a fishway is also important for American shad migrating upstream to spawning areas. Researchers found that water velocities of 0.6 to 0.9 m/s at the entrance to a pool-and-weir fishway was needed to attract American shad to the structure (Walburg and Nichols 1967). The Conowingo Dam fish lift on the Susquehanna River uses entrance velocities of 2 to 3 m/s to attract American shad to the lift (R. St. Pierre, U.S. Fish and Wildlife Service, personal communication). At other sites, such as the Holyoke Dam in Massachusetts, American shad have trouble locating fishway entrances among turbulent discharges and avoid the area; thus, too much water velocity and/or turbulence may actually deter this species (Barry and Kynard 1986).

Ross et al. (1993) noted that habitat selection among spawning adult American shad favored relatively shallow (0.5 to 1.5 m) mid-river runs with moderate to high current velocity (0.3-0.7 m/s). To a lesser degree, adults also were located in channels (deeper, greater current velocities, little if any SAV) and SAV shallows (inshore, high densities of SAV, low current velocities). The researchers found adults seemed to avoid pools (wide river segment, deep, low current velocities) and riffle pools (immediately downstream of riffles, deep water, variable current velocity and direction) that contained both deep and slow water. This avoidance of pools and riffle pools may be explained by the fact that the preferred run habitat contained both swift and shallow water characteristics. Channels and SAV shallows may be either swift or shallow; these characteristics may lead to higher survivability of newly spawned eggs compared to deep pool habitat (Ross et al. 1993). Similarly, Bilkovic et al. (2002) found the greatest level of spawning activity in runs.

Water velocity may also contribute in some way to weight loss and mortality during the annual spawning migration, especially for male American shad. Males typically migrate upstream earlier in the season when water velocities are greater, thus expending more energy than females (Glebe and Leggett 1973; DBC 1980).

In addition, areas with high water flows provide a cue for spawning American shad (Orth and White 1993). In 1985, a redirection canal and hydroelectric dam constructed between the Cooper River and Santee River, South Carolina, increased the average flow of the Santee River from 63 m³/s to 295 m³/s. (Cooke and Leach 2003). The increased river flow and access to spawning grounds through the fish passage facility have contributed to increases in American shad populations. Although the importance of instream flow requirements has been previously recognized with regard to spawning habitat requirements or recruitment potential (Crecco and

Savoy 1984; ASMFC 1985; Crecco et al. 1986; Ross et al. 1993; Moser and Ross 1994), Cooke and Leach (2003) suggested that river flow might be an important consideration for restoring alosine habitat.

Water flow may have additional importance for American shad populations in the future. Although Summers and Rose (1987) did not detect direct relationships between stock size and river flow or water temperature, they found that spawning stock size, river flow rate, and temperature were important predictors of future American shad population sizes. These researchers suggested that future studies incorporate a combination of environmental variables, rather than a single environmental variable, to determine what stimuli affect stock size.

Spawning suspended solid associations

Adults appear to be quite tolerant of turbid water conditions. In the Shubenacadie River, Nova Scotia, suspended solid concentrations as high as 1000 mg/L did not deter migrating adults (Leim 1924). Furthermore, Auld and Schubel (1978) found that suspended solid concentrations of 1000 mg/L did not significantly affect hatching success of eggs.

Spawning feeding behavior

Early research suggested that adult American shad did not feed in freshwater during upstream migration or after spawning (Hatton 1940; Moss 1946; Nichols 1959) because the most available food source in the freshwater community was too small to be retained by adult gillrakers (Walburg and Nichols 1967). Atkinson (1951) suggested that American shad stopped feeding due to the physical separation from suitable food sources rather than a behavioral or physiological reduction in feeding.

More recent studies of feeding habits of American shad in the York River, Virginia, found that individuals did, in fact, feed as they migrated from the oceanic to coastal waters (Chittenden 1969, 1976b; Walters and Olney 2003). Walters and Olney (2003) compared stomach fullness of migrating American shad with individuals in the ocean and estuary, and found that as American shad moved from oceanic waters to coastal and estuarine waters their diet composition changed from oceanic copepods, such as *Calanus finmarchicus*, to other copepods, such as *C. typicus* and *Acartia* spp. (Walters and Olney 2003). The estuarine mysid shrimp *Neomysis americana* became an important component, replacing euphausiids in spent and partially spent adults. Minor amounts of other crustaceans were also found in spent American shad stomachs including cumaceans, sevenspine bay shrimp (*Crangon septemspinosa*), and gammarid amphipods, as well as woody and green plant debris that had little or no nutritional value (Walters and Olney 2003). This finding suggested that these fish fed if there was suitable prey available (Atkinson 1951).

The ability to feed during migration and after spawning may be an important factor in decreasing post-spawning mortality of American shad (Walters and Olney 2003). Migration requires significant energetic expenditures and causes weight loss (Glebe and Leggett 1981a; 1981b); the resumption of feeding likely represents a return to natural feeding patterns, which allows the fish to begin regaining lost energy reserves (Walter and Olney 2003). Finally, the ability to survive spawning has been correlated with the degree of energy lost (Glebe and Leggett 1981b; Bernatchez and Dodson 1987). Therefore, American shad that feed actively before and

after spawning may have a higher likelihood of repeat spawning. Additionally, individuals whose spawning grounds are in closer proximity to estuarine food sources (and do not expend as much energy as those that have to travel farther), and emigrating fish that have partially spent ovaries that can be reabsorbed for energy (Olney et al. 2001), may have a higher frequency of repeat spawning and lower energy expenditures (Walter and Olney 2003).

Spawning competition and predation

Early studies found that seals and humans preyed upon adult American shad (Scott and Crossman 1973), but the species appeared to have few other predators (Scott and Scott 1988). Erkan (2002) found that predation of alosines has increased in Rhode Island rivers, noting that the double-crested cormorant often takes advantage of American shad staging near fishway entrances. Predation by otters and herons has also increased, but to a lesser extent (D. Erkan, Rhode Island Division of Fish and Wildlife, personal communication). A recent study strongly supports the hypothesis that striped bass predation on adult American shad in the Connecticut River has resulted in a dramatic and unexpected decline in American shad abundance since 1992 (Savoy and Crecco 2004). Researchers further suggest that striped bass prey primarily on spawning adults because their predator avoidance capability may be compromised at that time, due to a strong drive to spawn during upstream migration. Rates of predation on ages 0 and 1 alosines was also much lower (Savoy and Crecco 2004).

In south Atlantic coastal rivers where the percentage of repeat spawning is low or non-existent, adult American shad that die after spawning may contribute significant nutrient input from the marine system into freshwater interior rivers (ASMFC 1999). Garman (1992) hypothesized that before recent declines in abundance, the annual input of marine-derived biomass of post-spawning alosines was an important seasonal source of energy and nutrients for the non-tidal James River.

Part B. American Shad Egg and Larval Habitat

Geographical and temporal movement patterns

American shad eggs and larvae have been found at, or downstream of, spawning locations. Upstream areas typically have extensive woody debris where important larval and juvenile American shad prey items reside, and spawning there may ensure that eggs develop within favorable habitats (Bilkovic et al. 2002).

Once American shad eggs are released into the water column, they are initially semi-buoyant or demersal. Survival of eggs is dependent on several factors, including current velocity, dissolved oxygen, water temperature, suspended sediments, pollution, and predation (Krauthamer and Richkus 1987; Bailey and Houde 1989). Whitworth and Bennett (1970) monitored American shad eggs after they were broadcast and found that they traveled a distance of 5 to 35 m downstream before they sank or became lodged on the bottom. Other researchers reported similar observations (Barker 1965; Carlson 1968; Chittenden 1969).

Laboratory experiments suggested that sinking rates for American shad eggs were around 0.5 to 0.7 m/min (1.6 to 2.4 ft/min), with newly spawned eggs sinking at a quicker rate, although hydrodynamic and tidal effects were not accounted for in the experiments (Massmann 1952; Chittenden 1969). Other factors, such as amount of woody debris, influence how far eggs travel and may prevent eggs from settling far from the spawning site (Bilkovic 2000). Once eggs sink to the bottom, they are swept under rocks and boulders and are kept in place by eddy currents. In addition, eggs may become dislodged and swept downstream to nearby pools (DBC 1980).

American shad yolk-sac larvae may not use inshore habitat as extensively as post-yolk-sac larvae (Limburg 1996). One early study (Mitchell 1925, cited by Crecco et al. 1983) found that yolk-sac larvae were near the bottom and swam to shore as the yolk-sac reabsorbed. Metzger et al. (1992) also found yolk-sac larvae mostly in offshore areas along the bottom, while post yolk-sac larvae were more concentrated in quiet areas near shorelines (Cave 1978; Metzger et al. 1992). Yolk-sac larvae are typically found deeper in the water column than post-larvae, due to their semi-buoyant nature and aversion to light. Post-larvae, in contrast, are more abundant in surface waters, especially downstream of spawning sites (Marcy 1976).

Yolk-sac larvae exhaust their food supply within 4 to 7 days of hatching (Walburg and Nichols 1967), usually when they are approximately 10 to 12 mm total length (TL) (Marcy 1972). Survival is affected by water temperature, water flow, food production and density, and predation (State of Maryland 1985; Bailey and Houde 1989; Limburg 1996). Larvae may drift passively into brackish water shortly after hatching occurs, or can remain in freshwater for the remainder of the summer (State of Maine 1982); often they aggregate in eddies and backwaters (Stier and Crance 1985). Ross et al. (1993) reported that American shad larvae frequent riffle pools where water depth is moderate and velocity and direction vary. Alternatively, larvae in the Mattaponi and Pamunkey rivers, Virginia, were dispersed from the upper through the downriver areas. Unlike the presence of eggs, which can be predicted in most cases using physical habitat and shoreline/land use ratings, distinct habitat associations could not be discerned for larval distributions. This may be due to the fact that larvae were carried further downstream than eggs, dispersing them into more variable habitats (Bilkovic et al. 2002).

Eggs, larvae, and the saltwater interface

Although American shad eggs are generally deposited in freshwater, it is unknown whether they hatch in freshwater, brackish water, or in both (Weiss-Glanz 1986). Early attempts to acclimate larval shad to seawater resulted in high mortality rates (Milner 1876). Leim (1924) purported that successful development of embryos and larvae occurs under low salinity conditions. In the Shubenacadie River, Canada, eggs and larvae were most often observed in areas with a salinity of 0 ppt (range 0 to 7.6 ppt). Additionally, while larvae may tolerate salinities as high as 15 ppt, these conditions often result in death. Leim (1924) also found that temperature may influence salinity sensitivities, with lower temperatures (i.e., 12°C) resulting in more abnormalities at 15 and 22.5 ppt than higher temperatures (i.e., 17°C).

In another study, Limburg and Ross (1995) found that salinities of 10 to 20‰ were favorable for post-yolk sac American shad larvae, and concluded that estuarine salinities neither depressed growth rates nor elevated mortality rates of larval American shad compared with freshwater conditions. These researchers concluded that other ecological factors may play a greater role in influencing spawning site selection by American shad than the physiological effects of salinity.

Egg and larval substrate associations

Areas with sand or gravel substrates may be better for egg and larval survival because they allow sufficient water velocity to remove silt or sand that can suffocate eggs (Walburg and Nichols 1967). Additionally, survival rates of American shad eggs have been found to be highest among gravel and rubble substrates (Layzer 1974). According to Krauthamer and Richkus (1987), bottom composition is not a critical factor in the selection of spawning locations for American shad. After American shad eggs are fertilized, they either sink to the bottom where they become lodged under rocks and boulders, or they are swept by currents to nearby pools (Chittenden 1969). Bilkovic (2000) concluded that substrate type was not a good predictor of spawning and nursery habitat in rivers.

Egg and larval depth associations

Eggs are slightly heavier than water, but may be buoyed by prevailing currents and tides. Most eggs settle at, or near, the bottom of the river during the water-hardening stage (Leim 1924; Jones et al. 1978). In the Connecticut River, American shad eggs are distributed almost uniformly between the surface and the bottom of the river. Larvae are more than twice as abundant in surface waters, and are even more abundant in the water column as they move downstream (Marcy 1976).

Walburg and Nichols (1967) found 49% of American shad eggs in waters shallower than 3.3 m (10 ft), 30% in water 3.7 to 6.7 m (11 to 20 ft), and 21% in water 7 to 10 m (21 to 30 ft). Similarly, Massman (1952) reported that five times more eggs per hour were collected at depths ranging from 1.5 to 6.1 m (4.9 to 20.0 ft), than in deeper waters of the Pamunkey and Mattaponi rivers. In the same river systems, Bilkovic et al. (2002) found eggs at depths of 0.9 to 5.0 m, and larvae at 1 to 10 m.

Egg and larval water temperature

Days	Temperature	Reference
15.5	12° C	Leim 1924
17	12° C	Ryder 1887
7	17° C	Leim 1924
3	24° C	MacKenzie et al. 1985
2	27° C	Rice 1878

Table 2-4. American shad egg development time at various temperatures

Rate of development of shad eggs is correlated with water temperature (Table 2-4; Mansueti and Kolb 1953). According to Limburg (1996), within the temperature range of 11 to 27°C, the time it takes for eggs to develop can be expressed as:

$\log_e(\text{EDT}) = 8.9 - 2.484 \times \log_e(T)$, where EDT is egg development time in days and T is temperature in degrees Celsius

Estimates of near-surface water temperatures suitable for development and survival of American shad eggs range from 8 to 30°C (Walburg and Nichols 1967; Bradford et al. 1968; Stier and Crance 1985; Ross et al. 1993). Leim (1924) suggests that optimal conditions for American shad egg development occur in the dark at 17°C and 7.5 ppt salinity.

Characterization	Temperature (°C)	Citation
Suitable	10 - 27	Bradford et al. 1968
Suitable	13.0 - 26.2	Ross et al. 1993
Suitable	10 - 30	Stier and Crance 1985
Optimal	15.5 - 26.5	Leim 1924
Optimal	15 - 25	Stier and Crance 1985

Table 2-5. American shad larval temperature tolerance ranges

Water temperatures above 27°C can cause abnormalities or a total cessation of larval American shad development (Bradford et al. 1968). Few larvae have been found living in temperatures above 28°C (Table 2-5; Marcy 1971; 1973), and no viable larvae develop from eggs incubated above 29°C (Bradford et al. 1968). Ross et al. (1993) recommend that further sampling be conducted for post-larval stages at temperatures greater than or equal to 27°C to confirm upper optimal temperature preferences. In this study, the researchers found no reduction in density of larvae at the upper thermal limit (26 to 27°C) in areas sampled along the Delaware River (Ross et al. 1993).

Laboratory experiments have shown that American shad eggs can tolerate extreme temperature changes as long as the exposure is of relatively short duration (Klauda et al. 1991). Temperature increases after acclimation at various temperatures produced variable results; however, some eggs were found to withstand temperatures of 30.5°C for 30 minutes and 35.2°C for 5 minutes (Schubel and Koo 1976). Furthermore, sensitivity to temperature change decreases as eggs mature (Koo et al. 1976).

Shoubridge (1977) analyzed temperature regimes in several coastal rivers throughout the range of American shad, and found that as latitude increases: 1) the duration of the temperature optima for egg and larval development decreases, and 2) the variability of the temperature regime increases. Based on Shoubridge's work, Leggett and Carscadden (1978) suggest that variation in American shad egg and larval survival, year-class strength, and recruitment also increases with latitude.

Crecco and Savoy (1984) found that low water temperatures (with high rainfall and river flow) were significantly correlated with low American shad juvenile abundance during the month of June in the Connecticut River, while high water temperatures (with low river flow and rainfall) were significantly correlated with high juvenile abundance. In addition, depressed water temperatures can retard the onset and duration of American shad spawning (Leggett and Whitney 1972), larval growth rate (Murai et al. 1979), and the production of riverine zooplankton (Chandler 1937; Beach 1960).

Egg and larval dissolved oxygen associations

Miller et al. (1982) concluded that the minimum dissolved oxygen level for both eggs and larvae of American shad is approximately 5 mg/L. This is the value that Bilkovic (2000) assigned for optimum conditions for survival, growth, and development of American shad.

Although specific tolerance or optima data for eggs and larvae is limited, there are studies that note the presence or absence of eggs and larvae under certain dissolved oxygen conditions (Bilkovic et al. 2002). In the Neuse River, North Carolina, American shad eggs were collected in waters with dissolved oxygen levels ranging from 6 to 10 mg/L (Hawkins 1979). Marcy (1976) did not find any American shad eggs in waters of the Connecticut River where dissolved oxygen concentrations were less than 5 mg/L. Bilkovic (2000) found variations in dissolved oxygen concentrations for eggs (10.5 mg/L), yolk-sac larvae (9.0 mg/L), and post-larvae (8.1 mg/L) in the Mattaponi and Pamunkey rivers.

Marcy (1976) determined that the dissolved oxygen LC₅₀ values (i.e., concentration that causes 50% mortality) for American shad eggs in the Connecticut River were between 2.0 and 2.5 mg/L. In the Columbia River, the LC₅₀ was close to 3.5 mg/L for eggs and at least 4.0 mg/L for a high percentage of hatched eggs and healthy larvae; less than 1.0 mg/L dissolved oxygen resulted in total mortality (Bradford et al. 1968). Klauda et al. (1991) concluded that a good hatch with a high percentage of normal larvae required dissolved oxygen levels during egg incubation of at least 4.0 mg/L, based on observations by both Maurice et al. (1987) and Chittenden (1973a). Finally, it is worth noting that cleanup of the Delaware River has had a measurably positive effect on increasing dissolved oxygen concentrations in that system (Maurice et al. 1987).

Egg and larval pH and aluminum associations

Level	pH	Citation
Tolerance- egg	5.5 - 9.5	Bradford et al. 1968
Tolerance- egg	6.0 – 7.5	Klauda 1994
Tolerance- egg	6.5 - 8.5	Bilkovic et al. 2002
LD ₅₀ - egg	5.5	Klauda 1994
Mortality- egg	<5.2	Bradford et al. 1968
Tolerance- larvae	6.7 – 9.9	Klauda 1994
Tolerance- larvae	6.5 - 9.3	Bilkovic et al. 2002
Optimal- larvae	>7.0	Leach and Houde 1999
Tolerance- both	6.0 - 9.0	Leim 1924

Table 2-6. American shad egg and larval environmental pH tolerance ranges

A number of researchers have examined the effects of pH on American shad eggs and larvae (Table 2-6). Klauda (1994) hypothesized that even infrequent and temporary episodes of critical or lethal pH and aluminum exposures in spawning and nursery areas could contribute to significant reductions in egg or larval survival and slow stock recovery. Similarly, Leach and Houde (1999) noted that sudden drops in pH levels, such as those associated with rainfall, could cause sudden mortalities for American shad larvae.

In a laboratory study, Klauda (1994) subjected eggs, yolk-sac larvae, and post-larvae to an array of acid and aluminum conditions; larvae appeared to be more sensitive to acid and aluminum pulses than eggs. When eggs were subjected to aluminum pulses, critical conditions were met at pH 5.7 (with 50 or 200 µg/L Al) and pH 6.5 (with 100 µg/L Al) for 96-hour treatments. The least severe treatment that resulted in critical conditions for 1 to 3 day old yolk-sac larvae was a 24 h exposure to pH 6.1 with 92 µg/L Al. The least severe treatment that resulted in a lethal condition for yolk-sac larvae was a 24 h exposure to pH 5.5 with 214 µg/L Al. Furthermore, post-larvae (6 to 16 days old) were found to be more sensitive to acid and aluminum pulses than both eggs and yolk-sac larvae. Critical conditions occurred at pH 5.2 (with 46 µg/L Al) and pH 6.2 (with 54 or 79 µg/L Al) for 8 hours, and lethal conditions occurred at pH 5.2 (with 63 µg/L Al) for 16 hours (Klauda 1994).

Egg and larval water velocity/flow

Several studies report water velocity preferences for larval American shad, with 0 to 1.0 m/s the most commonly reported range (Walburg 1960; Walburg and Nichols 1967; Stier and Crance 1985; Bilkovic et al. 2002). Kuzmeskus (1977) found freshly spawned eggs in areas with water velocity rates between 0.095 and 1.32 m/s. Williams and Bruger (1972) noted that increased siltation may result if water velocities are less than 0.3 m/s, causing increased egg mortality from suffocation and bacterial infection.

Freshwater discharge can influence both eggs and larvae of American shad. Increased river flow can carry eggs from favorable nursery habitat to unfavorable areas that reduce their chance for survival. Lower flows may result in favorable hydrodynamic, thermal, and feeding conditions (Crecco and Savoy 1987a; Limburg 1996). Larval and juvenile American shad may select eddies and backwater areas where water flow is reduced (Crecco and Savoy 1987b). Limburg (1996) found that high spring river discharges coupled with low temperatures and low food availability contributed to high larval mortality in the Hudson River. Larvae that hatched after May, when the highest discharges occurred, had a higher survival rate (Limburg 1996). Furthermore, year-class strength and river flow showed a significant negative correlation in studies conducted on the Connecticut River (Marcy 1976). Larval survival rates have also been negatively correlated with increased river flow in June, but positively correlated with June river temperatures (Savoy and Crecco 1988).

Although hydrographic turbulence may affect larval American shad survival rates, the precise mechanisms of this influence are uncertain because daily river flow and rainfall levels are nonlinear, time-dependent processes that may act singularly or in combination with other factors, such as temperature and turbidity (Sharp 1980). Decreased temperatures can affect larval growth rates (Murai et al. 1979) and riverine zooplankton production that American shad may require for nourishment (Chandler 1937; Beach 1960). Turbulence can also cause turbidity, which may compromise the ability of larval fish to see their prey (Theilacker and Dorsey 1980). Increased turbidity may also affect the food web. Turbidity can cause reduced photosynthesis by phytoplankton, which in turn may lead to elimination of the cladocerans and copepods that American shad feed upon (Chandler 1937; Hynes 1970; Crecco and Blake 1983; Johnson and Dropkin 1995).

Egg and larval suspended solid associations

American shad eggs are less vulnerable to the effects of suspended solids than larvae. For example, Auld and Schubel (1978) found that suspended solid concentrations of up to 1000 mg/L did not significantly reduce hatching success, while larvae exposed to concentrations of 100 mg/L, or greater, had significantly reduced survival rates.

Egg and larval feeding behavior

Predation and starvation are considered the primary causes of mortality among larval fish of many marine species (May 1974; Hunter 1981). Newly hatched American shad larvae must begin feeding within 5 days, or they will die from malnutrition (Wiggins et al. 1984). Furthermore, older larvae have significantly reduced survival rates if they are deprived of food for as little as 2 days (Johnson and Dropkin 1995). Researchers have also found that larvae fed at intermediate prey densities of 500 L⁻¹ survived as well as those fed at high prey densities, and significantly higher than starved larvae, which indicates that some minimal level of feeding in riverine reaches can increase survival (Johnson and Dropkin 1995).

Crecco et al. (1983) suggest that larval American shad survival rates are related to spring and summer zooplankton densities. Additionally, despite larval American shad abundance being highest during May, Limburg (1996) determined that year-class was established by cohorts

hatched after June 1 due to more favorable conditions, including warmer temperatures, lower flow rates, and higher zooplankton densities.

Once the yolk-sac is absorbed, American shad larvae consume zooplankton, copepods, immature insects, and adult aquatic and terrestrial insects (Leim 1924; Mitchell 1925; Maxfield 1953; Crecco and Blake 1983; Facey and Van Den Avyle 1986). Several researchers have noted varying levels of selectivity for copepods and cladocerans (Crecco and Blake 1983; Johnson and Dropkin 1995), but zooplankton and chironomids generally comprise the bulk of larval diets (Maxfield 1953; Levesque and Reed 1972). Larval American shad feeding occurs most actively in late afternoon or early evening, usually peaking between 1200 h and 2000 h (Johnson and Dropkin 1995); feeding is least intensive near dawn (Massman 1963; Grabe 1996). Larval American shad are opportunistic feeders, shifting their diet depending on availability, river location, and their size (Leim 1924; Maxfield 1953; Walburg 1956; Levesque and Reed 1972; Marcy 1976).

Researchers have also attempted to determine if the patchiness of planktonic prey has any effect on cohort survival. Letcher and Rice (1997) found that increasing levels of patchiness enhances survival when productivity or average prey density is low, but will reduce cohort survival when productivity is high. Thus, except when average prey densities of plankton are particularly high, prey patchiness may be a requirement for survival of fish larvae (Letcher and Rice 1997).

Egg and larval competition and predation

American shad eggs and larvae are preyed upon primarily by American eels (*Anguilla rostrata*) and striped bass (*Morone saxatilis*) (Mansueti and Kolb 1953; Walburg and Nichols 1967; Facey et al. 1986), although they may be preyed upon by any fish that is large enough to consume them (McPhee 2002). According to Johnson and Ringler (1998), American shad larvae that were stocked in the Susquehanna River, Pennsylvania, experienced the lowest percentage mortality at releases of 400,000 to 700,00 larvae. A high rate of larval mortality at releases up to 400,000 may have been due to depensatory mechanisms, and releases above 700,000 may have resulted in increased predator aggregation at the site. Although some individual predators consumed up to 900 American shad larvae, mortality of larvae at the stocking site was usually less than 2% (an insignificant source of mortality) (Johnson and Ringler 1998).

Eggs, larvae, and contaminants

Bradford et al. (1968) found that the lethal dose (LD₅₀) of sulfates for American shad eggs is >1000 mg/L at 15.5° C. The LD₅₀ of iron for eggs is greater than 40 mg/L between pH 5.5 and 7.2 (Bradford et al. 1968). American shad eggs that are exposed to zinc and lead concentrations of 0.03 and 0.01 mg/L experience high mortality rates within 36 hours (Meade 1976). In addition, when water hardness is low (i.e., 12 mg/L), the toxicity of the zinc and lead are intensified (Klauda et al. 1991).

Part C. American Shad Juvenile Riverine/Estuarine Habitat

Geographical and temporal movement patterns

American shad larvae are transformed into juveniles 3 to 5 weeks after hatching at around 28 mm total length (TL) (Jones et al. 1978; Crecco and Blake 1983; Klauda et al. 1991; McCormick et al. 1996); they disperse at, or downstream of, the spawning grounds, where they spend their first summer in the lower portion of the same river. While most young American shad use freshwater nursery reaches (McCormick et al. 1996), it is thought that their early ability to hypo-osmoregulate allows them to utilize brackish nursery areas during years of high juvenile abundance (Crecco et al. 1983). Juveniles are typically 7 to 15 cm in length before they leave the river and enter the ocean (Talbot and Sykes 1958). For example, in the Hudson River, juvenile American shad and blueback herring were found inshore during the day, while alewives predominated inshore at night (McFadden et al. 1978; Dey and Baumann 1978). Additionally, American shad juveniles use the headpond of the Annapolis River, Nova Scotia, as a nursery area, which has surface water salinities of 25 to 30‰; they were observed remaining in the offshore region of the estuary for almost a month before the correct cues triggered emigration (Stokesbury and Dadswell 1989). Farther south, O'Donnell (2000) found that juvenile American shad in the Connecticut River began their seaward emigration at approximately 80 days post-hatch.

In addition, juvenile American shad may demonstrate temporal and latitudinal migration trends. It seems that juveniles in northern rivers emigrate seaward first, and those from southern rivers emigrate progressively later in the year (Leggett 1977a). For example, downstream emigration peaks at night (i.e., at 1800-2300 hours) (O'Leary and Kynard 1986; Stokesbury and Dadswell 1989) in September and October in the Connecticut River, late October in the Hudson River (Schmidt et al. 1988), and late October through late November in the Upper Delaware River and Chesapeake Bay (Krauthamer and Richkus 1987) and the Cape Fear River, North Carolina (Fischer 1980). Interestingly, some researchers (Chittenden 1969; Limburg 1996; O'Donnell 2000) found evidence that juvenile emigration was already underway by mid-summer, indicating that movement may be triggered by cues other than declining fall temperatures.

The combination of factors that trigger juvenile American shad emigration is uncertain, but some researchers suggest that decreased water temperatures, reduced water flow, or a combination of both during autumn appear to be key factors (Sykes and Lehman 1957; Walburg and Nichols 1967; Moss 1970). In the Susquehanna River, an increase in river flow from October through November may actually help push juveniles downstream (R. St. Pierre, U.S. Fish and Wildlife Service, personal communication). Miller et al. (1973) suggest that water temperature is more important than all other factors, because it directly affects the juvenile American shad. The lower lethal temperature limit that triggers the final movement of juveniles from fresh water is approximately 4 to 6°C (Chittenden 1969; Marcy 1976). In addition, Zydlewski and McCormick (1997a) observed changes in osmoregulatory physiology in migrating juvenile American shad, and concluded that these changes were part of a suite of physiological alterations that occur at the time of migration. While these changes are strongly affected by temperature, researchers suggest that other environmental and/or ontogenetic factors may have an influence on timing of migration (Zydlewski and McCormick 1997a).

Another migration theory deals with the age and growth of juvenile American shad. Limburg (1996) suggested that at the population level, temperature may provide the stimulus for fish to emigrate, or it may be a gradual process that is cued by size of fish, with early cohorts leaving first. Several researchers (Chittenden 1969; Miller et al. 1973; Limburg 1996; O'Donnell 2000) have observed younger, smaller young-of-the-year American shad in upstream reaches, while older and larger individuals within the same age cohorts are found downstream earlier in the season. This apparent behavior has lead researchers to hypothesize that as American shad grow and age, they move downstream (Chittenden 1969; Miller et al. 1973; Limburg 1996; O'Donnell 2000). Similarly, both Chittenden (1969) and Marcy (1976) suggest that factors associated with size appear to initiate the earlier stages of seaward emigration.

In contrast, Stokesbury and Dadswell (1989) suggest that size at emigration may not be the important factor that triggers migration, but that environmental stress may reach a point where seaward movement is necessary regardless of a critical size. O'Leary and Kynard (1986) and Stokesbury and Dadswell (1989) found that American shad movement typically occurred during quarter to new moon periods when water temperatures dropped below 19°C and 12°C, respectively. In these cases, decreasing water temperatures and the new moon phase, which provided dark nights, were considered to be more important in providing cues for emigration than increased river flow.

Habitat Type	Location	Citation
sound	Long Island	Savoy 1993
offshore estuary	New Jersey	Milstein 1981; Cameron and Pritchard 1963
brackish/ freshwater	Potomac River	Hammer 1942
estuary	Neuse River, NC	Holland and Yelverton 1973

Table 2-7. Overwintering habitats for juvenile American shad along the Atlantic coast

Following downstream migration in late fall, juvenile American shad may spend their first year near the mouths of streams, in estuaries, or in other nearshore waters (Hildebrand 1963; Colette and Klein-MacPhee 2002), or they may move to deeper, higher salinity areas, such as in portions of the lower Chesapeake Bay (Table 2-7; Hildebrand and Schroeder 1928). In their southern range, some juveniles may stay in the river for up to one full year (Williams and Bruger 1972). In South Carolina, juvenile American shad were found predominantly in deeper, channel habitats of estuarine systems, during fall and winter. Small crustaceans preyed upon by American shad are generally abundant near the bottom in these areas (McCord 2003).

Juveniles and the saltwater interface

Early studies of juvenile American shad describe a variety of responses to changes in salinity. When accompanied by temperature changes, juveniles generally adapt to abrupt transfers from freshwater to saltwater, but high mortality results when transferred from saltwater to freshwater (Tagatz 1961). For example, Tagatz (1961) observed 60% mortality for juveniles in isothermal transfers (21°C) from freshwater to 30 ppt saltwater; however, no individuals

survived transfers from freshwater (21.1°C) to 33 ppt saltwater (7.2 to 12.8°C). Freshwater transfers to 15 ppt in association with a temperature decrease less than 4°C also resulted in high mortalities (30 to 50%). Conversely, at temperature increases greater than 14°C, all juvenile American shad survived abrupt transfers from saltwater (15 ppt and 33 ppt) to freshwater (Tagatz 1961).

In another study, Chittenden (1973b) observed 0% mortality in isothermal transfers (17°C) from freshwater or 5 ppt to 32 ppt seawater. Additionally, juveniles transferred from 30 ppt seawater to freshwater suffered 100% mortality, but no mortalities resulted when they were transferred from 5 ppt to freshwater. In general, American shad are considered to be capable of surviving a wide range of salinities at early life stages, especially if salinity changes are gradual (Chittenden 1969).

Experiments conducted on American shad and other anadromous fish (Rounsefell and Everhart 1953; Houston 1957; Tagatz 1961; Zydlewski and McCormick 1997a, 1997b) have demonstrated that most fish undergo physiological changes before emigrating to saltwater. This ability to adapt to changes in salinity occurs at the onset of metamorphosis for American shad, between 26 and 45 days post-hatch. Zydlewski and McCormick (1997b) noted that the ability to osmoregulate in full-strength seawater is an important factor that limits American shad early life history stages to freshwater and low-salinity estuaries. The researchers suggested that a decrease and subsequent loss of hyper-osmoregulatory ability may serve as a proximate cue for juveniles to begin their downstream migration (Zydlewski and McCormick 1997b).

Juvenile substrate associations

Although juvenile American shad are often most abundant where boulder, cobble, gravel, and sand are present (Walburg and Nichols 1967; Odom 1997), substrate type is not considered to be a critical factor in nursery areas (Krauthamer and Richkus 1987). Ross et al. (1997) found no overall effect of habitat type on juvenile American shad relative abundance in the upper Delaware River, indicating that juveniles use a wide variety of habitat types to their advantage in many nursery areas. These researchers suggest that in contrast to earlier life stages and spawning adults, pre-migratory juveniles may be habitat generalists; however, a positive relationship was found between abundance of juvenile American shad and percent of SAV cover in SAV habitats only. In addition, Odom (1997) found that juvenile American shad favored riffle/run habitat in the James River, especially areas with extensive beds of water stargrass (*Heteranthera dubia*). These areas provided flow-boundary feeding stations where juveniles could feed on drifting macroinvertebrates while reducing their energy costs (Odom 1997).

Estuarine productivity is linked to freshwater detrital nutrient input to the estuary (Biggs and Flemer 1972; Hobbie et al. 1973; Saila 1973; Day et al. 1975) and detritus production in the salt marsh (Teal 1962; Odum and Heald 1973; Reimhold et al. 1973; Stevenson et al. 1975). Based on the assumption that the amount of submerged and emergent vegetation will be a qualitative estimate of the estuary's secondary productivity, and therefore, food availability (zooplankton) to juvenile American shad, Stier and Crance (1985) suggest that estuarine habitat with 50% or more vegetation coverage is optimal.

It is important to note that, although no link has been made between the presence of SAV and abundance of alosines, there seems to be a general agreement that there is a correlation

between water quality and alosine abundance (B. Sadzinski, Maryland Department of Natural Resources, personal communication). Abundance of SAV is often used as an indirect measure of water quality, with factors such as available light (Livingston et al. 1998), salinity, temperature, water depth, tidal range, grazers, suitable sediment quality, sediment nutrients, wave action, current velocity, and chemical contaminants controlling the distribution of underwater grasses (Koch 2001). Maryland has made it a priority to increase the amount of SAV within the Chesapeake Bay watershed in order to improve water quality. According to B. Sadzinski (Maryland Department of Natural Resources, personal communication), if SAV in a given area increases, this can be used as an indicator of improved water quality, which in turn, will likely benefit alosine species.

Juvenile depth associations

Juveniles have been observed at depths ranging from 0.9 to 4.9 m in the Connecticut River (Marcy 1976); however, abundance is related to the distance upstream and not to depth (MacKenzie et al. 1985). In the Connecticut River, juveniles were caught primarily at the bottom during the day (87%) and all were caught at the surface at night (Marcy 1976). Chittenden (1969) observed juveniles in the Delaware River most often in deeper, non-tidal pools away from the shoreline during daylight hours; after sunset juveniles scattered and were found at all depths (Miller et al. 1973).

Although data was sparse for depth optima for juveniles, Stier and Crance (1985) developed a suitability index based on input provided by research scientists. They suggest that for all life history stages, including juveniles, the optimum range for river depth is between 1.5 and 6.1 m. Depths less than 0.46 m and greater than 15.24 m are unsuitable habitat according to the model.

Juvenile water temperature

Characterization	Temperature (°C)	Location	Citation
Optimal range	15.5 - 23.9	N/A	Crance 1985
Optimal range	10 - 25	N/A	Stier and Crance 1985
Range	10 - 30	Connecticut River	Marcy et al. 1972
Critical maximum	34 - 35	Neuse River, NC	Horton and Bridges 1973
Maximum tolerance	35	N/A	Stier and Crance 1985
Minimum preference	8	N/A	MacKenzie et al. 1985
Minimum tolerance	3	N/A	Stier and Crance 1985
Minimum tolerance	31.6	N/A	Ecological Analysts Inc. 1978
Begin migration	19	Connecticut River	Leggett 1976; O'Leary and Kynard 1986

Characterization	Temperature (°C)	Location	Citation
Begin migration	23 - 26	Connecticut River	Marcy 1976
Begin migration	18.3	Connecticut River	Watson 1970
Peak migration	16	Connecticut River	Leggett and Whitney 1972; O'Leary and Kynard 1986
Peak migration	15.1	North Carolina	Neves and Depres 1979; Boreman 1981
End migration	8.3	Delaware River	Chittenden and Westman 1967
End migration	8.3	Chesapeake Bay	Chesapeake Bay Program 1988

Table 2-8. Temperature tolerances, preferences, and cues for juvenile American shad

Juvenile American shad demonstrate some variability in temperature tolerances and preferences among river systems (Table 2-8). Leim (1924) found that juveniles captured in the Shubenacadie River, Canada, were usually found where temperatures tended to be the highest compared to other regions of the river. Additionally, temperature appears to have a significant impact on growth of juvenile American shad. Limburg (1996) found that juveniles in the laboratory had higher initial growth rates at 28.5°C than individuals reared at lower temperatures. O'Donnell (2000) concluded that it may be advantageous for eggs to hatch later in the year because temperatures are higher and growth rates are faster; however, competition and predation rates are also higher.

Juvenile American shad do not appear to be as tolerant to temperature changes as eggs of the same species. In fact, juveniles are sensitive to water temperature changes, and actively avoid temperature extremes, if possible. Laboratory tests suggest that juveniles can tolerate temperature increases between 1° and 4°C above ambient temperature, but beyond that they will avoid changes if given a choice (Moss 1970). For example, juveniles acclimated to 25° C suffered a 100% mortality rate when the temperature was decreased to 15°C. There was also a 100% mortality rate for juveniles acclimated to 15°C and then subjected to temperatures less than 5°C. Finally, no survival was reported for juveniles acclimated to 5°C and then exposed to 1°C (PSE&G 1982).

Juvenile dissolved oxygen associations

Minimum dissolved oxygen values have a more adverse effect upon fish than average dissolved oxygen values; therefore, minimum dissolved oxygen criteria have been recommended. Dissolved oxygen concentrations less than 5.0 mg/L are considered sub-lethal to juvenile American shad (Miller et al. 1982). As with spawning areas, Bilkovic (2000) assigned a value of greater than 5.0 mg/L dissolved oxygen as optimal for nursery areas.

Seemingly healthy juvenile American shad have been collected in the Hudson River, New York, where dissolved oxygen concentrations were 4 to 5 mg/L (Burdick 1954). Similarly, in headponds above hydroelectric dams on the St. John River, New Brunswick, dissolved oxygen must be at least 4 to 5 mg/L for migrating juveniles to pass through (Jessop 1975). In the

Delaware River, dissolved oxygen concentrations less than 3.0 mg/L blocked juvenile migration, and concentrations below 2.0 mg/L were lethal. Emigrating juveniles have historically arrived at the upper tidal section of the Delaware River by mid-October, but do not continue further seaward movement until November or December, when the pollution/low oxygen conditions dissipate (Miller et al. 1982).

Under laboratory conditions, juvenile American shad did not lose equilibrium until dissolved oxygen decreased to 2.5 to 3.5 mg/L (Chittenden 1969, 1973a). Juveniles have been reported to survive brief exposure to dissolved oxygen concentrations of as little as 0.5 mg/L, but survived only if greater than 3 mg/L was available immediately thereafter (Dorfman and Westman 1970).

Juvenile pH associations

Areas that are poorly buffered (low alkalinity) and subject to episodic or chronic acidification may provide less suitable nursery habitat than areas that have higher alkalinities and are less subject to episodic or chronic acidification (Klauda et al. 1991). Once juvenile American shad move downstream to brackish areas with a higher buffering capacity, they may be less impacted by changes in pH (Klauda 1989).

Juvenile water velocity/flow

Ideal water velocity rates are thought to range between 0.06 to 0.75 m/s for the juvenile non-migratory stage of American shad (Klauda et al. 1991). The rate of water velocity is also critical for fish migrating downstream that pass over spillways (MacKenzie et al. 1985). Furthermore, it has been suggested that water flow may serve to orient emigrating juveniles in the downstream direction. Studies conducted on American shad in the St. Johns River, Florida, led researchers to speculate that the lack of water flow as a result of low water levels could result in the inability of juveniles to find their way downstream (Williams and Bruger 1972).

Juvenile suspended solid associations

Ross et al. (1997) suggest that optimal turbidity values for premigratory American shad juveniles in tributaries is between 0.75 and 2.2 NTU. While preliminary, these results could be cautiously applied to other river systems, but consideration should be given to the range and diversity of habitat types in the river system under study before applying the models.

Juvenile feeding behavior

Juvenile American shad begin feeding in freshwater and continue into the estuarine environment. They favor zooplankton over phytoplankton (Maxfield 1953; Walburg 1956), and in general, have a wider selection of prey taxa than larvae due to their increased size and the estuaries' higher diversity. Long, closely-spaced gill rakers enable juveniles to effectively filter plankton from the water column during respiratory movements (Leim 1924). Juvenile American shad are opportunistic feeders, whose freshwater diet includes copepods, crustacean zooplankton, cladocerans, aquatic insect larvae, and adult aquatic and terrestrial insects (Leim

1924; Maxfield 1953; Massmann 1963; Levesque and Reed 1972; Marcy 1976). After juveniles leave coastal rivers and estuaries for nearshore waters, they may prey on some fish, such as smelt, sand lance, silver hake, bay anchovy, striped anchovy, and mosquitofish (Leidy 1868; Bowman et al. 2000).

Although juveniles obtain most of their food from the water column (ASMFC 1999), many of the crustaceans that juveniles prey upon are benthic (Krauthamer and Richkus 1987). Leim (1924) speculated that although American shad obtain a minor amount of food near the bottom of the water column, they do not pick it off the bottom, but rather capture items as they are carried up into the water column a short distance by tidal currents (including mollusks).

Walburg (1956) found that juvenile American shad fed primarily on suitable organisms that were readily available. In contrast, Ross et al. (1997) found that juveniles in SAV habitat fed principally on chironomids, while those feeding in tributaries consumed terrestrial insects almost exclusively, despite the fact that insects were less available than other food sources. Researchers did not attribute the differences to developmental limitations, but concluded that there were true feeding differences between habitats. Other studies have noted different selection of organisms along the same river, but at different locations, such as above a dam (Levesque and Reed 1972) or downstream of a dam (Domermuth and Reed 1980).

Feeding of juvenile American shad may also differ along a stream gradient. In waters of Virginia, Massman (1963) found that juvenile American shad upstream consume more food than juveniles that remain downstream near their spawning grounds. The upstream sections of the river have a higher shoreline to open water ratio that may provide a more abundant source of terrestrial insects, a favored prey item (Massman 1963; Levesque and Reed 1972), while the downstream sections contain more autochthonously-derived prey. In contrast, the lower reach of the Hudson River appears to be more productive (as a function of primary productivity and respiration rates) than upper and middle reaches (Sirois and Fredrick 1978; Howarth et al. 1992). This greater productivity may lead to higher fish production in the lower estuary, as well as a higher relative condition of downriver juvenile American shad earlier in the season, compared to upriver and midriver fish (Limburg 1994).

Juvenile American shad also demonstrate diel feeding patterns. Johnson and Dropkin (1995) found that juveniles increase feeding intensity as the day progresses, achieving a maximum feeding rate at 2000 h. Similarly, juveniles in the Mattaponi and Pamunkey rivers in Virginia, feed during the day with stomachs reaching maximum fullness by early evening (Massman 1963).

In addition, at least one non-native species has proven to have an impact on young-of-the-year American shad. In the Hudson River, there is strong evidence that zebra mussel colonization has reduced the planktonic forage base of the species (Waldman and Limburg 2003).

Juvenile competition and predation

Juveniles in freshwater may be preyed upon by American eel, bluefish, weakfish, striped bass, birds, and aquatic mammals (Mansueti and Kolb 1953; Walburg and Nichols 1967; Facey et al. 1986).

With regard to inter-species competition, differences among alosine species in terms of distribution, diel activity patterns, and feeding habits are evident in many systems, and are likely mechanisms that may reduce competition between juveniles of the different species (Schmidt et al. 1988). For example, several researchers have noted that larger American shad (Chittenden 1969; Marcy 1976; Schmidt et al. 1988) and alewife (Loesch et al. 1982; Schmidt et al. 1988) move downstream first, which helps to segregate size classes of the two species.

Secondly, there is the idea of diel, inshore-offshore segregation. Both American shad and blueback herring juveniles occur in shallow nearshore waters during the day. However, competition for prey between American shad and blueback herring is often reduced by: 1) more opportunistic feeding by American shad, 2) differential selection for cladoceran prey, and 3) higher utilization of copepods by blueback herring (Domermuth and Reed 1980). American shad feed most often in the upper water column, the air-water interface (Loesch et al. 1982), and even leap from the water (Massman 1963), feeding on *Chironomidae* larvae, *Formicidae*, and *Cladocera*; they are highly selective for terrestrial insects (Davis and Cheek 1966; Levesque and Reed 1972). Juvenile bluebacks are more planktivorous, feeding on copepods, larval dipterans, and *Cladocera* (Hirschfield et al. 1966), but not the same cladoceran families that alewife feed upon (Domermuth and Reed 1980).

Juveniles and contaminants

Tagatz (1961) found that the 48 h lethal concentrations (LC_{50}) for juvenile American shad range from 2,417 to 91,167 mg/L for gasoline, No. 2 diesel fuel, and bunker oil. The effects of gasoline and diesel fuel are exacerbated when the dissolved oxygen concentration is simultaneously reduced. Gasoline concentrations of 68 mg/L at 21 to 23°C resulted in a lethal time (LT_{50}) of 50 minutes for juveniles when dissolved oxygen was reduced to 2.6 to 3.2 mg/L. Additionally, juveniles that were exposed to 84 mg/L of diesel fuel at 21 to 23°C with dissolved oxygen between 1.9 and 3.1 mg/L experienced an LT_{50} of 270 minutes (Tagatz 1961).

Part D. American Shad Late Stage Juvenile and Adult Marine Habitat

Geographical and temporal patterns at sea

American shad typically live 5 to 7 years (Leggett 1969) and remain in the ocean for 2 to 6 years before becoming sexually mature, at which point they return to their natal rivers to spawn (Talbot and Sykes 1958; Walburg and Nichols 1967). Both sexes begin to mature at 2 years, with males maturing on average in 4.3 years and females maturing on average in 4.6 years. Fish north of Cape Hatteras are iteroparous and will return to rivers to spawn when temperatures are suitable (Leggett 1969).

Results from 50 years of tagging indicate that discrete, widely separated aggregations of juvenile and adult American shad occur at sea (Talbot and Sykes 1958; Leggett 1977a, 1977b; Dadswell et al. 1987; Melvin et al. 1992). These aggregations are a heterogeneous mixture of individuals from many river systems (Dadswell et al. 1987); it is unknown if American shad from all river systems along the east coast intermingle throughout the entire year (Neves and Depres 1979). Populations that return to rivers to spawn are a relatively homogeneous group (Dadswell et al. 1987), and fish from all river systems can be found entering coastal waters as far south as North Carolina in the winter and spring (Neves and Depres 1979).

Dadswell et al. (1987) presented the following seasonal movement timeline for American shad:

- 1) *January & February* –found offshore from Florida to Nova Scotia; spawning inshore from Florida to South Carolina;
- 2) *March & April* –moving onshore and northward from the Mid-Atlantic Bight to Nova Scotia; spawning from North Carolina to the Bay of Fundy;
- 3) *Late June* – concentrated in the inner Bay of Fundy, inner Gulf of St. Lawrence, Gulf of Maine, and off Newfoundland and Labrador; spawning fish are still upstream from Delaware River to St. Lawrence River;
- 4) *Autumn* –American shad leaving the St. Lawrence estuary are captured across the southern Gulf of St. Lawrence, while fish leaving the Bay of Fundy are found from Maine to Long Island; some individuals already migrated as far south as Georgia and Florida.

Through an analysis of tag returns, occurrence records, and trawl survey data, Dadswell et al. (1987) found that there are three primary offshore areas where aggregations of American shad overwinter: 1) off the Scotian Shelf/Bay of Fundy, 2) in the Mid-Atlantic Bight, and 3) off the Florida coast. It appears that the majority of American shad that overwinter along the Scotian Shelf spawn in rivers in Canada and New England (Vladykov 1936; Melvin et al. 1985). Fish aggregations that overwinter off the mid-Atlantic coast (from Maryland to North Carolina) are comprised of populations that spawn in rivers from Georgia to Quebec (Talbot and Sykes 1958; Miller et al. 1982; Dadswell et al. 1987).

The regional composition of American shad aggregations overwintering off the Florida coast is unknown. Leggett (1977a) proposed the following estimates for timing and origin of southern migrations for overwintering off Florida based on migration rates and an average departure date of October 1 from the Gulf of Maine/Bay of Fundy region: Rhode Island/Long

Island coast in mid-to-late October, off Delaware Bay in early November, and off the coast of North Carolina, Georgia, and Florida in early December. Additionally, early migration studies of American shad found that during mild winters, small aggregations sometimes enter the sounds of North Carolina during November and December, but disappear if the weather becomes cold (Talbot and Sykes 1958).

Most American shad populations that overwinter off the mid-Atlantic coast (between 36° to 40°N) migrate shoreward in the winter and early spring. Pre-spawning adults homing to rivers in the south Atlantic migrate shoreward north of Cape Hatteras, North Carolina, then head south along the coast to their natal rivers. The proximity of the Gulf Stream to North Carolina provides a narrow migration corridor at Cape Hatteras through which individuals may maintain travel in the preferred temperature range of 3 to 15°C. Although pre-spawning adults are not required to follow a coastal route to North Atlantic rivers because temperatures in the Mid-Atlantic Bight are generally well within a tolerable range in the spring, tag returns indicate that most individuals likely enter coastal waters in the lower mid-Atlantic region, and then migrate north along the coast (Dadswell et al. 1987).

South of Cape Cod, pre-spawning American shad migrate close to shore (Leggett and Whitney 1972), but north of that point the migration corridor is less clear (Dadswell et al. 1987). Pre-spawning adults may detour into estuaries during their coastal migration; however, the timing and duration of the stay is unknown (Neves and Depres 1979). Although poorly documented, immature American shad (age 1+) may also enter estuaries and accompany adults to the spawning grounds, more than 150 km upstream (Limburg 1995, 1998). Additionally, non-spawning adults have been recorded in brackish estuaries (Hildebrand 1963; Gabriel et al. 1976).

Dadswell et al. (1987) found three primary offshore summer aggregations of American shad: 1) Bay of Fundy/Gulf of Maine, 2) St. Lawrence estuary, and 3) off the coast of Newfoundland and Labrador. Neves and Depres (1979) also found distinct summer aggregations on Georges Bank and south of Nantucket Shoals. Furthermore, American shad from all river systems, including those from south Atlantic rivers, have been collected at the Gulf of Maine feeding grounds during the summer (Neves and Depres 1979). While individuals from north Atlantic rivers are most abundant in the Bay of Fundy in the early summer, the appearance of American shad from the southern range does not peak until mid-summer (Melvin 1984; Dadswell et al. 1987). These migrating groups are a mixture of juveniles, immature sub-adults, and spent and resting adults that originate from rivers along the entire East Coast (Dadswell et al. 1983). Since there are very few repeat spawners in the southern range, the majority (76%) of American shad that migrate to the Bay of Fundy from areas south of Cape Lookout, North Carolina, are juveniles (Melvin et al. 1992).

American shad enter the Bay of Fundy in early summer and move throughout the inner Bay of Fundy for four months in a counterclockwise direction with the residual current (Dadswell et al. 1987). As water temperatures decline in the fall, American shad begin moving through the Gulf of Maine, and continue to their offshore wintering grounds. This species has been captured in late fall and winter 80 to 95 km offshore of eastern Nova Scotia (Vladykov 1936), 65 to 80 km off the coast of Maine, 40 to 145 km off southern New England, and 175 km from the nearest land of southern Georges Bank (Colette and Klein-MacPhee 2002; Dadswell et al. 1987).

Salinity associations at sea

During their residence in the open ocean, American shad sub-adults and adults will live in seawater that is approximately 33 ppt. During coastal migration periods, pre-spawning adults may detour into estuaries where water is more brackish, but the timing and duration of the stay is unknown (Neves and Depres 1979).

Depth associations at sea

While it is known that adult American shad move offshore to deeper waters during the fall and early winter, information regarding preferred depths is lacking. American shad have been found throughout a broad depth range in the ocean, from surface waters to depths of 340 m (Walburg and Nichols 1967; Facey and Van Den Avyle 1986). Alternatively, catch data analyses showed that this species has been caught at depths ranging from surface waters to 220 m (Walburg and Nichols 1967), but are most commonly found at intermediate depths of 50 to 100 m (Neves and Depres 1979). Seasonal migrations are thought to occur mainly in surface waters (Neves and Depres 1979).

The summer and autumn months are a time of active feeding for American shad, and analyzing stomach contents has served as a means to infer distribution in the water column. Studies by Neves and Depres (1979) suggested that American shad follow diel movements of zooplankton, staying near the bottom during the day and dispersing in the water column at night. Other researchers (Dadswell et al. 1983) have suggested that light intensity may control depth selection by American shad. For example, American shad swim much higher in the water column in the turbid waters of Cumberland Basin, Bay of Fundy, than they do in clear coastal waters, where they are found in deeper water. Both areas are within the same surface light intensity range (Dadswell et al. 1983).

Temperature associations at sea

Early studies by Leggett and Whitney (1972) found that American shad move along the coast via a “migrational corridor” where water temperatures are between 13 and 18°C. Neves and Depres (1979) later modified the near-bottom temperature range from 3 to 15°C, with a preferred range of 7 to 13°C. These researchers also hypothesized that seasonal movements are broadly controlled by climate, and that American shad follow paths along migration corridors or oceanic paths of “preferred” isotherms. Melvin et al. (1985) and Dadswell et al. (1987) revised this theory with data indicating movement of American shad across thermal barriers. It was determined that American shad remain for extended periods in temperatures outside their “preferred” range; this species migrates rapidly between regions regardless of currents and temperatures (Melvin et al. 1985; Dadswell et al. 1987). For example, Dadswell et al. (1987) documented non-reproductive American shad migrating from wintering grounds in the Mid-Atlantic Bight through the Gulf of Maine in May-June, where a constant sub-surface temperature of 6°C prevails, to reach the Bay of Fundy by mid-summer.

Temperature change and some aspect of seasonality (i.e., day length) may initiate migratory behavior, but timing of the behavior by different individuals may be influenced by intrinsic (genetic) factors and life history stage of the individual. Chance may also play a small role in determining which direction a fish will travel, at least within a confined coastal region.

Dadswell et al. (1987) concluded that extrinsic factors related to ocean climate, seasonality, and currents may provide cues for portions of non-goal-oriented migration, while intrinsic cues and bi-coordinate navigation appear to be important during goal-oriented migration.

Suspended solid associations at sea

Due to extreme turbidity, the American shad preference zone for light intensity in summer and fall in the Bay of Fundy is limited to surface waters (2 to 10 m). Although this makes the fish more susceptible to fishing gear that operates near surface waters, these waters are highly productive sources of zooplankton. Sight-oriented planktivores may be at a disadvantage in these turbid waters, but American shad, which can use a filter-feeding mechanism, may have a competitive advantage (Dadswell et al. 1983).

Feeding behavior at sea

While offshore, American shad are primarily planktivorous, feeding on the most readily available organisms, such as copepods, mysid shrimps, ostracods, amphipods, isopods, euphausiids, larval barnacles, jellyfish, small fish, and fish eggs (Willey 1923; Leim 1924; Maxfield 1953; Massmann 1963; Levesque and Reed 1972; Marcy 1976). Themelis (1986) found that in the Bay of Fundy, American shad mostly consume planktonic and epibenthic crustaceans. Differences in dominant prey items may be attributed to changing availability of zooplankton assemblages and the size of the American shad. Juveniles feed more extensively on copepods than adults and a smaller proportion of their diet is composed of large prey items such as euphausiids and mysids (Themelis 1986). In earlier studies, Leim (1924) reported similar observations, with copepods decreasing in importance in the diets of American shad over 400 mm in length. Detritus has also been found in the stomachs of American shad, but it probably provides little nutritional value and is simply ingested during the course of feeding (Themelis 1986).

The Bay of Fundy is regarded as the primary summer feeding grounds for American shad, however, the entire bay does not provide optimal feeding conditions for adults. For example, although both adult and juvenile American shad feed readily in the oceanic lower Bay of Fundy, only juveniles feed to a large extent within the turbid and estuarine waters of the upper bay. This is attributed to the juvenile's ability to successfully filter smaller prey items that dominate the upper bay (Themelis 1982).

Competition and predation at sea

Once in the ocean, American shad are undoubtedly preyed upon by many species including sharks, tunas, king mackerel, bluefish, striped bass, Atlantic salmon, seals, porpoises, other marine mammals, and seabirds, given their schooling nature and lack of dorsal or opercular spines (Melvin et al. 1985; Weiss-Glanz et al. 1986).

Current laboratory research by Plachta and Popper (2003) has found that American shad can detect ultrasonic signals to at least 180 kHz, which is within the range that echolocating harbour porpoises and bottlenose dolphins use to track alosines. In this laboratory environment, American shad have been observed modifying their behavior in response to echolocation beams,

such as turning slowly away from the sound source, forming very compact groups, and displaying a quick “panic” response. Although behavior in a natural environment may be different from that observed in experimental tanks, this study suggests that American shad may have evolved a mechanism to make themselves less “conspicuous” or less easily preyed upon by echolocating odontocetes (Plachta and Popper 2003).

Section II. Significant Environmental, Temporal, and Spatial Factors Affecting Distribution of American Shad

Table 2-9. Significant environmental, temporal, and spatial factors affecting distribution of American shad. Please note that, although there may be subtle variations between systems, the following data include a broad range of values that encompass the different systems that occur along the East Coast. Where a specific range is known to exist, it will be noted. For the subadult–estuarine/oceanic environment and non-spawning adult–oceanic environment life history phases, the information is provided as a general reference, not as habitat preferences or optima. NIF = No Information Found.

Life Stage	Time of Year and Location	Depth (m)	Temperature (°C)	Salinity (ppt)	Substrate	Current Velocity (m/sec)	Dissolved Oxygen (mg/L)
Spawning Adult	Mid-November-August (south to north progression) in natal rivers and tributaries from St. Johns River, Florida to St. Lawrence River, Canada	Tolerable: 0.46-15.24 Optimal: 1.5-6.1 Reported: Variable	Tolerable: 8-26 Optimal: 14-24.5 Reported: Varies across range and may vary between years	Tolerable: NIF Optimal: NIF Reported: Mostly freshwater	Tolerable: NIF Optimal: NIF Reported: Sand, silt, gravel, boulder	Tolerable: NIF Optimal: 0.3-0.9 Reported: Avoid pools but prefer slow flow; velocity is an important factor	Tolerable: NIF Optimal: NIF Reported: Minimum 4
Egg	Mid-November-August (south to north progression) at spawning areas or slightly downstream	Tolerable: NIF Optimal: NIF Reported: Settle at bottom in shallow water	Tolerable: 8-30 Optimal: NIF Reported: Variable	Tolerable: NIF Optimal: NIF Reported: Variable	Tolerable: NIF Optimal: NIF Reported: Gravel, rubble, and sand have highest survival	Tolerable: NIF Optimal: 0.3-0.9 Reported: Low flow	Tolerable: NIF Optimal: NIF Reported: Minimum 5
Larvae	2-17 days after fertilization depending on temperature, downstream of spawning areas	Tolerable: 0.46-15.24 Optimal: 1.5-6.1 Reported: Surface and water column	Tolerable: 10-30 Optimal: 15-25 Reported: Variable	Tolerable: NIF Optimal: NIF Reported: Variable	Tolerable: NIF Optimal: NIF Reported: NIF	Tolerable: NIF Optimal: 0.3-0.9 Reported: Low flow	Tolerable: NIF Optimal: NIF Reported: Minimum 5

Life Stage	Time of Year and Location	Depth (m)	Temperature (°C)	Salinity (ppt)	Substrate	Current Velocity (m/sec)	Dissolved Oxygen (mg/L)
Early Juvenile – Riverine Environment	3-5 weeks after hatching Downstream of spawning areas as far as brackish waters	Tolerable: 0.46-15.24 Optimal: 1.5-6.1 Reported: Variable	Tolerable: 3-35 Optimal: 10-25 Reported: Variable; growth higher at higher temps	Tolerable: 0-30 Optimal: NIF Reported: Gradual change well tolerated	Tolerable: NIF Optimal: Possibly areas w/50%+ SAV Reported: Boulder, cobble, gravel, sand, SAV	Tolerable: NIF Optimal: 0.1-0.8 Reported: Moderate needed for migration	Tolerable: NIF Optimal: NIF Reported: Minimum 5
Subadult & Non-spawning Adult – Estuarine / Oceanic Environment	2-6 years after hatching; 1) Overwinter offshore of Florida, the Mid-Atlantic Bight, and Nova Scotia 2) Spring – migration route is unknown 3) Late June – inner Bay of Fundy, inner Gulf of St. Lawrence, Gulf of Maine, and Newfoundland and Labrador 4) Autumn – moving offshore	Tolerable: Surface waters to 340 m Optimal: 50-100 m Reported: Variable; possible diel migrations with zooplankton	Tolerable: Variable Optimal: 7-13 Reported: Generally travel in preferred isotherm	Tolerable: NIF Optimal: NIF Reported: Brackish to saltwater	Tolerable: NIF Optimal: NIF Reported: NIF	Tolerable: NIF Optimal: NIF Reported: NIF	Tolerable: NIF Optimal: NIF Reported: NIF

Section III. American Shad Literature Cited

- Arnold, D. A. 2000. Lehigh River American shad: The first six years. *Pennsylvania Angler and Boater* 69(3): 18-21.
- Atkins, C. G. 1887. The river fishes of Maine. Pages 673-728 in George B. Goode and Associates. *History and methods of the fisheries: The fisheries and fishery industry of the United States, volume I (Section 5)*. Bulletin of the United States Fish Commission, Washington, D.C.
- Atkinson, C. E. 1951. Feeding habits of adult shad (*Alosa sapidissima*) in fresh water. *Ecology* 32: 556-557.
- ASMFC (Atlantic States Marine Fisheries Commission). 1985. Fishery management plan for the anadromous alosid stocks of the eastern United States: American shad, hickory shad, alewife, and blueback herring. ASMFC Fishery Management Report No. 6, Washington, D.C.
- ASMFC (Atlantic States Marine Fisheries Commission). 1988. Supplement to the fishery management plan for the anadromous alosid stocks of the eastern United States: American shad, hickory shad, alewife, and blueback herring. ASMFC Fishery Management Report No. 12, Washington, D.C.
- ASMFC (Atlantic States Marine Fisheries Commission). 1999. Amendment 1 to the interstate fishery management plan for shad and river herring. ASMFC Fishery Management Report No. 35, Washington, D.C.
- Auld, A. H., and J. R. Schubel. 1978. Effects of suspended sediments on fish eggs and larvae: A laboratory assessment. *Estuarine and Coastal Marine Science* 6: 153-164.
- Bailey, K. M., and E. D. Houde. 1989. Predation on eggs and larvae of marine fishes and the recruitment problem. *Advances in Marine Biology* 25: 1-83.
- Barker, J. 1965. Observations on some areas of the Delaware River between Belvidere and Scudders Falls, New Jersey in respect to their utilization by American shad, *Alosa sapidissima* (Wilson), for spawning purposes in 1963 and 1964. New Jersey Department of Conservation and Economic Development Miscellaneous Report 28, Trenton, New Jersey.
- Barry, T., and B. Kynard. 1986. Attraction of adult American shad to fish lifts at Holyoke Dam, Connecticut River. *North American Journal of Fisheries Management* 6: 223-241.
- Beach, N. W. 1960. A study of the planktonic rotifers of the Oequeoe River system, Presque Isle County, Michigan. *Ecological Monographs* 30: 339-357.
- Beasely, C. A., and J. E. Hightower. 2000. Effects of a low-head dam on the distribution and characteristics of spawning habitat used by striped bass and American shad. *Transactions of the American Fisheries Society* 129: 1316-1330.
- Bernatchez, L., and J. J. Dodson. 1987. Relationship between bioenergetics and behavior in anadromous fish migrations. *Canadian Journal of Fisheries and Aquatic Sciences* 44: 399-407.

- Biggs, R. B., and D. A. Flemer. 1972. The flux of particulate carbon in an estuary. *Marine Biology* 12: 11-17.
- Bilkovic, D. M. 2000. Assessment of spawning and nursery habitat suitability for American shad (*Alosa sapidissima*) in the Mattaponi and Pamunkey Rivers. Doctoral dissertation. The College of William and Mary, Williamsburg, Virginia.
- Bilkovic, D. M., C. H. Hershner, and J. E. Olney. 2002. Macroscale assessment of American shad spawning and nursery habitat in the Mattaponi and Pamunkey Rivers, Virginia. *North American Journal of Fisheries Management* 22: 1176-1192.
- Boreman, J. 1981. Life histories of seven fish species that inhabit the Hudson River estuary. National Marine Fisheries Service, Northeast Fisheries Center Laboratory Reference Document No. 81-34, Woods Hole, Massachusetts.
- Boreman, J., and K. D. Friedland. 2003. Sensitivity of American shad to changes in fishing mortality. Pages 267-273 in K. E. Limburg and J. R. Waldman, editors. Biodiversity, status, and conservation of the world's shads. American Fisheries Society Symposium 35, Bethesda, Maryland.
- Bowman, S., and J. E. Hightower. 2001. American shad and striped bass spawning migration and habitat selection in the Neuse River, North Carolina. Final report to the North Carolina Marine Fisheries Commission, North Carolina Cooperative Fish and Wildlife Research Unit, North Carolina State University, Raleigh, North Carolina.
- Bowman, R. E., C. E. Stillwell, W. L. Michaels, and M. D. Grosslein. 2000. Food of Northwest Atlantic fishes and two common species of squid. NOAA Technical Memorandum No. NMFS-F/NE-155, Silver Spring, Maryland.
- Bradford, A. D., J. D. Miller, and K. Buss. 1968. Bio-assays on eggs and larval stages of American shad *Alosa sapidissima*. Pages 52-60 in F. T. Carlson, editor. Suitability of the Susquehanna River for restoration of shad. U.S. Department of the Interior, Maryland Board on Natural Resources, New York Conservation Department, and Pennsylvania Fish Commission.
- Brown, M., and B. Sleeper. 2004. Anadromous Fish Restoration in the Androscoggin River Watershed - 2003 Report on the Operation of the Brunswick Fishway FERC # 2284. Maine Department of Marine Resources in Cooperation with NMFS (P.L. 89-304), Augusta, Maine.
- Burdick, G. E. 1954. An analysis of the factors, including pollution, having possible influence on the abundance of shad in the Hudson River. *New York Fish and Game Journal* 1: 188-205.
- Cameron, W. M., and D. W. Pritchard. 1963. Estuaries. Pages 306-324 in M. N. Hill. The sea, volume 2: The composition of seawater comparative and descriptive oceanography. Interscience, New York, New York.
- Carlson, F. T., editor. 1968. Suitability of the Susquehanna River for restoration of shad. U.S. Department of the Interior, Maryland Board on Natural Resources, New York Conservation Department, and Pennsylvania Fish Commission.

- Carscadden, J. E., and W. C. Leggett. 1975. Life history variations in populations of American shad, *Alosa sapidissima* (Wilson), spawning in tributaries of the St. John River, New Brunswick. *Journal of Fish Biology* 32: 653-660.
- Cave, J. R. 1978. American shad, *Alosa sapidissima*, larval distribution, relative abundance and movement in the Holyoke Pool, Connecticut River, Massachusetts. Masters thesis. University of Massachusetts, Amherst, Massachusetts.
- Chandler, D. C. 1937. Fate of typical lake plankton in streams. *Ecological Monographs* 7: 445-479.
- Chesapeake Bay Program. 1988. Habitat requirements for Chesapeake Bay living resources. Chesapeake Executive Council, Annapolis, Maryland.
- Chittenden, M. E., Jr. 1969. Life history and ecology of the American shad, *Alosa sapidissima*, in the Delaware River. Doctoral dissertation. Rutgers University, New Brunswick, New Jersey.
- Chittenden, M. E., Jr. 1973a. Effects of handling on oxygen requirements of American shad (*Alosa sapidissima*). *Journal of the Fisheries Research Board of Canada* 30: 105-110.
- Chittenden, M. E., Jr. 1973b. Salinity tolerances of young American shad, *Alosa sapidissima*. *Chesapeake Science* 14: 207-210.
- Chittenden, M. E., Jr. 1976a. Present and historical spawning grounds and nurseries of American shad, *Alosa sapidissima*, in the Delaware River. *Fishery Bulletin* 74: 343-352.
- Chittenden, M. E., Jr. 1976b. Weight loss, mortality, feeding, and duration of residence of adult American shad, *Alosa sapidissima*, in fresh water. *Fishery Bulletin* 74: 151-157.
- Chittenden, M. E., Jr., and J. R. Westman. 1967. Highlights of the life history of the American shad in the Delaware River. Presentation of the Delaware River Basin Commission at a public hearing on water quality standards for the Delaware River, Trenton, New Jersey.
- Collette, B., and G. Klein-MacPhee, editors. 2002. Bigelow and Schroeder's fishes of the Gulf of Maine, 3rd edition. Smithsonian Institution Press, Washington, D.C.
- Cooke, D. W., and S. D. Leach. 2003. Beneficial effects of increased river flow and upstream fish passage on anadromous alosine stocks. Pages 331-338 in K. E. Limburg, and J. R. Waldeman, editors. Biodiversity, status, and conservation of the world's shads. American Fisheries Society Symposium 35, Bethesda, Maryland.
- Crecco, V. A., and M. M. Blake. 1983. Feeding ecology of coexisting larvae of American shad and blueback herring in the Connecticut River. *Transactions of the American Fisheries Society* 112: 498-507.
- Crecco, V. A., and T. F. Savoy. 1984. Effects of fluctuations in hydrographic conditions on year-class strength of American shad (*Alosa sapidissima*) in the Connecticut River. *Canadian Journal of Fisheries and Aquatic Sciences* 41: 1216-1223.

- Crecco, V. A., and T. F. Savoy. 1987a. Review of recruitment mechanisms of the American shad: The critical period and match-mismatch hypotheses reexamined. Pages 455-468 in M. J. Dadswell, R. J. Klauda, C. M. Moffitt, and R. L. Saunders, editors. Common strategies of anadromous and catadromous fishes. American Fisheries Society Symposium 1, Bethesda, Maryland.
- Crecco, V. A., and T. F. Savoy. 1987b. Effects of climatic and density-dependent factors on intra-annual mortality of larval American shad. Pages 69-81 in R. D. Hoyt, editor. Proceedings of the 10th annual larval fish conference. American Fisheries Society Symposium 2, Bethesda, Maryland.
- Crecco, V. A., T. F. Savoy, and L. Gunn. 1983. Daily mortality rates of larval and juvenile American shad (*Alosa sapidissima*) in the Connecticut River with changes in year-class strength. Canadian Journal of Fisheries and Aquatic Sciences 40: 1719-1728.
- Crecco, V. A., T. F. Savoy, and W. Whitworth. 1986. Effects of density-dependent and climatic factors on American shad, *Alosa sapidissima*, recruitment: A predictive approach. Canadian Journal of Fisheries and Aquatic Sciences 43: 457-463.
- Dadswell, M. J., G. D. Melvin, and P. J. Williams. 1983. Effect of turbidity on the temporal and spatial utilization of the inner Bay of Fundy by American shad (*Alosa sapidissima*) (Pisces: Clupeidae) and its relationship to local fisheries. Canadian Journal of Fisheries and Aquatic Sciences 40 Supplement 1: 322-330.
- Dadswell, M. J., G. D. Melvin, P. J. Williams, and D. E. Themelis. 1987. Influences of origin, life history, and chance on the Atlantic coast migration of American shad. Pages 313-330 in M. J. Dadswell, R. J. Klauda, C. M. Moffitt, and R. L. Saunders, editors. Common strategies of anadromous and catadromous fishes. American Fisheries Society Symposium 1, Bethesda, Maryland.
- Davis, J. R., and R. P. Cheek. 1966. Distribution, food habits, and growth of young clupeids, Cape Fear River system, North Carolina. Proceedings of the 20th Annual Conference of the Southeastern Association of Game and Fish Commissions: 250-260.
- Day, J. W., Jr., T. J. Butler, and W. H. Connor. 1975. Productivity and nutrient export studies in a cypress swamp and lake system in Louisiana. Pages 255-269 in M. Wiley, editor. Estuarine processes, Vol. 2: Circulation, sediments, and transfer of material in the estuary. Academic Press, New York, New York.
- DBC (Delaware Basin Fish and Wildlife Management Cooperative). 1980. Strategic fishery management plan for the American shad (*Alosa sapidissima*) in the Delaware River Basin.
- Dey W. P., and P. C. Baumann. 1978. Community dynamics of shore zone fish populations in the Hudson River estuary: 108th Annual American Fisheries Society Meeting, Kingston, Rhode Island.
- Dodson, J. J., W. C. Leggett, and R. A. Jones. 1972. The behavior of adult American shad (*Alosa sapidissima*) during migration from salt to freshwater as observed by ultrasonic tracking techniques. Journal of the Fisheries Research Board of Canada 29: 1445-1449.

- Domermuth, R. B., and R. J. Reed. 1980. Food of juvenile American shad, *Alosa sapidissima*, juvenile blueback herring, *Alosa aestivalis*, and pumpkinseed, *Lepomis gibbosus*, in the Connecticut River below Holyoke Dam, Massachusetts. *Estuaries* 3: 65-68.
- Dorfman, D., and J. Westman. 1970. Responses of some anadromous fishes to varied oxygen concentrations and increased temperatures. Office of Water Resources Research Project No. B-012-NJ, Rutgers University, New Brunswick, New Jersey.
- Ecological Analysts, Inc. 1978. Hudson River thermal effects studies for representative species: Second progress report. Prepared for Central Hudson Gas and Electric Corporation, Poughkeepsie, New York.
- Erkan, D. E. 2002. Strategic plan for the restoration of anadromous fishes to Rhode Island coastal streams. Rhode Island Department of Environmental Management, Division of Fish and Wildlife, Completion Report in fulfillment of Federal Aid in Sportfish Restoration Project No. F-55-R, Jamestown, Rhode Island.
- Facey, D. E., and M. J. Van Den Avyle. 1986. Species profiles: Life histories and environmental requirements of coastal fishes and invertebrates (South Atlantic) – American shad. U.S. Fish and Wildlife Service Biological Report No. 82 (11.45), and U.S. Army Corps of Engineers Report No. TR EL-82-4, Washington D.C.
- Fischer, C. A. 1980. Anadromous fisheries research program Cape Fear River System Phase II. North Carolina Department of Natural and Community Development, Division of Marine Fisheries Completion Report for Project No. AFCS-15, Morehead, City, North Carolina.
- Fredin, R. A. 1954. Causes of fluctuations in abundance of Connecticut River shad. U.S. Fish and Wildlife Service Fisheries Bulletin 54: 247-259.
- Gabriel, W. L., W. C. Leggett, J. E. Carscadden, and B. D. Glebe. 1976. Origin and characteristics of “fall-run” American shad (*Alosa sapidissima*) from the St. John River, New Brunswick. *Journal of the Fisheries Research Board of Canada* 33: 1764-1770.
- Garman, G. C. 1992. Fate and potential significance of postspawning anadromous fish carcasses in an Atlantic coastal river. *Transactions of the American Fisheries Society* 121: 390-394.
- Glebe, B. D., and W. C. Leggett. 1973. Weight loss and associated energy expenditure of American shad during the freshwater migration. Progress Report on Project No. AFC 8-2 Conn. National Marine Fisheries Service, Silver Spring, Maryland.
- Glebe, B. D., and W. C. Leggett. 1981a. Temporal, intra-population differences in energy allocation and use by American shad *Alosa sapidissima* during the spawning migration. *Canadian Journal of Fisheries and Aquatic Sciences* 38: 795-805.
- Glebe, B. D., and W. C. Leggett. 1981b. Latitudinal differences in energy allocation and use during the freshwater migrations of American shad (*Alosa sapidissima*) and their life history consequences. *Canadian Journal of Fisheries and Aquatic Sciences* 38: 806-820.
- Grabe, S. A. 1996. Feeding chronology and habits of *Alosa* spp. (Clupeidae) juveniles from the lower Hudson River estuary, New York. *Environmental Biology of Fishes* 47: 321-326.
- Hammer, R. C. 1942. The homing instinct of the Chesapeake shad, *Alosa sapidissima*, as revealed by a study of scales. Master’s thesis. University of Maryland, College Park, Maryland.

- Hatton, S. R. 1940. Progress report on Central Valley fisheries investigation. California Fish and Game 26: 335-373.
- Hawkins, J. H. 1979. Anadromous fisheries research program – Neuse River. North Carolina Department of Natural Resources and Community Development, Division of Marine Fisheries, Morehead City, North Carolina.
- Hendricks, M. L., R. L. Hoopes, D. A. Arnold, and M. L. Kaufman. 2002. Homing of hatchery-reared American shad to the Lehigh River, a tributary to the Delaware River. North American Journal of Fisheries Management 22: 243-248.
- Hightower, J. E., and K. L. Sparks. 2003. Migration and spawning habitat of American shad in the Roanoke River, North Carolina. Pages 193-199 in K. E. Limburg, and J. R. Waldman, editors. Biodiversity, status, and conservation of the world's shads. American Fisheries Society Symposium 35, Bethesda, Maryland.
- Hildebrand, S. F., and W. C. Schroeder. 1928. Fishes of Chesapeake Bay. United States Bureau of Fisheries Bulletin 53.
- Hildebrand, S. F. 1963. Family Clupeidae. Pages 257-454 in H. B. Bigelow, editor. Fishes of the Western North Atlantic, part 3. Sears Foundation for Marine Research, Yale University, New Haven, Connecticut.
- Hill, D. R. 1959. Some uses of statistical analysis in classifying races of American shad (*Alosa sapidissima*). U.S. Fish and Wildlife Service Fisheries Bulletin 59: 268-286.
- Hirschfield, H. I., J. W. Rachlin, and E. Leff. 1966. A survey of invertebrates from selected sites of the lower Hudson River. Pages 230-257 in Hudson River ecology. New York State Department of Environmental Conservation, Albany, New York.
- Hobbie, J. E., B. J. Copeland, and W. G. Harrison. 1973. Sources and fates of nutrients of the Pamlico River Estuary, North Carolina. Pages 287-302 in L. E. Cronin, editor. Estuarine research, volume 1: Chemistry, biology, and the estuarine system. Academic Press, New York, New York.
- Holland, B. F., Jr., and G. F. Yelverton. 1973. Distribution and biological studies of anadromous fishes offshore NC. North Carolina Department of Natural and Economic Resources Special Science Report No. 24, North Carolina.
- Horton, D. B., and D. W. Bridges. 1973. A study to predict the effects of thermal additions in the Bay River and Neuse River area of North Carolina. U.S. Department of the Interior Office of Water Research and Technology Report No. OWRT-004-NC, Washington, D.C.
- Houston, A. H. 1957. Responses of juvenile chum, pink, and coho salmon to sharp sea-water gradients. Canadian Journal of Zoology 35: 371-383.
- Howarth, R. H., R. Marino, R. Garritt, and D. Sherman. 1992. Ecosystem respiration and organic carbon processing in a large, tidally influenced river: The Hudson River. Biogeochemistry 16: 83-102.
- Howe, K. M. 1981. Preliminary checklist of the fishes of the northeastern Pacific Ocean (revised). Unpublished manuscript. School of Fisheries, University of Washington, Seattle, Washington.

- Hunter, J. R. 1981. Feeding ecology and predation of marine fish larvae. Pages 33-77 in R. Lasker, editor. Marine fish larvae: Morphology, ecology, and relation to fisheries. University of Washington Press, Seattle, Washington.
- Hynes, H. B. N. 1970. The ecology of running waters. University of Toronto Press, Toronto, Canada.
- Jessop, B. M. 1975. A review of the American shad (*Alosa sapidissima*) stocks of the St. John River, New Brunswick, with particular references to the adverse effects of hydroelectric development. Canadian Fisheries and Marine Services Resource Division, Branch Maritime Regulation, Technical Report No. 75-6: 1-23.
- Jones, P. W., F. D. Martin, and J. D. Hardy, Jr. 1978. Development of fishes of the mid-Atlantic Bight. An atlas of egg, larval and juvenile stages, volume I, Acipenseridae through Ictaluridae. U.S. Fish and Wildlife Service Report No. FWS/OBS-78/12, Washington D.C.
- Johnson, J. H., and D. S. Dropkin. 1995. Effects of prey density and short term food deprivation on the growth and survival of American shad larvae. Journal of Fish Biology 46: 872-879.
- Johnson, J. H., and N. H. Ringler. 1998. Predator response to releases of American shad larvae in the Susquehanna River basin. Ecology of Freshwater Fish 7: 192-199.
- Klauda, R. J. 1989. Definitions of critical environmental conditions for selected Chesapeake Bay finfishes exposed to acidic episodes in spawning and nursery areas. John's Hopkins University, Applied Physics Laboratory, Shady Side, Maryland.
- Klauda, R. J. 1994. Lethal and critical effects thresholds for American shad eggs and larvae exposed to acid and aluminum in the laboratory, with speculation on the potential role of habitat acidification on stock status in Maryland. Pages 7-39 in J. E. Cooper, R. T. Eades, R. J. Klauda, and J. G. Loesch, editors. Anadromous *Alosa* Symposium. American Fisheries Society Tidewater Chapter, Bethesda, Maryland.
- Klauda, R. J., S. A. Fischer, L. W. Hall, Jr., and J. A. Sullivan. 1991. American shad and hickory shad. Pages 9.1-9.27 in S. L. Funderburk, J. A. Mihursky, S. J. Jordan, and D. Riley, editors. Habitat requirements for Chesapeake Bay living resources, second edition. Chesapeake Bay Program Living Resources Subcommittee, Annapolis, Maryland.
- Koch, E. W. 2001. Beyond light: Physical, geological and geochemical parameters as possible submersed aquatic vegetation habitat requirements. Estuaries 24: 1-17.
- Koo, T. S. Y., C. F. Smith, M. C. Johnston, G. E. Galog, Jr., and H. L. Mathers. 1976. Effects of heat shock on fish eggs and larvae. Chesapeake Biological Laboratory, CEES Ref. No. 76-112-CBL, Solomons, Maryland.
- Krauthamer, J., and W. Richkus. 1987. Characterizations of the biology of and fisheries for Maryland stocks of American and hickory shad. Prepared for Maryland Department of Natural Resources, Tidewater Administration, Annapolis, Maryland.
- Kuzmeskus, D. M. 1977. Egg production and spawning site distribution of the American shad, *Alosa sapidissima*, in the Holyoke Pool, Connecticut River, Massachusetts. Master's thesis. University of Massachusetts, Amherst, Massachusetts.

- Layzer, J. B. 1974. Spawning sites and behavior of American shad, *Alosa sapidissima* (Wilson), in the Connecticut River between Holyoke and Turners Falls, Massachusetts, 1972. Master's thesis. University of Massachusetts, Amherst, Massachusetts.
- Leach, S. D., and E. D. Houde. 1999. Effects of environmental factors on survival, growth, and production of American shad larvae. *Journal of Fish Biology* 54: 767-786.
- Lee, D. S., C. R. Gilbert, C. H. Hocutt, R. E. Jenkins, D. E. McAllister, and J. R. Stauffer, Jr. 1980. Atlas of North American freshwater fishes. North Carolina State Museum of Natural History, Raleigh, North Carolina.
- Leggett, W. C. 1969. Studies on the reproductive biology of the American shad *Alosa sapidissima* (Wilson). A comparison of populations from four rivers of the Atlantic seaboard. Doctoral dissertation. McGill University, Montreal, Canada.
- Leggett, W. C. 1976. The American shad (*Alosa sapidissima*), with special reference to its migration and population dynamics in the Connecticut River. American Fisheries Society Monograph No. 1: 169-225.
- Leggett, W. C. 1977a. Ocean migration rates of American shad (*Alosa sapidissima*). *Journal of the Fisheries Research Board of Canada* 34: 1422-1426.
- Leggett, W. C. 1977b. The ecology of fish migrations. *Annual Review of Ecology and Systematics* 8: 285-308.
- Leggett, W. C., and J. E. Carscadden. 1978. Latitudinal variation in reproductive characteristics of American shad (*Alosa sapidissima*): Evidence for population specific life history strategies in fish. *Journal of the Fisheries Research Board of Canada* 35: 1469-1478.
- Leggett, W. C., and R. N. O' Boyle. 1976. Osmotic stress and mortality in adult American shad during transfer from saltwater to freshwater. *Journal of Fish Biology* 8: 459-469.
- Leggett, W. C., and R. R. Whitney. 1972. Water temperature and the migrations of American shad. *Fisheries Bulletin* 70: 659-670.
- Leidy, J. 1868. Remarks on shad brought to our markets during the late autumnal months which were caught in salt water, and their food. *Proceedings of the Academy of Natural Sciences*, Philadelphia, Pennsylvania.
- Leim, A. H. 1924. The life-history of the shad (*Alosa sapidissima* (Wilson)) with special reference to the factors limiting its abundance. *Contributions To Canadian Biology*, New Series 2: 161-284.
- Letcher B. H., and J. A. Rice. 1997. Prey patchiness and larval fish growth and survival: Inferences from an individual-based model. *Ecological Modeling* 95: 29-43.
- Levesque, R. C., and R. J. Reed. 1972. Food availability and consumption by young Connecticut River shad *Alosa sapidissima*. *Journal of the Fisheries Research Board of Canada* 29: 1495-1499.
- Limburg, K. E. 1994. Ecological constraints on growth and migration of juvenile American shad (*Alosa sapidissima* Wilson) in the Hudson River estuary, New York. Doctoral dissertation. Cornell University, Ithaca, New York.

- Limburg, K. E. 1995. Otolith strontium traces migratory histories of juvenile American shad, *Alosa sapidissima*. Marine Ecology Progress Series 119: 25-35.
- Limburg, K. E. 1996. Growth and migration of 0-year American shad (*Alosa sapidissima*) in the Hudson River estuary: Otolith microstructural analysis. Canadian Journal of Fisheries and Aquatic Sciences 53: 220-238.
- Limburg, K. E. 1998. Anomalous migrations of anadromous herrings revealed with natural chemical tracers. Canadian Journal of Fisheries and Aquatic Sciences 55: 431-437.
- Limburg, K. E., K. A. Hattala, and A. Kahnle. 2003. American shad in its native range. Pages 125-140 in K. E. Limburg, and J. R. Waldman, editors. Biodiversity, status, and conservation of the world's shads. American Fisheries Society Symposium 35, Bethesda, Maryland.
- Limburg, K. E., and R. M. Ross. 1995. Growth and mortality rates of larval American shad, *Alosa sapidissima*, at different salinities. Estuaries 18: 335-340.
- Livingston, R. J., S. E. McGlynn, and X. Niu. 1998. Factors controlling seagrass growth in a gulf coastal system: Water and sediment quality and light. Aquatic Botany 60: 135-159.
- Loesch, J. G., W. H. Kriete, Jr., and E. J. Foell. 1982. Effects of light intensity on the catchability of juvenile anadromous *Alosa* species. Transactions of the American Fisheries Society 111: 41-44.
- MacKenzie, C., L. Weiss-Glanz, and J. Moring. 1985. Species profiles: Life histories and environmental requirements of coastal fishes and invertebrates (mid-Atlantic)-American shad. U.S. Fish and Wildlife Service Biological Report No. 82(11.37), Washington, D.C.
- Mansueti, R. J., and H. Kolb. 1953. A historical review of the shad fisheries of North America. Chesapeake Biological Laboratory Publication No. 97, Solomons, Maryland.
- Marcy, B. C., Jr. 1971. Survival of young fish in the discharge canal of a nuclear power plant. Journal of the Fisheries Research Board of Canada 28: 1057-1060.
- Marcy, B. C., Jr. 1972. Spawning of the American shad, *Alosa sapidissima*, in the lower Connecticut River. Chesapeake Science 13: 116-119.
- Marcy, B. C., Jr. 1973. Vulnerability and survival of young Connecticut River fish entrained at a nuclear power plant. Journal of the Fisheries Research Board of Canada 30: 1195-1203.
- Marcy, B. C., Jr. 1976. Early life history studies of American shad in the lower Connecticut River and the effects of the Connecticut Yankee Plant. Pages 141-168 in D. Merriman, and L. M. Thorpe, editors. The Connecticut River ecological study: The impact of a nuclear power plant. American Fisheries Society Monograph No. 1, Bethesda, Maryland.
- Marcy, B. C., Jr., P. M. Jacobson, and R. L. Nankee. 1972. Observations on the reactions of young American shad to a heated effluent. Transactions of the American Fisheries Society 191: 740-743.
- Massmann, W. H. 1952. Characteristics of spawning areas of shad, *Alosa sapidissima* (Wilson), in some Virginia streams. Transactions of the American Fisheries Society 81: 78-93.
- Massmann, W. H. 1963. Summer food of juvenile American shad in Virginia waters. Chesapeake Science 4: 167-171.

- Massmann, W. H., and A. L. Pacheco. 1957. Shad catches and water temperature in Virginia. *Journal of Wildlife Management* 21: 351-352.
- Maurice, K. R., R. W. Blye, and P. L. Harmon. 1987. Increased spawning by American shad coincident with improved dissolved oxygen in the tidal Delaware River. Pages 79-88 *in* M. J. Dadswell, R. J. Klauda, C. M. Moffitt, and R. L. Saunders, editors. Proceedings of the international symposium on common strategies of anadromous and catadromous fishes. American Fisheries Society, Bethesda, Maryland.
- Maxfield, G. H. 1953. The food habits of hatchery-produced, pond-cultured shad (*Alosa sapidissima*) reared to a length of two inches. Chesapeake Biological Laboratory Publication No. 98, Solomons, Maryland.
- May, R. C. 1974. Larval mortality in marine fishes and the critical period concept. Pages 3-19 *in* J. H. S. Blaxter, editor. The early life history of fish. Springer-Verlag, Berlin, Germany.
- McCord, J. W. 2003. Alosid habitats for South Carolina watersheds. South Carolina Department of Natural Resources, Office of Fisheries Management, Diadromous Fisheries Program, Charleston, South Carolina.
- McCormick, S. D., J. M. Shrimpton, and J. D. Zydlewski. 1996. Temperature effects on osmoregulatory physiology of juvenile anadromous fish. Pages 279-301 *in* C. M. Wood, and D. G. McDonald, editors. Global warming: Implications for freshwater and marine fish. Cambridge University Press, Cambridge, United Kingdom.
- McFadden, J. T., Texas Instruments, and Lawler, Matusky, & Skelly Engineers. 1978. Influence of the proposed Cornwall pumped storage project and steam electric generating plants on the Hudson River estuary, with emphasis on striped bass and other fish populations, revised. Pages 7.1-7.227 *in* Report to Consolidated Edison Company of New York, New York.
- McPhee, J. A. 2002. The Founding Fish. Farrar, Straus, and Giroux, New York, New York.
- Meade, J. W. 1976. Experimental intensive rearing of shad at Van Dyke, Pennsylvania. Pages 211-234 *in* R. St. Pierre, editor. Proceedings of the workshop on American shad. U.S. National Marine Fisheries Service, Newton Corner, Massachusetts.
- Medcof, J. C. 1957. Nuptial or prenuptial behavior of the shad, *Alosa sapidissima* (Wilson). *Copeia*: 252-253.
- Melvin, G. D. 1984. The usefulness of meristic and morphometric characters in discriminating populations of American shad (*Alosa sapidissima*) inhabiting Cumberland Basin, N.B. Doctoral dissertation. University of New Brunswick, Fredericton, New Brunswick.
- Melvin, G. D., M. J. Dadswell, and J. A. McKenzie. 1992. Usefulness of meristic and morphometric characters in discriminating populations of American shad (*Alosa sapidissima*) (Osteichthyes: Clupeidae) inhabiting a marine environment. *Canadian Journal of Fisheries and Aquatic Sciences* 49: 266-280.
- Melvin, G. D., M. J. Dadswell, and J. D. Martin. 1985. Impact of lowhead hydroelectric tidal power development on fisheries: I. A preparation study of the spawning population of American shad *Alosa sapidissima* (Pisces: Clupeidae) in the Annapolis River, Nova Scotia, Canada. Canadian Fisheries and Aquatic Sciences Technical Report No. 1340, Nova Scotia, Canada.

- Melvin, G. D., M. J. Dadswell, and J. A. McKenzie. Usefulness of meristic and morphometric characters in discriminating populations of American shad (*Alosa sapidissima*) (Osteichthyes: Clupeidae) inhabiting a marine environment. *Canadian Journal of Fisheries and Aquatic Sciences* 49: 266-280.
- Metzger, S. G., R. G. Keppel, P. Geogahan, and A. W. Wells. 1992. Abundance of selected Hudson River fish species in previously unsampled regions: Effect on standing crop estimates. Pages 348-375 in C. L. Smith, editor. *Estuarine research in the 1980s*. State University of New York Press, Albany, New York.
- Miller, J. P., J. W. Friedersdorff, H. C. Mears, and C. W. Billingsley. 1973. Annual progress report Delaware River Basin Anadromous Fish Project, AFS-2-6: July 1972 – December 1972. U.S. Fish and Wildlife Service, Washington, D.C.
- Miller, J. P., J. W. Friedersdorff, H. C. Mears, J. P. Hoffman, F. R. Griffiths, R. C. Reichard, and C. W. Billingsley. 1975. Annual progress report Delaware River Basin Anadromous Fish Project, AFS-2-6: January 1973 -- January 1974. U.S. Fish and Wildlife Service, Washington, D.C.
- Miller, J. P., F. R. Griffiths, and P. A. Thurston-Rogers. 1982. The American shad (*Alosa sapidissima*) in the Delaware River Basin. Delaware Basin Fish and Wildlife Management Cooperative.
- Miller, J. P., W. M. Zarback, J. W. Friedersdorff, and R. W. Marshall. 1971. Annual progress report Delaware River Basin Anadromous Fish Project, AFS-2-4. U.S. Fish and Wildlife Service, Washington, D.C.
- Milner, J. W. 1876. On the transportation of shad for long distances: Experiments with a view to transporting shad in seawater. U.S. Fisheries Commission Report 3: 323-326.
- Milstein, C. B. 1981. Abundance and distribution of juvenile *Alosa* species off southern New Jersey. *Transactions of the American Fisheries Society* 110: 306-309.
- Mitchell, P. H. 1925. A report of investigations concerning shad in the rivers of Connecticut, part 1. Connecticut State Board of Fish and Game: 7-45.
- Morrow, J. E. 1980. The freshwater fishes of Alaska. Alaska Northwest Publishing Company, Anchorage, Alaska.
- Moser, M. L., and S. W. Ross. 1994. Effects of changing current regime and river discharge on the estuarine phase of anadromous fish migration. Pages 343-347 in K. R. Dryer, and R. J. Orth, editors. *Changes in fluxes in estuaries: Implications from science to management*. Olsen and Olsen, Fredensborg, Denmark.
- Moss, D. D. 1946. Preliminary studies of the shad (*Alosa sapidissima*) catch in lower Connecticut River, 1944. Pages 230-239 in E. M. Quee, editor. *Transactions of the 11th North American Wildlife Conference*.
- Moss, S. A. 1970. The responses of young American shad to rapid temperature changes. *Transactions of the American Fisheries Society* 99: 381-384.
- Murai, T., J. W. Muller, and J. W. Andrews. 1979. Dietary studies with American shad fry. *Progressive Fish-Culturist* 41: 61-63.

- Neves, R. J., and L. Depres. 1979. The oceanic migration of American shad, *Alosa sapidissima*, along the Atlantic coast. *Fishery Bulletin* 77: 199-212.
- Nichols, P. R. 1959. Extreme loss in body weight of an American shad (*Alosa sapidissima*). *Copeia* : 343-344.
- Nichols, P. R. 1966. Comparative study of juvenile American shad populations by fin ray and scute counts. U.S. Fish and Wildlife Service Special Science Report in Fisheries No. 525, Washington, D.C.
- O'Donnell, M. 2000. Age, size, hatch-date, and growth rate distribution of young-of-year American shad in the Connecticut River. Master's thesis. University of Massachusetts, Amherst, Massachusetts.
- O'Leary, J. A., and B. Kynard. 1986. Behavior, length, and sex ratio of seaward-migrating juvenile American shad and blueback herring in the Connecticut River. *Transactions of the American Fisheries Society* 115: 529-536.
- O'Leary, J. A., and B. Kynard. 1993. Evaluation of a bypass system for spent American shad at Holyoke Dam, Massachusetts. *North American Journal of Fisheries Management* 13: 782-789.
- Odom, M. 1997. Observations on habitat usage by juvenile American shad in the James River, Virginia, in 1997. Administrative report for U.S. Fish and Wildlife Service, Washington, D.C.
- Odum, W. E., and E. J. Heald. 1973. The detritus-based food web of an estuarine mangrove community. Pages 265-286 in L. E. Cronin, editor. *Estuarine research, volume 1: Chemistry, biology, and the estuarine system*. Academic Press, New York, New York.
- Olney, J. E., S. C. Denny, and J. M. Hoenig. 2001. Criteria for determining maturity stage in female American shad, *Alosa sapidissima*, and a proposed reproductive cycle. *Bulletin Francais de la Pêche et de la Pisciculture* 362/363: 881-901.
- Olney, J. E., and R. S. McBride. 2003. Intraspecific variation in batch fecundity of American shad: Revisiting the paradigm of reciprocal latitudinal trends in reproductive traits. Pages 185-192 in K. E. Limburg, and J. R. Waldman, editors. *Biodiversity, status, and conservation of the world's shads*. American Fisheries Society Symposium 35, Bethesda, Maryland.
- Orth, D. J., and R. J. White. 1993. Stream habitat management. Pages 205-230 in C. C. Kohler, and W. A. Hubert, editors. *Inland fisheries management in North America*. American Fisheries Society, Bethesda, Maryland.
- Parker, J. A. 1990. Migration patterns of American shad in the nearshore ocean waters of southeastern North Carolina. Completion Report No. 90-1-PASRH. North Carolina Department of Natural Resources and Community Development, Division of Marine Fisheries, Morehead City, North Carolina.
- Plachta, D. T. T., and A. N. Popper. 2003. Evasive responses of American shad (*Alosa sapidissima*) to ultrasonic stimuli. *Acoustics Research Letters Online* 4: 25-30.

- Provost, J. 1987. L'alse savoureuse (*Alosa sapidissima*, Wilson) du Fleuve Saint-Laurent: Etude comparative des phenotypes morphologiques et de certains aspects de la biologie de quelques populations. Master's thesis. University of Quebec, Quebec, Canada.
- Public Service Electric and Gas Company (PSE&G). 1982. American shad (*Alosa sapidissima*): A synthesis of information on natural history, with reference to occurrence in the Delaware River and estuary and involvement with the Salem Nuclear Generating Station. Salem Nuclear Generating Station 316(b) Report, Appendix III, Newark, New Jersey.
- Reimhold, R. J., J. L. Gallagher, R. A. Linthurst, and W. J. Pfeiffer. 1973. Detritus production in coastal Georgia salt marshes. Pages 217-228 in L. E. Cronin, editor. Estuarine research, volume 1: Chemistry, biology, and the estuarine system. Academic Press, New York, New York.
- Rice, H. J. 1878. Notes upon the development of the shad, *Alosa sapidissima*. Pages 95-106 in Report of the Commissioners of Fisheries of Maryland, Annapolis, Maryland.
- Richkus, W. A., and G. DiNardo. 1984. Current status and biological characteristics of the anadromous alosid stocks of the eastern United States: American shad, hickory shad, alewife, and blueback herring. Interstate Fisheries Management Program, Atlantic States Marine Fisheries Commission, Washington, D.C.
- Ross, R. M., R. M. Bennett, and T. W. H. Backman. 1993. Habitat use and spawning adult, egg, and larval American shad in the Delaware River. *Rivers* 4: 227-238.
- Ross, R. M., R. M. Bennett, and J. H. Johnson. 1997. Habitat use and feeding ecology of riverine juvenile American shad. *North American Journal of Fisheries Management* 17: 964-974.
- Rounsefell, G. A., and W. H. Everhart. 1953. Fishery science: Its methods and applications. John Wiley & Sons, Inc., New York, New York.
- Ryder, J. A. 1887. On the development of osseous fishes, including marine and freshwater forms. U.S. Commission on Fisheries Report 13: 488-604.
- Saila, S. B. 1973. Some aspects of fish production and cropping in estuarine systems. Pages 473-493 in L. E. Cronin, editor. Estuarine research, volume 1: Chemistry, biology, and the estuarine system. Academic Press, New York, New York.
- Savoy, T. F. 1993. Nearshore residence of juvenile clupeids in Long Island Sound. Paper presented at 49th Northeast Fish & Wildlife Conference, Atlantic City, New Jersey.
- Savoy, T. F., and V. A. Crecco. 1988. The timing and significance of density-dependent and density-independent mortality of American shad, *Alosa sapidissima*. *Fishery Bulletin* 86: 467-482.
- Savoy, T. F., and V. A. Crecco. 2004. Factors affecting the recent decline of blueback herring and American shad in the Connecticut River. American Fisheries Society Monograph 9, Bethesda, Maryland.
- Schmidt, R. E., R. J. Klauda, and J. M. Bartels. 1988. Distributions and movements of the early life stages of three species of *Alosa* in the Hudson River, community and a comparative analysis. *Canadian Journal of Fisheries and Aquatic Sciences* 49: 1060-1069.

- Schubel, J. R., and T. S. Y. Koo. 1976. Effects of various time-excess temperature histories on hatching success of blueback herring, American shad, and striped bass eggs. *Thermal Ecology II*, AEC Symposium Series Conference No. 750425: 165-170.
- Scott, W. B., and E. J. Crossman. 1973. *Freshwater fishes of Canada*. Fisheries Research Board of Canada Bulletin 184, Ottawa, Canada.
- Scott, W. B., and M. G. Scott. 1988. Atlantic fishes of Canada. *Canadian Bulletin of Fisheries and Aquatic Sciences* 219: 1-731.
- Sharp, G. D. 1980. Report of the workshop on effects of environmental variation on survival of larval pelagic fishes. Pages 15-66 *in* Workshop on the effects of environmental variation on the survival of larval pelagic fishes. Food and Agriculture Organization of the United Nations, Rome, Italy.
- Sholar, T. M. 1976. Status of American shad in North Carolina. Pages 17-31 *in* Proceedings of a workshop on American shad. U.S. Fish and Wildlife Service and U.S. National Marine Fisheries Service, Washington, D.C.
- Shoubridge, E. A. 1977. Reproductive strategies in local population of the American shad (*Alosa sapidissima*). Master's thesis. McGill University, Montreal, Quebec, Canada.
- Sirois, D. L. and S. W. Fredrick. 1978. Phytoplankton and primary productivity in the lower Hudson River estuary. *Estuarine and Coastal Marine Science* 7: 413-423.
- Smith, H. M. 1907. The fishes of North Carolina, volume II. North Carolina Geological and Economic Survey. E. M. Uzzell and Company, State Printers and Binders, Raleigh, North Carolina.
- State of Maine. 1982. Anadromous fisheries river management plan. Pages 1-29 *in* Statewide River Fisheries Management Plan. Prepared by the Maine Department of Marine Resources for the Governor's Cabinet Committee on Hydropower Policy, Section 1.
- State of Maryland. 1985. Notice of proposed action: Emergency regulation. Maryland Department of Natural Resources, Annapolis, Maryland.
- Stevenson, C. H. 1899. The shad fisheries of the Atlantic coast of the United States. Pages 101-269 *in* Report of the Commission for 1898, part 24. U.S. Commission of Fish and Fisheries.
- Stevenson, J. C., D. R. Heinle, D. A. Flemer, R. J. Small, R. A. Rowland, and J. F. Ustach. 1975. Nutrient exchanges between brackish water marshes and the estuary. Pages 219-240 *in* M. Wiley, editor. *Estuarine processes*, volume 2: Circulation, sediments, and transfer of material in the estuary. Academic Press, New York, New York.
- Stier, D. J., and J. H. Crance. 1985. Habitat suitability index models and instream flow suitability curves: American shad. U.S. Fish and Wildlife Service Biological Report No. 82(10.88), Washington D.C.
- Stokesbury, K. D. E., and M. J. Dadswell. 1989. Seaward migration of juveniles of three herring species, *Alosa*, from an estuary in the Annapolis River, Nova Scotia. *The Canadian Field-Naturalist* 103: 388-393.

- Summers, J. K., and K. A. Rose. 1987. The role of interactions among environmental conditions in controlling historical fisheries variability. *Estuaries* 10: 255-266.
- Sykes, J. E., and B. A. Lehman. 1957. Past and present Delaware River shad fishery and considerations for its future. U.S. Fish and Wildlife Service Research Report No. 46.
- Tagatz, M. E. 1961. Reduced oxygen tolerance and toxicity of petroleum products to juvenile American shad. *Chesapeake Science* 2: 65-71.
- Talbot, G. B. 1954. Factors associated with fluctuations in abundance of Hudson River shad. U.S. Fish and Wildlife Service Fishery Bulletin 56: 373-413.
- Talbot, G. B., and J. E. Sykes. 1958. Atlantic coast migrations of American shad. U.S. Fish and Wildlife Service Fishery Bulletin 58: 473-490.
- Teal, J. M. 1962. Energy flow in the salt marsh ecosystem of Georgia. *Ecology* 43: 614-624.
- Theilacker, G., and K. G. Dorsey. 1980. A review of larval fish behavior, physiology and their diversity. Pages 105-142 in G. D. Sharp, editor. Report of the workshop on the effects of environmental variation on the survival of larval pelagic fishes. Intergovernmental Oceanographic Commission, IOC Workshop Report 28, Paris, France.
- Themelis, D. E. 1986. Feeding ecology of American shad (*Alosa sapidissima*) in the lower Bay of Fundy and Minas Basin. Master's thesis. Acadia University, Wolfville, Nova Scotia.
- Vladykov, V. D. 1936. Capsules d'oeufs de raies de l'Atlantique canadien appartenant au genre Raja. *Le Naturaliste Canadien* 63: 211-231.
- Walburg, C. H. 1956. Observations on the food and growth of juvenile American shad, *Alosa sapidissima*. *Transactions of the American Fisheries Society* 86: 302-306.
- Walburg, C. H. 1955. Relative abundance of American shad, 1944-52. U.S. Fish and Wildlife Service Research Report 38, Washington, D.C.
- Walburg, C. H. 1960. Abundance and life history of the shad, St. Johns River, Florida. U.S. Fish and Wildlife Service Fishery Bulletin 60: 487-501.
- Walburg, C. H. 1963. Parent-progeny relation and estimation of optimum yield for American shad in the Connecticut River. *Transactions of the American Fisheries Society* 92: 436-439.
- Walburg, C. H., and P. R. Nichols. 1967. Biology and management of the American shad and status of the fisheries, Atlantic coast of the United States, 1960. U.S. Fish and Wildlife Service Special Science Report for Fisheries 550.
- Waldman, J. R., and K. E. Limburg. 2003. The world's shads: Summary of their status, conservation, and research needs. Pages 363-369 in K. E. Limburg, and J. R. Waldman, editors. Biodiversity, status, and conservation of the world's shads. American Fisheries Society Symposium 35, Bethesda, Maryland.
- Walters, J. F., III, and J. E. Olney. 2003. Feeding behavior of American shad during spawning migration in the York River, Virginia. Pages 201-209 in K. E. Limburg, and J. R. Waldman, editors. Biodiversity, status, and conservation of the world's shads. American Fisheries Society Symposium 35, Bethesda, Maryland.

- Watson, J. F. 1970. Distribution and population dynamics of American shad, *Alosa sapidissima* (Wilson), in the Connecticut River above the Holyoke Dam, Massachusetts. Doctoral dissertation. University of Massachusetts, Amherst, Massachusetts.
- Weaver, L. A., M. T. Fisher, B. T. Bosher, M. L. Claud, and L. J. Koth. 2003. Boshers Dam vertical slot fishway: A useful tool to evaluate American shad recovery efforts in the upper James River. Pages 339-347 in K. E. Limburg, and J. R. Waldman, editors. Biodiversity, status, and conservation of the world's shads. American Fisheries Society Symposium 35, Bethesda, Maryland.
- Weiss-Glanz, L. S., J. G. Stanley, and J. R. Moring. 1986. Species profiles: Life histories and environmental requirements of coastal fishes and invertebrates (North Atlantic) – American shad. U.S. Fish and Wildlife Service Biological Report No. 82 (11.59), and U.S. Army Corps of Engineers Report No. TR EL-82-4, Washington, D.C.
- Whitehead, P. J. P. 1985. Food and Agriculture Organization species catalogue, volume 7, clupeoid fishes of the world (suborder Clupeoidei), part I: An annotated and illustrated catalogue of the herrings, sardines, pilchards, sprats, shads, anchovies and wolf-herrings (Chirocentridae, Clupeidae and Pristigasteridae). FAO Fish Synopsis No. 125: 1-303.
- Whitney, R. R. 1961. A report on the desirability and feasibility of passing fish at Conowingo Dam. Pages 18-43 in R. R. Whitney. The Susquehanna fishery study, 1957-1960. Maryland Department of Research and Education, Solomons, Maryland.
- Whitworth, W. R., and D. H. Bennett. 1970. A limnological study of the lower Farmington River with special reference to the ability of the river to support American shad. Institute of Water Research Report No. 9, University of Connecticut, Storrs, Connecticut.
- Wiggins, T. A., T. R. Bender, V. A. Mudrak, and J. A. Coll. 1984. The development, feeding, growth and survival of cultured American shad larvae through the transition from endogenous to exogenous nutrition. Special Publication of the Pennsylvania Fish Commission, Benner Spring Fish Research Station.
- Willey, A. 1923. Notes on the distribution of free-living Copepoda in Canadian waters. Contributions to Canadian Biology 1: 303-334.
- Williams, R. G., and G. Daborn. 1984. Spawning of American shad in the Annapolis River, Nova Scotia, Canada. Proceedings of the Nova Scotian Institute of Science 34: 9-14.
- Williams, R. O., and G. E. Bruger. 1972. Investigations on American shad in the St. Johns River. Florida Department of Natural Resources Marine Research Laboratory Technical Series 66: 1-49.
- Witherell, D. B., and B. Kynard. 1990. Vertical distribution of adult American shad in the Connecticut River. Transactions of the American Fisheries Society 119: 151-155.
- Zydlewski, J., and S. D. McCormick. 1997a. The loss of hyperosmoregulatory ability in migration juvenile American shad, *Alosa sapidissima*. Canadian Journal of Fisheries and Aquatic Sciences 54: 2377-2387.
- Zydlewski, J., and S. D. McCormick. 1997b. The ontogeny of salinity tolerance in the American shad, *Alosa sapidissima*. Canadian Journal of Fisheries and Aquatic Sciences 54: 182-189.

Chapter 3

HICKORY SHAD

(Alosa mediocris)

Section I. Hickory Shad Description of Habitat

Hickory Shad General Habitat Description and Introduction

Hickory shad (*Alosa mediocris*) are anadromous fish that spend most of their adult lives at sea, entering brackish and freshwater only to spawn (Colette and Klein-MacPhee 2002). Little is known about the life history and specific habitat requirements of this species. However, coastal migrations and habitat requirements are thought to be similar to that of other alosine species, particularly American shad (Klauda et al. 1991). Very few spawning studies have been conducted in part due to a general lack of interest in this species relative to other alosines (Klauda et al. 1991).

Historically, hickory shad abundance has been lower than other alosine species in many areas (Atran et al. 1983; Speir 1987). The historical range of hickory shad is thought to have extended as far north as the Gulf of Maine and possibly to Campobello Island, New Brunswick (Hildebrand 1963). The current northern boundary of hickory shad is Cape Cod, Massachusetts (Batsavage and Rulifson 1998), with the highest abundances occurring from New York southward. According to Klauda et al. (1991), spawning does not frequently occur north of Maryland. Hickory shad are reported to occur as far south as central Florida (Hildebrand 1963; Williams et al. 1975; McBride 2000). Waters south of Cape Canaveral, Florida, are unsuitable for hickory shad due to semi-tropical water temperatures (Williams et al. 1975).

Hickory shad have only supported minor commercial fisheries because the bony meat is considered to be inferior to American shad (Whitehead 1985). However, some consider hickory shad roe to be more delectable than the roe of any of the other river herrings (Nichols 1959). Furthermore, adult hickory shad are highly sought after by sport fishermen when they ascend rivers and tributaries during their spawning run (Mansueti 1962; Pate 1972). Although hickory shad populations have not been adequately monitored, there is information indicating that some stocks are healthy (Street 1970; Batsavage and Rulifson 1998; ASMFC 1999). Since 1989, the Albemarle Sound, North Carolina, population of hickory shad has experienced a surge in numbers, which supports a growing sport fishery on the Roanoke River and increased commercial fishing in Albemarle Sound. A short life span and low fecundity, however, makes this North Carolina population vulnerable to overharvest (Batsavage and Rulifson 1998). In contrast, hickory shad have been found to be highly fecund in other areas. For example, egg production was estimated to be as high as 509,749 eggs per female in the Altamaha River, Georgia (Street 1970).

Since the mid-1990s, hickory shad numbers have increased in the upper Chesapeake Bay and its tributaries (ASMFC 1999), including the lower Susquehanna, Potomac near Washington, D.C., upper Rappahannock, and James rivers (R. St. Pierre, U.S. Fish and Wildlife Service, personal communication). Some landings data also support the idea that hickory shad populations are thriving. The National Marine Fisheries Service (NMFS) estimated that 5.6 metric tons of hickory shad were landed in 1990, and by 1999, estimated landings dramatically increased to 61.9 metric tons (Waldman and Limburg 2003).

Part A. Hickory Shad Spawning Habitat

Geographical and temporal patterns of migration

Little is known about hickory shad behavior or utilization of riverine or marine habitats (Colette and Klein-MacPhee 2002). It is assumed that female hickory shad broadcast their eggs into the water between dusk and midnight where one or more males fertilize them; this behavior is similar to the spawning behavior of American shad (Mansueti 1962; Jones et al. 1978). Hickory shad are known to be repeat spawners, with individuals spawning an average of three to five times before dying (Schaeffer 1976). Unlike American shad, there is no progressive increase in spawning frequency from south to north. Most river systems have 70 to 80% repeat spawners, although there are exceptions (Street and Adams 1969; Loesch et al. 1979; Rulifson et al. 1982; Richkus and DiNardo 1984). Data collected from Maryland rivers indicated that 72% of females and 62% of males had previously spawned (B. M. Richardson, Maryland Department of Natural Resources, personal communication). In sharp contrast, Sholar (1977) found that in the Cape Fear River, North Carolina, only 19% of males and 9% of females were repeat spawners.

The age distribution of adult hickory shad in coastal rivers from Florida to North Carolina ranges from two to eight years (Rulifson et al. 1982). Eighty percent of males in the Octoraro Creek, Maryland, were sexually mature at age 2 (Schaeffer 1976). Data collected from a group of Maryland rivers found that 50% of males and 36% of females were sexually mature at age 2; by age 3, 89% of males and 90% of females had spawned (B. M. Richardson, Maryland Department of Natural Resources, personal communication). Further south, in the Altamaha River, Georgia, 75% of females and 49% of males were sexually mature by age 2 (Street and Adams 1969). In general, the majority of females are likely to become sexually mature at least one year later than males (Klauda et al. 1991; Batsavage and Rulifson 1998).

Hickory shad ascend coastal rivers during spring migration. Although it is assumed that these fish return to their natal rivers to spawn, there is no documented evidence of this behavior (Batsavage and Rulifson 1998). Hickory shad distribution in the riverine environment is similar to that of American shad (Rulifson et al. 1982). In North Carolina, the freshwater reaches of coastal rivers are the major spawning sites for hickory shad. In the Roanoke River, eggs have been collected during April and early May from the main channel near Weldon, North Carolina (Sparks 1998; Harris and Hightower 2007), and larvae have been collected farther downstream (Walsh et al. 2005). In the Neuse River, North Carolina, Pate (1972) detected spawning in flooded swamps and sloughs off channels of tributary creeks, but not in the mainstem river. However, Burdick and Hightower (2006) detected spawning in both mainstem Neuse River and tributary sites. In Georgia, hickory shad apparently spawn in flooded areas off the Altamaha River, and not in the mainstem of the upper reaches (Adams 1970). Major spawning sites in Virginia have been discovered in mainstem rivers at the fall line, further downstream, and in tributaries (Davis et al. 1970). Mansueti (1962) found that hickory shad spawned approximately 6 to 10 km (3.7 to 6.2 miles) upriver of major spawning sites of American shad in the mainstem of the Patuxent River, Maryland. In contrast, hickory shad in the St. Johns River, Florida, did not migrate as far upstream as American shad (Moody 1961). Compared to American shad and striped bass, hickory shad in the Neuse River basin tended to spawn further downstream and made greater use of tributaries (Burdick and Hightower 2006).

Adult hickory shad can be found in the St. Johns River, Florida, as early as December or possibly even November (McBride 2000), but may be absent by late January to mid-February (Williams et al. 1975) or early March (McBride 2005). Spawning in the Santee and Cooper rivers, South Carolina, may occur between early March through mid-May (Bulak and Curtis 1979). In the Chesapeake Bay, spawning may begin in early April (Mansueti and Hardy 1967), and typically peaks in early May (Mansueti 1962). However, spawning may occur as late as June in freshwaters of Virginia (Davis et al. 1970). Furthermore, a weaker second run of spawners may also migrate later through the Chesapeake Bay (Hildebrand and Schroeder 1928). It is unknown if the hickory shad that spawn during the fall run also participate in the spring run (Schaeffer 1976).

Large variations in the size of young hickory shad have been reported at spawning sites. This has lead researchers to hypothesize that this species has a protracted spawning period, where small amounts of eggs are released over a long period of time (Mansueti 1962; DesFosse et al. 1994). Mansueti (1962) found very few ripe-running hickory shad on the spawning grounds in the Chesapeake Bay area, and suggested that gonads mature rapidly and spawning occurs at night.

In Albemarle Sound, North Carolina, hickory shad appear to have a prolonged spawning period when compared to other alosines, but that period occurs earlier in the season (Batsavage and Rulifson 1998). It is unknown how long adult hickory shad remain in freshwater after they have spawned.

Spawning substrate associations

B. M. Richardson (Maryland Department of Natural Resources, personal communication) has reported catching adult hickory shad in waters of Maryland rivers, where complex structures, such as ledges and fallen trees are present. Bottom composition in these waters tended to be mud, sand, and/or gravel. Harris and Hightower (2007) reported that hickory shad spawning in the Roanoke River were concentrated in areas of moderate to high water velocity and sediments dominated by cobble, gravel, and sand, but not silt.

Spawning depth associations

Little information is available on spawning depth preferences for hickory shad. Hawkins (1980) noted that hickory shad prefer to spawn in the deep, dark tributaries of the Neuse River, North Carolina. Similarly, Moody (1961) found that hickory shad were more abundant (by frequency of occurrence and by weight) in deeper water than American shad in the St. Johns River, Florida.

Spawning water temperature

Temperature (°C)	Location	Citation
13 - 21	Albemarle, NC	Street et al. 1975
14 - 19	Tar River, NC	Marshall 1976
15 - 22	Altamaha River, GA	Street 1970
7.8 - 20.5	Maryland rivers	B. M. Richardson, MD DNR, personal communication

Table 3-1. Hickory shad spawning temperatures for locations along the Atlantic coast of North America

Some studies have examined spawning temperature preferences for hickory shad (Table 3-1). Spawning activity occurs in water temperatures that range from 8 to 22°C (Rulifson et al. 1982; Batsavage and Rulifson 1998), but typically peaks in waters temperatures between 15 and 19°C (Mansueti 1962; Street 1970; Pate 1972; Schaeffer 1976; Rulifson et al. 1982). In the Neuse River, North Carolina, spawning occurred at water temperatures of 10 to 23°C, with peak numbers of eggs collected at 12 to 16°C (Burdick and Hightower 2006). Eggs were collected in the Roanoke River at temperatures ranging from 10.2 to 17.0°C (Harris and Hightower 2007).

Spawning dissolved oxygen associations

Adults have been found spawning in Maryland waters where the dissolved oxygen level was between 5.7 and 11.8 mg/L (B. M. Richardson, Maryland Department of Natural Resources, personal communication). Eggs were collected in the Roanoke River at dissolved oxygen levels ranging from 6.76 to 11.27 mg/L (Harris and Hightower 2007).

Spawning water velocity/flow

Hawkins (1980) reported that hickory shad might prefer slow-flowing areas of the Neuse River, North Carolina, for spawning. Conversely, hickory shad in Maryland have been reported to favor habitat with faster moving water than that of American shad (B. M. Richardson, Maryland Department of Natural Resources, personal communication). Roanoke River sites where hickory shad spawning occurred had significantly higher water velocities than nearby sites with no spawning (Harris and Hightower 2007). Main channel sites where spawning occurred had median current velocities of 0.20 to 0.39 m/s (Harris and Hightower 2007).

Spawning feeding behavior

Pate (1972) did not find any stomach contents in over 400 adult migrating hickory shad that he examined from the Neuse River, North Carolina. However, adult hickory shad in the St.

Johns River, Florida, were found actively feeding, with 62.4% of the food items consisting of fish, and to a lesser extent, crustaceans (Williams et al. 1975).

Spawning competition and predation

Although no information on predation was found in the literature, striped bass have been reported preying heavily on hickory shad beginning in early April at Deer Creek, Maryland (B. M. Richardson, Maryland Department of Natural Resources, personal communication).

Part B. Hickory Shad Egg and Larval Habitat

Geographical and temporal movement patterns

In general, little is known about the movement of hickory shad eggs and larvae. Eggs are generally adhesive and typically sink to the bottom in undisturbed or moderately agitated water, but are semi-demersal in slow moving currents and buoyant under turbulent conditions (Mansueti 1962).

Egg and larval depth associations

As with adult hickory shad, little habitat information is known about larval individuals. Mansueti (1962) found hickory shad (9 to 20 mm) at depths of 20 feet at approximately 35 to 40 miles upstream from the mouth of the Patuxent River, Maryland.

Egg and larval water temperature

In the wild, hickory shad eggs have been collected in water temperatures between 9.5 and 22°C in rivers of North Carolina (Street 1970; Pate 1972; Marshall 1976; Hawkins 1980). In the laboratory, early efforts to propagate hickory shad failed. Eventually, Mansueti (1962) successfully hatched eggs in the laboratory at 18.3°C and 21.1°C, with hatching occurring 5 to 10 hours sooner under the warmer conditions. Prolarvae hatching occurred 2 to 3 days after fertilization, with an average hatch time of 55 to 60 hours. Prolarvae fully absorb the yolk sac after 4 to 5 days, and postlarvae begin feeding exogenously at this point. The size range of postlarvae is from 5.5 to 7.0 mm (Mansueti 1962). The state of Maryland reported successful incubation of eggs at 17.8°C (64°F), with hatching occurring in 5 to 6 days (B. M. Richardson, Maryland Department of Natural Resources, personal communication). Newer aquaculture spawning methods have been highly successful, and larvae and fingerlings have been transplanted in large quantities to Chesapeake Bay tributaries (Hendricks 2003).

Egg and larval dissolved oxygen associations

Viable hickory shad eggs have been collected in the Neuse River, North Carolina, where dissolved oxygen concentrations were between 5 and 10 mg/L (Hawkins 1980).

Egg and larval pH associations

Hickory shad eggs were found in water with a pH range of 6.4 to 6.6 in the Neuse River, North Carolina (Hawkins 1980).

Part C. Hickory Shad Juvenile (Riverine/Estuarine) Habitat

Geographical and temporal movement patterns

Postlarval hickory shad begin transforming into juveniles when they are 10 to 35 mm long (Ulrich et al. 1979; Krauthamer and Richkus 1987); the minimum size at which they are considered fully developed juveniles is 35 mm (Mansueti and Hardy 1962). Capture of juvenile hickory shad in Maryland rivers often occurs at sharp drop-offs, in schools of several dozen, which suggests a strong schooling behavior (B. M. Richardson, Maryland Department of Natural Resources, personal communication).

Several studies suggest that most young hickory shad leave freshwater and brackish habitats in early summer and migrate to estuarine nursery areas at an earlier age than other anadromous alosines (Mansueti 1962; Adams 1970; Pate 1972; Sholar 1977). Juveniles have also been caught in the surf zone off Long Island, New York, from April to November, which supports this hypothesis (Schaefer 1967). In the Altamaha River, Georgia, juveniles drift downstream and reach the estuary by late spring (Street 1970). Juveniles also drift down the Pee Dee and Waccamaw rivers, in South Carolina, earlier than young American shad, and enter Winyah Bay by July, remaining there throughout the first summer. By early fall, juveniles have moved into oceanic waters (Crochet et al. 1976). Trippell et al. (2007) found a few juvenile hickory shad in the St. Johns River, Florida, near Palatka (rkm 127), from May to October, with the highest catch rates occurring in October.

Some juvenile hickory shad may forego estuarine waters altogether and move directly into saltwater, unlike other alosine species that use freshwater nurseries before moving into marine waters (Pate 1972; Sholar 1977; Batsavage and Rulifson 1998). This ability to move directly into saltwater is believed to occur in hickory shad at an earlier age than for other anadromous alosines (Mansueti 1962; Schaefer 1967; Adams 1970; Pate 1972; Sholar 1977; Batsavage and Rulifson 1998). Additionally, some researchers suggest that juvenile hickory shad initially move to shallow offshore areas in Georgia near the mouth of the Altamaha River, and then disperse farther by August and September (Godwin and Adams 1969; Street 1970). Juvenile hickory shad are thought to be larger in size than other alosines at similar ages due to an earlier spawning period and a faster growth rate (Godwin and Adams 1969). Juvenile hickory shad that are larger than average compared to other alosines have been captured in Maryland (Mansueti 1962; Virginia (Atran et al. 1983) and Georgia rivers (Adams 1970).

Juveniles and the saltwater interface

In Maryland, juvenile hickory shad were captured in waters with salinities that ranged from 0 to 7.2 ppt (B. M. Richardson, Maryland Department of Natural Resources, personal communication). In addition, juveniles were found during the summer in estuarine waters of the Altamaha River, Georgia, when salinities reached 10 ppt, and during the winter, when salinities ranged from 10 to 20 ppt (Street 1970). As noted above, juveniles may forego the oligohaline portion of the estuary in favor of a more saline nursery environment (Pate 1972).

Juvenile depth associations

In South Carolina, juvenile hickory shad are more predominant in shallow expanses of sounds and bays, compared to deeper, channel habitats occupied by juvenile American shad and blueback herring. The variation in distribution is likely the result of differences in food preferences. Small fishes preferred by hickory shad are likely more numerous in shallower habitats adjacent to marshlands (McCord 2003).

Juvenile water temperature

B. M. Richardson (Maryland Department of Natural Resources, personal communication) has caught juveniles in Maryland rivers with water temperatures between 16 and 31°C, usually corresponding to early July through early October. Davis (1973) reported that hickory shad remain in freshwater until temperatures drop in October and November, then move downstream as temperatures continue to decrease.

Juvenile dissolved oxygen associations

Juveniles in Maryland waters were captured where dissolved oxygen ranged from 4.1 to 10.9 mg/L (B. M. Richardson, Maryland Department of Natural Resources, personal communication).

Part D. Hickory Shad Late Stage Juvenile and Adult Marine Habitat

Geographical and temporal patterns at sea

As with many aspects of hickory shad life history, very little is known about the distribution and movements of hickory shad in the ocean (Street 1970; Richkus and DiNardo 1984). Adults have been caught along the southern New England coast in the summer and fall (Bigelow and Schroeder 1953) and off Long Island, New York (Schaefer 1967). Anglers report catching them in nearshore waters at Cape May, New Jersey, from May to November, and then capturing them in inlets from November through December (W. Gordon, recreational angler, personal communication). Unlike American shad, hickory shad rarely migrate to the Gulf of Maine or upper Bay of Fundy during the summer (M. J. Dadswell, Canada Department of Fisheries and Oceans, personal communication). Furthermore, some researchers believe that adults do not move far from land while at sea (Mansueti and Hardy 1967).

Temperature associations at sea

Little information is available on hickory shad habitat associations offshore. Anglers fishing for hickory shad have reported that they will move further offshore from the nearshore waters of New Jersey, when water temperatures reach above 21°C (W. Gordon, recreational angler, personal communication).

Feeding behavior at sea

Adult hickory shad are piscivorous; they generally feed on sand lance, anchovies, cunner, herring, scup, and silversides. This species may also feed on squid, fish eggs, small crabs, and pelagic crustaceans (Hildebrand and Schroeder 1928; Williams et al. 1975; Bigelow and Schroeder 2002).

Section II. Significant Environmental, Temporal, and Spatial Factors Affecting Distribution of Hickory Shad

Table 3-2. Significant environmental, temporal, and spatial factors affecting distribution of hickory shad. Given that there is very little information on hickory shad, this table should be used only as a general reference. The term “reported” is used to denote ranges that were found in the literature, but should not be regarded as the full range tolerated by this species. NIF = No Information Found.

Life Stage	Time of Year and Location	Depth (m)	Temperature (°C)	Salinity (ppt)	Substrate	Current Velocity (m/sec)	Dissolved Oxygen (mg/L)
Spawning Adult	Early December (FL) through late June (VA) in natal rivers and tributaries from Connecticut River southward to Halifax River, Florida (mostly found from Maryland rivers southward)	Tolerable: NIF Optimal: NIF Reported: May prefer deeper waters than American shad	Tolerable: 8-23 Optimal: 12-19 Reported: Variable	Tolerable: NIF Optimal: NIF Reported: Usually freshwater	Tolerable: NIF Optimal: NIF Reported: Cobble, gravel, sand	Tolerable: NIF Optimal: NIF Reported: Variable	Tolerable: NIF Optimal: NIF Reported: Found 5.7-11.8
Egg & Larvae	Early December (FL) through late June (VA) (eggs may be released in batches) at spawning areas or slightly downstream	Tolerable: NIF Optimal: NIF Reported: NIF	Tolerable: 9.5-22 (egg) Optimal: NIF Reported: NIF	Tolerable: NIF Optimal: NIF Reported: NIF	Tolerable: NIF Optimal: NIF Reported: NIF	Tolerable: NIF Optimal: NIF Reported: NIF	Tolerable: NIF Optimal: NIF Reported: Minimum 5
Early Juvenile – Riverine/ Estuarine Environment	When they reach 35 mm TL (begin moving downstream at an earlier age than other alosines); reach estuaries by late spring/ early summer and ocean by early fall; or may forego estuarine waters and move directly to saltwater	Tolerable: NIF Optimal: NIF Reported: Generally shallow waters	Tolerable: 16-31 Optimal: NIF Reported: Variable	Tolerable: NIF Optimal: NIF Reported: Freshwater, brackish, and saltwater	Tolerable: NIF Optimal: NIF Reported: NIF	Tolerable: NIF Optimal: NIF Reported: NIF	Tolerable: NIF Optimal: NIF Reported: Minimum 4

Life Stage	Time of Year and Location	Depth (m)	Temperature (°C)	Salinity (ppt)	Substrate	Current Velocity (m/sec)	Dissolved Oxygen (mg/L)
Subadult & Non- spawning Adult– Estuarine / Oceanic Environment	Up to 8 years in Cape Cod, Massachusetts to Cape Canaveral, Florida (concentrated from NY southward)	Tolerable: NIF Optimal: NIF Reported: NIF	Tolerable: NIF Optimal: NIF Reported: Move offshore when temperatures reach 21°C	Tolerable: NIF Optimal: NIF Reported: NIF	Tolerable: NIF Optimal: NIF Reported: NIF	Tolerable: NIF Optimal: NIF Reported: NIF	Tolerable: NIF Optimal: NIF Reported: NIF

Section III. Hickory Shad Literature Cited

- Adams, J. G. 1970. Clupeids in the Altamaha River, Georgia. Georgia Game and Fisheries Commission, Coastal Fisheries Division Contribution Series No. 20, Brunswick, Georgia.
- ASMFC (Atlantic States Marine Fisheries Commission). 1999. Amendment 1 to the interstate fishery management plan for shad & river herring. Fishery Management Report No. 35, Washington, D.C.
- Atran, S. M., J. G. Loesch, and W. H. Kriete, Jr. 1983. An overview of the status of *Alosa* stocks in Virginia. Virginia Institute of Marine Science, Marine Resources Report No. 82-10, Gloucester Point, Virginia.
- Batsavage, C. F., and R. A. Rulifson. 1998. Life history aspects of the hickory shad (*Alosa mediocris*) in the Albemarle Sound/Roanoke River watershed, North Carolina. Report to the North Carolina Marine Fisheries Commission, Fishery Resource Grant No. M6057, ICMR Contribution Series No. ICMR-98-02, Morehead City, North Carolina.
- Bigelow, H. B., and W. C. Schroeder. 1953. Fishes of the Gulf of Maine. Fishery Bulletin 74 of the Fishery Bulletin of the Fish and Wildlife Service, volume 53. United States Government Printing Office, Washington, D.C.
- Bulak, J. S., J. S. Tuten, and T. A. Curtis. 1979. Santee-Cooper blueback herring studies. Annual Progress Report Project No. SCR 1-3: 1 Jan. 1979 to 30 Sept. 1979. South Carolina Wildlife and Marine Resources Department, Division of Wildlife and Freshwater Fisheries, Barnwell, South Carolina.
- Burdick S. M., and J. E. Hightower. 2006. Distribution of spawning activity by anadromous fishes in an Atlantic slope drainage after removal of a low-head dam. Transactions of the American Fisheries Society 135: 1290.
- Collette, B., and G. Klein-MacPhee, editors. 2002. Bigelow and Schroeder's fishes of the Gulf of Maine, 3rd edition. Smithsonian Institution Press, Washington, D.C.
- Crochet, D. W., D. E. Allen, and M. L. Hornberger. 1976. Commercial anadromous fishery Waccamaw and Pee Dee Rivers. South Carolina Wildlife and Marine Resources Department, Division of Wildlife and Freshwater Fisheries, Barnwell, South Carolina.
- Davis, J. 1973. Spawning sites and nurseries of fishes of the genus *Alosa* in Virginia. Proceedings of the Workshop on Egg, Larval and Juvenile Stages of Fish in Atlantic Coast Estuaries, NOAA Technical Publication No. 1, Silver Spring, Maryland.
- Davis, J., J. P. Miller, and W. L. Wilson. 1970. Biology and utilization of anadromous alosines. Completion Report from 1967-1970. Virginia Institute of Marine Science, Gloucester Point, Virginia.
- DesFosse, J. C., J. G. Loesch, N. M. Burkhead, and R. E. Jenkins. 1994. Herrings, family Clupeidae. Pages 209-228 in R. E. Jenkins, and N. M. Burkhead, editors. Freshwater fishes of Virginia. American Fisheries Society, Bethesda, Maryland.
- Godwin, W. F., and J. G. Adams. 1969. Young clupeids of the Altamaha River, Georgia. Georgia Game and Fisheries Commission, Division of Marine Fisheries Contribution Series No. 15, Brunswick, Georgia.

- Harris, J. E., and J. E. Hightower. 2007. Relative abundance of migratory fishes within a restored braided-channel habitat below the Roanoke Rapids Dam. Annual Report to Dominion. North Carolina Cooperative Fish and Wildlife Research Unit, North Carolina State University, Raleigh, North Carolina.
- Hawkins, J. H. 1980. Investigation of anadromous fishes of the Neuse River North Carolina. Special Science Report No. 34, North Carolina Department of Natural Resources and Community Development, Division of Marine Fisheries, Morehead City, North Carolina.
- Hendricks, M. L. 2003. Culture and transplant of alosines in North America. Pages 303-312 in K. E. Limburg, and J. R. Waldman, editors. Biodiversity, status, and conservation of the world's shads. American Fisheries Society Symposium 35, Bethesda, Maryland.
- Hildebrand, S. F. 1963. Family Clupeidae. Pages 257-454 in H. B. Bigelow, editor. Fishes of the Western North Atlantic, part 3. Sears Foundation for Marine Research, Yale University, New Haven, Connecticut.
- Hildebrand, S. F., and W. C. Schroeder. 1928. Fishes of Chesapeake Bay. Bulletin of the U.S. Bureau of Fisheries 43: 1-366.
- Jones, P. W., F. D. Martin, and J. D. Hardy, Jr. 1978. Development of fishes of the mid-Atlantic Bight. An atlas of egg, larval and juvenile stages, volume I.: Acipenseridae through Ictaluridae. U.S. Fish and Wildlife Service Report No. FWS/OBS-78/12, Washington, D.C.
- Klauda, R. J., S. A. Fischer, L. W. Hall, Jr., and J. A. Sullivan. 1991. American shad and hickory shad. Pages 9.1-9.27 in S. L. Funderburk, J. A. Mihursky, S. J. Jordan, and D. Riley, editors. Habitat requirements for Chesapeake Bay living resources, 2nd edition. Chesapeake Bay Program, Living Resources Subcommittee, Annapolis, Maryland.
- Krauthamer, J., and W. Richkus. 1987. Characterization of the biology of and fisheries for Maryland stocks of American and hickory shad. Prepared for Maryland Department of Natural Resources, Tidewater Administration, Annapolis, Maryland.
- Loesch, J. G., W. H. Kriete, Jr., J. G. Travelstead, E. J. Foell and M. A. Hennigar. 1979. Biology and management of mid-Atlantic anadromous fishes under extended jurisdiction. Special Report No. 236, Virginia Institute of Marine Science, Gloucester Point, Virginia.
- Mansueti, A. J., and J. D. Hardy, Jr. 1967. Development of fishes of the Chesapeake Bay region: An atlas of egg, larval, and juvenile stages, part I. Natural Resources Institute, University of Maryland, College Park, Maryland.
- Mansueti, R. J. 1962. Eggs, larvae, and young of the hickory shad, *Alosa mediocris*, with comments on its ecology in the estuary. Chesapeake Science 3: 173-205.
- Marshall, M. D. 1976. Anadromous fisheries research program, Tar River, Pamlico River, and northern Pamlico Sound. Completion Report Project No. AFCS-10, North Carolina Division of Marine Fisheries, Morehead City, North Carolina.
- McBride, R. S. 2000. Florida's shad and river herring (*Alosa* species): A review of population and fishery characteristics. Florida Fish and Wildlife Conservation Commission, Florida Marine Research Institute Technical Report No. TR-5, St. Petersburg, Florida.

- McBride, R. S. 2005. Develop and evaluate a decision-making tool for rebuilding American and hickory shad. Final Performance Report for Sport Fish Restoration Grant Number F-106. Fish and Wildlife Research Institute, St. Petersburg, Florida.
- McCord, J. W. 2003. Investigation of fisheries parameters for anadromous fishes in South Carolina. Completion Report to NMFS, 1 Mar. 1998 – 28 Feb. 2001, Project No. AFC-53. South Carolina Department of Natural Resources, Charleston, South Carolina.
- McLane, W. M. 1955. Fishes of the St. Johns River system. Doctoral dissertation, University of Florida, Tallahassee, Florida.
- Moody, H. L. 1961. Exploited fish populations of the St. Johns River, Florida. *Quarterly Journal of the Florida Academy of Sciences* 24: 1-18.
- Nichols, P. R. 1959. St. Johns shad fever. *Florida Wildlife* 12: 22-39.
- Pate, P. P. 1972. Life history aspects of the hickory shad, *Alosa mediocris* (Mitchill), in the Neuse River, North Carolina. Masters thesis. North Carolina State University, Raleigh, North Carolina.
- Richkus, W. A., and G. DiNardo. 1984. Current status and biological characteristics of the anadromous alosid stocks of the eastern United States: American shad, hickory shad, alewife, and blueback herring. Interstate Fisheries Management Program, Atlantic States Marine Fisheries Commission, Washington, D.C.
- Rulifson, R. A., M. T. Huish, and R. W. Thoesen. 1982. Anadromous fish in the southeastern United States and recommendations for development of a management plan. U.S. Fish and Wildlife Service, Atlanta, Georgia.
- Schaefer, R. H. 1967. Species composition, size and seasonal abundance of fish in the surf waters of Long Island. *New York Fish and Game Journal* 14: 1-46.
- Schaeffer, J. E., Jr. 1976. The hickory shad – an endangered species in Maryland? Pages 78-89 in *Proceedings of the 1st Annual Meeting of the Potomac Chapter of the American Fisheries Society, Maryland/Virginia*.
- Sholar, T. M. 1977. Anadromous fisheries research program, Cape Fear River system, phase I. North Carolina Department of Natural Resources and Community Development, Division of Marine Fisheries, Morehead City, North Carolina.
- Sparks, K. L. 1998. Identification of major spawning habitats used by American shad (*Alosa sapidissima*) in the Roanoke River, North Carolina. Master's thesis. North Carolina State University, Raleigh, North Carolina.
- Speir, H. J. 1987. Status of some finfish stocks in the Chesapeake Bay. *Water, Air, Soil, Pollution* 35: 49-62.
- Street, M. W. 1970. Some aspects of the life histories of hickory shad, *Alosa mediocris* (Mitchill), and blueback herring, *Alosa aestivalis* (Mitchill), in the Altamaha River, Georgia. Masters thesis. University of Georgia, Athens, Georgia.
- Street, M. W., and J. G. Adams. 1969. Aging of hickory shad and blueback herring in Georgia by the scale method. Georgia Game and Fisheries Commission, Marine Fisheries Division, Contribution Series No. 18, Brunswick, Georgia.

- Street, M. W., P. P. Pate, B. F. Holland, Jr., and A. B. Powell. 1975. Anadromous fisheries research program, northern coastal region. Completion Report Project No. AFCS-8, North Carolina Division of Marine Fisheries, Morehead City, North Carolina.
- Trippel, N. A., M. S. Allen, and R. S. McBride. 2007. Seasonal trends in abundance and size of juvenile American shad, hickory shad, and blueback herring in the St. Johns River, Florida, and comparison with historical data. *Transactions of the American Fisheries Society* 136: 988-993.
- Ulrich, G., N. Chipley, J. W. McCord, and D. Cupka. 1979. Development of fishery management plans for selected anadromous fishes in South Carolina/Georgia. Special Science Report No. 14, South Carolina Wildlife and Marine Resources Department, Marine Research Center, South Carolina.
- Waldman, J. R., and K. E. Limburg. 2003. The world's shads: A summary of their status, conservation, and research needs. Pages 363-369 *in* K. E. Limburg, and J. R. Waldman, editors. Biodiversity, status, and conservation of the world's shads. American Fisheries Society Symposium 35, Bethesda, Maryland.
- Walsh, H. J., L. R. Settle, and D. S. Peters. 2005. Early life history of blueback herring and alewife in the lower Roanoke River, North Carolina. *Transactions of the American Fisheries Society* 134: 910-926.
- Whitehead, P. J. P. 1985. Food and Agriculture Organization species catalogue, volume 7, clupeoid fishes of the world (suborder Clupeoidei), part I: An annotated and illustrated catalogue of the herrings, sardines, pilchards, sprats, shads, anchovies and wolf-herrings (Chirocentridae, Clupeidae and Pristigasteridae). FAO Fish Synopsis No. 125: 1-303.
- Williams, R., W. Gray, and J. Huff. 1975. Study of anadromous fishes of Florida. Completion Report for the period 1 May 1971 to 30 June 1974 for research funded by the Anadromous Fish Act (PL 89-304), National Marine Fisheries Service, St. Petersburg, Florida.

Chapter 4

ALEWIFE

(Alosa pseudoharengus)

Section I. Alewife Description of Habitat

Alewife General Habitat Description and Introduction

The alewife (*Alosa pseudoharengus*) is an anadromous, highly migratory, euryhaline, pelagic, schooling species. The species spends the majority of its life at sea, returning to freshwater river systems along the Atlantic coast of the United States to spawn (ASMFC 1985). While most alewife are native-anadromous fish, some have been introduced to landlocked systems. Researchers examined two distant anadromous alewife stocks to test whether landlocked stocks were more closely related to St. Croix anadromous stocks or to more geographically distant anadromous stocks. Landlocked alewife were found to be distantly related to all the anadromous stocks tested. A variety of statistical tests confirmed that anadromous and landlocked populations of alewife in the St. Croix are genetically divergent ($F_{ST} = 0.244$). These results implied that very little, if any, interbreeding occurs between the two life history types (Bentzen and Paterson 2006; Willis 2006). Furthermore, significant genetic differences were observed between anadromous alewife populations in the St. Croix and anadromous populations in the LaHave and Gaspereau Rivers, as well as between the two anadromous St. Croix samples (Dennis Stream and Milltown). These results imply homing of alewives to their natal streams and, consequently, at least partial reproductive isolation between spawning runs, even at the level of tributaries within the St. Croix River (Willis 2006).

The historical coastal range of the anadromous alewife was from South Carolina to Labrador, Nova Scotia, and northeastern Newfoundland (Berry 1964; Winters et al. 1973; Burgess 1978). However, more recent surveys indicate that they do not currently occur in the southern range beyond North Carolina (Rulifson 1982; Rulifson et al. 1994). Alewife from the southernmost portion of the species' range migrate long distances (over 2000 km) in ocean waters of the Atlantic seaboard. Patterns of migration may be similar to those of American shad (*Alosa sapidissima*) (Neves 1981). Although alewife and blueback herring co-occur throughout much of their respective ranges, alewife are typically more abundant than blueback herring in the northern portion of their range (Schmidt et al. 2003).

Recent analyses to determine the current status of alewife in the Connecticut, Hudson, and Delaware River systems, suggest that alewife are showing signs of overexploitation (for example, lower mean age, fewer returning spawners, and lower overall abundance) in all of these rivers. However, researchers noted that recently some runs in the northeastern U.S. and Canada have shown increased alewife abundance (Schmidt et al. 2003). Furthermore, alewife appeared to be thriving in inland waters, colonizing many freshwater bodies, including all five Great Lakes (Waldman and Limburg 2003).

While this document will focus primarily on the anadromous alewife populations, much of the research on 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 (Klauda et al. 1991).

Part A. Alewife Spawning Habitat

Geographical and temporal patterns of migration

The spring adult alewife migration to spawning grounds in freshwater and brackish water progresses seasonally from south to north, with populations further north returning later in the season as water temperatures rise. Neves (1981) suggested that alewife migrate from offshore waters north of Cape Hatteras, encountering the same thermal barrier as American shad. Alewife then move south along the Atlantic coast for fish homing to southern rivers, while northbound pre-spawning adults continue traveling up the coast (Stone and Jessop 1992). The species spawns in rivers, ponds, and lakes (lacustrine habitat), as far south as North Carolina and as far north as the St. Lawrence River, Canada (Neves 1981; S. Lary, U.S. Fish and Wildlife Service, personal communication).

State or region	Spawning season	Citations
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
	mid-May to mid-June	S. Lary, U.S. Fish and Wildlife Service, personal communication
Massachusetts	early to mid-April	Belding 1921; 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

Table 4-1. Reported spawning seasons for alewife along the Atlantic coast of North America

Alewife typically spawn from late February to June in the south, and from June through August in the north (Table 4-1) (Marcy 1976a; Neves 1981; Loesch 1987). Spawning is

triggered most predictably by a change in the water temperature. Movement upstream may be controlled by water flow, with increased movement occurring during higher flow periods (Collins 1952; Richkus 1974). However, extreme high flows can act as a velocity barrier delaying or preventing upstream migration and access to spawning habitat (S. Lary, U.S. Fish and Wildlife Service, personal communication).

Although adult alewife will move upstream at various times of the day, peak migration typically occurs between dawn and noon, and from dusk to midnight (Richkus 1974; Rideout 1974; Richkus and Winn 1979). Researchers have found that high midday movement is restricted to overcast days, and nocturnal movement occurs when water temperatures are abnormally high (Jones et al. 1978). Typically, males arrive before females at the mouths of spawning rivers (Cooper 1961; Tyus 1971; Richkus 1974).

There is strong evidence suggesting that alewife home to their natal rivers to reproduce; however, some individuals have been found to colonize new areas. Alternatively, alewife may 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 pre-spawning period (late winter, early spring), but not during the spawning run. It appears that olfaction is the primary means for homing behavior (Ross and Biagi 1990).

Spawning location (ecological)

Alewife select slow-moving sections of rivers or streams to spawn, where the water may be as shallow as 30 cm (Jones et al. 1978). The species may also spawn in lakes or ponds, including freshwater coves behind barrier beaches (Smith 1907; Belding 1921; Leim and Scott 1966; Richkus 1974; Colette and Klein-MacPhee 2002). In watersheds where dams are an impediment, spawning may occur in shore-bank eddies or deep pools below the dams (Loesch and Lund 1977). Additionally, in New England and Nova Scotia, alewife spawn in lakes and ponds located within coastal watersheds (Loesch 1987). For this reason, they are typically more abundant than blueback herring in rivers with abundant headwater ponds. In rivers where headwater ponds are absent or scarce, alewife are less abundant in headwater reaches; however, blueback herring utilize the mainstream proper for spawning in those systems (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 ascend further upstream than blueback herring (Hildebrand 1963; Scott and Crossman 1973), Loesch (1987) noted that both species have the ability to ascend rivers far upstream.

Boger (2002) found that river herring within the Rappahannock River watershed spawned in larger, elongated watersheds with greater mean elevation and greater habitat complexity. This researcher suggested that such areas are likely to have more stable base flows that can maintain suitable spawning habitat even during dry years. Additionally, spawning areas had a greater percentage of deciduous forest and developed areas and less grassland areas (Boger 2002).

Temporal spawning patterns

Alewife usually spawn 3 to 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 to 3 weeks (Jones et al. 1978). In a tributary of the Rappahannock River, Virginia, O’Connell and Angermeier (1997) found that blueback herring eggs and larvae were more abundant than those of alewife, but alewife used the stream over a longer period of time. The researchers also reported a minor three-day overlap of spawning by these two alosine species. It has been hypothesized that alewife and blueback herring 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 due to a temporal, rather than spatial, segregation that minimizes the competition between the two species.

Alewife may spawn throughout the day, however, most spawning occurs at night (Graham 1956). One female fish and up to 25 male fish broadcast eggs and sperm simultaneously just below the surface of the water or over the substrate (Belding 1921; McKenzie 1959; Cooper 1961). Spawning lasts two to three 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 1921; Cooper 1961; Libby 1981, 1982). Following spawning, the adult spent fish quickly return downstream (Colette and Klein-MacPhee 2002).

Maturation and spawning periodicity

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

Table 4-2. Percentage of repeat spawners for alewife along the Atlantic coast of North America

Many alewife are repeat spawners, with some individuals completing seven or eight spawning events in a lifetime (Table 4-2) (Jessop et al. 1983). It is not clear whether there is a clinal trend from south to north for repeat spawning (i.e., more in the north than south) (Klauda et al. 1991), or if there is a typical percent of the annual return population that repeat spawns (i.e., 30 to 40% repeat spawners throughout their range) (Richkus and DiNardo 1984). Furthermore, Kissil (1974) suggested that alewife might spawn more than once in a season.

Adults will typically spend two to four years at sea before returning to their natal rivers to spawn (Neves 1981). The majority of adults reach sexual maturity at 3, 4, or 5 years of age, although some adults from North Carolina (Richkus and DiNardo 1984) have returned to spawn at age-2 (Jessop et al. 1983). The oldest alewife recorded in North Carolina were age-9 (Street et

al. 1975; Johnson et al. 1979); age-10 fish have been caught in New Brunswick (Jessop et al. 1983) and Nova Scotia (O'Neill 1980). Additionally, Kissil (1974) found that alewife spawning in Bride Lake, Connecticut, spent three to 82 days on the spawning grounds, while Cooper (1961) reported that most fish left within five days of spawning in Rhode Island.

Spawning and the saltwater interface

While it is known that alewife can adjust to a wide range of salinities, published data on alewife tolerance ranges are 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. In the north, Leim (1924) studied the life history of American shad 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 saltwater for development (Leim 1924). Also, unlike American shad, some populations of alewife have become landlocked and are not at all dependent on saltwater (Scott and Crossman 1973).

Spawning substrate associations

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). In contrast, areas with little or no spawning activity were dominated by organic matter and finer sediments (usually associated with lower-gradient streams and comparatively more agricultural land use) (Boger 2002).

Pardue (1983) evaluated studies of cover component in alewife 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 (Pardue 1983). Pardue (1983) suggested that substrates with 75% silt (or other soft material containing detritus and vegetation) and sluggish waters are optimal for alewife.

Spawning depth associations

Water depth in spawning habitat may be a mere 15 cm deep (Bigelow and Schroeder 1953; Rothschild 1962), or as deep as 3 m (Edsall 1964); however, spawning typically occurs at less than 1 m (Murdy et al. 1997). Adults may utilize deeper water depths when not spawning in order to avoid high light intensities (Richkus 1974).

Spawning water temperature

Temperature (°C)	Location	Citation
14.0 – 15.5 (peak)	Rhode Island	Jones et al. 1978
7.0 – 10.9	Lower Connecticut River	Marcy et al. 1976a
10.5 – 21.6	Chesapeake Bay	Jones et al. 1978
11 - 19	Patuxent River, MD	J. Mowrer, Morgan State University, unpublished data
13 (peak)	Lake Mattamuskeet, NC	Tyrus 1974

Table 4-3. Alewife spawning temperatures for locations along the Atlantic coast of North America

Adult alewife have been collected in temperatures ranging from 5.7°C to 32°C (Marcy 1976b; Jones et al. 1978). Spawning temperatures along the Atlantic coast fall within this broader range (Table 4-3). There is some discrepancy regarding the minimum spawning temperature 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), some researchers suggest that the minimum spawning temperature for adult alewife is 10.5°C (Cianci 1965; Loesch and Lund 1977). Additionally, lower temperatures may be dangerous for spawning alewife. Otto et al. (1976) found that the lower incipient lethal temperature range for adults acclimated at 15.0°C and 21.0°C was between 6°C and 8°C. In this study, no fish survived below 3°C, regardless of acclimation temperature (Otto et al. 1976). Furthermore, at temperatures below 4.5°C, normal schooling behavior was significantly reduced for adult alewife from Lake Michigan (Colby 1973).

As water temperatures rise, alewife migration eventually slows. 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. Ultimately, higher temperatures may cause problems for alewife. In fact, Otto et al. (1976) found that upper incipient lethal temperatures (temperature at which 50% of the population survives) ranged from 23.5°C to 24.0°C for adults that were acclimated at temperatures of 10°C, 15°C, and 20°C. Another study reported upper incipient lethal temperatures of 29.8°C and 32.8°C at acclimation temperatures of 16.9°C and 24.5°C, respectively (Stanley and Holzer 1971). In addition, McCauley and Binkowski (1982) reported upper incipient lethal temperatures of 31°C to 34°C after acclimation at 27°C for a northern population of adults.

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 their relationship to a changing baseline temperature, and not on the basis of the absolute value of temperature. Stanley and Colby (1971) found that decreasing temperatures (from 16°C 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).

Spawning dissolved oxygen associations

There is little information regarding sensitivities of various life history stages of alewife to dissolved oxygen (Klauda et al. 1991). In one study, adults exposed to dissolved oxygen concentrations ranging from 2.0 to 3.0 mg/L for 16 hours in the laboratory experienced a 33% mortality rate. Alewife were able to withstand dissolved oxygen concentrations as low as 0.5 mg/L for up to 5 minutes, as long as a minimum of 3.0 mg/L was available, thereafter (Dorfman and Westman 1970). Additionally, Jones et al. (1988) suggested that the minimum dissolved oxygen concentration for adult alewife is 5.0 mg/L.

Spawning 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 alewife (Smith 1907; Belding 1921; Marcy 1976a). Some researchers have noted differential selection of spawning areas in alewife. For example, in Connecticut, alewife choose slower moving waters in Bride Lake (Kissil 1974) and Higganum and Mill creeks, while blueback herring select fast-moving waters in the upper Salmon River and Roaring Brook (Loesch and Lund 1977). In other areas where alewife and blueback herring are forced to spawn in the same vicinity due to blocked passage (Loesch 1987), alewife generally spawn along shorebank eddies or deep pools, whereas, blueback herring will typically select the main stream flow for spawning (Loesch and Lund 1977). In North Carolina, alewife utilize slow moving streams and oxbows (Street et al. 2005).

Spawning pH associations

Few researchers have reported on 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. Laboratory tests found that fish from those streams could successfully spawn at a pH as low as 4.5 (Byrne 1988). In another study, adult alewife tolerated a pH range of 6.5 to 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 to 137 µg/L for a pulse duration of 8 to 96 hours (Klauda 1989). Klauda et al. (1991) suggested a pH range of 5 to 8.5 as suitable for alewife eggs, but no range was provided for spawning.

Spawning feeding behavior

Adult alewife typically do not feed during their upstream spawning run (Bigelow and Schroeder 1953; Colby 1973). Spent fish that have reached brackish waters on their downstream migration will feed voraciously, mostly on mysids (Colette and Klein-MacPhee 2002). While adults may consume their own eggs during the spawning run (Edsall 1964; Carlander 1969), juveniles reportedly feed more actively on them (Colette and Klein-MacPhee 2002).

Spawning competition and predation

Adult alewife and blueback herring play an important role in the food web and in maintaining the health of the ecosystem. In the inland freshwater and coastal marine environments they provide forage for bass, trout, salmonids, other fish, ospreys, herons, eagles, kingfishers, cormorants, and aquatic fur-bearing mammals (Colby 1973; Royce 1943; Scott and Scott 1988; Loesch 1987; S. Lary, U.S. Fish and Wildlife Service, personal communication). In the marine environment, they are eaten by a variety of predators, such as bluefish, weakfish, striped bass, cod, pollock, and silver hake, as well as marine mammals and sea birds. Additionally, alewife are a host to native freshwater mussels, which they carry up and down rivers in their gills. Furthermore, spawning alewife heading upriver give cover to out-migrating Atlantic salmon smolts in the spring (S. Lary, U.S. Fish and Wildlife Service, personal communication).

Erkan (2002) notes that predation of alosines 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 cormorant colonies have increased in size and expanded into new areas. Predation by otters and herons has also increased, but to a lesser extent (D. Erkan, Rhode Island Department of Environmental Management, personal communication).

In many coastal communities, the annual alewife run is an integral part of the local culture, and local residents have initiated efforts to protect and restore their cultural link to this fishery, to develop effective management strategies for restoration, to establish self-sustaining harvest levels, and to enhance community education (S. Lary, U.S. Fish and Wildlife Service, personal communication).

Factors affecting stock size

At low stock levels, Havey (1973) and Walton (1987) demonstrated a weak relationship between spawning stock and abundance of 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 due to natural and manmade environmental impacts, the size of the spawning stock will likely become a factor in determining juvenile abundance (Kosa and Mather 2001).

Part B. Alewife Egg and Larval Habitat

Geographical and temporal movement patterns

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 near the bottom than at the surface in the Connecticut River. Eggs may hatch anywhere from 50 to 360 hours (2 to 15 days) after spawning, depending on water temperature (Fay et al. 1983); however, eggs most often hatch within 80 to 95 hours (3 to 5 days) (Edsall 1970).

Within two to five days of hatching, the yolk-sac is absorbed and larvae 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, 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).

Eggs, larvae, and the saltwater interface

Dovel (1971) found that 99% of alewife eggs in the upper Chesapeake Bay were in freshwater (0 ppt). Larvae were collected where salinities ranged from 0 to 8 ppt, but again, most (82%) were collected in freshwater (Dovel 1971). Klauda et al. (1991) suggested that the optimal range for alewife egg development is 0 to 2 ppt. Additionally, growth rates of larval alewife are considerably faster in saltwater compared to freshwater at temperatures of 26.4°C (Klauda et al. 1991).

Egg and larval substrate associations

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

Egg and larval water temperature

For alewife 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 are comparable: 2 to 4 days at 22°C (Belding 1921); 3 days at 23.8°C to 26.8°C, and 3 to 5 days at 20°C (Mansueti and Hardy 1967); 6 days at 15.5°C (Bigelow and Welsh 1925).

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 ranging from 6.9°C to 29.4°C for eggs from Lake Michigan; however, temperatures below 11°C caused a high percentage of deformed larvae. The optimum hatching performance occurred between 17.2°C and 21.1°C. Although this was the suggested optimal range, it was determined that considerable hatch rates and proper development could occur over a broader range from 10.6°C to 26.7°C

(Edsall 1970). Furthermore, in the upper Chesapeake Bay, alewife eggs were collected where temperatures ranged from 7°C to 14°C, with 70% of eggs found between 12°C and 14°C (Dovel 1971).

Edsall (1970) correlated egg mortality with incubation temperature. His equation follows for predicting incubation time of alewife eggs using a relationship with temperature:

$$t = 6.335 \times 10^6 (T)^{-3.1222}$$

where t = time in days

T = incubation temperature in degrees Fahrenheit

Several researchers have attempted to determine the effects of temperature on alewife eggs. One study on the effects of power plants on alewife eggs found that they suffered no significant mortality or abnormal egg development after acclimation at 17° C, and subsequent exposure to 24.5° C for 6 to 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 to 10 minutes.

Larval alewife were collected at water temperatures between 4°C and 27°C in the upper Chesapeake Bay, although 98% were collected at water temperatures of 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 around 15°C was 31°C (Kellogg 1982); their preferred range when acclimated at 20° C appears to be 23°C to 29°C (EA 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 slightly saline water (1.0 to 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 with 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°C to 13°C, it was suggested that the survival and early development of young alewife would not likely be threatened by rapid warming trends following spawning or by moderate thermal discharges. Furthermore, it was indicated that above normal temperature elevations following spawning and hatching would probably be beneficial to alewife populations (Kellogg 1982).

Egg and larval dissolved oxygen associations

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

Egg and larval pH and aluminum associations

Klauda et al. (1991) suggest that a range of pH 5.0 to 8.5 for both the alewife egg and prolarva life stage is optimal. Klauda et al. (1987) suggested that during an acidic pulse between pH 5.5 and 6.2, critical conditions associated with more than 50% direct mortality could occur. 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 (Klauda et al. 1991).

Egg and larval water velocity/flow

Sismour (1994) observed a rapid decline in abundance of early preflexion river herring larvae in the Pamunkey River, Virginia, following high river flow in 1989. This observation led to speculation that high flow leads to increased turbidity, which reduces prey visibility, leading to starvation of larvae (Sismour 1994). Additionally, O'Connell and Angermeier (1997) found that current velocity and dissolved oxygen were the strongest predictors of alewife early egg presence in a Virginia stream. Further north, drought conditions in Rhode Island 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).

Egg and larval suspended solid associations

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 infection from naturally occurring fungi, as was witnessed in earlier experiments (Schubel and Wang 1973); this can lead to delayed mortality (Klauda et al. 1991).

Egg and larval feeding behavior

Once alewife 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).

Egg and larval competition and predation

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

Part C. Alewife Juvenile Riverine/Estuarine Habitat

Geographical and temporal movement patterns

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 mid-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).

Further north, juveniles in the Hudson River usually remain in freshwater tributaries until June (Schmidt et al. 1988). In contrast to the inshore abundance of American shad and blueback herring during the day, juvenile alewife were found to be most abundant in inshore areas at night in the Hudson River (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 (Schmidt et al. 1988). Alewife typically spend three to nine months in their natal rivers before returning to the ocean (Kosa and Mather 2001).

In the summer in the Potomac River, juveniles are abundant near surface waters during the day; however, they shift to mid-water and bottom depths in September, where they remain until they emigrate in November (Warriner et al. 1970). Juvenile alewife respond negatively to light and follow diel movement patterns similar to blueback herring. Nevertheless, there appears to be some separation between the alewife and blueback herring as they emigrate from nursery grounds in the fall. The difference occurs most notably at night when alewife can be found more frequently at mid-water depths, while blueback herring are found mostly at the surface (Loesch and Kriete 1980). This behavior may reduce interspecific competition for food, given that the species' 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 have found that movement of alewife peaks in the afternoon (Richkus 1975a; Kosa and Mather 2001), while others have found that it peaks 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 only a minor role in providing migration cues under riverine conditions. Rather, these researchers think that migration timing is triggered by water temperature and moon phases that provide dark nights (i.e., new and quarter moons) (O'Leary and Kynard 1986; Stokesbury and Dadswell 1989). Additionally, Stokesbury and Dadswell (1989) found that alewife remained in the offshore region of the Annapolis estuary, Nova Scotia, for nearly one month before the correct migration cues triggered emigration. Furthermore, large juveniles begin moving downstream before smaller juveniles (Schmidt et al. 1988), inhabiting saline waters before they begin their seaward migration (Loesch 1969; Marcy 1976a; Loesch and Kriete 1980).

The influence and magnitude of migration cues on emigrating alewife may vary considerably. Richkus (1975a) observed waves of juvenile alewife leaving systems following environmental changes (e.g., changes in water flow, water levels, precipitation, and light

intensity), but the number of fish leaving was unrelated to the level of magnitude of the change. Most fish (60% to 80%) emigrated during a small percentage (approximately 8%) of available days. These waves also lasted two to three days, regardless of the degree of environmental change (Richkus 1975a). Similarly, other researchers have observed that the majority (>80%) of river herring emigrate in waves (Cooper 1961; Huber 1978; Kosa and Mather 2001). Richkus (1975a) also noted that in some instances, high abundances of juvenile alewife 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. Additionally, juvenile migration of alewife occurs about one month earlier than that of blueback herring (Loesch 1969; Kissil 1974).

Although most juveniles emigrate offshore during their first year, some overwinter in the Chesapeake (Hildebrand 1963) and Delaware bays (Smith 1971). Marcy (1969) suggested that many juveniles (age-1+) spend their first winter close to the mouth of their natal river due to their presence in the lower portion of the Connecticut River in early spring. Other researchers concur that 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). Conversely, 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).

Juveniles and the saltwater interface

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

Juvenile substrate associations

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. No other information was available regarding substrate preferences for juvenile alewife.

Juvenile depth associations

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.

Juvenile water temperature

Characterization	Acclimation Temp (°C)	Temp Range (°C)	Location	Citation
Optimal	N/A	15 - 20	Many	Pardue 1983
Suitable	N/A	10 - 28	Many	Klauda et al. 1991
Present	N/A	4 - 27	Upper Chesapeake Bay	Dovel 1971
Present	N/A	13.5 – 29.0	Cape Fear River, NC	Davis and Cheek 1966
Avoidance	26	>34	Delaware River	PSECG 1984
Preferred	15 - 21	17 – 23 (at 4 – 7 ppt)	Delaware River	Meldrim and Gift 1971; PSE&G 1982
Preferred	15 - 18	25.0	Lake Michigan	Otto et al. 1976

Table 4-4. Juvenile alewife temperature tolerances/preferences along the Atlantic coast

Temperature tolerance range estimates for juvenile alewife vary somewhat between researchers (Table 4-4). Dovel (1971) found that ninety-eight percent of juvenile alewife in the upper Chesapeake Bay were collected at 25°C.

According to McCauley and Binkowski (1982), the upper lethal temperature for juvenile alewife is approximately 30°C. Concurrently, in Lake Michigan, upper incipient lethal limits (i.e., temperature at which 50% of the population survives) for young-of-the-year alewife acclimated to 10°C, 20°C, 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). Another study found that juveniles exposed to water at 35°C for 24 hours, after acclimation to water at 18.9 to 20.6°C, had a 20% survival rate (Dorfman and Westman 1970). Moreover, young-of-the-year alewife seem to have critical thermal maxima (CTM) that are 3 to 6°C higher than adults (Otto et al. 1976).

Alternatively, when juvenile alewife were subjected to decreasing temperatures (15.6°C down to 2.8°C) over the course of 15 days, they suffered greater than 90% mortality (Colby 1973). In another study, juvenile alewife 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 to 60% mortality (PSE&G 1984). Comparatively, the lower limit at which juvenile river herring are unable to survive is 3°C or less (Otto et al. 1976).

Juvenile dissolved oxygen associations

Jones et al. (1988) determined that the minimum dissolved oxygen concentration for juveniles is 3.6 mg/L. Dorfman and Westman (1970) reported that at dissolved oxygen

concentrations below 2.0 mg/L, juvenile alewife became physically stressed. At concentrations as low as 0.5 mg/L, juveniles survived for approximately five minutes in oxygen (Dorfman and Westman 1970). In the Cape Fear River system, juveniles preferred waters where dissolved oxygen levels ranged from 2.4 to 10.0 mg/L (Davis and Cheek 1966).

Juvenile pH and aluminum associations

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

Juvenile water velocity/flow

Water discharge is an important variable influencing 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 that 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 juvenile alewife leaving Lake Bride, Connecticut, between June and October; they 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. Furthermore, Jessop (1994) found that the juvenile abundance index (JAI) of alewife decreased with mean river discharge during the summer. Daily instantaneous mortality also increased with mean river discharge from July to August at the Mactaquac Dam headpond on the Saint John River, New Brunswick, Canada (Jessop 1994).

Juvenile feeding behavior

Juvenile alewife are opportunistic feeders that usually favor seasonally available items (Gregory et al. 1983). For example, in the Hamilton Reservoir, Rhode Island, juveniles feed 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 is a behavior utilized more at night (Janssen 1976). Grabe (1996) found that juvenile alewife fed on chironomids, odonates, and other amphipods during the day and early evening hours in the Hudson River. Juveniles have also been observed consuming epiphytic fauna especially at night (Weaver 1975; Grabe 1996). Juveniles may also feed extensively on benthic organisms, including ostracods, chironomid larvae, and oligochaete worms (Watt and Duerden 1974).

The number of zooplankton per liter consumed is assumed to be critical for the survival and growth of juvenile alewife. Pardue (1983) suggests that habitats containing 100 or more zooplankton per liter are optimal. Walton (1987) found that juvenile alewife 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 to synchronize the larval stage with the optimal phase of annual plankton production cycles (Blaxter and Hunter 1982). In addition, Morsell and Norden (1968) found that juvenile alewife consume zooplankton until they reach 12 cm TL, and may then switch to increasing amounts of the benthic amphipod *Pontoporeia* sp. 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.

Unfortunately, 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).

Juvenile competition and predation

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 may consume different sizes of prey (Crecco and Blake 1983). Juvenile alewife in the Minas Basin, Nova Scotia, Canada, favor larger benthic prey (particulate-feeding strategy) compared to juvenile blueback herring (filter-feeding strategy) (Stone 1985; Stone and Daborn 1987). In the Cape Fear River, North Carolina, juvenile alewife consume more ostracods, insect eggs, and insect parts than blueback herring (Davis and Cheek 1966).

Alewife also spawn earlier than blueback herring, thereby giving juvenile alewife a relative size advantage over juvenile bluebacks, allowing them a larger selection of prey (Jessop 1990). Differences in juvenile diel feeding activity further reduce competition. One study noted that 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). In comparison, juvenile blueback herring begin to feed actively at dawn, increasing throughout the day and maximizing at dusk, then diminishing from dusk until dawn (Burbidge 1974).

With regard to 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 the estuarine waters of Maine, juvenile bluefish prey heavily on alewife (Creaser and Perkins 1994). In Massachusetts rivers, juvenile alewife are energetically valuable and a key food source for largemouth bass during late summer (Yako et al. 2000).

Juveniles and contaminants

A 24-hour LC₅₀ (i.e., concentration at which 50% of the population dies) of 2.25 mg/L for total residual chlorine (TRC) was reported for juvenile alewife exposed for 30 minutes at 10°C (Seegert and Latimer 1977). Thirty-minute LC₅₀ values for TRC were 2.27 and 0.30 mg/L for juveniles exposed at 10°C and 30°C, respectively (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 (PSE&G 1980). Juveniles held at 19 to 24°C in freshwater exhibited an

avoidance response at <0.03 mg/L TRC; fish subjected to 0.48 mg/L TRC for 2 hours at 22°C suffered 100% mortality (Bogardus et al. 1978).

Part D. Alewife Late Stage Juvenile and Adult Marine Habitat

Geographical and temporal patterns at sea

Some young-of-the-year alewife over-winter 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 juvenile alewife over-wintered in waters approximately 0.6 to 7.4 km from the shore of New Jersey, at depths of 2.4 to 19.2 m, in what is considered an offshore estuary. This area is warmer with higher salinity than the cooler, lower salinity river-bay estuarine nurseries where alewife reside in fall. The majority of alewife are present in March when bottom temperatures range from 4.4 to 6.5°C and salinity is between 29.0 and 32.0 ppt (Cameron and Pritchard 1963).

Young alewife have been found overwintering off the North Carolina coast from January to March, concentrated at depths of 20.1 to 36.6 m (Holland and Yelverton 1973; Street et al. 1973). However, other sources have noted that juvenile alewife tend to remain near the surface during their first year in saltwater (Bigelow and Schroeder 1953). In Lake Michigan, age-1 fish are usually pelagic, except in spring and fall, where they often occur on the bottom; age-2 fish are 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). Sexual maturity of alewife is reached at a minimum of age-2, but timing 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). 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). 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). In fact, alewife typically migrate in large schools of similar sized fish, and may even form mixed schools with other herring species (Colette and Klein-MacPhee 2002).

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. Commercial catch data indicates that alewife are most frequently caught on Georges Bank and south of Nantucket Shoals (Neves 1981; Rulifson et al. 1987). Distribution in the fall is similar to the summer, but alewife concentrate along the northwest perimeter of the Gulf of Maine. In the fall, individuals move offshore and southward to the mid-Atlantic coast between latitude 40°N and 43°N, where they remain until early spring (Neves 1981). It is not known to what extent alewife overwinter in deep water off the continental shelf, but they have rarely been found more than 130 km from the coast (Jones et al. 1978).

Alewife also experience diel movement patterns. At sea alewife are more available to bottom trawling gear during the day, suggesting that they follow the diel movement of plankton in the water column and are sensitive to light (Neves 1981). It also seems that feeding and vertical migration are likely controlled by light intensity patterns within thermal preference zones (Richkus and Winn 1979; Neves 1981).

Results from Canadian spring surveys show river herring distributed along the Scotian Gulf, southern Gulf of Maine, and off southwestern Nova Scotia from the Northeast Channel to the central Bay of Fundy; they are found 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 (and possibly some of the U.S. Gulf of Maine population) moves inshore during spring to spawn in Canadian waters. 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 1960s, it was believed that coastal river herring stocks did not mingle to the extent that American shad stocks apparently did, at least during the seasons that foreign harvests were made (ASMFC 1985).

Salinity associations at sea

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

Depth associations at sea

National Marine Fisheries Service catch data found that in offshore areas, alewife were caught most frequently in waters with depths of 56 to 110 m. The vertical position of alewife in the water column may be influenced by zooplankton concentrations (Neves 1981). Zooplankton usually concentrate at depths <100 m in the Gulf of Maine (Bigelow 1926). Stone and Jessop (1992) found that alewife offshore of Nova Scotia, the Bay of Fundy, and the Gulf of Maine, were at depths of 101 to 183 m in the spring; they were in shallower nearshore waters (46 to 82 m) in the summer, and in deeper offshore waters (119 to 192 m) in the fall.

Stone and Jessop (1992) also found differences in depth distribution between smaller fish (sexually immature) and larger fish. Smaller fish occurred in shallow regions (<93 m) during spring and fall, while larger fish were found in deeper areas (≥ 93 m) throughout the year (Stone and Jessop 1992). Furthermore, Jansen and Brandt (1980) reported that the nocturnal depth distribution of adult landlocked alewife differed by size class, with the smaller fish present at shallower depths.

Interestingly, in coastal waters juvenile alewife are found in deeper water than blueback herring despite their identical diets (Davis and Cheek 1966; Burbidge 1974; Watt and Duerden 1974; Weaver 1975).

Temperature associations at sea

From Cape Hatteras to Nova Scotia, alewife have been caught offshore where surface water temperatures ranged from 2 to 23°C and bottom water temperatures ranged from 3 to

17°C. Catches in this area were most frequent where the average bottom water temperature was between 4 and 7°C (Neves 1981). Stone and Jessop (1992) reported a temperature range of 7 to 11°C for alewife in the northern range off Nova Scotia, the Bay of Fundy, and the Gulf of Maine. The researchers also noted that the presence of a cold (<5°C) intermediate water mass over warmer, deeper waters on the Scotian Shelf, 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, vertical migration may have been confined by a water temperature inversion in this area during the spring (Stone and Jessop 1992).

Alewife may prefer and be better adapted to cooler water than blueback herring (Loesch 1987; Klauda et al. 1991). Northern populations may also 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 in any captured in Virginia (Duman and DeVries 1974).

Feeding behavior at sea

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 (Colette and Klein-MacPhee 2002). They feed either by selectively preying on individuals or non-selectively filter-feeding with 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 shift from micro-zooplankton in small fish to mysids and amphipods in larger fish. Feeding intensity also decreases with increasing age of fish (Stone 1985).

Alewife generally feed most actively during the day; nighttime predation is usually restricted to larger zooplankton that are easier to detect (Janssen 1978b; Janssen and Brandt 1980; Stone and Jessop 1993). In Nova Scotia, alewife feeding peaks at midday during the summer and mid-afternoon during the winter. Alewife also have a higher daily ration in the summer than in the winter (Stone and Jessop 1993). Although direct evidence is lacking, alewife catch 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 (Bowman et al. 2000; R. Rountree, University of Massachusetts, unpublished data). Of these species, spiny dogfish appears to have the greatest affinity for alewife (R. Rountree, University of Massachusetts, unpublished data). Also, see Part C of this chapter for additional information.

Section II. Significant Environmental, Temporal, and Spatial Factors Affecting Distribution of Alewife

Table 4-5.

Significant environmental, temporal, and spatial factors affecting distribution of alewife. Please note that, although there may be subtle variations between systems, the following data include a broad range of values that encompass the different systems that occur along the East Coast. Where a specific range is known to exist, it will be noted. For the subadult–estuarine/oceanic environment and non-spawning adult–oceanic environment life history phases, the information is provided as a general reference, not as habitat preferences or optima. NIF = No Information Found.

Life Stage	Time of Year and Location	Depth (m)	Temperature (°C)	Salinity (ppt)	Substrate	Current Velocity (m/sec)	Dissolved Oxygen (mg/L)
Spawning Adult	Late February (south) through August (north); slow-moving sections of streams/ponds/lakes, and shorebank eddies or deep pools, from North Carolina to Labrador & Newfoundland	Tolerable: 0.2-3 Optimal: NIF Reported: Typically spawn in shallower (<1) areas	Tolerable: 7-27.8 Optimal: 13-20 Reported: Broad range; disagreement on minimum temperature for spawning	Tolerable: NIF Optimal: NIF Reported: Migrate as far upstream in freshwater as possible	Tolerable: NIF Optimal: NIF Reported: Usually sand, gravel, cobble, and other coarse stone; some report SAV and detritus	Tolerable: NIF Optimal: NIF Reported: Slow-moving waters	Tolerable: >5.0 Optimal: NIF Reported: Only tolerate low DO for short periods
Egg	Late February (south) through August (north); hatch 50-360 hours after fertilization, but usually within 80-95 hours at spawning site or slightly downstream	Tolerable: NIF Optimal: NIF Reported: NIF	Tolerable: 10.6-26.7 Optimal: 17.2-21.1 Reported: Average time to median hatch varies inversely w/temperature	Tolerable: NIF Optimal: 0-2 Reported: Mostly found in freshwater	Tolerable: NIF Optimal: NIF Reported: NIF	Tolerable: NIF Optimal: NIF Reported: Usually found in low flow; w/DO, strongest predictor of egg presence	Tolerable: ≥5.0 Optimal: NIF Reported: With velocity, strongest predictor of egg presence
Prolarvae	Hatch in 50 to 360 hours, but usually within 80-95 hours downstream of spawning site	Tolerable: NIF Optimal: NIF Reported: NIF	Tolerable: 8-31 Optimal: 15-24 Reported: Variable	Tolerable: NIF Optimal: 0-3 Reported: Mostly found in freshwater	Tolerable: NIF Optimal: NIF Reported: NIF	Tolerable: NIF Optimal: NIF Reported: Usually found in low flow	Tolerable: ≥5.0 Optimal: NIF Reported: NIF

Life Stage	Time of Year and Location	Depth (m)	Temperature (°C)	Salinity (ppt)	Substrate	Current Velocity (m/sec)	Dissolved Oxygen (mg/L)
Postlarvae	2 to 5 days downstream of spawning site after prolarvae stage is reached	Tolerable: NIF Optimal: NIF Reported: NIF	Tolerable: 14-28 Optimal: 20-26 Reported: Variable	Tolerable: NIF Optimal: NIF Reported: Larvae grow faster in saltwater	Tolerable: NIF Optimal: NIF Reported: NIF	Tolerable: NIF Optimal: NIF Reported: Usually found in low flow	Tolerable: ≥5.0 Optimal: NIF Reported: NIF
Early Juvenile – Riverine	3-9 months in natal rivers after reaching juvenile stage in brackish waters or upstream in freshwater	Tolerable: NIF Optimal: NIF Reported: Absent from near-surface during daylight	Tolerable: 10-28 Optimal: 15-20 Reported: 4-29	Tolerable: NIF Optimal: NIF Reported: Variable	Tolerable: NIF Optimal: NIF Reported: SAV for protection	Tolerable: NIF Optimal: NIF Reported: Avoid > 10cm/s; high migration rates in heavy flow	Tolerable: ≥3.6 Optimal: NIF Reported: NIF
Subadult & Non-spawning Adult – Estuarine/Oceanic	2-5 years after hatching in nearshore estuarine waters or offshore marine waters	Tolerable: NIF Optimal: 46-192 Reported: Zooplankton may influence depth; smaller fish generally in shallower water	Tolerable: 2-23 Optimal: 4-7 (bottom temp) Reported: Northern populations may be more cold tolerant	Tolerable: NIF Optimal: NIF Reported: Brackish to saltwater	Tolerable: NIF Optimal: NIF Reported: NIF	Tolerable: NIF Optimal: NIF Reported: NIF	Tolerable: NIF Optimal: NIF Reported: NIF

Section III. Alewife Literature Cited

- ASMFC (Atlantic States Marine Fisheries Commission). 1985. Fishery management plan for the anadromous alosid stocks of the eastern United States: American shad, hickory shad, alewife, and blueback herring. Fishery Management Report No. 6, Washington, D.C.
- Auld, A. H., and J. R. Schubel. 1978. Effects of suspended sediment on fish eggs and larvae: A laboratory assessment. *Estuarine, Coastal, and Marine Science* 6: 153-164.
- Belding, D. L. 1921. A report upon the alewife fisheries of Massachusetts. Massachusetts Division of Marine Fisheries Contribution No. 11, Department of Conservation, Boston, Massachusetts.
- Bentzen, P., and I.G. Paterson. 2006. Genetic analyses of freshwater and anadromous alewife (*Alosa pseudoharengus*) populations from the St. Croix River, Maine/New Brunswick. Final Report to Maine Rivers, Hallowell, Maine.
- Berry, F. H. 1964. Review and emendation of family Clupeidae. *Copeia* 1964: 720-730.
- Bigelow, H. B. 1926. Plankton of the offshore waters of the Gulf of Maine. *Bulletin of the United States Bureau of Fisheries* 40: 1-509.
- Bigelow, H. B., and W. C. Schroeder. 1953. Fishes of the Gulf of Maine. *Fishery Bulletin* 74 of the Fishery Bulletin of the Fish and Wildlife Service, volume 53. United States Government Printing Office, Washington, D.C.
- Bigelow, H. B., and W. W. Welsh. 1925. Fishes of the Gulf of Maine. *Fishery Bulletin* 40 of the United States Fish and Wildlife Service, volume 1. U.S. Government Printing Office, Washington, D.C.
- Blaxter, J. H. S., and J. R. Hunter. 1982. The biology of clupeoid fishes. *Advances in Marine Biology* 20: 3-194.
- Bogardus, R. B., D. B. Boies, T. C. Teppen, and F. J. Horrath. 1978. Avoidance of monochloramine: Test tank results for rainbow trout, coho salmon, alewife, yellow perch and spotted shiner. Pages 149-161 in R. L. Julley, H. Gorchev, and D. H. Hamilton, editors. *Water chlorination – Environmental impact and health effects*, volume 2. Ann Arbor Science Publishers, Ann Arbor, Michigan.
- Boger, R. A. 2002. Development of a watershed and stream-reach spawning habitat model for river herring (*Alosa pseudoharengus* and *A. aestivalis*). Doctoral dissertation. The College of William and Mary, Williamsburg, Virginia.
- Bowman, R. E., C. E. Stillwell, W. L. Michaels, and M. D. Grosslein. 2000. Food of northwest Atlantic fishes and two common species of squid. NOAA Technical Memorandum NMFS-F/NE-155, Silver Spring, Maryland.
- Brooks, A. A., and G. L. Seegert. 1978. The effects of intermittent chlorination on the biota of Lake Michigan. Special Report No. 31, Center for Great Lakes Studies, University of Wisconsin, Milwaukee, Wisconsin.
- Burbidge, R. G. 1974. Distribution, growth, selective feeding, and energy transformation of young-of-the-year blueback herring, *Alosa aestivalis* (Mitchill), in the James River, Virginia. *Transactions of the American Fisheries Society* 103: 297-311.

- Burgess, G. H. 1978. *Alosa pseudoharengus* (Wilson), alewife. Page 65 in D. S. Lee, C. R. Bilber, C. H. Hocutt, R. E. Jenkins, D. E. McAllister, and J. R. Stauffer, Jr., editors. Atlas of North American freshwater fishes. North Carolina State Museum of Natural History, Raleigh, North Carolina.
- Byrne, D. M. 1988. Anadromous herring run restoration. New Jersey Department of Environmental Protection, Bureau of Marine Fisheries, Project No. AFC-10-1, Trenton, New Jersey.
- Cameron, W. M., and D. W. Pritchard. 1963. Estuaries. Pages 306-324 in M. N. Hill, editor. The Sea, volume 2. Wiley-Interscience, New York.
- Carlander, K. D. 1969. Handbook of freshwater fishery biology, volume I: Life history data on freshwater fishes of the United States and Canada, exclusive of the Perciformes. Iowa State University Press, Ames, Iowa.
- Cianci, J. M. 1965. Larval development of the alewife, *Alosa pseudoharengus* (Wilson), and the glut herring, *Alosa aestivalis* (Mitchill). Masters thesis. University of Connecticut, Storrs, Connecticut.
- Colby, P. J. 1973. Response of the alewife, *Alosa pseudoharengus*, to environmental changes. Pages 163-198 in W. Chavin, editor. Response of fish to environmental changes. Charles C. Thompson, Springfield, Illinois.
- Collette, B., and G. Klein-MacPhee, editors. 2002. Bigelow and Schroeder's fishes of the Gulf of Maine, 3rd edition. Smithsonian Institution Press, Washington, D.C.
- Collins, G. B. 1952. Factors influencing the orientation of migrating anadromous fishes. Fishery Bulletin 52 of the United States Fish and Wildlife Service: 373-396.
- Cooper, R. A. 1961. Early life history and spawning migration of the alewife, *Alosa pseudoharengus*. Masters thesis. University of Rhode Island, Kingston, Rhode Island.
- Creaser, E. P., and H. C. Perkins. 1994. The distribution, food, and age of juvenile bluefish, *Pomatomus saltatrix*, in Maine. Fishery Bulletin 92 of the United States Fish and Wildlife Service: 494-508.
- Crecco, V. A., and M. M. Blake. 1983. Feeding ecology of coexisting larvae of American shad and blueback herring in the Connecticut River. Transactions of the American Fisheries Society 112: 498-507.
- Crecco, V. A., and T. Savoy. 1984. Effects of fluctuations in hydrographic conditions on year-class strength of American shad (*Alosa sapidissima*) in the Connecticut River. Canadian Journal of Fisheries and Aquatic Sciences 42: 1640-1648.
- Dadswell, M. J., G. D. Melvin, P. J. Williams, and D. E. Themelis. 1987. Influences of origin, life history, and chance on the Atlantic coast migration of American shad. Pages 313-330 in M. J. Dadswell, R. J. Klauda, C. M. Moffitt, and R. L. Saunders, editors. Common strategies of anadromous and catadromous fishes. American Fisheries Society Symposium 1, Bethesda, Maryland.

- Davis, J. R., and R. P. Cheek. 1966. Distribution, food habits, and growth of young clupeids, Cape Fear River system, North Carolina. Proceedings of the 20th Annual Conference of the Southeastern Association of Game and Fish Commissions: 250-260.
- Dey, W. P., and P. C. Baumann. 1978. Community dynamics of shore zone fish populations in the Hudson River estuary: Proceedings of the 108th Annual American Fisheries Society meeting, Kingston, Rhode Island.
- Dixon, D. A. 1996. Contributions to the life history of juvenile blueback herring (*Alosa aestivalis*): Phototactic behavior and population dynamics. Doctoral dissertation. College of William and Mary, Virginia Institute of Marine Science, School of Marine Science, Gloucester Point, Virginia.
- Dominy, C. L. 1971. Evaluation of a pool and weir fishway for passage of alewife (*Alosa pseudoharengus*) at White Rock, Gaspereau River, Nova Scotia. Canada Department of Fisheries and Forestry, Resource Development Branch, Progress Report No. 3, Halifax, Canada.
- Dorfman, D., and J. Westman. 1970. Responses of some anadromous fishes to varied oxygen concentrations and increased temperatures. Office of Water Resources Research Project No. B-012-NJ, Rutgers University, New Brunswick, New Jersey.
- Dovel, W. L. 1971. Fish eggs and larvae of the upper Chesapeake Bay. Natural Resources Institute Special Report 4: 1-71.
- Duman, J. G., and A. L. DeVries. 1974. The effects of temperature and photoperiod on antifreeze production in cold water fishes. Journal of Experimental Zoology 190: 98-97.
- Ecological Analysts, Inc. (EA). 1978. Hudson River thermal effects studies for representative species: Second progress report. Prepared for Central Hudson Gas and Electric Corporation, Poughkeepsie, New York.
- Edsall, T. A. 1964. Feeding by three species of fishes on the eggs of spawning alewife. Copeia 1964: 226-227.
- Edsall, T. A. 1970. The effect of temperature on the rate of development and survival of alewife eggs and larvae. Transactions of the American Fisheries Society 102: 376-380.
- Edwards, R. L., and R. E. Bowman. 1979. Food consumed by continental shelf fishes. Pages 387-406 in H. Clepper, editor. Predator-prey systems in fish communities and their role in fisheries management. Sport Fishing Institute, Washington, D.C.
- Erkan, D. E. 2002. Strategic plan for the restoration of anadromous fishes to Rhode Island coastal streams. Rhode Island Department of Environmental Management, Division of Fish and Wildlife, Completion Report in fulfillment of Federal Aid in Sportfish Restoration Project No. F-55-R, Jamestown, Rhode Island.
- Fay, C. W., R. J. Neves, and G. B. Pardue. 1983. Species profiles: Life histories and environmental requirements of coastal fishes and invertebrates (mid-Atlantic) – alewife/blueback herring. United States Fish and Wildlife Service, Division of Biological Services Report No. FWS/OBS-82/11.9, and United States Army Corps of Engineers Report No. TR EL-82-4, Washington, D.C.

- Frankensteen, E. D. 1976. Genus *Alosa* in a channelized and an unchannelized creek of the Tar River basin, North Carolina. Masters thesis. East Carolina University, Greenville, North Carolina.
- Gibson, M. R. 1994. Status of alewife populations in Rhode Island. Rhode Island Division of Fish and Wildlife and Estuarine Resources, Wakefield, Rhode Island.
- Gordon, N. D., T. A. McMahon, and B. L. Finlayson. 1992. Stream hydrology: An introduction for ecologists. John Wiley and Sons, Ltd., England.
- Grabe, S. A. 1996. Feeding chronology and habits of *Alosa* spp. (Clupeidae) juveniles from the lower Hudson River estuary, New York. *Environmental Biology of Fishes* 47: 321-326.
- Graham, J. J. 1956. Observations on the alewife in freshwater. University of Toronto Biological Series No. 62, Toronto, Canada.
- Gregory, R. S., G. S. Brown, and G. R. Daborn. 1983. Food habits of young anadromous alewife, *Alosa pseudoharengus*, in Lake Ainslie, Nova Scotia. *Canadian Field Naturalist* 97: 423-426.
- Havey, K. A. 1961. Restoration of anadromous alewife at Long Pond, Maine. *Transactions of the American Fisheries Society* 90: 281-286.
- Havey, K. A. 1973. Production of juvenile alewife, *Alosa pseudoharengus*, at Love Lake, Washington County, Maine. *Transactions of the American Fisheries Society* 102: 434-437.
- Henderson, B. A., and E. H. Brown, Jr. 1985. Effects of abundance and water temperature on recruitment and growth of alewife (*Alosa pseudoharengus*) near South Bay, Lake Huron. *Canadian Journal of Fisheries and Aquatic Sciences* 42: 1608-1613.
- Hildebrand, S. F. 1963. Family Clupeidae. Pages 257-454 in H. B. Bigelow, editor. *Fishes of the Western North Atlantic*, part 3. Sears Foundation for Marine Research, Yale University, New Haven, Connecticut.
- Hildebrand, S. F., and W. C. Schroeder. 1928. *Fishes of Chesapeake Bay*. Fishery Bulletin 43 of the United States Fish and Wildlife Service, volume 1: 1-366.
- Holland, B. F., and G. F. Yelverton. 1973. Distribution and biological studies of anadromous fishes offshore North Carolina. North Carolina Department of Natural and Economic Resources, Division of Commercial and Sport Fisheries, Special Scientific Report No. 24, Beaufort, North Carolina.
- Howell, M. H., J. P. Mowrer, R. J. Hochberg, A. A. Jarzynski, and D. R. Weinrich. 1990. Investigation of anadromous alosines in Chesapeake Bay. Maryland Department of Natural Resources, Annapolis, Maryland.
- Huber, M. E. 1978. Adult spawning success and emigration of juvenile alewife (*Alosa pseudoharengus*) from the Parker River, Massachusetts. Masters thesis. University of Massachusetts, Amherst, Massachusetts.
- Janssen, J. 1976. Feeding modes and prey size selection in the alewife *Alosa pseudoharengus*. *Journal of the Fisheries Research Board of Canada* 33: 1972-1975.

- Janssen, J. 1978a. Feeding-behavior repertoire of the alewife, *Alosa pseudoharengus*, and ciscoes, *Coregonus hoyi* and *C. artedii*. Journal of the Fisheries Research Board of Canada 35: 249-253.
- Janssen, J. 1978b. Will alewife *Alosa pseudoharengus* feed in the dark? Environmental Biology of Fishes 3: 239-240.
- Janssen, J., and S. B. Brandt. 1980. Feeding ecology and vertical migration of adult alewife *Alosa pseudoharengus* in Lake Michigan. Canadian Journal of Fisheries and Aquatic Sciences 37: 177-184.
- Jessop, B. M. 1990. Diel variation in density, length composition, and feeding activity of juvenile alewife, *Alosa pseudoharengus* (Wilson), and blueback herring, *A. aestivalis* (Mitchill), at near-surface depths in a hydroelectric dam impoundment. Journal of Fish Biology 37: 813-822.
- Jessop, B. M., W. E. Anderson, and A. H. Vromans. 1983. Life-history data on alewife and blueback herring of the Saint John River, New Brunswick, 1981. Canadian Fisheries and Aquatic Sciences Data Report No. 426, New Brunswick, Canada.
- Jessop, B. M. 1994. Relations between stock and environmental variables, and an index of abundance, for juveniles alewife and blueback herring. North American Journal of Fisheries Management 14: 564-579.
- Johnson, H. B., S. E. Winslow, D. W. Crocker, B. F. Holland, Jr., J. W. Gillikin, and D. L. Taylor. 1979. Biology and management of mid-Atlantic anadromous fishes under extended jurisdiction, part I: North Carolina. Special Science Report No. 36, North Carolina Department of Natural Resources and Community Development, Division of Marine Fisheries, Morehead City, North Carolina.
- Johnson, J. H. 1983. Summer diet of juvenile fish in the St. Lawrence River. New York Fish and Game Journal 30: 91-99.
- Jones, P. W., F. D. Martin, and J. D. Hardy, Jr. 1978. Development of fishes of the mid-Atlantic Bight, an atlas of egg, larval and juvenile stages, volume I: Acipenseridae through Ictaluridae. United States Fish and Wildlife Service Report No. FWS/OBS-78/12, Arlington, Virginia.
- Jones, P. W., H. J. Speir, N. H. Butowski, R. O'Reilly, L. Gillingham and E. Smoller. 1988. Chesapeake Bay fisheries: Status, trends, priorities and data needs. Maryland Department of Natural Resources and Virginia Marine Resources Commission.
- Joseph, E. B., and J. Davis. 1965. A progress report to the herring industry. Virginia Institute of Marine Science, Special Science Report No. 51, Gloucester Point, Virginia.
- Kellogg, R. L. 1982. Temperature requirements for the survival and early development of the anadromous alewife. The Progressive Fish-Culturist 44: 63-73.
- Kissil, G. W. 1969. A contribution to the life history of *Alosa pseudoharengus* (Wilson). Doctoral dissertation. University of Connecticut, Storrs, Connecticut.
- Kissil, G. W. 1974. Spawning of the anadromous alewife, *Alosa pseudoharengus*, in Bride Lake, Connecticut. Transactions of the American Fisheries Society 103: 312-317.

- Klauda, R. J. 1989. Definitions of critical environmental conditions for selected Chesapeake Bay finfishes exposed to acidic episodes in spawning and nursery areas. Johns Hopkins University, Applied Physics Laboratory, Shady Side, Maryland.
- Klauda, R. J., S. A. Fischer, L. W. Hall, Jr., and J. A. Sullivan. 1991. Alewife and blueback herring; *Alosa pseudoharengus* and *Alosa aestivalis*. Pages 10.1-10.29 in S. L. Funderburk, J. A. Mihursky, S. J. Jordan, and D. Riley, editors. Habitat requirements for Chesapeake Bay living resources, 2nd edition. Chesapeake Bay Program, Living Resources Subcommittee, Annapolis, Maryland.
- Klauda, R. J., R. E. Palmer, and M. J. Lenkevich. 1987. Sensitivity of early life stages of blueback herring to moderate acidity and aluminum in soft freshwater. *Estuaries* 10: 44-53.
- Koo, T. S. Y., M. L. Johnston, G. E. Galog, Jr., D. Hepner, and D. F. Ludwig. 1976. Effects of heat shock on fish eggs and larvae. Chesapeake Biological Laboratory CEES Reference No. 77-60-CBL, Solomons, Maryland.
- Kosa, J. T., and M. E. Mather. 2001. Processes contributing to variability in regional patterns of juvenile river herring abundance across small coastal systems. *Transactions of the American Fisheries Society* 130: 600-619.
- Leim, A. H. 1924. The life history of the shad (*Alosa sapidissima*) (Wilson) with special reference to the factors limiting its abundance. Biological Board of Canada, Contributions to Canadian Biology 2: 163-284.
- Leim, A. H., and W. B. Scott. 1966. Fishes of the Atlantic coast of Canada. Fisheries Research Board of Canada Bulletin 155.
- Libby, D. A. 1981. Difference in sex ratios of the anadromous alewife, *Alosa pseudoharengus*, between the top and bottom of a fishway at Damariscotta Lake, Maine. United States National Marine Fisheries Service Fishery Bulletin 79: 207-211.
- Libby, D. A. 1982. Decrease in length at predominant ages during a spawning migration of the alewife, *Alosa pseudoharengus*. *Fisheries Bulletin* 80: 902-905.
- Loesch, J. G. 1969. A study of the blueback herring, *Alosa aestivalis* (Mitchill), in Connecticut waters. Doctoral dissertation. University of Connecticut, Storrs, Connecticut.
- Loesch, J. G. 1987. Overview of life history aspects of anadromous alewife and blueback herring in freshwater habitats. Pages 89-103 in M. J. Dadswell, R. J. Klauda, C. M. Moffitt, and R. L. Saunders, editors. Common strategies of anadromous and catadromous fishes. American Fisheries Society Symposium 1, Bethesda, Maryland.
- Loesch, J. G., and W. H. Kriete, Jr. 1980. Anadromous fisheries research program, Virginia. Annual Report for NMFS Project No. AFC10-1, Virginia Institute of Marine Science, Gloucester Point, Virginia.
- Loesch, J. G., and W. A. Lund, Jr. 1977. A contribution to the life history of the blueback herring, *Alosa aestivalis*. *Transactions of the American Fisheries Society* 106: 583-589.
- Mansueti, R. J. 1956. Alewife herring eggs and larvae reared successfully in lab. Maryland Tidewater News 13: 2-3.

- Mansueti, R. J., and J. D. Hardy, Jr. 1967. Development of fishes of the Chesapeake Bay region, and atlas of egg, larval, and juvenile stages, part I. Natural Resources Institute, University of Maryland, Baltimore, Maryland.
- Marcy, B. C., Jr. 1969. Age determination from scales of *Alosa pseudoharengus* (Wilson) and *Alosa aestivalis* (Mitchill) in Connecticut waters. Transactions of the American Fisheries Society 98: 622-630.
- Marcy, B. C., Jr. 1976a. Planktonic fish eggs and larvae of the lower Connecticut River and effects of the Connecticut Yankee plant including entrainment. Pages 115-139 in D. Merriman, and L. M. Thorper, editors. The Connecticut River ecological study: The impact of a nuclear power plant. American Fisheries Society Monograph No. 1, Bethesda, Maryland.
- Marcy, B. C., Jr. 1976b. Fishes of the lower Connecticut River and the effects of the Connecticut Yankee plant. Pages 61-114 in D. Merriman, and L. M. Thorper, editors. The Connecticut River ecological study: The impact of a nuclear power plant. American Fisheries Society Monograph No. 1, Bethesda, Maryland.
- McCauley, R. W., and F. P. Binkowski. 1982. Thermal tolerance of the alewife. Transactions of the American Fisheries Society 111: 389-391.
- McFadden, J. T., Texas Instruments, and Lawler, Matusky, and Skelly Engineers. 1978. Influence of the proposed Cornwall pumped storage project and steam electric generating plants on the Hudson River estuary with emphasis on striped bass and other fish populations. Consolidated Edison Company of New York, New York, New York.
- McKenzie, R. A. 1959. Marine and freshwater fishes of the Miramichi River and estuary, New Brunswick. Journal of the Fisheries Research Board of Canada 16: 807-833.
- Meldrim, J. W., and J. J. Gift. 1971. Temperature preference, avoidance and shock experiments with estuarine fishes. Ichthyological Association Bulletin No. 7, Ichthyological Association, Middletown, Delaware.
- Messieh, S. N. 1977. Population structure and biology of alewives *Alosa pseudoharengus* and blueback herring *A. aestivalis* in the Saint John River, New Brunswick. Environmental Biology of Fishes 2: 195-210.
- Milstein, C. B. 1981. Abundance and distribution of juvenile *Alosa* species off southern New Jersey. Transactions of the American Fisheries Society 110: 306-309.
- Morsell, J. W., and C. R. Norden. 1968. Food habits of the alewife, *Alosa pseudoharengus* (Wilson), in Lake Michigan. Proceedings of the 11th Conference on Great Lakes Research: 96-102.
- Murdy, E. O., R. S. Birdsong, and J. A. Musick. 1997. Fishes of Chesapeake Bay. Smithsonian Institution, Washington, D.C.
- Neves, R. J. 1981. Offshore distribution of alewife, *Alosa Pseudoharengus*, and blueback herring, *Alosa Aestivalis*, along the Atlantic coast. Fishery Bulletin 79: 473-485.
- Neves, R. J., and L. Depres. 1979. The oceanic migration of American shad, *Alosa sapidissima*, along the Atlantic coast. National Marine Fisheries Service Fisheries Bulletin 77: 199-212.

- Nigro, A. A., and J. J. Ney. 1982. Reproduction and early life accommodations of landlocked alewife to a southern range extension. *Transactions of the American Fisheries Society* 96: 387-393.
- Norden, C. R. 1967. Age, growth, and fecundity of the alewife, *Alosa pseudoharengus* (Wilson), in Lake Michigan. *Transactions of the American Fisheries Society* 96: 387-393.
- Norden, C. R. 1968. Morphology and food habits of larval alewife, *Alosa pseudoharengus* in Lake Michigan. *Proceedings of the 11th Conference on Great Lakes Research*: 70-78.
- O'Connell, A. M., and P. L. Angermeier. 1997. Spawning location and distribution early life stages of alewife and blueback herring in a Virginia stream. *Estuaries* 20: 779-791.
- O'Leary, J. A., and B. Kynard. 1986. Behavior, length, and sex ratio of seaward migrating juvenile American shad and blueback herring in the Connecticut River. *Transactions of the American Fisheries Society* 115: 529-536.
- O'Neill, J. T. 1980. Aspects of the life histories of anadromous alewife and the blueback herring, Margaree River and Lake Ainsle, Nova Scotia, 1978-1979. Masters thesis. Acadia University, Wolfville, Nova Scotia, Canada.
- O'Rear, C. W. 1983. A study of river herring spawning and water quality in Chowan River. North Carolina Department of Natural Resources and Community Development, Division of Marine Fisheries Report for Project No. AFC-17, Raleigh, North Carolina.
- Odell, T. T. 1934. The life history and ecological relationships of the alewife *Pomolobus pseudoharengus* (Wilson) in Seneca Lake, New York. *Transactions of the American Fisheries Society* 64: 118-124.
- Olney, J. E., and G. W. Boehlert. 1988. Nearshore ichthyoplankton associated with seagrass beds in the lower Chesapeake Bay. *Marine Ecology Progress Series* 45: 33-43.
- Otto, R. G., M. A. Kitchell, and J. O. Rice. 1976. Lethal and preferred temperatures of the alewife (*Alosa pseudoharengus*) in Lake Michigan. *Transactions of the American Fisheries Society* 105: 96-106.
- Pardue, G. B. 1983. Habitat suitability index models: Alewife and blueback herring. U.S. Fish and Wildlife Service Report No. FWS/OBS-82/10.58, Washington, D.C.
- PSE&G (Public Service Electric and Gas Company). 1980. Comparative evaluation of effects of ozonated and chlorinated thermal discharges on estuarine and freshwater organisms. Public Service Electric and Gas Company, Newark, New Jersey.
- PSE&G (Public Service Electric and Gas Company). 1982. Blueback herring (*Alosa aestivalis*): A synthesis of information on natural history, with reference to occurrence in the Delaware River and estuary and involvement with Salem Nuclear Generating Station. Salem Nuclear Generating Station, 316 (b) Report, Appendix VI, Newark, New Jersey.
- PSE&G (Public Service Electric and Gas Company). 1984. Alewife (*Alosa pseudoharengus*): A synthesis of information on natural history, with reference to occurrence in the Delaware River and estuary and involvement with Salem Nuclear Generating Station, 316 (b) Report, Appendix V, Newark, New Jersey.

- Richkus, W. A. 1974. Factors influencing the seasonal and daily patterns of alewife (*Alosa pseudoharengus*) migration in a Rhode Island river. *Journal of the Fisheries Research Board of Canada* 31: 1485-1497.
- Richkus, W. A. 1975a. Migratory behavior and growth of juvenile anadromous alewife, *Alosa pseudoharengus*, in a Rhode Island drainage. *Transactions of the American Fisheries Society* 104: 483-493.
- Richkus, W. A. 1975b. The response of juvenile alewife to water currents in an experimental chamber. *Transactions of the American Fisheries Society* 104: 494-498.
- Richkus, W. A., and G. DiNardo. 1984. Current status and biological characteristics of the anadromous alosid stocks of the eastern United States: American shad, hickory shad, alewife, and blueback herring. Interstate Fisheries Management Program, Atlantic States Marine Fisheries Commission, Washington, D.C.
- Richkus, W. A., and H. E. Winn. 1979. Activity cycles of adult and juvenile alewife, *Alosa pseudoharengus*, recorded by two methods. *Transactions of the American Fisheries Society* 108: 358-365.
- Rideout, S. G. 1974. Population estimate, movement, and biological characteristics of anadromous alewife (*Alosa pseudoharengus*) utilizing the Parker River, Massachusetts in 1971-1972. Masters thesis. University of Massachusetts, Amherst, Massachusetts.
- Ross, R. M. 1991. Recreational fisheries of coastal New England. University of Massachusetts Press, Amherst, Massachusetts.
- Ross, R. M., and R. C. Biagi. 1990. Marine recreational fisheries of Massachusetts: River herring. University of Massachusetts Cooperative Extension, Massachusetts Division of Marine Fisheries, Marine Recreational Fisheries Series Informational Pamphlet No. CR 162: 6/90-10M, Amherst, Massachusetts.
- Rothschild, B. J. 1962. The life history of the alewife, *Alosa pseudoharengus* (Wilson) in Cayuga Lake, New York. Doctoral dissertation. Cornell University, Ithaca, New York.
- Royce, W. F. 1943. The reproduction and studies of the life history of the lake trout, *Cristovomer namaycush* (Walbaum). Masters thesis. Cornell University, Ithaca, New York.
- Rulifson, R. A. 1982. Anadromous fish in the southeastern United States and recommendations for development of a management plan. U.S. Fish and Wildlife Service Research Region 4, Atlanta, Georgia.
- Rulifson, R. A., M. T. Huish, and R. W. Thoesen. 1994. Status of anadromous *Alosa* along the east coast of North America. Pages 134-159 in J. E. Cooper, R. T. Eades, R. J. Klauda, and J. G. Loesch, editors. *Proceedings of the Anadromous Alosa Symposium*, American Fisheries Society, Bethesda, Maryland.
- Rulifson, R. A., S. A. McKenna, and M. L. Gallagher. 1987. Tagging studies of striped bass and river herring in upper Bay of Fundy, Nova Scotia. North Carolina Division of Marine Fisheries, Completion Report No. AFC-28-1, East Carolina University, Greenville, North Carolina.

- Schmidt, R. E., B. M. Jessop, and J. E. Hightower. 2003. Status of river herring stocks in large rivers. Pages 171-182 in K. E. Limburg, and J. R. Waldman, editors. Biodiversity, status, and conservation of the world's shads. American Fisheries Society Symposium 35, Bethesda, Maryland.
- Schmidt, R. E., R. J. Klauda, and J. M. Bartels. 1988. Distributions and movements of the early life stages of three species of *Alosa* in the Hudson River, with comments on mechanisms to reduce interspecific competition. Pages 193-215 in C. L. Smith, editor. Fisheries research in the Hudson River. State University of New York Press, Albany, New York.
- Schubel, J. R., and A. H. Auld. 1972. Thermal effects of a model power plant on the hatching success of American shad, *Alosa sapidissima*, eggs. Proceedings of the Southeastern Association of Game and Fish Commissioners 26: 644-648.
- Schubel, J. R., and J. C. S. Wang. 1973. The effects of suspended sediments on the hatching success of yellow perch, white perch, striped bass and alewife eggs. Ichthyological Association Special Report No. 30, Reference 73-3.
- Scott, W. B., and E. J. Crossman. 1973. Freshwater fishes of Canada. Fisheries Research Board of Canada Bulletin 184, Ottawa, Canada.
- Scott, W. B., and M. G. Scott. 1988. Atlantic fishes of Canada. Canadian Bulletin of Fisheries and Aquatic Sciences 219: 1-731.
- Seegert, G. L., and A. S. Brooks. 1978. The effects of intermittent chlorination on coho salmon, alewife, spotted shiner, and rainbow trout. Transactions of the American Fisheries Society 107: 346-353.
- Seegert, G. L., and D. L. Latimer. 1977. The effects of a 30-minute exposure on selected Lake Michigan fishes and invertebrates to residual chlorine. Pages 91-100 in L. L. Jensen, editor. Biofouling control procedures, technology and ecological effects. Marcel Dekker, Inc., New York. New York.
- Sismour, E. N. 1994. Contributions to the early life histories of alewife (*Alosa pseudoharengus*) and blueback herring (*A. aestivalis*): rearing, identification, ageing, and ecology. Doctoral dissertation. Virginia Institute of Marine Science, Gloucester Point, Virginia.
- Smith, H. M. 1907. The fishes of North Carolina, volume II. North Carolina Geological and Economic Survey. E. M. Uzzell and Company, State Printers and Binders, Raleigh, North Carolina.
- Smith, B. A. 1971. The fishes of four low-salinity tidal tributaries of the Delaware River estuary. Masters thesis. Cornell University, Ithaca, New York.
- Stanley, J. G., and P. J. Colby. 1971. Effects of temperature on electrolyte balance and osmoregulation in the alewife (*Alosa pseudoharengus*) in fresh and sea water. Transactions of the American Fisheries Society 100: 624-638.
- Stanley, J. G., and J. A. Holzer. 1971. Electrolyte metabolism of moribund alewife from Lake Michigan. Proceedings of the 14th Conference on Great Lakes Research: 220-221.
- Stokesbury, K. D. E., and M. J. Dadswell. 1989. Seaward migration of juveniles of three herring species *Alosa*, from an estuary in the Annapolis River, Nova Scotia. The Canadian Field-Naturalist 103: 388-393.

- Stone, H. H. 1985. Composition, morphometric characteristics and feeding ecology of alewife (*Alosa pseudoharengus*) and blueback herring (*Alosa aestivalis*) (Pisces: Clupeidae) in Minas Basin. Masters thesis. Acadia University, Wolfville, Nova Scotia, Canada.
- Stone, H. H., and G. R. Daborn. 1987. Diet of alewife, *Alosa pseudoharengus* and blueback herring, *A. aestivalis* (Pisces: Clupeidae) in Minas Basin, Nova Scotia, a turbid, macrotidal estuary. *Environmental Biology of Fishes* 19: 55-67.
- Stone, H. H., and B. M Jessop. 1992. Seasonal distribution of river herring *Alosa pseudoharengus* and *A. aestivalis* off the Atlantic coast of Nova Scotia. *Fisheries Bulletin* 90: 376-389.
- Stone, H. H. 1993. Feeding habits of anadromous alewife, *Alosa pseudoharengus*, off the Atlantic coast of Nova Scotia. *Fisheries Bulletin* 92: 157-170.
- Street, M. W., A. S. Deaton, W. S. Chappell, and P. D. Mooreside. 2005. North Carolina Coastal Habitat Protection Plan. North Carolina Division of Marine Fisheries, Morehead City, North Carolina.
- Street, M. W., P. P. Pate, B. F. Holland, Jr., and A. B. Powell. 1975. Anadromous fisheries research program, northern coastal region. North Carolina Division of Marine Fisheries Completion Report for Project No. AFCS-8, Morehead City, North Carolina.
- Street, M. W., P. P. Pate, B. F. Holland, Jr., and B. F. Yelverton. 1973. Anadromous fisheries research program, northern coastal region. North Carolina Federal Aid Project No. AFCS-8-1 (Job 3). North Carolina Division of Commercial and Sports Fisheries, Raleigh, North Carolina.
- Thunberg, B. E. 1971. Olfaction in parent stream selection by the alewife (*Alosa pseudoharengus*). *Animal Behavior* 19: 217-225.
- Tyus, H. M. 1971. Population size, harvest and movements of alewife during spawning migrations to Lake Mattamuskeet, North Carolina. Doctoral dissertation. North Carolina State University, Raleigh, North Carolina.
- Tyus, H. M. 1974. Movements and spawning of anadromous alewife, *Alosa pseudoharengus* (Wilson) at Lake Mattamuskeet, North Carolina. *Transactions of the American Fisheries Society* 103: 392-395.
- Vigerstad, T. J., and J. S. Colb. 1978. Effects of predation by sea-run juvenile alewife (*Alosa pseudoharengus*) on the zooplankton community at Hamilton reservoir, Rhode Island. *Estuaries* 1: 36-45.
- Vinogradov, V. I. 1984. Food of silver hake, red hake and other fishes on Georges Bank and adjacent waters, 1968-74. Northwest Atlantic Fisheries Organization Science Council Study No. 7: 87-94.
- Waldman, J. R., and K. E. Limburg. 2003. The world's shads: Summary of their status, conservation, and research needs. Pages 363-369 in K. E. Limburg, and J. R. Waldman, editors. *Biodiversity, status, and conservation of the world's shads*. American Fisheries Society Symposium 35, Bethesda, Maryland.

- Walton, C. J. 1981. Population biology and management of the alewife (*Alosa pseudoharengus*) in Maine. Maine Department of Marine Resources, Division of Sea and Shore Fisheries Project No. AFC-21-2, Augusta, Maine.
- Walton, C. J. 1987. Parent-progeny relationship for an established population of anadromous alewife in a Maine lake. American Fisheries Society Symposium 1: 451-454.
- Wang, J. C. S., and R. J. Kernehan. 1979. Fishes of Delaware estuaries: A guide to the early life histories. Ecological Analysts, Inc., Towson, Maryland.
- Warriner, J. E., J. P. Miller, and J. Davis. 1970. Distribution of juvenile river herring in the Potomac River. Proceedings of the Southeastern Association of Game and Fish Commissioners 23: 384-388.
- Watt, W. D., and F. C. Duerden. 1974. Aquatic ecology of the Saint John River. The Saint John River Basin Board Volume 2, Report No. 15g, Fredericton, New Brunswick.
- Weaver, J. E. 1975. Food selectivity, feeding chronology, and energy transformations of juvenile alewife (*Alosa pseudoharengus*) in the James River near Hopewell, Virginia. Doctoral dissertation. University of Virginia, Charlottesville, Virginia.
- Weinrich, D. R., N. H. Butowski, E. W. Franklin, and J. P. Mowrer. 1987. Investigation of anadromous alosines. Maryland Department of Natural Resources, Annapolis, Maryland.
- Wells, L. 1968. Seasonal depth distribution of fish in southeastern Lake Michigan. U.S. Fish and Wildlife Service Fisheries Bulletin 67: 1-15.
- Willis, T. V. 2006. St. Croix River alewife – smallmouth bass interaction study. Final Report to Maine Rivers, Hallowell, Maine.
- Winslow, S. E. 1995. North Carolina alosid management program. Completion Report for Project AFC-47, Segments 1-3. North Carolina Division of Marine Fisheries, Morehead City, North Carolina.
- Winters, G. H., J. A. Moores, and R. Chaulk. 1973. Northern range extension and probably spawning of gaspereau (*Alosa pseudoharengus*) in the Newfoundland area. Journal of the Fisheries Research Board of Canada 30: 860-861.
- Yako, L. A. 1998. Community interactions influencing juvenile anadromous herring in freshwater: migration cues and predation. Masters thesis. University of Massachusetts, Amherst, Massachusetts.
- Yako, L. A., M. E. Mather, and F. Juanes. 2000. Assessing the contribution of anadromous herring to largemouth bass growth. Transactions of the American Fisheries Society 129: 77-88.
- Zich, H. E. 1978. Existing information on anadromous clupeid spawning in New Jersey. New Jersey Department of Environmental Protection, Division of Fish, Game, and Shellfish, Bureau of Fisheries, Miscellaneous Report No. 41, Lebanon, New Jersey.

Chapter 5

BLUEBACK HERRING

(Alosa aestivalis)

Section I. Blueback Herring Description of Habitat

Blueback Herring General Habitat Description and Introduction

Blueback herring (*Alosa aestivalis*) are an anadromous, highly migratory, euryhaline, pelagic, schooling species. Both blueback herring and alewife are often referred to as “river herring,” which is a collective term for these two often inter-schooling species (Murdy et al. 1997). This term is often used generically in commercial harvests with no distinction between the two species (ASMFC 1985); to further this lumping tendency, landings for both species are reported as alewife (Loesch 1987). Blueback herring spend most of their lives at sea, returning to freshwater only to spawn (Colette and Klein-MacPhee 2002). Their range is commonly cited as spanning from the St. Johns River, Florida (Hildebrand 1963; Williams et al. 1975) to Cape Breton, Nova Scotia (Scott and Crossman 1973) and the Miramichi River, New Brunswick (Bigelow and Schroeder 1953; Leim and Scott 1966). However, Williams et al. (1975) have reported that blueback herring occur as far south as Tomoka River, a small freshwater tributary of the Halifax River in Florida (a brackish coastal lagoon). Additionally, some landlocked populations occur in the Southeast (Klauda et al. 1991), but landlocking occurs less frequently in blueback herring than in alewife (Schmidt et al. 2003).

Blueback herring from the South are capable of migrating extensive distances (over 2000 km) along the Atlantic seaboard, and their patterns of migration may be similar to those of American shad (Neves 1981). This species is most abundant south of the warmer waters of the Chesapeake Bay (Manooch 1988; Scott and Scott 1988), occurring in virtually all tributaries to the Chesapeake Bay, the Delaware River, and in adjacent offshore waters (Jones et al. 1978). Although blueback herring and alewife co-occur throughout much of their range, blueback herring are more abundant by one or perhaps two orders of magnitude along the middle and southern parts of their ranges (Schmidt et al. 2003).

Several long-term data sets were recently analyzed to determine the current status of blueback herring in large river systems along the East Coast, including the Connecticut, Hudson, and Delaware rivers. Blueback herring show signs of overexploitation in all of these rivers, including reductions in mean age, decreases in percentage of returning spawners, and decreases in abundance. Although researchers did not include smaller drainages in the analysis, they did note that some runs in the northeastern U.S. and Atlantic Canada have observed increased population abundance of blueback herring in recent years (Schmidt et al. 2003).

Please note that some of the data presented in this chapter have been derived from studies of landlocked populations and the applicability of environmental requirements is unknown; therefore, they should be interpreted with discretion (Klauda et al. 1991).

Part A. Blueback Herring Spawning Habitat

Geographical and temporal patterns of migration

Adult blueback herring populations in the South return earliest to spawn in freshwater and sometimes brackish waters, with populations further north migrating inland later in the spring when water temperatures have increased. Researchers believe that blueback herring migrate inland from offshore waters north of Cape Hatteras, North Carolina, encountering the same thermal barrier as American shad. Individuals then turn south along the coast if they are homing to South Atlantic rivers (Neves 1981); northbound pre-spawning adults head north along the coast (Stone and Jessop 1992). Adults begin migrations from the offshore region in response to changes in water temperature and light intensity (Pardue 1983). It is assumed that adults return to the rivers in which they were spawned, but some may stray to adjacent streams or colonize new areas; some individuals have even reoccupied systems in which the species was previously extirpated (Messieh 1977; Loesch 1987).

Blueback herring will ascend freshwater far upstream (Massman 1953; Davis and Cheek 1966; Perlmutter et al. 1967; Crecco 1982); their distribution is a function of habitat suitability and hydrological conditions, such as swift flowing water (Loesch and Lund 1977). Earlier hypotheses that blueback herring do not ascend as far upstream as alewife are unfounded (Loesch 1987). In fact, in tributaries of the Rappahannock River, Virginia, upstream areas were found to be more important for blueback herring spawning than downstream areas (O'Connell and Angermeier 1997).

Spawning location (ecological)

Generally, blueback herring and alewife attempt to occupy different freshwater spawning areas. However, if blueback herring and alewife are forced to spawn in the same vicinity (i.e., due to blocked passage) (Loesch 1987), some researchers have suggested that the two species occupy separate spawning sites to reduce competition. For example, Loesch and Lund (1977) note that blueback herring typically select the main stream flow for spawning, while neighboring alewife spawn along shorebank eddies or deep pools. In rivers where headwater ponds are absent or poorly-developed, alewife may be most abundant farther upstream in headwater reaches, while blueback herring utilize the mainstream proper for spawning (Ross and Biagi 1990). However, in some areas blueback herring are abundant in tributaries and flooded low-lying areas adjacent to main streams (Erkan 2002).

In the allopatric range, where there is no co-occurrence with alewife (south of North Carolina), blueback herring select a greater variety of spawning habitat types (Street 1970; Frankensteen 1976; Christie 1978), including small tributaries upstream from the tidal zone (ASMFC 1999), seasonally flooded rice fields, small densely vegetated streams, cypress swamps, and oxbows, where the substrate is soft and detritus is present (Adams and Street 1969; Godwin and Adams 1969; Adams 1970; Street 1970; Curtis et al. 1982; Meador et al. 1984). Furthermore, despite the fact that blueback herring generally do not spawn in ponds in their northern range (possibly to reduce competition), they have the ability to do so (Loesch 1987).

Loesch (1987) has reported that blueback herring can adapt their spawning behavior under certain environmental conditions and disperse to new areas if the conditions are suitable.

This behavior was demonstrated in the Santee-Cooper System, South Carolina, where hydrological alterations resulting from the creation of a diversion canal led to changes in spawning site selection in both rivers. In the Cooper River, blueback herring lost access to formerly impounded rice fields along the river, which were important spawning areas. Following the construction of the diversion canal, there was an increase in the number and length of tributaries along the river that were used as spawning habitat. In the adjacent Santee River, adults dispersed into the diversion canal itself in favor of their former habitat, which was further upstream (Eversole et al. 1994).

Temporal spawning patterns

Spawning of blueback herring typically commences in the given regions at the following times: 1) Florida – as early as December (McLane 1955); 2) South Carolina (Santee River) – present in February (Bulak and Christie 1981), but spawning begins in early March (Christie 1978; Meador 1982); 3) Chesapeake Bay region - lower tributaries in early April and upper reaches in late April (Hildebrand and Schroeder 1928); 4) Mid-Atlantic region – late April (Smith 1971; Zich 1978; Wang and Kernehan 1979); 5) Susquehanna River - abundance peaks in early to mid-May (R. St. Pierre, U.S. Fish and Wildlife Service, personal communication); 6) Connecticut River – present in lower river mid-April, but spawning begins in mid-May (Loesch and Lund 1977); and 7) Saint John River, New Brunswick – present in May (Messieh 1977; Jessop et al. 1983), but spawning doesn't commence until June and may run through August (Leim and Scott 1966; Marcy 1976b).

Blueback herring generally spawn 3 to 4 weeks after alewife in areas where they co-occur; however, there may be considerable overlap (Loesch 1987) and peak spawning periods may differ by only 2 to 3 weeks (Hildebrand and Schroeder 1928). In a tributary of the Rappahannock River, Virginia, researchers found that blueback eggs and larvae were more abundant than those of alewife, but that alewife used the stream over a longer period of time. In addition, there was only a three-day overlap of spawning by alewife and blueback herring (O'Connell and Angermeier 1997). Although it has been suggested that alewife and blueback herring select separate spawning sites in sympatric areas to reduce competition (Loesch 1987), O'Connell and Angermeier (1997) did not find that the two species used different spawning habitat in the areas they examined. The researchers suggested that there was a temporal, rather than spatial, segregation that minimized the competition between the two species (O'Connell and Angermeier 1997).

Spawning may occur during the day, but blueback herring spawning activity is normally most prolific from late afternoon (Loesch and Lund 1977) into the night (Johnston and Cheverie 1988). During spawning, a female and two or more males will swim approximately one meter below the surface of the water; subsequently, they will dive to the bottom (Loesch and Lund 1977), simultaneously releasing eggs and sperm over the substrate (Colette and Klein-MacPhee 2002). Spawning typically occurs over an extended period, with groups or "waves" of migrants staying 4 to 5 days before rapidly returning to sea (Hildebrand and Schroeder 1928; Bigelow and Schroeder 1953; Klauda et al. 1991). In a temporal context, the majority of spent adult blueback herring emigrating from the Connecticut River moved through fish passage facilities between 1700 and 2100 hours (Taylor and Kynard 1984).

Maturation and spawning periodicity

Blueback herring are repeat spawners at an average rate of 30 to 40% (Richkus and DiNardo 1984). In general, there appears to be an increase in repeat spawning from south to north (Rulifson et al. 1982). Researchers have found that approximately 44 to 65% of the blueback herring in Chesapeake Bay tributaries had previously spawned (Joseph and Davis 1965), while 75% of those in Nova Scotia had previously spawned (O'Neill 1980). In the Chowan River, North Carolina, as many as 78% of individuals were first-time spawners (Winslow and Rawls 1992). First spawning occurs when adults are between 3 and 6 years old, but most first-time spawners are age 4 fish (Messieh 1977; Loesch 1987). Joseph and Davis (1965) reported that some blueback herring spawn as many as six times in Virginia.

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; Jessop 1994). Researchers have suggested that although year-class is driven mostly by environmental factors, 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). To the extent that environmental factors have been linked to year-class abundance, they will be discussed in subsequent sections.

Spawning and the saltwater interface

Blueback herring generally spawn in freshwater above the head of tide; brackish and tidal areas are rarely used for spawning by this species (Nichols and Breder 1927; Hildebrand 1963; Fay et al. 1983; Murdy et al. 1997). Adults, eggs, larvae, and juveniles can tolerate a wide range of salinities, but seem to prefer a more narrow range, depending on life history stage. For example, while spawning may occur in salinities ranging from 0 to 6 ppt, it typically takes place in waters that are less than 1 ppt (Klauda et al. 1991). Boger (2002) presented a modified salinity range for Virginia rivers, suggesting that a suitable salinity range for spawning adults is 0 to 5 ppt. Alternatively, spawning adult blueback herring have been found in brackish ponds at Woods Hole, Massachusetts (Nichols and Breder 1927; Hildebrand 1963).

Spawning substrate associations

In areas where blueback herring and alewife co-occur (sympatric region), blueback herring prefer to spawn over gravel and clean sand substrates where the water flow is relatively swift, and actively avoid areas with slow-moving or standing water (Bigelow and Welsh 1925; Marcy 1976b; Loesch and Lund 1977; Johnston and Cheverie 1988).

In the allopatric range, there seems to be some variation in blueback herring spawning substrate. Where water flow is more sluggish, there is ample opportunity for detritus and silt to accumulate. Pardue (1983) considered substrates with 75% or more silt and other soft materials (e.g., detritus and vegetation) as optimal for blueback herring spawning because it provides cover for eggs and larvae. However, more recently 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).

Spawning depth associations

During their freshwater migration, blueback herring swim at mid-water depths (compared to deeper water used by American shad) (Witherell 1987). This species is reported to spawn in both shallow (Jones et al. 1978) and deep streams (Johnston and Cheverie 1988).

Spawning water temperature

O'Connell and Angermeier (1997) found that temperature was the strongest predictor of blueback herring adult and early egg presence in a tributary of the Rappahannock River, Virginia. Blueback herring are reported to spawn at temperatures ranging from a minimum of 13°C (Hawkins 1979; Rulifson et al. 1982) to a maximum of 27°C (Loesch 1968). Loesch and Lund (1977) noted that spawning adults were found in the lower Connecticut River in mid-April when water temperatures were as low as 4.7°C, but spawning did not occur until several weeks later when the water temperature had risen. Meador et al. (1984) noted that rapid changes in water temperature appeared to be an important factor influencing the timing of spawning. Optimal spawning temperature range is suggested to be 21 to 25°C (Cianci 1969; Marcy 1976b; Klauda et al. 1991) and 20 to 24° C (Pardue 1983). Fish in the laboratory acclimated to 15°C and 29 ppt salinity exhibited a final temperature preference of 22.8°C (Terpin et al. 1977).

Spawning dissolved oxygen associations

Adult blueback herring require a minimum of 5.0 mg/L of dissolved oxygen (Jones et al. 1978). For example, adults caught in the Cooper and Santee Rivers, South Carolina, were always captured in areas that had a dissolved oxygen concentration of 6 mg/L or higher (Christie et al. 1981).

Spawning water velocity/flow

In the sympatric range, blueback herring prefer to spawn in large rivers and tributaries where the water flow is relatively swift, actively avoiding areas with slow-moving or standing water (Bigelow and Welsh 1925; Marcy 1976b; Johnston and Cheverie 1988). In such areas, blueback herring will concentrate and spawn in the main-stream flow, while alewife favor shorebank eddies or deep pools for spawning (Loesch and Lund 1977). In Connecticut, blueback herring select the fast-moving waters of the upper Salmon River and Roaring Brook, while alewife are found in the slower-moving waters of Higganum and Mill creeks (Loesch and Lund 1977) and Bride Lake (Kissil 1974). Researchers suggest that there is differential selection of spawning in these areas (Loesch and Lund 1977).

In the allopatric range, blueback herring favor lentic sites, but may also occupy lotic sites (Loesch 1987; Klauda et al. 1991). Additionally, they may select slower-flowing tributaries and flooded low-lying areas adjacent to main streams with soft substrates and detritus (Street et al. 1975; Sholar 1975, 1977; Fischer 1980; Hawkins 1979).

Meador et al. (1984) found that high flows (and accompanying low water temperatures) associated with flood control discharges in the Santee River, South Carolina, immediately prior to the spawning season, resulted in lower numbers of blueback herring larvae that year. In the preceding year without flood control discharges, spawning occurred farther upstream (Meador et al. 1984). Furthermore, ripe adults were found below the sampling site heading downstream the year that high flows occurred, apparently without having spawned (Bulak and Christie 1981). Concurrently, other studies (Bulak and Curtis 1977; West et al. 1988) have found spawning adults moving downstream from spawning areas following a sudden change in water discharge.

In a similar example in the same river system, a redirection canal and hydroelectric dam with a fish passage facility were constructed between the Cooper River and Santee River, which increased the average flow of the Santee River from 63 m³/s to 295 m³/s (Cooke and Leach 2003). Following the redirection, blueback herring did not concentrate below the dam and few were attracted into the fish lock during periods of zero discharge. Too much water flow also posed a problem, as adults were found concentrating below the dam during periods of discharge, but were unable to locate the entrance to the fish lock due to high turbulence (Chappelear and Cooke 1994). As a result, blueback herring changed migration patterns by abandoning the Santee River, and following the dredged canal to the higher flow of the St. Stephen Dam. Subsequently, access to spawning grounds was increased, which contributed to increases in blueback herring populations (Cooke and Leach 2003). Although the importance of instream flow requirements has been previously recognized (Crecco and Savoy 1984; ASMFC 1985; Crecco et al. 1986; Ross et al. 1993), it has usually been with regard to spawning habitat requirements or recruitment potential (Moser and Ross 1994). Cooke and Leach (2003) concluded that the study of, and possible adjustment of, river flow may be an important consideration for restoring alosine habitat.

Spawning pH and aluminum associations

Adult blueback herring captured in the Santee-Cooper River system, South Carolina, were found within a range of pH 6.0 to 7.5 (Christie and Barwick 1985; Christie et al. 1981). Further north, within tributaries of the Delaware River, New Jersey, spawning runs were found within a broader range of pH 4.7 to 7.1 (mean pH 6.2) (Byrne 1988). Based on suggested ranges for eggs (cited in Klauda et al. 1991), Boger (2002) suggested a suitable range of pH 6 to 8, and an optimal range of pH 6.5 to 8 for spawning habitat.

Spawning feeding behavior

Adult blueback herring feed during upstream spawning migrations (Rulifson et al. 1982; Frankenstein 1976), consuming large and diverse quantities of copepods, cladocerans, ostracods, benthic and terrestrial insects, molluscs, fish eggs, hydrozoans, and stratoblasts (Creed 1985). Sampling of adult blueback herring along the St. Johns River, Florida, found that they also consume vegetation (FWC 1973).

Spawning competition and predation

Information is lacking that identifies which predator species prey on adult blueback herring during their spawning runs, but it is assumed that they are consumed by other fish, reptiles (e.g., snakes and turtles), birds (e.g., ospreys, eagles, and cormorants), and mammals (e.g., mink) (Loesch 1987; Scott and Scott 1988). Erkan (2002) notes that predation of alosines 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 cormorant colonies have increased in size and have expanded into areas in which they were not previously observed. Predation by otters and herons has also increased, but to a lesser extent (Erkan 2002).

Several researchers have found evidence of striped bass predation on blueback herring (Trent and Hassler 1966; Manooch 1973; Gardinier and Hoff 1982). A recent study by Savoy and Crecco (2004) strongly supports the hypothesis that striped bass predation in the Connecticut River on adult blueback herring has resulted in a dramatic and unexpected decline in blueback herring abundance since 1992. The researchers further suggest that striped bass prey primarily on spawning adults because their predator avoidance capability may be compromised at that time, due to the strong drive to spawn during upstream migration. Rates of predation on age 0 and 1 alosines was much lower than that of adults (Savoy and Crecco 2004).

Part B. Blueback Herring Egg and Larval Habitat

Geographical and temporal movement patterns

On average, blueback herring eggs are hatched within 38 to 60 hours of fertilization (Adams and Street 1969). Yolk-sac larvae drift passively downstream with the current to slower moving water, where they grow and develop into juveniles (Johnston and Cheverie 1988). Yolk-sac absorption occurs in 2 to 3 days after hatching, and soon thereafter larvae begin to feed exogenously (Cianci 1969). Larvae are sensitive to light, so larval abundance at the surface increases as dusk approaches and reaches a maximum by dawn (Meador 1982).

Eggs, larvae, and the saltwater interface

Although spawning often occurs in freshwater, blueback herring eggs and larvae can survive in salinities as high as 18 to 22 ppt (Johnston and Cheverie 1988). Klauda et al. (1991) suggest an optimal range of 0 to 2 ppt for eggs only.

Egg and larval substrate associations

As with spawning habitat, Pardue (1983) suggested that substrates with 75% silt or other soft materials containing detritus and vegetation were optimal for egg and larval habitat. In contrast, Johnston and Cheverie (1988) found eggs adhered to sticks, stones, gravel, and aquatic vegetation along the bottom of a fast-flowing stream in the Gulf of St. Lawrence.

Egg and larval depth associations

Both Wang and Kernehan (1979) and Meador et al. (1984) observed that larval blueback herring achieved the greatest density at the surface during the night. This pattern of diel periodicity has also been described for the juvenile life stage of blueback herring (Loesch and Lund 1977; Loesch et al. 1982; Johnson et al. 1978).

Egg and larval water temperature

Blueback herring eggs were collected in the upper Chesapeake Bay where temperatures ranged from 7 to 14°C; 90% were collected at 14°C (Dovel 1971). Researchers did not report a significant reduction in hatching success for eggs acclimated at 15 to 18.3°C and exposed to temperatures of 22 to 28.3°C for 5 to 30 minutes in the laboratory (Schubel 1974), as well as those acclimated at 17.9 to 21.1°C and then exposed to 31.1°C for 30 minutes (Schubel and Koo 1976). Eggs acclimated at 32.9 to 36.1°C for 5 to 15 minutes experienced significant mortality, with total egg mortality occurring at 37.9°C. In their review of the literature, Klauda et al. (1991) concluded that suitable and optimal temperature ranges for eggs were 14 to 26°C and 20 to 24°C, respectively.

Blueback herring egg incubation is complete after 80 to 94 hours at 20 to 21°C (Kuntz and Radcliffe 1917; Jones et al. 1978) and 55 to 58 hours at 22.2 to 23.7°C (Cianci 1969; Klauda

et al. 1991). Following incubation, blueback herring eggs typically require 38 to 60 hours for hatching (Adams and Street 1969; Cianci 1969; Morgan and Prince 1976).

Larval blueback herring have been collected in the upper Chesapeake Bay where water temperatures ranged from 13 to 28°C; 96% were collected at 23 to 28°C (Dovel 1971). Blueback herring eggs and larvae collected from the Washademoak River, New Brunswick, were acclimated at 19°C, and then exposed to 29 and 34°C for 1 to 3 hours in the laboratory. While egg mortality and hatchability were deemed poor indicators of the effects of temperatures, larval deformity was considered a good indicator. Deformity rates over the three hour period were 0 to 25% at 29°C, and 100% at 34°C; such deformities were permanent and would have been lethal in the natural environment (Koo and Johnston 1978). In their review of the literature, Klauda et al. (1991) concluded that suitable temperature ranges for prolarvae and postlarvae were 14 to 26°C and 14 to 28°C, respectively.

Egg and larval dissolved oxygen associations

Larvae require a minimum of 5.0 mg/L of dissolved oxygen for survival (Jones et al. 1978).

Egg and larval pH and aluminum associations

Klauda (1989) conducted laboratory research on blueback herring fertilized eggs and yolk-sac larvae, and suggested that critical acidity conditions (defined as laboratory and field test exposures associated with greater than 50% direct mortality) for successful blueback herring reproduction in Maryland coastal plain streams occur during a single 8 to 96 hour pulse of acid (pH 5.5 to 6.2), with concomitant total monomeric aluminum concentrations of 15 to 137 µg/L. Eggs that were subjected to four treatments ranging from pH 5.7 to 7.5 and five aluminum treatments of 0 to 400 µg/L at a continuous exposure time between 96 and 120 h revealed the following results: 4-hour old embryos were sensitive to aluminum in the test treatments of pH 5.7 to 6.7; 12-hour old embryos were most sensitive to pH 5.7 with no aluminum present; and 24-hour old embryos suffered no mortality at all pH and aluminum levels (Klauda and Palmer 1987a).

Laboratory tests by Klauda et al. (1987) found a pH-induced mortality threshold for yolk-sac larvae of pH 5.7 to 6.5, and a 96-hour LC₅₀ pH of 6.37 (pH that induced 50% mortality); no aluminum was administered. Additional tests by Klauda and Palmer (1987b) found that as the exposure time was doubled (12 to 24 hours), mortality rates increased among yolk-sac larvae (25 to 49%) at a pH value of 5.5. When coupled with a concomitant exposure of total aluminum maxima of 100 to 150 µg/L, mortality increased to 19, 66, 98, and 100% after 4, 8, 12, and 24 hours exposure, respectively. Tests also revealed highly variable mortality rates (3 to 75%) for yolk-sac larvae at a pH of 6.7. In general, the data indicated that blueback herring larvae were more sensitive to lower pH values (5.7 and 6.2) with no aluminum added, and were more tolerant of higher pH values (6.7 and 7.5) (Klauda and Palmer 1987b). Furthermore, yolk-sac larvae were more sensitive than 4-hour old embryos to pH and aluminum treatments (Klauda and Palmer 1987a). Klauda et al. (1991) suggested overall suitable ranges for eggs and prolarvae of 5.7 to 8.5 and 6.2 to 8.5, respectively; optimal ranges were suggested to be 6.0 to 8.0 and 6.5 to 8.0, respectively.

Median pH values (6.27) where blueback herring were spawning in the Rappahannock River, Virginia, reported by O'Connell and Angermeier (1997) were within the lethal range (5.7 to 6.5) and below a 96-h LC_{50} of 6.37 for larvae. Reduced pH levels may represent episodic events, such as acid precipitation, but additional study is required to determine what the effects of occasional pH depressions might be.

Egg and larval water velocity/flow

Initially, blueback herring eggs are demersal, but during the water-hardening stage, they are less adhesive and become pelagic (Johnston and Cheverie 1988). In general, blueback herring eggs are buoyant in flowing water, but settle along the bottom in still water (Ross and Biagi 1990).

Water flow rates may have a notable impact on larval populations of blueback herring. For example, year-class size of blueback herring decreased with increasing discharge during May-June from the headpond at the Mactaquac Dam (Saint John River, New Brunswick) (Jessop 1990). Researchers speculated that this was due to a low abundance of phytoplankton and zooplankton that larvae rely on at first feeding; these reductions can result when high discharges occur (Laberge 1975). This effect was not observed for alewife, which spawn 2 to 3 weeks earlier than blueback herring. Sismour (1994) also 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. Similar to Jessop (1990), Sismour (1994) speculated that high flow led to increased turbidity, which reduced prey visibility, leading to starvation of larvae. Furthermore, in tributaries of the Chowan system, North Carolina, water flow was determined to be related to recruitment of larval river herring (O'Rear 1983).

Dixon (1996) found that seasonally high river flow and low water temperature during one season in several Virginia rivers were associated with delayed larval emergence, reduced relative abundance, depressed growth rate, and increased mortality compared with the previous season. It was suggested that high river flow may be a forcing mechanism on another abiotic factor, perhaps turbidity, which directly affects larval growth and survival (Dixon 1996).

Egg and larval suspended solid associations

As with alewife, blueback herring eggs have proven extremely tolerant to suspended solids, with no significant reduction in hatching success at concentrations up to 1000 mg/L (Auld and Schubel 1972). Schubel and Wang (1973) demonstrated that high levels of suspended solids during and after spawning significantly increase the rate of egg infections from naturally occurring fungi in alewife, which cause delayed mortalities; it may be likely that the same effects would be observed in blueback herring eggs (Klauda et al. 1991). Two *in situ* studies (Klauda and Palmer 1987b; Greening et al. 1989) note that yolk-sac larvae appear to be more sensitive to suspended solids than eggs, but given that observations were made following storm events, which also resulted in changes to pH and current velocity, the effects of turbidity alone were inconclusive. Klauda et al. (1991) later noted a suitable concentration range of less than 500 mg/L for the prolarva life stage.

Egg and larval feeding behavior

First-feeding larvae in the Connecticut River primarily consumed rotifers; they shift to cladocerans as they grow larger (Crecco and Blake 1983). In general, it has been suggested that clupeids have evolved to synchronize the larval stage with the optimal phase of annual plankton production cycles (Blaxter et al. 1982).

Egg and larval competition and predation

All life stages of blueback herring, including the egg and larval stages, are important prey for freshwater fishes, birds, amphibians, reptiles, and mammals (Klauda et al. 1991). The ability of blueback herring to feed extensively on rotifers is offered as an explanation for their dominance over American shad in some rivers along the East Coast (Marcy 1976a; Loesch and Kriete 1980).

Eggs, larvae, and chlorine

Morgan and Prince (1977) reported an 80 h LC₅₀ of 0.33 mg/L total residual chlorine (TRC) for blueback herring eggs incubated at 20.9°C in freshwater. The LC₅₀ for 1-day old larvae exposed to TRC for 48 and 54 h ranged from 0.24 to 0.32 mg/L; LC₅₀ for 2-day old larvae was between 0.25 and 0.32 mg/L (Morgan and Prince 1977). TRC concentrations that were greater than or equal to 0.30 mg/L increased the percentage of abnormally developed larvae (Morgan and Prince 1978).

Part C. Blueback Herring Juvenile Riverine/Estuarine Habitat

Geographical and temporal movement patterns

Recruitment to the juvenile stage for blueback herring begins later in the year than for other alosines because they spawn later and have a shorter growing season (Hildebrand and Schroeder 1928; Schmidt et al. 1988). The juvenile stage is reached when fish are about 20 mm TL (Klauda et al. 1991), with growth occurring very rapidly (Colette and Klein-MacPhee 2002).

Massman (1953), Warriner et al. (1970), and Burbidge (1974) have reported that juvenile blueback herring are most abundant upstream of spawning grounds in waters of Virginia. While Burbidge (1974) noted a greater prey density at these locations, he was unsure if fish were actually moving upstream in large numbers, if survival rates upstream were higher compared to survival rates downstream, or if fish were simply moving out of tributaries and oxbows into these areas. Michael Odom (U.S. Fish and Wildlife Service, personal communication) has noted that juvenile blueback herring select the pelagic main channel portion of tidal waters of the Potomac River, while American shad juveniles select shallower nearshore flats adjacent to and within submerged aquatic vegetation (SAV) beds. Odom speculates that these two species tend to partition the habitat in this river.

In North Carolina waters, Street et al. (1975) found that juveniles typically reside in the lower ends of the rivers in which they were spawned. In Chesapeake Bay tributaries, young-of-the-year blueback herring can be found throughout tidal freshwater nursery areas in spring and early summer; they subsequently head upstream later in the summer when saline waters encroach on their nursery grounds (Warriner et al. 1970). Schmidt et al. (1988) reasoned that juvenile blueback herring in the Hudson River remained in the vicinity of their natal areas throughout the summer because they were relatively absent downriver until late September.

Nursery areas of the Neuse River, North Carolina, have been characterized as relatively deep, slow-flowing, black waters that drain hardwood swamps (Hawkins 1979). In South Carolina, juvenile blueback herring and American shad were found to co-occur predominantly in deeper, channel habitats of estuarine systems, during fall and winter, while hickory shad selected shallow expanses of sounds and bays. Small crustaceans, favored by blueback herring and American shad, are generally abundant near the bottom in estuarine channels (McCord 2005).

Juvenile blueback herring spend three to –nine months in their natal rivers before returning to the ocean (Kosa and Mather 2001). Observations by Stokesbury and Dadswell (1989) found that blueback herring remained in the offshore region (25 to 30% seawater) of the Annapolis estuary (Nova Scotia) for almost a month before the correct migration cues triggered emigration. 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). Migration downstream is also thought by some researchers to be prompted by changes in water flow, water levels, precipitation, and light intensity (Kissil 1974; Pardue 1983). In contrast, other researchers have suggested that water flow plays little role in providing the migration cue under riverine conditions; these researchers think that migration timing is more dependent on water temperature and new to quarter moon phases, which provide dark nights (O’Leary and Kynard 1986; Stokesbury and Dadswell 1989).

In the Connecticut River, juvenile blueback herring were found to move out of river systems rapidly, within a 24-hour period, with peak migration occurring in the early evening at 1800 hours (O'Leary and Kynard 1986). Kosa and Mather (2001) studied juvenile river herring movement from 11 small coastal systems in Massachusetts, and found that most individuals emigrated between 1200 and 1600 hours. Farther north, emigration by juvenile blueback herring in the Annapolis River, Nova Scotia, peaked at night between 1800 and 2300 hours (Stokesbury and Dadswell 1989).

Juvenile blueback herring (age 1+) were found in the lower portion of the Connecticut River in early spring by Marcy (1969), which led him to speculate that many juveniles likely spend their first winter close to the mouth of the river. To the South, some young-of-the-year may overwinter in deeper, higher salinity areas of the Chesapeake Bay (Hildebrand and Schroeder 1928). In fact, Dovel (1971) reported juvenile populations in the upper Chesapeake Bay that did not emigrate until the early spring of their second year. Juveniles have also been reported overwintering in the Delaware Bay (Jones et al. 1978). Since juvenile river herring do not survive temperatures of 3°C or less (Otto et al. 1976), they would not be expected to overwinter in coastal systems where such temperatures persist (Kosa and Mather 2001).

Juveniles and the saltwater interface

Juvenile blueback herring are found most often in waters of 0 to 2 ppt prior to fall migration (Jones et al. 1988), but are tolerant of much higher salinities early in life. Pardue (1983) concluded that juveniles prefer low salinities in the spring and summer, with an optimal range between 0 and 5 ppt. Chittenden (1972) captured older juveniles in freshwater and subjected them to 28 ppt salinity at 22°C and all but one fish survived (mortality may have been due to handling stress). Furthermore, Klauda et al. (1991) suggested that 0 to 28 ppt was a suitable range for juveniles. Their ability to tolerate salinities as low as 0 ppt, and as high as 28 ppt, allows them to utilize both freshwater and marine nursery areas. However, both Loesch (1968) and Kissil (1968) found that juvenile blueback herring remained in freshwater up to one month longer than juvenile alewife.

In some cases, changes in one environmental factor may impact other environmental factors causing changes in behavior patterns. For example, in the Chowan River, North Carolina, juvenile blueback herring became scarce in sampling areas following drought conditions during the summer of 1981, which resulted in saline waters encroaching farther upriver into nursery areas. Researchers suggested that blueback herring had possibly moved further upstream to freshwater areas to avoid the saltwater intrusion (Winslow et al. 1983).

Juvenile substrate associations

Juvenile blueback herring have been found among submerged aquatic vegetation (SAV) beds of the lower Chesapeake Bay, and researchers have suggested that juveniles may benefit from reduced predation in such areas (Olney and Boehlert 1988). It is important to note, however, that no link has been made between the presence of SAV and abundance of alosines. Rather, SAV is known to improve the water quality, which may increase the abundance of alosines (B. Sadzinski, Maryland Department of Natural Resources, personal communication). Moreover, juvenile blueback herring are a pelagic schooling fish that likely do not rely on SAV

to the extent of other anadromous fishes, such as striped bass (D. A. Dixon, Electric Power Research Institute, personal communication).

Juvenile depth associations

Unlike alewife, juvenile blueback herring in the Potomac River remained at the surface or at mid-water depths during daylight hours from July through November, with almost no fish appearing at the bottom. However, at night over half of juvenile blueback herring captured were taken in bottom trawls (Warinner et al. 1970). Burbidge (1974) also reported that juvenile blueback herring were more abundant in surface waters of the James River, Virginia, during the day. Contrary to these results, Jessop (1990) found that abundance of juvenile bluebacks was greater in surface waters at night than during the day, but fish did not exhibit a strict negative phototropism. One explanation for these observed differences is the minimal sewage treatment that was required during the 1970's, which led to major phytoplankton and algal blooms in freshwater areas, reducing light penetration. Since that time, water clarity has greatly improved (Dennison et al. 1993).

In an additional study, Dixon (1996) found that juvenile blueback herring were more available to surface sampling gear approximately 30 minutes after sunset and before sunrise, where there was a corresponding light intensity of 10^{-2} to 10^{-3} $\mu\text{E}/\text{m}^2/\text{s}$. Because he did not detect a corresponding change in availability of primary zooplankton prey, he concluded that juveniles migrate to the surface water within a specific isolume with changes in incident light intensity, not as a response to prey movement. A light intensity of 10^{-2} to 10^{-3} $\mu\text{E}/\text{m}^2/\text{s}$ may be a threshold that controls retinomotor responses to support selective feeding and schooling behavior in this species. Dixon (1996) concluded that juveniles find a depth and isolume that optimizes schooling (for predation protection) and selective feeding during the day, balancing predation risks versus preferred food availability. These results further support and refine the observations of Loesch et al. (1982), who first reported the diel changes in movement of juveniles.

Juvenile water temperature

Characterization	Temperature Range (°C)	Acclimation Temperature (°C)	Salinity (ppt)	Location	Citation
Present	11.5 – 32.0	N/A		Cape Fear River, NC	Davis and Cheek 1966
Present	6.7 – 32.5	N/A		Connecticut River	Marcy 1976b
Suitable	10 – 30	N/A		Chesapeake Bay	Klauda et al. 1991
Optimal	20 – 30			Many	Pardue 1983
Selection	20 – 22	15 – 20	4 – 6	Delaware River,	Meldrim and

Characterization	Temperature Range (°C)	Acclimation Temperature (°C)	Salinity (ppt)	Location	Citation
				NJ	Gift 1971
Preference	24 – 28	25 – 26	7 – 8	Laboratory	PSE&G 1978
Avoidance	36	25 – 26	7 – 8	Laboratory	PSE&G 1978
62% Mortality	32 – 33 for 4 to 6 minutes	19		Laboratory	Marcy and Jacobson 1976
100% Mortality	32 – 33 for 4 to 6 minutes	22.7		Laboratory	Marcy and Jacobson 1976
100% Mortality	30.5 for 6 minutes	15		Laboratory	PSE&G 1984
100% Mortality	32 for 6 minutes	15	29	Laboratory	Terpin et al. 1977
100% Mortality	10	25	6.5 – 7	Laboratory	PSE&G 1978
100% Mortality	0.2	5	8.5 – 10	Laboratory	PSE&G 1978

Table 5-1. Juvenile blueback herring water temperature associations

Juvenile blueback herring have a wide range of temperature tolerances (Table 5-1). Additionally, certain temperatures create cues for the juveniles to begin migration. For example, in the Connecticut River, emigration began when the water temperatures dropped to 21°C in September, peaked at 14 to 15°C, and ended when the temperature dropped to 10°C, in late October and early November (O’Leary and Kynard 1986). Milstein (1981) found juveniles overwintering in an estuary off the coast of New Jersey where bottom temperatures ranged from 2.0 to 10.0°C. These waters were warmer and had a higher salinity than the cooler, lower salinity estuarine nurseries where the juveniles reside in the fall.

Juvenile dissolved oxygen associations

Juvenile blueback herring have been collected in waters of the Cape Fear River, North Carolina, where dissolved oxygen concentrations ranged from 2.4 to 10.0 mg/L (Davis and Cheek 1966). In the laboratory, juveniles that were exposed to dissolved oxygen concentrations of 2.0 to 3.0 mg/L for 16 hours experienced a 33% mortality rate. Researchers determined that the juveniles were unable to detect and avoid waters with low dissolved oxygen (Dorfman and

Westman 1970). As a result, mass mortalities of juveniles resulted from low dissolved oxygen in the Connecticut River over several years during June and July, most notably in the early morning hours when dissolved oxygen was below 3.6 mg/L and temperature was 27.6°C (Moss et al. 1976). In addition, Klauda et al. (1991) concluded that juveniles require a minimum of 4.0 mg/L of dissolved oxygen.

Juvenile pH and aluminum associations

In the Cape Fear River, North Carolina, juvenile blueback herring were collected where pH was between 5.2 and 6.8 (Davis and Cheek 1966), but the length of time spent within these areas was unknown. In contrast, Kosa and Mather (2001) found that abundance of juvenile river herring peaked at a pH of 8.2 in coastal systems in Massachusetts. Researchers speculated that between 7.2 and 8.2, increases in river herring abundance may be related to changes in system productivity. Although researchers were unable to determine the exact mechanism for the impact of pH on river herring, they suggested that pH does appear to contribute to variations in juvenile abundance (Kosa and Mather 2001).

Juveniles and water velocity/flow

Discharge is an important factor influencing variability in relative abundance and emigration of juvenile river herring across smaller systems. Extremely high discharge may adversely affect juvenile emigration, and high or fluctuating discharge may decrease relative abundance of adult and juvenile blueback herring (Meador et al. 1984; West et al. 1988; Kosa and Mather 2001). In laboratory experiments, juvenile river herring avoided water velocities greater than 10 cm/s, especially in narrow channels (Gordon et al. 1992). However, 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). Jessop (1994) found that the juvenile abundance index (JAI) of blueback herring decreased, and daily instantaneous mortality increased, with mean July-August river discharge from the Mactaquac Dam headpond on the Saint John River, New Brunswick, Canada. Impacts may have been the result of advection from the headpond, or from mortality as a result of reduced phytoplankton and zooplankton prey (Jessop 1994).

Juvenile feeding behavior

Juvenile blueback herring in nursery areas feed mostly on copepods, cladocerans (Domermuth and Reed 1980), and larval dipterans (Davis and Cheek 1966; Burbidge 1974). In fact, as much as 40% of the juvenile's diet may consist of benthic organisms (Watt and Duerden 1974). Additionally, Burbidge (1974) found that juveniles often select larger items in the James River, Virginia, such as adult copepods, rather than smaller prey, such as *Bosminia* sp., except where there is a high relative abundance of smaller prey. Several researchers (Vigerstad and Colb 1978; O'Neill 1980; Yako 1998) have hypothesized 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.

Juvenile blueback herring feed mostly at the surface, below the surface of the water, and to a lesser degree, on benthic prey (Domermuth and Reed 1980; Colette and Klein-MacPhee 2002). Some researchers (Burbidge 1974; Jessop 1990) observed juveniles feeding somewhat at dawn, and increasing feeding throughout the day with a maximum at dusk, then declining overnight. It is suggested that during the day, juveniles will remain within, or near, their zone of preferred light intensity, and feed in a selective mode (Dixon 1996), such as a “particulate” feeding mode (Janssen 1982).

Dixon (1996) noted that the size and age of juvenile blueback herring in the nursery zone increased in the downstream direction. Burbidge (1974) made similar observations that larger juveniles were found in downstream reaches of the James River. Dixon (1996) noted that the relative age distribution and density of juveniles (center of abundance) persisted in the nursery zone throughout the sampling season, which precluded the hypothesis that cohorts move downriver as a function of age and size. Instead, Dixon (1996) referenced Sismour’s (1994) theory that as river herring larvae hatch at different times and locations along the river, they will encounter varying concentrations and combinations of potential prey. It is these differences that will affect larval nutrition and survival. In early spring, larvae that are closer to the center of the chlorophyll maxima along the river (which likely support development and expansion of zooplankton assemblages) are more likely to find suitable prey items. Early in the season, sufficient prey in upriver areas may be lacking. As the season progresses and the zooplankton prey field expands to upriver reaches, larvae in these areas may find suitable prey quantities and grow to the juvenile stage (Sismour 1994; Dixon 1996). Pardue (1983) considered habitats that contained 100 or more zooplankton per liter as optimum, which he suggested was critical for survival and growth at this stage. Burbidge (1974) demonstrated a direct relationship between density of zooplankton and distribution and growth of blueback herring. This differential survival rate within the nursery zone over time may account for younger juveniles in upstream reaches (Dixon 1996).

Juvenile competition and predation

Young-of-the-year blueback herring are preyed upon by many freshwater and marine fishes, birds, amphibians, reptiles, and mammals. Eels, yellow perch, white perch, and bluefish are among the fish species that prey on blueback herring (Loesch (1987; Juanes et al. 1993). Researchers have suggested that excessive predation by striped bass may be contributing to the decline of blueback herring stocks in the Connecticut River (Savoy and Crecco 1995). Furthermore, suitably sized juvenile blueback herring were found to be energetically valuable and potentially a key prey item for largemouth bass in two Massachusetts rivers during the late summer. Although largemouth bass do not consistently consume blueback herring, they are energy-rich prey, which provide the highest growth potential (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, leading researchers to conclude that intraspecific competition may be greater than interspecific competition (Crecco and Blake 1983). This behavior is also evident in the Minas Basin, Nova Scotia, where juvenile blueback herring favor smaller and more planktonic prey (filter feeding strategy) than do juvenile alewife (particulate-feeding strategy)

(Stone 1985; Stone and Daborn 1987). In addition, alewife spawn earlier than blueback herring, thereby giving juvenile alewife a relative size advantage over juvenile blueback herring, which allows them access to a larger variety of prey (Jessop 1990).

Furthermore, differences in juvenile diel feeding activity serve to reduce competition. One study noted that diurnal feeding by juvenile alewife is 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 begin to feed actively at dawn, with feeding increasing throughout the day and maximizing at dusk, then diminishing from dusk until dawn (Burbidge 1974). Blueback herring are also found closer to the surface at night than alewife that are present at mid-water depths; this behavior may further reduce interspecific competition for food between the two species (Loesch 1987).

Blueback herring and American shad juveniles also co-occur in shallow nearshore waters during the day, but competition for prey is often reduced by: 1) more opportunistic feeding by American shad; 2) differential selection for cladoceran prey; and 3) higher utilization of copepods by blueback herring (Domermuth and Reed 1980). Juvenile blueback herring are more planktivorous, feeding on copepods, larval dipterans, and cladocerans (Hirschfield et al. 1966, Burbidge 1974).

Blueback herring have shown signs of being impacted by invasive species as well. For example, 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).

Juveniles and alkalinity, carbon dioxide, and chlorine

Davis and Cheek (1966) captured juvenile blueback herring in the Cape Fear River, North Carolina, where the alkalinity ranged from 5 to 32 mg/L. This same study also found that juveniles selected areas where free carbon dioxide concentrations were between 4 and 22 ppm (Davis and Cheek 1966). Another study found that juvenile blueback herring held in freshwater avoided 0.1 mg/L total residual chlorine (TRC) at 17.5°C (PSE&G 1978).

Part D. Blueback Herring Late Stage Juvenile and Adult Marine Habitat***Geographical and temporal patterns at sea***

Juvenile river herring have been found overwintering in an offshore estuary (Cameron and Pritchard 1963) 0.6 to 7.4 km from the shore of New Jersey, at depths of 2.4 to 19.2 m (Milstein 1981). This estuary is warmer and has a higher salinity than the cooler, lower salinity river-bay estuarine nurseries where river herring reside in the fall. The majority of river herring are present in this offshore estuary during the month of March, when bottom temperatures range from 4.4 to 6.5°C and salinity varies between 29.0 and 32.0 ppt (Cameron and Pritchard 1963). Further south, young blueback herring have been found overwintering off the North Carolina coast from January to March, concentrated at depths of 5.5 to 18.3 m (Holland and Yelverton 1973; Street et al. 1975).

Sexual maturity is reached between ages 3 and 6 for blueback herring. Life history information for young-of-the-year and adult blueback herring after they emigrate to the sea, and before they return to freshwater to spawn, is incomplete (Klauda et al. 1991). Researchers assume that most 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; changes in temperature likely drive oceanic migration (Neves 1981).

Neves (1981) reported that 16 years of catch data showed that blueback herring were distributed throughout the continental shelf from Cape Hatteras, North Carolina, to Nova Scotia during the spring. Most were found south of Cape Cod, but, unlike alewife, no blueback herring catches were recorded for Georges Bank. During the summer, blueback herring moved north and inshore, but catch records were too infrequent to determine summer occurrence for the species, although several catches were made near Nantucket Shoals and Georges Bank. This species was never collected south of 40° N in the summer. By early fall, the blueback herring were found along Nantucket Shoals, Georges Bank, and the inner Bay of Fundy, but were concentrated mostly along the northwest perimeter of the Gulf of Maine (Neves 1981). In the autumn, they began moving southward and offshore for overwintering along the mid-Atlantic coast until early spring (Neves 1981; Rulifson et al. 1987). Although winter sampling stations were inadequate to define wintering grounds, the few catches that were reported were primarily between latitude 40° N and 43° N. It is unknown to what extent blueback herring overwinter in deep water off the continental shelf of the United States (Neves 1981). This species has been found offshore as far as 200 km (Bigelow and Schroeder 1953; Netzel and Stanek 1966), but they are rarely collected more than 130 km from shore (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 to the central Bay of Fundy. They are also found to a lesser degree along the southern edge of Georges Bank and in the canyon between Banquereau and Sable Island Banks. 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 (Stone and Jessop 1992).

Salinity associations at sea

Adult blueback herring have been collected in salinities ranging from 0 to 35 ppt (Klauda et al. 1991). Chittenden (1972) subjected adults to gradual and abrupt changes in salinity, including direct transfers from fresh to saltwater and vice versa, with no mortality. Non-spawning adults that do not ascend freshwater streams will likely be found mostly in seawater, and possibly brackish estuaries as they make their way up the coast to their summer feeding grounds (Chittenden 1972).

Depth associations at sea

The extent to which blueback herring overwinter in deep waters off the continental shelf is unknown. Individuals have been caught most frequently at 27 to 55 m throughout their offshore range. While at sea, blueback herring are more susceptible to bottom trawling gear during the day; this concept led early researchers to conclude that the species is averse to light and follows the diel movement of plankton in the water column (Neves 1981). In the Gulf of Maine region, zooplankton concentrations are at depths less than 100 m (Bigelow 1926). Since blueback herring are rarely found in waters greater than 100 m in this area, it is speculated that zooplankton influence the depth distribution of blueback herring at sea (Neves 1981). A more recent study of juveniles within the riverine environment (see ***Juvenile depth*** under Part C of this chapter) found that they migrate to the surface within a specific isolume as light intensity changes (Dixon 1996).

Stone and Jessop (1992) found blueback herring offshore of Nova Scotia, the Bay of Fundy, and the Gulf of Maine, at mid-depths of 101 to 183 m in the spring, in shallower nearshore waters of 46 to 82 m in the summer, and in deeper offshore waters of 119 to 192 m in the fall. The researchers 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 (Stone and Jessop 1992). In addition, the semi-pelagic nature of juveniles may provide them with protection from the effects of overfishing (Dadswell 1985).

Temperature associations at sea

Although data on offshore temperature associations is limited, researchers speculate that blueback herring are similar to other anadromous clupeids, in that they may undergo seasonal migrations within preferred isotherms (Fay et al. 1983). Neves (1981) found that blueback herring were caught in an offshore area where surface water temperatures were between 2 and 20°C and bottom water temperatures ranged from 2 to 16°C; almost all of the fish were caught in water temperatures less than 13°C. Catches were most frequent where bottom temperatures averaged between 4 and 7°C (Neves 1981).

Stone and Jessop (1992) found 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 less than 5°C during the spring, researchers concluded that vertical migration may be confined by a water temperature inversion in this area (Stone and Jessop 1992).

Feeding behavior at sea

Blueback herring are size-selective zooplankton feeders (Bigelow and Schroeder 1953), whose diet at sea consists mainly of ctenophores, calanoid copepods, amphipods, mysids and other pelagic shrimps, and small fish (Brooks and Dodson 1965; Neves 1981; Stone 1985; Stone and Daborn 1987; Scott and Scott 1988; Bowman et al. 2000). In Minas Basin, Bay of Fundy, smaller blueback herring feed mostly on microzooplankton, while larger fish consume larger prey, including mysids and amphipods; feeding intensity also decreases with increasing age of fish (Stone 1985).

Neves' (1981) analysis of offshore survey results led to the conclusion that blueback herring follow the diel movement of zooplankton while at sea. As discussed above (see ***Juvenile depth*** under Part C of this chapter), Dixon's (1996) study in freshwater concluded that juvenile blueback herring followed diel movements in response to light intensity, not prey movement. Although direct evidence is lacking, catches of blueback herring 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

Complete information on predation at sea is lacking for blueback herring (Scott and Scott 1988). Fish that are known to prey on blueback herring in the marine environment include spiny dogfish, American eel, cod, Atlantic salmon, silver hake, white hake, and Atlantic halibut, as well as larger schooling species, including bluefish, weakfish, and striped bass (Dadswell 1985; Ross 1991; Bowman et al. 2000). Seals, gulls, and terns may also feed on blueback herring in the ocean.

Section II. Significant Environmental, Temporal, and Spatial Factors Affecting Distribution of Blueback Herring

Table 5-2. Significant environmental, temporal, and spatial factors affecting distribution of blueback herring. Please note that, although there may be subtle variations between systems, the following data include a broad range of values that encompass the different systems that occur along the East Coast. Where a specific range is known to exist, it will be noted. For the subadult–estuarine/oceanic environment and non-spawning adult–oceanic environment life history phases, the information is provided as a general reference, not as habitat preferences or optima. NIF = No Information Found.

Life Stage	Time of Year and Location	Depth (m)	Temperature (°C)	Salinity (ppt)	Substrate	Current Velocity (m/sec)	Dissolved Oxygen (mg/L)
Spawning Adult	December (Florida) through late August (Nova Scotia) in Atlantic coast rivers from St. Johns River, FL to Nova Scotia Sympatric range: Freshwater or brackish water above the head of the tide in fast-moving waters, also brackish ponds Allopatric range: Slower-flowing tributaries and flooded low-lying areas adjacent to main streams	Tolerable: NIF Optimal: NIF Reported: Variable	Tolerable: 13-27 Optimal: 20-25 Reported: Variable	Tolerable: 0-6 Optimal: <1 Reported: Generally freshwater	Tolerable: NIF Optimal: NIF Reported: Sympatric: gravel, sand; Allopatric: Variable	Tolerable: NIF Optimal: NIF Reported: Fast flow	Tolerable: NIF Optimal: NIF Reported: Minimum 5
Egg	December to August (south to north progression) at spawning site or slightly downstream of spawning site	Tolerable: NIF Optimal: NIF Reported: Usually found at bottom	Tolerable: 7-14 Optimal: NIF Reported: Variable	Tolerable: 0-22 Optimal: 0-2 Reported: Usually freshwater	Tolerable: NIF Optimal: NIF Reported: Variable	Tolerable: NIF Optimal: NIF Reported: NIF	Tolerable: NIF Optimal: NIF Reported: Minimum 5
Larvae	38-60 hours after fertilization downstream of spawning site	Tolerable: NIF Optimal: NIF Reported: Diel movement	Tolerable: 13-28 Optimal: NIF Reported: Variable	Tolerable: 0-22 Optimal: NIF Reported: Usually freshwater	Tolerable: NIF Optimal: NIF Reported: Variable	Tolerable: NIF Optimal: NIF Reported: NIF	Tolerable: ≥ 5 Optimal: NIF Reported: Minimum 5

Life Stage	Time of Year and Location	Depth (m)	Temperature (°C)	Salinity (ppt)	Substrate	Current Velocity (m/sec)	Dissolved Oxygen (mg/L)
Early Juvenile – Riverine Environment	3-9 months in natal rivers after reaching juvenile stage upstream or downstream of spawning sites, as far as offshore estuaries	Tolerable: NIF Optimal: NIF Reported: Surface or mid-water (daytime); bottom (nighttime)	Tolerable: 11-32 Optimal: 20-30 Reported: Variable; temp gives migration cues	Tolerable: 0-28 Optimal: 0-5 (summer) Reported: Variable	Tolerable: NIF Optimal: NIF Reported: SAV	Tolerable: NIF Optimal: NIF Reported: Variable	Tolerable: NIF Optimal: NIF Reported: Minimum 4
Subadult & Non-spawning Adult – Estuarine / Oceanic Environment	3-6 years after hatching in nearshore estuarine waters or offshore marine waters	Tolerable: NIF Optimal: NIF Reported: Diel migrations with zooplankton; most frequently caught at 27-55	Tolerable: NIF Optimal: NIF Reported: Probably travel in preferred isotherm like other alosines	Tolerable: NIF Optimal: NIF Reported: Brackish to saltwater	Tolerable: NIF Optimal: NIF Reported: NIF	Tolerable: NIF Optimal: NIF Reported: NIF	Tolerable: NIF Optimal: NIF Reported: NIF

Section III. Blueback Herring Literature Cited

- Adams, J. G. 1970. Clupeids in the Altamaha River. Georgia. Georgia Game and Fish Commission, Coastal Fisheries Division, Contribution Series No. 20, Brunswick, Georgia.
- Adams, J. G., and M. W. Street. 1969. Notes on the spawning and embryological development of blueback herring, *Alosa aestivalis* (Mitchill), in the Altamaha River, Georgia. Georgia Game and Fish Commission, Coastal Fisheries Division, Contribution Series No. 16, Brunswick, Georgia.
- ASMFC (Atlantic States Marine Fisheries Commission). 1985. Fishery management plan for the anadromous alosid stocks of the Eastern United States: American shad, hickory shad, alewife, and blueback herring. ASMFC Fishery Management Report No. 6, Washington, D.C.
- ASMFC (Atlantic States Marine Fisheries Commission). 1999. Amendment 1 to the interstate fishery management plan for shad and river herring. ASMFC Fishery Management Report No. 35, Washington, D.C.
- Auld, A. H., and J. R. Schubel. 1972. Effects of suspended sediment on fish eggs and larvae: A laboratory assessment. *Estuarine and Coastal Marine Science* 6: 153-164.
- Baker, W. D. 1968. A reconnaissance of anadromous fish runs into the inland fishing waters of North Carolina. North Carolina Wildlife Resources Commission Final Report for Project No. AFS-3, Raleigh, North Carolina.
- Bigelow, H. B. 1926. Plankton of the offshore waters of the Gulf of Maine. *Bulletin of the United States Bureau of Fisheries* 40, Washington, D.C.
- Bigelow, H. B., and W. W. Welsh. 1925. Fishes of the Gulf of Maine. *Bulletin of the United States Bureau of Fisheries* 40, Washington, D.C.
- Bigelow, H. B., and W. C. Schroeder. 1953. Fishes of the Gulf of Maine. U.S. Fish and Wildlife Service Fisheries Bulletin 53, Washington, D.C.
- Blaxter, J. H. S., F. S. Russell, and M. Yonge. 1982. *Advances in marine biology*, volume 20. Academic Press, Inc., London, England.
- Boger, R. A. 2002. Development of a watershed and stream-reach spawning habitat model for river herring (*Alosa pseudoharengus* and *A. aestivalis*). Doctoral dissertation. The College of William and Mary, Williamsburg, Virginia.
- Bowman, R. E., C. E. Stillwell, W. L. Michaels, and M. D. Grosslein. 2000. Food of Northwest Atlantic fishes and two common species of squid. NOAA Technical Memorandum No. NMFS-F/NE-155, Silver Spring, Maryland.
- Brooks, J. L., and S. I. Dodson. 1965. Predation, body size and composition of the plankton. *Science* 150: 28-35.
- Bulak, J. S., and R. W. Christie. 1981. Santee-Cooper blueback herring studies. South Carolina Wildlife and Marine Resources Department, Annual Progress Report No. SCR 1-5, Columbia, South Carolina.

- Bulak, J. S., and T. A. Curtis. 1977. Santee-Cooper rediversion project-annual progress report. South Carolina Wildlife and Marine Resources Department, Columbia, South Carolina.
- Burbidge, R. G. 1974. Distribution, growth, selective feeding, and energy transformation of young-of-the-year blueback herring, *Alosa aestivalis* (Mitchill), in the James River, Virginia. Transactions of the American Fisheries Society 103: 297-311.
- Byrne, D. M. 1988. Anadromous herring run restoration. New Jersey Department of Environmental Protection, Bureau of Marine Fisheries Project No. AFC-10-1, Trenton, New Jersey.
- Cameron, W. M., and D. W. Pritchard. 1963. Estuaries. Pages 306-324 in M. N. Hill, editor. The sea, volume 2: The composition of sea-water comparative and descriptive oceanography. Interscience, New York, New York.
- Chappelear, S. J., and D. W. Cooke. 1994. Blueback herring behavior in the tailrace of the St. Stephen dam and fishlock. Pages 108-112 in J. E. Cooper, R. T. Eades, R. J. Klauda, and J. G. Loesch, editors. Anadromous Alosa Symposium, Tidewater Chapter, American Fisheries Society, Bethesda, Maryland.
- Chittenden, M. E., Jr. 1972. Salinity tolerance of young blueback herring, *Alosa aestivalis*. Transactions of the American Fisheries Society 101: 123-125.
- Christie, R. W. 1978. Spawning distributing of blueback herring, *Alosa aestivalis* (Mitchill) in abandoned rice fields and tributaries of the west branch of the Cooper River, South Carolina. Masters thesis. Clemson University, Clemson, South Carolina.
- Christie, R. W., and D. H. Barwick. 1985. Santee-Cooper blueback herring studies. South Carolina Wildlife Marine Resources Department, Division of Wildlife and Freshwater Fisheries Completion Report No. SCR 1-8, Columbia, South Carolina.
- Christie, R. W., P. T. Walker, A. G. Eversole, and T. A. Curtis. 1981. Distribution of spawning blueback herring on the West Branch of Cooper River and the Santee River, South Carolina. Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies 35: 632-640.
- Cianci, J. M. 1969. Larval development of the alewife, *Alosa pseudoharengus* Wilson, and the glut herring, *Alosa aestivalis* Mitchill. Masters thesis. University of Connecticut, Storrs, Connecticut.
- Collette, B., and G. Klein-MacPhee, editors. 2002. Bigelow and Schroeder's fishes of the Gulf of Maine, 3rd edition. Smithsonian Institution Press, Washington, D.C.
- Cooke, D. W., and S. D. Leach. 2003. Beneficial effects of increased river flow and upstream fish passage on anadromous alosine stocks. Pages 331-338 in K. E. Limburg, and J. R. Waldeman, editors. Biodiversity, status, and conservation of the world's shads. American Fisheries Society Symposium 35, Bethesda, Maryland.
- Crecco, V. A. 1982. Overview of alewife and blueback herring runs in Connecticut. Report to Atlantic States Marine Fisheries Commission, Alosid Scientific and Statistical Committee, Washington, D.C.

- Crecco, V. A., and M. M. Blake. 1983. Feeding ecology of coexisting larvae of American shad and blueback herring in the Connecticut River. *Transactions of the American Fisheries Society* 112:498-507.
- Crecco, V. A., and T. Savoy. 1984. Effects of fluctuations in hydrographic conditions on year-class strength of American shad (*Alosa sapidissima*) in the Connecticut River. *Canadian Journal of Fisheries and Aquatic Sciences* 41: 1216-1223.
- Crecco, V. A., T. Savoy, and W. Whitworth. 1986. Effects of density-dependent and climatic factors on American shad, *Alosa sapidissima*, recruitment: A predictive approach. *Canadian Journal of Fisheries and Aquatic Sciences* 43: 457-463.
- Creed, R. P., Jr. 1985. Feeding, diet, and repeat spawning of blueback herring, *Alosa aestivalis*, from the Chowan River, North Carolina. *Fisheries Bulletin* 83: 711-716.
- Curtis, T. A., R. W. Christie, and J. S. Bulak. 1982. Santee-Cooper blueback herring studies. South Carolina Wildlife and Marine Resources Department, Annual Progress Report No. SCR-1-6, Columbia, South Carolina.
- Dadswell, M. J. 1985. Status of the blueback herring, *Alosa aestivalis*, in Canada. *Canadian Field Naturalist* 99: 409-412.
- Davis, J. R., and R. P. Cheek. 1966. Distribution, food habits, and growth of young clupeids, Cape Fear river system, North Carolina. *Proceedings of the Annual Conference of the Southeastern Association of Game and Fish Commissioners* 20: 250-260.
- Dennison, W. C., R. J. Orth, K. A. Moore, J. C. Stevenson, V. Carter, S. Kollar, P. W. Bergstrom, and R. A. Batiuk. 1993. Assessing water quality with submerged aquatic vegetation. *Bioscience* 43: 86-94.
- Dixon, D. A. 1996. Contributions to the life history of juvenile blueback herring (*Alosa aestivalis*): Phototactic behavior and population dynamics. Doctoral dissertation. College of William and Mary, Virginia Institute of Marine Science, School of Marine Science, Gloucester Point, Virginia.
- Dorfman, D., and J. Westman. 1970. Responses of some anadromous fishes to varied oxygen concentrations and increased temperatures. Rutgers University OWRR Project No. B-012-NJ, New Brunswick, New Jersey.
- Domermuth, R. B., and R. J. Reed. 1980. Food of juvenile American shad, *Alosa sapidissima*, juvenile blueback herring, *Alosa aestivalis*, and pumpkinseed, *Lepomis gibbosus*, in the Connecticut River below Holyoke Dam, Massachusetts. *Estuaries* 3: 65-68.
- Dovel, W. L. 1971. Fish eggs and larvae of the upper Chesapeake Bay. NRI Special Report 4: 1-71.
- Erkan, D. E. 2002. Strategic plan for the restoration of anadromous fishes to Rhode Island coastal streams. Rhode Island Department of Environmental Management, Division of Fish and Wildlife, Completion Report in fulfillment of Federal Aid in Sportfish Restoration Project No. F-55-R, Jamestown, Rhode Island.

- Eversole, A. G., C. J. Kempton, C. S. Thomason, and R. S. Slack. 1994. Blueback herring distribution and relative abundance in the Santee-Cooper system: Before and after rediversion. Pages 64-71 in J. E. Cooper, R. T. Eades, R. J. Klauda, and J. G. Loesch, editors. Anadromous Alosa Symposium, Tidewater Chapter, American Fisheries Society, Bethesda, Maryland.
- Fay, C. W., R. J. Neves, and G. B. Pardue. 1983. Species profiles: Life histories and environmental requirements of coastal fishes and invertebrates (mid-Atlantic) – alewife/blueback herring. U.S. Fish and Wildlife Service, Division of Biological Services Report No. FWS/OBS-82/11.9, and U.S. Army Corps of Engineers Report No. TR EL-82-4, Washington, D.C.
- Fischer, C. A. 1980. Anadromous fisheries research program. Cape Fear River system, phase II. North Carolina Department of Natural Resources and Community Development, Division of Marine Fisheries Completion Report Project No. AFCS-15, Morehead City, North Carolina.
- Fowler, H. W. 1921. Spawning habits of pike, killifishes, etc. *The Fish Culturist* 1: 36-37.
- Frankensteen, E. D. 1976. Genus *Alosa* in a channelized and an unchannelized creek of the Tar River basin, North Carolina. Masters thesis. East Carolina University, Greenville, North Carolina.
- Gardinier, M. N., and T. B. Hoff. 1982. Diet of striped bass in the Hudson River estuary. *New York Fish and Game Journal* 29: 152-165.
- Godwin, W. F., and J. G. Adams. 1969. Young clupeids of the Altamaha River, Georgia. Georgia Game and Fish Commission, Marine Fisheries Division Contribution Series No. 15, Atlanta, Georgia.
- Gordon, N. D., T. A. McMahon, and B. L. Finlayson. 1992. Stream hydrology: An introduction for ecologists. John Wiley and Sons, Ltd., England.
- Greening, H. A., A. J. Janicki, R. J. Klauda, D. M. Baudler, D. M. Levin, and E. S. Perry. 1989. An evaluation of stream liming effects on water quality and anadromous fish spawning in Maryland coastal plain streams: 1988 results. International Science and Technology, Sterling, Virginia, and John's Hopkins University, Applied Physics Laboratory, Shady Side, Maryland.
- Hardy, J. D., Jr. 1978. Development of fishes of the Mid-Atlantic Bight: An atlas of the egg, larval, and juvenile stages, volume III: Aphredoderidae through Rachycentridae. U. S. Fish and Wildlife Service Biological Services Program Report No. FWS/OBS-78/12, Washington, D.C.
- Hatchey, H. B. 1942. The waters of the Scotian Shelf. *Journal of the Fisheries Research Board of Canada* 5: 377-397.
- Hawkins, J. H. 1979. Anadromous fisheries research program – Neuse River. North Carolina Department of Natural Resources and Community Development, Division of Marine Fisheries Progress Report No. AFCS13-2, Raleigh, North Carolina.
- Hawkins, J. H. 1980. Investigations of anadromous fishes of the Neuse River, North Carolina. North Carolina Department of Natural Resources and Community Development, Division of Marine Fisheries Special Scientific Report No. 34, Morehead City, North Carolina.

- Henderson, B. A., and E. H. Brown, Jr. 1985. Effects of abundance and water temperature on recruitment and growth of alewife (*Alosa pseudoharengus*) near South Bay, Lake Huron, 1954-1982. *Canadian Journal of Fisheries and Aquatic Sciences* 42: 1608-1613.
- Hildebrand, S. F. 1963. Family Clupeidae. Pages 257-454 in H. B. Bigelow, editor. *Fishes of the Western North Atlantic*, part 3. Sears Foundation for Marine Research, Yale University, New Haven, Connecticut.
- Hildebrand, S. F., and W. C. Schroeder. 1928. *Fishes of Chesapeake Bay*. Bulletin of the U.S. Bureau of Fisheries 43, Washington, D.C.
- Hirschfield, H. I., J. W. Rachlin, and E. Leff. 1966. A survey of invertebrates from selected sites of the lower Hudson River. Pages 230-257 in *Hudson River Ecology*. New York State Department of Environmental Conservation, Albany, New York.
- Holland, B. F., and G. F. Yelverton. 1973. Distribution and biological studies of anadromous fishes offshore North Carolina. North Carolina Department of Natural and Economic Resources, Division of Commercial and Sport Fisheries, Special Scientific Report No. 24, Beaufort, North Carolina.
- Janssen, J. 1982. Comparison of searching behavior for zooplankton in an obligate planktivore, blueback herring *Alosa aestivalis* and a facultative planktivore, bluegill *Lepomis macrochirus*. *Canadian Journal of Fisheries and Aquatic Sciences* 39: 1649-1654.
- Jessop, B. M. 1990. Diel variation in density, length composition, and feeding activity of juvenile alewife, *Alosa pseudoharengus* Wilson, and blueback herring, *A. aestivalis* Mitchill, at near-surface depths in a hydroelectric dam impoundment. *Journal of Fish Biology* 37: 813-822.
- Jessop, B. M. 1994. Relations between stock and environmental variables, and an index of abundance for juvenile alewife and blueback herring. *North American Journal of Fisheries Management* 14: 564-579.
- Jessop, B. M., W. E. Anderson, and A. H. Vromans. 1983. Life-history data on alewife and blueback herring of the Saint John River, New Brunswick, 1981. *Canadian Fisheries and Aquatic Sciences Data Report No. 426*, New Brunswick, Canada.
- Johnson, H. B., D. W. Crocker, B. F. Holland, Jr., J. W. Gilliken, D. W. Taylor, M. W. Street, J. G. Loesch, W. H. Kriete, Jr., and J. G. Travelstead. 1978. Biology and management of mid-Atlantic anadromous fishes under extended jurisdiction. North Carolina Division of Marine Fisheries and Virginia Institute of Marine Science Report No. NC-VA AFSC 9-2.
- Johnson, H. B., B. F. Holland, Jr., and S. G. Keefe. 1977. Anadromous fisheries research program, northern coastal area. North Carolina Division of Marine Fisheries Completion Report for Project No. AFCS-11, Morehead City, North Carolina.
- Johnson, H. B., S. E. Winslow, D. W. Crocker, B. F. Holland, Jr., J. W. Gillikin, D. L. Taylor, J. G. Loesch, W. H. Kriete, Jr., J. G. Travelstead, E. J. Foell, and M. A. Hennigar. 1981. Biology and management of mid-Atlantic anadromous fishes under extended jurisdiction. North Carolina Division of Marine Fisheries and Virginia Virginia Institute of Marine Science Special Report No. 36.

- Johnston, C. E., and J. C. Cheverie. 1988. Observations on the diel and seasonal drift of eggs and larvae of anadromous rainbow smelt, *Osmerus mordax*, and blueback herring, *Alosa aestivalis*, in a coastal stream on Prince Edward Island. Canadian Field Naturalist 102: 508-514.
- Jones, P. W., F. D. Martin, and J. D. Hardy, Jr. 1978. Development of fishes of the mid-Atlantic Bight: An atlas of egg, larval and juvenile stages, volume I, Acipenseridae through Ictaluridae. U.S. Fish and Wildlife Service Report No. FWS/OBS-78/12, Washington, D.C.
- Jones, P. W., H. J. Speir, N. H. Butowski, R. O'Reilly, L. Gillingham and E. Smoller. 1988. Chesapeake Bay fisheries: Status, trends, priorities and data needs. Maryland Department of Natural Resources and Virginia Marine Resources Commission.
- Jordan, S. J., and V. A. Vaas. 1990. Long term trends in abundance indices for 19 species of Chesapeake Bay fishes: Reflections of trends in the bay ecosystem. Chesapeake Research Consortium Publication, Baltimore, Maryland.
- Joseph, E. B., and J. Davis. 1965. A progress report to the herring industry. Virginia Institute of Marine Science Special Report No. 51, Gloucester Point, Virginia.
- Juanes, F., R. E. Marks, K. A. McKowan, and D. O. Conover. 1993. Predation by age-0 bluefish on age-0 anadromous fishes in the Hudson River Estuary. Transactions of the American Fisheries Society 122: 348-356.
- Kissil, G. W. 1968. A contribution to the life history of *Alosa pseudoharengus* (Wilson). Masters thesis. University of Connecticut, Storrs, Connecticut.
- Kissil, G. W. 1974. Spawning of the anadromous alewife, *Alosa pseudoharengus*, in Bride Lake, Connecticut. Transactions of the American Fisheries Society 103: 312-317.
- Klauda, R. J. 1989. Definitions of critical environmental conditions for selected Chesapeake Bay finfishes exposed to acidic episodes in spawning and nursery areas. John's Hopkins University, Applied Physics Laboratory, Shady Side, Maryland.
- Klauda, R. J., and R. E. Palmer. 1987a. Laboratory and field bioassay experiments with blueback herring and American shad. John's Hopkins University, Applied Physics Laboratory Report No. PPSP-AD-87-9, Shady Side, Maryland.
- Klauda, R. J., and R. E. Palmer. 1987b. Responses of blueback herring eggs and larvae to pulses of acid and aluminum. Transactions of the American Fisheries Society 116: 561-569.
- Klauda, R. J., R. E. Palmer, and M. J. Lenkevich. 1987. Sensitivity of early life stages of blueback herring to moderate acidity and aluminum in soft freshwater. Estuaries 10: 453.
- Klauda, R. J., S. A. Fischer, L. W. Hall, Jr., and J. A. Sullivan. 1990. Habitat requirements for hickory shad (*Alosa mediocris*), American shad (*Alosa sapidissima*), alewife herring (*Alosa pseudoharengus*), and blueback herring (*Alosa aestivalis*). University of Maryland System, Agricultural Experiment Station, Wye Research and Education Center, Queenstown, Maryland.

- Klauda, R. J., S. A. Fischer, L. W. Hall, Jr., and J. A. Sullivan. 1991. Alewife and blueback herring; *Alosa pseudoharengus* and *Alosa aestivalis*. Pages 10.1-10.29 in S. L. Funderburk, J. A. Mihursky, S. J. Jordan, and D. Riley, editors. Habitat requirements for Chesapeake Bay living resources, 2nd Edition. Chesapeake Bay Program, Living Resources Subcommittee, Annapolis, Maryland.
- Koo, T. S. Y., and M. L. Johnston. 1978. Larval deformity in striped, *Morone saxatilis*, and blueback herring, *Alosa aestivalis*, due to heat shock treatment of developing eggs. *Environmental Pollution* 16: 137-149.
- Kosa, J. T., and M. E. Mather. 2001. Processes contributing to variability in regional patterns of juvenile river herring abundance across small coastal systems. *Transactions of the American Fisheries Society* 130: 600-619.
- Kuntz, A., and L. Radcliffe. 1917. Notes on the embryology and larval development of twelve teleostean fishes. *Bulletin of the U.S. Bureau of Fisheries* 35: 87-134.
- Laberge, E. 1975. The importance of water discharge in determining phytoplankton biomass in a river impoundment. Masters thesis. Dalhousie University, Halifax, Nova Scotia.
- Leim, A. H., and W. B. Scott. 1966. Fishes of the Atlantic coast of Canada. *Bulletin of the Fisheries Research Board of Canada* 155.
- Lippson, A. J., and R. L. Moran, editors. 1974. Manual for identification of early developmental stages of fishes of the Potomac River estuary. Maryland Power Plant Siting Program Miscellaneous Publication No 13, Annapolis, Maryland.
- Loesch, J. G. 1968. A contribution to the life history of *Alosa aestivalis* (Mitchill). Masters thesis. University of Connecticut, Storrs, Connecticut.
- Loesch, J. G. 1987. Overview of life history aspects of anadromous alewife and blueback herring in freshwater habitats. Pages 89-103 in M. J. Dadswell, R. J. Klauda, C. M. Moffitt, and R. L. Saunders, editors. Common strategies of anadromous and catadromous fishes. *American Fisheries Society Symposium* 1, Bethesda, Maryland.
- Loesch, J. G., and W. H. Kriete, Jr. 1980. Anadromous fisheries research program, Virginia. Annual Report for NMFS Project No. AFC10-1, Virginia Institute of Marine Science, Gloucester Point, Virginia.
- Loesch, J. G., and W. A. Lund, Jr. 1977. A contribution to the life history of the blueback herring, *Alosa aestivalis*. *Transactions of the American Fisheries Society* 106: 583-589.
- Loesch, J. G., W. H. Kriete, Jr., and E. J. Foell. 1982. Effects of light intensity on the catchability of juvenile anadromous *Alosa* species. *Transactions of the American Fisheries Society* 111: 41-44.
- Manooch, C. S., III. 1988. Fisherman's guide. Fishes of the southeastern United States. North Carolina State Museum of Natural History, Raleigh, North Carolina.
- Manooch, C. S., III. 1973. Food habits of yearling and adult striped bass, *Morone saxatilis* (Walbaum), from Albemarle Sound, North Carolina. *Chesapeake Science* 14: 73-86.

- Marcy, B. C., Jr. 1969. Age determination from scales of *Alosa pseudoharengus* (Wilson) and *Alosa aestivalis* (Mitchill) in Connecticut waters. Transactions of the American Fisheries Society 98: 622-630.
- Marcy, B. C., Jr. 1976a. Early life history studies of American shad in the lower Connecticut River and the effects of the Connecticut Yankee plant. Pages 141-168 in D. Merriman, and L. M. Thorpe, editors. The Connecticut River ecological study: The impact of a nuclear power plant. American Fisheries Society Monograph No. 1, Bethesda, Maryland.
- Marcy, B. C., Jr. 1976b. Planktonic fish eggs and larvae of the lower Connecticut River and effects of the Connecticut Yankee plant including entrainment. Pages 115-139 in D. Merriman, and L. M. Thorpe, editors. The Connecticut River ecological study: The impact of a nuclear power plant. American Fisheries Society Monograph No. 1, Bethesda, Maryland.
- Marcy, B. C., Jr., and P. Jacobsen. 1976. Early life history studies of American shad in the lower Connecticut River and the effects of the Connecticut Yankee plant. Pages 141-168 in D. Merriman, and L. M. Thorpe, editors. The Connecticut River ecological study: The impact of a nuclear power plant. American Fisheries Society Monograph No. 1, Bethesda, Maryland.
- Marshall, M. D. 1976. Anadromous fisheries research program: Tar River, Pamlico River, and Northern Pamlico Sound. North Carolina Department of Natural and Economic Resources, Division of Marine Fisheries Completion Report for Project No. AFCS-10, Morehead City, North Carolina.
- Massman, W. H. 1953. Relative abundance of young fishes in Virginia estuaries. Transactions of the North America Wildlife Conference 18: 439-449.
- McLane, W. M. 1955. The fishes of the St. Johns River system. Doctoral dissertation. University of Florida, Gainesville, Florida.
- Meador, M. R. 1982. Occurrence and distribution of larval fish in the Santee River system. Masters thesis. Clemson University, Clemson, South Carolina.
- Meador, M. R., A. G. Eversole, and J. S. Bulak. 1984. Utilization of portions of the Santee River system by spawning blueback herring. North American Journal of Fisheries Management 4: 155-163.
- Meehan, W. E. 1895. Fish, fishing and fisheries of Pennsylvania. Pennsylvania State Commission on Fisheries Official Document No. 20: 257-392.
- Meldrim, J. W., and J. J. Gift. 1971. Temperature preference, avoidance and shock experiments with estuarine fishes. Ichthyological Association Bulletin 7, Middletown, Delaware.
- Messieh, S. N. 1977. Population structure and biology of alewife *Alosa pseudoharengus* and blueback herring *A. aestivalis* in the Saint John River, New Brunswick. Environmental Biology of Fishes 2: 195-210.
- Milstein, C. B. 1981. Abundance and distribution of juvenile *Alosa* species off southern New Jersey. Transactions of the American Fisheries Society 110: 306-309.

- Morgan, R. P., II, and R. D. Prince. 1976. Chlorine toxicity to estuarine fish egg and larvae. Chesapeake Biological Laboratory, University of Maryland Reference No. 76-116 CBL, Solomons, Maryland.
- Morgan, R. P., II, and R. D. Prince. 1977. Chlorine toxicity to eggs and larvae of five Chesapeake Bay fishes. *Transactions of the American Fisheries Society* 106: 380-385.
- Morgan, R. P., II, and R. D. Prince. 1978. Chlorine effects on larval development of striped bass (*Morone saxatilis*), white perch (*Morone americana*) and blueback herring (*Alosa aestivalis*). *Transactions of the American Fisheries Society* 107: 636-641.
- Moser, M. L., and S. W. Ross. 1994. Effects of changing current regime and river discharge on the estuarine phase of anadromous fish migration. Pages 343-347 in K. R. Dyer, and R. J. Orth, editors. *Changes in fluxes in estuaries: Implications from science to management*. Olsen and Olsen, Fredensborg, Denmark.
- Moss, S. A., W. C. Leggett, and W. A. Boyd. 1976. Recurrent mass mortalities of the blueback herring, *Alosa aestivalis*, in the lower Connecticut River. *American Fisheries Society Monographs* 1: 227-234.
- Murdy, E. O., R. S. Birdsong, and J. A. Musick. 1997. *Fishes of Chesapeake Bay*. Smithsonian Institution Press, Washington, D.C.
- Netzel, J., and E. Stanek. 1966. Some biological characteristics of blueback, *Pomolobus aestivalis* (Mitchill), and alewife, *Pomolobus pseudoharengus* (Wilson), from Georges Bank, July and October 1964. *International Commission on Northwestern Atlantic Fisheries Research Bulletin* 3: 106-110.
- Neves, R. J. 1981. Offshore distribution of alewife, *Alosa pseudoharengus*, and blueback herring, *Alosa aestivalis*, along the Atlantic coast. *Fisheries Bulletin* 79: 473-485.
- Nichols, J. T., and C. M. Breder, Jr. 1927. The marine fishes of New York and southern New England. *Zoologica (New York)* 9: 1-192.
- O'Connell, A. M., and P. L. Angermeier. 1997. Spawning location and distribution early life stages of alewife and blueback herring in a Virginia stream. *Estuaries* 20: 779-791.
- O'Leary, J. A., and B. Kynard. 1986. Behavior, length, and sex ration of seaward-migrating juvenile American shad and blueback herring in the Connecticut River. *Transactions of the American Fisheries Society* 115: 529-536.
- O'Neill, J. T. 1980. Aspects of the life histories of anadromous alewife and the blueback herring, Margaree River and Lake Aninsle, Nova Scotia, 1978-1979. Masters thesis. Acadia University, Wolfville, Nova Scotia.
- O'Rear, C. W. 1983. A study of river herring spawning and water quality in Chowan River. North Carolina Department of Natural Resources and Community Development, Division of Marine Fisheries Complete Report for Project No. AFC-17, Raleigh, North Carolina.
- Olney, J. E., and G. W. Boehlert. 1988. Nearshore ichthyoplankton associated with seagrass beds in the lower Chesapeake Bay. *Marine Ecology Progress Series* 45: 33-43.
- Otto, R. G., M. A. Kitchel, and J. O. Rice. 1976. Lethal and preferred temperatures of the alewife in Lake Michigan. *Transactions of the American Fisheries Society* 105: 96-106.

- Pardue, G. B. 1983. Habitat suitability index models: Alewife and blueback herring. U.S. Fish and Wildlife Service Report No. FWS/OBS-82/10.58, Washington, D.C.
- Pate, P. P. 1975. Anadromous fisheries research program: Tar River, Pamlico River, and Northern Pamlico Sound. North Carolina Department of Natural and Economic Resources, Division of Marine Fisheries Annual Report for Project No. AFCS-10-1, Morehead City, North Carolina.
- Perlmutter, A., E. E. Schmidt, and E. Leff. 1967. Distribution and abundance of fish along the shores of the lower Hudson River during the summer of 1965. *New York Fish and Game Journal* 14: 46-75.
- PSE&G (Public Service Electric and Gas Company). 1978. Annual environmental operating report (nonradiological), Salem Nuclear Generating Station – Unit 1: 1977 Report, volume 3. Public Service Electric and Gas Company, Newark, New Jersey.
- Rawls, K. B. 2001. North Carolina alosid management program. North Carolina Department of Environment and Natural Resources, Division of Marine Fisheries, Morehead City, North Carolina.
- Richkus, W. A., and G. DiNardo. 1984. Current status and biological characteristics of the anadromous alosid stocks of the eastern United States: American shad, hickory shad, alewife, and blueback herring. Atlantic States Marine Fisheries Commission Interstate Fisheries Management Program, Washington, D.C.
- Ross, R. M. 1991. Recreational fisheries of coastal New England. University of Massachusetts Press, Amherst, Massachusetts.
- Ross, R. M., R. M. Bennett, and T. W. H. Backman. 1993. Habitat use and spawning adult, egg, and larval American Shad in the Delaware River. *Rivers* 4: 227-238.
- Ross, R. M., and R.C. Biagi. 1990. Marine recreational fisheries of Massachusetts: River herring. University of Massachusetts Cooperative Extension, Massachusetts Division of Marine Fisheries, Marine Recreational Fisheries Series Informational Pamphlet No. CR 162: 6/90-10M, Amherst, Massachusetts.
- Rulifson, R. A., M. T. Huish, and R. W. Thoesen. 1982. Anadromous fish in the southeastern United States and recommendations for development of a management plan. U.S. Fish and Wildlife Service, Fisheries Research Region 4, Atlanta, Georgia.
- Rulifson, R. A., S. A. McKenna, and M. L. Gallagher. 1987. Tagging studies of striped bass and river herring in upper Bay of Fundy, Nova Scotia. North Carolina Department of Natural Resources and Community Development, Division of Marine Fisheries Completion Report No. AFC-28-1, East Carolina University, Greenville, North Carolina.
- Rulifson, R. A., and V. Crecco. 1995. Factors affecting the recent decline of blueback herring and American shad in the Connecticut River. A report to the Atlantic States Marine Fisheries Commission, Washington, D.C.
- Savoy T. F., and V. A. Crecco. 2004. Factors affecting the recent decline of blueback herring and American shad in the Connecticut River. *American Fisheries Society Monograph* 9: 361–377.

- Schmidt, R. E., B. M. Jessop, and J. E. Hightower. 2003. Status of river herring stocks in large rivers. Pages 171-182 in K. E. Limburg, and J. R. Waldman, editors. Biodiversity, status, and conservation of the world's shads. American Fisheries Society Symposium 35, Bethesda, Maryland.
- Schmidt, R. E., R. J. Klauda, and J. M. Bartels. 1988. Distributions and movements of the early life stages of three species of *Alosa* in the Hudson River, with comments on mechanisms to reduce interspecific competition. Pages 193-215 in C. L. Smith, editor. Fisheries research in the Hudson River. State University of New York Press, Albany, New York.
- Schmidt, R. E., and T. R. Lake. 2000. Alewives in Hudson River tributaries, two years of sampling. Hudsonia Final Report to the Hudson River Foundation. Hudsonia Ltd., Bard College Field Station, Annandale, New York.
- Schubel, J. R. 1974. Effects of exposure to time-excess temperature histories typically experienced at power plants on the hatching success of fish eggs. Coastal Marine Science 2: 105-116.
- Schubel, J. R., and T. S. Y. Koo. 1976. Effects of various time-excess temperature histories on hatching success of blueback herring, American shad, and striped bass eggs. Thermal Ecology II, AEC Symposium Series, Conference No. 750425: 165-170.
- Schubel, J. R., and J. C. S. Wang. 1973. The effects of suspended sediment on the hatching success of *Perca flavescens* (yellow perch), *Morone americana* (white perch), *Morone saxatilis* (striped bass), and *Alosa pseudoharengus* (alewife) eggs. Chesapeake Bay Institute Reference No. 73-3, John's Hopkins University, Baltimore, Maryland.
- Scott, W. B., and E. J. Crossman. 1973. Freshwater fishes of Canada. Fisheries Research Board of Canada Bulletin 184, Ottawa, Canada.
- Scott, W. B., and M. G. Scott. 1988. Atlantic fishes of Canada. Canadian Bulletin of Fisheries and Aquatic Sciences 219: 1-731.
- Sholar, T. M. 1975. Anadromous fisheries survey of the New and White Oak River systems. North Carolina Division of Marine Fisheries Completion Report for Project No. AFCS-9, Morehead City, North Carolina.
- Sholar, T. M. 1977. Anadromous fisheries research program, Cape Fear River system, phase I. North Carolina Division of Marine Fisheries Progress Report for Project No. AFCS-12, Morehead City, North Carolina.
- Sismour, E. N. 1994. Contributions to the early life histories of alewife (*Alosa pseudoharengus*) and blueback herring (*A. aestivalis*): Rearing, identification, ageing, and ecology. Doctoral Dissertation. College of William and Mary, Virginia Institute of Marine Science, Gloucester Point, Virginia.
- Smith, B. A. 1971. The fishes of four low-salinity tidal tributaries of the Delaware River estuary. Masters thesis. Cornell University, Ithaca, New York.
- Stokesbury, K. D. E., and M. J. Dadswell. 1989. Seaward migration of juveniles of three herring species *Alosa*, from an estuary in the Annapolis River, Nova Scotia. The Canadian Field-Naturalist 103: 388-393.

- Stone, H. H. 1985. Composition, morphometric characteristics and feeding ecology of alewife (*Alosa pseudoharengus*) and blueback herring (*Alosa aestivalis*) (Pisces: Clupeidae) in Minas Basin. Masters thesis. Acadia University, Wolfville, Nova Scotia.
- Stone, H. H., and G. R. Daborn. 1987. Diet of alewife, *Alosa pseudoharengus* and blueback herring, *A. aestivalis* (Pisces: Clupeidae) in Minas Basin, Nova Scotia, a turbid, macrotidal estuary. *Environmental Biology of Fishes* 19: 55-67.
- Stone, H. H., and B. M Jessop. 1992. Seasonal distribution of river herring *Alosa pseudoharengus* and *A. aestivalis* off the Atlantic coast of Nova Scotia. *Fisheries Bulletin* 90: 376-389.
- Street, M. W. 1970. Some aspects of the life histories of hickory shad, *Alosa mediocris* (Mitchill), and blueback herring, *Alosa aestivalis* (Mitchill), in the Altamaha River, Georgia. Masters thesis. University of Georgia, Athens, Georgia.
- Street, M. W., P. P. Pate, Jr., B. F. Holland, Jr., and A. B. Powell. 1975. Anadromous fisheries research program, northern coastal region. North Carolina Division of Marine Fisheries Completion Report for Project No. AFCS-8, Morehead City, North Carolina.
- Taylor, R., and B. Kynard. 1984. Studies of downrunning adult alosids in the Holyoke Dam canal system – 1983. Final Report to Northeast Utilities Service Company, Hartford, Connecticut.
- Terpin, K. M., M. C. Wyllie, and E. R. Holmstrom. 1977. Temperature preference, avoidance, shock and swim speed studies with marine and estuarine organisms from New Jersey. *Ichthyological Association Bulletin* 17, Middletown, Delaware.
- Trent, W. L., and W. W. Hassler. 1966. Feeding behavior of adult striped bass, *Roccus saxatilis*, in relation to stages of sexual maturity. *Chesapeake Science* 7: 189-192.
- Vigerstad, T. J., and J. S. Colb. 1978. Effects of predation by sea-run juvenile alewife (*Alosa pseudoharengus*) on the zooplankton community at Hamilton reservoir, Rhode Island. *Estuaries* 1: 36-45.
- Waldman, J. R., and K. E. Limburg. 2003. The world's shads: Summary of their status, conservation, and research needs. Pages 363-369 in K. E. Limburg, and J. R. Waldman, editors. *Biodiversity, status, and conservation of the world's shads*. American Fisheries Society Symposium 35, Bethesda, Maryland.
- Wang, J. C. S., and R. J. Kernehan. 1979. Fishes of Delaware estuaries: A guide to the early life histories. *Ecological Analysts, Inc.*, Towson, Maryland.
- Warriner, J. E., J. P. Miller, and J. Davis. 1970. Distribution of juvenile river herring in the Potomac River. *Proceedings of the Annual Conference Southeastern Association of Game and Fish Commissioners* 23: 384-388.
- Watt, W. D., and F. C. Duerden. 1974. Aquatic ecology of the Saint John River, volume 2: Report 15g. The Saint John River Basin Board, Fredericton, New Brunswick.
- Weaver, J. E. 1975. Food selectivity, feeding chronology, and energy transformation of juvenile alewife (*Alosa pseudoharengus*) in the James River near Hopewell, Virginia. Doctoral dissertation. University of Virginia, Charlottesville, Virginia.

- West, J. C., A. G. Eversole, and R. W. Christie. 1988. Influence of river discharge on blueback herring abundance. *Proceedings of the Annual Conference Southeastern Association of Fish and Wildlife Agencies* 42: 166-174.
- Williams, R. O., W. F. Grey, and J. A. Huff. 1975. Anadromous fish studies in the St. Johns River. Florida Department of Natural Resources, Marine Research Laboratory Completion Report for the project 'Study of Anadromous Fishes of Florida' for the period 1 May 1971 to 30 June 1974, St. Petersburg, Florida.
- Winslow, S. E. 1989. North Carolina alosid fisheries management program. North Carolina Division of Marine Fisheries, Project Report No. AFC-27, Morehead City, North Carolina.
- Winslow, S. E. 1995. North Carolina alosid management program. Completion Report for Project AFC-47, Segments 1-3. North Carolina Division of Marine Fisheries, Morehead City, North Carolina.
- Winslow, S. E., S. C. Mozley, and R. A. Rulifson. 1985. North Carolina Division of Marine Fisheries, Project Report No. SFCS-22, Morehead City, North Carolina.
- Winslow, S. E., and K. B. Rawls. 1992. North Carolina alosid management program. North Carolina Division of Marine Fisheries Completion Report for Project No. AFC-36, Morehead City, North Carolina.
- Winslow, S. E., N. S. Sanderlin, G. W. Judy, J. H. Hawkins, B. F. Holland, Jr., C. A. Fischer, and R. A. Rulifson. 1983. North Carolina anadromous fisheries management program. North Carolina Division of Marine Fisheries Completion Report for Project No. AFCS-16, Morehead City, North Carolina.
- Winters, G. H., and J. P. Wheeler. 1987. Recruitment dynamics of spring-spawning herring in the Northwest Atlantic. *Canadian Journal of Fisheries and Aquatic Sciences* 44: 882-900.
- Witherell, D. B. 1987. Vertical distribution of adult American shad and blueback herring during riverine movement. Masters thesis. University of Massachusetts, Amherst, Massachusetts.
- Yako, L. A. 1998. Community interactions influencing anadromous herring in freshwater: Migration cues and predation. Masters thesis. University of Massachusetts, Amherst, Massachusetts.
- Yako, L. A., M. E. Mather, and F. Juanes. 2000. Assessing the contribution of anadromous herring to largemouth bass growth. *Transactions of the American Fisheries Society* 129: 77-88.
- Zich, H. E. 1978. Existing information on anadromous clupeid spawning in New Jersey. New Jersey Department of Environmental Protection, Division of Fish, Game and Shellfish, Bureau of Fisheries Miscellaneous Report No. 41, Lebanon, New Jersey.