

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 coast 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 “alosines”).

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

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