Chapter 4

ALEWIFE

(*Alosa pseudoharengus*)

Section I. Alewife Description of Habitat

Alewife General Habitat Description and Introduction

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

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

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

While this document will focus primarily on the anadromous alewife populations, much of the research on specific environmental requirements of alewife, such as temperature, dissolved oxygen, salinity, and pH, has been conducted on landlocked populations, not anadromous stocks; therefore data should be interpreted with discretion (Klauda et al. 1991).

Part A. Alewife Spawning Habitat

Geographical and temporal patterns of migration

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

State or region	Spawning season	Citations
Bay of Fundy tributaries	late April or early May	Leim and Scott 1996; Dominy 1971, 1973
Gulf of St. Lawrence tributaries	late May or early June	Leim and Scott 1996; Dominy 1971, 1973
Maine	late April to mid-May	Rounsefell and Stringer 1943; Bigelow and Schroeder 1953; Havey 1961; Libby 1981
	mid-May to mid-June	S. Lary, U.S. Fish and Wildlife Service, personal communication
Massachusetts	early to mid-April	Belding 1921; Bigelow and Schroeder 1953
Mid-Atlantic and southern New England	late March or early April	Cooper 1961; Kissil 1969; Marcy 1969; Smith 1971; Saila et al. 1972; Richkus 1974; Zich 1978; Wang and Kernehan 1979
Chesapeake Bay region	mid-March	Jones et al. 1978; Loesch 1987
North Carolina	late February	Holland and Yelverton 1973; Frankensteen 1976

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

Alewife typically spawn from late February to June in the south, and from June through August in the north (Table 4-1) (Marcy 1976a; Neves 1981; Loesch 1987). Spawning is triggered most predictably by a change in the water temperature. Movement upstream may be controlled by water flow, with increased movement occurring during higher flow periods (Collins 1952; Richkus 1974). However, extreme high flows can act as a velocity barrier delaying or preventing upstream migration and access to spawning habitat (S. Lary, U.S. Fish and Wildlife Service, personal communication).

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

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

Spawning location (ecological)

Alewife select slow-moving sections of rivers or streams to spawn, where the water may be as shallow as 30 cm (Jones et al. 1978). The species may also spawn in lakes or ponds, including freshwater coves behind barrier beaches (Smith 1907; Belding 1921; Leim and Scott 1966; Richkus 1974; Colette and Klein-MacPhee 2002). In watersheds where dams are an impediment, spawning may occur in shore-bank eddies or deep pools below the dams (Loesch and Lund 1977). Additionally, in New England and Nova Scotia, alewife spawn in lakes and ponds located within coastal watersheds (Loesch 1987). For this reason, they are typically more abundant than blueback herring in rivers with abundant headwater ponds. In rivers where headwater ponds are absent or scarce, alewife are less abundant in headwater reaches; however, blueback herring utilize the mainstream proper for spawning in those systems (Ross and Biagi 1990). In tributaries of the Rappahannock River, Virginia, upstream areas were found to be more important than downstream areas for spawning alewife (O'Connell and Angermeier 1997). Although earlier studies suggested that alewife ascend further upstream than blueback herring (Hildebrand 1963; Scott and Crossman 1973), Loesch (1987) noted that both species have the ability to ascend rivers far upstream.

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

Temporal spawning patterns

Alewife usually spawn 3 to 4 weeks before blueback herring in areas where they co-occur; however, there may be considerable overlap (Loesch 1987) and peak spawning periods may differ by only 2 to 3 weeks (Jones et al. 1978). In a tributary of the Rappahannock River, Virginia, O'Connell and Angermeier (1997) found that blueback herring eggs and larvae were more abundant than those of alewife, but alewife used the stream over a longer period of time. The researchers also reported a minor three-day overlap of spawning by these two alosine species. It has been hypothesized that alewife and blueback herring select separate spawning sites in sympatric areas to reduce competition (Loesch 1987). O'Connell and Angermeier (1997) reported that the two species used different spawning habitat due to a temporal, rather than spatial, segregation that minimizes the competition between the two species.

Alewife may spawn throughout the day, however, most spawning occurs at night (Graham 1956). One female fish and up to 25 male fish broadcast eggs and sperm simultaneously just below the surface of the water or over the substrate (Belding 1921; McKenzie 1959; Cooper 1961). Spawning lasts two to three days for each group or "wave" of fish that arrives (Cooper 1961; Kissil 1969; Kissil 1974), with older and larger fish usually spawning first (Belding 1921; Cooper 1961; Libby 1981, 1982). Following spawning, the adult spent fish quickly return downstream (Colette and Klein-MacPhee 2002).

Maturation and spawning periodicity

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

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

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

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

Spawning and the saltwater interface

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

Spawning substrate associations

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

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

Spawning depth associations

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

Spawning water temperature

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

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

Adult alewife have been collected in temperatures ranging from 5.7°C to 32°C (Marcy 1976b; Jones et al. 1978). Spawning temperatures along the Atlantic coast fall within this broader range (Table 4-3). There is some discrepancy regarding the minimum spawning temperature for alewife. Although running ripe fish of both sexes have been reported at temperatures as low as 4.2°C in the Chesapeake Bay area (Mansueti and Hardy 1967), some researchers suggest that the minimum spawning temperature for adult alewife is 10.5°C (Cianci 1965; Loesch and Lund 1977). Additionally, lower temperatures may be dangerous for spawning alewife. Otto et al. (1976) found that the lower incipient lethal temperature range for adults acclimated at 15.0°C and 21.0°C was between 6°C and 8°C. In this study, no fish survived below 3°C, regardless of acclimation temperature (Otto et al. 1976). Furthermore, at temperatures below 4.5°C, normal schooling behavior was significantly reduced for adult alewife from Lake Michigan (Colby 1973).

As water temperatures rise, alewife migration eventually slows. Cooper (1961) noted that upstream migration ceased in a Rhode Island stream when temperatures reached 21°C, while Edsall (1970) reported that spawning ceases altogether at 27.8°C. Ultimately, higher temperatures may cause problems for alewife. In fact, Otto et al. (1976) found that upper incipient lethal temperatures (temperature at which 50% of the population survives) ranged from 23.5°C to 24.0°C for adults that were acclimated at temperatures of 10°C, 15°C, and 20°C. Another study reported upper incipient lethal temperatures of 29.8°C and 32.8°C at acclimation temperatures of 16.9°C and 24.5°C, respectively (Stanley and Holzer 1971). In addition, McCauley and Binkowski (1982) reported upper incipient lethal temperatures of 31°C to 34°C after acclimation at 27°C for a northern population of adults.

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

Spawning dissolved oxygen associations

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

Spawning water velocity/flow

Increased movement upstream occurs during higher water flows (Collins 1952; Richkus 1974), while spawning typically takes place in quiet, slow-moving waters for alewife (Smith 1907; Belding 1921; Marcy 1976a). Some researchers have noted differential selection of spawning areas in alewife. For example, in Connecticut, alewife choose slower moving waters in Bride Lake (Kissil 1974) and Higganum and Mill creeks, while blueback herring select fast-moving waters in the upper Salmon River and Roaring Brook (Loesch and Lund 1977). In other areas where alewife and blueback herring are forced to spawn in the same vicinity due to blocked passage (Loesch 1987), alewife generally spawn along shorebank eddies or deep pools, whereas, blueback herring will typically select the main stream flow for spawning (Loesch and Lund 1977). In North Carolina, alewife utilize slow moving streams and oxbows (Street et al. 2005).

Spawning pH associations

Few researchers have reported on pH sensitivity in alewife (Klauda et al. 1991). Byrne (1988) found that the average pH level was 5.0 in several streams in New Jersey where alewife spawning was known to occur. Laboratory tests found that fish from those streams could successfully spawn at a pH as low as 4.5 (Byrne 1988). In another study, adult alewife tolerated a pH range of 6.5 to 7.3 (Collins 1952). When aluminum pulses were administered in the laboratory, critical conditions for spawning could occur during an acidic pulse between pH 5.5 and 6.2, with concomitant concentrations of total monomeric aluminum ranging from 15 to 137 µg/L for a pulse duration of 8 to 96 hours (Klauda 1989). Klauda et al. (1991) suggested a pH range of 5 to 8.5 as suitable for alewife eggs, but no range was provided for spawning.

Spawning feeding behavior

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

Spawning competition and predation

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

Erkan (2002) notes that predation of alosines has increased dramatically in Rhode Island rivers in recent years, especially by the double-crested cormorant, which often takes advantage of fish staging near the entrance to fishways. Populations of nesting cormorant colonies have increased in size and expanded into new areas. Predation by otters and herons has also increased, but to a lesser extent (D. Erkan, Rhode Island Department of Environmental Management, personal communication).

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

Factors affecting stock size

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

Part B. Alewife Egg and Larval Habitat

Geographical and temporal movement patterns

Fertilized eggs remain demersal and adhesive for several hours (Mansueti 1956; Jones et al. 1978), after which they become pelagic and are transported downstream (Wang and Kernehan 1979). Marcy (1976a) observed eggs more often near the bottom than at the surface in the Connecticut River. Eggs may hatch anywhere from 50 to 360 hours (2 to 15 days) after spawning, depending on water temperature (Fay et al. 1983); however, eggs most often hatch within 80 to 95 hours (3 to 5 days) (Edsall 1970).

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

Eggs, larvae, and the saltwater interface

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

Egg and larval substrate associations

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

Egg and larval water temperature

For alewife in general, average time to median hatch varies inversely with temperature. Edsall (1970) reported the following hatch times for alewife eggs taken from Lake Michigan: 2.1 days at 28.9°C, 3.9 days at 20.6°C, and 15 days at 7.2°C. Reported hatch times in saltwater are comparable: 2 to 4 days at 22°C (Belding 1921); 3 days at 23.8°C to 26.8°C, and 3 to 5 days at 20°C (Mansueti and Hardy 1967); 6 days at 15.5°C (Bigelow and Welsh 1925).

Kellogg (1982) found that eggs from the Hudson River, New York, achieved maximum hatching success at 20.8°C. Edsall (1970) reported some hatching at temperatures ranging from 6.9°C to 29.4°C for eggs from Lake Michigan; however, temperatures below 11°C caused a high percentage of deformed larvae. The optimum hatching performance occurred between 17.2°C and 21.1°C. Although this was the suggested optimal range, it was determined that considerable hatch rates and proper development could occur over a broader range from 10.6°C to 26.7°C

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

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

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

where t = time in days

T = incubation temperature in degrees Fahrenheit

Several researchers have attempted to determine the effects of temperature on alewife eggs. One study on the effects of power plants on alewife eggs found that they suffered no significant mortality or abnormal egg development after acclimation at 17° C, and subsequent exposure to 24.5° C for 6 to 60 minutes (Schubel and Auld 1972). Koo et al. (1976) determined that the critical thermal maximum (CTM) for alewife eggs was 35.6° C, acclimated at 20.6° C, with a critical exposure period of 5 to 10 minutes.

Larval alewife were collected at water temperatures between 4°C and 27°C in the upper Chesapeake Bay, although 98% were collected at water temperatures of 25°C (Dovel 1971). In laboratory experiments, larvae acclimated at 18.6°C withstood temperatures as high as 33.6°C for one hour (Koo et al. 1976). The upper temperature tolerance limit for yolk-sac larvae from the Hudson River, New York, acclimated at around 15°C was 31°C (Kellogg 1982); their preferred range when acclimated at 20° C appears to be 23°C to 29°C (EA 1978; Kellogg 1982). Although alewife eggs taken from Lake Michigan were able to hatch at temperatures as low as 6.9°C, larvae held at incubation temperatures below 10.6°C had a 69% rate of deformities (Edsall 1970).

Dovel (1971) found that growth rates of alewife larvae were much lower in freshwater compared to slightly saline water (1.0 to 1.3 ppt) at 26.4°C. He also observed substantial growth increases with small temperature increases above 20.8°C. Average daily weight gain for alewife larvae has been directly correlated with water temperature. The maximum larval growth rate was 0.084 g/day at 29.1°C; net gain in biomass (a function of survival and growth) was highest at 26.4°C (Kellogg 1982).

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

Egg and larval dissolved oxygen associations

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

Egg and larval pH and aluminum associations

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

Egg and larval water velocity/flow

Sismour (1994) observed a rapid decline in abundance of early preflexion river herring larvae in the Pamunkey River, Virginia, following high river flow in 1989. This observation lead to speculation that high flow leads to increased turbidity, which reduces prey visibility, leading to starvation of larvae (Sismour 1994). Additionally, O’Connell and Angermeier (1997) found that current velocity and dissolved oxygen were the strongest predictors of alewife early egg presence in a Virginia stream. Further north, drought conditions in Rhode Island in the summer of 1981 were strongly suspected of impacting the 1984-year class, which was only half of its expected size (ASMFC 1985). In tributaries of the Chowan system, North Carolina, water flow was related to recruitment of larval river herring (O’Rear 1983).

Egg and larval suspended solid associations

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

Egg and larval feeding behavior

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

Egg and larval competition and predation

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

Part C. Alewife Juvenile Riverine/Estuarine Habitat

Geographical and temporal movement patterns

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

Further north, juveniles in the Hudson River usually remain in freshwater tributaries until June (Schmidt et al. 1988). In contrast to the inshore abundance of American shad and blueback herring during the day, juvenile alewife were found to be most abundant in inshore areas at night in the Hudson River (McFadden et al. 1978; Dey and Baumann 1978). Hudson River juveniles were observed in shallow portions of the upper and middle estuary in late June and early July, where they remained for several weeks before moving offshore (Schmidt et al. 1988). Alewife typically spend three to nine months in their natal rivers before returning to the ocean (Kosa and Mather 2001).

In the summer in the Potomac River, juveniles are abundant near surface waters during the day; however, they shift to mid-water and bottom depths in September, where they remain until they emigrate in November (Warriner et al. 1970). Juvenile alewife respond negatively to light and follow diel movement patterns similar to blueback herring. Nevertheless, there appears to be some separation between the alewife and blueback herring as they emigrate from nursery grounds in the fall. The difference occurs most notably at night when alewife can be found more frequently at mid-water depths, while blueback herring are found mostly at the surface (Loesch and Kriete 1980). This behavior may reduce interspecific competition for food, given that the species' diets are similar (Davis and Cheek 1966; Burbidge 1974; Weaver 1975).

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

The influence and magnitude of migration cues on emigrating alewife may vary considerably. Richkus (1975a) observed waves of juvenile alewife leaving systems following environmental changes (e.g., changes in water flow, water levels, precipitation, and light intensity), but the number of fish leaving was unrelated to the level of magnitude of the change. Most fish (60% to 80%) emigrated during a small percentage (approximately 8%) of available days. These waves also lasted two to three days, regardless of the degree of environmental change (Richkus 1975a). Similarly, other researchers have observed that the majority (>80%) of river herring emigrate in waves (Cooper 1961; Huber 1978; Kosa and Mather 2001). Richkus (1975a) also noted that in some instances, high abundances of juvenile alewife may trigger very early (i.e., summer) emigration of large numbers of small juveniles from the nursery area, which is likely a response to a lack of forage. Additionally, juvenile migration of alewife occurs about one month earlier than that of blueback herring (Loesch 1969; Kissil 1974).

Although most juveniles emigrate offshore during their first year, some overwinter in the Chesapeake (Hildebrand 1963) and Delaware bays (Smith 1971). Marcy (1969) suggested that many juveniles (age-1+) spend their first winter close to the mouth of their natal river due to their presence in the lower portion of the Connecticut River in early spring. Other researchers concur that some juvenile alewife may remain in deep estuarine waters through the winter (Hildebrand and Schroeder 1928). There is some indication that alewife in northern states may remain in inshore waters for one to two years (Walton 1981). Conversely, since juvenile river herring cannot survive water temperatures of 3°C or below (Otto et al. 1976), they likely do not overwinter in coastal systems where temperatures are below 3°C (Kosa and Mather 2001).

Juveniles and the saltwater interface

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

Juvenile substrate associations

Olney and Boehlert (1988) found juvenile alewife among submerged aquatic vegetation (SAV) beds of the lower Chesapeake Bay and suggested that SAV likely confers some level of protection from predation. No other information was available regarding substrate preferences for juvenile alewife.

Juvenile depth associations

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

Juvenile water temperature

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

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

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

According to McCauley and Binkowski (1982), the upper lethal temperature for juvenile alewife is approximately 30°C. Concurrently, in Lake Michigan, upper incipient lethal limits (i.e., temperature at which 50% of the population survives) for young-of-the-year alewife acclimated to 10°C, 20°C, and 25°C, was estimated to be slightly less than 26.5°C, 30.3°C, and 32.1°C, respectively (Otto et al. 1976). Another study found that juveniles exposed to water at 35°C for 24 hours, after acclimation to water at 18.9 to 20.6°C, had a 20% survival rate (Dorfman and Westman 1970). Moreover, young-of-the-year alewife seem to have critical thermal maxima (CTM) that are 3 to 6°C higher than adults (Otto et al. 1976).

Alternatively, when juvenile alewife were subjected to decreasing temperatures (15.6°C down to 2.8°C) over the course of 15 days, they suffered greater than 90% mortality (Colby 1973). In another study, juvenile alewife exposed to 9°C, following acclimation at 20°C in 5.5 ppt salinity, suffered no mortality. However, when the temperature was decreased to 7°C for 96 h, they suffered 27 to 60% mortality (PSE&G 1984). Comparatively, the lower limit at which juvenile river herring are unable to survive is 3°C or less (Otto et al. 1976).

Juvenile dissolved oxygen associations

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

Juvenile pH and aluminum associations

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

Juvenile water velocity/flow

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

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

Juvenile feeding behavior

Juvenile alewife are opportunistic feeders that usually favor seasonally available items (Gregory et al. 1983). For example, in the Hamilton Reservoir, Rhode Island, juveniles feed primarily on dipteran midges in July, and cladocerans in August and September (Vigerstad and Colb 1978). Juveniles either select their prey individually or switch to a non-selective filter-feeding mode, which is a behavior utilized more at night (Janssen 1976). Grabe (1996) found that juvenile alewife fed on chironomids, odonates, and other amphipods during the day and early evening hours in the Hudson River. Juveniles have also been observed consuming epiphytic fauna especially at night (Weaver 1975; Grabe 1996). Juveniles may also feed extensively on benthic organisms, including ostracods, chironomid larvae, and oligochaete worms (Watt and Duerden 1974).

The number of zooplankton per liter consumed is assumed to be critical for the survival and growth of juvenile alewife. Pardue (1983) suggests that habitats containing 100 or more zooplankton per liter are optimal. Walton (1987) found that juvenile alewife abundance in

Damariscotta Lake, Maine, was controlled by competition for zooplankton, rather than parental stock abundance and recruitment. It has been suggested that clupeids evolved to synchronize the larval stage with the optimal phase of annual plankton production cycles (Blaxter and Hunter 1982). In addition, Morsell and Norden (1968) found that juvenile alewife consume zooplankton until they reach 12 cm TL, and may then switch to increasing amounts of the benthic amphipod *Pontoporeia* sp. Several researchers (Vigerstad and Colb 1978; O'Neill 1980; Yako 1998) hypothesize that a change in food availability may provide a cue for juvenile anadromous herring to begin emigrating seaward, but no causal link has been established.

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

Juvenile competition and predation

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

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

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

Juveniles and contaminants

A 24-hour LC_{50} (i.e., concentration at which 50% of the population dies) of 2.25 mg/L for total residual chlorine (TRC) was reported for juvenile alewife exposed for 30 minutes at 10°C (Seegert and Latimer 1977). Thirty-minute LC_{50} values for TRC were 2.27 and 0.30 mg/L for juveniles exposed at 10°C and 30°C, respectively (Brooks and Seegert 1978; Seegert and Brooks 1978). Juvenile alewife held at 15°C in 7 ppt salinity exhibited an avoidance response to 0.06 mg/L TRC (PSE&G 1980). Juveniles held at 19 to 24°C in freshwater exhibited an avoidance response at <0.03 mg/L TRC; fish subjected to 0.48 mg/L TRC for 2 hours at 22°C suffered 100% mortality (Bogardus et al. 1978).

Part D. Alewife Late Stage Juvenile and Adult Marine Habitat

Geographical and temporal patterns at sea

Some young-of-the-year alewife over-winter in deep, high salinity areas of the Chesapeake Bay (Hildebrand and Schroeder 1928). Dovel (1971) reported juvenile populations in the upper Chesapeake Bay that did not emigrate until early spring of their second year. Milstein (1981) found that juvenile alewife over-wintered in waters approximately 0.6 to 7.4 km from the shore of New Jersey, at depths of 2.4 to 19.2 m, in what is considered an offshore estuary. This area is warmer with higher salinity than the cooler, lower salinity river-bay estuarine nurseries where alewife reside in fall. The majority of alewife are present in March when bottom temperatures range from 4.4 to 6.5°C and salinity is between 29.0 and 32.0 ppt (Cameron and Pritchard 1963).

Young alewife have been found overwintering off the North Carolina coast from January to March, concentrated at depths of 20.1 to 36.6 m (Holland and Yelverton 1973; Street et al. 1973). However, other sources have noted that juvenile alewife tend to remain near the surface during their first year in saltwater (Bigelow and Schroeder 1953). In Lake Michigan, age-1 fish are usually pelagic, except in spring and fall, where they often occur on the bottom; age-2 fish are typically found on the bottom (Wells 1968).

Information on the life history of young-of-the-year and adult alewife after they emigrate to the sea is sparse (Klauda et al. 1991). Sexual maturity of alewife is reached at a minimum of age-2, but timing may vary regionally. In North Carolina, sexual maturity occurs mostly at age-3. In Connecticut, most males achieve maturity at age-4, and most females at age-5 (Jones et al. 1978). It is generally accepted that juveniles join the adult population at sea within the first year of their lives and follow a north-south seasonal migration along the Atlantic coast, similar to that of American shad (Neves 1981). Despite a lack of conclusive evidence, it is thought that alewife are similar to other anadromous clupeids in that they may undergo seasonal migrations within preferred isotherms (Fay et al. 1983). In fact, alewife typically migrate in large schools of similar sized fish, and may even form mixed schools with other herring species (Colette and Klein-MacPhee 2002).

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

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

Results from Canadian spring surveys show river herring distributed along the Scotian Gulf, southern Gulf of Maine, and off southwestern Nova Scotia from the Northeast Channel to the central Bay of Fundy; they are found to a lesser degree along the southern edge of Georges Bank and in the canyon between Banquereau and Sable Island Banks (Stone and Jessop 1992). A large component of the overwintering population on the Scotian Shelf (and possibly some of the U.S. Gulf of Maine population) moves inshore during spring to spawn in Canadian waters. Summer aggregations of river herring in the Bay of Fundy/eastern Gulf of Maine may consist of a mixture of stocks from the entire Atlantic coast, as do similar aggregations of American shad (Dadswell et al. 1987). However, based on commercial offshore catches by foreign fleets in the late 1960s, it was believed that coastal river herring stocks did not mingle to the extent that American shad stocks apparently did, at least during the seasons that foreign harvests were made (ASMFC 1985).

Salinity associations at sea

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

Depth associations at sea

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

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

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

Temperature associations at sea

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

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

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

Feeding behavior at sea

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

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

Competition and predation at sea

Schooling fish such as bluefish, weakfish, and striped bass, prey upon alewife (Bigelow and Schroeder 1953; Ross 1991). Other fish such as dusky shark, spiny dogfish, Atlantic salmon, goosefish, cod, pollock, and silver hake, also prey on alewife (Bowman et al. 2000; R. Rountree, University of Massachusetts, unpublished data). Of these species, spiny dogfish appears to have the greatest affinity for alewife (R. Rountree, University of Massachusetts, unpublished data). Also, see Part C of this chapter for additional information.

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

Table 4-5. Significant environmental, temporal, and spatial factors affecting distribution of alewife. Please note that, although there may be subtle variations between systems, the following data include a broad range of values that encompass the different systems that occur along the East Coast. Where a specific range is known to exist, it will be noted. For the subadult–estuarine/oceanic environment and non-spawning adult–oceanic environment life history phases, the information is provided as a general reference, not as habitat preferences or optima. NIF = No Information Found.

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

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

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