River Herring Habitat in the Northeast United States

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- methods in ecological modeling

We propose that there are temporal and spatial differences in the larval growth and mortality of river herring and that these differences are species specific. (Overton et al., 2012)

Due to their differences in biology, a single management plan will affect each species differently and exploitation within a river system may be biased towards one species (Schmidt et al 2003).

- how hsi breakpoints were derrived
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Chapter 4

Alewife (*Alosa pseudoharengus*)

This chapter is dedicated to the habitat preferences and life cycle of alewives (*Alosa pseudoharengus*) for the Northeastern United States. Despite their historical significance, alewife populations have encountered significant declines, leading to their classification as a "species of concern" by the U.S. National Marine Fisheries Service (National Marine Fisheries Service 2009). Various factors contribute to this decline, including deteriorating water quality, habitat loss, offshore bycatch/overfishing, increased predation, and dam construction (Kocovsky et al. 2008; National Marine Fisheries Service 2009; Bethoney, Stokesbury, and Cadrin 2014; Waldman and Quinn 2022). The consideration for inclusion in the U.S. Endangered Species List has also been raised, as indicated in reports by the National Marine Fisheries Service in 2013 (National Marine Fisheries Service 2013).

Recent stock assessments reveal diverse trends in documented alewife runs over the last ten years, with some populations showing signs of stabilization or even growth (ASMFC 2017). In 2019, the National Marine Fisheries Service concluded that listing the alewife as threatened or endangered under the Endangered Species Act (ESA) was not warranted (National Marine Fisheries Service 2019).

Alewives are widely distributed throughout the Northeastern United States, thriving in freshwater rivers and estuaries along the Atlantic coast (ASMFC 1985). While historically known for extensive migrations to spawn in freshwater tidal systems, limited information is available about estuary movements for alewives. This chapter aims to explore the favorable habitat conditions for spawning alewife adults, non-migratory juveniles, as well as eggs and larvae, considering factors such as temperature, depth, salinity, flow velocity, and substrate.

4.1 Life cycle overview

Alewives have a complex life cycle with distinct stages and behaviors. Spawning occurs in waves during spring, triggered by rising water temperatures and increasing day length (ASMFC 2009; McCartin et al. 2019; Able et al. 2020). Adult alewives migrate upstream from marine environments to suitable brackish or freshwater spawning habitats (Pardue 1983; Collette and Klein-MacPhee 2002). Recent observations also suggest a correlation between alewife migration and the lunar phase (Legett et al. 2021).

Alewife migration and spawning precedes blueback herring by 2-3 weeks (Fay, Neves, and Pardue 1983). Alewives exhibit a north-south seasonal migration pattern, with migrating adults potentially detouring into estuaries (Greene et al. 2009). Upon arrival at the spawning grounds, adult alewives engage in immense spawning runs, where large groups gather to deposit their adhesive eggs over a variety of substrates (O'Connell and Angermeier 1997; Able et al. 2020). After spawning, both males and females return to the marine environment.

In the spawning habitat, the incubation period for eggs lasts 3-6 days (Munroe 2000; Collette and Klein-MacPhee 2002). The eggs hatch into yolk-sac larvae, representing an early developmental stage where larvae rely on an attached yolk sac for nutrients before transitioning to external feeding. For alewives, this stage typically lasts 2-5 days (Bourne 1990).

After this stage, larvae remain in the estuary to grow and migrate downstream towards more brackish areas, maturing into juvenile fish (Pardue 1983). These brackish areas serve as nurseries until the juvenile alewives migrate to the sea (Laney 1997; Kosa and Mather 2001). Alewife larvae can adapt to high salinity (35 psu) by 50 days post-hatch (DiMaggio et al. 2016). However, the survival rate for larvae is relatively low, with only a small percentage successfully reaching the sea, potentially as low as 1%, depending on ecosystem conditions (Kissil 1974). Similarly, mortality rates for migratory adults during a spawning season can reach as high as 90% (Brady et al. 2005).

4.2 Habitat Requirements

4.2.1 Spawning Adult Alewives

Spawning adult alewives exhibit specific habitat preferences and requirements. Their annual migration during spawning is energetically demanding, with notable variations in behavior. Some studies suggest fasting during the day and extensive feeding at night, while others report refraining from eating until their return downstream to productive tidal habitats (Janssen and Brandt 1980; Collette and Klein-MacPhee 2002; Greene et al. 2009).

Preferred spawning habitats include lacustrine and fluvial environments rather than riverine ones (Reback et al. 2004; Frank et al. 2011). Alewives spawn and rear in upper river pools (Turner and Limburg 2016; Greene et al. 2009).

4.2.1.1 Temperature

Spawning adult alewives exhibit distinct temperature preferences crucial to their reproductive success and migration patterns. The spawning process commences at temperatures around 10.5 °C, with upstream migration initiating within the range of 5°C to 10°C (Cianci 1969; Mullen, Fay, and Moring 1986; Loesch 1987; Munroe 2000; Reback et al. 2004). Notably, limited in-stream movement is observed below 8°C or over 18°C, emphasizing the species' preference for moderate temperature conditions (Durbin, Nixon, and Oviatt 1979; Collette and Klein-MacPhee 2002). Spawning ceases at temperatures exceeding 27°C, indicating an upper limit for optimal reproductive activity (Kissil 1974; Pardue 1983; Brown et al. 2000; Reback et al. 2004). The optimal temperature range for successful spawning is broadly identified as 10°C to 22°C, with consensus suggesting peak spawning occurring within the narrower range of 12 to 16 degrees Celsius (Tyus 1974; Pardue 1983; O'Connell and Angermeier 1997; Collette and Klein-MacPhee 2002). While deviations from the optimal temperature range can impact spawning success and migration timing, the overall consensus indicates that alewives thrive in moderate temperature conditions.

4.2.1.2 Depth

Spawning adult alewives exhibit specific depth preferences during their reproductive activities. Notably, adult alewives migrating inland show an overall preference for depths below 100 meters (Pardue 1983; Munroe 2000). Species of herring from the same clupeid family have been known to spawn at depths ranging from 0.5 to 15 meters (Haegele and Schweigert 1985). Alewives generally favor depths from Mean Low Tide (MLT) to 10 meters (Brown et al. 2000). Other studies report that alewives favor more shallow spawning habitats ranging from 0.15 to 3 meters (Pardue 1983; Greene et al. 2009), with significant spawning recorded around 0.5 meters (Kosa and Mather 2001). Additional field observations, reveal a significant proportion of alewives occupying habitats as shallow as 2 meters (Mather et al. 2012), with the majority of spawning occurring at less than 1 m (Murdy, Birdsong, and Musick 1997). This variability in depth preferences reflects the adaptability of alewives to shallow conditions during their spawning and migration phases.

4.2.1.3 Salinity

The documented behavior of alewives challenges conventional beliefs about anadromous species exclusively relying on freshwater environments for spawning. Observations reveal that alewives engage in spawning activities in freshwater tidal habitats with minimal salinity concentrations, demonstrating adaptability to environments with salinity levels below 0.5 psu (Pardue 1983; Brown et al. 2000). This adaptability extends to tolerating higher salinity levels, with successful spawning observed in concentraions of 8 psu (Able et al. 2020). Other research by Brown et al. (2000) emphasizes a heightened preference for habitats with salinity concentrations below 15 psu, deeming concentrations exceeding 20 psu unsuitable for spawning adults.

Field studies further document that adult alewives exhibit spawning activities across diverse estuary habitats with varying salinity levels, including coastal ponds, pond-like regions in coastal rivers and streams, oxbows, eddies, backwaters, stream pools, and flooded swamps (Pardue 1983; Mullen, Fay, and Moring 1986; Collette and Klein-MacPhee 2002; Walsh, Settle, and Peters 2005). Remarkably, species of herring from the same clupeid family have been known to spawn in a wide range of salinity, from freshwater to levels exceeding 35 psu (Haegele and Schweigert 1985). This highlights the versatility of alewives in utilizing estuarine habitats with varying salinity conditions for their spawning activities.

4.2.1.4 Flow Velocity

The flow velocity preferences for adult alewives are crucial for understanding spawning habitat (Tommasi et al. 2015). Haro et al. (2004) highlighted the challenges faced by smaller species, including alewives, when subjected to high velocities above 3.5 m/s, leading to impingement issues and poor performance. In contrast, lower velocities, particularly below 1.7 m/s, as observed by Walsh, Settle, and Peters (2005), are favored by alewives. Consistently, Mather et al. (2012) found that tagged alewives spent minimal time in riffle–run habitats but preferred pools, with varying locations of pool occupancy.

While conventional wisdom suggests that alewives spawn in slow-moving habitats with little to no current, Haro et al. (2004) swimming experiments also revealed that migratory alewives can travel farther distances upstream when flow velocities are increased to 1.5 m/s, compared to 3.5 m/s. However, these experiments indicated very little suitability for upstream migration when velocities reach above 3.5 m/s, suggesting no suitability if tested at 4.5 m/s (Haro et al. 2004). Older findings identify velocities up to 0.3 m/s as optimal for spawning (Pardue 1983). Understanding the influence of flow velocity is key for effective management and preservation of the habitat conditions required for successful alewife spawning.

4.2.1.5 Substrate

Previous studies have presented conflicting information regarding the substrate preferences of spawning adult alewives, often stemming from the generalization of alewives with blueback herring as river herring. Despite Brown et al. (2000) arguing that substrate composition holds no significance in alewife models, contrasting observations from various sources, including studies by Fay, Neves, and Pardue (1983), Killgore, Morgan, and Hurley (1988), O'Connell and Angermeier (1997), and Able et al. (2020), present compelling evidence of a more defined range of substrate preferences. These preferences span a variety of unconsolidated substrates, such as small gravel, pebbles, small cobbles, sand, detritus, and other softer substrates (Esdall 1964; Pardue 1983; Bourne 1990; O'Connell and Angermeier 1997; Greene et al. 2009). These substrates are usually associated with higher-gradient streams. Observations from Boger (2002) found that river herring spawning areas along the Rappahannock River, Virginia, had substrates that consisted of sand, pebbles, and cobbles, and little accumulation of vegetation and detritus. Further, there is an indication that spawning adult alewives may avoid habitats containing sub-aquatic vegetation (SAV), according to findings by Killgore, Morgan, and Hurley (1988), Laney (1997) and Greene et al. (2009). This suggests that spawning adult alewives may favor habitat without SAV.

4.2.2 Non-Migratory Juveniles

Habitat preferences of non-migratory juvenile alewives differ from those of spawning adult alewives, but similar factors, including temperature, depth, salinity, flow velocity, and substrate, impact the abundance and successful development of young alewives, as evidenced in studies conducted by Pardue (1983), Walsh, Settle, and Peters (2005), and Tommasi et al. (2015). A comprehensive understanding of the preferred habitats for juvenile alewives is essential for meeting their ecological needs.

4.2.2.1 Temperature

Temperature plays a pivotal role in shaping the distribution, behavior, and early development of non-migratory juvenile alewives (Tommasi et al. 2015). Specific river observations, including the Delaware River at 22°C, Potomac River at 22.3°C, and Nanticoke River at 21.8°C, identify critical temperature thresholds associated with peak juvenile recruitment (Tommasi et al. 2015). The optimal temperature for nursery rearing is found to be 20–23°C (Tommasi et al. 2015), with a some preference for young alewives estimated at 26.3°C (Kellogg 1982). Supporting these findings, observations in the Eel River showed a mean temperature of 23.1°C, while the Herring River exhibited a mean temperature of 25.1°C (Ames and Lichter 2013; Bourne 1990).

The broader suitability range for juvenile recruitment spans 11°C to 28°C [Pardue (1983); Fay, Neves, and Pardue (1983); Klauda, Fischer, and Sullivan (1991); Brown et al. (2000); Munroe (2000); Tommasi et al. (2015)). Juvenile alewives do not survive temperatures below 3°C (Otto, Kitchel, and Rice

1976; Kellogg 1982; Pardue 1983; Munroe 2000). Specific thresholds, such as feeding behavior disruption at 6.7°C and schooling behavior disruption at 4.5°C, underscore the vulnerability of juvenile alewives to temperature fluctuations, with complete disorientation occurring at 2.8°C (Mullen, Fay, and Moring 1986). Exposure to temperature extremes outside the suitable range can negatively impact juvenile growth and performance (Kellogg 1982; Henderson and Brown Jr. 1985; Pörtner and Farrell 2008; Overton, Jones, and Rulifson 2012). Maintaining temperatures within the suitable thresholds is crucial for ensuring successful development and overall health of non-migratory juvenile alewives as they transition to adulthood.

4.2.2.2 Depth

The depth preferences of non-migratory juvenile alewives, as observed in studies such as Brown et al. (2000) and Mullen, Fay, and Moring (1986), differ significantly from their adult counterparts. Juveniles exhibit a preference for depths ranging from 0 to 10 meters, and no observed habitat suitability beyond 20 meters (Brown et al. 2000; Höök et al. 2008). Additional research by Pardue (1983) reinforces this trend, indicating that juveniles favor depths between 0.5 to 5 meters, and their abundance notably increases around five-meter depths. Similarly, other juvenile cluepids were found abundant in 4.6 meters (Mullen, Fay, and Moring 1986). After leaving the estuary, juveniles can be found in deeper waters off-shore before swimming farther out to sea (Greene et al. 2009). These combined field observations show that the optimal depth for juvenile alewives is equal to or less than 5 meters.

4.2.2.3 Salinity

Juvenile alewives display considerable adaptability to varying salinity levels, as evidenced by physiological changes observed in response to seawater exposure. This adaptation suggests capacity for osmoregulation, enabling them to regulate salt and water balance and maintain stability in seawater environments (Christensen et al. 2012). Additional studies, such as Leim (1924), Pardue (1983), and Brown et al. (2000), provide further insights into the versatility of alewives in diverse salinity conditions and imply that alewives can thrive in environments with fluctuating salinity, emphasizing adaptability to both freshwater and saltwater habitats during different life stages.

Research by Richkus (1975) indicates that juvenile alewives, transferred between freshwater and saline water, experienced zero mortality, suggesting a robust tolerance to salinity changes. However, DiMaggio et al. (2016) note lower survival rates when transferred from higher salinities to lower ones, emphasizing a potential preference for higher salinity environments. The presence of juvenile alewives in estuarine waters, where they are preyed upon by bluefish (Creaser and Perkins 1994), underscores their distinct salinity preference, spanning from areas exceeding 10 psu to levels as high as 30 psu (Pardue 1983; Brown et al. 2000). Turner and Limburg (2016) and Able et al. (2020) highlight juvenile preference for estuarine habitats with salinity concentrations ranging from 0.5 to 25 psu, promoting an ideal balance between freshwater and marine conditions for growth. Overall, juvenile alewives exhibit a wide range salinity preferences, showcasing their adaptability to diverse environments for optimal growth and survival.

4.2.2.4 Flow Velocity

Flow velocity preferences play a pivotal role in the development and survival of non-migratory juvenile alewives. Laboratory experiments suggest that juvenile alewives tend to avoid water velocities exceeding 0.1 m/s (Greene et al. 2009). Other observations document the presence of juvenile alewives in habitats with flow velocities ranging from 0.05 to 0.17 m/s (Richkus 1975; O'Connell and Angermeier 1999). Slower flow rates are conducive to energy conservation and effective foraging, while higher flow velocities may impede access to critical food resources, and disrupt their position in the water column (Haro et al. 2004; Able et al. 2020). Understanding flow velocity preferences is essential for informed habitat management, ensuring successful transitions for non-migratory juvenile alewives to adulthood.

4.2.2.5 Substrate

Non-migratory juvenile alewives have broad substrate preferences, underscoring their adaptability to diverse aquatic environments. While earlier studies, such as Fay, Neves, and Pardue (1983), indicated a preference for sandy substrates, recent observations suggest a potential inclination towards rocky substrates (Janssen and Luebke 2004; Kornis and Janssen 2011; Boscarino et al. 2020). Alewife catches at rocky sites have been reported to be much higher than those at sandy sites, possibly attributed to the increased profitability of rocky habitats for feeding on zooplankton (Janssen and Luebke 2004; Kornis and Janssen 2011). These substrate preferences have implications for habitat management,and creating environments conducive to the successful development and survival of juvenile alewives.

The presence of seagrass and SAV is important to non-migratory juvenile alewife habitat. Despite some studies suggesting avoidance of areas with aquatic vegetation (Ingel 2013), research by Olney and Boehlert (1988), Laney (1997), Greene et al. (2009), and Smith and Rulifson (2015) contradict this, emphasizing that seagrass beds provide essential nursery habitats for juvenile alewives. These vegetated areas serve as refuge from predators and offer abundant food sources. Seagrass beds also contribute to enhanced water quality by stabilizing sediments and promoting nutrient cycling, creating an optimal environment for the thriving of juvenile alewives. The significance of SAV extends to overwintering habitats, as suggested by Killgore, Morgan, and Hurley (1988). The understanding of these diverse substrate preferences and seagrass coverage is vital for effective habitat management, ensuring the successful development of non-migratory juvenile alewives in varied aquatic environments.

4.2.3 Eggs & Larvae

The early life stages of alewives, particularly their planktonic larval phases, are characterized by vulnerability to passive transport dispersal (Schmidt and Kiviat 1988). Understanding the habitat preferences exhibited by alewife eggs and larvae is essential for comprehending their developmental dynamics and ensuring optimal conditions for survival. This section will delve into key environmental parameters influencing the distribution and behavior of alewife eggs and larvae. Factors such as temperature, depth, salinity, flow velocity, and substrate play crucial roles in shaping the habitat preferences of these early life stages. Notably, studies, such as those by O'Connell and Angermeier (1997), emphasize current velocity as one of the strongest predictors for the presence of alewife eggs.

4.2.3.1 Temperature

Water temperature significantly shapes the growth, survival, and overall development of alewife eggs and larvae. Pardue (1983) and Kellogg (1982) reveal the optimal temperature for larval growth at approximately 26.4°C, with the estimated peak at 26.3°C. A broad suitable temperature range is evident as egg survival occurs between 12°C and 30°C, and temperatures exceeding 31°C lead to larvae mortality. Beyond direct developmental impacts, temperature influences the suitability of nursery areas, as noted by Tommasi et al. (2015). Specific river systems, like the Chowan River, experience temperatures surpassing the upper thermal tolerance of alewife larvae, influencing their distribution (Kellogg 1982).

The association between peak densities of alewife larvae and water temperature peaks highlights temperature sensitivity in early life stages of alewife. Lower temperatures and peaks in river flow negatively affect alewife larvae, indicating a complex interplay between temperature and environmental conditions (O'Connell and Angermeier 1999). Optimal temperature ranges for egg density peaks fall between 16-21°C and 11-28°C, showcasing the adaptability of alewife eggs to varying temperature conditions (O'Connell and Angermeier 1999; Klauda, Fischer, and Sullivan 1991). This is supported in observations from Kellogg (1982) where maximum hatching success occurred at 12.7°C, 15.0°C, and 20.8°C. Optimal hatching temperature is defined at 16°C (Esdall 1970), with hatching success ceasing above 29.7°C (Kellogg 1982; Pardue 1983). Temperature is a crucial factor impacting the development and survival of alewife eggs and larvae.

4.2.3.2 Depth

Alewife eggs and larvae exhibit clear depth preferences, primarily favoring shallow-water habitats during their early life stages. Observations from Lake Ontario, as documented by Klumb et al. (2003) and Ingel (2013), reveal that alewife larvae are uniformly distributed in nearshore areas, with a significant presence in waters less than 5 meters deep. In the same lake, early post-hatch larvae are particularly abundant in depths less than 3 meters, while larger larvae progressively inhabit deeper habitats (Ingel 2013; Dunstall 1984). Studies conducted in Nova Scotia's Margaree River and other locations further emphasize this trend, indicating that alewife larvae predominantly reside in depths shallower than 2 meters (Mullen, Fay, and Moring 1986). The preference for shallow-water habitats is linked to the benefits these environments offer, providing protection from predators and facilitating access to essential food sources, crucial for the growth and development of alewife larvae into juveniles.

4.2.3.3 Salinity

While there are observations indicating that alewives utilize freshwater streams for their early life stages (Kosa and Mather 2001; Tommasi et al. 2015), Mullen, Fay, and Moring (1986) provides evidence of their high tolerance to salinity changes. Pardue (1983) reports the presence of alewife eggs and larvae in environments with salinity levels below 12 ppt, suggesting a potential inclination towards slightly saline conditions. This inclination is corroborated by Dovel and Edmunds (1971), who notes that the growth rates of larvae are significantly lower in freshwater compared to slightly saline water, ranging from 1.0 to 1.3 ppt. The adaptability of alewives to a range of salinities is evident in their ability to thrive in different conditions.

Similarly, other clupeid eggs display tolerance to salinities in the range of 3-33%, and herring eggs and larvae are reported to develop abundantly in seawater with healthy and active larvae (Haegele and Schweigert 1985; Ford 1929). DiMaggio et al. (2016) offer valuable insights into the survival rates of alewives at different salinities, with the highest mean survival rate observed at 15‰ salinity (76.0%). As salinity increases to 20‰ and 30‰, the mean survival rates for alewives decrease to 69.3% and 64.7%, respectively. This pattern suggests a potential preference for moderate salinity conditions, supported by the higher survival rates at 15‰ compared to higher salinities. dimaggio_effects_2016 further highlights the adaptability of alewife embryos, showing survival rates above 97% at low salinities (2, 5, and 10 g/L) and decreased survival at salinities above 15 g/L. Overall, these findings highlight the broad salinity preferences that promote successful early development and survival of alewife eggs and larvae.

4.2.3.4 Flow Velocity

The early egg stages of alewives exhibit a positive relationship with flow velocity, particularly in the range of 0.03-0.2 m/s (O'Connell and Angermeier 1999). However, there is a rapid decline in larvae abundance associated with high flows, suggesting that extreme water velocities can be detrimental to their survival (O'Connell and Angermeier 1999). Insights from the Delaware River indicate that excessively high flows may negatively impact alewife recruitment, as elevated water velocity can create barriers that hinder the swimming performance of anadromous fish (Haro et al. 2004).

In specific habitats, larval alewives tend to be consistently found in water velocities up to 0.12 m/sec, avoiding faster currents (Ingel 2013). The distribution of alewife larvae is not primarily influenced by overall tidal fluctuations or the highest speeds of water flow; rather, it is influenced by more localized and instantaneous changes in velocity (Ingel 2013). Previous studies, such as Pardue (1983), observed optimal velocities for larvae and egg development ranging from 0 to 0.3 m/s. These findings collectively highlight the importance of flow velocity in shaping the distribution and development of alewife eggs and larvae, emphasizing the significance of suitable flow conditions for their early life stages.

4.2.3.5 Substrate

Substrate preferences significantly influence the distribution and habitat selection of alewife eggs and larvae. The sandy substrate on the eastern side of Lake Michigan was identified as a favorable environment for the primary and secondary production, limiting dreissenid mussel biomass and providing better support for prey available to larval alewife (Prendergast 2019). Detritus concentrations, a key variable associated with larval growth rate, are positively correlated with productive regions in Lake Michigan, indicating increased prey availability for larval alewife in areas with high detritus concentrations (Prendergast 2019). Pardue (1983) also suggests that optimal egg and larval habitat is found in substrates composed of 75% silt or other soft material containing detritus and vegetation. Soft substrates, such as sand, are considered conducive to the successful development of alewife eggs and larvae. Further, larvae have not been commonly reported in abundance over hard substrates. Reports of eggs on hard substrates might be attributed to the temporary adhesive property of alewife eggs rather than a preference for hard substrate habitats.

Although SAV is thought to provide spawning and nursery habitat for most anadromous and resident fishes, alewife larval catch is inversely related to SAV density, with larvae most frequently found in areas with less than 10 percent vegetation density and never in areas exceeding 30 percent vegetation density (Ingel 2013). Observations by Schmidt and Kiviat (1988) further highlight the impact of vegetation cover, like water-chestnut and water celery beds, on the distribution of larval alewife, with a decline in larval abundance following the establishment of dense water-chestnut cover. These findings collectively highlight the substrate preferences of alewife eggs and larvae, emphasizing the importance of soft substrates and vegetation coverage in their habitat.

4.3 Habitat suitability models

Existing alewife habitat suitability models, originally developed by Brown et al. (2000) and Pardue (1983), with reliance on similar sources such as Bigelow and Schroeder (1953) and the updated version Collette and Klein-MacPhee (2002), possess several limitations that make them inadequate for current applications.

Primarily, these models are constructed solely on observations of alewives' daytime behavior, neglecting their significant nocturnal activity patterns. Recent studies have revealed that alewives are substantially active at night, engaging in feeding and exhibiting substantial downstream movement during these nocturnal periods (Janssen 1978; Janssen and Brandt 1980; Greene et al. 2009; McCartin et al. 2019). Collette and Klein-MacPhee (2002) and Greene et al. (2009) even note that groups of alewives spawn in the evening. Consequently, the primary focus on daytime behavior in the existing models fails to capture the true habitat preferences and requirements of alewives, particularly in estuary and brackish environments.

Current models predominantly consider variables such as temperature, depth, and substrate, while disregarding other crucial factors that significantly influence alewives' habitat selection, including flow velocity, sub-aquatic vegetation, and life stage differences. Stevens, Saunders, and Duffy (2021) suggests that considerable diversity in these life history patterns may exist and that life cycle diversity may be an under-examined aspect of the ecology and management of river herring. This limited scope results in incomplete assessments of habitat suitability. Further, existing models fall short of encompassing the total knowledge available for alewives, as inconsistencies and potential inaccuracies emerge from conflicting information concerning substrate, salinity, and depth preferences. These limitations undermine the models' effectiveness in predicting habitat suitability for alewives, and since the release of these models, updated observations and stock assessments have been published that offer more detailed information on the habitat for alewives.

To address these shortcomings, habitat models should encompass a more comprehensive understanding of alewives' behavior, specifically acknowledging their use of estuarine and brackish habitats. These habitats serve as critical areas for alewives, exhibiting relatively high levels of habitat use (Greene et al. 2009; McCartin et al. 2019; Stevens, Saunders, and Duffy 2021). Incorporating these estuarine and brackish areas into management strategies is of paramount importance to ensure the conservation and successful management of the species.

Notably, utilizing estuaries and brackish habitats for spawning may offer energetically favorable conditions for alewives, as it eliminates the need for them to acclimate to complete freshwater environments (DiMaggio et al. 2015). This recognition highlights the significance of incorporating these habitats into conservation efforts and management plans to safeguard the species and support their reproductive success. The objective of this section is to define an updated habitat model for the spawning adult, non-migratory juvenile, and egg and larvae life stages of the alewife.

4.3.1 Spawning Adult Alewives

The updated Habitat Suitability Index (HSI) model for alewives introduces several environmental factors that relate to habitat preferences for spawning adult alewives. In terms of temperature preferences, the model introduces specific temperature ranges in which spawning behavior can be expected, such as the optimal suitability range of 12 to 16 degrees Celsius, offering a more precise depiction of alewives' thermal requirements. The upper limit of 27 degrees Celsius is also emphasized, underlining the critical need for suitable thermal conditions in spawning habitats.

The depth preferences in the model offer a more detailed assessment of habitat suitability, specifying a peak range of 0 to 2 meters for spawning adult alewives. Beyond 20 meters, the model identifies unsuitable depths for spawning, contributing to a clearer view of alewives' depth requirements. Similarly, the updated salinity preferences are characterized by a broader range, with the highest suitability observed at 0 to 8 psu, and moderate suitability expected from 8 to 15 psu.

In the realm of flow velocity, the model introduces distinct ranges, highlighting the optimal conditions at 0 to 0.3 meters per second and extending high suitability to 0.3 to 1.7 meters per second. An upper threshold of 4.5 meters per second is defined, aligning with observed behaviors and contributing to a more detailed view of the flow velocity requirements for alewives. The model also emphasizes the importance of diverse substrate types, including both soft (e.g., small gravel, sand, silt, detritus) and hard substrates (e.g., rock, boulders, clam beds), as well as the consideration of SAV presence or absence in spawning habitats. This update enhances the understanding of alewife spawning habitat and provides valuable insights for effective management and conservation efforts.

Table 4.1: Model Parameters and Habitat Suitability Values for Spawning Adult Alewives

Parameter	Range	**Habitat Suitability Value**
A. Temperature (°C)	$0.0 < t < 3.0$	0.0
	$3.0 <= t < 5.0$	0.1
	$5.0 <= t < 8.0$	0.5
	$8.0 <= t < 10.5$	0.7
	$10.5 <= t < 12$	0.8
	$12 <= t < 16$	1.0
	$16 <= t < 22$	0.8
	$22 <= t < 27$	0.5
	$t >= 27$	0.0
B. Depth (*meters*)	$0.0 < d < 2.0$	1.0
	$2.0 <= d < 5.0$	0.8
	$5.0 <= d < 10.0$	0.5
	$10.0 <= d < 15.0$	0.3
	$15.0 <= d <= 20.0$	0.1
	$d > 20.0$	0.0
C. Salinity (*psu*)	$0.5 <= s < 8.0$	1.0
	$8.0 <= s < 15.0$	0.5
	$15.0 <= s <= 20.0$	0.3
	$s > 20$	0.0
D. Flow Velocity (*m/s*)	$0 < v < 0.3$	1.0
	$0.3 <= v < 1.7$	0.8
	$1.7 <= v < 3.5$	0.5
	$3.5 <= v < 4.5$	0.1
	$v >= 4.5$	0.0
E. Substrate	Hard Substrate	0.3
	Soft Substrate	1.0
	Present SAV	0.1
	Absent SAV	1.0

4.3.2 Non-Migratory Juveniles

The updated Habitat Suitability Index (HSI) model for non-migratory juvenile alewives takes into account temperature, depth, salinity, flow velocity, and substrate, which influence habitat availability. The model defines habitat preferences for non-migratory juveniles using these parameters to provide an understanding of suitable conditions for the development and survival of non-migratory juveniles.

Temperature preferences are detailed, highlighting the critical range of 20 to 23 degrees Celsius as optimal for alewives' habitat. Depth considerations underscore the importance of depths below 5.0 meters, with higher depths exceeding 20.0 meters identified as unsuitable. The model recognizes the adaptability of alewives to varying salinity conditions, emphasizing their high suitability in habitats ranging from 0.5 to 25.0 psu.

A specific range is introduced for flow velocity to address optimal conditions for juvenile habitat. The model provides valuable insights into the impact of flow velocity on survival during development, helping inform habitat management practices. The substrate parameter delves into substrate type and the presence of SAV. Hard substrate receives the highest suitability value, while the presence of SAV contributes positively to habitat suitability. This detailed substrate analysis enhances our understanding of alewives' preferences for specific environmental conditions.

In summary, the HSI model offers a detailed perspective on habitat preferences for non-migratory juvenile alewives, providing detailed ranges and suitability values for each parameter. This approach contributes to comprehension of the conditions essential for the successful development and survival of alewives in their aquatic habitats.

Table 4.2: Model Parameters and Habitat Suitability Values for Non-Migratory Juvenile Alewives

Parameter	Range	**Habitat Suitability Value**
A. Temperature (°C)	$0 > t < 3$	0.0
	$3 <= t < 7$	0.1
	$7 <= t < 11$	0.5
	$11 <= t < 20$	0.8
	$20 <= t < 23$	1.0
	$23 <= t < 28$	0.5
	$t >= 28$	0.1
B. Depth (*meters*)	$0 < d < 5.0$	1.0
	$5.0 <= d < 10.0$	0.7
	$10.0 <= d < 20.0$	0.5
	$d >= 20$	0.0
C. Salinity (*psu*)	$0 < s < 0.5$	0.0
	$0.5 <= s < 10.0$	0.5
	$10.0 <= s <= 25.0$	1.0
	$s > 25$	0.8
D. Flow Velocity (*m/s*)	$0 < v < 0.1$	1.0
	$0.1 <= v < 0.17$	0.7
	$0.17 <= v < 0.3$	0.5
	$0.3 <= v < 3.5$	0.3
	$3.5 <= v < 4.5$	0.1
	$v >= 4.5$	0.0

Parameter	Range	**Habitat Suitability Value**
E. Substrate	Hard Substrate	1.0
	Soft Substrate	0.1
	Present SAV	1.0
	Absent SAV	0.5

4.3.3 Eggs & Larvae

The habitat suitability model for alewife eggs and larvae encompasses specified ranges and corresponding suitability values for temperature, depth, salinity, flow velocity, and substrate. The temperature parameter delineates thermal tolerances, emphasizing an optimal range between 16 and 28 degrees Celsius. Beyond these limits, suitability sharply declines, with extreme temperatures below 3 degrees or above 30 degrees Celsius deemed unsuitable. This highlights the significance of maintaining specific temperature conditions for alewife development to ensure optimal conditions for their survival.

The depth parameter provides insights into the preferred distribution of alewives, with a peak suitability observed in depths ranging from 0 to 3 meters. As depths increase, the suitability progressively decreases, indicating that eggs and larvae are more commonly found in shallower waters. Salinity considerations are also integrated, indicating a higher suitability in habitats with salinity levels between 0.5 and 12 psu. As salinity exceeds 20 psu, the suitability diminishes, suggesting an upper limit for suitable salinity conditions at this life stage in alewives.

The model specifies an optimal range of 0.03 to 0.12 meters per second for flow velocity. This parameter highlights the importance of low flow rates for alewife habitats, while higher velocities result in reduced suitability. The substrate parameter emphasizes the significance of substrate type and the presence of SAV for alewife eggs and larvae. Hard substrates and the absence of SAV are associated with increased abundance, underlining the importance of substrate variety in alewife habitats. Overall, this model defines environmental factors influencing habitat suitability for alewife eggs and larvae, aiding in effective conservation and management strategies.

Table 4.3: Model Parameters and Habitat Suitability Values for Alewife Larvae and Egg Development Stages

Parameter	Range	**Habitat Suitability Value**
A. Temperature (°C)	$0 < t < 3$	0.0
	$3 <= t < 7$	0.1
	$7 <= t < 11$	0.3
	$11 <= t < 16$	0.5
	$16 <= t < 28$	1.0
	$28 <= t < 30$	0.1
	$t >= 30$	0.0
B. Depth (*meters*)	$0 < d < 3$	1.0
	$3 <= d < 5$	0.8
	$5 <= d < 10$	0.5
	$10 <= d < 20$	0.1
	$d >= 20$	0.0
C. Salinity (*psu*)	$0 < s < 0.5$	0.8
	$0.5 <= s < 12.0$	1.0
	$12.0 <= s < 15.0$	0.75
	$15.0 <= s <= 20.0$	0.7
	$s > 20$	0.65
D. Flow Velocity (m/s)	$0 < v < 0.03$	0.7
	$0.03 <= v < 0.12$	1.0
	$0.12 <= v < 0.3$	0.5
	$0.3 <= v < 3.5$	0.3
	$3.5 <= v < 4.5$	0.1
	$v >= 4.5$	0.0
E. Substrate	Hard Substrate	0.5
	Soft Substrate	1.0
	Present SAV	0.1
	Absent SAV	1.0

Chapter 5

Blueback Herring (*Alosa aestivalis*)

This chapter aims to explore the habitat preferences and life cycle of blueback herring (*Alosa aestivalis*) in the northeastern United States. Blueback herring have faced significant declines,

This chapter explores the favorable habitat conditions for spawning blueback adults, non-migratory juveniles, as well as eggs and larvae, which are influenced by factors such as suitable spawning habitats, water quality conditions, and availability of appropriate food resources (Lynch et al. 2015).

blueback herring spawn in higher salinity, faster-moving waters in the lower river (Turner & Limburg, 2016)

5.1 Life cycle overview

- Alewives enter the river first, followed by blueback herring 2-3 weeks later (Jessop 2003).
- juveniles may take longer to move into brackish waters (Schmidt et al. 1988).
- Blueback larvae demonstrate the ability to adapt to marine environments by 58 days post-hatch (DiMaggio et al., 2015).

5.2 Habitat Requirements

5.2.1 Spawning Adults

5.2.1.1 Temperature

- move into estuary begins at 14 and ceases at 27 Pardue (1983)
- 16 - 16 klauda et al 1991
- Our results indicate that blueback herring adults require temperatures of at least 16.8"C to spawn. (O'Connell & Angermeier, 1999)
- range 17 - 26 and optimal 20 - 24 Pardue (1983)
- spawning stops at 27 Pardue (1983)
- Our results demonstrate that the spawning temperature that maximized juvenile blueback herring abundance in the Delaware River was 11 °C (tommasi 2015)
- spawning begins at 14 C (Mullen et al., 1986)
- Alewives begin spawning when water temperatures reach 51 and bluebacks 57 degrees F (Reback et al., 2004).
- Both species cease spawning when the water warms to 81°F (Reback et al., 2004).

5.2.1.2 Depth

- 0.15–3 m Pardue (1983)
- spawning habitat were all 0.5 m or less (Kosa & Mather, 2001)
- Species of herring from the same cluepid family have been known to spawn majority 0.5-5m and up to 15 m (Haegele & Schweigert, 1985).

5.2.1.3 Salinity

- spawning begins then or shortly thereafter. Although this species apparently spawns primarily in fresh water, spawning also occurs in brackish ponds at Woods Hole (Nichols and Breder, 1926; Hildebrand, 1963).
- I found that the chief spawning grounds in the Delaware River were in tidal water (Chittenden, 1972)
- Species of herring from the same cluepid family have been known to spawn in a range of salinities from freshwater to 35+ psus (Haegele & Schweigert, 1985).

- Alewives have been widely observed spawning in freshwater tidal habitats with minimal salinity concentrations, revealing a habitat use in environments with salinity levels below 0.5 psu (Pardue 1983).

- Blueback herring in Winnegance Lake and Patten Pond show a preference for high salinity environments for spawning, indicated by their limited residency time in freshwater. The immediate transition of fish from Winnegance Lake to the estuary after spawning suggests a preference for high salinity spawning, with the estuarine environment supporting early egg and larvae development (Payne Wynne et al., 2015).

5.2.1.4 Flow Velocity

- blueback herring show a preferance for higher velocities than alewives (haro 2004)
- Low velocities (0.0–1.7 m/s) (Walsh et al 2005)
- 0.11 m/s (O'Connell & Angermeier, 1997)
- blueback tend to favor running water and a fairly clean hard bottom, Bourne 1990
- Both species spawn primarily in habitats with little or no current Walsh 2005

5.2.1.5 Substrate

- Blueback herring do not usually spawn as far upstream as the alewife and selectively choose spawning sites in fast-flowing water over a hard substrate, particularly in shared spawning grounds (Loesch and Lund 1977; Jones et al. 1978; Scott and Scott 1988).

- blueback tend to favor running water and a fairly clean hard bottom, bourne 1990

- prefer hard substrate (Loesch and Lund 1977)

5.2.2 Non-Migratory Juveniles

5.2.2.1 Temperature

- supported in observations where Eel River had a mean temperature of 23.1°C, while the Herring River (Bourne) had temperatures with a mean of 25.1°C (Ames & Lichter, 2013).

5.2.2.2 Depth

- Juvenile Blueback herring in Potomac River, Virginia abundant in 4.6 m(Mullen et al., 1986)

5.2.2.3 Salinity

Bluebacks:

Bluebacks exhibit high survival rates when transferred between certain salinities, particularly from 3‰, 15‰, and 30‰ into 3‰ salinity. The high survival rates indicate that Bluebacks are well-adapted and can thrive under a range of salinity conditions within the specified experimental scenarios. While the information does not explicitly state a preference for specific salinities, the high survival rates suggest that Bluebacks may have a relatively broad salinity tolerance in the studied range.(DiMaggio et al., 2015)

- blueback herring is highly salinity tolerant early in life (28 psu) (Chittenden, 1972)
- herring eggs and larvae developing in abundance in sea-water with healthy and active larvae (Ford, 1929)

5.2.2.4 Flow Velocity

- Previous optimal velocities for larvae and egg development were observed from 0 to 0.3 m/s (Pardue 1983).

5.2.2.5 Substrate

- blueback tend to favor running water and a fairly clean hard bottom, bourne 1990

5.2.3 Eggs and Larvae

5.2.3.1 Temperature

- blueback herring early egg stages were positively related to water temperature (14-22°C). (O'Connell & Angermeier, 1999)
- Blueback herring eggs have been found in water temperatures ranging from 7 to 14°C in the upper Chesapeake Bay, with most being collected at 14°C (Dove1 1971).

- Temperatures observed in our study were always below those known to impair hatching success (32.9 to 36.1°C) or cause larval deformities (34°C). (O'Connell & Angermeier, 1999)
- eggs recorded at 20-24 C (Mullen et al., 1986)
- 19 C 0-5% deformities, 20 0-24% deformities, Complete larval deformities in eggs exposed to 34 C (Koo and Johnston 1978)
- 11.48C to 23.08C, 10.98C to 20.88C walsh 2005
- Larvae were not found in the canal oroxbow until late April and were never abundantat water temperatures below 148C (walsh 2005).
- peak densities were positively associated with peaks in water temperature (within the range of 4-19 C) (O'Connell & Angermeier, 1999).

5.2.3.2 Depth

- In Lake Ontario, early post-hatch larvae were most abundant in shallow areas less than 3m in depth, with larger larvae progressively occupying deeper habitat (Dunstall 1984).
- Larval Alosa in Nova Scotian fmgs rivers inhabite-i-waters that were relatively shallow (<2 m) (Mullen et al., 1986)

5.2.3.3 Salinity

- Bluebacks:

The mean survival rates for Bluebacks consistently increase with higher salinities. The highest mean survival rate for Bluebacks is observed at 30‰ salinity (95.3%). This pattern indicates that Bluebacks may exhibit a preference for higher salinity conditions, as indicated by their higher survival rates at 30‰ compared to lower salinities. (DiMaggio et al., 2015)

- highly tolerant of salinity changes (Mullen et al., 1986)

- Pacific herring eggs are tolerant to salinities in the range of 3-33% (Haegele & Schweigert, 1985).

- blueback herring embryos displayed a wide salinity tolerance throughout the range. Embryos of both species exhibited high survival in tidal salinity exposures. Survival of acutely-transferred alewife and blueback herring larvae decreased with increasing salinity (>20 g/L)(DiMaggio et al., 2016).

5.2.3.4 Flow Velocity

- lower temperatures and peaks in river flow negatively impacted early life stages (O'Connell & Angermeier, 1999)

5.2.3.5 Substrate

- thought to provide spawning and nursery habitat for anadromous and resident fishes (Miller et al 2006); however, in the case of alewives, larval catch was inversely related to vegetation density. larvae were most frequently found in areas with less than 10 percent vegetation density and were never found in areas where vegetation density exceeded 30 percent (Ingel, 2013).

5.3 Habitat suitability models

5.3.1 Spawning Adults

Table 5.1: **Table 1.** Model Parameters and Habitat Suitability Values for Spawning Adult Blueback Herring.

Parameter	Range	**Habitat Suitability Value**
A. Temperature (°C)	$0 < t < 8$	0.0
	$8 <= t < 12$	0.5
	$12 <= t < 16$	1.0
	$16 <= t < 22$	1.0
	$22 <= t < 27$	0.5
	$27 <= t < 30$	0.1
	$t > 30$	0.0
B. Depth (*meters*)	$MLT < d < 2$	0.0
	$2 <= d < 10$	0.5
	$10 <= d < 20$	1.0
	$20 <= d < 50$	0.5
	$50 <= d < 100$	0.5
	$d > 100$	0.5
C. Salinity (*psu*)	$0 < s < 0.5$	1.0
	$0.5 <= s < 5.0$	1.0
	$5.0 <= s < 15.0$	1.0
	$15.0 <= s < 20.0$	0.5
	$s > 20$	0.0
D. Flow Velocity (*m/s*)	$0 < v < 0.3$	1.0
	$0.3 <= v < 1.5$	1.0
	$1.5 <= v < 3.5$	0.5
	$3.5 <= v < 4.5$	0.3
	$v > 5$	0.0

Parameter	Range	**Habitat Suitability Value**
E. Substrate	Hard Substrate	0.5
	Soft Substrate	1.0
	Present SAV	1.0
	Absent SAV	0.5

5.3.1.1 Temperature

5.3.1.2 Depth

5.3.1.3 Salinity

5.3.1.4 Flow Velocity

5.3.1.5 Substrate

5.3.2 Non-Migratory Juveniles

Table 5.2: **Table 2.** Model Parameters and Habitat Suitability Values for Non-Migratory Juvenile Blueback Herring.

Parameter	Range	**Habitat Suitability Value**
A. Temperature (°C)	$0 < t < 8$	0.0
	$8 <= t < 12$	0.5
	$12 <= t < 16$	1.0
	$16 <= t < 22$	1.0
	$22 <= t < 27$	0.5
	$27 <= t < 30$	0.1
	$t > 30$	0.0
B. Depth (*meters*)	$MLT < d < 2$	0.0
	$2 <= d < 10$	0.5
	$10 <= d < 20$	1.0
	$20 <= d < 50$	0.5
	$50 <= d < 100$	0.5
	$d > 100$	0.5
C. Salinity (*psu*)	$0 < s < 0.5$	1.0
	$0.5 <= s < 5.0$	1.0
	$5.0 <= s < 15.0$	1.0
	$15.0 <= s < 20.0$	0.5
	$s > 20$	0.0

Parameter	Range	**Habitat Suitability Value**
D. Flow Velocity (m/s)	$0 < v < 0.3$	1.0
	$0.3 <= v < 1.5$	1.0
	$1.5 <= v < 3.5$	0.5
	$3.5 <= v < 4.5$	0.3
	$v > 5$	0.0
E. Substrate	Hard Substrate	0.5
	Soft Substrate	1.0
	Present SAV	1.0
	Absent SAV	0.5

5.3.2.1 Temperature

5.3.2.2 Depth

5.3.2.3 Salinity

5.3.2.4 Flow Velocity

5.3.2.5 Substrate

Previous studies have presented conflicting information regarding the substrate preferences of spawning adult blueback herring, likely stemming from the generalization of alewives with blueback herring as river herring. Adult blueback herring spawn over both soft and hard substrates (Pardue 1983; O'Connell and Angermeier 1997; Brown et al. 2000).

Aside from their demonstrated dependence on soft substrates, spawning adult alewives also exhibit a pronounced inclination toward habitats containing subaquatic vegetation (Killgore, Morgan, and Hurley 1988; Laney 1997). Comprehending and defining these substrate preferences is crucial to effectively manage and conserve the appropriate spawning habitats for alewives.

5.3.3 Larvae

Table 5.3: **Table 3.** Model Parameters and Habitat Suitability Values for Blueback Herring Larvae Stage.

Parameter	Range	**Habitat Suitability Value**
A. Temperature (°C)	$0 < t < 8$	0.0
	$8 <= t < 12$	0.5
	$12 <= t < 16$	1.0
	$16 <= t < 22$	1.0
	$22 <= t < 27$	0.5
	$27 <= t < 30$	0.1
	$t > 30$	0.0
B. Depth ($meters$)	$MLT < d < 2$	0.0
	$2 <= d < 10$	0.5
	$10 <= d < 20$	1.0
	$20 <= d < 50$	0.5
	$50 <= d < 100$	0.5
	$d > 100$	0.5
C. Salinity (psu)	$0 < s < 0.5$	1.0
	$0.5 <= s < 5.0$	1.0
	$5.0 <= s < 15.0$	1.0
	$15.0 <= s < 20.0$	0.5
	$s > 20$	0.0
D. Flow Velocity (m/s)	$0 < v < 0.3$	1.0
	$0.3 <= v < 1.5$	1.0
	$1.5 <= v < 3.5$	0.5
	$3.5 <= v < 4.5$	0.3
	$v > 5$	0.0
E. Substrate	Hard Substrate	0.5
	Soft Substrate	1.0
	Present SAV	1.0
	Absent SAV	0.5

5.3.3.1 Temperature

5.3.3.2 Depth

5.3.3.3 Salinity

5.3.3.4 Flow Velocity

5.3.3.5 Substrate

Chapter 6

Application

example of application to martha's vineyard

6.1 Study Area

We do not know right now the precise places where the herring spawn within Squibnocket and its tributary brooks and pond and salinity conditions where spawning occurs. spawn successfully in the slightly brackish water at the west end of the Pond (or elsewhere within it), or whether they manage to work their way up little tributaries. Bourne 1990.

6.2 Input Data

6.3 Pre-Processing

6.4 Post-Processing

6.5 Results

6.5.1 Spawning Adults

- Alewives
- Blueback Herring

6.5.2 Non-Migratory Juveniles

- Alewives
- Blueback Herring

6.5.3 Eggs and Larvae

- Alewives
- Blueback Herring

Chapter 7

Evaluation

7.1 Qualitative Evaluation

- Tribal evaluation of quality
- confidence language

7.2 Quantitative Evaluation

- Historic Herring Map?
- Spatial accuracy (Area)?

Chapter 8

Discussion

- Utility
  - management
  - what do the results tell us
- Limitations
  - regional
  - accuracy based on current knowledge
  - prediction power
- Compare to similar models (Pardue & Brown)

other factors impacting habitat health that could be added in the future - nitrogen - dissolved oxygen - PH levels "Blueback eggs and larvae to pulses of acidified water (pH 5.5 to 5.6) was reported to increase their mortality rate substantially (Klauda, 1987; see also Byrne, 1988). The pH of many Cape and Island soils is roughly in tnis range, and the ability of these soils to neutralize additional acidic inputs is limited. Bourne 1990)

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Chapter 9

Summary

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Appendices

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