

Alewife Habitat Suitability Models

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Alewives

This chapter aims to explore the habitat preferences and life cycle of alewives (*Alosa pseudoharengus*) in the northeastern United States. Alewives have faced significant declines, leading to their classification as a “species of concern” by the U.S. National Marine Fisheries Service (National Marine Fisheries Service 2009). A combination of factors that have contributed 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). They have also been considered for inclusion in the U.S. Endangered Species List, as indicated in reports by the National Marine Fisheries Service in 2013 (National Marine Fisheries Service 2013).

Recent stock assessment reports reveal diverse trends in documented alewife runs over the last ten years, with some populations showing signs of stabilization or even growth (ASMFC 2017). Additionally, 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). Historically, alewives have undertaken extensive migrations to spawn in freshwater tidal systems, but limited information is available about estuary and marine movements during the juvenile and adult phases for alewives (McCartin et al. 2019).

This chapter explores the favorable habitat conditions for spawning alewife adults, nonmigratory juveniles, 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).

Life cycle overview

Alewives exhibit a complex life cycle characterized by distinct stages and behaviors. Spawning typically occurs in waves during the spring season, 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 reach suitable brackish or freshwater spawning habitats (H. B. Bigelow and Schroeder 1953; A. F. Bigelow et al. 2002). Recent observations show that alewife migration can also be correlated with the lunar phase (Legett et al. 2021).

Upon arrival at the spawning grounds, adult alewives engage in immense spawning runs, where large aggregations 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 (H. B. Bigelow and Schroeder 1953; A. F. Bigelow et al. 2002).

In the spawning habitat, the incubation period for eggs typically lasts for 3-7 days (H. B. Bigelow and Schroeder 1953; A. F. Bigelow et al. 2002). Once hatched, the larvae begin their rapid migration downstream, eventually making their way towards estuary habitats where they will reside as they grow (Pardue 1983). This estuary environment serves as a nursery for juvenile alewives until they eventually migrate to the sea

(Laney 1997; Kosa and Mather 2001). It is noteworthy that the survival rate for larvae is relatively low, with only a small percentage successfully reaching the sea for each female alewife that entered the spawning grounds. This percentage can be as low as 1% or even less, depending on the specific conditions of the ecosystem (Kissil 1974). Similarly, mortality rates for migratory adults during a spawning season can reach as high as 90% in southern regions (Brady et al. 2005).

Habitat Requirements

Spawning Adult Alewives

Spawning adult alewives exhibit specific preferences and requirements related to habitat characteristics. Their annual migration during spawning is energetically demanding and notable variations in behavior have been observed. Some studies report fasting during the day and extensive feeding at night, while others document refraining from eating until their return downstream to productive tidal habitats (H. B. Bigelow and Schroeder 1953; Janssen and Brandt 1980; A. F. Bigelow et al. 2002). The preferred habitats for spawning are lacustrine and fluvial environments rather than riverine (Reback et al. 2004; Frank et al. 2011).

Temperature preferences during spawning vary across studies, but there is a consensus that optimal temperatures for successful spawning fall within the range of 12 to 16 degrees Celsius (Brown et al. 2000). Suitable spawning temperatures broadly span from 8 to 22 degrees Celsius (Tyus 1974; Pardue 1983; Collette and Klein-MacPhee 2003; Mather et al. 2012) and spawning activity significantly diminishes above 27 degrees Celsius (Kissil 1974; Pardue 1983). Deviations from the optimal temperature range can significantly impact spawning success and the timing of migration. Water temperature also plays a critical role in alewife abundance and movement patterns (Legett et al. 2021).

In terms of depth preferences, spawning adult alewives are generally known to favor depths ranging from Mean Low Tide (MLT) to 10 meters (Brown et al. 2000), but recent field observations indicate that a significant proportion of alewives can be found in habitats as shallow as 2 meters (Mather et al. 2012). As such, alewives are capable of spawning in both shallow and deep water environments, highlighting their adaptability in selecting suitable spawning locations.

Further, documented behavior of alewives challenges the conventional belief that anadromous species exclusively depend on freshwater environments for spawning. Alewives have been observed spawning in freshwater habitats with minimal salinity concentrations, revealing a preference for environments with salinity levels below 0.5 psu. However, they can tolerate salinity levels as high as 5 psu for successful spawning, as documented in the study conducted by Pardue (1983). More recently, Brown et al. (2000) emphasizes an additional heightened preference for habitats with salinity concentrations below 15 psu, while concentrations surpassing 20 psu are deemed unsuitable for spawning adults. Additionally, field studies have documented that adult alewives engage in spawning activities across a diverse array of estuarine habitats with varying salinity levels, including ponds within coastal systems, pond-like regions within coastal rivers and streams, oxbows, eddies, backwaters, stream pools, and flooded swamps (Pardue 1983; Mullen, Fay, and Moring 1986; Collette and Klein-MacPhee 2003; Walsh, Settle, and Peters 2005).

Flow velocity is a crucial factor influencing the spawning of alewives (Tommasi et al. 2015). Alewives are thought to spawn in habitat that are slow moving with little or no current (Walsh, Settle, and Peters 2005). Pardue (1983) identifies velocities up to 0.3 m/s as suitable for spawning. However, Haro et al. (2004) conducted laboratory experiments showing that migratory alewives can travel farther distances upstream when flow velocities are up to 1.5 m/s, compared to 3.5 m/s. Notably, these experiments indicate some suitability at these flow velocities and very little suitability for upstream migration when velocities reach 4.5 m/s (Haro et al. 2004). Understanding the preferred flow velocities is essential in managing and preserving the habitat conditions required for successful alewife spawning.

Previous studies have presented conflicting information regarding the substrate preferences of spawning adult alewives. While some studies suggest that alewives appear to prefer spawning over hard substrates such as gravel and rock Brown et al. (2000), possibly due to the eggs' better adhesion to such surfaces, recent

research provides evidence supporting a broader range of substrate utilization by spawning alewives Able et al. (2020). Notably, Able et al. (2020) documented observations of alewives spawning over sandy substrates, alongside the presence of eggs near hard substrates. Additionally, O’Connell and Angermeier (1997) also support the idea that alewives spawn over a range of substrates, including gravel, sand, vegetation, and other soft substrates. Furthermore, spawning adult alewives do not appear to show a strong preference for habitat containing sub-aquatic vegetation (Killgore, Morgan, and Hurley 1988; Rozas and Odum 1988). Understanding these substrate preferences is crucial for managing and preserving suitable spawning habitats for alewives.

Premigratory Juvenile Alewives and Larvae

Premigratory juvenile alewives and larvae exhibit distinct habitat preferences and requirements, which play a crucial role in influencing their survival and growth. Several factors influence the abundance and successful development of these young alewives, including river flow, temperature, salinity, depth, and substrate (Pardue 1983; Walsh, Settle, and Peters 2005; Tommasi et al. 2015). The preferred habitats for juveniles and alewife larvae are also lacustrine and fluvial environments (Overton, Jones, and Rulifson 2012).

Temperature significantly influences the distribution, behavior, and early development of premigratory juvenile alewives and larvae (Tommasi et al. 2015). Optimal temperatures for juvenile alewife development and larvae hatching fall within the range of 20°C to 23°C, with a broader suitability range for juvenile and larvae recruitment from 11°C to 27°C (Pardue 1983; Fay, Neves, and Pardue 1983; Klauda, Fischer, and Sullivan 1991; Brown et al. 2000; Tommasi et al. 2015). Juvenile river herring do not survive temperatures of 3°C or less and hatching success ceases entirely above 29.7°C (Otto, Kitchel, and Rice 1976; Pardue 1983). Maintaining water temperatures within these ranges is crucial for the successful development and overall health of premigratory juvenile alewives and larvae.

The depth preferences of premigratory juvenile alewives differ from their adult counterparts, as juveniles exhibit a preference for depths ranging from 0 to 10 meters, with no habitat suitability observed beyond 20 meters (Brown et al. 2000; Höök et al. 2008). Research by Pardue (1983) further supports this finding, indicating that juveniles prefer depths between 0.5 to 5 meters. Lake Ontario research by Ingel (2013) found that early post-hatch larvae are abundant in depths less than 3 meters, while larger larvae occupy progressively deeper habitats. Similarly, observations in Nova Scotia’s Margaree River indicate that alewife larvae predominantly reside in depths shallower than 2 meters, while juvenile abundance increases around five meters deep (Gibson and Myers 2003). Overall, these field observations indicate that optimal depth for juvenile alewives and larvae is <5 meters. These shallow-water habitats provide protection from predators and access to food sources, facilitating growth before downstream migration.

Juvenile alewives exhibit a distinct salinity preference, favoring concentrations exceeding 10 psu and even tolerating levels up to 30 psu (Pardue 1983; Brown et al. 2000). Research by Fay, Neves, and Pardue (1983) notes their presence in areas with salinity below 12 psu, indicating adaptability to lower salinity environments. Turner and Limburg (2016) along with Able et al. (2020) emphasize the preference of juveniles for estuarine habitats with salinity concentrations spanning 0.5 to 25 psu, promoting an ideal balance between freshwater and marine conditions for growth. While salinities exceeding 20 psu might impede suitability by affecting feeding and physiological processes (Fabrizio et al. 2021), higher salinities up to 30 psu show minimal adverse effects on the health and survival of juvenile alewives, with a 100% survival rate observed at 15 psu (DiMaggio et al. 2015). In summary, juvenile alewives exhibit a versatile salinity preference that ranges from thriving in concentrations exceeding 10 psu up to tolerating levels as high as 30 psu, highlighting their adaptability to diverse environments for optimal growth and survival.

Flow velocity is a crucial determinant of the development and survival of premigratory juvenile alewives (Tommasi et al. 2015). Previous optimal velocities for larvae and egg development were observed from 0 to 0.3 m/s (Pardue 1983). Other studies document juvenile alewife preference for habitats with flow velocities ranging from 0.05 to 0.17 m/s (Richkus 1975; O’Connell and Angermeier 1999). Larval alewives are consistently found in water velocities up to approximately 0.12 m/s, but they are absent in faster currents (Ingel 2013). Slower flow rates offer suitable conditions for juveniles and larvae to conserve energy while

effectively foraging for food (Haro et al. 2004). Conversely, higher flow velocities may hinder their ability to access critical food resources, maintain their position in the water column, and displace recently spawned eggs from their initial location (Haro et al. 2004; Able et al. 2020). Understanding the flow velocity preferences and effects on premigratory juvenile alewives and larvae is crucial for effective habitat management and successful transition from egg to adulthood.

Premigratory juvenile alewives exhibit diverse substrate preferences that reflect their adaptability to various environments. While previous studies suggest a preference for sandy substrates Fay, Neves, and Pardue (1983), more recent observations by Janssen and Luebke (2004) indicate a potential preference for rocky substrates. Seagrass coverage also plays a vital role in the habitat of these juveniles. Despite some studies suggesting avoidance of areas with aquatic vegetation Ingel (2013), research by Laney (1997) and Smith and Rulifson (2015) demonstrates that seagrass beds provide essential nursery habitat, offering refuge from predators and abundant food sources. Seagrass beds enhance water quality by stabilizing sediments and promoting nutrient cycling, creating a favorable environment for juvenile alewives to thrive. These vegetated areas are also crucial for overwintering habitat (Killgore, Morgan, and Hurley 1988). Understanding these diverse substrate preferences and the importance of seagrass coverage is essential for effective habitat management and the successful development of premigratory juvenile alewives.

Habitat suitability models

The Alewives Habitat Suitability models, originally developed by Brown et al. (2000) and Pardue (1983), with reliance on similar sources such as H. B. Bigelow and Schroeder (1953) and A. F. Bigelow et al. (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 primarily active at night, engaging in feeding and exhibiting substantial downstream movement during these nocturnal periods (Janssen 1978; Janssen and Brandt 1980; McCartin et al. 2019). Collette and Klein-MacPhee (2003) even notes that groups of alewives spawn in the evening. Consequently, the exclusive 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. Since the release of these models, updated observations and stock assessments have been published that offer more detailed information on the habitat for alewives.

Furthermore, the 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 and life stage differences. This limited scope results in incomplete assessments of habitat suitability. Moreover, the existing models fall short of encompassing the comprehensive spectrum of 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.

To address these shortcomings, updated 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 (McCartin et al. 2019). 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.

Spawning Adult Alewives

```
## Warning: package 'dplyr' was built under R version 4.1.3
```

```
##
## Attaching package: 'dplyr'

## The following objects are masked from 'package:stats':
##
##   filter, lag

## The following objects are masked from 'package:base':
##
##   intersect, setdiff, setequal, union

## Warning: package 'knitr' was built under R version 4.1.3

## Warning: package 'kableExtra' was built under R version 4.1.3

##
## Attaching package: 'kableExtra'

## The following object is masked from 'package:dplyr':
##
##   group_rows

## Warning in kable_styling(., full_width = T): Please specify format in kable.
## kableExtra can customize either HTML or LaTeX outputs. See
## https://haozhu233.github.io/kableExtra/ for details.

## Warning in column_spec(., 4, width_min = "20em"): Please specify format in
## kable. kableExtra can customize either HTML or LaTeX outputs. See
## https://haozhu233.github.io/kableExtra/ for details.

## Warning in column_spec(., 5, width_min = "20em"): Please specify format in
## kable. kableExtra can customize either HTML or LaTeX outputs. See
## https://haozhu233.github.io/kableExtra/ for details.
```

Table 1: Habitat Suitability Indices for Spawning Adult Alewives

	Variable	Parameter	Range	HSI	Formulas
Spawning Adults	A	Temperature	$temp_C = 0 - 8$	0	$0 + (0.0625 * temp_C)$
			$temp_C = 8 - 12$	0.5	$-0.5 + (0.125 * temp_C)$
			$temp_C = 12 - 16$	1	$1 + (0 * temp_C)$
			$temp_C = 16 - 22$	1	$2.33 + (-0.0833 * temp_C)$
			$temp_C = 22 - 27$	0.5	$2.26 + (-0.0800 * temp_C)$
			$temp_C = 27 - 30$	0.1	$1.00 + (-0.0333 * temp_C)$
	B	Depth	$temp_C = 30+$	0	$0 + (0 * temp_C)$
			$depth_m = 0 - 2$	0	$0 + (0.005 * depth_m)$
			$depth_m = 2 - 10$	0.5	$0.38 + (0.0625 * depth_m)$
			$depth_m = 10 - 20$	1	$1.5 + (-0.05 * depth_m)$
			$depth_m = 20 - 50$	0.5	$0.5 + (0.0 * depth_m)$
			$depth_m = 50 - 100$	0.5	$0.5 + (0.0 * depth_m)$

Variable	Parameter	Range	HSI	Formulas
C	Salinity	$depth_m = 100+$	0.5	$0.0 + (0.005 * depth_m)$
		$sal_{psu} = 0 - 0.5$	1	$1 + (0 * sal_{psu})$
		$sal_{psu} = 0.5 - 5$	1	$1 + (0 * sal_{psu})$
		$sal_{psu} = 5 - 15$	1	$1.25 + (-0.05 * sal_{psu})$
		$sal_{psu} = 15 - 20$	0.5	$2.0 + (-0.1 * sal_{psu})$
		$sal_{psu} = 20+$	0	$0 + (0 * sal_{psu})$
D	Flow Velocity	$vel(m/s) = 0 - 0.3$	1	$1 + (0 * vel_{m/s})$
		$vel(m/s) = 0.3 - 1.5$	1	$1.13 + (-0.4167 * vel_{m/s})$
		$vel(m/s) = 1.5 - 3.5$	0.5	$0.65 + (-0.1 * vel_{m/s})$
		$vel(m/s) = 3.5 - 4.5$	0.3	$1.35 + (-0.3 * vel_{m/s})$
		$vel(m/s) = 4.5+$	0	$0 + (0 * vel_{m/s})$
E	Substrate		Substrate	

Juvenile Alewives

Figures & Tables

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