Atlantic Silverside Spawning Phenology in Response to Warming Temperature Cues in Casco Bay

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ABSTRACT

Atlantic silversides (*Menidia menidia*) are a key forage fish along the east coast of North America. They are known for their responsiveness to environmental cues, like temperature, as a result of their rapid growth and short lifespans. Using Casco Bay Aquatic Systems Survey (CBASS) data collected from 2014 to 2023, this study examines how the spawning phenology of silversides is changing in the Gulf of Maine, an area of intense warming. Analysis of these data revealed that from 2014 to 2023, the timing of silverside spawning shifted to be 5 to 10 weeks earlier in the year. Spawning peaked anytime between week 9 and 15, which represents dates from early March to the end of April. This is earlier than spawning times expected for the Gulf of Maine, in which silversides have been observed spawning from May to July. The earlier shift in silverside spawning has benefits and costs, as it allows for a longer growing season, but could cause phenological mismatches with primary food sources like plankton. These findings highlight the complex tradeoffs that climate change causes to marine ecosystems. They also reveal the importance of long-term monitoring as a way to inform the management of marine species.

INTRODUCTION

This study investigates how climate change, specifically rising ocean temperatures, is affecting the spawning phenology of Atlantic silversides (*Menidia menidia*; hereafter, silverside) in the Gulf of Maine. Silversides are an ecologically important species found along the eastern coast of North America. They play a crucial part in the food web, serving as prey to a variety of species such as larger fish and seabirds. Their high abundance supports higher trophic levels, and they significantly contribute to the biomass of waters of the western Atlantic. Silversides are often studied as ecological indicators of climate change as they have short lifespans and rapid growth rates. Global climate change has driven sea surface temperatures in the Gulf of Maine to increase faster than 99% of all other ocean ecosystems (Pershing et al., 2015). As a result, the dynamics of marine ecosystems are changing at unprecedented rates. Understanding the impacts of climate change to marine community ecology is critical, and silversides will be useful indicators of the magnitude and direction of these impacts.

Silversides have a well-documented life history. They are annual spawners, and most silversides only live up to one year. They spawn in the late spring and early summer in shallow nearshore waters and then rapidly grow until they migrate to the inner continental shelf over winter to find warmer waters (Conover & Ross, 1982). Fewer than 1% of each cohort survives the winter and returns to nearshore regions to spawn in the next spring (Conover & Murawski 1982, Conover, 2025). Because reproduction happens only once in their lifetime for most individuals, the timing and success of each spawning season plays an important role in silverside population size.

Silverside spawning is influenced by both lunar phases and sunlight. Many studies have observed maximum silverside spawning during high tides (Conover & Kynard, 1984, Middaugh et al., 1984, Middaugh, 1981). In particular, it has been found that spawning is common with new and full moons, when spring tides occur (Conover & Kynard, 1984). It has also been observed that maximum spawning occurs in the hours right after sunrise, suggesting that spawning may be linked to the amount of sunlight (Middaugh et al., 1984).

In the Gulf of Maine, silversides typically spawn during early summer, from May to July, suggesting that spawning cues are temperature-dependent (Conover & Ross, 1982). According to a paper looking at silverside spawning habits in Massachusetts, spawning temperatures in the field ranged from 9-21°C (Conover & Kynard, 1984). Another field study found that silverside spawning started at a minimum water temperature of 16 °C and a maximum water temperature of 29-30°C (Middaugh, 1981). As environmental cues that regulate silverside spawning, like ocean temperatures, change in Gulf of Maine spawning areas like Casco Bay, the timing of silverside spawning could shift.

While it is known that environmental cues like temperature impact silverside spawning, it is not known exactly how temperature changes spawning phenology. In a rapidly warming environment, understanding these changes is crucial. It is predicted that the warming waters will result in earlier silverside spawning. By using weekly length distributions of Atlantic silversides sampled in the Gulf of Maine from 2014-2023 to back-calculate spawning dates, this study aims to determine the impacts of recent warming on Atlantic silverside spawning phenology.

METHODS

The data used for this project were pulled from the Casco Bay Aquatic Systems Survey (CBASS), a program run by the Gulf of Maine Research Institute (GMRI) that monitors species relative abundance at 12 sites from the Presumpscot River to Trundy Point in Casco Bay, Maine (Fig. 1). CBASS data have been collected biweekly from late May to early September every year since 2014. In 2023, the Quahog Bay Conservancy joined the CBASS program and expanded spatial coverage to include an additional six sites in the eastern portion of Casco Bay. CBASS sampling is conducted using a 45.7 m long, 2.4 m tall seine net constructed of 4.8 mm knotless delta-style nylon mesh with a 2.4 m by 2.4 m by 2.4 m bag. The seine was deployed in nearshore shallows using a small Carolina skiff. At each site, one person held the end of the net on shore while the boat backed up. As the boat backed up, two other people slowly flaked the net out. When the net unfolded to the point of the bag the boat then looped back to shore, and a second person held the other end of the net. Each set was conducted so the ends of the net were approximately 20m apart. Next, the net was checked for any snags and rocks and corrected if needed to ensure a good set. The two people on shore then slowly pulled the float line of the net in while each working their way inward to the center of the net. When the bag reached the shoreline, the bottom lead line was pulled in until the end of the bag reached the shoreline. All fish were then collected out of the net and identified. The length of the first 25 fish for each species were recorded, and all individual fish after 25 were counted and recorded without being measured.

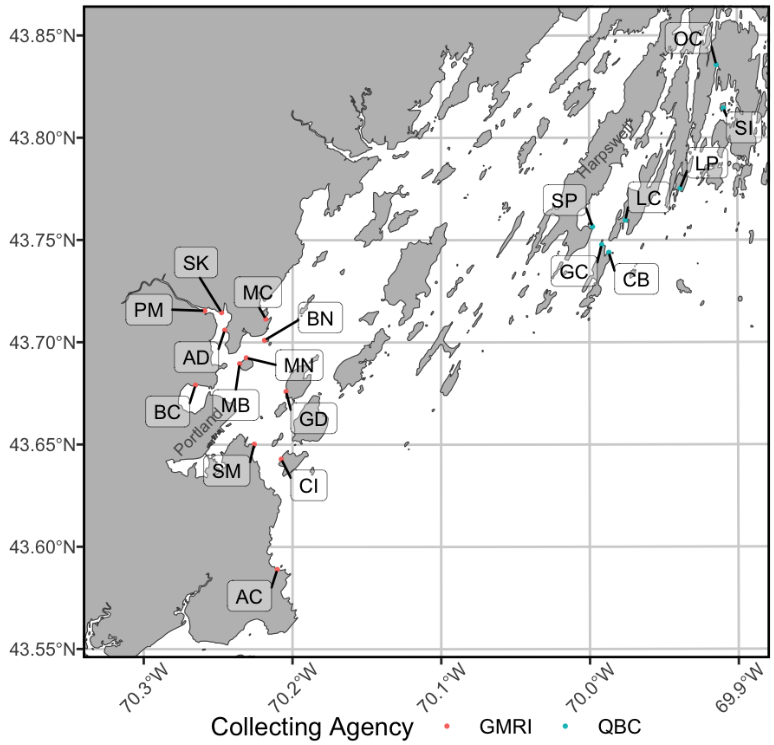

Figure 1. Map of CBASS seine sites in Casco Bay.

This study used CBASS data from 2014 to 2023. Data from 2019 were excluded as funding constraints limited the number of seines conducted. Length data were first filtered to only include silversides. To isolate newly spawned juvenile silversides (age-0), a mixed distribution modeling approach was applied to distinguish them from older individuals.

To assess the growth rates of age-0 silversides for each year, a linear regression was applied. A linear model was used because only a small period of growth was being evaluated, limiting the applicability of more common logistic growth models. Length of selected age-0 silversides per week supported the use of a linear model (Fig. 2). Variance of length distributions was not consistent over any year. Therefore, a weighted least squares regression approach was used to estimate weekly growth rates in millimeters for silversides. The next step was to back-calculate from observed lengths to get the predicted hatch date of silversides for each year. Studies show that silversides are 4-6 mm post-hatch, so we used our modeled growth rates and observed lengths to determine the date silversides were a length of 5 mm (Bengtson et al 1987).

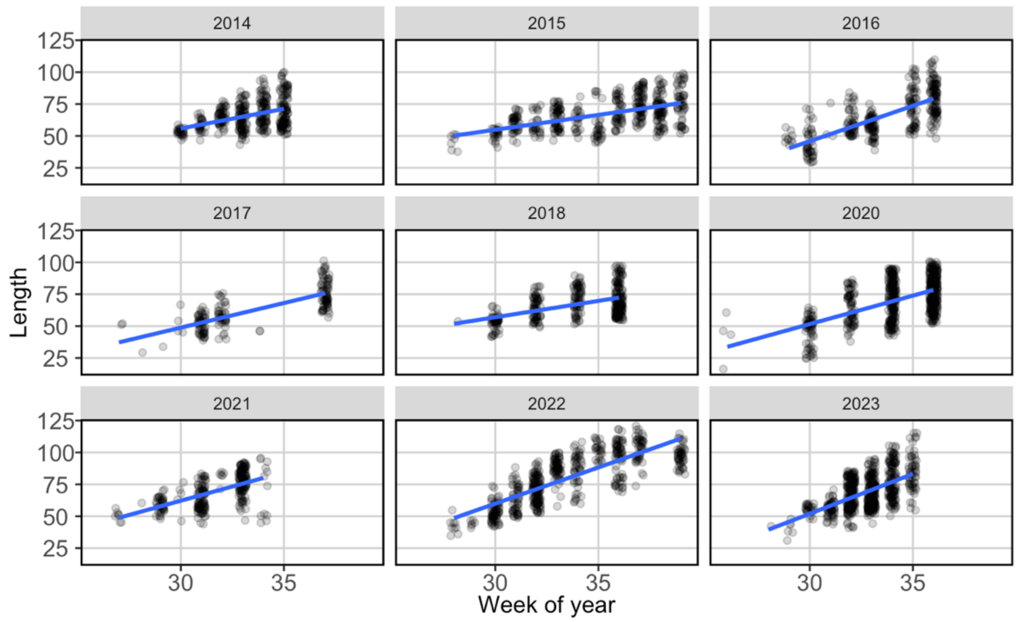

Figure 2. Length of age-0 silversides caught by CBASS surveys from 2014-2023 (excluding 2019), highlighting a linear relationship between length and week of the year.

To find optimal silverside spawning times, sunrise and high tide times for Portland, Maine were extracted for each year. Portland was selected as the example location because it is centrally located among study sites. The difference in tide times and sunrise times between the east and west edges of Casco Bay is on the order of minutes, which is unlikely to have a significant ecological impact. We identified optimal spawning conditions (daylight high tides) that occurred up to three weeks before the estimated silverside hatch date, because previous studies showed that silversides hatched 5–20 days after being laid (The Chesapeake Bay Program, 2025). Days during this period that contained daylight high tides were retained as potential spawning dates. Next, the earliest, midpoint, and latest weeks spawning could have occurred were plotted for each year.

Finally, the relationship between spawning dates and the average surface temperature during the potential spawning period was assessed. Data from the Portland Harbor Tide Gauge (NOAA Station ID: 8418150) were used to calculate daily average Casco Bay surface water temperature in each year. Though this instrument represents only a single spatial point in Casco Bay, it is the most consistent and complete record of local water temperature. Temperature was extracted at its native 6-minute frequency. The average temperature during the potential spawning period, defined as the earliest and latest weeks of potential spawning across any year, was calculated as the average of these values. A linear regression was used to estimate how the temperature affected the average spawning week of each year.

RESULTS

Most hatching occurred between week 5 and week 25, with peak hatching times occurring between weeks 9 and 15 (Fig. 3). The distribution is right-skewed, with a long tail extending to hatch weeks as late as week 35. The year 2014 shows a broad and later distribution of hatch weeks, with a peak around week 15. In contrast, 2023 shows a narrower and earlier distribution of hatch weeks, with a peak around week 9. Overall, hatching dates show varying patterns from 2014-2023 and the earlier years tend to have later and broader, hatching periods compared to the later years (Fig. 3).

Spawning times of silversides have shifted to be earlier in the year in the Gulf of Maine in the past 10 years. The average spawning week has shifted earlier by about 5 weeks from 2014 to 2023 (Fig. 4). In recent years such as 2021–2023, a greater proportion of silversides spawned earlier in the season, with the peak occurring as early as weeks 9–12. In the earlier years such as 2014–2016, the peak was around weeks 14–17 (Fig. 4). To put this into dates on the calendar, peak silverside spawning in earlier years such as 2014-2016 occurred in mid-April to early May, while peak spawning in recent years such as 2021-2023 was predicted to occur in early to late March. This suggests a phenological shift towards earlier silverside spawning over the years.

There is a significant negative relationship between average spring sea surface temperature and spawning week ($F_{1,7}$=9.40, p=0.018). The slope of this significant relationship indicates that for every degree Casco Bay spring surface waters warm, average silverside spawning week will be about 4 weeks earlier. As Casco Bay spring surface temperatures increased from about 4.8 °C to 7.0 °C from 2014 to 2023, the mean spawning week got pushed earlier in the year by almost 10 weeks (Fig. 5).

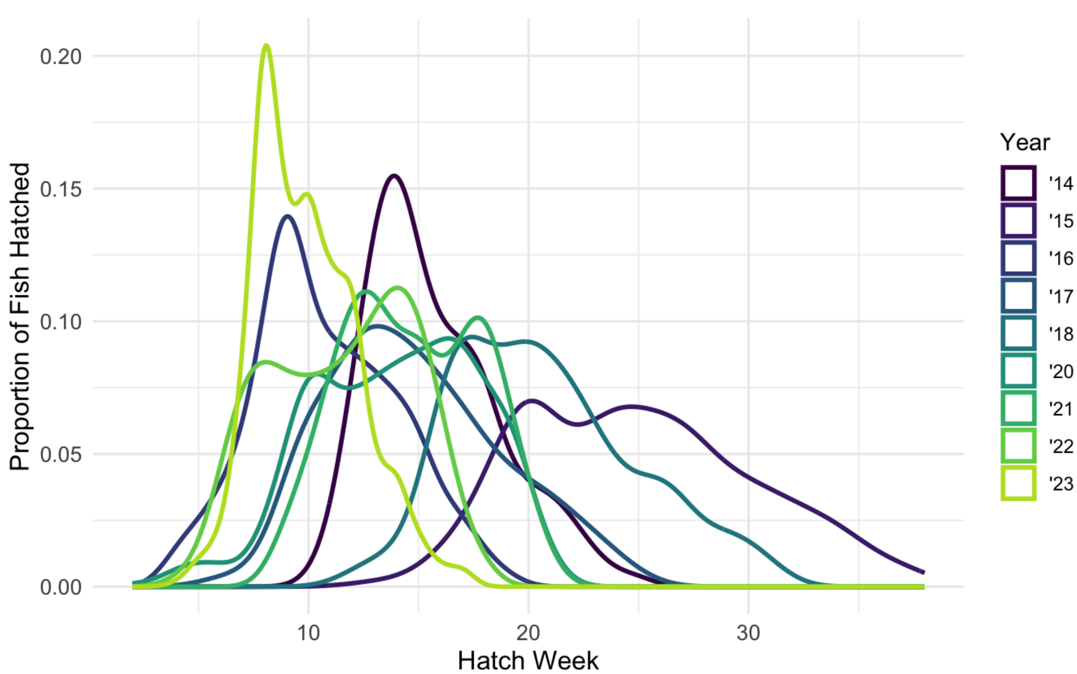

Figure 3. Weekly hatch distribution of Atlantic silverside from 2014-2023 (excluding 2019). Colors represent years from 2014 (dark purple) to 2023 (light green).

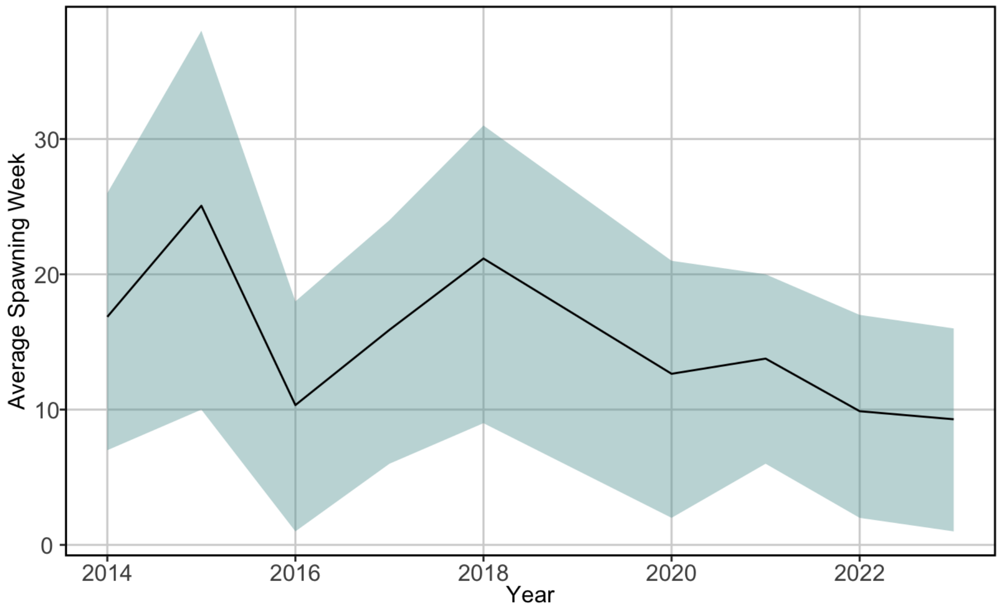

Figure 4. Predicted average spawning weeks from 2014 to 2023 with regard to optimal spawning conditions such as high tides during daylight. The blue shaded region represents the 95% confidence interval.

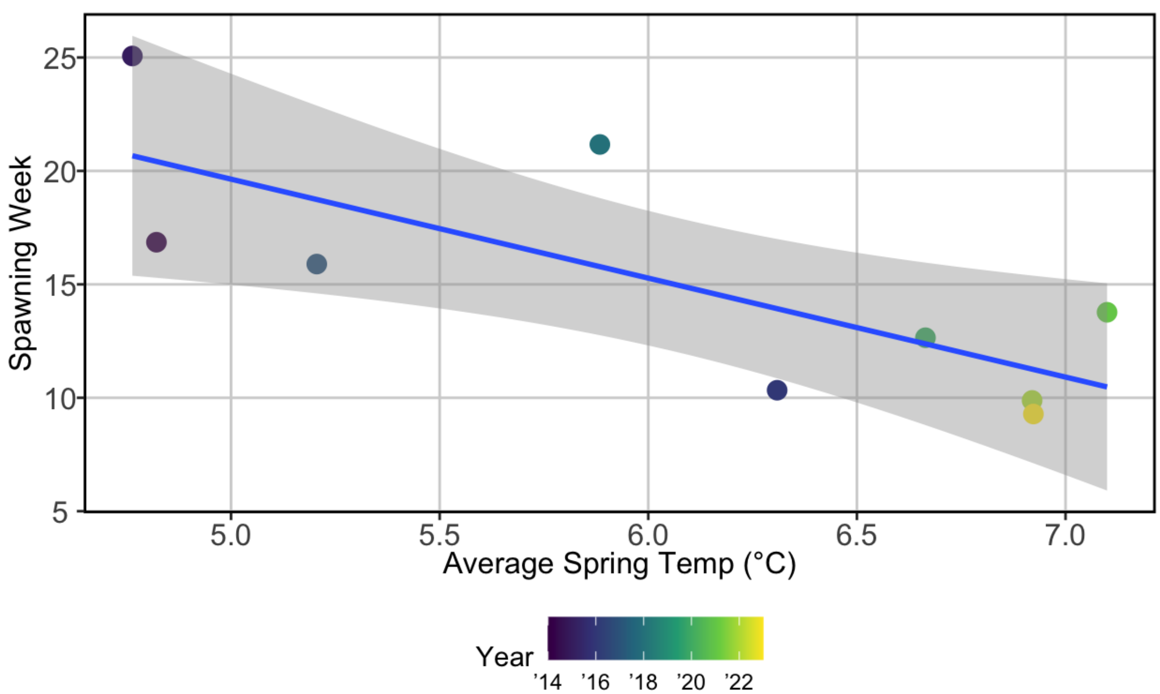

Figure 5. Relationship between average spring sea surface temperature (°C) for each year, and the estimated spawning week of Atlantic silversides from 2014 to 2023. Each point represents a year, colored according to time from 2014 (dark purple) to 2023 (yellow). The blue regression line indicates a significant negative relationship, with earlier spawning associated with warmer spring temperatures. The shaded gray area represents the 95% confidence interval.

DISCUSSION

From 2014 to 2023, the average spawning week pushed forward by about five to ten weeks, with recent peak spawning occurring in early to late March compared to mid-April to early May in earlier years (Fig. 4). This shift is driven by the strong negative correlation between temperature and spawning week (Fig. 5).

These findings are consistent with previous research, suggesting that silverside spawning is greatly impacted by environmental cues such as temperature (Conover & Kynard, 1984; Middaugh et al., 1984). The trend towards spawning earlier in the spring coincides with the rapid increase in ocean water temperatures in the Gulf of Maine, an area that has experienced some of the highest warming rates in the world (Pershing et al., 2015). As seen in Figure 5, for every 1°C increase in average spring sea surface temperature, the average silverside spawning week shifts earlier by about four weeks, which is an ecologically significant change in spawning phenology.

While the direction of the predicted phenological spawning timing is consistent with what has been observed in other marine fishes, the magnitude of change may be exaggerated. There are physiological limits to how early silversides can successfully spawn. Spawning too early in the year may expose larvae to suboptimal temperatures, leading to high larval-to-juvenile mortality and a decline in the silverside population. In addition, early spawning may lead to limited food availability and could increase predation risk due to phenological mismatches with other species in the ecosystem (Cushing, 1990). However, earlier spawning during years when spring conditions support larval growth could be advantageous, as it could provide silversides with longer growing seasons which they can use to increase their size before winter, increasing winter survival rates (Conover & Ross, 1982). It is this tradeoff between the benefits of a longer growing season and the risk of limited food availability and high predation that looms over the silverside population as the climate continues to change.

Silverside spawning events have not been recorded in the Gulf of Maine as early as our projections would indicate. There are limitations to our approach, and some model assumptions can be improved. One assumption made that may not be true was that silversides grow at a consistent rate from hatch. Assuming a uniform growth rate across all silversides ignores the genetic and environmental variations that can cause uneven growth rates. For example, there is a study that suggests silversides from northern latitudes have higher growth rates than those from southern latitudes so they can compensate for their shorter growing season (Conover & Present, 1990). This reveals that growth rates are not just influenced by temperature, but they can also be influenced by genetic differences which lead to inconsistent growth rates. In addition, this study assumed that food resources and water temperatures across the spatial and temporal of an entire spring were consistent, which may not be true.

Understanding spawning phenological shifts is essential for fisheries management. It is particularly important to understand the reproductive phenology of silversides and other forage fishes as they play a crucial role in coastal food webs. Looking in the short term, spawning earlier in the year may increase growth opportunities and winter survival. However, long-term outcomes of phenological shifts in spawning depend on how these shifts align with food availability and predator presence. If phenological mismatches develop, the availability of silversides to their predators could change, which would impact higher trophic levels including commercially important fish.

This study highlights the importance of long-term monitoring programs like CBASS. By tracking species' responses to environmental changes over time, programs like CBASS can give us insight into how a species' population dynamics and phenology change. This will reveal how different marine ecosystems will be reshaped by climate change. Continuing to monitor marine ecosystems in the future is essential and will determine how managers make decisions to ensure the longevity of coastal biodiversity.

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WORKS CITED

Conover, & Murawski. (1982). Offshore winter migration of the Alantic silverside, Menidia menidia. *Fishery Bulletin United States, National Marine Fisheries Service*, *80*. https://agris.fao.org/search/en/providers/123819/records/64735d4053aa8c896309351d

Conover, D. O., & Ross, M. R. (1982). Patterns in seasonal abundance, growth and biomass of the atlantic silverside, Menidia menidia, in a New England estuary. *Estuaries*, *5*(4), 275–286. https://doi.org/10.2307/1351750

Conover, D. O., & Kynard, B. E. (1984). Field and laboratory observations of spawning periodicity and behavior of a northern population of the Atlantic silverside, Menidia menidia (Pisces: Atherinidae). *Environmental Biology of Fishes*, *11*(3), 161–171. https://doi.org/10.1007/BF00000462

Conover, D. O., & Present, T. M. C. (1990). Countergradient variation in growth rate: Compensation for length of the growing season among Atlantic silversides from different latitudes. *Oecologia*, *83*(3), 316–324. https://doi.org/10.1007/BF00317554

Conover, D. O. (2025). The extraordinary Atlantic silverside and me. *ICES Journal of Marine Science*, *82*(2), fsae136. https://doi.org/10.1093/icesjms/fsae136

Cushing, D. H. (1990). Plankton Production and Year-class Strength in Fish Populations: An Update of the Match/Mismatch Hypothesis. In J. H. S. Blaxter & A. J. Southward (Eds.), *Advances in Marine Biology* (Vol. 26, pp. 249–293). Academic Press. https://doi.org/10.1016/S0065-2881(08)60202-3

Middaugh, D. P. (1981). Reproductive Ecology and Spawning Periodicity of the Atlantic Silverside, Menidia menidia (Pisces: Atherinidae). *Copeia*, *1981*(4), 766–776. JSTOR. https://doi.org/10.2307/1444176

Middaugh, D. P., Domey, R. G., & Scott, G. I. (1984). Reproductive Rhythmicity of the Atlantic Silverside. *Transactions of the American Fisheries Society*, *113*(4), 472–478. https://doi.org/10.1577/1548-8659(1984)113<472:RROTAS>2.0.CO;2

Pershing, A. J., Alexander, M. A., Hernandez, C. M., Kerr, L. A., Le Bris, A., Mills, K. E., Nye, J. A., Record, N. R., Scannell, H. A., Scott, J. D., Sherwood, G. D., & Thomas, A. C. (2015). Slow adaptation in the face of rapid warming leads to collapse of the Gulf of Maine cod fishery. *Science*, *350*(6262), 809–812. https://doi.org/10.1126/science.aac9819

The Chesapeake Bay Program. (2025). *Atlantic Silverside*. https://www.chesapeakebay.net/discover/field-guide/entry/atlantic-silverside