Time-lagged Environmental Signals Impact Juvenile Atlantic Herring Abundance in Casco Bay, ME

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Abstract

Atlantic herrings (*Clupea harengus*) are an economically and ecologically important resource in the Gulf of Maine. As a result of overfishing and climate change, herring relative abundance is currently in decline. There are mixed interpretations within the scientific community of how environmental signals impact herring physiology, distribution, and abundance over time, and little data specific to the juvenile life stages. Using data sourced from the Casco Bay Aquatic Systems Survey (CBASS) program run by the Gulf of Maine Research Institute, time series analyses were performed to understand potential time-lagged effects of various environmental variables on juvenile Atlantic herring abundance. Abiotic covariates such as sea surface temperature (SST) and Atlantic multidecadal oscillation (AMO), and biotic covariates such as adult herring spawning stock biomass (SSB) and zooplankton abundance, were each analyzed to identify the length of time it takes for changes in conditions to impact juvenile herring abundance. Ultimately, significant positive relationships at a lag of one year were established between juvenile herring abundance and SSB, as well as between juvenile herring abundance and large copepod abundance. Significant negative correlations occurred between average Casco Bay summer and annual temperatures at a lag of 3 years, and annual average AMO at a lag of 4 years. These results indicate that time-lagged effects of various environmental conditions must be taken into account when formulating predictive models and structuring regulations surrounding this important fishery.

Introduction

The small-bodied Atlantic herring (*Clupea harengus*) is an ecologically and economically valuable schooling fish found in the North Atlantic Ocean (Bekkevold et al. 2023). As a prominent prey source, Atlantic herring play a central role in supporting trophic interactions between primary producers and high-level consumers (Trochta et al. 2020). This species can be found in much of the summer and early fall off the coasts of Maine, Nova Scotia, and Georges Bank, where it is distributed into at least three spatially and temporally distinct spawning populations (Kelly 1986, Farrell et al. 2022). Within the Gulf of Maine, Atlantic herring have served as the main source of bait for the lobster industry, with 70-90% of total herring landings sold to support the fishery as recently as the early 2000s (Stoll et al. 2022). However, the Gulf of Maine herring population has drastically declined in the last few decades. Several biotic and abiotic factors have been proposed as drivers of this change, including increased fishing pressure (Stoll et al. 2022).

In addition to increased fishing pressure, Atlantic herring are also impacted by changing environmental conditions. The Gulf of Maine region in particular has experienced rapid change as a result of northward incursions of the Gulf Stream, increased development of warm-core eddies off the Gulf Stream, and the slowing of the Atlantic Meridional Overturning Current (AMOC) (Saba et al. 2016, Caesar et al. 2021). Linked to AMOC, the Atlantic multidecadal oscillation (AMO) is a cyclical mode of temperature anomalies in the Atlantic Ocean. With a 0.4°C range between the 60-75 year cycles, AMO impacts a wide range of atmosphere-ocean dynamics and has been linked to modulating patterns of migration in highly transitory species such as Atlantic herring (Nye et al. 2014).

While herring are impacted by temperatures and AMO fluctuations throughout the duration of their life span, physiological impacts present differently depending on their life stage. Positive AMO, which has occurred since 1999, is correlated with weak recruitment years in Norwegian spring-spawning herring in which larval herring experienced increased temperatures during lifestage transitions (Tiedemann et al. 2021). Historical records show that in the 1930s, when AMO was last in a positive phase in European waters, Atlantic herring experienced increased egg production as a result of increased temperatures (Nye et al. 2014). A study looking at adult Atlantic herring populations using mean length-at-age 4 data indicated that herring experience decreased growth in response to a warming environment, with populations in the southern limits of the species range exhibiting slower growth rates than those in cooler, northern latitudes (Beaudry‐Sylvestre et al. 2024).

Not only do environmental conditions impact herring physiological functioning directly, they also destabilize the food webs that herring rely on. In the Gulf of Maine, warming waters have been associated with a decline in the zooplankton *Calanus finmarchicus*, an important prey species for herring and many other marine organisms (Prokopchuk & Sentyabov 2006, Pershing et al. 2021, Randall et al. 2022). Other zooplankton prey species, like euphausiids, have shifted their distributions northwards, particularly in spring months (Lasley-Rasher et al. 2015). This may cause a mismatch in the spatiotemporal distributions of herring and their prey. Although decreasing Atlantic herring recruitment has occurred concurrently with these abundance declines and distribution shifts in prey items, few studies have provided direct evidence that these trends can be attributed to one another (Pershing et al. 2021).

The combined effects of biotic and abiotic factors can culminate in changes in the Atlantic herring spawning stock biomass (SSB). As oceanic conditions shift in the Gulf of Maine, factors such as larval drift, growth rates, and survival are all impacted and may influence SSB over the course of years and decades (Ojaveer et al. 2021). As SSB and survival, both drivers of population collapse and recovery, are closely associated with one another, understanding how spawning stock biomass may vary over the scale of years is important when assessing how climate change may impact this valuable fishery in the future (Ojaveer et al. 2021). Comparing metrics of Atlantic herring spawning stock biomass to collected data of juvenile herring abundance is particularly valuable as juvenile phenotypic changes during this life stage have been shown to have a disproportionate impact on life-time egg production in the species (Beaudry‑Sylvestre et al. 2024).

Although much is known about how these various environmental and biotic conditions impact Atlantic herring in larval and adult life stages, few studies investigate how climate change and warming in the Gulf of Maine impact juvenile Atlantic herring. Previous studies have established a relationship between metabolic rate and temperature in juvenile Atlantic herring, with metabolic rates increasing between 9 and 14°C, optimum temperature for metabolism between 15 and 16°C, and metabolic rate decreasing with further temperature increases (Bernreuther et al. 2013). Metabolic rate and spawning are also known to be closely related, with faster growing individuals spawning at year 1 compared to those growing slower spawning at year 2 or 3 (Brophy & Danilowicz 2003).

Despite the known impacts of these factors on herring abundance and growth, few studies have investigated how biotic and abiotic variables may impact juvenile herring throughout different time scales. As the causes of the recent herring population collapse are still under investigation, exploring how a changing climate may impact the understudied juvenile stages may highlight the existence of a bottleneck at this stage, which would prevent recruitment to the adult population. This research aims to understand the relationship between juvenile herring population dynamics and a variety of biotic and abiotic signals by performing time series analyses using 11 years of abundance data of Atlantic herring collected within Casco Bay, ME. Associations between variables such as sea surface temperature (SST), zooplankton abundance, SSB, AMO, and Atlantic herring abundance in Casco Bay are expected to become apparent only when aggregated over the scale of years. Biotic factors may have significant correlations at shorter lags. Abiotic factors may only have significant correlations at lags of 3-4 years, which may indicate an indirect effect through action on the parent generation.

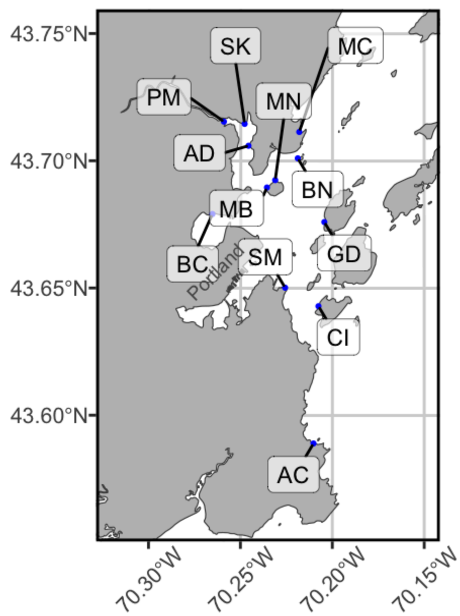

Figure 1. Casco Bay Aquatic Systems Survey (CBASS) sites sampled annually from the years 2014 to 2024 in Casco Bay, Maine US.

Methods

Field Data Collection

Field data was sourced from the Casco Bay Aquatic Systems Survey (CBASS), a summer beach seining program launched in 2014 by the Gulf of Maine Research Institute. The project encompasses 12 sites throughout the western half of Casco Bay, with sampling locations along the coast from the Presumpscot River mouth to just north of Trundy Point, Cape Elizabeth, Maine (Figure 1). Sampled every 2 weeks from early summer through early fall, sites vary in salinity and substrate material from fine-grain mud to coarse gravel.

Samples of organisms were taken using a 45.7 m long and 2.4 m tall seine with a central 2.4 m^3 bag. Outfitted with 4.8 mm knotless delta-style nylon mesh, the seine had lead weights installed at the bottom line and spongex floats on the top. At either end of the seine was a bridle with 2 m of excess line extending from the net. The seine was deployed in a U-shaped fashion using a skiff, with one end anchored to shore as the net was flaked off the bow until returning to shore with 20 m between the two ends on the beach. At this point, two researchers at either end of the seine hand-hauled the net to shore, ensuring the bag was at least partially immersed in water to limit specimen mortality. Tidal stage was recorded and the greatest depth sampled was limited to 1.5 - 2.2 m. Seine contents were sorted and target species were counted with the first 25 individuals of a given species being measured before release. Once seine operations were concluded, general weather conditions were recorded and sea surface temperature, salinity, and oxygen concentration were measured using a YSI multiparameter sonde.

For each year of the survey program, juvenile Atlantic herring annual catch per unit effort was calculated as the total number of herring observed divided by the total number of seine hauls conducted. All herring captured in seining efforts were between 14 and 139 mm long. As most herring within the Northeast US continental shelf large marine ecosystem reach 160 mm total length by the end of their first year and 275 mm by the time they sexually mature (Boyar 1968), the smaller size of our sampled herring suggests that they are all likely to be recently spawned individuals. Since this means they would all be less than 1 year old, there is no need to subset our data to include only juveniles.

Environmental Data

Prey Availability

To estimate prey availability for Atlantic herring in the Gulf of Maine, data from zooplankton surveys conducted seasonally by the Northeast Fisheries Science Center, including data from the ECOMON survey program, was accessed through the Ecodata package (https://github.com/NOAA-EDAB/ecodata). From this data source, estimates for seasonal relative indices of zooplankton abundance for large species (including *Calanus* spp., *Metridia lucens*, and *Eucalanus* spp.), small species (including *Pseudocalanus*, *Centropages*, and *Temora* spp.), and euphausiids were obtained and cleaned. As data was only available for years through to 2022, herring abundances in 2023 and 2024 were not compared to this dataset.

Casco Bay SST

Due to the highly migratory nature of Atlantic herring, data for sea surface temperatures (SST) were sourced from both large spatial scales (Gulf of Maine) and finer spatial scales (nearshore Casco Bay). The Casco Bay sea surface temperature data was accessed from the Portland Harbor tide gauge deployed and monitored by NOAA (https://tidesandcurrents.noaa.gov/met.html?id=8418150). Seasonal and yearly averages were calculated, with seasons defined as the following: winter includes December, January, and February; spring includes March, April, and May; summer includes June, July, and August; and lastly, fall includes September, October, and November. Due to these seasonal distributions, and to match the beginning of an observation period to the expected timing of peak spawning, each modeled year begins on December 1st. Though the tide gauge represents only one small spatial point within the larger Casco Bay, it collects the most consistent and complete record of surface water temperatures near our seining sites.

Gulf of Maine SST

SST for the Gulf of Maine at large was sourced from the Gulf of Maine Research Institute (GMRI) annual warming update (2024 Gulf of Maine Warming Update 2025) which used NOAA OI SST V2 High Resolution Dataset data provided by the NOAA PSL, Boulder, Colorado, USA, from their website at https://psl.noaa.gov (Huang et al. 2021). GMRI has assembled yearly warming reports since 2021. Average annual and seasonal temperatures were calculated, with season definitions following those of the Casco Bay SST data.

Monthly AMO

Monthly AMO values were retrieved from the NOAA record of the AMO SST Index, calculated from the Kaplan SST dataset (https://psl.noaa.gov/gcos_wgsp/Timeseries/AMO/). Monthly AMO values were aggregated to find average annual AMO index values.

Data Analysis in R

Retrieved and sampled data were sorted, cleaned, and analyzed using the tidyverse (Wickham et al., 2019), forecast (Hyndman et al., 2025), and tseries packages (Trapletti & Hornik, 2020). All data were converted to time series. It was assumed that no time series had seasonality, as calculating average annual trends or seasonal average trends removed any seasonal signal present in the raw data. The auto.arima() function was used to determine the ideal p, d, and q values to achieve time series stationarity, with the Kwiatkowski-Phillips-Schmidt-Shin (KPSS) test used as the method for determining stationarity. If stationarity was not achieved after applying differencing as recommended by the KPSS test, a second attempt to achieve stationarity using the Augmented Dickey-Fuller (ADF) test and de-trending was used instead. All time series achieved stationarity using one of these methods. After doing so, cross correlation functions were run to detect statistically significant relationships between juvenile Atlantic herring abundances found in the aforementioned CBASS sampling and various abiotic and biotic factors. Residuals were checked for independence using the Box-Ljung test.

Results

Abiotic Variables

Juvenile Atlantic herring abundance is strongly correlated with the Casco Bay average annual temperature with a negative association at a lag of 3 years (Figure 2 and 3, cross-correlation coefficient = -0.613). Similarly, average summer temperature in Casco Bay and juvenile herring abundance had a strong, negative correlation with each other at a lag of 3 years (Figure 3; cross-correlation coefficient = -0.639). AMO was determined to have a strong, negative association with juvenile Atlantic herring abundance at a lag of 4 years (Figure 4; cross-correlation coefficient = -0.718). When average winter, spring, and fall temperatures in Casco Bay and all average seasonal temperatures in the GOM were checked for potential correlations with juvenile Atlantic herring abundances, no significant correlations were found.

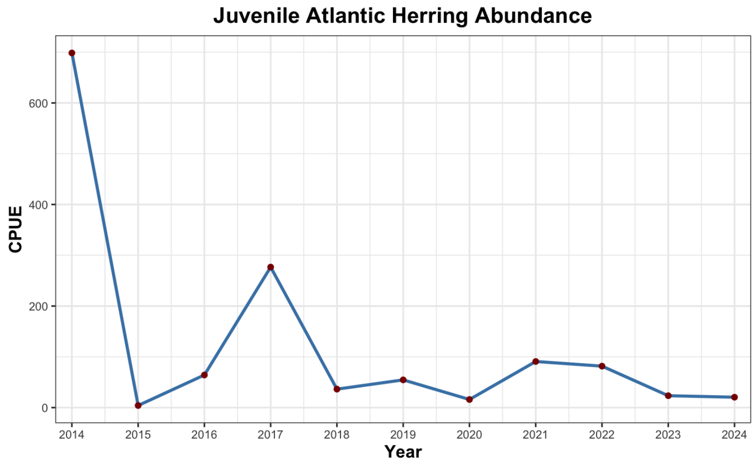

Figure 2. Yearly catch per unit effort (CPUE) of juvenile Atlantic herring as part of the GMRI CBASS study.

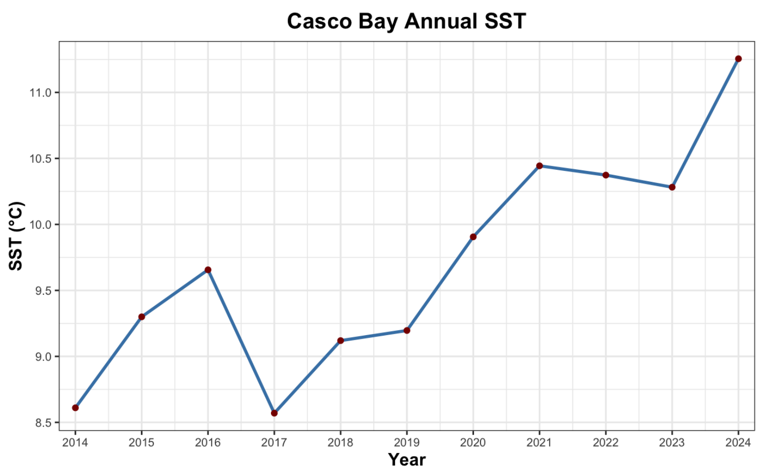

Figure 3. Casco Bay annual sea surface temperature (SST).

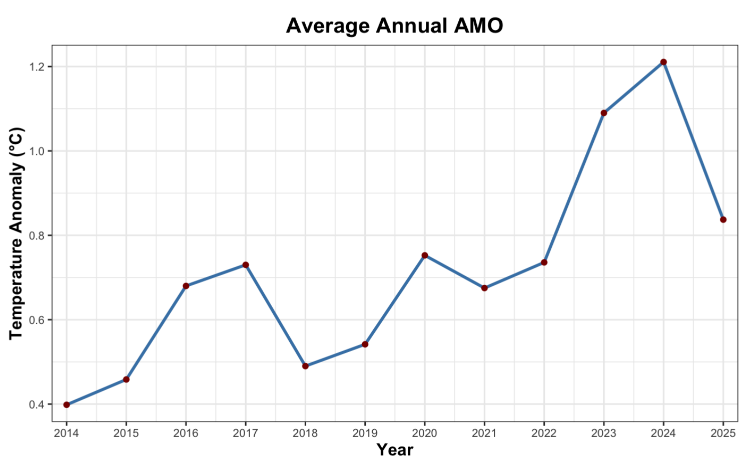

Figure 4. Average annual Atlantic multidecadal oscillation (AMO).

Biotic Variables

Atlantic herring SSB had a strong positive correlation with juvenile herring abundance at a lag of 1 year (Figure 5, cross-correlation coefficient = 0.674). Similarly, large copepod abundance and juvenile herring abundance had a strong positive correlation at 1 year (Figure 6; cross-correlation coefficient = 0.721). Correlations were not found between small prey and euphausiid abundance and Atlantic herring abundance.

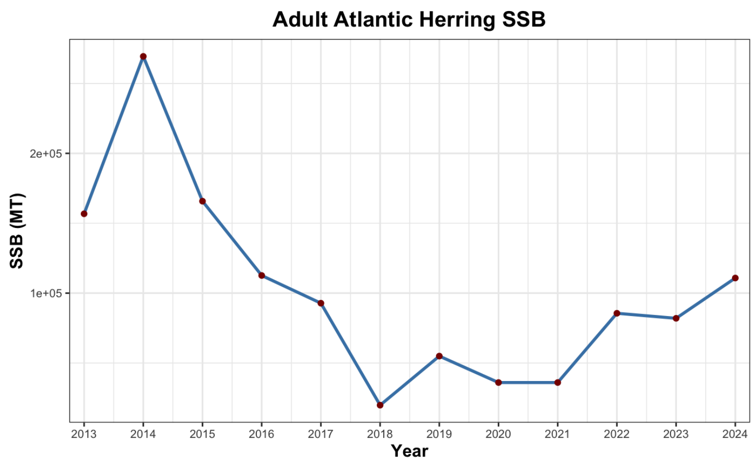

Figure 5. Yearly juvenile Atlantic herring spawning stock biomass (SSB) in the Gulf of Maine.

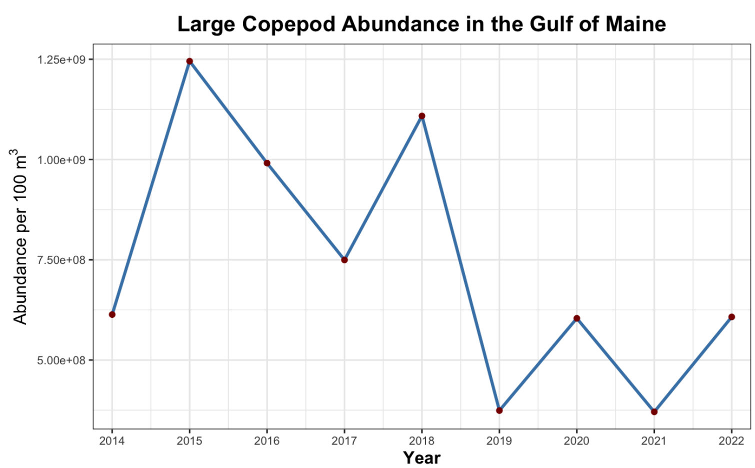

Figure 6. Yearly large copepod abundance in the Gulf of Maine.

Discussion

As the association between juvenile Atlantic herring abundance and Casco Bay average annual temperature is negatively correlated at a lag of three years, increased temperatures experienced by the parent generation appear to negatively impact juvenile herring abundance three years later (Figure 3). This is congruent with studies mentioned previously, which indicate that warmer temperatures are associated with slower growth rates (Beaudry-Sylvestre et al. 2024). Slower growth rates are in turn associated with later spawning during years three and four

(Brophy & Danilowicz 2003). This pattern of significant negative correlations at later lags is also found when comparing juvenile herring abundance in Casco Bay during the summer season, but not for other seasons. The strong negative correlation between summer temperatures and juvenile Atlantic herring abundance may be attributed to behavioral changes, such as movement towards deeper, offshore waters as a response to increased temperature pressure during the summer months (Nye et al. 2009). As spawning sites are often located in nearshore regions, adult herring may move to other spawning grounds in times of increased temperature, thus affecting herring abundances in the next generation. This impact on spawning behavior in herring may account for the longer lagged signal of 3 years.

The relationship between AMO and juvenile herring abundance had a similar correlation with a strong negative association at 4 year lag. The reason for this relationship is likely similar to that of average SST and abundance described above. As positive AMO is associated with increased SST, the effects of AMO on adult spawning herring behavior would be the same as the effects of SST on adult herring. These behavioral changes then have an indirect, trickle down effect on juvenile herring in later generations as spawning locations and migration, fertility, and growth are variables all impacted by increased temperatures (Nye et al. 2014, Beaudry‐Sylvestre et al. 2024). The later lag time of AMO compared to SST may be attributed to the length of time it takes for changes in AMO to appear in temperatures, as changes in SST temperature lags behind changes in AMO due to the inertia of the ocean (Börgel et al. 2020).

Large copepods had an expected positive correlation at a lag of one year with juvenile Atlantic herring abundance. This group includes the species' main source of prey – *Calanus* spp.. Such a signal indicates that impacts from changing prey populations and availability have direct and fast-moving impacts on herring abundances. Although the relationship between food availability and associated growth and survival of predator species has been well established, the cumulative effect of prey abundances and temperature on growth and survival is less clear. Studies have shown that temperature and food availability may jointly affect herring physiology and growth, with larval herring in a food-limited, warm environment growing slower than those grown in food-limited, cooler environments. However, this relationship was flipped in food-rich environments, with larvae exposed to cooler temperatures growing slower than those exposed to warmer temperatures (Allan et al. 2022). Further research looking into how temperature and food availability act together in impacting herring abundances across a temporal scale may be beneficial in better defining the relationship between these two variables.

Ultimately, these findings indicate that Atlantic herring continue to experience impacts from their environment years down the line. With temperatures in one year determining juvenile herring abundance three to four years later, herring have a much more nuanced and indirect relationship with SST and AMO than what can be observed in real-time. These findings call for a more nuanced approach to fisheries management in the herring industry, where population assessments and predictive models should take into account the potentially lagged effects of temperature anomalies and primary production in an area. Additionally, as SSB was found to predict juvenile herring abundance, more thought must be taken to protect SSB levels. With a strong positive lag at only one year, they have an immediate and disproportional impact on the growth of the herring population. In summary, herring have a much more complex temporal and spatial relationship with their environment than what may be assumed at face value. Together with proper action, these findings have the potential to offer insight to regulations that may strengthen a collapsing fishing industry.

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