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Charles K. Cobb

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The Impact of Climate Change on the Migration Phenology of New England’s Anadromous River Herring and American Shad

Charles K. Cobb
Environmental Studies Program
Colby College
Waterville, Maine

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ABSTRACT

Anadromous fish play important roles in food webs and nutrient cycling in both aquatic and marine ecosystems. As a result of climate change however, anadromous fish's migration timing has begun to change, with potentially deleterious consequences to both anadromous fish, and the species that depend on them. Western coastal US studies have linked earlier anadromous fish returns to warming marine temperatures and changes in river flow regimes, but the exact temperatures thresholds that anadromous fish respond to, and the relative importance of temperatures and river flows, remain somewhat unknown. Additionally, there has been relatively little research on anadromous fish phenology on the east coast, especially in the Gulf of Maine, which is warming faster than 99% of the world's oceans. This research addresses this gap by using time series datasets to determine how river discharge and marine sea-surface temperatures have altered migration timing of river herring and American shad in New England. River herring and American shad return times got significantly earlier over the 30-year study period, a trend driven mainly by the earlier onset of warming in the fish's marine habitat. River discharge was not as strongly related to migratory timing as marine temperature phenological indices, but played an important secondary role, especially in years with spring high flows. Overall, this research shows that climate change is having significant impacts on anadromous fish in New England, and highlights the need to account for climate impacts in fisheries management.

ACKNOWLEDGEMENTS

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CHAPTER I:

Phenology and Anadromous Fish

Phenology is the study of recurring seasonal events and how they relate to biological processes (Staudinger et al., 2019). In the Gulf of Maine, phenological processes include the onset/collapse of water-column stratification, the spring phytoplankton bloom, and the return/departure of migratory and anadromous fish. However, as the Gulf of Maine rapidly warms (Pershing et al., 2015), the timing of these phenological events has begun to change. Spring and fall phytoplankton blooms are happening later in the year (Staudinger et al., 2019). In the Eastern Gulf of Maine, stratification now begins about one week earlier than historical averages (Staudinger et al., 2019). Summer in the Gulf of Maine (as defined by sea-surface temperature (SST) thresholds) is also beginning earlier and ending later at a rate of about one day (earlier and later) per year (Thomas et al. 2017).

As seasons shift and temperatures warm, fish migration times and patterns are also changing (Staudinger et al., 2019). Many fish species prefer a certain temperature range, and likely use temperature cues to determine when to migrate (Henderson et al., 2017; Humston et al., 2000). In the Columbia River in Oregon, warmer spring temperatures have caused American Shad and Chinook Salmon to return to rivers earlier each year (Quinn & Adams, 1996; Keefer et al., 2008). New England alewives are also returning to rivers earlier in the spring (Staudinger et al., 2019; Ellis & Vokoun, 2009; Marjadi et al., 2019). While earlier anadromous fish return times are believed to be driven by temperature, the exact relationship between temperature and return times is still somewhat unknown. Furthermore, very little research has been conducted to determine how earlier return times may affect overall anadromous fish abundance (Staudinger et al., 2019). Relationships between earlier return times and population abundance could be very important to the future of anadromous fish populations in New England.

Impacts on Anadromous Fish in New England

Until about the mid-1800s, river herring (collectively alewives, *Alosa pseudoharengus*, and blueback herring, *Alosa aestivalis*) and American shad (*Alosa sapidissima*) were some of the most abundant anadromous fish species in New England

and played key roles in both freshwater and marine ecosystems (Hall et al., 2012; Mattocks et al., 2017; Limburg and Waldman, 2009). It is estimated that New England river herring populations were 10-20 times greater than they are today (Hall et al., 2012; Mattocks et al., 2017). American shad populations were also about an order of magnitude greater than current populations across the east coast of the United States (Limburg and Waldman, 2009).

Due to their abundance and predictable migration patterns, river herring and shad were a key food source for many larger predators. Alewives were the preferred prey of cod, haddock, white hake, and pollock, which led these species to stay in coastal waters, creating a strong coastal fishery (Ames & Lichter, 2013). When alewife populations collapsed, these predatory species all moved offshore and, due in part to lower prey concentrations, experienced population declines (Ames & Lichter, 2013). In freshwater systems, anadromous fish were prey for piscivorous freshwater fish, ospreys, cormorants, and other large waterfowl (Cronin-Fine et al., 2013; Hall et al., 2012; Mattocks et al., 2017). Anadromous fish also brought marine-derived nutrients to freshwater systems through their excretions and mortality, boosting primary and secondary production (Hall et al., 2012, Mattocks et al., 2017, Walters et al., 2009). Since the early 1800s however, anadromous fish's roles in marine and aquatic ecosystems have been greatly diminished by a massive population decline.

Anadromous fish populations were devastated by 19th and 20th century damming, to the point where anadromous species have gone locally extinct in many rivers (Limburg and Waldman, 2009, Hall et al., 2010, Moffitt et al., 1982). In the state of Maine, damming began in 1634 (Hall et al., 2010). Dams were first constructed to help transport goods from rural inland areas, which lacked sufficient roads, to coastal cities (Moffitt et al., 1982). While the pace of dam construction in New England was relatively slow at first, damming took off in the early 1800s with the growth of industrialization, and by the 1860s, damming was quite extensive (Hall et al., 2010, Moffitt et al., 1982, Limburg and Waldman, 2009). The state of Maine alone has had at least 1,356 dams built since 1630 (Hall et al., 2010). This damming drastically reduced anadromous fish's habitat, leading to a massive population decline across New England

(Hall et al., 2010; Mattocks et al., 2017). In several large New England rivers, alewife populations have decreased by 99.9% (Limburg and Waldman, 2009).

While damming and the resulting habitat loss have been the main driver of anadromous fish's decline in New England, these declines have been exacerbated by fishing. Historically, river herring and shad have been commercially and recreationally fished in both rivers and the ocean (Davis and Schultz, 2009, Kahnle and Hattala, 2010, Olney et al., 2001). Many river herring and shad are also taken as bycatch in the Atlantic herring fishery (Davis and Schultz, 2009, Kahnle and Hattala, 2010). This fishing pressure has prevented river herring and shad from recovering despite ongoing efforts since the late 1950s to build fishways on dams, and/or remove dams to expand anadromous fish habitat (Kahnle and Hattala, 2010, Davis and Schultz, 2009). In 2005, commercial fishing for shad was banned everywhere in New England except for the Connecticut River, and commercial fishing for river herring was banned in Connecticut, Massachusetts, and Rhode Island (Kahnle and Hattala, 2010, Davis and Schultz, 2009). However, likely due to bycatch and inefficient fish passage technology, these efforts have not led to a population recovery (Kahnle and Hattala, 2010, Davis and Schultz, 2009). Furthermore, the life history traits of both river herring and American Shad make them vulnerable to further population declines at the hands of climate change.

Life History

River herring are comprised of two species: alewives and blueback herring, which share many of the same habitats, life history traits, and cannot be distinguished from one another with the naked eye. The main differences between alewives and blueback herring are that alewives typically make earlier spawning runs and prefer to spawn in still waters of small ponds or lakes, whereas blueback herring prefer flowing rivers and streams (Mattocks et al., 2017; Rosset et al., 2017). All river herring are born in freshwater and spend the first 3-12 months of their lives there (Mattocks et al., 2017). They then migrate to the ocean, where they live until they reach sexual maturity at 3-6 years old (Mattocks et al., 2017). Once sexually mature, river herring return each spring, typically to their natal river/lake, to spawn. In New England, river herring usually return to the rivers sometime between March and June (Rosset et al., 2017). Once they arrive at their spawning site, river herring will spawn several times, and typically spend 1.5-2.5 months at their spawning site before returning to the sea (Rosset et al, 2017; McCartin et al., 2019). While in freshwater, river herring feed on freshwater zooplankton, smaller fish, and benthic invertebrates (Simonin et al., 2007).

While American shad's migration is similar to that of river herring, there are a few important differences. Like river herring, American shad return to their natal rivers to spawn each spring. The timing and number of times shad make this migration however, varies with latitude. In the southeastern US, shad are semelparous (they only make one migration and die after spawning), whereas in the northeastern US, shad are iteroparous, and return to the ocean after spawning to make another migration next year (Castro-Santos and Letcher, 2010). This difference in spawning patterns is due to the fact that southern rivers are warmer, which increases fish metabolism and the amount of energy that is required for migrations, but also much more stable and predictable, so a semelparous strategy maximizes fitness (Castro-Santos and Letcher, 2010). In the north, rivers are colder and require less energy to travel through, but ice-outs and spring flooding are unpredictable, so fish pursue an iteroparous strategy (Castro-Santos and Letcher, 2010). Another difference between the migrations of shad and river herring is that shad do not feed during their migrations, and only spawn for 1-2 weeks before leaving the spawning grounds (Grote et al., 2014; Carscadden and Legget, 1975).

Temperature and Migration Timing

Larval survival of both shad and river herring is determined by river temperature and flow in the months following spawning (Hasselman et al., 2013, Tommasi et al., 2015). Survival of these juveniles to recruitment age, in turn, determines overall population abundance (Hasselman et al., 2013). To ensure the survival of their larvae, river herring and shad use temperature, tidal, and river discharge cues to time their migrations (Ellis and Vokoun, 2009, Rosset et al., 2017). While the mechanisms behind this process are not yet fully understood, studies have shown that river herring tend to begin migrations when both marine and freshwater temperatures are between 9 and 13 degrees Celsius (Ellis and Vokoun, 2009, Rosset et al., 2017). However, more research is needed to confirm these findings and determine how temperature and river discharge interact to shape migration timing.

Summary of Research Goals

To investigate migratory timing of American shad and river herring, and add to the growing base of knowledge on anadromous fish phenology, this thesis investigates how warming Northwest Atlantic Ocean temperatures, variable river discharge rates, and changes in population abundance have affected return times of river herring and American shad in seven New England Rivers. Specifically, I use time-series datasets on river herring runs in the Cocheco, Exeter, Lamprey, Oyster, Taylor, and Winnicut rivers in New Hampshire and American shad runs on the Connecticut River at the Holyoke Dam in Massachusetts. I then compare these annual fish return time and abundance datasets with time-series datasets of annual marine spring and summer start dates (defined by temperature thresholds) for the entire Northwest Atlantic Continental Shelf margin from the Bay of Fundy to Chesapeake Bay (University of Maine), time-series datasets of annual Gulf of Maine SST anomaly, and time-series datasets of daily river discharge from the Connecticut, Lamprey, Oyster, and Exeter rivers (United States Geological Survey (USGS)). By comparing return times to these temperature indices and river discharge rates, this thesis sheds light on the way temperature, river discharge, and population abundance are related to shad and river herring migration timing, and quantifies how warming temperatures have affected return times.

Current Status of Anadromous Fish at the Study Sites

River Herring in New Hampshire Rivers:

Like most New England rivers, the six New Hampshire rivers were dammed by the late 1800s, devastating anadromous fish populations (Patterson et al., 2016). As scientists and fisheries managers have begun to recognize anadromous fish’s importance as a forage fish for larger piscivorous fish and as a key transporter of nutrients between marine and freshwater systems however, there have been many efforts to help river herring recover. On the New Hampshire rivers, fishways were constructed on the dams from the 1950s to the 1970s to allow river herring to return to their original and optimal spawning grounds (Patterson et al., 2016). Since the 1970s, river herring populations have increased on the two largest New Hampshire rivers (the Cocheco and Lamprey rivers, *Figure 1*), and these rivers now have the largest river herring populations of all the New Hampshire rivers (Piscataqua Region Estuaries Partnership (PREP), 2018). Despite this, total river herring population across all six rivers has steadily declined since the 1970s (PREP, 2018).

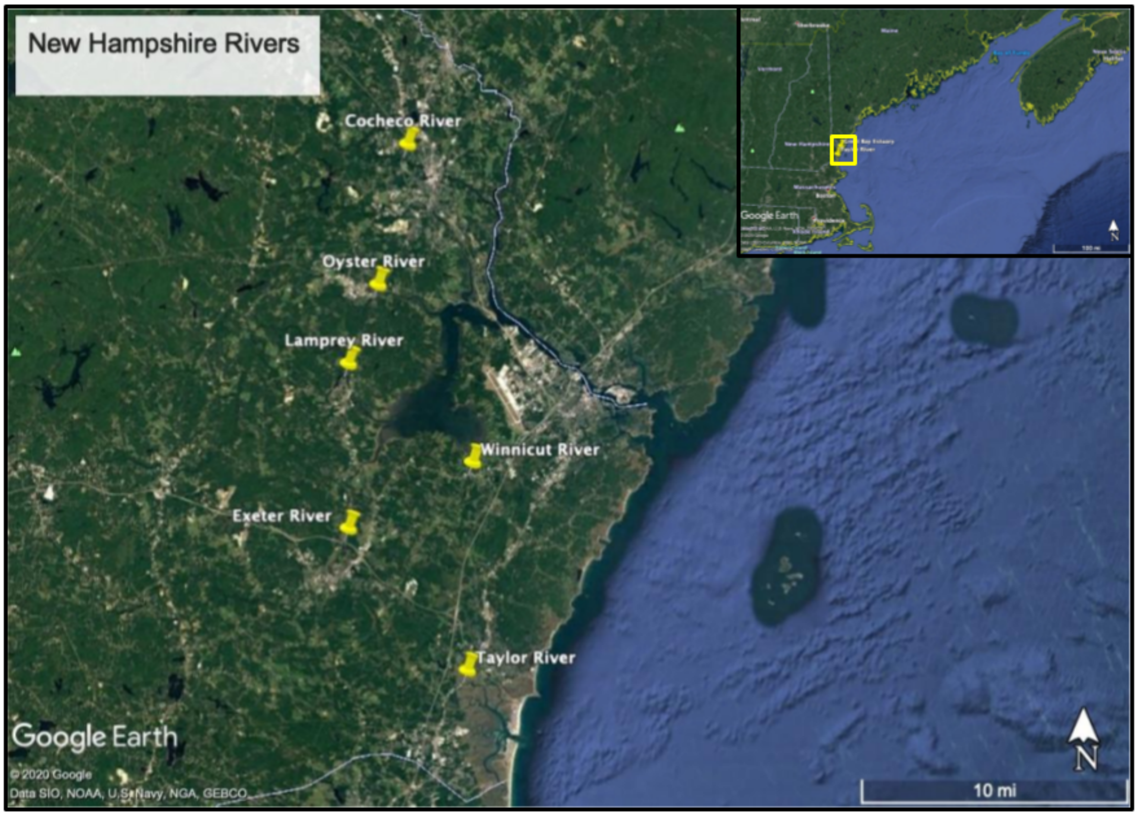


Figure 1: The Gulf of Maine (inset) and the six New Hampshire rivers from the river herring dataset. Thin blue lines represent state borders, and the placement of the pins roughly represents the data collection points. All the rivers outlet into the Great Bay estuary near Portsmouth, New Hampshire along the New Hampshire-Maine border, except for the Taylor River which outlets further south.

Connecticut River Shad

The Connecticut River is the longest and largest river in New England, and prior to damming, supported an abundant shad population that typically traveled from Long Island Sound to Southern Vermont during spawning runs (Moffitt et al., 1982). The

Connecticut river was first dammed in 1798, and was dammed more extensively throughout the 1800s, ultimately limiting shad to the lower 110 km of the river (Moffitt et al., 1982, Leggett et al., 2004). This habitat loss drastically reduced shad population (Moffitt et al., 1982). In the late 1970s however, the Enfield Dam was removed and fish-lifts were constructed at the Holyoke Dam, giving shad access to 198 km of river habitat (Leggett et al., 2004). Despite this, shad populations have yet to recover (Leggett et al., 2004).

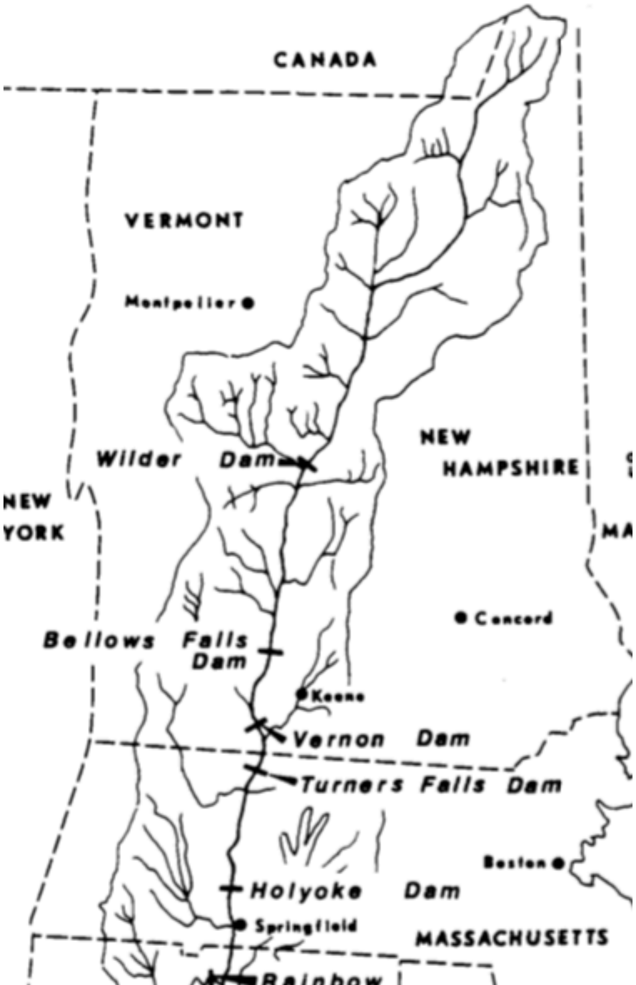


Figure 2: Connecticut River and tributaries. The first dam was the Turners Falls Dam, constructed 198 km from the mouth of the river in 1798. Today the first dam on the river

is the Holyoke Dam at 140 km from the mouth of the river. *Taken from Moffit et al., 1982*.

Broader Significance

River herring and American shad's importance as forage fish and in nutrient exchanges between freshwater and marine ecosystems combined with their declining populations make them very important species to monitor. Range-shifts and/or earlier or later runs of river herring and american shad could hurt species that rely on predictable river herring and shad runs as a foodsource. Such shifts could also have implications for how the fisheries are managed, especially if there are geographical or time of year restrictions on fishing. Additionally, the effects of warming temperatures and earlier return times on anadromous fish abundance are unknown, and it's possible that these climatic changes could be preventing shad and river herring from recovering. With this project I hope to add to ongoing efforts to restore anadromous fish populations in coastal New England and incorporate climate change into fisheries management.

CHAPTER II:

Introduction:

Over the past decade, the Gulf of Maine has warmed faster than 99% of the world's oceans (Pershing et al., 2015). This rapid warming has had a significant effect on the timing of the Gulf of Maine's phenological processes. Spring and fall phytoplankton blooms are occurring later and later each year, and in the Eastern Gulf of Maine, stratification now begins about one week earlier than historical averages (Staudinger et al., 2019). Additionally, summer in the Gulf of Maine (as defined by sea-surface temperature (SST) thresholds) is beginning earlier and ending later at a rate of about one day (earlier and later) per year (Thomas et al. 2017).

As seasons shift and temperatures warm, fish migration times and patterns are also changing (Staudinger et al., 2019). However, these changes are difficult to quantify for many large marine species because they are hard to track (Henderson et al., 2017). Due to their predictable migration patterns, anadromous fish have become the focus of much of the phenological research on larger marine species (Staudinger et al., 2019). Despite a massive, dam-induced population decline, anadromous fish continue to play important roles as forage fish and facilitators of freshwater-marine nutrient exchange in coastal New England ecosystems (Hall et al., 2012; Mattocks et al., 2017; Walters et al., 2009). The most abundant species of anadromous fish in New England are river herring (collectively alewives, *Alosa pseudoharengus*, and blueback herring, *Alosa aestivalis*) and American shad (*Alosa sapidissima*). River herring and American shad use temperature and river discharge cues to time their migrations, and as a result, their migratory timing has been altered by climate change (Ellis & Vokoun, 2009; Rosset et al., 2017). Warming spring temperatures have led New England alewives and American shad in Oregon and New York, to migrate and spawn earlier in the spring (Ellis & Vokoun, 2009; Marjadi et al., 2019; Quinn & Adams, 1996; Nack et al., 2019). Additionally, climate change-induced changes to river flow regimes have affected migratory timing of Chinook salmon, and are believed to affect the migratory timing of river herring and shad as well (Keefer et al., 2008).

While the effects of temperature on migration and spawning are well documented, the importance of marine and freshwater temperatures relative to river flow rates, and the exact temperature thresholds cueing fish migrations remain unknown. Furthermore, prior studies of New England anadromous fish phenology have not accounted for fish population declines, and would therefore miss any potential effects of population declines on return times. To address this gap, I used time series datasets to determine how river discharge, marine SSTs, and changes in population abundance are related to the return times of river herring and American shad in seven New England rivers. I hypothesized that return times would be most-strongly correlated with marine temperature phenology indices, and that SST would play a larger role in determining return times than discharge. Additionally, I hypothesized that population abundance would be positively correlated with return time, as I suspected that the first fish return would be earlier in a larger population. Lastly, I hypothesized that return times would have gotten earlier over time across all rivers.

Methods:

Datasets:

To investigate migratory timing of American shad and river herring in New England, I obtained 30+-year time-series datasets on river herring and American shad return times on seven New England rivers from the Gulf of Maine Research Institute (GMRI). The river herring return time dataset covers river herring runs on the Cocheco, Exeter, Lamprey, Oyster, Taylor, and Winnicut rivers in New Hampshire from 1980-2016 (Figure 1), and records the julian day of the year that the first river herring returned to the fishway on the dam at each river. The river herring population dataset records the total number of fish that passed through the fishway on each river from 1972-2008. For both datasets, the data was collected by the NH Fish and Game Department (Patterson et al., 2016). The American shad return time/population abundance dataset spans from 1981-2011 and records shad passage in fish per day at the fishways on the Holyoke Dam on the Connecticut River in Massachusetts (Figure 2).

Daily fish-passage monitoring allowed me to calculate four metrics that I used in my analyses: (1) the first shad return (the first day of each year that at least one American shad passed through the fishway), (2) the annual day of peak passage of the shad run (the day of the year that the greatest number of shad passed through the fishway), (3) the annual run duration (the number of days between the first shad return and the last shad return), and (4) the annual population abundance.

To investigate the role of marine temperatures in determining fish return times, I obtained time series datasets on both marine temperature phenology and annual sea surface temperature (SST) anomaly. The marine temperature phenology dataset from Thomas et al. (2017) spans from 1982-2016, and records daily SST and spring and summer start dates at a 0.25 degree resolution (all data points are 0.25 degrees away from each other) for the entire Northwest Atlantic Ocean. Raw SST data were collected by satellites, and then subsequently smoothed using a 15 day mean to represent daily SST. This smoothed daily SST data was then used to calculate the spring and summer start dates. Spring start was defined as the first day of the year after the winter minimum SST that smoothed SST exceeded 8 degrees Celsius for 8 straight days at each location. Summer start was defined as the first day that SST was warmer than 0.5 degrees Celsius colder than the coldest maximum summer SST of the 33-yr study period at each location. The second temperate dataset that I used recorded the SST anomaly for the Gulf of Maine region, the Atlantic Multidecadal Oscillation (AMO), and the North Atlantic Oscillation (NAO) for each year from 1981-2014. I obtained this data from the National Oceanic and Atmospheric Administration's (NOAA) Optimum Interpolation Sea Surface Temperature (OISST) project, which uses a combination of satellites, buoys, and ship data to interpolate daily SSTs across the world (NOAA, n.d.).

Time-series datasets of mean daily river discharge were obtained from the USGS waterdata website (waterdata.usgs.gov). The USGS only had a time-series of appropriate length (at least ten years) for four of my six rivers (the Exeter, Oyster, Lamprey, and Connecticut rivers). For each of these rivers, the data was recorded at either the same dam where the return time data was collected (Connecticut and Lamprey) or within 5 miles of the dam where the return time data was collected (Exeter and Oyster). For both the Oyster and Lamprey rivers, the time-series were long, and spanned from 1934-2020, whereas for the Exeter and Connecticut rivers the time-series were shorter and spanned from 1996-2016 and 1984-2002 respectively. For each river I used the daily discharge values to calculate the mean monthly discharge for March, April, May, and June, as well as the mean spring discharge from March-June for each year.

Analyses:

To determine the strength of the relationship between return time and my independent variables, I performed a Pearson's product moment correlation test between return time and each variable. For the shad data, I correlated each independent variable with both the day of peak shad passage and the first shad return, so as to identify any differences between metrics. I also correlated shad run duration with population abundance to determine whether or not larger populations had a longer run duration, which I hypothesized would contribute to earlier return times. Lastly, I ran a two-way ANOVA to determine whether annual SST anomaly or spring river discharge played a stronger role in determining fish return times.

All of the correlation and ANOVA analyses were conducted in R. Missing years were not included in the correlation analyses, and datasets of varying time-spans were trimmed such that only the overlapping years were analyzed. Correlations between return times and marine SST phenological indices were mapped and plotted with the tmap package using a WGS 1984 projection.

Expectations:

I hypothesized that SST would be the strongest determinant of return time, and as a result, return times would be most-strongly correlated with marine temperature phenology indices, and second-most strongly correlated with annual SST anomaly. Additionally, I expected that the ANOVA would show that annual SST anomaly plays a larger role in determining return times than discharge. As a result of warming temperatures and shifting marine temperature phenology, I expected that return times would have gotten earlier over time across all rivers.

I also expected that both river discharge and the AMO and NAO may be weakly related to return time for some rivers, but would be more weakly correlated than the marine temperature phenology indices and the annual SST anomaly. Additionally, I hypothesized that population abundance would be positively correlated with return time, as I suspected that the first fish return would be earlier in a larger population.

Results:

Return Time Trends:

There were significant ($p<0.05$) trends in first fish return time for both the Cocheco and Connecticut rivers where return time got earlier by 0.35 and 0.40 days per year respectively (Figure S1, S2). There was also a significant ($p<0.05$) trend in timing of the peak day of the Connecticut River shad run which got earlier at a rate of 0.33 days per year (Figure S2). No significant trends were detected in the other five rivers (Table S1).

Temperature Anomaly and River Discharge:

The results of the two-way ANOVA between annual GOM SST anomaly, and mean spring discharge show that spring discharge accounts for much more of the variance in return times than annual temperature anomaly (Table 1). For all rivers except the Lamprey River, spring discharge was significantly related to return time ($p < 0.05$), whereas SST anomaly was only significantly ($p <0.05$) related to return time in the Exeter River. Additionally, there were no significant interaction effects between mean spring discharge and SST anomaly.

Table 1: Two-way ANOVA between annual temperature anomaly and spring discharge. All reported values are p-values.

River	Annual Anomaly	Spring Discharge	Annual Anomaly*Spring Discharge
Lamprey	0.34	0.22	0.66
Exeter	0.002	0.035	0.95
Oyster	0.85	0.003	0.57

Connecticut (peak passage)	0.25	0.088	0.086
Connecticut (first return)	0.43	0.03	0.64

There was substantial interannual variability in discharge across all rivers. Despite this variability, mean spring discharge increased over time for all rivers (Figures S3-S6). For the New Hampshire rivers, mean discharge was high in March and April and much lower in June and May (Figure 3). In the Connecticut River, mean discharge was similar across all months, except for April, which had much greater discharge than other months (Figure 3).

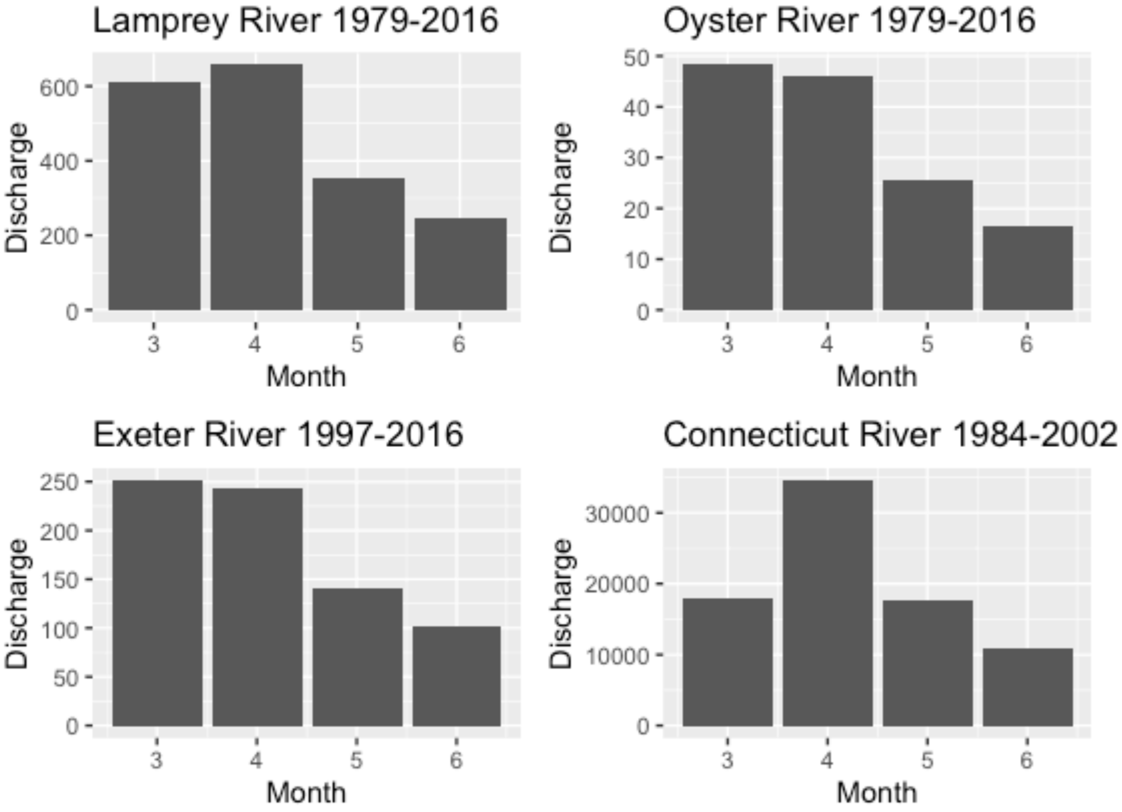


Figure 3: Mean monthly discharge for all rivers. Discharge was measured in cubic feet per second. Differences in magnitude of discharge are mainly due to differences in cross-sectional area of the rivers rather than differences in flow rates. Note that the time period varies between rivers.

Across all rivers, return times were more strongly and significantly positively correlated with mean April discharge than they were with mean discharge in any other month (Table 1, Table S2, S3). The only exception to this trend was in the Oyster River, where return time had a significant negative correlation (r = -0.42, p=0.01) with March discharge and no significant correlation with April discharge. These results suggest that fish return earlier when April discharge is lower and March discharge is higher; a trend likely driven by earlier occurrence of high spring river flows.

Peak Connecticut River shad passage was also significantly correlated with discharge. However unlike Connecticut River return times, peak shad passage was most significantly positively correlated with May (r= 0.55, p=0.01) and June (r=0.49, p=0.03) discharge, rather than April discharge (Table S2). This difference is likely due to the fact peak passage occurs 20-30 days later than first return, and as a result is more heavily impacted by late spring discharge than early spring discharge.

Table 2: Correlation between mean April discharge and fish return time

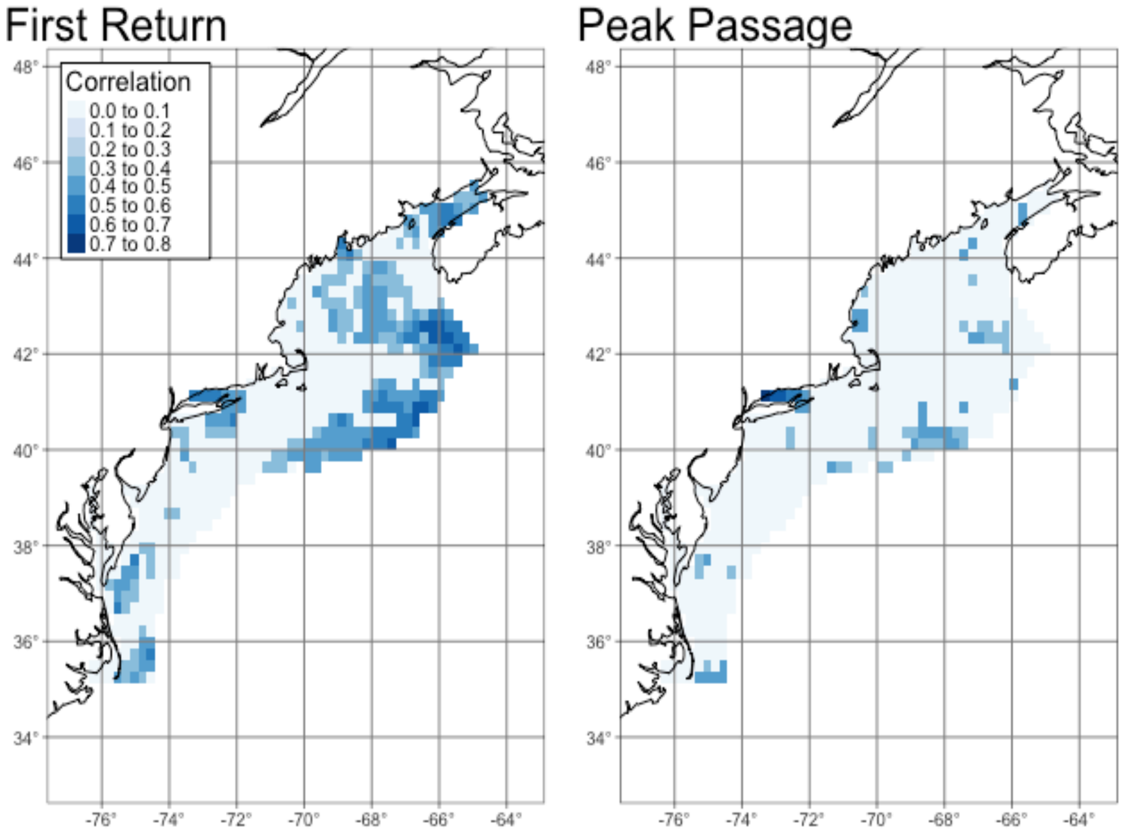
River	**r**	**p-value**
Lamprey	0.49	0.002
Exeter	0.57	0.01
Oyster	0.13	0.46
Connecticut (peak passage)	-0.08	0.75
Connecticut (first return)	0.53	0.02

There were significant correlations between return time and annual GOM SST anomaly for two of the seven rivers (Table S4). All significant correlations (and most insignificant correlations) were negative, suggesting that for most rivers warming SSTs have led to earlier fish return times (Figure S7, Table S4). Correlations between return times and the AMO and NAO were generally weaker and less significant than the correlations between annual SST anomaly, suggesting that these large-scale climatic processes have little impact on anadromous fish return times (Table S5-6).

Temperature Phenology:

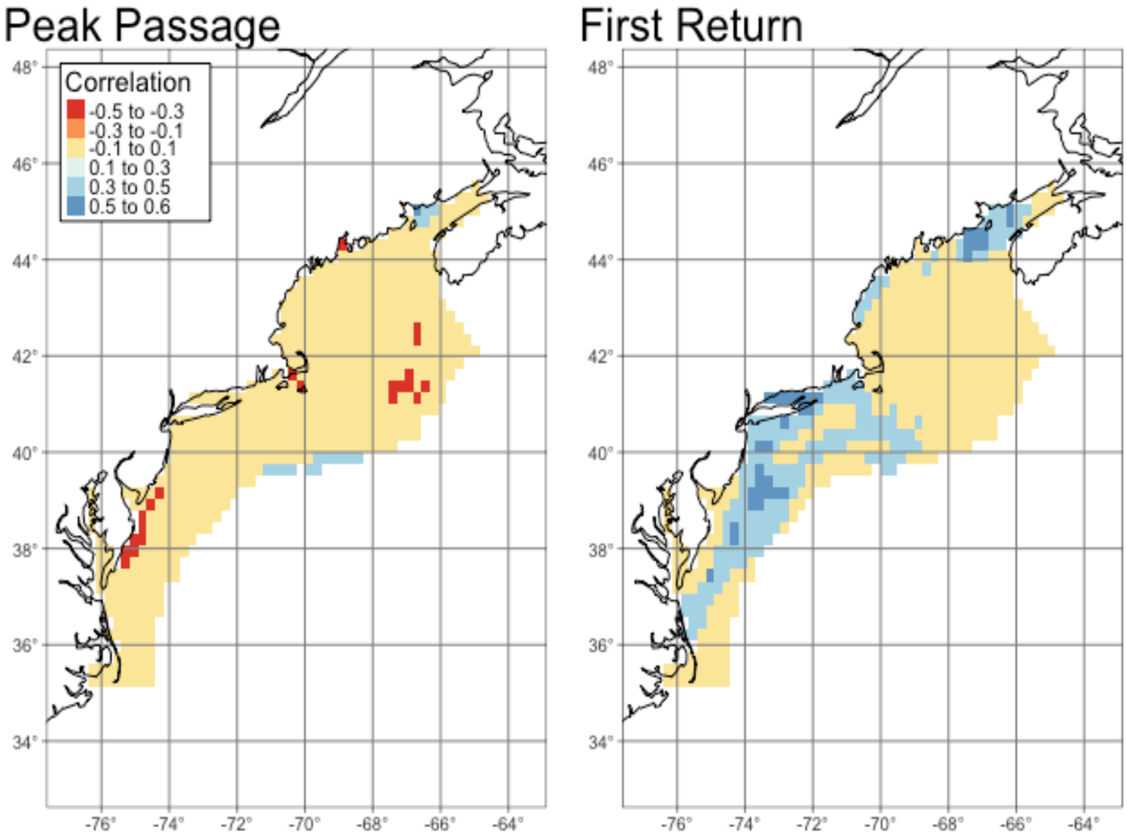
Return time was significantly positively correlated with both spring start and summer start. However, there were noticeable differences in location and magnitude of correlations with SST indices between species (Figure 4-8). River herring returns were generally more strongly correlated with spring start (Figure 6), whereas American shad returns were more strongly correlated with summer start (Figure 4, 5). Additionally, the spatial regions of high correlation varied, with the strongest correlations for river herring typically coming from the GOM, and the strongest correlations for shad coming from Long Island Sound. Magnitude of correlation with summer start was greatest for peak shad passage (r=0.7+), and greater overall for shad than for river herring (Figure 4, 7). However, the magnitude of correlation with spring start was greater overall for river herring (Figure 5, 6).

There were also significant differences in location and magnitude of correlations between river herring in each river (Figure 6, 7). Correlations were generally strongest for the Cocheco River and weakest for the Winnicut and Taylor rivers. While return times were more strongly correlated to spring start for most rivers, return times for the Exeter and Taylor rivers were more strongly correlated with summer start (Figure 6, 7). Though there was little overlap in regions of correlation between all New Hampshire rivers and summer start, there was significant overlap in regions of correlation between all New Hampshire rivers and spring start (Figure 8). Additionally, the regions of highest correlation with spring start (0.5-0.7) were very similar for the Cocheco, Exeter, Lamprey, and Oyster Rivers (Figure 6).


First Return

Peak Passage

Figure 4: Significant correlations between Connecticut River shad return times and summer's start. Light blue regions denote insignificant correlations (p>0.05). Fewer regions were correlated with peak shad passage than with shad return time. Despite this, there was a significant amount of overlap in regions of correlation between the two metrics. Additionally, correlations in Long Island Sound were stronger for peak shad passage (0.7+), than they were for shad return time (0.6-0.7).


Peak Passage

First Return

Figure 5: Significant correlations between Connecticut River shad return times and spring start. Tan regions denote insignificant correlations (p>0.05). Correlations were much stronger for first return than for peak passage, but were weaker than the correlations with summer start for both metrics (Figure 7).

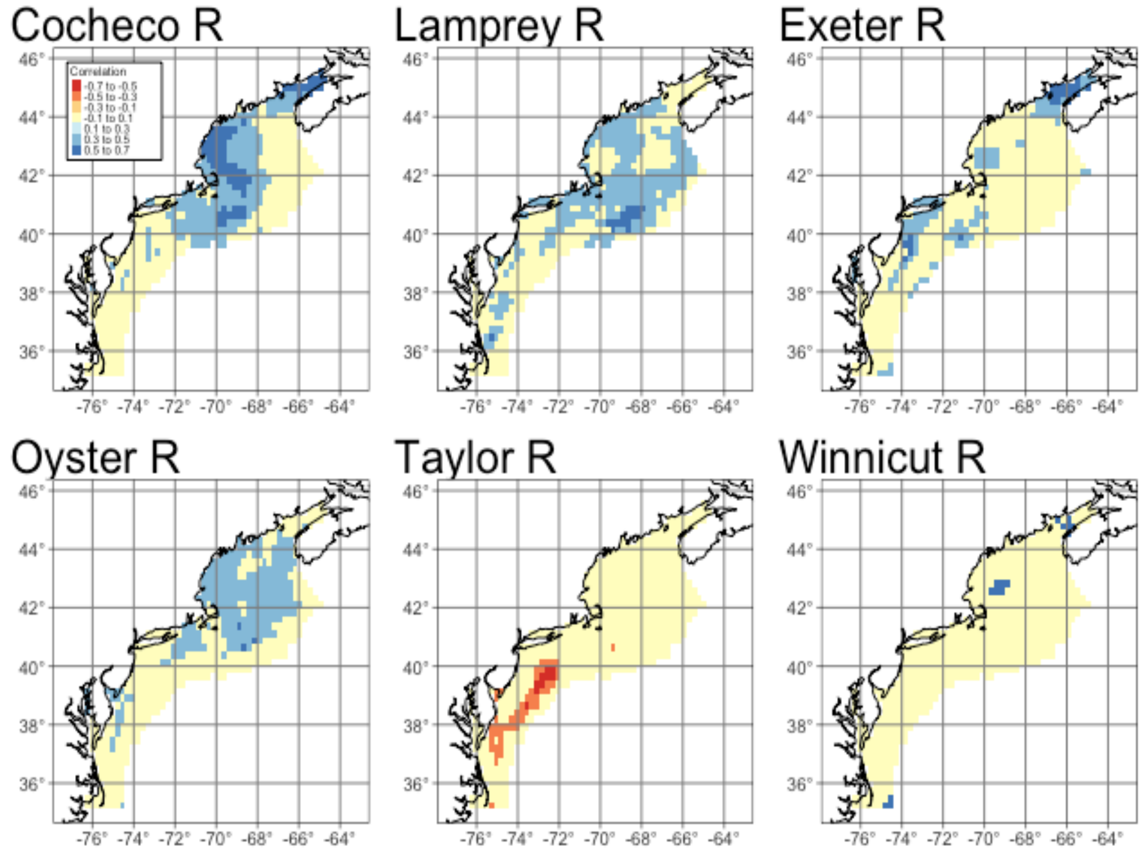


Figure 6: Significant correlations between spring start and river herring return time. Warm colors indicate negative correlation, while beige areas indicate insignificant correlations. Correlations were greatest in the Cocheco, Lamprey, Exeter, and Oyster rivers.

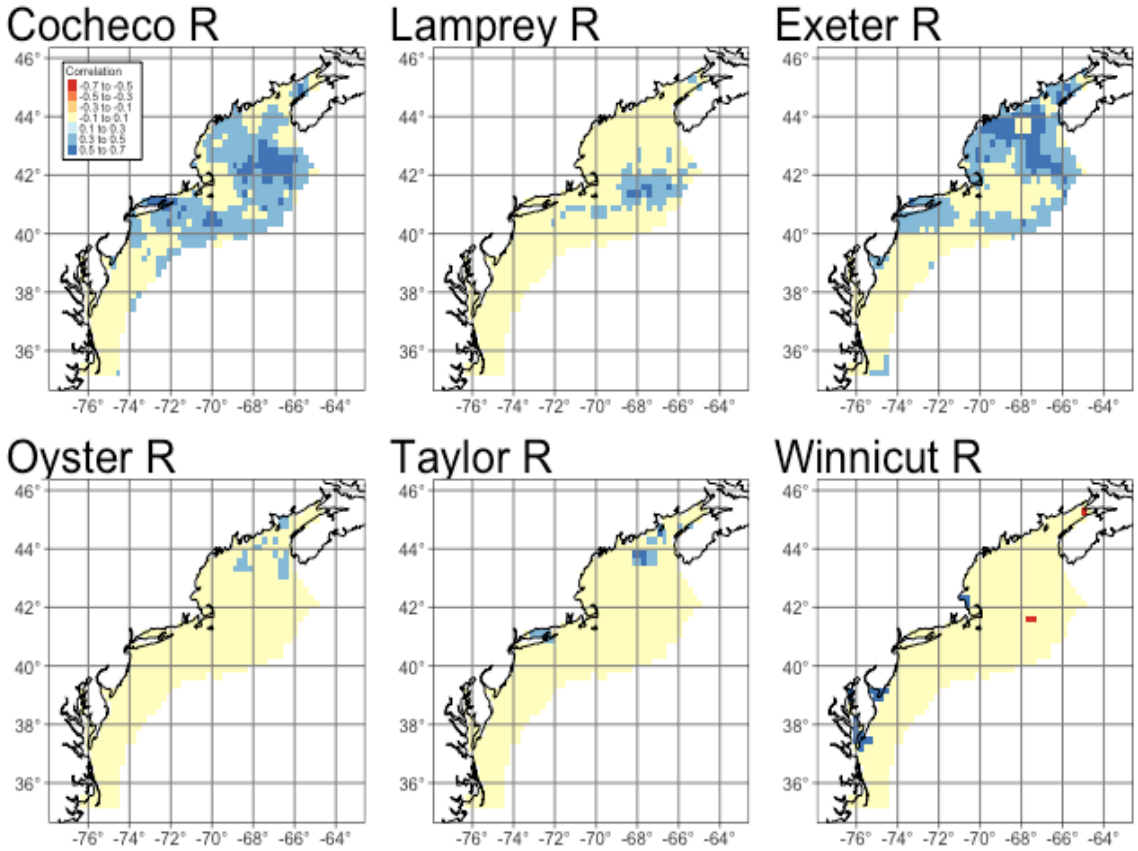


Figure 7: Significant correlations between summer start and river herring return time. Warm colors indicate negative correlation, while beige areas indicate insignificant correlations and cold colors indicate positive correlations. Correlations with summer start are weaker than correlations with spring start for all rivers except for the Exeter and Taylor rivers (Figure 9).

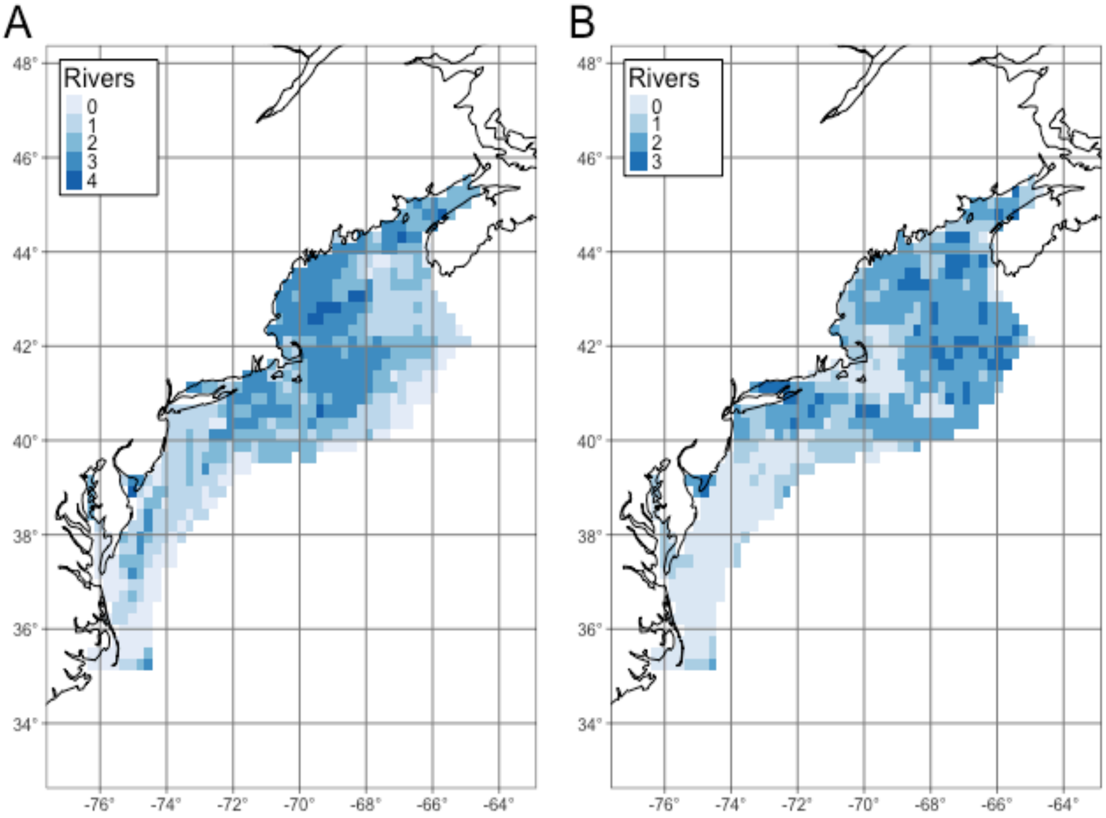


Figure 8: Areas of overlapping significant ($p<0.05$) correlation between return time and spring start (A) and summer start (B) across all New Hampshire rivers. Note the difference in legends between figures. There is much greater overlap in correlations with spring start than with summer start. The greatest overlap of correlations is seen in the Southwestern Gulf of Maine for spring start and in the Eastern Gulf of Maine for summer start.

Population:

I had hypothesized that there would be a significant positive correlation between run duration and population abundance and as a result, fish would return earlier in larger populations. However, my correlation analyses suggested that this was not the case. There was no correlation between shad run duration and population abundance. Correlations between abundance and return time were generally weak and insignificant (Table S7). While there was a significant negative correlation ($r= -0.54$, $p<0.1$) between return time and population abundance for river herring in the Exeter and Winnicut rivers, it is likely that this correlation was a product of large outliers and data gaps rather than my hypothesized mechanism (Table S7, Figure S10, S14). Overall, my analysis suggests that population abundance has little relationship to return time.

Discussion:

Overall, river herring and American shad return times across the study area have gotten significantly earlier over time, a trend likely driven by both earlier thermal onset of spring start and summer start in the fish's marine habitat, and earlier peak river flows (Staudinger et al., 2019). As I hypothesized, temperature phenology indices were more strongly correlated with return time than any of the other independent variables for most rivers. This result supports the results of other studies that have found water temperature to be the main driver of anadromous fish migrations (Nack et al., 2019; Quinn & Adams, 1996; Hodgson et al., 2006). For many rivers however, spring discharge was more strongly correlated with return time than annual SST anomaly. This suggests that spring river discharge is also a significant determinant of return time, and that changes in return times are driven by changes in the timing of specific temperature thresholds, rather than general ocean warming. Lastly, population abundance does not appear to be related to fish return time, suggesting that population declines have had little effect on return times.

Rates of phenological change

These results confirm the results of many other studies (Ellis & Vokoun, 2009; Nack et al., 2019; Huntington et al., 2003) that show anadromous fish return times are getting significantly earlier over time, and further illustrate the impact that climate change is having on phenological processes within the GOM. My rates of change in return time are much lower than the 1.2 days and 1.3 days earlier/year reported by Huntington et al. (2003) for alewives on the Androscoggin River (Maine) and Atlantic salmon on the Penobscot River (Maine) respectively, but are comparable to the rates of 0.33-0.43 days earlier/year estimated by Ellis & Vokoun (2009) for alewives in four Massachusetts streams. This difference between my results and those reported by

Huntington et al. (2003) may reflect uneven rates of warming across the GOM. However, more research is needed to confirm this hypothesis.

River Discharge

The strong role of spring river discharge as a determinant of fish return times is somewhat surprising, as most studies of anadromous fish phenology on the east coast either ignore discharge or have found only weak relationships between river discharge and return times (Nack et al., 2019; Ellis and Vokoun, 2009). On the west coast however, high river flows have been associated with later return times in American shad, Chinook salmon, and sockeye salmon (Quinn & Adams, 1996; Hodgson et al., 2006; Keefer et al., 2008). It is hypothesized that high flows are harder for fish to swim against, causing them to delay their migrations until flow decreases and/or preventing them from locating and passing through fishways (Hodgson et al., 2006; NH Fish and Game, 2006). New Hampshire Fish and Game department reports support this hypothesis, noting that very high spring discharge in 2005 led to significant decreases in total fish passage across all of the six New Hampshire rivers in my dataset (NH Fish and Game, 2006; NH Fish and Game, 2008). The strong positive correlations between April discharge and return time in the Connecticut, Exeter, and Lamprey rivers further support this hypothesis, and point to the need for future studies of anadromous fish migration phenology to include river discharge as a variable in their analysis.

If this hypothesized mechanistic relationship between high flows and return times is supported, then we can understand river discharge to be a confounding factor that alters migrations when flows are high, rather than a driver of migratory timing. River discharge's role as a confounding factor, rather than a driver of migratory timing, would explain why most studies of anadromous fish migration phenology have found that water temperature is much more strongly related to return times than river discharge.

Phenology Indices and Fish presence

The strong correlations between river herring return times and the marine spring start index, and the proximity of these areas of correlation to the mouths of the New Hampshire rivers (Figure 8), might suggest that these areas of correlation indicate fish presence. As alewives have been reported to begin migrations when freshwater temperatures warm to 9 degrees Celsius (Ellis & Vokoun, 2009), it is likely that they would amass near the mouths of rivers at the time of the spring start index (the first day of the year that SST gets above 8 degrees Celsius for eight days). Comparisons between overlapping regions of correlation and blueback herring and alewife spring (February-April) trawl data from 2010-2017, further support this hypothesized relationship (Figure 9). While more research is needed to confirm this relationship, the strong similarity between regions of overlapping correlation and spring river herring presence suggest that 8 degree Celsius marine temperatures may be used to track spring coastal New England river herring distribution.

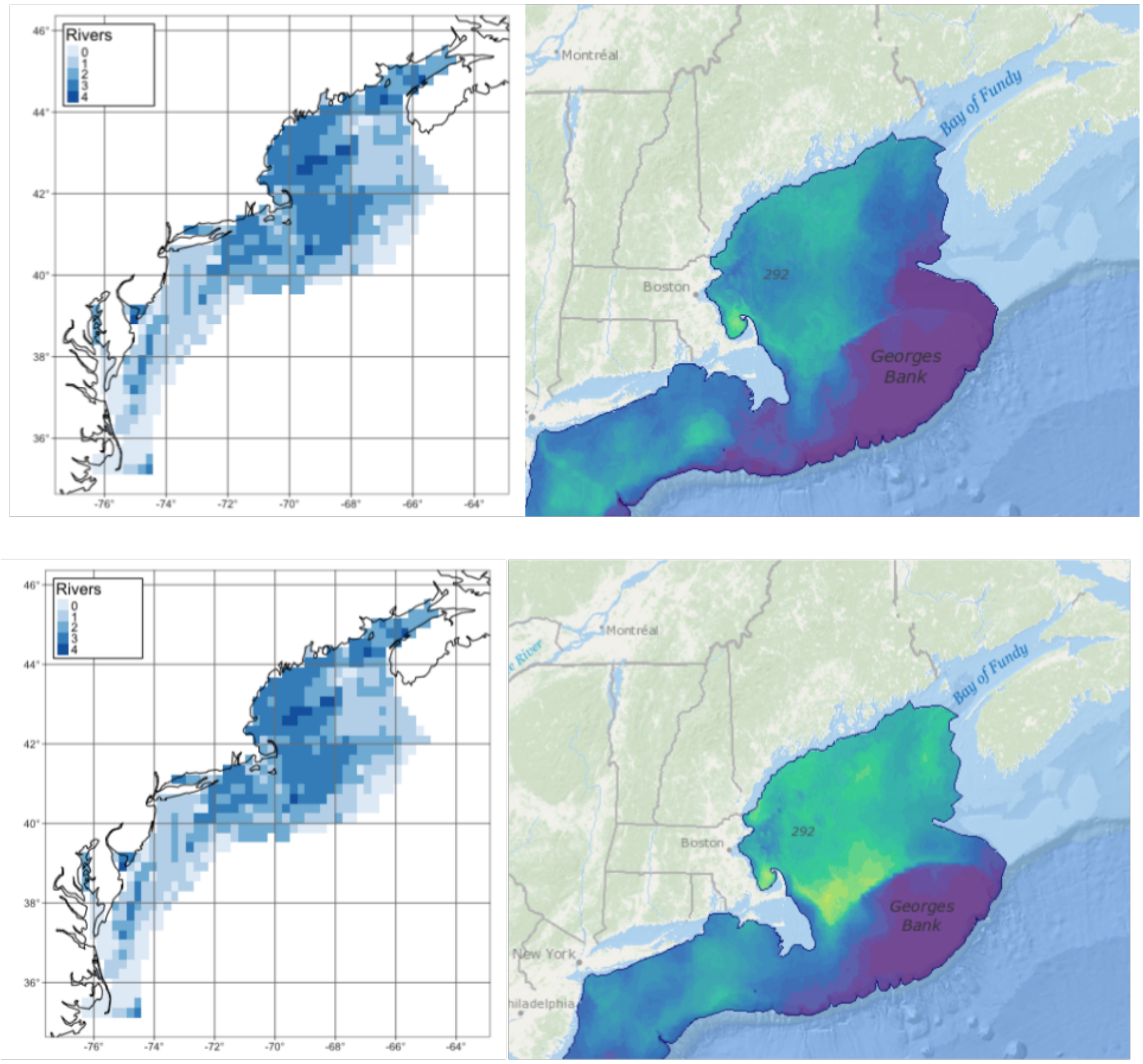


Figure 9: Comparisons between areas of overlapping significant ($p<0.05$) winter's end/return time correlation and 2010-2017 blueback herring (top) and alewife (bottom) spring (February-April) trawl distribution. Light green denotes greatest fish biomass, while dark purple denotes lowest fish biomass. Trawl data were sourced from the Northeast Ocean Data Portal (Ribera et al., 2019; Fogarty and Peretti, 2016; Gottschall and Pacileo, 2014; Curtice et al., 2019, Marine Life Data Analysis Team).

American shad return times were much more strongly correlated with the summer's start index than the winter's end index, suggesting that shad migrations are cued by warmer temperatures than the migrations of river herring. Although there was no relationship between areas of correlation and shad spring trawl data (Ribera et al., 2019; Fogarty and Peretti, 2016; Gottschall and Pacileo, 2014; Curtice et al., 2019, Marine Life Data Analysis Team), strong correlations in the region surrounding the mouth of the Connecticut River (Long Island Sound) may also indicate fish presence (Figure 4). However, more research is needed to determine the relationship between shad presence, migratory timing and SST.

Limitations/Sources of Error

As with any study of river herring phenology, differences in migratory timing between alewives and blueback herring likely weakened my analysis. Alewives typically migrate earlier than Blueback Herring, and as both were present in varying abundance on all of my New Hampshire rivers, this difference could have led to inconsistencies in the data and obscured return time trends for both species (Mattocks et al., 2017; Rosset et al., 2017). Such inconsistencies may have contributed to weaker correlations between temperatures and return time. High discharge rates in some years may also have weakened correlations between temperature and return time.

Another potential source of error is the presence of false positives in my correlations. It is likely that some of my correlations are a product of chance rather than any relationship between variables. Furthermore, strong correlations do not necessarily mean that a variable is related to return time. Some of my correlations might be the product of two independent trends, rather than a mechanistic relationship between variables and return time.

Lastly, my research was limited by data availability. Without any data on year-class and daily fish passage on 6 of my 7 rivers, I was unable to find any significant relationship between population and return time. While relationships between population and return time may exist, I found no evidence for them with the data that I had.

Conclusion:

Overall, my findings are consistent with those of other studies of anadromous fish migration phenology and suggest that river herring and American shad migrations are triggered by specific water temperature thresholds. While it is unlikely that river discharge is a driver of anadromous fish migration timing, my findings suggest that it may play an important role in delaying migrations in years with high spring flows in dammed rivers. After reviewing the literature, it is clear to me that much remains unknown about the phenology of New England river herring and American shad. Future research efforts should focus on determining the specific temperature thresholds that trigger fish migrations, and the influence of river discharge on return times, particularly in undammed rivers.

The earlier return times of anadromous fish that I have documented, have important implications for the conservation of river herring and American shad in New England. As most fishways do not operate year-round, earlier fish migrations could result in a mismatch between migrations and fishway operation (Ellis & Vokoun, 2009). It is therefore essential to continue to monitor migration timing and adjust fishway operation times accordingly. As the GOM continues to warm, and New England's hydrology changes (Staudinger et al., 2019), such monitoring will become increasingly important in the efforts to protect and restore New England's anadromous fish populations.

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APPENDIX:

Supplementary Data:

Table S1: Return time trends (based on a linear regression)

River	p-value	R-squared (adjusted)	slope
Cocheco	0.000708	0.262	-0.35
Lamprey	0.328	-0.0004	0.104
Exeter	0.135	0.0436	-0.24
Taylor	0.148	0.0401	-0.39
Winnicut	0.793	-0.058	0.11
Oyster	0.965	-0.029	-0.0054
Connecticut (peak passage)	0.04	0.11	-0.33
Connecticut (first return)	0.05	0.1	-0.4

Table S2: Correlations (r) between monthly discharge and return time

River	March r	p	April r	p	May r	p	June r	p
Lamprey	-0.02	0.92	0.49	0.002	0.04	0.84	-0.14	0.41
Exeter	0.09	0.71	0.57	0.01	0.32	0.17	0.17	0.48
Oyster	-0.42	0.01	0.13	0.46	0.04	0.83	-0.16	0.37
Connecticut (peak passage)	0.1	0.69	-0.08	0.75	0.55	0.01	0.49	0.03
Connecticut (first return)	-0.42	0.07	0.53	0.02	0.39	0.1	0.36	0.13

Table S3: Correlations between spring discharge and return time

River	r	p-value
Lamprey	0.19	0.27
Exeter	0.55	0.01

Oyster	-0.22	0.21
Connecticut (peak passage)	0.41	0.08
Connecticut (first return)	0.48	0.04

Table S4: Correlation between annual GOM SST anomaly and fish return time

River	**r**	**p-value**
Cocheco	-0.47	0.006
Lamprey	-0.16	0.37
Exeter	-0.33	0.08
Taylor	0.05	0.79
Winnicut	-0.11	0.69
Oyster	-0.53	0.002
Connecticut (peak passage)	0.13	0.47
Connecticut (first return)	-0.14	0.44

Table S5: Correlations between Atlantic Multidecadal Oscillation and return time

River	**r**	**p-value**
Cocheco	0.36	0.04
Lamprey	0.07	0.71
Exeter	0.29	0.13
Taylor	0.07	0.71
Winnicut	0.61	0.02
Oyster	0.09	0.63
Connecticut (peak passage)	0.54	0.002
Connecticut (first return)	0.24	0.19

Table S6: Correlations between North Atlantic Oscillation and return time

River	**r**	**p-value**
Cocheco	-0.31	0.08
Lamprey	-0.04	0.82
Exeter	-0.24	0.21
Taylor	-0.23	0.23
Winnicut	-0.11	0.7
Oyster	-0.03	0.85
Connecticut (peak passage)	-0.33	0.07

Connecticut (first return)	-0.53	0.002

Table S7: Correlations (r) between population abundance and return time

River	**r**	**p-value**
Cocheco	-0.12	0.54
Lamprey	-0.38	0.04
Exeter	-0.54	0.009
Taylor	0.33	0.1
Winnicut	-0.54	0.085
Oyster	-0.03	0.87
Connecticut (peak passage)	0.38	0.03
Connecticut (first return)	0.32	0.08
Connecticut (run duration)	0.12	0.52

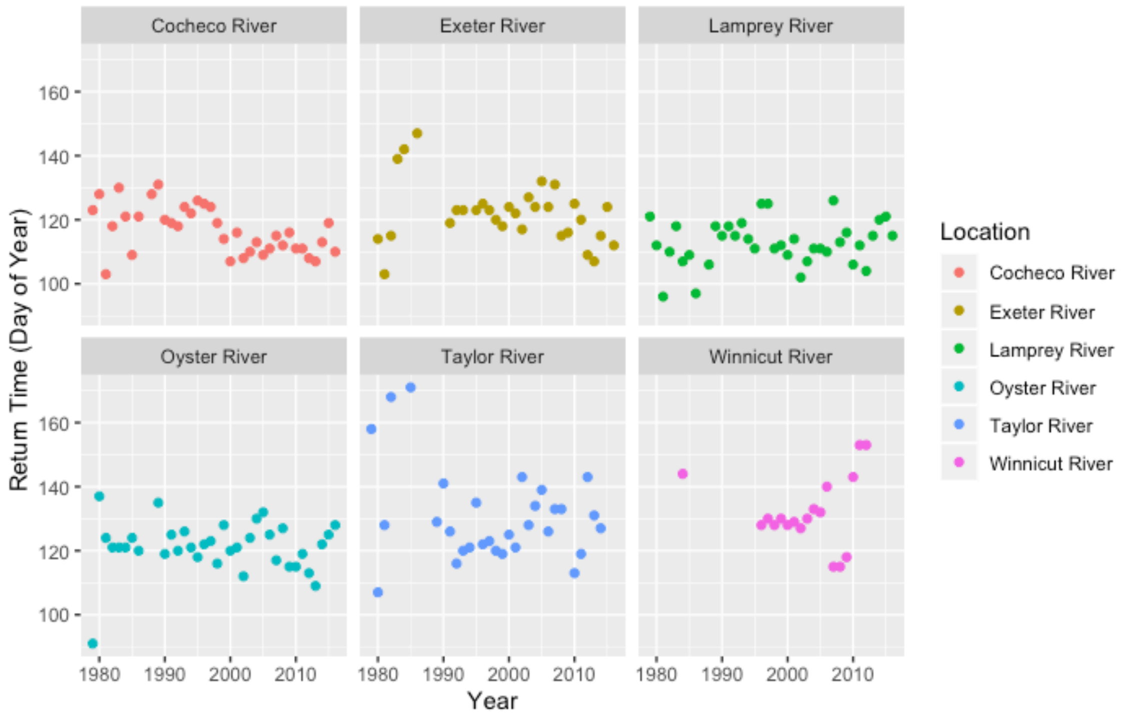


Figure S1: River herring return time trends 1979-2016. There is substantial annual variation in fish return time for all six rivers. Fish return time has gotten significantly earlier ($p<0.05$) over the study period in the Cocheco River. The return time trends in the other rivers are not significant.

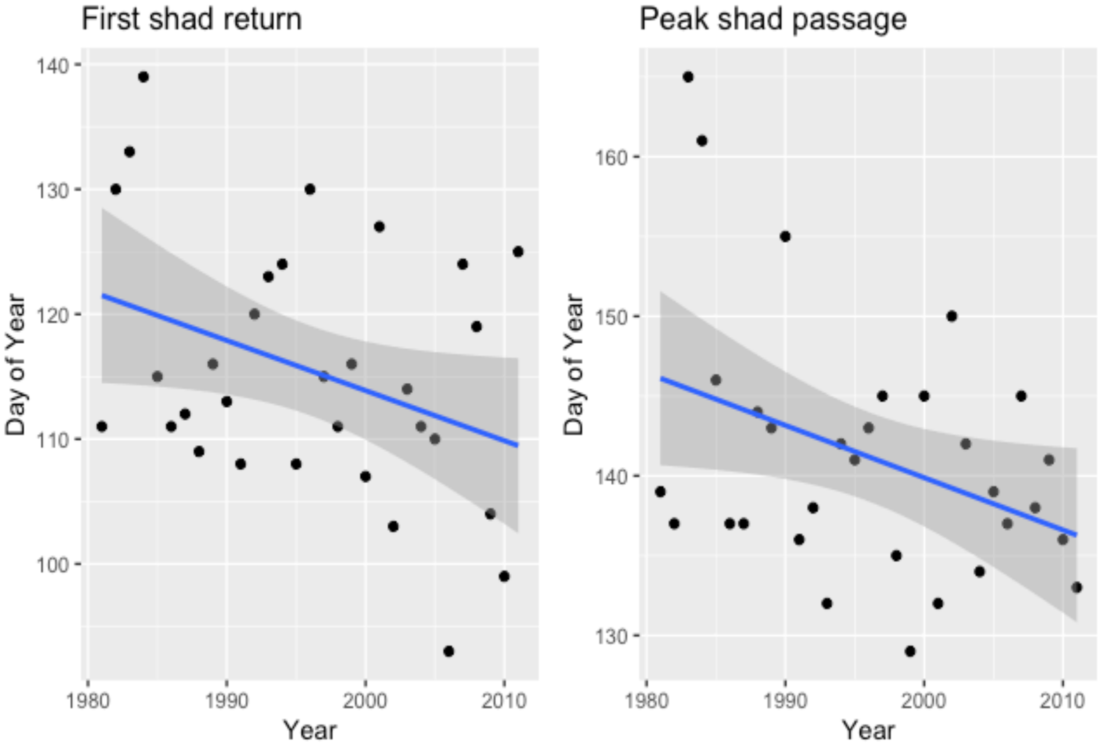


Figure S2: Connecticut River shad return times 1981-2011. Over the 30 year period, both first shad return time and peak shad passage have gotten significantly earlier (p<0.05) at a rate of 0.4 and 0.33 days per year respectively.

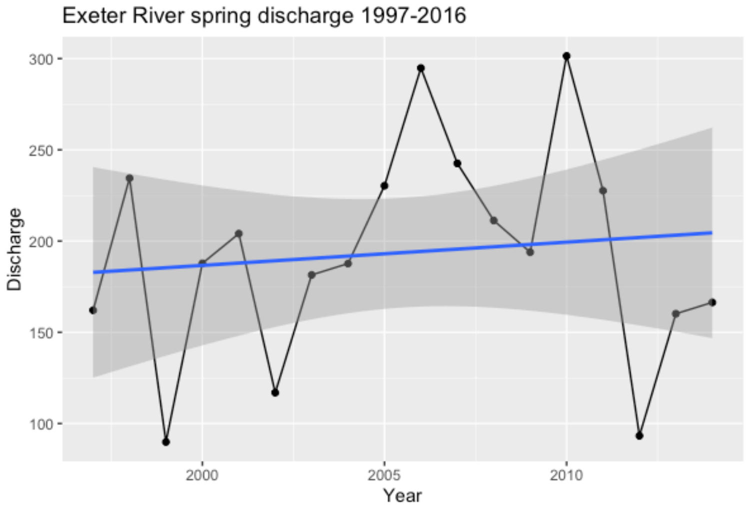


Figure S3: Exeter river spring discharge 1997-2016. Values represent the mean annual March-June daily discharge for each year. Discharge increased by an average of 1.27 ft^3/s/yr however this trend was not significant (p=0.65).

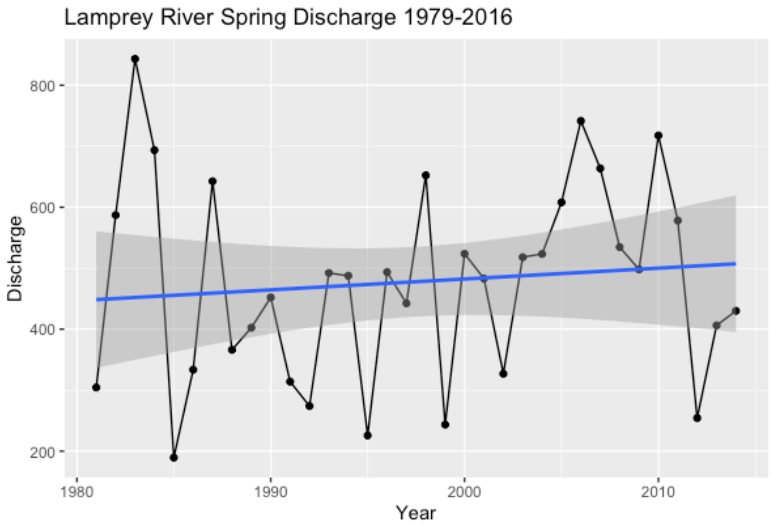


Figure S4: Lamprey River spring discharge 1979-2016. Values represent the mean annual March-June daily discharge for each year. Discharge increased by an average of 1.78 ft^3/s/yr however this trend was not significant (p=0.54).

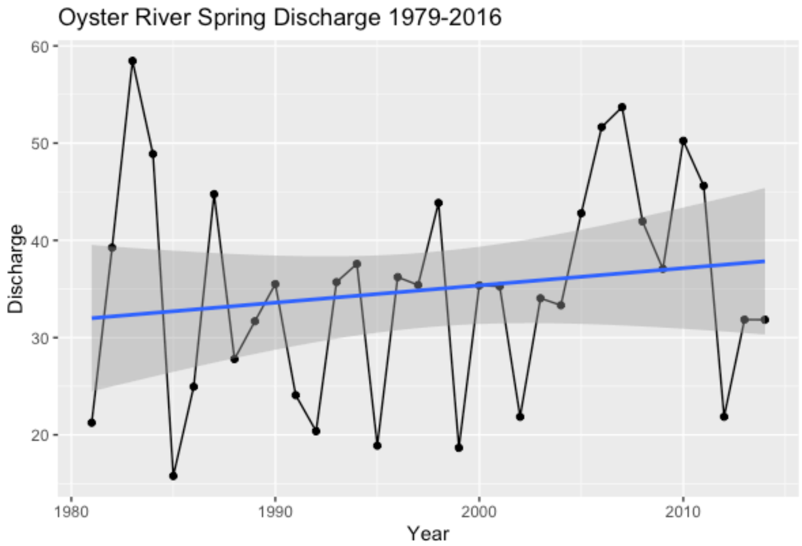


Figure S5: Lamprey River spring discharge 1979-2016. Values represent the mean annual March-June daily discharge for each year. Discharge increased by an average of 0.18 ft^3/s/yr however this trend was not significant (p=0.36).

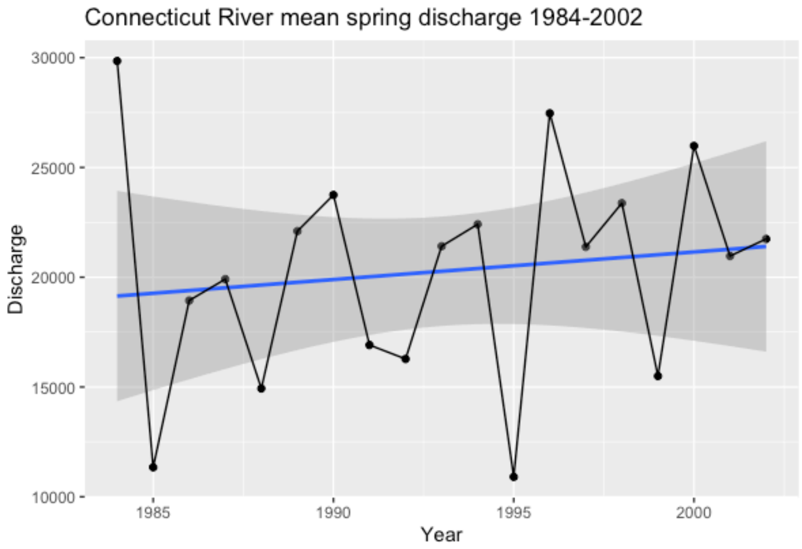


Figure S6: Connecticut River spring discharge 1984-2002. Values represent the mean annual March-June daily discharge for each year. Discharge increased by an average of 125.4 ft^3/s/yr however this trend was not significant (p=0.57).

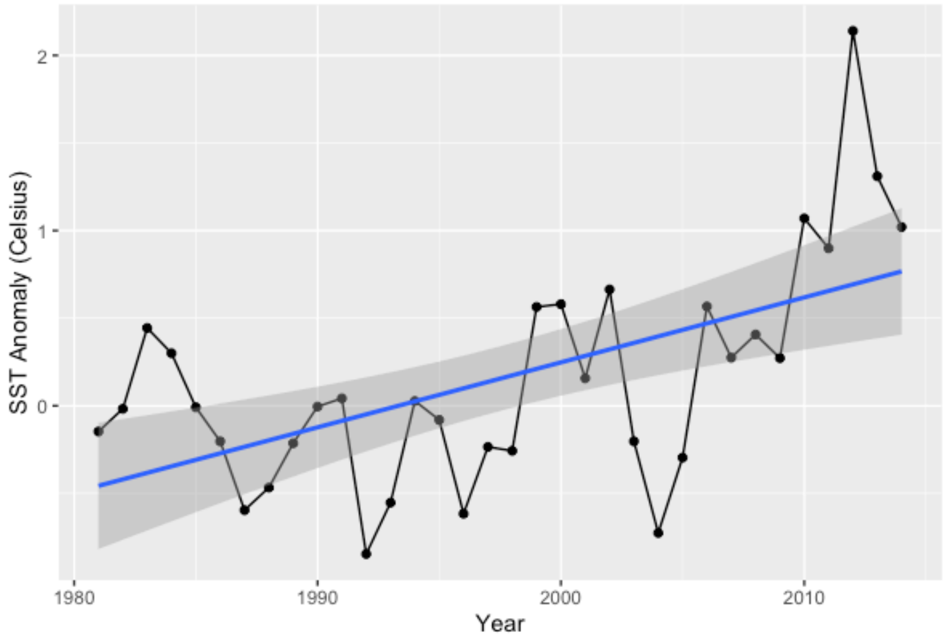
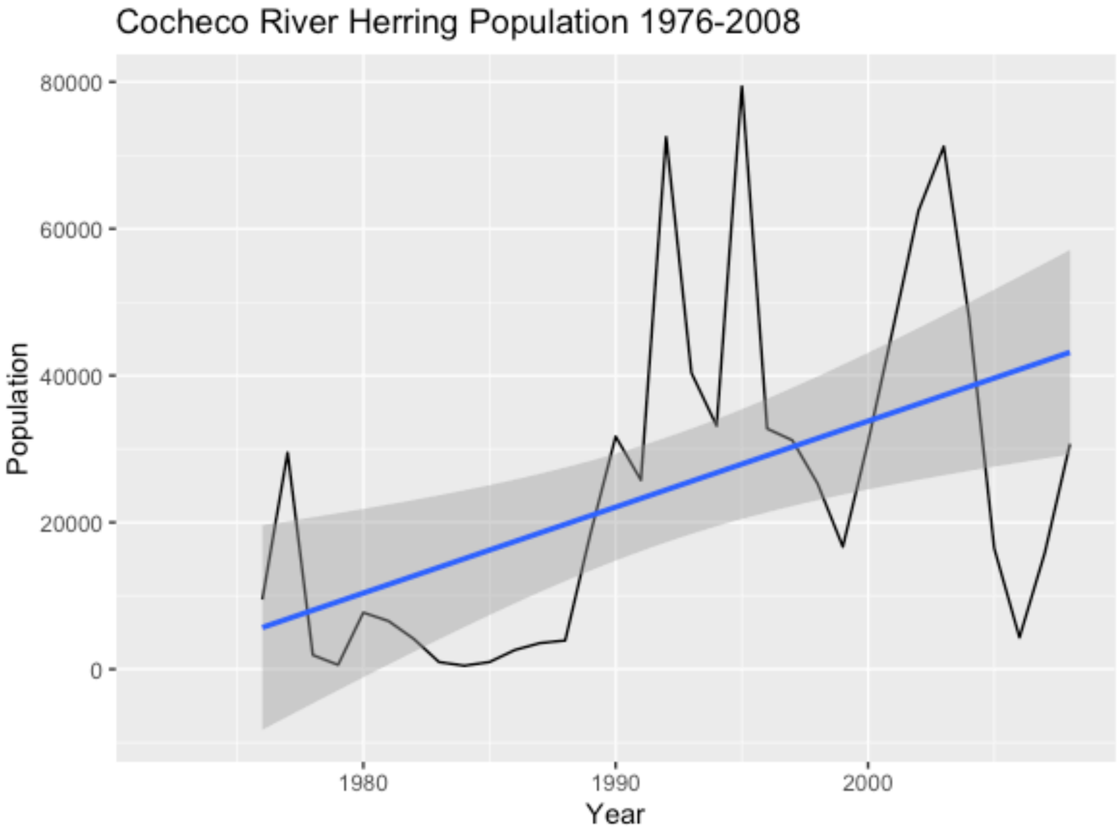
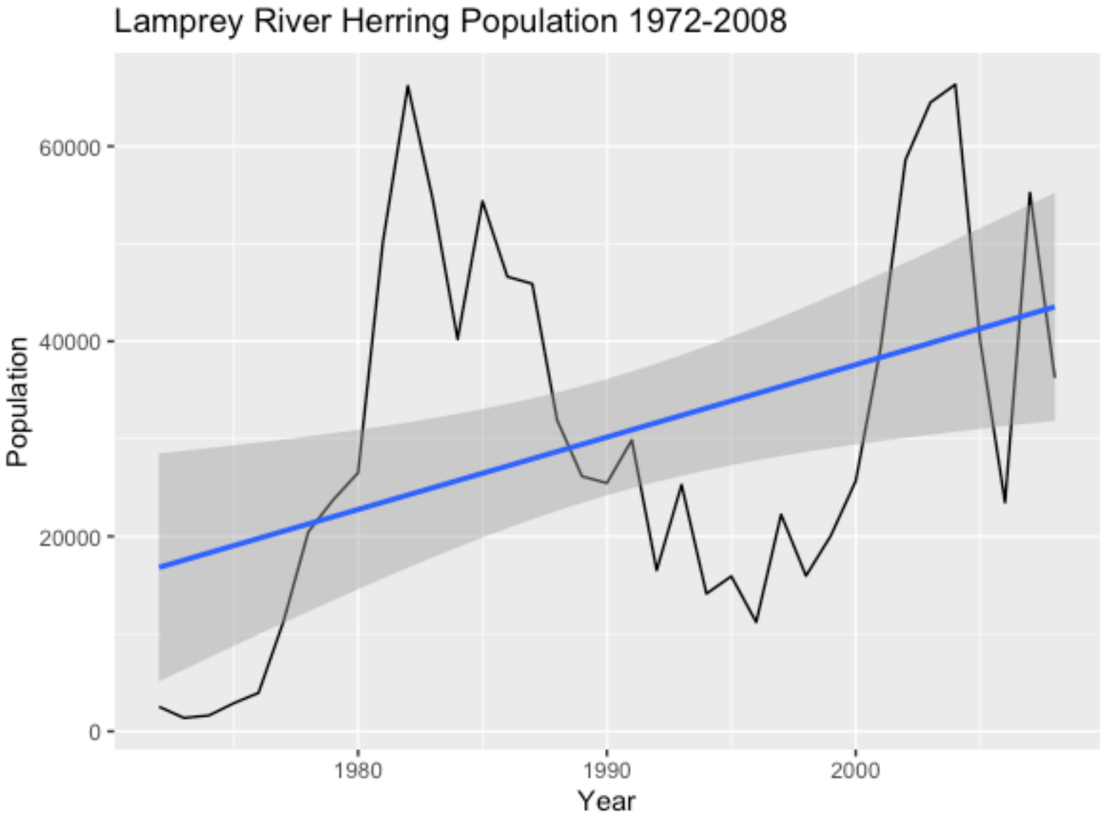
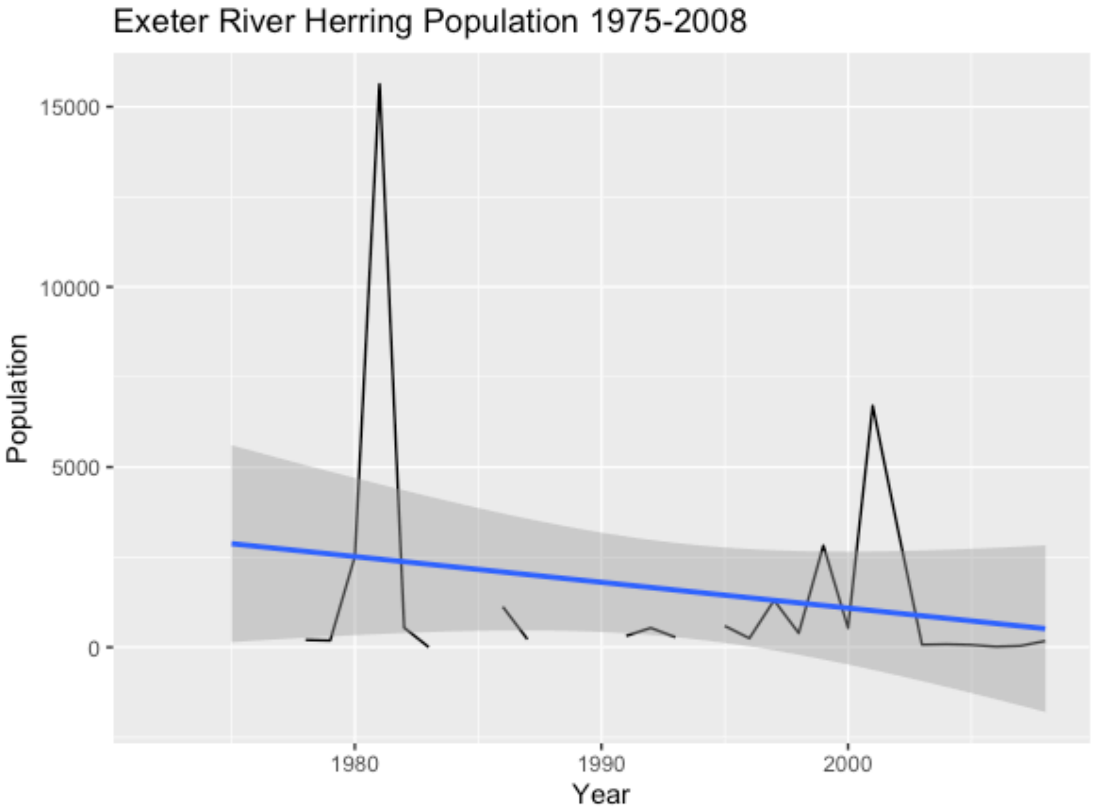


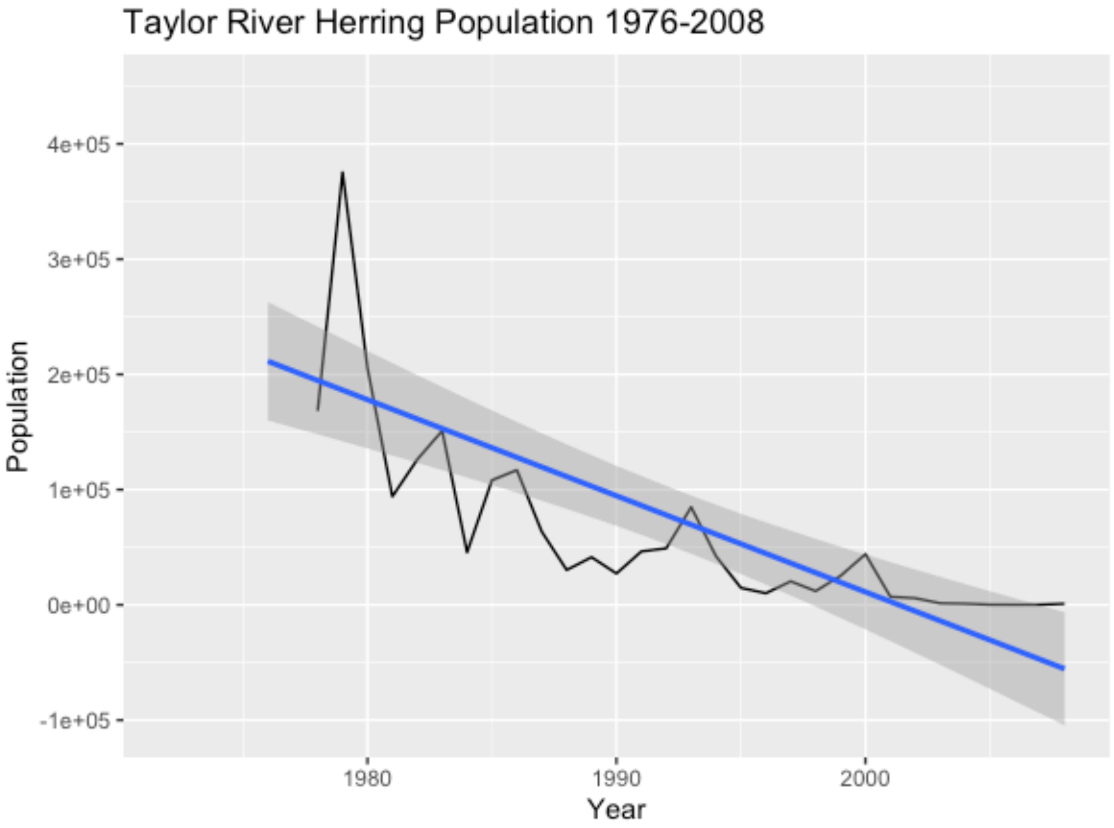
Figure S7: Annual GOM SST anomaly 1981-2014. Over the 33-yr period annual SST anomaly has significantly increased (p = 0.0003) by an average of 0.04 degrees Celsius (C) per year. Additionally, SST anomaly has increased at an even greater rate over the last 10 years, suggesting that warming is accelerating in the Gulf of Maine.

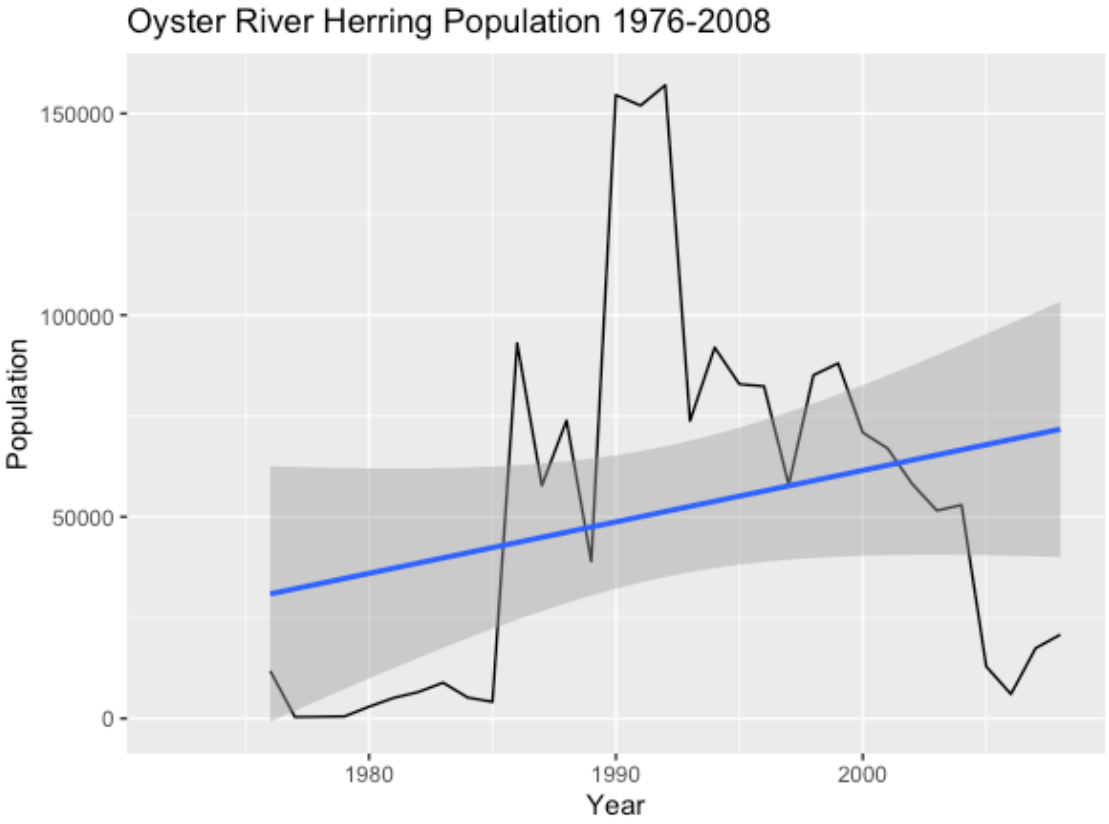
Figures S8-S14: Trends in Population abundance

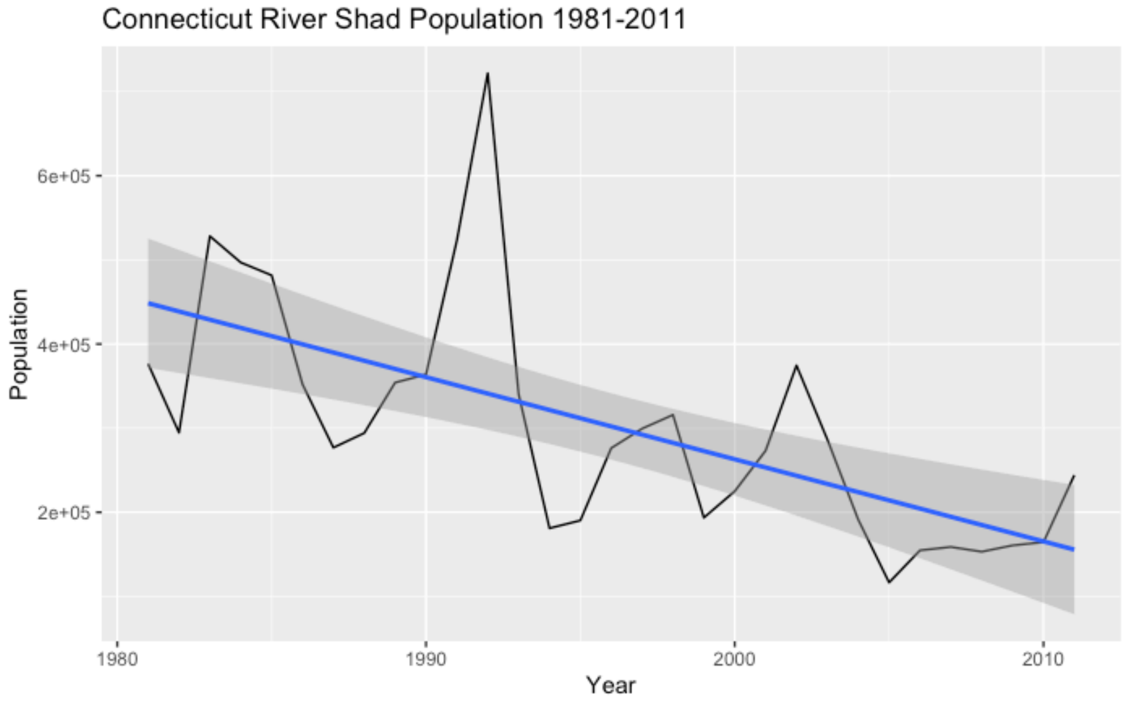


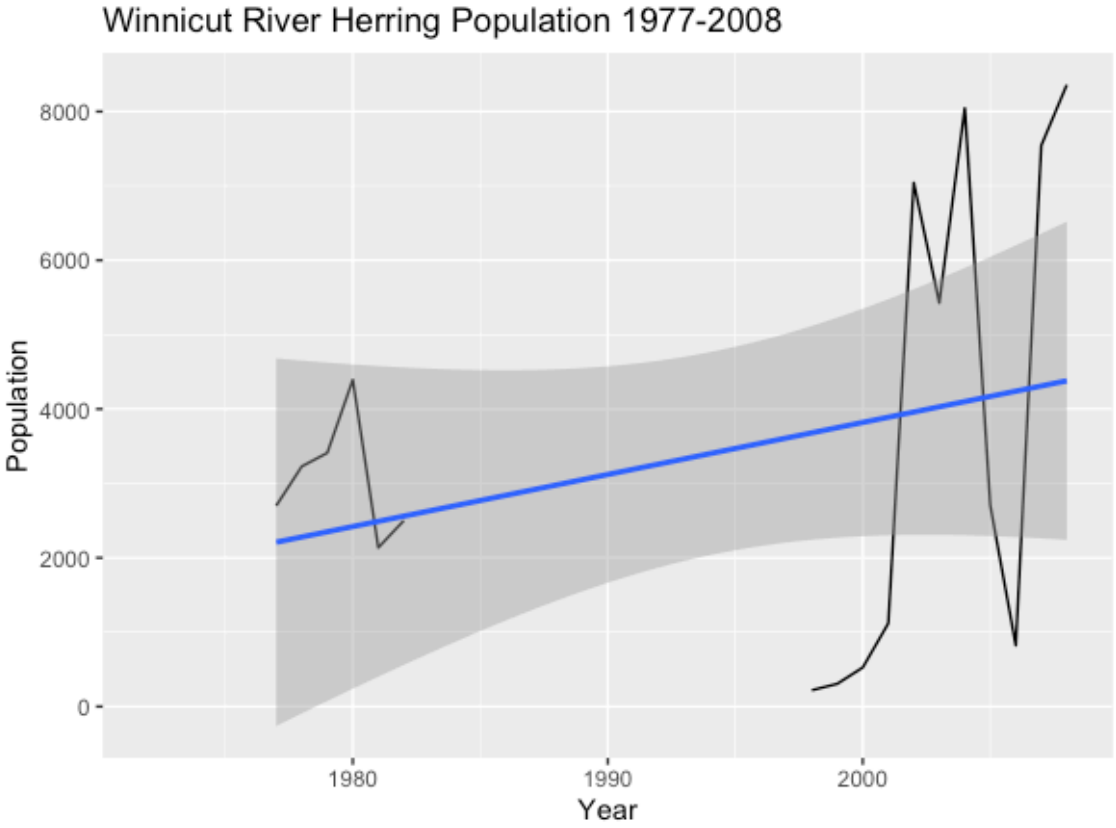

Lamprey River Herring Population 1972-2008
Population
60000
40000
20000
0
1980
1990
2000
Year


Exeter River Herring Population 1975-2008
Population
15000
10000
5000
0
1980
1990
2000
Year


Taylor River Herring Population 1976-2008
Population
4e+05
3e+05
2e+05
1e+05
0e+00
-1e+05
1980
1990
2000
Year


Oyster River Herring Population 1976-2008
Population
150000
100000
50000
0
1980
1990
2000
Year


Connecticut River Shad Population 1981-2011
Population
6e+05
4e+05
2e+05
1980
1990
2000
2010
Year


Winnicut River Herring Population 1977-2008
Population
8000
6000
4000
2000
0
1980
1990
2000
Year