November 2016

Ecological Consequences of Lost Anadromous Forage Fish in Freshwater Ecosystems

Steven R. Mattocks
University of Massachusetts Amherst

Recommended Citation

Mattocks, Steven R., "Ecological Consequences of Lost Anadromous Forage Fish in Freshwater Ecosystems" (2016). *Masters Theses*. 433.
https://scholarworks.umass.edu/masters_theses_2/433

ECOLOGICAL CONSEQUENCES OF LOST ANADROMOUS FORAGE FISH IN FRESHWATER ECOSYSTEMS

A Thesis Presented

by

STEVEN RICHARDSON MATTOCKS

Submitted to the Graduate School of the
University of Massachusetts Amherst in partial fulfillment
of the requirements for the degree of

MASTER OF SCIENCE

September 2016

Wildlife and Fisheries Conservation

ECOLOGICAL CONSEQUENECES OF LOST ANADROMOUS FORAGE FISH IN FRESHWATER ECOSYSTEMS

A Thesis Presented

by

STEVEN RICHARDSON MATTOCKS

Approved as to style and content by:

____
Adrian Jordaan, Chair

____
Allison Roy, Member

____
Michelle Staudinger, Member

____
Eve Vogel, Member

____
Curtice R. Griffin, Department Head
Department of Environmental Conservation

ACKNOWLEDGEMENTS

I would like the thank my advisor Adrian Jordaan for all of his advice and guidance throughout this process, and for trusting me with this project. I am indebted to Allison Roy for taking me into her lab and allowing me to engage and learn in such a constructive environment. I would also like to thank Michelle Staudinger for her advice and support during the last 2 years. This project would not have been completed without significant contributions from Matthew Devine and Julianne Rosset, who were major collaborators throughout this process. Thanks to Vasili Luzanau for his field and lab expertise, and impressive design skills. I owe many thanks to a team of undergraduate students who provided major assistance with otolith reading.

I owe Carolyn Hall a great deal of appreciation for her contributions and guidance throughout this project, and for her help with historical dam and river herring population data and analysis. This research benefited from many conversations with Karen Alexander and William Leavenworth, who provided historical interpretations and feedback on earlier drafts, plus many wonderfully insightful conversations. Jason Carmignani, Eve Vogel, Steve Bittner, Chris Sutherland, Jack Finn, Mike Akresh, and Habib Mohamadi also contributed to the success of this project. I would also like to thank my parents, Tom and Becky Mattocks, for always being there for me, and for the constant love, support, and encouragement. I thank Pew Charitable Trust and the Lenfest Ocean Program, McIntire Stennis Fund, and UMass Department of Environmental Conservation for funding this research.

ABSTRACT

ECOLOGICAL CONSEQUENCES OF LOST ANADROMOUNS FORAGE FISH IN FRESHWATER ECOSYSTEMS

SEPTEMBER 2016

STEVEN RICHARDSON MATTOCKS, B.S., EAST CAROLINA UNIVERSITY

M.S., UNIVERSITY OF MASSACHUSETTS AMHERST

Directed by: Professor Adrian Jordaan

Beginning in the early 1600s, dam construction in New England obstructed anadromous fish access to spawning grounds during migration. As a result, anadromous forage fish populations have declined, which has impacted freshwater, marine, and terrestrial ecosystems. To determine the impacts of dams on anadromous forage fish and freshwater ecosystems, I used historical and current data to estimate population changes in alewives (*Alosa pseudoharengus*) from 1600-1900. A significant reduction in spawning habitat occurred in New England as a result of 1,642 dams constructed between 1600 and 1900, resulting in 14.8% and 16.6% lake and stream habitat remaining by 1900, respectively. In eight New England watersheds, this translates to an estimated cumulative annual loss of 30 B juvenile alewives available as freshwater forage and 538 M year 1, 2 and 3 alewives available as marine forage. The cumulative annual lost number of adult return spawners was conservatively 17 M fish, or 3,642 metric tons. Lost marine-derived nutrients from adult return spawners were 11 T phosphorus, 64 T nitrogen, and 410 T carbon. A comparison of predator fish growth and condition in alewife and non-alewife lakes showed that white perch (*Morone Americana*) and yellow perch (*Perca flavescens*) have higher condition in early summer in lakes with alewives. Predator growth rates (length-at-age) were significantly higher in early life stages (ages 1 and 2) when alewives were present, but significantly lower in late life stages (ages 3 and older). Results indicate a greater maximum length obtained by mature fish when alewives are absent, and an earlier age and length at maturity when alewives are present. These results indicate significant ecosystem impacts of lost anadromous forage fish, with bottom-up trophic effects across multiple time scales and biological processes. An ecosystem-based management approach should be used by inland and marine aquatic managers, and ecosystem connectivity and trophic interactions should be considered when managing migratory fish and prioritizing restoration goals.

TABLE OF CONTENTS

Page

CHAPTER

LIST OF TABLES

Table Page

LIST OF FIGURES

CHAPTER 1

INTRODUCTION

The European settlement of New England in the seventeenth century sparked an increased demand for natural resources. Resulting landscape changes included deforestation, erosion, water and air pollution, and aquatic habitat fragmentation from damming (Foster 2002, Hall et al. 2011). All of these landscape disturbances had compounding effects, and as a result, ecosystem structure and function was altered. Native predators were extirpated, forests were cleared, waterways were polluted, and local fish populations declined (Colligan et al 1999, Cumbler 2001, Limburg and Waldman 2009). Landscape changes from historical dam construction were particularly imperiling for native migratory fish, which are susceptible to habitat fragmentation because their life history and reproductive cycle require annual movements between freshwater and marine habitats (Hall et al 2012).

The damming of New England rivers and streams began in the early 1600s when waterways became fragmented by wood-crib and rock mill dams (Fleishman 1978, Hall et al. 2011, Mattocks et al. 2016). Colonial towns had high demands for saw and mill dams, which provided a reliable source of power needed to process timber for structural needs, as well as corn and wheat for flour and cooking. This demand increased as towns commerce increased and settlers turned more and more towards market economies, and as a result, dam construction increased across the region. By the nineteenth century, dam construction became more sophisticated and large rivers were dammed through the construction of mainstem concrete dams (Steinberg 1994). These dams were particularly deleterious to aquatic organisms because they obstructed a disproportionate amount of river, stream, and lake habitat. By 1850, most major rivers in New England had mainstem dams, leaving aquatic habitat severely fragmented (Hall et al 2011).

River herring, collectively alewives (*Alosa pseudoharengus*) and blueback herring (*A. aestivalis*), are anadromous clupeids that live in marine habitats but spawn in freshwater every spring. Alewives are distinguishable from blueback herring in that they spawn in coastal lakes and ponds, while bluebacks spawn in rivers and streams, although both species have been observed spawning in both habitat types (Pardue 1984). River herring require multiple movement events between freshwater and marine habitats at adult and juvenile stages. They are important mid-trophic level forage fish that transfer nutrients from plankton to larger commercially and recreationally important fish, as well as birds and marine mammals. As such, river herring are essential to aquatic, terrestrial, and marine food webs (Yako and Mather 2000, Dalton et al. 2009, Ames and Licher 2013).

Alewives are known to be important prey items for a number of organisms, and they play an essential role in food web dynamics. Returning adult spawners provide forage for freshwater, marine, and terrestrial predators, and bring a significant amount of nutrients to freshwater systems through excretion and mortality (Durbin et al. 1979). Every summer, juvenile alewives emerge from eggs in coastal ponds, where they spend the following 3-7 months feeding on plankton and serving as important prey items for freshwater predator fish (Yako and Mather 2000, Moring and Mink 2002). In the fall, juvenile alewives out-migrate from coastal ponds to marine environments where they spend the next 3-5 years reaching sexual maturity (Pardue 1984). Sexually mature adult alewives ascend freshwater streams in the spring to spawn. Alewives are iteroparous, or capable of multiple spawning events. Adults that survive spawning continue their life cycle, providing abundant, seasonally predictable sources of energy and nutrients to freshwater systems and marine ecosystems.

River herring were an important aspect of colonial life in New England, and were widely used for purposes of trade, fertilizer, and bait. River herring may also have had an earlier importance for Native Americans as fertilizer (Goode 1980), although the degree of use is unclear. As dam construction prospered, river herring populations declined, and domino ecosystem-effects occurred. In 2006, river herring were listed as species of concern by the National Maine Fisheries Service (NOAA 2006) with the primary causes of population decline reported as overfishing, waterway degradation, and habitat obstructions (ASMFC 2007).

New England towns struggled to restore aquatic habitat connectivity; there have been many efforts to protect alewives from harvest, as well as efforts to move fish over dams so they could reach spawning habitat (Steinberg 1994). Working fishways (fish ladders) have been installed to allow fish to bypass dams, and laws were implemented requiring dam operators to open dams and remove flash boards during certain days of the week. However, the high demand for hydropower and the expense of fish ladders has prevented widespread adoption of these strategies. The inefficiency of fishways and the abundance of mainstem dams continue to hinder the recovery of river herring populations.

There are many challenges in assessing historical population trends of species with centuries of exploitation. River herring experienced significant exploitation and population declines prior to accurate catch records, leaving historical baseline population estimates unclear. Consistent catch data began in the 1950s and current population assessments are often based on this historical data. Understanding how historical damming and natural resource use have impaired alewife populations can improve our estimates of historical fish populations (Alexander et al. 2009) and aid in management and research in evaluating current restoration goals (Hall et al 2012). Here, I estimate the lost river herring productivity at multiple life stages as a result of dams, and investigate impacts on freshwater and marine ecosystems. In addition, I investigate the short term and long term impacts of alewives on predator fish condition and growth in coastal pond ecosystems.

The second chapter of this thesis focuses on determining the consequences of historical dams on anadromous alewife populations and the resulting changes in freshwater and marine ecosystem dynamics. I address this by asking the questions: 1) How much alewife spawning habitat became inaccessible from 1600 to 1900? 2) How many alewives have been lost across different life stages, representing freshwater forage, marine forage, and adult return spawners? 3) How have dams impacted influxes of marine-derived nutrients (MDN) into freshwater ecosystems? and 4) Do freshwater predator fish rely on alewives as an important component of their diet? This information can be used to better understand the consequences of lost access to spawning habitat and resulting declines in forage fish populations, and how these changes have altered freshwater food web dynamics.

The third chapter of this thesis investigates the short and long term impacts of alewife presence and density on native predator fish condition and growth in coastal ponds. Alewives have a high fat content, making them energetically more important diet items compared to other species of prey (Iverson et al. 2002, FAO 2016). Because of this, juvenile alewives may be important in determining predator fish condition and may enhance overwinter survival and overall growth. I focus on two species of predator fish, yellow perch (*Perca flavescens*) and white perch (*Morone americana),* and incorporate zooplankton and other environmental data to better understand ecological changes at multiple trophic levels and time scales. Specifically, I ask the questions: 1) Does the presence and density of juvenile alewives impact the condition of perch? 2) Does the presence and density of juvenile alewives impact the growth of perch? To answer these questions, I investigated ponds where alewives were present and absent. This analysis elucidates the trophic changes and ecosystem consequences that have occurred as an indirect result of habitat fragmentation. Evaluating the response of predators to the removal of an important prey item is important for understanding food web complexity, habitat use, and community interactions, as well as consequences of the removal of anadromous forage fish from freshwater ecosystems.

CHAPTER 2

HISTORICAL DAMMING, ANADROMOUS FISH, AND ECOSYSTEM CONNECTIVITY

2.1 Abstract

The damming of New England watersheds obstructed anadromous fish access to spawning habitat beginning in the 1630s. This reduction in habitat has contributed to large-scale population declines of anadromous river herring; however, historical population estimates of river herring are unclear due to a paucity of historical catch data. To assess historical populations of river herring in New England, I combined historical habitat obstruction records with current freshwater productivity information. I produced a timeline of lost river herring production due to dams and detail the decline of adult spawning alewife and alewives available as freshwater and marine forage. Using nutrient data from previous research, I estimated lost marine-derived nutrients from adult river herring through mortality and excretion. These results indicate a significant decline in river herring production and marine-derived nutrients by 1900. Juvenile river herring are important to the diets of freshwater fishes, as evidenced through the diets of predator fishes from 28 coastal ponds where alewife are currently present. I conclude that declines in production due to dams have dramatically affected freshwater food webs. A more comprehensive view of freshwater and marine ecosystem function and connectivity is required to inform restoration goals and to adequately assess the ecological significance of lost river herring.

2.2 Introduction

2.2.1 Aquatic Habitat Connectivity

Migratory anadromous fishes rely on habitat connectivity between freshwater and marine ecosystems to complete their life cycle. River habitat fragmentation beginning in the early 1600s in northeastern United States has disrupted this connectivity, occluding anadromous fishes from spawning grounds (Hall et al. 2011). The damming of rivers and streams has been a primary driver in population declines of north Atlantic anadromous fishes (Limburg and Waldman 2009, Hall et al. 2011, ASMFC 2007), particularly forage fish that are essential prey items for marine, aquatic, and terrestrial organisms.

Quantitative and qualitative historical information such as log books, export data, and anecdotal information has been used to inform fish population estimates for ecosystem modelling (Pauly 1995, Swetnam et al. 1999, Jackson et al. 2001, Alexander et al. 2009, Hall et al. 2012). In many northeastern United States rivers and streams, dams may mark the first major disturbance to anadromous river herring, collectively alewives (*Alosa pseudoharengus*) and blueback herring (*A. aestivalis*). Dams directly disrupt spawning migrations by reducing access to spawning habitat; thus, a timeline of habitat loss can be used as a proxy for reduced abundance (Hall et al. 2011, Hall et al. 2012). Here, I focus on river herring to elucidate the consequences of lost access to spawning habitat, with an emphasis on lost production. Using obstruction records and freshwater productivity information, I reconstructed historical populations of river herring. Historical documents were used to validate obstruction dates and locations, as well as the historical presence of river herring. In addition, I explore how lost alewife productivity from centuries of damming influenced freshwater and marine ecosystems. Finally, I quantified the importance of juvenile river herring to predator fish in coastal New England ponds and discuss ecosystem impacts of lost forage fish.

River herring are an economically and ecologically important species that inhabit coastal waters from Canada to Florida. River herring migrate annually from marine to freshwater habitat to spawn from March to July, depending on temperature and other environmental conditions (Neves 1981, Pardue 1983). Alewives typically spawn in lakes and ponds, while blueback herring predominately spawn in rivers and streams, although both species have been documented as potentially spawning in both habitat types (Pardue 1983). River herring return to natal streams, and are iteroparous, capable of multiple spawning events over their life cycle (Jessop 1994). After three months to one year in fresh or brackish water, juveniles emigrate to the marine environment where they primarily feed on zooplankton (Bigelow and Schroeder 1953). River herring become sexually mature at three to five years (Pardue 1983) after which they begin their first of several potential spawning migrations to freshwater.

This dynamic spatial behavior throughout their life cycle makes river herring particularly vulnerable to habitat obstructions. These obstructions have led to the decline of this forage fish (Limburg and Waldman 2009, Hall et al. 2012), altering food webs and reducing nutrient exchange between marine and freshwater ecosystems.

2.2.2 Historical Dams

The New England hydrologic landscape was drastically altered by damming. Early seventeenth century dams were constructed on small rivers and streams and typically functioned to power saw and grist mills which were integral to the economic growth and development of early New England towns (Cumbler 2001). Dams constructed in the eighteenth and nineteenth century began to serve larger industrial purposes that included powering large industries such as cotton factories, iron forges, and brick manufacturers (Steinberg 1994). Diversion dams were also constructed to direct water to canals, bypassing waterfalls to serve navigational purposes (Spence 1930). By the nineteenth century, dams became ubiquitous throughout New England, with nearly every river and stream dammed by 1900 (Cumbler 2001, Hall et al. 2011). Mainstem dams, those that span the main channel of rivers, were present on most major rivers in New England by 1850, substantially reducing access to upstream habitats for migratory fish (Hall et al. 2011). Many towns made efforts to reduce the disturbance of dams on anadromous fishes by requiring the construction of fish passage systems (fishways) or by requiring dams to be open seasonally (Secretary of the Commonwealth 1887). However, a lack of maintenance and enforcement stymied the efficacy of fish passages, and due to a plethora of issues including privatization of ponds and rivers, year-round demands for milling, and poor fishway design, fish passage systems have been largely unsuccessful (Steinberg 1994, Noonan and Grant 2012, Brown et al. 2013).

Dams not only prevent fish passage; they significantly alter ecosystems (Ben-David et al. 1998). Dams prevent the downstream flow of organic material, sediment, and nutrients, thus decreasing alluvial deposition and altering biological productivity in downstream ecosystems (Zhou 2015). Nutrients in watersheds are currently dominated by anthropogenic sources, whereas historical nutrient inputs would have been higher quality marine-derived nutrients from migratory fish. With the construction of dams, riverine habitat becomes characteristic of pond, lake, and reservoir habitat, with altered water clarity, temperature, and biotic assemblages (Ward et al. 2015). Additionally, aquatic invasive plant species such as didymo (*Didymosphenia geminate*) can thrive in near dams, further altering aquatic ecosystems (Kirkwood et al. 2009). Dams can also have adverse energetic costs for anadromous fish that can reduce survival and iteroparity (Castro-Santos and Letcher 2010), further contributing to their declines. It is important to note that beavers played an essential role in altering aquatic habitats, however, it is relatively unclear how these alterations impacted river herring spawning migrations and habitat quality.

2.2.3 River Herring Populations

In 2006, river herring were listed as species of concern under the Federal Endangered Species Act by the National Marine Fisheries Service (NOAA 2006). In the Atlantic States Marine Fisheries Commission (ASMFC) 2007 benchmark report, a similar anadromous forage fish species, American shad (*Alosa sapidissima*) were reported to be at an all-time low due to a combination of excess total mortality, habitat degradation, and habitat access impediments (ASMFC 2007). Thus, overfishing and damming constitute major population recovery impediments for multiple anadromous fish species.

A lack of historical catch data has resulted in unclear population estimates, making it difficult to establish baselines for restoration. Current river herring populations are often evaluated by regulatory and research agencies by comparison to populations in the 1950s when consistent landings records began. Because anthropogenic disturbances predate population assessments, the 1950s data is a poor reference for understanding population changes due to human harvesting and landscape disturbances. Accurate population baselines are needed to inform current restoration efforts and improve ecosystem understanding, and are essential for stock evaluation by federal and state agencies. Establishing a chronology of dam construction can give insight to historical anadromous fish populations and resulting ecosystem consequences.

2.3 Methods and Results

2.3.1 Documenting Historical Dams

In order to establish a timeline of lost access to spawning habitat for river herring, I documented dams erected between 1600 and 1900 in five southern New England watersheds: Merrimack, Connecticut, Thames-Pawcatuck, Narragansett, and Coastal Massachusetts. I documented 1642 dams in these five watersheds using historical documents, and used an additional 121 dams from The Nature Conservancy (Martin and Apse 2011) dam database (Figure 2.1).

To determine the amount of river herring spawning habitat prior to colonial dam construction, I used a published historical map from an early US Fish Commissioner Report detailing the natural migration limits of the American shad prior to dams along the east coast (Baird 1884). Historical accounts and sightings from town histories, commissioner reports, and anecdotal information were used to confirm American shad migration limits and establish historical river herring limits (Figure 2.3). Historical accounts revealed river herring and American shad native ranges to be nearly identical; therefore, I used American shad boundaries to represent river herring migration limits.

2.3.2 GIS Network Analysis

I used the U.S. Geological Survey's National Hydrography Dataset (NHD) and Watershed Boundary Dataset (WBD), along with the Utility Network Analyst tool in ArcGIS 10.2, to calculate the length of stream habitat and area of lake habitat upstream of dams within the historical migration limits of river herring. Because alewives preferentially spawn in lakes and bluebacks preferentially spawn in rivers, I used pond and lake habitat lost (km^2) to represent alewife spawning habitat, and stream and river habitat lost (km) to represent blueback herring habitat.

My analyses found that all five watersheds in Southern New England experienced a significant reduction in available spawning habitat by 1900. The mean lake and stream habitat remaining in 1900 for the five focus watersheds was 14.8% ± 12.2% and 16.6% ± 15.5% of original habitat, respectively. The greatest reduction in river and stream habitat occurred in the Connecticut and Merrimack River watersheds, with 6.7% and 7.9% habitat remaining by 1900, respectively. The greatest loss in lake and pond habitat occurred in the Merrimack and Thames-Pawcatuck River watersheds, with 2.8% and 6.4% habitat remaining in 1900. The coastal Massachusetts watershed had the most spawning habitat available in 1900, with 43.5% river and 51.8% lake habitat remaining (Figure 2.2).

The first known man-made structure that obstructed migratory fish (not including Native American weirs) was built in Coastal Massachusetts on the Charles River in 1632 (Francis 1871, Fleishman 1978) and eight years later over 25% of river habitat and over 21% of lake habitat within the Charles River watershed were occluded by dams. The coastal Massachusetts watershed had significantly more dams constructed from 1600-1750 compared to other watersheds; however, due to the interconnectivity of streams and a plethora of undammed intertidal creeks that are potential spawning grounds for blueback herring, a higher percentage of habitat remained in coastal Massachusetts compared to inland streams by 1900. Coastal streams were practically the only available habitat remaining by 1900. Although waterway obstructions existed in coastal New England towns, such as tide mill-dams, the morphology of the landscape was less ideal for waterpower compared to the sloped landscape inland. Because of the pattern of habitat loss across the landscape, a shift in habitat use by river herring from inland rivers and lakes to coastal streams and ponds may have occurred.

In order to provide a more comprehensive view of habitat loss in New England, I compared habitat loss in five southern New England watersheds with three Gulf of Maine watersheds (Hall et al. 2012). The Gulf of Maine watersheds used for this comparison were the Androscoggin, Kennebec, and Penobscot, which are similar to southern New England watersheds in size and in landscape development pattern, and contain historically important spawning habitat for river herring. These two major regions for river herring and American shad production experienced a near complete loss in spawning habitat by 1900, with reductions to 6.5% and 16.6% of original available river habitat for the Gulf of Maine and southern New England watersheds, respectively. This similar pattern of habitat loss from Maine to Connecticut is reflective of the industrial history within the region. Southern New England watersheds had a greater number of dams constructed before 1718 compare to Gulf of Maine watersheds (Figure 2.1). Due to the landscape features and settlement patterns, southern New England watersheds experienced earlier but less severe habitat loss. The reduction in spawning habitat from dams is the first large-scale disturbance that significantly altered river herring production (Hall et al. 2011, Hall et al. 2012).

2.3.3 Lost River Herring Production

In order to understand the consequences of lost spawning habitat on river herring production, I investigated juvenile alewife productivity in Massachusetts lakes and ponds where spawning habitat is currently accessible. To estimate current alewife productivity, I used juvenile alewife data from 18 coastal New England ponds. All ponds are located in eastern Massachusetts and are accessible to anadromous fish through single or multiple fish ladders. Young-of-year (YOY) alewife density data were obtained from pelagic purse-seine netting (30.5 m x 4.3 m) at night during the summer of 2014, with sampling occurring in June, July, and August. Densities were calculated using the number of alewives captured per pond surface area (km^2) covered by the net. I used the maximum monthly YOY alewife densities to represent peak YOY alewife production for each pond.

To estimate potential YOY alewife productivity from all lake habitats, I applied the median value of peak emigrating alewife densities from the 18 ponds to the total pond and lake area within eight New England watersheds. This represents a conservative estimate of the number of potential fish produced under the scenario of restored spawning habitat, represented by

$$N_{\mathrm{t}} = A_h D_y$$

where YOY density (D) is expressed as number of YOY fish/km^2, area (A) is the total area (km^2) of pond and lake habitat within the eight New England watersheds, and production (N) is the potential number of YOY fish emigrating to marine habitat produced from ponds and lakes in New England. I then applied a conservative mortality rate of 99% (Rosset 2016) to each lake to estimate the number of fish (N_0) emigrating to the ocean.

To estimate subsequent year classes of alewives, I used the exponential model of population growth (Gotelli 1998)

$$N_{t+1} = N_t^{e-Z}$$

and predicted abundances of alewives at year- 2, 3, and 4 (Figure 2.4). N represents the number of fish at time t, and Z is the annual instantaneous (total) mortality rate. I used a conservative annual mortality rate of 0.8 to estimate historical alewife age structure

(Hall et al. 2012). I assumed an average juvenile emigration date of 1 September and an average adult spawn date of 1 May to calculate population estimates, which were used to inform time steps of the population model. I used an average age of 4 for adult returning fish (Davis and Schultz 2009, Hall et al. 2012) and an average fish weight of 0.204 kg (Bigelow and Schroeder 1953, Hall et al. 2012) to indicate lost biomass of adult returning fish. I calculated lost alewife productivity at multiple life history stages: (1) YOY as food for freshwater predators, (2) emigrating YOY (N_0), year-1 (N_1), year-2 (N_2), and year-3 (N_3) fish as food for marine predators, and (3) adult spawners (N_3) returning to freshwater habitat. The age structure of spawning river herring has changed over time, which has implications for spawning productivity and fecundity; thus, our populations estimates are likely conservative.

Alewives that experienced mortality in freshwater systems represented forage available to aquatic, terrestrial, and bird predators. The cumulative annual lost number of alewives as freshwater and marine forage were 3.0×10^{10} and 5.3×10^{8}, respectively (Figure 2.5). In addition, the estimated cumulative annual lost number of adult returning alewife was 1.7×10^{7}, which is equivalent to 3,642 metric tons.

Adult production (fish/km^2) variability was high for the 18 ponds (mean: 92,871; SD: 251,771) compared to adult-derived estimates from the Damariscotta system (mean: 63,535; SD: 34,462) in Maine (Crecco and Gibson 1990, Hall et al. 2012). Due to the high production variance among the 18 Massachusetts systems (mean: 92,871; median: 16,135), I used the median value of juvenile densities as a conservative measure to estimate populations. The 18 ponds used in this analysis vary in size, depth, fish accessibility, and adult spawning density, which contribute to high variance in production estimates.

2.3.4 Alewives in Marine and Freshwater Ecosystems

The importance of adult river herring as prey is well understood (Dalton et al. 2009, Davis et al. 2009), particularly in marine environments (Bowman 1975, Bowman et al. 2000, Ames and Lichter 2013). Due to their marine trophic importance and the value for commercial harvest, research has primarily focused on the marine consequences of lost river herring populations. Research has shown that a decrease in forage fish was linked to declining condition of the semi-anadromous striped bass (*Morone saxatilis*) in the 1990s (Hartman and Margraf 2003), which may have occurred with other predators of anadromous forage fish. Distributions of marine fishes may also be directly influenced by alewives, evidenced by the movement of white hake (*Urophyci tenuis*) in the Gulf of Maine (Ames 2012, Ames and Lichter 2013), which was correlated with juvenile alewife out-migrations.

Consumption of alewives by predators is not exclusive to marine ecosystems. Alewives spend a large portion of time in freshwater ecosystems during the juvenile stage where they are particularly vulnerable and widely available to a variety of aquatic and terrestrial consumers. In particular, white perch (*M. americana*), yellow perch (*Perca flavescens*), largemouth bass (*Micropterus salmoides*), and smallmouth bass (*Mi. dolomieu*) may be important consumers, as they have a large temporal and spatial overlap with YOY river herring.

Previous research regarding river herring in freshwater food webs has largely focused on negative interactions, with concerns about alewives competing with non-native sport fish during juvenile and adult stages (Kircheis et al. 2002). Follow-up studies in anadromous systems showed that alewives are not direct competitors of sport fish and do not hinder condition of YOY smallmouth bass (Willis 2006).

Only a handful of other studies have focused on river herring as prey in natural communities of freshwater systems (Yako and Mather 2000, Moring and Mink 2002). Yako and Mather (2000) created bioenergetics models for two coastal ponds to evaluate the importance of river herring as prey items for largemouth bass. In their study, alewives were the most numerically and energetically important fish. Moring and Mink (2002) showed that alewives were also an important diet item for white perch during the summer months in Maine pond, which is likely true for a number of resident predators in other coastal New England ponds. Ecosystems historically had more abundant influxes of YOY alewives, providing freshwater predator fish with a predictable lipid-rich forage base for a portion of the year.

2.3.5 Freshwater Predators

To better understand the ecological importance of alewives, I explored alewives' role in freshwater ecosystems by employing gut content analysis (GCA) on nine species of predator fish from 28 coastal ponds in eastern Massachusetts where anadromous alewives are currently present (Figure 2.3). Predator fish included black crappie (*Pomoxis nigromaculatus*), largemouth bass, smallmouth bass, chain pickerel (*Esox* *niger*), white perch, yellow perch, brown bullhead (*Ameiurus nebulosus*), bluegill (*Lepomis macrochi*rus), and pumpkinseed (*L. gibbosus*). Ponds were sampled using pelagic purse seine nets and beach seine nets in the summer (27 July-15 August 2014; 2 June-11 September 2015), after the emergence of juvenile alewives from eggs, but before emigration of alewives to marine habitat.

Diets of predators (n=645) were described by % occurrence (%O), % number (%N), and % weight (%W). These dietary measures provide different insights into feeding behaviors of fish. Occurrence represents population wide food habits (Cailliet 1977), numeric is informative for feeding behavior (Macdonald and Green 1983), and volumetric is reflective of dietary nutritional importance (Macdonald and Green 1983). I calculated Pinka's index of relative importance (IRI),

$$IRI = (\%W + \%N)\ \%O$$

which was expressed as a percentage to make prey categories comparable across predator species (Pinkas et al. 1971),

$$\%\ IRI = 100\ IRI\ /\ \sum^{n} IRI$$

with n representing the total number of food categories considered at a given taxonomic level. Fish in guts were identified to species using voucher specimens and identification guides (Werner 2004). Invertebrates and unidentifiable matter were grouped into separate categories.

Predation on YOY alewives was observed by eight of the nine freshwater predator species examined: black crappie, largemouth bass, smallmouth bass, chain pickerel, white perch, yellow perch, brown bullhead, and bluegill. Pumpkinseed was the only predator fish that did not consume alewives. Alewife %IRI values were highest for brown bullhead (50.5%), white perch (36.9%), black crappie (20.9%), and smallmouth bass (16.8%) (Figure 2.6). Alewife %W values were also highest for white perch (49%), black crappie (29%), brown bullhead (21%), and smallmouth bass (21%), which may be more relevant for advanced ecosystem modelling (Table 2.1). Most of these fish feed primarily on invertebrates and small fish throughout their life history and YOY alewives may be utilized by more aggressive, opportunistic feeders (Hartel et al. 2002). Smaller predator fish, particularly bluegill and pumpkinseed, may be physically limited earlier in life history as a function of gape size and prey body depth (Staudinger and Juanes 2010).

The presence of YOY alewives in the stomachs of various predator species indicates their dietary and energetic importance to consumers in freshwater ponds. Seasonal influxes of organisms may contribute to increased condition and overwintering survivorship of predators. The use of YOY anadromous fish by freshwater predators occurs in rivers as well as ponds, and has been found to be important for predator diets (Trippel et al. 2015). Trippel and colleagues (2015) outlined the importance of seasonally available forage fish to largemouth bass diets in St. John’s River, Florida. Although migratory forage fish are seasonally available to predators in many coastal river systems, many landlocked-systems where anadromous forage fish are absent are stocked with lower trophic level fish in order to provide a reliable forage base (Noble 1981). Gizzard shad (*Dorosoma cepedianum*) are often stocked in freshwater impoundments as a forage item for freshwater predators; however, due to rapid growth and morphological constraints, gizzard shad quickly reach sizes that exclude them from predation (Bonds 2000, Evans et al. 2015). The lack of prey can result in unstable food supplies and declining growth rates for competing predators (Bonds 2000). Gizzard shad are functionally comparable to alewives in impoundments due to similar feeding habits, habitat use, and growth rates (Willis 1987, Bonds 2000, Rosset 2016). As a result of dammed systems, the loss of juvenile river herring likely altered trophic dynamics, causing predators to shift diets to other native fishes and invertebrates.

The increased productivity of connected systems is evident when compared to dammed systems. Undammed lakes with open access to rivers and streams are able to support pulses of forage fish at high magnitudes because of the transience of anadromous fish. Freshwater lakes and ponds support anadromous adult alewife populations for 2-4 months and anadromous juvenile alewife populations for 3-9 months (Pardue 1983, Gahagan et al. 2010). With shorter residency times compared to landlocked populations, anadromous river herring obtain most of their biomass from marine ecosystems, reducing the pertinence of carrying capacity as a limiting factor (Bigelow and Schroeder 1953). Thus, landlocked alewives exhibit slower growth, with smaller size and earlier age at maturity compared to anadromous populations (Graham 1956, Davis and Schultz 2009).

2.3.6 Lost Marine-Derived Nutrients

The loss of annual influxes of marine-derived nutrients (MDN) from river herring as a result of damming impacts trophic dynamics in freshwater ecosystems (Bilby et al. 1996, Hicks et al. 2005, Twining et al. 2013, Childress et al. 2014). Anadromous fish provide an important and reliable source of MDN through excretion (feces and gametes) and mortality (carcasses). With open access to spawning habitat, MDN from anadromous fish become widely available for transport by predators (Hilderbrand et al. 1999), and can have a significant positive impact on riparian production (Hicks et al. 2005, Childress et al. 2014). The importance of habitat connectivity was exemplified by Pacific salmon, as shown by Reimchen and colleagues (2002) who identified a relationship between the spawning density of Pacific salmon and nitrogen enrichment in soil, riparian vegetation, and riparian insects. In addition, MDN from anadromous fish can increase growth of juvenile offspring in streams (Bilby 1996). Juvenile emigrating anadromous fish also export a significant amount of nitrogen and phosphorous to marine environments (Moore and Schindler 2004, West et al. 2010), further connecting aquatic ecosystems.

Gresh and colleagues (2000) estimated that current levels of MDN from salmon in the Pacific Northwest are at 6-7% of historical levels. This reduction began in the 1880’s with the peak commercial harvest of salmon in areas south of the Fraser River (Cobb 1930). Yet anthropogenic disturbances on the east coast began impacting Atlantic anadromous fish stocks 200 years earlier (Hall et al. 2011, Hall et al. 2012). Unlike Pacific salmon, the Atlantic salmon (*Salmo salar*) became severely depleted in the early 1800s, with three of the five largest salmon populations (Connecticut, Merrimack, and Androscoggin River) eliminated by the end of the 19th Century (Colligan et al. 1999). These earlier disturbances to Atlantic anadromous fish stocks are largely the result of habitat access impediments (Hall et al. 2011, Brown et al. 2013). Although river herring are iteroparous and experience less post-spawn mortality than Pacific salmon, due to their high historical abundances, they likely contributed significantly to nutrient loading in freshwater systems.

I estimated the loss of MDN from adult return spawning alewives using nutrient values of adult fish pre- and post-spawn from published research (Durbin et al. 1979). Values of carbon (C), nitrogen (N), and phosphorous (P) for adult alewives were 33.7, 6.11, and 1.04 g, respectively, and values for excretion (nutrients pre-spawn – nutrients post-spawn) were 12.9, 1.17, and .18 g for C, N, and P, respectively (Durbin et al. 1979). Mortality rates of spawning alewives vary between 30 and 90% depending on physical, geographical, and environmental variables, thus I assumed a conservative mortality rate of 50% (Havey 1961; Dalton et al. 2009; Kissil 1974).

The cumulative annual loss of MDN from historical damming from 1600-1900 for C, N, and P were 410, 64, and 11 metric tons, respectively (Figure 2.5). Most of the nutrients were transferred through mortality events, by which they were available to the food web at multiple trophic levels. Nutrients from excretion were 38, 19, and 17% of the pre-spawn whole fish nutrient content of adult alewives for C, N, and P, respectively (Durbin et al. 1979). The reported loss in magnitude of historical nutrients is only reflective of alewives and does not include bluebacks. Other Atlantic anadromous species that would have significantly contributed to food web productivity and ecosystem connectivity are bluebacks, Atlantic salmon, American shad, and particularly the sea lamprey (*Petromyzon marinus*), which leaves carcasses after spawning (Weaver et al. 2015). The contributions of marine derived nutrients were particularly important for freshwater productivity due to their higher quality compared to nutrients from nearby landscapes.

Many techniques have been used to estimate historical trends of MDN to better understand past ecosystems. Paleolimnological analysis of sedimentary diatoms has been used to reflect historical salmon abundances (Gregory-Eaves 2003). Similarly, Gresh and colleagues (2000) evaluated historical cannery records to estimate salmon abundance in past ecosystems. Stable nitrogen isotope analysis (ratio of 15N to 14N) of wood has been used to elucidate nitrogen cycling on millennial timescales in anadromous fish habitat (Drake et al. 2011, Gerhart and McLauchlan 2014). The emergence of these techniques to assess historical fish populations and MDN can further our understanding of past ecosystems and the consequences of lost ecosystem connectivity.

2.4 Indirect Effects of Dams

A significant reduction in alewife spawning habitat and productivity occurred by 1900 as a result of dams. This resulted in significant ecosystem consequences that impacted freshwater and marine ecosystems; freshwater and marine forage, as well as marine-derived nutrients declined significantly. Although these are direct impacts, the damming of rivers and streams can have indirect effects on ecosystem processes (Marczak et al. 2007) through the creation of landlocked populations of river herring. Intraspecific variation in alewife morphology between landlocked and anadromous populations has a major influence on the trophic dynamics in freshwater systems

(Twining and Post 2013), which can have a cascading effect on lower trophic organisms (Post et al. 2008). Phenotypic divergence of morphological traits can also regulate community structure of alewife prey (Post et al. 2008) and competitors (Huss et al. 2014), lending more credence to the widespread ecosystem effects of dams.

Habitat obstructions may have additional significant effects on alewives that are not fully understood. Current alewife runs are comprised of smaller, younger alewives than runs in the 1960s (Davis and Schultz 2009). Although this shift in demography and life history is credited to predation pressure and fisheries mortality of older individuals, dams exacerbate these divergences by truncating habitat availability and altering migratory behavior. In addition, fish passage systems can select for various physiological traits (Volpato et al. 2009), which can further alter ecosystem structure and function. It is unclear how altered age structure and morphology from dams impacted these estimates. My estimates are likely conservative because I only used one age class of spawning fish, whereas multiple age classes actually spawn. Historical alewife populations lived up to eight years; these fish likely produced more eggs than age-4 fish.

The combination of habitat truncation from damming and climate change may have compounded negative effects for recovering anadromous populations. Rising sea surface temperatures have been negatively correlated with the condition and lipid content of spawning adult Atlantic salmon (Todd et al. 2008). Temperature has been shown to drive life-history modifications of migratory fishes, influencing the proportion of residents and migrants (Morita et al. 2014). In addition, increased hydrologic variability with climate change is expected to have negative effects on depleted anadromous fish populations (Ward et al. 2015), which is exacerbated by dams. Changes in the timing, magnitude, and duration of stream and river flows as well as extreme events and temperatures expected with climate change can decrease recruitment, survival, and productivity of anadromous salmonids (Jonsson and Jonsson 2009, Ward et al. 2015). The presence of natural barriers can influence response to climate change for freshwater resident fish by further altering temperatures and restricting migration routes (Daufresne and Boët 2007). All of these factors add to the uncertainty and unintended ecological consequences for recovering migratory fish populations.

2.4.1 Future Restoration in New England

New England has undergone extensive landscape transformations throughout the last 400 years, including deforestation (Foster 2002), urbanization (Steinburg 1994, Cumbler 2001), and altered morphology of river networks (Walter and Merritts 2008). In a comprehensive review of river restoration projects in the United States, Bernhardt and colleagues (2005) highlighted fish passage as one of the primary goals of river restoration projects. This aspect of restoration has become increasingly the focus of scientific inquiry. As such, dam removal has been prioritized by many restoration groups. It is clear that mainstem dams blocked more spawning habitat than smaller dams; however, when combined, smaller obstructions such as high order stream dams and culverts can block a significant amount of habitat. As many major dams in New England are currently in the relicensing process, our estimates provide robust ecological support for dam removal and increased ecosystem connectivity.

Enhancing our understanding of habitat use by juvenile river herring would help prioritize habitat restoration projects. Although alewives are known to predominately use pond and lake habitat for spawning, little is known about spawning success below dams or in estuarine habitat. This paucity of research makes interpreting productivity data difficult. Because of a shift in available spawning habitat from ponds and lakes to streams and estuaries occurred from dams, assessing juvenile river herring productivity in various aquatic habitats would inform future management strategies and restoration scenarios.

Annual influxes of forage fish provide a predictable pulse of nutrients that are available to a variety of freshwater predator fish. The assimilation of these resources into freshwater food webs is incorporated at multiple trophic levels, influencing interactions at different scales. It is clear that recovering lost anadromous populations will require large scale habitat restoration, primarily dam removal, and in cases where this is not plausible, adequate fish passage systems should be used. Although river herring were the focus of this study, the negative impacts of dams have similar consequences for all diadromous fish species. If other diadromous fish productivity data were incorporated into estimates, lost production values would be orders of magnitudes higher. Accurate estimates of historical anadromous fish populations will only be developed with the inclusion of historical, cultural, and ecological data. Restoration projects using dam removal should consider ecological gains in terms of quality and quantity of spawning habitat gained, with life history, anthropogenic impacts, and changing climatic conditions in mind. When designing restoration projects, understanding ecosystem consequences to fragmented habitat in freshwater and marine environments will maximize benefits of restored habitat and will help prioritize future restoration efforts.

Table 2.1: Diet items from nine freshwater predators expressed as percent frequency of occurrence (%O), percent by number (%N), percent by weight (%W), and percent index of relative importance (%IRI).

	White Perch (n=95)				Yellow Perch (n=150)				Largemouth Bass (n=35)			
Prey Category	%O	%N	%W	%IRI	%O	%N	%W	%IRI	%O	%N	%W	%IRI
alewife *Alosa pseudoharengus*	23.16	58.20	49.20	36.91	6.00	7.69	16.98	1.54	17.14	15.00	9.42	7.62
bluegill *Lepomis macrochirus*	-	-	-	-	-	-	-	-	5.71	5.00	16.68	2.26
yellow perch *Perca flavescens*	-	-	-	-	-	-	-	-	2.86	2.50	4.44	0.36
white perch *Morone americana*	-	-	-	-	0.67	0.59	0.37	0.01	-	-	-	-
largemouth bass *Micropterus salmoides*	-	-	-	-	-	-	-	-	-	-	-	-
golden shiner *Notemigonus crysoleucas*	1.05	0.53	0.81	0.02	-	-	-	-	-	-	-	-
tessellated darter *Etheostoma olmstedi*	-	-	-	-	-	-	-	-	-	-	-	-
banded killifish *Fundulus diaphanus*	1.05	0.53	0.79	0.02	-	-	-	-	2.86	2.50	9.19	0.61
invertebrates	54.74	27.51	40.37	55.14	64.67	57.40	53.42	74.62	42.86	37.50	20.54	45.29
unidentifiable matter	26.32	13.23	7.02	7.91	38.00	33.73	26.50	23.83	42.86	37.50	18.71	43.86

	Smallmouth Bass (n=10)				Black Crappie (n=105)				Chain Pickerel (n=35)			
Prey Category	%O	%N	%W	%IRI	%O	%N	%W	%IRI	%O	%N	%W	%IRI
alewife	20.00	26.67	20.95	16.75	25.71	49.12	28.66	20.94	2.86	4.17	0.43	0.51
bluegill	-	-	-	-	-	-	-	-	2.86	4.17	4.97	1.01
yellow perch	-	-	-	-	-	-	-	-	5.71	8.33	58.50	14.84
white perch	-	-	-	-	-	-	-	-	-	-	-	-
largemouth bass	-	-	-	-	-	-	--	-	11.43	16.67	11.22	12.39
golden shiner	-	-	-	-	-	-	-	-	-	-	-	-
tessellated darter	10.00	6.67	8.05	2.59	-	-	-	-	5.71	8.33	0.69	2.00
banded killifish	30.00	20.00	38.80	31.03	-	-	-	0.00	2.86	4.17	0.26	0.49
invertebrates	30.00	20.00	10.63	16.16	69.52	42.69	62.68	76.71	5.71	8.33	3.97	2.73
unidentifiable matter	40.00	26.67	20.89	33.46	13.33	8.19	8.65	2.35	31.43	45.83	8.21	66.02

	Brown Bullhead (n=12)				Bluegill (n=138)				Pumpkinseed (n=64)			
Prey Category	%O	%N	%W	%IRI	%O	%N	%W	%IRI	%O	%N	%W	%IRI
alewife	50.00	69.64	21.04	50.48	1.45	1.43	0.16	0.01	-	-	-	-
bluegill	-	-	-	-	-	-	-	-	-	-	-	-
yellow perch	8.33	1.79	14.10	1.47	-	-	-	-	-	-	-	-
white perch	-	-	-	-	-	-	-	-	-	-	-	-
largemouth bass	-	-	-	-	-	-	-	-	-	-	-	-
golden shiner	-	-	-	-	-	-	-	-	-	-	-	-
tessellated darter	-	-	-	-	-	-	-	-	-	-	-	-
banded killifish	8.33	5.36	1.86	0.67	-	-	-	-	-	-	-	-
invertebrates	75.00	16.07	16.35	27.08	87.68	86.43	85.88	97.90	71.88	62.16	66.18	74.63
unidentifiable matter	33.33	7.14	47.55	20.30	12.32	12.14	13.96	2.08	43.75	37.84	33.82	25.37

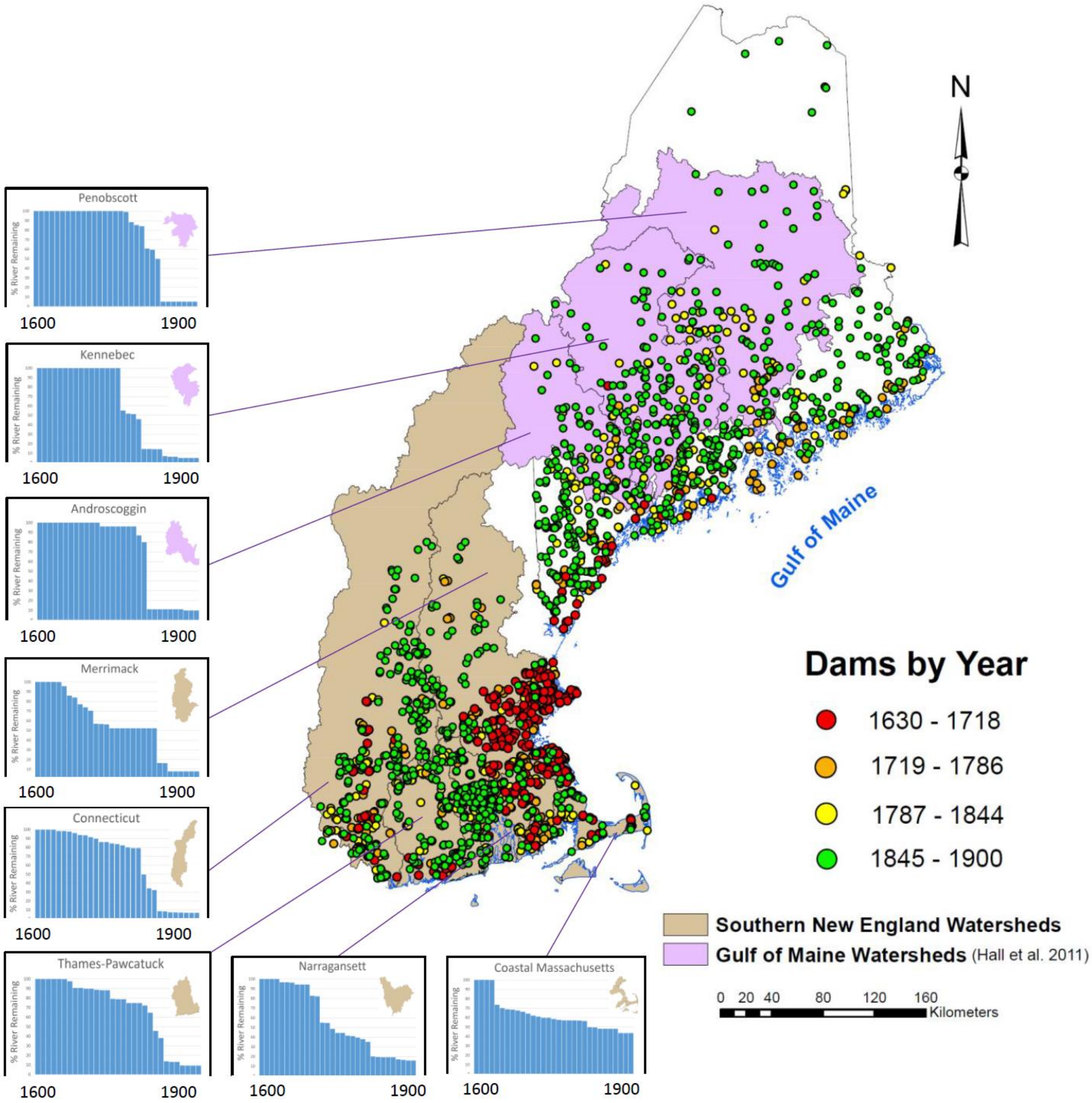


Figure 2.1: Historical dams and resulting timelines of habitat loss (inset graphs) from 8 watersheds in New England. Dams were classified using natural breaks and projected using Massachusetts State Plane 2001 projection.

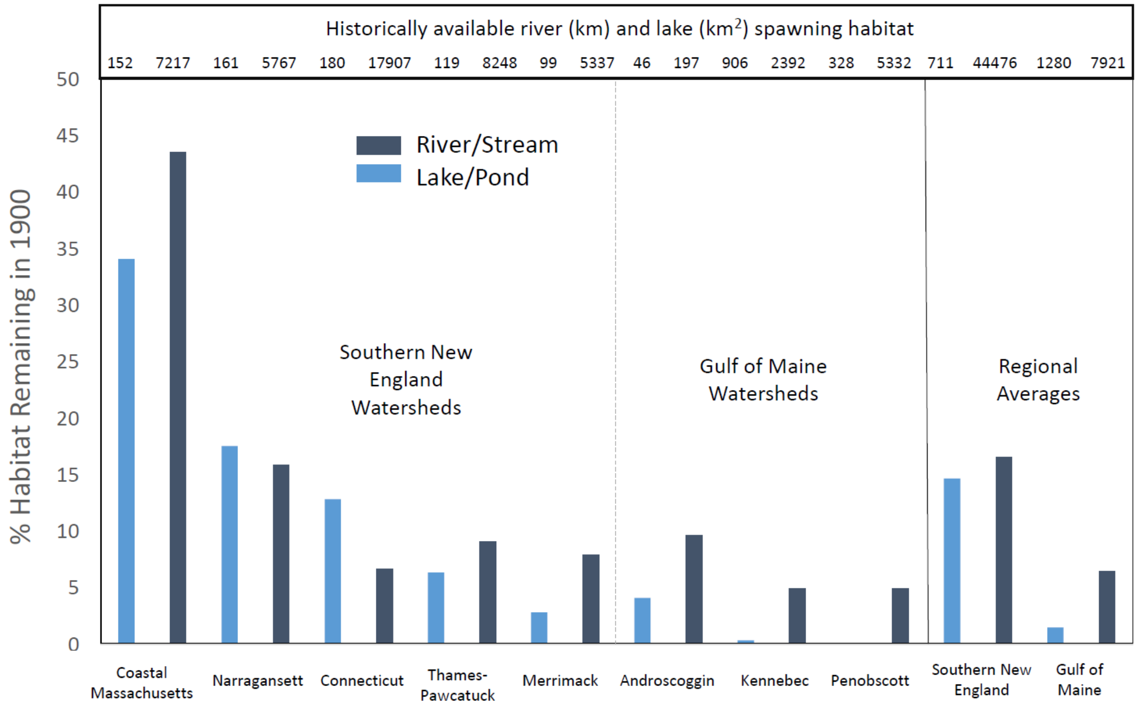


Figure 2.2: Percent lake and stream habitat remaining in 1900 for 5 watersheds in Southern New England and 3 watersheds in the Gulf of Maine (Hall et al. 2011).

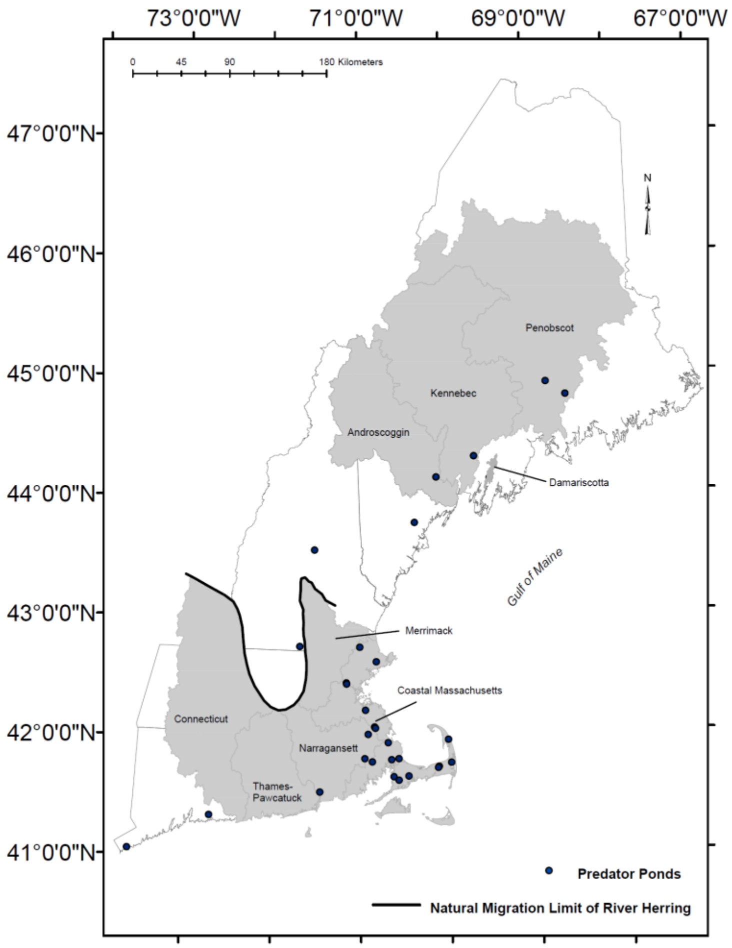


Figure 2.3: Five New England watersheds and three Gulf of Maine watersheds with points showing lakes where predators were collected. Solid black line represents the natural migration limit of American shad and river herring in Southern New England (Baird 1884). Historical map was georeferenced and projected using Massachusetts State Plane Coordinate System with 3rd order polynomial transformation.

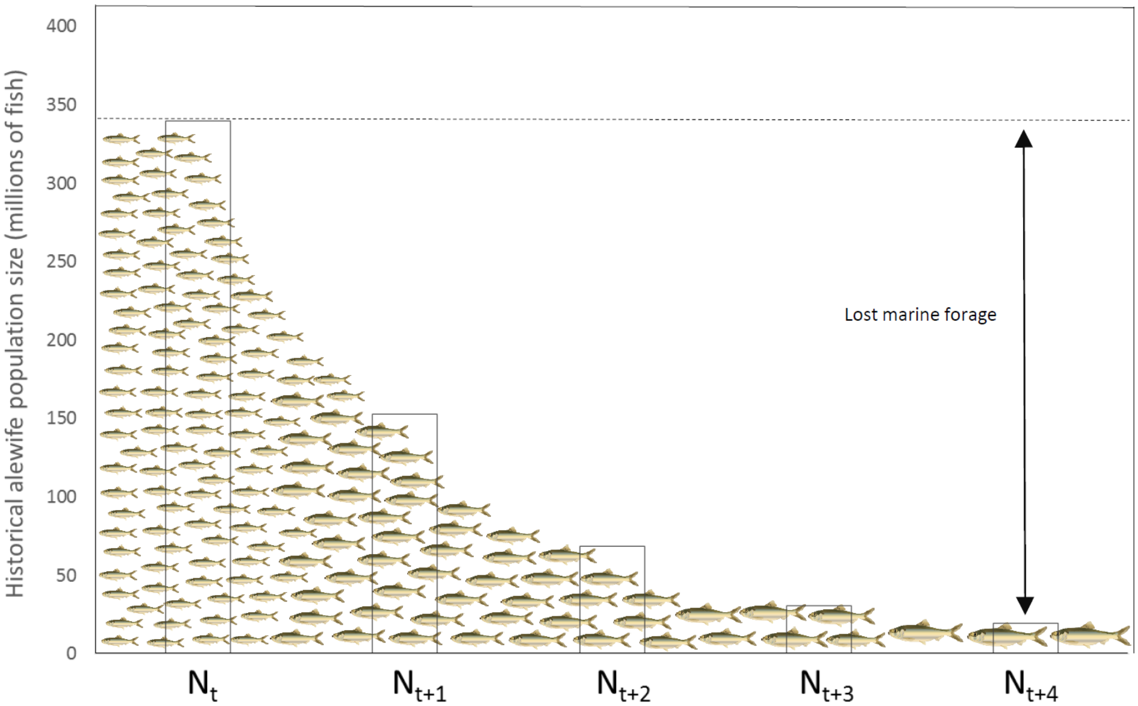


Figure 2.4: Population estimates (N) for different age classes (black bars) of alewife with full access to lakes and ponds in New England. I used the exponential model of population growth with an annual instantaneous mortality rate of 0.8. Population estimates for age 0 (N_t) through age 4 (N_{t+3}) were calculated for 1 September (emigration date) and N_{t+4} was calculated for 1 May (spawn date). Lost marine forage is 1-, 2-, and 3-year-old fish.

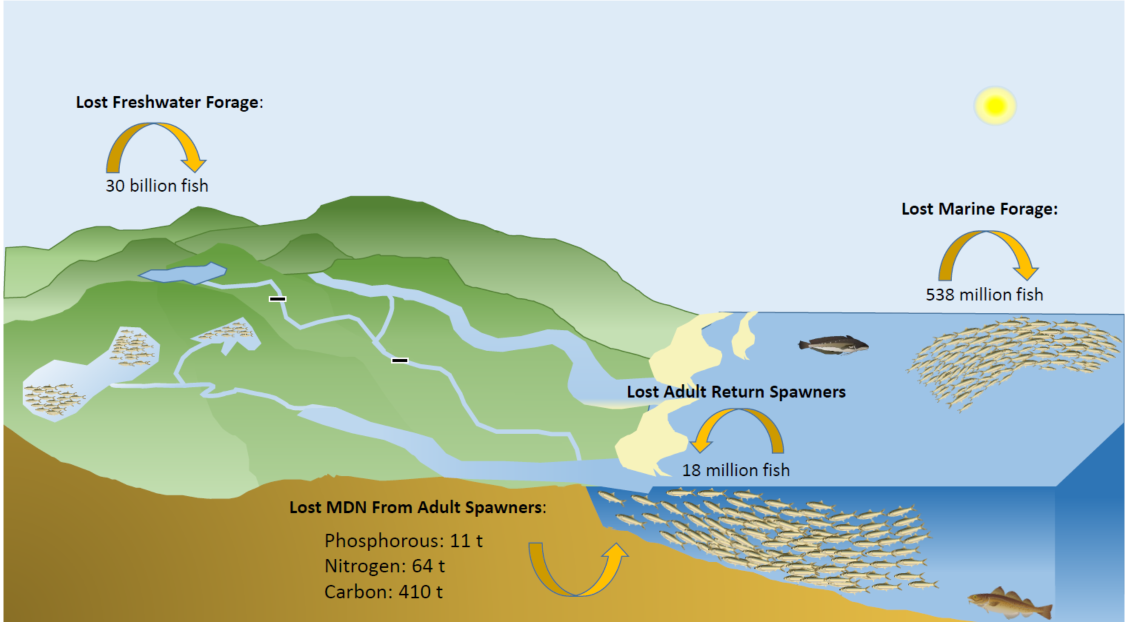


Figure 2.5: Conceptual model of cumulative annual lost forage (freshwater and marine) and adult return spawners. Nutrient values were calculated from previous research (Durbin et al. 1979) and give the cumulative annual lost MDN (metric tons) from adult return spawners for 8 New England watersheds. Current alewife production was applied to pre-damming habitat access to obtain estimates.

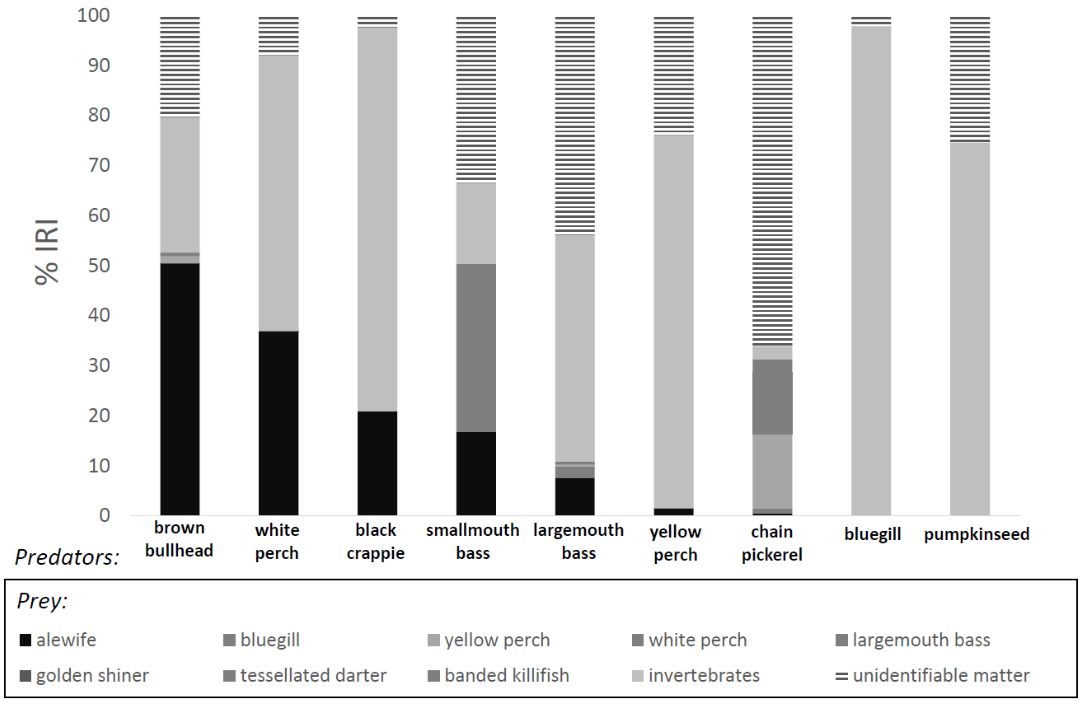


Figure 2.6: Index of relative importance (IRI) of prey for 9 freshwater predators based on gut contents of fish (n=645) collected from 28 coastal ponds.

CHAPTER 3

BOTTOM-UP EFFECTS THROUGH THE PRESENCE OF ANADROMOUS RIVER HERRING IN COASTAL POND ECOSYSTEMS

3.1 Abstract

Anadromous river herring have experienced population declines throughout New England, largely from reduced access to spawning habitat from the construction of dams. The current conservation response has been to re-establish spawning populations through improved access or stocking efforts. The decision to re-connect ocean and freshwater systems, and the consequences of past elimination of populations on freshwater dynamics is not well understood, despite the important role river herring play in trophic dynamics when present. Freshwater predator fish that rely on seasonally available juvenile river herring may have been impacted by reduced river herring runs from historical damming. To evaluate whether juvenile river herring abundance and presence predicts predator condition and growth, I collected white perch and yellow perch from three alewife and three non-alewife ponds in eastern Massachusetts. I used a linear mixed-effects model approach to compare perch morphometric and physiological indices of condition, as well as length-at-age among alewife and non-alewife ponds. Understanding short and long term ecosystem data, such as condition and growth of fish permitted a multi-scaled analysis of processes driven by the presence of alewives. Perch grew faster and had earlier age-at-maturity when alewives were present. Perch length-at-age was significantly higher in non-alewife ponds after maturity, indicating a higher maximum length obtained without alewife. Alewives play a

significant role in shaping freshwater food webs, and impact coastal ponds at multiple trophic levels and time scales.

3.2 Introduction

The historical construction of dams has severely truncated the freshwater spawning habitat of many anadromous fish populations (Hall et al. 2011, Hall et al. 2012, Brown et al. 2013). Over the past few centuries, many anadromous fish populations have experienced severe population declines due to lost spawning and recruitment. Alewives (*Alosa pseudoharengus*), anadromous clupeids inhabiting coastal waters from Canada to Florida, were listed as a species of concern by the National Marine Fisheries Services in 2006 (NOAA 2006). In New England, alewife spawning habitat has been reduced to 2-15% of their original range (Hall et al. 2011, Mattocks et al. 2016 *in review*), resulting in dramatic alteration of marine, freshwater, and terrestrial food webs (Post et al. 2008, Limburg and Waldman 2009).

Alewives are important prey items for a host of marine (Bowman 1975, Bowman et al. 2000, Ames and Lichter 2013, McDermott et al. 2015), freshwater (Yako and Mather 2000, Davis et al. 2009), and terrestrial (Dalton et al. 2009) predators. In freshwater systems, consumption of alewife has been shown to improve predator condition (Porath et al. 2003, Crade and Terrell 2008). Freshwater predator fish in New England consume juvenile river herring at high rates, with alewives often dominating the diets of largemouth bass, brown bullhead, black crappie, and white perch (Yako and Mather 2000, Mooring and Mink 2002, Mattocks et al. 2016 *in review*). The high caloric value of alewives compared to other energetically important anadromous fish may contribute to high predation rates in systems where they occur (Schulze 1996, Yako and Mather 2000, Saunders et al. 2006) and increase their ecological role. Due to their high fat content (Iverson et al. 2002, FAO 2016), predators may partially rely on alewives for energy reserves for metabolic and reproductive processes, as well as overwinter survival. Thus, juvenile alewives provide important seasonal nutrition in freshwater ponds.

A large body of alewife research focuses on the Great Lakes region where alewives are invasive and have been shown to adversely affect native fishes (Madenjian et al. 2008). Resident fish declines have been attributed to increased predation on indigenous larval fish by adult alewives and early mortality from egg thiamine deficiencies. Egg thiamine deficiency, a result of alewife consumption, has been shown to reduce lake trout (*Salvelinus namaycush)* (Fitzsimons and Brown 1998, Fitzsimons et al. 2010) and Atlantic salmon (*Salmo salar)* (Ketola et al. 2000) populations via early mortality syndrome. However, the effects of thiamine remain unclear. Lake trout egg survival can be highly variable (10-90%) and survival of adults with low levels of thiamine has been observed (Madenjian et al. 2008). Adverse effects on other species, such as yellow perch (*Perca flavescens*), have been presumed to result from indirect effects, including habitat overlap and physical displacement during spawning (Wells 1977). Although alewives have been observed consuming juvenile yellow perch (Kircheis et al. 2004), overall population impacts on perch growth and condition are poorly understood.

Predator condition has been widely used by managers and researchers to indicate the supply and quality of food sources (Blackwell et al. 2000, Hartman and Margraf 2003, Brown and Murphy 2004). Fish condition is estimated from physiological and morphometric indices of energy reserves, fat content, or overall fish fitness. Physiological measures of condition include hepatosomatic index (liver index) (Jensen 1979), body-water content (Shackley et al. 1994, Peters et al. 2007), and percent lipid or fat in body tissues (Hakanson 1989). These physiological measures directly relate to composition of body tissues, which represent accurate estimates of energy reserves reflecting environmental changes over short durations such as weeks (Heidinger and Crawford 1977, Lambert and Dutil 1997). Morphometric measures of condition include Fulton's condition factor (*K*) (Fulton 1904), Relative Weight (W_r) (Wege and Anderson 1978, Blackwell et al. 2000), and body-height and length factor (*B*) (Jones et al. 1999). Morphometric indices reflect fish condition based on body form, which may reflect longer monthly time scales (Fulton 1904, Wege and Anderson 1978, Anderson and Gutreuter 1983). Condition indices based on body form can be influenced by temperature, food supply, and photoperiod (Pope and Willis 1996). Since common condition indices represent different processes and time scales, the use of multiple condition factors may enhance understanding of ecological systems and changing food supply.

Lipids play an important role in fish condition by mediating overwinter starvation and survival, as well as through energy allocation, reproductive performance, early life history, and response to environmental stress (Adams 1999). During winter starvation, energetic lipids (triacylglycerols) are mobilized to structural lipids to support biological function. Although necessary for metabolism and reproduction, energetic lipids cannot be replenished without feeding. Hence, fish typically increase their energy stores prior to seasonal stressors such as winter and spawning (Foltz and Norden 1977). In northern coastal ponds, the ability to increase energy reserves through summer foraging may be a limiting factor for the overwinter survival of many fish. For temperate species in the northern part of their range, overwinter mortality is often high (Shuter and Post 1990, Fullerton et al. 2000), and the proportion of energy stores can fluctuate more compared to fish living in warmer climates (Schultz et al. 1996).

Lipid-rich prey items, such as alewives, may be particularly important for securing energy reserves for white perch (*Morone americana*) and yellow perch. The distribution of these perch species overlaps with the range of anadromous alewives leading to likely trophic interactions between March and October when juvenile alewives reside in freshwater ponds. Both white perch and yellow perch reside in a variety of freshwater habitats, including lakes, rivers, and large impoundments throughout most of the eastern United States. Both perch species have similar feeding habits, temperature requirements, body size, and metabolic rates. After scaling for temperature and body size, the metabolic rate for perciforms is estimated to be 0.193 mmol h^{-1} (SE=.013) (Clarke and Johnston 1999). These species differ in their salinity tolerance; yellow perch tolerate salinities of about 13 ppt (Krieger et al. 1983), while semi-anadromous white perch can bear salinities as high as 30 ppt (Stanley et al. 1983). This distinction determines distribution patterns and even reproduction strategies.

Many white perch populations are riverine or estuarine, exhibiting resident and migratory life history strategies depending on environmental conditions (Kerr and Secor 2012). Yellow perch populations primarily occur in clear freshwater lakes with areas of littoral vegetation (Krieger et al. 1983). Yet, when present in lakes, both species are known to dominate pelagic habitats. Differences in habitat, movement patterns, body form, and feeding habits may result from different responses and adaptations to environmental conditions (Stanley and Danie 1983, Jones et al. 2013), including the presence of anadromous alewives.

In addition to providing energy and nutrients to predators, alewives can alter freshwater food webs through effects on zooplankton communities. Zooplankton play a vital role in lake ecosystems by consuming phytoplankton (Wetzel 1983, Carpenter et al. 1985), and serving as a food source for planktivorous fish and macroinvertebrates (Bergman and Greenberg 1994). Nutrients deposited by adult alewives during spawning are believed to trigger primary plankton production in lakes, resulting in a larger biomass of zooplankton food for juvenile fish (Durbin et al 1976); zooplankton are consumed by both juvenile and adult alewives. Previous studies illustrate that the presence of alewife in lakes usually favors smaller forms of zooplankton because of their size-selectivity towards consumption of larger-bodied zooplankton (Brooks and Dodson 1965, Warshaw 1972, Post et al. 2008). Because of predation on larger zooplankton such as *Daphnia*, small zooplankton species such as *Bosmina* are released from competition and predation pressure (Twinning and Post, 2012). This shift in zooplankton alters the food web of lakes (Kircheis et al. 2004) and therefore changes food availability for other fish. For example, in Lake George, ME, the re-introduction of alewives significantly altered zooplankton community structure and subsequently altered the diet of another planktivore, the rainbow smelt (*Osmerus mordax*) (Kircheis et al. 2004).

It is unclear how alewives impact the growth and condition of freshwater predators; a better understanding of this could inform management and restoration goals. The objectives of this research are: 1) to better understand the effects of alewife presence and density on the growth and condition of perch in coastal ponds. Specifically, I ask the questions: 1) Does the presence and density of juvenile alewives' impact perch condition? and 2) Does the presence and density of juvenile alewives' impact perch growth? Investigating these research questions could help in understanding the complex ecosystem changes that have occurred as a result of habitat exclusion from dams and the changes that occur when historically abundant forage fish are occluded from freshwater ecosystems.

3.3 Methods

3.3.1 Study Area

Six ponds in eastern Massachusetts were selected for this study: three alewife ponds and three non-alewife ponds (Figure 3.1). Alewife ponds were Pentucket Pond (Georgetown, MA), Upper Mystic Lake (Arlington, MA), and Whitman's Pond (Weymouth, MA), and non-alewife ponds were Rock Pond (Georgetown, MA), Fresh Pond (Cambridge, MA), and Weymouth Great Pond (Weymouth, MA). Non-alewife ponds were similar to alewife ponds in size, location, and predatory fish species assemblage. Yellow perch are present in all ponds, and white perch were present in all ponds except for Pentucket. Ponds range in depth from 26 m to 6 m, and range in size from 0.8 km^2 to 0.2 km^2.

3.3.2 Fish Collection

Predator fish were collected using four, 4-panel multi-mesh experiment gillnets (2.5, 5, 7.5, and 10 cm mesh, 75 m length x 2.5 m height) in June, July, and August 2015. Two nets were deployed in the pelagic zone (>200 m from shore) and two nets were deployed in the littoral zone (<100 m from shore) for each lake sample. I used a random number generator and the fishnet tool in ArcGIS 10.1 to select net locations (50 m x 50 m grids). Pelagic nets floated on the surface and were set with a haphazard aspect. Littoral nets were set perpendicular to shoreline, with one net small-mesh-to-shoreline and the other large-mesh-to-shoreline. Nets were deployed overnight (set at dusk and retrieved at dawn) and all predator fish were immediately placed on an ice bath and later frozen.

Although yellow perch and white perch were the primary target species, I collected additional predator species that are known to be potentially significant predators of alewives in coastal ponds. Other species include largemouth bass (*Micropterus salmoides*), black crappie (*Pomoxis nigromaculatus*), chain pickerel (*Esox niger*), and brown bullhead (*Ameiurus nebulosus)*. In addition, three daytime beach seines were conducted at each pond each month using a 25 m x 2 m bag-type beach seine (7 mm mesh). Locations were chosen haphazardly wherever suitable beaches existed. Beach seines were conducted primarily to verify fish assemblages and species composition, and to confirm presence or absence of alewives. All sampling was conducted from south to north to account for subtle differences in season, with one pond sampled per day.

Catch per unit effort (CPUE) for perches was used as a covariate and was calculated as the total number of perches (combined yellow and white perch) per net per night. Perch CPUE reflects an index of predator abundance for the six study ponds. Yellow perch and white perch were combined because of their similar feeding habits and ecological roles, and non-perch CPUEs were overall very low. CPUE was averaged across June, July, and August because: (1) true perch abundance is not expected to fluctuate much within one season, and (2) different seasons have different catchabilities thus a combination allows for more accurate abundance estimates.

Alewife densities were provided by Matt Devine (MS student, University of Massachusetts Amherst, unpublished data). Alewife densities were obtained using a pelagic purse seine (30.5 m x 4.3 m) at night in June, July, and August 2015. Purse seining for each month was conducted within 48 hours of predator fish collection. The purse seine was deployed and immediately retrieved at 5 random locations each night for two consecutive nights each month following methods by Rosset (2016). Random locations were selected using the fishnet tool in ArcGIS 10.2, using 50 m x 50 m grids and a 100 m shoreline buffer.

3.3.3 Gut Content Analysis

All predator fish were thawed in cold water, patted dry, then weighed and measured (total length) to the nearest mm. Gape height and width were also recorded (mm) for potential evaluation of gape-limited feeding effects. Stomachs were removed behind the esophagus and wet weight of full stomachs, empty stomachs, and livers were taken to the nearest 0.001 gram. Predator stomachs were emptied and sorted into categories: (1) fish, (2) invertebrates, (3) unidentifiable matter, and (4) vegetation and detritus.

Fish prey were identified to species using identification guides (Werner 2004) and voucher specimens. For heavily digested prey items, I used otolith shape with published documents and vouchers to identify fish to species (Ross et al. 2005), although many otoliths were from immature individuals or highly eroded and prevented identification of prey. When prey fish were discernable, I measured wet weight (nearest 0.001 gram), body length and depth (mm), and stage of digestion (1, 2, 3).

Prey categories were described as percent weight (%W), percent number (%N), and percent frequency of occurrence (%O). I calculated an index of relative importance (IRI) using the following equation:

$$\mathrm{IRI} = (\%W + \%N)\ \%O \qquad \text{(i)}$$

which was expressed as a percentage to make prey and predator categories comparable following Pinkas et al. (1971):

$$\%\ \mathrm{IRI} = 100\ \mathrm{IRI} / \sum^{n} \mathrm{IRI} \qquad \text{(ii)}$$

with n representing the total number of food categories considered at a given taxonomic level.

3.3.4 Age and Growth Analysis

White perch and yellow perch otoliths were extracted and processed using the "crack and burn" method, where otoliths were cross-sectioned and held above a flame to reveal annuli. Otoliths were aged under a compound microscope to the nearest year using 2 readers, and all age discrepancies between readers were re-evaluated. Fish with a coefficient of variation between two readers greater that 10% were analyzed a second time, and a final age was determined by the more experienced ager. Overall, ages were precise, with an average coefficient of variation of 3.5%, which is below the suggested threshold of 5% (Campana 2001). I compared growth rates of white perch and yellow perch from alewife and non-alewife ponds using the Von Bertalanffy growth equation:

$$L_t = L\infty \, [1 - e^{-k\,(t - t0)}] \qquad \text{(vi)}$$

where parameters are maximum length ($L\infty$), theoreticaxl length at age-0 (t_0), and the growth parameter (k).

3.3.5 Condition Analysis

We used Fulton's condition factor (K), hepatosomatic index (HSI), and relative weight (W_r) to represent condition of white perch (n=406) and yellow perch (n=126) from all six ponds. These indices were chosen because their ubiquitous use and ease of application, and because they represent different ecological, physiological, and morphometric processes across different time scales. Fulton's K (K) is expressed as

$$K = (W/TL^3) * 100 \tag{iii}$$

where W is somatic weight and TL is fish total length. Hepatosomatic index (HSI) is a function of liver weight (LW) and somatic weight (W):

$$HSI = (LW/W) * 100{,}000 \tag{iv}$$

Relative Weight (W_r) is

$$W_r = 100 * (W/W_s) \tag{v}$$

where W is somatic weight and W_s is standard weight. I used standard weight regression coefficients from Blackwell et al. (2000) which were produced from many fish populations from multiple state management agencies.

3.3.6 Water Quality

I collected pH, conductivity, temperature, and maximum depth from each lake using a multi-probe YSI 6 series. Measurements were taken at dusk within 48 hours of predator fish and YOY (young of year) alewife data collection. Measurements were taken at the deepest part of the lake at three vertical locations: surface (0.5 m depth), middle (half of max depth), and bottom (0.5 m from bottom).

3.3.7 Zooplankton Sampling

Plankton samples were collected with an 80-µm mesh (0.3-m diameter) plankton net, towed vertically near the deepest portion of each pond. The samples were filtered to approximately 20 mL and preserved in 4% formalin. In the lab, rose bengal stain was added to each lake sample to facilitate organism sorting and identification. A Hensen-Stempel pipette was used to extract three, 1-mL aliquots and place onto a Sedgewick-Rafter counting cell. All zooplankton were identified under an Olympus compound microscope at 10X magnification or more and measured to the nearest mm with the Olympus CellSens program. Zooplankton were identified according to Haney et al. (2013), Johnson and Allen (2005), and Balcer et al. (1984) identification guides.

The average number and size of each species or genera was computed to use in density and biomass calculations for each month and lake. Biomass (µg/L) and density (invid./L) were calculated according to Kamaladasa (2007) and US EPA (2004).

3.4 Data Analysis

3.4.1 Perch Condition

I tested the null hypothesis of no difference in effect of alewife density/alewife presence on predator condition. In addition, I tested the effects of temperature, zooplankton density, perch abundance (adult), month, and habitat type (pelagic vs. littoral) on fish condition. I modeled Fulton's K, HSI, and W_r as response variables for yellow perch and white perch separately using linear mixed-effects models. I used the "lmer" function in the package "lme4" in R studio (R Core Team 2013). Mixed effects models were used to account for similar conditions of fish within each pond, as each pond has structural and functional variability that may influence condition. I compared the full model with a random effect of pond to the full model with no random effect of pond, and used restricted maximum likelihood estimation and AIC to estimate parameters and to determine if random effects were appropriate. Fulton's K is often criticized for its length bias (assumption of isometric growth), and other indices may be influenced by fish size, therefore fish (perch) length was included in all models.

I compared predictive models of fish condition using maximum likelihood and conditional AIC (AICc). Full models with maximized fixed variables were visually assessed to evaluate model assumptions. For the random effect of pond, I assessed conditional modes for intercept estimates for each pond. Normality and heterogeneity of residuals were assessed with normal and Pearson's R standardized residual plots; collinearity was also checked using a correlation matrix (Appendix B). All models included fixed effects for length and month, with a random effect of pond, plus 17 different combinations of remaining fixed variables (alewife density/presence, zooplankton density, perch abundance, temperature, and habitat). I ran separate models for alewife density as a continuous predictor variable, and alewife presence as a factor with two classes (present/absent). P-values for parameter estimates were obtained using normal approximation (Barr et al. 2013). To assess goodness of fit, I obtained R^2 values using the "r.squaredGLMM" function in the "MuMIn" package in R (Nakagawa and Schielzeth 2013, Barton 2014). Final models were described using restricted maximum likelihood estimation (Zuur et al 2010).

I visually assessed co-plots for inclusion of interaction terms for the variables month, zooplankton density, and alewife density or alewife presence (depending on model set). I used a likelihood ratio test and the "anova" function in the "car" package to assess different interaction terms (Fox and Weisberg 2011, R Core Team 2013). I tested 2-way interactions between zooplankton density and month, alewife density and month, and alewife presence and month. Interactions between alewife density and month, and alewife presence and month were significant in all model sets. I ran two distinct sets of models, with the first set containing no interaction terms, and second set containing interaction terms between alewife density/presence and month. For models with interactions, I used a z-score standardization on continuous variables in order to scale data.

Because the model selection process did not reveal a single unequivocally best model, parameter estimates and significance terms were derived from averaging the set of most plausible models (Table 3.5). I used the top 5 models with respect to each condition index to calculate parameter estimates. Final model averaging only included models with interaction terms for alewife density, alewife presence, and month. Model averaging and confidence intervals were obtained using ‘model.avg’ in the ‘MuMIn’ package in R.

In order to determine the effect of age on fish condition, a separate set of mixed-effects models were created. This was done because the short term variables in the condition models are not representative of the longer time scales represented by growth. I modeled the three indices of condition using an interaction between fish age (factor) and alewife presence, as well as various combinations of environmental variables used in previous condition models. Fixed effects for month and fish length, as well as a random effect of pond were used in all model combinations.

3.4.2 Perch Growth

Growth curves can provide ecological insight related to life history, such as early growth, mature growth, maximum length, and can even hint at age at reproduction and energy allocation (Hutchings 1993). Parameter estimates for growth were obtained using the non-linear least squares fit method of Von Bertalanffy growth equations. Confidence intervals were obtained at the 95% level using non-parametric bootstrapping. Differences in models were determined to be significant when parameter confidence intervals did not overlap.

Linear mixed-effect models were employed to predict perch growth between alewife and non-alewife ponds. For both yellow and white perch, I tested three model combinations with three different variables, all of which included an interaction between alewife presence/absence and age. Age was converted to a factor in order to perform and interaction in an ANOVA-type framework, and to answer specific questions about how lengths differ between alewife present and absent ponds with varying ages. Three variables were considered representative of ponds over long time scales (~10-20 years) and therefore could be used to better understand growth: (1) ponds size (km^2), maximum depth (m), and perch (yellow and white) abundance (CPUE). Both perch species were combined in this index due to similarity in feeding and ecological roles, and although perch abundance was only collected during 2015, it was assumed to remain relatively stable in the sampled ponds. I initially used CPUE data from all species to represent predator abundance, but this was highly correlated with perch abundance ($r = 0.91$), and perch abundance may reflect a more appropriate index of competition.

Because perch abundance was highly correlated with pond area and maximum depth, I modeled each variable separately and used AICc to compare among models. A random effect on pond was used to account for variability among ponds.

3.5 Results

White and yellow perch were captured to determine the growth and condition with the presence and absence of alewives. We captured 122 white perch in June, 165 in July, and 268 in August (Table 3.1) 2015 using gillnets. For yellow perch, we caught 21 in June, 36 in July, and 66 in August 2015. Perch abundances differed substantially among ponds (Table 3.1). Results were consistent among models that used alewife density and models that used alewife presence. Results were also similar among models with and without interaction terms.

3.5.1 Condition

While most top models included alewife density or alewife presence, all of the other predictor variables were included in the top 5 averaged models for both yellow and white perch. Perch length was selected in all final models as having a significant positive effect on condition for K and W_r. Temperature had a weak negative effect on condition for both species. Perch abundance had an overall negative effect on the condition of perches throughout the summer, which is likely an indication of density-dependence and carrying capacity. Although zooplankton was in many top models, its effect on condition was a weak to moderate trend, with slightly varying effects for both species. Habitat was selected in final models for white perch, but the effect was not significantly different in alewife and non-alewife ponds. Results obtained for regular models were similar to those from interaction models with standardized variables.

White Perch

White perch condition was variable across lakes and months. All top models for white perch condition included an alewife effect. Alewives had a significant positive effect on white perch condition in June, with significant terms for K, HSI, and W_r (Figure 3.2). By July and August, alewife density had a moderate to slightly negative effect on white perch condition. Top K models including alewife density or alewife presence, month, temperature, and length had marginal and conditional R^2 values of 0.329 and 0.474, respectively. Top K models with alewife presence/absence, month temperature, and length had marginal (fixed effects) and conditional (fixed and random effects) R^2 values of 0.304 and 0.485, respectively. Other top models for HSI and W_r has similar R^2 values, with conditional R^2 ranging from 0.38 to 0.57, and marginal R^2 values ranging from 0.16 to 0.45.

Model combinations that included an interaction between age and alewife presence revealed little information. Age was only significantly different between alewife and non-alewife ponds for age-6 fish ($p < 0.001$). Although age was generally not significantly different between the two populations, the interaction was included in top models for Fulton's condition factor k and relative weight W_r.

Yellow Perch

Yellow perch condition varied across months and ponds. Yellow perch top models included an effect on alewives, perch abundance, temperature, and zooplankton density. Similar to white perch, yellow perch K and W_r were positively influenced by alewife density/alewife presence in June, but this effect decreased and became slightly negative for July and August (Figure 3.2). However, with HSI models, alewife density had a negative effect in June. For all three condition indices, there was a significant difference in condition in June, July, and August. Top K models that included alewife density, month, temperature, and length had marginal and conditional R^2 values of 0.56 and 0.72, respectively. Top *K* models that included perch abundance, zooplankton density, length, and month had marginal and conditional R^2 values of 0.51 and 0.73, respectively. Top models for HSI and W_r had marginal R^2 values ranging from 0.2 to 0.4, and conditional R^2 values ranging from 0.47 to 0.54.

Model combinations that included an interaction between age and alewife presence showed a difference in length-at-age between alewife present and absent ponds, with a significantly higher condition at ages 3 ($p = 0.024$), 4 ($p = 0.006$), and 7 ($p = 0.015$) in non-alewife ponds relative to age-1 fish. Although age was generally not significantly different between the two populations, the interaction was included in the top model for relative weight W_r.

3.5.2 Growth

White Perch

Maximum length parameter estimates (*Linf*) for white perch were significantly higher in non-alewife ponds (Figure 3.3, Table 3.6). Growth parameter *K* for white perch was greater in alewife ponds compared to non-alewife ponds, but the difference was not significant. White perch length-at-age was greater for two-year-old fish in alewife ponds. Conversely, white perch length at age was significantly greater in non-alewife ponds at ages 3, 7, 8, 9, 10, 12, and 13 (Appendix C). Maximum depth had a negative effect on white perch, although not statistically significant.

Yellow Perch

Maximum length of yellow perch was also greater in non-alewife ponds, although the difference was not statistically significant. Growth parameter *K* was slightly higher, but not statistically significant for yellow perch in non-alewife ponds. The only environmental variable that significantly predicted yellow perch growth was maximum depth. Yellow perch length-at-age was greater for one and two-year-old fish in alewife ponds (Appendix C). Yellow perch length at age was significantly greater in non-alewife ponds at age 5. Overall, perch early growth (ages 1-2) tended to be slower, and late growth tended to be faster, and eventual size-at-age greater when alewives were absent.

3.5.3 Dietary Analysis

Diets of yellow and white perch were dominated by invertebrates in both alewife (93% IRI) and non-alewife ponds (95% IRI) (Figure 3.7). In ponds where alewives were present, alewives were only observed in white perch (0.02% IRI), largemouth bass (3% IRI), and black crappie (0.08 % IRI). Unidentifiable matter comprised of 54% IRI for yellow perch diets in alewife ponds and 21% IRI in non-alewife ponds.

3.6 Discussion

Overall, these results show evidence that the presence and density of juvenile alewives have strong bottom-up effects on lake ecosystems. Bottom up effects were: (1) increased perch condition in June as a result of juvenile alewife presence and increased density, and (2) increased immature growth and decreased mature growth of perch, resulting in a smaller size and earlier age at maturity; a result of alewife presence and increased density. These ecosystem changes occurred across multiple time scales, evidenced by short term physiological and longer term morphometric indices of condition. Further, differences in growth between perch populations in alewife and non-alewife ponds revealed ecosystem impacts across multiple years. The presence of alewives modified the life history and reproductive strategy of both species of perch. This research revealed the complex trophic dynamics that occur in coastal ponds, and highlighted multi-dimensional food web changes that occurred from the exclusion of alewives.

Alewife presence and density explained a significant amount variation in perch condition, and positively influenced the condition of perch in June. This bottom-up effect is likely due to perch consumption of alewife eggs and small size of YOY alewife, although these were rarely observed in guts. Juvenile alewives are highly abundant and vulnerable to predation in early summer months, and are likely easily accessible to predator fish. Previous observations suggest that perch consume juvenile alewives of smaller length during a relatively small window of time (Mattocks et al. *In review*). For the three alewife ponds, average alewife lengths in June, July, and August were 20mm, 27mm, and 64mm, respectively. Larger fish are better swimmers and may escape predation easier; this may represent properties of optimal foraging theory. In mid-late summer when YOY alewives reach larger sizes, it may be less energetically efficient for perch to consume juvenile alewives. Although YOY alewives were not consumed by largemouth bass until late summer in similar coastal New England ponds (Yako and Mather 2000), perches may opportunistically exploit juvenile alewives when they are in high abundances in the early summer (Mattocks et al. 2016 *In review*). Perch predation on alewives may be explained by perch feeding habits and habitat use. Both white and yellow perch are known to utilize pelagic zones of lakes during the summer, while largemouth bass dominate littoral habitats with structural complexity (Werner 2004). Thus, perch may overlap in habitat with juvenile alewives in early summer, while alewives may become more available to largemouth bass in the fall when larger alewife are in littoral areas, and when alewife are energetically beneficial for bass to pursue (Schielke et al. 2011.).

The density of alewives may have multiplicative effects on the condition of predators. For instance, ponds with high alewife densities often have slower growing YOY alewife populations, causing alewives to remain within the edible size window for perch for a longer period of time (Rose et al. 2001). This indirect effect could potentially contribute to increased consumption by predators that benefit from increased energetic reserves in summer months. Alewife length was not incorporated into this study because of collinearity with alewife density, but it should be considered separately in future studies as prey size is an important aspect of predator-prey interactions, and is particularly useful in disentangling the effects of density, abundance and length on predator condition.

When alewives were present, growth of perch trended towards faster growth during ages 1 and 2, and smaller size-at-age during later stages after fish reached maturity. For many fish populations, faster early growth leads to increased energy allocation towards reproduction, leading to slower somatic growth during mature life stages (Hutchings 1993, Kuparinen et al. 2008). Importantly, faster early growth is also linked to increased adult mortality, which has been observed in perch populations as a result of predation and competition (Heibo and Magnhagen 2005). Thus, perch are becoming sexually mature at an earlier age and smaller size when alewives are present. Previous work has in New England freshwater system revealed that alewives have a higher index of relative importance (IRI) for white perch compared to yellow perch; thus, it is not surprising that the effects of alewife presence and density had a lesser effect on yellow perch condition and growth (Mattocks et al. 2016 *In review*) (Figure 3.2, 3.3). Because only six lakes were sampled in this study, results for environmental variables at this scale should be interpreted with caution.

Many challenges are associated with gut content analysis using gillnet sampling. Increased digestion and decomposition rates of prey fish are much higher compared to active sampling methods such as purse seining. Because gillnets were set overnight, predator fish captured in early evening that experienced mortality at night were exposed to longer periods of high temperatures and time for active digestion compared to fish captured with active sampling methods, such as seines, which can be immediately placed on ice. Because identification of larval fish can be nearly impossible just 60 minutes after consumption (Schooley et al. 2008, Legler et al. 2010), diet analysis using gillnet capture methods is not ideal. Although I identified some prey fish using hard parts, the amount of unidentifiable matter and the number of empty stomachs reduced diet resolution. The indeterminate shape of larval fish otoliths, along with stomach acid further dissolving hard parts obfuscated interpretation of stomach contents. For these reasons, diet data were presented as descriptions rather than metrics in the mixed effects models.

A better understanding of food web dynamics could be obtained from lake-specific bioenenergetics models. These techniques have previously been used in coastal Massachusetts to quantify the role of alewives as prey for largemouth bass (*Micropterus salmoides)* (Yako and Mather 2000). Lake-specific energy densities of prey items would further illustrate the energetic importance of prey fish. However, bioenergetics models are complicated by seasonal and ontogenetic changes in energy densities of prey and predator fish, size-based predator-prey interactions, and habitat use (Bryan et al. 1996, Yako and Mather 2000). Ecosystem models that incorporate functional nodes with multiple species' interactions are the logical next step for interpreting consequences of lost fish populations, as they capture spatial and temporal complexities of fish assemblages.

Predator binge feeding on juvenile anadromous fish in freshwater has been documented (Fury et al. 2015), as seasonal prey is an important aspect of many fish populations (Trippel et al. 2015). Prey availability likely determines foraging strategies of predators that rely on seasonal pulses of fish; thus, alewives subsidize consumers during summer months when they are available (Mattocks et al. *In review*). My research provides data useful to understanding the importance and timing of juvenile anadromous fish occurrence in ponds and sheds light on bottom-up ecosystem effects.

Damming of streams has decreased the amount of lake and pond habitat occupied by alewives, which has likely altered predator diets, and has likely altered fish assemblages and community structure. River restoration aiming to restore aquatic connectivity is a key aspect to reestablishment of anadromous fish runs where previously excluded from spawning habitat. Managers should apply ecosystem-based management approaches when managing coastal ponds, and should prioritize river connectivity when managing fish populations in coastal ecosystems. By allowing native anadromous forage fish populations to persist, predator populations can benefit without the need to stock forage fish, and by prioritizing dam removal, anadromous fish populations can be restored, reestablishing important links to freshwater and marine food webs.

Table 3.1: Catch Per Unit Effort (CPUE) of adult fish captured from gillnets in coastal ponds. Whitman's, Upper Mystic, and Pentucket contained alewives. Juvenile fish captured from beach seines were identified as present (x) in ponds but were not quantified due to non-standardized sampling techniques. Ponds (alewife and non-alewife) were Whitman's and Weymouth Great, Upper Mystic and Fresh, and Pentucket and Rock, respectively.

Adult Fish	Whitman's	Weymouth Great	Upper Mystic	Fresh	Pentucket	Rock
Brown Bullhead (*Ameiurus nebulosus*)	0.54	0.16	-	-	0.18	0.27
White Sucker (*Catostomus commersonii*)	-	-	0.67	-	-	-
Common Carp (*Cyprinus carpio*)	-	-	0.08	-	-	-
Gizzard shad (*Dorosoma cepedianum*)	-	-	-	-	-	-
Chain Pickerel (*Esox niger*)	0.45	1	-	0.42	0.64	0.18
Pumpkinseed (*L. gibbosus*)	0.18	0.08	-	0.08	-	-
Bluegill (*Lepomis macrochirus*)	0.18	0.58	-	0.08	0.64	0.73
Largemouth Bass (*Micropterus salmoides*)	0.45	0.92	0.33	0.5	0.18	0.09
Golden Shiner (*Notemigonus crysoleucas*)	11.63	-	0.5	-	4.27	3.36
Rainbow Trout (*Oncorhynchus mykiss*)	-	-	-	-	0.82	-
Yellow Perch (*Perca flavescens*)	3.73	2.25	0.33	2.5	1.18	2.1
Black Crappie (*Pomoxis nigromaculatus*)	2.18	0.08	-	-	0.36	0.55
White Perch (*Morone americana*)	14.1	20.58	4.42	3.92	-	7.18
Brook Trout (*Salvelinus fontinalis*)	-	-	-	-	0.18	-
Juvenile Fish						
banded killifish (*Fundulus diaphanus*)	x	-	x	-	-	-
bluegill	x	x	x	x	x	x
brown bullhead	x	-	-	-	-	-
chain pickerel	x	x	-	x	x	-
golden shiner	-	-	-	-	x	-
largemouth bass	x	x	x	x	x	x
pumpkinseed	x	-	x	x	x	x
tessellated darter (*Etheostoma olmstedi*)	x	-	-	-	-	-
yellow perch	x	-	-	x	-	-

Table 3.2: Combinations of models testing alternative hypothesis for predicting perch condition. Perch length, month, and pond (random intercept) were included in all models. All models were tested for white perch and yellow perch.

	Condition indices predicted by the following models:
1	alewife density, zooplankton density, perch abundance, temperature, habitat, length, month, pond
2	alewife density, zooplankton density, perch abundance, temperature, length, month, pond
3	alewife density, zooplankton density, perch abundance, length, month, pond
4	zooplankton density, perch abundance, temperature, length, month, pond
5	alewife density, zooplankton density, temperature, length, month, pond
6	alewife density, perch abundance, temperature, length, month, pond
7	alewife density, zooplankton density, habitat, length, month, pond
8	zooplankton density, habitat, temperature, length, month, pond
9	alewife density, temperature, habitat, length, month, pond
10	temperature, zooplankton density, length, month, pond
11	alewife density, perch abundance, length, month, pond
12	perch abundance, temperature, length, month, pond
13	alewife density, temperature, length, month, pond
14	habitat, alewife density, length, month, pond
15	temperature, habitat, length, month, pond
16	alewife density, length, month, pond
17	length, month, pond

Table 3.3: Table represents candidate models for white perch. Variables used in final models for Fulton's K (K), Hepatosomatic Index (HSI), and Relative Weight (Wr). Sets of models were run with either non-standardized continuous predictor variables or with z-score standardized (Z) continuous variables with an interaction between alewife density/alewife presence and month (*). Variables with three asterisks (***) indicate significance at p<0.05 level. Variables with an X made final models.

White Perch	alewife data type	alewife density/ present-yes	perch abundance	zooplankton density	habitat-pelagic	temp	length	july	august	alewife density/ present-yes: july	alewife density/ present-yes: august
K	density	X *** (-)					X*** (+)	X (-)	X (-)		
K	present/absent	X (+)			X*** (-)		X*** (-)	X (-)	X(-)		
K: Z, *	density	X *** (+)				X *** (-)	X *** (+)	X (+)	X (+)	X *** (-)	X *** (-)
K: Z, *	present/absent	X *** (+)					X *** (+)	X (-)	X (-)	X *** (-)	X *** (-)
HSI	density	X *** (-)	X (-)				X (+)	X *** (-)	X *** (-)		
HSI	present/absent						X (+)	X *** (-)	X *** (-)		
HSI: Z, *	density	X (+)				X *** (-)	X (+)	X (-)	X (-)	X (-)	X *** (-)
HSI: Z, *	present/absent	X *** (+)				X *** (-)	X (+)	X (-)	X *** (-)	X *** (-)	X *** (-)
W_r	density	X *** (-)					X *** (+)	X (-)	X (-)		
W_r	present/absent	X (+)			X ***(-)		X *** (+)	X (-)	X (-)		
Wr : Z, *	density	X *** (+)				X *** (-)	X *** (+)	X (+)	X (+)	X *** (-)	X *** (-)
Wr : Z, *	present/absent	X *** (+)				X (-)	X *** (+)	X (+)	X (+)	X *** (-)	X *** (-)

Table 3.4: Table represents candidate models for yellow perch. Variables used in final models for Fulton's K (K), Hepatosomatic Index (HSI), and Relative Weight (Wr), with each condition factor modeled with alewife as a continuous variable (density) and as a factor (present/absent). Sets of models were run with either non-standardized continuous predictor variables or with z-score standardized (Z) continuous variables with an interaction between alewife density/alewife presence and month (*). Variables with three asterisks (***) indicate significance.

Yellow Perch	alewife data type	alewife density/ present-yes	perch abundance	zooplankton density	habitat-pelagic	temp	length	july	august	alewife density/ present-yes: july	alewife density/ present-yes: august
K	density	X *** (-)			X (-)		X (+)	X (-)	X (-)		
K	present/absent	X (+)			X ***(-)		X *** (+)	X *** (-)	X (+)		
K: Z, *	density	X (+)				X (+)	X *** (+)	X *** (-)	X *** (-)	X *** (-)	X (+)
K: Z, *	present/absent		X (-)	X *** (-)			X *** (+)	X (-)	X *** (-)		
HSI	density	X *** (-)			X (+)		X (+)	X *** (-)	X *** (-)		
HSI	present/absent	X (+)			X (-)		X (+)	X *** (+)	X *** (-)		
HSI: Z, *	density		X *** (-)				X *** (+)	X *** (-)	X *** (-)		
HSI: Z, *	present/absent	X *** (-)	X *** (-)			X (+)	X *** (+)	X *** (-)	X *** (-)	X (+)	X (+)
Wr	density	X (+)		X *** (-)		X (+)	X (+)	X (-)	X *** (-)		
Wr	present/absent			X *** (-)		X (-)	X (+)	X (-)	X *** (-)		
Wr : Z, *	density	X (-)				X (+)	X (+)	X *** (-)	X *** (-)	X *** (-)	X (+)
Wr : Z, *	present/absent			X *** (-)		X (-)	X (+)	X (-)	X *** (-)		

Table 3.5: Model selection for Fulton's K as the predictor variable for white and yellow perch. Statistics shown are number of parameters estimated (*k*), conditional AIC (AICc), AICc difference (Δ_i), and Akaike weight (w_i). All models included month, temperature, and length. Upper section of table includes alewife density; lower section includes alewife presence/absence.

Candidate Models - White Perch	*k*	*AICc*	*Δi*	*wi*
alewife density, month, temp, length	10	-606.94	0.00	0.50
alewife density, month, temp, length, habitat	11	-604.85	2.10	0.17
alewife density, month, temp, length, perch abundance	11	-604.83	2.11	0.17
alewife density, month, habitat, length	10	-601.85	5.09	0.04
alewife density, month, zooplankton density, perch abundance, length	10	-601.85	5.09	0.04

Candidate Models - Yellow Perch	*k*	*AICc*	*Δi*	*wi*
alewife density, month, temp, length	8	-213.70	0.00	0.32
alewife density, month, perch abundance, length, zooplankton density	8	-213.70	0.00	0.32
zooplankton density, month, temp, length,	10	-213.28	0.42	0.26
temp, month, zooplankton density, length	11	-210.92	2.78	0.08
alewife density, month, perch abundance, length, temp	6	-208.08	5.62	0.02

Candidate Models - White Perch	*k*	*AICc*	*Δi*	*wi*
alewife presence, month, perch abundance, temp, length	10	-606.73	0.00	0.24
alewife presence, month, temp, length	10	-605.96	0.76	0.16
alewife presence, month, length	10	-605.96	0.76	0.16
alewife presence, month, length, perch abundance, zooplankton density	11	-605.57	1.16	0.13
alewife presence, month, length, zooplankton density, habitat	11	-605.34	1.39	0.12

Candidate Models - Yellow Perch	*k*	*AICc*	*Δi*	*wi*
perch abundance, zooplankton density, length, month	8	-213.70	0.00	0.25
zooplankton density, month, temp, length	8	-213.70	0.00	0.25
temp, zooplankton density, length, month	8	-213.70	0.00	0.25
zooplankton density, month, temp, length, perch abundance	10	-213.28	0.42	0.20
alewife presence, month, temp, length	11	-210.92	0.42	0.06

Table 3.6: Parameter estimates, confidence intervals, and residual sum of squares from Von Bertalanffy growth models. Yellow perch and white perch growth were modeled in alewife and non-alewife ponds.

White Perch	Estimate	95% LCI	95% UCI	Resid SSQ
Alewife Present				
Linf	235.8752	229.74	242.955	
K	0.6138	0.511	0.737	
T0	-0.2744	-0.557	-0.061	
				40144
Alewife Absent				
Linf	273.448	264.04	282.885	
K	0.428	0.363	0.518	
T0	-0.411	-0.079	-0.074	
				135427
Yellow Perch	estimate	95% LCI	95% UCI	Resid SSQ
Alewife Present				
Linf	280.827	248.5989	353.2996	
K	0.260188	0.13405	0.45637	
T0	-1.1737	-2.4344	-0.328	
				38733
Alewife Absent				
Linf	288.3782	266.944	320.2007	
K	0.26495	0.18412	0.35678	
T0	-0.6686	-1.38917	-0.20135	
				55715

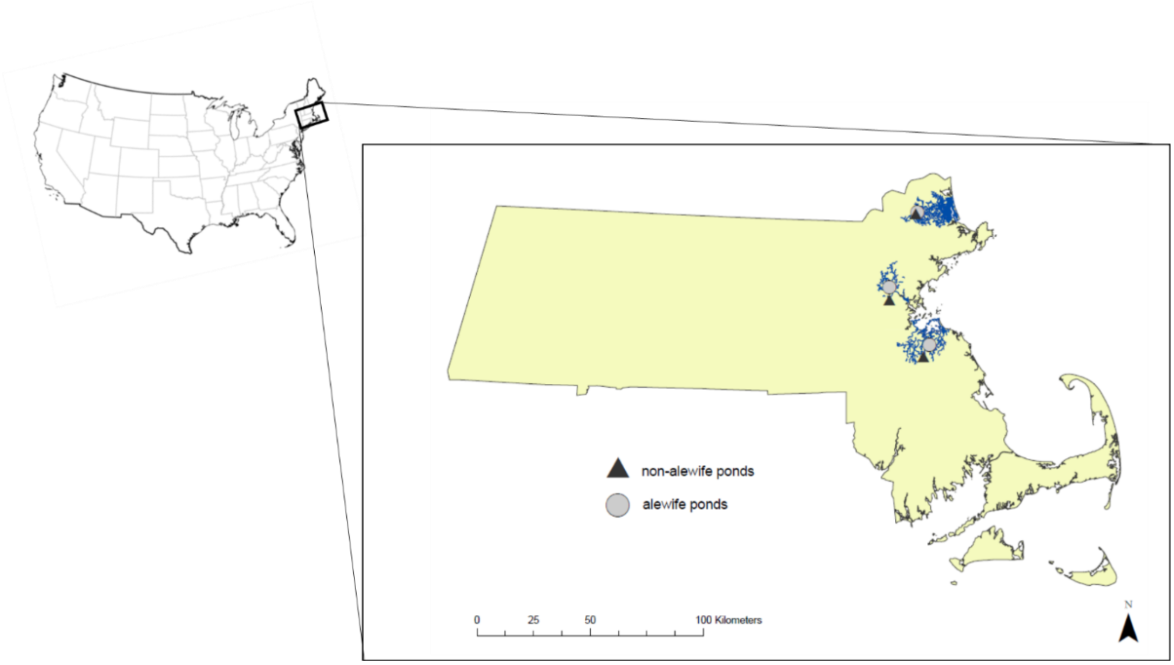


Figure 3.1: Map of 3 alewife (circles) and 3 non-alewife (triangles) ponds in eastern Massachusetts where predator sampling occurred. From south to north, pond pairs (alewife and non-alewife) were Whitman's and Weymouth Great, Upper Mystic and Fresh, and Pentucket and Rock, respectively.

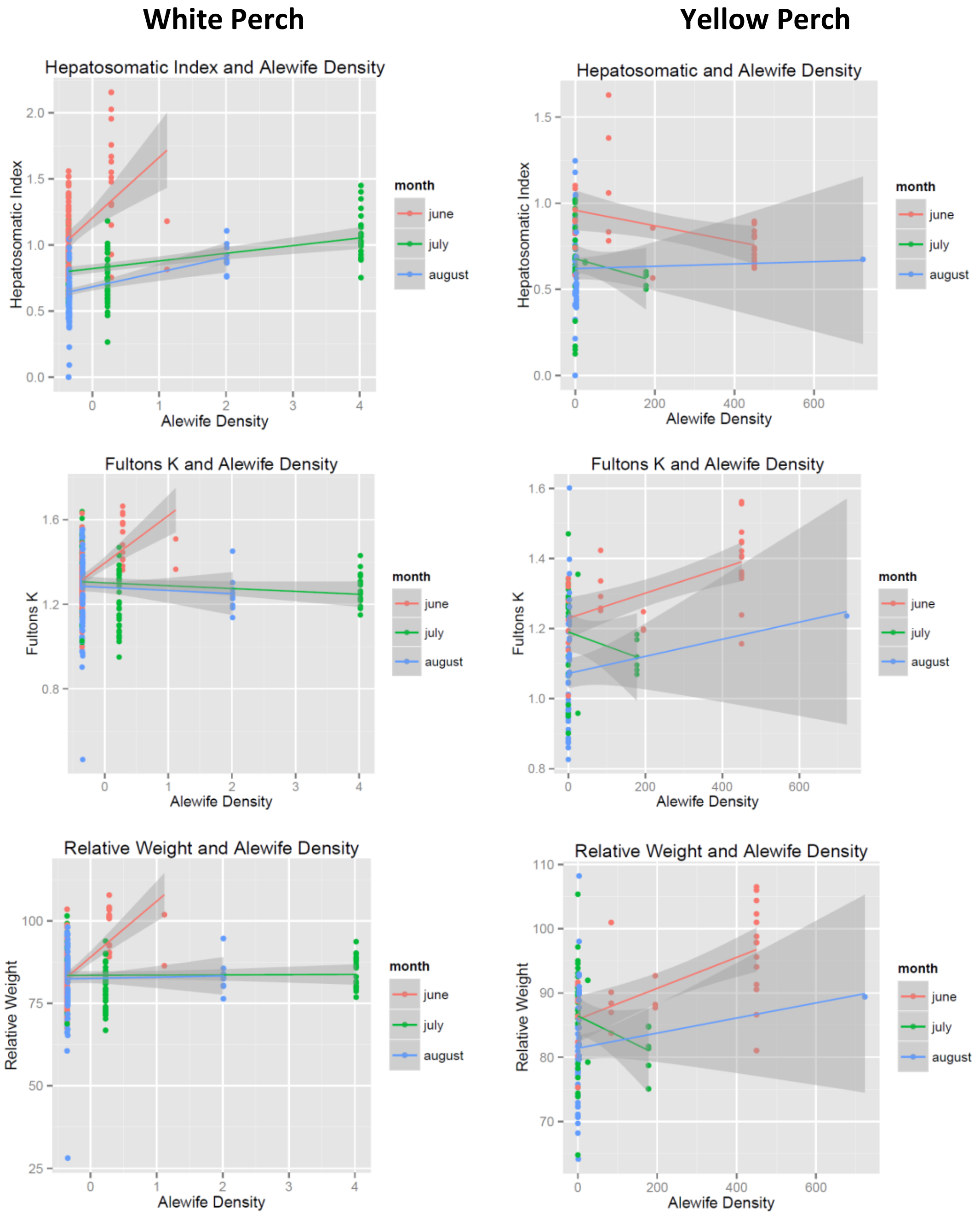


Figure 3.2: Plots show the relationship between condition (*K, HSI, Wr*) and alewife density during summer months. These plots show an interaction between month and alewife density. Alewife densities are z-score standardized for white perch, and expressed as fish/net.

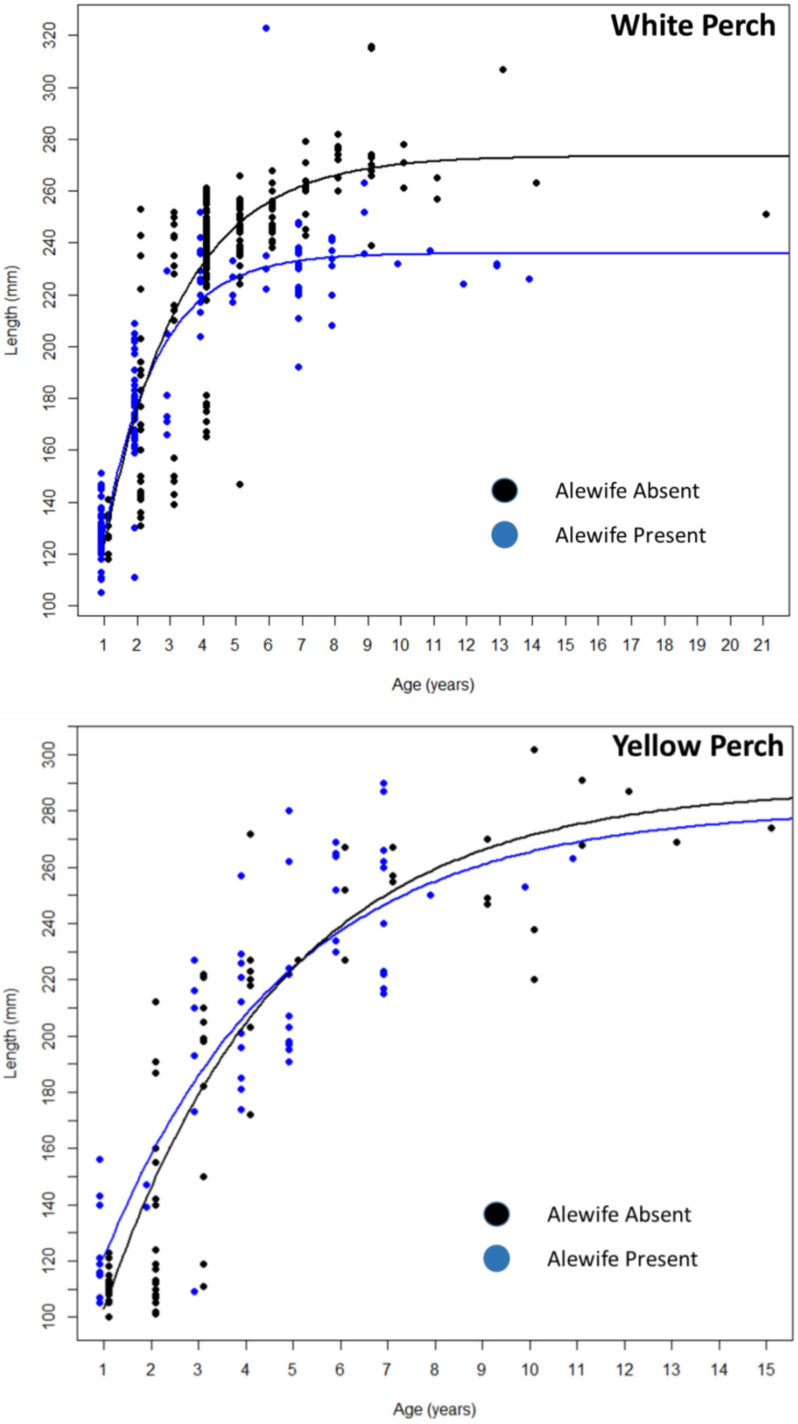


Figure 3.3: Fitted Von Bertalanffy models for white perch (top) and yellow perch (bottom) in alewife ponds (blue) and non-alewife ponds (black).

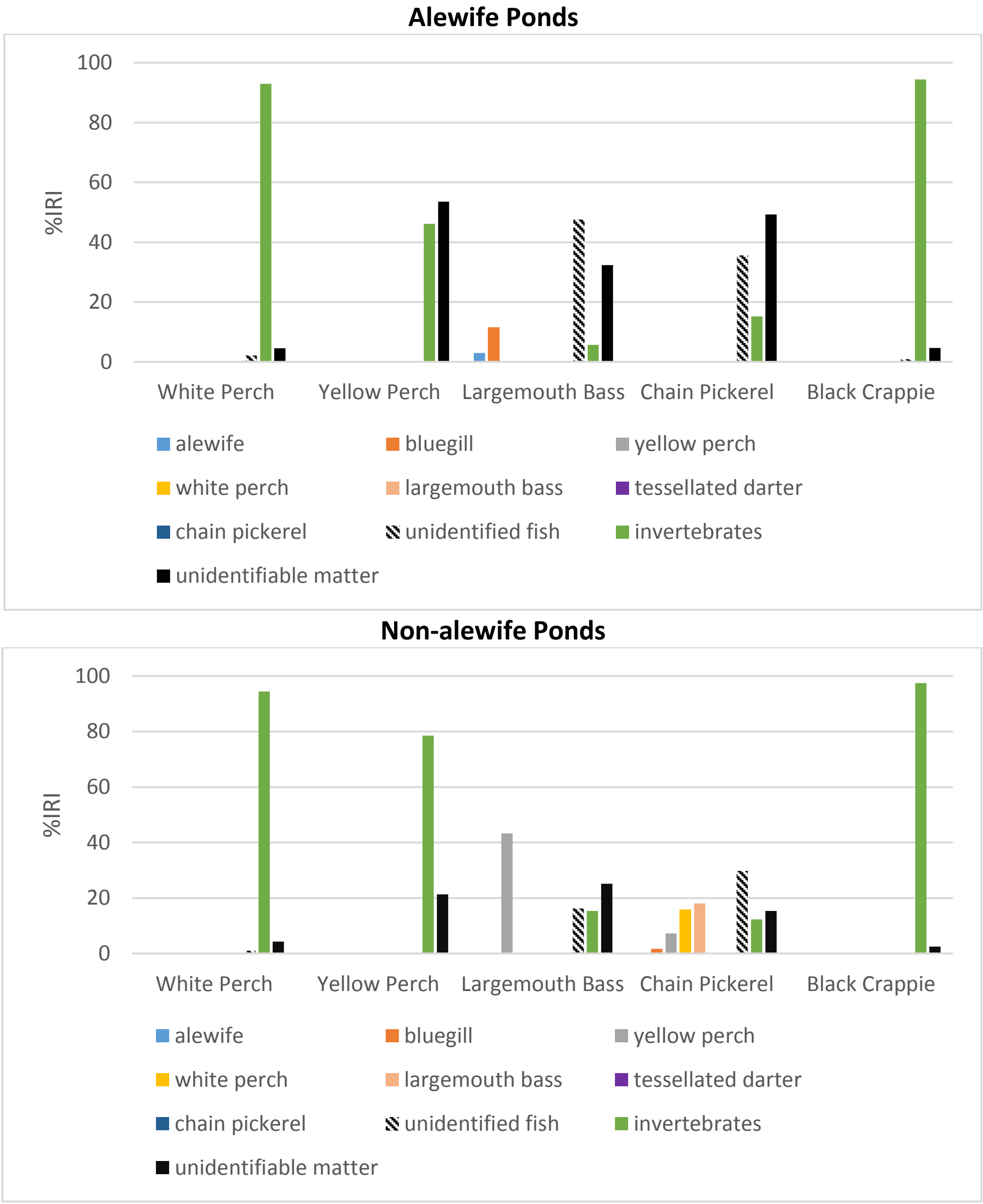


Figure 3.4: Diet graphs depicting diet index of relative importance expressed as a percentage for predators when alewives are present (top) and absent (bottom).

CHAPTER 4

CONCLUSION

This thesis provides novel insight into the impacts of river herring on freshwater food web dynamics. Using historical records, current juvenile density data, freshwater predator diet, condition and growth data, as well as a suit of biotic and abiotic observations including zooplankton analysis, I quantified various ecosystem changes that occurred as the result of the damming of New England rivers and streams. I demonstrated how changes in ecosystem structure and function have occurred from the exclusion of river herring from freshwater ecosystems. Short term ecosystems effects were observed using condition indices, and longer term ecosystem effects were observed from changes in growth rates and age and size at maturity of alewife predators. Perhaps most importantly, century long ecosystem changes occurred from damming, which resulted in estimated significant declines in river herring populations and MDN. This research has implications for management and future research in ecosystems with anadromous fish, and offers a novel approach for quantifying the consequences of damming and the loss of anadromous forage fish in freshwater ecosystems.

Historical ecological data is an important tool that can be used to better understand ecosystem changes that have occurred through time. In many fields, historical baselines for species' distribution and population data are scant. As a result, ecological baselines have shifted, and understanding and appreciation of pre-exploited conditions are lost (Pauly 1995). As researchers and managers exit their careers, new incoming scientists have different baseline references, and management strategies and expectations shift. By comparing current scientific data with historical information detailing resource use and ecosystem change, a holistic view can be obtained and ecological baselines are better understood.

River herring are important resources for humans, and were particularly essential during the development of colonial and industrial New England. They provided an abundant source of cheap food, and were widely used for bait and fertilizer. River herring were likely utilized by Native Americans for various aspects of life, although the details of this are unclear. There is evidence that Native Americans used river herring as fertilizer, and likely consumed them to some degree, although this remains unclear. Native Americans were skilled builders of fish weirs built from wood, brush, and rocks, which may have impeded anadromous fish spawning migrations. These weirs were constructed to target more desirable species such as salmon, but because river herring have poor swimming abilities compared to salmon, river herring migrations may have been disrupted. Native Americans also altered ecosystems through the burning of brush and trees in order to maintain hunting grounds.

This research has implications for climate change adaptation strategies, as anadromous fish are among the most vulnerable aquatic species to climate change (Hare et al. 2016). The complex life history of anadromous forage fish creates both challenges and opportunities when managing for adaptation. Habitat obstructions likely have significant compounding effects with changing climatic conditions. Migratory fish populations will be restricted from spawning habitat as their distribution shifts, further impeding their ability to recover.

This research also serves as a guide for freshwater and marine fisheries managers aiming to restore anadromous fish populations. By prioritizing river restoration and dam removal, ecological benefits can be achieved and native fish communities can be reestablished, supporting higher potential abundances of anadromous fish and potentially their predators. Restored fish runs would greatly benefit commercial and recreational fishing communities, as well as ecological and economic interests. If managers and environmental decision-makers prioritize dam removal, anadromous forage fish populations could be restored, which would reduce the need to stock non-native forage fish to maintain sportfish populations. Because of their transient life history, the productivity of forage fish would likely be higher with anadromous migrations when compared to stocked forage fish that are year-round residents of ponds. This has the potential to reduce long term costs of forage fish stocking in ponds, while providing ecological benefits to other freshwater, marine, and terrestrial ecosystems. As exemplified by this thesis, there are a plethora of ecosystem benefits to restored river herring runs. As anthropogenic stressors persist and environmental and climatic conditions continue to change at high rates, restoring river herring populations may become more difficult. Future scenarios that incorporate multiple stressors should include historical data, with current ecosystem structure and function in consideration in order to better understand the interaction between alewives and their ecosystems.

APPENDICES

APPENDIX A

DAMMING, HABITAT LOSS, AND ALEWIFE POPULATION DATA

Figure A.1: Unobstructed stream habitat in 1600 prior to damming (top map) and stream habitat remaining by 1900 after damming (bottom map).

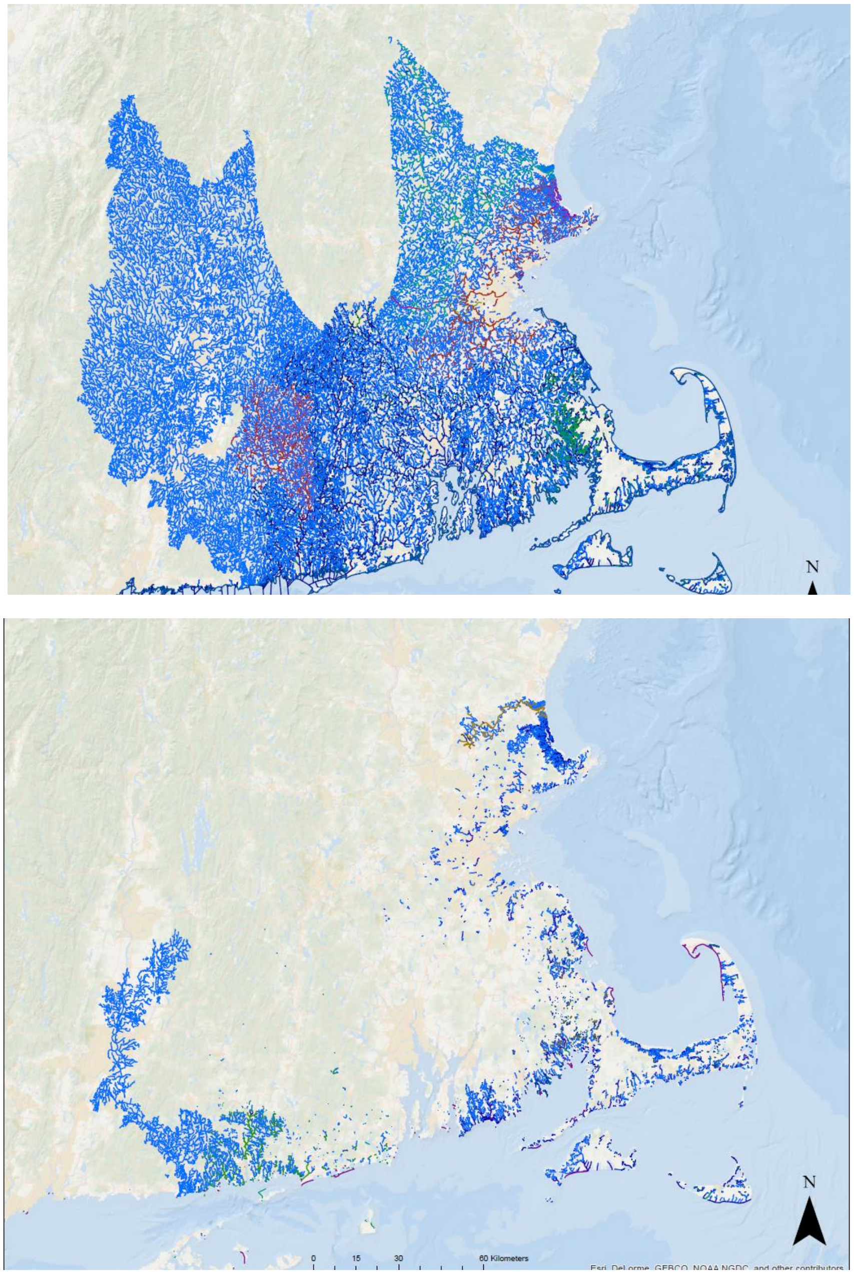


Figure A.2: Lake and pond habitat loss from dams constructed form 1600-1900 in 5 New England watersheds.

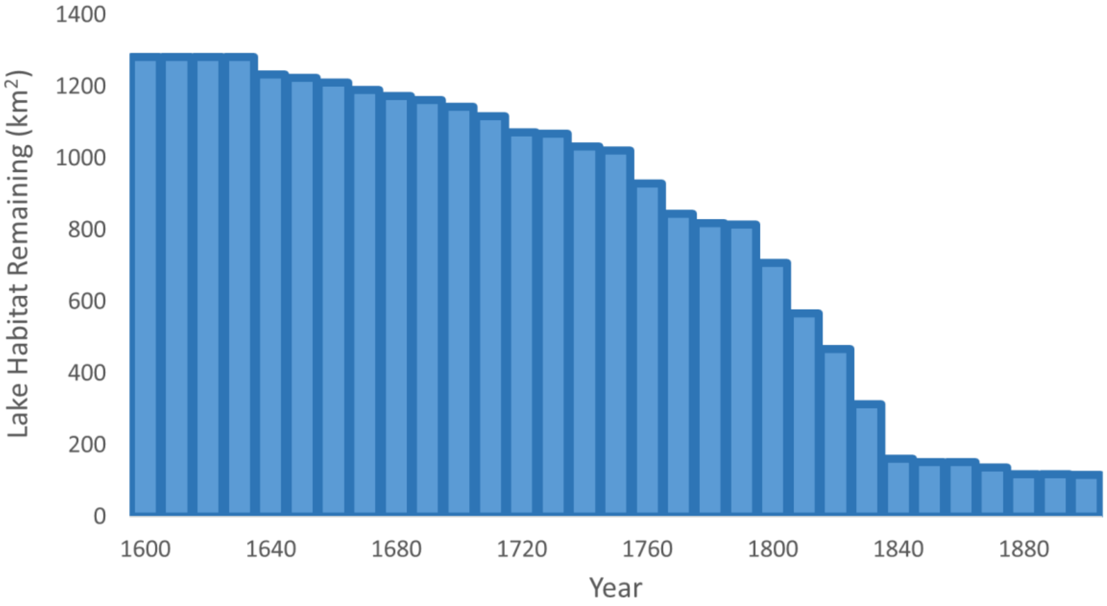
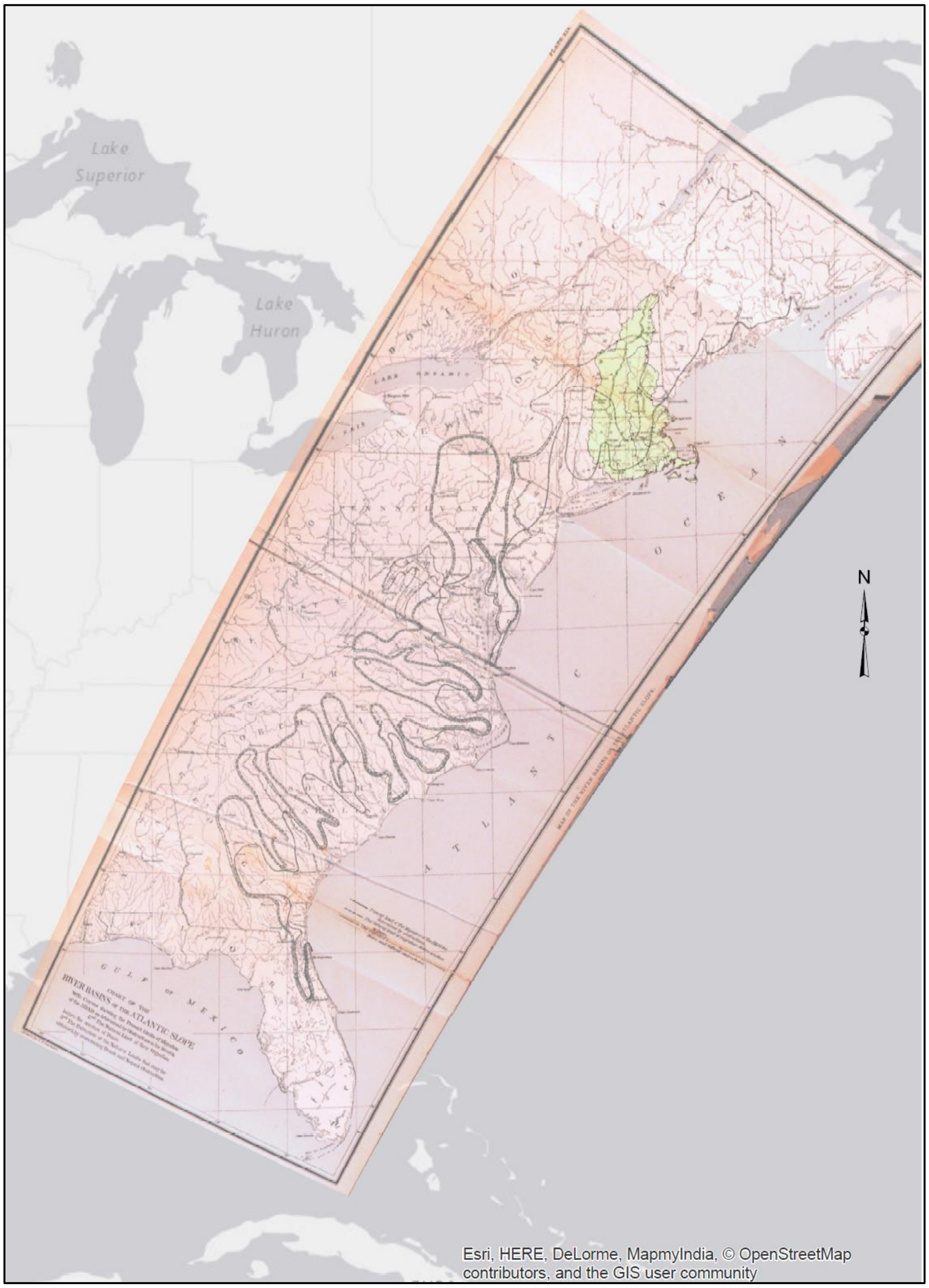


Figure A.3: Historical American shad range map georeferenced to New England watersheds, and used as a proxy for river herring migration limits.



Esri, HERE, DeLorme, MapmyIndia, © OpenStreetMap contributors, and the GIS user community

Figure A.4: Historical map detailing the natural migration limit of American shad prior to colonial damming was used to determine virgin spawning habitat of American shad, and was used as a proxy for river herring native ranges. The historical map was digitized and georeferenced, and was used to clip watershed boundaries to perform a network analysis. Watersheds: CT-Connecticut, TP-Thames-Pawcatuck, NR-Narragansett, CM-Coastal Massachusetts, MK-Merrimack.

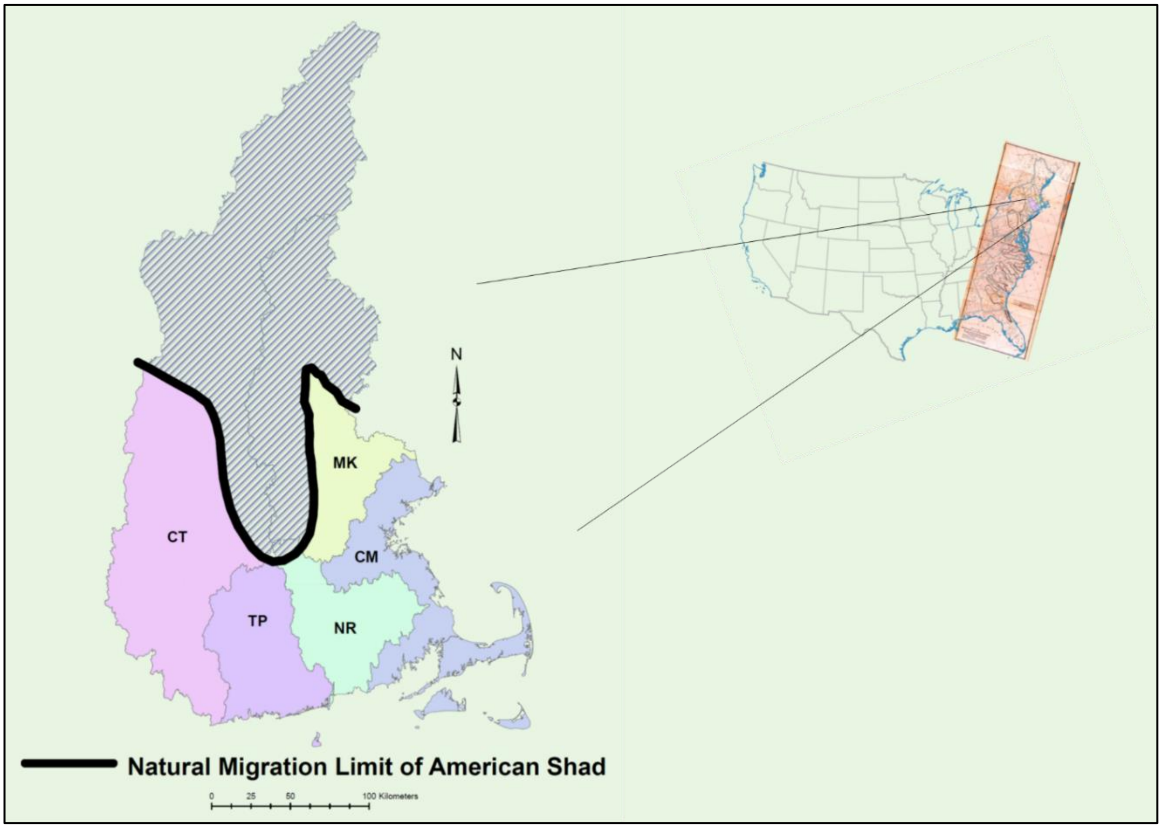


Figure A.5: Network analysis and lost habitat calculated for each dam in the Thames-Pawcatuck watershed.

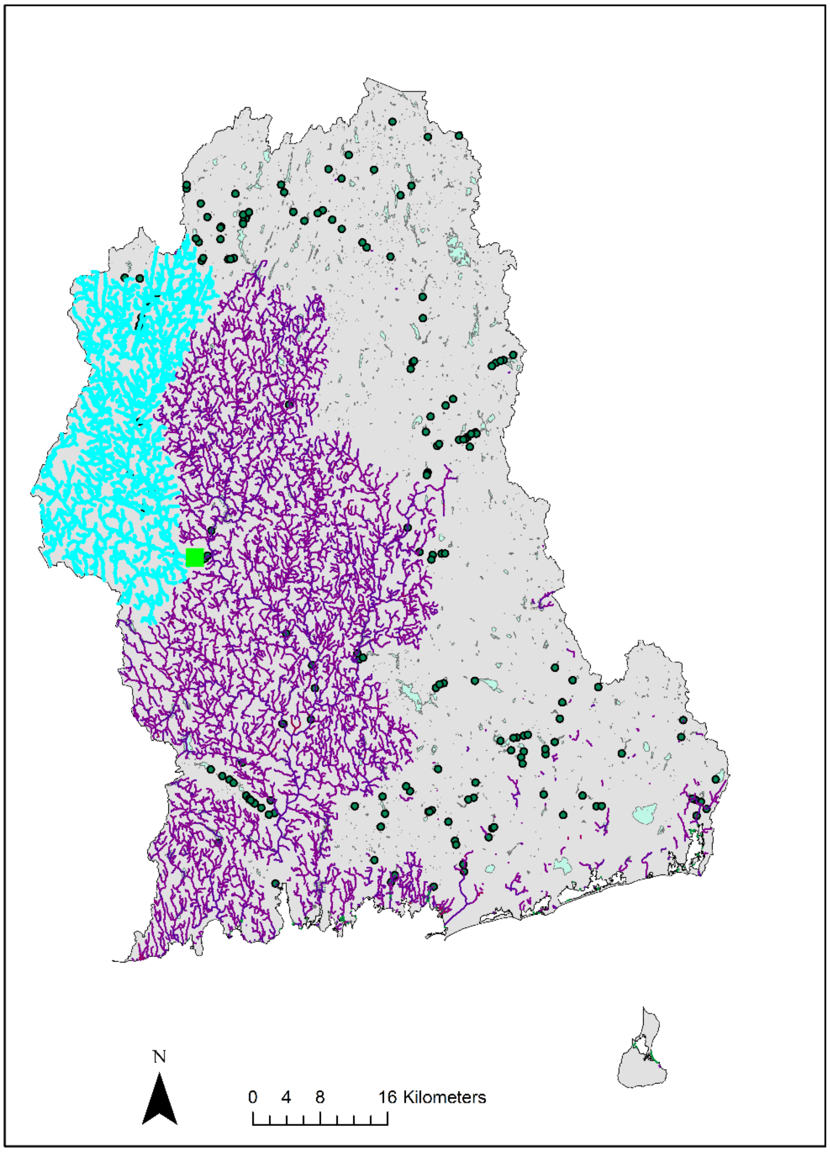


Figure A.6: Obstructed (red) and unobstructed (blue) river habitat after construction of the Pawtucket Falls Dam on the Merrimack River, Massachusetts.

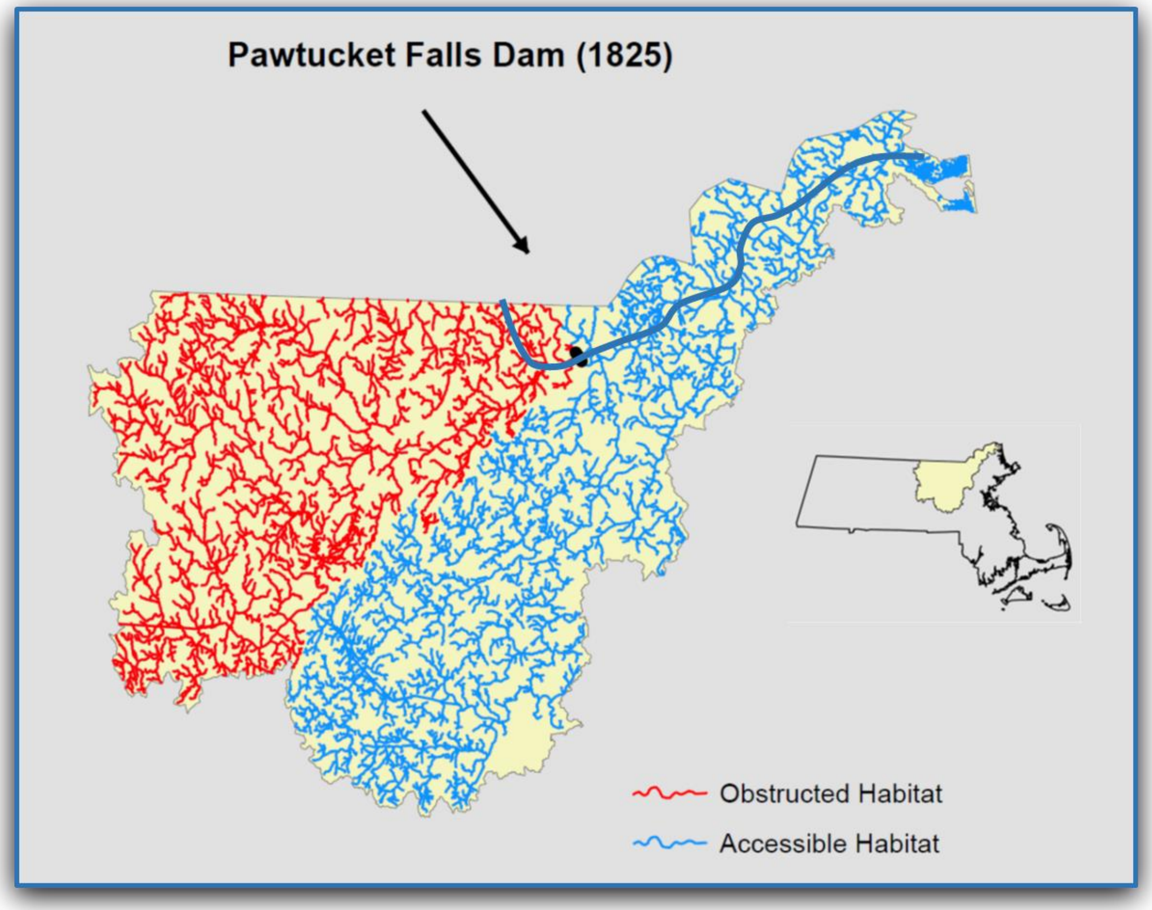


Figure A.7 Merrimack River habitat loss by decade.

Year	River Habitat Remaining (km)	Percent River	Lake Habitat Remaining (km^2)	Percent Lake
1600	5337	100.0	98.9	100.0
1610	5337	100.0	98.9	100.0
1620	5337	100.0	98.9	100.0
1630	5337	100.0	98.9	100.0
1640	5327	99.8	90.6	91.6
1650	5107	95.7	88.1	89.1
1660	4582	85.9	81.3	82.2
1670	4482	84.0	79.8	80.7
1680	4112	77.0	67.3	68.0
1690	3944	73.9	64.1	64.8
1700	3752	70.3	59.1	59.8
1710	3037	56.9	43.7	44.2
1720	3025	56.7	43.7	44.2
1730	3006	56.3	43.6	44.1
1740	2792	52.3	40.7	41.2
1750	2792	52.3	40.7	41.2
1760	2792	52.3	40.7	41.2
1770	2792	52.3	40.7	41.2
1780	2792	52.3	40.7	41.2
1790	2792	52.3	40.7	41.2
1800	2792	52.3	40.7	41.2
1810	2792	52.3	40.7	41.2
1820	2792	52.3	40.7	41.2
1830	879	16.5	10.1	10.2
1840	872	16.3	10.1	10.2
1850	422	7.9	2.8	2.8
1860	422	7.9	2.8	2.8
1870	422	7.9	2.8	2.8
1880	422	7.9	2.8	2.8
1890	422	7.9	2.8	2.8
1900	422	7.9	2.8	2.8

Figure A.8 Coastal Massachusetts habitat loss.

Year	River Habitat Remaining (km)	Percent River	Lake Habitat Remaining (km^2)	Percent Lake
1600	7217	100.00	151.8	100.00
1610	7217	100.00	151.8	100.00
1620	7217	100.00	151.8	100.00
1630	7210	99.90	151.8	100.00
1640	5315	73.65	118.8	78.26
1650	5058	70.08	112	73.78
1660	4966	68.81	109.9	72.40
1670	4940	68.45	108.2	71.28
1680	4873	67.52	106.9	70.42
1690	4778	66.20	101.5	66.86
1700	4637	64.25	98.6	64.95
1710	4483	62.12	97.2	64.03
1720	4408	61.08	93.9	61.86
1730	4317	59.82	90.6	59.68
1740	4317	59.82	90.6	59.68
1750	4223	58.51	89.4	58.89
1760	4160	57.64	89.2	58.76
1770	4120	57.09	84.4	55.60
1780	4120	57.09	84.4	55.60
1790	4117	57.05	84.3	55.53
1800	4107	56.91	84.2	55.47
1810	4064	56.31	83.4	54.94
1820	3588	49.72	72.6	47.83
1830	3577	49.56	71.1	46.84
1840	3478	48.19	66.9	44.07
1850	3478	48.19	66.9	44.07
1860	3474	48.14	66.9	44.07
1870	3469	48.07	65.8	43.35
1880	3147.3	43.61	52.2	34.39
1890	3142.3	43.54	51.8	34.12
1900	3142.3	43.54	51.8	34.12

Figure A.9 Narragansett River watershed habitat loss.

Year	River Habitat Remaining (km)	Percent River	Lake Habitat Remaining (km^2)	Percent Lake
1600	5767	100	161.3	100
1610	5767	100	161.3	100
1620	5767	100	161.3	100
1630	5767	100	161.3	100
1640	5576	97	157.7	98
1650	5576	97	157.7	98
1660	5555	96	157.2	97
1670	5442	94	156.5	97
1680	5442	94	156.5	97
1690	5442	94	156.5	97
1700	4771	83	146.8	91
1710	4739	82	145.9	90
1720	3165	55	112.2	70
1730	3151	55	111.1	69
1740	2804	49	91.9	57
1750	2561	44	84.2	52
1760	2561	44	84.2	52
1770	2397	42	79.7	49
1780	2368	41	79.6	49
1790	2278	40	78.2	48
1800	2188	38	76	47
1810	2026	35	72.9	45
1820	1155	20	37.5	23
1830	1122	19	36.5	23
1840	1111	19	34.5	21
1850	1111	19	34.5	21
1860	1111	19	34.5	21
1870	988	17	30.9	19
1880	952	17	29.3	18
1890	916	16	28.3	18
1900	915	16	28.3	18

Figure A.10 Thames-Pawcatuck watershed habitat loss.

Year	River Habitat Remaining (km)	Percent River	Lake Habitat Remaining (km^2)	Percent Lake
1600	8248.3	100.00	119.2	100.00
1610	8248.3	100.00	119.2	100.00
1620	8248.3	100.00	119.2	100.00
1630	8248.3	100.00	119.2	100.00
1640	8248.3	100.00	119.2	100.00
1650	8234.7	99.84	119	99.83
1660	8054.8	97.65	116.7	97.90
1670	7473	90.60	100.3	84.14
1680	7473	90.60	100.3	84.14
1690	7401.5	89.73	100	83.89
1700	7401.5	89.73	100	83.89
1710	7316.9	88.71	98.9	82.97
1720	7283.8	88.31	98.7	82.80
1730	7283.8	88.31	98.7	82.80
1740	6526.3	79.12	87.3	73.24
1750	6495.8	78.75	87.2	73.15
1760	6495.8	78.75	87.2	73.15
1770	6173.1	74.84	80.7	67.70
1780	6173.1	74.84	80.7	67.70
1790	6173.1	74.84	80.7	67.70
1800	5958.1	72.23	72.9	61.16
1810	5338.2	64.72	58.1	48.74
1820	3763	45.62	40.3	33.81
1830	3149.3	38.18	31	26.01
1840	1134.1	13.75	14.4	12.08
1850	1088.9	13.20	14.1	11.83
1860	1088.9	13.20	14.1	11.83
1870	764.3	9.27	9	7.55
1880	756.9	9.18	7.8	6.54
1890	750.3	9.10	7.6	6.38
1900	750.3	9.10	7.6	6.38

Figure A.11 Connecticut River watershed habitat loss.

Year	River Habitat Remaining (km)	Percent River	Lake Habitat Remaining (km^2)	Percent Lake
1600	17907	100.00	179.7	100.00
1610	17907	100.00	179.7	100.00
1620	17907	100.00	179.7	100.00
1630	17907	100.00	179.7	100.00
1640	17626	98.43	176	97.94
1650	17626	98.43	176	97.94
1660	17521	97.84	174.7	97.22
1670	17227	96.20	173.3	96.44
1680	16835	94.01	170.1	94.66
1690	16778	93.70	168.7	93.88
1700	16414	91.66	167.7	93.32
1710	16078	89.79	159.8	88.93
1720	15413	86.07	152.8	85.03
1730	15413	86.07	152.8	85.03
1740	15136	84.53	150.7	83.86
1750	15007	83.81	148.7	82.75
1760	14749	82.36	148	82.36
1770	14336	80.06	144.9	80.63
1780	14203	79.32	144.1	80.19
1790	14196	79.28	144.1	80.19
1800	8884	49.61	110.5	61.49
1810	6105	34.09	71	39.51
1820	5779	32.27	64.4	35.84
1830	1519	8.48	28.6	15.92
1840	1485	8.29	28.3	15.75
1850	1292	7.22	25.9	14.41
1860	1270	7.09	25.3	14.08
1870	1241	6.93	25.2	14.02
1880	1200	6.70	23.6	13.13
1890	1200	6.70	23.6	13.13
1900	1199	6.70	23.1	12.85

Figure A.12 Lost nutrients from adult return spawning alewives through mortality and excretion, estimated from Durbin et al. (1979).

year	Total P (mort + excretion) g	Total N (mort + excretion) g	Total C (mort + excretion) g	Total P (kg)	Total N (kg)	Total C (kg)
1600	0	0	0	0.0	0.0	0.0
1610	0	0	0	0.0	0.0	0.0
1620	0	0	0	0.0	0.0	0.0
1630	0	0	0	0.0	0.0	0.0
1640	447613	2671001	17097341	447.6	2671.0	17097.3
1650	535109	3193110	20439414	535.1	3193.1	20439.4
1660	654841	3907575	25012776	654.8	3907.6	25012.8
1670	854701	5100183	32646774	854.7	5100.2	32646.8
1680	1011273	6034483	38627325	1011.3	6034.5	38627.3
1690	1106138	6600560	42250836	1106.1	6600.6	42250.8
1700	1277446	7622795	48794263	1277.4	7622.8	48794.3
1710	1523357	9090196	58187246	1523.4	9090.2	58187.2
1720	1931541	11525918	73778543	1931.5	11525.9	73778.5
1730	1972987	11773233	75361630	1973.0	11773.2	75361.6
1740	2300868	13729769	87885608	2300.9	13729.8	87885.6
1750	2402179	14334316	91755377	2402.2	14334.3	91755.4
1760	3253485	19414236	124272443	3253.5	19414.2	124272.4
1770	4034170	24072753	154092070	4034.2	24072.8	154092.1
1780	4270042	25480249	163101595	4270.0	25480.2	163101.6
1790	4298777	25651721	164199202	4298.8	25651.7	164199.2
1800	5297433	31610911	202344565	5297.4	31610.9	202344.6
1810	6583776	39286796	251478664	6583.8	39286.8	251478.7
1820	7497883	44741463	286394529	7497.9	44741.5	286394.5
1830	8923336	53247447	340842172	8923.3	53247.4	340842.2
1840	10316369	61559975	394051489	10316.4	61560.0	394051.5
1850	10408471	62109564	397569460	10408.5	62109.6	397569.5
1860	10413997	62142539	397780538	10414.0	62142.5	397780.5
1870	10548557	62945488	402920294	10548.6	62945.5	402920.3
1880	10714340	63934748	409252643	10714.3	63934.7	409252.6
1890	10729076	64022682	409815518	10729.1	64022.7	409815.5
1900	10733681	64050161	409991417	10733.7	64050.2	409991.4

Figure A.13 Abundance of alewives in each age class estimated from juvenile densities from purse seines in June and July 2014.

pond	jun avg	jul avg	max_jun_jul	N(0) fw	*.99 (mort)	N(0) sw	N+1	N+2	N+3	N+4	lost marine forage
Lower Millpond	12884	954	128884	1741675676	1724258919	17416757	7825853	3516383	1580013	1059114	75812
Pilgrim Lake	35692	249	35692	482319865	477496666	4823199	2167203	973787	437551	293299	277526
Upper Mystic	88	18060	18059	244040541	241600135	2440405	1096545	492709	221389	148401	113802
Lower Mystic	5	3351	3351	45283784	44830946	452838	203473	91426	41081	27537	310313
Long Pond	2912	33	2911	39337838	38944459	393378	176756	79422	35686	23921	27287
Coonamessett	2445	723	2445	33040541	32710135	330405	148461	66708	29974	20092	271180
Oldham	2197	489	2196	29675676	29378919	296757	133341	59914	26921	18046	138509
Cedar Lake	2187	512	2187	29549459	29253965	295495	132774	59659	26807	17969	3681
Great Herring	2137	105	2137	28873784	28585046	288738	129738	58295	26194	17558	369457
Whitmans	1790	12	1790	24193649	23951712	241936	108709	48846	21948	14712	16357643
Gull	38	1091	1091	14747703	14600226	147477	66266	29775	13379	8968	425301
Chebacco	897	16	897	12117027	11995857	121170	54445	24464	10992	7368	278711
Billington Sea	597	282	597	8072027	7991307	80720	36270	16297	7323	4909	4529900
Santuit	564	140	564	7626081	7549820	76261	34266	15397	6918	4637	71623
Furnace	138	215	215	2905405	2876351	29054	13055	5866	2636	1767	24114
Upper Mill/Walkers	116	194	194	2621622	2595405	26216	11780	5293	2378	1594	24622
Snipatuit	190	60	190	2567568	2541892	25676	11537	5184	2329	1561	2292004
Johns	29	10	29	391892	387973	3919	1761	791	356	238	227224

Figure A.14 Available habitat in 8 New England watersheds and resulting population structure of alewives.

year	total ne habitat	N($_0$)	N+1	N+2	N+3	N+3.583
1600	1281.618	340060883	152799204	68657108	30849627	19350624
1610	1281.618	340060883	152799204	68657108	30849627	19350624
1620	1281.618	340060883	152799204	68657108	30849627	19350624
1630	1281.618	340060883	152799204	68657108	30849627	19350624
1640	1233.018	327165497	147004934	66053575	29679784	18616833
1650	1223.518	324644794	145872309	65544653	29451111	18473396
1660	1210.518	321195411	144322401	64848235	29138190	18277114
1670	1188.818	315437594	141735248	63685752	28615853	17949475
1680	1171.818	310926863	139708445	62775051	28206649	17692799
1690	1161.518	308193890	138480441	62223273	27958719	17537283
1700	1142.918	303258619	136262881	61226859	27511001	17256450
1710	1116.218	296174116	133079609	59796523	26868310	16853317
1720	1071.899	284414639	127795735	57422325	25801514	16184163
1730	1067.399	283220622	127259228	57181257	25693195	16116219
1740	1031.799	273774619	123014866	55274142	24836273	15578710
1750	1020.799	270855910	121703405	54684865	24571494	15412625
1760	928.3677	246330451	110683406	49733260	22346594	14017043
1770	843.604	223839491	100577567	45192414	20306261	12737230
1780	817.994	217044207	97524249	43820470	19689806	12350556
1790	814.874	216216355	97152271	43653329	19614705	12303448
1800	706.444	187445846	84224848	37844664	17004704	10666308
1810	566.778	150387266	67573354	30362665	13642825	8557548
1820	467.528	124052553	55740405	25045778	11253794	7059013
1830	312.758	82986320	37288157	16754649	7528349	4722205
1840	161.508	42854074	19255577	8652088	3887634	2438543
1850	151.508	40200703	18063340	8116382	3646925	2287557
1860	150.908	40041500	17991806	8084240	3632483	2278498
1870	136.298	36164925	16249948	7301572	3280808	2057908
1880	118.298	31388856	14103922	6337301	2847533	1786133
1890	116.698	30964316	13913164	6251588	2809019	1761975
1900	116.198	30831648	13853552	6224802	2796984	1754426

Figure A.15 Juvenile alewife densities (# fish/net purse seine haul) from coastal ponds sampled during summer 2014.

Average of average # per net				
Ponds	**(June)**	**(July)**	**(August)**	**Average**
Billington Sea	597	282	93	324
Cedar Lake	2187	512	93	931
Chebacco	897	16	49	321
Coonamessett	2445	723	153	1107
Furnace	138	215	22	125
Great Herring	2137	105	366	869
Gull	38	1091	622	584
Johns	29	10	25	21
Long Pond	2912	33	1	982
Lower Millpond	12884	954	370	4736
Lower Mystic	5	3351	506	1287
Oldham	2197	489	188	958
Pentucket	51	24	4	26
Pilgrim Lake	35692	249	284	12075
Robbins	9	5	0	5
Santuit	564	140	93	266
Snipatuit	190	60	0	83
Upper Mill/Walkers	116	194	376	229
Upper Mystic	88	18060	551	6233
Whitmans	1790	12	8	603
Average	**3248**	**1326**	**190**	**1588**

Figure A.16: Map of historical sightings of fish in Massachusetts freshwater habitats. Historical documents and anecdotal information were used to locate fish references.

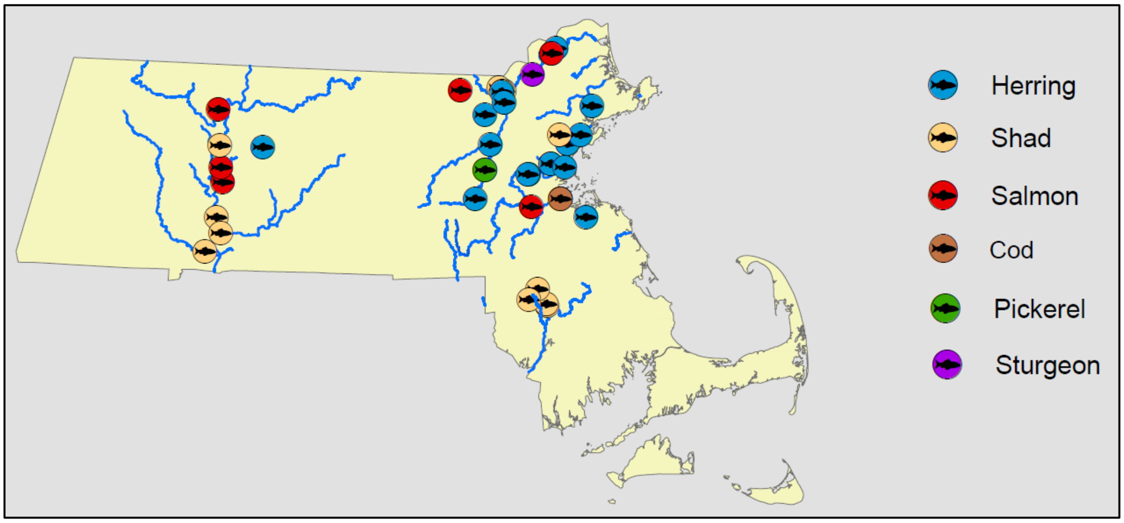


Figure A.17: Graph of percent weight of juvenile alewives in the diets of freshwater predators. Fish were collected from daytime beach seines and nighttime purse seines from 20 coastal ponds where juvenile alewives were present (n=301).

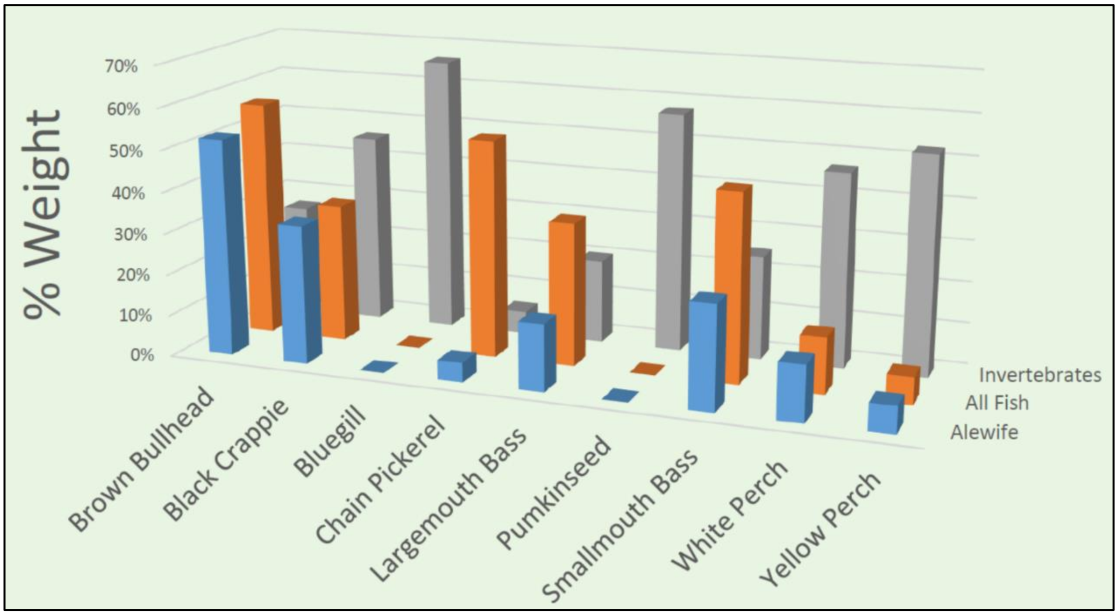


Figure A.18: Graph of the cumulative annual lost marine forage from 1600-1900 for eight New England watersheds. Marine forage was calculated as the difference between the number of 4-year-old fish and the number of emigrated YOY fish (N3 – N0). Solid line represents YOY-based estimates from 18 coastal ponds; dashed line represents recruit - based estimates from adult return data (Crecco and Gibson 1990, Hall et al. 2012) from the Damariscotta watershed. Graph displays the mean productivity with 75% confidence intervals.

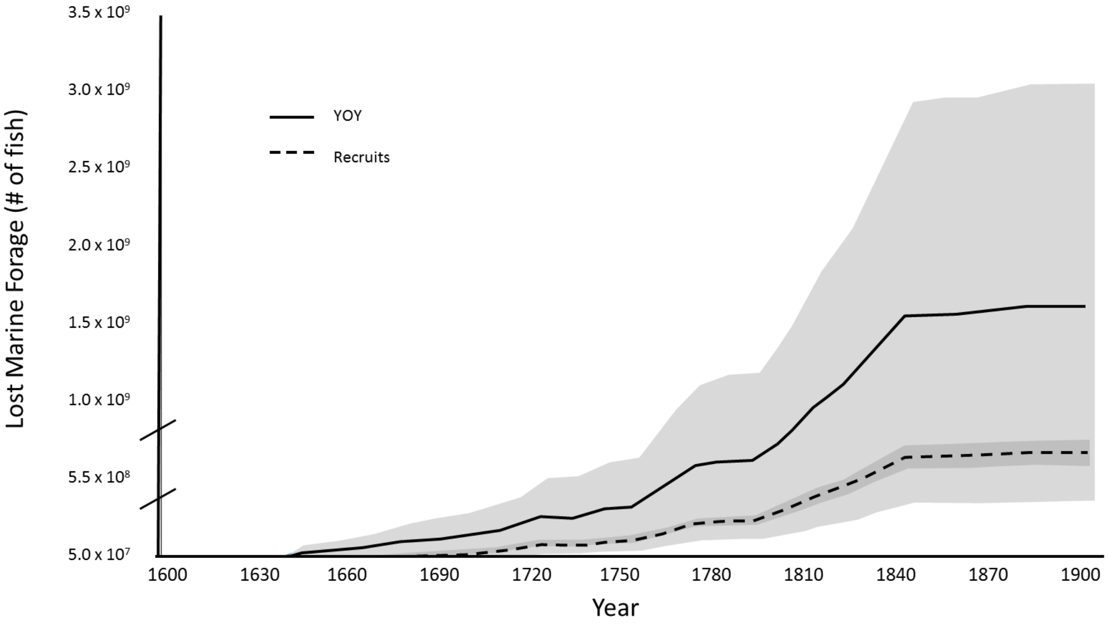


Figure A.19: Production of adult return spawners expressed as number of 4-year-old fish/km^2 for YOY and recruits. YOY estimates were derived from 18 coastal ponds in MA, and recruit estimates are from adult run count data for the Damariscotta River, ME (Crecco and Gibson 1990, Hall et al. 2012). Box plots show the mean (center dark line), the lower and upper bounds for 50% confidence intervals, and the maximum/minimum value or 1.5 times the interquartile range, whichever is smaller (error bars).

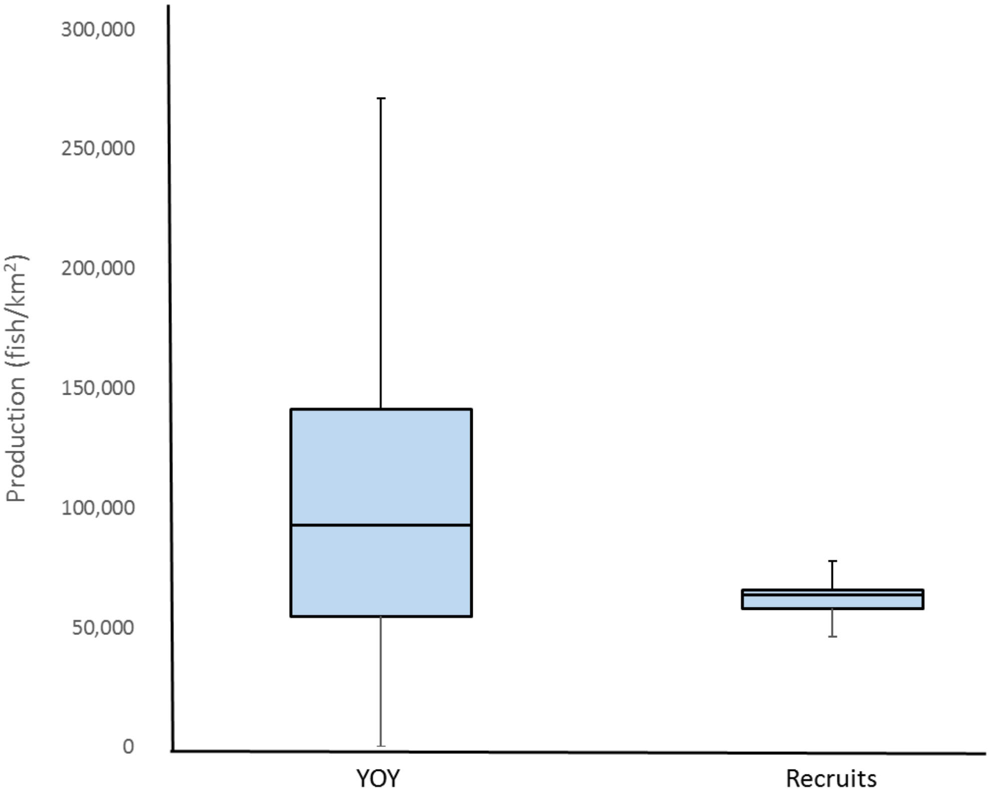


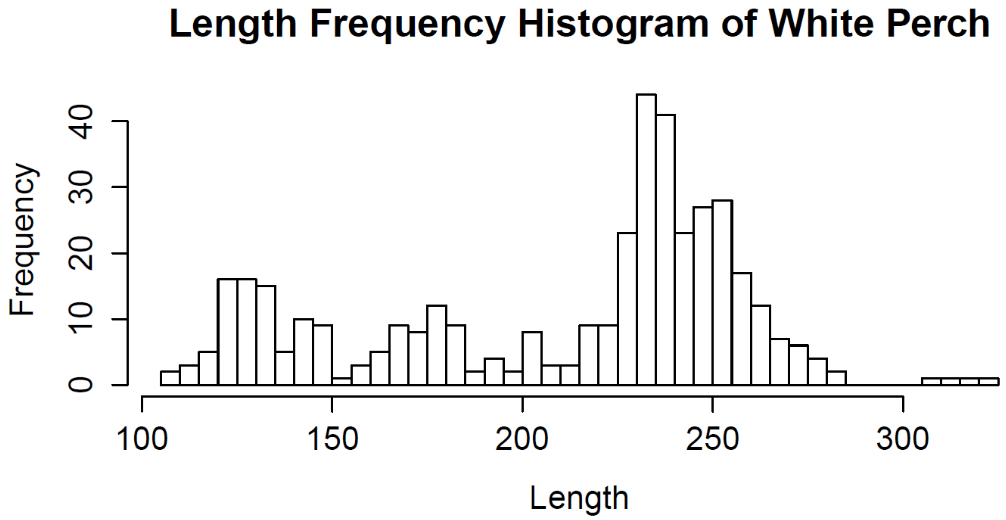
Figure A.20 Assumptions of habitat loss and model calculations and associated direction of change in alewife population estimates.

Assumption	Predicted direction of change in population estimates
American shad spawning range = alewife spawning range	↑ ↓
Pond habitat used equally by alewife	↑ ↓
Greater pond habitat available = greater alewife productivity	↑ ↓
Mill indicates presence of dam	↓
Dams = complete habitat obstruction of alewives	↓
Spawn date = May 1, juvenile emigration date = Sept. 1	↑ ↓
Average adult spawner = age 4	↑
Only age 4 alewives are spawning	↑
Juvenile sampling occurred at highest alewife densities	↑
Juvenile mortality = 99%	↑ ↓
Adult mortality (Z) = 0.8	↑ ↓

APPENDIX B

CONDITION DATA AND MODELS

Figure B.1: Length frequency histograms of white and yellow perch captured using gillnets from 6 coastal ponds.



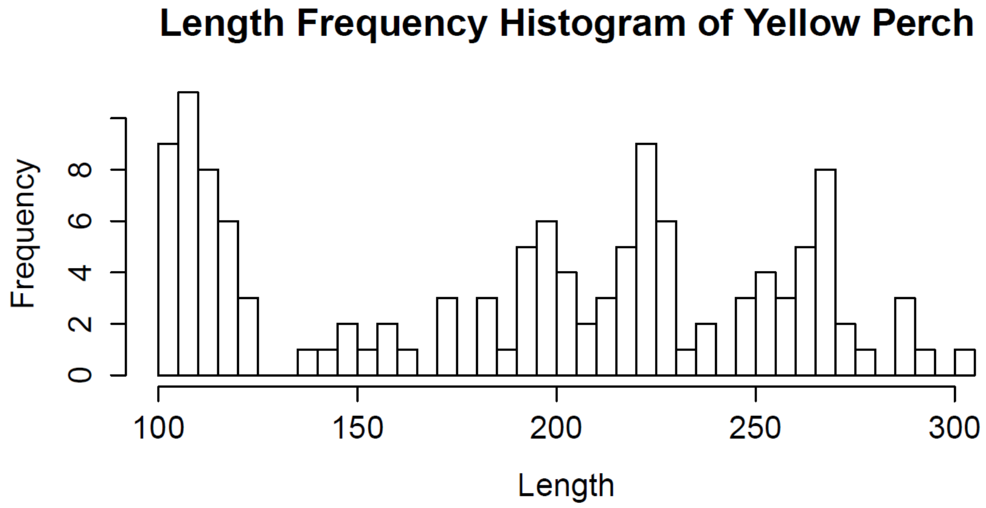


Figure B.2: Box plots of white perch condition across coastal ponds. Center black lines represent means and boxes represent the interquartile range.

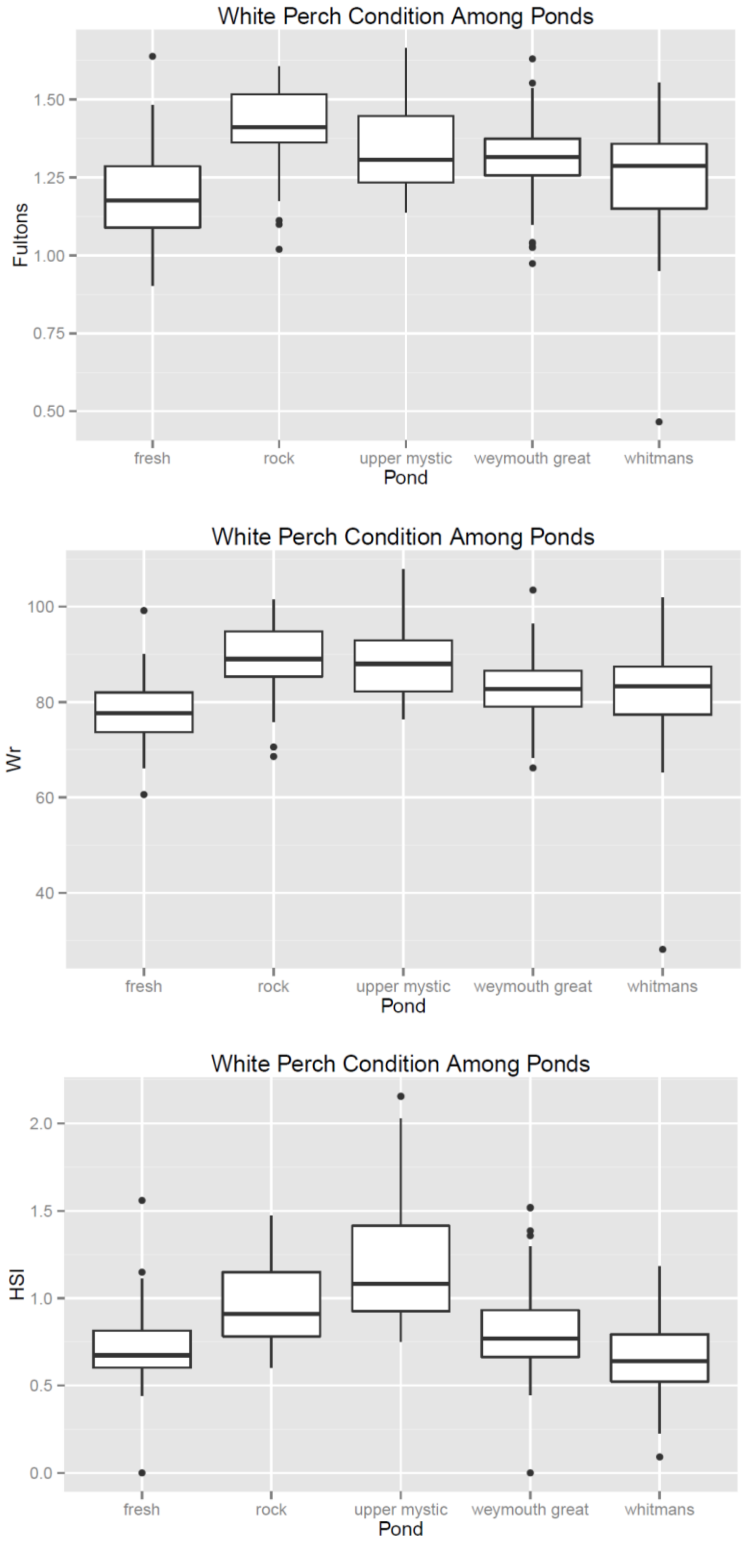


Figure B.3: Box plots and yellow perch condition across coastal ponds.

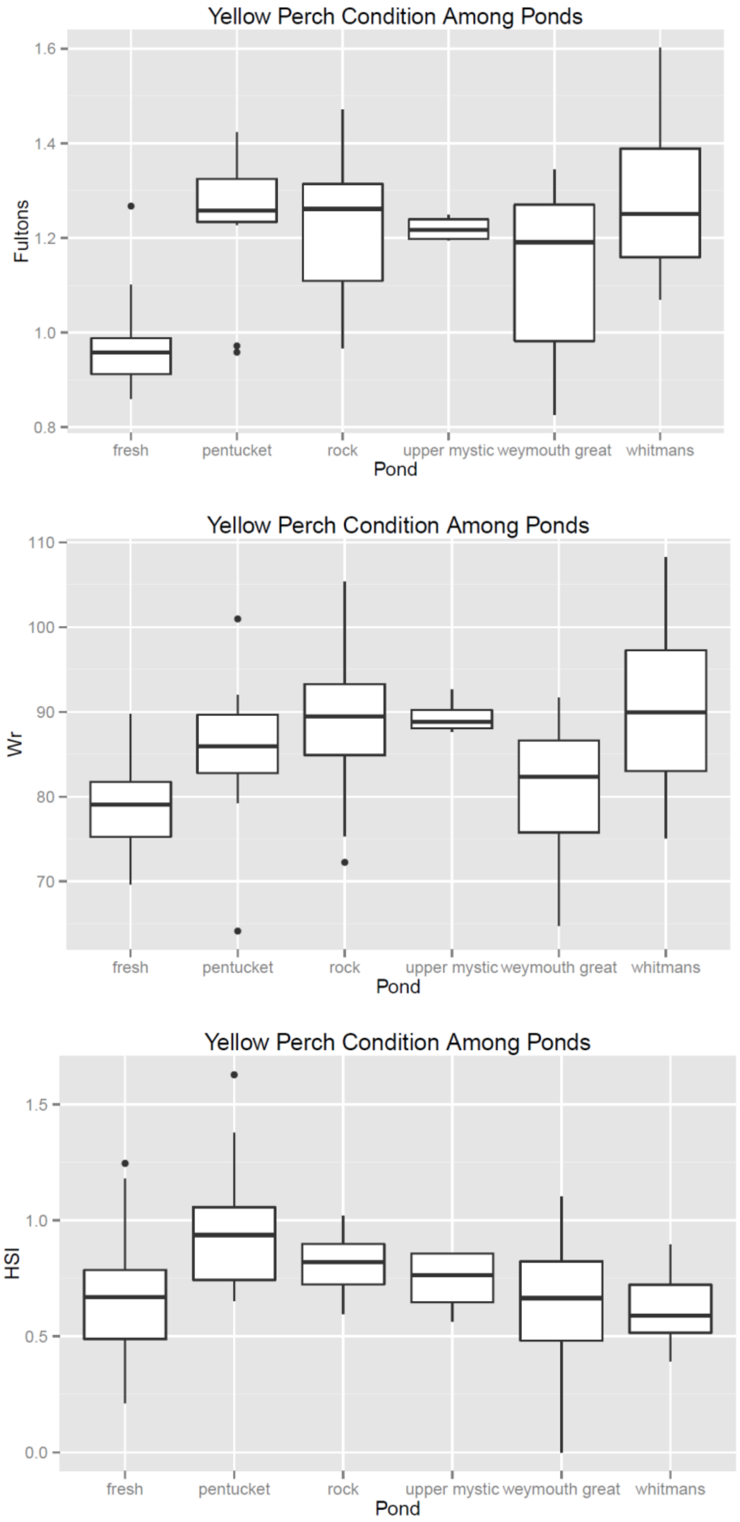


Figure B.4: Box plots of white perch condition by month collected.

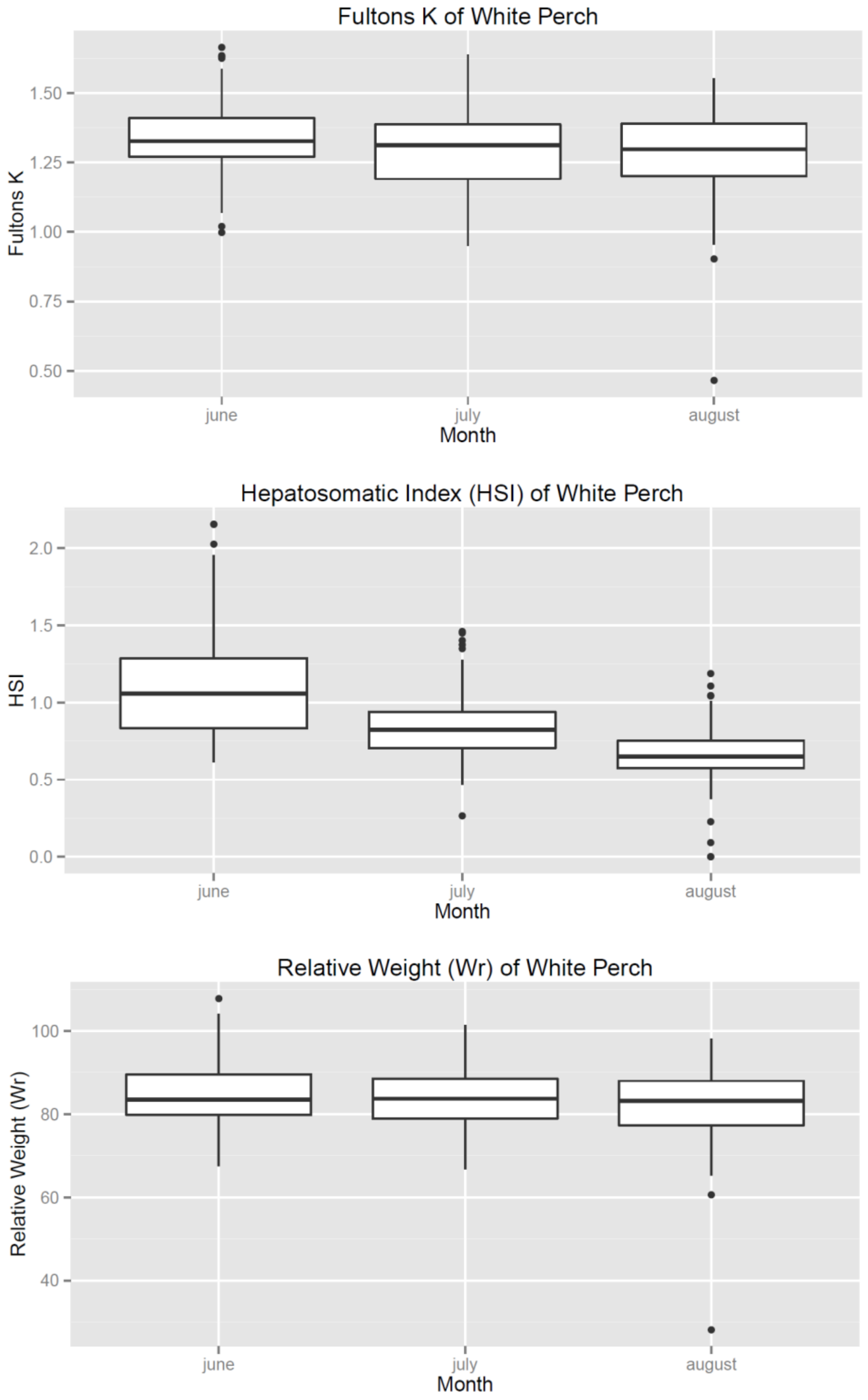


Figure B.5: Box plots of yellow perch condition by month collected.

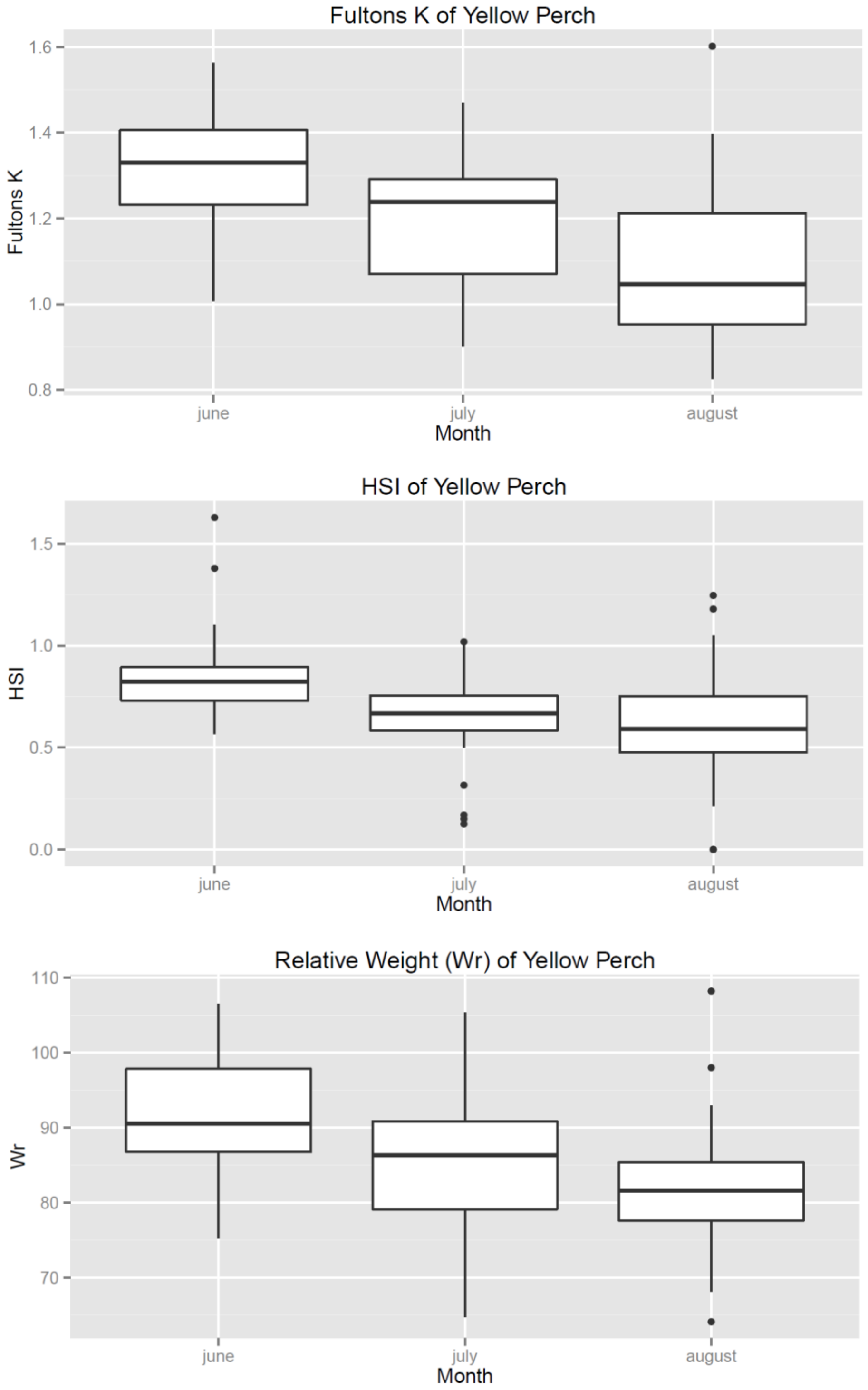
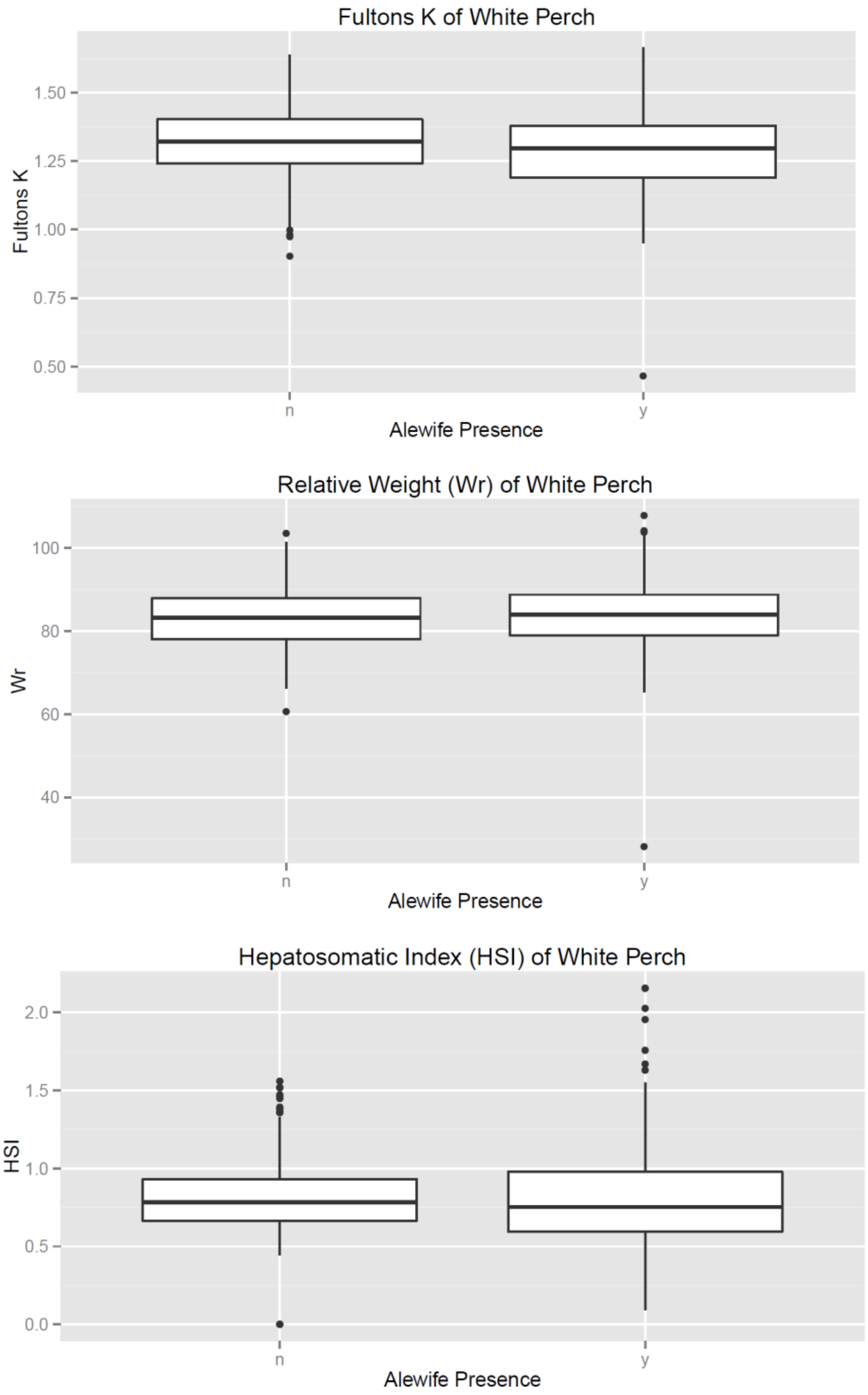


Figure B.6: Boxplots of white perch condition factors in alewife (y) and non-alewife (n) ponds.

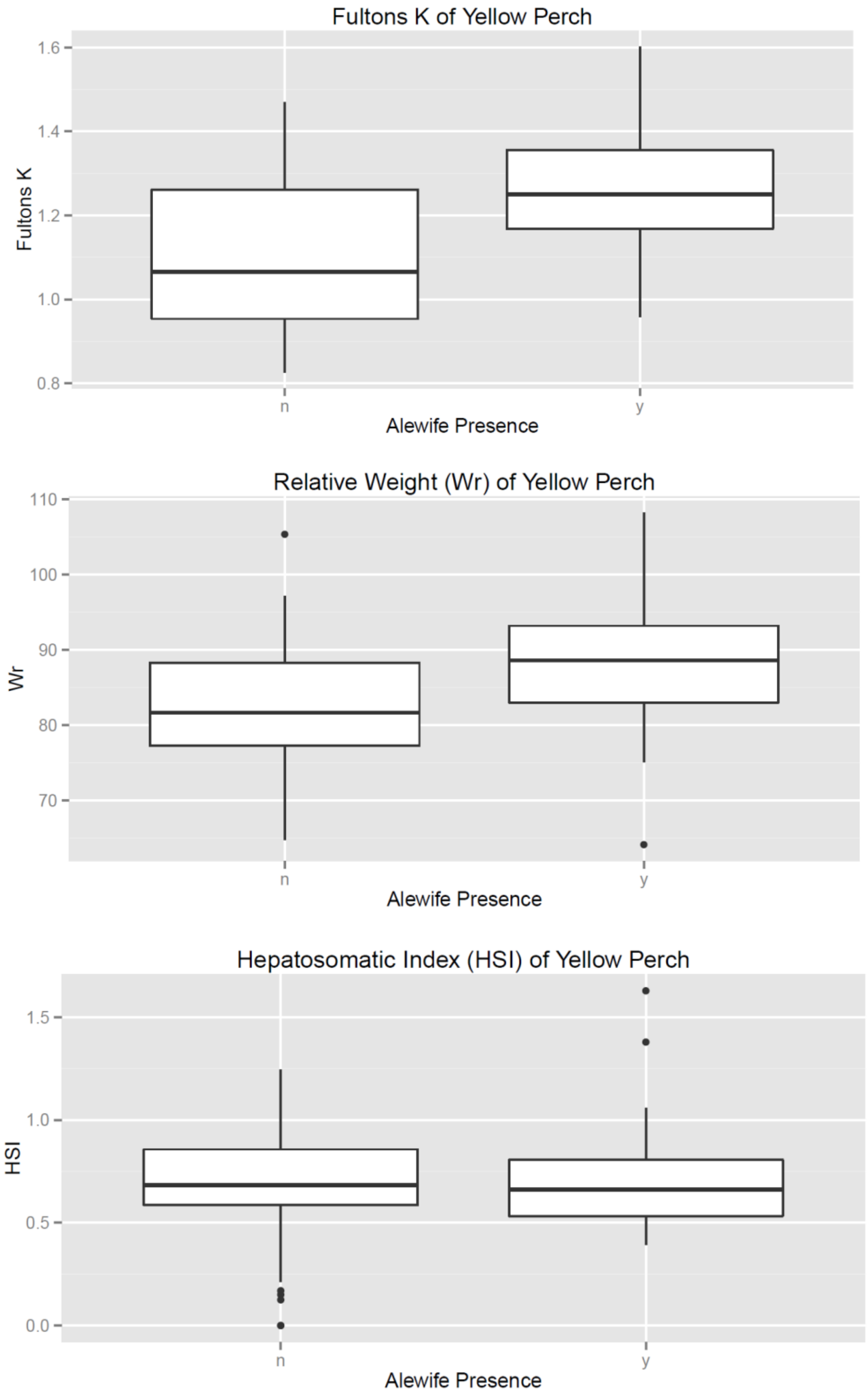


Fultons K of White Perch

Relative Weight (Wr) of White Perch

Hepatosomatic Index (HSI) of White Perch

Figure B.7: Boxplots of yellow perch condition factors in alewife (y) and non-alewife (n) ponds.



Fultons K of Yellow Perch

Relative Weight (Wr) of Yellow Perch

Hepatosomatic Index (HSI) of Yellow Perch

Figure B.8: Histograms of 3 indices of condition showing normality of distribution for response variables.

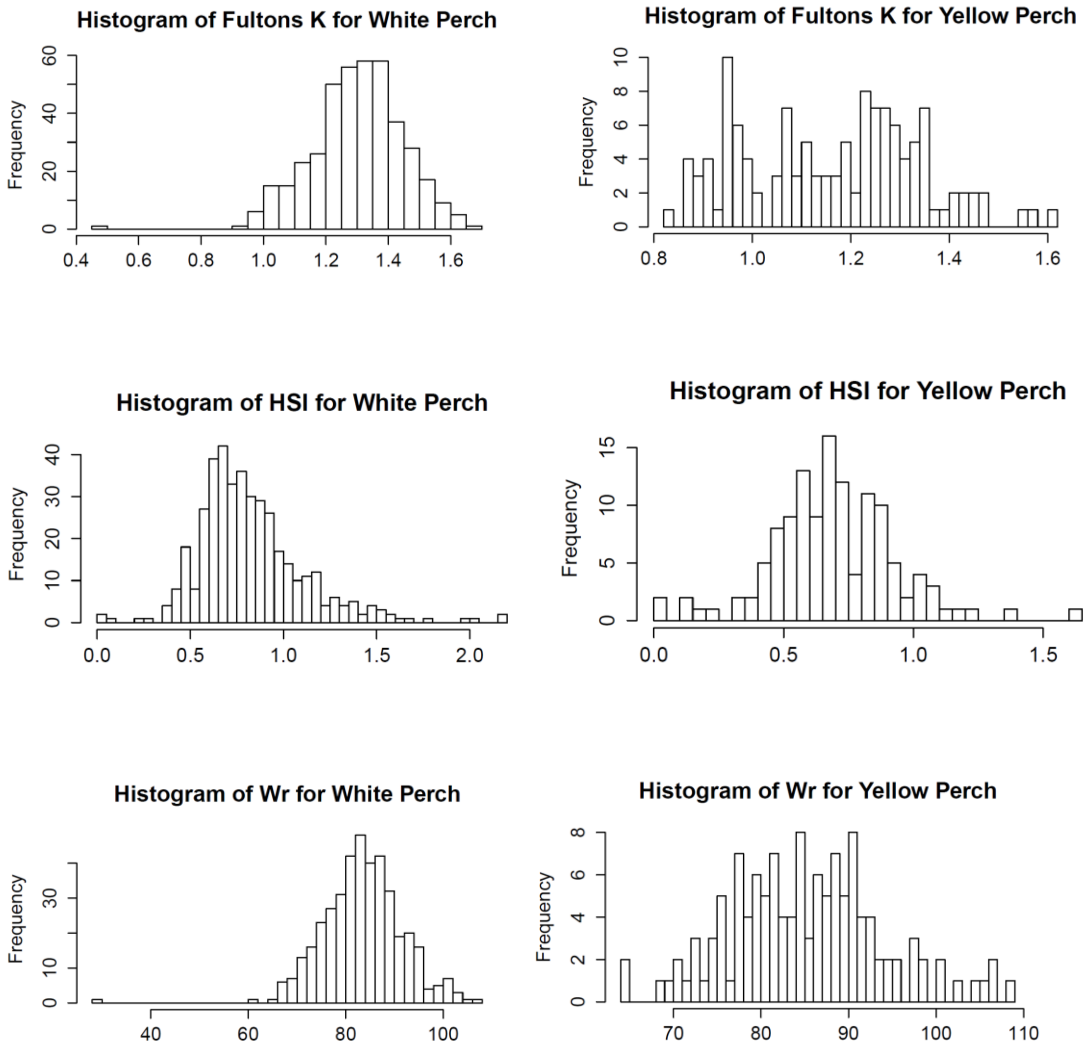


Figure B.9: Scatterplots of 3 condition indices with regression lines. Plots show a strong relationship between Wr and Fulton's K, and a weak relationship between HSI and Fulton's K, and HSI and Wr.

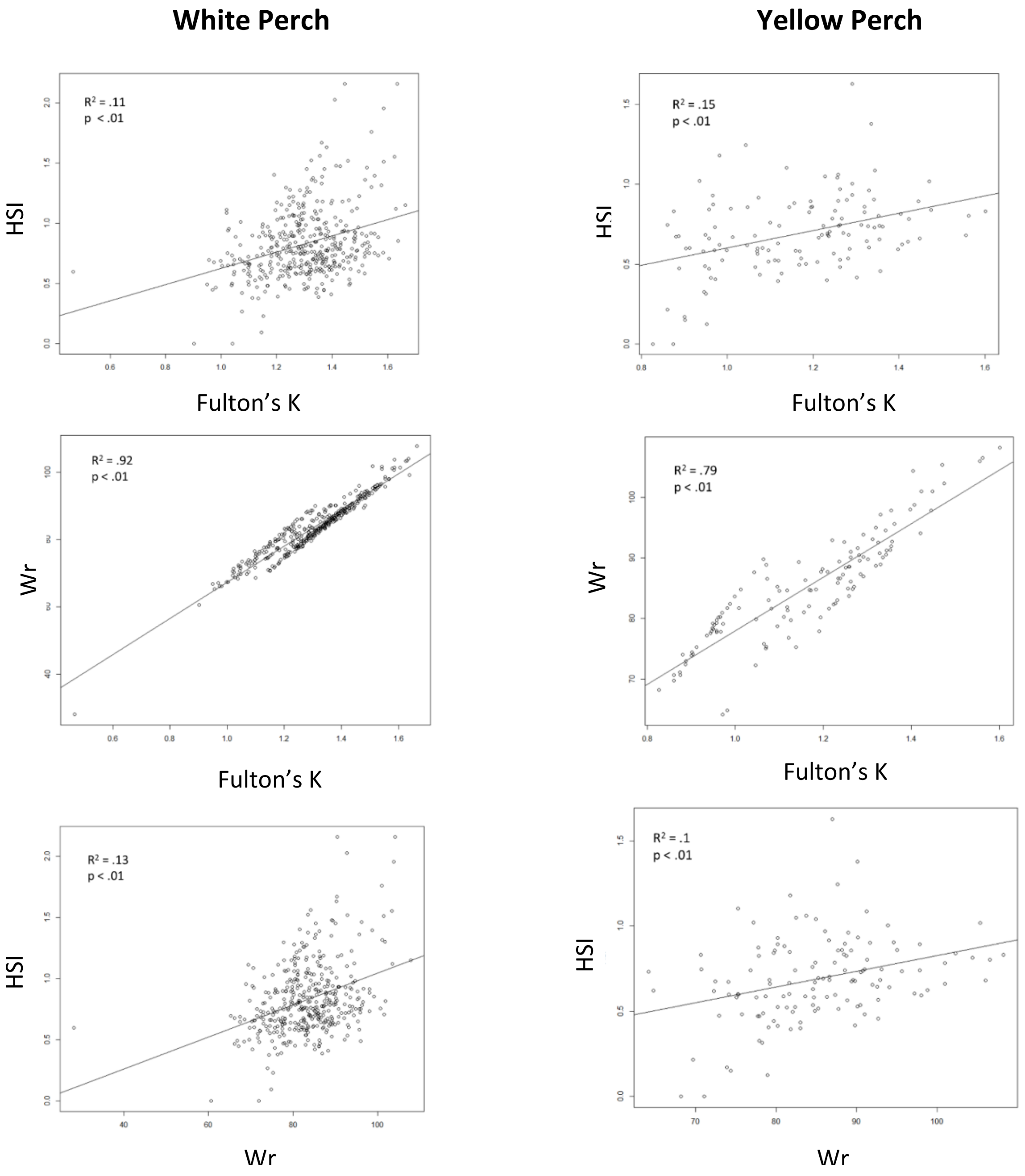
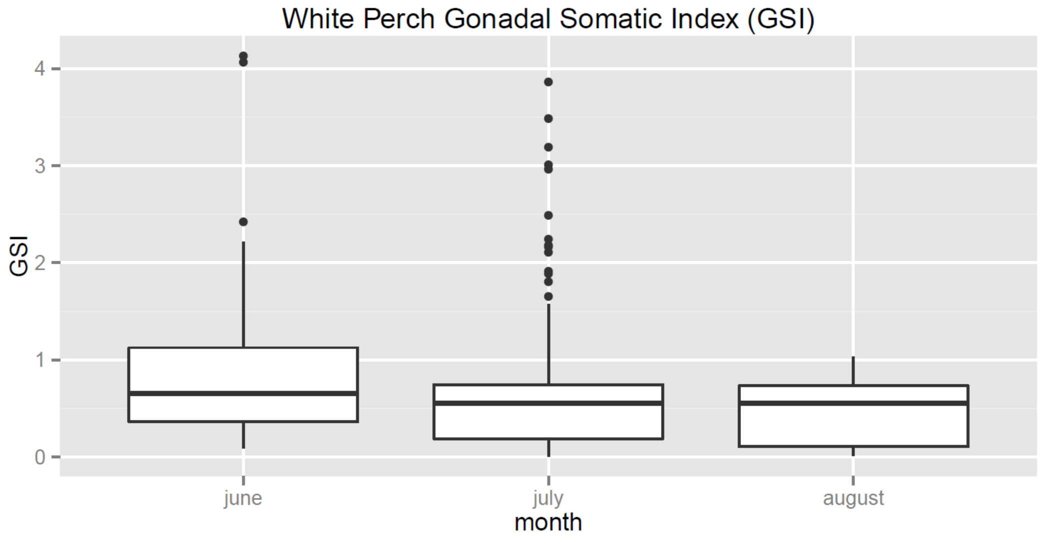


Figure B.10: White Perch (top) and yellow perch (bottom) maturity using gonadal somatic index. White perch appear to spawn in June and yellow perch seem to spawn in August.



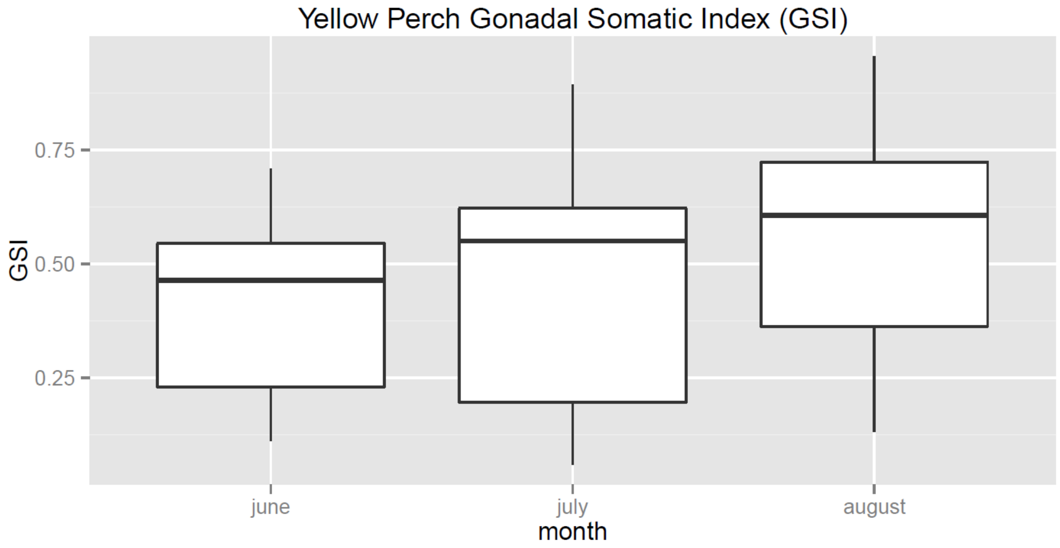


Figure B.11: Scatterplots of 3 condition indices with varying alewife densities for white perch (left) and yellow perch (right).

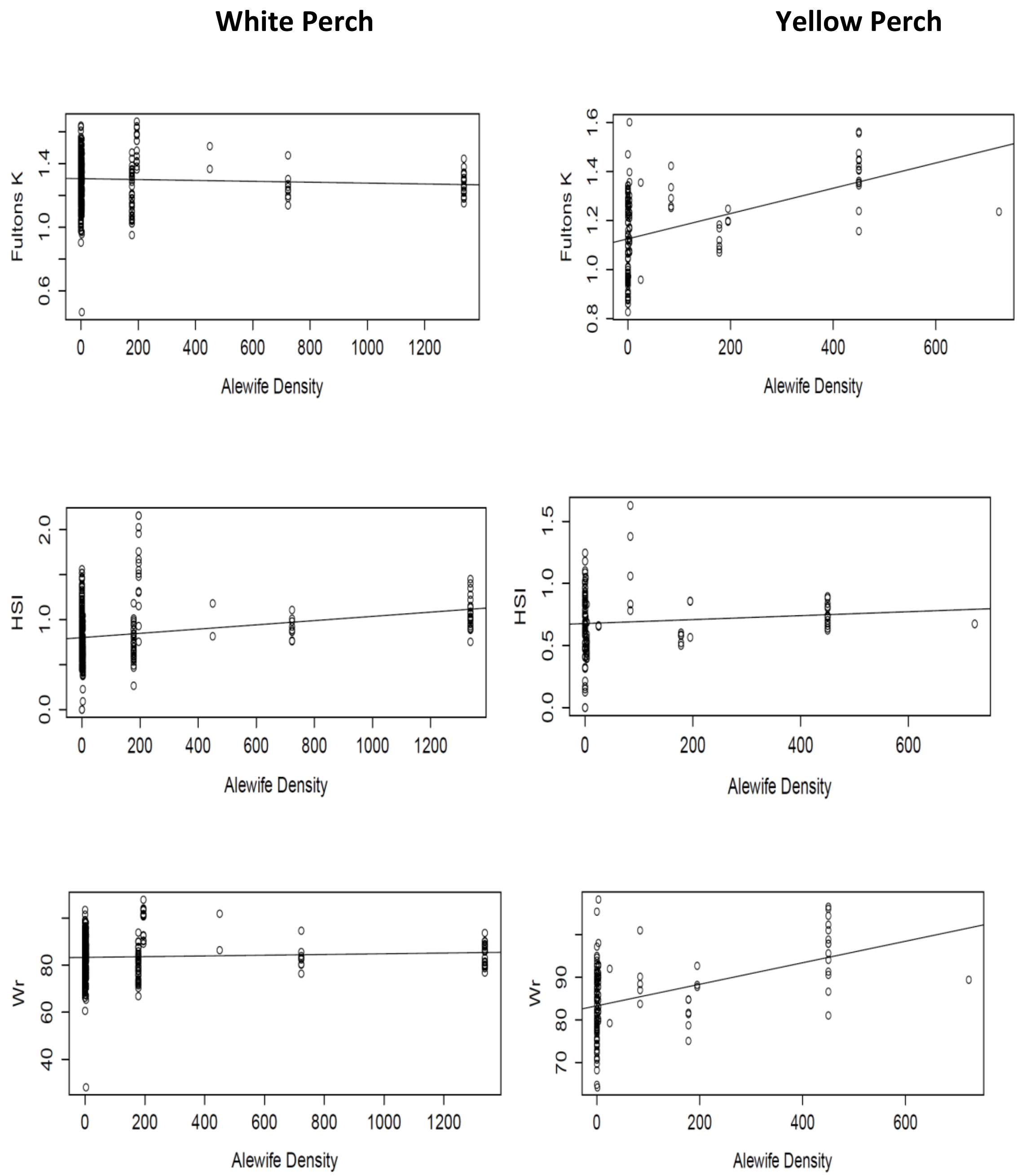


Figure B.12: Box plots of condition indices with alewives present and absent in June, July, and August. Gray boxes indicate juvenile alewives are present, and white boxes indicate juvenile alewives are absent.

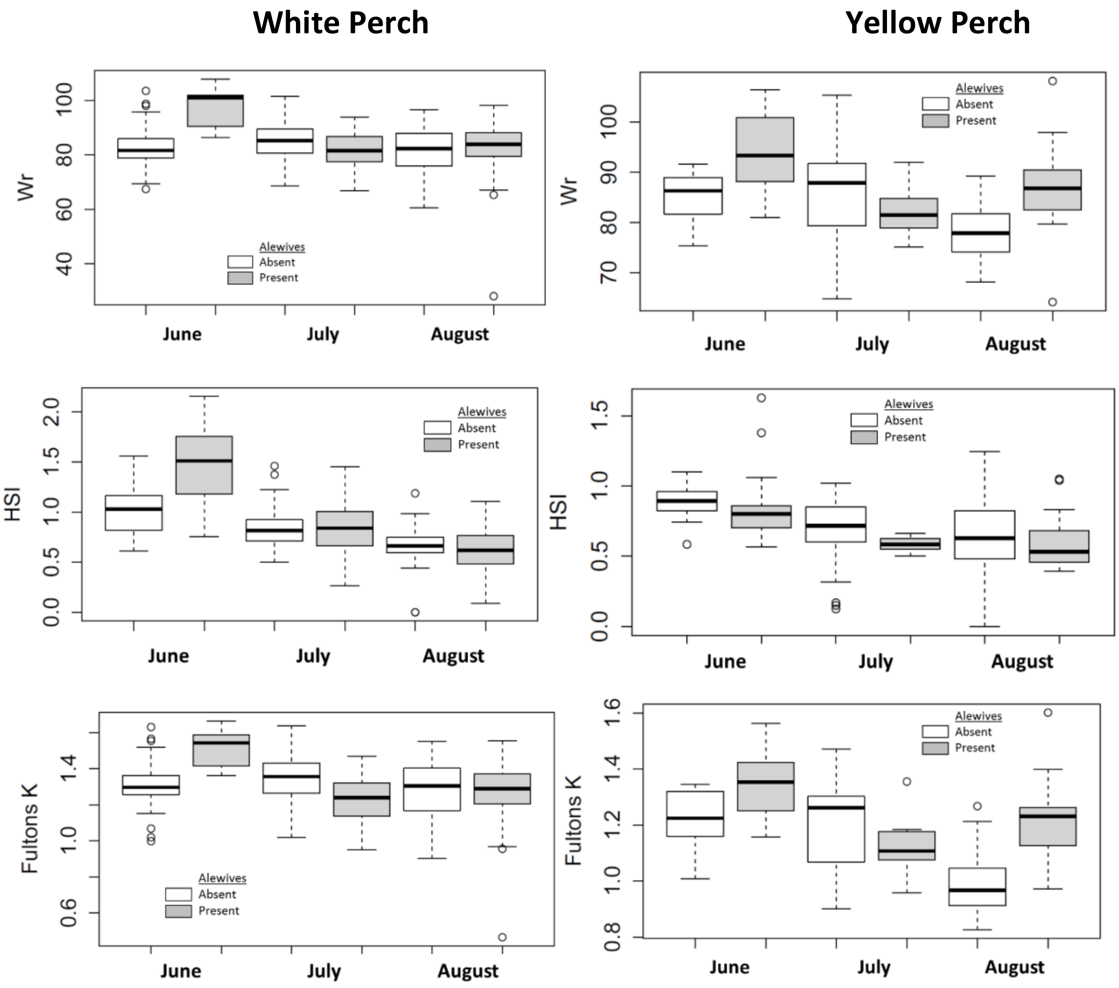


Figure B.13: Conditional mode plots for random effect on pond (water) for Fulton's K (top), Hepatosomatic Index (middle), and Relative Weight (bottom) models. Plots are for white perch.

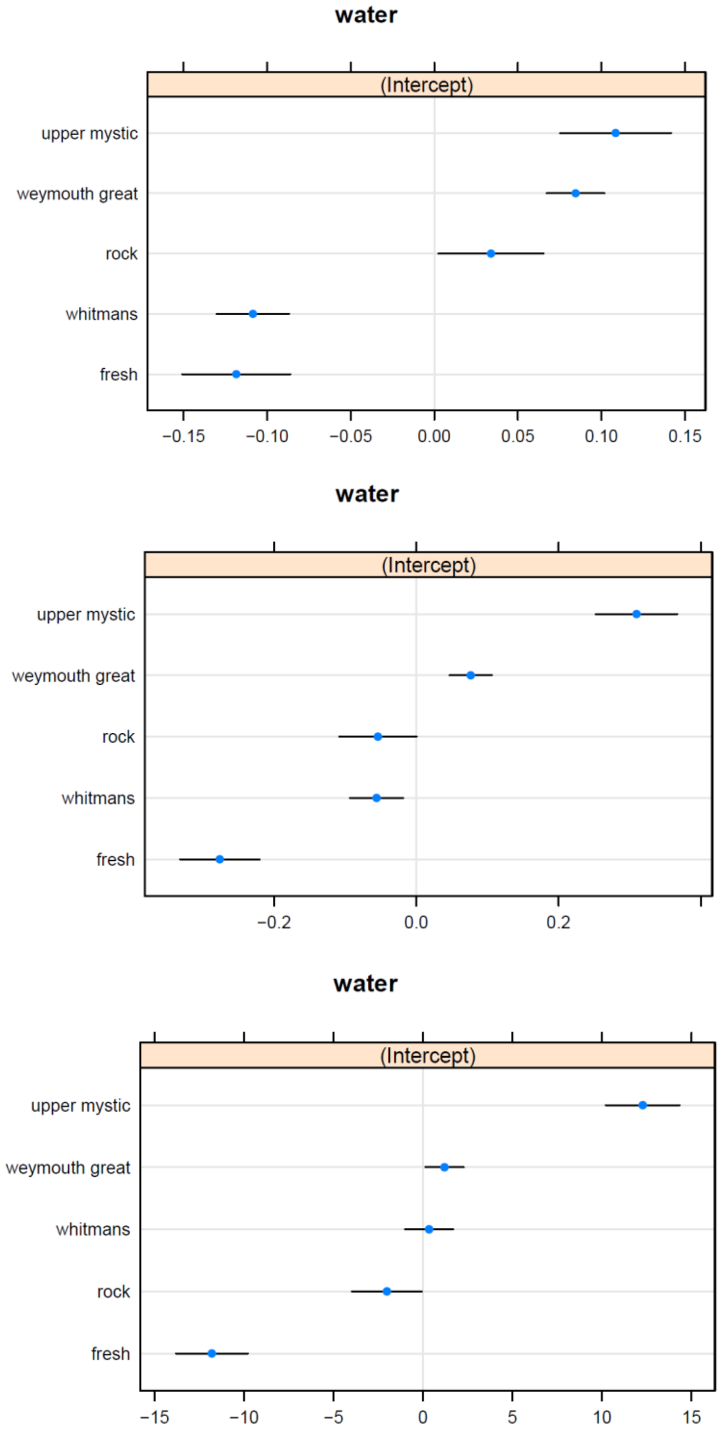


Figure B.14: Conditional mode plots for random effect on pond (water) for Fulton's K (top), Hepatosomatic Index (middle), and Relative Weight (bottom) models. Plots are for yellow perch.

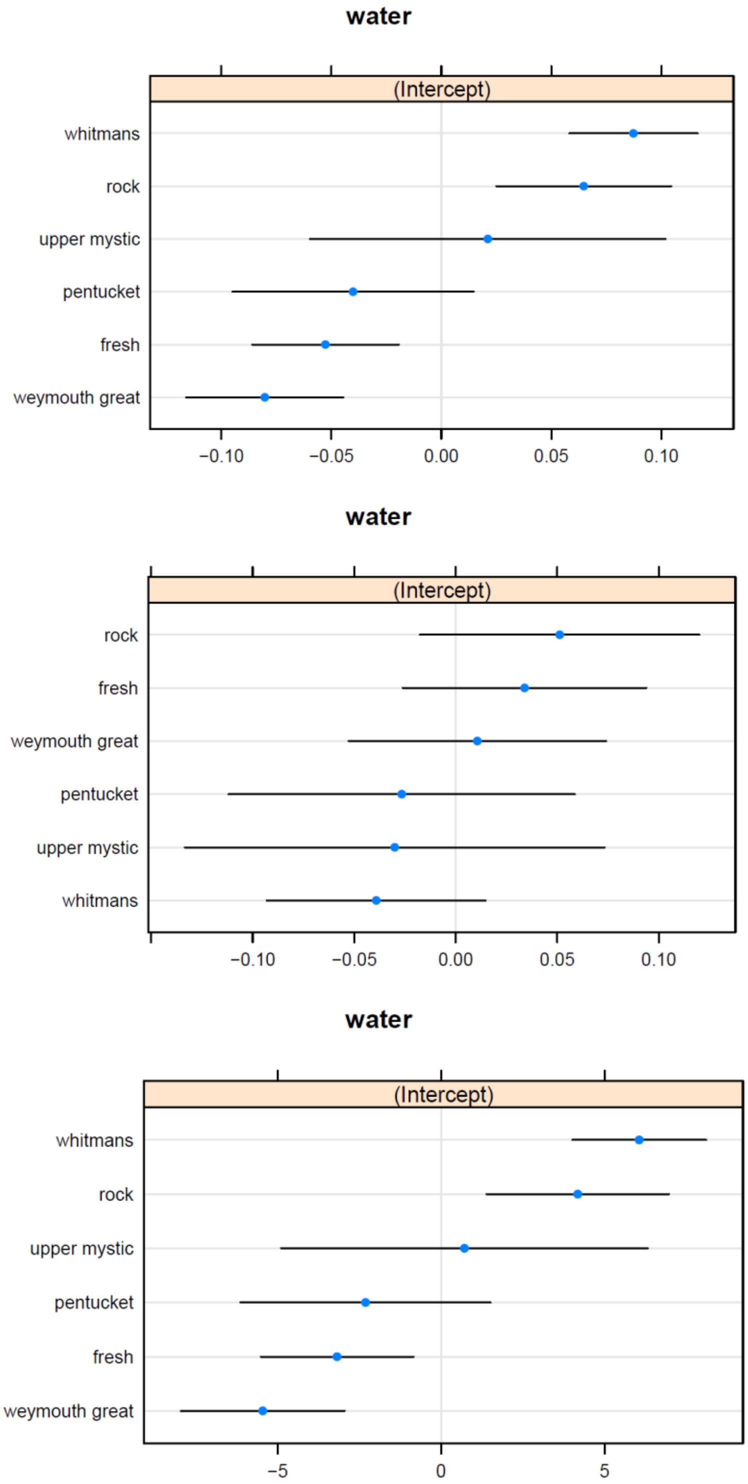
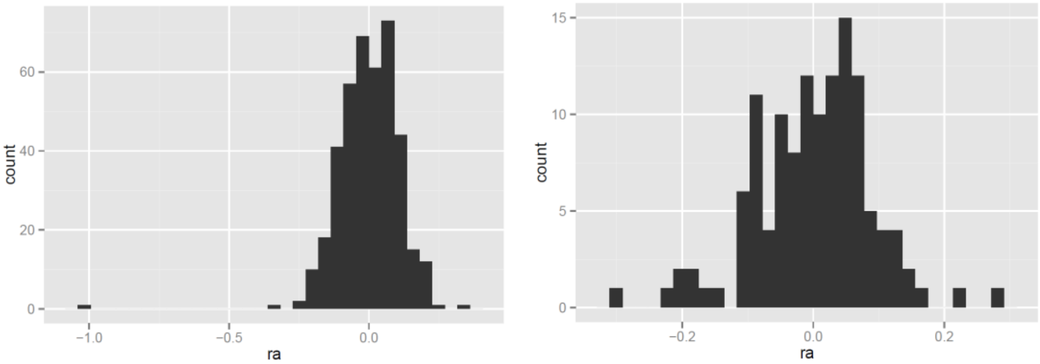
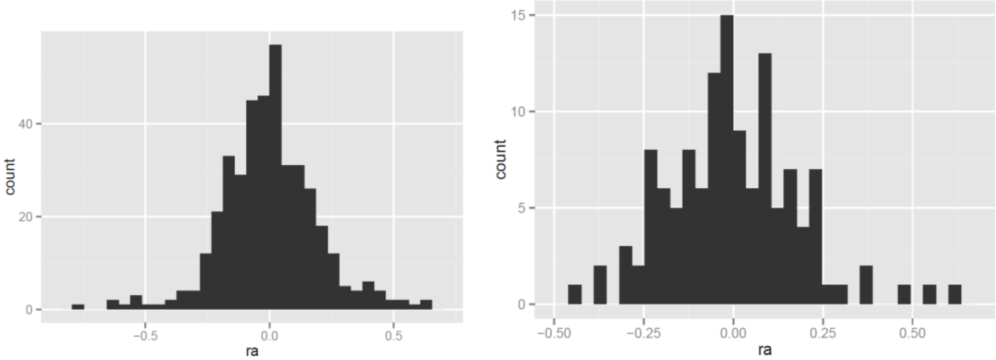


Figure B.15: Non-standardized residuals (count) for 3 condition indices for white and yellow perch. Graphs show normality among residuals.

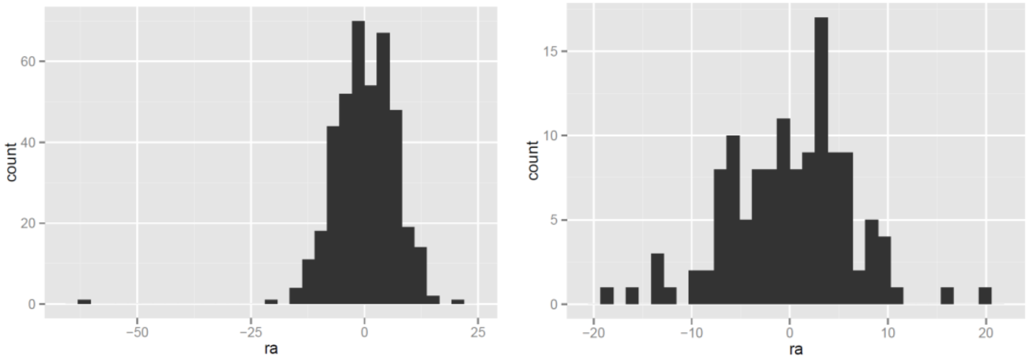
White Perch **Yellow Perch**



Fulton’s K



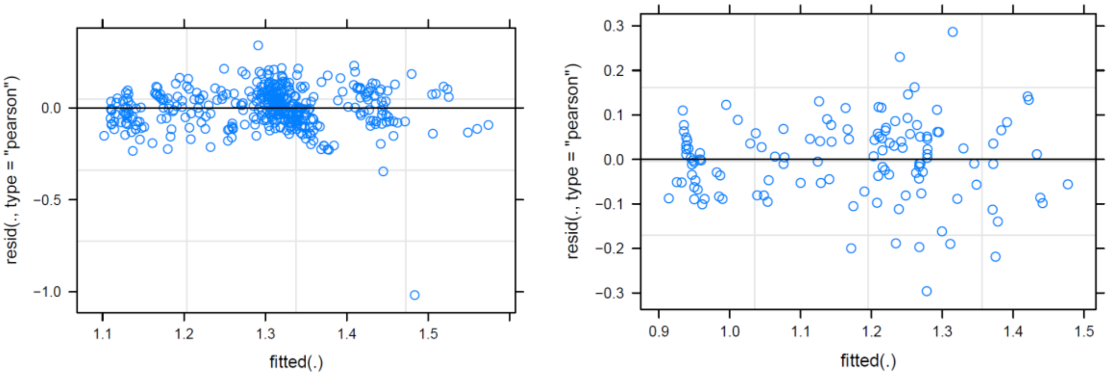
Hepatosomatic Index



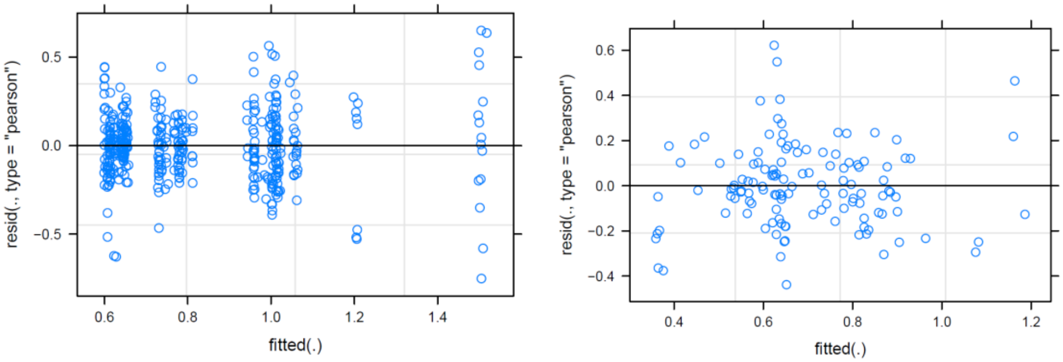
Relative Weight

Figure B.16: Pearson’s R standardized residuals for 3 condition indices for white and yellow perch. Graphs show independence of residuals.

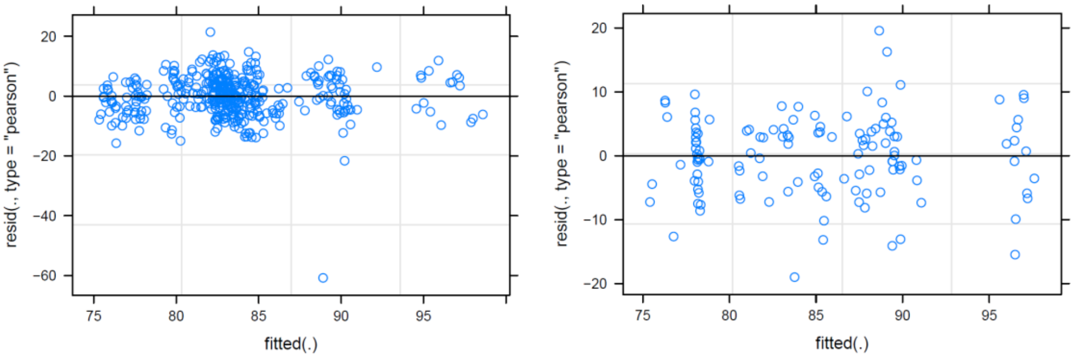
White Perch **Yellow Perch**



Fulton’s K



Hepatosomatic Index



Relative Weight

APPENDIX C

GROWTH AND DIET DATA AND MODELS

Figure C.1: Histograms of the frequency of bootstrapped parameter estimates for Von Bertalanffy models of white perch in alewife ponds.

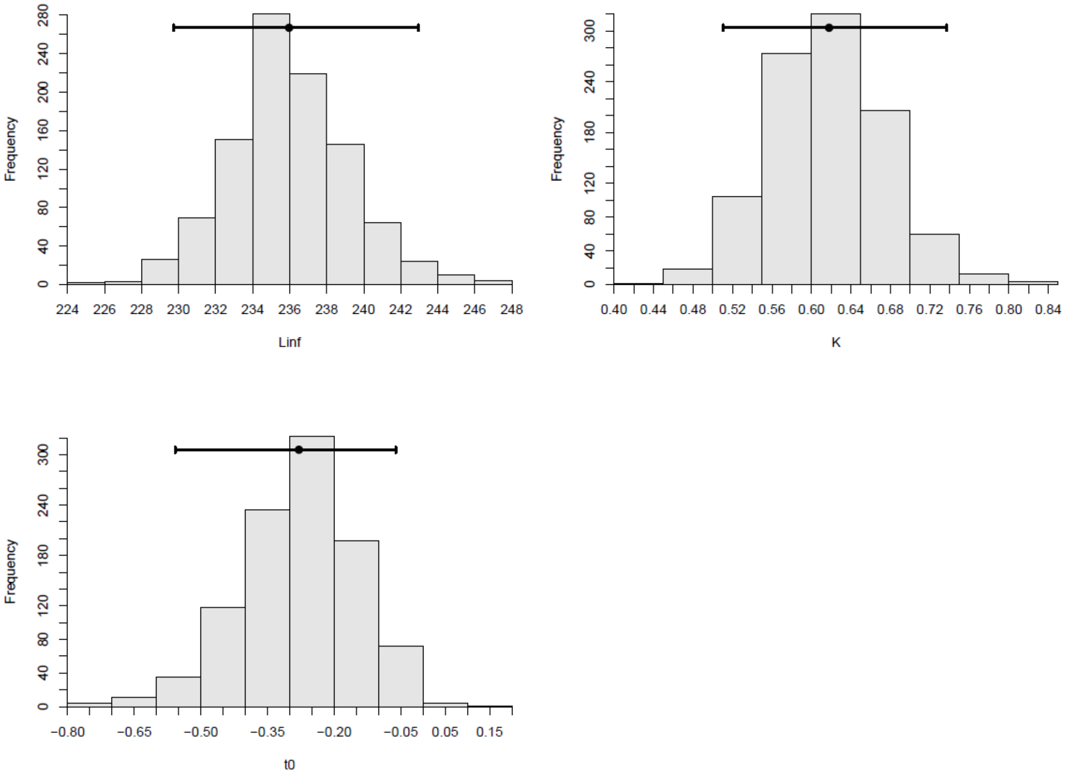


Figure C.2: Histograms of the frequency of bootstrapped parameter estimates for Von Bertalanffy models of white perch in non-alewife ponds.

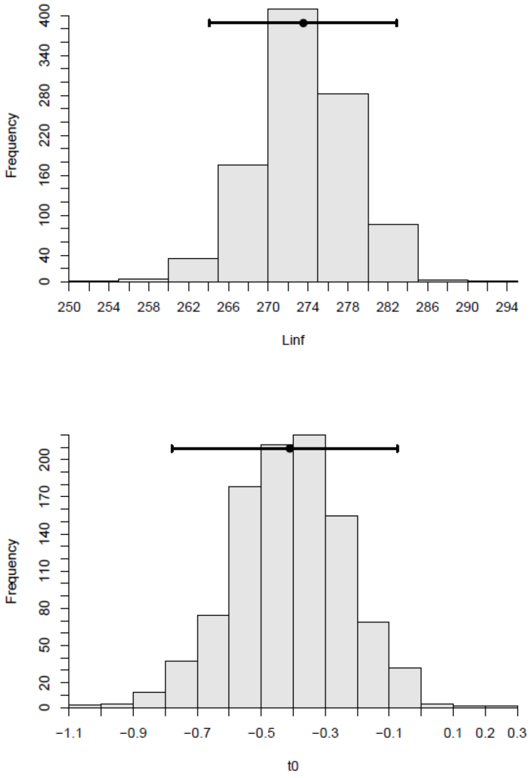


Figure C.3: Histograms of the frequency of bootstrapped parameter estimates for Von Bertalanffy growth models of yellow perch in alewife ponds.

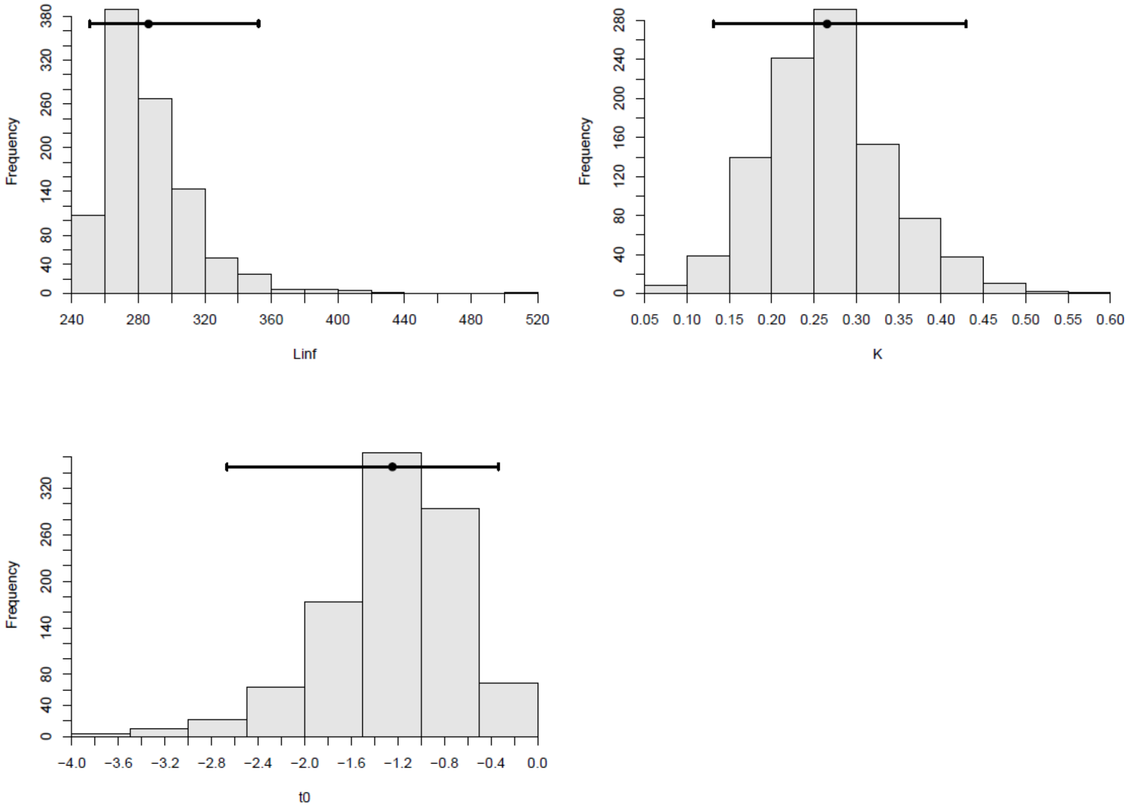


Figure C.4: Histograms of the frequency of bootstrapped parameter estimates for Von Bertalanffy growth models of yellow perch in alewife-absent ponds.

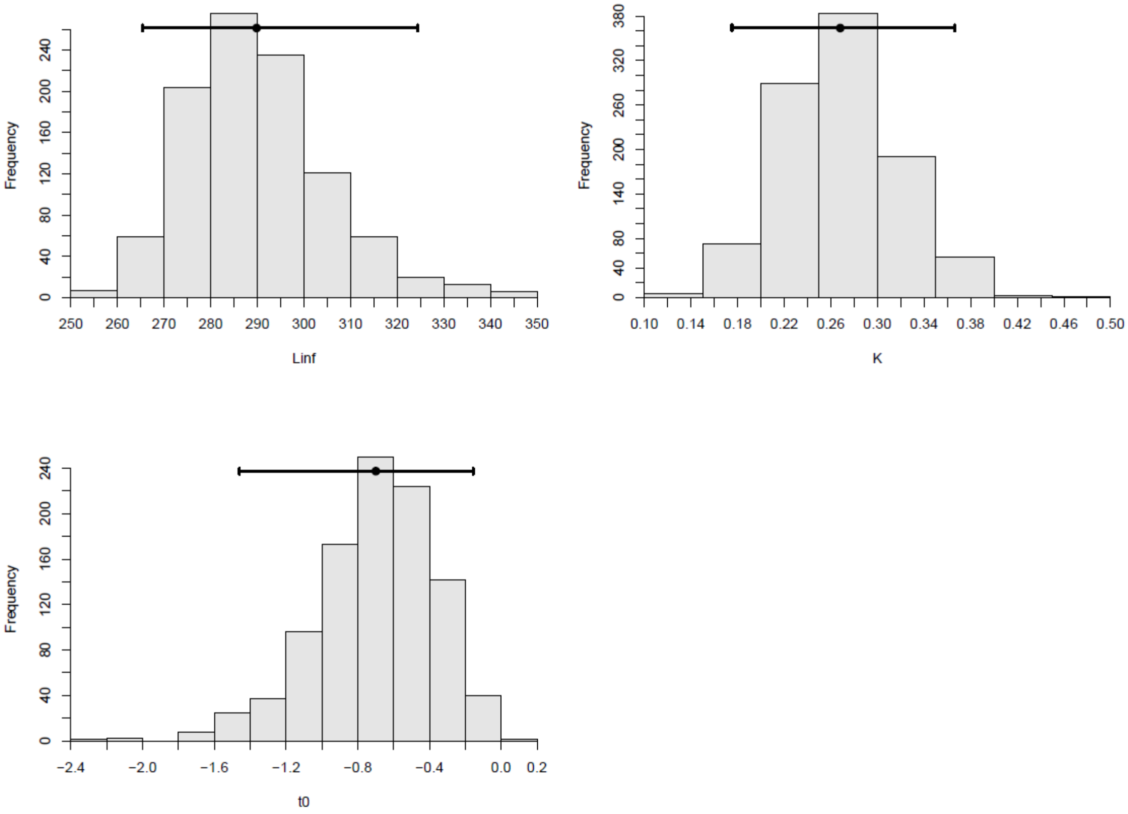


Figure C.5 Partial plot for residuals of linear mixed effects model of length-at-age for white perch, with alewife presence and maximum depth as predictor variables.

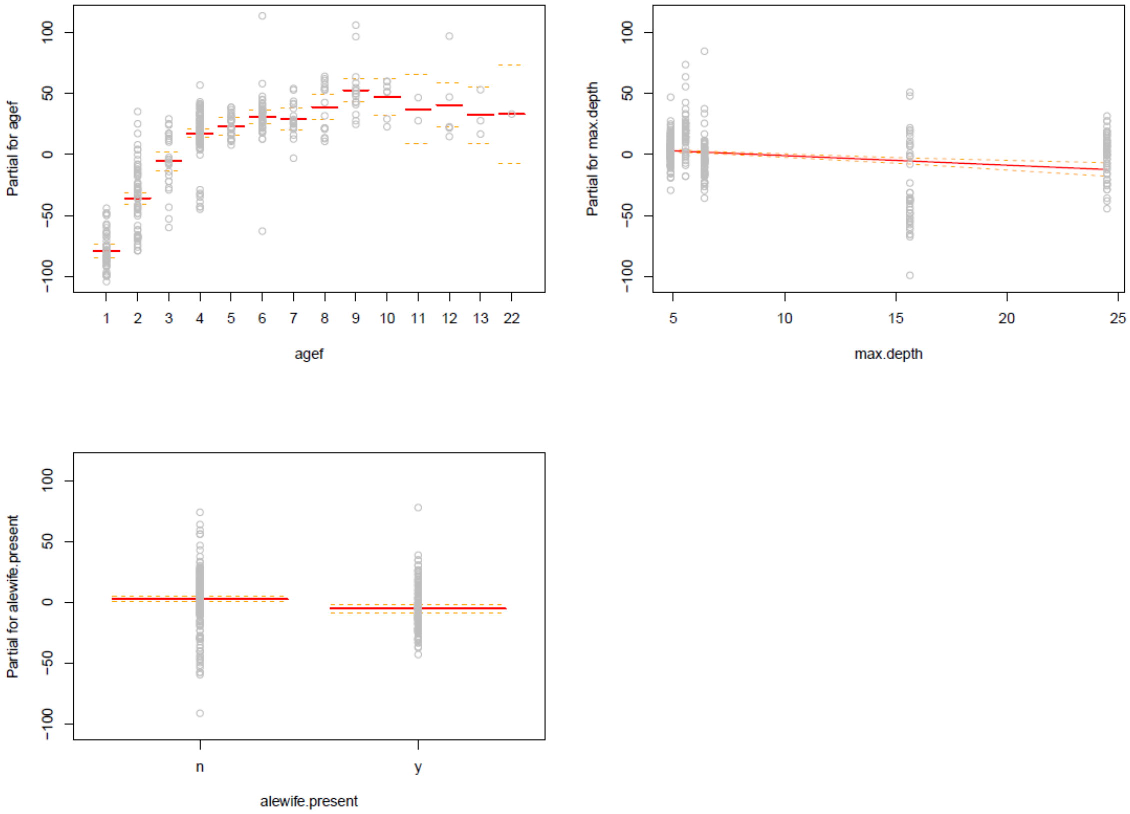


Figure C.6 Partial plot for residuals of linear mixed effects model of length-at-age for yellow perch, with alewife presence and maximum depth as predictor variables.

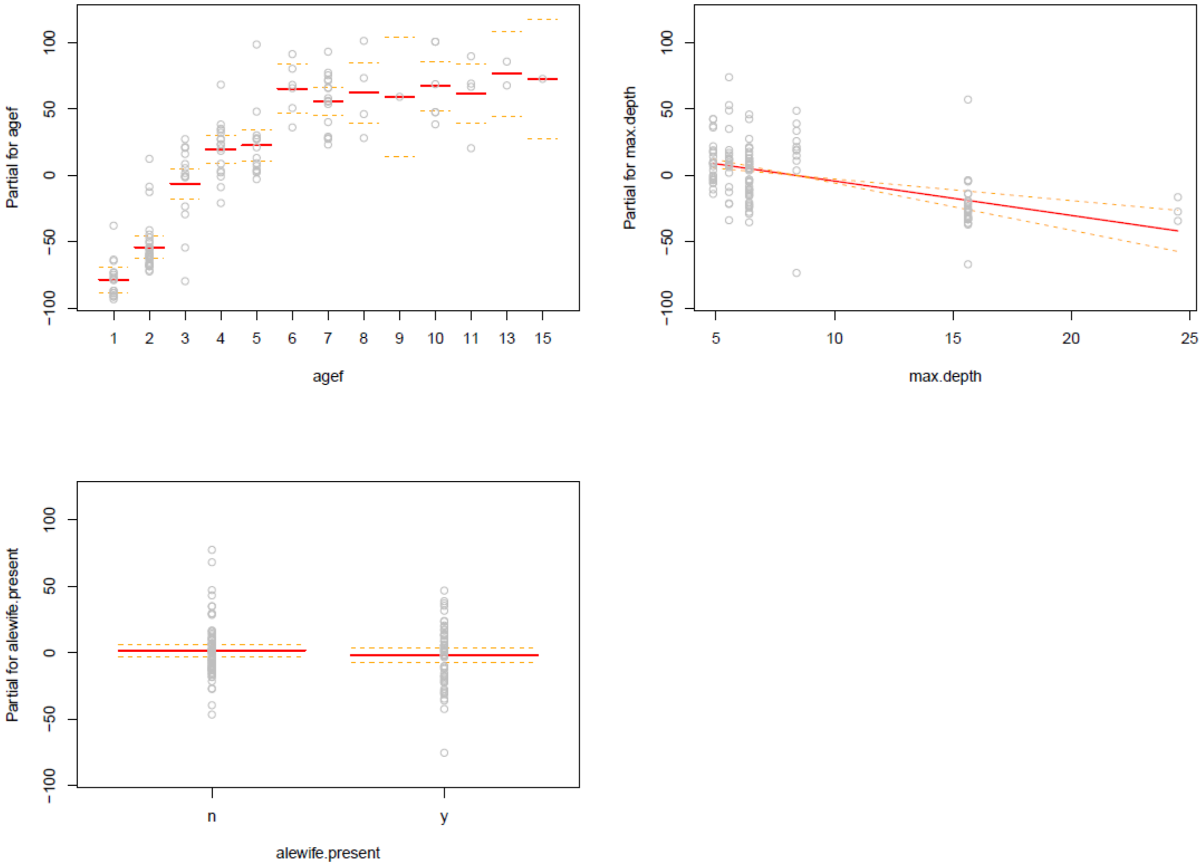


Figure C.7 Partial plot for residuals of linear mixed effects model of length-at-age for white perch, with alewife presence and perch abundance as predictor variables.

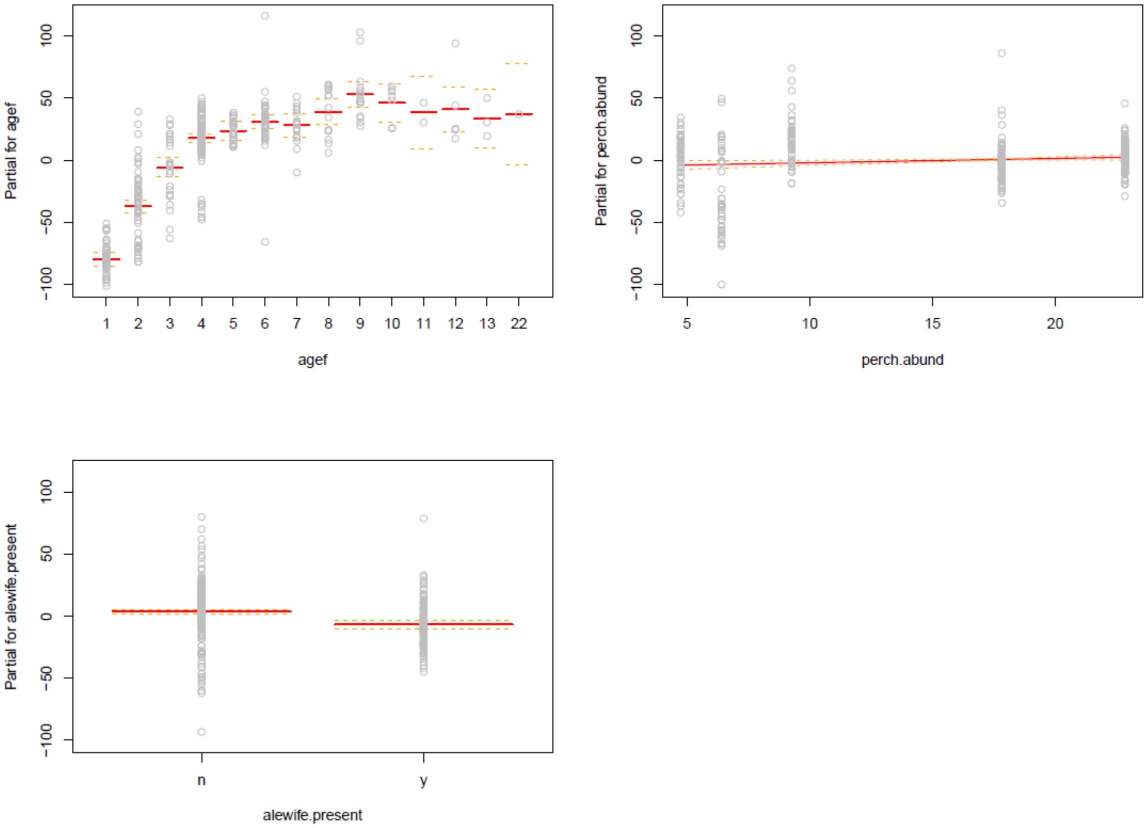


Figure C.8 Partial plot for residuals of linear mixed effects model of length-at-age for yellow perch, with alewife presence and perch abundance as predictor variables.

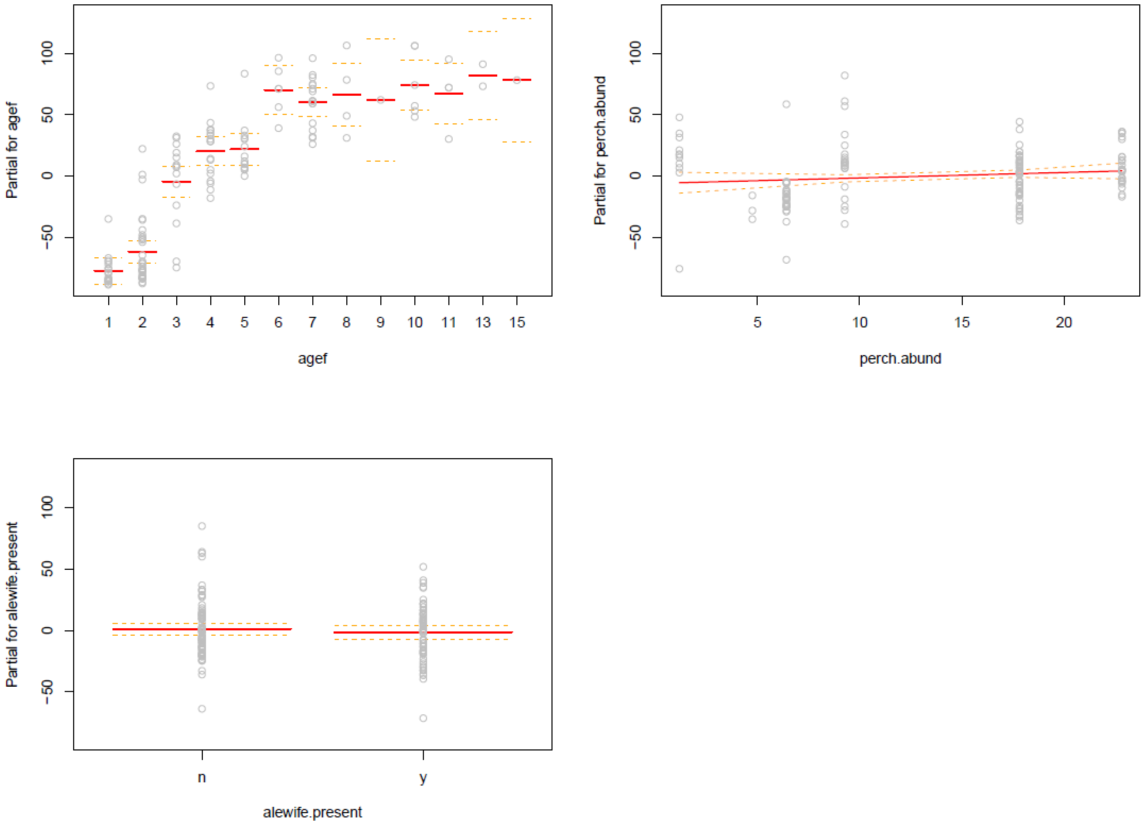


Figure C.9 Partial plot for residuals of linear mixed effects model of length-at-age for white perch, with alewife presence and pond size as predictor variables.

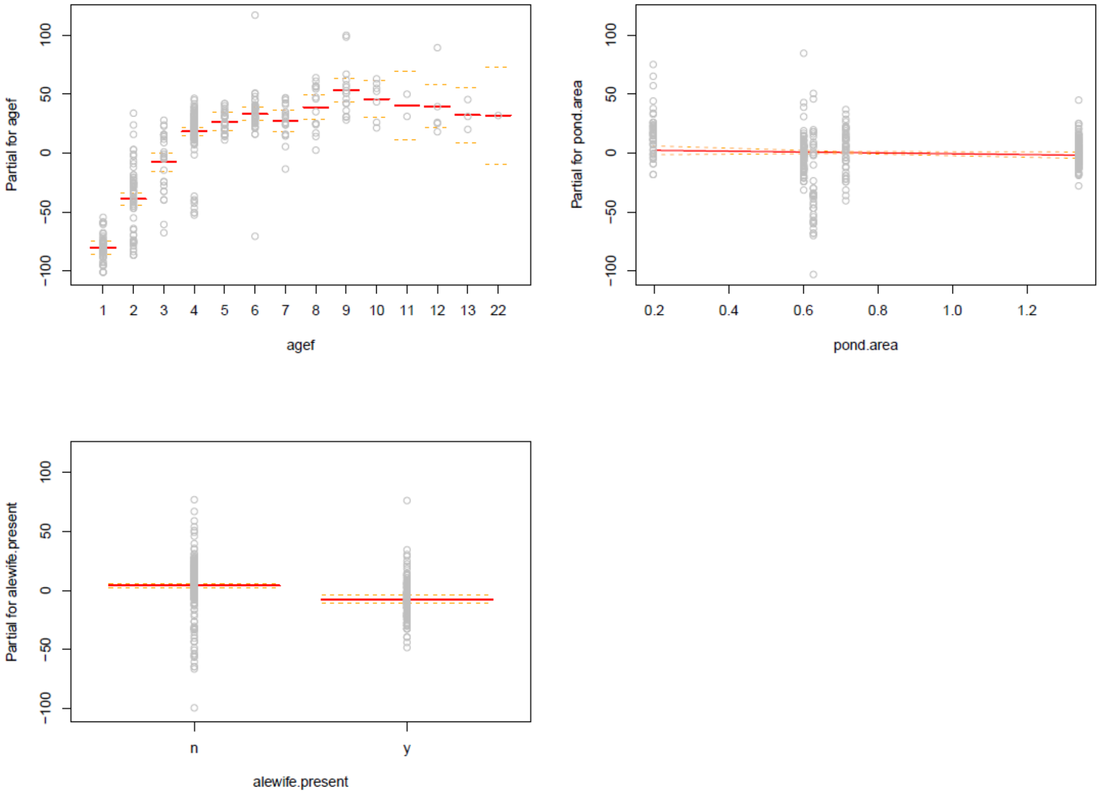


Figure C.10 Partial plot for residuals of linear mixed effects model of length-at-age for yellow perch, with alewife presence and pond size as predictor variables.

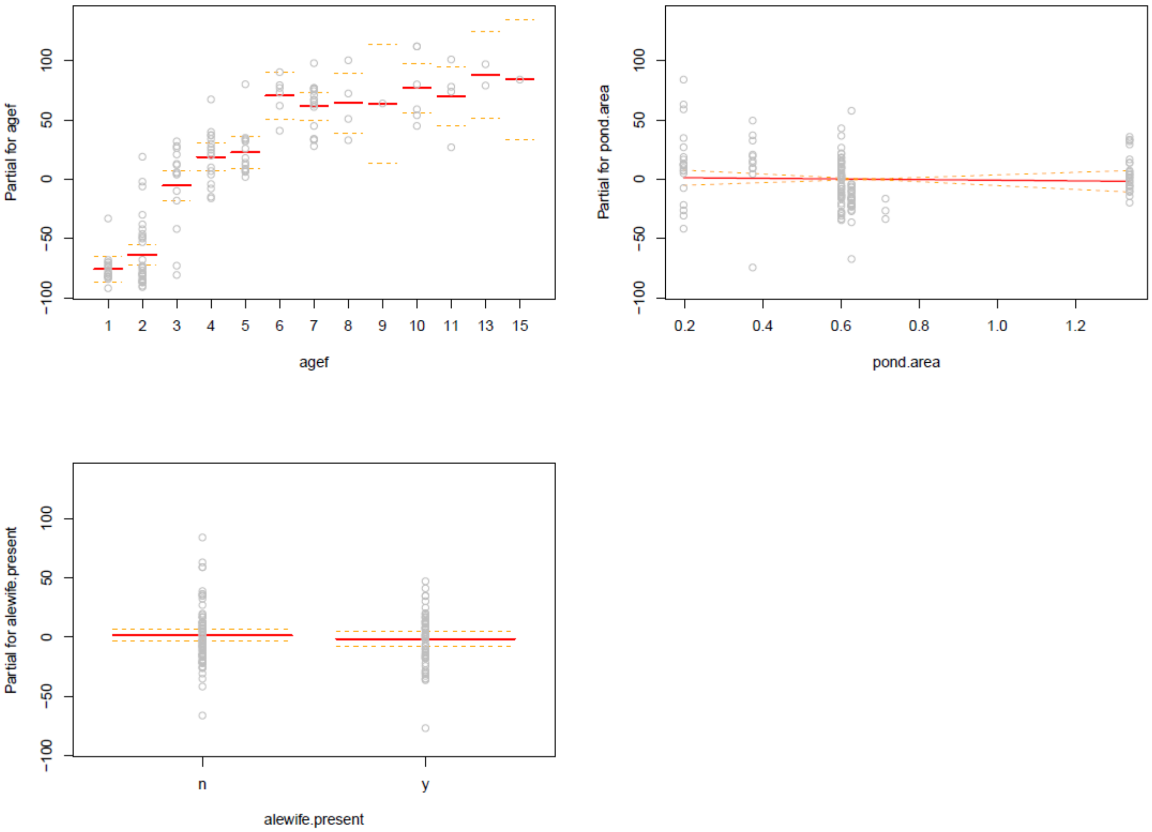


Figure C.11: Age bias plot of all perch aged by two readers (ACV = 3.5).

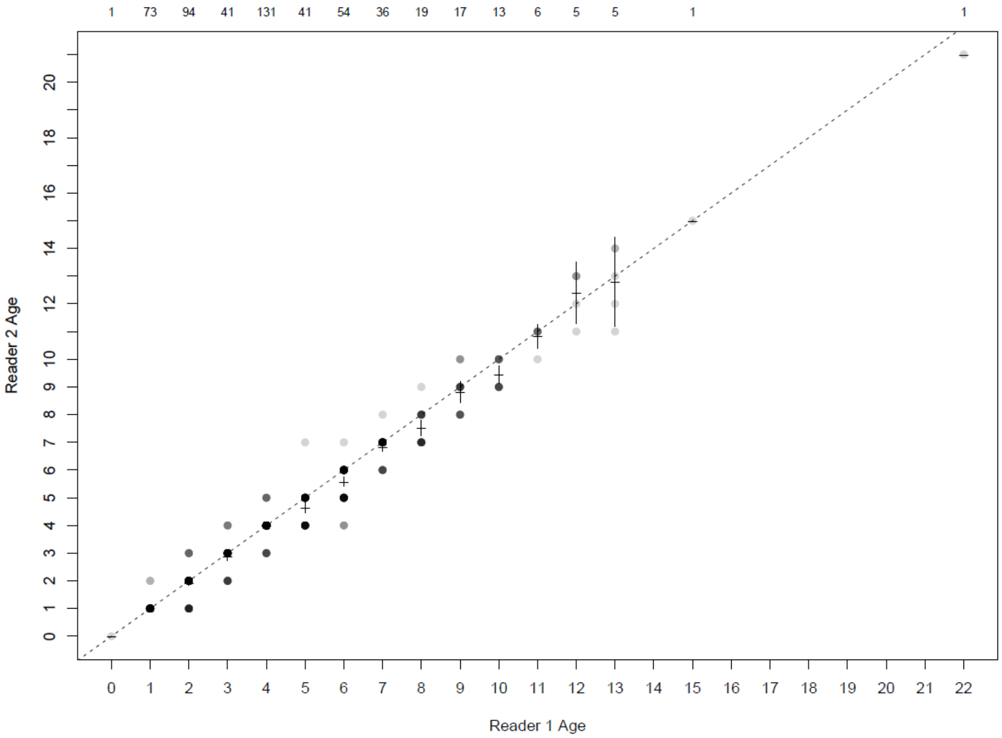


Figure C.12 Diets of white perch and yellow perch in alewife present and alewife absent ponds.

Alewife Ponds

	White Perch						Yellow Perch					
Prey	%O	%N	%W	IRI	%IRI	% empty	%O	%N	%W	IRI	%IRI	% empty
alewife	0.7	1.7	1.0	2.0	-	9.5	-	-	-	-	-	13.5
bluegill	-	-	-	-	-		-	-	-	-	-	
yellow perch	0.7	0.8	2.5	2.5	-		-	-	-	-	-	
white perch	-	-	-	-	-		-	-	-	-	-	
largemouth bass	-	-	-	-	-		2.2	4.3	12.2	36.8	0.3	
tessellated darter	-	-	-	-	-		-	-	-	-	-	
chain pickerel	-	-	-	-	-		-	-	-	-	-	
unidentified fish	12.7	15.8	5.5	270.5	2.2		-	-	-	-	-	
inverts	73.1	81.6	78.7	11717.9	93.0		48.8	95.6	35.7	6406.5	46.2	
Unidentified matter	19.4	17.8	11.9	575.6	4.6		68.9	57.4	50.5	7434.9	53.6	

Non-alewife Ponds

	White Perch						Yellow Perch					
Prey	%O	%N	%W	IRI	%IRI	% empty	%O	%N	%W	IRI	%IRI	% empty
alewife	-	-	-	-	-	10.9	-	-	-	-	-	9.3
bluegill	1.3	1.6	0.1	2.1	-		1.5	2.1	9.4	16.9	0.1	
yellow perch	3.4	3.9	4.8	29.1	0.2		-	-	-	-	-	
white perch	-	-	-	-	-		-	-	-	-	-	
largemouth bass	0.4	0.4	-	0.2	-		-	-	-	-	-	
tessellated darter	0.4	0.8	0.1	0.4	-		-	-	-	-	-	
chain pickerel	0.4	0.4	0.1	0.2	-		-	-	-	-	-	
unidentified fish	9.7	8.9	4.6	130.8	1.0		-	-	-	-	-	
inverts	81.1	75.1	78.7	12474.1	94.5		67.6	97.9	66.9	11147.1	78.6	
unidentified matter	22.3	17.1	8.3	565.0	4.3		47.1	40.5	23.7	3021.1	21.3	

Figure C.13 White perch length-at-age. Significant differences between alewife and non-alewife ponds are ages with the red squares.

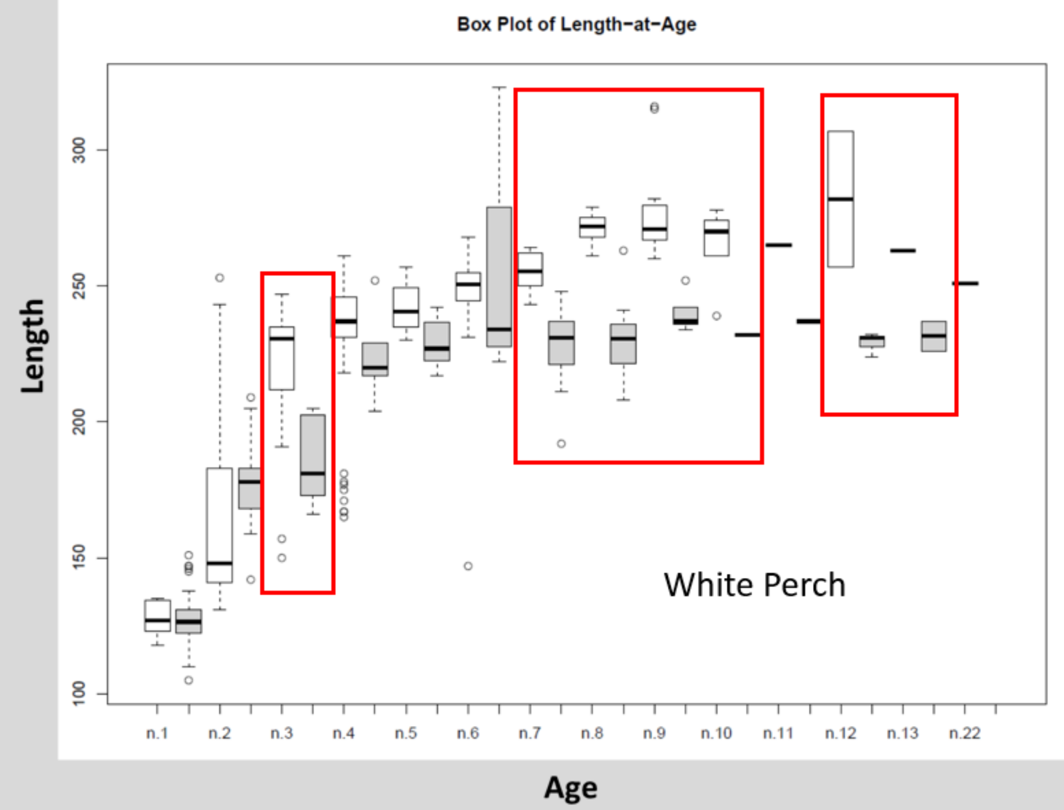
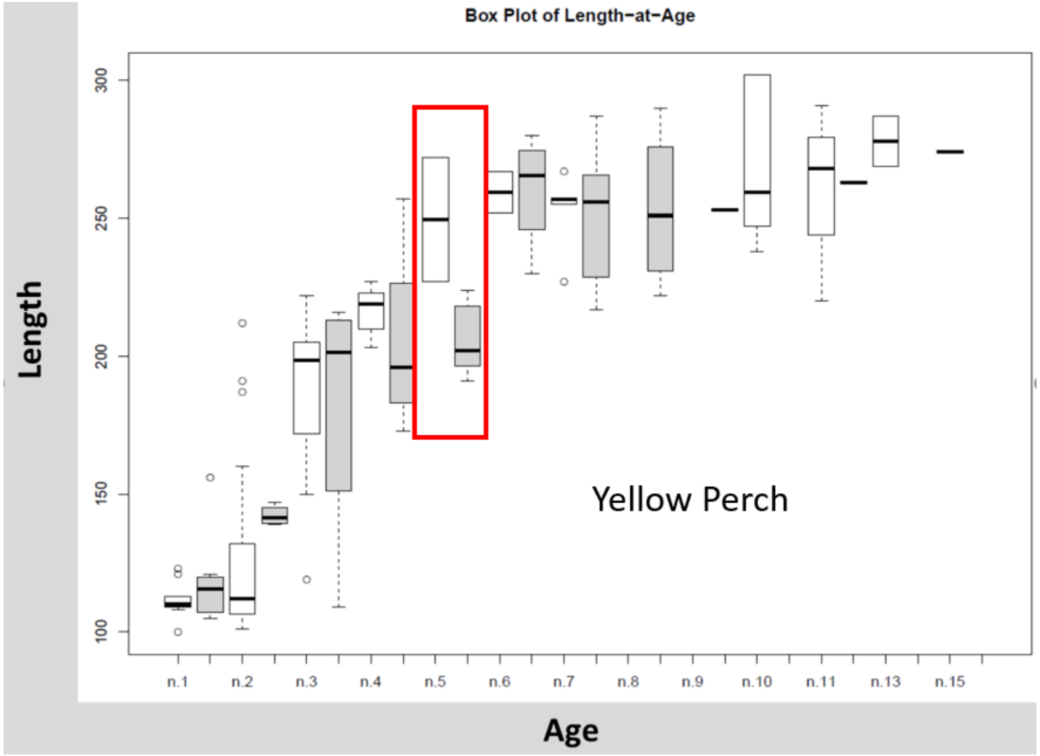


Figure C.14 Yellow perch length-at-age. Significant differences between alewife and non-alewife ponds are ages with the red squares.



LITERATURE CITED

Adams, S.M. 1999. Ecological role of lipids in the health and success of fish populations. In Lipids in freshwater ecosystems, eds. M.T. Arts and B.C. Wainman, pp. 132–160. New York, NY: Springer-Verlag.

Alexander KE, et al. 2009. Gulf of Maine cod in 1861: Historical analysis of fishery logbooks, with ecosystem implications. Fish and Fisheries 10: 428–449.

Ames, EP. 2012. White hake (Urophycis tenuis) in the Gulf of Maine: Population structure insights from the 1920s. Fisheries Research 114: 56-65.

Ames, EP, and Lichter, J. 2013. Gadids and Alewives: Structure within complexity in the Gulf of Maine. Fisheries Research 141:70-78.

Anderson, RO, Gutreuter, SJ. 1983. Length, weight, and associated structural indices. Pages 283-300 in L. A. Nielson and D. L. Johnson, editors. Fisheries techniques. American Fisheries Society, Bethesda, Maryland.

[ASMFC] Atlantic States Marine Fisheries Commission. 2007. Stock Assessment Report No. 07-01. ASMFC American Shad Stock Assessment Peer Review Panel.

[ASMFC] Atlantic State Marine Fisheries Commission. 2013. Fisheries Focus: River Herring. 22 (3).

Baird, SF. 1884. United States Commission of Fish and Fisheries. The Fisheries and Fishery Industry of the United States. Section 1 Plates. Washington.

Balcer MD, Korda NL, Dodson SD (1984) Zooplankton of the Great Lakes: A Guide to the Identification and Ecology of the Common Crustacean Species (Univ Wisconsin Press, Madison, WI).

Barr, DJ, Levy, R, Scheepers, C, Tily, HJ. 2013. Random effects structure for confirmatory hypothesis testing: Keep it maximal. Journal of Memory and Language 68: 255-278.

Barton, K. 2014. MuMIn: Multi-Model Inference. R package version 1.12.1. http://CRAN.R-project.org/package=MuMIn.

Bates, D, Maechler, M, Bolker, B, Walker, S. (2014). _lme4: Linear mixed-effect models using Eigen and s4_. R package version 1.1-7, <URL: http://CRAN.R-project.org/package=lme4>.

Ben-David, M, Hanley, TA, Schell, DM. 1998. Fertilization of terrestrial vegetation by spawning Pacific Salmon: the role of flooding and predator activity. OIKOS 83:47-55.

Bergman E, and Greenberg LA. 1994. Competition between a planktivore, a benthivore, and a species with ontogenic diet shifts. Ecology 75:1233-1245.

Bernhardt, ES, et al. 2005. Synthesizing U.S. River Restoration Efforts. Science 308: 636-637.

Bigelow HB, Schroeder WC. 1953. Fishes of the Gulf of Maine. Bulletin no. 74, vol. 53. US Government Printing Office.

Bilby, RE, Fransen, BR, Bisson, PA. 1996. Incorporation of nitrogen and carbon from spawning adult coho salmon into the trophic system of small streams: evidence from stable isotopes. Canadian Journal of Fisheries Aquatic Science 53: 164-173.

Blackwell, B. G., M. L. Brown, and D. W. Willis. 2000. Relative weight (Wr) status and current use in fisheries assessment and management. Reviews in Fisheries Science 8:1–44.

Bonds CC. 2000. Assessment of the Response of Piscivorous Sportfishes to the Establishment of Gizzard Shad in Claytor Lake, Virginia. Master’s thesis. Virginia Polytechnic Institute and State University, Blacksburg.

Bowman, RE. 1975. Food Habits of Atlantic Cod, Haddock, and Silver Hake in the Northwest Atlantic, 1969-1972. Northeast Marine Fisheries Center. Woods Hole, Massachusetts. Ref. No. 75-1.

Bowman, RE, Stillwell, CE, Michaels, WL, Grosslein, MD. 2000. Food of Northwest Atlantic Fishes and Two Common Species of Squid. National Marine Fisheries Service. Woods Hole Lab.

Brooks, J. L., and Dodson, S. I. 1965. Predation, body size, and the composition of plankton. Science 150:28-35.

Brown, ML, Murphy, BR. 2004. Seasonal dynamics of direct and indirect condition indices in relation to energy allocation in largemouth bass *Micropterus salmoides* (Lacepede). Ecology of Freshwater Fish. 13: 23-36.

Brown, JJ, Limburg, KE, Waldman, JR, Stephenson, K, Glenn, E, Juanes, F, Jordaan, A. 2013. Fish and hydropower on the U.S. Atlantic coast: failed fisheries policies from half-way technologies. Conservation letters 6:4 280-286.

Cade, BS, Terrell, JW. 2008. Estimating Fish Body Condition with Quantile Regression. North American journal of Fisheries Management. 28: 349-359.

Cailliet, GM, Barry, JP. 1979. Comparison of food array overlap measures useful in fish feeding habit analysis. *In* Fish Food Habits Studies: Proceedings of the 2nd Pacific Northwest Technical Workshop. *Edited by* S.J. Lipovsky and C.A. Simenstad. Washington Sea Grant publication. Washington Sea Grant Program, University of Washington, Seattle.

Carpenter, SR, Kitchell, JF, and Hodgson, JR. 1985. Cascading Trophic Interactions and Lake Productivity. Bioscience 35: 634-639.

Castro-Santos, T, Letcher, BH. 2010. Modeling migratory energetics of Connecticut River American shad (Alosa sapidissima): implications for the conservation of an iteroparous anadromous fish. Canadian Journal of Fisheries and Aquatic Sciences 67: 806-830.

Childress, ES, Allan, JD, McIntyre, PB. 2014. Nutrient Subsidies from Iteroparous Fish Migrations Can Enhance Stream Productivity. Ecosystems 17: 522-534.

Clarke, A, Johnston, NM. 1999. Scaling of metabolic rate with body mass and temperature in teleost fish. Journal of Animal Ecology. 68: 893-905.

Cobb, JN. 1930. Pacific salmon fisheries. US Bureau of Fisheries. Document No. 1092. Washington, DC.

Colligan, MA, Kocik, JF, Kimball, DC, Marancik, J, McKeon, JF, Nickerson, PR. 1999. Status Review for anadromous Atlantic Salmon in the United States. National Marine Fisheries Service/US Fish and Wildlife Service Joint Publication. Gloucester, Massachusetts.

Crecco VA, Gibson MR. 1990. Stock Assessment of River Herring from Selected Atlantic Coast Rivers. Atlantic States Marine Fisheries Commission. Special Report no. 19.

Cumbler, John T. 2001. Reasonable Use: The people, the Environment, and the State, New England 1790-1930. Oxford University Press.

Dalton, CM, Ellis, D, Post, DM. 2009. The impact of double-crested cormorant (*Phalacrocorax auritus*) predation on anadromous alewife (*Alosa Pseudoharengus*) in south-central Connecticut, USA. Canadian Journal of Fisheries and Aquatic Sciences 66: 177-186.

Daufresne, M, Boët, P. 2009. Climate change impacts on structure and diversity of fish communities in rivers. Global Change Biology 13: 2467-2478.

Davis, JP, Schultz, ET. 2009. Temporal Shifts in Demography and Life History of an Anadromous Alewife Population in Connecticut. Marine and Coastal Fisheries 1: 90-106.

Davis, JP, Schultz, ET, Vokoun, JC. 2012. Striped Bass Consumption of Blueback Herring during Vernal Riverine Migrations: Does Relaxing Harvest Restrictions on a Predator Help Conserve a Prey Species of Concern? Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science 4: 239-251.

Drake, DC, Sheppard, PJ, Naiman, RJ. 2011. Relationships between salmon abundance and tree-ring $\delta^{15}N$: three objective tests. 2011. Canadian Journal of Forest Research 41: 2423-2432.

Durbin, AG, Nixon, SW, Oviatt, CA. 1979. Effects of the Spawning Migration of the Alewife, Alosa Pseudoharengus, on Freshwater Ecosystems. Ecology 60: 8-17.

Evans, NT, Shoup, DE, Glover, DC. A simplified approach for estimating age-0 gizzard shad prey supply and predator demand. Fisheries Management and Ecology 21: 140-154.

[FAO] Food and Agriculture Organization of the United Nations. The Composition of Fish. Torrey Research Station. http://www.fao.org/wairdocs/tan/x5916e/x5916e01.htm. Accessed 2/16/2016.

Fitzsimons, J. D., Brown, S.B. 1998. Reduced egg thiamine levels in inland and Great Lakes lake trout and their relationship with diet. In: G. McDonald, J. Fitzsimons and D. C. Honeyfield (Eds.), *Early life stage mortality syndrome in fishes of the Great Lakes and the Baltic Sea*., pp. 160–171. American Fisheries Society, Symposium 21, Bethesda, Maryland.

Fitzsimons, JD, Brown, S, Brown, L, Honeyfield, D, He, J, Johnson, JE. 2010. Increase in lake trout reproduction in Lake Huron following the collapse of alewife: Relief from thiamine deficiency or larval predation? Aquatic Ecosystem Health and Management 13: 74-84.

Fleishman, T. 1978. Charles River Dams Booklet, Charles River Watershed Association.

Foltz, JW, Norden, CR. 1977. Seasonal changes in consumption and energy content of smelt (*Osmerus mordax*) in Lake Michigan. Transactions of the American Fisheries Society. 106: 230-234.

Foster, DR. 2002. Thoreau's country: a historical-ecological perspective to conservation in the New England landscape. Journal of Biogeography 29: 1537–1555.

Fox, J, Weisberg. 2011. An {R} Companion to Applied Regression, Second Addition. Thousand Oaks, CA. Sage. URL: http://socserv.socsci.mcmaster.ca/jfox/Books/Companion

Fullerton, AH, Garvey, JE, Russell, AW, Stein, RA. 2000. Overwinter Growth and Survival of Largemouth Bass: Interactions among Size, Food, origin, and Winter Severity. Transactions of the American Fisheries Society. 129: 1-12.

Fulton, TW. 1904. The rate of growth of fishes. Twenty-second annual report of the fishery research board for Scotland. 3: 141-241.

Francis, Convers. 1871. A Historical Sketch of Watertown, in Massachusetts: From the first settlement of the town to the close of its second century. E. W. Metcalf and Company. p. 23.

Gahagan, B, Gherard, KE, Schultz, ET. 2010. Environmental and Endogenous Factors Influencing Emigration in Juvenile Anadromous Alewives. Transactions of the American Fisheries Society 139: 1069-1082.

Geode, RW, Barton, BA. 1990. Organismic indices and an autopsy-based assessment as indicators of health condition of fish. In: Adams, SA, ed. Biological indicators of stress. American Fisheries Society. Bethesda, Maryland.

Gerhart, LM, McLauchlan, KK. 2014. Reconstructing terrestrial nutrient cycling using stable isotopes in wood. Biogeochemistry 120:1-21.

Goode GB. 1880. The use of agricultural fertilizers by the American Indians and the early English colonists. American Naturalist 14: 473–479.

Gotelli, NJ. 1998. A Primer of Ecology, 2nd ed. Sinauer.

Graham, J. J. 1956. Observations on the alewife, Pomolobus pseudoharengus (Wilson), in fresh water. University of Toronto Biological Series Number 62, Publications of the Ontario Fisheries Research Laboratory 74.

Gregory-Eaves, I, Smol, J, Douglas, MSV, Finney, BP. 2003. Diatoms and sockeye salmon (Oncorhynchus nerka) population dynamics: Reconstruction of salmon-derived nutrients over the past 2,200 years in two lakes from Kodiak Island, Alaska. Journal of Paleolimnology 30: 35-53.

Gresh, T, Lichatowich, J, Schoonmaker, P. 2000. An estimation of historic and current levels of salmon production in the Northeast Pacific ecosystems: evidence of a nutrient deficit in the freshwater systems of the Pacific Northwest. Fisheries 25: 15-21.

Hakanson, J.L. 1989. Analysis of lipid components for determining the condition of anchovy larvae (*Engraulis mordax*) Marine Biology 102:143-151.

Hall CJ, Jordaan A, Frisk MG. 2011. The historic influence of dams on diadromous fish habitat with a focus on river herring and hydrologic longitudinal connectivity. Landscape Ecology 26: 95-107.

Hall, CJ, Jordaan, A, Frisk, MG. 2012. Centuries of Anadromous Forage Fish Loss: Consequences for Ecosystems Connectivity and Productivity. Bioscience 62: 723-731.

Haney, J.F., et al., 2014. An-Image-based Key to the Zooplankton of North America. version 5.0 released 2013, University of New Hampshire Center for Freshwater Biology (http://cfb.unh.edu/cfbkey/html/index.html).

Hanson, PC, Johnson, TB, Schindler, DE, Kitchell, JF. 1997. Bioenergetics Manual. Fish Bioenergetics 3.0. Center of Limnology, Wisconsin-Madison. Sea Grant Institute. pp. 109.

Hare, J.A., et al. 2016. A Vulnerability Assessment of Fish and Invertebrates to Climate Change on the Northeast U.S. Continental Shelf. PloS One 11. pp.30.

Hartman KJ, Margraf FJ. 2003. US Atlantic coast striped bass: Issues with a recovered population. Fisheries Management and Ecology 10: 309–312.

Hartel, KM, Halliwell, DB, Launer, AE. 2002. Inland Fishes of Massachusetts. Massachusetts Audubon Society. pp. 376.

Havey, KA. 1961. Restoration of anadromous alewives at Long Pond, Maine. Transactions of the American Fisheries Society 90: 281–286.

Heibo, E, and Magnhagen, C. 2005. Variation in age and size at maturity in perch (*Perca fluviatilis L.*), compared across lakes with different predation risk. Ecology of Freshwater Fish **14**:344-351.

Heidinger, RC, Crawford, SD. 1977. Effect of temperature and feeding rate on the liver-somatic index of the largemouth bass, *Micropterus salmoides.* Journal of the Fisheries Research Board of Canada 34: 633-638/

Hicks, BJ, Wipfli, MS, Lang, DW. 2005. Marine-derived nitrogen and carbon in freshwater-riparian food webs of the Copper River Delta, southcentral Alaska. Oceologia 144: 558-569.

Hilderbrand, GV, Hanley, TA, Robbins, CT, Schwartz, CC. 1999. Role of brown bears (Ursus arctos) in the flow of marine nitrogen into a terrestrial ecosystem. Oecologia 121: 546-550.

Huss M, Howeth JG, Osterman JI, Post DM. 2014. Intraspecific phenotypic variation among alewife populations drives parallel phenotypic shifts in bluegill. Proceedings of the Royal Society B: 281.

Hutchings, JA. 1993. Adaptive Life Histories Effected by Age-Specific Survival and Growth Rates. Ecology 74:673-684.

Iverson, SJ, Frost, KJ, Lang, and SLC. 2002. Fat content and fatty acid composition of forage fish and invertebrates and invertebrates in Prince William Sound, Alaska: factors contributing to among and within species variability. Marine Ecology Progress Series. 241: 161-181.

Jackson JBC, et al. 2001. Historical overfishing and the recent collapse of coastal ecosystems. Science 293: 629–637.

Jensen, A. J. 1979. Energy content analysis from weight and liver index measurements of immature Pollock. (Pollachius virens). J. Fish res. Bd Can. 36:1207-1213

Johnson,W.S., Allen, D.M., 2005. Zooplankton of the Atlantic and Gulf Coasts: A Guide to Their Identification and Ecology. Johns Hopkins University Press, Baltimore

Jones, RE, Petrell, RJ, Pauly, D. 1999. Using modified length-weight relationships to assess the condition of fish. Aquaculture Engineering. 20: 261-276.

Jones, AW, Palkovacs, EP, Post, DM. 2013. Recent parallel divergence in body shape and diet source of alewife life history forms. Evolutionary Ecology 27: 1175-1187.

Jonsson, B, Jonsson, N. 2009. A review of the likely effects of climate change on anadromous Atlantic salmon Salmo salar and brown trout Salmo trutta, with particular reference to water temperature and flow. Journal of Fish Biology 75: 2381-2447.

Kamaladasa AI, Jayatunga YNA, 2007. Composition, density and distribution of zooplankton in South West and East Lakes of Beira Lake soon after the restoration of South West Lake, Cey. J. Sci. (Bio. Sci.), 36 (1), 1–7.

Kerr, LA, Secor, DH. 2012. Partial Migration Across Populations of White Perch (*Morone Americana):* A Flexible Life History Strategy in a Variable Estuarine Environment. Estuaries and Coasts. 35: 227-236.

Ketola, G. H., P. R. Bowser, G. A. Wooster, L. R. Wedge, and S. S. Hurst. 2000. Effects of thiamine on reproduction of Atlantic salmon and a new hypothesis for their extirpation in Lake Ontario. Transactions of the American Fisheries Society 129: 607–612.

Kircheis et al. 2002. Analysis of Impacts Related to the Introduction of Anadromous Alewives into a small Freshwater Lake in Central Maine, USA. Maine Department of Inland Fisheries And Wildlife Report. pp. 1-53.

Kircheis, F. W., Trial, J. G., Boucher, D. P., Mower, B., Squiers, T., Gray, N., O'Donnell, M., Stahlnecker, J. 2004. Analysis of impacts related to the introduction of anadromous alewives into a small freshwater lake in central Maine, USA. Friends of Merry Meeting Bay.

Kirkwood AE, Jackson LJ, McCauley, E. 2009. Are dams hotspots for *Didymosphenia geminate* blooms? Freshwater Biology 54: 1856-1863.

Kissil, GW. 1974. Spawning of anadromous alewife, *Alosa pseudoharengus*, in Bride Lake, Connecticut. Transactions of the American Fisheries Society 103: 312– 317.

Krieger, D. A., J. W. Terrell, and P. C. Nelson. 1983. Habitat suitability information: Yellow perch. U.S. Fish Wildl. Servo FWS/OBS-83/10.55. 37 pp.

Kuparinen, A, O'Hara, RB, and Merila, J. 2008. The role of growth history in determining age and size at maturity in exploited fish populations. Fish and Fisheries **9**:201-207.

Lambert, Y, Dutil, JD. 1997. Can simple condition indices be used to monitor and quantify seasonal changes in the energy reserves of Atlantic cod (Gadus morhua)? Canadian Journal of Fishereis and Aquatic Science. 54: 104-112.

Legler, ND, Johnson, TB, Health, DD, Ludsin, SA. 2010. Water Temperature and Prey Size Effects on the Rate of Digestion of Larval and Early Juvenile Fish. Transactions of the American Fisheries Society. 139: 868-875.

Limburg KE, Waldman, JR. 2009. Dramatic declines in North Atlantic diadromous fishes. BioScience 59: 955–965.

Macdonald, JS, Green, RH. 1983. Redundancy of variables used to describe importance of prey species in fish diets. Canadian Journal of Fisheries and Aquatic Science 40: 635-637.

Madenjian, C.P, O'Gorman, R, Bunnell, D.B., Argyle, R.L, Roseman, E. F., Warner, D. M., Stockwell, J. D., Stapanian, M. A. 2008. Adverse Effects of Alewives on Laurentian Great Lake Fish Communities. North American Journal of Fisheries Management. 28: 263-282.

Malone, PM. 2009. Waterpower in Lowell: Engineering and Industry in Nineteenth-Century America. JHU Press.

Marczak, LB, Thompson, RM, Richardson, JS. 2007. Meta-Analysis: Trophic Level, Habitat, Productivity Shape the Food Web Effects of Resource Subsidies. Ecology 88: 140-148.

Martin, EH and Apse, CD. 2011. Northeast Aquatic Connectivity: An Assessment of Dams on Northeastern Rivers. The Nature Conservancy, Eastern Freshwater Program.,

Mattocks, S., C.J. Hall, A. Jordaan. *In review*. Damming, connectivity and the historical role of anadromous fish in freshwater ecosystem dynamics. Submitted to *Bioscience.*

McDermott, SP, Bransome, NC, Sutton, SE, Smith, BE, Link, JS, Miller, TJ. 2015. Quantifying alosine prey in the diets of marine piscivores in the Gulf of Maine.Journal of Fish Biology. pp. 1-19.

Moore, JW, Schindler, DE. 2004. Nutrient export from freshwater ecosystems by anadromous sockeye salmon (Oncorhynchus nerka). Canadian Journal of Fisheries and Aquatic Science 61: 1582-1589.

Moring, JR, Mink, LH. 2002. Anadromous alewives, *Alosa pseudoharengus*, as prey for white perch, *Morone americana*. Hydrobiologia 479: 125-130.

Morita, K, Tamate, T, Kuroki, M, Nagasawa, T. 2014. Temperature-dependent variation in alternative migratory tactics and its implications for fitness and population dynamics in a salmonid fish. Journal of Animal Ecology 83: 1268-1278.

Nakagawa, S, Schielzeth, H. 2013. A general and simple method for obtaining R^2 from generalized linear mixed-effects models. Methods in Ecology and Evolution. 4: 133-142.

Neves RJ. 1981. Offshore distribution of alewife, *Alosa pseudoharengus*, and blueback herring, *Alosa aestivalis*, along the Atlantic Coast. US Fisheries Bulletin 79: 473–485

[NOAA] National Oceanic and Atmospheric Administration. 2006. Endangered and threatened species: Revision of species of concern list, candidate species definition, and candidate species list. Federal Register71: 61022–61025.

Noble, RL. 1981. Management of forage fishes in impoundments of the southern United States. Transactions of the American Fisheries Society 110: 738–750.

Noonan, MJ, Grant, JWA. 2012. A quantitative assessment of fish passage efficiency. Fish and Fisheries 13: 450-464.

O'Gorman, R., B. F. Lantry, and C. P. Schneider. 2004. Effect of stock size, climate, predation, and trophic status on recruitment of alewives in Lake Ontario, 1978–2000. Transactions of the American Fisheries Society 133: 855– 867.

Pardue, GB. 1983. Habitat suitability index models: alewife and blueback herring. U.S. Department of the Intterior. Fish and Wildlife Service FWS. OBS-82: 10.58.

Pauly, D. 1995. Anecdotes and the shifting baseline syndrome of fisheries. Trends in Ecology and Evolution 10: 430.

Peters, AK, Jones, MJ, Honeyfield, DC, Bence, JR. 2007. Monitoring Energetic Status of Lake Michigan Chinook Salmon Using Water Content as a Predictor of Whole-fish Lipid Content. Journal of Great Lake Research. 33: 253-263.

Pinkas, L, Oliphant, MS, Iverson, ILK. 1971. Food habits of albacore, bluefin tuna, and bonita in Californian waters. California Department of Fish and Game. Fish Bull. 152: 1-105.

Pope, KL, Willis, DW. 1996. Seasonal Influences on Freshwater Fisheries Sampling Data. Reviews in Fisheries Science. 4: 57-73.

Porath, M. T., E. J. Peters, and D. L. Eichner. 2003. Impact of alewife introduction on walleye and white bass condition in Lake McConaughy, Nebraska, 1980–1995. North American Journal of Fisheries Management 23: 1050–1055.

Post, DM, Palkovacs, EP, Schielke, EG, Dodson, SI. 2008. Intraspecific variation in a predator affects community structure and cascading trophic interactions. Ecology 89: 2019-2032.

R Core Team (2013). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://R-preoject.org/.

Reimchen, TE, Mathewson, D, Hocking, MD, Morgan, J. 2002. Isotopic Evidence for Enrichment of Salmon-Derived Nutrients in Vegetation, Soil, and Insects in Riparian Zones in Coastal British Columbia. American Fisheries Society Symposium XX:00-000.

Ricker, W.E. 1973. Linear regression in fishery research. J. Fish. Res. Bd Can. 30:409-434.

Rose, KA, JH Cowan, Jr., KO Winemiller, RA Myers, and R Hilborn. 2001. Compensatory density dependence in fish populations: importance, controversy, understanding and prognosis. Fish and Fisheries 2:293-327.

Ross, RM, Johnson, JH, Adams, CM. 2005. Use of Fish-Otolith-Length Regressions to Infer Size of Double-Crested Cormorant Prey Fish from Recovered Otoliths in Lake Ontario. Northeast Naturalist. 12: 133-140.

Rosset, J. 2016. The Life History Characteristics, Growth, and Mortality of Juvenile Alewife, *Alosa Pseudoharengus*, In Coastal Massachusetts. Master's Thesis. pp. 109.

Saunders, R., Hachey, M.A., Fay, and C.W. 2006. Maine's diadromous fish community: past, present, and implications for Atlantic salmon recovery. Fisheries 31:537–547.

Schielke, E.G., E.P. Palkovacs, and D.M. Post 2011. Eco-Evolutionary Feedbacks Drive Niche Differentiation in the Alewife. Biol. Theory 6:211-219.

Schooley, JD, Karam, AP, Kesner, BR, Marsh, PC, Pacey, CA, Thornbrugh, DJ. 2008. Detection of Larval Remains after Consumption by Fishes. Transactions of the American Fisheries Society. 137: 1044-1049.

Schultz, ET, Conover, DO. 1996. Latitudinal differences in somatic energy storage: adaptive responses to seasonality in an estuarine fish (*Atherinidae: Menidia menidia*). Oecologia 109: 516-529.

Schulze, M. B. 1996. Using a field survey to assess potential temporal and spatial overlap between piscivores and their prey and a bioenergetics model to examine potential consumption of prey, especially juvenile anadromous fish, in the Connecticut River estuary. Master's thesis. University of Massachusetts, Amherst.

Secretary of the Commonwealth. 1887. Laws Relating to Inland Fisheries in Massachusetts. 1623-1886.

Shackley, P.E., C. Talbot, A. Cowan, and A. Watt. 1994. The use of body water, sodium, potassium and calcium content to investigate the nutritional status of first year Atlantic salmon parr in two Scottish Highlands streams. Journal of Fish Biology 44:693-706.

Shuter, B. J., and J. R. Post. 1990. Climate, population viability, and zoogeography of temperate fishes. Transactions of the American Fisheries Society 119: 314–336

Smith, S. H. 1970. Species interactions of the alewife in the Great Lakes. Transactions of the American Fisheries Society 99:754–765.

Spence, VE. 1930. Manufacturing Industries of the city of Chicopee, Massachusetts. Clark University. pp. 7 -50.

Stanley, J.G., and D.S. Danie. 1983. Species profiles: life histories and environmental requirements of coastal fishes and invertebrates (North Atlantic -- white perch. U.S. Fish and Wildlife Service, Division of Biological Services, FWS/OBS-82/11.7. U.S. Army Corps of Engineers, TR EL- 82-4. 12 pp.

Staudinger, MD, Juanes, F. 2010. A size-based approach to quantifying predation on longfin inshore squid *Loligo pealeii* in the northwest Atlantic. Mar. Ecol. 399: 225-241.

Steinberg, Theodore. 1994. Nature Incorporated: Industrialization and the Waters of New England. The University of Massachusetts Press.

Swetnam TW, Allen CD, Betancourt JL. 1999. Applied historical ecology: Using the past to manage for the future. Ecological Applications 9: 1189–1206.

Todd, CD, Hughes, SL, Marshall, CT, Macleans, JC, Lonerhan, Michael E, Biuw, EM. 2008. Detrimental effects of recent ocean surface warming on growth condition of Atlantic salmon. Global Change Biology. 14: 958-970.

Tran, G, Heuze, V and Makkar, HPS. 2015. Insects in fish diets. Animal Frontiers 5:37-44.

Trippel, NA, Allen, MS, McBride, RS. 2015. Importance of Resident and Seasonally Transient Prey to Largemouth Bass in the St. Johns River, Florida. Transactions of the American Fisheries Society. 144: 140-149.

Twining, CW, West, DC, Post, DM. 2013. Historical Changes in Nutrient Input from Humans and Anadromous Fishes in New England's Coastal Watersheds. Limnology and Oceanography 58: 1286-1300.

U.S. Environmental Protection Agency. 2003. Standard operating procedure for zooplankton analysis. Washington, DC. LG403

Volpato, GL, Barreto, RE, Marcondes, AL, Moreira, PSA, Ferreira, MFB. 2009. Fish ladders select fish traits on migration – still a growing problem for natural fish populations. Marine and Freshwater Behaviour and Physiology. 42: 307-313.

Walter, RC, Merrits, DJ. 2008. Natural streams and the legacy of water-powered mills. Science 319: 299.

Ward, EJ, Anderson, JH, Beechie, TJ, Pess, GR, Ford, MJ. 2015. Increased hydrologic variability threatens depleted anadromous fish populations. Global Change Biology. 21: 2500-2509.

Warshaw, S. J. 1972. Effects of alewives (*Alosa pseudoharengus*) on the zooplankton of lake Wononskopomuc, Connecticut. Limnology and Oceanography 17:816-825.

Weaver, DM, Coghlan, SM Jr, Zydlewski, J, Hogg, RS, Canton, M. 2015. Decomposition of sea lamprey *Petromyzon marinus* carcasses: temperature effects, nutrient dynamics, and implications for stream food webs. Hydrobiologia. 760: 57-67.

Wege, GJ, Anderson, RO. 1978. Relative Weight (W_r): a new index of condition for largemouth bass. Pages 79-91 in G. Novinger and J. Dillard, editors. New approaches to the management of small impoundments. American Fisheries Society, North Central Division, Special Publication 5, Bethesda, Maryland.

Wells, L. 1977. Changes in yellow perch (Perca flavescens) populations of Lake Michigan, 1954–75. Journal of the Fisheries Research Board of Canada 34:1821–1829.

Werner, RG. 2004. Freshwater Fishes of the Northeastern United States. Syracuse University Press. pp. 304.

West, DC, Walters, AW, Gephard, S, Post, DM. 2010. Nutrient loading by anadromous alewife (*Alosa pseudoharengus*): contemporary patterns and predictions for restoration efforts. Canadian Journal of Fisheries and Aquatic Science. 67: 1211-1220.

Wetzel, R.G. 1983. Attached algal–substrate interactions: fact or myth, and when and how*? Periphyton of Freshwater Ecosystems* (ed.R.G. Wetzel), pp. 207–215. Dr W. Junk Publishers, The Hague, the Netherlands.

Willis, DW. 1987. Reproduction and Recruitment of Gizzard Shad in Kansas Reservoirs. North American Journal of Fisheries Management. 7: 71-80.

Willis, T. V. 2006. St. Croix River Alewife-Smallmouth Bass Interaction Study. Maine Rivers

Yako, LA, Mather, ME. 2000. Assessing the Contribution of Anadromous Herring to Largemouth Bass Growth. Transactions of the American Fisheries Society. 129: 77-88.

Zhou, J, Zhang, M, Lin, B, and Lu, P. 2015. Lowland fluvial phosphorus altered by dams. *Water Resources Research* 51: 2211-2226.

Zuur, AF, Ieno, EN, Walker, NJ, Saveliev, AA, and Smith, GM. 2010. Mixed Effects Models and Extensions in Ecology with R. Springer Science + Business Media. pp. 574.