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Juvenile River Herring in Freshwater Lakes: Sampling Approaches for Evaluating Growth and Survival

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**JUVENILE RIVER HERRING IN FRESHWATER LAKES:
SAMPLING APPROACHES FOR EVALUATING GROWTH AND SURVIVAL**

A Thesis Presented

by

MATTHEW THOMAS DEVINE

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

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Environmental Conservation

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ABSTRACT

JUVENILE RIVER HERRING IN FRESHWATER LAKES: SAMPLING APPROACHES FOR EVALUATING GROWTH AND SURVIVAL

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River herring, collectively alewives (*Alosa pseudoharengus*) and blueback herring (*A. aestivalis*), have experienced substantial population declines over the past five decades due in large part to overfishing, combined with other sources of mortality, and disrupted access to critical freshwater spawning habitats. Anadromous river herring populations are currently assessed by counting adults in rivers during upstream spawning migrations, but no field-based assessment methods exist for estimating juvenile densities in freshwater nursery habitats. Counts of 4-year-old migrating adults are variable and prevent understanding about how mortality acts on different life stages prior to returning to spawn (e.g., juveniles and immature adults in lakes, rivers, estuaries, and oceans). This in turn makes it challenging to infer a link between adult counts and juvenile recruitment and to develop effective management policy. I used a pelagic purse seine to investigate juvenile river herring densities, growth, and mortality across 16 New England lakes. First, I evaluated the effectiveness and sampling precision of a pelagic purse seine for capturing juvenile river herring in lakes, since this sampling gear has not been systematically tested. Sampling at night in June or July resulted in highest catches. Precision, as measured by the coefficient of variation, was lowest in July (0.23) compared to June (0.32), August (0.38), and September (0.61). Simulation results indicated that the

effort required to produce precise density estimates is largely dependent on lake size with small lakes (<50 ha) requiring up to 10 purse seine hauls and large lakes (>50 ha) requiring 15–20 hauls. These results suggested that juvenile recruitment densities can be effectively measured using a purse seine at night in June or July with 10–20 hauls. Using juvenile fishes captured during purse seining in June–September 2015, I calculated growth and mortality rates from sagittal otoliths. Density, growth, and mortality were highly variable among lakes, and mixed-effects regression models explained 11%–76% of the variance in these estimates. Juvenile densities ranged over an order of magnitude and were inversely related to dissolved organic carbon. Juvenile growth rates were higher in productive systems (i.e., low secchi depth, high nutrients) and were strongly density-dependent, leading to much larger fish at age in productive lakes with low densities of river herring compared to high density lakes. Water temperature explained 56%–85% of the variation in juvenile growth rates during the first 30 days of life. Mortality was positively related to total phosphorous levels and inversely related to hatch date, with earlier hatching cohorts experiencing higher mortality. These results indicate the importance of water quality and juvenile densities in nursery habitats for determining juvenile growth and survival. This study encourages future assessments of juvenile river herring in freshwater and contributes to an understanding of factors explaining juvenile recruitment that can guide more effective and comprehensive management of river herring.

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CHAPTER 1

INTRODUCTION

1.1 Marine Forage Fishes

Marine forage fish species are small to medium-sized (<30-90 cm in length) planktivorous fish that often form large schools in pelagic habitats. Common marine forage fish species include many clupeids (menhadens, herrings, sardines, sprat), osmerids (capelin, smelt), and engraulids (anchovies), among others. Forage fish consume phytoplankton and zooplankton by filter-feeding, thus serve as major conduits between primary and secondary production and higher trophic levels (Bakun et al. 2010). Forage fish are generally found across broad latitudinal ranges in all the world's oceans (FAO 2010), but shifts in their planktonic food due to changing oceanographic conditions can result in large fluctuations of these relatively short-lived species (Cury et al. 2000).

As a primary food source, forage fish help sustain many marine predators. For example, the diets of mammals such as sea lions (Weise and Harvey 2008), seals (Thompson et al. 1996), whales, and otters (Pauly et al. 1998) rely heavily on various species of forage fish. Seabirds including penguins, gannets, cormorants, kittiwake, and terns also consume large quantities of forage fish (Crawford and Dyer 1995; Furness 2007; Liechty et al. 2016). Finally, large commercial fish species like cod (Magnussen 2011), striped bass (Walter and Austin 2003), and tuna (Logan et al. 2011), are dependent on globally abundant forage fish stocks. Schools of forage fish are essentially concentrated sources of fuel, and their distribution in marine habitats can drive the presence or absence of other organisms.

In addition to a food source for marine predators, forage fish are also an important source of food or other processed product for humans. For centuries, humans all over the world have fished for, consumed, and used forage fish. Forage fish represent a major source of protein for nations globally (FAO 2010) and the fact that they can be easily preserved through salting or smoking methods, and are high in essential nutrients, make them extremely valuable. Forage fish are also an important input for animal feed and aquaculture. Large markets exist for forage fish byproducts such as fish meal and fish oils. Almost 90% of the global forage fish catch is used to provide feed for domestic animals such as pigs and chickens (Alder et al. 2008). The industrialized byproduct markets compete against fish for sustenance and ecosystem function, and increasing demand, when paired with predicted population growth, is worrisome for the future of forage fish stocks and their management (Rice and Garcia 2011).

Forage fish can be captured in relatively inexpensive small mesh nets, and vessels require considerably less fuel than other fisheries such as trawl and line (Tyedmers et al. 2005). Major fisheries exist in a few concentrated parts of the world including North America, Northern Europe, and the west coast of South America. To give some perspective, five of the top ten species caught in 2008 (by weight) were forage fish, and their catch constitutes 30% of all wild fish caught annually (Alder et al. 2008). Additionally, forage fish contribute roughly \$16.9 billion USD to global fisheries annually (Pikitch et al. 2012).

The United States has taken measures to manage stocks of marine forage fish along its maritime boundary. The Magnuson–Stevens Fishery Conservation and Management Act, commonly referred to as the Magnuson–Stevens Act (MSA), was

enacted in 1976 by Congress, and serves as the primary federal law governing the management of offshore marine resources. The MSA was passed in part to address heavy fishing and exploitation from foreign fleets, and the law has been updated and reauthorized several times since its inception. Under this law, eight regional fishery management councils were formed and given authorization to prepare management plans towards the conservation and management of federally managed fishery resources. These eight management councils operate under the oversight of the National Marine Fisheries Service (NMFS); a division of the National Oceanic and Atmospheric Administration (NOAA). The jurisdictional boundaries of NMFS are the Exclusive Economic Zone (EEZ). The U.S. EEZ extends between 3–200 nautical miles offshore and allows the U.S. exclusive rights on the use and exploitation of marine resources, including water and wind for energy production (United Nations 1983).

While the Magnuson–Stevens Act ensures the protection and management of marine fisheries, this law does not specifically apply to North America’s diadromous fishes, which occupy marine waters for only part of their life. Instead, diadromous fishes are managed by federal and state agencies and local municipalities. Because diadromous fishes do not obey political boundaries, individual states deemed that their best opportunity to sustain coastal fisheries would be accomplished by working cooperatively, in collaboration with the federal government. Thus, three Interstate Marine Fisheries Commissions were approved by Congress in the 1940’s with the mission to manage these shared migratory fishery resources: the Atlantic States Marine Fisheries Commission, the Pacific States Marine Fisheries Commission, and the Gulf States Marine Fisheries Commission. Each regional commission is made up of three commissioners from each

state: the director of the state's marine fisheries program, a state legislator, and an individual appointed by the governor to represent stakeholder interests. Funding for interstate commissions is largely provided by NMFS and the U.S. Fish and Wildlife Service (USFWS).

1.2 Diadromous Forage Fishes: Biology, Use, and Decline

Diadromous species migrate between marine and freshwater environments to complete their life cycles, and in North America, include fishes such as sturgeons, salmon, and shads. Diadromy takes place in two forms: anadromy, where spawning occurs in freshwater, and catadromy, in which spawning occurs at sea. Like the marine species described above, diadromous fishes are economically and ecologically important, providing services such as nutrient transport, prey for both marine (Hall et al. 2012) and freshwater food chains (Mattocks et al. 2017), food for direct human consumption, and food for domestic animals (Bolster 2008).

Shad and river herrings in the family Clupeidae (collectively referred to as alosines) are the most well-known anadromous forage fishes along the Atlantic coast of North America. Four species are native to the region: American shad (*Alosa sapidissima*), hickory shad (*A. mediocris*), alewife (*A. pseudoharengus*), and blueback herring (*A. aestivalis*). These species share similar life histories--they all are iteroparous, spend most of their adult life at sea, and have relatively short lifespans. While these species can be difficult to discriminate and are often grouped as simply herrings or shads in commercial landings, each can be distinguished based on morphological characteristics and meristics.

River herring use a variety of habitats throughout their lifecycle. As adults, they reside at sea most of the year, mixing with other stocks of river herring and Atlantic

herring, before returning each spring to their natal freshwater habitats to spawn. While at sea, river herring are subject to incidental bycatch in fisheries targeting other species such as Atlantic herring and mackerel (Bethoney et al. 2014). Historically, river herring (collectively, alewives and blueback herring) were not as well documented in fisheries accounts, though their abundances appear to have greatly exceeded American shad (Hall et al. 2011). Alewives and blueback herring occupied the majority of coastal rivers and estuaries along the Atlantic coast (ASMFC 2008). Maryland, North Carolina, Virginia, and Massachusetts were responsible for a large portion of commercial landings during the late 19th and early 20th century using primarily pound nets, although prior to 1950 significant commercial catches of river herring were recorded in each Atlantic State. Many states experienced peak or substantial harvest in the years following World War II and coastwide landings reached almost 75 million pounds in 1958 (ASMFC 2012). Commercial landings peaked in the late 1960's, quickly declined through the next two decades, and have remained at less than 3% of the peak levels, partly as the result of moratoria on harvest (ASMFC 2012). Much of the harvest from 1950 through the 1970's came from Massachusetts purse seine fisheries that were targeting Atlantic herring (*Clupea harengus*) offshore. Additionally, the increase in landings depicted on many figures can be attributed to heavy offshore fishing pressure from foreign fleets that began in the 1960's. Results from the most recent stock assessment indicated that 22 of 52 river herring stocks for which data were available were depleted. Of these 52, data was inadequate for 28 stocks, and one stock was increasing. Today, river herring stocks are considered to be depleted on a coast-wide basis (ASMFC 2012) and designated as a species of concern throughout their range (Dalton et al 2009; NOAA 2009).

1.3 River Herring Conservation and Management

Alewives and blueback herring are managed by the Atlantic States Marine Fisheries Commission, through River Herring Fisheries Management Plans (FMPs). Member states of the Commission include (from north to south), Maine, New Hampshire, Massachusetts, Rhode Island, Connecticut, New York, New Jersey, Pennsylvania, Delaware, Maryland, Virginia, North Carolina, South Carolina, Georgia, and Florida. Member states are required to collect data on, monitor, and calculate population indices for river herring in their jurisdiction.

Two amendments to the FMP's have been enacted since Crecco and Gibson (1990) conducted the Commission's first assessment of Atlantic coastal river herring stocks. Amendment I (1999) required states to "keep fishing mortality sufficiently low to ensure survival and enhancement of depressed stocks and the maintenance of stabilized stocks" (ASMFC 1999). However, large data gaps, uncertainties about population trends, and concerns over appropriate mortality levels and whether they were low enough to prevent further stock decline led to a second amendment. Amendment II (2009) requires states to close their river herring fishery unless they develop and implement approved Sustainable Fishery Management Plans (SFMPs). These plans need to clearly demonstrate that the state's river herring fisheries will not negatively affect future stock production or recruitment (ASMFC 2009). Currently, approved SFMPs are in effect for some rivers in Maine, New Hampshire, Massachusetts, New York, North Carolina, and South Carolina, with the remaining states' commercial and recreational fisheries closed (ASMFC 2016). This amendment seeks to prevent further declines by improving our understanding of stock dynamics and sources of mortality on an annual basis.

Amendment II puts an emphasis on data collection that will improve our understanding of the complex population dynamics of river herring and allow for more knowledgeable management decisions.

1.4 River Herring Data Gaps

Assessments of anadromous river herring ideally would include data from freshwater systems where geographically distinct stocks can be evaluated, yet to date, assessments are conducted where feasible and in a haphazard fashion. Adult population size and juvenile indices of abundance are derived from a variety of fishery-independent methods. The most common metric to evaluate river herring population size is counts of returning adults at river fishways. Most states conduct adult counting at select fishways using either electronic counters, video monitoring, or citizen science programs.

Massachusetts relies heavily on this approach--all 38 streams monitored in the state do so via counts of upstream migrants. In most cases, relative abundance estimates are made, but absolute abundance is sometimes achieved during stocking events or at sites with low density runs. Fixed gill nets are less commonly used, but can be effective on large rivers when used as an “intercept fishery”. The New York Department of Environmental Conservation (NYDEC) uses fixed gill nets on the same stretches of the Hudson River annually to capture adults migrating to spawning grounds. Virginia and North Carolina also sample with passive gill nets. Beach seining and electrofishing are widely used among states (ME, NH, CT, RI, VA, FL) with surveys being conducted in littoral estuarine habitats, large rivers, or accessible stretches of stream. Estuary trawl surveys are used by some states (RI, CT, NJ, DE, GA, FL), and NMFS conducts a bi-annual bottom trawl survey at sea. The non-standardized sampling approach used across the

various fishery-independent surveys presents challenges when assessing river herring populations coastwide because fisheries data collected using different gears that is not consistent in time or space is difficult to interpret (Bonar and Hubert 2002). The complex life cycle of anadromous river herring makes it difficult to partition lacustrine, riverine, estuarine, and marine factors determining population dynamics (ASMFC 2012), and long-term trend data is needed to inform river herring management across life stages. However, if collected in a standardized fashion, these data will aid in large-scale population analysis by streamlining regionwide data comparisons and reducing levels of uncertainty cast by model predictions.

1.5 Social Benefits of Restoring River Herring

Restoring river herring populations to coastal rivers and streams can have important social benefits. Traditional and immediate economic (Lewis et al. 2008) and ecological (Benayas et al. 2009) benefits typically determine restoration success without accounting for important social connections to the resource. Each spring, festivals draw thousands of people from small towns to coastal streams and rivers to celebrate the return of river herring. Often, 50–75% of a town's population will attend these festivals, resulting in the largest gathering of the year (McClenachan et al. 2015). These physical gatherings create a sense of pride and community and allow people to feel connected to the resource as they watch fish migrate with their children, taste smoked herring, and participate in learning about the species history and biology. This connectedness in turn can generate strong feelings of identity and ownership, which can quickly translate into a desire to protect and enhance the resource. For river herring, this scenario is playing out in many states, particularly in Maine, where harvest is still allowed on select rivers and

river herring are a deep part of the culture and local economy (McClenachan et al. 2015). Towns that have licenses to harvest river herring look to keep the fishery sustainable because it enhances local economies and diversifies local fisheries (Alden 2011). Because river herring return to their natal rivers, local towns have an opportunity to steer the future of these fish through the management and consumption practices they impose. This places strong value on maintaining local benefits, which may be easier to support than a fishery at sea where connectedness is less tangible. Broad support for river herring restoration may be boosted by a social attachment to the fishery that begins with a simple walk along a stream during spring migration.

River herring have historically been given low monitoring priority compared to other species. The 2012 ASMFC stock assessment identified specific data gaps that need to be addressed prior to the next benchmark assessment, which is scheduled for 2022. Specific areas of research that are supported by the commission and the federal government include developing juvenile sampling methods that can be used to estimate abundance, investigating the relationship between juvenile production and subsequent year class strength, quantifying sources of freshwater mortality, and implementing monitoring protocols that can determine river herring responses to restoration measures such as dam removal, fishways, stocking, and moratoria (ASMFC 2012). This thesis aims to fill data gaps identified in the 2012 ASMFC stock assessment by testing sampling methods for juveniles in freshwater lakes, and investigating factors that influence productivity.

The second chapter of this thesis evaluates the capture efficiency and sampling precision of a purse seine for estimating juvenile herring densities in freshwater lakes.

Specifically, I ask the questions: 1) When is the most appropriate time to sample? 2) How much sampling is required to produce precise estimates? and 3) How does the efficiency of a purse seine compare to gill nets and beach seines? This information can be used to estimate juvenile abundances in a standardized fashion, and should help managers better understand the relationship between adult escapement and juvenile production.

Additionally, the sampling protocols discussed here will help optimize future sampling efforts, if adopted by the states.

The third chapter of this thesis investigates the density, growth, and survival of juvenile river herring in lakes throughout their northern range and biological and environmental factors influencing productivity. Specifically, the objectives of Chapter 3 are to: 1) investigate how density, growth, and mortality vary within and among lakes, 2) examine patterns in daily growth rates and relationships with temperature, and 3) evaluate how abiotic and biotic variables influence density, growth, and mortality. The results of this study can help identify the role of freshwater mortality in determining population size and inform river herring population models used to predict abundance.

CHAPTER 2

CAPTURE EFFICIENCY AND SAMPLING PRECISION FROM A PURSE SEINE

2.1 Introduction

Estimating the abundance of larval and juvenile fish populations is necessary for the applied management of fish stocks, as long as they are accurate (unbiased) and precise (low variance) enough to inform population modeling and instruct decision-making (Cyr et al. 1992). A common challenge for fisheries managers looking to estimate larval and juvenile fish densities is determining a sampling design and gear that minimizes spatial and temporal capture efficiency. Gear selection and sampling design is dependent upon logistical challenges (i.e., cost, personnel), behavior of the target species, study objectives, and practical challenges of gear (Baker and Wolff 1987; Bonar and Hubert 2002). The heterogenous spatial distribution commonly exhibited by age-0 fish often leads to high variance among replicate samples (Silliman 1946; Hilden and Urho 1988), and if left unaccounted for can be deeply problematic for population estimates and predictive modeling.

To develop standardized protocols for population assessments, it is critical to consider sampling precision. Gear selection should be designed to maximize capture efficiency (the proportion of target species initially enclosed by the gear) and recovery efficiency (the proportion of target species retained from the gear and enumerated), thus minimizing active (e.g., swimming to avoid capture) and passive (e.g., failed detection in habitats) gear avoidance (Rozas et al. 1997). While many studies have compared the accuracy of age-0 fish sampling methods (Kriete and Loesch 1980; Gallagher and Connor

1983; Thayer et al. 1983; Gregory and Powles 1988; DeAlteris et al. 1989; Tischler et al. 2000; Claramunt et al. 2005; Overton and Rulifson 2007), less often quantified is the precision. In this study, I evaluate the effectiveness and sampling precision of a small-sized purse seine for estimating juvenile river herring densities in pelagic freshwater lake habitats.

River herring are an economically and ecologically important species that have supported commercial fisheries for centuries (ASMFC 2009; Davis and Schultz 2009). Once abundant across North America's Atlantic coast, anadromous river herring, collectively alewives (*Alosa pseudoharengus*) and blueback herring (*A. aestivalis*), have experienced sharp population decline in recent decades due in large part to habitat degradation, overfishing, and disrupted access to critical spawning habitat (Limburg and Waldman 2009; Hall et al. 2011). Consequently, the U.S. federal government has listed river herring as a species of concern throughout their range, prompting states to close commercial and recreational fisheries for both species and implement caps on bycatch at sea (Dalton et al. 2009, NOAA 2009). Inhabiting coastal waters from Canada to Florida, river herring use a wide range of habitats during their anadromous life cycle, with sexually mature individuals migrating each spring from offshore habitats into coastal rivers, streams, and headwater lakes and ponds to spawn (Pardue 1983; Walsh 2005). This migration to spawning habitats can begin as early as March and continue through June, and appears to be largely dependent on water temperature and flow (Mullen et al. 1986; Loesch 1987).

Effective management of river herring remains a challenge (NOAA 2009). Current approaches that rely on counting adults during upstream migration are hampered

by high costs, and logistical and biological constraints including: equipment and technical failure, required personnel, financial limitations, and unfavorable weather. Further, the relationship between enumerated adults and the resulting number of offspring is unclear, due to habitat complexity upstream of counting stations, and the possibility of complex behaviors that result in multiple counts of the same individual (Nelson et al. 2011). Understanding the biological link between adult run size and recruitment is essential for developing population models that can partition mortality among different life stages and sources. Counts of 4-5-year-old migrating adults make it difficult to infer the sources of mortality prior, and current surveys exhibit such high variability that trends are not decipherable, generating uncertainty around stock assessments. Because there is considerable uncertainty regarding the potential drivers of recent declines, quantifying age-0 abundance would aid in understanding whether in-system productivity or at-sea mortality is more important for determining population size.

Previous studies of anadromous river herring have focused on adults or juveniles in lotic and estuarine habitats (Graham 1982; Walsh et al. 2005; Gahagan et al. 2010; Tommasi et al. 2015; Ogburn et al. 2017), primarily focusing on the timing and triggers of movement. Others have evaluated freshwater lake habitat use and aspects of production (Havey 1973; Ney and Kelso 1982; Post et al. 2008; Davis and Schultz 2009; Kircheis et al. 2002; Mather et al. 2012). While these studies provide important contributions to our understanding of river herring biology and life history, river herring management could be improved by estimating accurately and precisely juvenile recruitment in freshwater nursery habitats.

Purse seines are widely used in commercial fisheries today and are particularly effective at capturing schooling pelagic species such as Pacific tuna and Atlantic menhaden (McNeely 1961; Schaaf and Huntsman 1972). This active fishing method has been successfully used at varying scales for centuries in subsistence fisheries (Ben-Yami 1994). Scientists have also adopted the gear for sampling in freshwater and marine environments, experimenting with different sized nets in the absence of satisfactory sampling gears. For example, Hunter et al. (1966) conducted one of the first investigations using a 'miniature' purse seine to capture juvenile pelagic fishes beneath drifting materials off the California coast. Levi (1981) described a two-boat purse seine method and found it highly successful for capturing juvenile menhaden for mark-recapture studies. Wessel and Winner (2003) used a modified purse seine to effectively monitor juvenile estuarine fishes, showing high retention rates as well as an ability to capture a wide range of sizes. Emerging from this initial work, researchers began evaluating catch rates and avoidance from a purse seine compared to other gears (Charles-Dominique 1989; Murphy and Clutter 1972; Steele et al. 2007), and support has grown for its various applications. In inland freshwater habitats, the use of a small-sized purse seine has also been shown to be effective at sampling a variety of age-0 fishes (Nellen and Schnack 1974). Durkin and Park (1967) successfully captured age-0 salmonids in large western United States impoundments, and suggested this method 'could be successfully used to obtain samples of virtually any species that concentrates at or near the surface.' Tischler et al. (2000) compared different sized purse seines and concluded that purse seines are appropriate for sampling rapidly growing age-0 Eurasian perch (*Perca fluviatilis*): a schooling pelagic species during its first year.

Purse seines have been used to sample juvenile river herring in freshwater lakes for ecological and evolutionary studies (Post et al. 2008), and for estimating summer densities within and across lakes (Rosset 2016). However, the timing and effort needed to gain accurate and precise estimates of river herring densities with good capture efficiency has not been formally tested. Thus, my study objectives were to 1) determine the optimal month and time of day to sample to obtain peak capture rates with the highest precision, 2) determine the sampling effort (number of hauls) required to precisely estimate age-0 river herring densities, and 3) evaluate the capture efficiency of a purse seine compared to other gears (beach seines, gill nets). My intention is that methods discussed in this paper lead to the development of an efficient, cost-effective, and reliable sampling protocol to assess age-0 river herring densities in freshwater lakes.

2.2 Methods

2.2.1 Study Lakes

Sixteen freshwater lakes spanning from Greenwich, Connecticut to Old Town, Maine were sampled in this study. Sites were selected to include all coastal New England states and a wide range of physical and chemical characteristics (Table 2.1; Figure 2.1). Study waters were 28–1773 ha, had mean depths of 2.5–15.2 m, and had summer surface temperatures of 18.1–28.7 °C. River herring entered lakes naturally using fish passage structures or were introduced via stocking. Adult upstream migration monitoring programs had been established at each natural run and estimates of adult escapement were available from run counts or stocking numbers. River distance, measured from lake outlet to ocean, ranged from 4.5–199.7 km, and preference was given to lakes that were

the only lake upstream of an adult run count. Finally, priority was given to lakes where study would strengthen ongoing research efforts by management agencies.

2.2.2 Study Design

Lakes were sampled for fishes with a purse seine and water quality one to four times between 02 June and 21 September 2015. Sampling began at the southernmost site (Mianus Pond, CT) and continued north through Rhode Island, Massachusetts, New Hampshire and Maine. This progression was repeated each month as part of our longitudinal study design, and ensured equal intervals of time (one month) between sampling events at each lake. Lakes were assigned to three levels of sampling intensity: high, medium, and low. High intensity sites (Damariscotta, Upper Mystic, Pentucket, Winnisquam, Gilbert-Stuart) were sampled 4 times (June–September), and provided significant replication across time and space. Medium intensity sites (Lower Guilford, Glen Charlie, Potanipo, Highland, Sabattus, and Whitmans) were sampled 3 times (June–August) with slightly less effort (i.e., fewer sampling nights) than high intensity sites. Low intensity sites (Chemo, Mianus, Snipatuit, Pushaw, and Togus) were sampled one night in July or August. Beach seines were used only one time (July or August) at all sites. Gill net sampling was conducted at 3 lakes (Upper Mystic, Whitmans, Pentucket) in June-September, concurrent with purse seining. In July 2016, we additionally sampled 4 lakes (Pentucket, Potanipo, Upper Mystic, Whitmans) with a purse seine during the day (1230–1800) to test for differences in detectability and size structure between day and night.

Water quality data was collected following protocols specified by Chase (2010). Samples were taken during dusk, preceding fish sampling, at the deepest point in each

lake. Water temperature (°C) and dissolved oxygen (mg/L) were measured vertically every 1-m using a multi-parameter YSI-650MDS (YSI Inc, Yellow Springs, OH). Water samples for total nitrogen and phosphorous were collected just below the lake surface in an acid-washed 60-mL bottle. Dissolved organic carbon (DOC) and chlorophyll-a (chl-a) were sampled by filtering water through a glass fiber filter. All samples were placed on ice and frozen completely within 10 hours.

2.2.3 Gear Descriptions

Purse seine samples were collected after sunset (2000–0200). A minimum of 3 samples were taken at randomly selected locations within each lake. To choose sampling locations, I used ArcGIS 10.2.2 to construct 50 x 50-m grids, excluding a 50-m shoreline buffer at each lake, then select grid locations using the random number generator and fishnet tools. In larger lakes with multiple basins or greater than 1,000 ha, I selected random locations in each basin. No other stratification criteria were used in our sampling design due to the limited knowledge of within-lake habitat preference and diel movement of age-0 river herring.

A 30.5 x 4.3 m purse seine with 2 mm mesh was set by a crew of 3 people from a 5-m aluminum Jon boat, powered by a 25-horsepower outboard engine and equipped with a stern-mounted 22-kg thrust electric trolling motor. The electric motor was used for setting and retrieving the net to minimize noise and possible disturbance to fish following Levi (1981). Headlamps with red lights were used during sampling to preserve night vision and to minimize the potential bias of behavioral effects of artificial light. One end of the net was attached to a large buoy with a 30-m rope and thrown overboard. This prevented the net from being towed during the set, demarcated our haul location, and

provided a visual marker for the boat operator. Nets were set over the starboard side by 2 crew members while the third member reversed the boat, in a counterclockwise circle, and returned to the buoy. When correctly set, the purse seine sampled 485 m³ of water. Hauls that were not correctly set due to strong wind gusts, net snags, or operator error were retrieved, discounted, and repeated at a new location. Immediately after being set, the net was retrieved by pulling the purse line ends until the bottom of the net was closed, trapping all fish encircled. Simultaneously, the float line was slowly pulled into the boat, reducing the net diameter. When pursing was completed, all weights and rings were lifted from the water, and the float line and net-wall retrieved to form a small pocket containing the catch that remained submerged in water alongside the boat (Figure 2.2). River herring were captured from the purse seine pocked using dip nets, enumerated, and returned immediately to open water. Only individuals being collected for aging (n=30 per haul) were enumerated, measured, and handled on-board the boat. This entire process was considered 1 haul.

Sampling coordinates, time of day, processing time, sample depth, wind speed, and substrate (when observed from net encountering lake bottom) were recorded for each haul. High intensity sites (n=5) were sampled 2–3 consecutive nights in June, July, and August, and 1 night in September (30–54 total hauls). Medium intensity sites (n=6) were sampled 1 night in June and August, and 2 consecutive nights in July (16–30 total hauls), with the exception of Potanipo and Highland lakes which were additionally sampled 1 night in September. Low intensity sites (n=5) were sampled 1 night in either July or August (2–5 total hauls).

A 25-m long by 2-m deep bag-type beach seine (7-mm mesh) was used to evaluate the presence of age-0 river herring in littoral habitats and to test the effectiveness of this gear type for capturing our target species. Two to three beach seine hauls were conducted at 13 of the 16 lakes in July 2015. Beach seining was conducted in early evening, prior to purse seine sampling. Sampling locations were chosen haphazardly based on accessible shoreline by boat or foot. All river herring captured were enumerated, measured for total length to the nearest millimeter, and released. Other species captured were identified, counted, measured, and released. If more than 50 individuals of a species were caught in a single seine, a random subsample of not less than 50 fish were measured and the remaining individuals counted.

We used gill nets at 3 Massachusetts lakes (Upper Mystic, Whitmans, Pentucket) to compare sampling methods and effectiveness at capturing river herring. Four multi-mesh gill nets were deployed concurrently with purse seines (± 1 day) at randomly selected locations in 4 months (June–September). Each net was 75-m long and 2.5-m tall, and included 4 monofilament panels with mesh sizes of 2.5, 5, 7.5, and 10 cm. A crew of 2 people deployed 2 nets in the pelagic zone (>200 m from shore) and 2 nets in the littoral zone (<100 m from shore) at each lake in a haphazard fashion. Nets were set prior to dusk (1800–2200) and retrieved the following morning (0800–1230), with an average soak time of 16.5 h (SD = 1.6 h). Due to lethal entanglement, most river herring were deceased upon retrieval. Mesh size, total length (mm), and direction fish entered the net were recorded, and specimens were placed on an ice bath and later frozen. River herring observed to be alive during retrieval were immediately removed from the net and released. No biological information was recorded for these individuals.

2.2.4 Data Analysis

Densities of age-0 river herring were estimated from purse seine samples only. Density (no. m⁻³) was calculated as the number of individuals captured within each net haul divided by 485. If water depth was <4.3 m (depth of seine), as was the case in 30% (100 of 344) of hauls, the volume was adjusted accordingly. Per-haul densities were averaged each month to estimate monthly density, and monthly densities were averaged to estimate an overall density for each lake.

I used analysis of variance (ANOVA) to test for statistically significant differences in densities among months. Density estimates were log-transformed to meet normality assumptions of the linear models. If a significant difference was found by the ANOVA, I subsequently performed a Tukey's post-hoc test (alpha = 0.05) to determine which months differed.

I compared precision of catch-per-unit-effort (CPUE; total fish captured in 1 purse seine haul) estimates from a purse seine using the coefficient of variation of the mean ($CV_{\bar{x}} = SE/\bar{x}$), where \bar{x} = mean CPUE from repeat samples and SE = standard error of the mean. For each lake, monthly CV values were calculated. Those estimates were then averaged across all lakes each month to determine the month when sampling precision was optimized. High values of CV indicate relatively imprecise data and would suggest the need for greater sampling effort, while low CV values yield more precise estimates and reduce uncertainty (Cyr et al. 1992), and I used this rationale to guide interpretation of the results. I compared 5 daytime hauls with 5 nighttime hauls on the same day at 4 lakes. I calculated the CV of mean CPUE for each lake and each diel period to determine when precision was highest. I used a Student's t-test (alpha = 0.05) to

test for diel differences in mean lengths among lakes and within each lake, and employed a two-sample Kolmogorov-Smirnov (K-S) test to determine whether length frequency distributions were statistically different among sampling periods.

I used statistical simulation to determine the effort required from a purse seine to obtain repeatable CPUE estimates. Our CPUE data was highly right-skewed, where 300 or fewer individuals were captured in 90% of purse seine hauls (Table 2.2). Non-parametric bootstrap resampling was performed to test the effect of sample size on mean CPUE estimates. This approach is effective when data do not adequately fit a probability distribution, or when the underlying population distribution is unknown (Haddon 2010).

I simulated CPUE data from the 5 high intensity lakes sampled in July 2015. The number of hauls for these 5 sites in July ranged from 10 (Pentucket) to 18 (Upper Mystic), and I simulated data for a range of sampling effort ($n = 2-30$ hauls). For each lake, I performed 1000 repetitions for each level of sampling effort and calculated simulation statistics (mean, standard deviation (SD), and coefficient of variation (CV)) for each iteration, which were assumed to be normally distributed given the high number of replicates (Appendix A). The rate of change of CV with increasing sample size was also calculated. The CV and the rate of change in CV were plotted against sampling effort and fit with ordinary least squares regression. The number of hauls where the rate of change in CV reached 1% was interpreted as the point at which increasing sampling effort resulted in a negligible increase in precision.

For each gear type in each month, I calculated the mean total length of captured river herring, the percent of river herring in the total catch, and the CV of the number of fish per sample. I used a two-sample bootstrap K-S test for pairwise comparisons of age-

0 river herring length distributions between purse seines and gill nets. Cumulative Distribution Functions (CDFs) of fish lengths for both gears were calculated, and length frequency histograms were constructed for Pentucket, Upper Mystic, and Whitmans. A bootstrapped version of the K-S test was used to overcome the assumption that length data is continuous and “ties” are theoretically impossible (Hollander et al. 2014). All statistical analyses were performed in Program R (Version 3.3.2).

2.3 Results

Age-0 herring were captured in 309 of 344 purse seine hauls (90%), 12 of 34 gill net sets (36%), and 6 of 44 beach seine hauls (14%). A total of 41893 age-0 river herring were captured from 16 lakes using a purse seine, 640 were captured from 3 lakes using gill nets, and 404 were captured from 5 lakes using beach seines.

Average densities across lakes varied over an order of magnitude from 0.03 (Pentucket) to 0.87 (Gilbert-Stuart) river herring/m³ (Figure 2.3). Densities were generally highest in June (mean \pm SE = 200.6 \pm 72.6), and decreased throughout the summer (Figure 2.4).

Mean juvenile densities differed significantly among months (one-way ANOVA: $F_{3,335} = 12.14$, $p < 0.001$), with densities significantly higher in early summer months (June/July) than later months (August/September). Notably, mean densities were not significantly different between June and July. For 8 of 11 lakes sampled June-August, density was highest in June and lowest in August (Table 2.2); however, 3 lakes (Damariscotta, Highland, Upper Mystic) exhibited highest densities in July. On average, it took a crew of 3 people 3 min to set the purse seine, 10 min to retrieve the seine, and depending on the density of fish, 0-55 min for counting and measuring fish from one haul.

2.3.1 Sampling Time of Day

There was a strong effect of sampling time of day on capture efficiency and size structure of age-0 river herring. We sampled a total of 206 age-0 herring during the day and 987 fish at night from 5 purse seine hauls in 4 lakes. No fish were captured during daytime sampling at Potanipo. Pooled length frequency distributions were significantly different among sampling periods (K-S test; $D = 0.284$, $p < 0.001$) and we collected significantly larger fish at night ($36.6 \text{ mm} \pm 0.39$) compared to the day ($30.7 \text{ mm} \pm 0.59$) (Student's T-test; $t_{(1191)} = 3.10$, $p < 0.005$). Fish sampled at night in Upper Mystic and Whitmans were significantly larger than fish sampled during the day. In Pentucket, larger fish were captured during the day (Table 2.3). Our nighttime sampling detected a variety of size classes, and variability in fish length was greater at night for all lakes (Figure 2.8).

I observed 56% higher in sampling precision at night ($CV = 0.30$) compared to day ($CV = 0.68$) across all lakes. Median CPUE values across all lakes for day and night sampling were 2 and 91 respectively, and this difference was significant ($p < 0.001$). Median values are perhaps more representative of total catch than mean values because I observed strong schooling behavior during the day that led to very similar mean CPUE values (day = 206.5; night = 203.7), despite 11 of 20 (55%) day hauls capturing 2 fish or less. Individually, Upper Mystic showed the most difference in CV between day and night, Pentucket had similar precision between day and night, and a comparison was not possible at Potanipo because no fish were captured during the day.

2.3.2 Precision and Resampling Simulation

Average CV of the mean ranged from 0.23 to 0.61, and was lowest in July when CPUE and sampling effort were highest (Table 2.2; Figure 2.5). The highest CV values

were observed in September where densities were lowest and sample size was small (< 5 hauls per lake). In simulations, precision increased rapidly for all 5 lakes with increasing sampling effort, and larger lakes (Winnisquam, Damariscotta) exhibited the greatest variability (Figure 2.6). Curve inflection points were different between large and small waterbodies, and these curves stabilized faster for smaller lakes (Pentucket, Gilbert-Stuart, Mystic). The point at which additional sampling effort resulted in a negligible increase in precision ($\Delta CV \leq 1\%$) corresponded to 10 hauls for lakes ≤ 50 ha, and 17 hauls for lakes greater than 50 ha (Figure 2.7).

2.3.3 Capture Efficiency and Size Selectivity

Capture efficiency varied strongly between sampling gears. River herring were captured most frequently in purse seines, making up 97, 90, 81, and 79% of all fish caught across lakes (mean values) in June, July, August, and September respectively. In contrast, capture efficiency increased over time for gill nets; river herring making up 0, 12, 44, and 77% of the total catch June-September respectively. River herring were poorly represented in beach seine sampling, occurring in low numbers at 4 lakes during July only.

Pooled length frequency distributions were significantly different among gear types (K-S test; $D = 0.981$, $p < 0.001$) (Figure 2.9). The mean, minimum, and maximum total length of fish captured by purse seine among lakes were 35.6, 4.0, and 124.0 mm respectively. Only 1% of all fish were larger than 100 mm, and no adults were caught by purse seining. Gill nets captured river herring averaging 144 mm, with a minimum and maximum length of 93–267 mm respectively, including spawning adults during June (Upper Mystic; $n = 540$). All fish captured by gill nets were entangled in 4-cm mesh

panels. Gill nets produced the smallest range of length-frequency data, with most fish between the size of 130-170 mm regardless of sampling location (Figure 2.9).

2.4 Discussion

A small sized purse seine fished at night is an effective sampling tool for estimating age-0 river herring densities in freshwater lakes. I observed high precision and capture efficiency, and have demonstrated its use for collecting valuable biological information from post-hatch larvae and juveniles up to 100 mm total length. River herring catch rates varied by summer month, diel period, and gear type. Purse seines are easy to operate with 3 people, do not require much maintenance, and produce reliable results. Methods used in this study can be implemented into a standardized sampling protocol across the region to strengthen population assessments and enhance monitoring.

2.4.1 What Sampling Gear to Use

Catch data can produce inaccurate abundance estimates without knowing the capture efficiency of the gear being used (Kjelson and Colby 1977). In this study, we compared the capture efficiency of a purse seine to gill nets and beach seines. Murphy and Clutter (1972) observed a dramatic improvement at night in capture efficiency from a purse seine while sampling anchovy larvae, and our study suggests nighttime sets are necessary to maintain high capture efficiency when targeting river herring. Efficiency was highest in June (97%), and decreased throughout the summer, falling to 79% in September. Special attention should be given to the growth rates and size structure of age-0 river herring during the summer and if additional biological samples are needed once fish exceed 100 mm, gill nets should be employed.

Purse seining was effective for sampling post-hatch larvae from 4 mm to up to 100 mm, whereas gill nets are more effective for capturing larger fish. Mean total length of all fish sampling by purse seine in June was 20.6 mm, while mean length for gill nets was 257 mm. Multi-mesh gill nets are inappropriate for capturing larval fish due to larger mesh sizes, but perform well at catching spawning adults May-July, and thus provide a tool for managers to evaluate their body condition, age, and diet of spawning individuals. The size-selectivity of the purse seine appears similar to results from Charles-Dominique (1989) who documented low catch efficiency for individuals greater than 100 mm. Possible reasons for net avoidance include an increased swimming ability from larger individuals, visual detection of the purse seine mesh, or an onset of schooling behavior that creates patchy distributions that become difficult to sample compared to more evenly distributed populations of larvae. Net avoidance due to an increased swimming ability and visual net detection are most plausible. Larger individuals may be capable of swimming under the opening in the net prior to being pursed, or evade capture by swimming over the float line during retrieval. Evaluating net avoidance and retention rates were beyond the scope of our study, thus future research should incorporate estimates of avoidance and detection probability into abundance models.

Purse seines may be effective at capturing fish, including larger individuals, where there is low visibility. Murphy and Clutter (1972) proposed that fish vision is the most important avoidance cue, and our diel capture efficiency results appear to agree. However, water clarity may play a role in detection as well. Interestingly, high chl-a levels may prevent river herring from detecting, and thus avoiding the purse seine. For example, I observed catches with larger individuals more frequently in eutrophic systems.

Specifically, in Sabattus Pond, length frequencies of herring captured by purse seine were 2–3 times larger than other study lakes, and this coincided with acute levels of chl-a. I also observed severe algal blooms during sampling, and suspect that herring were limited in their ability to see the mesh. Larger individuals were present in several of our study lakes (as shown by gill net length frequencies), and I was not able to capture them in purse seine sampling, though their abundance is not clear. However, sampling for larger individuals may be slightly more effective in hypereutrophic lakes, particularly during an algal bloom.

Purse seines are generally not effective at sampling littoral habitats with aquatic vegetation, large wood, and uneven lake bottom. Beach seines can be used in littoral habitats; however, we only captured juvenile river herring in beach seines at 4 lakes, with river herring making up only about 11% of the total catch. There are several explanations for the low capture efficiency observed from beach seines in this study. Beach seining was not conducted in complete darkness, which may have allowed river herring to avoid capture. However, it is more likely that age-0 river herring were not present in littoral habitats during sampling, as we captured other species of similar size in beach seines and did not observe net avoidance during sampling. I observed schools of river herring in littoral areas near outlet structures prior to emigration, and beach seines may be effective at sampling river herring there, although such targeted sampling would not lead to an accurate estimate of whole lake densities. I suggest using beach seines for collecting presence-absence data, not estimating abundance, as catch efficiencies are generally low and variable (Connolly 1994).

I did not test the efficiency of different sized purse seines. Steele et al. (2007) found a larger purse seine (36.4 m x 3.6 m) produced higher density estimates of another open water species (Topsmelt; *Atherinops affinis*), captured more species, and was more time efficient than a smaller net (18.2 m x 2.4 m). The dimensions of our net were similar to the large net used by (Steele et al. 2007) thus it may be valuable to test even larger purse seines.

I did not directly test other gear types that have been successfully used to capture age-0 clupeids, such as push-nets, tow-nets, or acoustics. For example, Tischler et al. (2000) concluded a push-net system mounted to a 7-m wooden boat is effective for sampling newly hatched pelagic larvae and juveniles up to *ca.* 30 mm. Kriete and Loesch (1980) and Claramunt et al. (2005) both concluded that push nets perform better than trawls, and could efficiently capture larvae over a wide range of sizes. While I recognize other types of gear may be moderately to highly effective at capturing age-0 river herring, gear selection must also consider the cost (e.g., equipment and personnel), feasibility to operate, ability to validate results, and environmental and biological impact. The purse seine used in this study was custom made for our application and costs about USD \$3,000. This seine needs little maintenance and requires no additional accessories. I assume most state and federal fisheries agencies already own or have access to a vessel big enough to set and retrieve the seine with appropriate propulsion, and those costs are not discussed here. Acoustic technology such as dual frequency identification sonar (DIDSON) or side-scanning sonar may cost up to USD \$80,000 per unit. Sampling with acoustics requires more technical training, may be more difficult to operate, requires long

data processing hours, and does not allow collection of biological samples so it must be validated through another method.

Fishing mortality is another important factor when considering gear selection, particularly for a species of concern. Fish collected in pushed or towed gears become susceptible to mortality from clumping and being compressed against the net during operation. Push-nets and tow-nets tend to collect surface debris that can congest the net, possibly sacrificing sensitive larvae unable to sustain the physiological stress of being towed for standardized amounts of time (Isermann et al. 2002; Overton and Rulifson 2007). While barge electrofishing is effective for sampling resilient warm and coldwater gamefish, age-0 river herring struggle to recover from the effects of pulsed direct or alternating current, even when performed correctly, and suffer extreme mortality (personal communication: Ben Gahagan, Massachusetts Division of Marine Fisheries; Ken Sprankle, U.S. Fish and Wildlife Service). In contrast, mortality from the purse seine methods used in our study was extremely low.

Additional limitations of using a purse seine include being susceptible to strong winds (e.g., 10 mph sustained or 15–20 mph gusts), which caused improper sets, restricted boat maneuverability, and caused inconsistencies in the float line remaining on the surface of the water. Further, newly hatched larvae less than 5 mm may be underestimated in the sample. Larvae of this size may simply drift through the seine mesh, or become difficult to see against the backdrop of the net.

2.4.2 When to Sample

Our results indicate densities of age-0 river herring in freshwater lakes generally peak in June or July, then decline as the summer progresses. This pattern is consistent

with river herring life history characteristics, as emigration from freshwater lakes into estuarine environments typically occurs mid-June through October (Bigelow and Schroeder 1953; Richkus 1975). The timing of emigration is dependent on body condition, water levels, and diel period (Walsh 2005; Gahagan et al. 2010), which may explain the large variation in age-0 river herring densities among sites. Our seasonal density estimates conducted at a large geographic scale are similar to regional estimates provided by Rosset (2016), who observed peak densities in June for 16 of 20 coastal Massachusetts lakes. Our study also identified several lakes where densities peaked in July as opposed to June (Damariscotta, Highland, Upper Mystic) (Table 2.2), reflecting the temporal recruitment variability that can occur, and may be attributed to physical or phenological delays. For example, adult spawning migration timing and strength may be altered due to a prolonged winter and cooler stream temperatures, ephemeral blockages to passage (e.g., beaver dams and fallen woody debris), or delays between the arrival of adults to lakes and subsequent spawning events (Marjadi 2017; Rosset et al. 2017). However, these differences between June and July densities were not significant in my study, and suggest sampling in either June or July should produce similar results and effectively estimate maximum densities prior to emigration.

Time of day is also an important consideration for sampling age-0 river herring. Purse seine catch rates were higher at night in all 4 lakes sampled during day and night, suggesting strong diel effects on sampling efficiency, and thus estimates of density. Consistent with other studies, I found increased detection of juvenile fishes occurred after nightfall in both lentic and lotic habitats, regardless of sampling gear. For example, Kratochvil et al. (2014) documented higher abundances of juvenile perch, roach, and

dace at night vs day in a reservoir using electrofishing. Similarly, Cada et al. (1980) observed greater nocturnal densities of threadfin shad in a Tennessee reservoir, independent of habitat. For clupeid-like ichthyoplankton and juvenile fishes, vertical migration in the water column at night make sampling at night (vs. day) more effective (Loesch et al. 1982; Gallagher and Connor 1983; Batty and Blaxter 1986; Dixon 1996; Overton and Rulifson 2007). These published studies were conducted at small spatial scales involving a selected reach of river or singular waterbody. In contrast, my study provides evidence from lakes in the Northeast varying in size, trophic conditions, species compositions, and river herring densities. Diel migratory behavior from age-0 river herring must be accounted for in future sampling designs.

2.4.3 How Much to Sample

Oversampling leads to increased labor costs that are unnecessary and undersampling may produce density estimates that are inaccurate, imprecise, or both. As such, researchers conducting fishery-independent surveys constantly strive to achieve an optimal level of sampling effort, reaching target levels of precision at the lowest cost. Increasing the precision of age-0 fish density estimates can be achieved by either increasing the sample volume, thus changing the average number of individuals captured per sample, or increasing the number of samples collected (Cyr et al. 1992). My study chose the latter, and I showed through both empirical data and a resampling simulation; that sample size (i.e., number of hauls) greatly affected density estimates. For data derived from field collection, precision was highest in July among lakes, which coincided with greater sampling effort. In contrast to what might be expected, the density of age-0 river herring did not appear to influence sampling precision, as I observed high precision

in lakes with both high and low fish densities in each month. This is consistent with the findings of Kell (1991) and Smith (2006), who concluded that precision is likely to vary based on gear type and specifications, target species, and size classes rather than fish densities. This suggests that reduced sampling precision for species occurring in patchy or variable densities, like age-0 river herring, can be overcome by increasing sample size or modifying gear selection.

Using data from 5 lakes sampled intensively in July 2015, my simulation results suggest that lake size should be used to determine the effort required to produce precise density estimates. Two large lakes in this study (Damariscotta and Winnisquam) displayed greater variability in CPUE estimates across all levels of effort than smaller impoundments. Damariscotta and Winnisquam have similar surface areas (1773 and 1704 hectares respectively), and considerably different densities, which supports the conclusion that lake size, rather than fish density, determines sampling effort. Specifically, I expect small lakes (<50 ha) to require up to 10 hauls, while larger lakes will require between 15-20 purse seine hauls to achieve precise density estimates. The resampling simulation used in this study aimed to achieve a 1% change in the coefficient of variation, though I emphasize this target is arbitrary in nature and highly conservative. Given my estimates of the time required to properly set, retrieve, and process samples, I expect smaller lakes to require about 7.5 hours (1-2 nights) of effort, and larger lakes to require about 15 hours (2-3 nights) of effort.

The classification of large and small lakes characterized in this study remains coarse, and I recognize the gradient of lake sizes and habitat complexity are more wide-ranging than presented here. For lakes larger than 50 hectares, total effort may be

determined by adding one seine haul per additional 10 hectares. However, investigators should combine my results with their a priori knowledge of local waterbodies and habitat complexity to determine optimal sampling effort required to meet objectives.

2.4.4 Conclusion

Standardized sampling methods for North American inland fishes have been developed by the American Fisheries Society by waterbody type (e.g., large standing water, small standing water, large river, wadable stream) and for both warmwater and coldwater species (Bonar et al. 2009). However, methods to evaluate diadromous fishes present unique challenges, and there is no standard assessment protocol for juvenile river herring. I described a method for assessing age-0 river herring using a pelagic purse seine at night which was evaluated in a variety of lakes that are representative of the range of coastal New England freshwater habitats occupied by anadromous river herring. Widespread application of this sampling method can be used to fill gaps in our knowledge about the species and provide insights into strategies and tools that may be valuable when researching other diadromous fishes.

Fisheries data collected in a standardized fashion is particularly essential to the integrity of long-term datasets. Given that more research is needed to assess recruitment dynamics and the extent to which interannual variability in production exists, it is important that standardized sampling methods become incorporated prior to large-scale initiatives. Haphazard study of age-0 river herring in freshwater lakes will produce results that lack acceptable levels of certainty and will continue to hinder data comparison for studies conducted at a large spatial scale. My suggested methodologies should help

managers better understand the relationships that exists between adult escapement and juvenile production, and lead to implementation of effective management strategies.

Table 2.1: Mean and range (min, max) of physical and chemical characteristics for 16 study lakes sampled June–August 2015. Water samples were collected at dusk, preceding fish sampling, at the deepest point in each lake. Site numbers correspond with lakes in Figure 1.

Lake	Site #	State	Surface area (ha)	Elevation (m)	Mean depth (m)	Max depth (m)	Surface Temperature (°C)			^a Dissolved Oxygen (mg/L)			Chlorophyll-a (µg/L)			Total Phosphorous (µg/L)			Total Nitrogen (mg/L)			Dissolved Organic Carbon (mg C/L)		
							Mean	Min	Max	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max
Chemo	1	ME	464	38.4	3.5	8.7	25.3	–	–	NA	–	–	4.0	–	–	19.3	–	–	0.26	–	–	4.53	–	–
Damariscotta	2	ME	1773	16.4	7.5	34.7	23.3	19.8	25.7	5.68	5.57	5.90	13.8	9.0	17.3	20.2	4.0	43.0	0.22	0.19	0.25	3.62	3.51	3.73
Gilbert Stuart	3	RI	28	2.7	3.7	4.5	24.3	19.8	28.7	5.79	4.87	7.47	19.6	7.5	25.7	24.5	13.9	32.6	0.47	0.41	0.52	4.45	3.52	6.29
Glen Charlie	4	MA	75	10.6	2.5	5.3	23.4	19.1	27.3	1.32	1.01	1.86	13.9	11.7	16.7	23.1	14.3	40.6	0.27	0.19	0.40	2.65	1.49	4.92
Highland	5	ME	259	57.9	6.4	19.8	24.2	21.3	26.6	5.36	4.75	6.09	9.1	5.1	15.3	12.4	1.3	19.4	0.26	0.22	0.33	3.52	3.14	3.99
Guilford	6	CT	52	11.8	3.0	6.5	23.1	19.2	28.0	4.62	3.40	6.60	24.7	12.1	34.3	16.8	11.5	19.5	0.39	0.33	0.50	5.74	5.59	6.03
Mianus	7	CT	44	4.2	1.8	4.2	25.4	25.4	25.4	NA	–	–	55.0	–	–	12.6	–	–	0.31	–	–	4.01	–	–
Pentucket	8	MA	33	7.3	5.1	8.4	24.9	23.8	26.5	5.64	4.95	6.85	13.4	4.9	28.1	35.0	21.3	47.4	0.47	0.42	0.52	5.02	4.65	5.51
Potanipo	9	NH	55	80.5	4.0	8.2	25.4	24.6	26.9	1.25	1.09	1.37	9.7	6.8	14.1	9.2	1.0	16.0	0.24	0.22	0.25	4.93	4.41	5.28
Pushaw	10	ME	1894	35.3	3.4	8.1	25.8	25.8	25.8	NA	–	–	16.9	–	–	15.0	–	–	0.31	–	–	4.41	–	–
Sabattus	11	ME	794	74.2	4.3	6.3	24.4	20.9	26.9	7.50	6.69	8.50	63.8	24.0	90.6	39.2	23.1	69.5	0.47	0.35	0.64	3.68	3.55	3.81
Snipatuit	12	MA	258	16.1	1.5	1.8	23.9	23.9	23.9	1.09	1.09	1.09	10.5	10.5	10.5	28.2	–	–	0.37	–	–	5.89	–	–
Togus	13	ME	262	55.1	6.0	14.9	25.2	25.2	25.2	NA	–	–	160.8	–	–	6.5	6.5	6.5	0.79	0.79	0.79	3.25	3.25	3.25
Upper Mystic	14	MA	64	0.9	15.0	28.9	22.9	18.0	25.3	0.34	0.23	0.51	38.5	20.1	72.8	19.7	0.6	35.2	1.14	0.68	1.64	3.77	3.65	3.96
Whitmans	15	MA	64	6.2	4.0	7.9	24.6	20.7	26.6	5.13	4.83	5.38	16.4	2.3	38.5	27.5	23.6	32.5	0.53	0.38	0.74	6.52	5.67	8.05
Winnisquam	16	NH	1704	146.9	15.2	53.1	23.5	21.0	25.6	5.53	4.80	6.10	3.0	1.6	3.8	19.1	3.7	34.4	0.82	0.30	1.86	2.48	2.22	2.80

^a Values are averages from a vertical profile; measurements taken at 0.5 m below surface, middle, and 0.5 m above bottom

– Lake only sampled once

NA Measurements not taken due to YSI calibration

Table 2.2: Adult run counts and juvenile river herring sampling statistics from purse seines. Catch-per-unit-effort (CPUE) was calculated as the number of individuals per haul. Density was calculated as the number per volume of water. CV = coefficient of variation. Site numbers correspond with lakes in Figure 1.

Lake	Site #	River/stream	Distance to ocean (km)	Adult run	Counter method	# Hauls	June					July					
							Total herring	Median CPUE	CV	Mean juvenile density (no. m ⁻³)	Mean total length (mm)	# Hauls	Total herring	Median CPUE	CV	Mean juvenile density (no. m ⁻³)	Mean total length (mm)
Chemo	1	Blackman	56.1	309,128	Electronic	–	–	–	–	–	–	–	–	–	–	–	–
Damariscotta	2	Damariscotta	41.2	689,669	Visual	13	1135	66	0.25	0.18	20.3	11	2084	93	0.37	0.40	28.6
Gilbert Stuart	3	Pettaquamscutt	12.5	11,135	Visual	10	7935	938	0.18	2.10	22.1	10	1478	119	0.17	0.39	28.0
Glen Charlie	4	Agawam	11.8	24,398	Electronic	3	1157	421	0.26	1.08	21.7	9	1693	194	0.17	0.45	24.9
Highland	5	Mill	21.5	8,686	Electronic	4	371	77	0.44	0.19	15.7	10	1995	205	0.16	0.44	27.6
Guilford	6	East	11.3	2,414	Electronic	3	138	49	0.20	0.11	18.9	9	290	39	0.18	0.09	26.9
Mianus	7	Mianus	4.5	18,642	Electronic	–	–	–	–	–	–	3	585	178	0.20	0.66	33.0
Pentucket	8	Parker	13.4	410	Stocking	7	335	33	0.32	0.10	21.8	10	125	11	0.20	0.03	25.0
Potanipo	9	Nissitissit	124.4	503	Stocking	5	226	36	0.18	0.10	24.7	10	267	25	0.18	0.06	49.7
Pushaw	10	Pushaw	72.1	30,304	Stocking	–	–	–	–	–	–	–	–	–	–	–	–
Sabattus	11	Sabattus	101.9	12,748	Stocking	3	193	9	0.87	0.17	25.1	8	238	18	0.40	0.07	89.1
Snipatuit	12	Mattapoissett	15.5	42,332	Electronic	–	–	–	–	–	–	5	26	3	0.40	0.04	33.1
Togus	13	Togus	71.3	30,304	Stocking	–	–	–	–	–	–	–	–	–	–	–	–
Upper Mystic	14	Mystic	17.5	477,827	Visual	12	974	66	0.23	0.17	20.7	15	6685	414	0.14	0.95	27.0
Whitmans	15	Herring run	7.8	339,554	Electronic	3	1349	542	0.23	0.93	18.7	10	892	90	0.17	0.22	28.1
Winnisquam	16	Merrimack	199.7	24,625	Stocking	12	1363	46	0.35	0.23	17.5	15	1191	18	0.30	0.19	37.8

– Lake not sampled

Site #	# Hauls	Total herring	Median CPUE	CV	Mean juvenile density (no. m-3)	Mean total length (mm)	# Hauls	Total herring	Median CPUE	CV	Mean juvenile density (no. m-3)	Mean total length (mm)
August							September					
1	5	205	42	0.28	0.12	41.2	–	–	–	–	–	–
2	15	362	25	0.23	0.06	36.9	5	36	5.0	0.53	0.01	69.8
3	10	504	27	0.36	0.13	55.7	–	–	–	–	–	–
4	4	329	97	0.34	0.23	45.1	–	–	–	–	–	–
5	5	864	152	0.29	0.36	35.6	5	545	21.0	0.83	0.26	49.1
6	4	10	2	0.50	0.01	28.7	–	–	–	–	–	–
7	–	–	–	–	–	–	–	–	–	–	–	–
8	10	6	0	0.57	0.00	120.1	3	0	0.0	–	0.00	NA
9	6	20	2	0.43	0.01	84.4	5	10	2.0	0.55	0.01	104.1
10	2	53	27	0.36	0.07	58.0	–	–	–	–	–	–
11	5	112	14	0.46	0.05	107.0	–	–	–	–	–	–
12	–	–	–	–	–	–	–	–	–	–	–	–
13	2	162	81	0.75	0.17	48.8	–	–	–	–	–	–
14	18	3996	154	0.22	0.46	48.9	9	346	18.0	0.48	0.08	74.4
15	4	17	3	0.17	0.01	58.5	–	–	–	–	–	–
16	16	970	32	0.37	0.12	42.4	5	122	15.0	0.43	0.08	62.0

– Lake not sampled

Table 2.3: Diel sampling statistics for river herring captured using a purse seine at four lakes in July 2016 and two-sample t-test results comparing day vs night mean lengths are presented far right. TL = total length, n is the number of fish measured to estimate mean total length, CPUE = catch-per-unit-effort, CV = coefficient of variation.

	Day				Night				t	df	p
	Mean TL (mm)	n	Median CPUE	CV %	Mean TL (mm)	n	Median CPUE	CV %			
Pentucket	25	78	16	36	22	221	23	37	3.101	105	<0.001
Potanipo	-	-	-	-	41	147	90	26	-	-	-
Upper Mystic	44	32	0	99	46	236	600	37	-2.299	54	<0.04
Whitmans	31	98	21	71	32	251	44	22	-2.287	153	<0.05

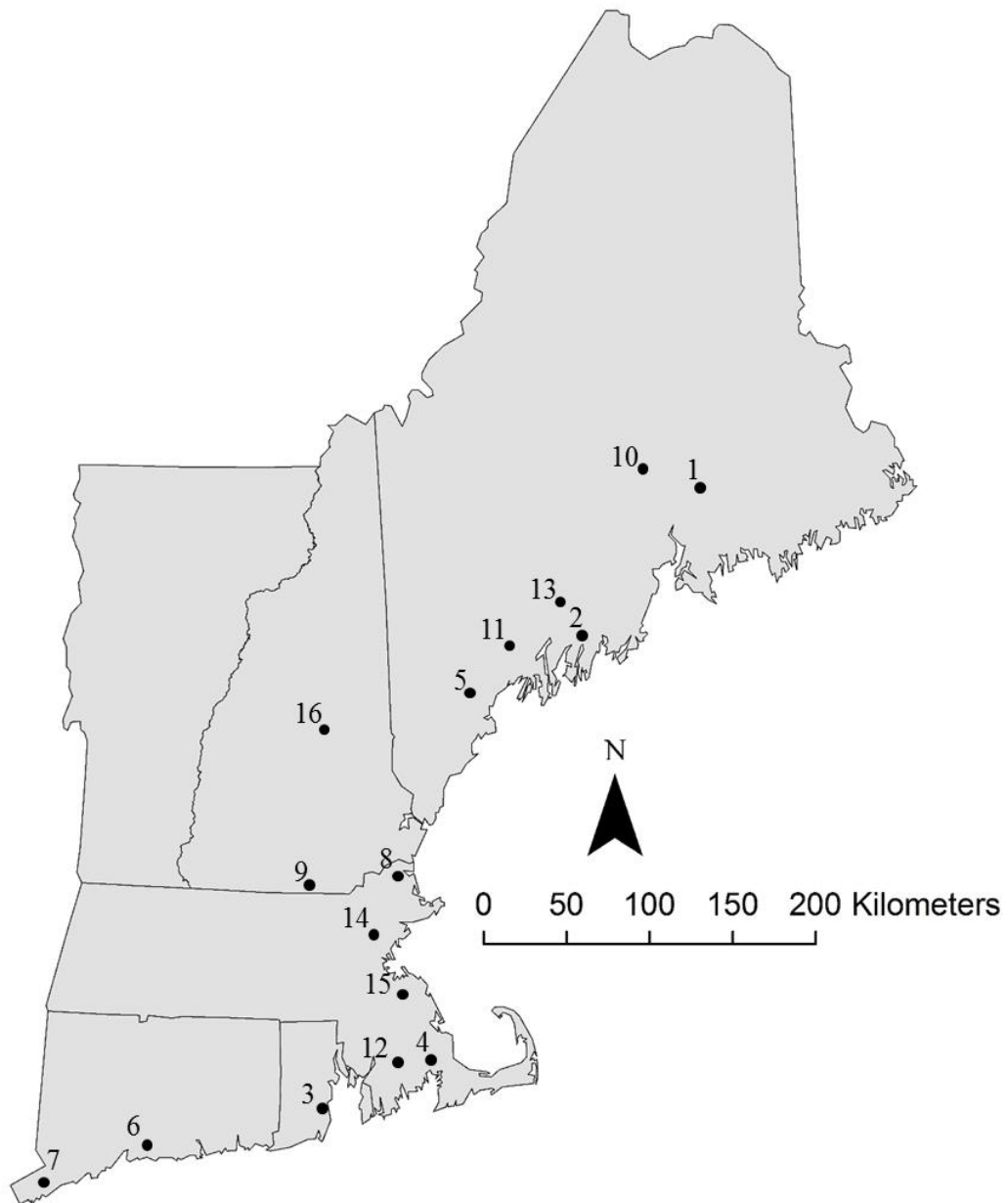


Figure 2.1: Map of 16 coastal New England lakes used in this study. Numbers correspond with lakes in Table 1.

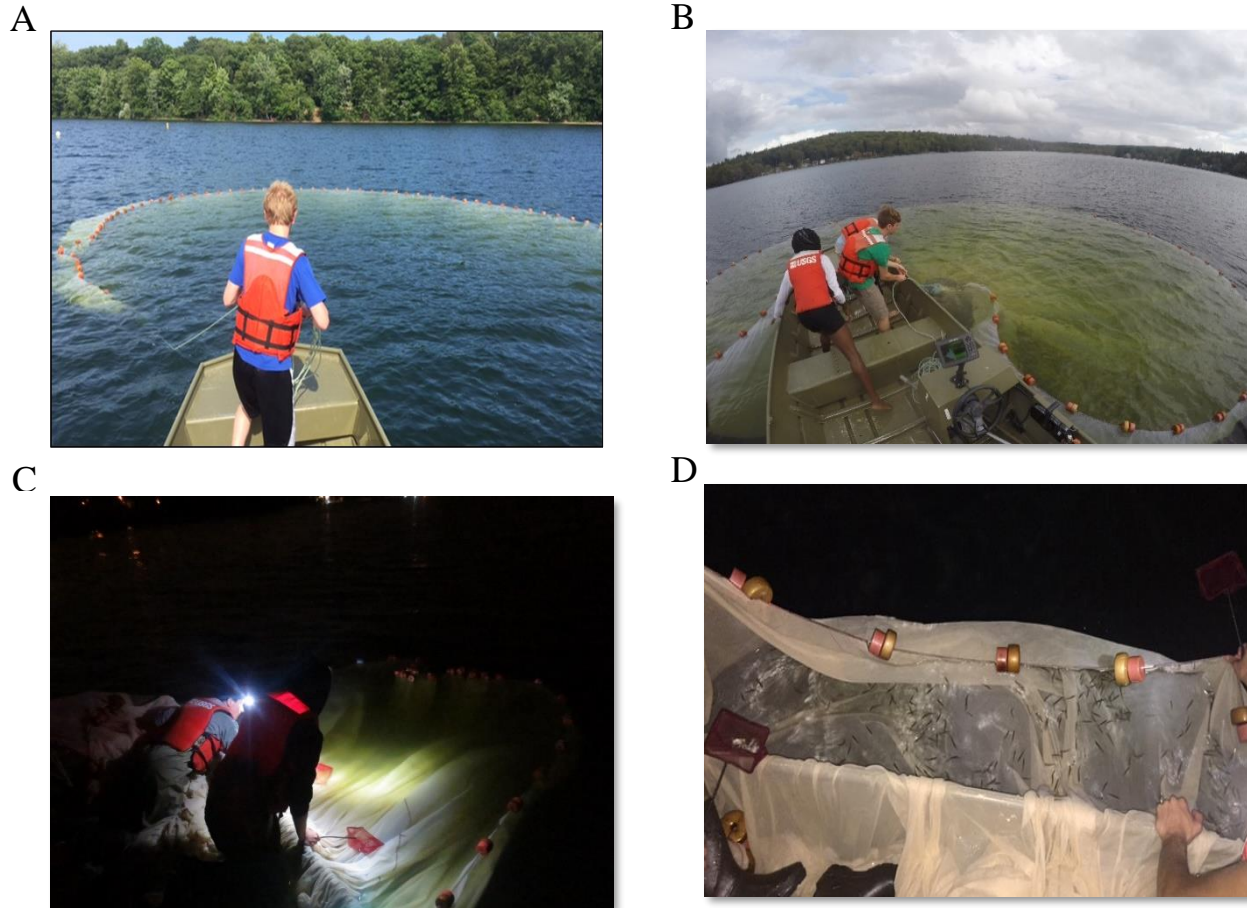


Figure 2.2: Methods for purse seine sampling. A) Proper set with full circle; B) Retrieving net on starboard side of boat; C) Forming net pocket while looking for fish; D) River herring in final net pocket.

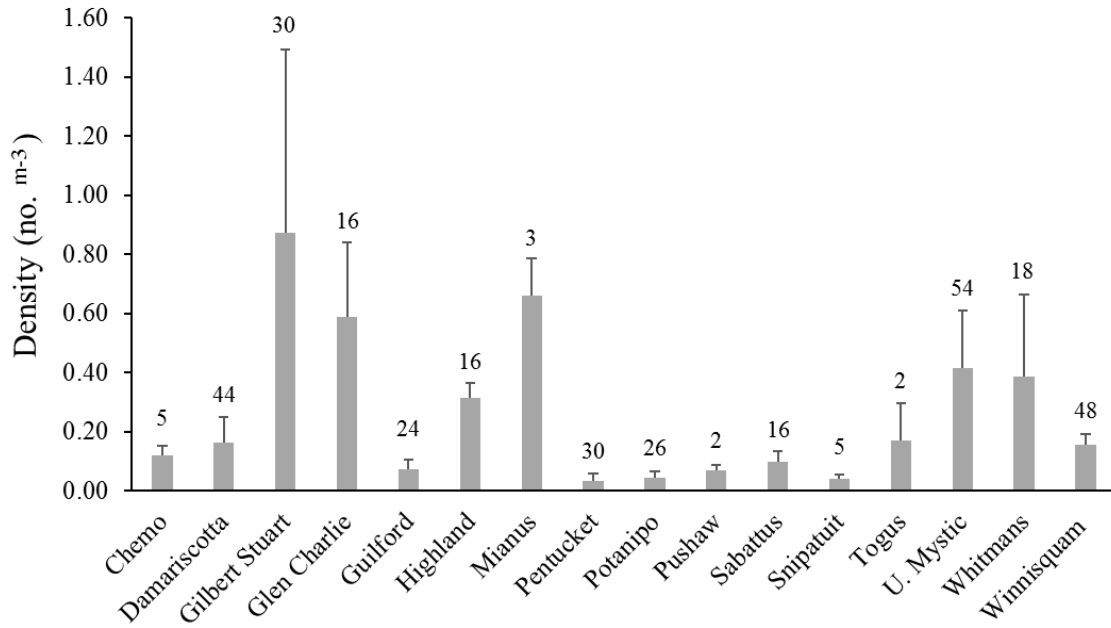


Figure 2.3: Average density (+ SE) of juvenile river herring from purse seines across sampling months in each study lake. Number of samples averaged to estimate density are shown above error bars.

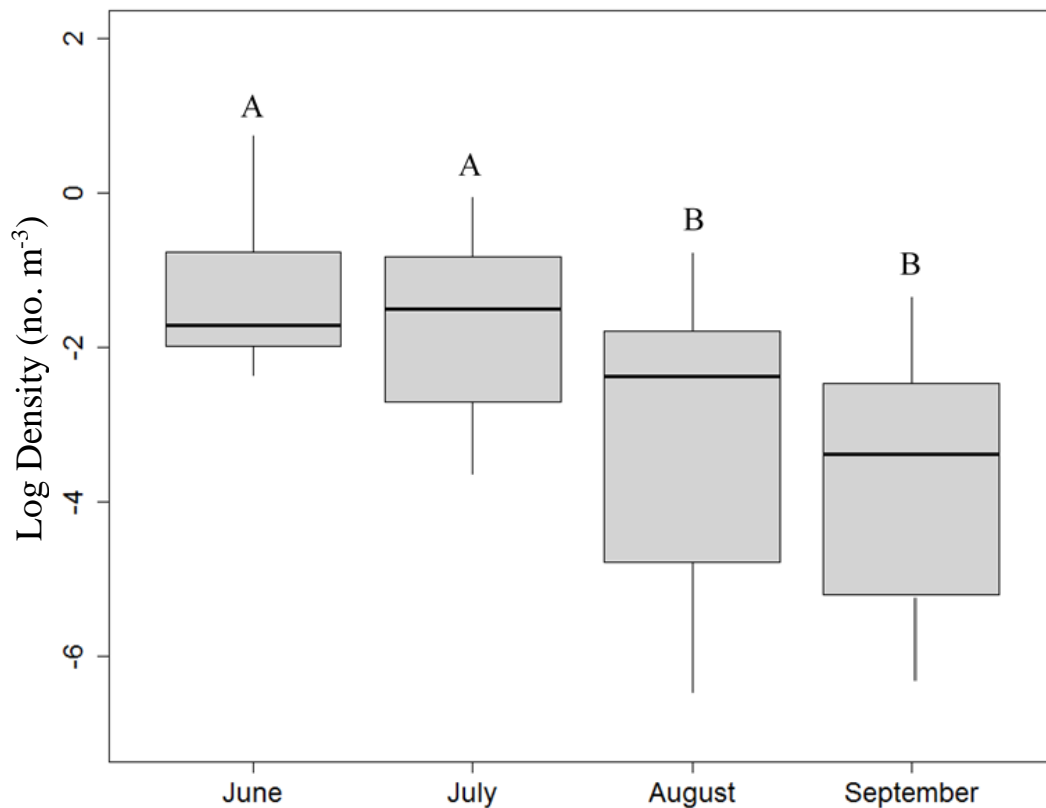


Figure 2.4: Mean density (log-transformed) of river herring by month for 16 lakes sampled June–September 2015. Months not connected by same letter are significantly different (one-way ANOVA; $p < 0.05$). Box plots show the median (center dark line), the lower and upper bounds for 50% confidence intervals, and the maximum/minimum value (whiskers).

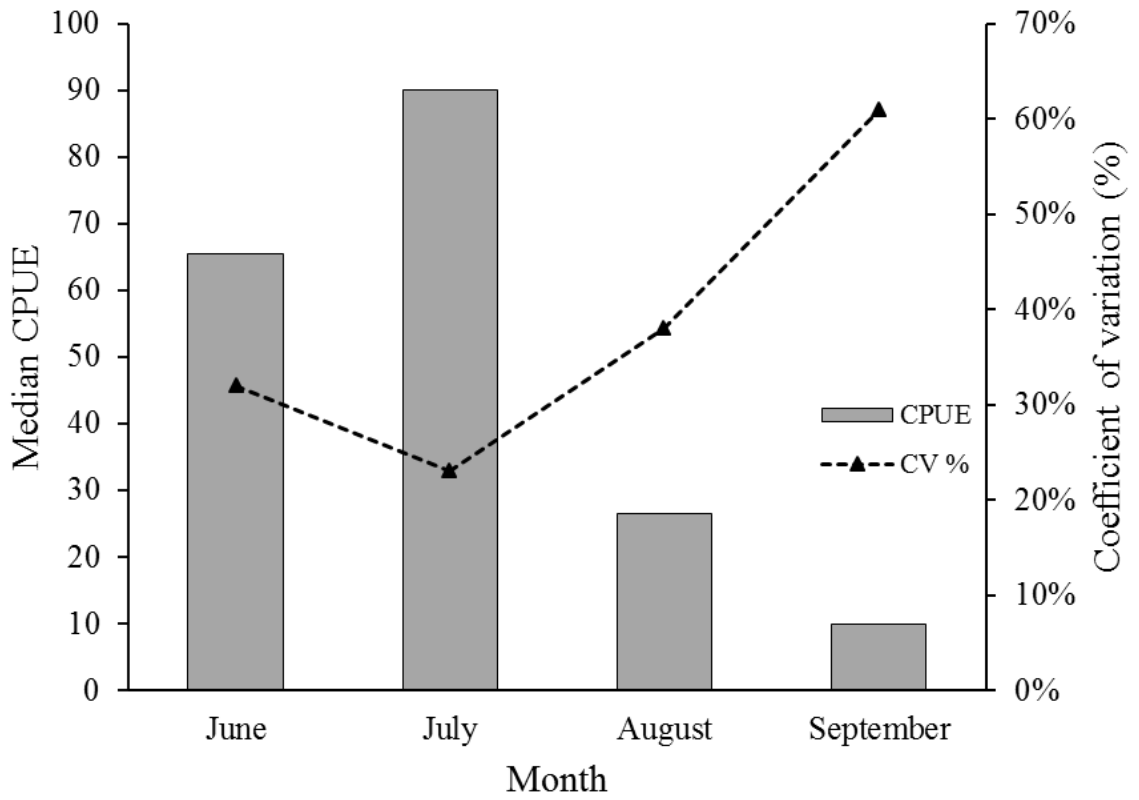


Figure 2.5: Median catch-per-unit-effort (CPUE) and coefficient of variation percent (CV) among 16 lakes sampled for age-0 river herring June–September 2015.

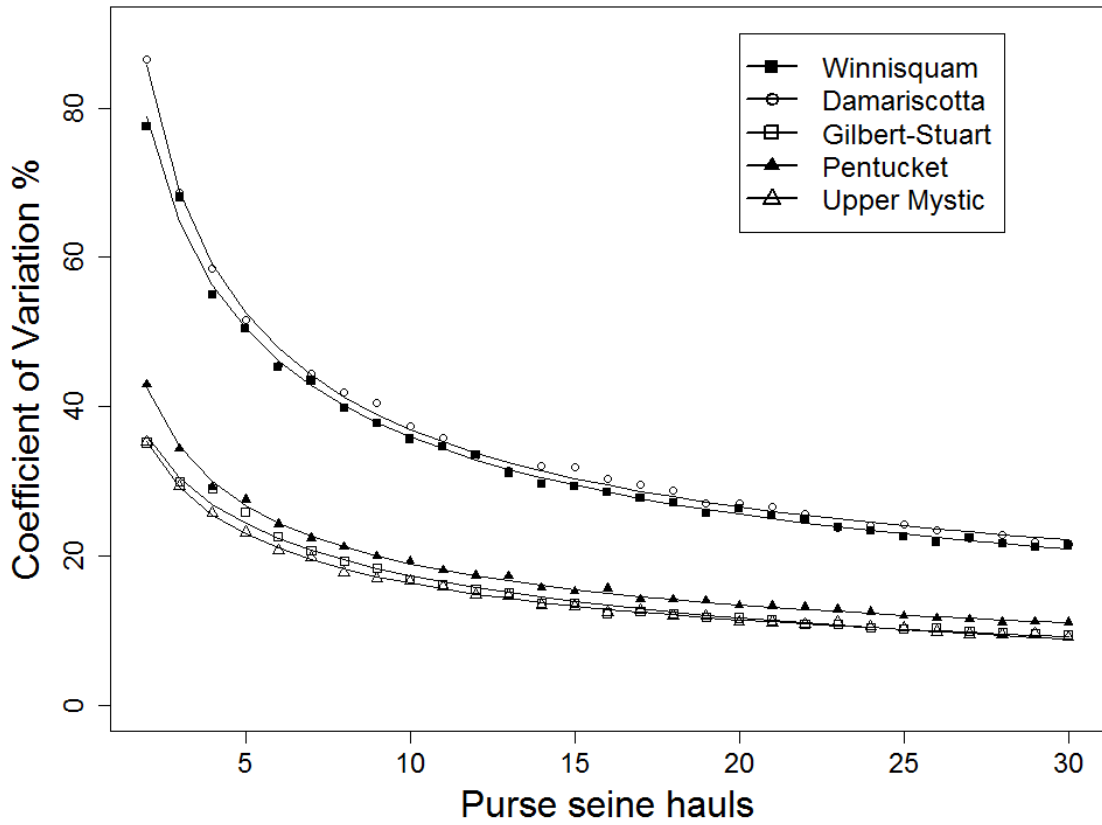


Figure 2.6: Bootstrapped coefficient of variation (CV) values from a resampling analysis of 1000 iterations, plotted against a range of sampling efforts for five New England lakes sampled for juvenile river herring in July 2015.

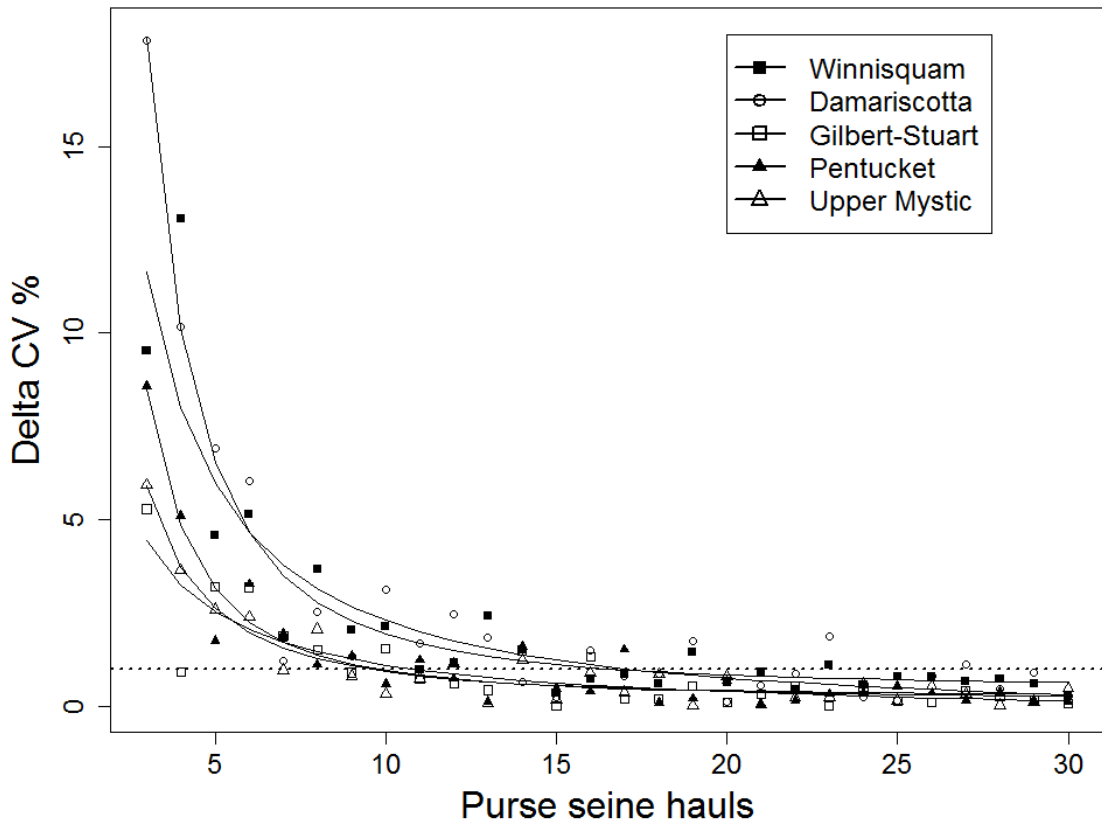


Figure 2.7: The change in coefficient of variation (CV) values with an increase in sampling effort, derived from a bootstrap resampling analysis, using 1000 iterations. Dotted horizontal line depicts a change in cv of 1%, and was used as my target precision.

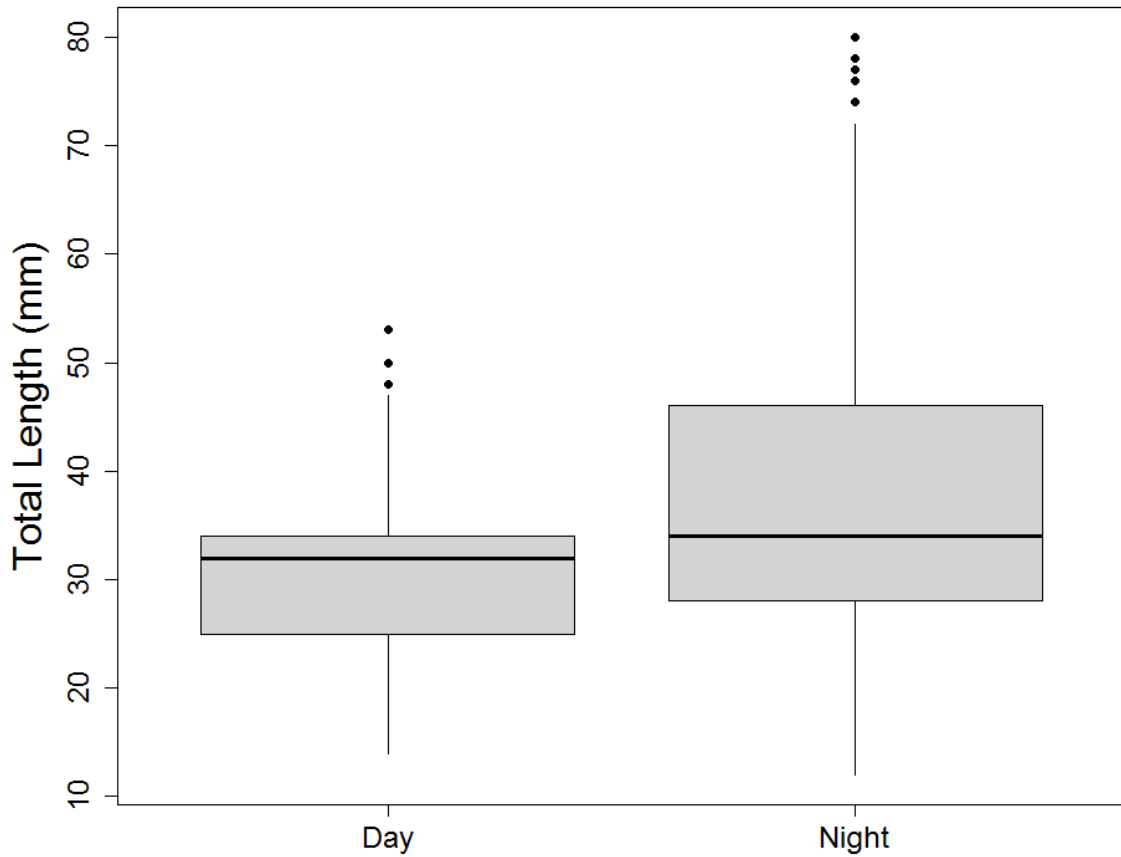


Figure 2.8: Total lengths (mm) of age-0 river herring sampled by purse seine during day and night sampling at four lakes (Pentucket, Potanipo, Whitmans, Upper Mystic). Box plots show the median (center dark line), the lower and upper bounds for 50% confidence intervals, and the maximum/minimum value (whiskers). and outliers (black circles).

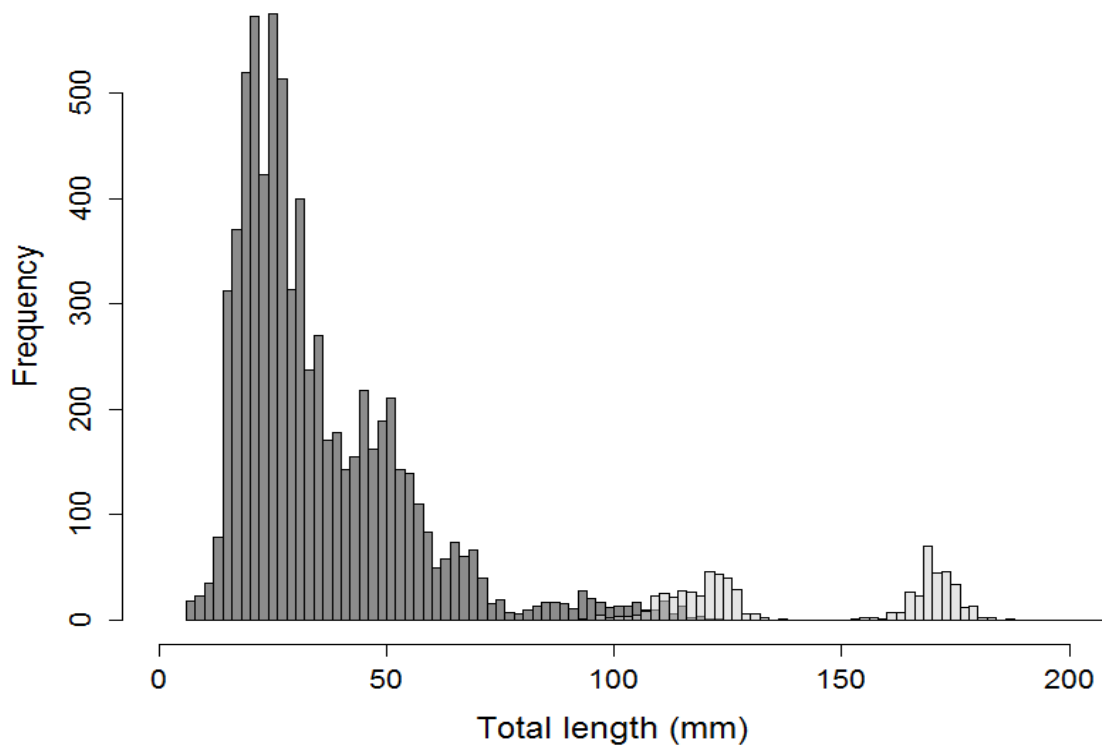


Figure 9. Length frequency histogram for all river herring sampled by purse seine (dark grey) and gill nets (light grey) at 16 New England lakes June–October 2015.

CHAPTER 3

GROWTH AND MORTALITY OF JUVENILE RIVER HERRING IN FRESHWATER LAKES

3.1 Introduction

Growth and mortality for various life-stages are fundamental for fisheries management as they can be used to determine productivity, predict recruitment potential, and inform future patterns in adult abundance (Rothschild 1986; Leggett and DeBlois 1994). For larval and juvenile fishes, there is high variability in mortality (Dahlberg 1979; McGurk 1986) and growth rates (Houde 1987; Pepin and Myers 1991). These two processes typically interact and contribute to recruitment of biomass from early life stages (Cushing 1975). For example, an accepted recruitment theory in fisheries is the “growth-mortality” hypothesis proposed by Ware (1975) and Shepherd and Cushing (1980) which suggests that survival of early-stage fishes is a direct function of growth such that as growth increases the probability of mortality decreases. Thus, conditions that determine growth will ultimately determine survival.

Anadromous river herring [collectively alewife (*Alosa pseudoharengus*) and blueback herring (*A. aestivalis*)] play an important role in both marine and freshwater food web dynamics (Dalton et al. 2009; Demi et al. 2012, Mattocks 2016) and provide a multitude of ecosystem (Belding and Corwin 1921; Fay et al. 1983; West et al. 2010) and socioeconomic services (Bigelow and Schroeder 1953; Mullen et al. 1986). Populations have undergone a dramatic decline over the past five decades (Limburg and Waldman 2009; ASMFC 2012; NFWF 2012) prompting a species of concern designation at both federal and state levels, a closure on commercial and recreational fisheries for both species, a moratorium on directed harvest, and caps on bycatch. Several data gaps were

identified during the Endangered Species Act (ESA) and Benchmark stock assessment processes including a better analysis of freshwater production (ASMFC 2012).

The life history of anadromous river herring poses monitoring and assessment challenges and currently, river herring are managed as a single species. River herring use a wide range of freshwater and marine habitats to complete their life cycle; adults migrating from offshore habitats into freshwater environments to spawn each spring (Bigelow and Schroeder 1953; Loesch 1987). Further complicating assessments is the spatiotemporal overlap that exists between the two species. Their ranges are sympatric from Canada to Georgia (Hildebrand 1963) and peak migration and spawning events may only differ by 2–3 weeks (Hildebrand and Schroeder 1927). Blueback herring typically spawn in coastal rivers and streams, while alewives prefer headwater lake and pond habitats (Pardue 1983; Loesch 1987). Each species has been observed in both habitats, and hybridization does occur, though hybrids are relatively rare (McBride 2013; Hasselman et al. 2014; Marjadi 2016).

Population productivity estimates for river herring are dependent on monitoring adult spawning migrations within rivers (Crecco and Gibson 1990; Hasselman et al. 2016), although fisheries surveys at sea, and in large rivers and estuaries do contribute additional understanding (Neves 1981). These estimates provide only a snapshot into the complex life history of the species by not incorporating evaluations of freshwater productivity, and do not fully account for biological and environmental factors mediating production across life stages. Estimates of freshwater growth and mortality for juvenile anadromous river herring in freshwater and marine ecosystems are sparse. Although several previous studies have estimated juvenile river herring growth and mortality rates

in freshwater (Essig and Cole 1986; Walsh 2005; Höök et al. 2007; Overton 2012; Simonin et al. 2016), these studies were conducted over short time-scales, in single systems, or on landlocked populations in the Great Lakes, making range-wide inferences about demographic rates and the interannual variability that exists nearly impossible.

Juvenile fish growth rates are often highly influenced by juvenile densities (Rothschild 1986). High stocking or recruitment rates of juvenile fish can suppress growth rates through intraspecific competition for resources, particularly habitat and food (Myers and Cadigan 1993). Larger-bodied individuals are more successful at predator avoidance (Cowan et al. 1996) and more easily attain favorable prey items (Dower et al. 2009), thus increasing their probability of survival. Density-dependent growth has been observed for juvenile-stage species occupying lentic environments such as rainbow trout (*Oncorhynchus mykiss*) (Post et al. 1999), bluegill (*Lepomis macrochirus*) (Mittelbach and Osenberg 1993), and yellow perch (*Perca flavescens*) (Irwin et al. 2009), and for anadromous species like Atlantic salmon (*Salmo salar*) (Jonsson et al. 1998) and American shad (*Alosa sapidissima*) (Crecco et al. 1986). Although density-dependent growth for river herring has been suggested in mesocosm experiments (West et al. 2010), this hypothesis has not been formally tested in wild fish across a gradient of lakes, and it is unclear how this relationship may change with fish size and early life-stage.

Temperature fundamentally shapes the growth and survival of fish (Houde 1989; Blaxter 1992; Houde and Zastrow 1993). Water temperature may affect the success and timing of biological processes such as spawning, egg incubation (Pepin 1991), and hatching. Moreover, changes in temperature over a fine temporal scale (daily) may influence fish demographics equally or have cumulative effects similar to those measured

on coarse time-steps (seasonal or annual). Studies evaluating juvenile river herring growth have used equations that assume constant growth over time (Walsh et al. 2005; Höök et al. 2007; Simonin et al. 2016), which make interactions with environmental variables experienced by organisms at sub-daily scale -- like temperature -- difficult to detect if growth does not remain constant. Daily fluctuations in water temperature during the growing season will influence the daily growth of juvenile river herring and have consequences for survival, yet these relationships have not been examined in the wild. Allometric relationships between otolith increment width and fish growth have been shown for other species (Neilson and Geen 1982; Volk et al. 1984), and may exist for river herring. Otoliths provide a means to reconstruct growth histories in fish, and since the first discovery of daily ring deposition in teleost fish (Pannella 1971, 1974), researchers have used otoliths to estimate daily growth rates in several species (Campana and Neilson 1985). Because daily ring deposition occurs in river herring (Essig and Cole; Höök et al. 2007), it is possible to determine if and how growth varies with during the first few months of life.

In this study, I examine how abiotic and biotic factors influence productivity at both monthly and daily scales at 16 coastal New England lakes. I provide region-wide estimates of juvenile river herring density, growth, and mortality rates and evaluate the effects of density, nutrients, temperature, zooplankton biomass, fish size, and hatch date on these estimates. Additionally, I examine patterns in daily growth among lakes in relation to temperature. Linking biological and environmental factors to vital rates such as growth and mortality can substantially enhance population assessments (Rochet and Rice 2009), thus improving river herring management.

3.2 Methods

3.2.1 Study Design

Sixteen freshwater lakes spanning from Greenwich, Connecticut to Old Town, Maine were sampled in this study. These sites represented a wide range of physical and chemical characteristics (Table 3.1; Figure 3.1). Study waters were 28–1773 ha, had mean depths of 2.5–15.2 m, were 0.9–146.9 m above sea level, and had summer surface temperatures of 18.1–28.7 °C. River herring entered lakes naturally using fish passage structures with established monitoring stations or were introduced in known numbers via stocking. River distance, measured from lake outlet to ocean, ranged from 4.5–199.7 km, and preference was given to lakes that were the only lake upstream of an adult run count. Priority was given to systems where study would strengthen ongoing research efforts by management agencies. All lakes were sampled for fishes and water quality approximately monthly one to four times between 02 June and 21 September 2015. Four lakes (Potanipo, Pentucket, Upper Mystic, Whitmans) were additionally sampled twice in 2016 (between 14 June and 20 July). In both years, sampling began at the southernmost site and continued north through Rhode Island, Massachusetts, New Hampshire, and Maine respectively. This progression was repeated each month as part of my longitudinal study design, and ensured equal intervals of time (one month) between sampling events at each lake.

3.2.2 Fish Sampling

Each night, 3–5 samples were taken using a 30.5 x 4.3 m purse seine with 2 mm mesh at randomly selected locations (50 x 50 m grids) within each lake. The purse seine was set in a circle by a crew of 3 people using an electric motor, and immediately

retrieved. When correctly set, the purse seine sampled 485 m³ of water. Hauls that were not correctly set due to strong wind gusts, net snags, or operator error were retrieved, discounted, and repeated at a new location. To reduce bias associated with diel variations in the vertical distribution of juveniles (Meador et al. 1984; also see Chapter 2), sampling began after sunset (2000–0200).

After each haul, all river herring were enumerated using dip nets and a subset (n = 30) were euthanized using Tricaine methanesulfonate (MS-222), measured to the nearest millimeter, and preserved in 95% ethanol for aging. All remaining river herring were returned immediately to open water. Sampling coordinates, time of day, processing time, sample depth, wind speed, and substrate (when observed from net encountering lake bottom) were recorded for each haul.

3.2.3 Water Quality and Zooplankton

Water quality was sampled during dusk, preceding fish sampling, at the deepest point in each lake. Water temperature (°C), conductivity (mS/cm), pH, and dissolved oxygen (mg/L) were measured using a multi-parameter YSI-650MDS (YSI Inc, Yellow Springs, OH) at depths of 0.5 m off the bottom, 0.5 m below the surface, and the middle of each lake's water column. The average of two secchi depth measurements was used to characterize turbidity. Surface water samples for total nitrogen (TN) and total phosphorous (TP) were collected just below the lake surface in an acid-washed 60 mL bottle. Additionally, dissolved organic carbon (DOC) and chlorophyll-a (chl-a) samples were collected by filtering surface water through a 42- mm Whatman® glass fiber filter. All samples were placed on ice and frozen completely within 10 hours. Zooplankton was sampled vertically in the water column in conjunction with water quality sampling. A

weighted plankton net (80 μ m mesh; 0.30-m diameter) was lowered to just above the lake bottom and slowly retrieved. The sample was poured into a 125-mL plastic bottle and preserved in 5% formalin.

I deployed three temperature loggers (Onset HOBO® Water Temp Pro V2) at 4 lakes (Pentucket, Potanipo, Upper Mystic, Whitmans) in 2016. Loggers were contained in custom white Polyvinyl chloride (PVC) flow-through housing units and programmed to record temperature in 15-min intervals. Prior to deployment, loggers underwent an ice bath calibration following Dunham et al. (2005). Two loggers were deployed along a line at the deepest part of each lake using a surface buoy (float) and a cinderblock (weight). The first logger was placed approximately 1 m below the surface, and the second was placed approximately 1 m above the bottom. The third logger was installed near each lake's outlet structure, secured to a rebar stake and anchored into the sediment. MDMF had loggers already installed in fishways at Pentucket and Upper Mystic lakes as part of ongoing temperature monitoring, thus outlet loggers were added in Potanipo and Whitmans. All loggers were installed between 24 April and 30 April, and removed no later than 3 December. I maintained and downloaded data once per month May–November.

3.2.4 Otolith Processing

Sagittal otoliths from juvenile river herring and daily increments were used to estimate age (in days), hatch date, growth, and mortality. A minimum of 50 fish per lake per month were selected using a two-stage sampling approach. For each month, I selected five 50-mL vials (each vial representing a different purse seine haul) and randomly chose 10 fish from each vial. This ensured that demographic data would be derived from

juveniles sampled throughout each lake, rather than a cluster of fish sampled from the same haul. In lakes where less than 50 fish were captured, all fish were aged. Prior to otolith extraction, each fish was measured to the nearest millimeter.

Left and right sagittal otoliths from each fish were extracted under a dissecting microscope with jeweler forceps, dried for 24 hours, and mounted on a glass slide using Crystalbond 509® adhesive. A drop of mineral oil was placed on otoliths to improve resolution of daily increments, and otoliths from older juveniles were lightly polished with 1500–2000 grit wet-dry sandpaper (Brothers 1987). Otoliths were imaged using a Lumenera® camera mounted to a Micro Optical Solutions® compound microscope and catalogued using Image Pro® Insight Version 09 (MediaCybernetics, Rockville, MD, USA). All images were captured under reflected light at 20 x 1.5-micron magnification.

Age of individuals was determined by counting microincrements along the major posterior axis of the sagittal plane, opposite the rostrum (Pannella 1980). Two readers first independently examined both otoliths from 50 randomly selected fish collected in June (10 fish each from 5 different lakes), and fish age was calculated as the mean of both estimates. Linear regression analysis showed strong correlation between age estimates from left and right otoliths ($\text{left otolith} = 1.8029 + 0.9457 \times \text{right otolith}$; $R^2 = 0.955$; $P < 0.001$) (Appendix B), so thereafter only one otolith was examined per fish. All fish collected in June were double-aged, and a subsample ($n = 15\text{-}30$ per lake) were double-aged for fish collected in subsequent months. To reduce reader bias and encourage precision in age determination, an Average Percent Error index (APE) was calculated following equations developed by Chang (1982). Otolith ages with more than 10% disagreement were excluded from analysis. As expected, otolith age discrepancy

increased with age (Appendix B). Two days were added to all final age estimates—an estimate of the time between hatching and the date of first ring deposition (Sismour 1994; Essig and Cole 1986).

Hatch dates were determined by subtracting individual fish age from their capture date, and were averaged for each month. Otolith increment widths were measured along the posterior axis from the core (hatching) to the outermost increment (day of capture). I operated under the assumption that the width from the core to the first distinct increment represented growth on day one. Though larval otoliths appear nearly circular, juvenile otoliths deviate and rapidly become asymmetrical, forming three axes (rostral, antirostral, and posterior), each with varying increment sequences and clarity. This makes accurate measurements more of a challenge than simple counts of those same increments.

Whereas the counting path of increments need not be linear, great care must be taken to select the orientation of the measurement axis. Thus, I standardized the posterior axis for measuring increment widths for consistency and to reduce potential bias in measurements, as other regions of the otolith become depressed and distorted. The maximum radial distance was measured in millimeters from the core to the posterior edge and all increment widths were recorded. All measurements were made using calibrated Image Pro® software. When increments were not continuously interpretable throughout the region due to cracks, overgrinding, or inconsistent imaging, that otolith was discarded and the second was inspected.

3.2.5 Water Quality and Zooplankton Processing

TP, TN, and DOC samples were processed at the University of New Hampshire Water Quality Lab. Alkaline persulfate digestion methods were used to process TP and

TN, and DOC samples were processed using high temperature catalytic oxidation. Chl-a samples were processed at the University of Massachusetts Amherst. Filters containing the field sample were placed in 90% acetone solution and stored frozen for 24 hours. An AquaFluor® handheld fluorometer (Turner Designs, Sunnyvale, California, USA) was used to extract and analyze the sample.

Rose bengal stain was applied to each lake sample to facilitate zooplankton sorting. A Hensel-Stempel pipette was used to extract three 1-mL subsamples from each pond. Samples were placed on a Sedgewick-Rafter counting cell, and zooplankton were identified, enumerated, and measured to the nearest μm under a compound microscope at 5x or 10x magnification. Zooplankton were identified using Haney et al. (2013), Johnson and Allen (2005), and Balcer et al. (1984) identification guides. Zooplankton density (no. L^{-1}) and biomass ($\mu\text{g L}^{-1}$) were computed for each sampling date per lake using the average number and size of each genera following methods by Kamaladasa (2007) and US EPA (2003).

3.2.6 Data Analysis

3.2.6.1 Estimates of Density, Growth, and Mortality

Juvenile river herring density (no. m^{-3}) was calculated as the number of individuals captured within each net haul divided by 485. If water depth was <4.3 m (depth of seine), as was the case in 30% (100 of 344) of hauls, the volume was adjusted accordingly. Per-haul densities were averaged each month to estimate monthly density, and subsequently, monthly densities were averaged to estimate an overall density for each lake. I used linear regression to test the relationship between adult run size and juvenile density, and to assess the ability of one month's juvenile density to predict the

next. I used analysis of variance (ANOVA) to test for statistically significant differences in juvenile densities among months. Density estimates were log-transformed to meet normality assumptions, and month was used as categorical predictor variable. If a significant difference was found by the ANOVA, I subsequently performed a Tukey's post-hoc test ($\alpha = 0.05$) to determine which months differed from one another.

I calculated growth in three ways, using two different scales. First, I calculated somatic growth rates for each lake using Höök et al. (2007) instantaneous growth (IG) equation, which defines individual river herring growth as

$$IG = (L-3.5) / (A+2)$$

where L is length (mm) and A is age (days). I used 3.5 mm as an estimate of size-at-hatch for river herring (Auer 1982), and added 2 days to age estimates to account for a delay in daily increment deposition (Sismour 1994). Individual growth rates from 50 fish were averaged each month for each lake to determine monthly somatic growth estimates, and subsequently monthly estimates were averaged to determine an overall growth rate for each lake.

I developed length-at-age linear growth models for 12 lakes using length and age data collected June–August, 2015. I fit a linear model for each lake and used the resulting parameter estimates to model the age of juvenile river herring captured and measured in the field, but not aged. By substituting age for length, I could increase the sample size and range of ages in this study, and subsequently used these data in estimating mortality. Lakes sampled only once during the summer were omitted in this analysis.

Secondly, I calculated otolith-based growth by dividing the otolith radial distance by the estimated age for that fish. As before, individual growth rates from 50 fish were

averaged each month for each lake to determine monthly otolith growth rates, and monthly estimates were averaged to determine overall growth rates for each lake. I used least squares regression to investigate the strength of an allometric relationship between otolith length and fish total length, and to investigate the relationship between otolith growth and somatic growth.

Lastly, I estimated daily growth of juveniles in 9 lakes using otolith increment widths. Only fish sampled in June were used in this analysis, and I did not estimate daily growth past 30 days. Increment widths from 31–50 juveniles were averaged each day for each lake. I tested the hypothesis that increment width varies by lake with age using an Analysis of Covariance (ANCOVA). Increment width was modeled as a function of age (continuous covariate) and lake (categorical factor), plus an interaction term between the two. Estimates of regression lines were compared between lakes using a Tukey's post-hoc test ($\alpha = 0.05$).

Otolith increment widths were also used to test the response of otolith growth to varying lake temperatures at 4 lakes in 2016. Increment widths from up to 50 individuals were averaged for each day for each lake. I excluded the first day post-hatch and fish ages (days) where less than 5 increment widths were measured. For each lake, mean daily surface water temperatures were calculated by averaging all 15-minute logger recordings for each Julian day. I used linear regression to evaluate the relationship between daily surface temperature and mean daily increment width.

Instantaneous mortality rates (Z) were calculated monthly and overall for each lake using two catch-curve estimation methods: 1) weighted linear regression and 2) Chapman-Robson. I used two methods for several reasons. First, linear regression has

been previously used to estimate juvenile river herring mortality (Essig and Cole 1986; Walsh et al 2005; Rosset 2016), thus my estimates will be directly comparable. However, I also used the Chapman-Robson estimator because its estimates have been shown to be more precise and less bias than traditional catch-curve methods (Dunn et al 2002; Gary Nelson, MDMF personal communication). For both methods, I used ages estimated from otoliths, and additionally applied the ages from the well performing growth models previously discussed. Mortality estimates were based on the juveniles sampled with a purse seine, but because these lakes weren't closed systems, mortality includes emigrating individuals.

First, I performed a weighted linear regression on the natural log of catches-at-age using the 'catchcurve' function in the "FSA" package in R. Maceina and Bettoli (1998) suggested that a weighted regression be used instead of a non-weighted regression in order to reduce the relative impact of older ages with fewer fish (in part attributable to emigration): which is the case with this longitudinal dataset. The first age included in these analyses is the age where the peak catch occurred, and I only included age-classes older than and including the age with the maximum catch (Smith et al. 2012). The mortality estimate is the resulting slope on the descending limb of the catch-curve, and I report estimates of Z plus standard errors for monthly mortality rates.

The Chapman-Robson method was also used to estimate mortality. For this analysis, I used all ages after the age where the peak catch occurred, and excluded all age-classes with less than 5 individuals (Chapman Robson 1960). In this method, ages are "recoded" such that the first full-recruited age on the descending limb of the catch-

curve is set to 0. The “ChapmanRobson” function in the “FSA” package in R was used to perform this analysis.

3.2.6.2 Mixed-Effects Regression Models

I fit linear mixed-effects models to examine the influence of several biotic (zooplankton biomass, juvenile mean length, hatch date) and abiotic (lake surface temperature, TP, TN, DOC, chl-a, secchi depth) variables on river herring density, growth, and mortality. Density, growth, and mortality were also used as biotic predictor variables when appropriate. I fit separate models for biotic and abiotic variables using all possible additive combinations with lake as the single random intercept. I included a temporal interactive term (Julian date) with all abiotic variables because I expected the relationships between dependent and independent variables to change with time. I also included an interaction term between juvenile river herring mean length and each biotic variable. A total of 6 abiotic and 6 biotic variables were used in models prior to adding interactions. Mixed-effect models were used to account for dependency in the structure of the data, as multiple observations were taken from each lake over time. Ages were not estimated or sample sizes were too small for Chemo, Pushaw, and Togus lakes due to poor otolith quality, thus estimates of growth and mortality do not exist. Therefore, I dropped these observations from all models that included growth and mortality as either dependent or independent variables. The resulting abiotic models included 44 observations each for density, growth, and mortality, and biotic models included 41 observations for each.

Prior to analysis, all dependent variables were tested for normality using a Shapiro-Wilk test ($\alpha = 0.05$). Otolith growth was the only variable normally

distributed, so density, somatic growth, and mortality were log-transformed to meet model assumptions. Cleveland dotplots were used to inspect both dependent and independent variables for outliers. Models were fit both with and without outliers, although removing outliers did not strongly influence parameter estimates, and results reported here are derived from the full dataset. Pairplots and variance inflation factor (VIF) scores were used to assess collinearity in predictor variables (Appendix C); only variables with low Pearson's r correlations (<0.5) and VIF scores of ≤ 2 were kept in models. Multi-panel scatterplots were used to visualize relationships and I investigated square terms, though their addition did not improve model fits and curve linear relationships were not supported. Covariates were normalized with a Z-score transformation. I used Akaike's Information Criterion (AICc-corrected for small sample size; Burnham and Anderson 1998) to evaluate support for the most parsimonious model, and I report only the top 5 models. Mixed-effects models were fit using functions implemented in the "lme4" package (Bates et al. 2014), and I report the conditional R^2 for top models in each analysis as an indication of goodness-of-fit (Nakagawa and Schielzeth 2013). All analyses were performed in R version 3.2.2 (R Core Team 2015).

3.3 Results

Measurements were recorded for 5998 fish, and of these, 1834 were used for aging. Individuals used in this study hatched as early as 16 April and as late as 6 August (Appendix D). Estimates of density, growth, and mortality were variable among lakes and months, and single-variable mixed-effects models performed best. Juvenile densities influenced both juvenile growth and mortality. Mortality was highest in lakes with high

juvenile densities and growth and mortality were inversely related. Model results and relationships are described in detail below.

3.3.1 Density

Average densities across lakes varied over an order of magnitude from 0.03 (Pentucket) to 0.87 (Gilbert-Stuart) river herring/m³ (Table 3. 2; Figure 3.2). Densities were generally highest in June (mean \pm SE = 200.6 \pm 72.6), and decreased throughout the summer. Mean juvenile densities differed significantly among months (one-way ANOVA: $F_{3,335} = 12.14$, $p < 0.001$), with densities significantly higher in early summer months (June/July) than later months (August/September). For 8 of 11 lakes sampled June–August 2015, density was highest in June and lowest in August (Figure 3.3).

Juvenile density was not explained by adult run size ($F_{1,11} = 1.363$; $R^2 = 0.11$; $P = 0.267$). Instead, juvenile density was positively correlated with the previous month's density ($F_{1,20} = 52.76$; $R^2 = 0.71$; $P < 0.001$). The top-ranked mixed-effects model using abiotic variables included the interaction between DOC and Julian date, and explained 76% of the variance in juvenile density (Table 3.3; Figure 3.4A, 3.4B). This model shows a significant negative relationship between juvenile density and DOC, with the effect of DOC on density increasing with time. The top-ranked biotic model included the additive terms river herring mortality and length, which were both negatively related to density (Figure 3.4C, 3.4D). This model had almost 3 times the support of the second-ranked model.

3.3.2 Growth

Fish length in June ranged from 7–39 mm and age ranged from 6–48 days old across all study lakes. In July, length and age was 9–105 mm and 8–96 days old. In

August, length and age was 17–133 mm and 22–105 days old, while fish caught in September were 40–124 mm and 44–127 days old (Appendix E; Appendix F). Pentucket, Potanipo, and Sabattus consistently contained the largest river herring, while Damariscotta, Highland, and Lower Guilford contained the smallest fish. There was a strong linear relationship between length and age. Length increased over time for all lakes sampled more than one month. Linear regression model fits for 11 lakes were highly significant ($p < 0.001$), and R^2 values ranged from 0.58–0.97 (Appendix G).

Overall length-based growth estimates in 2015 ranged from 0.58 mm/day (Snipatuit) to 0.94 mm/day (Potanipo), and averaged 0.74 mm/day across all study lakes (Table 3.2). When averaged across all lakes, growth rates increased throughout the summer and were generally higher for older fish. Estimates pooled across all lakes were 0.75, 0.72, 0.85, and 0.95 mm/day in June, July, August, and September respectively; however, these temporal trends varied by lake.

Overall otolith-based growth estimates ranged from 0.023 mm/day (Mianus) to 0.031 mm/day (Potanipo), and averaged 0.026 mm/day across all lakes. For 10 of 11 lakes sampled June–August, otolith growth peaked in August, and in all but two lakes (Glen Charlie and Gilbert Stuart), otolith growth steadily increased throughout the summer (Figure 3.5). Somatic and otolith growth estimates were moderately correlated ($F_{1,13} = 11.03$; $R^2 = 0.50$; $P < 0.001$; Figure 3.6A), however this relationship was largely improved by removing a single outlier (Sabattus) that was identified upon inspection of residuals ($F_{1,12} = 28.66$; $R^2 = 0.74$; $P < 0.0001$). There was a strong allometric relationship between fish total length and sagittal otolith radius length (Figure 3.6B).

Otolith length was particularly well correlated with fish length for individuals smaller than 40 mm.

In terms of abiotic variables, somatic growth was best explained by secchi depth. There was a negative linear relationship between secchi depth and juvenile growth, and this model explained 50% of the variance (Table 3.4, Figure 3.7A). Juvenile river herring density was the strongest predictor of growth rate, with growth rates decreasing with increased fish densities (Figure 3.7B). The top model explained 51% of the variance in growth (Table 3.4). Density-dependent effects were more pronounced for faster growing individuals, and correlations between density and growth were stronger later in the season (Figure 3.8). Growth rates were highest in lakes that were stocked with adult river herring.

Juvenile river herring daily growth during the first 30 days (as measured by otolith increment widths) varied by lake and by age (ANCOVA, $F_{17,213} = 113$; $R^2 = 0.90$; $P < 0.0001$; Table 3.6; Figure 3.9). Daily growth did not increase in a linear fashion, and patterns in increment width became more variable with age. An immediate decline in increment width was observed for all lakes following hatch followed by a steady increase in growth after day two. Highest growth rates (based on model intercept values) were in Pentucket, Potanipo, and Sabattus. Otolith increment widths from Pentucket and Potanipo were significantly larger than fish in all other lakes (Table 3.6). Increases in growth through time (slope) was lowest for Sabattus and highest for Highland and Whitmans.

Otolith growth patterns revealed an increasing increment width with increasing lake surface temperature in all four lakes examined, with correlation coefficients of 0.56, 0.85, 0.62, and 0.81 for Upper Mystic, Whitmans, Pentucket, and Potanipo, respectively

(Figure 3.10A-D). Measurements of increment widths were consistently most variable for fish from Upper Mystic and Pentucket, and variation in increment estimates increased for all lakes over time. Upper Mystic and Whitmans increased in otolith increment width through 30 days old, whereas after increment growth was more variable from 31–50 days. Declines in increment widths were observed during or soon after periods of lowered lake temperatures.

3.3.3 Mortality

Mortality was variable within and among lakes, as well as among estimation methods. Estimates of overall mortality between two estimation methods varied over an order of magnitude. Overall weighted linear regression estimates in 2015 ranged from 0.021 (Pentucket) to 0.164 (Upper Mystic) and averaged 0.092 across all lakes (Table 3.2). Overall Chapman-Robson mortality estimates in 2015 ranged from 0.059 (Damariscotta) to 0.307 (Snipatuit), and averaged 0.172 across all study lakes. For both estimators, mortality was typically highest in June, and decreased throughout the summer; however, this temporal trend was not true for Sabattus and Whitmans, where mortality increased over time (Appendix H).

Mortality was positively related to total phosphorous levels and negatively related to Julian hatch date (Figure 3.11). Mortality was poorly explained by abiotic water quality variables; the top-ranked mixed-effects model with TP explained only 11% of the variance (Table 3.5) and was largely driven by a single site (Sabattus) with high TP. Julian hatch date explained 47% of the variance in juvenile river herring mortality. The top 5 models all included Julian hatch date, and all were equally supported ($\Delta AICc < 2$)

and parameter estimates were highly significant (Appendix I). Overall mortality across lakes was negatively correlated with growth (Figure 3.12).

3.4 Discussion

This study evaluated the production of juvenile river herring and factors that influence the variation observed among lakes. This is the first study to document density-dependent growth of juvenile river herring among lakes in the wild. Results indicate that growth rates immediately post-hatch vary among lakes but follow similar trajectories during the first two weeks. Earlier hatching individuals experienced higher mortality rates than those hatching later in the summer. Juvenile density was poorly explained by adult density, but fairly well explained by the previous month's juvenile density and dissolved organic carbon (DOC) levels.

3.4.1 Environmental Factors, Not Spawning Stock, Affect Density

Results indicate that adult run size has little effect on the density of young-of-year in the lake, a finding consistent with previous work in 20 lakes in Massachusetts (Rosset 2016) and by Tommasi et al. (2015). This result has critical implications for management, as management agencies exclusively measure adult run size as a measure of productivity to manage river herring populations. Inconsistent patterns in stock-recruitment relationships are not uncommon (Myers and Barrowman 1996). Environmental and biological factors like temperature and climate (Clapp et al. 1997; Casselman 2002), food and competition (DeVries and Stein 1992; Hoxmeier et al. 2004), and predation (Brandt et al. 1987; Kim and DeVries 2001) can act independently or interact to affect mortality during early life stages, thus mediating fish densities.

Density estimates observed in this study ranged over an order of magnitude, and the abiotic variables best explaining variation were an interaction between DOC and Julian date. Although juvenile densities decline throughout the summer due to emigration and natural mortality, DOC levels appeared to have an amplified effect on this decline. DOC can have complex physical and biological effects on lakes, and recent literature has linked increases in DOC with reduced fish productivity (Karlsson et al. 2009; Finstad et al. 2014; Craig et al. 2017). As terrestrial DOC naturally flushes into lakes, the water becomes stained with a dark brown color (Jones 1992; Wilkinson et al. 2013). This “browning” of the water can reduce penetration of light and heat, and thus reduce thermocline depths and restrict available well-oxygenated epilimnion habitat (Wetzel 2001; Read and Rose 2013). As a result of light abatement, primary productivity is reduced, which negatively effects secondary production (Kelly et al. 2014; Craig et al. 2015) and can set-up poor biological characteristics of fishes such as slower growth rate and smaller size-at-age.

Lakes in my study showing the strongest negative relationship between DOC and density (Glen Charlie, Gilbert-Stuart, Whitmans) were generally shallow with mean depths less than 4-m. In these lakes, restricted epilimnion area could drive reduced productivity at the lake level, generating interspecific resource-limitation. River herring in these lakes were observed to have a smaller size-at-age, and may have less available energy to dedicate to foraging and growth due to indirect effects of elevated levels of DOC; a phenomenon observed in other studies (Karlsson et al. 2009; Finstad et al. 2014; Craig et al. 2017). Additionally, I found no difference in chl-a concentrations along the DOC gradient. In fact, the highest levels of chl-a were observed in the darkest lakes

where size-at-age was lowest, suggesting that the high availability of phytoplankton did not compensate for the negative effects of increased DOC.

Density-dependent interactions also influence fish productivity (Myers and Hilborn 2001; Downing and Plante 1993) and may potentially confound the results shown in this study. Juvenile densities were high in Glen Charlie, Gilbert-Stuart, and Whitmans, and competitive pressure may contribute to increased mortality in these lakes. Model results showed a negative effect of mortality on density, and although this is to be expected, this relationship may mask the extent to which declines in juvenile densities are attributable to changes in DOC levels. Additional modeling or laboratory experiments that are able to explicitly separate the potential confounding effects of densities and other environmental variables will be useful to infer patterns across the landscape. Previous work has demonstrated the effect of DOC concentrations on recreational fisheries, yet this study begins to illustrate how DOC can impact a commercially important species, and incorporating these relationships into fisheries models and restoration initiatives might suggest improvements in water quality can lead to higher freshwater productivity.

3.4.2 Size-Dependent Mortality

Average mortality estimates within lakes (Chapman Robson: 0.059–0.307; weighted regression: 0.021–0.164) observed in this study were comparable to previous work. For example, Essig and Cole (1986) estimated daily instantaneous mortality at 0.12 in Pentucket Pond, Massachusetts, and in my study mortality was estimated to be 0.13; Walsh et al. (2005) calculated mortality to be 0.34–0.48 in the Roanoke River, North Carolina; Höök et al. (2007) estimated mortality in Lake Michigan to be 0.22–0.30 and 0.14–0.16 in Muskegon Lake; Overton et al. (2012) reported rates of 0.06–0.27 in the

Tar-Pamlico River in North Carolina; and Rosset (2016) provided estimates of 0.01–0.20 in 20 Massachusetts lakes. Estimates from my study are within the range of previous estimates regardless of the estimator used in calculation. However, comparison is not possible for studies that derive mortality estimates using different methods. For example, whereas instantaneous values (Z) were used in this study and the ones described above, West et al. (2010) used a measure of fish per day in a Connecticut pond mesocosm, and Simonin et al. (2016) used a percentage of fish per day metric in Lake Champlain. Calculations used will surely depend on study objectives, though future work estimating juvenile river herring mortality rates in freshwater should strongly consider using a standardized metric to aid in comparisons throughout their range and inform management. Chapman-Robson estimations in this study were slightly more inflated than weighted linear regression estimates, and more reflective of the variation captured by other studies. By “re-coding” ages and using only those ages where more than 5 individuals are captured, more precise estimates of mortality are possible, and future work should consider adopting this approach.

This study provides strong evidence that earlier hatching cohorts experience elevated mortality; a finding consistent with what Crecco and Savoy (1985) found with American shad (*Alosa sapidissima*), a species closely related to river herring. The highest mortality rates among lakes were observed in June, when densities within lakes were also highest. This is not surprising, given mortality of larval-stage river herring in nursery habitats has been estimated at 91–99% (Havey 1973; Kissil 1974; Walsh et al. 2005). Additionally, Mansfield and Jude (1986) found river herring mortality rates to vary with fish size, with smaller larvae exhibiting higher mortality than larger individuals.

The temporal trends in mortality among lakes observed in my study are consistent with size-dependent mortality theory that suggests that smaller individuals spend more time vulnerable to early life stage risks including fluctuations in the physical environment (Roseman et al. 1999), predation (Miller et al. 1988), and energetic costs related to finding and consuming fruitful prey items (Schael et al. 1991). While a mechanism for this relationship cannot be directly inferred from my research, several possibilities exist. First, cooler water temperatures during early summer may create conditions that promote slower growth compared to fish hatched in later months. Individual growth was closely linked to water temperature in this study, and it is likely that earlier hatching larvae are more temperature-limited. Secondly, predation on river herring larvae by yellow and white perch (*Morone americana*) is high (Mattocks 2016). Yellow and white perch are pelagic predators that were observed in most of the lakes sampled in this study, and have been shown to regulate the abundance of larval river herring (Couture and Watzin 2008). Yellow and white perch most likely have an increased desire to feed after winters of less prey, and their gape-width limitations may drive them to seek river herring that hatch early and exhibit slower growth. Lastly, earlier hatching individuals may be forced towards unfavorable prey items immediately post-hatch due to reduced foraging abilities (i.e., shorter burst duration and smaller gape-width). River herring generally select the largest and most abundant items available to them, which in freshwater are *Daphnia*, cyclopoid and calanoid copepods, and *Bosmina* (Wells 1970; Cohen 1976; Crecco and Blake 2011). Biomass and density of these preferable zooplankton prey were greatest in June and July in my study, however these items would have been unavailable to small

larvae. Instead, smaller individuals may have been forced to feed on less favorable rotifers, resulting in slower growth rates and starvation.

The hatch date-mortality relationships shown in my study are not supported for alewives in the Great Lakes, as reported by Höök et al. (2007), who observed on average that earlier hatching individuals grew faster, were in better condition, and had greater survival than those that hatched in later periods. Additionally, Simonin et al. (2016) did not find any significant effect of hatch date on the mortality of river herring. These studies were conducted in large, cool, waterbodies in northern latitudes, and on landlocked river herring, and may not be representative of interactions occurring in shallower, productive lakes in southern New England (Connecticut, Rhode Island, and Massachusetts) where fish were hatched on average as early as 4 May, compared to New Hampshire and Maine that were hatched on average on 21 May.

The work on mortality described in this thesis has limitations. Estimates of mortality assume no recruitment to or emigration from the system. The lakes in this study were not closed systems and I did not account for juvenile river herring emigration. Thus, the estimates provided here are a combination of mortality and emigration and should be considered apparent mortality rather than true mortality. Without controlling for emigration, the relationship between hatch date and mortality may simply be a function of earlier hatching individuals leaving lakes earlier and it is possible my mortality values are overestimations. Monthly mortality estimates may be more accurate than overall mortality estimates because I expect relatively minimal emigration to occur during 2–3 consecutive nights of sampling. Additionally, during this study, several lakes experienced drought conditions which created low lake water levels and prevented juvenile

emigration during some summer months (e.g., Highland, Upper Mystic), and these mortality estimates are most likely reflective of true mortality. Nonetheless, future work estimating juvenile mortality should occur in closed systems or laboratory experiments where juvenile emigration events can be limited.

3.4.3 Density-Dependent Growth

The results of this study support the hypothesis that growth of juvenile river herring is density-dependent. Low-density sites (primarily stocked lakes) produced higher growth rates. Although West et al. (2010) speculated this to be true, my study demonstrates this relationship using study lakes throughout New England that are characterized by a wide range of densities and habitat characteristics. There was substantial variation in size-at-age among lakes, particularly towards August and September. For example, fish sampled in August at Pentucket, Potanipo, and Sabattus were dramatically larger than those in other lakes. These differences appear to be driven by strong density-dependent growth that became more pronounced later in the summer.

Top-down pressure of river herring on zooplankton communities has been well documented (Brooks and Dodson 1965; Post et al. 2008) and my results indicate density-dependent growth may be linked to limited prey resources for young of year individuals. Zooplankton biomass, however, was not a significant variable in mixed-models, and several explanations are possible. First, zooplankton sampling was coarse at each lake across space and time in this study (one tow at sunset, once per month, in the deepest point in the lake) and most likely did not capture the nuanced seasonal and diel fluctuations in biomass. Limiting sampling to one lake location may not fully represent how zooplankton are distributed throughout each lake, and may have created sampling

bias, as certain species are known to make both vertical (Hutchinson 1967) and horizontal (Lauridsen et al. 1998) diel migrations. Secondly, this study did not account for possible diet shifts by juvenile river herring over time. For example, I combined genera (Copepods, Cladocerans, Rotifers) when calculating biomass, and future studies may benefit from including separate variables for each genus in modeling, thus providing a level of detail not demonstrated here. Finally, the interactions between prey availability and growth are complex (Buckley et al. 2004) and likely to vary with other environmental factors like temperature. Laboratory studies that can control for these effects may be better suited to determine how prey type and density affect growth.

Heavy predation on larger, more favorable zooplankton in lakes with high densities of juvenile river herring will likely force a shift in diet towards smaller and less energy-rich items such as rotifers. This diet shift was observed in Upper Mystic Lake, Massachusetts (Steven Bittner, personal communication) and it is reasonable to suspect diet shifts are occurring in other high density sites where growth is reduced (Damariscotta, Gilbert Stuart, Glen Charlie, Highland). Additionally, the size-dependent mortality observed in this study may be mediated by the effects of density-dependent growth. These effects are expected to be compounded when emigration from nursery habitat is delayed due to low lake water levels (a phenomenon observed during my study).

The results presented here can be immediately implemented into dynamic life history models and provide strong predictive power for managers. Density-dependent growth parameters have been developed and incorporated into assessment models for several capture fisheries (Beverton and Holt 1957; Patterson 1997), but these data are

lacking for river herring and other under-studied clupeids whose recruitment levels are sensitive to subtle hydrographic and meteorological disturbances (Sutcliffe et al. 1977; Yako et al. 2002). Crecco et al. (1986) demonstrated that including known relationships with environmental variables and density-dependent effects into stock-recruitment models improves predictions of recruitment variability for American shad. Similar environment and density-dependent stock-recruitment models for river herring are now possible using the information provided in this study, and should increase the predictive capability of current modeling frameworks.

Density-dependent growth has implications for river herring stocking. Managers need to consider the tradeoffs between large numbers or large sizes of fish. Research on other anadromous species like Atlantic salmon and American shad reveal that early marine survival is related to their size at outmigration (Parker 1971; Healey 1982), and it is reasonable to suspect the same occurs for anadromous river herring. However, stocking approaches that manage for large sizes would need to consider emigration access for juveniles and the implications of larger fish being unable to leave the lake. For example, larger individuals looking to transition to more productive estuarine environments that become trapped in freshwater lakes may be susceptible to decreasing prey availability or deteriorating water quality. Thus, when implementing restoration actions like stocking, site selection should consider water quality and emigration access but monitor fish densities, growth, and survival as well. The results from this study provide empirical relationships between density and growth that should be helpful in decision making. However, they should not replace site-specific evaluations of juvenile

production or additional stock-recruitment modeling; instead, they should supplement them.

3.4.4 Water Quality Influences on Growth and Mortality

The observed positive relationship between phosphorous levels and mortality, while not particularly strong, may suggest an indirect effect on survival. Phosphorous can be a major controlling factor of lake eutrophication, where increased nutrient loading often results in a pulse of phytoplankton, which may then drive oxygen deficiency, decreased water clarity, and changes in species composition (Dillon and Rigler 1974; Correll 1998). TP was well correlated with chl-a in this study ($R^2 = 0.69$) and mortality rates were generally highest in shallow, more eutrophic systems. Interestingly, mortality rates were highest in August at two lakes (Sabattus and Whitmans) where high acute levels of chl-a were observed and significant algal blooms were witnessed while sampling. These observations further support the empirical evidence suggesting that mortality rates increase with excess nutrients. Although certain levels of phosphorous are natural and enable primary productivity, perpetual inputs (particularly from anthropogenic sources) may have pronounced negative effects on fish communities during summer months.

Phosphorous levels at spring turnover is one of the most common measures of lake productivity, as it is generally the nutrient that limits production in lakes, regardless of latitude (Schindler 1978). Control measures that prevent anthropogenic phosphorous from entering lake ecosystems may benefit river herring and can include manure management plans, the use of zero-phosphorous lawn fertilizers, “buffer ditches” on farmland, healthy riparian areas along waterways, and limiting pet and wildlife waste.

Additionally, summer lake water levels that allow juvenile egress are critical to restricting excess nutrients. While it is well established that river herring contribute phosphorous to lake ecosystems during adult spawning migrations through mortality and excretion (Walters et al. 2009), juveniles are capable of driving a net export of phosphorous during egress (West et al. 2010). Juveniles retain phosphorous in their muscle tissue and their annual egress from freshwater, and thus removal of large amounts of phosphorous, has been shown to improve lake water quality (Mower 1979). Lake associations and dam operators can play a role in facilitating phosphorous export by ensuring appropriate flows are present at spillways and bypass structures during summer months or periods of juvenile egress.

The negative relationship between secchi depth and growth rate observed in this study indicate that juvenile river herring growth rates are higher when water transparency is low. Transparency can be affected by phytoplankton biomass, chl-a (Carlson 1977), and terrestrial DOC (Wetzel 2001; Read and Rose 2013). Phytoplankton biomass has been shown to be linearly related to chl-a (Desortová et al. 1981; Jones et al. 1996; Kalchev et al. 1996), and I observed a negative relationship between secchi depth and chl-a ($R^2 = 0.38$), suggesting increased periods of growth occur when primary productivity is high. River herring can indirectly influence algal communities by decreasing the size and abundance of zooplankton (Brooks and Dodson 1965) and the changes observed in chl-a in this study may be a response to changes in zooplankton biomass due to top-down pressure from river herring.

3.4.5 Patterns in Fine-Scale Growth

Previous researchers have successfully shown and used linear relationships to describe juvenile river herring growth (Höök et al. 2007; Walsh et al. 2005; Rosset 2016). However, because larval-stage dynamics have so much potential to influence recruitment, I examined daily growth rates. Changes in length or weight are unlikely to occur at a daily scale; however, otoliths formed by calcium deposits are influenced by environmental and physiological factors (Gutierrez and Morales-Nin; Savoy and Crecco 1987; Thorrold et al. 1989; Campana 1992; Limburg 1996 and others) and may be useful in evaluating fine-scale growth. The suggestion that otolith microstructure can predict fish growth is not new (Volk et al. 1984), and my study demonstrates otolith development to be proportional to fish growth.

I observed an initial decline in increment widths across all lakes during the first two days post-hatch. This is not an uncommon phenomenon in fishes, and represents a transition from yolk-sac to active feeding, a period described as the “critical period” by Hjort (1914). During the critical period, high mortality is expected, and year-class strength is often determined. After this period, growth increased, but not in a linear fashion, and large daily fluctuations in increment widths were present.

Growth during the first several weeks is, at least in part, a function of temperature. For instance, surface water temperatures during June 2015 sampling at Pentucket, Potanipo, and Sabattus were 24.3, 24.7, and 25.4°C respectively. These three lakes warmed the fastest among study lakes and their initial increment widths (first 2 days post-hatch) and subsequent widths (larval-phase) were highest. Although these three lakes were stocked at low densities, and density likely plays a role in structuring growth,

density does not appear to have pronounced effects on growth until individuals reach larger sizes. This is supported by the fourth stocked lake, Winnisquam, where June surface water temperatures of 19.95°C were observed with the smallest increment widths across all ages.

More work is needed to better understand the thermal limits in growth, and how these relationships may change with fish size and density. Kellog (1982) observed maximum growth rates for herring larvae reared in tanks at 29.1°C, and my study confirms these results for fish in the wild. For example, individuals from Upper Mystic lake in 2016 experienced steady growth until about 27°C, and growth for fish sampled at Whitmans appeared to stabilize at around 23°C. I was unable to interpret growth patterns in fish from Pentucket and Potanipo beyond Julian day 160, though it is possible that growth in these low-density lakes is more temperature-limited because fish are released from any density-dependent effects. How density and temperature interact to affect growth may be lake-dependent or vary by year, but this study provides evidence that growth is temperature-limited immediately post-hatch, before being mediated by density.

3.4.6 Conclusion

This study directly links juvenile river herring freshwater survival to growth and highlights the importance of environmental conditions in nursery habitats in explaining productivity. Quantifying juvenile production in freshwater was identified as a high priority research need for managers ahead of the next Benchmark Stock Assessment in 2022 (ASMFC 2012), and the region-wide estimates of juvenile density, growth, and mortality in freshwater provided here can be incorporated into population models and help determine more precise estimates of production. Additionally, this study

demonstrates that density-dependent mechanisms may affect recruitment variability for river herring. Incorporating density-dependent parameters into stock-recruitment models may help forecast recruitment in response to years with particularly large or small adult runs. This information is also useful for predicting the abundance of system-specific stocks and determining freshwater mortality and its role in population dynamics.

This study provides evidence that lake water quality may have large impacts on juvenile production, and thus population recovery. This suggests that site selection for restoration efforts such as dam removal and stocking should be based on lakes with high productivity, warm water temperatures, and limited excess nutrients rather than proximity to the sea or adult run strength. Moreover, communities and individual landowners can contribute to increased river herring productivity by improving water quality conditions. For example, planting riparian buffers, diverting runoff to catch ponds, fencing off stream networks from livestock, and limiting lawn fertilizers that contain phosphorous are a few ways to reduce excess nutrient loading, limit thermal pollution, and restrict anthropogenic-driven changes in primary productivity. These can then potentially offset mortality later in life. Ultimately, this study provides novel information to inform decision-making towards recovery of river herring.

Table 3.1: Physical and chemical characteristics for 16 study lakes sampled June–August 2015. Water samples were collected at dusk, preceding fish sampling, at the deepest point in each lake. Site numbers correspond with map in Figure 1. Temp = surface temperature (0.5-m below surface), DO = Dissolved oxygen, TP = Total phosphorous, TN = Total nitrogen, DOC = Dissolved organic carbon.

Lake	Site #	State	Surface area (ha)	Elevation (m)	Mean depth (m)	Max depth (m)	Temp (°C)	DO (mg/L) ^a	Chl-a (µg/L)	TP (µg/L)	TN (mg/L)	DOC (mg C/L)	Temp (°C)	DO (mg/L) ^a	Chl-a (µg/L)	TP (µg/L)	TN (mg/L)	DOC (mg C/L)	Temp (°C)	DO (mg/L) ^a	Chl-a (µg/L)	TP (µg/L)	TN (mg/L)	DOC (mg C/L)
							June						July						August					
Chemo	1	ME	464	38.4	3.5	8.7	–	–	–	–	–	–	–	–	–	–	–	–	25.3	NA	4.0	19.3	0.26	4.53
Damariscotta	2	ME	1773	16.4	7.5	34.7	19.8	5.57	15.1	4.0	0.19	3.73	24.5	5.9	9.0	13.7	0.22	3.63	25.7	5.57	17.3	43.0	0.25	3.51
Gilbert Stuart	3	RI	28	2.7	3.68	4.5	19.8	7.47	25.7	32.6	0.49	6.29	24.6	5.03	25.5	13.9	0.41	3.52	28.7	4.87	7.5	27.1	0.52	3.54
Glen Charlie	4	MA	75	10.6	2.5	5.3	19.1	1.08	11.7	40.6	0.40	1.54	23.7	1.86	16.7	14.3	0.24	1.49	27.3	1.01	13.3	14.3	0.19	4.92
Highland	5	ME	259	57.9	6.4	19.8	21.3	6.09	15.3	16.5	0.22	3.43	24.6	5.25	6.8	19.4	0.23	3.14	26.6	4.75	5.1	1.3	0.33	3.99
Guilford	6	CT	52	11.8	3	6.5	19.2	6.6	34.3	19.5	0.35	6.03	22.2	3.87	27.7	11.5	0.33	5.59	28.0	3.4	12.1	19.5	0.50	5.61
Mianus	7	CT	44	4.2	1.8	4.2	–	–	–	–	–	–	25.4	NA	55.0	12.6	0.31	4.01	–	–	–	–	–	–
Pentucket	8	MA	33	7.3	5.1	8.4	24.3	4.95	28.1	36.5	0.52	4.91	26.5	6.85	4.9	21.3	0.42	4.65	23.8	5.12	7.2	47.4	0.47	5.51
Potanipo	9	NH	55	80.5	4	8.2	24.7	1.09	8.1	10.7	0.22	4.41	26.9	1.3	14.1	1.0	0.25	5.28	24.6	1.37	6.8	16.0	0.25	5.10
Pushaw	10	ME	1894	35.3	3.35	8.1	–	–	–	–	–	–	–	–	–	–	–	–	25.8	NA	16.9	15.0	0.31	4.41
Sabattus	11	ME	794	74.2	4.26	6.3	20.9	8.5	76.9	23.1	0.35	3.67	25.4	6.69	24.0	24.9	0.43	3.81	26.9	7.3	90.6	69.5	0.64	3.55
Snipatuit	12	MA	258	16.1	1.5	1.8	–	–	–	–	–	–	23.9	1.09	10.5	28.2	0.37	5.89	–	–	–	–	–	–
Togus	13	ME	262	55.1	6	14.9	–	–	–	–	–	–	–	–	–	–	–	–	25.2	NA	160.8	6.5	0.79	3.25
Upper Mystic	14	MA	64	0.9	15	28.9	18.0	0.51	72.8	35.2	1.64	3.65	25.3	0.27	20.1	23.2	1.10	3.96	25.3	0.23	22.5	0.6	0.68	3.71
Whitmans	15	MA	64	6.2	4	7.9	20.7	5.38	38.5	23.6	0.48	5.85	26.6	5.19	8.3	26.4	0.38	8.05	26.4	4.83	2.3	32.5	0.74	5.67
Winnisquam	16	NH	1704	146.9	15.2	53.1	21.0	5.7	1.6	3.7	0.30	2.42	23.9	6.1	3.8	34.4	0.32	2.22	25.6	4.8	3.7	19.0	1.86	2.80

^a Values are averages from a vertical profile; measurements taken at 0.5 m below surface, middle, and 0.5 m above bottom

– Lake not sampled

NA Measurements not taken due to YSI calibration

Table 3.2: Total sample nights, total number of purse seine hauls, overall density, overall somatic growth, and overall Chapman-Robson (CR) and weighted linear regression (WLR) instantaneous mortality estimates for 13 coastal New England lakes. Estimates are averages of monthly estimates. Site numbers correspond with map in Figure 1.

Lake	Site #	Sample nights	# Hauls	Density (no. m ³)	Growth (mm/d)	Mortality (CR)	Mortality (WLR)
Damariscotta	2	4	44	0.164	0.666	0.059	0.023
Gilbert Stuart	3	3	30	0.870	0.680	0.202	0.143
Glen Charlie	4	3	16	0.585	0.677	0.167	0.107
Highland	5	4	24	0.312	0.685	0.259	0.130
Guilford	6	3	16	0.070	0.783	0.207	0.144
Mianus	7	1	3	0.656	0.619	0.153	0.101
Pentucket	8	4	30	0.033	0.936	0.136	0.021
Potanipo	9	4	26	0.042	0.949	0.067	0.030
Sabattus	11	3	16	0.094	0.817	0.117	0.059
Snipatuit	12	1	5	0.039	0.581	0.307	0.121
Upper Mystic	14	4	54	0.413	0.758	0.222	0.164
Whitmans	15	3	18	0.385	0.775	0.277	0.109
Winnisquam	16	4	48	0.164	0.773	0.067	0.042

Table 3.3: Model selection results for the top-ranked mixed-effects models explaining variation in juvenile river herring density as a function of abiotic water quality variables and biotic fish demographic and prey variables in 16 coastal New England lakes, June–September 2015. All models include lake as random intercept term. Abbreviations: Julian = Julian date, Temp = lake surface temperature, Chl-a = chlorophyll-a, DOC = dissolved organic carbon, Zoops = zooplankton biomass, Hatch = mean Julian hatch date, Length = mean fish total length. Asterisk represents an interaction.

Abiotic Candidate Models	<i>k</i>	AICc	Δ AICc	w_i	R^2
DOC * Julian	6	153.31	0.00	0.94	0.76
Temp	4	160.52	7.21	0.03	0.30
Chl-a	4	161.51	8.26	0.02	0.34
DOC + Julian	4	162.33	9.02	0.01	0.23
Temp + Chl-a	5	163.24	9.82	0.01	0.33
Biotic Candidate Models	<i>k</i>	AICc	Δ AICc	w_i	R^2
Mortality + Length	5	106.91	0.00	0.68	0.74
Mortality * Length	5	110.33	3.41	0.12	0.73
Length + Hatch	5	110.43	3.51	0.12	0.69
Mortality + Zoops + Length	6	112.32	5.41	0.05	0.76
Zoops + Length	6	112.96	6.05	0.03	0.70

Table 3.4: Model selection results for the top-ranked mixed-effects models explaining variation in juvenile river herring growth as a function of abiotic water quality variables and biotic fish demographic and prey variables in 16 coastal New England lakes, June–September 2015. All models include lake as random intercept term. Abbreviations: Temp = lake surface temperature, Secchi = secchi disk depth, TP = total phosphorous, TN = total nitrogen, Zoops = zooplankton biomass, Hatch = mean Julian hatch date.

Abiotic Candidate Models	<i>k</i>	AICc	Δ AICc	w_i	R ²
Secchi	4	-10.30	0.00	0.84	0.50
Temp	4	-5.83	4.47	0.09	0.49
Secchi + Tn	5	-3.55	6.75	0.03	0.53
Secchi + Tp	5	-3.21	7.09	0.02	0.46
Tp + Tn	5	-2.20	8.11	0.01	0.49
Biotic Candidate Models	<i>k</i>	AICc	Δ AICc	w_i	R ²
Density	4	-17.86	0.00	0.94	0.51
Density + Mortality	5	-10.67	7.19	0.03	0.49
Density + Hatch	5	-9.69	8.17	0.02	0.51
Density + Zoops	5	-8.52	9.34	0.01	0.48
Mortality + Hatch	5	-7.65	10.21	0.01	0.47

Table 3.5: Model selection results for the top-ranked mixed-effects models explaining variation in juvenile river herring mortality as a function of abiotic water quality variables and biotic fish demographic and prey variables in 16 coastal New England lakes, June–September 2015. All models include lake as random intercept term. Abbreviations: Temp = lake surface temperature, DOC = dissolved organic carbon, TP = total phosphorous, TN = total nitrogen, Hatch = mean Julian hatch date, Length = mean fish total length. Asterisk represents an interaction.

Candidate Models	k	AICc	Δ AICc	w_i	R^2
TP	4	70.98	0.00	0.54	0.11
TN + TN ²	4	72.99	2.01	0.20	0.05
Temp	4	74.24	3.26	0.11	0.07
TN	4	74.92	3.94	0.08	0.05
DOC	4	74.95	3.97	0.07	0.05

Candidate Models	k	AICc	Δ AICc	w_i	R^2
Hatch	4	60.36	0.00	0.84	0.47
Density + Hatch	5	65.34	0.07	0.07	0.60
Length + Hatch	5	66.16	0.05	0.05	0.47
Hatch + Hatch ²	4	66.31	0.04	0.04	0.47
Density * Hatch	6	70.36	0.01	0.01	0.50

Table 3.6: Parameter estimates for regression lines from an ANCOVA testing how the relationship between increment width and age changes by lake. Tukey post-hoc test results are included and lakes not connected by the same letter are significantly different ($p < 0.05$). Fish used in this analysis were sampled in June 2015, and only the first 30 days of life are used.

Lake	Sample Size		Slope	Intercept
Pentucket	35	A	0.00060	0.02270
Potanipo	31	A	0.00049	0.01926
Damariscotta	47	B	0.00047	0.01050
Guilford	46	B	0.00045	0.01297
Highland	48	B	0.00088	0.00879
Mystic	50	B	0.00054	0.01138
Whitmans	37	B	0.00073	0.01029
Winnisquam	39	B	0.00049	0.00880
Sabattus	31	C	0.00012	0.01754

Model output: $F_{(17,213)} = 113$; $R^2 = 0.90$; $p\text{-value} < 0.0001$

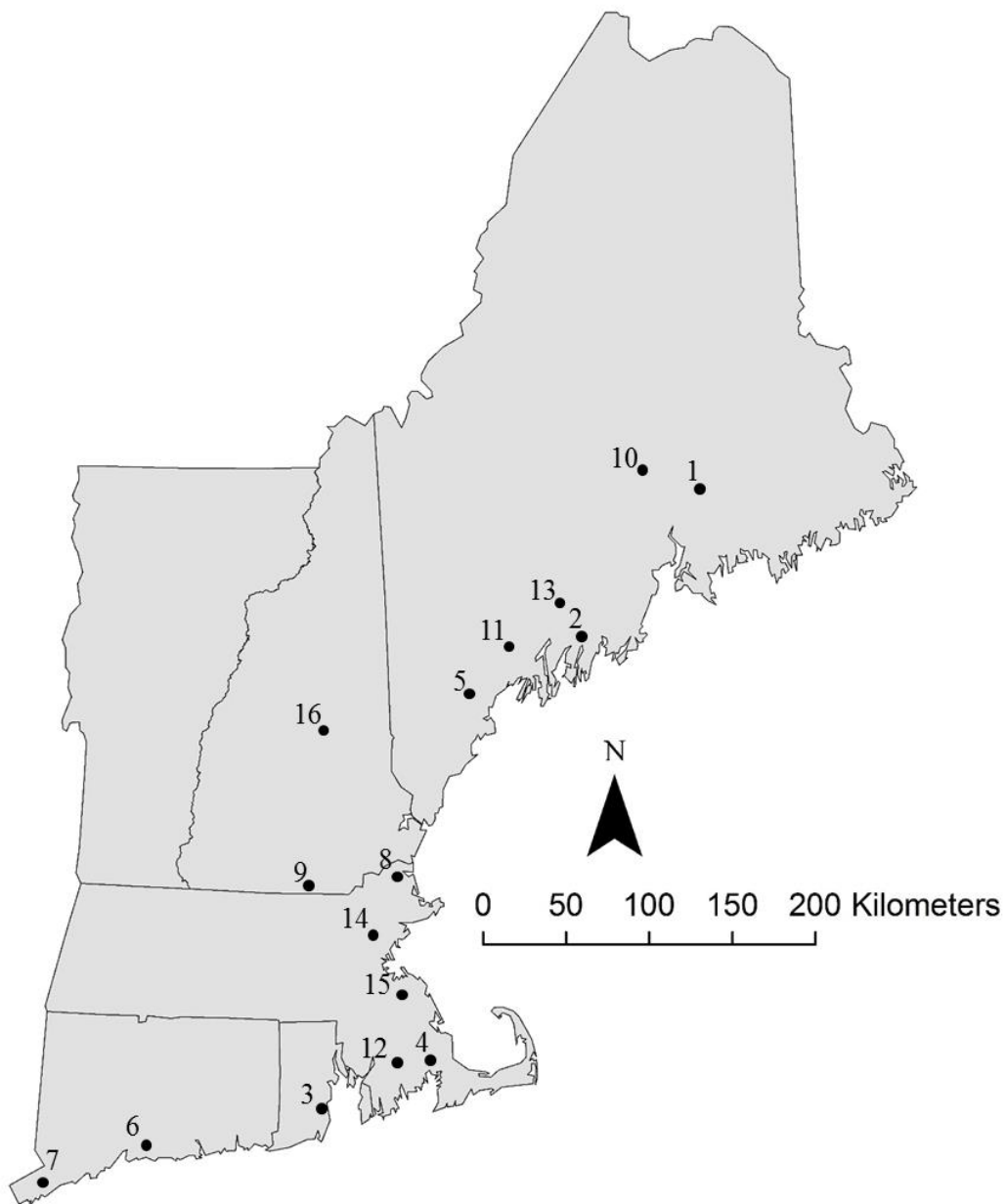


Figure 3.1: Map of 16 coastal New England lakes studied 2015–2016. Numbers are associated with Table 1.

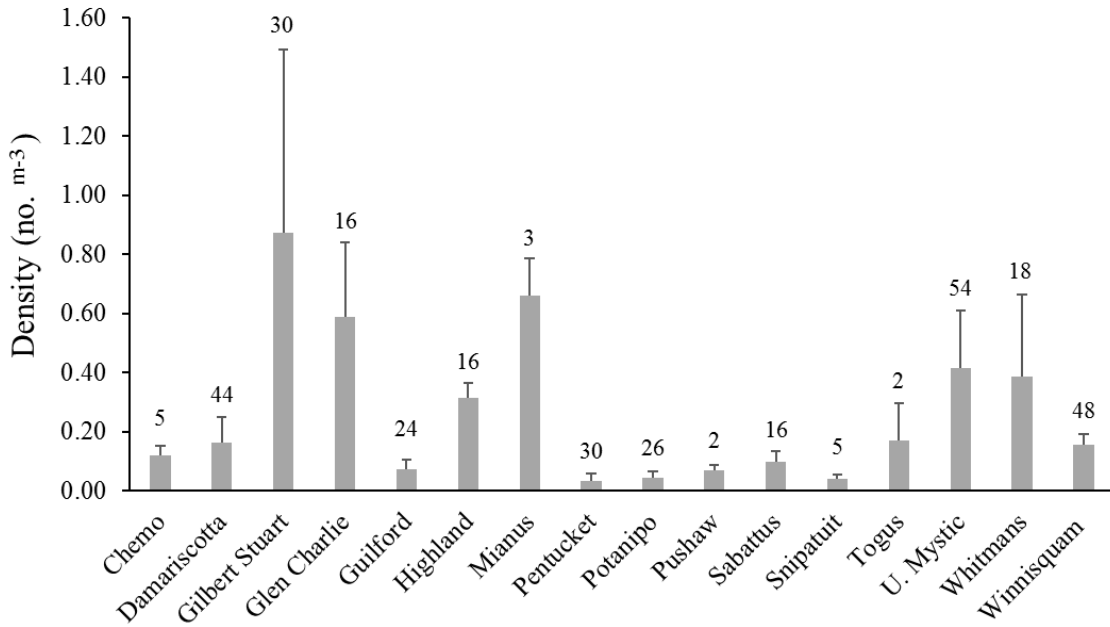


Figure 3.2: Average density (+ SE) of juvenile river herring across sampling months in each study lake. Number of samples (purse seine hauls) averaged to estimate density are shown above error bars.

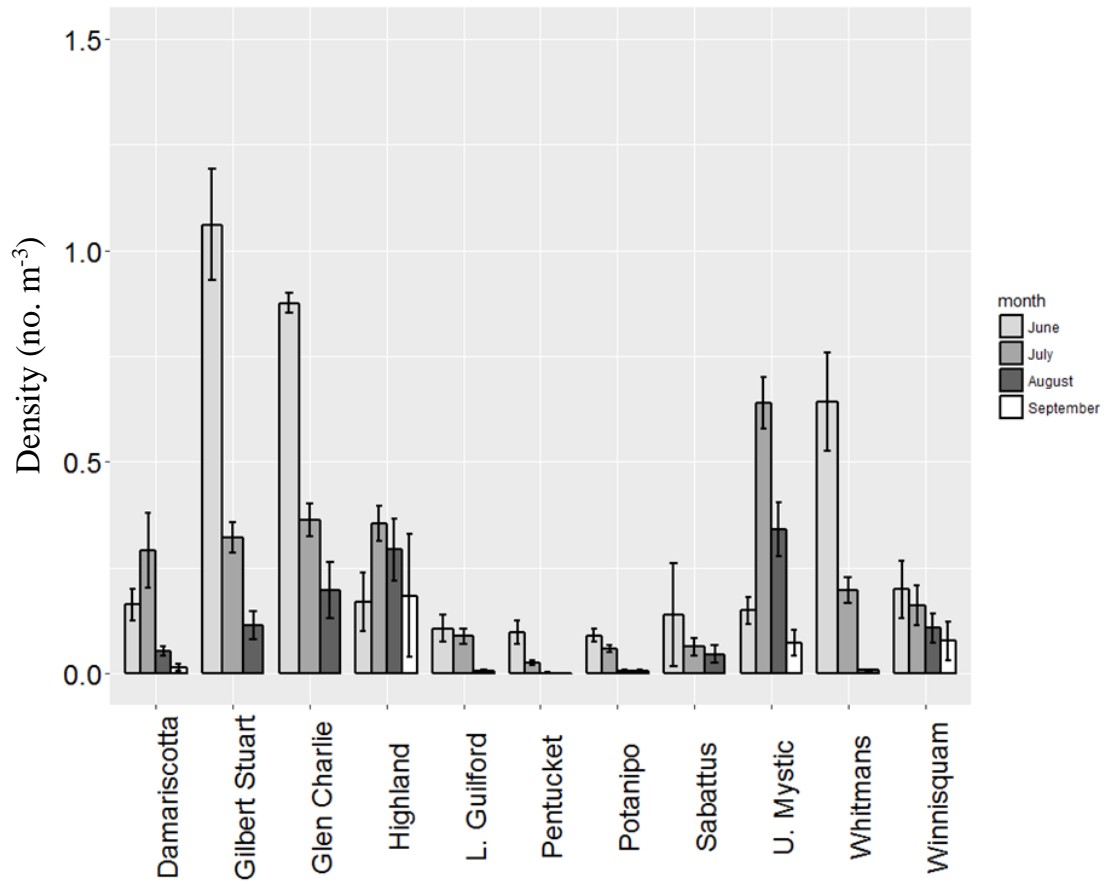


Figure 3.3: Average (\pm SE) juvenile river herring densities in each lake in each month for lakes sampled three times during 2015.

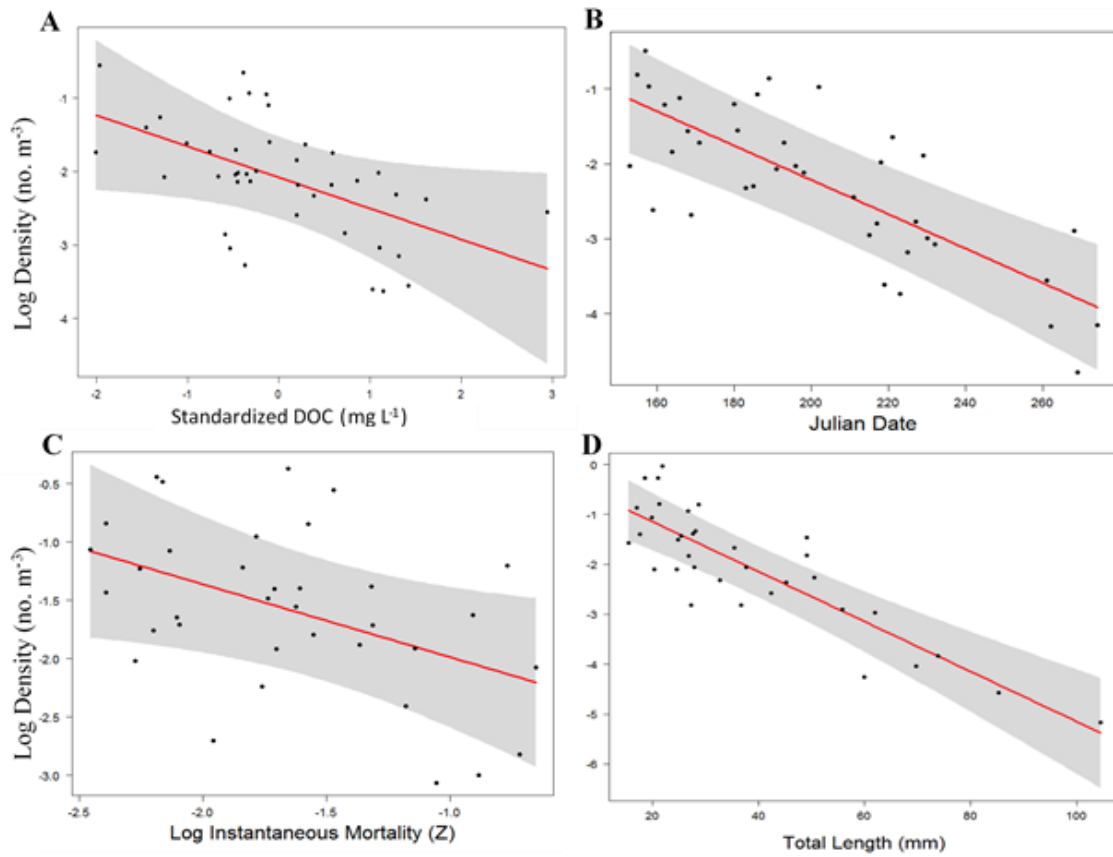


Figure 3.4: Regressions from top abiotic and biotic mixed-effects models predicting juvenile river herring density in relation to A) DOC, B) Julian date (while holding DOC constant at its mean), C) Chapman-Robson instantaneous mortality, and D) juvenile mean total length (while holding mortality constant at its mean).

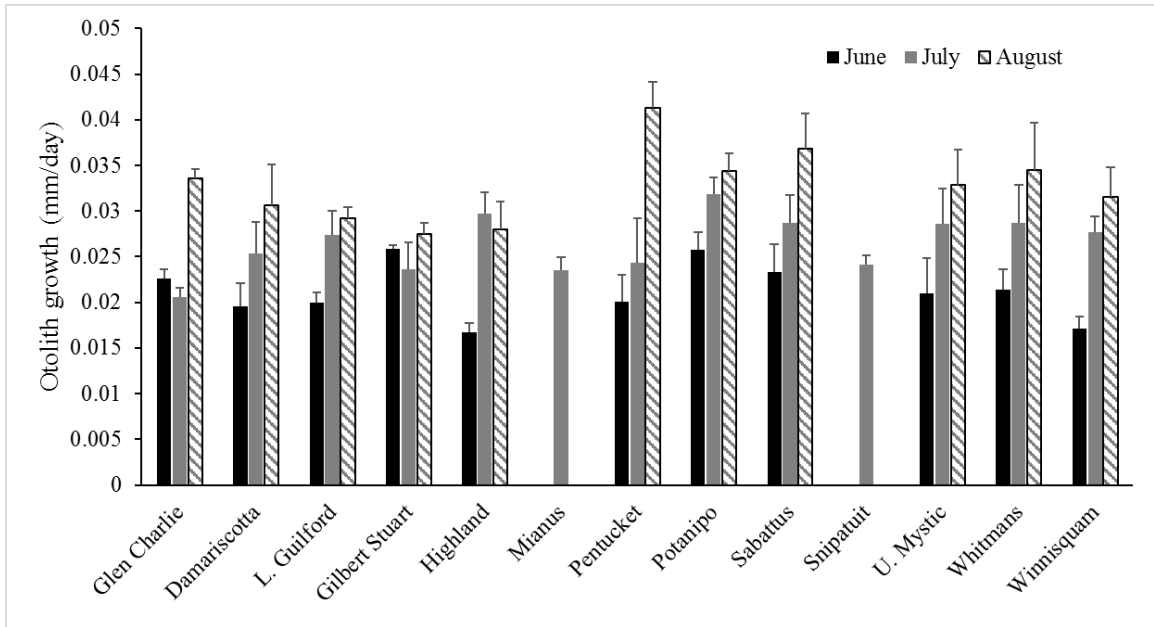


Figure 3.5: Monthly otolith-based growth estimates (mean \pm SE) for juvenile river herring sampled June–August 2015. Estimates were derived using sagittal otoliths to estimate age (days) for 50 juveniles per month, per pond. Black bars represent standard error of the mean.

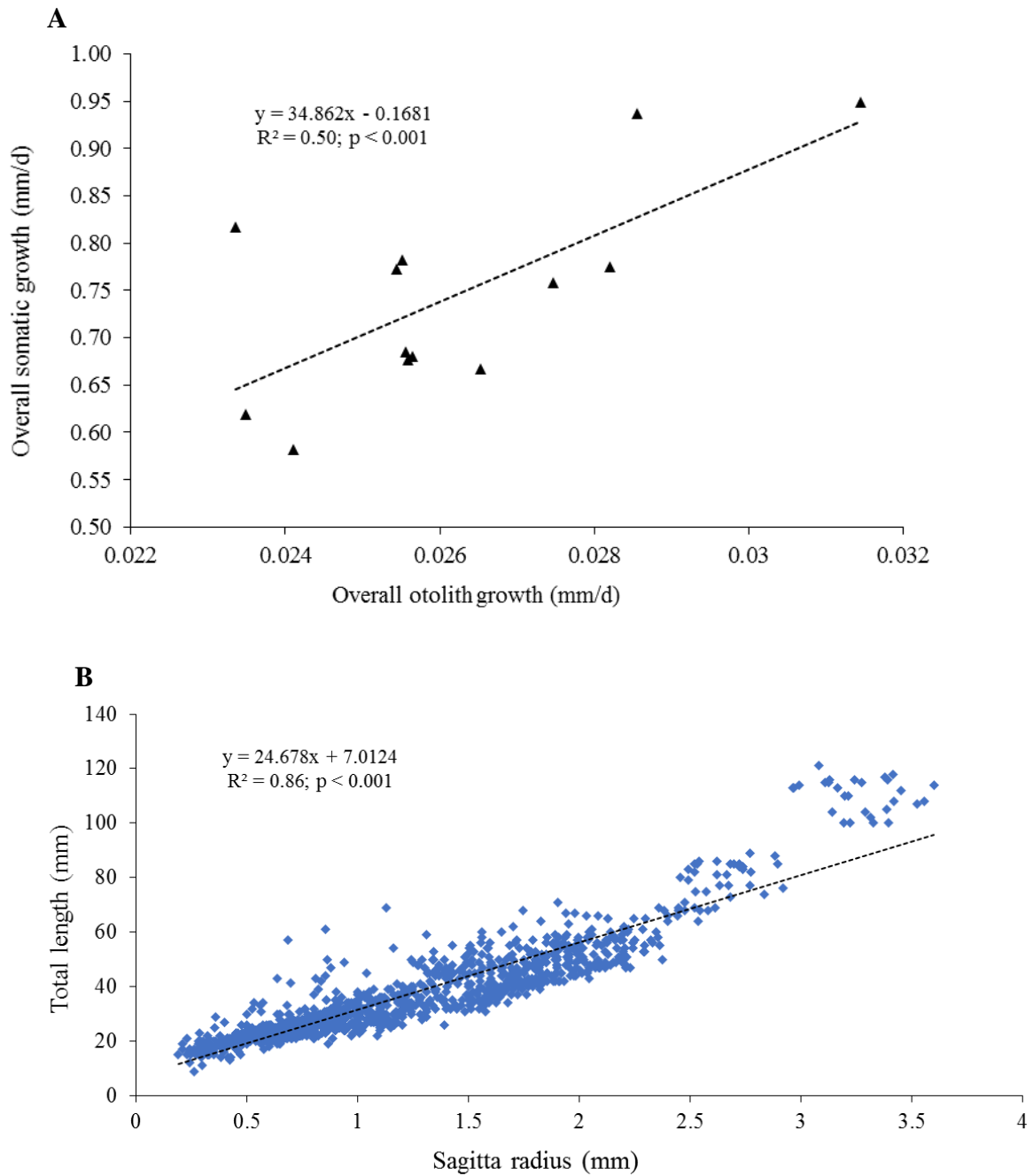


Figure 3.6: Linear regressions of A) overall otolith-based growth versus overall length-based growth averaged across three months, and B) otolith radius length versus fish total length for individual juvenile river herring.

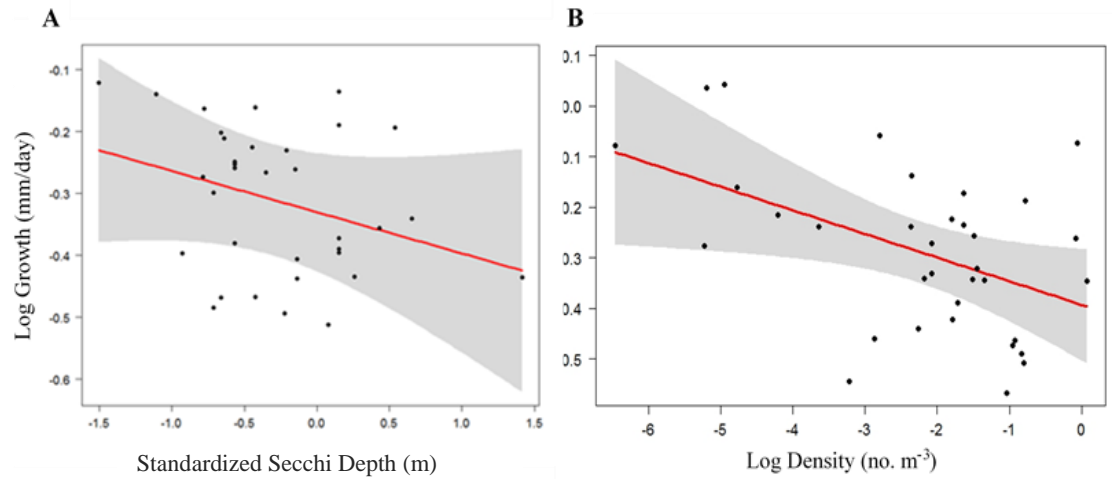


Figure 3.7: Regressions from top abiotic and biotic mixed-effects models predicting juvenile river herring somatic growth in relation to A) secchi disk depth and B) juvenile river herring density.

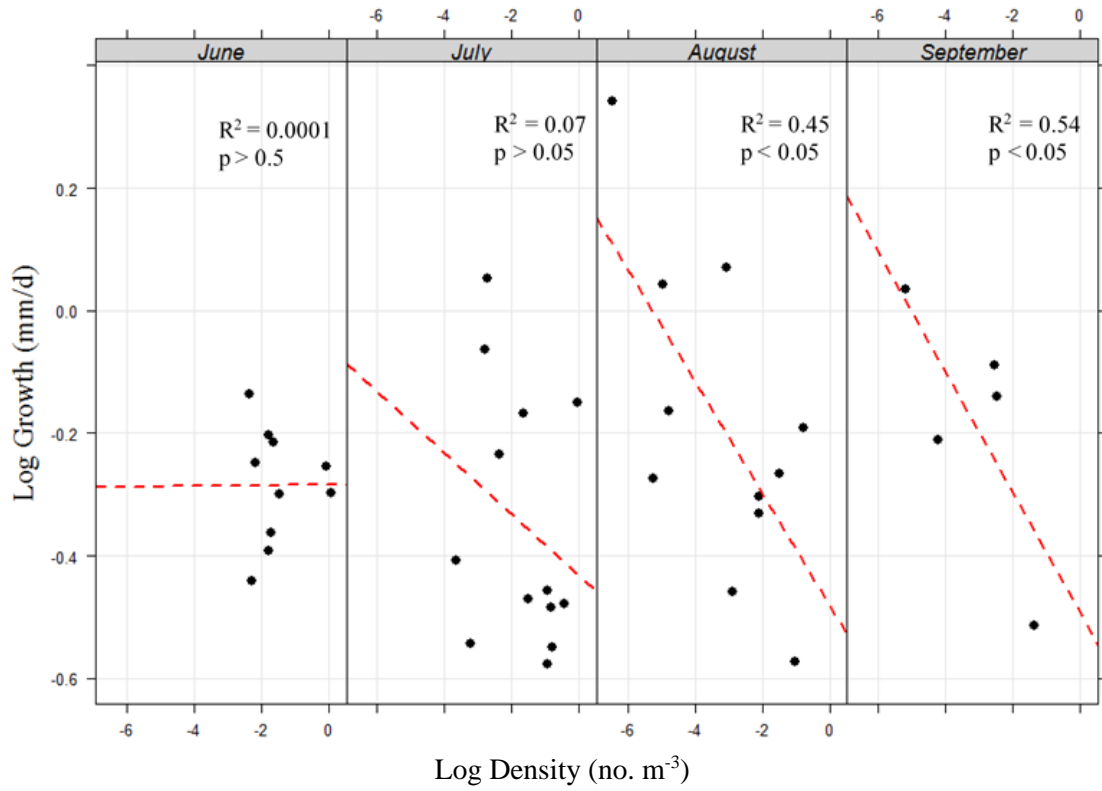


Figure 3.8: Linear regressions showing the relationship between density and growth by month for 2015. Red dashed line shows the linear model fit.

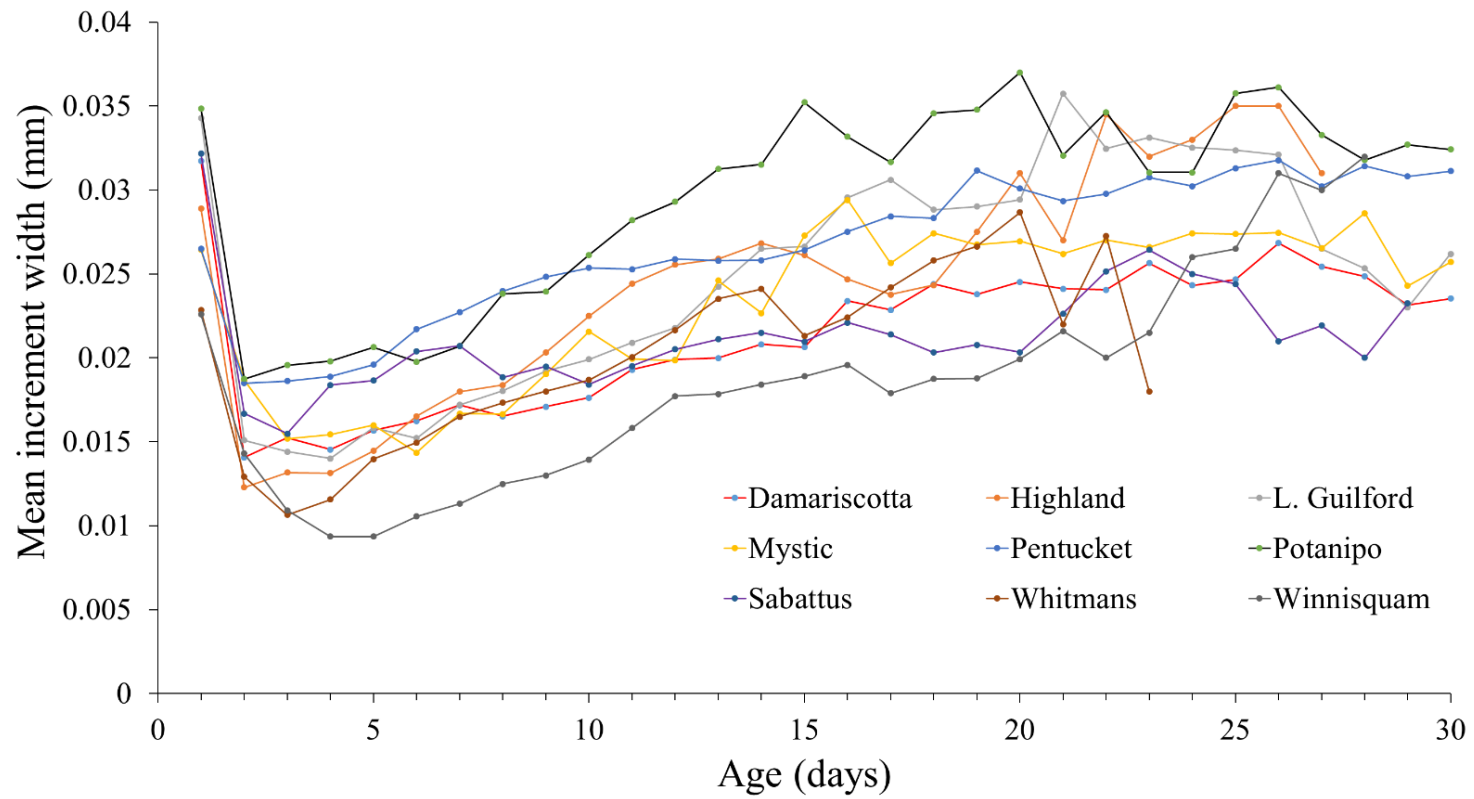
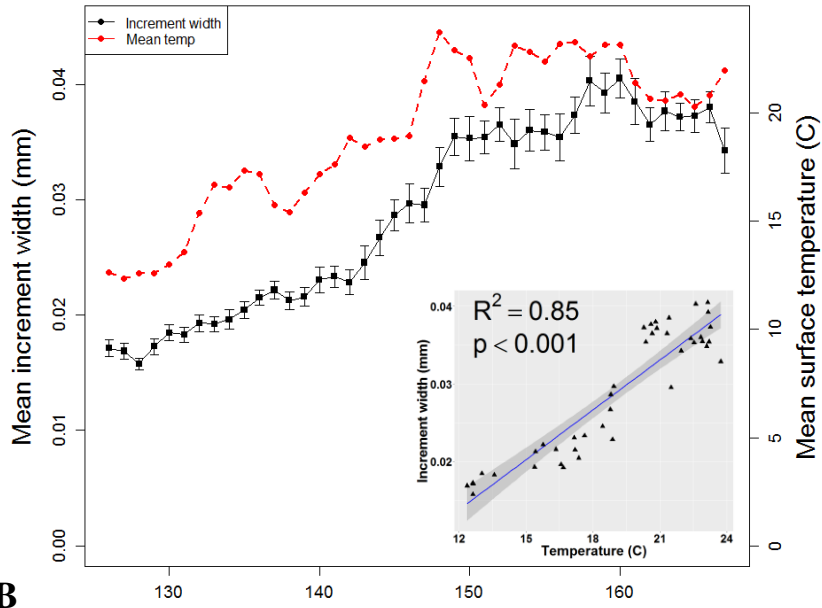
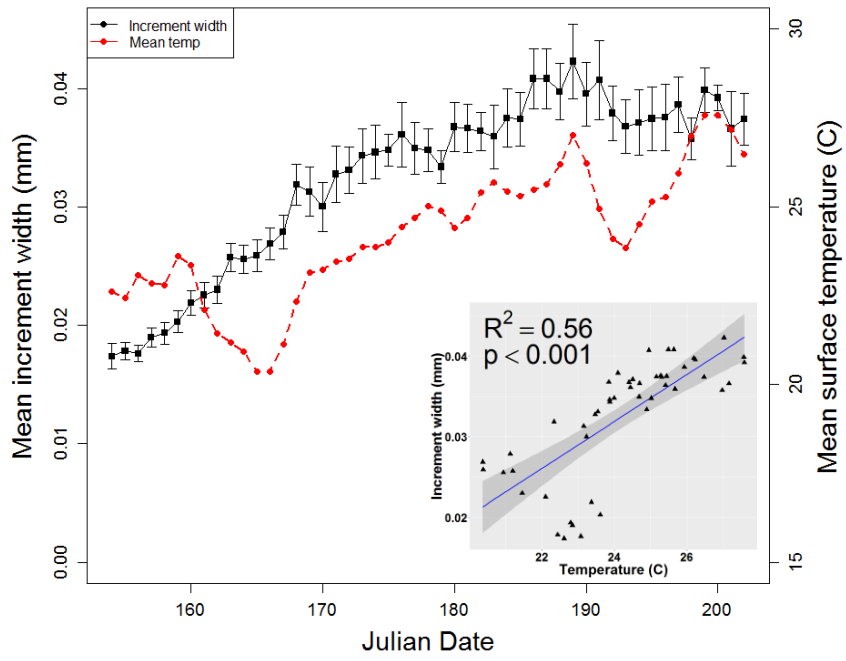


Figure 3.9: Mean sagittal otolith increment width during the first 30 days of life for nine lakes sampled in June 2015.

A**B**

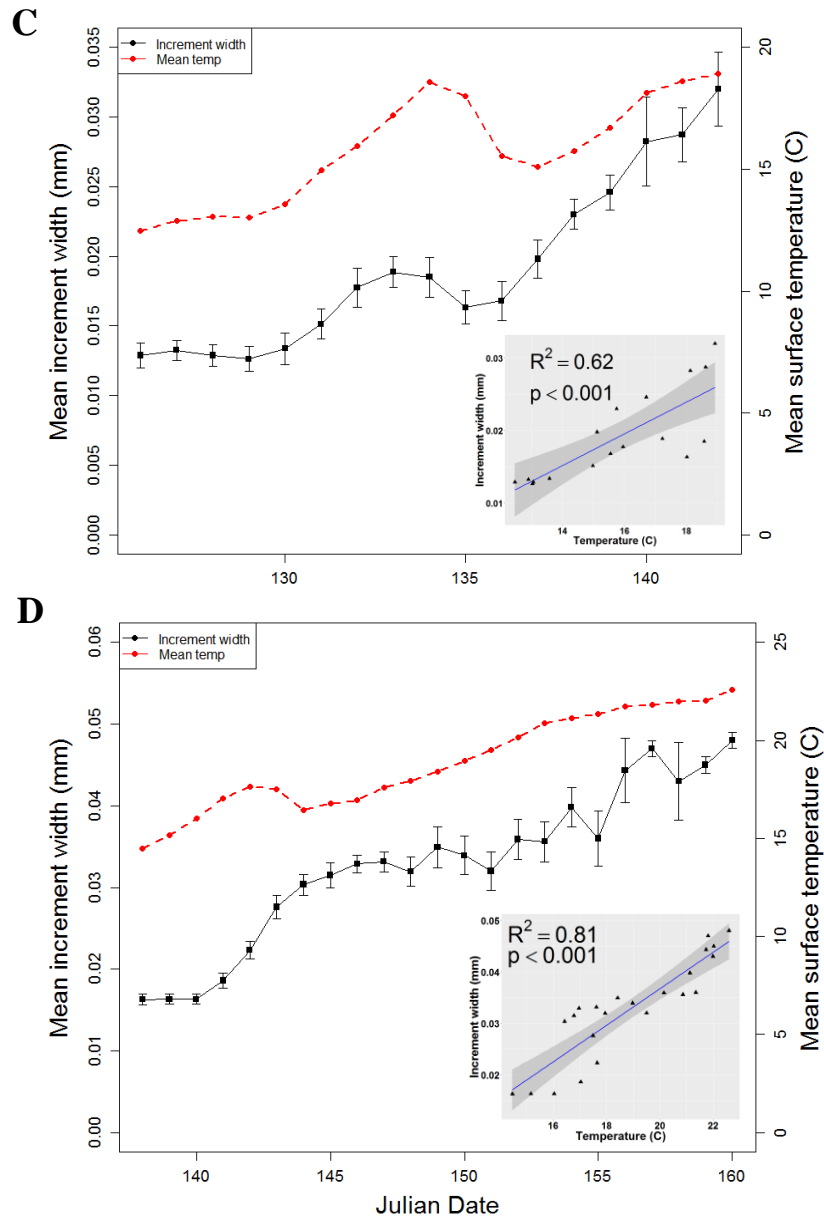


Figure 3.10: Mean daily increment width (\pm SE) and mean daily surface lake temperature in June and July 2016 for A) Whitmans, B) Upper Mystic, C) Pentucket, and D) Potanipo. Black bars represent standard error of the mean. Inset are results from linear regressions fitting increment width as a function of lake temperature. Correlation coefficients and p-values are shown, and gray band represents the 95% confidence interval.

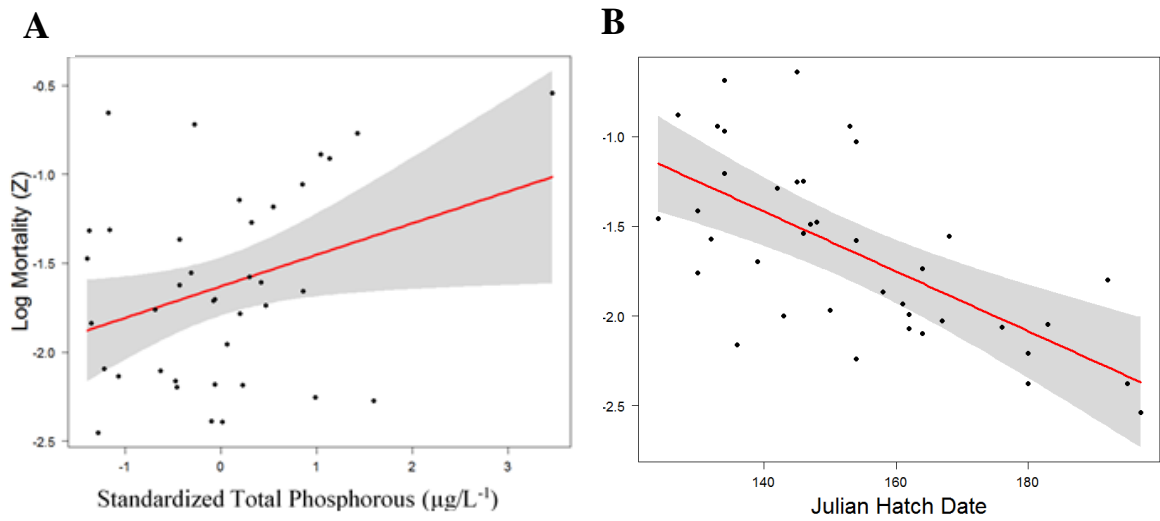


Figure 3.11: Regressions from top abiotic and biotic mixed-effects models predicting juvenile river herring instantaneous mortality calculated using Chapman-Robson method in relation to A) standardized total phosphorous and B) Julian hatch date.

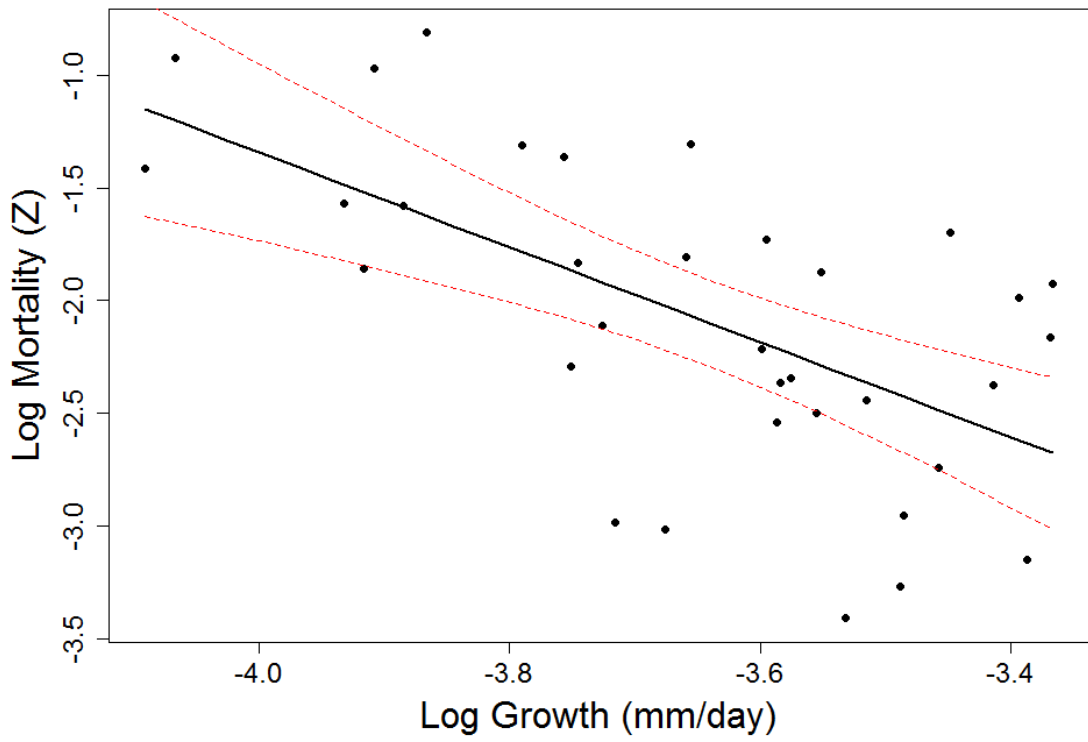


Figure 3.12: The relationship between juvenile river herring growth and mortality.

CHAPTER 4

CONCLUSION

This thesis contributes new data collection techniques for juvenile river herring in freshwater, and provides important new insights into how recruitment is affected by interactions that occur during early growth and development. In this thesis, I tested the efficiency and sampling precision of a small-sized purse seine, and determined the time of year, time of day, and sampling effort required to produce precise density estimates. A purse seine fished at night in June or July is most efficient. Sampling effort is largely dependent on lake size, and a crew of 3 people could estimate river herring densities with up to 10 purse seine hauls (1-2 nights) in a small lake (<50 ha), and with 15-20 hauls (2-3 nights) in a large lake (>50 ha). Purse seines are effective at capturing pelagic species in the upper portion of the water column (Loesch et al. 1982; Dixon 1996; Overton and Rulifson 2007), making them an extremely suitable and attractive gear type for sampling juvenile river herring. While purse seines have been used by previous researchers to capture juvenile river herring (Post et al. 2008; Rosset 2016), this study is the first to explicitly test its effectiveness compared to other gear types (beach seine and gill net) and quantify necessary sampling effort. My study helps to fill large gaps in our sampling regimes, which when employed annually by state fisheries agencies, should help researchers, technical working groups, and decision-makers better understand patterns in recruitment.

Sampling juvenile river herring with a purse seine is limited to pelagic areas and thresholds still need to be determined to understand at what size individuals exhibit net

avoidance. Furthermore, sampling protocols are still lacking for emigrating fish and those occupying estuarine habitats. Considering their complex life history, river herring sampling protocols should continue to be developed and tested for fish transitioning into the marine environment. Future work should focus on several areas including late summer within-lake densities, emigration patterns, and densities in estuary habitats. Estimating densities of fish during out-migration and into estuaries will be valuable to accurate assessments of survival at different life stages.

Results from Chapter 3 suggest that juvenile growth is density-dependent, and that survival in freshwater is directly linked to growth. Larger individuals are released from predation and successfully compete for the most valuable prey items. The tradeoff will need to be examined more closely, but managing for large sizes and densities may increase freshwater survival. The results from this study may be particularly beneficial to stocking initiatives. Managers employing stocking practices as a restoration tool have the benefit of controlling the number of introduced fish. This presents an opportunity to directly test the effects of adult stocking density on juvenile density, growth, and mortality. This study design was employed at one site in this study (Lake Potanipo) and revealed that a four-fold increase in stocked adults (500–2000) resulted in a marked increase in juvenile density and a significant reduction in average growth. Additionally, a second stocked lake did not alter stocking densities during my study (Pentucket Pond – 500 both years), and the result was comparable densities and growth rates both years.

While this information has practical benefits for stocking practices, management decisions on systems with natural runs are much less clear. Aquatic connectivity continues to be restored in many systems in New England through dam removal. While

qualitative observations suggest that dam removal may positively impact movement and productivity of river herring, evidence is lacking that can point to changes in biological characteristics (i.e., fecundity, size and age structure) and the use of newly available habitat for river herring following dam removal. This limits our understanding of production potential and how river herring may respond to dam removal. There is an emphasis to conduct studies that quantify the efficacy of restoration actions for river herring (ASMFC 2012). Considering the current emphasis on dam removal, future work should evaluate the effect completely opening a run has on the magnitude and the timing of recruitment and the time it takes (number of years) to build a new, recovered population. Understanding how river herring productivity responds to dam removal can greatly enhance restoration prioritization models, fisheries management plans, and inform appropriate harvest targets.

I intentionally do not make the distinction between alewife and blueback herring in this study because these two species are managed as a mixed stock. I did not identify by species when processing fish in the field or the laboratory, although blueback herring occurred in less than 5% of the samples that were genotyped in 2015 for a parallel study (A.R. Whiteley, University of Montana, unpublished data). Additionally, preliminary results suggest little differences in growth rates (Grasso and Devine, unpublished data), and I expect the sampling methods described here to be effective for both species.

An understanding of how juvenile production affects year class strength is a high priority for managers (ASMFC 2012) and this thesis has taken steps to address this data gap. First, I have developed a technique that state management agencies could adopt that can achieve precise estimates of juvenile densities in freshwater lakes. Second, I have

provided new insights into the growth-mortality relationship for juvenile river herring which can be used to support dynamic population models used by managers at the state level. An increased understanding of juvenile production can inform stock-recruitment models for single river systems, and when generated over a sufficient time-span, as required by the ASMFC, can be used in addition to trend analysis. Finally, I have characterized temporal patterns in juvenile freshwater density, growth, and mortality throughout New England and have described abiotic and biotic factors that influence their variation. This new information can serve as a guide for freshwater and marine fisheries managers whose objectives are to recover anadromous populations of river herring.

APPENDICES

APPENDIX A

MEAN CATCH-PER-UNIT-EFFORT FROM SIMULATIONS AND FIELD SAMPLING

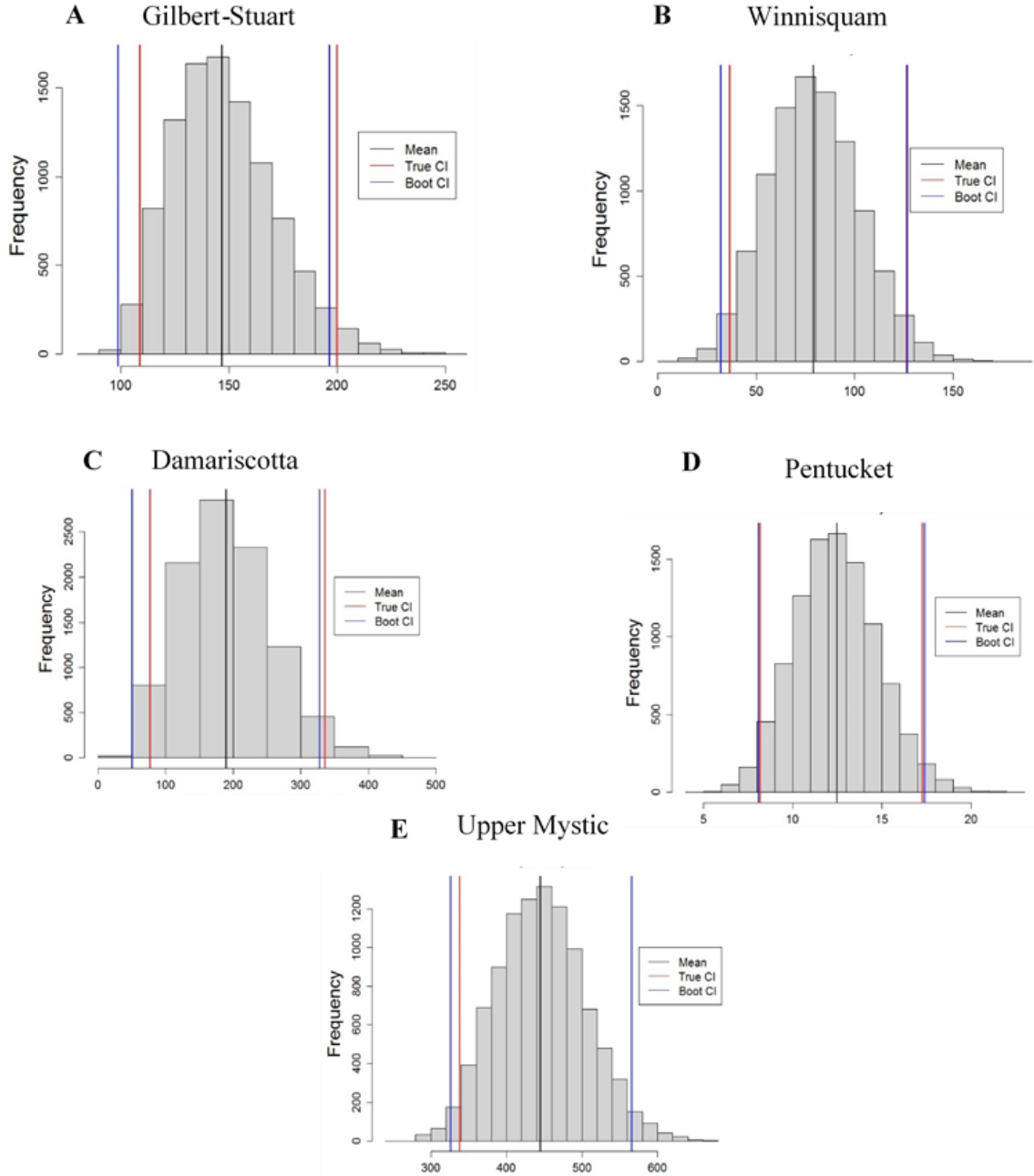


Figure A.1: Histograms of bootstrapped mean catch-per-unit-effort (CPUE) values resulting from 1,000 iterations for A) Gilbert-Stuart, B) Winnisquam, C) Damariscotta, D) Pentucket, and E) Upper Mystic lakes. Black vertical line represents the mean, blue line is 95% bootstrapped confidence intervals, and red line is empirical 95% confidence intervals.

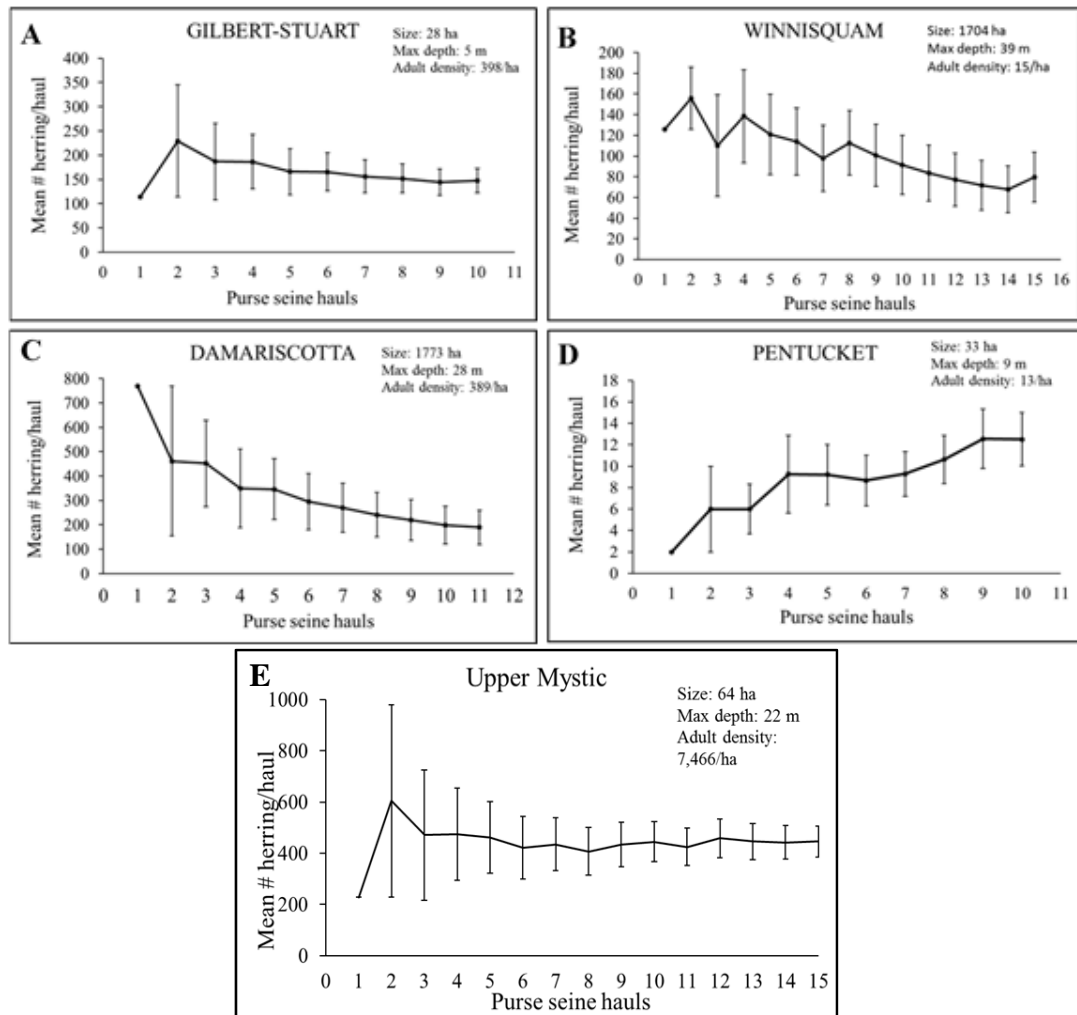


Figure A.2: Mean number of river herring (\pm SE) per seine haul across increasing sampling effort for A) Gilbert-Stuart, B) Winnisquam, C) Damariscotta, D) Pentucket, and E) Upper Mystic lakes sampled in July, 2015.

APPENDIX B

OTOLITH AGE COMPARISONS AND AGE-BIAS PLOTS

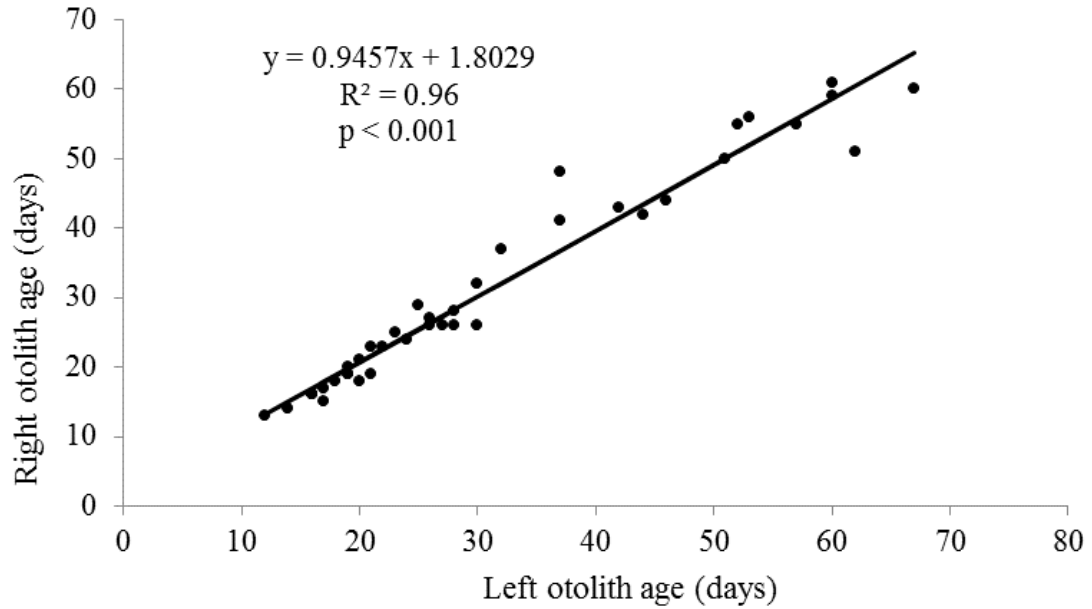


Figure B.1: Linear regression of age estimates (in days) for left and right sagittal otoliths extracted from 50 juvenile river herring caught using a purse seine in June 2015 at five lakes (Damariscotta, Whitmans, Highland, Glen Charlie, Winnisquam).

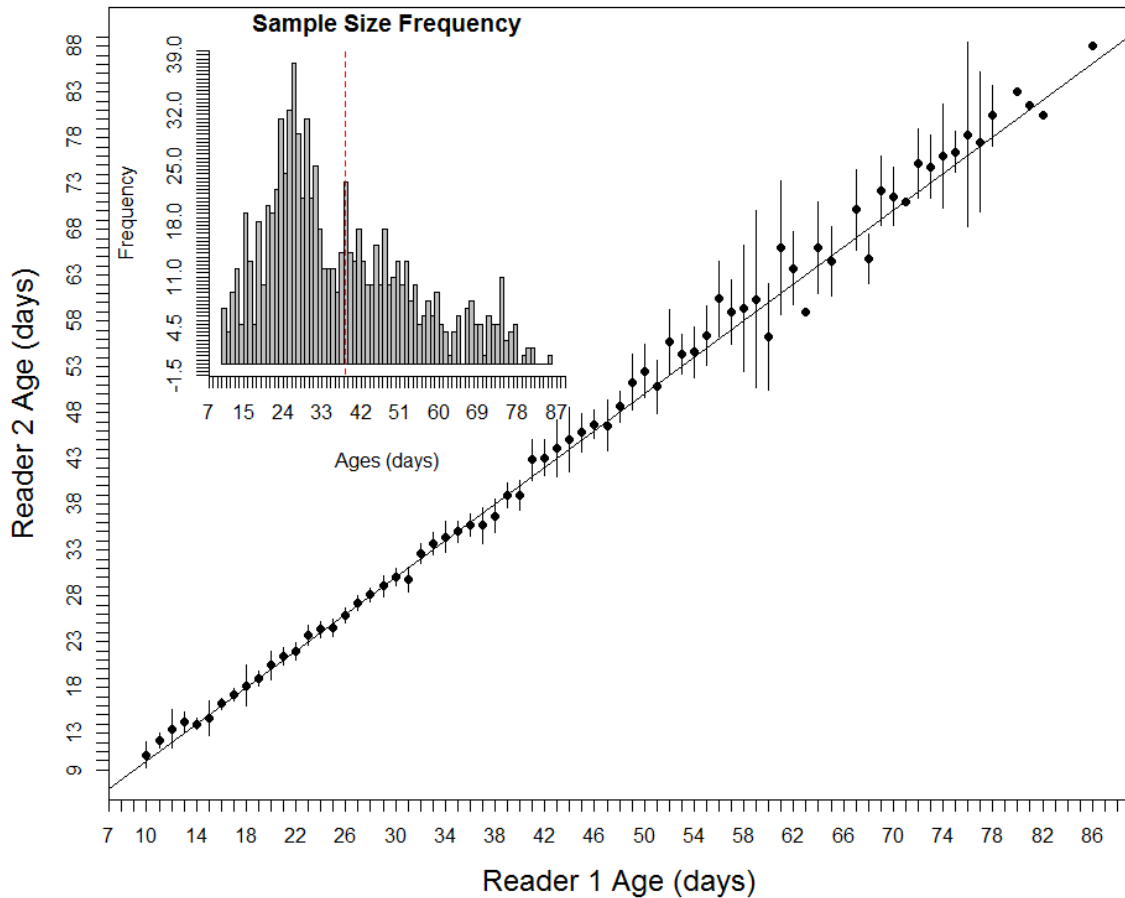


Figure B.2: Age bias plot for the mean (points) and 95% confidence intervals (black bars) of reader 2 age estimates at each reader 1 age estimate for juvenile alewife sampled in coastal New England lakes June-September 2015. The dashed 1:1 gray line represents age estimates that agree. Confidence intervals that do not capture this “agreement line” suggest a significant difference in the two age estimates at that reference age. Points with no confidence intervals had too few observations. A histogram is included to show the distribution (and sample sizes) of the age estimates used. The vertical red dash indicates the mean (37).

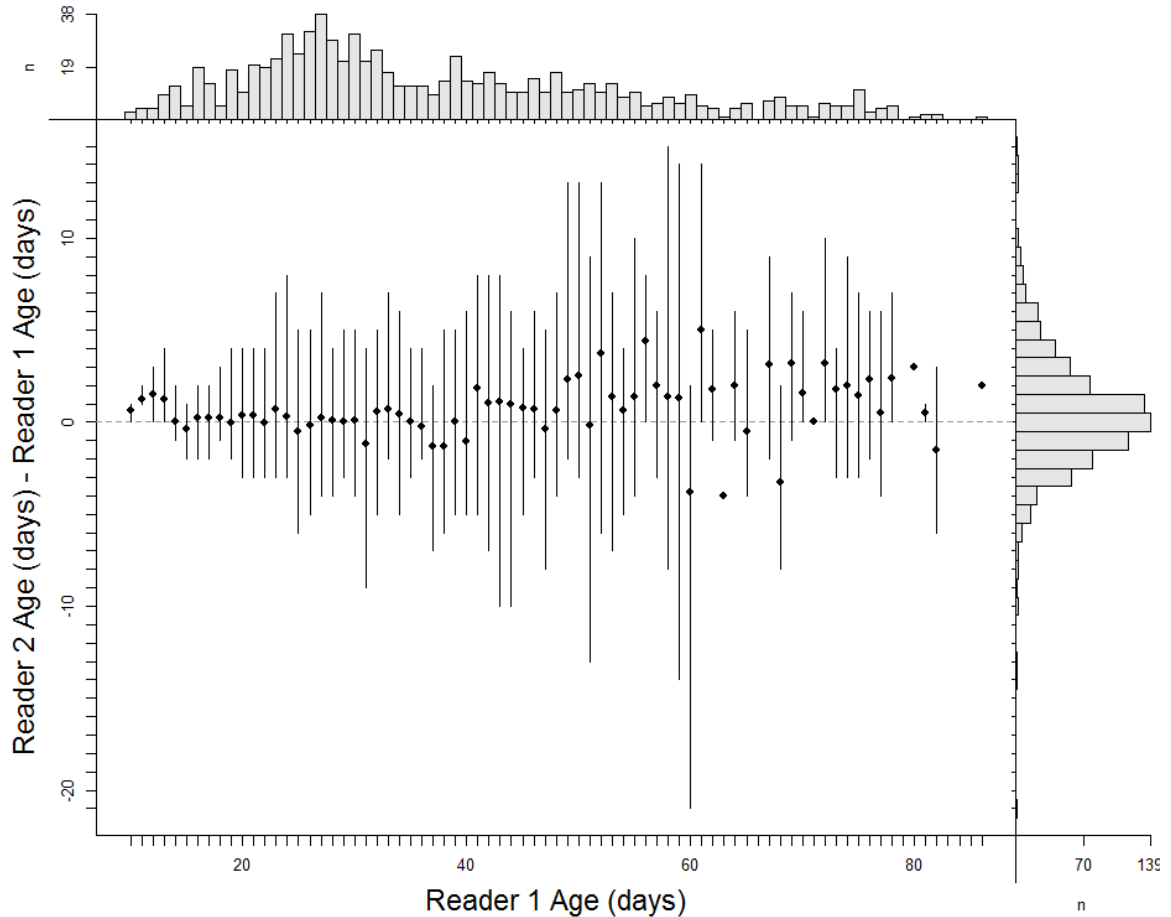


Figure B.3: Mean (points) and range (intervals) of differences in sagittal otolith age estimates between two readers at the estimates for the first reader for juvenile alewife sampled June-September 2015. Intervals that do not overlap zero (dashed gray horizontal line) represent significant differences in age estimates. Marginal histograms are for age estimates of the first reader (top) and differences in age estimates between readers (right).

APPENDIX C

PAIRWISE CORRELATIONS FOR VARIABLES USED IN MIXED-MODELS

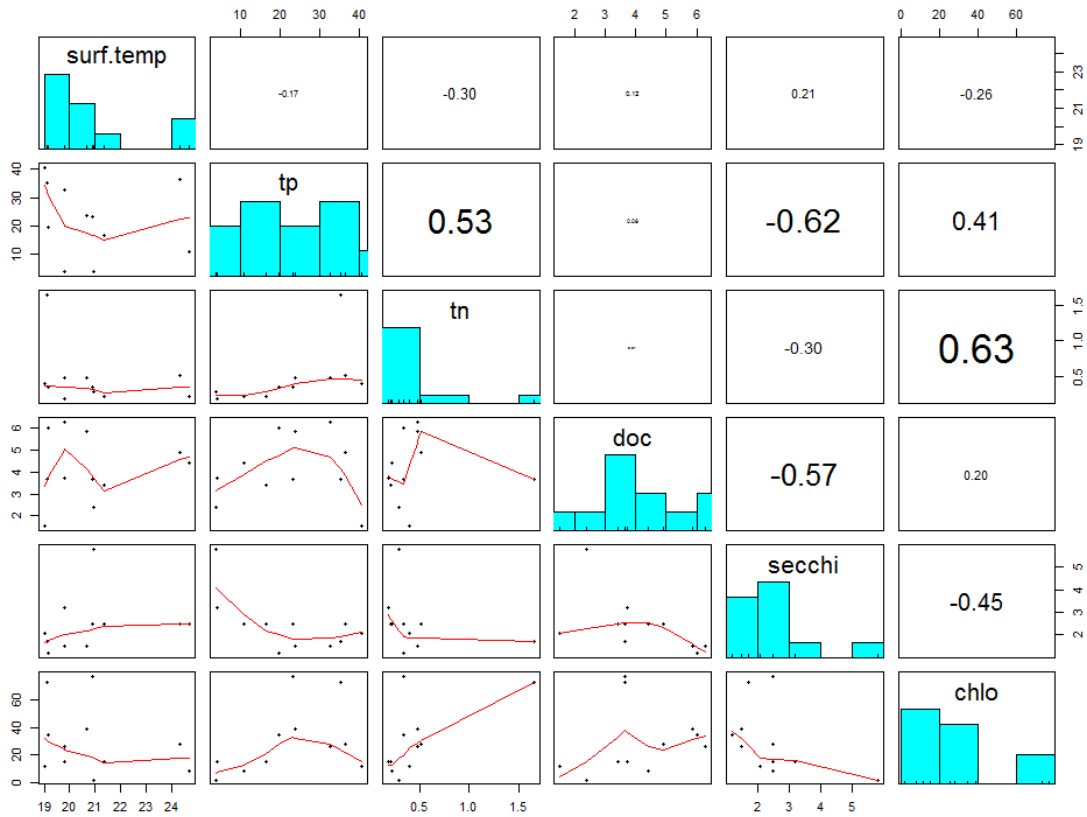


Figure C.1: Pairwise regressions of independent variables for June 2015 sampling. Variables include lake surface temperature (surf.temp), total phosphorous (tp), total nitrogen (tn), dissolved organic carbon (doc), secchi disk depth (secchi), and chlorophyll-a (chlo).

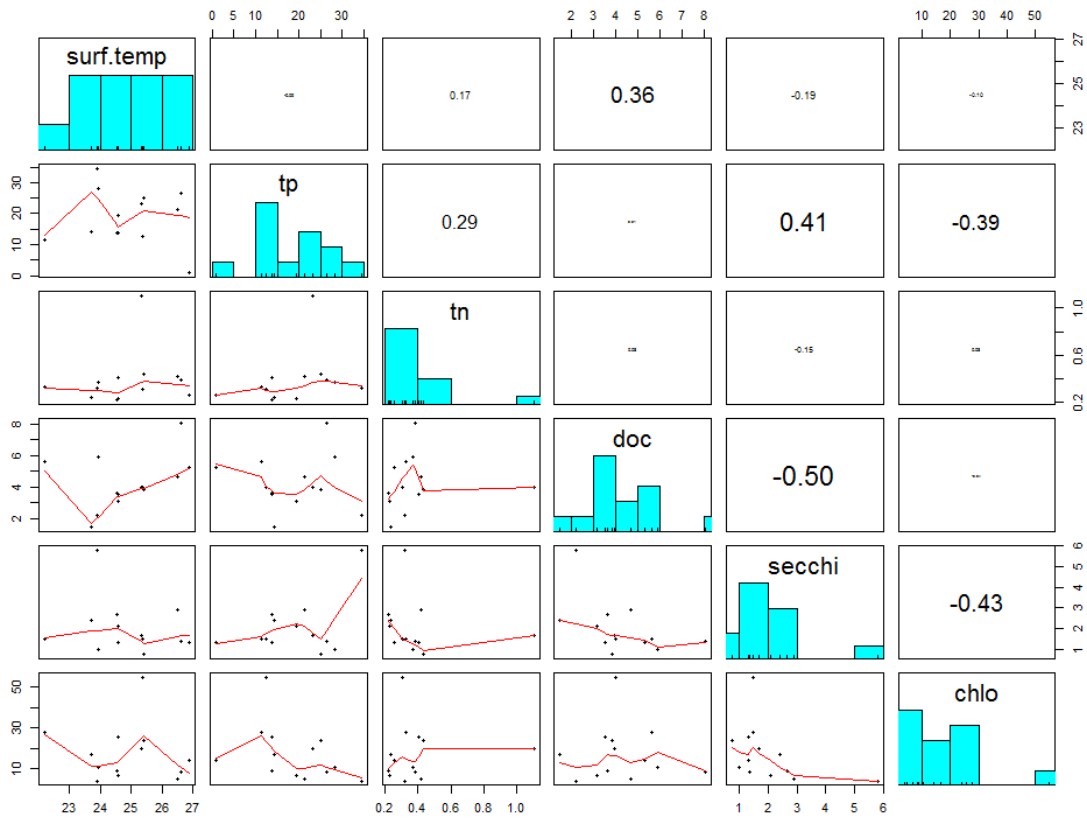


Figure C.2: Pairwise regressions of independent variables for July 2015 sampling. Variables include lake surface temperature (surf.temp), total phosphorous (tp), total nitrogen (tn), dissolved organic carbon (doc), secchi disk depth (secchi), and chlorophyll-a (chlo).

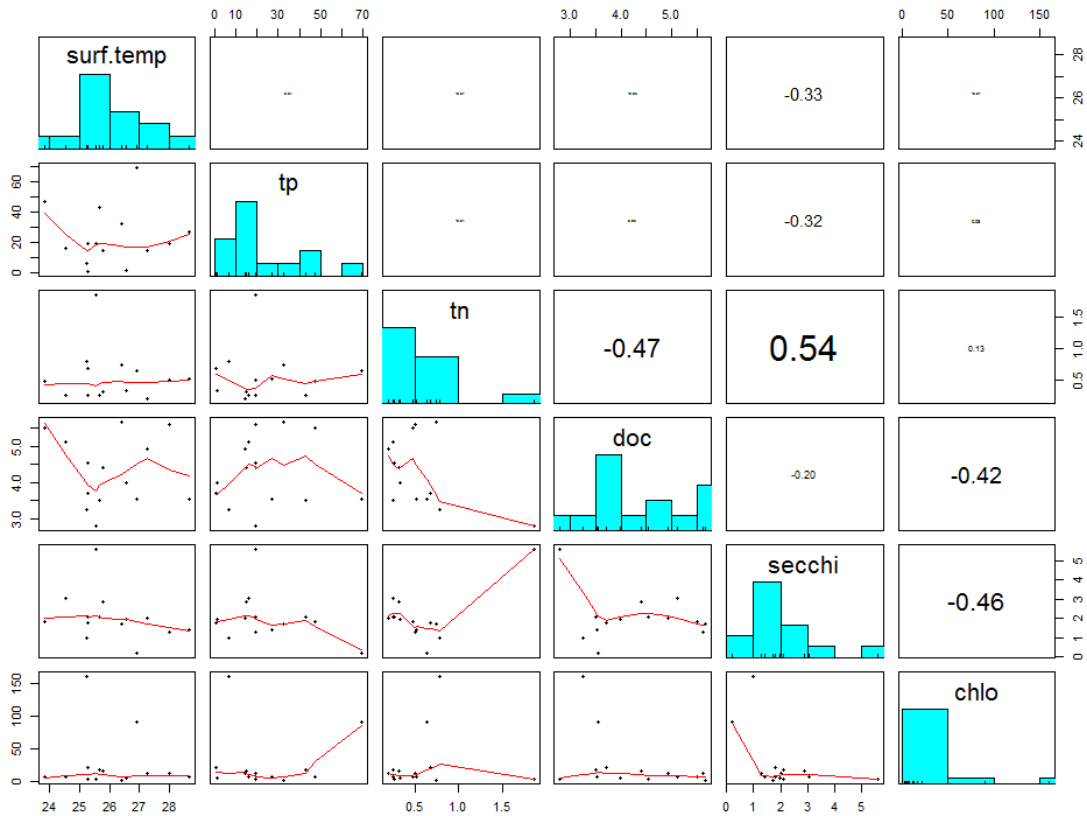


Figure C.3: Pairwise regressions of independent variables for August 2015 sampling. Variables include lake surface temperature (surf.temp), total phosphorous (tp), total nitrogen (tn), dissolved organic carbon (doc), secchi disk depth (secchi), and chlorophyll-a (chlo).

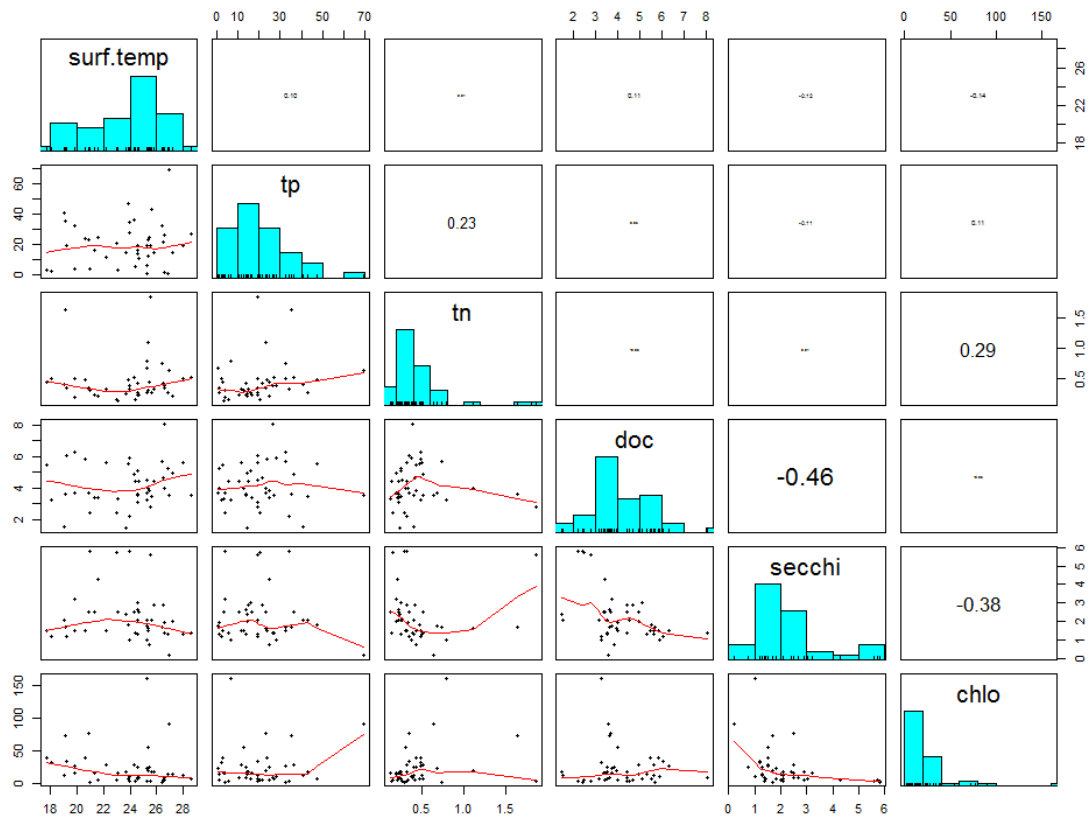
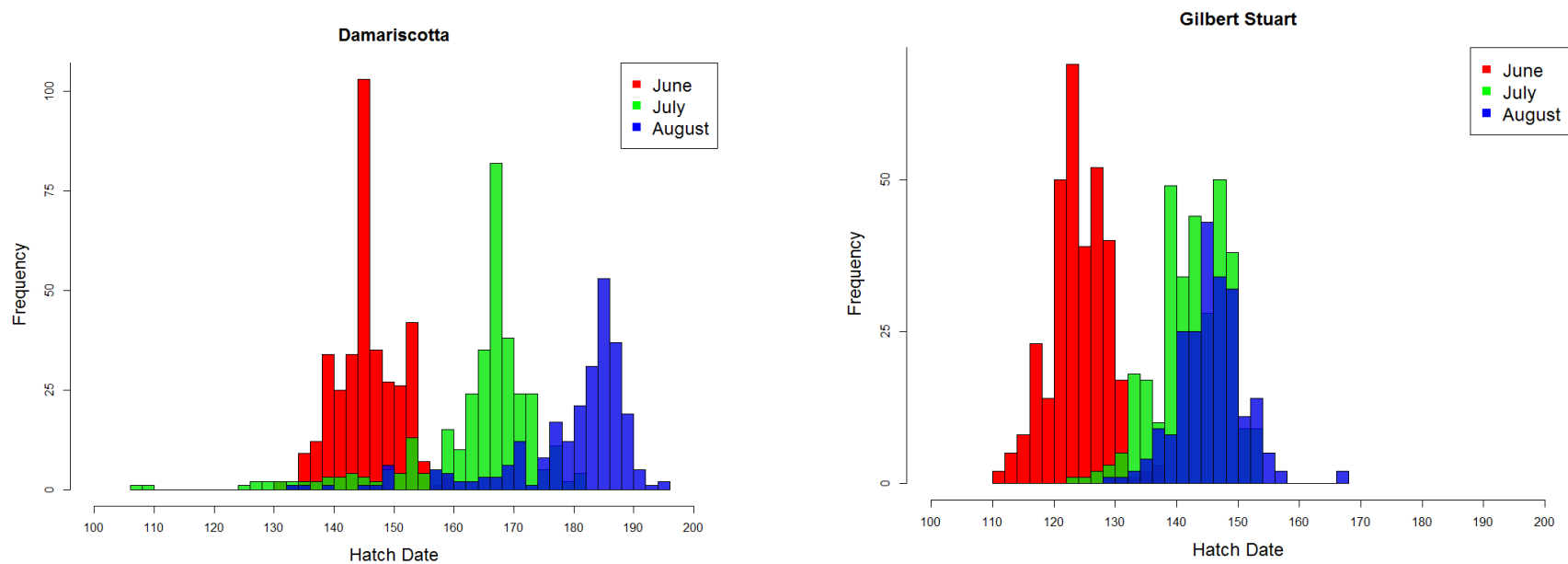


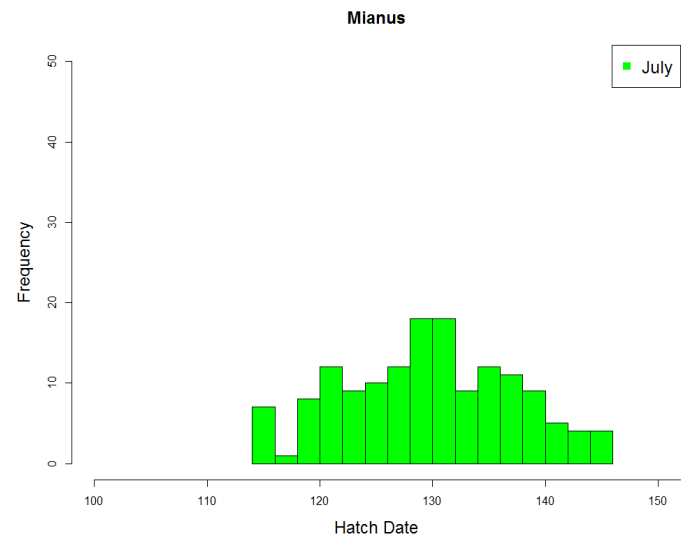
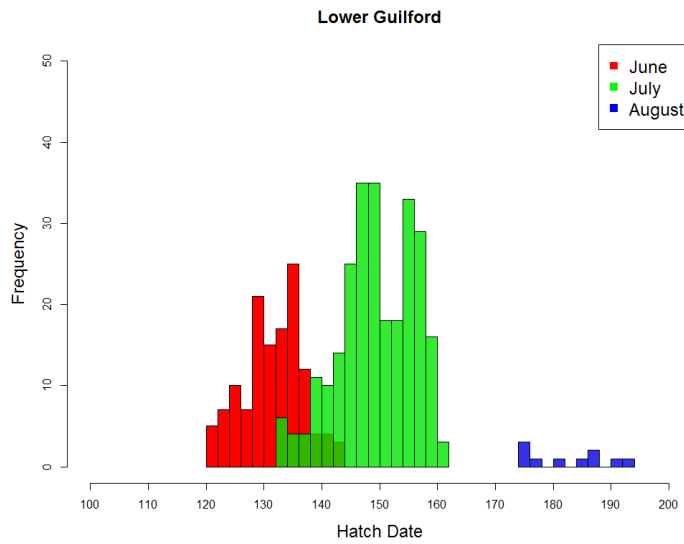
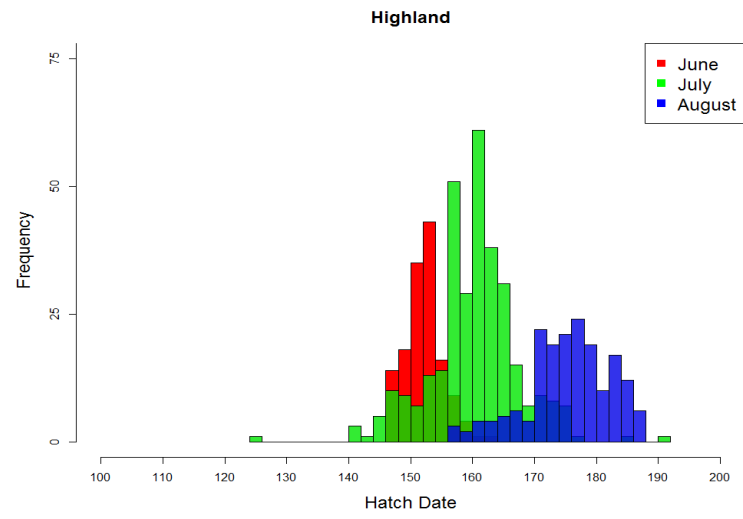
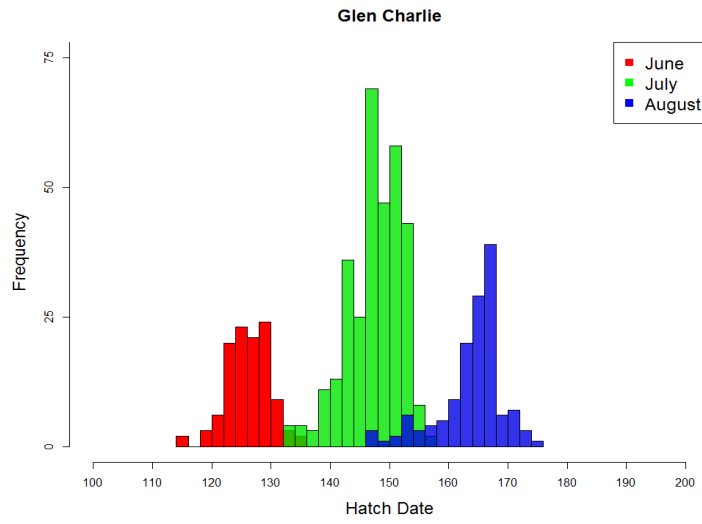
Figure C.4: Pairwise regressions of independent variables averaged across June–August 2015 sampling. Variables include lake surface temperature (surf.temp), total phosphorous (tp), total nitrogen (tn), dissolved organic carbon (doc), secchi disk depth (secchi), and chlorophyll-a (chlo).

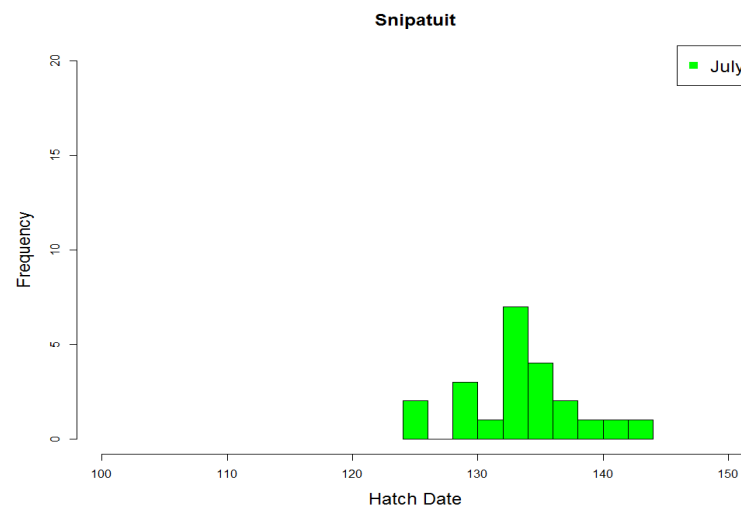
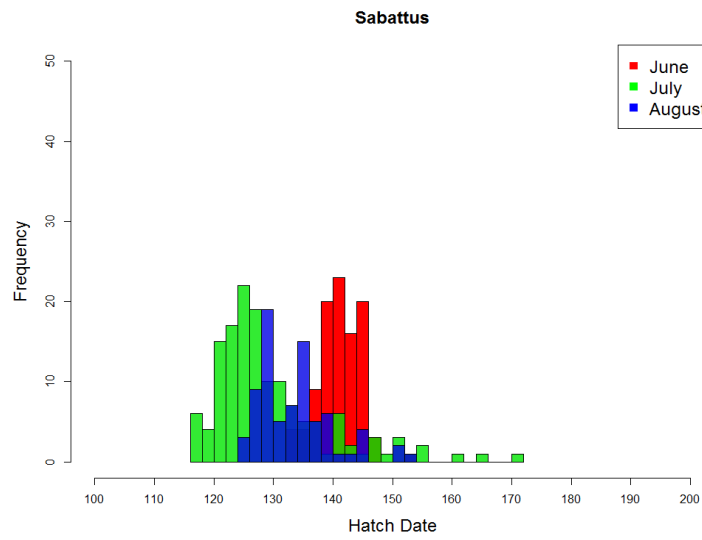
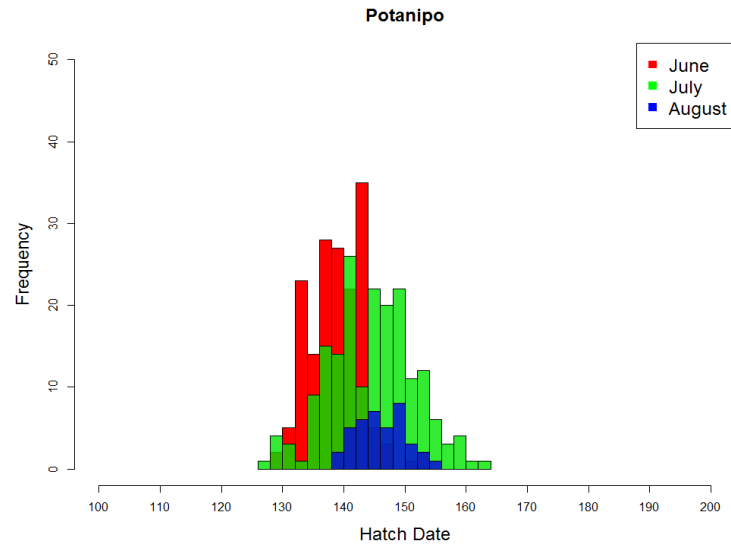
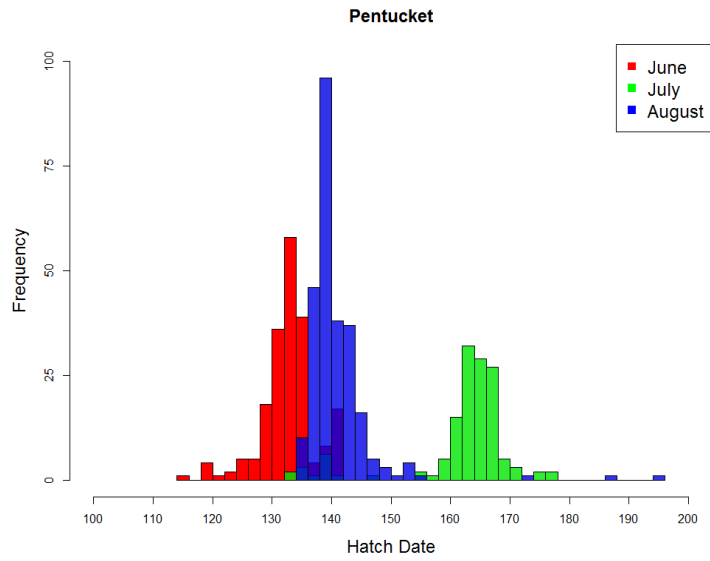
APPENDIX D

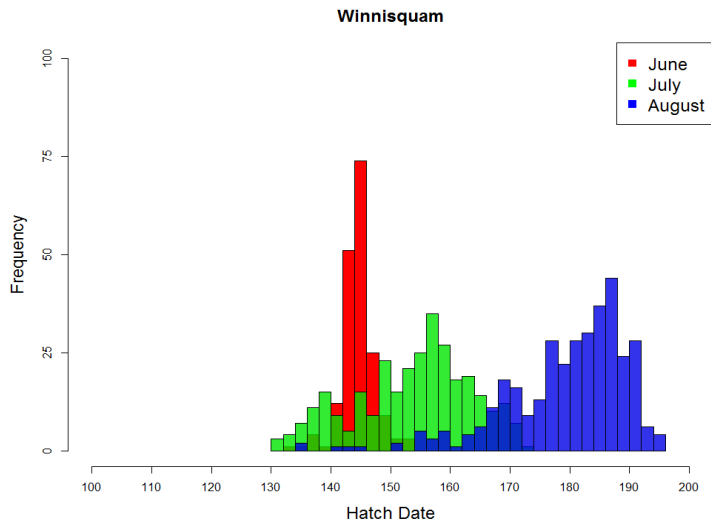
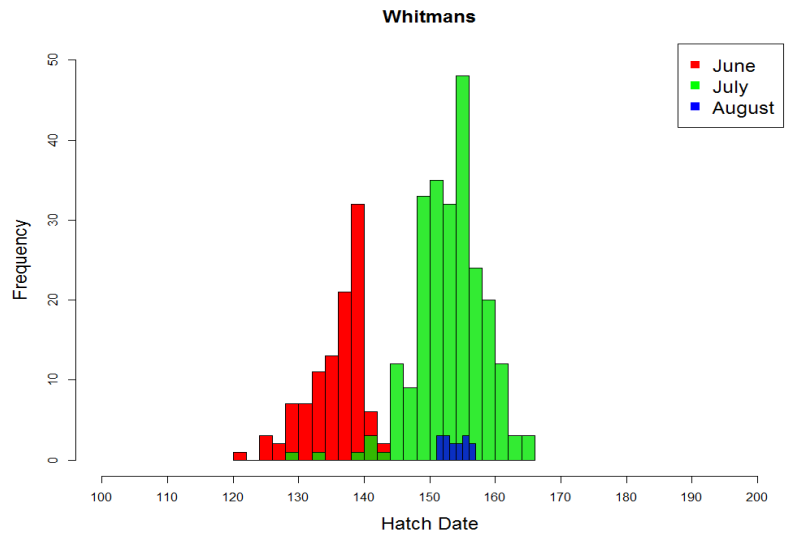
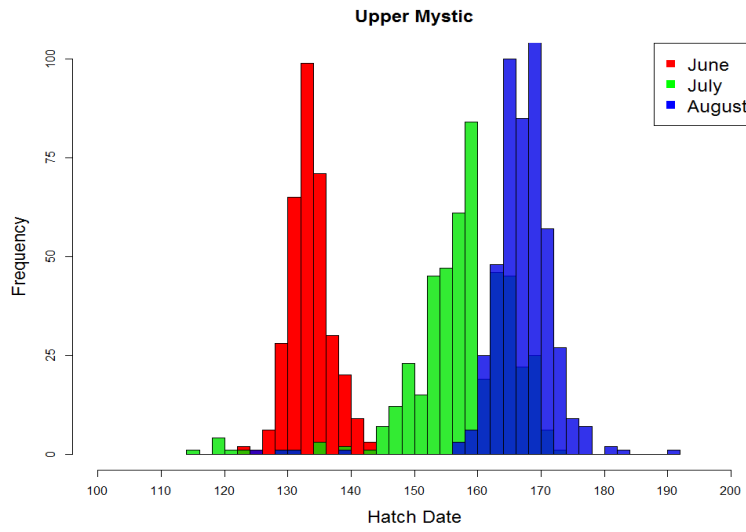
HATCH DATE FREQUENCY DISTRIBUTIONS BY LAKE ACROSS ALL SAMPLING MONTHS

Figure D.1: Hatch-frequency distributions by month for each study lake sampled in 2015. Simulated ages from length-age regressions are included. Note differences in x and y-axis ranges.





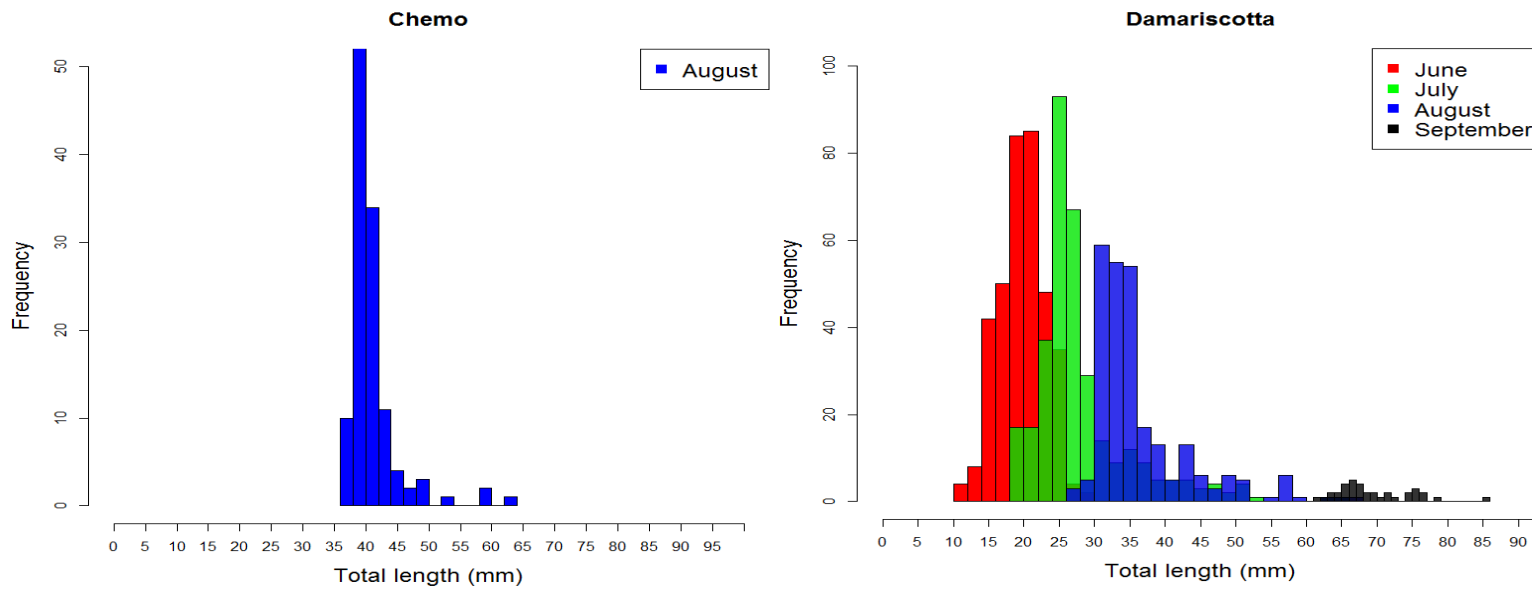


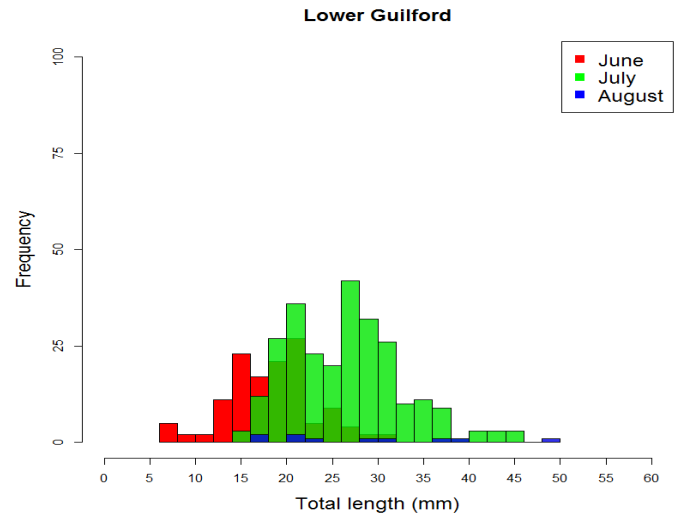
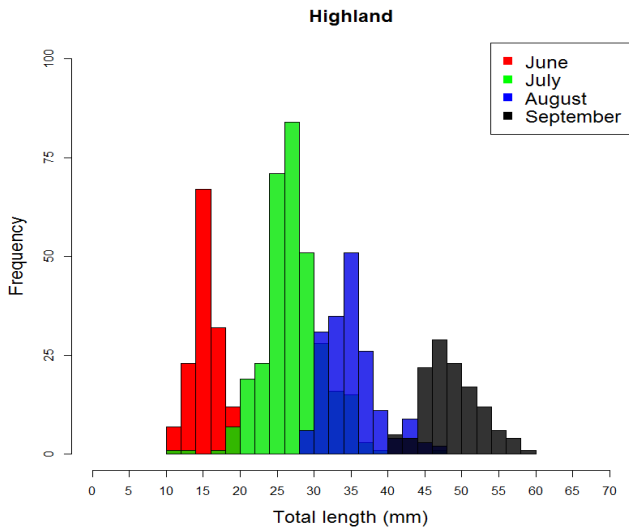
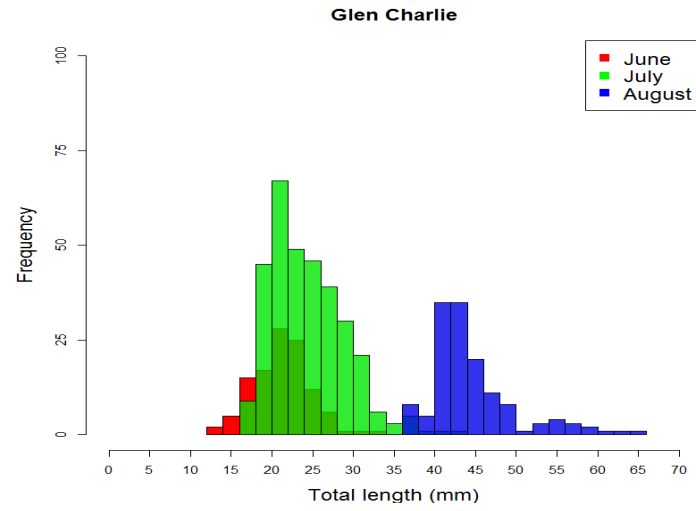
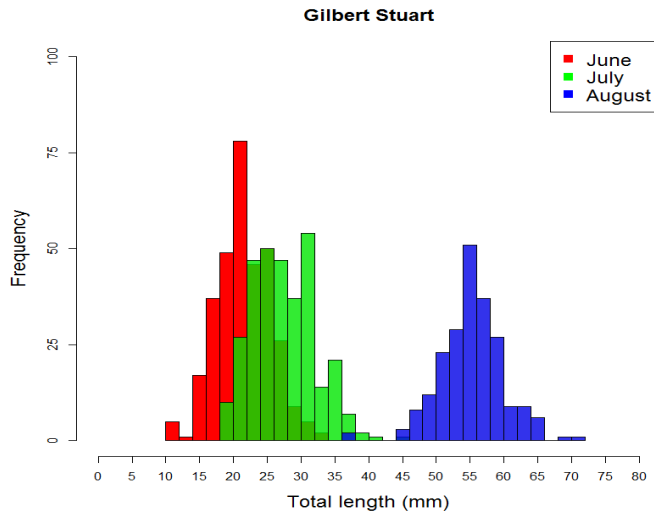


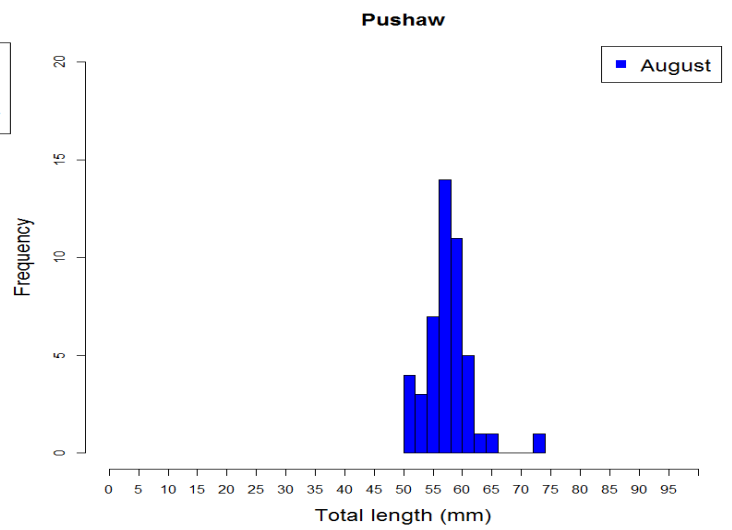
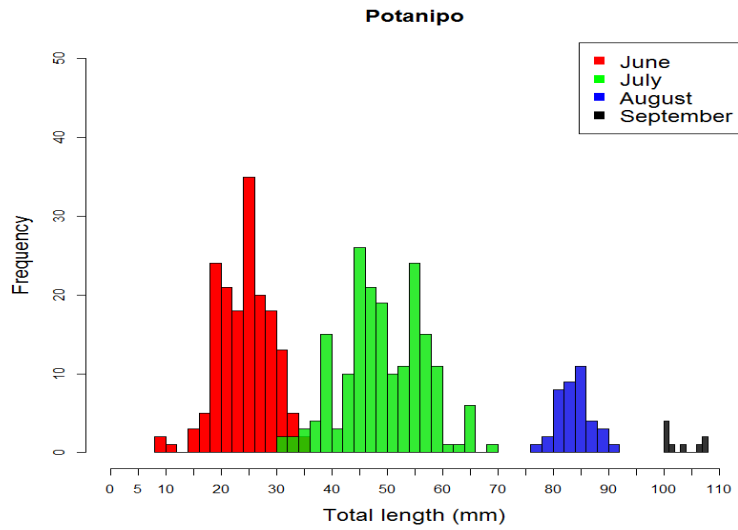
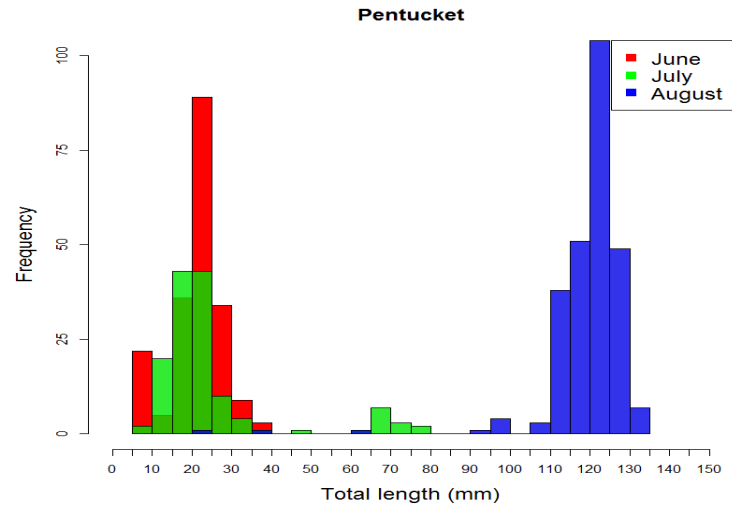
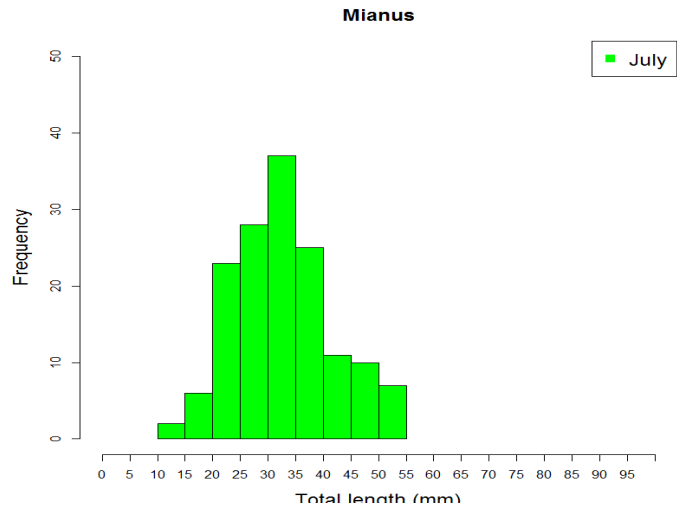
APPENDIX E

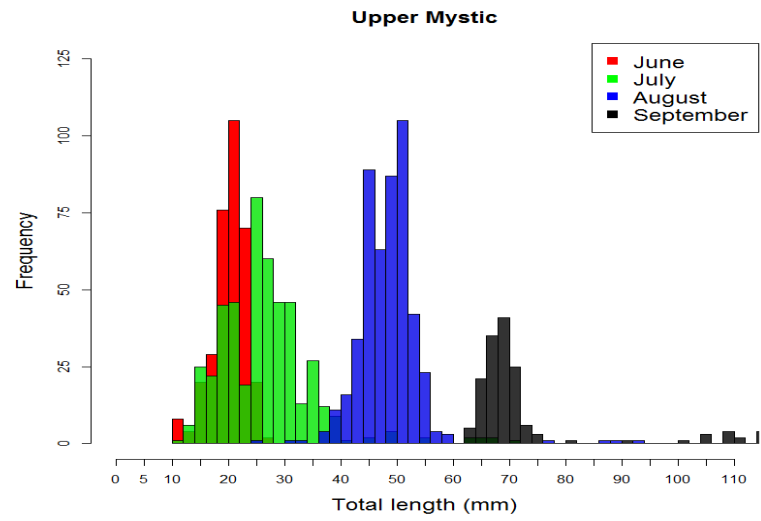
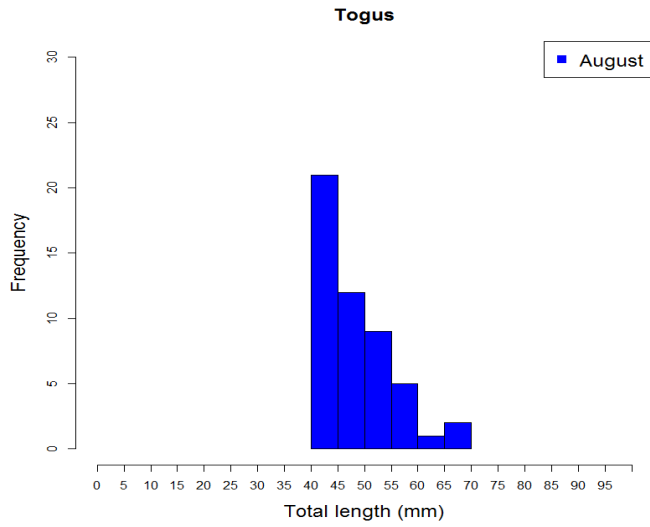
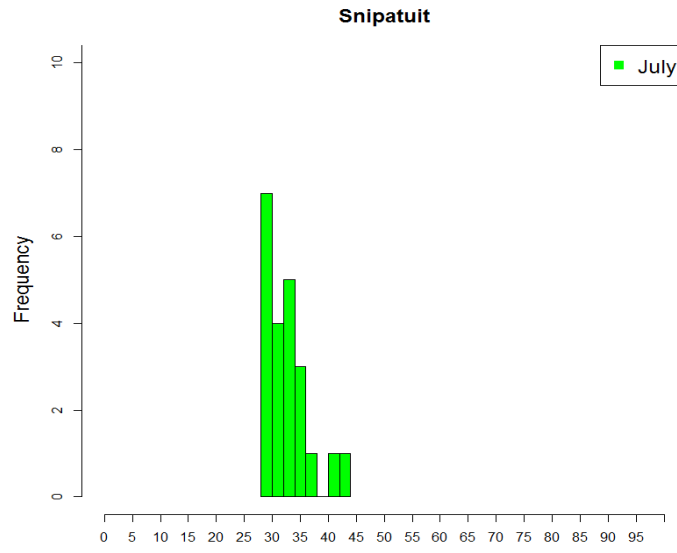
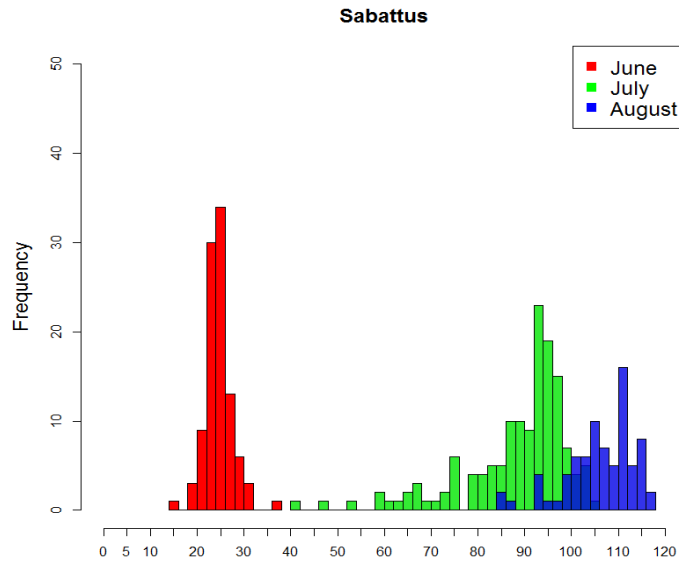
LENGTH FREQUENCY DISTRIBUTIONS BY LAKE ACROSS ALL SAMPLING MONTHS

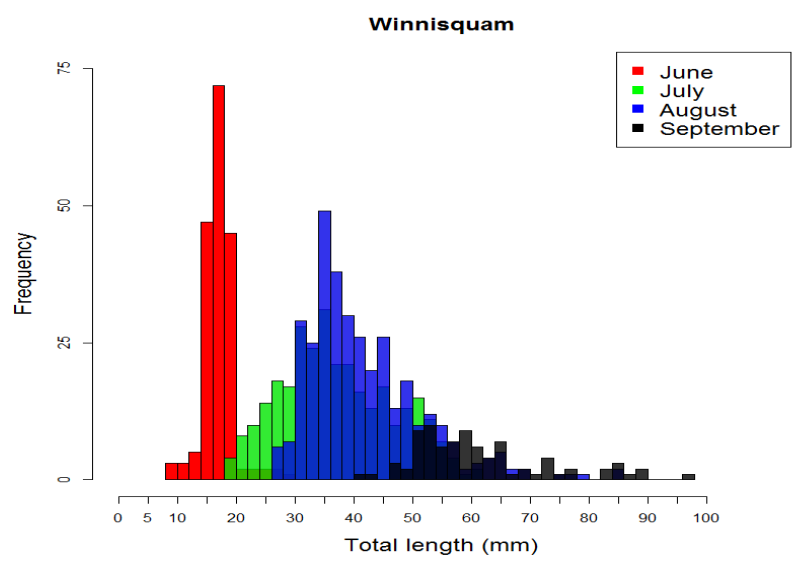
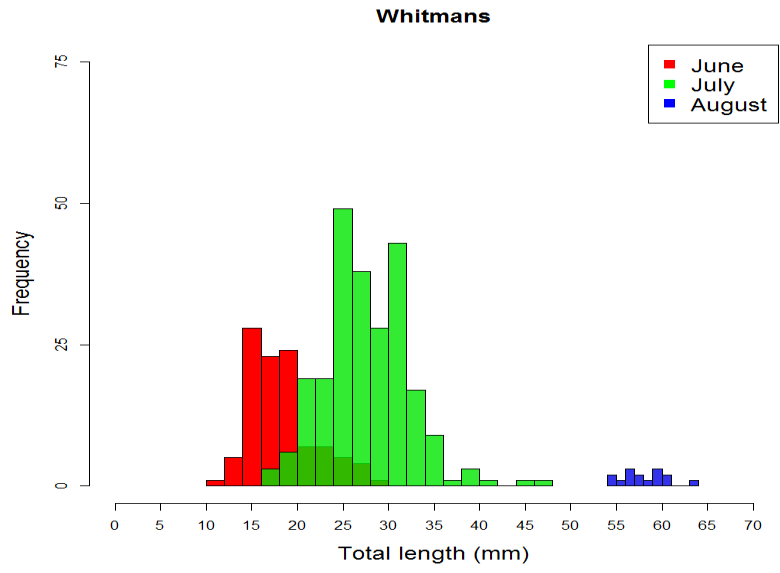
Figure E.1: Length-frequency distributions by month for each study lake sampled in 2015. Note differences in x and y-axis ranges.







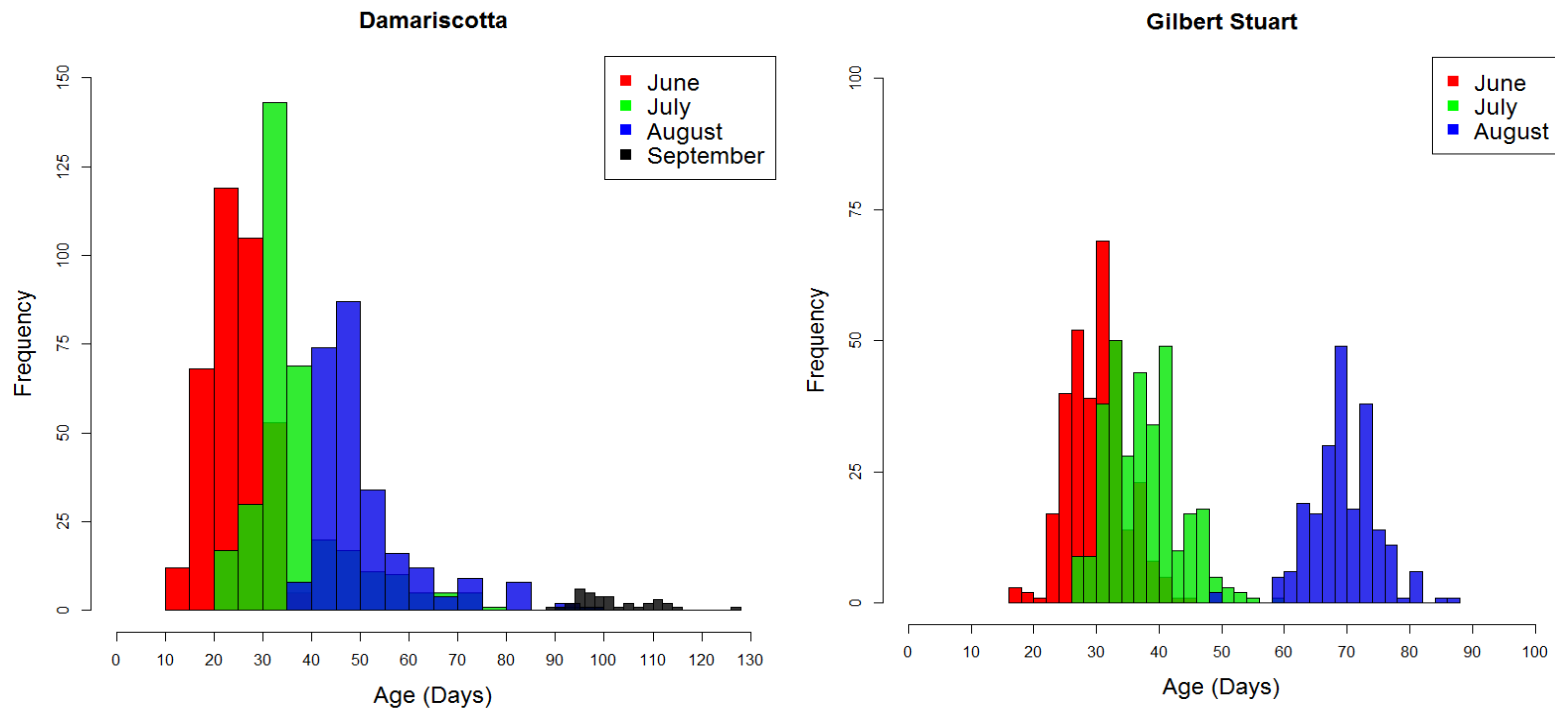


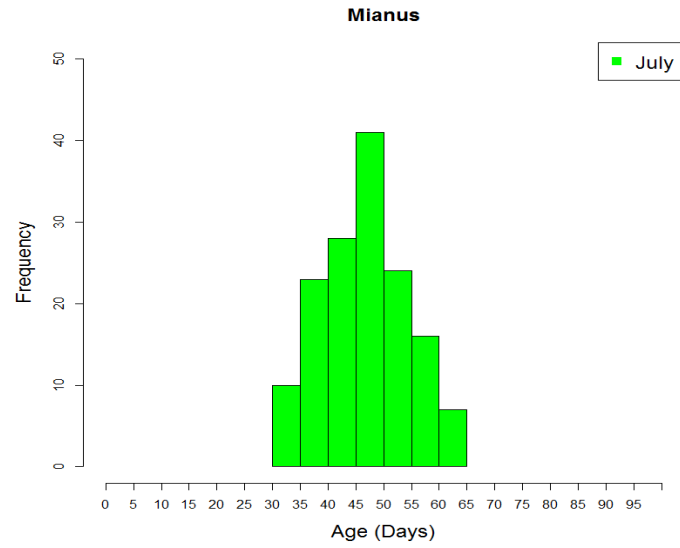
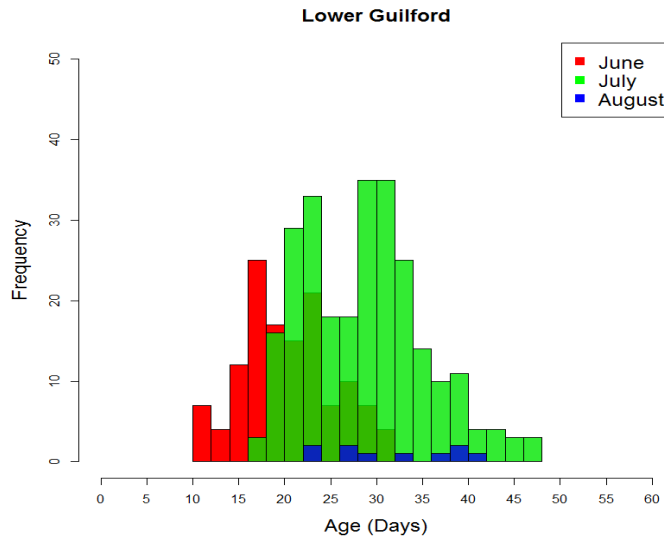
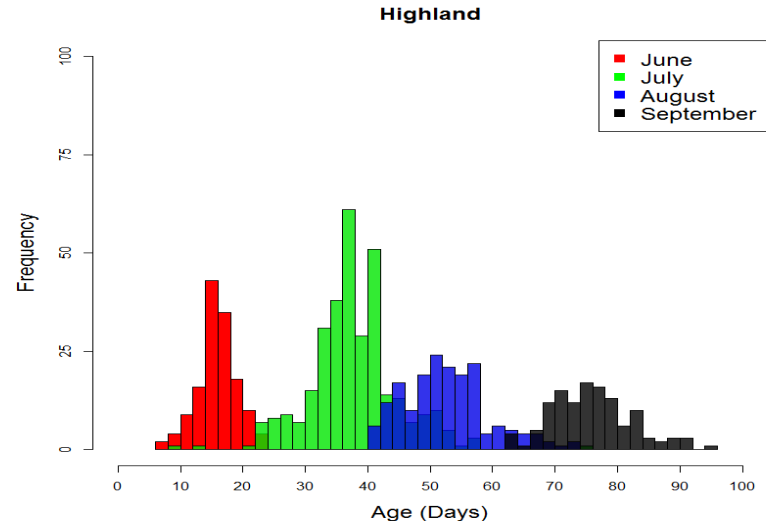
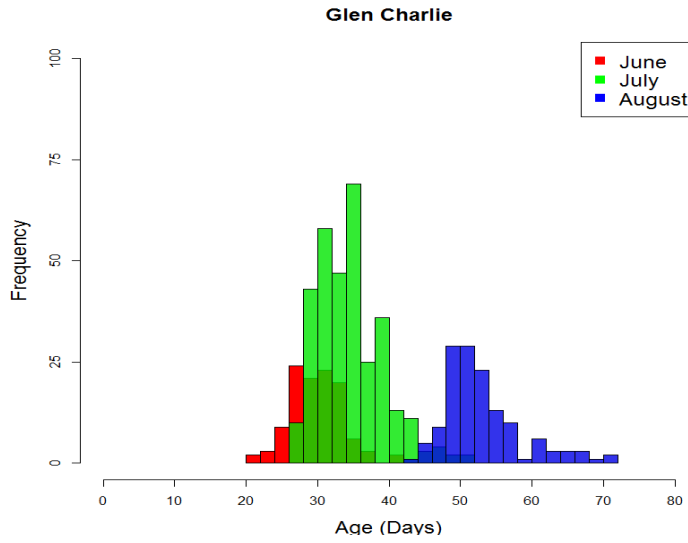


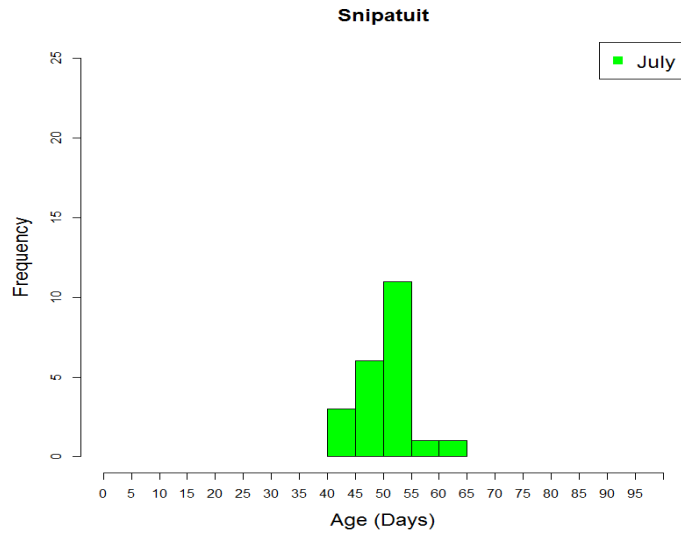
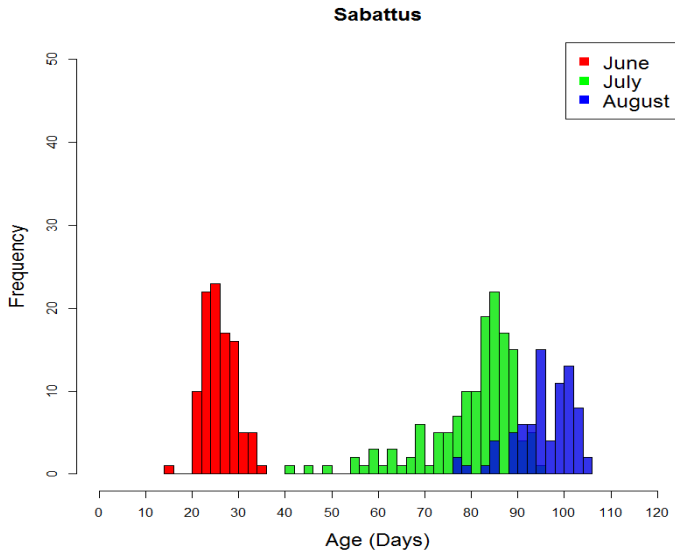
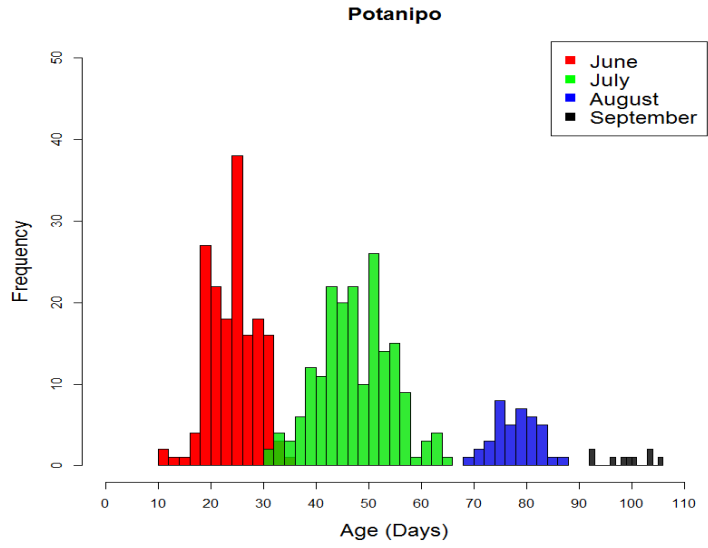
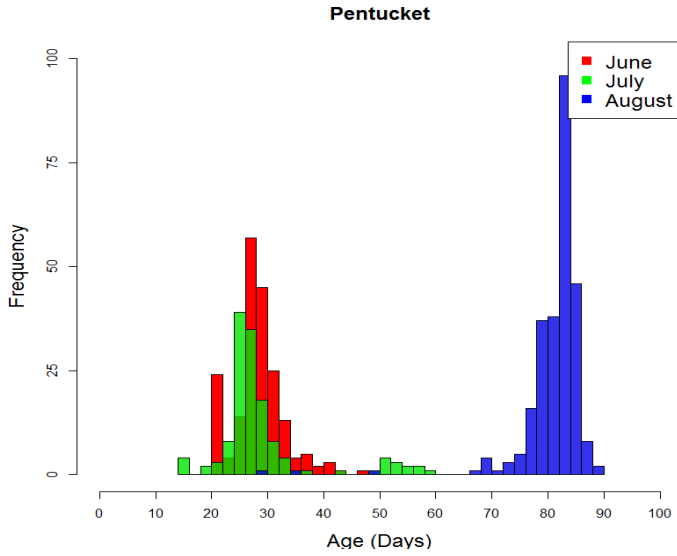
APPENDIX F

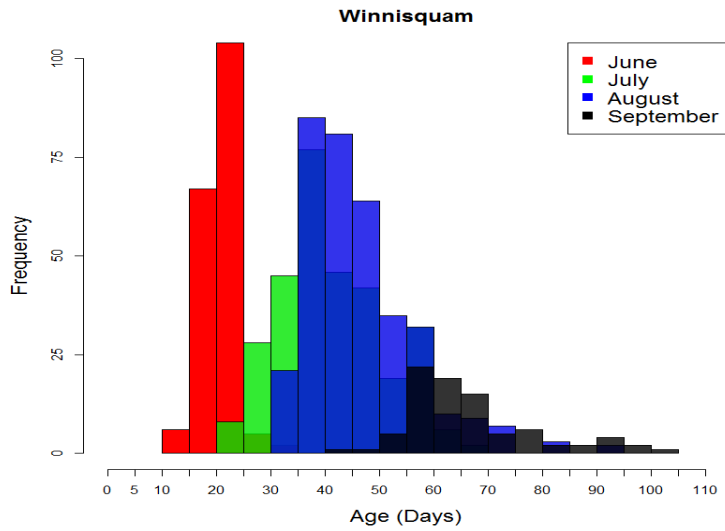
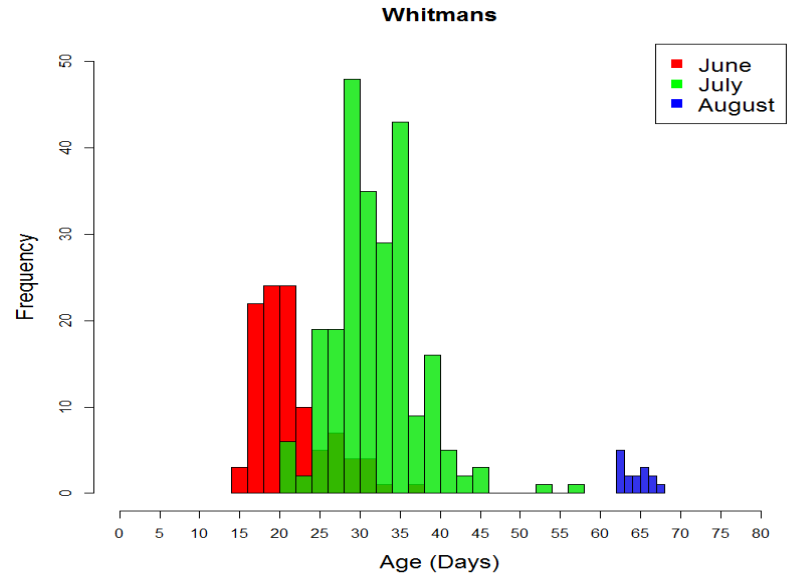
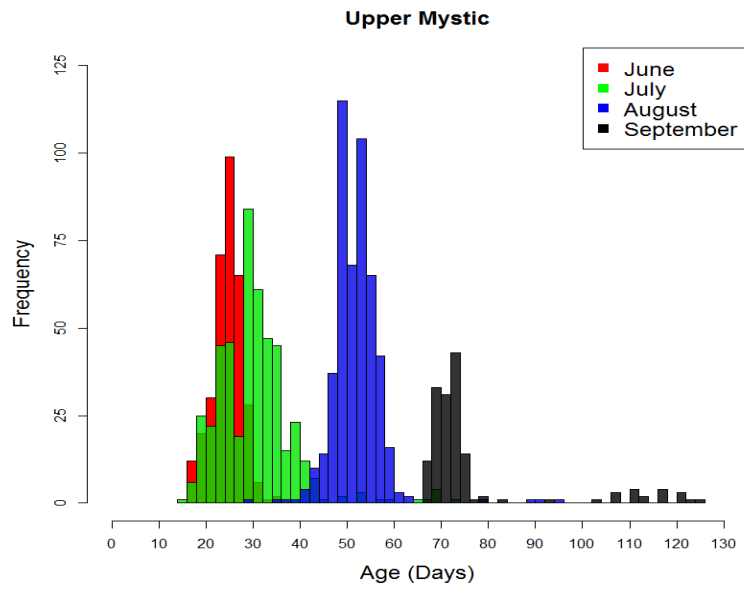
AGE FREQUENCY DISTRIBUTIONS BY LAKE ACROSS ALL SAMPLING MONTHS

Figure F.1: Age-frequency distributions by month for each study lake sampled in 2015. Simulated ages from length-age regressions are included. Note differences in x and y-axis ranges.









APPENDIX G

LENGTH-AGE REGRESSIONS

Table G.1: Length-age regression equations for 11 lakes sampled June–August 2015.

Lake	Equation	R ²	P-value	F-stat	DF
Damariscotta	$A = -6.04172 + 1.55454 * t_l$	0.84	<0.001	474.7	88
Gilbert Stuart	$A = 5.68373 + 1.16106 * t_l$	0.88	<0.001	494	64
Glen Charlie	$A = 11.62192 + 0.93675 * t_l$	0.76	<0.001	365.2	116
Highland	$A = -10.99017 + 1.79351 * t_l$	0.93	<0.001	1458	105
Guilford	$A = 3.15692 + 0.98455 * t_l$	0.71	<0.001	219.6	93
Upper Mystic	$A = 5.36113 + 0.97084 * t_l$	0.91	<0.001	988.8	98
Pentucket	$A = 16.9580 + 0.5426 * t_l$	0.96	<0.001	1946	78
Potanipo	$A = 2.71528 + 0.91397 * t_l$	0.97	<0.001	3827	91
Sabattus	$A = 5.1228 + 0.8570 * t_l$	0.58	<0.001	19.79	51
Whitmans	$A = 2.49952 + 1.07528 * t_l$	0.95	<0.001	686.1	36
Winnisquam	$A = 3.5262 + 1.0297 * t_l$	0.82	<0.001	389.2	85

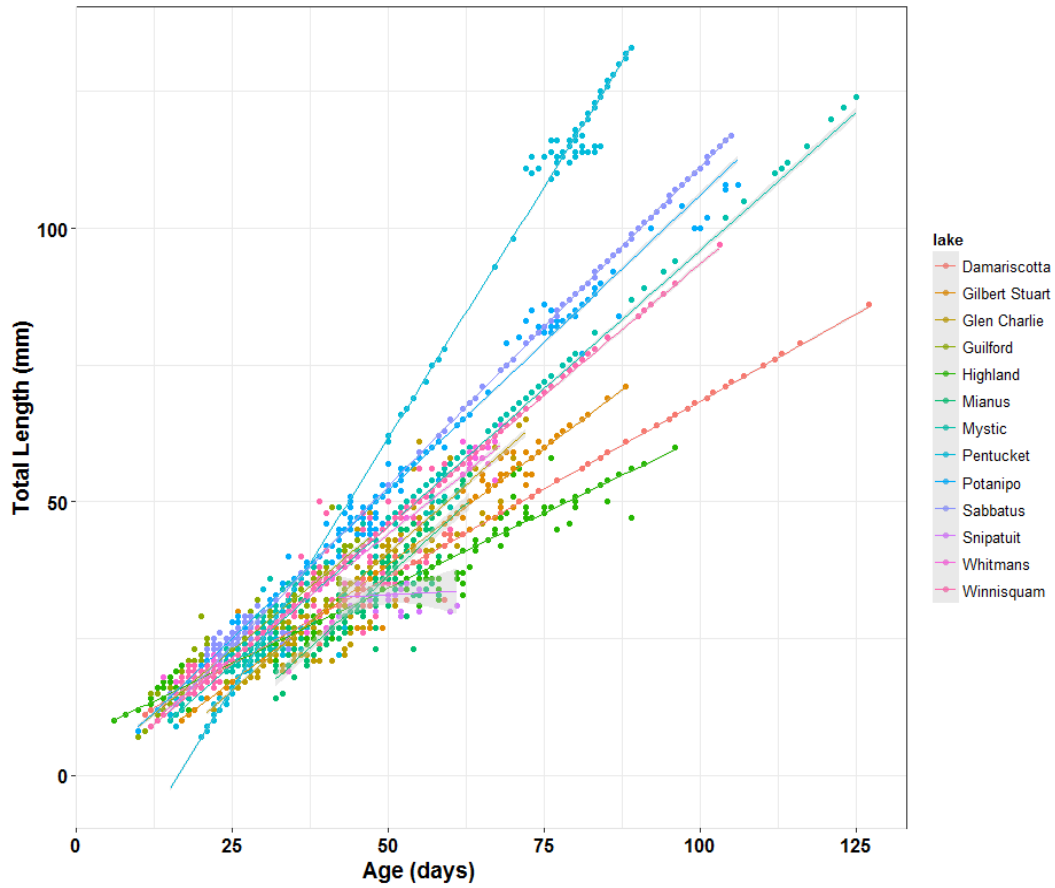


Figure G.1: Length-age regressions for juvenile river herring sampled at 13 lakes, June–September 2015 using true and simulated ages. Lakes are color-coded and a best-fit line from a linear regression model is added. Gray bands represent 95% confidence intervals.

APPENDIX H

INSTANTANEOUS MORTALITY ESTIMATES

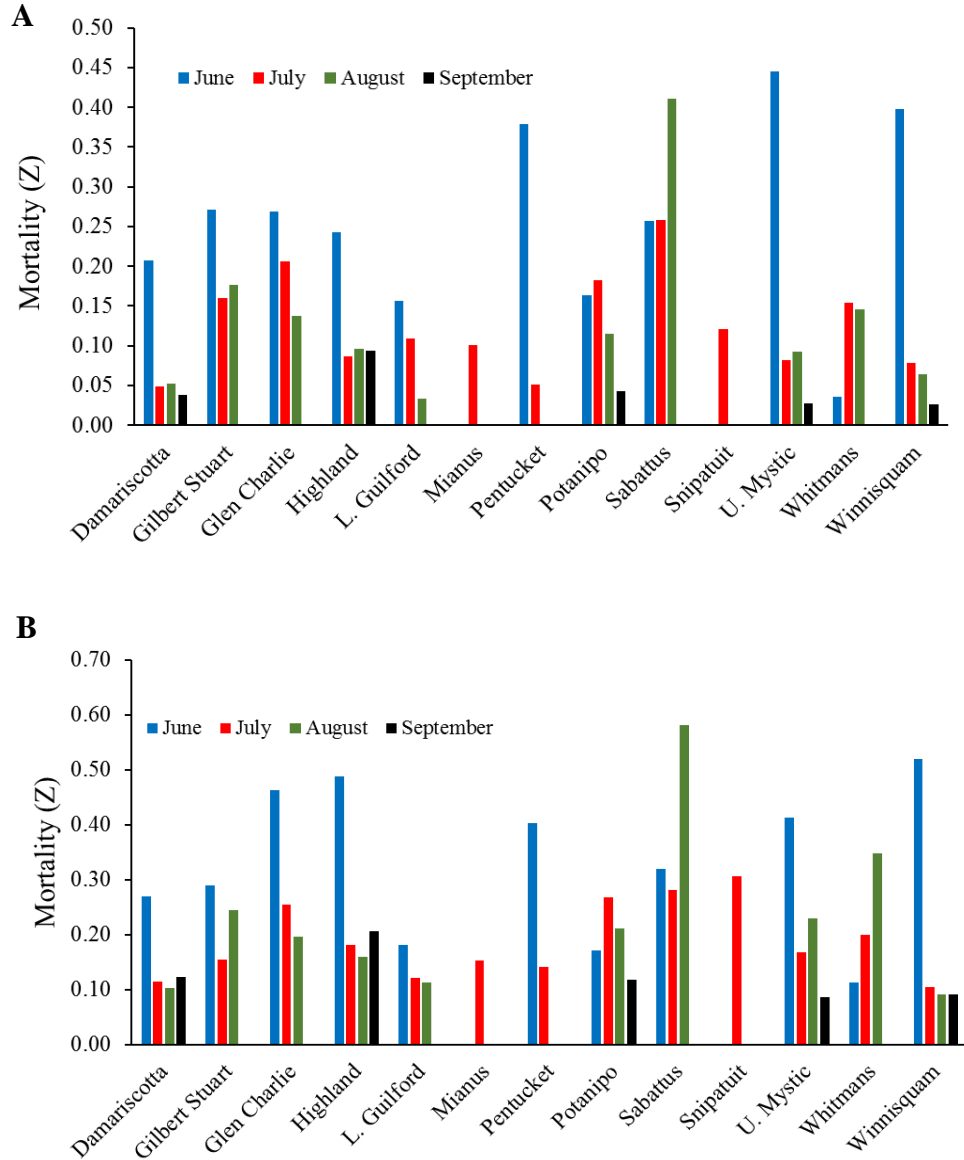


Figure H.1: Monthly instantaneous mortality estimates (Z) for 13 lakes sampled June–September 2015 using A) weighted linear regression and B) Chapman-Robson estimators.

Table H.1: Monthly instantaneous mortality estimates (Z) with standard errors (SE) for 13 lakes sampled June–September 2015 using A) weighted linear regression and B) Chapman-Robson estimators.

Lake	Month	Linear Regression		Chapman-Robson	
		Z	SE	Z	SE
Damariscotta	June	0.208	0.065	0.269	0.030
Damariscotta	July	0.049	0.008	0.115	0.015
Damariscotta	August	0.052	0.011	0.103	0.013
Damariscotta	September	0.038	0.017	0.123	0.024
Gilbert Stuart	June	0.271	0.052	0.289	0.025
Gilbert Stuart	July	0.160	0.022	0.154	0.018
Gilbert Stuart	August	0.177	0.036	0.245	0.025
Glen Charlie	June	0.269	0.056	0.463	0.050
Glen Charlie	July	0.206	0.021	0.255	0.019
Glen Charlie	August	0.137	0.015	0.197	0.015
Highland	June	0.243	0.349	0.487	0.131
Highland	July	0.087	0.030	0.181	0.024
Highland	August	0.096	0.029	0.159	0.020
Highland	September	0.094	0.050	0.207	0.030
L. Guilford	June	0.156	0.029	0.182	0.020
L. Guilford	July	0.109	0.016	0.122	0.014
L. Guilford	August	0.033	0.016	0.113	0.021
Mianus	July	0.101	0.021	0.153	0.017
Pentucket	June	0.378	0.067	0.403	0.048
Pentucket	July	0.051	0.017	0.141	0.029
Pentucket	August	-	-	-	-
Potanipo	June	0.164	0.034	0.172	0.024
Potanipo	July	0.183	0.045	0.268	0.026
Potanipo	August	0.115	0.031	0.212	0.032
Potanipo	September	0.043	0.017	0.118	0.023
Sabattus	June	0.256	0.036	0.319	0.030
Sabattus	July	0.258	0.039	0.281	0.022
Sabattus	August	0.410	0.274	0.581	0.074
Snipatuit	July	0.121	0.082	0.307	0.063
U. Mystic	June	0.445	0.049	0.412	0.044
U. Mystic	July	0.082	0.010	0.168	0.022
U. Mystic	August	0.093	0.017	0.229	0.062
U. Mystic	September	0.027	0.012	0.086	0.021
Whitmans	June	0.035	0.016	0.112	0.015
Whitmans	July	0.154	0.020	0.200	0.020

Whitmans	August	0.145	0.079	0.348	0.103
Winnisquam	June	0.397	0.072	0.520	0.050
Winnisquam	July	0.079	0.015	0.105	0.009
Winnisquam	August	0.065	0.007	0.092	0.007
Winnisquam	September	0.026	0.011	0.092	0.013

APPENDIX I

MIXED-MODEL PARAMETER ESTIMATES AND RESIDUAL PLOTS

Table I.1: Parameter estimates for a) abiotic and b) biotic factors affecting juvenile river herring density, growth, and mortality.

Density Models							
Effect	^a DOC x Julian + (1 lake)				^b Mortality + Length + (1 lake)		
	β	SE	P		β	SE	P
Intercept	3.6633	0.8594	<0.0001*	Intercept	-3.1000	0.5432	<0.0001*
DOC	3.7660	0.9486	<0.0001*	Mortality	-0.6250	0.2923	0.0325*
Julian	-0.0291	0.0040	<0.0001*	Length	-1.0490	0.1560	<0.0001*
DOC x Julian	-0.0212	0.0050	<0.0001*				

Growth Models							
Effect	^a Secchi+ (1 lake)				^b Density + (1 lake)		
	β	SE	P		β	SE	P
Intercept	-0.3173	0.0477	<0.0001*	Intercept	-0.3942	0.0531	<0.0001*
Secchi	-0.0501	0.0547	<0.05*	Density	-0.0389	0.0174	<0.05*

Mortality Models							
Effect	^a TP + (1 lake)				^b Hatch + (1 lake)		
	β	SE	P		β	SE	P
Intercept	-1.6298	0.0837	<0.0001*	Intercept	-1.6440	0.0856	<0.0001*
TP	0.1774	0.0848	<0.05	Hatch	-0.3260	0.0721	<0.0001*

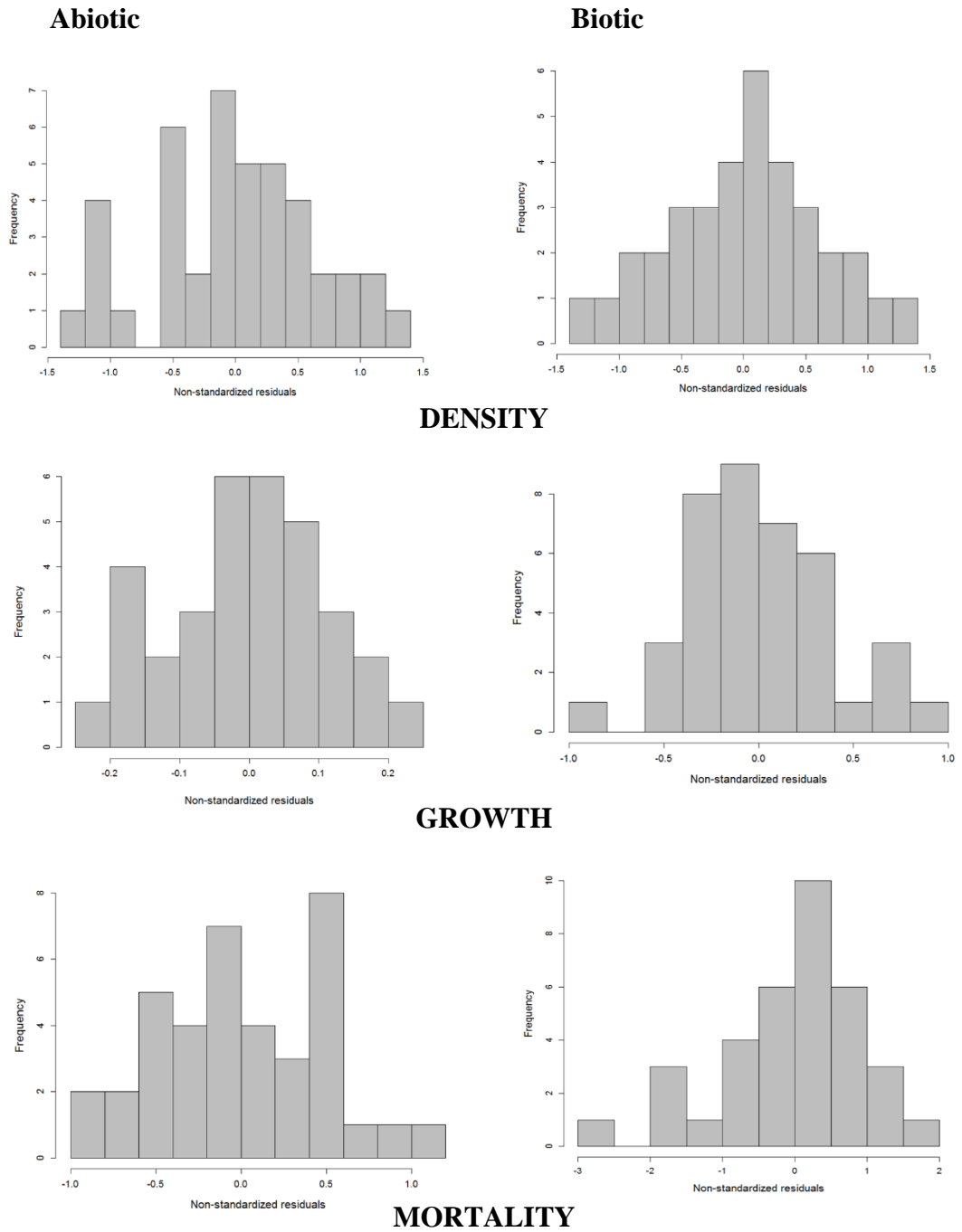


Figure I.1: Histograms of non-standardized residuals from top abiotic and biotic mixed-effect models explaining variation in juvenile river herring density, growth, and mortality.

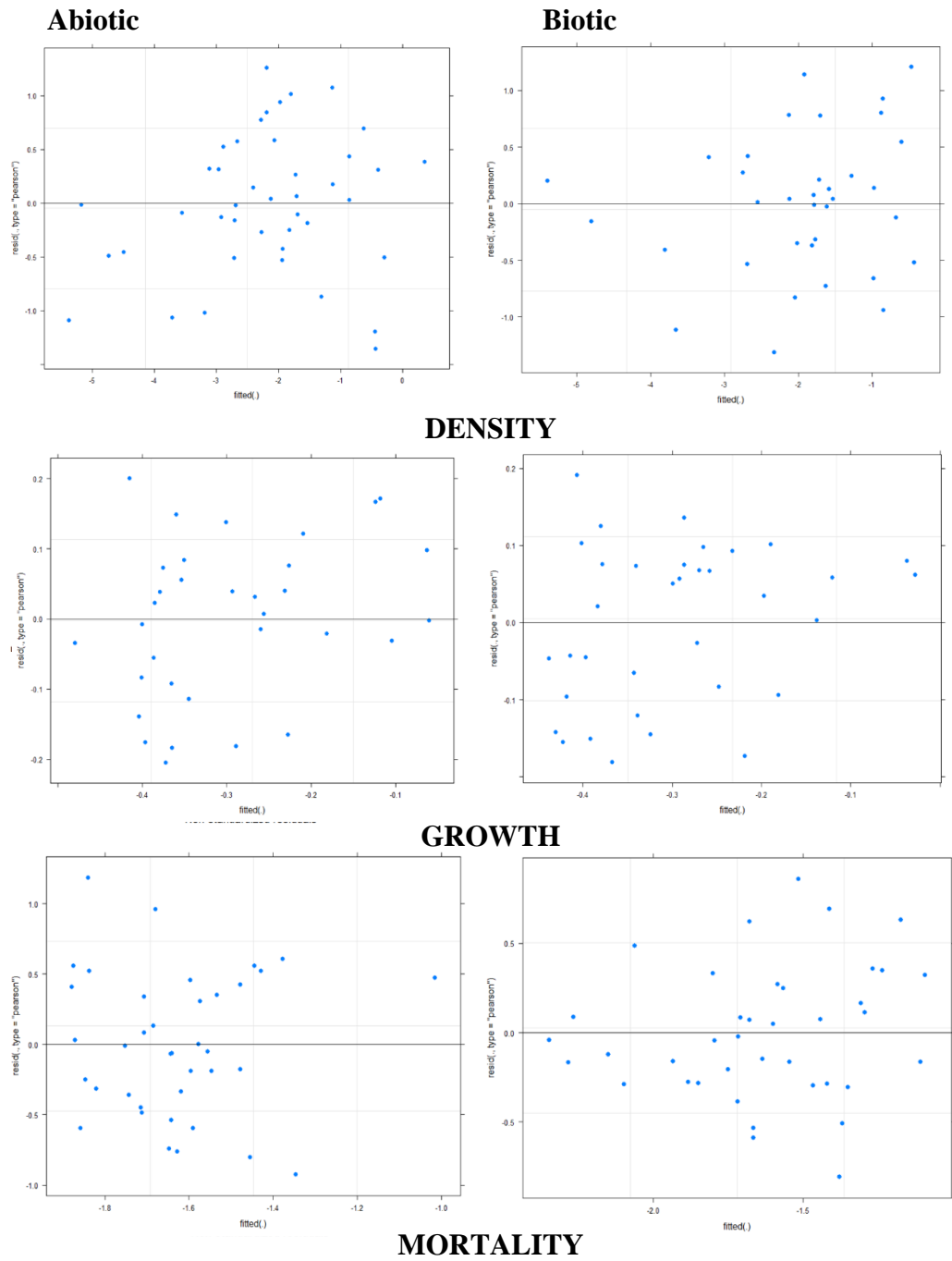


Figure I.2: Pearson’s R residuals vs. fitted plots from top abiotic and biotic mixed-effect models explaining variation in juvenile river herring density, growth, and mortality.

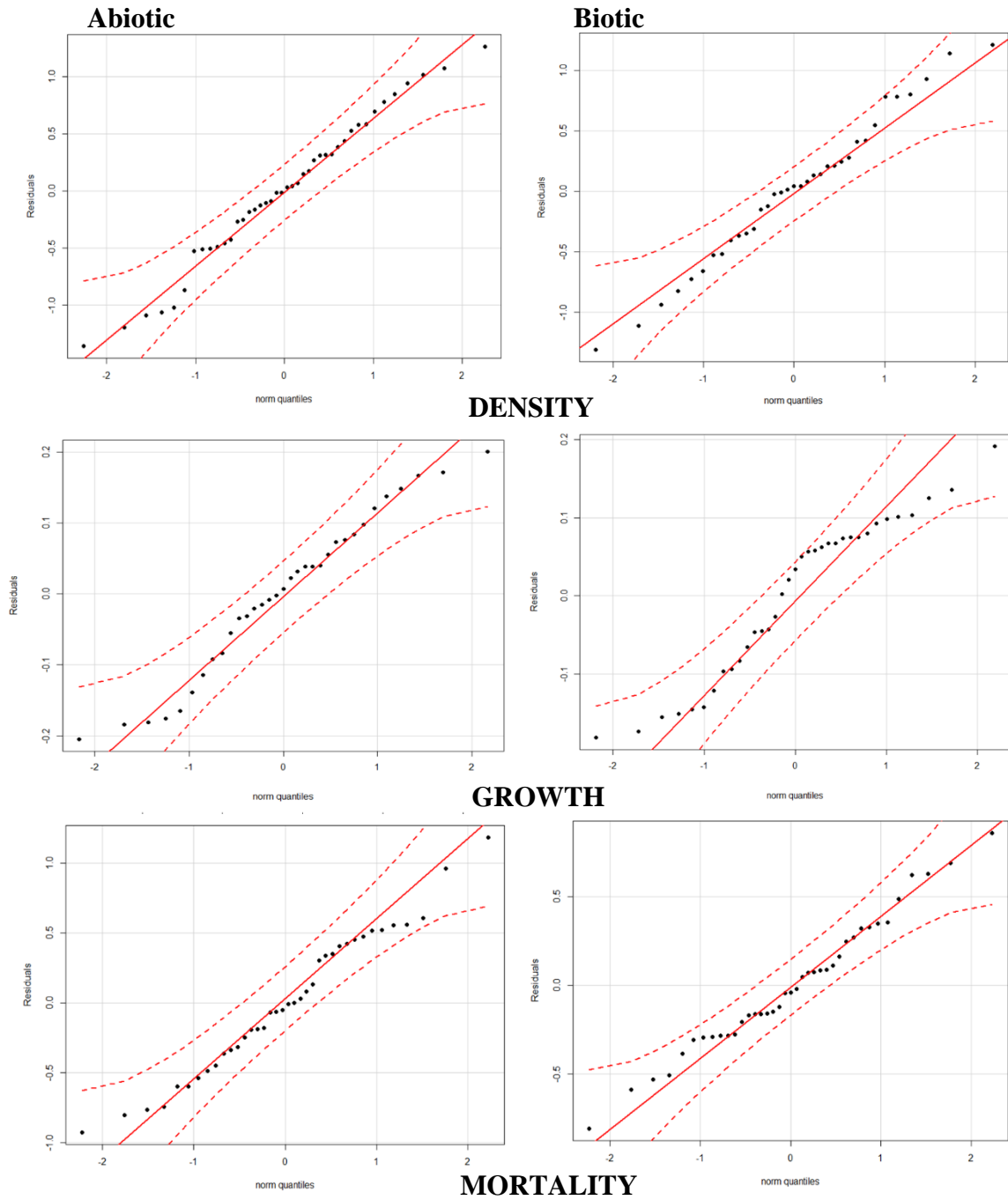


Figure H.3: Quantile-quantile residual plots from top abiotic and biotic mixed-effect models explaining variation in juvenile river herring density, growth, and mortality. Solid red line indicates normally distributed residuals. Dashed lines are 95% confidence intervals.

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