

SPATIAL COMMUNITY ECOLOGY, CANNIBALISM, AND THE RESILIENCE  
OF LAKE CHAMPLAIN FORAGE FISH

A Dissertation

Presented to the Faculty of the Graduate School  
of Cornell University

In Partial Fulfillment of the Requirements for the Degree of  
Doctor of Philosophy

by

Paul Warren Simonin

August 2015

© 2015 Paul Warren Simonin

SPATIAL COMMUNITY ECOLOGY, CANNIBALISM, AND THE RESILIENCE  
OF LAKE CHAMPLAIN FORAGE FISH

Paul Warren Simonin, Ph. D.

Cornell University 2015

Nonnative species and changes in the abiotic environment are current drivers of ecological change around the world. Understanding and forecasting the response of fish populations and communities to these types of changes is the focus of the following research conducted in Lake Champlain. Three general themes run throughout this work: adaptation to change, fish early life history, and spatial ecology.

In the first section of this work, we compared hatch timing, abundance, growth rates, and subsequent survival of age 0 rainbow smelt *Osmerus mordax* and alewife *Alosa pseudoharengus*. Rainbow smelt hatched almost a month earlier than alewife. Later hatching individuals of both species grew faster than those hatching earlier. Because cannibalism by rainbow smelt is likely the mortality source for age-0 Rainbow smelt, early hatching may not be advantageous as the overlap between adult and age-0 rainbow smelt is highest early in the season. However, alewife, first found in Lake Champlain in 2003, may increase age 0 rainbow smelt summer mortality. Increased summer mortality in rainbow smelt should, in turn, favor selection for early hatching.

Using stable isotopes of C and N, we found that alewife are now a large component of predator diets, and in particular of the diets of Atlantic salmon and walleye. Walleye and rainbow smelt  $\delta^{15}\text{N}$  values changed significantly from pre-alewife  $\delta^{15}\text{N}$  values of the late 1990's. These changes represent a preferential switch to feeding on alewife by Atlantic salmon which was likely caused by the distribution patterns of these species.

Distribution patterns of adults and age 0 fish were simulated on a daily basis, and subsequent age 0 mortality rates calculated. Rainbow smelt age 0 mortality rates are highest when rainbow smelt adults are abundant and alewife age 0 mortality rates are highest when alewife adults are abundant, allowing the two species to co-exist. Mortality rates were higher under normal temperature regimes, but late-summer mortality rates were higher in our climate change scenario because of increased overlap of adult and age 0 distributions. Our simulation suggests spatial distribution patterns should be accounted for when forecasting the interacting effects of climate change aquatic nonnative species.

## **BIOGRAPHICAL SKETCH**

Paul W. Simonin was born in Hamilton, New York, and grew up in the central part of New York State. His interest in nature was instilled at a young age through his family and through time spent in the Adirondack region of New York. His father, an aquatic biologist with the New York State Department of Environmental Conservation (NY DEC), was and remains an inspiration for Paul, and his example demonstrated that one could have a career in the field of environmental science. After graduating from Holland Patent High School, Paul attended the State University of New York College of Environmental Science and Forestry, where he studied ecology. After work with the NY DEC during summers and vacations, and a fellowship working with the National Oceanic and Atmospheric Administration, Paul began his Masters studies in 2007 at the University of Vermont. This research on Lake Champlain included collaboration with Lars Rudstam and Pat Sullivan at Cornell, and led to his acceptance into the Natural Resources PhD program at Cornell in 2009.

## ACKNOWLEDGMENTS

My time at Cornell working toward a PhD taught me many lessons both professionally and personally. Reaching the end of this path would not have been possible alone, and I am grateful to the many colleagues, friends, and family who have guided me and walked with me along the way.

I am grateful for my advisor Lars Rudstam, who has been an enthusiastic support for me all these years. Thank you, Lars, for your investment in me as a professional ecologist. I have appreciated your patience and support for my wandering and wide interests, and for your steady guidance regarding our Lake Champlain research. Thank you for taking time to meet and work through challenges even when my data, models, and ideas were still quite raw. Your curiosity and thoughtfulness as an ecologist combined with your positive and lighthearted nature have been a great example to me, and one I will continue to reflect on and learn from.

My committee members have been helpful and supportive throughout the various phases of my time here at Cornell. Pat Sullivan has been involved in this Lake Champlain research from its very beginning. Thank you, Pat, for you working with me through all of the quantitative aspects of this research, and for your kind patience with me as I tried to build quantitative skills. Thank you also for pushing to refine my writing and communication of this work in these later stages of the project. Norman Uphoff has been a helpful presence and advisor for my work in Indonesian fishing communities, and has allowed me to learn about participatory rural development from his decades of experience around the world. Thank you, Norman. Cliff Kraft has been

helpful both as an aquatic ecologist with kindred interests and work in the Adirondacks, and also as one interested in the methods and practice of science. In addition to your helpful guidance regarding alewife and smelt ecology, thank you Cliff for your thoughtfulness regarding the interplay between science and the humanities, and for our many interesting conversations in this regard.

I must also thank many individuals in Vermont and at the Cornell Biological Field Station. Donna Parrish has been a supportive advisor and colleague, and in addition to her skill as a fisheries biologist, we are all grateful for her smooth handling of the logistical and financial aspects of our Lake Champlain research. Bernie Pientka's presence, advice, and feedback throughout this work has been a tremendous help as I sought to ask questions relevant to managers and others in the Lake Champlain fisheries community. Many thanks also must go to Dave Gibson, Nick Staats, and others with Vermont Fish and Wildlife for your partnership in this work. While at the Cornell Biological Field Station I have enjoyed and benefited from working alongside many great people in addition to Lars. I would be remiss if I did not thank Allison, Amy, Annie, Brent, Brian, Chris, Dave, Ed, Ellen, Jim, John, Kristen, Randy, Robin, Sam, Sarah, Scott, Toby, Tom, and Willie. Thank you for all the ways you have helped and taught me.

I thank the National Oceanic and Atmospheric Administration for funding this research through the Lake Champlain Sea Grant program. Additional support for research during my time at Cornell came from the Atkinson Center for a Sustainable Future and from the Kieckhefer Adirondack Fellowship.

I would finally like to thank many friends and family who have walked with me through my years here at Cornell. Thank you, Abby, Annise, Bill, Brian, Casey, Christian, Claire, David, Jenny, Jim, Karen, Kim, Micah, Michelle, Michelle, Mark, Morgan, Peter, Phil, Robin, Stephen, Steven, Theo, and TJ, for your encouragement and for making these past 5 years fun, worthwhile, and meaningful. Dad and Mom, thank you for your constant love, support, and prayers for me. Dad, thank you also for your professional support, example, and inspiration through these many years. Thank you Mark for your encouragement, help, and friendship. Finally, thank you Abby for your love and support, and for the joyful and life-giving example you are to me. I look forward to many more adventures together!

## TABLE OF CONTENTS

Biographical sketch	v
Acknowledgements	vi
List of figures	x
List of tables	xii
Chapter One: Thematic introduction and literature review	1
Chapter Two: Hatch dates, abundance, growth rates, and mortality	40
Chapter Three: Piscivore diet shifts and trophic level change	62
Chapter Four: Early mortality and forage fish recruitment	88
Chapter 5: Concluding summary	126
Appendix I: model code	132

## LIST OF FIGURES

- 2.1. Lake Champlain (right panel), located between the states of New York and Vermont, and the Province of Quebec, Canada. Location of survey transects in the main lake (left) of Lake Champlain. Contour lines represent 5-m depth intervals.
- 2.2. Density of age 0 fish observed ( $\leq 45$  days old) with given hatch date. Values calculated by partitioning total acoustic age 0 ( $\leq 45$  days old) density estimates into cohorts using age data from fish caught in Tucker trawl.
- 2.3. Abundance (number per square meter) of age 0 Rainbow Smelt (A) and Alewife (B) in our main lake survey transect in 2007 and 2008.
- 2.4. Lengths of age 0 Rainbow Smelt (A) and Alewife (B) less than 45 days old, with linear regression lines for 2007 and 2008.
- 2.5. Mortality rates of age 0 Rainbow Smelt and Alewife hatching at different times in 2007 and 2008. Cohorts are groups of age 0 fish which hatched the same week (1 = earliest, 9 = latest). Significant linear regression line for Rainbow Smelt is also shown.
- 3.1. Lake Champlain, located between the U.S. states of New York and Vermont, and the Province of Quebec, Canada.
- 3.2. Carbon and nitrogen stable isotope ratios of forage fish, salmonids and walleye in Lake Champlain. Samples were collected in 2011. Lines represent range of forage fish values.
- 3.3. Estimated proportion of prey items in lake trout (A), Atlantic salmon (B) and walleye (C) diets. Plot shows Bayesian posterior distributions of proportion estimates, with 50, 75 and 95% credible intervals in shaded boxes.

- 3.4. Rainbow smelt and alewife adult (large), age 1 (medium) and YOY (small)  $\delta^{15}\text{N}$  values. Boxes represent interquartile range.
- 3.5. Walleye (A) and rainbow smelt (B) tissue  $\delta^{15}\text{N}$ . Fish are from the Main Lake section of Lake Champlain.
- 4.1. Lake Champlain (right panel), located between the states of New York and Vermont, and the Province of Quebec, Canada. Location of survey transects in the main lake (left) of Lake Champlain. Contour lines represent 5-m depth intervals.
- 4.2. Temperature, light, and fish density vertical patterns in the water column in June, August, and September in Lake Champlain
- 4.3. Rainbow smelt and alewife distribution and early mortality simulation model structure.
- 4.4. Daily experienced density values through the season for adults and YOY rainbow smelt and alewife in Lake Champlain.
- 4.5. Daily mortality rates of YOY alewife and YOY rainbow smelt from 1 June through 15 October with only adult rainbow smelt present (A), and with both rainbow smelt and alewife present (B).
- 4.6. Mean daily YOY mortality rates from 1 June through 15 October when preyed upon by an adult fish group consisting of different proportions of rainbow smelt and alewife. Predictions are shown with only density-dependent relationships (A) and with spatial dimensions added (B).
- 4.7. Mortality rates from 1 June through 15 October under normal conditions (A), and under a climate change scenario in which epilimnion temperatures are 3C warmer than 2008 (B).

## LIST OF TABLES

- 1.1-4 Temperature preferences of adult and young rainbow smelt and alewife reported in previous studies.
- 3.1 Mean and standard deviation (s.d.)  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  for each species and age class sampled.
- 4.1. Functions used in our simulation of alewife and rainbow smelt density and YOY mortality in Lake Champlain.
- 4.2. Parameters and parameter values used in simulation functions, with Table 4.1 symbols identified.
- A4.1 Model parameters, parameter descriptions, and values.

# CHAPTER 1

## THEMATIC INTRODUCTION AND LITERATURE REVIEW

Ecological change is happening on a global scale (Mack et al. 2000, Brook et al. 2008, Intergovernmental Panel on Climate Change (IPCC) 2014) at a rate unprecedented in recent millennia, with consequences for both terrestrial and aquatic ecosystems (Rockström et al. 2009, Nickus et al. 2010, Barnosky et al. 2012, Cardinale et al. 2012). The response of fish populations and communities to current and future change, such as species introductions and climate changes, is unknown, but of great interest (e.g., Roessig et al. 2005, Ficke et al. 2007). Understanding and forecasting species and community response to change is of both intellectual and management interest, and is the focus of the following research I have conducted in Lake Champlain. In this introduction I will briefly review three core themes of the work described in subsequent chapters, and will provide background information regarding the species and ecosystem studied. These three themes are: adaptation to change, fish early life history and spatial ecology.

### ***Key concepts:***

#### 1) Adaptation to change

Understanding adaptations to change is not a new topic of study in ecology or fisheries science. However, it is too often true that, “despite the dramatic example of the cod collapse and the rise of non-equilibrium perspectives in ecology, fisheries management is still based largely on a single equilibrium worldview” (Vert-pre et al. 2013). While this may be too harsh a critique (adaptive management, for example, recognizes the need for change), recent analyses have

suggested that nonstationary relationships (e.g., relating stock size and recruitment) are common, and that the stationary assumptions of many of our most commonly-used models and management guidelines reduce model accuracy and management effectiveness significantly (e.g., Feiner et al. 2015). Furthermore, current drivers of ecological change (e.g., climate change, invasive species) require that additional assumptions of stochasticity and nonstationarity be built into analyses of population and community dynamics. We should explicitly measure this additional complexity and quantify changing conditions as they occur.

## 2) Fish early life history

In the study of fish community change, the second theme of my work is fish early life history. The past forty years have seen an increasing focus on fish early life history, which represents a change from fisheries science in earlier years that focused almost solely on adult individuals (Fuiman and Werner 2009). This change likely happened for several reasons, including technological improvements to research techniques and the growing application of early life history information in fishery management decisions (e.g., Rice 2002).

In Lake Champlain, previous studies of rainbow smelt (*Osmerus mordax*), which will be reviewed in more detail later, had focused on survey methods (Kirn and Labar 1991, Parker-Stetter et al. 2009), growth and diet (Stritzel Thomson et al. 2011), adult cannibalism rates (Parker Stetter et al. 2007), and salmonid and walleye predation (Kirn and Labar 1996, Overman and Parrish 2001, Pientka and Parrish 2002). Rainbow smelt early life history remained understudied in this system with the exception of preliminary surveys in the early 1900's searching for lake spawning habitat. Therefore, one of the early goals of my research was to increase our

understanding of rainbow smelt early life history; a topic of interest to both academic and management communities.

A lewife (*Alosa pseudoharengus*) was documented in Lake Champlain in 2003 and was abundant by 2007, the first field sampling year of my study (Marsden and Hauser 2009). We thus had the opportunity to both study the response of rainbow smelt to alewife and to study alewife as they became a part of the forage fish community in this system. Alewife and rainbow smelt are both cannibalistic and known to affect the early life history of salmonids as well, through predation on larvae and eggs (Rhodes et al. 1974, Parker Stetter et al. 2007, Madenjian et al. 2008). Rainbow smelt and alewife recruitment are of interest in large freshwater lakes throughout North America, and particularly in the Laurentian Great Lakes (e.g., Lantry and Stewart 1993, 2000, Madenjian et al. 2002, 2005). Many questions remain, and attempts to understand recruitment patterns of both species are ongoing (O'Brien et al. 2014, Collingsworth et al. 2014, He et al. 2015, Feiner et al. 2015). My work will build on known aspects of the biology of both species to forecast future early life history stage mortality and recruitment change.

### 3) Spatial ecology

The third theme of this study is spatial ecology. Traditional fish stock assessment techniques are commonly based on a “dynamic pool” model in which a stock is assumed to exist in a well-mixed environment (Walters and Martell 2004). While helpful for simplifying dynamic processes for analysis, this assumption can lead to unrealistic predictions of population dynamics (Walters and Martell 2004). The aquatic environment must be understood as structured by temperature, light, oxygen, and nutrients (e.g., Magnuson et al. 1979, 1990). This structure

affects species interactions and should be incorporated in predictive models (e.g., Walters et al. 1999, Pauly et al. 2000).

Rainbow smelt cannibalism is also a function of both density and spatial overlap of adults and young (Parker Stetter et al. 2007). Cannibalism is often understood as a density dependent process (Kellison et al. 2002), but spatial overlap between predator and prey can also be important (Lloyd 1967, Williamson and Stoeckel 1990). Understanding predation as a function of distribution also allows the inclusion of information regarding temperature, light, and other habitat preferences into predation analyses. Furthermore, this allows comparisons of niche breadth (a measure of species similarity), and other metrics of species interaction and overlap such as “experienced density” (Feinsinger et al. 1981, Parker Stetter et al. 2007).

## LITERATURE REVIEW

### *Lake Champlain*

Lake Champlain is a large north-temperate lake located between New York (USA) and Vermont (USA), with a northern section in the Canadian province of Quebec. The lake itself is about 200 km long, has a maximum width of 21 km, roughly 800 km of shoreline, 1124 km<sup>2</sup> of surface area, and a drainage basin of almost 20,000 km<sup>2</sup> (Manley and Manley 1999).

Phytoplankton community composition differs throughout the lake and seasonally. Protected bays and shallower regions such as Missisquoi Bay and the south lake have had greater phytoplankton densities in general, and have seen seasonally large Cyanobacteria populations (Shambaugh et al. 1999). Cryptophyta are dominant taxa, with *Chroomonas* spp. especially common, and Bacillariophyta, Chlorophyta, Chrysophyta, Euglenophyta, and Pyrrophyta are also present (Shambaugh et al. 1999).

Zooplankton communities are also variable, with slightly higher densities in southern sections of the lake during early summer (Carling et al. 2004a). Throughout the lake, the three main taxa are Rotifera, Copepoda, and Cladocera, but there have been changes since the establishment of zebra mussels in 1993 (Carling et al. 2004b). Microzooplankton, and specifically rotifers, are the most abundant zooplankton, but have declined in abundance since the mid-1990s (Carling et al. 2004b). There has been a change in rotifer community composition as well, and it may be possible that this too is a result of the invasive alien zebra mussel (Smith 1985). The spiny water flea (*Bythotrephes longimanus*) is the latest nonnative addition to Lake Champlain's zooplankton fauna (B. Pientka, personal communication), and the effects of its presence are yet unknown.

Relative to the Laurentian Great Lakes, fish communities in Lake Champlain have not changed dramatically since the time of European colonization. Cyprinids have the largest number of representatives of any fish taxa in the basin, although they are less studied than other more economically valuable species. The invertebrate *Mysis diluviana* is an abundant part of the lake's pelagic food web, both in numbers and biomass. This glacial relic species is also native to the Great Lakes, and is an influential predator and prey in systems it inhabits (Kitchell et al. 2000, Mills et al. 2003c).

The dominant planktivorous fish species in Lake Champlain has historically been rainbow smelt. Rainbow smelt are native to the basin, and adults inhabit all parts of the lake with adequate thermal stratification to sustain colder hypolimnetic temperatures. A second very abundant fish in the lake is yellow perch (*Perca flavescens*), which inhabit shallower water. Pumpkinseed sunfish (*Lepomis gibbosus*), rock bass (*Ambloplites rupestris*), bluegill (*Lepomis macrochirus*), white perch (*Morone americana*), black crappie (*Pomoxis nigromaculatus*), small and largemouth bass (*Micropterus dolomieu* and *Micropterus salmoides*), pickerel (*Esox niger* and *Esox americanus*), northern pike (*Esox lucius*), suckers, common carp (*Cyprinus carpio*), gar (*Lepisosteus osseus*), brown bullhead (*Ictalurus nebulosus*), and channel catfish (*Ictalurus punctatus*) are other fish species present in shallower warmer water (Langdon et al. 2006). Pelagic species include several salmonids, including native lake trout (*Salvelinus namaycush*). Other salmonids include landlocked Atlantic salmon (*Salmo salar*), steelhead or rainbow trout (*Oncorhynchus mykiss*), and brown trout (*Salmo trutta*). In addition, the Lake Champlain fish fauna includes walleye (*Stizostedion vitreum*), sauger (*Stizostedion canadense*), cisco (*Coregonus artedii*), whitefish (*Coregonus clupeaformis* and *Prosopium cylindraceum*), burbot (*Lota lota*), bowfin (*Amia calva*), drum (*Aplodinotus grunniens*), lake sturgeon (*Acipenser*

*fulvescens*), and American eel (*Anguilla rostrata*) (Langdon et al. 2006). Sea lamprey (*Petromyzon marinus*) have an interesting history in the basin, and although once assumed to be an alien invasive, recent evidence is conflicted (e.g., Waldman et al. 2006). However, the current sea lamprey population size is likely much larger than historically.

Today the Lake Champlain basin is home to over 600,000 people, with many visitors drawn to the region each year (Stickney et al. 2001). In the late 1990's, visitors spent approximately \$228 million on water-based recreation each year, with residents (within 35 miles of the lake) spending approximately \$118 million. The ecological and social importance of the natural landscape of the Champlain – Adirondack region, of which Lake Champlain is an integral part, was underscored by its 1989 United Nations designation as a Biosphere Reserve (Stickney et al. 2001).

### ***Rainbow smelt***

Rainbow smelt is an anadromous species native to the east coast of North America from eastern Labrador and the Gulf of St. Lawrence south to the Delaware River, and to some freshwater lakes and ponds with coastal access (Smith 1985, Buckley 1989). Rainbow smelt have been stocked in inland lakes including some in the Great Lakes basin (Smith 1985), and have thereby spread into other freshwater systems. Rainbow smelt are part of the family Osmeridae, which has about six genera and twelve species worldwide. To narrow the scope of this review, the focus will be on the ecology of landlocked rainbow smelt.

Freshwater rainbow smelt populations are most successful in larger and relatively deep lakes (Smith 1985, Buckley 1989). Native inland populations are found close to the Atlantic

seaboard, and larger rivers such as the St. Lawrence facilitated natural establishment of further inland as well; this is thought to be the case for Lake Champlain's rainbow smelt (Cobb 1905, Moore 1929). In Lake Champlain, rainbow smelt were also stocked for a period of 10 years beginning in 1919. This strain was from the Cold Spring hatchery on Long Island, New York, and has reportedly survived in Lake Champlain (Moore 1929).

In larger lakes, adult rainbow smelt prefer cooler metalimnion and hypolimnion waters throughout the summer, then spread more widely in the water column during spring and fall turnover, and possibly during winter isothermal conditions (Table 1.1) (Ferguson 1958, 1965, Hart and Ferguson 1966, Dryer 1966, Wells 1968, Jude et al. 1975, Brandt 1980, Heist and Swenson 1983, Burczynski et al. 1987, Parker Stetter et al. 2006, Stockwell et al. 2007). The utilization of coldwater habitats is further demonstrated in the ability of adults to decrease their freezing point by accumulating glycerol during winter months (Lewis et al. 2004). Larval and young-of-the-year (YOY) fish generally occupy relatively warmer habitats in both freshwater and estuarine environments (Table 1.2) (Tin and Jude 1983, Dunstall 1984, Evans and Loftus 1987, Urban and Brandt 1993, Sirois and Dodson 2000, Lecomte and Dodson 2004, Ayer et al. 2005, Bradbury et al. 2006, Parker Stetter et al. 2006). Therefore, interaction between adult and young fish depends on spawning and hatching dates, and periods of stratification.

Table 1.1) Adult rainbow smelt habitat preferences in nature and laboratory.

<b>Waterbody</b>	<b>Lake zone(s)</b>	<b>Vertical distribution</b>	<b>Temp. pref. (C°)</b>	<b>Seasons</b>	<b>Reference</b>
Lake Champlain	Entire water column	Hypolimnion and lower metalimnion		June, July, September	Parker Stetter et al. 2006
Lake Huron	Entire water column	Spring:closer to bottom Fall:more "demersal"		1 "Spring," 1 "Summer," 1 "Fall" survey	Argyle 1982
Lake Michigan	Nearshore benthic isotherms		Day:7-8°C Night:11-16°C	September	Brandt et al. 1980
Lake Michigan			6-8°		Jude et al. 1975
Lake Michigan			6-14°C		Wells 1968
Lake Oahe	Entire water column	Hypolimnion and metalimnion; Day:near bottom, Night:pelagic	5-14°C	July-August	Burczynski et al. 1987
Lake Superior			6-16°C		Heist and Swenson 1983
Lake Superior: Apostle Islands	Water near bottom (bottom trawls, gill nets on bottom)	Spring:<18-70m Summer:18-90m Fall:<18-90m		Spring, Summer, Fall (specific months not mentioned)	Dryer 1966
Laboratory			6-8°C		Ferguson 1965, Hart and Ferguson 1966
n/a		Water column thermal stratification			Nellbring 1989

Table 1.2) Young-of-the-year rainbow smelt habitat use.

<b>Waterbody</b>	<b>Lake zone(s)</b>	<b>Vertical distribution</b>	<b>Temp. pref. (C°)</b>	<b>Seasons</b>	<b>Reference</b>
Lake Champlain	Entire water column	June and July: epilimnion September: epilimnion and metalimnion		June, July, September	Parker Stetter et al. 2006
Lake Michigan	Above nearshore depth contours (1-15m)	No distribution pattern observed	10-16°C	May-September	Tin and Jude 1983
Lake Ontario	Above nearshore depth contours (1-13m)	May-June: densities highest at 0.5m depth over 3m depth contour		May-October but not at any set frequency	Dunstall 1984
Lake Ontario	8-75m depths in two locations	August:10-30m September: wide distribution, generally deeper than August	August-September:8-12°C October: day(7-8°C) night(8-12°C) November: wide distribution	August-November (2 year study, not all months sampled either year)	Urban and Brandt 1993
Lake Superior	One "shallow" one "deep" sample	Day: found only in "deep" samples Night: found in both "shallow" and "deep" samples	First collected in June at temp. of 10.8-17.4°C	May-July	Oyadomari and Auer 2004

Landlocked rainbow smelt populations generally spawn in rivers and streams (Smith 1985, Buckley 1989, Urho 1992). In coastal populations, adults typically begin spawning migrations before ice breakup, migrating upstream to beyond the head of the tide (Buckley 1989, Locke and Courtenay 1995), and behavior of lake populations is generally similar in that adults move into lake tributaries in early spring (Kendall 1927, Hoover 1936). Spawning runs typically begin in the evening, with most fish returning to the lake the next morning, unless cloudy conditions exist (Kendall 1927, Hoover 1936, Smith 1985).

Despite this general tendency toward anadromous behavior, exceptions may not be unusual. Landlocked rainbow smelt spawn in shoals and shallow near-shore areas in a number of temperate lakes (Rupp 1965, Dunstall 1984). Survival of eggs and larvae in these situations does not differ significantly from estimates of stream survival, and mortality comes mainly from water level changes, grinding from surf, and trampling by humans and other forces (Rupp 1965).

More rare than shore spawning, however, is deep-water spawning (Plosila 1984). This behavior was documented in Lake Heney, Quebec, and also in Lake Champlain (Legault and Delisle 1968, Plosila 1984). Lake Heney, like Lake Champlain, was a lake that supported a population of “giant” rainbow smelt (Legault and Delisle 1968). Details regarding this spawning behavior, and exact spawning locations, have proven difficult to determine (e.g. Plosila 1984).

Rainbow smelt egg incubation times are dependent on water temperature, with warmer waters facilitating earlier hatching (Akielaszek et al. 1985, Buckley 1989, Ayer et al. 2005). Hatching takes place 160 to 200 hours after fertilization at 13 to 20° C, with newly hatched larvae around 5 mm long (Cooper 1978, Smith 1985). In marine systems, these larvae develop

through summer months in estuaries and tidal regions, whereas in lakes initial development occurs in near-shore shallow water for at least a limited period of time (Tin and Jude 1983, Oyadomari and Auer 2004). This time spent in near-shore water appears to be variable, and is followed by general movement offshore with larvae remaining in shallower depth strata. For example, in Lake Michigan, larval rainbow smelt were most common at water temperatures of 10 to 16° C (Tin and Jude 1983), but may tolerate a “wide range of environmental conditions” (Ayer et al. 2005).

When the yolk sac and oil globule food sources are depleted, larvae join adults as mainly pelagic feeders (Foltz and Norden 1977, Sirois and Dodson 2000). Zooplankton are the dominant prey items during this first summer, with cyclopoid copepods and cladocerans often comprising the vast majority of the diet (Urban and Brandt 1993, Mills et al. 1995). Adults feed on zooplankton as well, but also consume *Mysis*, amphipods, insect larvae, oligochaetes, and small fish including young rainbow smelt (Foltz and Norden 1977, Mills et al. 1995, Lantry and Stewart 2000, Parker et al. 2001, Stetter et al. 2005, Parker Stetter et al. 2007). The diets of both young and adult rainbow smelt change relative to prey availability, and now often include non-native species such as dreissenid veligers and *Bythotrephes* (e.g., Mills et al. 1995, Parker et al. 2001).

Cannibalism complicates rainbow smelt population dynamics (LaBar 1993, He and LaBar 1994, Lantry and Stewart 2000, Parker Stetter et al. 2007). Large rainbow smelt year classes exert stronger pressure on larval populations thus leading to cyclical population levels (Parker Stetter et al. 2007). In some systems, adults are the major predator of young, but this interaction is dependent on fish density and habitat overlap between these groups. In Lake

Champlain, “experienced density,” and thus cannibalism, was highest in June, lowest in July, and then again high in September (Parker Stetter et al. 2007).

Rainbow smelt have been introduced as a forage fish for larger species in many systems (e.g., Evans and Loftus 1987, Jones et al. 1994, Kirn and Labar 1996, Johnson and Goettl Jr 1999). Predators ranging from walleye to lake trout to common terns eat rainbow smelt (Burness et al. 1994), but introductions of the species into other systems for this purpose has had mixed results (Johnson and Goettl Jr 1999, Mercado-Silva et al. 2006). In Lake Champlain native rainbow smelt populations support not only native species, but non-natives as well (Kirn and Labar 1996). Native lake trout, Atlantic salmon, and walleye are the three main predatory fish species reliant on rainbow smelt for food (LaBar 1993, He and LaBar 1994, Pientka and Parrish 2002). Lake Champlain rainbow smelt are also a significant target of human fisheries, both commercial and recreational, and have been for many decades (Moore 1929).

There are at least two characteristics of the Lake Champlain rainbow smelt population that distinguish it from other populations. First, Lake Champlain is one of the few large lakes in which rainbow smelt are native, and, of these lakes, Champlain is the largest. Second, in the recent past there has been no other ecologically similar fish (“forage fish”) species present in similar abundance.

### *Alewife*

Alewife (*Alosa pseudoharengus*), like rainbow smelt, is an anadromous species native to coastal Atlantic waters. It is found along the coast and in rivers and estuaries from Newfoundland to South Carolina, with non-native landlocked populations now present in inland lakes (Bozeman and Van Den Avyle 1989). Some of these populations have been establish

purposefully, and others not (Smith 1985, Hendricks 2003). Given the context of this study, freshwater alewife populations will be the focus of this review.

Much of the research conducted on freshwater alewife populations has been done in the Laurentian Great Lakes region (Bozeman and Van Den Avyle 1989). Alewife had become established in these lakes by 1954, but was not abundant until several years later (Miller 1957), and did not become established in Lake Champlain (Smith 1985). Within the Northeastern U.S., the species is already present in numerous other water bodies (Smith 1985, Bozeman and Van Den Avyle 1989), and at different times has been regarded as either desirable or undesirable (e.g., Smith 1968, Stewart et al. 1981, Krueger et al. 1995).

Freshwater alewife populations in the northern U.S. prefer slightly warmer temperatures than many other fish species in the region, but this has not appeared to hinder their success (Otto et al. 1976). In laboratory studies, adults prefer temperatures in the range of 16 to 21° C from spring to fall, with the maximum temperature preference occurring at the time of spring spawning, whereas during winter months adults prefer temperatures of roughly 11° C (Otto et al. 1976). Lethal temperatures are more extreme than these values, and ideal habitat preferences may be influenced by the avoidance of these extremes when ideal preferences are not available, as extreme cold temperatures (near freezing) can cause large-scale winter die-offs (Lepak and Kraft 2008).

Young-of-year alewife in laboratory experiments prefer consistently up to 9 C warmer temperatures than their adult counterparts, (Otto et al. 1976). In summer months these fish preferred a temperature in the range of 25° C, and this preference only decreased to 19 to 21° C by early winter (Otto et al. 1976). Lethal temperatures were consistently higher than those of

adults as well, with a summer maximum in the range of 30 to 32° C (Otto et al. 1976). Adult and young alewife preferences may overlap with those of rainbow smelt, although adult and young rainbow smelt seem to prefer cooler water than alewife (Tables 1.3 & 1.4).

Table 1.3) Adult alewife habitat use in various environments.

<b>Waterbody</b>	<b>Lake zone(s) sampled</b>	<b>Vertical distribution preferences</b>	<b>Temperature preferences (C°)</b>	<b>Seasons / timeframe of study</b>	<b>Reference</b>
Lake Huron	Entire water column	Spring: closer to bottom Fall: more "demersal"		1 "Spring," 1 "Summer," 1 "Fall" survey	Argyle 1982
Lake Michigan	Nearshore benthic isotherms	Night: not present on bottom	Day: 11-14°C	September	Brandt et al. 1980
Lake Michigan			16-22°C		Jude et al. 1975
Lake Michigan			11-16°C		Wells 1968
Laboratory			May: 21°C June- August: 16-21°C September- November: 16°C December- January: 11°C	Acclimated to L. Michigan temperatures from May-January	Otto et al. 1976

Table 1.4) Young-of-the-year alewife habitat use in various environments.

<b>Waterbody</b>	<b>Lake zone(s) sampled</b>	<b>Vertical distribution preferences</b>	<b>Temperature preferences (C°)</b>	<b>Seasons / timeframe of study</b>	<b>Reference</b>
Lake Michigan	Nearshore benthic isotherms	Night: not present on bottom	Day: 17-20°C	September	Brandt et al. 1980
Lake Michigan			16-20°C and 24-28°C		Jude et al. 1975
Lake Ontario	Above nearshore depth contours (1-13m)	Densities highest at 0.5m depth "immediately following hatching"	13-20°C (highest densities at warmer end of range)	May-October but not at set frequency	Dunstall 1984
Lake Ontario	Bays		Highest densities in July-August when water was 18+ °C	May-September	Klumb et al. 2003
Lake Ontario	8-75m depths in two locations (bottom and mid-water trawls)	August-September: 10-15m, pelagic; "dense scattering layer" present at night (10-15m) October: <25 m November: 30-40m	"Warmest water available"	August-November (2 year study, not all months sampled both years)	Urban and Brandt 1993

Marine alewife move up coastal rivers to spawn (Bozeman and Van Den Avyle 1989). This behavior has been noted in some freshwater populations, but it appears spawning in shallow lake waters, river or stream mouths, and embayments is the more common behavior in freshwater (Graham 1956, Klumb et al. 2003). After hatching, larvae most commonly prefer shallow depths in these near-shore habitats (Dunstall 1984). In Lake Ontario, alewife historically preferred depths of 0 to 3 m., with densities dropping significantly in deeper strata (O'Gorman 1983), though this has changed in more recent years, with alewife found deeper in the water column. Along the north shore of Ontario, alewife are the dominant pelagic ichthyoplankton from July to September (Dunstall 1984).

Adult and young alewife are pelagic feeders, feeding on a variety of plankton and other items in the water column. When young, their main prey are similar to rainbow smelt, and small cladocerans and copepods are favored (Bozeman and Van Den Avyle 1989, Mills et al. 1995), but zooplankton sizes consumed increase steadily with gape size. Compared to rainbow smelt adults, however, alewife adults are the more efficient planktivore (e.g., Mills et al. 1995).

The efficiency of river herring species (blueback herring and alewife) as zooplanktivores was first documented in coastal lakes, but has since been noted in other inland systems (Brooks and Dodson 1965, Hendricks 2003, Mills et al. 2003a). Young alewife particulate feed, but adults exhibit a variety of feeding methods. Adults can pick out larger items in the plankton, but often pump feed which allows the consumption of microzooplankton as well (Janssen 1978, Mills et al. 1995). Due to this high efficiency, many lakes have seen significant changes in the body size of the zooplankton community after alewife become established (e.g., Brooks and Dodson 1965, Mills et al. 2003c).

In addition to invertebrate zooplankton, adult alewife prey on fish larvae in a number of systems. Great Lake salmonid species such as lake trout have been likely affected by this predation (e.g., Krueger et al. 1995), and other native pelagic populations have declined in part due to predation on pelagic larvae by both alewife and rainbow smelt, with alewife being the more efficient predator (Crowder 1980, Madenjian et al. 2008). In other lakes, walleye larvae are likely consumed, and fish community effects such as these have raised concerns regarding the integrity of sport fisheries and native fish populations (Crowder 1980, Brooking et al. 1998, Marsden et al. 2005, Fielder et al. 2007, Madenjian et al. 2008). Larvae size, as expected, influences whether alewife will efficiently capture these fish, and younger (smaller) larvae are more susceptible to predation (Brooking et al. 1998).

The forage base provided by alewife to salmonids has been the reason for this species' introduction in many areas (Hendricks 2003). In the Great Lakes, perception of alewife as either a pest or a beneficial forage fish changes over time and with stakeholder groups (Smith 1968, Stewart et al. 1981, Hendricks 2003, Madenjian et al. 2008). Concerns regarding the large alewife population of the Great Lakes basin led to the introduction of additional non-native predatory species in the form of Pacific salmon, recognizing that these fish would likely feed heavily upon adult alewife (Smith 1968, Christie 1974, Rand and Stewart 1998a, 1998b, Mills et al. 2003b). This predation has happened, and sport fisheries supported by the current Pacific salmon population motivate continued stocking of these species, while restoration efforts for native salmonids continue (Krueger et al. 1995, Rand and Stewart 1998b, Madenjian et al. 2008).

Alewife consumption by some salmonids may actually be detrimental (Fisher et al. 1996). Alewife can contain thiaminase in a form that retains its effectiveness even after exposure to digestive processes, and thus is effective within the bodies of alewife predators (Brown et al.

2005a, Fitzsimons et al. 2005, Tillitt et al. 2005). The reaction of thiamine (Vitamin B1) with thiaminase (an enzyme that breaks down thiamine) is potentially harmful in that it may cause deficiencies of this essential nutrient (Brown et al. 2005b, Honeyfield et al. 2005, Fitzsimons et al. 2007).

There are two ways in which thiamine deficiency may affect predators that feed on alewife, and while research concerning this topic is on-going the main harmful interaction occurs when fish produce eggs, and thus larvae, with lower than normal thiamine levels (Fisher et al. 1996, Brown et al. 2005b, 2005c, Honeyfield et al. 2005). This deficiency leads to “early mortality syndrome,” and larvae have impaired feeding ability, among other necessary activities (Honeyfield et al. 2005). Given that this interaction may be occurring, alewife consumption is likely an additional factor inhibiting native salmonid reproduction in the Great Lakes (Mills et al. 2003b, Brown et al. 2005b, 2005c, Fitzsimons et al. 2007). Consumption of alewife by predatory species may be detrimental to adult predators themselves. For example, in both the Great Lakes and Baltic Sea, abnormal behavior and other neurological changes in adult fish may be associated with thiamine deficiency, which in turn can result from consumption of alewife or other herring species (Wistbacka 2002, Brown et al. 2005a).

Alewife were first found in Lake Champlain in 2003 by the Quebec Ministry of Wildlife and Parks, and fish were subsequently found in other regions of the lake in 2004 through 2006 (Marsden and Hauser 2009). In spring of 2007, adult alewife were seen congregating in shallow water near a river mouth, and many young fish were collected by our study later in that year.

## *Survey methods*

### Hydroacoustics

Recognition of sound in the aquatic realm can be traced to at least the 1400's when Leonardo da Vinci first mentions hearing "ships at a great distance" by listening underwater (Urick 1983). It was not until the early 20<sup>th</sup> century, though, that technological advancements suggested underwater sound may be utilized as an information gathering tool (Simmonds and MacLennan 2008).

The field of underwater acoustics developed sporadically with major advances occurring around the first and second World Wars, and the first use in fish detection occurring in 1929 (Kimura 1929, Simmonds and MacLennan 2008). Since that time, advances have enabled the recording of sound in the form of echograms, and the development of instruments designed specifically for fish detection. The initial motivation for this fish detection technology, and its major use still today, was in fishing (Simmonds and MacLennan 2008). Technological advances have continued, with many sonar arrangements now used including single and multiple transducers, scanning sonars, multiple frequency configurations, and others (Simmonds and MacLennan 2008). Whereas hydroacoustics began in marine systems, fishers and researchers are now using the technology in freshwater as well, and effectively observing organisms of increasingly smaller sizes (Argyle 1992, Rudstam et al. 2002).

Hydroacoustic-derived biomass assessment data are used by fisheries managers, in addition to other data, to set catch limits, stocking levels, etc., and the Great Lakes have been a major testing ground for freshwater hydroacoustics in the United States. Acoustic surveys are now conducted in all of these lakes, with interest in both smaller forage fish species and larger stocked predators (e.g., Fabrizio et al. 1997, Rudstam 2003, Mason et al. 2005, Stockwell et al.

2007). Hydroacoustic data are consistently compared with trawl and historic trawl data to maintain assessment continuity, and combined trawl-acoustic surveys are conducted on many systems (Appenzeller and Leggett 1992, 1995, Fabrizio et al. 1997, Rudstam et al. 2002, Malinen et al. 2005, Stockwell et al. 2007).

Hydroacoustics has been used for studies for organisms of all sizes, including larval fish down to roughly 15 mm in length (Rudstam et al. 2002), and larger fish such as adult Atlantic salmon (Pientka and Parrish 2002). Studies of invertebrates have also been possible, including *Mysis diluviana*, an important ecological player in many glacial relict lakes (Gal et al. 1999a, 1999b, 2004, Boscarino et al. 2007), and freshwater insects (Kubecka et al. 2000). Using hydroacoustics along with other tools, it is possible to determine fish and invertebrate distributions, and correlate these with abiotic and biotic factors also measured (e.g., Gliwicz and Jachner 1992, Appenzeller and Leggett 1995, Pientka and Parrish 2002, Gal et al. 2004).

### *Dissertation focus*

The work presented herein adds to our understanding of rainbow smelt and alewife ecology, and addresses the challenge of studying adaptation to change, in three chapters:

- 1) Chapter 2 presents an analysis of how a species (rainbow smelt) and system (fish in Lake Champlain) change in response to a new species (alewife), specifically in relation to hatch timing and early life history.
- 2) Chapter 3 studies prey switching and the extent to which piscivores in Lake Champlain now consume alewife instead of rainbow smelt.
- 3) In the final Chapter 4, I use early life history and fish distribution data, combined with previous cannibalism research, to forecast future recruitment and early mortality patterns for rainbow smelt and alewife in light of alewife presence and a likely climate change scenario.

## REFERENCES

- Akielaszek, J.J., Moring, J.R., Chapman, S.R., and Dearborn, J.H. 1985. Experimental culture of young rainbow smelt *Osmerus mordax*. *Trans. Am. Fish. Soc.* **114**(4): 596–603.
- Appenzeller, A.R., and Leggett, W.C. 1992. Bias in hydroacoustic estimates of fish abundance due to acoustic shadowing - evidence from day night surveys of vertically migrating fish. *Can. J. Fish. Aquat. Sci.* **49**(10): 2179–2189.
- Appenzeller, A.R., and Leggett, W.C. 1995. An evaluation of light-mediated vertical migration of fish based on hydroacoustic analysis of the diel vertical movements of rainbow smelt (*Osmerus mordax*). *Can. J. Fish. Aquat. Sci.* **52**(3): 504–511.
- Argyle, R.L. 1992. Acoustics as a tool for the assessment of Great Lakes forage fishes. *Fish. Acoust.* **14**(2–3): 179–196. doi: 10.1016/0165-7836(92)90052-U.
- Ayer, M., Benton, C., King, W., Kneebone, J., Elzey, S., Toran, M., Grange, K., and Berlinsky, D. 2005. Development of practical culture methods for rainbow smelt larvae. *North Am. J. Aquac.* **67**(3): 202–209. doi: 10.1577/A04-064.1.
- Barnosky, A.D., Hadly, E. a, Bascompte, J., Berlow, E.L., Brown, J.H., Fortelius, M., Getz, W.M., Harte, J., Hastings, A., Marquet, P. a, Martinez, N.D., Mooers, A., Roopnarine, P., Vermeij, G., Williams, J.W., Gillespie, R., Kitzes, J., Marshall, C., Matzke, N., Mindell, D.P., Revilla, E., and Smith, A.B. 2012. Approaching a state shift in Earth’s biosphere. *Nature* **486**(7401): 52–8. doi: 10.1038/nature11018.
- Boscarino, B.T., Rudstam, L.G., Mata, S., Gal, G., Johannsson, O.E., Lr, O., and Mills, E.L. 2007. The effects of temperature and predator – prey interactions on the migration behavior and vertical distribution of *Mysis relicta*. **52**(4): 1599–1613.

- Bozeman, E.L., and Van Den Avyle, M.J. 1989. Species profiles: life histories and environmental requirements of coastal fishes and invertebrates (South Atlantic) -- alewife and blueback herring. U.S. Fish and Wildlife Service Biological Report 82(11.111). U.S. Army Corps. of Engineers, TR EL-82-4.
- Brandt, S.B. 1980. Spatial segregation of adult and young-of-the-year Alewives across a thermocline in Lake Michigan. *Trans. Am. Fish. Soc.* (September): 469–478.
- Brook, B.W., Sodhi, N.S., and Bradshaw, C.J.A. 2008. Synergies among extinction drivers under global change. *Trends Ecol. Evol.* **23**(8): 453–460. doi: 10.1016/j.tree.2008.03.011.
- Brooking, T.E., Rudstam, L.G., Olson, M.H., and Vandevalk, A.J. 1998. Size-dependent alewife predation on larval walleyes in laboratory experiments. *North Am. J. Fish. Manag.* **18**(4): 960–965.
- Brooks, J.L., and Dodson, S.I. 1965. Predation, body size, and composition of the plankton. *Science* **150**: 28–35 ST – Predation, body size, and composition.
- Brown, S.B., Arts, M.T., Brown, L.R., Brown, M., Moore, K., Villella, M., Fitzsimons, J.D., Honeyfield, D.C., Tillitt, D.E., Zajicek, J.L., Wolgamood, M., and Hnath, J.G. 2005a. Can diet-dependent factors help explain fish-to-fish variation in thiamine-dependent early mortality syndrome? *J. Aquat. Anim. Health* **17**(1): 36–47. doi: 10.1577/H03-072.1.
- Brown, S.B., Fitzsimons, J.D., Honeyfield, D.C., and Tillitt, D.E. 2005b. Implications of thiamine deficiency in Great Lakes salmonines. *J. Aquat. Anim. Health* **17**(1): 113–124. doi: 10.1577/H04-015.1.
- Brown, S.B., Honeyfield, D.C., Hnath, J.G., Wolgamood, M., Marcquenski, S.V., Fitzsimons, J.D., and Tillitt, D.E. 2005c. Thiamine status in adult salmonines in the Great Lakes. *J. Aquat. Anim. Health* **17**(1): 59–64. doi: 10.1577/H04-059.1.

- Buckley, J. 1989. Species profiles: life histories and environmental requirements of coastal fishes and invertebrates (North Atlantic)--rainbow smelt. U.S. Fish and Wildlife Service Biological Report 82(11.106). U.S. Army Corps of Engineers, TR EL-82-4.
- Burczynski, J.J., Michaletz, P.H., and Marrone, G.M. 1987. Hydroacoustic assessment of the abundance and distribution of rainbow smelt in Lake Oahe. *North Am. J. Fish. Manag.* **7**(1): 106–116.
- Burness, G.P., Morris, R.D., and Bruce, J.P. 1994. Seasonal and annual variation in brood attendance, prey type delivered to chicks, and foraging patterns of male common terns (*Sterna hirundo*). *Can. J. Zool.-Rev. Can. Zool.* **72**(7): 1243–1251.
- Cardinale, B.J., Duffy, J.E., Gonzalez, A., Hooper, D.U., Perrings, C., Venail, P., Narwani, A., Mace, G.M., Tilman, D., Wardle, D.A., Kinzig, A.P., Daily, G.C., Loreau, M., Grace, J.B., Larigauderie, A., Srivastava, D.S., and Naeem, S. 2012. Biodiversity loss and its impact on humanity. *Nature* **486**(7401): 59–67. doi: 10.1038/nature11148.
- Carling, K.J., Ater, I.M., Pellam, M.R., Bouchard, A.M., and Mihuc, T.B. 2004a. A Guide to the zooplankton of Lake Champlain. Plattsbg. State Univ. N. Y. Available from <http://www.plattsburgh.edu/files/686/files/2004-A-guide-to-the-Zooplankton-of-Lake-Champlain.pdf> [accessed 25 March 2014].
- Carling, K.J., Mihuc, T.B., Siegfried, C., Bonham, R., and Dunlap, F. 2004b. Where have all the rotifers gone? Zooplankton community patterns in Lake Champlain from 1992-2001. *In* Lake Champlain: partnership and research in the new millennium. *Edited by* T.O. Manley, P. Manley, and T.B. Mihuc. Kluwer Academic/Plenum Publishers, New York. pp. 259–270.

- Christie, W. 1974. Changes in the fish species composition of the Great Lakes. J. Fish. Res. Board Can. **31**(5): 827–854.
- Cobb, J.N. 1905. The commercial fisheries of the interior lakes and rivers of New York and Vermont. U.S. Commission of Fish and Fisheries, 1903 (1905), Washington.
- Collingsworth, P.D., Bunnell, D.B., Madenjian, C.P., and Riley, S.C. 2014. Comparative recruitment dynamics of alewife and bloater in Lakes Michigan and Huron. Trans. Am. Fish. Soc. **143**(1): 294–309.
- Cooper, J.E. 1978. Identification of eggs, larvae, and juveniles of the rainbow smelt, *Osmerus mordax*, with comparisons to larval alewife, *Alosa pseudoharengus*, and gizzard shad, *Dorosoma cepedianum*. Trans. Am. Fish. Soc. **107**(1): 56–62.
- Crowder, L.B. 1980. Alewife, rainbow smelt and native fishes in Lake Michigan: competition or predation? Environ. Biol. Fishes **5**(3): 225–233. doi: 10.1007/BF00005356.
- Dryer, W.R. 1966. Bathymetric distribution of fish in the Apostle Islands region, Lake Superior. Trans. Am. Fish. Soc. **95**(3): 248–259.
- Dunstall, T.G. 1984. Distribution of Rainbow Smelt and Alewife Larvae Along the North Shore of Lake Ontario. J. Gt. Lakes Res. **10**(3): 273–279.
- Evans, D.O., and Loftus, D.H. 1987. Colonization of inland lakes in the great lakes region by rainbow smelt, *Osmerus mordax*: their freshwater niche and effects on indigenous fishes. Can. J. Fish. Aquat. Sci. **44**(S2): s249–s266. doi: 10.1139/f87-327.
- Fabrizio, M.C., Adams, J.V., and Curtis, G.L. 1997. Assessing prey fish populations in Lake Michigan: comparison of simultaneous acoustic-midwater trawling with bottom trawling. Fish. Res. **33**(1): 37–54.

- Feiner, Z.S., Bunnell, D.B., Höök, T.O., Madenjian, C.P., Warner, D.M., and Collingsworth, P.D. 2015. Non-stationary recruitment dynamics of rainbow smelt: The influence of environmental variables and variation in size structure and length-at-maturation. *J. Gt. Lakes Res.* **41**(1): 246–258.
- Feinsinger, P., Spears, E.E., and Poole, R.W. 1981. A simple measure of niche breadth. *Ecology* **62**(1): 27.
- Ferguson, R.G. 1958. The preferred temperature of fish and their midsummer distribution in temperate lakes and streams. *J. Fish. Res. Board Can.* **15**(4): 607–624.
- Ferguson, R.G. 1965. Bathymetric distribution of American smelt *Osmerus mordax* in Lake Erie. *J. Gt. Lakes Res.* **13**: 47–60.
- Ficke, A.D., Myrick, C.A., and Hansen, L.J. 2007. Potential impacts of global climate change on freshwater fisheries. *Rev. Fish Biol. Fish.* **17**(4): 581–613.
- Fielder, D.G., Schaeffer, J.S., and Thomas, M.V. 2007. Environmental and ecological conditions surrounding the production of large year classes of walleye (*Sander vitreus*) in Saginaw Bay, Lake Huron. *J. Gt. Lakes Res.* **33**(sp1): 118–132.
- Fisher, J.P., Fitzsimons, J.D., Combs Jr, G.F., and Spitsbergen, J.M. 1996. Naturally occurring thiamine deficiency causing reproductive failure in Finger Lakes Atlantic salmon and Great Lakes lake trout. *Trans. Am. Fish. Soc.* **125**(2): 167–178.
- Fitzsimons, J.D., Williston, B., Williston, G., Brown, L., El-Shaarawi, A., Vandenbyllaardt, L., Honeyfeld, D., Tillitt, D., Wolgamood, M., and Brown, S.B. 2007. Egg thiamine status of Lake Ontario salmonines 1995-2004 with emphasis on lake trout. *J. Gt. Lakes Res.* **33**(1): 93–103.

- Fitzsimons, J.D., Williston, B., Zajicek, J.L., Tillitt, D.E., Brown, S.B., Brown, L.R., Honeyfield, D.C., Warner, D.M., Rudstam, L.G., and Pearsall, W. 2005. Thiamine content and thiaminase activity of ten freshwater stocks and one marine stock of alewives. *J. Aquat. Anim. Health* **17**(1): 26–35.
- Foltz, J.W., and Norden, C.R. 1977. Food habits and feeding chronology of rainbow smelt, *Osmerus mordax*, in Lake Michigan. *Fish. Bull.* **75**(3): 637–640.
- Fuiman, L.A., and Werner, R.G. 2009. *Fishery Science: The unique contributions of early life stages*. John Wiley & Sons.
- Gal, G., Loew, E.R., Rudstam, L.G., and Mohammadian, A.M. 1999a. Light and diel vertical migration: spectral sensitivity and light avoidance by *Mysis relicta*. *Can. J. Fish. Aquat. Sci.* **56**(2): 311–322.
- Gal, G., Rudstam, L.G., and Greene, C.H. 1999b. Acoustic characterization of *Mysis relicta*. *Limnol. Oceanogr.* **44**(2): 371–381.
- Gal, G., Rudstam, L.G., and Johannsson, O.E. 2004. Predicting *Mysis relicta* vertical distribution in Lake Ontario. *Arch. Für Hydrobiol.* **159**(1): 1–23.
- Gliwicz, Z.M., and Jachner, A. 1992. Diel migrations of juvenile fish - a ghost of predation past or present. *Arch. Hydrobiol.* **124**(4): 385–410.
- Graham, J.J. 1956. *Observations of the alewife (Pomolobus pseudoharengus) in fresh water*. University of Toronto, Toronto.
- Hart, J.L., and Ferguson, R.G. 1966. The American smelt. *Trade News* **18**: 22–23.
- Heist, B.G., and Swenson, W.A. 1983. Distribution and abundance of rainbow smelt in western Lake Superior as determined from acoustic sampling. *J. Gt. Lakes Res.* **9**: 343–353.

- He, J.X., Bence, J.R., Madenjian, C.P., Pothoven, S.A., Dobiesz, N.E., Fielder, D.G., Johnson, J.E., Ebener, M.P., Cottrill, R.A., Mohr, L.C., and Koproski, S.R. 2015. Coupling age-structured stock assessment and fish bioenergetics models: a system of time-varying models for quantifying piscivory patterns during the rapid trophic shift in the main basin of Lake Huron. *Can. J. Fish. Aquat. Sci.* **72**(1): 7–23.
- Hendricks, M.L. 2003. Culture and transplant of alosines in North America. *In* Biodiversity, status, and conservation of the world's shads. pp. 303–312. Available from <://BIOSIS:PREV200300480720>.
- He, X., and LaBar, G.W. 1994. Interactive effects of cannibalism, recruitment, and predation on rainbow smelt in Lake Champlain - a modeling synthesis. *J. Gt. Lakes Res.* **20**(1): 289–298.
- Honeyfield, D.C., Brown, S.B., Fitzsimons, J.D., and Tillitt, D.E. 2005. Early mortality syndrome in Great Lakes Salmonines. *J. Aquat. Anim. Health* **17**(1): 1–3.
- Hoover, E.E. 1936. The spawning activities of freshwater smelt, with special reference to the sex ratio. *Copeia* **2**: 85–91.
- Intergovernmental Panel on Climate Change (IPCC). 2014. Climate change 2013: The physical science basis: working group I contribution to the fifth assessment report of the intergovernmental panel on climate change. Cambridge University Press.
- Janssen, J. 1978. Feeding-behavior repertoire of the alewife, *Alosa pseudoharengus*, and the ciscos, *Coregonus hoyi* and *C. artedii*. *J. Fish. Res. Board Can.* **35**: 249–253.
- Johnson, B.M., and Goettl Jr, J.P. 1999. Food web changes over fourteen years following introduction of rainbow smelt into a Colorado reservoir. *North Am. J. Fish. Manag.* **19**(3): 629–642.

- Jones, M.S., Goettl JR, J.P., and Flickinger, S.A. 1994. Changes in walleye food habits and growth following a rainbow smelt introduction. *North Am. J. Fish. Manag.* **14**(2): 409–414.
- Jude, D., Tesar, F.J., Dorr, J.A., Miller, T.J., Rago, P.J., and Stewart, D.J. 1975. Inshore lake Michigan fish population near the Donald C. Cook Nuclear Power Plant, 1973. *Univ. Mich. Gt. Lakes Res. Div. Spec. Rep.* **52**: 267 p.
- Kellison, G.T., Eggleston, D.B., and Tanaka, M. 2002. Density-dependent predation and implications for stock enhancement with Japanese flounder. *J. Fish Biol.* **60**(4): 968–980.
- Kendall, W. 1927. The smelts. *Bull. U. S. Bur. Fish.* **41**: 217–375.
- Kimura, K. 1929. On the detection of fish-groups by an acoustic method. *J. Imp. Fish. Inst. Tokyo* **24**: 41–45.
- Kirn, R.A., and Labar, G.W. 1991. Stepped-oblique midwater trawling as an assessment technique for rainbow smelt. *North Am. J. Fish. Manag.* **11**(2): 167–176.
- Kirn, R.A., and Labar, G.W. 1996. Growth and survival of rainbow smelt, and their role as prey for stocked salmonids in Lake Champlain. *Trans. Am. Fish. Soc.* **125**(1): 87–96.
- Kitchell, J.F., Cox, S.P., Harvey, C.J., Johnson, T.B., Mason, D.M., Schoen, K.K., Aydin, K., Bronte, C., Ebener, M., Hansen, M., Hoff, M., Schram, S., Schreiner, D., and Walters, C.J. 2000. Sustainability of the Lake Superior fish community: interactions in a food web context. *Ecosystems* **3**(6): 545–560.
- Klumb, R.A., Rudstam, L.G., Mills, E.L., Schneider, C.P., and Sawyko, P.M. 2003. Importance of Lake Ontario embayments and nearshore habitats as nurseries for larval fishes with emphasis on alewife (*Alosa pseudoharengus*). *J. Gt. Lakes Res.* **29**(1): 181–198.

- Krueger, C.C., Perkins, D.L., Mills, E.L., and Marsden, J.E. 1995. Predation by alewives on lake trout fry in Lake Ontario: Role of an exotic species in preventing restoration of a native species. *J. Gt. Lakes Res.* **21**: 458–469.
- Kubecka, J., Frouzová, J., Cech, M., Peterka, J., Ketelaars, H.A., Wagenwoort, A.J., and Papáček, M. 2000. Hydroacoustic assessment of pelagic stages of freshwater insects. *Aquat. Living Resour.* **13**(05): 361–366.
- LaBar, G.W. 1993. Use of bioenergetics models to predict the effect of increased lake trout predation on rainbow smelt following sea lamprey control. *Trans. Am. Fish. Soc.* **122**(5): 942–950.
- Langdon, R.W., Ferguson, M.T., and Cox, K.M. 2006. *Fishes of Vermont*. Vermont Fish and Wildlife Department, Montpelier, VT.
- Lantry, B.F., and Stewart, D.J. 1993. Ecological energetics of rainbow smelt in the Laurentian Great Lakes: An interlake comparison. *Trans. Am. Fish. Soc.* **122**(5): 951–976.
- Lantry, B.F., and Stewart, D.J. 2000. Population dynamics of rainbow smelt (*Osmerus mordax*) in Lakes Ontario and Erie: a modeling analysis of cannibalism effects. *Can. J. Fish. Aquat. Sci.* **57**(8): 1594–1606.
- Legault, R., and Delisle, C. 1968. The spawning of a population of giant smelt, *Osmerus eperlanus mordax*, in Lake Heney, Gatineau County, Quebec. *J. Fish. Res. Board Can.* **25**(9): 1813–1830.
- Lepak, J.M., and Kraft, C.E. 2008. Alewife mortality, condition, and immune response to prolonged cold temperatures. *J. Gt. Lakes Res.* **34**(1): 134–142.
- Lewis, J.M., Ewart, K.V., and Driedzic, W.R. 2004. Freeze resistance in rainbow smelt (*Osmerus mordax*): Seasonal pattern of glycerol and antifreeze protein levels and liver

- enzyme activity associated with glycerol production. *Physiol. Biochem. Zool.* **77**(3): 415–422.
- Lloyd, M. 1967. 'Mean Crowding'. *J. Anim. Ecol.* **36**(1): 1. doi: 10.2307/3012.
- Locke, A., and Courtenay, S.C. 1995. Effects of environmental-factors on ichthyoplankton communities in the Miramichi Estuary, Gulf of St-Lawrence. *J. Plankton Res.* **17**(2): 333–349.
- Mack, R.N., Simberloff, D., Lonsdale, W.M., Evans, H., Clout, M., and Bazzaz, F.A. 2000. Biotic invasions: causes, epidemiology, global consequences, and control. *Ecol. Appl.* **10**(3): 689–710.
- Madenjian, C.P., Fahnenstiel, G.L., Johengen, T.H., Nalepa, T.F., Vanderploeg, H.A., Fleischer, G.W., Schneeberger, P.J., Benjamin, D.M., Smith, E.B., and Bence, J.R. 2002. Dynamics of the Lake Michigan food web, 1970–2000. *Can. J. Fish. Aquat. Sci.* **59**(4): 736–753.
- Madenjian, C.P., Höök, T.O., Rutherford, E.S., Mason, D.M., Croley, T.E., Szalai, E.B., and Bence, J.R. 2005. Recruitment variability of alewives in Lake Michigan. *Trans. Am. Fish. Soc.* **134**(1): 218–230.
- Madenjian, C.P., O’Gorman, R., Bunnell, D.B., Argyle, R.L., Roseman, E.F., Warner, D.M., Stockwell, J.D., and Stapanian, M.A. 2008. Adverse effects of alewives on Laurentian Great Lakes fish communities. *North Am. J. Fish. Manag.* **28**(1): 263–282.
- Magnuson, J.J., Crowder, L.B., and Medvick, P.A. 1979. Temperature as an ecological resource. *Am. Zool.* **19**(1): 331–343. doi: 10.1093/icb/19.1.331.
- Magnuson, J.J., Meisner, J.D., and Hill, D.K. 1990. Potential changes in the thermal habitat of Great Lakes Fish after global climate warming. *Trans. Am. Fish. Soc.* **119**(2): 254–264.

- Malinen, T., Tuomaala, A., and Peltonen, H. 2005. Hydroacoustic fish stock assessment in the presence of dense aggregations of *Chaoborus* larvae. *Can. J. Fish. Aquat. Sci.* **62**(2): 245–249. doi: 10.1139/f05-038.
- Manley, T.O., and Manley, P. 1999. Lake Champlain in transition: from research toward restoration. American Geophysical Union, Washington, DC.
- Marsden, J.E., Ellrott, B.J., Claramunt, R.M., Jonas, J.L., and Fitzsimons, J.D. 2005. A comparison of lake trout spawning, fry emergence, and habitat use in lakes Michigan, Huron, and Champlain. *J. Gt. Lakes Res.* **31**(4): 492–508.
- Marsden, J.E., and Hauser, M. 2009. Exotic species in Lake Champlain. *J. Gt. Lakes Res.* **35**(2): 250–265. doi: 10.1016/j.jglr.2009.01.006.
- Mason, D.M., Johnson, T.B., Harvey, C.J., Kitchell, J.F., Schram, S.T., Bronte, C.R., Hoff, M.H., Lozano, S.J., Trebitz, A.S., and Schreiner, D.R. 2005. Hydroacoustic estimates of abundance and spatial distribution of pelagic prey fishes in western Lake Superior. *J. Gt. Lakes Res.* **31**(4): 426–438.
- Mercado-Silva, N., Olden, J.D., Maxted, J.T., Hrabik, T.R., and Zanden, M.J.V. 2006. Forecasting the spread of invasive rainbow smelt in the Laurentian Great Lakes region of North America. *Conserv. Biol.* **20**(6): 1740–1749. doi: 10.1111/j.1523-1739.2006.00508.x.
- Miller, R.R. 1957. Origin and dispersal of the alewife, *Alosa pseudoharengus*, and the gizzard shad, *Dorosoma cepedianum*, in the Great Lakes. *Trans. Am. Fish. Soc.* **86**(1): 97–111.
- Mills, E.L., Casselman, J.M., Dermott, R., Fitzsimons, J.D., Gal, G., Holeck, K.T., Hoyle, J.A., Johannsson, O.E., Lantry, B.F., and Makarewicz, J.C. 2003a. Lake Ontario: food web

- dynamics in a changing ecosystem (1970-2000). *Can. J. Fish. Aquat. Sci.* **60**(4): 471–490.
- Mills, E.L., Dermott, R., Munawar, M., Millard, S., Johannsson, O., and Rudstam, L.G. 2003c. Status of the Lake Ontario food web in a changing ecosystem: the 2003 Lake Ontario lower aquatic food web assessment (LOLA). Available from [http://digitalcommons.brockport.edu/tech\\_rep/73/](http://digitalcommons.brockport.edu/tech_rep/73/) [accessed 8 April 2014].
- Mills, E.L., Ogorman, R., Roseman, E.F., Adams, C., and Owens, R.W. 1995. Planktivory by alewife (*Alosa pseudoharengus*) and rainbow smelt (*Osmerus mordax*) on microcrustacean zooplankton and dreissenid (*Bivalvia, Dreissenidae*) veligers in southern Lake-Ontario. *Can. J. Fish. Aquat. Sci.* **52**(5): 925–935.
- Moore, E. 1929. A biological survey of the Champlain watershed. New York State Conservation Department, Albany, NY.
- Nickus, U., Bishop, K., Erlandsson, M., Evans, C.D., Forsius, M., Laudon, H., Livingstone, D.M., Monteith, D., and Thies, H. 2010. Direct impacts of climate change on freshwater ecosystems. *Clim. Change Impacts Freshw. Ecosyst.*: 38–64.
- O'Brien, T.P., Taylor, W.W., Roseman, E.F., Madenjian, C.P., and Riley, S.C. 2014. Ecological factors affecting rainbow smelt recruitment in the Main Basin of Lake Huron, 1976–2010. *Trans. Am. Fish. Soc.* **143**(3): 784–795.
- Otto, R.G., Kitchel, M.A., and Rice, J.O. 1976. Lethal and preferred temperatures of the alewife (*Alosa pseudoharengus*) in Lake Michigan. *Trans. Am. Fish. Soc.* **105**(1): 96–106.
- Overman, N.C., and Parrish, D.L. 2001. Stable isotope composition of walleye:  $\delta^{15}\text{N}$  accumulation with age and area-specific differences in  $\delta^{13}\text{C}$ . *Can. J. Fish. Aquat. Sci.* **58**(6): 1253–1260.

- Oyadomari, J.K., and Auer, N.A. 2004. Inshore-offshore distribution of larval fishes in Lake Superior off the western coast of the Keweenaw Peninsula, Michigan. *J. Gt. Lakes Res.* **30**: 369–384.
- Parker, S.L., Rudstam, L.G., Mills, E.L., and Einhouse, D.W. 2001. Retention of *Bythotrephes* spines in the stomachs of eastern Lake Erie rainbow smelt. *Trans. Am. Fish. Soc.* **130**(5): 988–994.
- Parker Stetter, S.L., Rudstam, L.G., Stritzel Thomson, J.L., and Parrish, D.L. 2006. Hydroacoustic separation of rainbow smelt (*Osmerus mordax*) age groups in Lake Champlain. *Fish. Res.* **82**(1-3): 176–185.
- Parker-Stetter, S.L., Rudstam, L.G., Sullivan, P.J., and Warner, D.M. 2009. Standard operating procedures for fisheries acoustic surveys in the Great Lakes. Great Lakes Fishery Commission.
- Parker Stetter, S.L., Thomson, J.L.S., Rudstam, L.G., Parrish, D.L., and Sullivan, P.J. 2007. Importance and predictability of cannibalism in Rainbow Smelt. *Trans. Am. Fish. Soc.* **136**(1): 227–237.
- Pauly, D., Christensen, V., and Walters, C. 2000. Ecopath, Ecosim, and Ecospace as tools for evaluating ecosystem impact of fisheries. *ICES J. Mar. Sci. J. Cons.* **57**(3): 697–706. doi: 10.1006/jmsc.2000.0726.
- Pientka, B., and Parrish, D.L. 2002. Habitat selection of predator and prey: Atlantic salmon and rainbow smelt overlap, based on temperature and dissolved oxygen. *Trans. Am. Fish. Soc.* **131**(6): 1180–1193.
- Plosila, D.S. 1984. Spatial distribution of rainbow smelt spawning in the New York waters of Lake Champlain. *N. Y. Fish Game J.* **31**(1): 109–111.

- Rand, P.S., and Stewart, D.J. 1998a. Prey fish exploitation, salmonine production, and pelagic food web efficiency in Lake Ontario. *Can. J. Fish. Aquat. Sci.* **55**(2): 318–327.
- Rand, P.S., and Stewart, D.J. 1998b. Dynamics of salmonine diets and foraging in Lake Ontario, 1983-1993: a test of a bioenergetic model prediction. *Can. J. Fish. Aquat. Sci.* **55**(2): 307–317.
- Rhodes, R.J., Webb, D.A., and McComish, T.S. 1974. Cannibalism by the adult alewife (*Alosa pseudoharengus*) in southern Lake Michigan. *In Proceedings, Seventeenth Conference on Great Lakes Research.*
- Rice, J.A. 2002. Cascading effects of human impacts on fish populations in the Laurentian Great Lakes. *In Fishery Science: The unique contributions of early life stages. Edited by L.A. Fuiman and R.G. Werner.* Blackwell Science Ltd., Malden, MA. p. 326.
- Rockström, J., Steffen, W., Noone, K., Persson, A.A.S., Chapin, F.S., Lambin, E.F., Lenton, T.M., Scheffer, M., Folke, C., and Schellnhuber, H.J. 2009. A safe operating space for humanity. *Nature* **461**(7263): 472–475.
- Roessig, J.M., Woodley, C.M., Jr, J.J.C., and Hansen, L.J. 2005. Effects of global climate change on marine and estuarine fishes and fisheries. *Rev. Fish Biol. Fish.* **14**(2): 251–275.
- Rudstam, L. 2003. Application of in situ target-strength estimations in lakes: examples from rainbow-smelt surveys in Lakes Erie and Champlain. *ICES J. Mar. Sci.* **60**(3): 500–507.
- Rudstam, L.G., VanDeValk, A.J., and Scheuerell, M.D. 2002. Comparison of acoustic and Miller high-speed sampler estimates of larval fish abundance in Oneida Lake, New York. *Fish. Res.* **57**(2): 145–154.
- Rupp, R.S. 1965. Shore-spawning and survival of eggs of the American smelt. *Trans. Am. Fish. Soc.* **94**(2): 160–168.

- Shambaugh, A.D., Duchovnay, A., and McIntosh, A. 1999. A survey of Lake Champlain's plankton. *In* Lake Champlain in transition: from research toward restoration. *Edited by* T.O. Manley and P. Manley. American Geophysical Union, Washington, DC. pp. 323–340.
- Simmonds, J., and MacLennan, D.N. 2008. Fisheries acoustics: Theory and practice. John Wiley & Sons.
- Sirois, P., and Dodson, J.J. 2000. Critical periods and growth-dependent survival of larvae of an estuarine fish, the rainbow smelt *Osmerus mordax*. *Mar. Ecol.-Prog. Ser.* **203**: 233–245.
- Smith, C.L. 1985. The inland fishes of New York State. New York State Department of Environmental Conservation, Albany, NY.
- Smith, S.H. 1968. That little pest the alewife. *Limnos* **1**: 12–20.
- Stetter, S.P., Witzel, L.D., Rudstam, L.G., Einhouse, D.W., and Mills, E.L. 2005. Energetic consequences of diet shifts in Lake Erie rainbow smelt ( *Osmerus mordax* ). *Can. J. Fish. Aquat. Sci.* **62**(1): 145–152.
- Stewart, D.J., Kitchell, J.F., and Crowder, L.B. 1981. Forage fishes and their salmonid predators in Lake Michigan. *Trans. Am. Fish. Soc.* **110**(6): 751–763.
- Stickney, M., Hickey, C., and Hoerr, R. 2001. Lake Champlain basin program: working together today for tomorrow. *Lakes Reserv. Res. Manag.* **6**(3): 217–223.
- Stockwell, J.D., Yule, D.L., Hrabik, T.R., Adams, J.V., Gorman, O.T., and Holbrook, B.V. 2007. Vertical distribution of fish biomass in Lake Superior: Implications for day bottom trawl surveys. *North Am. J. Fish. Manag.* **27**(3): 735–749.

- Stritzel Thomson, J.L., Parrish, D.L., Parker-Stetter, S.L., Rudstam, L.G., and Sullivan, P.J. 2011. Growth rates of rainbow smelt in Lake Champlain: effects of density and diet: Growth rates of rainbow smelt. *Ecol. Freshw. Fish* **20**(4): 503–512.
- Tillitt, D.E., Zajicek, J.L., Brown, S.B., Brown, L.R., Fitzsimons, J.D., Honeyfield, D.C., Holey, M.E., and Wright, G.M. 2005. Thiamine and thiaminase status in forage fish of salmonines from Lake Michigan. *J. Aquat. Anim. Health* **17**(1): 13–25.
- Tin, H.T., and Jude, D.J. 1983. Distribution and growth of larval rainbow smelt in Eastern Lake Michigan, 1978–1981. *Trans. Am. Fish. Soc.* **112**(4): 517–524.
- Urban, T.P., and Brandt, S.B. 1993. Food and habitat partitioning between young-of-year alewives and rainbow smelt in southeastern Lake Ontario. *Environ. Biol. Fishes* **36**(4): 359–372.
- Urho, L. 1992. Morphological and ecological differences in the development of smelt and herring larvae in the Northern Baltic Sea. *Sarsia* **77**(1): 1–10.
- Urick, R.J. 1983. Principles of Underwater Sound. *In* 3rd edition. Peninsula Publishing, Los Altos, California.
- Vert-pre, K.A., Amoroso, R.O., Jensen, O.P., and Hilborn, R. 2013. Frequency and intensity of productivity regime shifts in marine fish stocks. *Proc. Natl. Acad. Sci.* **110**(5): 1779–1784.
- Waldman, J.R., Grunwald, C., and Wirgin, I. 2006. Evaluation of the native status of sea lampreys in Lake Champlain based on mitochondrial DNA sequencing analysis. *Trans. Am. Fish. Soc.* **135**(4): 1076–1085.
- Walters, C.J., and Martell, S.J.D. 2004. Fisheries ecology and management. Princeton University Press.

- Walters, C., Pauly, D., and Christensen, V. 1999. Ecospace: prediction of mesoscale spatial patterns in trophic relationships of exploited ecosystems, with emphasis on the impacts of marine protected areas. *Ecosystems* **2**(6): 539–554.
- Wells, L. 1968. Seasonal depth distribution of fish in southeastern Lake Michigan. US Fish Wildl. Service Fish. Bull. *67*: 15 p.
- Williamson, C.E., and Stoeckel, M.E. 1990. Estimating predation risk in zooplankton communities: the importance of vertical overlap. *In* Intrazooplankton predation. *Edited by* H.J. Dumont, J.G. Tundisi, and K. Roche. Springer Netherlands. pp. 125–131. Available from [http://link.springer.com/chapter/10.1007/978-94-009-2067-5\\_12](http://link.springer.com/chapter/10.1007/978-94-009-2067-5_12) [accessed 20 March 2015].
- Wistbacka, S. 2002. Thiaminase activity of gastrointestinal contents of salmon and herring from the Baltic Sea. *J. Fish Biol.* **60**(4): 1031–1042.

**CHAPTER 2**

**HATCH DATES, ABUNDANCE, GROWTH RATES, AND MORTALITY OF AGE 0  
RAINBOW SMELT AND ALEWIFE IN LAKE CHAMPLAIN: IMPLICATIONS FOR  
SPECIES INTERACTIONS<sup>1</sup>**

---

<sup>1</sup> *Simonin, P.W., L.G. Rudstam, D.L. Parrish, B. Pientka, P. Sullivan. Hatch dates, abundance, growth rates, and mortality of age 0 rainbow smelt and alewife in Lake Champlain. Transactions of the American Fisheries Society. In revision.*

## ABSTRACT

Timing of hatch in fish can be critical for first-year survival and therefore year – class strength and subsequent species interactions. We compared hatch timing, abundance, growth rates, and subsequent survival of age 0 Rainbow Smelt *Osmerus mordax* and Alewife *Alosa pseudoharengus*, two common open-water fish of northern North America. In our study site, Lake Champlain, Rainbow Smelt hatched almost a month earlier than Alewife (hatching began on 26 May for Rainbow Smelt and 20 June for Alewife). Abundance in the sampling area was highest in July for age 0 Rainbow Smelt and August for Alewife. Later hatching individuals of both species grew faster than those hatching earlier (0.6 mm/d vs. 0.4 for Rainbow Smelt; 0.7mm/d vs. 0.6 for Alewife). Mean mortality rate for age 0 Rainbow Smelt was 3.4% /d and for Alewife was 5.5%/d during the first 45 days of life. Alewife mortality rates did not differ with hatch timing but daily mortality rates of Rainbow Smelt were highest for earlier hatching fish. Because cannibalism by Rainbow Smelt is likely the primary mortality source for age-0 Rainbow Smelt in this lake, early hatching may not be advantageous as the overlap between adult and age-0 Rainbow Smelt is highest early in the season. However, Alewife, first found in Lake Champlain in 2003, may increase age 0 Rainbow Smelt summer mortality. Increased summer mortality in Rainbow Smelt should, in turn, favor selection for early hatching.

## INTRODUCTION

Hatch timing in fish can be critical for first-year growth and survival, and therefore recruitment. Most fish larvae do not survive their first few months of life, and individual survival is often a function of time spent vulnerable to predators (Cushing 1975). Growth may increase the probability of survival, with larger, faster-growing, and faster-developing individuals more likely to survive (Chambers and Leggett 1987; Miller et al. 1988; Hare and Cowen 1997; Takasuka et al. 2003). Growth in turn is a function of hatch timing because temperature regimes, prey availability and predation vary seasonally.

Alewife and Rainbow Smelt *Osmerus mordax* are ecologically important components of Laurentian Great Lakes ecosystems and many smaller lakes in North America, both as major zooplankton and *Mysis diluviana* predators and as the forage base for salmonid and Walleye *Sander vitreus* fisheries (Christie 1974; Stewart et al. 1981). Both species have highly variable annual recruitment, and in their native marine habitat are anadromous spring spawners (Smith 1985; Parker Stetter et al. 2007; Höök et al. 2008). In freshwater systems, Rainbow Smelt and Alewife either move into tributaries or embayments to spawn, or spawn along shorelines (Klumb et al. 2003; O'Brien et al. 2012).

Recruitment success can be habitat-specific (Höök et al. 2007), but there are few studies of these important species which investigate interactions between hatch timing, growth rates, abundance, and mortality over the first growing season in lake systems. In Lake Michigan in 1978-81, the predominant Rainbow Smelt cohort hatched in early to mid-May, and growth rates from May through August were approximately 0.31-0.36 mm/day (Tin and Jude 1983). Rainbow Smelt recruitment was studied in Lake Erie and found to be related to adult Rainbow Smelt

densities (Henderson and Nepszy 1989), but hatch timing was not included in this analysis. In 1966-67, Alewife adults were observed spawning in the Kalamazoo River in late May and early June (Edsall 1970), but hatch dates and mortality were not recorded. Alewife daily mortality over the first summer of growth in Lake Michigan was in the range of 12-27% for larvae before yolk absorption, and 2-5% after absorption during 1974-1982 (Mansfield and Jude 1986). However, mortality in relation to seasonal hatch timing was not recorded in this study.

Our study examines young-of-the-year (age 0) Alewife and Rainbow Smelt hatch dates, abundance, growth, and mortality in a large north-temperate lake. Rainbow Smelt are native to Lake Champlain (Moore 1929), but Alewife were first observed in 2003 and the population increased by 2007 (Marsden and Hauser 2009). Prior to our study in 2007, relatively few age 0 alewives had been collected from Lake Champlain. Our objectives were to determine hatch date, abundance, growth rate, and mortality patterns of these species to infer differential survival and recruitment related to hatch timing. We hypothesized individual growth rates would be slower and mortality rates higher for early-hatching age 0 of both species.

## **METHODS**

Lake Champlain is a large inland lake bordered by New York (USA), Vermont (USA), and Québec (Canada). Our primary survey site included two inshore-to-offshore transects, and one offshore transect, in the main lake (Figure 2.1). These transects were surveyed using the Vermont Department of Fish and Wildlife's (VTFW) *Doré* every two to three weeks from June to October of 2007 and 2008. Nighttime hydroacoustic data were collected to estimate fish abundance, with surveys starting at least one hour after sunset. Age 0 fish were collected during night and dusk, with dusk defined as one hour before sunset until one hour after sunset.

A BioSonics DT-X, 120-kHz split-beam echo sounder using a 0.4 ms pulse duration at an interval of 2 pulses/sec ( $7.5^\circ$  half – power beam width) was used to collect hydroacoustic data. The transducer was mounted on a 1.3-m long tow body (BioSonics BioFin) suspended alongside the survey vessel at a depth of ~1 m below the surface and towed at ~2 m/s. The unit was calibrated at least once per month using a standard 33-mm dia. tungsten carbide calibration sphere. Sphere target strength (TS) measurements remained within  $\pm 0.2$  dB, so no adjustments were necessary. Hydroacoustic data used in this study were collected during nighttime surveys (Simonin et al. 2012).

Fish were collected using a 1 m x 1 m opening-closing trawl (Tucker) and 5 m x 5 m mid-water otter trawl. The Tucker trawl (1000  $\mu\text{m}$  mesh) had three separate nets that could be opened and closed at depth and was used to target age 0 fish at specific depths, whereas the mid-water trawl (12.7 mm mesh in the codend) targeted larger fish and could not be closed at depth. Each tow was 15 min long, with 5 min for each net in the Tucker trawl. A net transponder was attached to the headrope of each trawl to provide real-time tow depths. Fish collected verified the identity of targets recorded acoustically, and samples were frozen in the field for preservation and use in later analyses. We recorded total lengths of both adult (fresh, in field) and age 0 (thawed, in lab) fish. All age 0 Rainbow Smelt and Alewife were defrosted in the lab, given an identification number, and photographed. We measured total length (mm) digitally using Image Tool software (University of Texas UTHSCSA, San Antonio, Texas, USA).

Daily ring deposition has been verified for both species, so otolith ring counts were used to estimate hatch dates (Essig and Cole 1986; Sirois et al. 1998; Ganger 1999; Höök et al. 2007). Otoliths were aged using light microscopy with cross polarization. If there were more than 20 individuals of a species caught for a time-depth category (e.g., nighttime, 10 m trawl depth), 20

were haphazardly selected for aging. Standard procedures were used to verify precision of readings (e.g., Lochet et al. 2008), with blind increment counting done twice by the same reader, counting first from primordium to edge, then edge to primordium, and a second reader following the same procedure to check a subset of otoliths read by the first. Daily growth rate was calculated in mm/d by dividing measured lengths with estimated age.

Hydroacoustic data were processed using Myriax Software's *Echoview* program (Version 4.6, Myriax Software Pty Ltd., Hobart, TAS Australia) and followed the standard operating procedures for hydroacoustic surveys in the Great Lakes (Rudstam et al. 2009). Target strength (TS) distributions and trawl catches from the same depth layers confirmed that TS ranges for different age groups of Rainbow Smelt were the same as previously-determined ranges for Rainbow Smelt at 70 kHz in Lake Champlain (age-1 and older: -60 to -35 dB, age-0: -80 to -45 dB), and overlapping TS distributions for young and adult fish were analyzed as outlined in Parker Stetter et al. (2006). Simultaneous collections of both 70- and 120-kHz data in June of 2007 showed very similar target strength distributions (Rudstam et al. 2009). The abundance of each age 0 weekly cohort was then calculated from the total acoustics estimate of age 0 of each species and the proportion of the fish aged that were in each weekly cohort.

Instantaneous mortality rates were calculated for age 0, grouped in cohorts of fish hatching the same week, from the decline in abundance of the particular cohort during the first 45 days of life. The hatching periods included a maximum of seven weeks for Rainbow Smelt (in 2007) and eight weeks for Alewife (also in 2007). Mortality was only calculated when cohorts were observed during two or more sampling occasions. Multivariate linear model regression (R Development Core Team 2013), was used to test for significance of changes in mortality related to cohort, and regression included year as well.

## RESULTS

We determined hatch dates for age 0 Rainbow Smelt (406 fish) and Alewife (230 fish) using fish aged through 45 days. Otolith reading error for both species increased with age, as was expected. For fish younger than 45 days, there was no significant difference between ages from the two readers (t-test,  $p=0.63$ ), and  $< 5\%$  of readings were discarded due to discrepancies between readers.

Rainbow Smelt hatched from late May through early July 2007 and 2008 whereas most age 0 Alewife hatched in July. In both 2007 and 2008, Rainbow Smelt in the main lake began hatching in late May, and hatching continued until July (Figure 2.2). Ninety percent of the population hatched in June both years. The earliest fish hatched on 26 May, and the latest hatched on 31 July. The Rainbow Smelt population had a median hatch date of 17 June in 2007 and 12 June in 2008. Alewife hatched from late June until August in 2007 and 2008. The earliest hatch recorded was 18 June, 2008 and the latest was 6 August, 2007, with a median hatch date of 9 July in 2007 and 8 July in 2008.

Overall abundance of age 0 Rainbow Smelt in our survey region was similar in 2007 and 2008 (Figure 2.3). Age 0 Alewives were more abundant in August 2008 than August 2007 (Figure 2.3). Rainbow Smelt age 0 were most abundant in late July in 2007 and 2008. Alewife age 0 abundance increased most rapidly (from about 0 to 6 fish per square meter in 2008) at the same time age 0 Rainbow Smelt abundance declined most rapidly (from about 11 to 1 fish per square meter in 2008).

Rainbow Smelt growth rates ranged from 0.2 to 1 mm /day, with a mean of 0.57 mm/day. Alewife growth rates ranged from 0.3 to 1.3 mm/day, with a mean of 0.65 mm/day. Early-

hatching Rainbow Smelt and Alewife grew significantly slower than later-hatching individuals (Rainbow Smelt:  $p=0.0499$ ; Alewife:  $p<0.0001$ ). Age also significantly affected growth rate, with older fish growing faster (Rainbow Smelt:  $p=0.0023$ ; Alewife:  $p<0.0001$ ). Lengths at age were similar for the two years, although faster-growing Alewife were collected in 2007 at age 40 to 45 days (Figure 2.4).

Rainbow Smelt mortality rates (%/day) ranged from 0.3 to 5.9, with a mean rate of 3.4. Alewife mortality rates ranged from 2.5%/day to 7.7, with a mean of 5.5 (Figure 2.5). Early hatching Rainbow Smelt in 2007 had a mortality rate of 5.9%/day, compared to  $<1\%$  for late-hatching individuals (Figure 2.5). Early hatching Rainbow Smelt have a significantly higher mortality rate than later hatching Rainbow Smelt ( $p=0.03$ ), whereas Alewife mortality rates show no significant trend with hatch date ( $p=0.57$ , Figure 2.5).

## **DISCUSSION**

Because of lower water temperatures and predation by adult Rainbow Smelt, we hypothesized that early hatching Rainbow Smelt and Alewife would have slower growth rates and higher mortality rates than later hatching individuals. As hypothesized, growth rates were significantly slower and mortality rates significantly higher for early-hatching Rainbow Smelt. Alewife growth rate was also significantly slower for early-hatching individuals. However, Alewife mortality rates did not differ significantly as a function of hatch date.

Rainbow Smelt and Alewife hatching took place during a period of over two months in the main lake of Lake Champlain. Most Rainbow Smelt hatched in June, but hatch dates ranged from late May through early July in both 2007 and 2008. Alewife hatched in July, with some fish also hatching in late June and early August. Both species were most abundant in the area a few

weeks after the last observed hatching date indicating either recruitment to the gear, or to the area sampled, or both.

Hatch dates in July are common for Alewife at this latitude. In Lake Ontario, larval Alewife were most abundant in nearshore and embayment habitats during late July and early August, and most Alewife hatched in late June through July. (Klumb et al. 2003). In Lake Michigan, Alewife also hatch primarily during July, but Alewife hatch time stretches from mid-May through early August in smaller lakes near Lake Michigan (Höök et al. 2007). In these systems, like in others, it is thought that variable and wide-ranging hatch time minimizes inter-annual variation in recruitment under varying environmental conditions (Garvey et al. 2002; Höök et al. 2008).

Rainbow Smelt typically hatch earlier in other systems at similar latitudes. In Crystal Lake, Wisconsin, Rainbow Smelt began hatching on 9 May in 1995 although in 1996, a year with a colder spring, hatch started on 30 May (Hrabik et al. 2001). In this system, the mean hatching date calculated from long-term temperature records was 4 May, with a mean hatch date range of 23 April to 18 May. Evidence from other systems suggests Rainbow Smelt hatch dates generally range from April through May elsewhere in North American lakes (Smith 1985; Buckley 1989).

In contrast, Lake Champlain Rainbow Smelt hatched primarily in June with some fish hatching as late as early July. Late Rainbow Smelt hatching could be a response to the dominance of adult Rainbow Smelt as predators on fish larvae in this system (Parker Stetter et al. 2007). Selection by cannibalism for late hatching would not only select for later spawning, but also for spawning grounds that slow incubation, such as the deep substrate (17-23 m) preferred

by Lake Champlain Rainbow Smelt (Plosila 1984). Preference for deep spawning sites also delays spawning, because water at these depths warms more slowly than in near-shore or stream areas.

Changes in age 0 abundance, and therefore estimates of mortality, in our main lake section through the season could be caused by several factors, including sampling bias. Many studies whose goal is to capture larval fish within one to two weeks of hatching use 300-600  $\mu\text{m}$  mesh sizes (e.g., Klumb et al. 2003), and thus the 1000 micron mesh Tucker trawl we used likely does not catch age 0 fish immediately after hatching. Likewise, fish larger than 60mm begin to avoid the Tucker trawl (P.W. Simonin, personal communication). Thus, the range of fish sizes for which this gear is effective is approximately 15 – 60mm, which is appropriate for our study..

Predation is the most common mortality source for age 0 fish in general (Bailey and Houde 1989), and Lake Champlain Rainbow Smelt in particular (Parker Stetter et al. 2007). Over annual and longer time cycles, larger individuals of a given species generally survive better (Miller et al. 1988), and we may expect early-hatched individuals to be larger and more fit prior to winter (Höök et al. 2007). However, early-hatched individuals were slower growing than later-hatching fish, and thus late hatching Rainbow Smelt and Alewife in Lake Champlain progress more rapidly through vulnerable larval stages.

Both Rainbow Smelt and Alewife particulate feed and are known to be predators on larval fish, (Rhodes et al. 1974; He and LaBar 1994). We observed larval fish in the stomachs of several alewives collected in 2008. Rainbow Smelt cannibalism rate in Lake Champlain is a function of adult and age 0 abundance and spatial overlap (Parker Stetter et al. 2007). Thus,

cannibalism rates are likely highest in spring when the lake is not thermally stratified, leading to higher age 0 Rainbow Smelt mortality rates for early hatching than late hatching individuals.

In Lake Champlain, Alewife may alter the selection forces (risk of mortality through cannibalism and large size in the fall) that we believe have been responsible for the late hatching of this population. Alewife in the Great Lakes have affected other fish species through both competition and predation (Crowder 1980), specifically via predation on larvae of native fish (Madenjian et al. 2008). Rainbow Smelt larvae were historically shielded from intense cannibalism by hatching late, after thermal stratification. However, summer mortality could increase if adult alewives continue occupying the epilimnion. Increased summer mortality in Rainbow Smelt should, in turn, favor selection for early hatching.

## REFERENCES

- Bailey, K. M., and E. D. Houde. 1989. Predation on eggs and larvae of marine fishes and the recruitment problem. *Advances in Marine Biology* 25:1-83.
- Buckley, J. 1989. Species profiles: life histories and environmental requirements of coastal fishes and invertebrates (North Atlantic)--rainbow smelt. U.S. Fish and Wildlife Service Biological Report 82(11.106). U.S. Army Corps of Engineers, TR EL-82-4.
- Chambers, R. C., and W. C. Leggett. 1987. Size and age at metamorphosis in marine fishes: an analysis of laboratory-reared winter flounder (*Pseudopleuronectes americanus*) with a review of variation in other species. *Canadian Journal of Fisheries and Aquatic Sciences* 44:1936-1947.
- Christie, W. 1974. Changes in the fish species composition of the Great Lakes. *Journal of the Fisheries Research Board of Canada* 31:827-854.
- Crowder, L. B. 1980. Alewife, smelt and native fishes in Lake Michigan: competition or predation? *Environmental Biology of Fishes* 5:225-233.
- Cushing, D. H. 1975. *Marine ecology and fisheries*. Cambridge University Press, Cambridge; New York.
- Edsall, T. A. 1970. The effect of temperature on the rate of development and survival of alewife eggs and larvae. *Transactions of the American Fisheries Society* 99:376-380.
- Essig, R. J., and C. F. Cole. 1986. Methods of estimating larval fish mortality from daily increments in otoliths. *Transactions of the American Fisheries Society* 115:34-40.

- Ganger, M. T. 1999. The spatial and temporal distribution of young-of-the-year *Osmerus mordax* in the Great Bay Estuary. *Environmental Biology of Fishes* 54:253-261.
- Garvey, J. E., T. P. Herra, and W. C. Leggett. 2002. Protracted reproduction in sunfish: the temporal dimension in fish recruitment revisited. *Ecological Applications* 12:194-205.
- Hare, J. A., and R. K. Cowen. 1997. Size, growth, development, and survival of the planktonic larvae of *Pomatomus saltatrix* (Pisces: Pomatomidae). *Ecology* 78:2415-2431.
- He, X., and G. W. LaBar. 1994. Interactive effects of cannibalism, recruitment, and predation on rainbow smelt in Lake Champlain - a modeling synthesis. *Journal of Great Lakes Research* 20:289-298.
- Henderson, B. A., and S. J. Nepszy. 1989. Factors Affecting Recruitment and Mortality-Rates of Rainbow Smelt (*Osmerus mordax*) in Lake Erie, 1963-85. *Journal of Great Lakes Research* 15:357-366.
- Höök, T. O., E. S. Rutherford, T. E. Croley, D. M. Mason, and C. P. Madenjian. 2008. Annual variation in habitat-specific recruitment success: implications from an individual-based model of Lake Michigan alewife (*Alosa pseudoharengus*). *Canadian Journal of Fisheries & Aquatic Sciences* 65:1402-1412.
- Höök, T. O., E. S. Rutherford, D. M. Mason, and G. S. Carter. 2007. Hatch dates, growth, survival, and overwinter mortality of age-0 alewives in Lake Michigan: implications for habitat-specific recruitment success. *Transactions of the American Fisheries Society* 136:1298-1312.

- Hrabik, T. R., M. P. Carey, and M. S. Webster. 2001. Interactions between young-of-the-year exotic rainbow smelt and native yellow perch in a northern temperate lake. *Transactions of the American Fisheries Society* 130:568-582.
- Klumb, R. A., L. G. Rudstam, E. L. Mills, C. P. Schneider, and P. M. Sawyko. 2003. Importance of Lake Ontario embayments and nearshore habitats as nurseries for larval fishes with emphasis on alewife (*Alosa pseudoharengus*). *Journal of Great Lakes Research* 29:181-198.
- Lochet, A., P. Jatteau, J. Tomas, and E. Rochard. 2008. Retrospective approach to investigating the early life history of a diadromous fish: allis shad *Alosa alosa* (L.) in the Gironde-Garonne-Dordogne watershed. *Journal of Fish Biology* 72:946-960.
- Madenjian, C. P., and coauthors. 2008. Adverse effects of alewives on Laurentian Great Lakes fish communities. *North American Journal of Fisheries Management* 28:263-282.
- Mansfield, P. J., and D. J. Jude. 1986. Alewife (*Alosa pseudoharengus*) survival during the first growth season in southeastern Lake Michigan. *Canadian Journal of Fisheries and Aquatic Sciences* 43:1318-1326.
- Marsden, J. E., and M. Hauser. 2009. Exotic species in Lake Champlain. *Journal of Great Lakes Research* 35:250-265.
- Miller, T. J., L. B. Crowder, J. A. Rice, and E. A. Marschall. 1988. Larval size and recruitment mechanisms in fishes: toward a conceptual framework. *Canadian Journal of Fisheries and Aquatic Sciences* 45:1657-1670.

- Moore, E. 1929. A biological survey of the Champlain watershed. New York State Conservation Department, Albany, NY.
- O'Brien, T. P., W. W. Taylor, A. S. Briggs, and E. F. Roseman. 2012. Influence of water temperature on rainbow smelt spawning and early life history dynamics in St. Martin Bay, Lake Huron. *Journal of Great Lakes Research* 38:776-785.
- Parker Stetter, S. L., L. G. Rudstam, J. L. Stritzel Thomson, and D. L. Parrish. 2006. Hydroacoustic separation of rainbow smelt (*Osmerus mordax*) age groups in Lake Champlain. *Fisheries Research* 82:176-185.
- Parker Stetter, S. L., J. L. Stritzel Thomson, L. G. Rudstam, D. L. Parrish, and P. J. Sullivan. 2007. Importance and predictability of cannibalism in rainbow smelt. *Transactions of the American Fisheries Society* 136:227-237.
- Plosila, D. S. 1984. Spatial distribution of rainbow smelt spawning in the New York waters of Lake Champlain. *New York Fish and Game Journal* 31:109-111.
- R Development Core Team. 2013. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Rhodes, R. J., D. A. Webb, and T. S. McComish. 1974. Cannibalism by the adult alewife (*Alosa pseudoharengus*) in southern Lake Michigan. *Proceedings of the Conference on Great Lakes Research* 17:593-595.
- Rudstam, L. G., S. L. Parker Stetter, P. J. Sullivan, and D. M. Warner. 2009. Towards a standard operating procedure for fisheries acoustic surveys in the Laurentian Great Lakes, North America. *ICES Journal of Marine Science* 66:1391-1397.

- Simonin, P. W., D. L. Parrish, L. G. Rudstam, P. J. Sullivan, and B. Pientka. 2012. Native rainbow smelt and nonnative alewife distribution related to temperature and light gradients in Lake Champlain. *Journal of Great Lakes Research* 38, Supplement 1:115-122.
- Sirois, P., F. Lecomte, and J. J. Dodson. 1998. An otolith-based back-calculation method to account for time-varying growth rate in rainbow smelt (*Osmerus mordax*) larvae. *Canadian Journal of Fisheries and Aquatic Sciences* 55:2662-2671.
- Smith, C. L. 1985. The inland fishes of New York State. New York State Department of Environmental Conservation, Albany, NY.
- Stewart, D. J., J. F. Kitchell, and L. B. Crowder. 1981. Forage fishes and their salmonid predators in Lake Michigan. *Transactions of the American Fisheries Society* 110:751-763.
- Takasuka, A., I. Aoki, and I. Mitani. 2003. Evidence of growth-selective predation on larval Japanese anchovy *Engraulis japonicus* in Sagami Bay. *Marine Ecology-Progress Series* 252:223-238.
- Tin, H. T., and D. J. Jude. 1983. Distribution and growth of larval rainbow smelt in eastern Lake Michigan, 1978-1981. *Transactions of the American Fisheries Society* 112:517-524.

## Figure captions

Figure 2.1. Lake Champlain (right panel), located between the states of New York and Vermont, and the Province of Quebec, Canada. Location of survey transects in the main lake (left) of Lake Champlain. Contour lines represent 5-m depth intervals.

Figure 2.2. Density of age 0 fish observed ( $\leq 45$  days old) with given hatch date. Values calculated by partitioning total acoustic age 0 ( $\leq 45$  days old) density estimates into cohorts using age data from fish caught in Tucker trawl.

Figure 2.3. Abundance (number per square meter) of age 0 Rainbow Smelt (A) and Alewife (B) in our main lake survey transect in 2007 and 2008.

Figure 2.4. Lengths of age 0 Rainbow Smelt (A) and Alewife (B) less than 45 days old, with linear regression lines for 2007 and 2008.

Figure 2.5. Mortality rates of age 0 Rainbow Smelt and Alewife hatching at different times in 2007 and 2008. Cohorts are groups of age 0 fish which hatched the same week (1 = earliest, 9 = latest). Significant linear regression line for Rainbow Smelt is also shown.

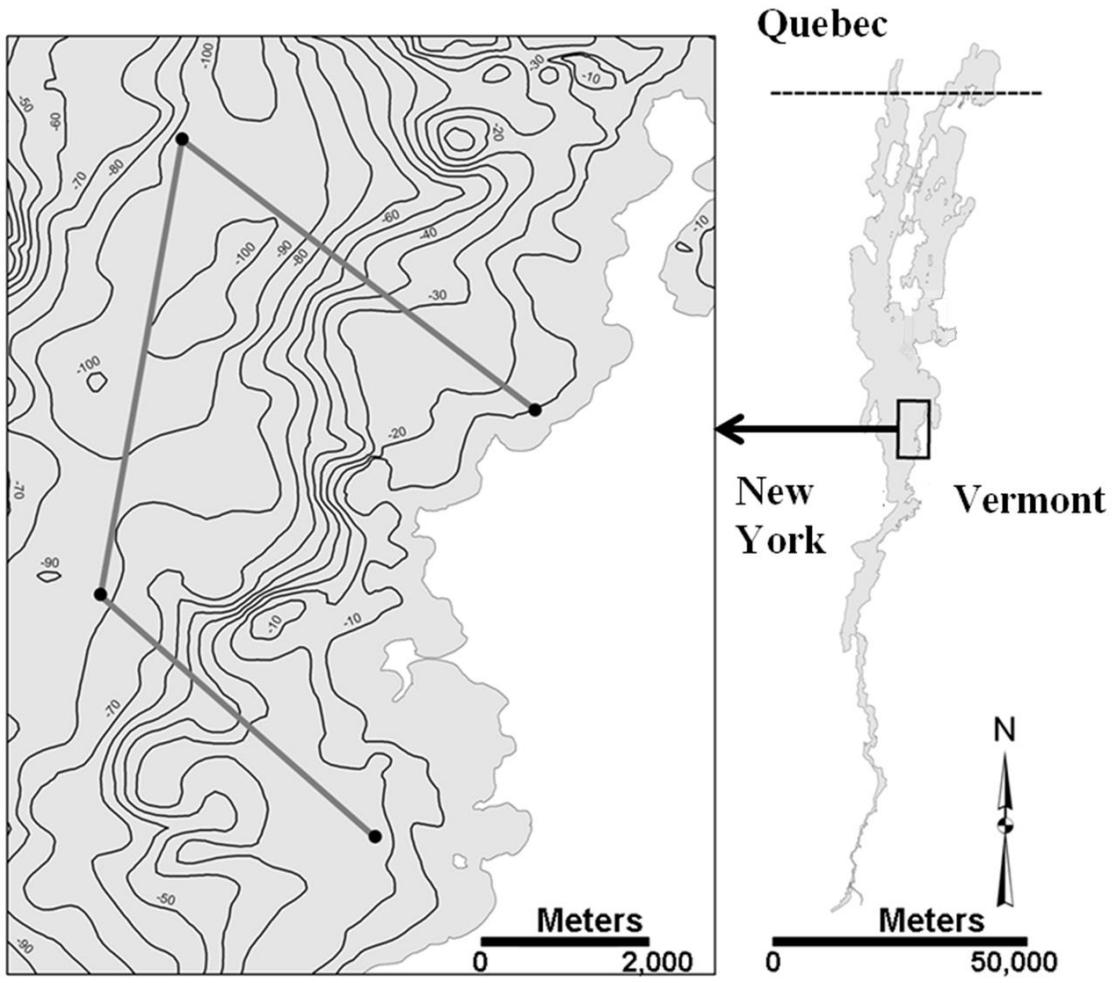


Figure 2.1

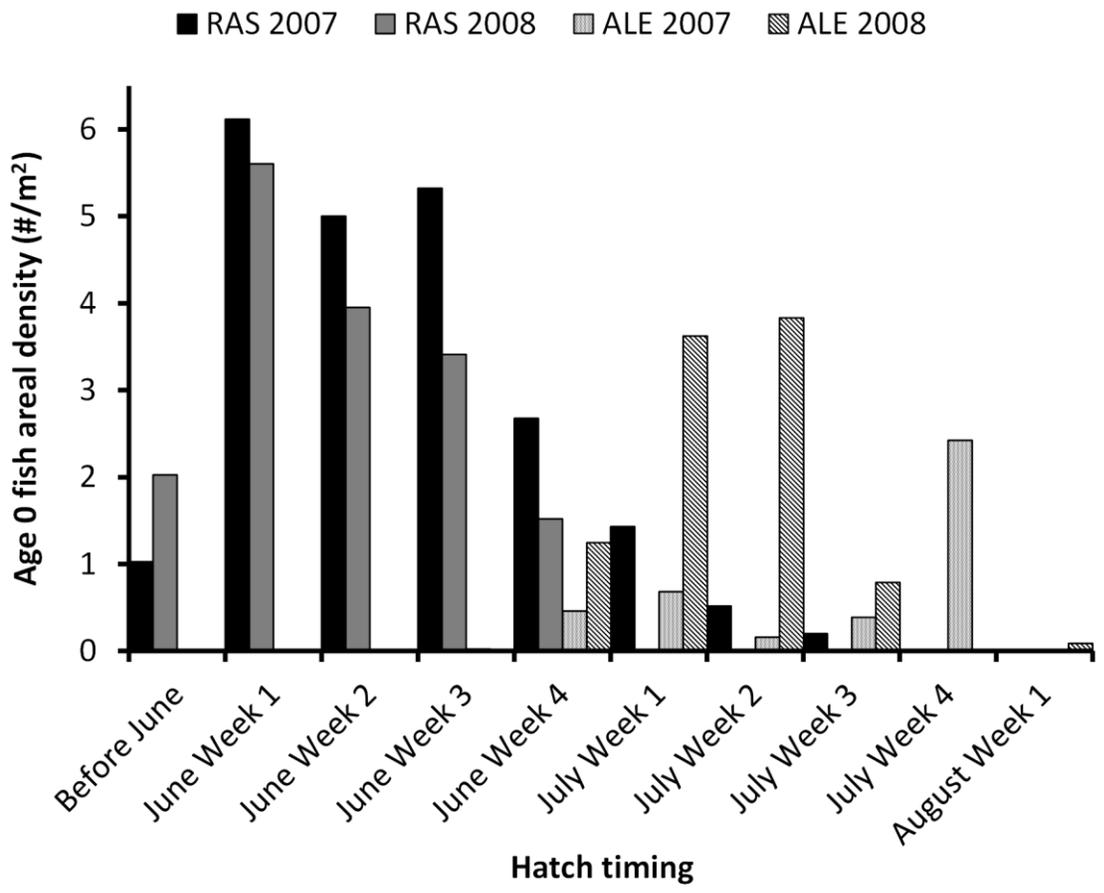


Figure 2.2

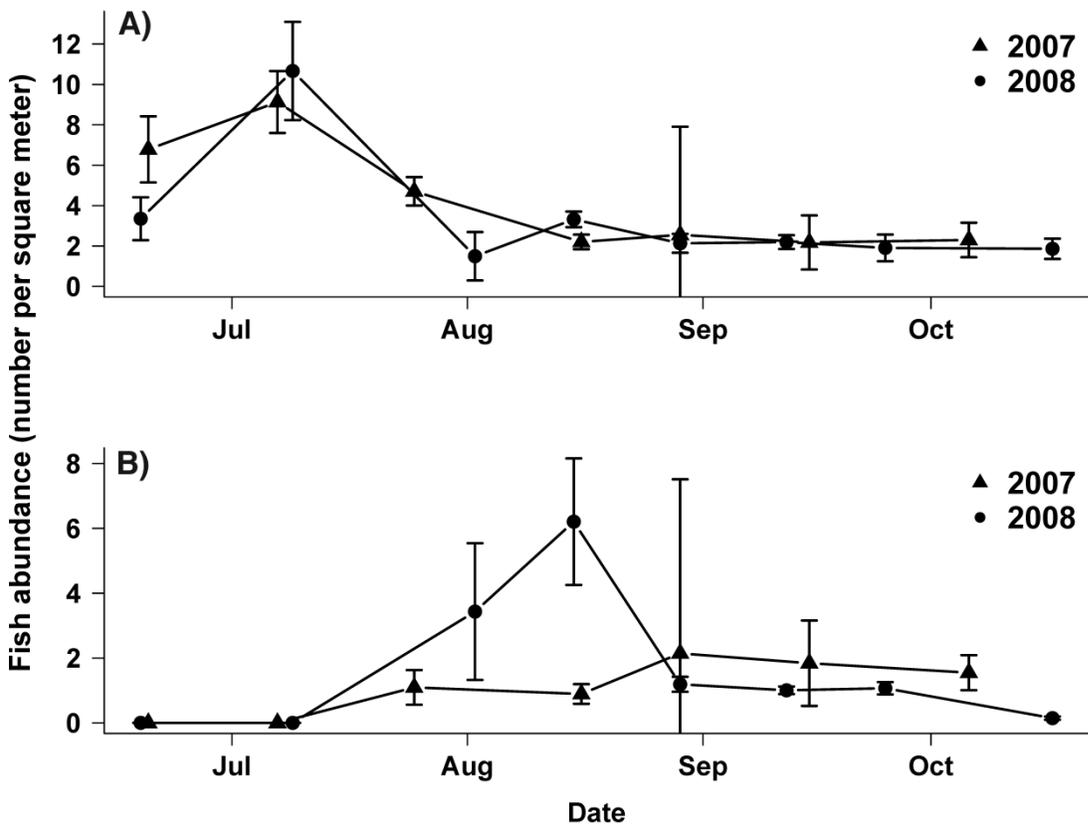


Figure 2.3

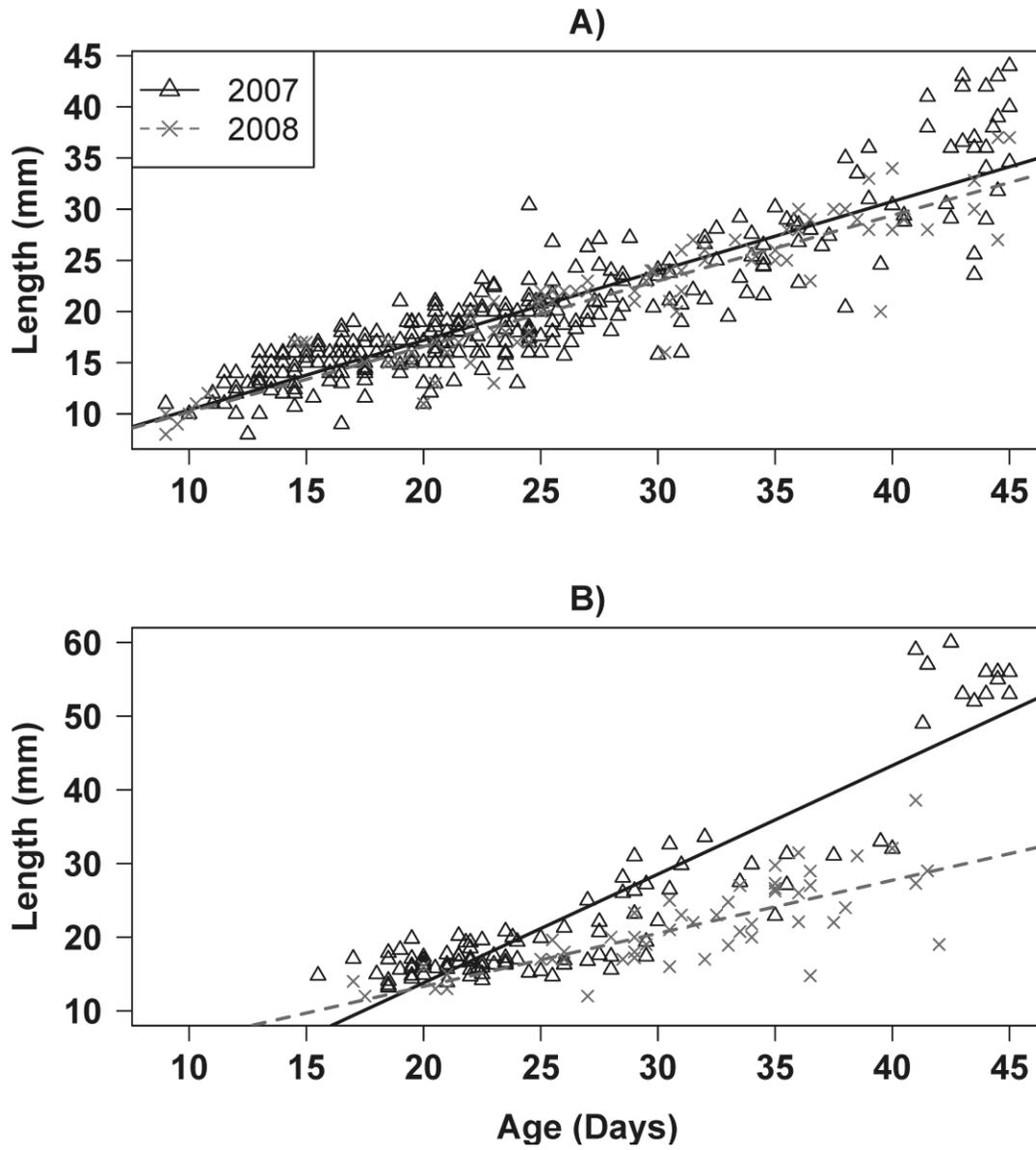


Figure 2.4

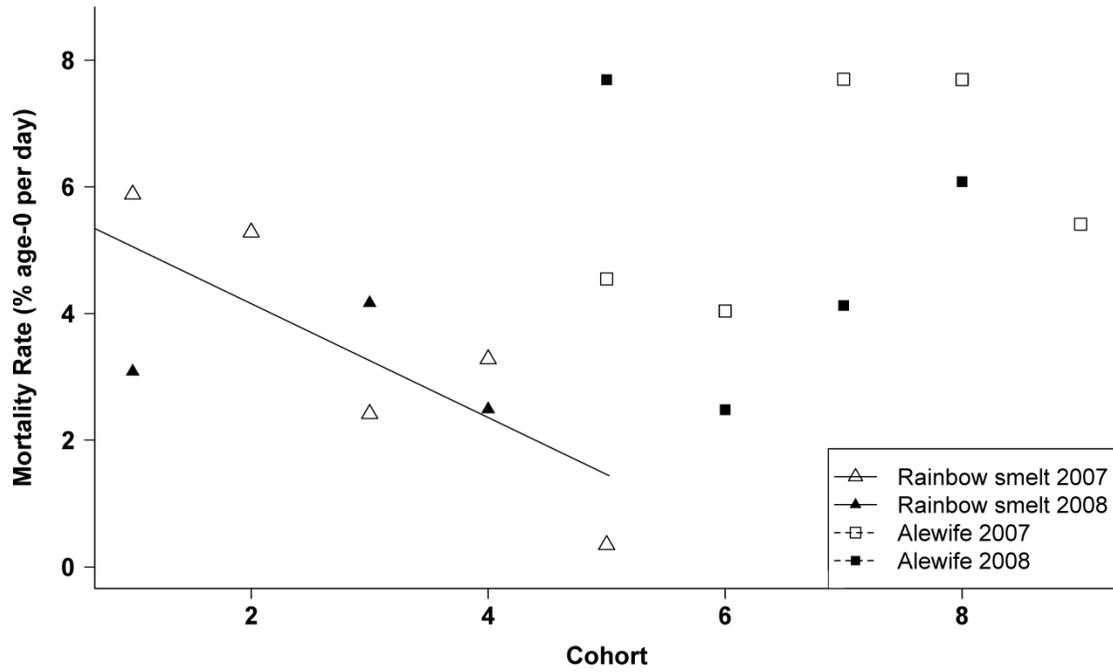


Figure 2.5

## CHAPTER 3

### PISCIVORE DIET SHIFTS AND TROPHIC LEVEL CHANGE AFTER ALEWIFE ESTABLISHMENT IN LAKE CHAMPLAIN<sup>2</sup>

#### ABSTRACT

Predators may consume prey in proportion to abundance or switch to abundant prey items as a function of changes in relative prey abundance. Introductions of nonnative species create opportunities to study changes in predation behavior. Rainbow smelt and alewife are common prey fish species in lakes throughout North America. The recent establishment of alewife in Lake Champlain offered a unique opportunity to study changes in the diet and trophic level of the major fish predators in this system. Using stable isotopes of C and N, we found that alewife are now a large component of predator diets, and in particular of the diets of Atlantic salmon and walleye. Lake trout also consumed alewife, but to a lesser extent than the other two species. Atlantic salmon fed primarily on young-of-year (YOY) alewife whereas walleye and lake trout incorporate larger alewife in their diets. Furthermore, walleye and rainbow smelt  $\delta^{15}\text{N}$  values changed significantly from pre-alewife  $\delta^{15}\text{N}$  values of the late 1990's. These changes represent a preferential switch to feeding on alewife by Atlantic salmon which was likely caused by the distribution patterns of these species, whereas lake trout and walleye also consume alewife, but do so in closer proportion to their abundance in the system.

---

<sup>2</sup> Simonin, P.W., L.G. Rudstam, D.L. Parrish, B. Pientka, P. Sullivan. *Piscivore diet shifts and trophic level change after alewife establishment in Lake Champlain. PLoS ONE. In prep.*

## INTRODUCTION

Predation can shape prey communities and stabilize or destabilize prey population sizes (Holling 1959, Murdoch 1969, Murdoch and Oaten 1975). Some predators consume prey in proportion to relative prey abundance and thus do not change prey community composition (Tilman 1982). Other predators stabilize prey communities by “switching” as the relative abundance of prey types in a community changes, and feed disproportionately on the most abundant prey (Murdoch et al. 1975, Rubega and Inouye 1994). In temperate lake communities, the diet of fish species at the highest trophic level is often composed of only one or two primary fish species, and these predators can be major drivers of prey abundance and community composition (Tsehaye et al. 2014).

Introductions of abundant nonnative prey fish can change predator diet composition. Lake trout (*Salvelinus namaycush*) are the top native predator in most of the Laurentian Great Lakes and consumed coregonid species, native cyprinids and other native planktivorous species prior to rainbow smelt (*Osmerus mordax*) and alewife (*Alosa pseudoharengus*) introduction (Crowder 1980). Post-rainbow smelt and -alewife introduction, these species compose a large proportion of lake trout diets (Jude et al. 1987, Evans and Loftus 1987). Atlantic salmon (*Salmo salar*), walleye (*Sander vitreus*) and chinook salmon (*Onchorhynchus tshawytscha*) consume alewife and rainbow smelt as well. Recent functional response analyses suggest salmonid consumption of rainbow smelt and alewife in the Great Lakes will decline only at very low prey densities (Tsehaye et al. 2014). Furthermore, understanding salmonid and walleye predation on forage fish is crucial since many salmonids are stocked and thus predator population size is largely decoupled from prey abundance.

Alewife is the dominant prey fish for most salmonids and walleye, but the degree to which different species incorporate alewife in their diet depends on the predator (e.g., Rand and Stewart 1998a, 1998b). Alewife are more abundant than rainbow smelt in most of the Great Lakes, meaning there have been few opportunities to study changes in predator diet composition caused by increasing and decreasing abundance of alewife relative to other prey fish such as rainbow smelt. For example, in Lake Michigan, salmonids continued to prey primarily upon alewife despite increases in abundance of bloater (*Coregonus hoyi*) (Jude et al. 1987), and consumed small alewife when large individuals became less abundant (Stewart and Ibarra 1991), but alewife populations never fluctuated enough to test functional response relationships or switching. Recent changes in Lake Huron alewife populations may for the first time allow these types of analyses if alewife again become abundant in the system.

The recent establishment of alewife in Lake Champlain offers a unique opportunity to study changes in predator diets as an alewife population grows, in a system with a well-established rainbow smelt population. Rainbow smelt are native to Lake Champlain, whereas alewife were first collected in the lake in 2003 and the population rapidly expanded since 2007 (Marsden and Hauser 2009)(Marsden and Hauser, 2009). Lake trout, Atlantic salmon and walleye are three native predators of rainbow smelt in Lake Champlain and are also important in the lake as sport fish (Kirn and Labar 1996a, Marsden and Langdon 2012)(Kirn and Labar, 1996a; Marsden and Langdon, 2012).

Our study examines prey switching and changes in trophic position of native rainbow smelt, Atlantic salmon, lake trout and walleye populations following the establishment of alewife in Lake Champlain. Our objectives were to, 1) determine whether, and to what extent, native lake trout and Atlantic salmon feed on alewife adults and young-of-year (YOY), 2) compare

current walleye stable isotope signatures to pre-alewife values to infer changes in walleye diet and trophic position, and 3) compare pre- and post-alewife invasion isotopic signatures of rainbow smelt to infer competitive or predatory interactions.

## **METHODS**

### *Study area*

Lake Champlain is a large inland lake on the border of New York (USA), Vermont (USA) and Québec (Canada) with a north-south dimension of 200 km and an east-west maximum dimension of 21 km (Manley and Manley 1999) (Figure 3.1). Though part of the Laurentian system, Lake Champlain has fewer resident nonnative species than the Great Lakes except Lake Superior and a native rainbow smelt population (Marsden and Hauser 2009). (Crowder 1980) In Lake Champlain, lake trout and Atlantic salmon were extirpated by 1900 and the current populations are sustained by stocking and thus are de-coupled from prey fish abundance, as is the case for salmonids in the Laurentian Great Lakes (Marsden and Langdon 2012). To understand the available forage base, a yearly forage fish survey has been conducted for the past 20 years, with a focus on monitoring rainbow smelt abundance (Kirn and Labar 1991, 1996b). However, alewife are now in the lake and the predators of interest to fisheries management may be switching from rainbow smelt to alewife, as observed for double-crested cormorants (DeBruyne et al. 2012).

### *Fish Sampling*

Fish from all deeper basins of Lake Champlain were collected (excluding the shallow Missisquoi Bay that does not support rainbow smelt). This broad range of sampling locations insured that the forage fish sampled were representative of those

consumed by predators across the lake. Atlantic salmon were collected from the Sand Bar Bridge, Lamoille River, Willsboro Bay and Winooski River via boat electrofishing and Hatchery Brook via backpack electrofishing. Walleye were collected from the Winooski River and lake trout from Whallon Bay, Grand Isle Cove and Willsboro Bay via boat electrofishing. A maximum of twenty salmonids and walleye per site were weighed, measured and tissue plugs were removed for stable isotope analyses before fish were released alive.

Two pelagic trawls and gill nets were used to collect rainbow smelt and alewife. Yearling-and-older (YAO) individuals were targeted with a 5m x 5m midwater trawl, with a graded mesh size of 203 mm to 1.3 mm. A 1m x 1m opening-closing Tucker trawl with 1mm mesh was used to target young-of-the-year fish. Tucker trawls were deployed for 5 minutes per sample, whereas midwater trawls were towed 30 minutes. Gill nets were 6 m deep x 21 m long, with seven mesh sizes (6.25, 8, 10, 12, 15, 18 and 25 mm bar mesh). These mesh sizes catch alewife in the size range 50 to 300 mm (selectivity curves in Warner et al. 2002). Species, length and age class of each fish was recorded and ten to twenty rainbow smelt and alewife of each species/size/age class from each location were frozen for stable isotope analysis.

### *Stable Isotope Analysis*

We used carbon and nitrogen stable isotope analyses to address all three of our objectives. Carbon stable isotope ratios indicate carbon source (pelagic versus littoral) and change little during trophic transfers, whereas nitrogen stable isotope ratio indicates trophic position because N-15 is enriched at each higher trophic level (Peterson and Fry 1987). Stable isotope ratios are given in the “del” notation, in which isotope ratios are measured against standards:  $\delta$ -value =  $(R_{\text{sample}} / R_{\text{standard}} - 1) \times 1,000$ , where  $R$  = ratio of heavier isotope to lighter isotope. Samples were analyzed with a Thermo Delta V isotope ratio mass spectrometer

interfaced to a NC2500 elemental analyzer at Cornell University's Stable Isotope laboratory. The reference standard for  $^{15}\text{N}$  is atmospheric air and for  $^{13}\text{C}$  is Vienna Pee Dee Belemnite. An internal laboratory standard of mink tissue was analyzed for every ten samples and a methionine standard was used to measure instrument accuracy.

Stable isotope data were analyzed using the Stable Isotope Analysis in R (SIAR) package version 4.2 in R (R Development Core Team 2015). This statistical package runs a Bayesian isotope mixing model, using a Gaussian likelihood with a Dirichlet (uninformative) prior mixture on the mean, to estimate the proportions of prey items consumed by predators. Lake trout, Atlantic salmon and walleye prey items included in the model were white perch (*Morone americana*), sculpin (*Cottus cognatus*) and small (<75mm), medium (75-150mm) and large (>150mm) rainbow smelt and alewife.

Walleye stable isotope measurements from 2011 were compared with stable isotope data from 1997 from Overman and Parrish (2001). Only fish from the Main Lake section of Lake Champlain were used in this comparison. We sampled the same size range of fish used in 1997 (400-600+ mm) because walleye age affects  $\delta^{15}\text{N}$  (Overman and Parrish 2001). Walleye growth rates are not known to have changed between 1997 and 2011.

Rainbow smelt isotope data were also available from 1997 (Overman and Parrish 2001) for comparison with our 2011 samples. Only fish from the Main Lake were used in this comparison and only fish of the same length were compared (103-138 mm, representing age 1-2 fish in both years). Changes in walleye and rainbow smelt  $\delta^{15}\text{N}$  values from 1997 to 2011 were determined by analysis of variance using R.

## **RESULTS**

### *Salmonid and walleye diets*

Lake trout had the highest mean  $\delta^{15}\text{N}$  value and thus highest trophic position of fish we sampled, followed by Atlantic salmon, then walleye. The mean  $\delta^{15}\text{N}$  value of lake trout were 18.36, the highest of any fish sampled (Table 3.1, Figure 3.2). Atlantic salmon  $\delta^{15}\text{N}$  mean was 16.82 and walleye  $\delta^{15}\text{N}$  mean was 16.44. Within-species variation of isotope ratios was higher for carbon than nitrogen (Figure 3.2).

Nitrogen stable isotope values and results from the SIAR mixing model indicate that lake trout, Atlantic salmon and walleye all consumed alewife in 2011. The proportion of alewife was higher in the diet of Atlantic salmon and walleye than in lake trout (Figure 3.3). For lake trout, the stable isotopes suggest they consume about equal parts (15-18%) large, medium and small rainbow smelt, small alewife and sculpin, with fewer (<10%) white perch, large alewife and medium alewife consumed (Figure 3.3A). Half of the Atlantic salmon diet was made up of small alewife, with small smelt the next largest component (18-20%), followed by white perch and medium and large alewife (5-8%; Figure 3.3B). Walleye diet consisted of white perch (25-30%), small alewife (20-22%), small smelt (18%) and medium and large alewife (15-18%, Figure 3.3C).

### *Rainbow smelt and alewife C and N isotopes*

Older and larger rainbow smelt had significantly higher mean  $\delta^{15}\text{N}$  values. Mean  $\delta^{15}\text{N}$  value for adult rainbow smelt was 1.4 units higher than age 1 rainbow smelt and 2.3 units higher than age 2 rainbow smelt. Mean  $\delta^{15}\text{N}$  value for adult rainbow smelt was 16.54 (SD=0.56), for age 1 rainbow smelt was 15.16 (SD=1.02) and for YOY rainbow smelt was 14.24 (SD=0.56) (Table 3.1; Figure 3.4). All three of these groups differed from each other significantly ( $p < 0.05$ ). Adult alewife mean  $\delta^{15}\text{N}$  was 13.68 (SD=0.87), age 1 alewife mean was 13.76 (SD=1.58) and

YOY mean was 13.09 (SD=0.93) (Table 3.1). There was a significant difference between YOY alewife and older alewife ( $p < 0.05$ ).

Mean  $\delta^{13}\text{C}$  differed significantly between some age groups of rainbow smelt and alewife. Mean  $\delta^{13}\text{C}$  value for adult rainbow smelt was -27.83 (SD=0.96), for age 1 rainbow smelt was -28.62 (SD=0.93) and for YOY rainbow smelt was -27.88 (SD=0.84) (Table 3.1). Only age 1 smelt were significantly different from the other two groups ( $p < 0.05$ ). Adult alewife mean  $\delta^{13}\text{C}$  was -28.79 (SD=1.14), age 1 alewife mean was -28.54 (SD=1.03) and YOY mean was -28.08 (SD=1.56) and there was a significant difference between YOY alewife and older alewife ( $p < 0.05$ ).

#### *Comparison of walleye and rainbow smelt trophic level in 1997 and 2011*

A significant difference was found in mean walleye  $\delta^{15}\text{N}$  values between 1997 and 2011 (Figure 3.5A) (ANOVA,  $F = 57.06$ ,  $p = 3.99 \times 10^{-8}$ ). This represents 2.1 unit decrease in mean  $\delta^{15}\text{N}$  values. Rainbow smelt  $\delta^{15}\text{N}$  values also changed significantly between 1997 and 2011 (ANOVA,  $F = 19.34$ ,  $p = 3.66 \times 10^{-5}$ ). Mean  $\delta^{15}\text{N}$  value of rainbow smelt in 1997 was 14.0 and in 2011 was 15.1, representing an increase in  $\delta^{15}\text{N}$  of 1.1 units (Figure 3.5B).

## **DISCUSSION**

Our study examines changes in the trophic position and diet of Atlantic salmon, lake trout and walleye following the establishment of an alewife population. We found that alewife was a large component of predator diets, particularly the diets of Atlantic salmon and walleye. Lake trout also incorporated alewife, but to a lesser extent than the other two species. Atlantic salmon fed primarily on YOY alewife whereas walleye and lake trout incorporate larger alewife in their diets. Furthermore, walleye and rainbow smelt  $\delta^{15}\text{N}$  values changed significantly from pre-alewife  $\delta^{15}\text{N}$  values of the late 1990's.

Species habitat differences and distribution patterns influence predator diets observed in this study. In Lake Champlain, rainbow smelt adults occupy the deepest part of the pelagic water column during times of thermal stratification and migrate to the bottom of the thermocline at night (Simonin et al. 2012), thus making them available to predators such as lake trout, which also are in these cooler depths. Alewife adults and YOY, and rainbow smelt YOY, are in the epilimnion and metalimnion when the lake is stratified (Simonin et al. 2012) and thus are more available to walleye and Atlantic salmon, which also prefer shallower habitat in Lake Champlain, than they are to lake trout, which inhabit deeper and cooler water.

Our results suggest Atlantic salmon may have switched to feeding on alewife in a way that is consistent with preferential switching behavior of predators in other systems (Murdoch et al. 1975, Rubega and Inouye 1994, Rennie et al. 2009). Atlantic salmon previously fed almost solely on small rainbow smelt (Pientka and Parrish 2002), but smelt now make up less than 25% of Atlantic salmon diets even though smelt still compose more than 25% of the biomass of Lake Champlain forage fish (Bernie Pientka, personal communication). This switch to alewife predation is likely because alewife are in the same part of the water column as Atlantic salmon when the lake is thermally stratified, emphasizing the importance of understanding spatial distribution patterns of predator and prey fish species throughout seasonal cycles (Simonin, Chapter 4).

Energy content and prey size also influence predatory choices (Kushlan 1979) and likely influence salmonid and walleye predation on rainbow smelt and alewife in Lake Champlain. In Lake Champlain, faster alewife growth rates have been observed than in other systems, with 300 mm adults present in the system during the period of rapid population increase in 2007-2008 (Simonin, Chapter 2). In Lake Ontario, salmonids increased alewife consumption rates as mean

alewife size and condition declined to compensate for reduced energy intake per alewife consumed (Rand et al. 1994, Rand and Stewart 1998c). We may expect to see something similar happen in Lake Champlain if alewife growth rates slow as alewife become established and increase in abundance.

The presence of alewife in the diets of salmonids is of interest to Lake Champlain fisheries managers for several reasons. First, lake trout, salmon and walleye populations are supported by stocking, as native salmonid populations were extirpated by 1900 (Marsden and Langdon 2012). Predator population sizes are thus no longer naturally coupled to prey population sizes. Previous forage fish surveys in Lake Champlain focused on rainbow smelt, but our study confirms that alewife abundance must also now be known so managers can appropriately adjust predator stocking rates as prey population abundance fluctuates.

The presence of alewife in the diets of salmonids is also of interest to managers because of concerns regarding thiamine deficiency. Staff at the Grand Isle fish hatchery run by the Vermont Department of Fish and Wildlife have begun to notice poor Atlantic salmon larval fish survival, which improved when eggs were treated with thiamine (B. Pientka, personal communication). Our results from tissue analysis of the same adult fish used for egg collection indicate that these fish indeed feed to a large extent on alewife and is therefore consistent with the results from the Great Lakes of an alewife source of thiaminase causing Early Mortality Syndrome in Atlantic Salmon (Fitzsimons et al. 1999, Honeyfield et al. 2005). However, natural reproduction of lake trout and Atlantic salmon was low in Lake Champlain in recent years prior to the alewife invasion (Riley and Marsden 2009, Marsden and Langdon 2012), so any additional decline in natural reproduction associated with increasing thiamine deficiency would be difficult to detect. Furthermore, alewife do not cause thiamine (e.g., Honeyfield et al. 2005) deficiency

and Early Mortality Syndrome in all systems in which they are present (Fitzsimons et al. 1999, 2005).

The observed change in walleye  $\delta^{15}\text{N}$  values since 1997 is consistent with our finding that Main Lake walleye now consume alewife to a larger extent than smelt. Overman and Parrish (2001) reported that in the Main Lake, “aside from one large cisco (*Coregonus* spp.) consumed by an 18-year-old walleye, all Main Lake diets consisted of rainbow smelt.” This is no longer the case. Further, the incorporation of alewife in walleye diets led to a decline in average trophic level position for walleye of 2/3 of a full trophic level (assuming a fractionation of 3.4 units per trophic level, (Post 2002). This change in walleye diets to prey feeding at lower trophic levels (like alewife) will likely decrease bio-magnification of contaminants and increase the efficiency of energy flow through the ecosystem to walleye.

The significant change in rainbow smelt mean  $\delta^{15}\text{N}$  was not expected. Larger predatory zooplankton were not, to our knowledge, preyed upon differently by rainbow smelt in 2011 compared with 1997 and we do not know whether smelt predation on mysids (*Mysis diluviana*) may have changed between these years. Isotope baseline values did not differ between these years, so was not the cause of this shift. Rainbow smelt are cannibalistic, but the shift is not likely to be caused by a switch from cannibalism to YOY alewife consumption, because  $\delta^{15}\text{N}$  did not differ significantly between YOY of these two species. It is possible that this change was caused by cycles of cannibalism that occur in Lake Champlain (Parker Stetter et al. 2007). In 1997, rainbow smelt of the size consumed by walleye may not have eaten YOY rainbow smelt to the same extent they did (or to the extent they ate YOY alewife) in 2011. Main Lake midwater trawl catches in 1998 management surveys were double those of 2007, suggesting high survival of the 1997 age class and low cannibalism in 1997 (B. Pientka, personal communication).

We base our inferences of diet shifts only on stable isotope data. Ideally, stomach contents would also have been examined, but that was not possible in this study as the predatory fish were sampled during spawning time and released live. (e.g., Overman and Parrish 2001) An advantage of tissue stable isotope analysis is that it integrates consumption patterns over a longer period of time. In calculating dietary proportions (objective 1), we also sampled several species in addition to rainbow smelt and alewife, so that they too could be included in our mixing models. We did not analyze yellow perch tissue and this species could also be a prey item of walleye in Lake Champlain as it is in other systems. However, yellow perch are not abundant in the main lake section of Lake Champlain where we collected walleye and therefore not likely a main diet item for these fish.

Alewife have substantially altered the trophic structure of the fish community in Lake Champlain, and are likely to remain influential here just as they have been in the Great Lakes basin since the mid-20<sup>th</sup> century (Crowder 1980, e.g., Bunnell et al. 2006, Madenjian et al. 2008). Since alewife entered the system, walleye trophic level declined significantly, increasing walleye production potential and decreasing contaminant burden. Atlantic salmon now a diet consisting of 50+% alewife, in particular YOY alewife, whereas they used to feed almost exclusively on rainbow smelt in certain parts of the lake (Pientka and Parrish 2002). Atlantic salmon growth may increase if alewife are energetically better prey, but thiamine deficiency may become more prevalent. Lake trout continue to feed primarily upon rainbow smelt, but eat a small amount of alewife as well. The insertion of alewife into the Lake Champlain food web has thus affected walleye, Atlantic salmon and lake trout differently, and these differences are likely caused in part by the spatial distribution of these species.

## REFERENCES

- Bunnell, D.B., Madenjian, C.P., and Claramunt, R.M. 2006. Long-term changes of the Lake Michigan fish community following the reduction of exotic alewife (*Alosa pseudoharengus*). *Can. J. Fish. Aquat. Sci.* 63(11): 2434–2446.
- Crowder, L.B. 1980. Alewife, rainbow smelt and native fishes in Lake Michigan: competition or predation? *Environ. Biol. Fishes* 5(3): 225–233.
- Evans, D.O., and Loftus, D.H. 1987. Colonization of inland lakes in the Great Lakes region by rainbow smelt, *Osmerus mordax*: Their freshwater niche and effects on indigenous fishes. *Can. J. Fish. Aquat. Sci.* 44(S2): s249–s266.
- Fitzsimons, J.D., Brown, S.B., Honeyfield, D.C., and Hnath, J.G. 1999. A review of early mortality syndrome (EMS) in Great Lakes salmonids: relationship with thiamine deficiency. *Ambio* 28(1): 9–15.
- Fitzsimons, J.D., Williston, B., Zajicek, J.L., Tillitt, D.E., Brown, S.B., Brown, L.R., Honeyfield, D.C., Warner, D.M., Rudstam, L.G., and Pearsall, W. 2005. Thiamine content and thiaminase activity of ten freshwater stocks and one marine stock of alewives. *J. Aquat. Anim. Health* 17(1): 26–35.
- Holling, C.S. 1959. The components of predation as revealed by a study of small-mammal predation of the European pine sawfly. *Can. Entomol.* 91(05): 293–320.
- Honeyfield, D.C., Brown, S.B., Fitzsimons, J.D., and Tillitt, D.E. 2005. Early mortality syndrome in great lakes salmonines. *J. Aquat. Anim. Health* 17(1): 1–3.
- Jude, D.J., Tesar, F.J., Deboe, S.F., and Miller, T.J. 1987. Diet and selection of major prey species by Lake Michigan salmonines, 1973–1982. *Trans. Am. Fish. Soc.* 116(5): 677–691.

- Kirn, R.A., and Labar, G.W. 1991. Stepped-oblique midwater trawling as an assessment technique for rainbow smelt. *North Am. J. Fish. Manag.* 11(2): 167–176.
- Kirn, R.A., and Labar, G.W. 1996. Growth and survival of rainbow smelt, and their role as prey for stocked salmonids in Lake Champlain. *Trans. Am. Fish. Soc.* 125(1): 87–96.
- Kushlan, J.A. 1979. Feeding ecology and prey selection in the white ibis. *The Condor* 81(4): 376–389.
- Madenjian, C.P., O’Gorman, R., Bunnell, D.B., Argyle, R.L., Roseman, E.F., Warner, D.M., Stockwell, J.D., and Stapanian, M.A. 2008. Adverse effects of alewives on Laurentian Great Lakes fish communities. *North Am. J. Fish. Manag.* 28(1): 263–282.
- Manley, T.O., and Manley, P. 1999. Lake Champlain in transition: from research toward restoration. American Geophysical Union, Washington, DC.
- Marsden, J.E., and Hauser, M. 2009. Exotic species in Lake Champlain. *J. Gt. Lakes Res.* 35(2): 250–265.
- Marsden, J.E., and Langdon, R.W. 2012. The history and future of Lake Champlain’s fishes and fisheries. *J. Gt. Lakes Res.* 38: 19–34.
- Murdoch, W.W. 1969. Switching in general predators: Experiments on predator specificity and stability of prey populations. *Ecol. Monogr.* 39(4): 335–354.
- Murdoch, W.W., Avery, S., and Smyth, M.E.B. 1975. Switching in predatory fish. *Ecology* 56(5): 1094–1105.
- Murdoch, W.W., and Oaten, A. 1975. Predation and population stability. *Adv. Ecol. Res.* 9: 1–131.

- Overman, N.C., and Parrish, D.L. 2001. Stable isotope composition of walleye:  $\delta^{15}\text{N}$  accumulation with age and area-specific differences in  $\delta^{13}\text{C}$ . *Can. J. Fish. Aquat. Sci.* 58(6): 1253–1260.
- Parker Stetter, S.L., Thomson, J.L.S., Rudstam, L.G., Parrish, D.L., and Sullivan, P.J. 2007. Importance and predictability of cannibalism in Rainbow Smelt. *Trans. Am. Fish. Soc.* 136(1): 227–237.
- Peterson, B.J., and Fry, B. 1987. Stable isotopes in ecosystem studies. *Annu. Rev. Ecol. Syst.* 18(1): 293–320.
- Pientka, B., and Parrish, D.L. 2002. Habitat selection of predator and prey: Atlantic salmon and rainbow smelt overlap, based on temperature and dissolved oxygen. *Trans. Am. Fish. Soc.* 131(6): 1180–1193.
- Post, D.M. 2002. Using stable isotopes to estimate trophic position: models, methods, and assumptions. *Ecology* 83(3): 703–718.
- Rand, P.S., Lantry, B.F., O’Gorman, R., Owens, R.W., and Stewart, D.J. 1994. Energy density and size of pelagic prey fishes in Lake Ontario, 1978–1990: implications for salmonine energetics. *Trans. Am. Fish. Soc.* 123(4): 519–534.
- Rand, P.S., and Stewart, D.J. 1998a. Dynamics of salmonine diets and foraging in Lake Ontario, 1983–1993: a test of a bioenergetic model prediction. *Can. J. Fish. Aquat. Sci.* 55(2): 307–317.
- Rand, P.S., and Stewart, D.J. 1998b. Prey fish exploitation, salmonine production, and pelagic food web efficiency in Lake Ontario. *Can. J. Fish. Aquat. Sci.* 55(2): 318–327.

- Rand, P.S., and Stewart, D.J. 1998c. Dynamics of salmonine diets and foraging in Lake Ontario, 1983-1993: a test of a bioenergetic model prediction. *Can. J. Fish. Aquat. Sci.* 55(2): 307–317.
- R Development Core Team. 2015. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available from <http://www.R-project.org>.
- Rennie, M.D., Sprules, W.G., and Johnson, T.B. 2009. Resource switching in fish following a major food web disruption. *Oecologia* 159(4): 789–802.
- Riley, J.W., and Marsden, J.E. 2009. Predation on emergent lake trout fry in Lake Champlain. *J. Gt. Lakes Res.* 35(2): 175–181.
- Rubega, M., and Inouye, C. 1994. Prey switching in red-necked phalaropes *Phalaropus lobatus*: Feeding limitations, the functional response and water management at Mono Lake, California, USA. *Biol. Conserv.* 70(3): 205–210.
- Simonin, P.W., Parrish, D.L., Rudstam, L.G., Sullivan, P.J., and Pientka, B. 2012. Native rainbow smelt and nonnative alewife distribution related to temperature and light gradients in Lake Champlain. *J. Gt. Lakes Res.* 38: 115–122.
- Stewart, D.J., and Ibarra, M. 1991. Predation and production by salmonine fishes in Lake Michigan, 1978–88. *Can. J. Fish. Aquat. Sci.* 48(5): 909–922.
- Tilman, D. 1982. Resource competition and community structure. Princeton University Press.
- Tsehaye, I., Jones, M.L., Bence, J.R., Brenden, T.O., Madenjian, C.P., and Warner, D.M. 2014. A multispecies statistical age-structured model to assess predator–prey balance: application to an intensively managed Lake Michigan pelagic fish community. *Can. J. Fish. Aquat. Sci.* 71(4): 627–644.

Warner, D.M., Rudstam, L.G., and Klumb, R.A. 2002. In situ target strength of alewives in freshwater. *Trans. Am. Fish. Soc.* 131(2): 212–223.

**Table captions**

Table 3.1. Mean and standard deviation (s.d.)  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  for each species and age class sampled.

## Figure captions

Figure 3.1. Lake Champlain, located between the U.S. states of New York and Vermont, and the Province of Quebec, Canada.

Figure 3.2. Carbon and nitrogen stable isotope ratios of forage fish, salmonids and walleye in Lake Champlain. Samples were collected in 2011. Lines represent range of forage fish values.

Figure 3.3. Estimated proportion of prey items in lake trout (A), Atlantic salmon (B) and walleye (C) diets. Plot shows Bayesian posterior distributions of proportion estimates, with 50, 75 and 95% credible intervals in shaded boxes.

Figure 3.4. Rainbow smelt and alewife adult (large), age 1 (medium) and YOY (small)  $\delta^{15}\text{N}$  values. Boxes represent interquartile range.

Figure 3.5. Walleye (A) and rainbow smelt (B) tissue  $\delta^{15}\text{N}$ . Fish are from the Main Lake section of Lake Champlain.

## Tables

Species	Age class	N	Carbon mean	Carbon s.d.	Nitrogen mean	Nitrogen s.d.
rainbow smelt	YOY	32	-27.88	0.84	14.24	0.56
rainbow smelt	age 1	78	-28.62	0.93	15.16	1.02
rainbow smelt	adult	32	-27.83	0.96	16.54	0.56
alewife	YOY	60	-28.08	1.56	13.09	0.93
alewife	age 1	77	-28.54	1.03	13.76	1.58
alewife	adult	66	-28.79	1.14	13.68	0.87
sculpin	n/a	25	-27.88	0.90	17.29	0.47
white perch	adult	5	-26.08	0.41	14.23	0.16
walleye	adult	20	-26.41	0.59	16.44	0.45
Atlantic salmon	adult	41	-27.28	1.38	16.82	0.40
lake trout	adult	40	-27.27	1.34	18.36	0.50

**Table 3.1**

**Figures**

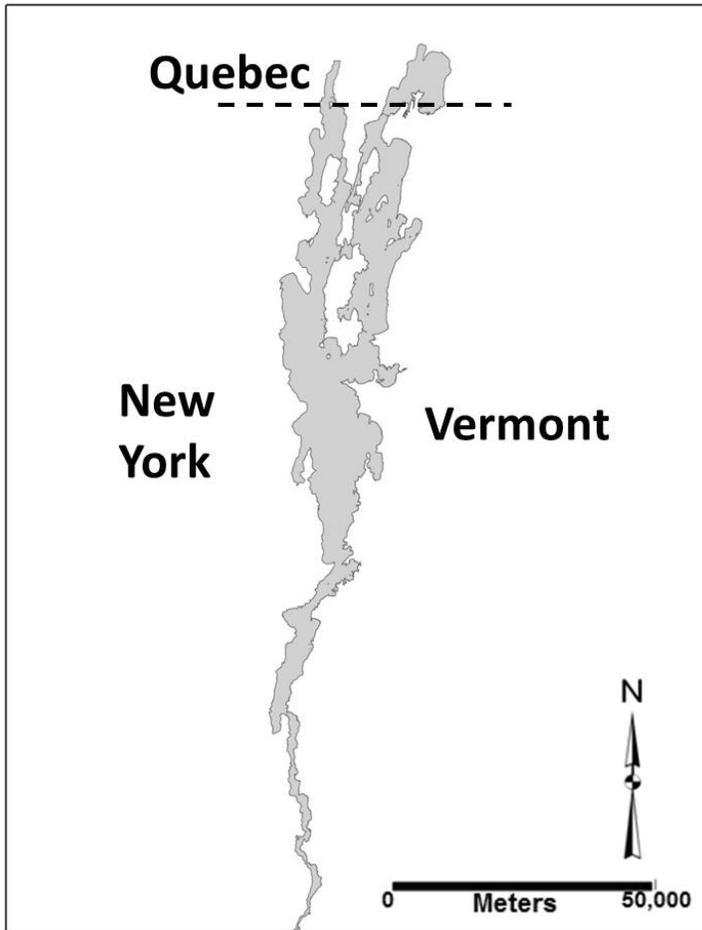


Figure 3.1

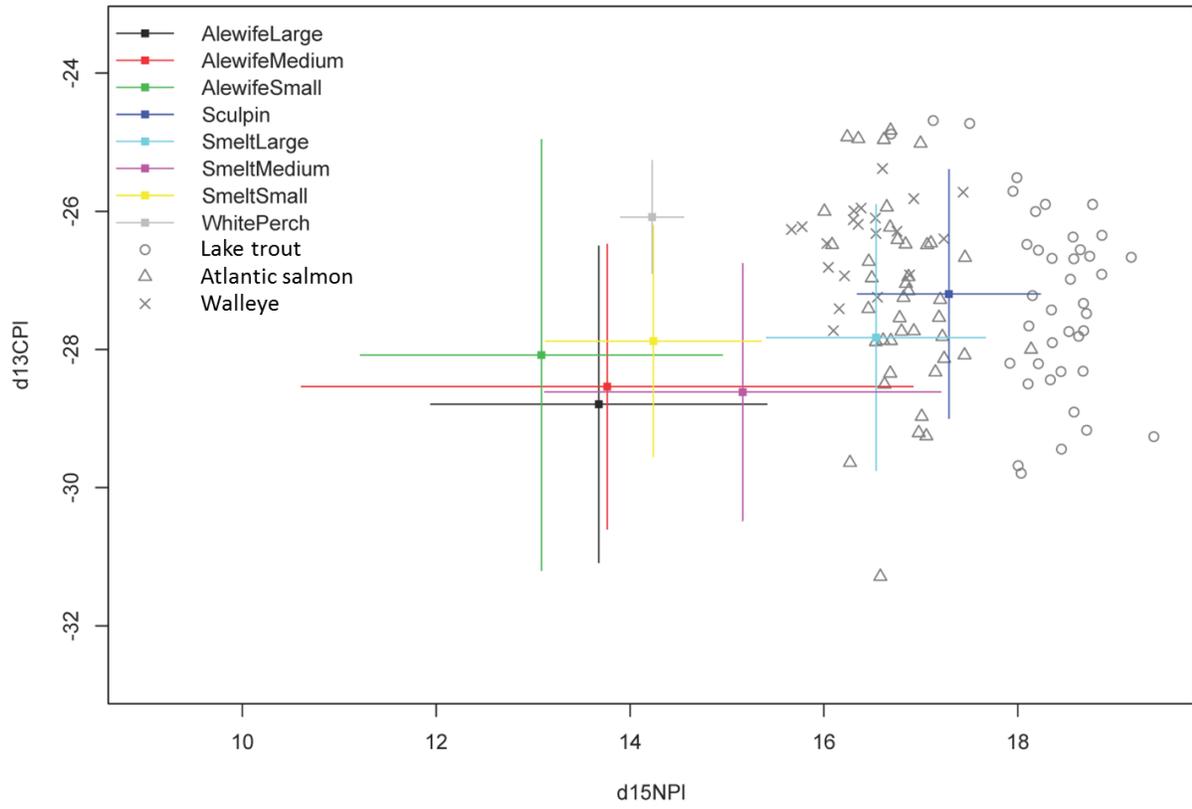


Figure 3.2

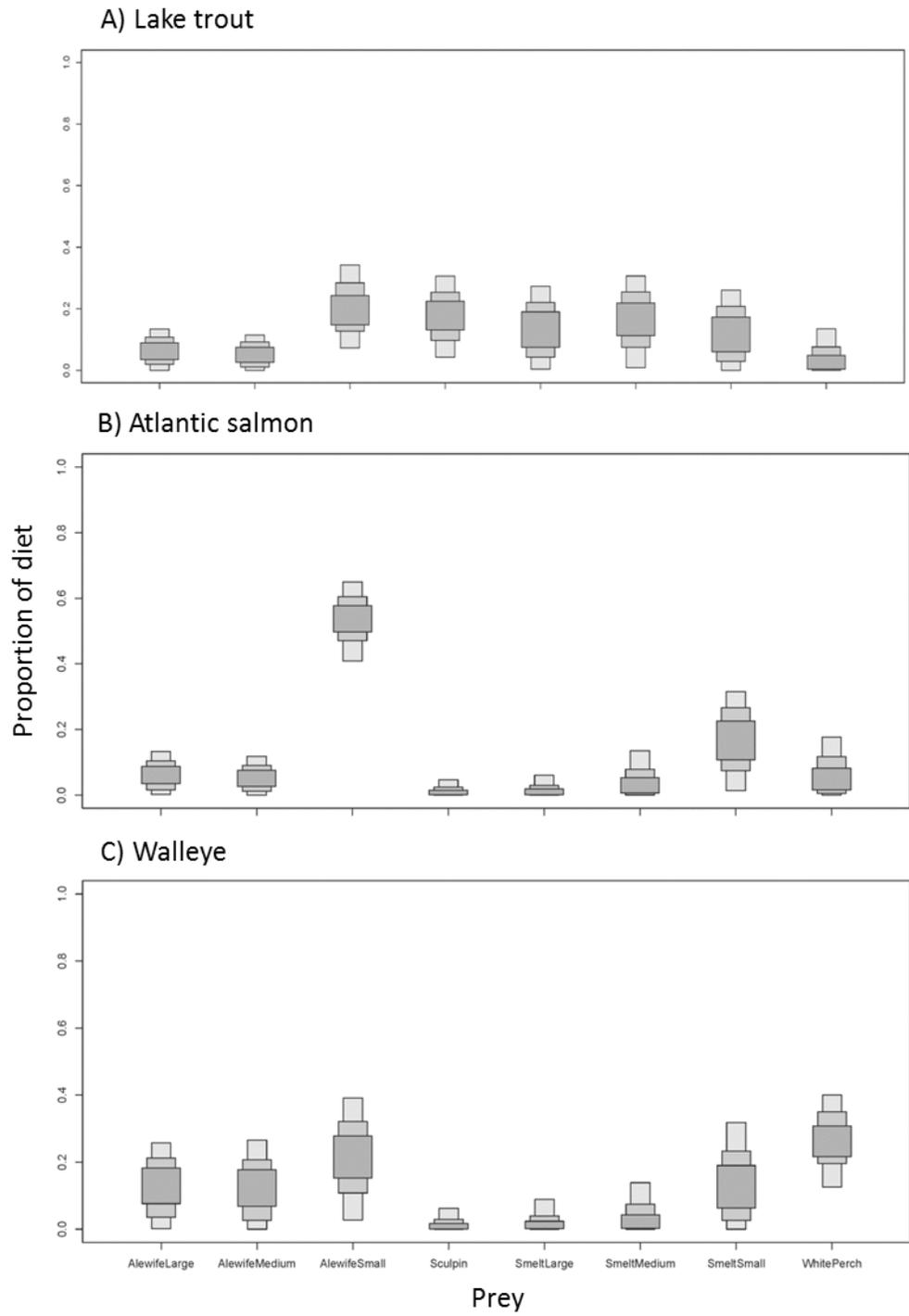


Figure 3.3

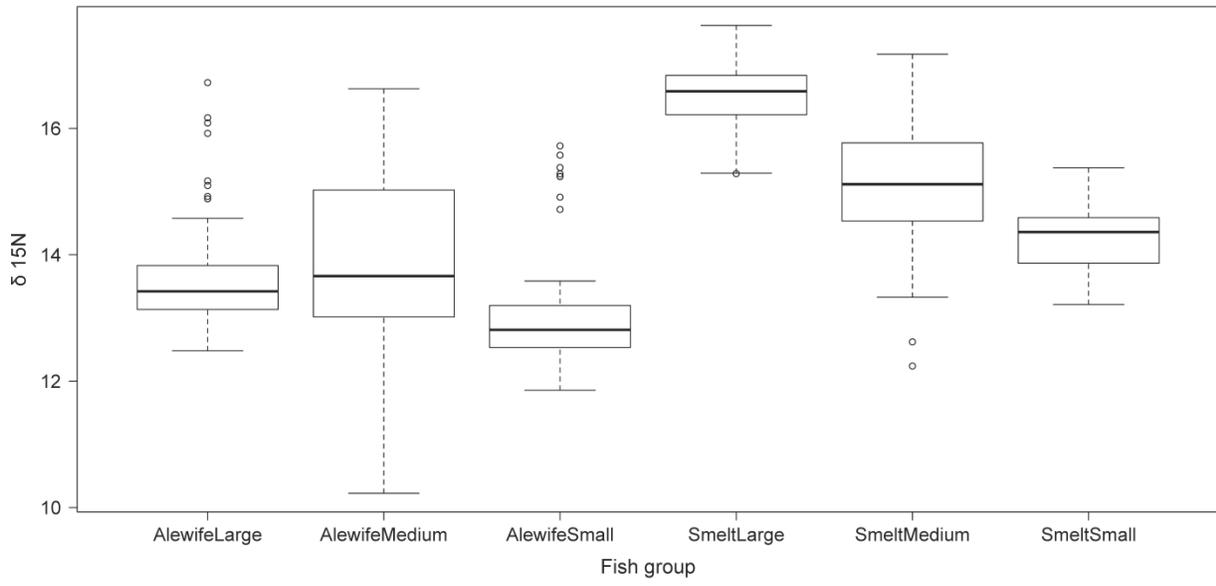
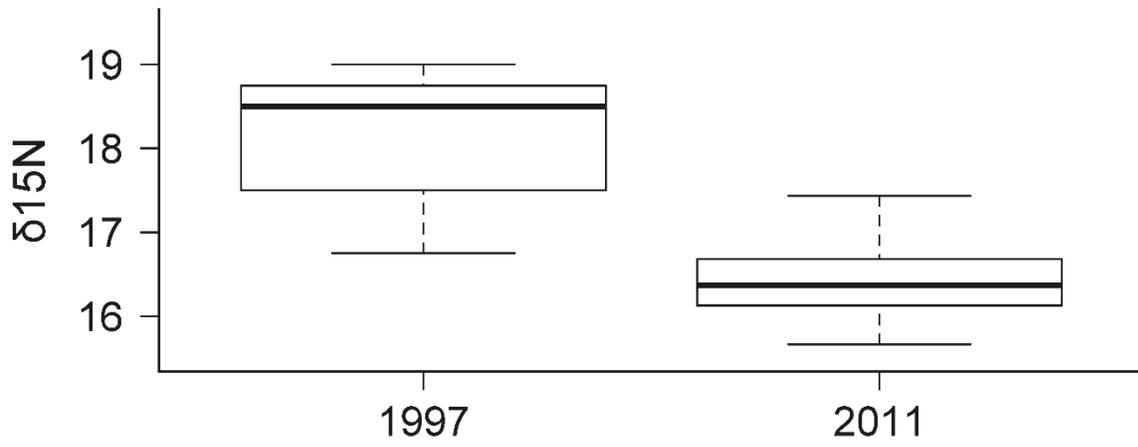


Figure 3.4

### A) Walleye



### B) Rainbow smelt

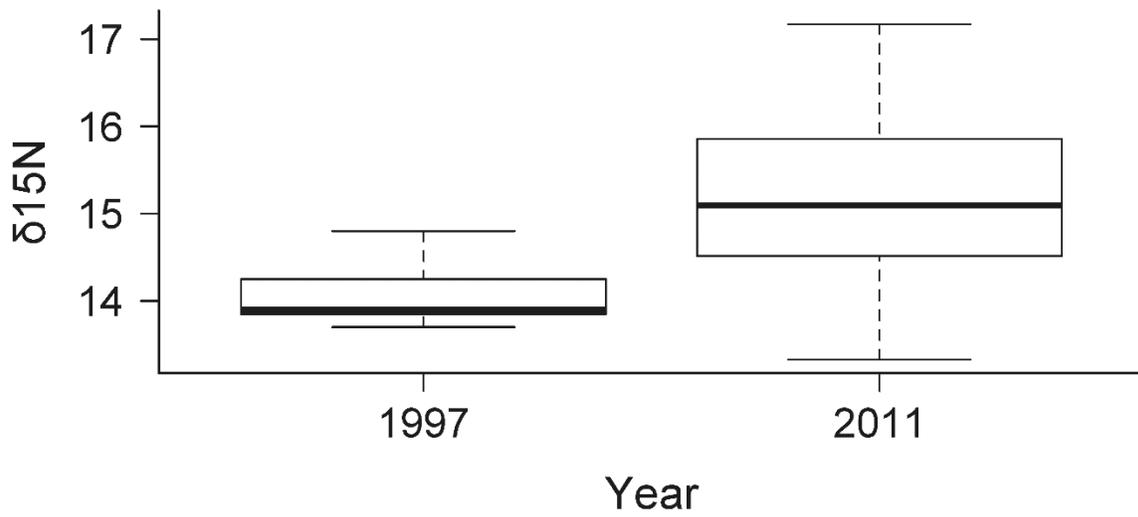


Figure 3.5

## CHAPTER 4

### EARLY MORTALITY AND FRESHWATER FORAGE FISH RECRUITMENT: NONNATIVE ALEWIFE AND NATIVE RAINBOW SMELT INTERACTIONS IN LAKE CHAMPLAIN<sup>3</sup>

---

<sup>3</sup> Simonin, P.W., L.G. Rudstam, P. Sullivan, D.L. Parrish, B. Pientka. Early mortality and freshwater forage fish recruitment: nonnative alewife and native rainbow smelt interactions in Lake Champlain. *Canadian Journal of Fisheries and Aquatic Sciences*. In prep.

## ABSTRACT

Current changes to aquatic systems caused by climate change and nonnative species may affect patterns of early mortality and recruitment in fish communities. We studied the consequences of nonnative species introduction and changes in temperature using a model simulating native rainbow smelt (*Osmerus mordax*) and nonnative alewife (*Alosa pseudoharengus*) in Lake Champlain. Distribution patterns of adults and young-of-year (YOY) fish were simulated on a daily basis, and mortality rates calculated as a function of fish densities and overlap between adults and YOY. Mortality rates of YOY were highest in the spring and early summer. Relative survival of YOY rainbow smelt and alewife in the model depends on which predator is most abundant. Rainbow smelt YOY mortality rates are highest when rainbow smelt adults are abundant and alewife YOY mortality rates are highest when alewife adults are abundant, allowing the two species to co-exist. Mortality rates were higher under normal temperature regimes, but late-summer mortality rates were higher in our climate change scenario because of increased overlap of adult and YOY distributions. Our simulation suggests spatial distribution patterns should be accounted for when forecasting the interacting effects of climate change aquatic nonnative species.

## INTRODUCTION

Environmental and biological mechanisms causing variable recruitment in fish populations are a topic of long-term interest in fisheries science (Cushing 1975, Wootton 1990, e.g., Diana 2004) and of increased current interest because of climate change (e.g., Vert-pre et al. 2013, Feiner et al. 2015). The characteristics and structure of the stock(s) in question also affect recruitment, and interact with the effects of climate and predation (Brander 2005, Ottersen et al. 2006). Forecasts of continuing climate change, in addition to continuing additions of nonnative species to many systems, suggest that it is increasingly important to understand ways these changes affect recruitment and young-of-the-year (YOY) fish survival.

The interactive effects of predation, recruitment and climate change have been studied in marine systems. Recently, North Sea herring recruitment was low for an unprecedented 6 years, despite a large adult population and low mortality from fishing (Payne et al. 2009). This change has been attributed to a warming trend in the North Sea since about 2000, which altered plankton populations. Environment and climate-induced changes, mostly of low frequency and high amplitude (e.g., “regime shifts”) have taken place in other marine fishery systems as well such as the North Pacific in 1977 and 1989 (Polovina 2005).

We are beginning to understand environment-driven recruitment dynamics in freshwater systems, with several recent studies conducted in the Laurentian Great Lakes of North America. In recent years, bloater (*Coregonus hoyi*) recruitment in Lake Huron has been predictable based on population demographics and alewife (*Alosa pseudoharengus*) abundance. Alewife recruitment was comparatively more variable and affected by salmon predation and environmental factors (Collingsworth et al. 2014). Temperature, and specifically spring-summer

temperature was influential in the production of strong alewife year classes in Lakes Huron and Michigan, with more recruitment in warmer years (Madenjian et al. 2005, Collingsworth et al. 2014). Thus, YOY survival has been correlated with environmental factors in many freshwater systems, but the underlying mechanisms of these correlations are not well-documented and are thus the focus of our study. Rainbow smelt and alewife recruitment is our focus because of the importance of these species in many lakes, and because of the recent establishment of alewife in Lake Champlain.

Rainbow smelt (*Osmerus mordax*) and alewife are pelagic fish species native to the Northwest Atlantic Ocean that are now found in many freshwater lakes in North America where they have been introduced as food for sportfish. These two species, in addition to native coregonids, now form the forage fish base of the commercially-valuable salmonids in the Laurentian Great Lakes and in lakes throughout North America. In Lake Champlain, a large freshwater lake on the border of New York (USA), Vermont (USA), and Quebec (Canada), rainbow smelt are native and alewife are not. Alewife were first collected in 2003, and the population expanded rapidly in 2007 (Marsden and Hauser 2009). Both species prey on smaller fish including members of their own species (Brandt 1980, Henderson and Nepszy 1989, Moring and Mink 2002, Parker Stetter et al. 2007, O'Brien et al. 2014). In many systems, cannibalism is a primary driver of the population dynamics of the species, particularly of rainbow smelt (Rhodes et al. 1974, Lantry and Stewart 2000, Parker Stetter et al. 2007). Predation rates are a function of density of YOY and spatial overlap between adults and YOY (Parker Stetter et al. 2007). In most species, including alewife and rainbow smelt, YOY fish prefer higher temperatures than adults, which affect the depth distribution and spatial overlap between age

groups (Ferguson 1958, Magnuson et al. 1979, Brandt et al. 1980, Crowder et al. 1981, Simonin et al. 2012).

Rainbow smelt recruitment was related to stock size more than to environmental variables in Lake Michigan, but accounting for non-stationarity in this relationship improved recruitment model fit and suggested there is a need to better understand environmental effects (Feiner et al. 2015). Environmental factors including spring precipitation are influential in the main basin of Lake Huron, likely because of their influence on stream spawning habitat (O'Brien et al. 2014). Cannibalism was also influential in this system, with a negative relationship between adult spawning biomass and recruitment (O'Brien et al. 2014), as is also the case in Lakes Erie and Champlain (Henderson and Nepszy 1989, Parker Stetter et al. 2007). In addition, rainbow smelt recruitment has been related to salmonid predation (Stewart et al. 1981), though the relationship is sometimes positive, with salmonid predation on age 1 smelt improving recruitment (O'Brien et al. 2014).

Here we develop a simulation model to explore the consequences of nonnative species introduction and changes in temperature on freshwater fish survival. We focused on the mortality pattern of YOY rainbow smelt and alewife over the first four months of life in Lake Champlain, VT, NY. The model estimates mortality of YOY fish of both species due to predation by the adults of both species while taken into account the spatial distribution of YOY and adults. Our objectives were to, 1) investigate the pattern of mortality of YOY rainbow smelt and YOY alewife through the first growing season with and without adult alewife present, 2) explore whether alewife are likely to replace rainbow smelt as a consequence of predation on YOY, and, 3) explore what effect climate-induced changes in temperature and light may have on

YOY rainbow smelt and YOY alewife mortality and recruitment as a result of changing distributions of YOY and adults of both species.

## **METHODS**

Surveys were conducted with hydroacoustics, trawls and gillnets in the Main Lake section of Lake Champlain, and included two inshore-to-offshore transects and one pelagic transect (Figure 4.1). Transects began about 100 m from shore and ranged in depth from about 10 to 100 m. Surveys were conducted from June through October of 2007 and 2008, with sampling (n=16 dates) conducted every two to three weeks using the VTFW *Doré*. Day and night surveys were conducted, with day surveys ending at least 1 h before sunset and night surveys beginning at least 1 h after sunset.

Hydroacoustic data was collected with a Biosonics DT-X, 120-kHz split beam echosounder using a 0.4 ms pulse duration at an interval of 2 pulses per second (7.5° half-power beam width). The transducer was mounted on a 1.3-m long BioSonics BioFin tow body suspended alongside the survey vessel at a depth of about 1 m below the surface and towed at about 2 m/s. The unit was calibrated at least once per month using a standard 33 mm diameter tungsten carbide calibration sphere. Data were recorded during the entire day and night surveys and stored on a PC aboard the vessel.

Two different trawls were used to collect fish. A 1 m x 1 m opening-closing trawl (Tucker) with 1 mm mesh was used to target YOY fish at specific depths. A 5 m x 5 m mid-water trawl with 12.7 mm mesh was used to target larger fish. Three Tucker trawl tows were conducted on each inshore-offshore transect during the day and night on each sampling occasion (12 tows per sampling date). Samples were collected using the mid-water trawl two to four times

per day to insure adequate coverage and identification of hydroacoustic targets. A depth sounder was attached to the head rope of each trawl to measure tow depths, and trawls were towed at depths with hydroacoustic targets to verify target identity.

We set two floating gill nets each night during the 2008 surveys to sample the upper epilimnion, which could not be sampled efficiently by our trawls. We did not catch any adult alewife in our trawls during 2007, suggesting that these fish were in the shallowest water layers. Floating gill nets were 6 m deep x 21 m long, with seven mesh sizes (6.25, 8, 10, 12, 15, 18, and 25 mm bar mesh). To determine adult alewife depth distributions for our models, additional gill nets were set in July 2011. These nets consisted of 7 separate nets, each 3 m wide and 20 m deep, each of a single mesh size representing one of the same 7 mesh sizes used in our previous 6x21m nets. These nets were suspended from the surface down to 20 m depth, which include the entire epilimnion and overlapped with the thermocline. Nets were set at sunset and pulled 5 h later, after the completion of our night survey. We noted mesh size and vertical location of each fish caught.

We previously determined that rainbow smelt and alewife vertical distributions are related to, and predictable based on, temperature and light gradients (Figure 4.2; Simonin et al. 2012). Because our previously-developed GAMM models (Simonin et al. 2012) were not appropriate for our simulations, we developed temperature and light preference functions from the observed distributions and measured light and temperature profiles following Boscarino et al. (2010, Appendix 1).

To predict fish vertical distribution through the growing season, these temperature and light preferences were coupled with temperature and light vertical water column profiles. Daily water temperature and light profiles were calculated from bi-weekly temperature profiles

recorded by Vermont Department of Fish and Wildlife using linear interpolation. With these inputs, we simulated the proportion of the areal density of adult and YOY rainbow smelt and alewife to be found at each 1-meter depth interval throughout the water column using the preference functions in Appendix 1 (Figure 4.3). Densities of all four fish groups were calculated for each depth by multiplying the expected proportion of the population at that depth with the simulated areal density for each fish group. Thus, the density at each meter depth changes daily during the simulated time period (1 June through 15 October) and is a function of both changes in temperature and light profiles through the season and changes in the simulated total population of each fish group.

Cannibalism is a function of the density of YOY encountered by the average adult, also known as experienced density ( $\text{YOY}/\text{m}^2$ ) (based on Parker Stetter et al. 2007), and a function of YOY and adult fish size (e.g., Brooking et al. 1998). Experienced density was calculated for only YOY fish small enough to be eaten by adults ( $<30\text{mm}$  for alewife adults,  $<80\text{mm}$  for rainbow smelt adults). To convert experienced density to predation, a new relationship (Table 4.1, “Predat.” stage) was fit to previously-published data (Parker Stetter et al. 2007). This relationship differs from previous work in that we do not first calculate a “proportion of cannibals” in the adult population (as in Parker Stetter et al. 2007). We assume that all adult rainbow smelt and alewife can be piscivorous, and thus that cannibalism is a function of experienced density and YOY fish size. Based on age and size data from our study (Simonin et al *in review*, Chapter 3), rainbow smelt YOY growth rate in the model was  $0.6 \text{ mm/day}$  and alewife growth rate was  $0.7 \text{ mm/day}$  (Table 4.1).

From these predation rates we then calculated YOY instantaneous daily mortality rates and changes in YOY abundance and cohort size. Adult rainbow smelt and alewife instantaneous

daily mortality rate was also included in the model, and was held at 0.002 throughout the simulation (Table 4.2). The model was run on a daily time step. Simulations included daytime and nighttime predation, using the same adult alewife distribution for day and night because our observations suggest they do not migrate vertically in Lake Champlain. We assumed daytime predation by adult rainbow smelt did not exist because they do not overlap with YOY during the day (Simonin et al. 2012). We ran the model from 1 June through 15 October (137 days), because this was the range over which field data were collected. Starting areal densities of adult fish were 0.05 fish per square meter, and 1 fish per square meter for YOY (Table 4.2). We simulated a basin area of 10000 square meters.

To compare the effects of predation by rainbow smelt vs. alewife, and to determine whether rainbow smelt will now experience higher mortality because of alewife presence, we ran our simulation with varying proportions of rainbow smelt and alewife but keeping the initial total number of adult fish constant. In addition to running our simulation under normal Lake Champlain conditions, we ran the model using conditions representing a warmer climate by increasing the epilimnion temperatures by 3 C.

We compared the importance of estimating mortality using experienced density vs. only density by setting temperature and light preferences to the same values (those of YOY rainbow smelt), and running the model using these conditions. This simulated a predation/cannibalism function that was only density-dependent.

## **RESULTS**

### *Distributions and experienced density*

In all interactions, experienced density was highest in the spring and early summer (Figure 4.4). This was the case partially because simulated densities of YOY fish were highest in

the spring. Also, springtime thermal stratification allowed adult rainbow smelt distributions to partially overlap with YOY distributions at night. In mid-summer, strong thermal stratification more effectively separated adult rainbow smelt from YOY of both species until late summer when YOY rainbow smelt moved into the thermocline because epilimnion temperatures increased above their preferred range.

#### *YOY mortality pattern*

If adult alewife are absent, our simulation shows that rainbow smelt instantaneous daily mortality rates were high in the spring, then decreased steadily through the summer and increased again in the fall. The highest rainbow smelt instantaneous daily mortality rates occurred in the fall (Figure 4.5A). With alewife in the system, spring mortality increased and is the time with the highest rates, with rainbow smelt mortality in the spring about twice as high as in the fall (Figure 4.5B).

#### *Mortality comparison*

When comparing the effects of predation by rainbow smelt vs. alewife on YOY mortality, we found that accounting for spatial dynamics is influential. When simulating recruitment and YOY mortality using only a density-dependent relationship, we found the highest overall mortality rates would take place when only rainbow smelt were in the system (Figure 4.6A). Furthermore, rainbow smelt YOY experienced consistently higher mortality rates than alewife in this simulation.

When spatial distributions of the two species are included, relative survival of YOY rainbow smelt and alewife in the model depends on which predator is most abundant. Rainbow smelt YOY mortality rates are highest when only rainbow smelt adults are present, and alewife

YOY mortality rates are highest when only alewife adults are present (Figure 4.6B). Both rainbow smelt and alewife YOY are included in the simulation independent of whether adults are present. When the system contains 50% alewife and 50% rainbow smelt adults, alewife YOY mortality rates are slightly higher than those of YOY rainbow smelt (Figure 4.6B).

#### *Changes in temperature and light*

We also compared YOY mortality rates under current (2008) conditions with rates under a scenario of 3 C higher epilimnetic temperature while maintaining the same thermocline depth as in 2008 (Figure 4.7) (Livingstone 2003). We found higher YOY early-spring mortality rates under normal conditions, but also a slightly longer period of springtime alewife cannibalism in the future conditions (Figure 4.7). Mortality rates in late summer and early fall were also higher in our climate change scenario, though they then decreased to a rate lower than the current rate by late fall. Higher springtime mortality rates, when YOY are most abundant, led to higher overall YOY mortality in the normal scenario.

## **DISCUSSION**

#### *Distributions and experienced density*

Simulated distribution patterns from our model are similar to field observations from other systems. Rainbow smelt generally prefer cooler temperatures than alewife as both adults and YOY (Ferguson 1965, Urban and Brandt 1993, Simonin et al. 2012). This preference for cooler water reduces the overlap between distributions of adult rainbow smelt and YOY of both species. Overlap between YOY alewife and adult rainbow smelt, and thus experienced density, is particularly low in the summer during periods of strong thermal stratification. Adult rainbow smelt experienced density values are therefore primarily a function of fish distribution patterns.

Adult alewife experienced density values are a function of YOY size and abundance to a greater extent than adult rainbow smelt experienced density values. Adult alewife overlap with YOY of both species, and declines in experienced density through the summer are caused by growth of YOY fish, not by thermal separation as is the case for adult rainbow smelt. Alewife prefer warmer temperatures, but also move into cooler depths to feed when necessary (Olson et al. 1988, Boscarino et al. 2009), and it is possible that alewife distributions currently observed in Lake Champlain could change with changes in zooplankton populations. This type of change, which would move alewife deeper in the epilimnion, would increase overlap between adult alewife and YOY rainbow smelt distribution and increase experienced density. Springtime YOY mortality would be increased by this change in distribution, but summer and fall YOY mortality would remain similar because of adult alewife's gape limitation.

#### *Patterns of YOY mortality*

Mortality patterns in our simulation are a function of interactions between YOY fish growth, lake thermal stratification, and fish habitat preferences. In the absence of adult alewife, we found the highest YOY rainbow smelt mortality rates in the fall. These maxima shifted to the spring if adult alewife were the main predator (Figure 4.5). In the springtime, YOY fish are smaller than the 30mm maximum size consumed by adult alewife, and are also in the same part of the water column (epilimnion) as adult alewife. Thus, experienced density is high, resulting in high predation and mortality rates. In the fall, YOY fish have grown to a size too large for adult alewife to consume, but not too large for rainbow smelt. Adult rainbow smelt overlap with YOY fish much more during the late summer when the thermocline covers only a very narrow range of depths. This is because the epilimnion temperatures are then warmer than those preferred by YOY, pushing them into the narrow thermocline and in closer proximity to adult rainbow smelt

that also reside in the thermocline. As temperatures decrease in the epilimnion in the fall, the spatial separation between YOY and adult smelt increases and this continues until fall mixing when overlap increases again.

Growth also influences YOY mortality. In our model, adult alewife can consume YOY up to 30mm, but this is likely the upper limit of what is possible (Brooking et al. 1998). Alewife currently have relatively fast growth rates in Lake Champlain (Simonin et al *in review*, Chapter 2), which reduces YOY alewife mortality via cannibalism. Rainbow smelt YOY have slower growth than alewife, and so are exposed to predation by alewife adults until 40-50 days post-hatching (Figure 4.5). Adult rainbow smelt can consume YOY for most of the period over which our model runs. This is based on observations in Lake Champlain, but it is likely that predation/cannibalism efficiency is reduced as YOY become more mobile and better able to escape adult rainbow smelt predators, even if gape size is not limiting. Thus, it is possible our model over-predicts fall mortality via adult rainbow smelt. Growth is also density dependent (Stritzel Thomson et al. 2011), and in years with particularly low YOY densities, YOY fish may grow more quickly and reach a larger size by fall, such thus adult rainbow smelt are less able to catch and consume them. If this happens, fall mortality will again be less than what we predict.

The addition of alewife to this system increases springtime mortality to levels not previously experienced, or at least not experienced by later-hatching YOY (see Simonin et al. *In review*, Chapter 3). In their native marine habitat, rainbow smelt and alewife YOY are typically more separated from adults because YOY are often in estuarine nursery areas whereas the adults return to coastal pelagic areas after spawning. Similarly, YOY rainbow smelt in Lake Champlain were previously partially protected from cannibalism by thermal stratification from the late spring through the summer (Parker Stetter et al. 2006, 2007, Overton et al. 2012). One primary

way alewife seem to affect native fish communities is through predation on larvae (Madenjian et al. 2008). In the Great Lakes, rainbow smelt larvae disperse offshore and thus are able to avoid alewife predation when small (Madenjian et al. 2008), and only move back into regions with adult alewife once they are larger than 40mm (Tin and Jude 1983). Thus, in these systems, alewife have been thought to not negatively affect rainbow smelt via predation on YOY (e.g., Madenjian et al. 2008), but we suggest a different pattern exists in Lake Champlain and smaller lakes, and that springtime alewife predation on YOY rainbow smelt may be influential.

Our model does not consider daytime predation by rainbow smelt adults, but we expect predation occurs mainly during the night because adult rainbow smelt are deeper than YOY fish by day, and so do not interact with YOY individuals (Simonin et al 2012). Alewife conversely are found in the epilimnion of Lake Champlain during both day and night. Alewife adults school during the day (Simonin, unpublished data), and we do not know the effect this has on their feeding behavior. Alewife are visual predators (Boscarino et al. 2010) and do feed in other systems during the day (e.g., Crowder et al. 1981), supporting our assumption that they feed during the day in Champlain.

### *Invasibility*

When including the spatial distribution of rainbow smelt and alewife in the model, our simulation suggests neither species is likely to extirpate the other from the Main Lake of Lake Champlain. This is because cannibalism is more influential than predation by other species for both alewife and rainbow smelt. However, if mortality is analyzed as only density dependent, and temperature, light, and subsequent distribution patterns are not accounted for, our simulations suggest YOY alewife will have consistently lower mortality rates than YOY rainbow

smelt. This finding indicates that an understanding of the environmental drivers of distribution and subsequent predation/mortality is important and changes our forecasts of YOY mortality rates after the alewife introduction.

When alewife became established in the Laurentian Great Lakes, few larval fish predators were abundant, as rainbow smelt had already begun to decline in abundance and native coregonids were not abundant (Smith 1972, Madenjian et al. 2008). Thus, YOY alewife mortality was likely low until cannibalism increased with higher abundance of adult alewife (Rhodes et al. 1974). In Lake Champlain, however, rainbow smelt are native and have been present in high abundances in recent years (Kirn and Labar 1996, Stritzel Thomson et al. 2011). Despite this, alewife were able to invade and become established. Our analysis suggests this is in part because YOY alewife distribution does not widely overlap with that of adult rainbow smelt.

Similarly, our simulation predicts that adult alewife predation is unlikely to cause higher YOY rainbow smelt mortality than that already caused by rainbow smelt cannibalism. (Figure 4). This is somewhat surprising, because alewife are known to cause higher levels of larval fish mortality in many species (e.g., Madenjian et al. 2008). Our analysis indicates that differences in temperature and light preferences, resulting in differences in distribution patterns, cause lower experienced density and thus predation rates than expected. Distribution-weighted density dependence (like our calculation of ‘experienced density’) (e.g., Lloyd 1967, Feinsinger et al. 1981, Williamson and Stoeckel 1990) ) may be more common in recruitment relationships, and possibly in fisheries and ecology generally, than is currently understood.

*Climate scenarios*

The climate scenario we analyzed was only one of many possible future scenarios, but it suggests changes in climate may cause unexpected changes in YOY rainbow smelt and alewife mortality. In our simulation, springtime mortality decreased slightly because the thermocline formed more quickly, but summer and fall mortality increased. This is because the 3 degree C increase in epilimnetic temperature caused the epilimnion to become warmer than is preferred by YOY rainbow smelt, and to a lesser extent alewife, thus causing them to move deeper and into the metalimnion in closer proximity to adult rainbow smelt, thus increasing experienced density and predation. In other parts of the summer and fall, YOY preferred temperatures were found in or throughout the epilimnion, and YOY fish were spread more widely through this layer, thus decreasing experienced density and mortality.

These results suggest effects of climate and abiotic environmental change on recruitment relationships deserve attention, as has been suggested elsewhere recently (e.g., Vert-pre et al. 2013, Feiner et al. 2015). The primary effects of climate change on abiotic aspects of aquatic systems may include changes in mixing and stratification regimes, ice cover patterns, and hydrology (Nickus et al. 2010). Effects of these changes up food webs are less well understood, but our approach directly links abiotic conditions to fish distribution patterns and subsequent species interactions. Future work could expand on this technique, and include additional nonlinearities in growth, in addition to stochasticity in abiotic conditions. Overwinter mortality is unknown for the species we studied, and for many north-temperate fish, and understanding this would allow us to calculate through a full year, and allow multi-year simulations and tests of longer-term community change.

Current climate and lake modeling efforts suggest changes in epilimnetic and thermocline structure may be expected if current climate trends continue. In stratified lakes, predictions are

that the epilimnion will be warmer and stratification more stable (Livingstone 2003). These trends intuitively suggest conditions that may reduce YOY mortality, because thermal stratification separates adult rainbow smelt from YOY in Lake Champlain and other similar systems (Brandt et al. 1980, Crowder et al. 1981, Crowder and Magnuson 1982, Kirn and Labar 1991, Simonin et al. 2012) and YOY typically prefer warmer conditions than adults (Magnuson et al. 1979, 1990). However, our simulation suggests that mortality rates may instead increase if adults and YOY are forced, by temperature preferences, into the same part of the water column. We therefore suggest that predictions of aquatic species interactions should include spatial components, and that this is increasingly important because of the influence of climate change on aquatic systems.

## REFERENCES

- Boscarino, B. T., L. G. Rudstam, E. R. Loew, and E. L. Mills. 2009. Predicting the vertical distribution of the opossum shrimp , *Mysis relicta* , in Lake Ontario : a test of laboratory-based light preferences 113:101–113.
- Brander, K. M. 2005. Cod recruitment is strongly affected by climate when stock biomass is low. *ICES Journal of Marine Science: Journal du Conseil* 62(3):339–343.
- Brandt, S. B. 1980. Spatial segregation of adult and young-of-the-year Alewives across a thermocline in Lake Michigan. *Transactions of the American Fisheries Society* (September):469–478.
- Brandt, S. B., J. J. Magnuson, and L. B. Crowder. 1980. Thermal habitat partitioning by fishes in Lake Michigan. *Canadian Journal of Fisheries and Aquatic Sciences* 37(10):1557–1564.
- Brooking, T. E., L. G. Rudstam, M. H. Olson, and A. J. Vandevalk. 1998. Size-dependent alewife predation on larval walleyes in laboratory experiments. *North American Journal of Fisheries Management* 18(4):960–965.
- Collingsworth, P. D., D. B. Bunnell, C. P. Madenjian, and S. C. Riley. 2014. Comparative recruitment dynamics of Alewife and Bloater in Lakes Michigan and Huron. *Transactions of the American Fisheries Society* 143(1):294–309.
- Crowder, L. B., and J. J. Magnuson. 1982. Thermal habitat shifts by fishes at the thermocline in Lake Michigan. *Canadian Journal of Fisheries and Aquatic Sciences* 39(7):1046–1050.
- Crowder, L. B., J. J. Magnuson, and S. B. Brandt. 1981. Complementarity in the use of food and thermal habitat by Lake Michigan fishes. *Canadian Journal of Fisheries and Aquatic Sciences* 38(6):662–668.
- Cushing, D. H. 1975. *Marine ecology and fisheries*. CUP Archive.

- Diana, J. S. 2004. Biology and ecology of fishes. Biological Sciences Press, a Division of Cooper Publishing Group.
- Feiner, Z. S., D. B. Bunnell, T. O. Höök, C. P. Madenjian, D. M. Warner, and P. D. Collingsworth. 2015. Non-stationary recruitment dynamics of rainbow smelt: The influence of environmental variables and variation in size structure and length-at-maturation. *Journal of Great Lakes Research* 41(1):246–258.
- Feinsinger, P., E. E. Spears, and R. W. Poole. 1981. A simple measure of niche breadth. *Ecology* 62(1):27.
- Ferguson, R. G. 1958. The preferred temperature of fish and their midsummer distribution in temperate lakes and streams. *Journal of the Fisheries Research Board of Canada* 15(4):607–624.
- Ferguson, R. G. 1965. Bathymetric distribution of American smelt *Osmerus mordax* in Lake Erie. *Journal of Great Lakes Research* 13:47–60.
- Henderson, B. A., and S. J. Nepszy. 1989. Factors affecting recruitment and mortality rates of rainbow smelt (*Osmerus Mordax*) in Lake Erie, 1963–85. *Journal of Great Lakes Research* 15(2):357–366.
- Kirn, R. A., and G. W. Labar. 1991. Stepped-oblique midwater trawling as an assessment technique for rainbow smelt. *North American Journal of Fisheries Management* 11(2):167–176.
- Kirn, R. A., and G. W. Labar. 1996. Growth and survival of rainbow smelt, and their role as prey for stocked salmonids in Lake Champlain. *Transactions of the American Fisheries Society* 125(1):87–96.

- Lantry, B. F., and D. J. Stewart. 2000. Population dynamics of rainbow smelt (*Osmerus mordax*) in Lakes Ontario and Erie: a modeling analysis of cannibalism effects. *Canadian Journal of Fisheries and Aquatic Sciences* 57(8):1594–1606.
- Livingstone, D. M. 2003. Impact of secular climate change on the thermal structure of a large temperate central European lake. *Climatic Change* 57(1-2):205–225.
- Lloyd, M. 1967. 'Mean Crowding'. *The Journal of Animal Ecology* 36(1):1.
- Madenjian, C. P., T. O. Höök, E. S. Rutherford, D. M. Mason, T. E. Croley, E. B. Szalai, and J. R. Bence. 2005. Recruitment variability of Alewives in Lake Michigan. *Transactions of the American Fisheries Society* 134(1):218–230.
- Madenjian, C. P., R. O’Gorman, D. B. Bunnell, R. L. Argyle, E. F. Roseman, D. M. Warner, J. D. Stockwell, and M. A. Stapanian. 2008. Adverse effects of alewives on Laurentian Great Lakes fish communities. *North American Journal of Fisheries Management* 28(1):263–282.
- Magnuson, J. J., L. B. Crowder, and P. A. Medvick. 1979. Temperature as an ecological resource. *American Zoologist* 19(1):331–343.
- Magnuson, J. J., J. D. Meisner, and D. K. Hill. 1990. Potential changes in the thermal habitat of Great Lakes fish after global climate warming. *Transactions of the American Fisheries Society* 119(2):254–264.
- Marsden, J. E., and M. Hauser. 2009. Exotic species in Lake Champlain. *Journal of Great Lakes Research* 35(2):250–265.
- Moring, J. R., and L. H. Mink. 2002. Anadromous alewives, *Alosa pseudoharengus*, as prey for white perch, *Morone americana*. *Hydrobiologia* 479(1-3):125–130.

- Nickus, U., K. Bishop, M. Erlandsson, C. D. Evans, M. Forsius, H. Laudon, D. M. Livingstone, D. Monteith, and H. Thies. 2010. Direct impacts of climate change on freshwater ecosystems. *Climate change impacts on freshwater ecosystems*:38–64.
- O'Brien, T. P., W. W. Taylor, E. F. Roseman, C. P. Madenjian, and S. C. Riley. 2014. Ecological factors affecting Rainbow Smelt recruitment in the main basin of Lake Huron, 1976–2010. *Transactions of the American Fisheries Society* 143(3):784–795.
- Olson, R. A., J. D. Winter, D. C. Nettles, and J. M. Haynes. 1988. Resource partitioning in summer by salmonids in south-central Lake Ontario. *Transactions of the American Fisheries Society* 117(6):552–559.
- Ottersen, G., D. Ø. Hjermmann, and N. C. Stenseth. 2006. Changes in spawning stock structure strengthen the link between climate and recruitment in a heavily fished cod (*Gadus morhua*) stock. *Fisheries Oceanography* 15(3):230–243.
- Overton, A. S., N. A. Jones, and R. Rulifson. 2012. Spatial and temporal variability in instantaneous growth, mortality, and recruitment of larval river herring in Tar—Pamlico River, North Carolina. *Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science*:218–227.
- Parker Stetter, S. L., L. G. Rudstam, J. L. Stritzel Thomson, and D. L. Parrish. 2006. Hydroacoustic separation of rainbow smelt (*Osmerus mordax*) age groups in Lake Champlain. *Fisheries Research* 82(1-3):176–185.
- Parker Stetter, S. L., J. L. S. Thomson, L. G. Rudstam, D. L. Parrish, and P. J. Sullivan. 2007. Importance and predictability of cannibalism in rainbow Smelt. *Transactions of the American Fisheries Society* 136(1):227–237.

- Payne, M. R., E. M. C. Hatfield, M. Dickey-Collas, T. Falkenhaus, A. Gallego, J. Gröger, P. Licandro, M. Llope, P. Munk, C. Röckmann, J. O. Schmidt, and R. D. M. Nash. 2009. Recruitment in a changing environment: the 2000s North Sea herring recruitment failure. *ICES Journal of Marine Science: Journal du Conseil* 66(2):272–277.
- Polovina, J. J. 2005. Climate variation, regime shifts, and implications for sustainable fisheries. *Bulletin of Marine Science* 76(2):233–244.
- R Development Core Team. 2015. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Rhodes, R. J., D. A. Webb, and T. S. McComish. 1974. Cannibalism by the adult alewife (*Alosa pseudoharengus*) in southern Lake Michigan. *Proceedings, Seventeenth Conference on Great Lakes Research*.
- Simonin, P. W., D. L. Parrish, L. G. Rudstam, P. J. Sullivan, and B. Pientka. 2012. Native rainbow smelt and nonnative alewife distribution related to temperature and light gradients in Lake Champlain. *Journal of Great Lakes Research* 38:115–122.
- Smith, S. H. 1972. Factors of ecologic succession in oligotrophic fish communities of the Laurentian Great Lakes. *Journal of the Fisheries Research Board of Canada* 29(6):717–730.
- Stewart, D. J., J. F. Kitchell, and L. B. Crowder. 1981. Forage fishes and their salmonid predators in Lake Michigan. *Transactions of the American Fisheries Society* 110(6):751–763.
- Stritzel Thomson, J. L., D. L. Parrish, S. L. Parker-Stetter, L. G. Rudstam, and P. J. Sullivan. 2011. Growth rates of rainbow smelt in Lake Champlain: effects of density and diet: Growth rates of rainbow smelt. *Ecology of Freshwater Fish* 20(4):503–512.

- Thornton, K. W., and A. S. Lessem. 1978. A temperature algorithm for modifying biological rates. *Transactions of the American Fisheries Society* 107(2):284–287.
- Tin, H. T., and D. J. Jude. 1983. Distribution and growth of larval Rainbow Smelt in Eastern Lake Michigan, 1978–1981. *Transactions of the American Fisheries Society* 112(4):517–524.
- Urban, T. P., and S. B. Brandt. 1993. Food and habitat partitioning between young-of-year alewives and rainbow smelt in southeastern Lake Ontario. *Environmental Biology of Fishes* 36(4):359–372.
- Vert-pre, K. A., R. O. Amoroso, O. P. Jensen, and R. Hilborn. 2013. Frequency and intensity of productivity regime shifts in marine fish stocks. *Proceedings of the National Academy of Sciences* 110(5):1779–1784.
- Williamson, C. E., and M. E. Stoeckel. 1990. Estimating predation risk in zooplankton communities: the importance of vertical overlap. Pages 125–131 in H. J. Dumont, J. G. Tundisi, and K. Roche, editors. *Intrazooplankton Predation*. Springer Netherlands.
- Wootton, R. J. 1990. *Ecology of teleost fishes*. Chapman and Hall.

## **Table captions**

Table 4.1. Functions used in our simulation of alewife and rainbow smelt density and YOY mortality in Lake Champlain.

Table 4.2. Parameters and parameter values used in simulation functions, with Table 4.1 symbols identified.

## Figure captions

Figure 4.1. Lake Champlain (right panel), located between the states of New York and Vermont, and the Province of Quebec, Canada. Location of survey transects in the main lake (left) of Lake Champlain. Contour lines represent 5-m depth intervals.

Figure 4.2. Temperature, light, and fish density vertical patterns in the water column in June, August, and September in Lake Champlain

Figure 4.3. Rainbow smelt and alewife distribution and early mortality simulation model structure.

Figure 4.4. Daily experienced density values through the season for adults and YOY rainbow smelt and alewife in Lake Champlain.

Figure 4.5. Daily mortality rates of YOY alewife and YOY rainbow smelt from 1 June through 15 October with only adult rainbow smelt present (A), and with both rainbow smelt and alewife present (B).

Figure 4.6. Mean daily YOY mortality rates from 1 June through 15 October when preyed upon by an adult fish group consisting of different proportions of rainbow smelt and alewife. Predictions are shown with only density-dependent relationships (A) and with spatial dimensions added (B).

Figure 4.7. Mortality rates from 1 June through 15 October under normal conditions (A), and under a climate change scenario in which epilimnion temperatures are 3C warmer than 2008 (B).

Tables

Model Stage	Equation
Density [young rainbow smelt]	$VD_{YRS}[vulnerable] = AD_{YRS} * V_{sp} * P_{YRS}$
Density [young alewife]	$VD_{YAW}[vulnerable] = AD_{YAW} * V_{sp} * P_{YAW}$
Exper. Density	$ExDens_{sp} = \sum P_{A[sp]} * VD_{YRS}$
Predat.	$C_{YRS[sp]} = 1.93 * (ExDens_{sp}) - 0.0217$
Total consumption by adults	$C_{YRS} = C_{YRS[sp1]} * (adult_{sp1} \text{ areal density}) + C_{YRS[sp2]} * (adult_{sp2} \text{ areal density})$
Density $t+1$ [young fish]	$AD_{YRS}[t + 1] = AD_{YRS}[t] - C_{YRS}$
Density $t+1$ [adult fish]	$AD_{ARS}[t + 1] = AD_{ARS}[t] * (1 - M_{ARS}[n])$
Total fish abundance in lake	$N_{sp} = AD_{sp} * B$
Fish length	$L_{sp}[t + 1] = L_{sp}[t] + G_{sp}$

Table 4.1

<b>Symbol</b>	<b>Parameter description</b>	<b>Adult rainbow smelt</b>	<b>YOY rainbow smelt</b>	<b>Adult alewife</b>	<b>YOY alewife</b>
<i>AD</i>	Areal density (#/m <sup>2</sup> , starting density shown)	0.05	1	0.05	1
<i>VD</i>	Volumetric fish density	n/a	n/a	n/a	n/a
<i>B</i>	Simulated basin area (m <sup>2</sup> )	10000	10000	10000	10000
<i>M</i>	Adult daily mortality rate	0.002	n/a	0.002	n/a
<i>G</i>	Growth rate (mm/day)	n/a	0.6	n/a	0.7
<i>V</i>	Proportion of YOY fish vulnerable to adult alewife	n/a	n/a	n/a	n/a
<i>S</i>	Maximum fish size consumed (mm)	n/a	n/a	30	n/a

Table 4.2

**Figures**

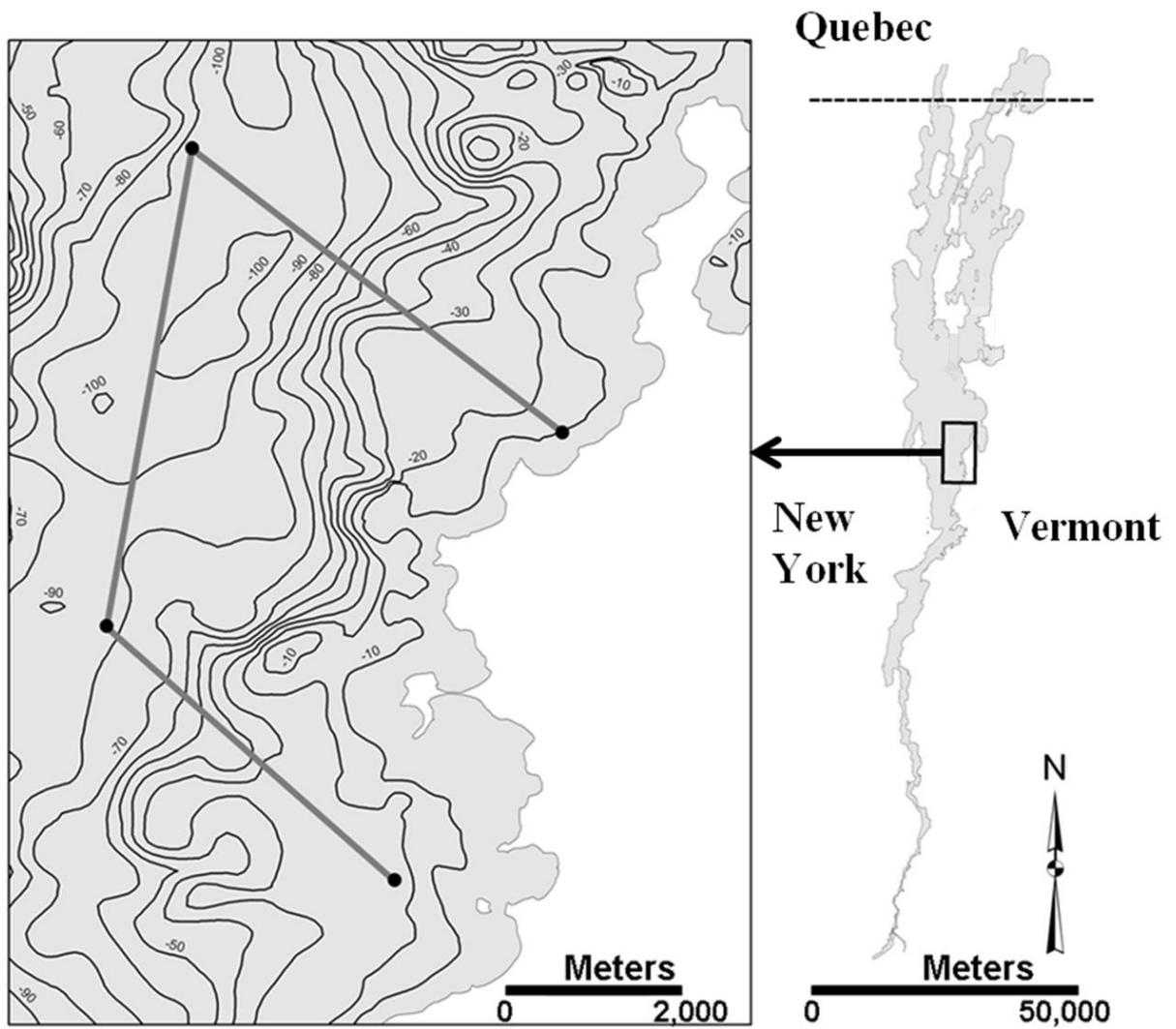


Figure 4.1

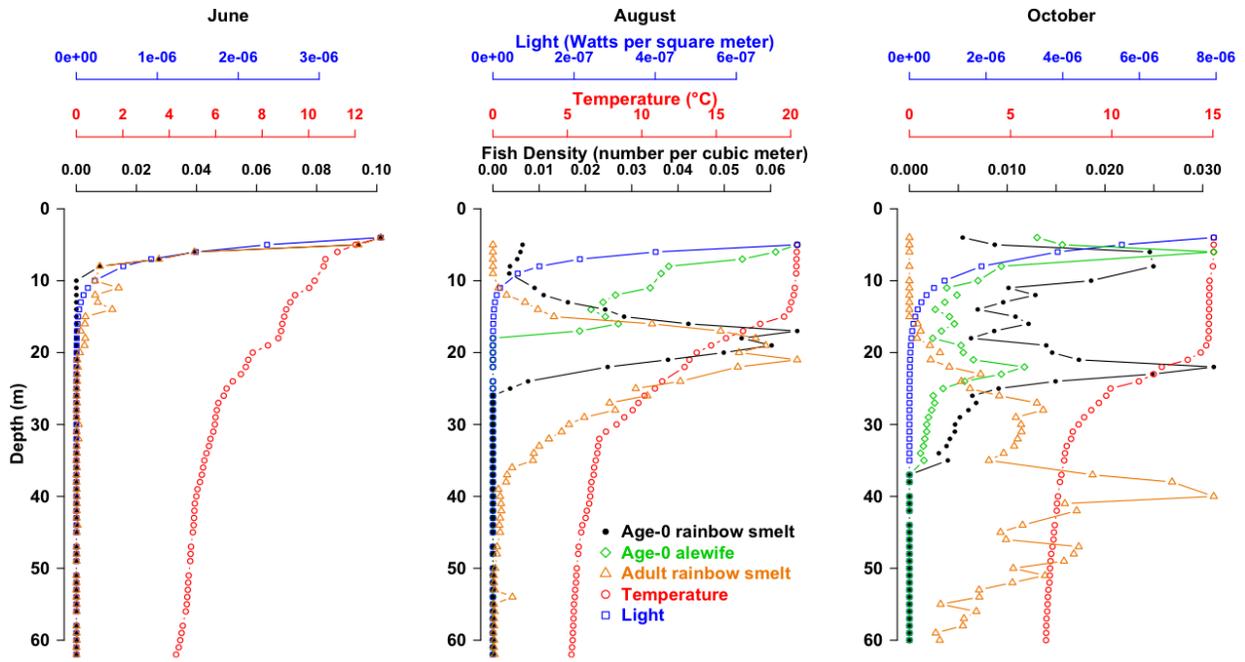


Figure 4.2

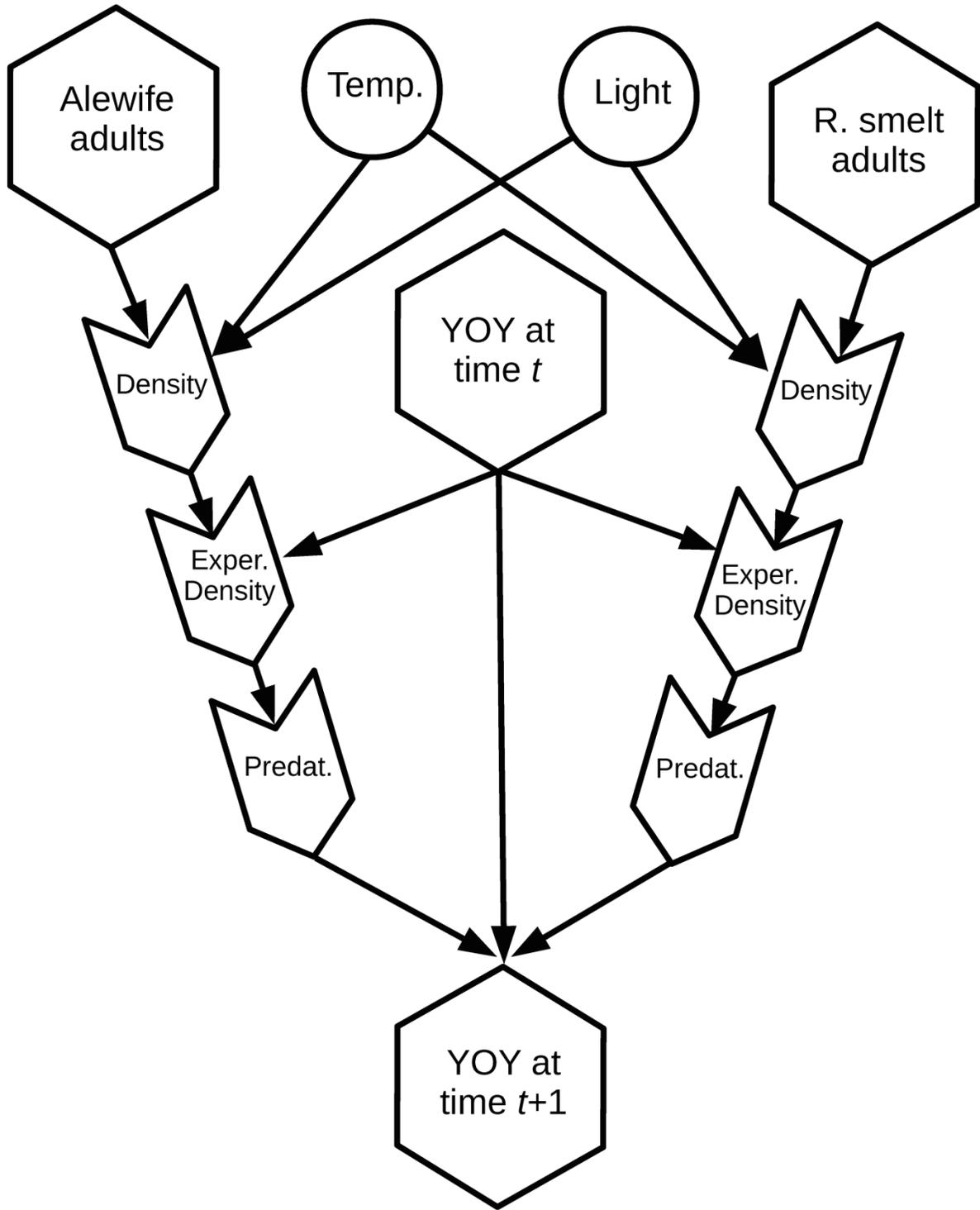


Figure 4.3

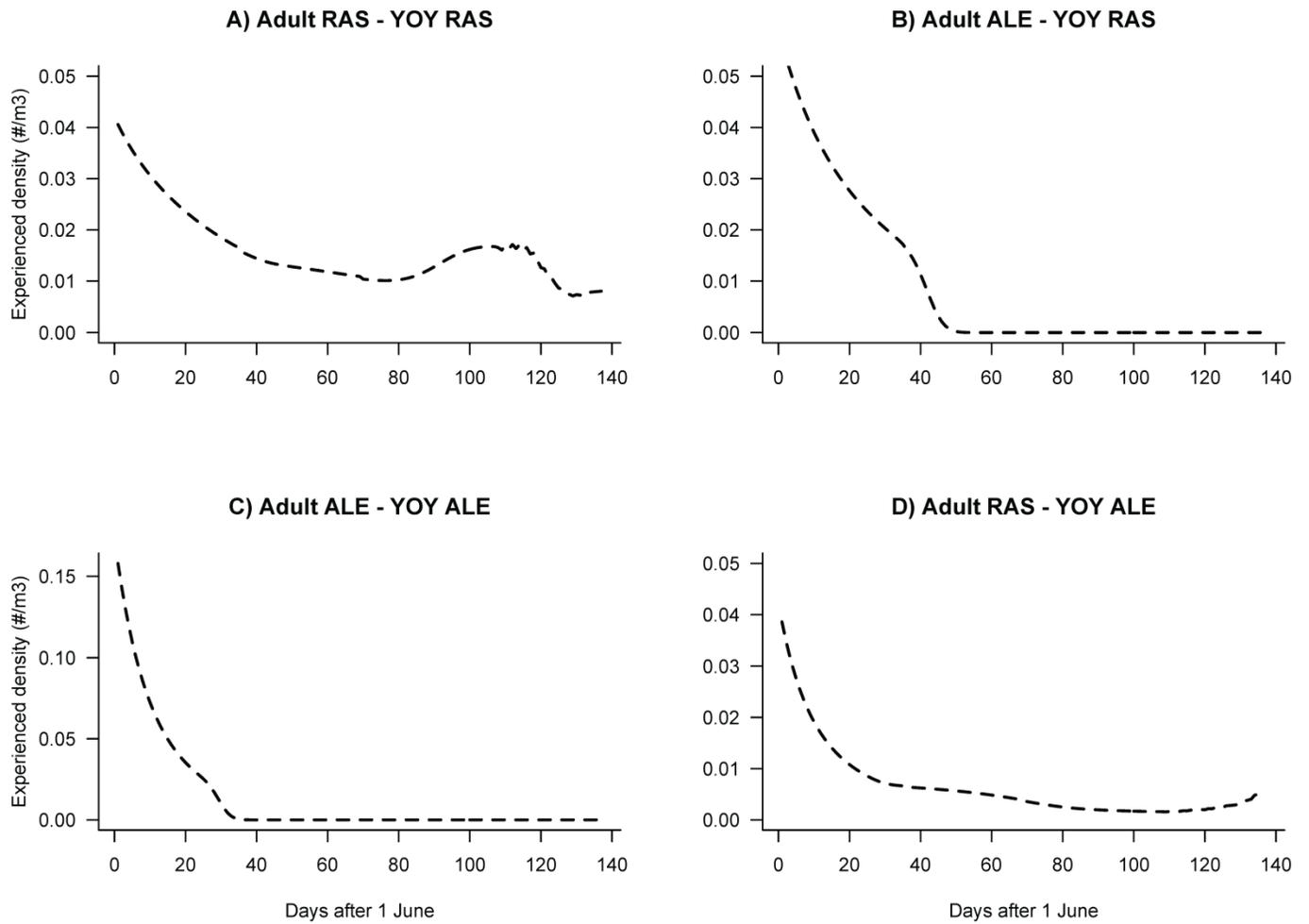


Figure 4.4

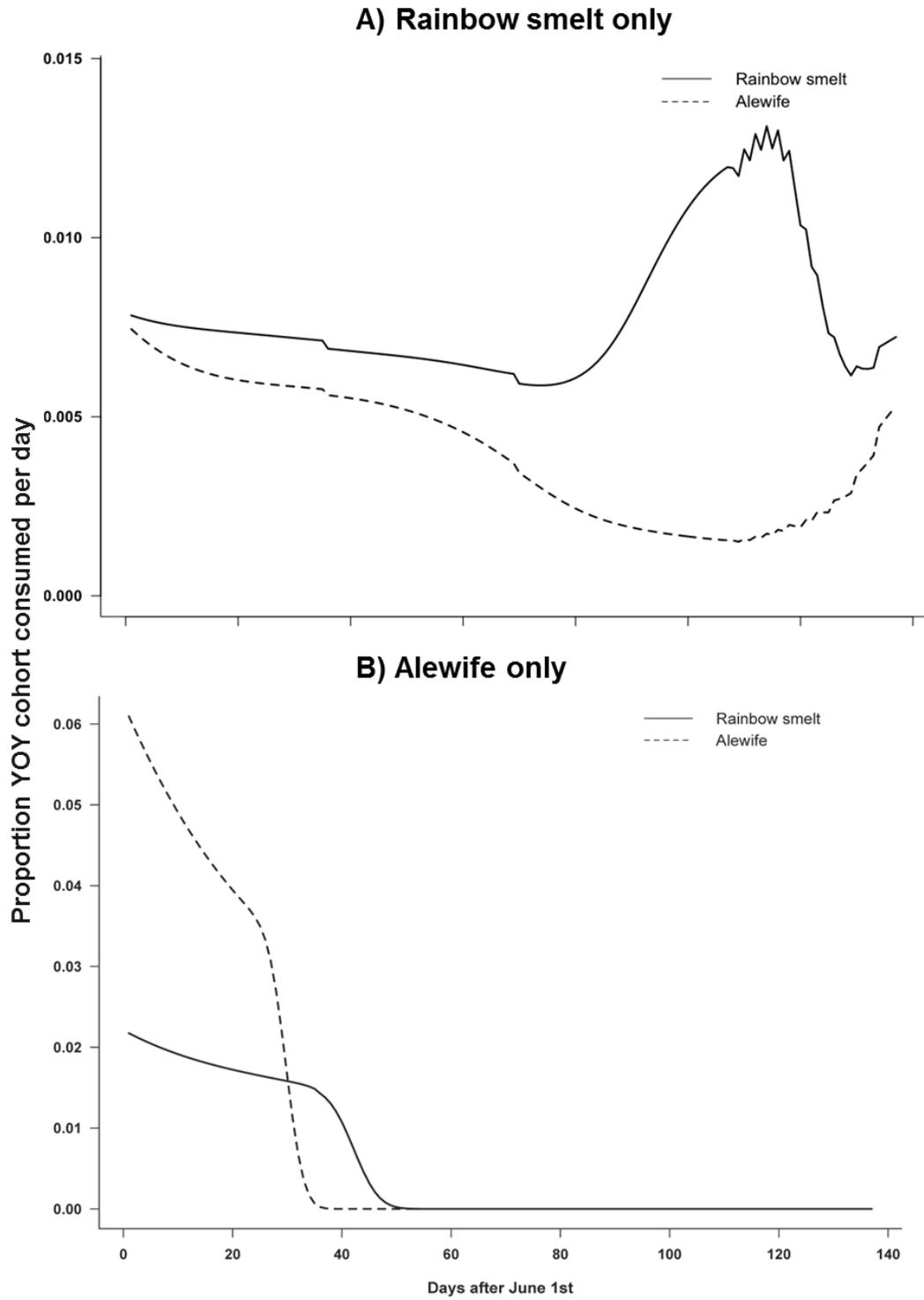


Figure 4.5

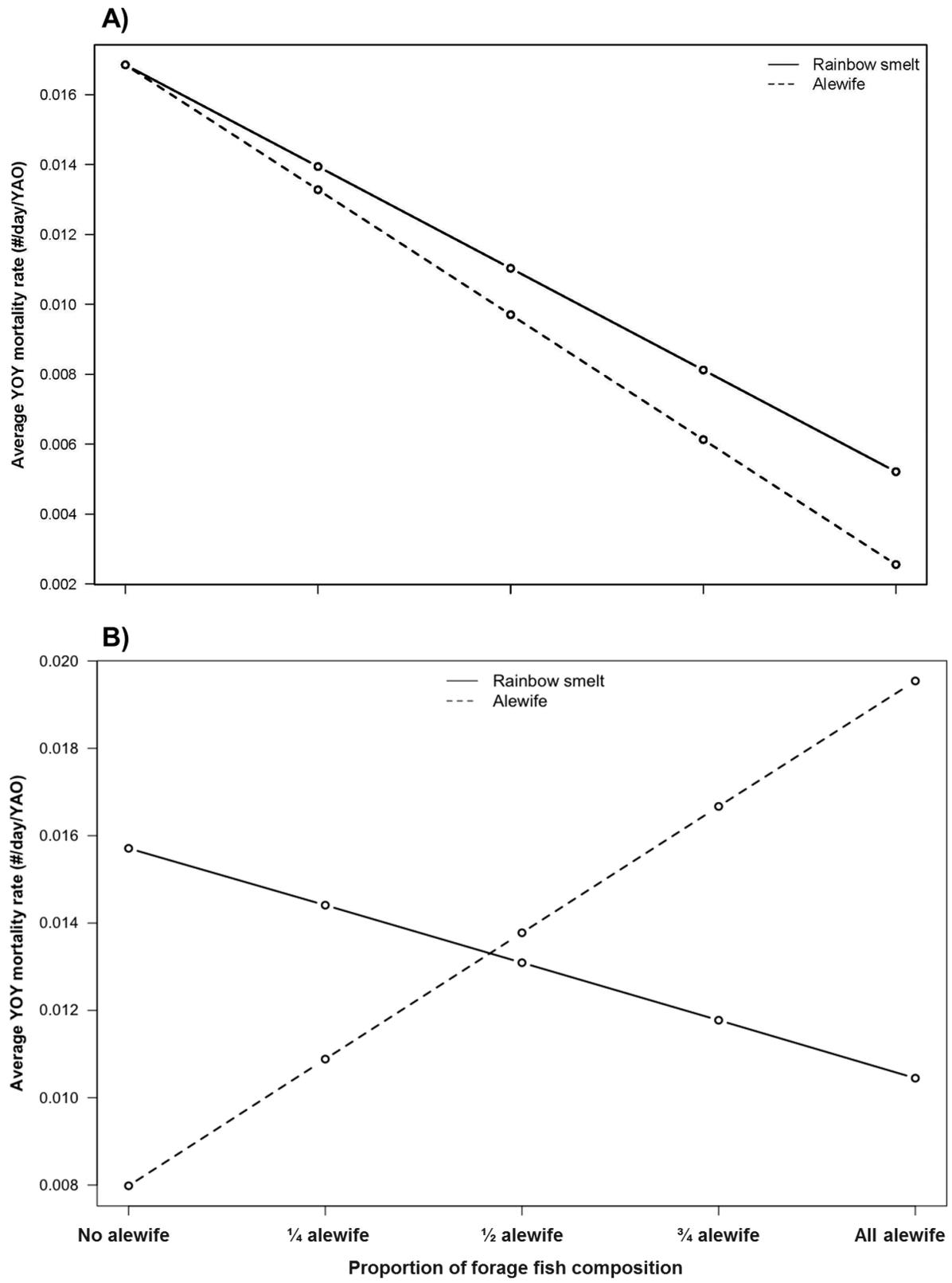


Figure 4.6

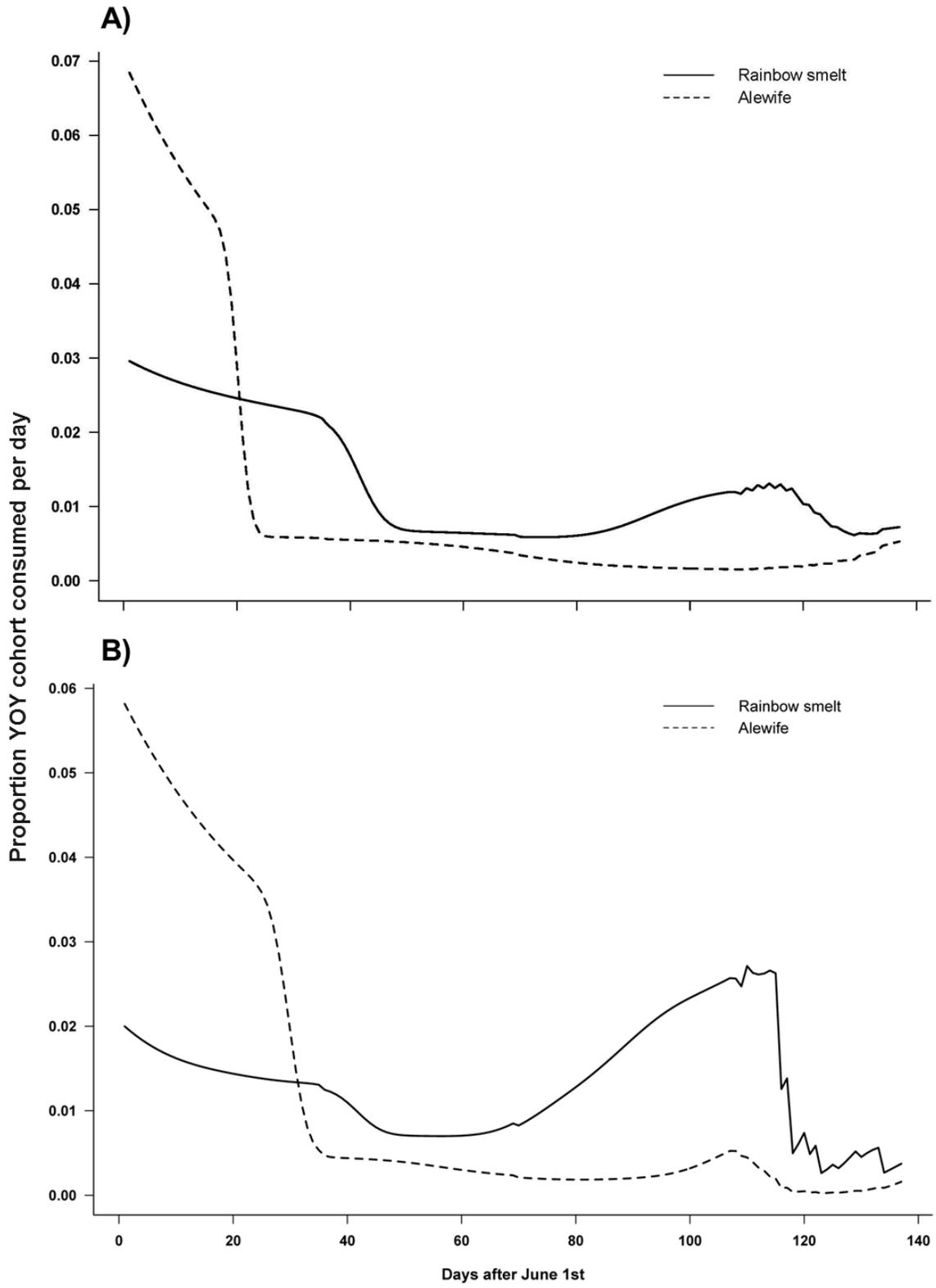


Figure 4.7

## Appendix: Calculation of temperature and light preferences

We previously determined that rainbow smelt and alewife vertical distributions are related to temperature and light gradients (Figure 4.2; Simonin et al. 2012). Our previously-developed GAMM models were not appropriate for use in our current simulation because they are not able to predict distributions accurately on dates when the full range of possible water temperatures are unavailable (e.g., pre- and post-thermal stratification). So, we developed temperature preference functions using Thornton and Lessem curves, a relationship originally developed as an algorithm for modifying biological rates as a function of temperature (Thornton and Lessem 1978). The Thornton and Lessem curve is defined as,

$$P_T(T) = P_A(T) * P_B(T)$$

And,

$$P_A(T) = \frac{P_1 e^{\gamma_1 (T - \theta_1)}}{1 + P_1 \{e^{\gamma_1 (T - \theta_1)} - 1\}}$$

$$\gamma_1 = \frac{1}{\theta_2 - \theta_1} \ln \frac{P_2(1 - P_1)}{P_1(1 - P_2)}$$

$$P_B(T) = \frac{P_4 e^{\gamma_2 (\theta_3 - T)}}{1 + P_4 \{e^{\gamma_2 (\theta_3 - T)} - 1\}}$$

$$\gamma_2 = \frac{1}{\theta_4 - \theta_3} \ln \frac{P_3(1 - P_4)}{P_4(1 - P_3)}$$

Where  $T$  is the observed temperature, and  $P_1$ ,  $P_2$ ,  $P_3$  and  $P_4$  are fixed and identified in Appendix Table A4.1, and  $\theta_3$  is 2° C greater  $\theta_2$ . Thus, three temperature preference parameters ( $\theta_1$ ,  $\theta_2$  and

$\theta_4$ ) were fit for each species/age category, with the upper and lower maximum preferences linked. A normal distribution was assumed for fish light preference rainbow smelt and YOY alewife as,

$$P_L(L) = \frac{1}{\sigma\sqrt{2\pi}} e^{-\frac{(L-\mu)^2}{2\sigma^2}}$$

Where  $L$  is the observed light level in the 460-580 nm wavelength range ( $\log W/m^2$ ),  $\mu$  is the preferred light level (also in  $\log W/m^2$ ) and  $\sigma$  is standard error of the light preference function. Temperature and light preferences were then multiplied together to calculate a final preference function as,

$$P_{sp}(T, L) = P_T(T) * P_L(L),$$

where  $P_{sp}$  is the preference of a given species-age group for the given combination of temperature and light conditions.

Preference models for adult rainbow smelt and YOY rainbow smelt and alewife were fit using data from combined hydroacoustic/trawl/gillnet surveys. Gillnet data were used to fit adult alewife preferences. Because adult alewife preference was calculated from gill net data, and light levels changed during the time gill nets were fishing, we used only temperature to predict adult alewife distribution. Preference functions were fit to nighttime data because of increased uncertainty in daytime data and little overlap between adults and YOY rainbow smelt during the day. Our observations (unpublished) also suggest adult alewife and YOY alewife and rainbow smelt do not migrate vertically in this system, and that YOY form dense shoals during daytime at the same depths as observed during the night.

Fish preferences were converted into the predicted proportion of fish at each depth interval on each day as,

$$B_i = \frac{P_{spi}}{\sum P_{sp}}$$

Where  $P_{spi}$  is the value of  $P_{sp}$  at depth  $i$ ,  $B_i$  is the proportion of fish found at that depth, and  $\sum P_{sp}$  is the sum of  $P_{sp}$  over all depths. Parameter optimization was done using the `optim` routine in R (R Development Core Team 2015) to minimize the sum of the squared difference between the proportion of fish present at an observed temperature-light combination during a sampling event, and the predicted proportion of fish present under those conditions, as in,

$$Z = \sum (A_i - B_i)^2$$

Where,  $A_i$  is the observed proportion of fish present at a depth,  $B_i$  is the predicted proportion present, and  $Z$  is the quantity minimized. This fitting used all observed data from June through October, without assuming any changes in preference functions for that time period.

Appendix Table A4.1

Symbol	Parameter description	Adult rainbow smelt	YOY rainbow smelt	Adult alewife	YOY alewife
$P_1$	Value of the curve at theta 1 (constant)	0.4	0.4	0.4	0.4
$P_2, P_3, P_4$	Value of the curve at theta 2 and theta 3 (constant)	0.98	0.98	0.98	0.98
	Value of the curve at theta 4 (constant)	0.01	0.01	0.01	0.01
$\theta_1$	Lower threshold temperature (°C)	6.1	5.8	20.1	9.1
$\theta_2$	Lower max. preference (°C)	10.4	13.0	26.9	17.1
$\theta_3$	Upper max. preference (°C)	12.4	15.0	28.9	19.1
$\theta_4$	Upper threshold temperature (°C)	17.2	19.0	34.0	23.1
$\mu$	Mean light preference (Log W/m <sup>2</sup> )	-7.74	-6.25	n/a	-4.9

## **CHAPTER 5:**

### **CONCLUDING SUMMARY**

My dissertation began with a brief mention of ecological changes, such as nonnative species introductions and climate change, and how those influence the adaptation of fish species and communities. . I continued in later chapters by focusing more specifically on the ecology of two important lower-trophic-level fish species in North America, rainbow smelt and alewife, and their early life history and interactions in Lake Champlain. These chapters (Chapters 2-4) focused on:

- 4) A study of hatch timing, abundance, growth, and early mortality of rainbow smelt and alewife.
- 5) What has changed, since the alewife invasion, in regard to predation on rainbow smelt and alewife by higher-trophic-level fish.
- 6) A forecast of future possible recruitment and early mortality patterns for rainbow smelt and alewife in light of alewife presence and a likely climate change scenario

I will now briefly review the conclusions from each of these chapters/papers.

### *Hatch timing and early mortality*

Our objectives in this section of the study were to determine hatch date, abundance, growth rate, and mortality patterns of rainbow smelt and alewife to infer differential survival and recruitment related to hatch timing. I hypothesized individual growth rates would be slower and mortality rates higher for early-hatching age 0 of both species. No previous studies of rainbow smelt or alewife hatch timing and early life history had been conducted in Lake Champlain, and few studies have been conducted elsewhere.

As hypothesized, growth rates were significantly slower and mortality rates higher for early-hatching rainbow smelt. Alewife growth rate was also significantly slower for early-hatching individuals, but alewife mortality rates did not differ significantly as a function of hatch timing. Previous to this study, YOY rainbow smelt of widely varying sizes had been observed throughout the summer, suggesting multiple hatching behaviors may exist in the lake. However, I did not find distinct groups of rainbow smelt or alewife hatching at different times (e.g., hatching in May and July, but not in June). Instead, hatching was spread evenly over a period of about two months for each species, and rainbow smelt hatched from late May through early July, whereas alewife hatched from late June through early August. The rainbow smelt hatch dates I observed differ from other systems where YOY rainbow smelt hatch in May, and suggest Lake Champlain rainbow smelt behave differently than those in other lakes.

Our finding that mortality rates were higher for early-hatching rainbow smelt suggests a reason for the later hatch timing of this population. Cannibalism is a major source of mortality for YOY of this species in this lake, and is a function of both fish densities and shared habitat (i.e., interaction between individuals). In the early spring, the lake has not yet stratified

thermally, and so adults and YOY are more mixed throughout the water column, potentially leading to higher cannibalism rates. This differs from times when thermal stratification exists, and adults are in the hypolimnion while YOY are in the epilimnion. Thus, I suggest that rainbow smelt in this system have adapted to reduce cannibalistic mortality by hatching later in Lake Champlain than they do in other systems.

### *Trophic changes post-alewife*

This section of our study examines changes in trophic positioning of native rainbow smelt, salmonid, and walleye populations following the establishment of alewife in a large north-temperate lake (Lake Champlain). Our objectives were to, 1) determine whether, and to what extent, native lake trout and Atlantic salmon are now feeding on alewife, 2) compare current walleye stable isotope signatures to pre-alewife values to infer changes in walleye diets, and 3) compare pre- and post-alewife invasion isotopic signatures of rainbow smelt to infer competitive or predatory interactions. I hypothesized that alewife will replace rainbow smelt in the diets of some predators, but that rainbow smelt trophic position will not change.

I found that alewife are now an important component of predator (salmonids and walleye) diets in Lake Champlain, and that Atlantic salmon feed on alewife to a large extent. This conclusion has implications for the management of both Atlantic salmon and alewife in Lake Champlain, as Atlantic salmon are a desired sportfish currently maintained in the lake by stocking. Stocking levels should match prey availability, and thus quantifying alewife population changes will be important in future years. Furthermore, those dealing with Atlantic salmon in the hatchery should look for symptoms of thiamine deficiency, and may need to address this to increase fish survival. This conclusion is also an interesting ecological shift for Atlantic salmon,

in that behavior and nutritional intake have changed. Atlantic salmon growth rates may thus change as well, as may their habitat preferences.

I also found significant changes in walleye and rainbow smelt trophic position between 1997 and 2011. Walleye decreased in trophic level, represented by a decrease in tissue  $\delta^{15}\text{N}$  of 2.1 units, and rainbow smelt increased by 1.1  $\delta^{15}\text{N}$  units. The change in rainbow smelt trophic position was unexpected, and, combined with the change in walleye position, indicate that walleye are no longer feeding predominantly on rainbow smelt in the main lake of Lake Champlain. I find it hard to conclude that rainbow smelt trophic position has changed in a biologically meaningful way since 1997, because mysid populations had already declined by this time (1995 decline), and zebra mussel (*Dreissena polymorpha*) were already in the system (1993 entry). Spiny water flea did not enter the lake until 2014, and so also could not have caused this increase. Thus, it seems cycles of cannibalism could be responsible for this change, or other unknown factors affecting baseline stable isotope ratios.

The walleye decrease in trophic level is notable and their diet now consists primarily of fish species not native to Lake Champlain, a shift causing the observed decrease in  $\delta^{15}\text{N}$ . A decrease in trophic level is ecologically interesting for multiple reasons, including that more energy/biomass should be available to them if almost an entire trophic step is removed, and that biomagnification of compounds and toxicants in their tissue (walleye are high in mercury in L. Champlain) should decrease. Prey switching theory and our knowledge of walleye and Atlantic salmon in Lake Champlain suggested they may now feed upon alewife, but the magnitude of the dietary change I found is both interesting and significant to managers of these fish populations.

### *Forage fish early mortality forecasts*

In this analysis, I focused on the mortality pattern of YOY rainbow smelt and alewife over the first four months of life in Lake Champlain. Our objectives were to, 1) investigate the pattern of mortality of YOY rainbow smelt and YOY alewife through the first growing season with and without adult alewife present, 2) explore whether alewife are likely to replace rainbow smelt as a consequence of predation on YOY, and, 3) explore what effect climate-induced changes in temperature and light may have on YOY rainbow smelt and YOY alewife mortality and recruitment.

I found that the presence of alewife in Lake Champlain switches the timing of maximum YOY rainbow smelt (and now alewife) seasonal mortality from the fall to the spring. This conclusion is significant, because our previous analysis of hatch timing and YOY mortality suggested that YOY rainbow smelt had historically been shielded from cannibalism during the early summer by thermal stratification. However, now they are vulnerable to predation from adult alewife, even after thermal stratification, until they reach a size too large for adult alewife capture (about 20-30mm). Regarding hatch timing, I theorized that the current timing of rainbow smelt hatching is a balance between natural selection forces that would push toward early hatching (i.e., overwinter mortality selecting for maximum size fall fish size) and those that push toward later hatching (i.e., rainbow smelt cannibalism). However, alewife predation in early summer may cancel out the benefits of later hatching, thus pushing the population toward the early hatch timing often observed to that in other lakes.

I also conclude that alewife are not likely to push rainbow smelt out of the main lake section of Lake Champlain via predation on YOY. This conclusion is due to the importance of

cannibalism driven by experienced density. I acknowledge this conclusion does not account for other ways alewife may out-compete rainbow smelt, such as competition for mysids or zooplankton. However, it is important to recognize that alewife are unlikely to cause a rainbow smelt population crash under current conditions via YOY predation, especially given that alewife predation on larval fish has been one of their primary effects in other systems.

Finally, I conclude that climate change-driven changes to abiotic lake conditions cause lower springtime YOY mortality but higher late-summer and fall mortality. I find this conclusion interesting, because intuitively it seems that warmer lake conditions may lead to more habitat for fish that prefer warmer temperatures. However, in our model, an increase in epilimnetic temperatures by 3°C pushes YOY rainbow smelt and alewife preferred temperatures into the thermocline, and thus pushes YOY individuals closer to adult rainbow smelt spatially. Similar patterns could likely occur in other lakes with thermal stratification.

The deconstruction of a recruitment relationship into the mechanisms of daily mortality, and subsequent simulation of these mechanisms into the future under varying conditions, is one of the additional unique contributions of this work. This was done in an attempt to simulate future fish community mortality patterns and test for potential changes in forage fish species dominance. This fish community ecology model led to intellectually interesting results while also being helpful in discussions with managers and non-specialists, because of its tractability. We suggest similar techniques may be possible in other system, where understanding and forecasting aquatic community change is the goal, and where historic data exist and the mechanisms of species interactions are understood.

## APPENDIX I

### R/S+ CODE FOR MODEL SIMULATIONS (USED IN CH. 5)

---

#### SECTION 1: DEMO CODE

#This script is meant to demonstrate a few of the types of functions and code used in the rest of the model.

```
trial.data = read.csv("AllData_trial_july08.csv") #trial data using one profile from July 31, 2008
```

```
AllData = read.csv("AllData.csv") #Dataset including all our 2007-08 surveys
```

```
#####
```

```
#####
```

#The function for which parameters will be estimated

```
YAO.RAS.Dist.T = function(MyPar, data=MyData)
```

```
{
```

```
temp=data$temp
```

```
yaoras=data$yaoras
```

```
CQ= MyPar[1]
```

```
CTO=MyPar[2]
```

```
CTM=MyPar[3]
```

```
CTL=MyPar[4]
```

```
CK1=0.4
```

```
CK4=0.01
```

```
length=15
```

```
G1 = (1/(CTO - CQ))*log((0.98*(1-CK1))/(CK1*0.02))
```

```
G2 = (1/(CTL - CTM))*log((0.98*(1-CK4))/(CK4*0.02))
```

```
Ka = (CK1*exp(G1*(temp-CQ)))/(1+CK1*(exp(G1*(temp-CQ))-1))
```

```
Kb = (CK4*exp(G2*(CTL-temp)))/(1+CK4*(exp(G2*(CTL-temp))-1))
```

```
TPref = Ka*Kb
```

```
Pref<<-TPref/sum(TPref)
```

```
SS = sum((yaoras-Pref)^2)
```

```
#LogLik=-1*sum(dnorm(yaoras,Pref,sqrt(SS/length(SS)),log=T))
```

```
#FuncAic<<-(-2*LogLik+2*(6+1))
```

```
return(SS)
```

```
}
```

```
#####
```

```
#####
```

```
#Demonstrating the fitting of this model to data from various dates
```

```
MyInitParam = c(6.10, 10.35, 12.36, 15.16)
```

```
i = 1
```

```
SampleID = sort(unique(AllData$code))
```

SECTION 2: FUNCTIONS USED IN MODEL, AND REFERED TO BY OTHER SECTIONS  
OF CODE

#Functions to estimate vertical fish distributions in the water column

#ESTIMATION OF DISTRIBUTION MODEL PARAMETERS

#####

#The function for which parameters will be estimated

DistTempLight = **function**(InitParams, data = AllData)

{

temp=data\$temp

DistData=data[, species]

logwm2 = data\$logwm2

CQ=InitParams[1]

CTO=InitParams[2]

CTM=CTO + 2

CTL=InitParams[3]

CK1=0.4

CK4=0.01

length=15

$G1 = (1/(CTO - CQ)) * \log((0.98 * (1 - CK1)) / (CK1 * 0.02))$

$G2 = (1/(CTL - CTM)) * \log((0.98 * (1 - CK4)) / (CK4 * 0.02))$

$Ka = (CK1 * \exp(G1 * (temp - CQ))) / (1 + CK1 * (\exp(G1 * (temp - CQ)) - 1))$

$Kb = (CK4 * \exp(G2 * (CTL - temp))) / (1 + CK4 * (\exp(G2 * (CTL - temp)) - 1))$

TPref = Ka \* Kb

#Light preference

Lmu = InitParams[4]

Lsd = 1.5 #InitParams[5]

LightPref =  $\exp(-0.5 * ((\log_{wm2} - Lmu)^2) / (Lsd^2))$

LPref = ifelse(logwm2 >= -7.94, LightPref, 0.01)

#Size effects

#Length = (data[, length]) \* InitParams[5]

#Overall Preferences

CombinePref = LPref \* TPref #\* Length

```
Pref<<- CombinePref/sum(CombinePref)
```

```
SS = sum((DistData-Pref)^2)
```

```
#LogLik=-1*sum(dnorm(species,Pref,sqrt(SS/length(SS)),log=T))
```

```
#FuncAic<<-(-2*LogLik+2*(6+1))
```

```
return(SS)
```

```
}
```

```
#Function which applies the above "DistTempLight" function to the entire dataset
```

```
GlobalDist = function(InitParams, data = AllData)
```

```
{
```

```
Squares = NULL
```

```
SampleID = sort(unique(AllData$code))
```

```
i = 1
```

```
for(i in seq(length(SampleID)))
```

```
{
```

```
  ChampData = AllData[AllData$code == SampleID[i], ]
```

```
  HoldSS = optim(InitParams, DistTempLight)
```

```
  Squares = rbind(Squares, HoldSS$value)
```

```
}
```

```
SumSquares = sum(Squares)
```

```
return(SumSquares)
```

```
}
```

```
#####
```

```
#PREDICTIONS OF DISTRIBUTIONS
```

```
#####
```

```
#Function used for predicting YOY and YAO RAS preferences --> distributions (Temperature  
AND Light)
```

```
#FitPar =
```

```
#PredTemp = seq(5,20, by = 0.25)
```

```
DistTempLightPred = function(Par, data = Profile) #switch to FitPar if we use output form  
above model
```

```
{
```

```
Temp = data$temp
```

logwm2 = data\$logwm2

CQ=Par[1]

CTO=Par[2]

CTM=Par[3]

CTL=Par[4]

CK1=0.4

CK4=0.01

length=15

$G1 = (1/(CTO - CQ)) * \log((0.98 * (1 - CK1)) / (CK1 * 0.02))$

$G2 = (1/(CTL - CTM)) * \log((0.98 * (1 - CK4)) / (CK4 * 0.02))$

$Ka = (CK1 * \exp(G1 * (Temp - CQ))) / (1 + CK1 * (\exp(G1 * (Temp - CQ)) - 1))$

$Kb = (CK4 * \exp(G2 * (CTL - Temp))) / (1 + CK4 * (\exp(G2 * (CTL - Temp)) - 1))$

TPref = Ka\*Kb

#Light preference

Lmu = Par[5]

Lsd = 1.5

```

LightPref=exp(-0.5*((logwm2-Lmu)^2)/(Lsd^2))
LPref = ifelse(logwm2 >= -7.94, LightPref, 0.01)

#Overall Preferences

CombinePref = LPref * TPref

Pref<<- CombinePref/sum(CombinePref)

return(data.frame(depth = data$depth, temp = Temp, light = logwm2, TPref = TPref, LPref =
LPref, Pref = Pref))
}

```

```
#####
```

```
#Function used for predicting YAO ALE preferences --> distributions (Temperature ONLY)
```

```
DistTempPred = function(Par, data = Profile) #switch to FitPar if we use output form above
model
```

```
{
```

```
Temp = data$temp
```

```
logwm2 = data$logwm2
```

```
CQ=Par[1]
```

CTO=Par[2]

CTM=Par[3]

CTL=Par[4]

CK1=0.4

CK4=0.01

length=15

$G1 = (1/(CTO - CQ)) * \log((0.98 * (1 - CK1)) / (CK1 * 0.02))$

$G2 = (1/(CTL - CTM)) * \log((0.98 * (1 - CK4)) / (CK4 * 0.02))$

$Ka = (CK1 * \exp(G1 * (Temp - CQ))) / (1 + CK1 * (\exp(G1 * (Temp - CQ)) - 1))$

$Kb = (CK4 * \exp(G2 * (CTL - Temp))) / (1 + CK4 * (\exp(G2 * (CTL - Temp)) - 1))$

TPref = Ka\*Kb

#Light preference

#Lmu = Par[5]

#Lsd = 1.5

$\#LightPref = \exp(-0.5 * ((\logwm2 - Lmu)^2) / (Lsd^2))$

#if (logwm2 >= -7.94)

{LPref <- LightPref}

```

#else

#{LPref <- 0.01}

#Overall Preferences

CombinePref = TPref #LPref * TPref

Pref<<- CombinePref/sum(CombinePref)

return(data.frame(depth = data$depth, temp = Temp, light = logwm2, TPref = TPref, Pref =
Pref))
}

```

```
#####
```

```
#Functions to pack simulation output into objects to be saved
```

```

PackScalar = function(){
  data.frame(
    date,
    YoyRasSize,
    YoyAleSize,
    MortRateYoyRas,
    MortRateYoyAle,
    ArealDensYaoRas,
    ArealDensYoyRas,

```

```
ArealDensYaoAle,  
ArealDensYoyAle,  
YaoRasPopSize,  
YoyRasPopSize,  
YaoAlePopSize,  
YoyAlePopSize  
)  
}
```

```
PackVectors = function(){  
  data.frame(  
    ERasRasAll,  
    EAleRasAll,  
    ERasAleAll,  
    EAleAleAll,  
    ConsumedYoyRasRasAll,  
    ConsumedYoyAleRasAll,  
    ConsumedYoyRasAleAll,  
    ConsumedYoyAleAleAll,  
    ConsumedYoyRasAll,  
    ConsumedYoyAleAll,  
    YoyRasMortRates,  
    YoyAleMortRates,
```

```
YoyRasTotalPop,  
YoyAleTotalPop,  
YaoRasTotalPop,  
YaoAleTotalPop  
)  
}
```

```
#####
```

```
#Functions to create plots of simulation output
```

```
#Plots of one-year simulation
```

```
Plots = function(input){
```

```
#YOY mortality rates
```

```
dev.new()
```

```
par(mar=c(4, 5, 4, 2) + 0.1)
```

```
plot(YoyRasMortRates, main = "Young fish mortality rates", xlab = "Days after June 1st", ylab
```

```
= "", type = "l", ylim = c(0, max(YoyRasMortRates, YoyAleMortRates)), las=1, font=2,
```

```
font.lab=2, cex.axis=1.01, cex.lab=1.1, bty = "l", lwd = 2)
```

```
lines(YoyAleMortRates, xlab = "", type = "l", lty = 2, lwd = 2)
```

```

mtext("Instant. daily mortality rate",side=2,line=3.5,font=2, cex=1.1)
legend("topright",legend=c("Rainbow smelt", "Alewife"), lty=c(1, 2), bty="n", cex=1.1)

#Population sizes
dev.new()
par(mar=c(4, 5, 4, 2) + 0.1)
plot(YoyRasTotalPop, main = "Young fish population size over time", xlab = "Days after June
1st", ylab = "", type = "l", ylim = c(0, max(YoyRasTotalPop, YoyAleTotalPop)), las=1, font=2,
font.lab=2, cex.axis=1.01, cex.lab=1.1, bty = "l", lwd = 2)
lines(YoyAleTotalPop, xlab = "Days after June 1st", type = "l", lty = 2, lwd = 2)
mtext("Fish population size",side=2,line=3.5,font=2, cex=1.1)
legend("topright",legend=c("Rainbow smelt", "Alewife"), lty=c(1, 2), bty="n", cex=1.1)

```

```

#Population sizes
dev.new()
par(mar=c(4, 5, 4, 2) + 0.1)
plot(YaoRasTotalPop, main = "Adult fish population size over time", xlab = "Days after June
1st", ylab = "", type = "l", ylim = c(0, max(YaoRasTotalPop, YaoAleTotalPop)), las=1, font=2,
font.lab=2, cex.axis=1.01, cex.lab=1.1, bty = "l", lwd = 2)
lines(YaoAleTotalPop, xlab = "Days after June 1st", type = "l", lty = 2, lwd = 2)
mtext("Fish population size",side=2,line=3.5,font=2, cex=1.1)
legend("topright",legend=c("Rainbow smelt", "Alewife"), lty=c(1, 2), bty="n", cex=1.1)

```

```
}
```

```
#Experienced density plots
```

```
PlotExperDens = function(input){
```

```
dev.new()
```

```
par(mar=c(4, 5, 4, 5) + 0.1)
```

```
plot(input, main = "Experienced density and consumption", xlab = "Days after June 1st", ylab =  
"", las=1, font=2, font.lab=2, cex.axis=1.01, cex.lab=1.1, bty = "l")
```

```
axis(side = 4, at = pretty(input), labels = pretty(input)*3.86, las=1, font=2, font.lab=2,  
cex.axis=1.01, cex.lab=1.1)
```

```
mtext("Experienced density (YOY / cubic meter / YAO)",side=2,line=4,font=2, cex=1.1)
```

```
mtext("Number of YOY consumed per adult per day",side=4,line=4,font=2, cex=1.1)
```

```
}
```

```
#####
```

```
#Plots of multi-year simulation
```

```
PlotsYears = function(input){
```

```
#YOY mortality rates
```

```
dev.new()
```

```
par(mar=c(4, 5, 4, 2) + 0.1)
```

```

plot(YoyRasMortRates, main = "", xlab = "Days after June 1st", ylab = "", type = "l", ylim = c(0,
max(YoyRasMortRates, YoyAleMortRates)), las=1, font=2, font.lab=2, cex.axis=1.01,
cex.lab=1.1, bty = "l", lwd = 2)
lines(YoyAleMortRates, xlab = "Days after June 1st", type = "l", lty = 2, lwd = 2)
mtext("Instant. daily mortality rate",side=2,line=3.5,font=2, cex=1.1)
legend("topright",legend=c("Rainbow smelt", "Alewife"), lty=c(1, 2), bty="n", cex=1.1)

```

#Population sizes

```

dev.new()
par(mar=c(4, 5, 4, 2) + 0.1)
plot(YaoRasYearPopSize, main = "Adult fish population size over time", xlab = "Years", ylab =
"", type = "l", ylim = c(0, max(YaoRasYearPopSize, YaoAleYearPopSize)), las=1, font=2,
font.lab=2, cex.axis=1.01, cex.lab=1.1, bty = "l", lwd = 2)
lines(YaoAleYearPopSize, xlab = "", type = "l", lty = 2, lwd = 2)
mtext("Fish population size",side=2,line=3.5,font=2, cex=1.1)
legend("topright",legend=c("Rainbow smelt", "Alewife"), lty=c(1, 2), bty="n", cex=1.1)

```

#Population sizes

```

dev.new()
par(mar=c(4, 5, 4, 2) + 0.1)
plot(YaoRasTotalPop, main = "Adult fish population size over time", xlab = "Days after June
1st", ylab = "", type = "l", ylim = c(0, max(YaoRasTotalPop, YaoAleTotalPop)), las=1, font=2,
font.lab=2, cex.axis=1.01, cex.lab=1.1, bty = "l", lwd = 2)

```

```

lines(YaoAleTotalPop, xlab = "Days after June 1st", type = "l", lty = 2, lwd = 2)
mtext("Fish population size",side=2,line=3.5,font=2, cex=1.1)
legend("topright",legend=c("Rainbow smelt", "Alewife"), lty=c(1, 2), bty="n", cex=1.1)

}

```

```
#####
```

```
#Functions to interpolate between different starting and ending water column profiles
```

```
#For June - Sept 15
```

```
myinterp1 = function(x,n=107) {
```

```
nn=dim(x)[1]
```

```
int = NULL
```

```
for(i in seq(nn)){
```

```
  j = x[i,]
```

```
  int = rbind(int,approx(j,n=n)$y)
```

```
}
```

```
return(int)
```

```
}
```

```
#For Sept 15 - Oct 15
```

```
myinterp2 = function(x,n=30) {
```

```
nn=dim(x)[1]
```

```
int = NULL
```

```
for(i in seq(nn)){  
  j = x[i,]  
  int = rbind(int,approx(j,n=n)$y)  
}  
return(int)  
}
```

```
#####
```

### SECTION 3: DISTRIBUTION MODEL FITTING FOR SPECIES/AGE CLASSES

#This script is meant to run functions in the RAS-AWF\_3... file and fit Thornton-Lessem curves for adult rainbow smelt, age-0 r. smelt, and age-0 alewife distributions in relation to temperature.

#Data used in fitting

trial.data = read.csv("AllData\_trial\_july08.csv") #trial data using one profile from July 31, 2008

AllData = read.csv("AllData.csv") #Dataset including all our 2007-08 surveys

source("RAS-AWF\_2\_Functions.R")

#INCLUDING TEMPERATURE AND LIGHT

#####

\*\*\*\*\*

#Setting code values to starting dates

SampleID = sort(unique(AllData\$code))

i = 1

#Fit for YaoRas

InitParams = c( 5, 10, 15, -8) #, 14)

```

species = "yaoras"

YaoRasJuly = optim(InitParams, DistTempLight, data = trial.data, hessian=TRUE)

YaoRasFit = optim(InitParams, GlobalDist, data = AllData, hessian=TRUE) #, method =
"SANN")

summary(YaoRasFit)

YaoRasFit

#Setting code values to starting dates

SampleID = sort(unique(AllData$code))

i = 1

#Fit for YoyRas

InitParams = c( 5, 12, 20, -7) #, 20)

species = "yoyras"

#length = "yoyrasL"

YoyRasJuly = optim(InitParams, DistTempLight, data = trial.data, hessian=TRUE)

YoyRasFit = optim(InitParams, GlobalDist, data = AllData, hessian=TRUE)

YoyRasFit

#Setting code values to starting dates

SampleID = sort(unique(AllData$code))

i = 1

#Fit for YoyAle

InitParams = c( 8, 16, 22, -6) #, 22)

```

```

species = "yoyale"

#length = "yoyaleL"

YoyAleJuly = optim(InitParams, DistTempLight, data = trial.data, hessian=TRUE)

YoyAleFit = optim(InitParams, GlobalDist, data = AllData, hessian=TRUE)

YoyAleFit

#*****

*****

#Parameters from models fit above

YaorasPar = c(6.10, 10.36, 12.36, 15.16, -7.74)

YaoalePar = c(13.94, 18.87, 23.68, 30.73)

YoyrasPar = c(5.75, 12.75, 14.75, 19.00, -6.25)

YoyalePar = c(9.10, 17.10, 19.10, 23.10, -4.90)

#*****

*****

#Uncertainty around parameters

YaoRasFisher = solve(-YaoRasFit$hessian)

YoyRasFisher = solve(-YoyRasFit$hessian)

YoyAleFisher = solve(YoyAleFit$hessian)

YaoRasSigma = sqrt(abs(diag(YaoRasFisher)))

```

```
YoyRasSigma = sqrt(abs(diag(YoyRasFisher)))
```

```
YoyAleSigma = sqrt(abs(diag(YoyAleFisher)))
```

```
YaoRasSigma = diag(YaoRasSigma)
```

```
YoyRasSigma = diag(YoyRasSigma)
```

```
YoyAleSigma = diag(YoyAleSigma)
```

```
YaoRasUpper = YaoRasFit$par+1.96* YaoRasSigma
```

```
YaoRasLower = YaoRasFit$par-1.96* YaoRasSigma
```

```
YoyRasUpper = YoyRasFit$par+1.96* YoyRasSigma
```

```
YoyRasLower = YoyRasFit$par-1.96* YoyRasSigma
```

```
YoyAleUpper = YoyAleFit$par+1.96* YoyAleSigma
```

```
YoyAleLower = YoyAleFit$par-1.96* YoyAleSigma
```

```
### INCLUDING TEMPERATURE ONLY
```

```
#####These are copied from DEMO file, so function names refer to functions there
```

```
#####
```

```
#Fit for YaoRas
```

```
InitParams = c( 8, 11, 20) #, 14)
```

```
species = "yaoras"
```

```
YaoRasTempJuly = optim(InitParams, DistLight, data = trial.data)
```

```
YaoRasTempFit = optim(InitParams, GlobalDist, data = AllData) #, method = "SANN")
```

```
YaoRasTempFit
```

```
#Fit for YoyRas
```

```
InitParams = c( 9, 14, 17) #, 20)
```

```
species = "yoyras"
```

```
YoyRasTempJuly = optim(InitParams, DistLight, data = trial.data)
```

```
YoyRasTempFit = optim(InitParams, GlobalDist, data = AllData)
```

```
YoyRasTempFit
```

```
#Fit for YoyAle
```

```
InitParams = c( 8, 16, 25) #, 22)
```

```
species = "yoyale"
```

```
YoyAleTempJuly = optim(InitParams, DistLight, data = trial.data)
```

```
YoyAleTempFit = optim(InitParams, GlobalDist, data = AllData)
```

```
YoyAleTempFit
```

```
#####
```

#### SECTION 4: SIMULATION OF DISTRIBUTIONS AND CANNIBALISM/PREDATION

#This script simulates future fish distributions and the community dynamics of rainbow smelt  
and alewife in Lake Champlain

#####

```
date = 1
YoyRasSize = 1
YoyAleSize = 1
ERasRasAll = NULL
EAleRasAll = NULL
ERasAleAll = NULL
EAleAleAll = NULL
ConsumedYoyRasRasAll = NULL
ConsumedYoyAleRasAll = NULL
ConsumedYoyRasAleAll = NULL
ConsumedYoyAleAleAll = NULL
ConsumedYoyRasAll = NULL
ConsumedYoyAleAll = NULL
YoyRasMortRates = NULL
YoyAleMortRates = NULL
YoyRasTotalPop = NULL
YoyAleTotalPop = NULL
```

```
YaoRasTotalPop      = NULL
```

```
YaoAleTotalPop      = NULL
```

```
for( date in seq(1:137 ))
```

```
{
```

```
  Profile      = data.frame(depth = Depth, temp = Temp[, date], logwm2 = Light[, date])
```

```
  #YaoRas
```

```
  YaorasDist = DistTempLightPred(YaorasPar, Profile)
```

```
  #YaoAle
```

```
  YaoaleDist = DistTempPred(YaoalePar, Profile)
```

```
  #YoyRas
```

```
  YoyrasDist = DistTempLightPred(YoyrasPar, Profile)
```

```
  #YoyAle
```

```
  YoyaleDist = DistTempLightPred(YoyalePar, Profile)
```

```
  #Volumetric density calculation for YOY
```

```
  #YOY vulnerable to RAS adults. Add size restricted predation if desired.
```

```
  DensYoyRas = YoyrasDist$Pref * ArealDensYoyRas  /* pnorm(RasMaxCons, mean =
```

```
  YoyRasSize, sd = 2.5)
```

```
  DensYoyAle = YoyaleDist$Pref * ArealDensYoyAle  /* pnorm(RasMaxCons, mean =
```

```
  YoyAleSize, sd = 2.5)
```

```
  #YOY vulnerable to ALE adults
```

```
DensYoyRas.ALE = YoyrasDist$Pref * ArealDensYoyRas * pnorm(AleMaxCons, mean =  
YoyRasSize, sd = 2.5)
```

```
DensYoyAle.ALE = YoyaleDist$Pref * ArealDensYoyAle * pnorm(AleMaxCons, mean =  
YoyAleSize, sd = 2.5)
```

```
#Experienced density (E) calculations
```

```
ERasRas = (sum(YaorasDist$Pref * DensYoyRas)) #Predation by adult smelt on young smelt
```

```
EAleRas = (sum(YaoaleDist$Pref * DensYoyRas.ALE)) #Predation by adult alewife on young  
smelt
```

```
ERasAle = (sum(YaorasDist$Pref * DensYoyAle)) #Predation by adult smelt on young alewife
```

```
EAleAle = (sum(YaoaleDist$Pref * DensYoyAle.ALE)) #Predation by adult alewife on young  
alewife
```

```
ERasRasAll = rbind(ERasRasAll, ERasRas)
```

```
EAleRasAll = rbind(EAleRasAll, EAleRas)
```

```
ERasAleAll = rbind(ERasAleAll, ERasAle)
```

```
EAleAleAll = rbind(EAleAleAll, EAleAle)
```

```
#Number of YOY consumed per YAO
```

```
#YOYRAS predation
```

```
ConsumedYoyRasRas = 3.86 * ERasRas #3.86 is original regression
```

```
ifelse(ConsumedYoyRasRas < 0, ConsumedYoyRasRas <- 0, ConsumedYoyRasRas <-  
ConsumedYoyRasRas)
```

```
ConsumedYoyAleRas = (3.86 * EAleRas)*2 #Doubled to account for daytime predation
ifelse(ConsumedYoyAleRas < 0, ConsumedYoyAleRas <- 0, ConsumedYoyAleRas <-
ConsumedYoyAleRas)
```

```
#YOYALE predation
```

```
ConsumedYoyRasAle = 3.86 * ERasAle
ifelse(ConsumedYoyRasAle < 0, ConsumedYoyRasAle <- 0, ConsumedYoyRasAle <-
ConsumedYoyRasAle)
```

```
ConsumedYoyAleAle = (3.86 * EAleAle)*2 #Doubled to account for daytime predation
ifelse(ConsumedYoyAleAle < 0, ConsumedYoyAleAle <- 0, ConsumedYoyAleAle <-
ConsumedYoyAleAle)
```

```
ConsumedYoyRasRasAll = rbind(ConsumedYoyRasRasAll, ConsumedYoyRasRas)
```

```
ConsumedYoyAleRasAll = rbind(ConsumedYoyAleRasAll, ConsumedYoyAleRas)
```

```
ConsumedYoyRasAleAll = rbind(ConsumedYoyRasAleAll, ConsumedYoyRasAle)
```

```
ConsumedYoyAleAleAll = rbind(ConsumedYoyAleAleAll, ConsumedYoyAleAle)
```

```
#Number of YOY consumed on a given night
```

```
ConsumedYoyRas = ConsumedYoyRasRas * ArealDensYaoRas + ConsumedYoyAleRas *
ArealDensYaoAle          #(DensCanRasRas * 1.348) + (DensCanAleRas * 1.348)
```

```
ConsumedYoyAle = ConsumedYoyRasAle * ArealDensYaoRas + ConsumedYoyAleAle *
ArealDensYaoAle          #(DensCanRasAle * 1.348) + (DensCanAleAle * 1.348)
```

```
ConsumedYoyRasAll = rbind(ConsumedYoyRasAll, ConsumedYoyRas)
```

ConsumedYoyAleAll = rbind(ConsumedYoyAleAll, ConsumedYoyAle)

#Total mortality rate for YOY on a night

MortRateYoyRas = ConsumedYoyRas / ArealDensYoyRas

MortRateYoyAle = ConsumedYoyAle / ArealDensYoyAle

YoyRasMortRates = rbind(YoyRasMortRates, MortRateYoyRas)

YoyAleMortRates = rbind(YoyAleMortRates, MortRateYoyAle)

#Updates before next day

ArealDensYaoRas = ArealDensYaoRas \* (1 - SalWalRasPRate)

ArealDensYoyRas = ArealDensYoyRas \* (1 - MortRateYoyRas)

ArealDensYaoAle = ArealDensYaoAle \* (1 - SalWalAlePRate)

ArealDensYoyAle = ArealDensYoyAle \* (1 - MortRateYoyAle)

#Total population size changes through the season

#YOY

YoyRasPopSize = ArealDensYoyRas \* BasinArea

YoyAlePopSize = ArealDensYoyAle \* BasinArea

YoyRasTotalPop = rbind(YoyRasTotalPop, YoyRasPopSize)

YoyAleTotalPop = rbind(YoyAleTotalPop, YoyAlePopSize)

#YAO

YaoRasPopSize = ArealDensYaoRas \* BasinArea

```
YaoAlePopSize = ArealDensYaoAle * BasinArea
YaoRasTotalPop = rbind(YaoRasTotalPop, YaoRasPopSize)
YaoAleTotalPop = rbind(YaoAleTotalPop, YaoAlePopSize)

date = date + 1

YoyRasSize = YoyRasSize + YoyRasGrowth
YoyAleSize = YoyAleSize + YoyAleGrowth
}
```

## SECTION 5: PLOTTING FUNCTIONS USED IN OTHER PARTS OF MODEL

#This script creates appropriate plots for various aspects of our Lake Champlain rainbow smelt  
and alewife model

```
#####
```

```
#DISTRIBUTION PREFERENCE PLOTS
```

```
#####
```

```
#Plots of preference model fit vs. data
```

```
SampleID = sort(unique(AllData$code))
```

```
i = 1
```

```
#####
```

```
#Making prediction (highlight this from here down to the "i + 1" line)
```

```
ChampData = AllData[AllData$code == SampleID[i], ]
```

```
#YaoRas
```

```
YaorasDist = DistTempLightPred(YaorasPar, ChampData)
```

```
#YaoAle
```

```
YaoaleDist = DistTempPred(YaoalePar, ChampData)
```

```
#YoyRas
```

```
YoyrasDist = DistTempLightPred(YoyrasPar, ChampData)
```

```
#YoyAle
```

```
YoyaleDist = DistTempLightPred(YoyalePar, ChampData)
```

```
#####

#Plotting

par(mfrow=c(2,2), mar=c(2,4,12.5,2)+0.1)

#YAORAS

par(mar=c(2,4,13.5,0)+0.1)

plot(x=YaorasDist$Pref,y=YaorasDist$depth,xlim=c(0,max(YaorasDist$Pref,ChampData$yaoras)),ylim=c(40,0),xaxt="n",yaxt="n",xlab="",ylab="",pch=20,type="b",bty="n",las=1)

par(new=T)

plot(x=ChampData$yaoras,y=ChampData$depth,xlim=c(0,max(YaorasDist$Pref,ChampData$yaoras)),ylim=c(40,0),xaxt="n",yaxt="n",xlab="",ylab="",pch=4,type="b",bty="n",las=1)

axis(side=2,lty = "solid",lwd = 1, lwd.ticks =1,las=1,font=2,cex.axis=1.5)

axis(side=3,lty = "solid",lwd = 1, lwd.ticks =1,font=2)

mtext("Fish Density (# per cubic meter)", side = 3, line=2,font=2)

mtext("YAO rainbow smelt",side=3, line=12,font=2)

mtext("Depth (m)",side=2,line=3,font=2)

par(new=T)

plot(x=ChampData$temp,y=ChampData$depth,xlim=c(0,max(ChampData$temp)),ylim=c(40,0),xlab="",ylab="",axes=F,pch=21,type="b",bty="n",col="red")

axis(side=3, xlim=c(0,max(ChampData$temp)),pos=-17,col="red",col.axis="red",font=2)

mtext("Temperature (C)",side=3,line=6,col="red",font=2)

par(new=T)
```

```

plot(x=ChampData$wm2,y=ChampData$depth,xlim=c(0,max(ChampData$wm2)),ylim=c(40,0),
     xlab="",ylab="",axes=F,pch=22,type="b",bty="n",col="blue",las=1)
axis(side=3, xlim=c(-11,-5),pos=-32,col="blue",col.axis="blue",font=2)
mtext("Light (Watts per square meter)",side=3,line=10,col="blue",font=2)

#YOYRAS

par(mar=c(2,4,13.5,0)+0.1)
plot(x=YoyrasDist$Pref,y=YoyrasDist$depth,xlim=c(0,max(YoyrasDist$Pref,ChampData$yoyr
as)),ylim=c(40,0),xaxt="n",yaxt="n",xlab="",ylab="",pch=20,type="b",bty="n")
par(new=T)
plot(x=ChampData$yoyras,y=ChampData$depth,xlim=c(0,max(YoyrasDist$Pref,ChampData$yo
oyras)),ylim=c(40,0),xaxt="n",yaxt="n",xlab="",ylab="",pch=4,type="b",bty="n",las=1)
axis(side=2,lty = "solid",lwd = 1, lwd.ticks =1,las=1,font=2,cex.axis=1.5)
axis(side=3,lty = "solid",lwd = 1, lwd.ticks = 1,xlim=c(0,max(YoyrasDist$Pref)),font=2)
mtext("Fish Density (# per cubic meter)", side = 3, line=2,font=2)
mtext("YOY rainbow smelt",side=3, line=12,font=2)
par(new=T)
plot(x=ChampData$temp,y=ChampData$depth,xlim=c(0,max(ChampData$temp)),ylim=c(40,0),
     xlab="",ylab="",axes=F,pch=21,type="b",bty="n",col="red")
axis(side=3, xlim=c(0,max(ChampData$temp)),pos=-17,col="red",col.axis="red",font=2)
mtext("Temperature (C)",side=3,line=6,col="red",font=2)
par(font=2)

```

```

legend(x=10,y=40,legend=c("Fish","Temp. ","Light"),text.col=c("black","red","blue"),pch=c(20,
21,22),col=c("black","red","blue"),bty="n")

par(new=T)

plot(x=ChampData$wm2,y=ChampData$depth,xlim=c(0,max(ChampData$wm2)),ylim=c(40,0),
xlab="",ylab="",axes=F,pch=22,type="b",bty="n",col="blue")

axis(side=3,xlim=c(0,max(ChampData$wm2)),pos=-32,col="blue",col.axis="blue",font=2)

mtext("Light (Watts per square meter)",side=3,line=10,col="blue",font=2)

#YAOALE

par(mar=c(2,4,4,0)+0.1)

plot(x=YaoaleDist$Pref,y=YaoaleDist$depth,xlim=c(0,max(YaoaleDist$Pref)),ylim=c(40,0),xax
t="n",yaxt="n",xlab="",ylab="",pch=20,type="b",bty="n",las=1)

axis(side=2,lty="solid",lwd=1,lwd.ticks=1,las=1,font=2,cex.axis=1.5)

axis(side=3,lty="solid",lwd=1,lwd.ticks=1,font=2)

mtext("Fish Density (# per cubic meter)",side=3,line=2,font=2)

mtext("Adult alewife",side=3,line=4,font=2)

mtext("Depth (m)",side=2,line=3,font=2)

par(new=T)

plot(x=ChampData$temp,y=ChampData$depth,xlim=c(0,max(ChampData$temp)),ylim=c(40,0),
xlab="",ylab="",axes=F,pch=21,type="b",bty="n",col="red")

par(new=T)

plot(x=ChampData$wm2,y=ChampData$depth,xlim=c(0,max(ChampData$wm2)),ylim=c(40,0),
xlab="",ylab="",axes=F,pch=22,type="b",bty="n",col="blue")

```

```
#YOYALE
```

```
par(mar=c(2,4,4,0)+0.1)
```

```
plot(x=YoyaleDist$Pref,y=YoyaleDist$depth,xlim=c(0,max(YoyaleDist$Pref,ChampData$yoyal  
e)),ylim=c(40,0),xaxt="n",yaxt="n",xlab="",ylab="",pch=20,type="b",bty="n")
```

```
par(new=T)
```

```
plot(x=ChampData$yoyale,y=ChampData$depth,xlim=c(0,max(YoyaleDist$Pref,ChampData$y  
oyale)),ylim=c(40,0),xaxt="n",yaxt="n",xlab="",ylab="",pch=4,type="b",bty="n",las=1)
```

```
axis(side=2,lty = "solid",lwd = 1, lwd.ticks =1,las=1,font=2,cex.axis=1.5)
```

```
axis(side=3,lty = "solid",lwd = 1, lwd.ticks =1,xlim=c(0,max(YoyaleDist$Pref)),font=2)
```

```
mtext("Fish Density (# per cubic meter)", side = 3, line=2,font=2)
```

```
mtext("YOY alewife",side=3, line=4,font=2)
```

```
par(new=T)
```

```
plot(x=ChampData$temp,y=ChampData$depth,xlim=c(0,max(ChampData$temp)),ylim=c(40,0),  
xlab="",ylab="",axes=F,pch=21,type="b",bty="n",col="red")
```

```
par(font=2)
```

```
par(new=T)
```

```
plot(x=ChampData$wm2,y=ChampData$depth,xlim=c(0,max(ChampData$wm2)),ylim=c(40,0),  
xlab="",ylab="",axes=F,pch=22,type="b",bty="n",col="blue")
```

```
i = i + 1
```

```
#####
#Plots of functional relationships, model fit vs. data

SampleID = sort(unique(AllData$code))

i = 1

#####

#Making prediction (run from here down to "i + 1" line)

ChampData = AllData[AllData$code == SampleID[i], ]

#YaoRas

YaorasDist = DistTempLightPred(YaorasPar, ChampData)

#YaoAle

YaoaleDist = DistTempPred(YaoalePar, ChampData)

#YoyRas

YoyrasDist = DistTempLightPred(YoyrasPar, ChampData)

#YoyAle

YoyaleDist = DistTempLightPred(YoyalePar, ChampData)

#####

par(mfrow=c(3,1))

plot(YaorasDist$Pref ~ YaorasDist$Temp, type = "b", ylim = c(0,
max(YaorasDist$Pref,ChampData$yaoras)), xlab = "Temperature (C)", ylab = "", main = "Adult
rainbow smelt", las=1,font=2,cex.axis=1.5)

lines(ChampData$yaoras ~ ChampData$Temp, type = "b", pch = 4)
```

```

plot(YoyrasDist$Pref ~ YoyrasDist$temp, type = "b", ylim = c(0,
max(YoyrasDist$Pref,ChampData$yoyras)), xlab = "Temperature (C)", ylab = "", main =
"YOY rainbow smelt", las=1,font=2,cex.axis=1.5)
lines(ChampData$yoyras ~ ChampData$temp, type = "b", pch = 4)
plot(YoyaleDist$Pref ~ YoyaleDist$temp, type = "b", ylim = c(0,
max(YoyaleDist$Pref,ChampData$yoyale)), xlab = "Temperature (C)", ylab = "", main = "YOY
alewife", las=1,font=2,cex.axis=1.5)
lines(ChampData$yoyale ~ ChampData$temp, type = "b", pch = 4)

```

```
i = i + 1
```

```
#####
```

```
#SIMULATION PLOTS
```

```
#####
```

```
#Plots of simulations under various conditions
```

```
#Mortality rates
```

```
par(mar=c(4, 5, 4, 2) + 0.1)
```

```
plot(YoyRasMortRates, main = "Fish mortality rates", xlab = "Days after June 1st", ylab = "",
type = "l", ylim = c(0, max(YoyRasMortRates, YoyAleMortRates)), las=1, font=2, font.lab=2,
cex.axis=1.01, cex.lab=1.1, bty = "l")
```

```
lines(YoyAleMortRates, xlab = "Days after June 1st", type = "l", lty = 2)
```

```
mtext("Mortality rate (#/day)",side=2,line=3.5,font=2, cex=1.1)
```

```
legend("topright",legend=c("Rainbow smelt", "Alewife"), lty=c(1, 2), bty="n", cex=1.1)
```

```

dev.new()

#Population sizes

par(mar=c(4, 5, 4, 2) + 0.1)

plot(YoyRasTotalPop, main = "Fish population size over time", xlab = "Days after June 1st",
      ylab = "", type = "l", ylim = c(min(YoyRasTotalPop, YoyAleTotalPop), max(YoyRasTotalPop,
      YoyAleTotalPop)), las=1, font=2, font.lab=2, cex.axis=1.01, cex.lab=1.1, bty = "l")

lines(YoyAleTotalPop, xlab = "Days after June 1st", type = "l", lty = 2)

mtext("Fish population size",side=2,line=3.5,font=2, cex=1.1)

legend("topright",legend=c("Rainbow smelt", "Alewife"), lty=c(1, 2), bty="n", cex=1.1)

#Number consumed per adult

#Ras - Ras

plot(ConsumedYoyRasRasAll, type = "l")

plot(ConsumedYoyRasAleAll, type = "l")

#Experienced densities

plot(ERasRasAll, bty = "l")

axis(side = 4, at = pretty(ERasRasAll), labels = pretty(ERasRasAll)*3.86)

plot(ERasAleAll)

plot(EAleRasAll)

plot(EAleAleAll)

```

```

#Mortalities of smelt and alewife under varying competitor densities

#Preparing data for plot

RasMortDiffAle = c(sum(RasOnlyV$YoyRasMortRates)/137,
sum(QuartAleV$YoyRasMortRates)/137, sum(HalfRasAleV$YoyRasMortRates)/137,
sum(TQuartAleV$YoyRasMortRates)/137, sum(AleOnlyV$YoyRasMortRates)/137)

AleMortDiffAle = c(sum(RasOnlyV$YoyAleMortRates)/137,
sum(QuartAleV$YoyAleMortRates)/137, sum(HalfRasAleV$YoyAleMortRates)/137,
sum(TQuartAleV$YoyAleMortRates)/137, sum(AleOnlyV$YoyAleMortRates)/137)

Proportions = c("No alewife", "1/4 alewife", "1/2 alewife", "3/4 alewife", "All alewife")

#Plotting

par(mar=c(4, 5, 4, 2) + 0.1)

plot(RasMortDiffAle, ylab = "", xlab = "", main = "YOY rainbow smelt and alewife mortality
rates", type = "b", las = 1, lwd = 2, ylim = c(min(RasMortDiffAle, AleMortDiffAle),
max(RasMortDiffAle, AleMortDiffAle)), font.lab=2, cex.axis=1.01, cex.lab=1.1)

mtext("Average YOY mortality rate (#/day/YAO)",side=2,line=3.8,font=2, cex=1.1)

lines(AleMortDiffAle, type = "b", las = 1, lwd = 2, lty = 2)

legend("top",legend=c("Rainbow smelt", "Alewife"), lty=c(1, 2), bty="n", cex=1.1)

#Plots of rainbow smelt vs. alewife mortality rates as a function of adult #'s, SAME Distributions

RasVsAleSame = read.csv("RasvsAleSameDist.csv")

Proportions = c("No alewife", "1/4 alewife", "1/2 alewife", "3/4 alewife", "All alewife")

par(mar=c(4, 5, 4, 2) + 0.1)

```

```
plot(yoyras~code, data=RasVsAleSame, type="b", main="YOY rainbow smelt vs alewife
mortality rates without spatial data", xlab="", ylab="", ylim = c(min(yoyras,yoyale),
max(yoyras, yoyale)), las = 1, lwd = 2)
lines(yoyale~code, data=RasVsAleSame, type="b", las = 1, lwd = 2, lty = 2)
mtext("Average YOY mortality rate (#/day/YAO)",side=2,line=3.8,font=2, cex=1.1)
legend("topright",legend=c("Rainbow smelt", "Alewife"), lty=c(1, 2), bty="n", cex=1.1)
```

```
#####
```

SECTION 6: ANALYSIS/COMMAND SCRIPT USED TO RUN DIFFERING SCENARIOS.  
REQUIRES OTHER FILES WHICH CONTAIN FUNCTIONS.

#Data used in fitting, listed here only FYI

trial.data = read.csv("AllData\_trial\_july08.csv") #trial data using one profile from July 31, 2008

AllData = read.csv("AllData.csv") #Dataset including all our 2007-08 surveys

#####

#Reading functions

source("RAS-AWF\_2\_Functions.R")

#Temperature and light must be also read in using scripts below for various scenarios

#####

#Parameters for each species/age distribution model

YaorasPar = c(6.10, 10.36, 12.36, 17.16, -7.74)

YaoalePar = c(20.13, 26.85, 28.85, 33.99)

YoyrasPar = c(5.75, 13.00, 15.00, 19.00, -6.25)

YoyalePar = c(9.10, 17.10, 19.10, 23.10, -4.90)

#Areal (#/sq. meter) RAS and ALE fish densities at start of season (\* 10000 to obtain  
fish/hectare)

ArealDensYaoRas = 0.05

ArealDensYaoAle = 0.05

ArealDensYoyRas = 1

ArealDensYoyAle = 1

#Basin area (square meters)

BasinArea = 10000

#Salmonid predation on adult RAS, ALE

SalWalRasPRate = 0.002

SalWalAlePRate = 0.002

#Growth rates (mm/day) (From Simonin et al, hatch date paper)

YoyRasGrowth = 0.7 # 0.6 in hatch date paper

YoyAleGrowth = 1 # 0.7 in hatch date paper

#Maximum size fish adult alewife can consume

AleMaxCons = 30

RasMaxCons = 80

#Depth range

Depth = seq(2, 80, by = 1)

```

#####
#Reading/running mortality simulation
source("RAS-AWF_4_Simulation.R")
#####

#Creating data frames to save simulations
NormRunV      = PackVectors()
NormRunS      = PackScalar()

#Creating data frames to save simulations
TrialV        = PackVectors()
TrialS        = PackScalar()

#Only smelt
RasOnlyV      = PackVectors()
RasOnlyS      = PackScalar()

#One quarter alewife
QuartAleV     = PackVectors()
QuartAleS     = PackScalar()

```

#Half smelt, half alewife

HalfRasAleV = PackVectors()

HalfRasAleS = PackScalar()

#Three quarters alewife

TQuartAleV = PackVectors()

TQuartAleS = PackScalar()

#Only alewife

AleOnlyV = PackVectors()

AleOnlyS = PackScalar()

#Mallets Bay Norm

MalletsNormV= PackVectors()

MalletsNormS= PackScalar()

#Reduced yoyras growth %30

RasRedGrowthV = PackVectors()

RasRedGrowthS= PackScalar()

#Reduced yoyras growth %10

RasRed10GrowthV = PackVectors()

RasRed10GrowthS= PackScalar()

#Reduced yoyras growth %50

RasRed50GrowthV = PackVectors()

RasRed50GrowthS= PackScalar()

#Half yoyras

HalfYoyRasV = PackVectors()

HalfYoyRasS= PackScalar()

#Half both

HalfBothRasV = PackVectors()

HalfBothRasS= PackScalar()

#Half yoyras

TenPerYoyRasV = PackVectors()

TenPerYoyRasS= PackScalar()

#Warm epi all, deeper cline

Warm1V = PackVectors()

Warm1S= PackScalar()

#Warm Ale (1600 & 300) epi all, deeper cliine

Warm1ALEV = PackVectors()

```
Warm1ALES= PackScalar()
```

```
#Brighter
```

```
BrightRunV = PackVectors()
```

```
BrightRunS = PackScalar()
```

```
#Ale faster growth
```

```
AleFast1.5V = PackVectors()
```

```
AleFast1.5S = PackScalar()
```

```
#Warm epi, deeper cline, darker summer
```

```
WarmDarkRunV = PackVectors()
```

```
WarmDarkRunS = PackScalar()
```

```
#####
```

```
#Plots of simulation output. *Enter the appropriate data frame from above (Plots is our function)
```

```
Plots(NormRunV)
```

```
Plots(TrialV)
```

```
Plots(RasOnlyV)
```

Plots(AleOnlyV)

Plots(MalletsNormV)

Plots(RasRedGrowthV)

Plots(RasRed10GrowthV)

Plots(RasRed50GrowthV)

Plots(HalfYoyRasV)

Plots(HalfBothRasV)

Plots(TenPerYoyRasV)

Plots(Warm1V)

Plots(Warm1ALES)

Plots(BrightRunV)

Plots(AleFast1.5V)

Plots(WarmDarkRunV)

#Experienced density

PlotExperDens(NormRunV\$ERasRasAll)

PlotExperDens(NormRunV\$ERasAleAll)

PlotExperDens(NormRunV\$EAleRasAll)

PlotExperDens(NormRunV\$EAleAleAll)

PlotExperDens(RasOnlyV\$ERasRasAll)

PlotExperDens(AleOnlyV\$ERasRasAll)

```

dev.new()

image(x=seq(137), y=seq(79,1), z=t(Temp))

Temp2=Temp[nrow(Temp):1,]

image(t(Temp2))

#####

#Elements found in the above-created data frames, listed here only for reference:

#SCALARS:

#date,

#YoyRasSize,

#YoyAleSize,

#MortRateYoyRas,

#MortRateYoyAle,

#ArealDensYaoRas,

#ArealDensYoyRas,

#ArealDensYaoAle,

#ArealDensYoyAle,

#YaoRasPopSize,

#YoyRasPopSize,

#YaoAlePopSize,

#YoyAlePopSize

#VECTORS:

```

```
#ERasRasAll,  
#EAleRasAll,  
#ERasAleAll,  
#EAleAleAll,  
#ConsumedYoyRasRasAll,  
#ConsumedYoyAleRasAll,  
#ConsumedYoyRasAleAll,  
#ConsumedYoyAleAleAll,  
#ConsumedYoyRasAll,  
#ConsumedYoyAleAll,  
#YoyRasMortRates,  
#YoyAleMortRates,  
#YoyRasTotalPop,  
#YoyAleTotalPop,  
#YaoRasTotalPop,  
#YaoAleTotalPop  
#####  
#Plots of elements from some data frames  
  
#####  
#Temperature scenario changes (run all of each section below to create temperature input)  
#####  
#Normal conditions, Main Lake
```

```
juneNorm = c(read.csv("JuneNorm.csv", header = F), recursive = TRUE)
```

```
septNorm = c(read.csv("SeptNorm.csv", header = F), recursive = TRUE)
```

```
octNorm = c(read.csv("OctNorm.csv", header = F), recursive = TRUE)
```

```
TempNorm1 = cbind(juneNorm, septNorm)
```

```
TempNorm2 = cbind(septNorm, octNorm)
```

```
TempSum = myinterp1(TempNorm1)
```

```
TempFall = myinterp2(TempNorm2)
```

```
Temp = cbind(TempSum, TempFall)
```

```
#-----
```

```
#Warmer conditions for entire water column
```

```
Temp = (read.csv("TempProfiles.csv") + 2)
```

```
#-----
```

```
#Warmer conditions for epilimnion and deeper thermocline in Sept.
```

```
juneWarmEpi = c(read.csv("JuneWarmEpi.csv", header = F), recursive = TRUE)
```

```
septWarmEpi = c(read.csv("SeptWarmEpi.csv", header = F), recursive = TRUE)
```

```
octWarmEpi = c(read.csv("OctWarmEpi.csv", header = F), recursive = TRUE)
```

```
TempWarmEpi1 = cbind(juneWarmEpi, septWarmEpi)
```

```
TempWarmEpi2 = cbind(septWarmEpi, octWarmEpi)
```

```
TempSum = myinterp1(TempWarmEpi1)
```

```

TempFall = myinterp2(TempWarmEpi2)
Temp     = cbind(TempSum, TempFall)
Temp     = Temp + 1
#-----

#Warm spring
juneWarmEpi= c(read.csv("JuneWarmEpi.csv", header = F), recursive = TRUE)
septNorm   = c(read.csv("SeptNorm.csv", header = F), recursive = TRUE)
octNorm    = c(read.csv("OctNorm.csv", header = F), recursive = TRUE)
TempNorm1  = cbind(juneWarmEpi, septNorm)
TempNorm2  = cbind(septNorm, octNorm)

TempSum    = myinterp1(TempNorm1)
TempFall   = myinterp2(TempNorm2)
Temp       = cbind(TempSum, TempFall)

#-----

#Warm summer
juneNorm   = c(read.csv("JuneNorm.csv", header = F), recursive = TRUE)
septWarmEpi= c(read.csv("SeptWarmEpi.csv", header = F), recursive = TRUE)
octNorm    = c(read.csv("OctNorm.csv", header = F), recursive = TRUE)
TempNorm1  = cbind(juneNorm, septWarmEpi)
TempNorm2  = cbind(septWarmEpi, octNorm)

```

```
TempSum = myinterp1(TempNorm1)
TempFall = myinterp2(TempNorm2)
Temp     = cbind(TempSum, TempFall)
```

```
#-----
```

```
#Warm fall
```

```
juneNorm = c(read.csv("JuneNorm.csv", header = F), recursive = TRUE)
septNorm  = c(read.csv("SeptNorm.csv", header = F), recursive = TRUE)
octWarmEpi = c(read.csv("OctWarmEpi.csv", header = F), recursive = TRUE)
TempNorm1  = cbind(juneNorm, septNorm)
TempNorm2  = cbind(septNorm, octWarmEpi)
```

```
TempSum = myinterp1(TempNorm1)
TempFall = myinterp2(TempNorm2)
Temp     = cbind(TempSum, TempFall)
```

```
#-----
```

```
#Normal conditions, *Mallets Bay*
```

```
juneNormMallets = c(read.csv("JuneNormMallets.csv", header = F), recursive = TRUE)
septNormMallets = c(read.csv("SeptNormMallets.csv", header = F), recursive = TRUE)
octNormMallets  = c(read.csv("OctNormMallets.csv", header = F), recursive = TRUE)
TempNormMallets1 = cbind(juneNormMallets, septNormMallets)
TempNormMallets2 = cbind(septNormMallets, octNormMallets)
```

```

TempSum = myinterp1(TempNormMallets1)

TempFall = myinterp2(TempNormMallets2)

Temp      = cbind(TempSum, TempFall)

#####

#Light scenario changes (run all of each section below to create light input)

#####

#Normal conditions

juneLNorm = c(read.csv("JuneLNorm.csv", header = F), recursive = TRUE)
septLNorm = c(read.csv("SeptLNorm.csv", header = F), recursive = TRUE)
octLNorm  = c(read.csv("OctLNorm.csv", header = F), recursive = TRUE)

LightNorm1 = cbind(juneLNorm, septLNorm)
LightNorm2 = cbind(septLNorm, octLNorm)

LightSum = myinterp1(LightNorm1)
LightFall = myinterp2(LightNorm2)
Light     = cbind(LightSum, LightFall)

#-----

#Brighter conditions for entire season

Light      = (read.csv("LightProfiles.csv") + 0.5)

#-----

```

```

#Brighter spring

juneLBrighter= c(read.csv("JuneLBrighter.csv", header = F), recursive = TRUE)

septLNorm = c(read.csv("SeptLNorm.csv", header = F), recursive = TRUE)

octLNorm = c(read.csv("OctLNorm.csv", header = F), recursive = TRUE)

LightNorm1      = cbind(juneLBrighter, septLNorm)

LightNorm2      = cbind(septLNorm, octLNorm)

LightSum = myinterp1(LightNorm1)

LightFall = myinterp2(LightNorm2)

Light = cbind(LightSum, LightFall)

#-----

#Brighter summer

juneLNorm = c(read.csv("JuneLNorm.csv", header = F), recursive = TRUE)

septLBrighter= c(read.csv("SeptLBrighter.csv", header = F), recursive = TRUE)

octLNorm = c(read.csv("OctLNorm.csv", header = F), recursive = TRUE)

LightNorm1      = cbind(juneLNorm, septLBrighter)

LightNorm2      = cbind(septLBrighter, octLNorm)

LightSum = myinterp1(LightNorm1)

LightFall = myinterp2(LightNorm2)

Light = cbind(LightSum, LightFall)

```

```

#-----

#Brighter fall

juneLNorm = c(read.csv("JuneLNorm.csv", header = F), recursive = TRUE)
septLNorm = c(read.csv("SeptLNorm.csv", header = F), recursive = TRUE)
octLBrighter= c(read.csv("OctLBrighter.csv", header = F), recursive = TRUE)

LightNorm1      = cbind(juneLNorm, septLNorm)
LightNorm2      = cbind(septLNorm, octLBrighter)

LightSum  = myinterp1(LightNorm1)
LightFall = myinterp2(LightNorm2)
Light     = cbind(LightSum, LightFall)

#-----

#Darker conditions for entire season

Light          = (read.csv("LightProfiles.csv") - 0.5)

#-----

#Darker spring

juneLDarker= c(read.csv("JuneLDarker.csv", header = F), recursive = TRUE)
septLNorm = c(read.csv("SeptLNorm.csv", header = F), recursive = TRUE)
octLNorm  = c(read.csv("OctLNorm.csv", header = F), recursive = TRUE)

LightNorm1      = cbind(juneLDarker, septLNorm)
LightNorm2      = cbind(septLNorm, octLNorm)

```

```
LightSum = myinterp1(LightNorm1)
LightFall = myinterp2(LightNorm2)
Light     = cbind(LightSum, LightFall)
```

```
#-----
```

```
#Darker summer
```

```
juneLNorm = c(read.csv("JuneLNorm.csv", header = F), recursive = TRUE)
septLDarker= c(read.csv("SeptLDarker.csv", header = F), recursive = TRUE)
octLNorm  = c(read.csv("OctLNorm.csv", header = F), recursive = TRUE)
LightNorm1    = cbind(juneLNorm, septLDarker)
LightNorm2    = cbind(septLDarker, octLNorm)
```

```
LightSum = myinterp1(LightNorm1)
LightFall = myinterp2(LightNorm2)
Light     = cbind(LightSum, LightFall)
```

```
#-----
```

```
#Darker fall
```

```
juneLNorm = c(read.csv("JuneLNorm.csv", header = F), recursive = TRUE)
septLNorm = c(read.csv("SeptLNorm.csv", header = F), recursive = TRUE)
octLDarker= c(read.csv("OctLDarker.csv", header = F), recursive = TRUE)
LightNorm1    = cbind(juneLNorm, septLNorm)
```

```
LightNorm2 = cbind(septLNorm, octLDarker)
```

```
LightSum = myinterp1(LightNorm1)
```

```
LightFall = myinterp2(LightNorm2)
```

```
Light = cbind(LightSum, LightFall)
```

```
#Other combinations of lighter/darker
```

```
#-----
```

```
#Darker spring, lighter fall
```

```
juneLDarker= c(read.csv("JuneLDarker.csv", header = F), recursive = TRUE)
```

```
septLNorm = c(read.csv("SeptLNorm.csv", header = F), recursive = TRUE)
```

```
octLBrighter = c(read.csv("OctLBrighter.csv", header = F), recursive = TRUE)
```

```
LightNorm1 = cbind(juneLDarker, septLNorm)
```

```
LightNorm2 = cbind(septLNorm, octLBrighter)
```

```
LightSum = myinterp1(LightNorm1)
```

```
LightFall = myinterp2(LightNorm2)
```

```
Light = cbind(LightSum, LightFall)
```

```
#-----
```

```
#Darker spring and summer
```

```
juneLDarker = c(read.csv("JuneLDarker.csv", header = F), recursive = TRUE)
```

```

septLDarker= c(read.csv("SeptLDarker.csv", header = F), recursive = TRUE)
octLNorm = c(read.csv("OctLNorm.csv", header = F), recursive = TRUE)
LightNorm1 = cbind(juneLDarker, septLDarker)
LightNorm2 = cbind(septLDarker, octLNorm)

LightSum = myinterp1(LightNorm1)
LightFall = myinterp2(LightNorm2)
Light = cbind(LightSum, LightFall)

#-----
#Darker spring and fall, brighter summer
juneLDarker= c(read.csv("JuneLDarker.csv", header = F), recursive = TRUE)
septLBrighter= c(read.csv("SeptLBrighter.csv", header = F), recursive = TRUE)
octLDarker= c(read.csv("OctLDarker.csv", header = F), recursive = TRUE)
LightNorm1 = cbind(juneLDarker, septLBrighter)
LightNorm2 = cbind(septLBrighter, octLDarker)

LightSum = myinterp1(LightNorm1)
LightFall = myinterp2(LightNorm2)
Light = cbind(LightSum, LightFall)

#-----
#Mallets Bay light

```

```
Light = (read.csv("LightProfilesMallets.csv"))
```

```
#####
```

```
#Reading out the average mortality rate for the season
```

```
sum(NormRunV$YoyRasMortRates)/137
```

```
sum(NormRunV$YoyAleMortRates)/137
```

```
#####
```

```
#Reading/running mortality simulation over years
```

```
source("RAS-AWF_5_Simulations_MultiYear.R")
```

```
rm(list=ls())
```

```
#####
```

SECTION 7: UNCERTAINTY AND ESTIMATION OF ERROR. THIS CODE CONTAINS SECTIONS COMMON TO OTHER SECTIONS(FILES) ALREADY GIVEN, BUT ADDS ESTIMATIONS OF UNCERTAINTY.

```
#This script is meant to run functions in the RAS-AWF_3... file and fit Thornton-Lessem curves for adult rainbow smelt, age-0 r. smelt, and age-0 alewife distributions in relation to temperature.
```

```
#Here we also compute the Cholesky decomposition of the Hessian
```

```
#Data used in fitting
```

```
trial.data = read.csv("AllData_trial_july08.csv") #trial data using one profile from July 31, 2008
```

```
AllData = read.csv("AllData.csv") #Dataset including all our 2007-08 surveys
```

```
source("RAS-AWF_2_Functions.R")
```

```
#INCLUDING TEMPERATURE AND LIGHT
```

```
#####
```

```
*****
```

```
#Setting code values to starting dates
```

```
SampleID = sort(unique(AllData$code))
```

```
i = 1
```

```

#Fit for YaoRas

InitParams = c( 5, 10, 15, -8) #, 14)

species = "yaoras"

YaoRasJuly = optim(InitParams, DistTempLight, data = trial.data, hessian=TRUE)

YaoRasFit = optim(InitParams, GlobalDist, data = AllData, hessian=TRUE) #, method =
  "SANN")

YaoRasFit

#Setting code values to starting dates

SampleID = sort(unique(AllData$code))

i = 1

#Fit for YoyRas

InitParams = c( 5, 12, 20, -7) #, 20)

species = "yoyras"

#length = "yoyrasL"

YoyRasJuly = optim(InitParams, DistTempLight, data = trial.data, hessian=TRUE)

YoyRasFit = optim(InitParams, GlobalDist, data = AllData, hessian=TRUE)

YoyRasFit

#Cholesky decomposition

YoyRas.VarCov=solve(YoyRasJuly$hessian) #var-cov matrix (JULY ONLY)

YoyRas.VarCov=solve(YoyRasFit$hessian) #var-cov matrix (ALL SEASON)

YoyRas.Cor.V=decompose.cov(YoyRas.VarCov) #decomposes var-cov into correlation and
var.

```

```

YoyRas.VarCov = round(YoyRas.VarCov, 3)

YoyRas.VarCov = abs(YoyRas.VarCov)

YoyRas.Chol=chol(YoyRas.VarCov)                #Cholesky decomposition of var-cov

YoyRas.CholCor=chol(YoyRas.Cor.V$r)           #Cholesky decomposition of Corr matrix

YoyRas.nvars=dim(YoyRas.CholCor)[1]           #just to count number of dims

#YoyRas.Chol.L=t(YoyRas.Chol)                 #transpose to get lower L

t(YoyRas.CholCor) %*% YoyRas.CholCor          #check

t(YoyRas.Chol) %*% YoyRas.Chol

nobs = 100

#Using correlation matrix

Rand.num = t(YoyRas.CholCor) %*% matrix(rnorm(YoyRas.nvars*nobs), nrow=YoyRas.nvars,
ncol=nobs)                                     #generates random numbers following corr.

Rand.num = t(Rand.num)

var(Rand.num)

#Using covariance matrix

Rand.num = t(YoyRas.Chol) %*% matrix(rnorm(YoyRas.nvars*nobs), nrow=YoyRas.nvars,
ncol=nobs)                                     #generates random numbers following cov.

Rand.num = t(Rand.num)

Sim=YoyRas.Chol.L*Rand.num

#multiply rand. num. by Cholesky decomp

```

```

diag(YoyRas.VarCov) #just gives diagonal
lower.tri(YoyRas.VarCov) #gives True/False
YoyRas.SE = sqrt(diag(YoyRas.VarCov)) #calculates standard errors
#Setting code values to starting dates
SampleID = sort(unique(AllData$code))
i = 1
#Fit for YoyAle
InitParams = c( 8, 16, 22, -6) #, 22)
species = "yoyale"
#length = "yoyaleL"
YoyAleJuly = optim(InitParams, DistTempLight, data = trial.data, hessian=TRUE)
YoyAleFit = optim(InitParams, GlobalDist, data = AllData, hessian=TRUE)
YoyAleFit
#*****
#Parameters from models fit above
YaorasPar = c(6.10, 10.36, 12.36, 15.16, -7.74)
YaoalePar = c(13.94, 18.87, 23.68, 30.73)
YoyrasPar = c(5.75, 12.75, 14.75, 19.00, -6.25)
YoyalePar = c(9.10, 17.10, 19.10, 23.10, -4.90)
#*****

```