DISTRIBUTION AND ABUNDANCE OF NATIVE RAINBOW SMELT AND NONNATIVE ALEWIFE IN LAKE CHAMPLAIN

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ABSTRACT

Nonnative species have been a powerful driver of ecological change in recent decades, and can complicate management, inflict economic costs, and threaten biodiversity. Rainbow smelt (*Osmerus mordax*) and alewife (*Alosa pseudoharengus*) are cannibalistic, pelagic fish species native to coastal regions of northeastern North America and elsewhere. Rainbow smelt are presumed to be native to Lake Champlain as well, and have been the main forage species supporting higher organisms, including the salmonid and walleye (*Sander vitreus*) sport fisheries in the lake. However, alewife have recently become established here, and thus have the potential to dramatically alter the Lake Champlain ecosystem.

Previous work in this lake focused on adult rainbow smelt, and found cannibalism is a function of fish distribution. In light of this, and alewife invasion, our study quantifies adult and particularly young-of-year (YOY) rainbow smelt and alewife distribution and abundance temporally in relation to their physical environment. We used hydroacoustic equipment, trawls, and gill nets to observe fish over inshore-to-offshore transects during day and night. Each trip we also collected temperature, dissolved oxygen, pH, conductivity, and light data throughout the water column, and recorded continuous surface light levels. Surveys were conducted every two to three weeks from June to October of 2007 and 2008.

In the main lake, YOY rainbow smelt were first observed June, whereas YOY alewife not until late July. In this region, YOY rainbow smelt were most abundant in mid-July, and YOY alewife in early-August, while Malletts Bay populations peaked earlier. Daily mortality rates were higher for earlier hatching fish. YOY alewife growth rates were faster than those of YOY rainbow smelt, and both species recruited to the adult population by October. We found YOY and adult alewife in shallower water than their rainbow smelt counterparts. YOY rainbow smelt distribution overlapped with adult rainbow smelt and YOY alewife, but adult alewife were shallower. Using a modeling approach with information criteria, we found YOY and adult rainbow smelt distributions were related to temperature, temperature gradients, and light, whereas YOY alewife distribution was related to temperature and light. Our study expands the current knowledge base in several ways by providing a uniquely comprehensive description of seasonal and diel dynamics of interacting cannibalistic populations in relation to physical habitat gradients. This explicit understanding of physical – biotic connections and species behavior clarifies our understanding of fish population dynamics and informs decisions regarding Lake Champlain and other systems.

Table of Contents

LIST OF TABLES

Table

LIST OF FIGURES

Figure

CHAPTER 1: INTRODUCTION

Ecology is the study of relations of organisms to each other and their surroundings, and an understanding of the distribution and abundance of life in relation to abiotic and biotic components of the environment forms the foundation of ecological knowledge (Ricklefs 2001). Also fundamental to this science are the concepts of predation and competition, and the inherent web of other interactions that shape both relatively pristine and human dominated ecosystems. Changes in any one player can pull the strings of this web and cause effects that ripple outward in multiple directions. Thus, the addition of a non-native organism to a system will alter this system by its mere presence. Aquatic ecosystems such as large freshwater lakes are systems made up of a myriad of biotic and abiotic components. Fish are one important component of these systems from both the human perspective and in terms of overall lake ecology.

Located between New York and Vermont, with a northern section in the Canadian province of Quebec, Lake Champlain is the sixth largest freshwater body in the United States. While rainbow smelt (*Osmerus mordax*) have historically been the dominant pelagic planktivore in Lake Champlain, and are likely native, this lake now supports a growing non-native alewife (*Alosa pseudoharengus*) population as well. Numerous questions have arisen as to the role and effect of this new species, and a door has been opened to study a system's ecology as a potentially influential species becomes established. Thus, the overall purpose of this study was to enhance our understanding of the interaction between ecologically similar native and alien species in aquatic systems, with the specific goal of gaining a better understanding of distribution and abundance dynamics of rainbow smelt and alewife in Lake Champlain.

Previous studies have documented habitat use and environmental preferences of alewife and rainbow smelt, but this study complements and builds upon current knowledge in several ways. First, relatively few studies have focused on young-of-the-year (YOY) rainbow smelt or alewife lake-wide distribution, and very few have attempted to follow a YOY population from hatching until recruitment to the adult population. Second, this complete dataset of biotic and abiotic data from spring to fall, day and night, is relatively novel and allows description of habitat preferences and relationships between abiotic and biotic variables in a comprehensive manner.

CHAPTER 2: LITERATURE REVIEW

In this review, general ecological principles will be touched upon in relation to resource use and invasive species, followed by a review of previous applicable Lake Champlain research. The current body of knowledge related to rainbow smelt (*Osmerus mordax*) and alewife (*Alosa pseudoharengus*) will be evaluated, and methods of data collection will also be discussed. Finally, I will discuss how this current study fills previous knowledge gaps.

Ecology: competition, predation, and abundance

The presence and abundance of a given species is ultimately a function of energy available in the system, and the species' relative ability to use this energy. Thus, this discussion will largely deal with competition and predation, as these fundamental ecological interactions largely dictate such energy flow and utilization. Given the nature of our study, I will focus on interactions regarding habitat.

Competition, and specifically competition for habitat, will result when one or more species have similar preferences. In aquatic systems this type of competition takes place at all life stages of organisms. However, some organisms seem to share habitat at early life stages but not as adults. The larvae of two zooplanktivorous fish species co-exist in some systems (Urban and Brandt 1993), while adult stages separate (Mills et al. 2003). This separation often seems to result from a preference for different conditions such as temperature, but one may ask whether this is simply the proximate cause whereas ultimately this separation is an evolutionary adaptation to avoid competition.

This is largely a rhetorical question, but it serves to remind one that it is ultimately the maintenance of individual fitness that is important for a population and species. This can ultimately lead to rather interesting adaptations within species themselves, which allows for the utilization of different habitats. Lake trout in Lake Superior are a perfect example in that several morphotypes exist. These morphotypes utilize different habitats in much the same manner in which different species often segregate (Kitchell et al. 2000). Rainbow smelt behave similarly in some estuarine and lake systems, which has led to genetic differentiation between these populations (Taylor and Bentzen 1993, Bernatchez 1997, Pigeon et al. 1998, Taylor 2001, Saint-Laurent et al. 2003, Lecomte and Dodson 2004, 2005).

Competition for habitat certainly includes simple competition for physical space, but competition for food and other resources likely plays just as important a role in dictating habitat choices. Cannibalism is one rather extreme example of food demands interacting with habitat choices. Several species of fish have been shown to exhibit this seemingly mal-adaptive behavior to varying degrees (He and LaBar 1994, Dong and DeAngelis 1998, Lantry and Stewart 2000, Parker Stetter et al. 2007), largely related to conditions facilitating habitat overlap. For example, rainbow smelt adults will cannibalize young smelt during isothermal lake conditions, whereas summer stratified conditions restrict this interaction to smaller regions where habitats overlap.

When direct competition for the same resource takes place one may predict several possible outcomes in the long run. Generally, in the first scenario one species eventually out-competes the other(s), and this is referred to as competitive exclusion

(Hardin 1960, Levin 1970, Connor and Simberloff 1986, Ricklefs 2001).This takes place in aquatic systems worldwide between species ranging from fish to invertebrates (Connell 1961, Zaret and Rand 1971, Selgeby et al. 1994, Hrabik et al. 2001). The second possible outcome of this competition is simply coexistence and the maintenance of all species in the system. This scenario requires either an abundance of resources, or adequate division of scarce resources. Coexistence of many organisms which seemingly rely on the same resources has been shown to take place in aquatic systems, and an example is the maintenance of diverse plankton communities which appear to be in constant inter-specific competition (Hutchinson 1961).

The complex topic of competition in ecosystems may be best summed up in a statement by G.E. Hutchinson (1957) in which he said: “Given a region of physical space in which two species do persist indefinitely at (or close to) a steady state, there exists one or more properties of the environment or species, or of both, that ensures an ecological distinction between the two species, and if one were able to construct the multi-dimensional, fundamental niche of these two species a region would be found in this multi-dimensional space that is part of the fundamental niche of one of the species but not of the other; and similarly, a region would be found that is part of the fundamental niche of the second species but not of the first. It would further be the case that the physical space in which the two species persist indefinitely at, or near, their steady state, represents a real-world projection of those portions of the fundamental niches of the two species that are not identical. If they seem identical the study is incomplete.”

As in much of ecology, topics of study are very much intertwined with each other, and such is the case with competition and predation. Nonetheless, the issue of predation in aquatic organism interactions deserves mention. Debates as to the true magnitude of predation's influence have arisen, but in terrestrial and aquatic systems alike, predator – prey interactions are often cited as shaping species and community population dynamics (Errington 1963, Ricklefs 2001).

A well known example of the influence of predation in aquatic systems is that of planktivores and plankton communities. Zooplanktivourous fish influence the composition of zooplankton communities through selective feeding (Brooks and Dodson 1965). The phytoplankton community is influenced due to changes in the predation characteristics of this new zooplankton community (Brooks and Dodson 1965, Reynolds 2006). Cascades such as this serve as vivid indicators of the importance of predation in ecosystems, and what are often called "top-down" influences (May et al. 1979).

In addition to being a purely academic exercise, such top-down influences (in addition to "bottom-up") play, or should play, a critical role in natural resource management decisions. Fisheries management in particular has proven challenging in freshwater and marine systems alike due in part to the lack of perfect knowledge concerning complex predator-prey interactions, and thus the influence of removing individuals from a population (Ranta et al. 1997). In terrestrial and aquatic systems alike, an added component of this complexity comes when populations move or shift to more suitable habitat (Pimentel et al. 2001). Predation can cause such a shift, as can other influences, and this phenomenon serves to again emphasize the interconnectedness of organism abundance, competition, and predation.

Ecology: habitat selection

Both homeothermic and poikilothermic organisms exhibit preference for specific abiotic environmental characteristics, and the determination of these preferences has been a component of ecological studies for many years (Ricklefs 2001). Questions revolving around an organism's preference for specific temperature, light, moisture, oxygen, and other abiotic conditions are still valid today however, as we seek to further understand new species and new ecosystems.

Biotic interactions also have obvious effects on distribution and resource use, and thus it is often the blend of living and non-living components that dictates preferences and behavior (Ricklefs 2001). In aquatic systems, research has documented definite environmental preferences for organisms of all types. At the base of the aquatic trophic pyramid, phytoplankton and macrophytes have been found to exhibit distinct preferences for variables such as temperature, pH, light, and nutrients (Wetzel 2001, Reynolds 2006). Further up the pyramid, zooplankton have been found to exhibit abiotic environmental preferences in lakes worldwide (e.g. Johnson et al. 2007). Predators also have obvious influences on these plankton communities and have been shown to shape plankton community structure (e.g. Brooks and Dodson 1965, Wetzel 2001).

In terms of higher planktivorous organisms, numerous studies have demonstrated ties between distribution and biotic and abiotic environmental characteristics. In the Great Lakes of North America, spatial distribution of mysids (*Mysis relicta*) has been correlated with light, temperature, and predator behavior (Gal et al. 1999a, Gal et al. 2004, Boscarino et al. 2007). The spectral sensitivity of these organisms has been determined, and techniques developed to measure light quantities in units valid for mysids (Gal et al. 1999a, Boscarino et al. 2007). Focusing only on light and temperature, however, was not enough to explain the distribution of these animals through the day. In addition, zooplanktivorous fish were found to influence mysid distribution through competition with, and direct predation on, mysids (Gal et al. 2004, Gal et al. 2006, Boscarino et al. 2007).

Higher predators such as zooplanktivorous fish have themselves been the focus of other studies, because in general most pelagic fish species do not spread evenly throughout the entire water column. Early research found that gradients of both dissolved oxygen and temperature influenced many fish species (Juday and Wagner 1908). Summer stratification produces these types of gradients in many temperate lakes, and this has been found to cause seasonal differences in fish distribution (Fry 1937). Despite strong preferences for specific abiotic conditions however, studies have found fish to occupy different habitat than would be dictated by abiotic preferences alone (Rudstam and Magnuson 1985). Instead, biotic characteristics such as predator or prey presence also seem to dictate fish distribution. In general it is an obvious fact that avoiding predation and finding food are priorities for all living beings, and that this may require an organism to leave its ideal comfort zone from time to time. The manifestation of this behavior, though, is different from one species to another. Cisco (*Coregonus artedii*), for instance, have been found to behave differently in eutrophic lakes with anaerobic hypolimnia, and also in lakes with restricted food supplies (Rudstam and Magnuson 1985). Food can influence the vertical distribution of other lake fishes such as rainbow smelt, alewife, yellow perch (*Perca flavescens*), and Atlantic salmon (*Salmo salar*) (Dahlberg 1981, Rudstam and Magnuson 1985, Ogorman et al. 1991, Urban and Brandt 1993, Appenzeller and Leggett 1995, Mills et al. 1995, Ganger 1999, O'Gorman et al. 2000, Pientka and Parrish 2002). Studies such as these demonstrate obvious links between fish at various trophic levels, but habitat preferences by fish can also influence, and be influenced by, higher non-aquatic predators. Common terns (*Sterna hirundo*), and other birds, vary their foraging pattern and type of prey delivered to chicks, due to water temperature that determines presence or absence of rainbow smelt and emerald shiner (Burness et al. 1994).

To ecologists, ties such as these may seem intuitive. However, the complexity of an organism's interaction with biotic and abiotic components of its environment can hardly be underestimated. It is rarely possible to understand an organism without first deciphering some of these other strands in the web.

Lake Champlain

Located between New York and Vermont, with a northern section in the Canadian province of Quebec, Lake Champlain is the sixth largest freshwater body in the United States. The lake itself is about 200 km long, has a maximum width of 21 km, roughly 800 km of shoreline, 1124 km^2 of surface area, and a drainage basin of almost 20,000 km^2 (Manley and Manley 1999). Affected geologically by both the Adirondack and Green

Mountains, Lake Champlain's current condition is only the most recent state in its long, varied, history.

Typical of many large lakes, Lake Champlain has a diversity of aquatic habitat suitable for species typically considered to prefer only warm or cold water habitat, pelagic or littoral, etc. 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. 2004). Throughout the lake the three main taxa are Rotifera, Copepoda, and Cladocera, but there have been possible changes since the establishment of zebra mussels in 1993 (Carling et al. 2004). Microzooplankton, specifically rotifers, are the most abundant zooplankton, but have declined in abundance since the mid-1990s (Carling et al. 2004). 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 story of fish communities in Lake Champlain is one of even more dramatic changes since the time of European colonization, as is the case in many freshwater bodies throughout North America. Currently, Lake Champlain fishes include species considered native and alien (Gilbert 2000). 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 lake has several generally planktivorous organisms, one of which deserves mention here despite not being a fish species. The invertebrate *Mysis relicta* 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 serves as an influential predator and prey item in systems it inhabits (Kitchell et al. 2000, Mills et al. 2003).

By far the dominant planktivorous fish species in Lake Champlain has historically been rainbow smelt. This species is likely native to the basin, and adults inhabit all parts of the lake with adequate thermal stratification to sustain cold 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 dolomieui and Micropterus salmoides*), pickerel (*Esox niger* and *Esox americanus*), northern pike (*Essox 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, with native lake trout (*Salvelinus namaycush*) generally atop this pelagic food web. Other salmonids include landlocked Atlantic salmon (*Salmo salar*), steelhead or rainbow trout (*Oncorhynchus mykiss*), and brown trout (*Salmo trutta*). Other taxa are also represented by species such as 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*), 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, this species is now believed to be native (Waldman et al. 2006). However, due to a number of factors, the current sea lamprey population size is likely much larger than historically.

It is not only fish that make up Lake Champlain's food web, though. Mammals, reptiles, and amphibians are represented by such diverse species as river otters (*Lontra canadensis*), soft-shell turtles (*Apalone spinifer spinifer*), and mudpuppies (*Necturus maculosus maculosus*). The lake also supports both resident and migratory bird populations, with species of gulls, herons, terns, ducks, cormorants, and others breeding in the basin, in addition to songbirds and other more terrestrial species.

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). It was estimated in the late 1990's that visitors spent approximately $228 million on water-based recreation each year, with residents (within 35 miles of the lake) spending approximately $118 million (Buckley 1989b). 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 naturally distributed along the east coast of North America from eastern Labrador and the Gulf of St. Lawrence south to the Delaware River, and are also native to some freshwater lakes and ponds with coastal access (Smith 1985). Rainbow smelt have been stocked in inland lakes including the Great Lakes (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 (e.g. Lewis et al. 2004). To narrow the scope of this review slightly, the focus will be on the biology of landlocked rainbow smelt.

When it comes to inland rainbow smelt populations, both native and non-native populations generally are most successful in larger relatively deep lakes (Smith 1985, Buckley 1989a). Native inland populations are mainly found close to the Atlantic seaboard, but larger rivers such as the St. Lawrence facilitated natural establishment of populations further inland as well, and this is believed to be the case for Lake Champlain's rainbow smelt (Cobb 1905, Moore 1929). In Lake Champlain, though, it must also be noted that rainbow smelt were 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) (Ferguson 1965, Dryer 1966, Hart and Ferguson 1966, Wells 1968, Jude et al. 1978, Brandt et al. 1980, Argyle 1982, 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, though, generally occupy relatively warmer habitats in both freshwater and estuarine studies (Table 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). One can therefore see that interaction between adult and young fish may largely depend on spawning and hatching dates, and periods of stratification.

Table 1) Adult rainbow smelt habitat parameters in water bodies and the laboratory.

Waterbody	Lake zone(s) sampled	Vertical distribution preferences	Temperature preferences (C°)	Seasons / timeframe of study	Reference
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 lower 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 (<10-39 fathoms) Summer:18-90m (10-49 fathoms) Fall:<18-90m (<10-49 fathoms)		Spring, Summer, Fall (specific months not mentioned)	Dryer 1966
Laboratory			6-8°C		Ferguson 1965, Hart and Ferguson 1966
n/a		Entire water column during periods without thermal stratification			Nellbring 1989

Table 2) Young-of-the-year rainbow smelt habitat use in various water bodies.

Waterbody	Lake zone(s) sampled	Vertical distribution preferences	Temperature preferences (C°)	Seasons / timeframe of study	Reference
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-November: 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
Lake Superior: Apostle Islands	Water near bottom (bottom trawls)	Spring and summer: <18-53m (<10-29 fathoms) Fall: <18-70m (<10-39 fathoms)		Spring, Summer, Fall (specific months not mentioned)	Dryer 1966

Landlocked rainbow smelt populations, such as, coastal Atlantic populations, generally spawn in rivers and streams (Smith 1985, Buckley 1989a, Urho 1992). In coastal populations, adults typically begin spawning migrations before ice breakup, migrating upstream to beyond the head of the tide (Buckley 1989a, 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-like behavior, exceptions may not be unusual. Indeed, landlocked rainbow smelt have been found to 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 has not been found to differ significantly from estimates of stream survival, and mortality comes mainly from water level changes, grinding from surf, and trampling by humans and others (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, interestingly much 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).

As in many fish species, incubation times have been found to be largely dependant on water temperature with warmer waters facilitating earlier hatching

(Akielaszek et al. 1985, Buckley 1989a, Ayer et al. 2005). In general, hatching takes place 160 to 200 hours after fertilization at 13 to 20° C, with newly hatched larvae being around 5 mm long (Cooper 1978, Smith 1985). In marine systems, these larvae develop through summer months in estuaries and tidal regions, while in lakes initial development generally 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 but 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), presumably within this relatively warmer water compared to adults.

When the yolk sac and oil globule food sources are depleted, these larvae join their adult counterparts 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, Parker 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).

The existence of cannibalism behavior in this species is the topic of several studies, and serves to complicate population dynamics (LaBar 1993, He and LaBar 1994, Lantry and Stewart 2000, Parker Stetter et al. 2007). For example, large rainbow smelt year classes may 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 it should be remembered that this interaction is dependent on habitat overlap between these groups in addition to fish densities. 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).

In lake systems such as these, larger predators prey upon rainbow smelt as well. This is certainly the case, and the value of rainbow smelt as a forage fish for larger species has been a reason for its introduction into water bodies in which it is not native (e.g. Evans and Loftus 1987, Jones et al. 1994, Kirn and LaBar 1996, Johnson and Goettl 1999). Predators ranging from walleye to lake trout to common terns have been found to naturally rely either entirely or partly on a food base of rainbow smelt (Burness et al. 1994), but introductions of the species into other systems for this purpose has had mixed results (Johnson and Goettl 1999, Mercado-Silva et al. 2006).

The situation in Lake Champlain is believed to be the opposite, in that the native rainbow smelt population supports not only native species, but non-natives as well (Kirn and LaBar 1996). Native lake trout, Atlantic salmon, and walleye are arguably 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 (1929 ref., others?).

However, is this situation in Lake Champlain truly that different from other systems? How important are rainbow smelt in this system? It seems there are at least two characteristics of the Lake Champlain system that distinguish it from others. First is the fact that Lake Champlain is one of the few large lakes in which rainbow smelt are believed to be native, and of these lakes Champlain is the largest. Second, in the past there has been no other ecologically similar fish species present.

Thus, the ecological structure of this system has evolved with rainbow smelt as an integral component. As they have been quite abundant, rainbow smelt may not fit the traditional definition of a keystone species, but using this term may not be an exaggeration of their importance in the natural community of Lake Champlain. If this rainbow smelt population declines it is safe to say no single species will entirely fill its niche. Putting these pieces together leads us to question how rainbow smelt and alewife will coexist, and what future may result. The current situation also lends itself to the broader study of ecological interactions such as these.

Alewife

Alewife *(Alosa pseudoharengus*), similar to rainbow smelt, is an anadromous species native to coastal Atlantic waters. It is naturally 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, while others not (Smith 1985, Hendricks 2003). Given the context of this study, these freshwater alewife populations will be the focus of this review.

Much of the research conducted on freshwater alewife populations has been done in the Great Lakes region due to the presence of this species in all five lakes (Bozeman and Van Den Avyle 1989). Alewife had become established in these lakes by 1954, but did not become truly abundant until several years later (Miller 1957), and remained conspicuous by its absence from the sixth Laurentian lake, 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 cases and times has interestingly been regarded as both desirable and 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, while 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) have been cited as a cause of large scale winter die-offs (Lepak and Kraft 2007).

Young-of-the-year alewife in laboratory experiments prefer consistently warmer temperatures than their adult counterparts, with a maximum preference 9° C warmer (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). As with adult habitat choices, these relationships to temperature will likely influence the distribution and habitat preferences of young alewife. With this in mind, one may note that adult and young alewife preferences may overlap with those of rainbow smelt, although adult and young rainbow smelt seem to prefer cooler water than their alewife counterparts (Tables 3 & 4). Few laboratory preference studies have been conducted to determine exact values for rainbow smelt, though, and it seems highly likely that other biotic or abiotic factors may also influence final habitat choice of both species.

Table 3) Adult alewife habitat use in various environments.

Waterbody	Lake zone(s) sampled	Vertical distribution preferences	Temperature preferences (C°)	Seasons / timeframe of study	Reference
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 4) Young-of-the-year alewife habitat use in various environments.

Waterbody	Lake zone(s) sampled	Vertical distribution preferences	Temperature preferences (C°)	Seasons / timeframe of study	Reference
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 Michigan and Muskegon Lake			Alewife from Muskegon L. were larger and of better condition than those from L. Michigan. Muskegon was warmer and had higher productivity.	May-October	Hook et al. 2007
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:<25m November:30-40m	"Warmest water available"	August-November (2 year study, not all months sampled either year)	Urban and Brandt 1993

Again much like rainbow smelt, marine alewife move up coastal rivers to spawn. This behavior has been noted in some freshwater populations, but it appears spawning in shallow lake waters, river or stream mouths, and embayments may be the more common behavior in freshwater populations (Graham 1956, Klumb et al. 2003). After hatching, larvae most commonly prefer shallow depths in these near-shore habitats (Dunstall 1984). In Lake Ontario, studies have documented an apparent preference for depths of 0 to 3 m., with densities dropping significantly in deeper strata (O'Gorman 1983). Along the north shore of this lake, alewife are the dominant pelagic ichthyoplankton from July to September (Dunstall 1984).

Much like rainbow smelt, both adult and young alewife are pelagic feeders feeding on a variety of plankton and other items in the water column. When young, the dominant prey items are similar to rainbow smelt in that 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 planktivorous feeders (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. 2003). Young alewife have been found to particulate feed, but adults exhibit a variety of feeding methods. These 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 freshwater bodies 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. 2003).

In addition to invertebrate zooplankton, however, adult alewife seasonally prey on fish larvae in a number of systems. Great Lake salmonid species such as lake trout have been one species likely affected by this predation (e.g., Krueger et al. 1995), and other native pelagic species populations have declined dramatically 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 as well, and fish community impacts such as these have raised concerns regarding the integrity of sport fisheries, predatory fish populations, and native populations (Crowder 1980, Brooking et al. 1998, Marsden et al. 2005, Fielder et al. 2007, Madenjian et al. 2008). In regards to the efficiency of this predation, laboratory studies show that larvae size, as expected, likely influences whether alewife will efficiently capture these fish, and thus younger (smaller) larvae are more susceptible to predation (Brooking et al. 1998).

The predator-prey relationship in these waters is turned around, though, as larval salmonids, walleye, etc. become adults. The food base provided by alewife is significant in many systems, and has been the reason for this species' introduction in some regions (Hendricks 2003). In the Great Lakes, scientist's and the public's perception of alewife as beneficial forage fish, or not, changes over time and between individual people and 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 to the system in the form of Pacific salmon species, recognizing that these fish would likely feed heavily upon adult alewife (Smith 1968, Christie 1974, Rand and Stewart 1998a, b, Mills et al. 2003). This predation has taken place, and sport fisheries supported by the current Pacific salmon population have provided motivation for the continued stocking of these species, while restoration efforts for native salmonids continue (Krueger et al. 1995, Rand and Stewart 1998b, Madenjian et al. 2008).

The fact that larger salmonids have become predators of alewife may not be surprising, but this discussion of native and non-native salmonids, and restoration efforts is necessary in light of current evidence that alewife consumption by some salmonids may actually be detrimental (Fisher et al. 1996). More specifically, alewife 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. 2005c, 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. 2005a, Honeyfield et al. 2005, Fitzsimons et al. 2007).

So, what does this mean for alewife predators? There are two ways in which thiamine deficiency may impact these fish, 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. 2005a, Brown et al. 2005b, Honeyfield et al. 2005). This deficiency leads to “early mortality syndrome,” i.e., larvae exhibit impaired feeding ability, among other necessary activities (Honeyfield et al. 2005). Given this interaction may be occurring, it seems alewife consumption could be one additional factor inhibiting native salmonid reproduction in the Great Lakes (Mills et al. 2003, Brown et al. 2005b, Brown et al. 2005c, Fitzsimons et al. 2007). In addition to reproduction effects, 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 et al. 2002, Brown et al. 2005c).

Thus, current research concerning the potential detrimental effect of feeding on alewife has once again raised questions as to the desirability of alewife in various water bodies. So, what is the final verdict? This question is best answered on a case by case basis, but one can certainly make use of our current knowledge when making this judgment. Alewife have been detrimental to the maintenance of native and non-native fish populations due to their competitive and predatory behaviors, and more complex interactions concerning their role as prey (Madenjian et al. 2008). On the other hand, in this role as prey they have also facilitated a higher growth rate in their predators, and larger predator populations.

Such interactions have now come into play in Lake Champlain as well. Alewife were first found in the lake 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. In spring of 2007 adult alewife were seen congregating in shallow water near a river mouth, and many young fish were collected later in the year. The ecological similarity of alewife to rainbow smelt leads us to question how these species will coexist. What habitat are they utilizing in the lake? What changes occur seasonally? Such questions seem fundamental to our understanding of rainbow smelt and alewife here, but also facilitate the study of ecological interactions such as these in general.

Research Tools: Hydroacoustics

Numerous tools could be utilized to address these questions, and while some need little explanation, the use of hydroacoustics is complex topic worthy of review. 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 20th century, though, that technological advancements suggested underwater sound may be utilized as an information gathering tool (Simmonds and MacLennan 2005).

This 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 2005). 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 2005). Fisheries use inherently led to use in research endeavors, as the realm of aquatic research and management itself began to grow through the 20th century. 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 2005). 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 (e.g., Rudstam et al. 2002).

Arguably the main use of hydroacoustics outside commercial and recreational fishing has been the assessment of fish biomass in various bodies of water, often with a focus on specific species or trophic groups (Simmonds and MacLennan 2005). Such 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 prey-fish species and larger stocked predators (e.g., Fabrizio et al. 1997, Rudstam et al. 2003, Mason et al. 2005, Stockwell et al. 2007). Concerns regarding the validity of acoustic data relative to historic and current trawl data are justifiable, but research concerning this issue is on-going (Appenzeller and Leggett 1992, 1996, Fabrizio et al. 1997, Rudstam et al. 2002, Malinen and Tuomaala 2005, Stockwell et al. 2007).

One significant way in which survey accuracy can be improved is by continually increasing our knowledge of the species of interest. Hydroacoustics has proven to be a viable tool for these types of ecological 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 relicta*, an important ecological player in many glacial relict lakes (Gal et al. 1999a, Gal et al. 1999b, Gal et al. 2004, Boscarino et al. 2007), and freshwater insects (Kubecka et al. 2000). Using hydroacoustics along with other tools, researchers can determine distribution of fish and invertebrates, and abiotic and biotic factors related to this distribution (e.g., Gliwicz and Jachner 1992, Appenzeller and Leggett 1995, Pientka and Parrish 2002, Gal et al. 2004). Overlap of predators and potential prey can be observed directly, or predicted, and thus relationships and models have been developed to address general ecological questions and direct management objectives (Pientka and Parrish 2002, Parker Stetter et al. 2006, Parker Stetter et al. 2007).

Studies such as these have been conducted on Lake Champlain by academic and government scientists since the 1990's, with an interest in first developing the correct methods of data collection, then applying these methods for assessment and study of fish populations. With this history in the basin, and previous use studying rainbow smelt and alewife, hydroacoustic techniques are a viable tool in our current study. Experienced practitioners, collaboration, and previous studies and techniques, are facilitating the expansion of hydroacoustic technology to new regions and uses worldwide.

What is lacking?

As this discussion illustrates, much previous work has been done generally concerning abundance, species interaction, and habitat use, and also pertaining specifically to rainbow smelt and alewife. So, why do we need this project?

First, reviewing previous work concerning these species, and historic fisheries-specific research in general, there seems to be a lack of comprehensive, holistic investigations. In other words, data collection is often limited by numerous factors, and many studies are rather case and time specific. This is not inherently bad, but it causes gaps in our knowledge base; such is the case for questions concerning seasonal abundance and habitat use patterns of YOY rainbow smelt and alewife. There is a need for study of these organisms at early ages over an entire growing season instead of simple snapshot data points. Where are these fish during the day compared to night? Do proximate abiotic preferences change as these fish develop? What are these changes and when do they occur?

Second, despite volumes of work concerning these species, specifically in the Great Lakes, they have typically been studied under the single “forage fish” lens. In reality, rainbow smelt and alewife are two distinct species, with inherently different niches. As fundamental as that sounds, it is a fact commonly glossed over when the focus is on larger sport fisheries. Thus, there is need for increased understanding of how rainbow smelt and alewife coexist in physical and ecological space.

Finally, with such rapid rates of nonnative species spread worldwide, such research concerning interactions between native and nonnative species is increasingly necessary. How do species partition resources ranging from physical space to energy? In such situations, gaining a comprehensive understanding of habitat use patterns is a critical first step to understanding questions such as: what effect a nonnative species may have, why it may or may not be successful, whether control measures are necessary, what is at stake ecologically, what is at stake economically, or how can we prevent future spread.

In the case of the Lake Champlain system, we now have the opportunity to add to our ecological knowledge base concerning such nonnative species issues as well as rainbow smelt and alewife ecology. Of course years of research have already been conducted, but we are still far from obtaining perfect knowledge of these species, Lake Champlain, habitat use patterns, and ecology as a whole.

CHAPTER 3:

DIFFERENTIAL SURVIVAL OF EARLY- VERSUS LATE-HATCHED RAINBOW SMELT AND ALEWIFE

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Abstract: Survival of young-of-the-year (YOY) alewife (*Alosa pseudoharengus*) and rainbow smelt (*Osmerus mordax*) was studied in relation to individual hatch dates. We hypothesized earlier hatching fish would have higher probability of survival, based on the "growth-mortality" hypothesis. Hydroacoustics and trawls were used to observe and collect fish in Lake Champlain. Rainbow smelt YOY in Lake Champlain hatched from June through early July, and were most abundant in mid-July, compared to YOY alewife that hatched in July and were most abundant in August. Daily mortality rates were higher for earlier hatching fish (0.41 vs. <0.05 for 2007 rainbow smelt). Mortality rates for both species were higher in 2007 than 2008, but only rainbow smelt were significantly different (rainbow smelt: 0.15 vs. 0.03, alewife: 0.12 vs. 0.10). Selection for later hatching is counter to our hypothesis, and is likely driven by cannibalism. Thus, selection for late hatching, by cannibalism, and selection for early hatching, by growth-mortality factors, compete, with the balance between forces varying annually. Alewife, first found in Lake Champlain in 2003, may alter historic hatch-date selection forces by increasing summer YOY mortality rates. Events occurring in early life can be the primary forces driving fish population, and even community, dynamics.

Introduction

Early life histories are influential in animal population dynamics (Oli and Dobson 2003), and particularly in aquatic systems (Moksnes 2004) and fish (Miller et al. 1988). For fish, early-life components include parental investment in young, hatch timing, and larval and juvenile growth and mortality rates (Fuiman and Werner 2002). These components are influenced by characteristics of the physical environment such as temperature, which influence distribution, hatch timing, and growth rates (Fonseca and Cabral 2007) and ultimately survival by affecting predation levels (Bradbury et al. 2004) and overwinter mortality (Hook et al. 2007). Thus, knowledge of early-life processes is important to understanding and managing fish populations (Fuiman and Werner 2002).

Most larvae do not survive their first summer, with predation the primary source of mortality (Bailey and Houde 1989). Thus, in most systems, individual survival is a function of time spent vulnerable to predators (Cushing 1975). Growth is generally viewed as the ultimate mechanism to decrease the time of vulnerability, with larger (Miller et al. 1988), faster-growing (Takasuka et al. 2003), and faster-developing (Chambers and Leggett 1987) individuals more likely to survive (Hare and Cowen 1997). These selection pressures could favor early- or late-hatching individuals depending on temperature regimes and predators.

Hatch timing also influences vulnerability, by affecting both growth rate (Rice et al. 1987), and exposure to predators (Crowder 1980). Earlier spring-hatching individuals may grow slower because of cooler temperatures (Power and Attrill 2007), thus prolonging vulnerability. Vulnerability is also affected by the relation between hatch and stratification timing in lakes, especially when hypolimnetic predators are abundant (Parker Stetter et al. 2007). These predators will generally be separated from epilimnetic larvae after stratification, so hatching later shortens the time until separation. Intra-season selection pressure thus favors late hatching, but selection is complex on longer time scales.

Selection caused by overwinter mortality likely favors early hatching because early hatching allows more time for growth, and starvation becomes less likely with increasing size. Alewife (*Alosa pseudoharengus*) condition decreases substantially overwinter, and individuals likely must reach a minimum size by fall to survive (Flath and Diana 1985). Thus, for this species, early hatching and growth can facilitate both ultimate recruitment success (Hook et al. 2007) and intra-season survival.

Our study examines survival of young-of-the-year (YOY) alewife and rainbow smelt (*Osmerus mordax*) in relation to individual hatch dates. We hypothesized earlier hatching fish would have higher probability of survival because of the reasons above, and the cannibalistic nature of both species (Rhodes et al. 1974; He and LaBar 1994). Bi-monthly hydroacoustic surveys were conducted from spring through autumn to obtain abundance of YOY rainbow smelt and alewife. Acoustic targets were groundtruthed with Tucker and mid-water trawls and floating gillnets. We determined age and hatch dates using daily otolith rings. Rainbow smelt are presumed to be native to Lake Champlain (Moore 1929), but alewife were first observed in 2003 and the population expanded dramatically in 2007. Our objective was to determine hatch dates, growth rates, and abundance and mortality patterns of these species to infer preferential survival and recruitment related to hatch timing.

Methods

Lake Champlain is a large inland lake bordered by New York (USA), Vermont (USA), and Québec (Canada). To observe fish in a range of habitats, our primary survey site included several inshore-to-offshore transects, and one pelagic transect, in the main lake (Fig. 1). Location was chosen to be representative of the variety of habitat present in the main lake, and so the northern transect coincided with the Vermont Department of Fish and Wildlife's (VTFW) multi-year, lake-wide, acoustic dataset.

In 2008, we conducted two surveys in another section of the lake, Malletts Bay (Fig. 1). The bay is isolated from the rest of Lake Champlain by manmade causeways, and thus little movement of young fish in or out of the bay is likely. We conducted surveys over four parallel transects to estimate YOY rainbow smelt and alewife total population size.

In the main lake, data collection was from June to October of 2007 and 2008, with surveys conducted every two to three weeks aboard the VTFW *Doré*. Surveys were conducted during daytime and nighttime, with daytime surveys ending at least one hour prior to sunset and nighttime surveys starting at least one hour after sunset (Parker Stetter et al. 2006).

A BioSonics DT-X split beam echosounder (120 kHz, 7.5° half – power beam width, 0.4 m·s pulse length, 2 pulses·s^{-1}) (BioSonics Inc., Seattle, WA USA) was used to collect hydroacoustic data. The transducer was mounted on a tow body and towed at ~ 2 $m \cdot s^{-1}$, and the unit was calibrated at least once per month. Hydroacoustic data were recorded during the entire daytime and nighttime survey and also during dusk hours.

Fish were collected using 1m x 1m opening-closing (Tucker) and mid-water trawls. The Tucker trawl (1000 μm mesh) was used to target YOY fish at specific depths, whereas the mid-water trawl (12.7 mm mesh) targeted larger fish. Each tow was 15 minutes long, with 5 minutes for each net in the Tucker trawl. A depth sounder was attached to the headrope of each trawl to measure tow depth. Fish collected served to verify 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 YOY (thawed, in lab) fish.

All rainbow smelt and alewife YOY 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). This method was used because measurement in the field was not possible, and no difference in length measurements was observed using this freeze-thaw-measure process compared with unfrozen measurement. A length-age relationship was developed using these length data and daily ages (see below).

Timing of first-ring deposition on otoliths, and daily deposition thereafter, has been verified (Essig and Cole 1986; Sirois et al. 1998; Ganger 1999; Hook et al. 2007), so 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).

Hydroacoustic data were processed using Myriax Software's *Echoview* program (Myriax Software Pty Ltd., Hobart, TAS Australia) and standard operating procedures for Great Lakes hydroacoustics (Rudstam et al. 2009). Plots were created of target strengths at all depths within each region, and frequency distribution data were exported for each date. Using these data and fish identification data from physical sampling at known depths, target strength ranges for YOY and adult rainbow smelt and alewife, in decibels (dB), were identified and we confirmed yearling-and-older (YAO) rainbow smelt TS range was within the -60 to -35 dB range in previous studies (Parker Stetter et al. 2006). Our analysis allowed the calculation of YOY rainbow smelt, YOY alewife, and YAO rainbow smelt density with high resolution. Total abundance in our survey region was obtained by summing abundance values from each analysis region and cell.

Mortality rates were calculated for YOY groups hatching during specific intervals. For rainbow smelt, the intervals (n=7) were: before June, first, second, third, and fourth week of June, first week of July, and after 7 July. For alewife, YOY hatching intervals (n=8) were: before the last week of June, last week of June, first, second, third, and fourth week of July, first week of August, and after 7 August. The abundance of YOY hatching during each interval was calculated through the season using densities from acoustics and hatch dates from YOY otoliths. To calculate mortality rates, the natural log of abundance values was taken, and a linear regression fit to the declining abundance values of each cohort through the season using least square regression.

Multivariate linear model regression (R Development Core Team 2010), was used to test for significance of changes in mortality through the season.

Results

Rainbow smelt YOY in Lake Champlain hatched from June through early July 2007 and 2008, reaching peak numbers in mid-July, compared to YOY alewife that hatched in July with numbers peaking in August. Mortality was higher for earlier hatching fish. Mortality rates for both species were higher in 2007 than 2008. YOY rainbow smelt are more abundant than YOY alewife at the main lake study site, although YOY alewife grew faster and reached a similar mean size before October.

We determined hatch dates for YOY rainbow smelt collected from 9 to 110 days post-hatch (n=614 fish) and alewife collected 15 to 100 days after hatching (n=234 fish). Generally, YOY rainbow smelt daily rings were more distinct than alewife, but for both species precision decreased with age. In both 2007 and 2008 rainbow smelt in the main lake section of Lake Champlain began hatching in late May, and hatching continued through July (Fig. 2). The earliest fish hatched on May 23 in 2008, and the latest hatched in August (August 15, 2007). The rainbow smelt population had a median hatch date of June 18 in 2007 and June 12 in 2008. In contrast, alewife in the main lake hatched from late June into August in 2007 and 2008 (Fig. 2). The earliest hatch recorded was June 15, 2008 (n=1 fish) and the latest August 11, 2007 (n=2 fish), with a population median hatch date of July 19 in 2007 and July 7 in 2008. Malletts Bay alewife hatched earlier in 2008 compared to main lake populations, but rainbow smelt did not. Rainbow smelt hatched from May 30 to June 22, and alewife from June 1 to July 7. This represents a 15-d difference in median hatch date (rainbow smelt=June 10, alewife=June 25) compared to main lake fish whose medians differed by 25 days.

In the main lake, abundance of YOY rainbow smelt in our survey region was similar in 2007 and 2008. However, in our samples, there were more alewife in August 2008 than in August 2007. Until 2007, there were few adult alewife, and no YOY fish collected from Lake Champlain. Rainbow smelt YOY abundance peaked in late July in 2007 and 2008 (Fig. 3). Alewife YOY abundance increased most rapidly during the same period YOY rainbow smelt abundance declined most rapidly.

We compared hatch dates of fish collected through the season. Earlier-hatching alewife and rainbow smelt were not collected later in the 2007 growing season (Fig. 4). In 2008, collections contained the full range of hatch dates throughout the season. Mortality was higher for earlier hatching rainbow smelt in 2007 (Fig. 5). Early hatching rainbow smelt in 2007 had a mortality rate of 0.41, compared to <0.05 for late hatching individuals. The mean rainbow smelt mortality rate in 2007 was 0.15, compared to 0.03 in 2008. In 2007 alewife had a mean rate of 0.12, and in 2008, 0.10.

Discussion

Survival of native rainbow smelt YOY and nonnative alewife YOY in Lake Champlain differs in relation to hatch timing and cannibalism rate. Later-hatching young of both species may survive better than earlier-hatched individuals in some years. Selection for later hatching is counter to our hypothesis that early hatched fish would survive better. Nonnative alewife in the main lake of Lake Champlain hatched and reached highest abundance later than native rainbow smelt, and hatching was earlier in a portion of the lake that warms faster.

The changes in YOY abundance in our main lake region through the season (Fig. 3) could be caused by several factors. Sampling bias is likely present, but should affect physical collections more than acoustic data. In this study, trawl samples were only used to identify targets, not estimate abundance. Trawl catches and acoustic fish density were correlated, indicating that acoustic targets represented trawled fish (Rudstam et al. 2009).

Fish collected via trawls were used to determine hatch dates, so it is possible that collection bias influences hatch data. However, YOY fish were consistently caught in both Tucker and mid-water trawls, and hatch date analyses use fish from both gears. So, it is unlikely that YOY at either end of the size spectrum were ignored, although mid-sized individuals could have been under-sampled on certain dates. Movement of fish out of the study area is possible, but summertime hydrodynamics of Lake Champlain keep the main lake horizontally well-mixed (Manley et al. 1999), and rainbow smelt and alewife are not known to congregate preferentially at any main lake location. Thus, while bias exists, it is most probable that data reflect the balance between hatching and mortality.

Mortality is the likely cause for decreased abundance of both species, and predation is the likely source (Bailey and Houde 1989). Our hypothesis that early-hatching fish would have lower mortality rates was not generally supported. Lack of selection for early hatching seemingly contradicts suggestions that larger individuals survive better (Miller et al. 1988), because we would expect early-hatched individuals to be larger and more fit (Hook et al. 2007). However, early-hatched individuals are slower growing, thereby providing support for two of three components of the "growth-mortality" hypothesis (Hare and Cowen 1997). Overwinter mortality likely selects for early hatching because of Lake Champlain's temperature trends (Flath and Diana 1985). Also, rainbow smelt winter die-offs may have occurred historically, and a large alewife die-off occurred in 2008. Thus, competing selection forces are at work in Lake Champlain.

Cannibalism is likely the ultimate driver interacting with these competing selection forces (Parker Stetter et al. 2007). Both rainbow smelt and alewife particulate feed and are known to be cannibalistic (Rhodes et al. 1974; He and LaBar 1994), with adult rainbow smelt in Lake Champlain probably the primary predator of YOY rainbow smelt from spring through autumn (Parker Stetter et al. 2007). Given adult rainbow smelt behavior in other systems (Crowder 1980), predation on YOY alewife seems possible . Adult alewife feeding behavior in Lake Champlain is unstudied, but in other systems they are cannibalistic and consume larvae of other species (Rhodes et al. 1974; Crowder 1980). Rainbow smelt cannibalism rate in Lake Champlain is a function of adult and YOY abundance and vertical distribution (Parker Stetter et al. 2007). Thus, cannibalism rates are highest in spring when the lake is not thermally stratified, and autumn when YOY begin to integrate with the adult population. This means changes in adult population size will differentially affect YOY mortality rate depending on hatch date, potentially conferring an advantage to late-hatched fish in years with large adult populations. The rainbow smelt adult population in Lake Champlain was larger in 2007 than 2008 (Vermont Fish and Wildlife 2008), likely causing higher spring cannibalism rates and the observed lower survival of early-hatching individuals (Fig. 5).

Selection for late hatching, by cannibalism, and selection for early hatching, by growth-mortality factors, compete and could theoretically lead to dominance of one. For native rainbow smelt, selection has likely already reduced the hatch-date range to its current length. However, this range of over one month is large for rainbow smelt and alewife from a given system (e.g., Bradbury et al. 2004; Hook et al. 2007). A large range is most plausible only in light of cannibalism, which confounds, and in some years dominates, traditional growth-mortality selection forces. 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 meters) preferred by native rainbow smelt (Plosila 1984).

In Lake Champlain, alewife may alter historic selection forces. In the Great Lakes, the effect of alewife has likely been via 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 after stratification, but summer-mortality could increase if adult alewife occupy the epilimnion. Increased summer mortality could, in tern, tip the selection balance to a more consistent preference for early hatching.

Events occurring in early life can be the primary forces driving fish population, and even community, dynamics (Fuiman and Werner 2002). Thus, understanding forces affecting larval and juvenile fish increases the efficacy of management and conservation.

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References

Bailey, K.M., and Houde, E.D. 1989. Predation on eggs and larvae of marine fishes and the recruitment problem. Advances in Marine Biology **25**: 1-83.

Bradbury, I.R., Campana, S.E., Bentzen, P., and Snelgrove, P.V.R. 2004. Synchronized hatch and its ecological significance in rainbow smelt *Osmerus mordax* in St. Mary's Bay, Newfoundland. Limnology and Oceanography **49**(6): 2310-2315.

Chambers, R.C., and Leggett, W.C. 1987. Size and age at metamorphosis in marine fishes: an analysis of laboratory-reared winter flounder (*Pseudopleutonectes americanus*) with a review of variation in other species Canadian Journal of Fisheries and Aquatic Sciences **44**(11): 1936-1947.

Crowder, L.B. 1980. Alewife, smelt and native fishes in Lake Michigan: competition or predation? Environ. Biol. Fishes **5**: 225-233.

Cushing, D.H. 1975. Marine ecology and fisheries. Cambridge University Press, Cambridge; New York.

Essig, R.J., and Cole, C.F. 1986. Methods of estimating larval fish mortality from daily increments in otoliths. Trans. Am. Fish. Soc. **115**: 34-40.

Flath, L.E., and Diana, J.S. 1985. Seasonal energy dynamics of the alewife in southeastern Lake Michigan. Trans. Am. Fish. Soc. **114**(3): 328-337.

Fonseca, V.F., and Cabral, H.N. 2007. Are fish early growth and condition patterns related to life-history strategies? Rev. Fish. Biol. Fish. **17**(4): 545-564. 10.1007/s11160-007-9054-x.

Fuiman, L.A., and Werner, R.G. 2002. Fishery science : the unique contributions of early life stages. Blackwell Science, Malden, MA.

Ganger, M.T. 1999. The spatial and temporal distribution of young-of-the-year *Osmerus mordax* in the Great Bay Estuary. Environ. Biol. Fishes **54**(3): 253-261.

Hare, J.A., and Cowen, R.K. 1997. Size, growth, development, and survival of the planktonic larvae of *Pomatomus saltatrix* (Pisces: Pomatomidae). Ecology **78**(8): 2415-2431.

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.

Hook, T.O., Rutherford, E.S., Mason, D.M., and Carter, G.S. 2007. Hatch dates, growth, survival, and overwinter mortality of age-0 alewives in Lake Michigan: implications for habitat-specific recruitment success. Trans. Am. Fish. Soc. **136**(5): 1298-1312.

Lochet, A., Jatteau, P., Tomas, J., and Rochard, E. 2008. Retrospective approach to investigating the early life history of a diadromous fish: allis shad *Alosa alosa* (L.) in the Gironde-Garonne-Dordogne watershed. J. Fish Biol. **72**(4): 946-960. 10.1111/j.1095-8649.2007.01776.x.

Madenjian, C.P., 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 American Journal of Fisheries Management **28**(1): 263-282.

Manley, T.O., Hunkins, K., Saylor, J., Miller, G.S., and Manley, P. 1999. Aspects of summertime and wintertime hydrodynamics of Lake Champlain. *In* Lake Champlain in transition: from research toward restoration. *Edited by* T.O. Manley and P. Manley. American Geophysical Union, Washington, DC. pp. 67-116.

Miller, T.J., Crowder, L.B., Rice, J.A., and Marschall, E.A. 1988. Larval size and recruitment mechanisms in fishes: toward a conceptual framework. Canadian Journal of Fisheries and Aquatic Sciences **45**(9): 1657-1670.

Moksnes, P.-O. 2004. Self-regulating mechanisms in cannibalistic populations of juvenile shore crabs *Carcinus maenas*. Ecology **85**(5): 1343-1354. doi:10.1890/02-0750.

Moore, E. 1929. A biological survey of the Champlain watershed, New York State Conservation Department, Albany, NY.

Oli, M.K., and Dobson, F.S. 2003. The relative importance of life-history variables to population growth rate in mammals: Cole's prediction revisited. Am. Nat. **161**(3): 422-440.

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**: 176-185.

Parker Stetter, S.L., Stritzel Thomson, J.L., 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.

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**(1): 109-111.

Power, M., and Attrill, M.J. 2007. Temperature-dependent temporal variation in the size and growth of Thames estuary smelt *Osmerus eperlanus*. Mar. Ecol.-Prog. Ser. **330**: 213-222.

R Development Core Team. 2010. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rhodes, R.J., Webb, D.A., and McComish, T.S. 1974. Cannibalism by the adult alewife (*Alosa pseudoharengus*) in southern Lake Michigan. Proceedings of the Conference on Great Lakes Research **17**: 593-595.

Rice, J.A., Crowder, L.B., and Holey, M.E. 1987. Exploration of mechanisms regulating larval survival in Lake Michigan bloater: a recruitment analysis based on characteristics of individual larvae. Trans. Am. Fish. Soc. **116**(5): 703-718. doi:10.1577/1548-8659(1987)116<703:EOMRLS>2.0.CO;2.

Rudstam, L.G., Parker Stetter, S.L., Sullivan, P.J., and Warner, D.M. 2009. Towards a standard operating procedure for fisheries acoustic surveys in the Laurentian Great Lakes, North America. Ices Journal of Marine Science **66**.

Sirois, P., Lecomte, F., and Dodson, J.J. 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**(12): 2662-2671.

Takasuka, A., Aoki, I., and Mitani, I. 2003. Evidence of growth-selective predation on larval Japanese anchovy *Engraulis japonicus* in Sagami Bay. Mar. Ecol.-Prog. Ser. **252**: 223-238.

Tables

Table 1. Hydroacoustic settings used in data collection and processing

Frequency (kHz)	**Beam width (◦)**	**Min. collect. thresh. (dB)**	**Transmitted pulse length (m·s)**	**Pulse rate (pulse / s)**	**Depth layer thickness (m)**	***In situ* TS settings**	**Noise at 1 m (S_v, dB)**
120 (BioSonics DtX)	7.5	-100	0.4	2	1	6 dB, 0.6	-115

Figure captions

Fig. 1.-- Lake Champlain (right panel), located between New York, Vermont, and Quebec. Location of surveys in the main lake (left) and Malletts Bay (right) of Lake Champlain. Contour lines represent 5-m depth intervals.

Fig. 2.-- Range of hatch dates for YOY rainbow smelt and alewife collected in 2007 (a) and 2008 (b). No fish were collected in Malletts Bay in 2007.

Fig. 3.-- YOY rainbow smelt and alewife abundance at the main lake survey location.

Fig. 4.-- Hatch dates of individual rainbow smelt (a, c) and alewife (b, d) caught through 2007 (a,b) and 2008 (c, d).

Fig. 5 -- Mortality rates of YOY rainbow smelt and alewife in the main lake of lake Champlain in 2007 and 2008.

Figures

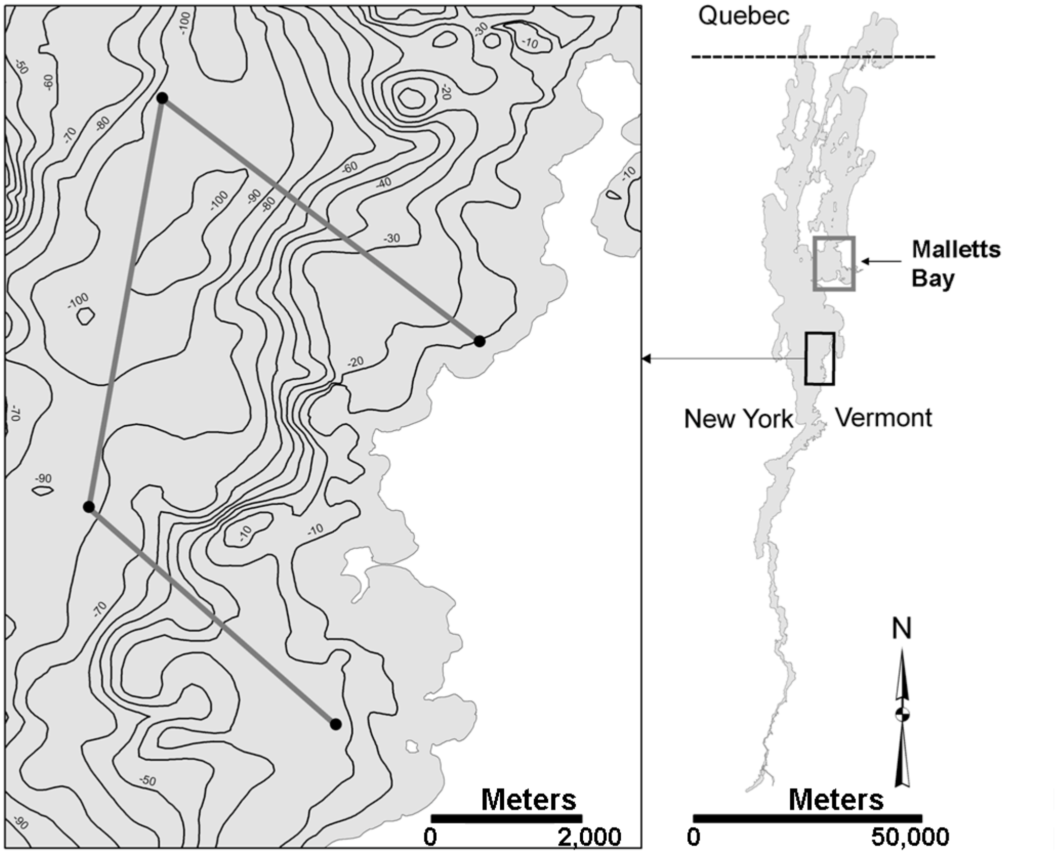


Fig. 1

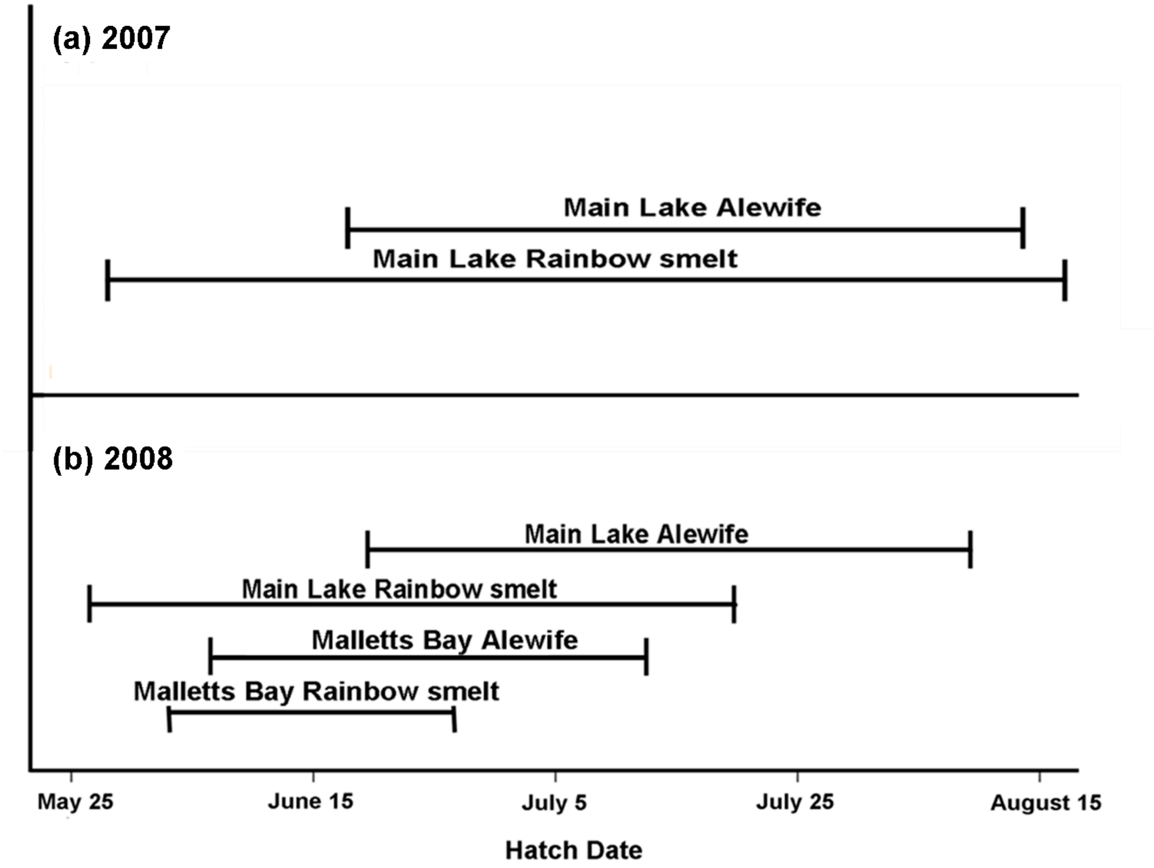

(a) 2007
Main Lake Alewife
Main Lake Rainbow smelt
(b) 2008
Main Lake Alewife
Main Lake Rainbow smelt
Malletts Bay Alewife
Malletts Bay Rainbow smelt
May 25
June 15
July 5
July 25
August 15
Hatch Date

Fig. 2

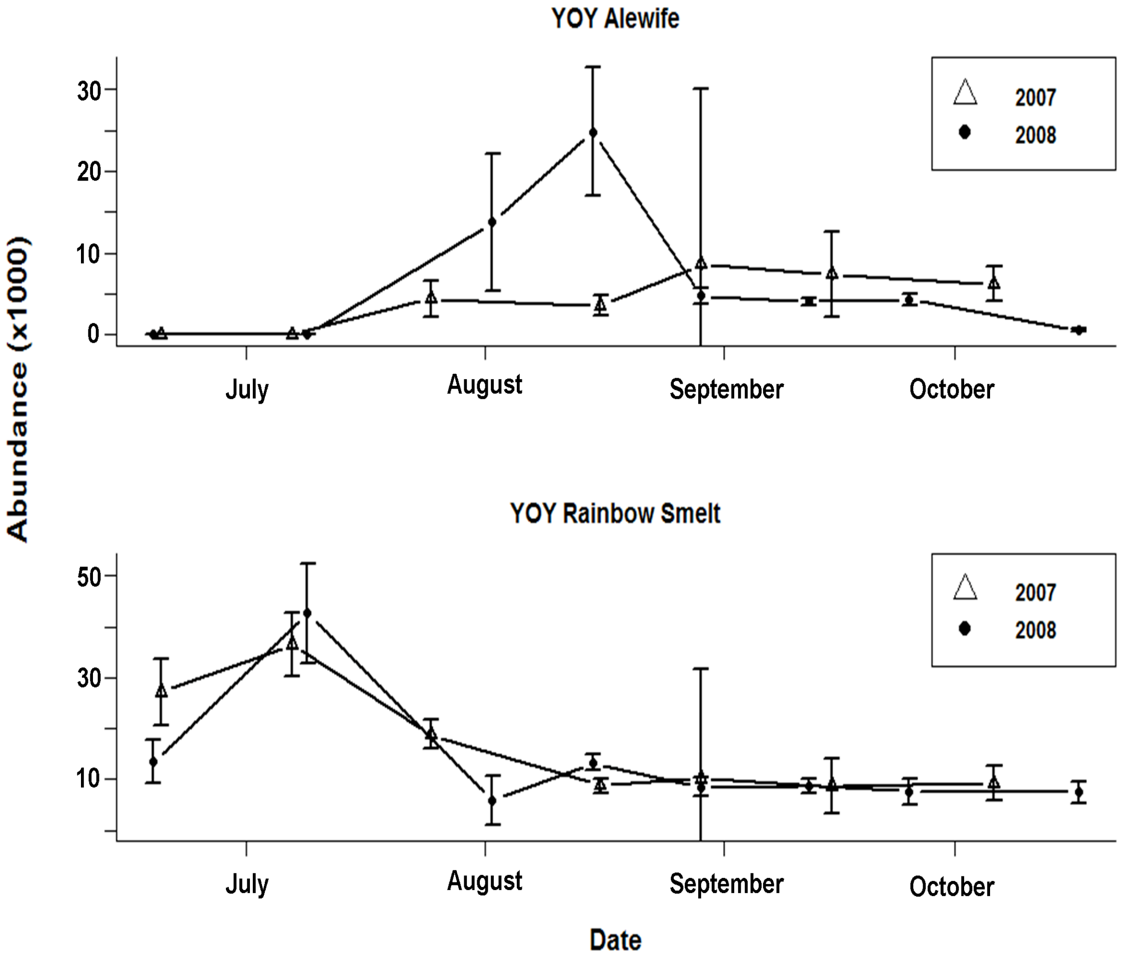
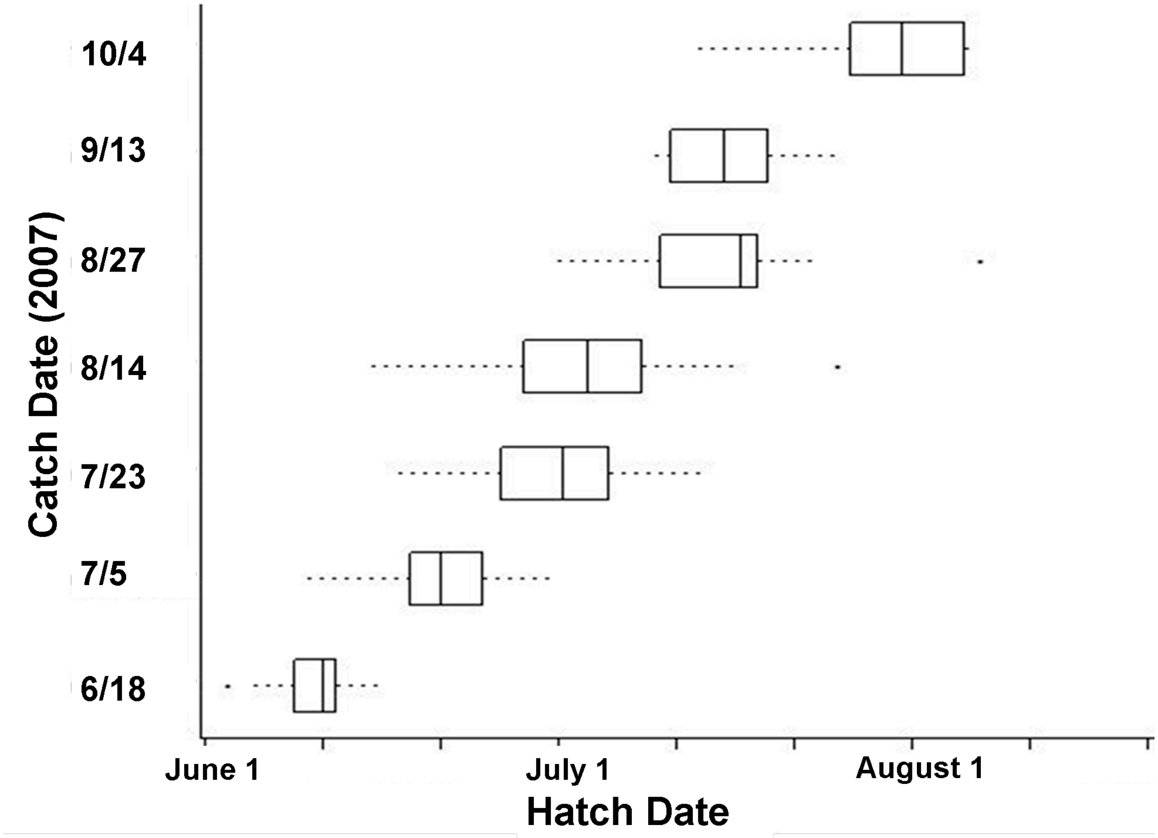
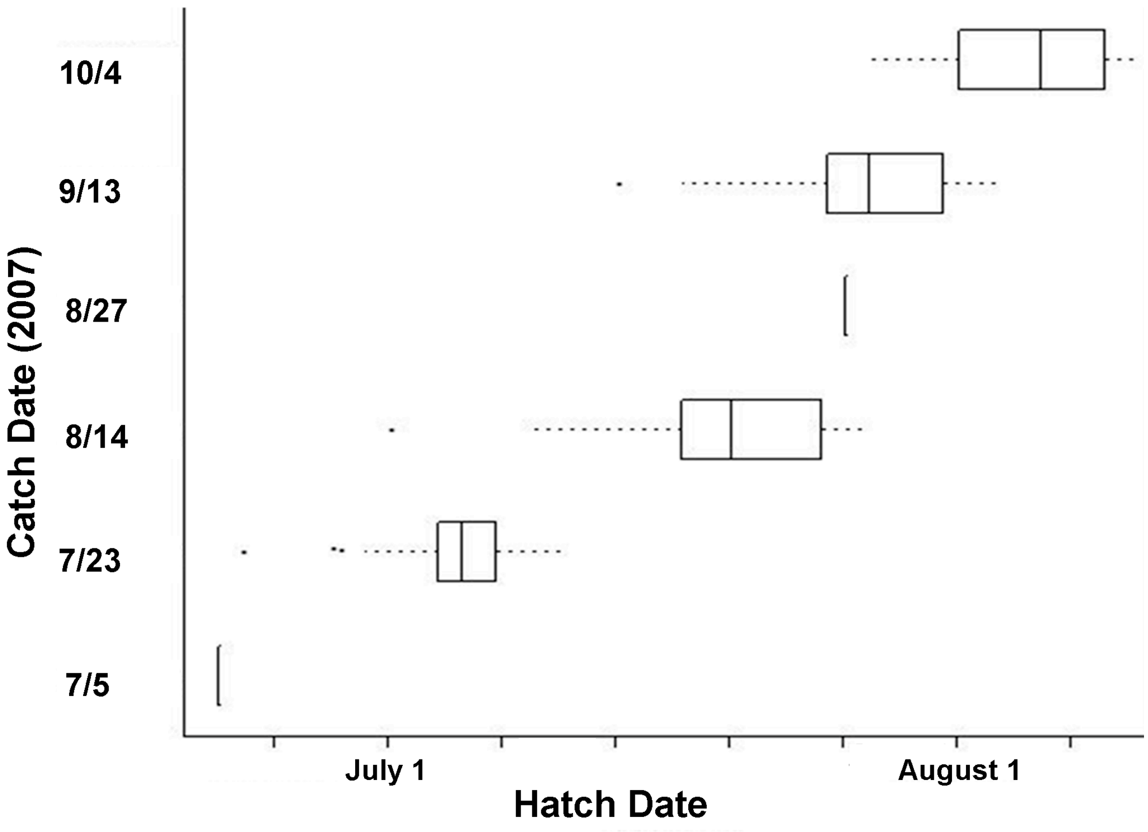

YOY Alewife
Abundance (x1000)
30
20
10
0
July
August
September
October
2007
2008
YOY Rainbow Smelt
50
30
10
July
August
September
October
2007
2008
Date

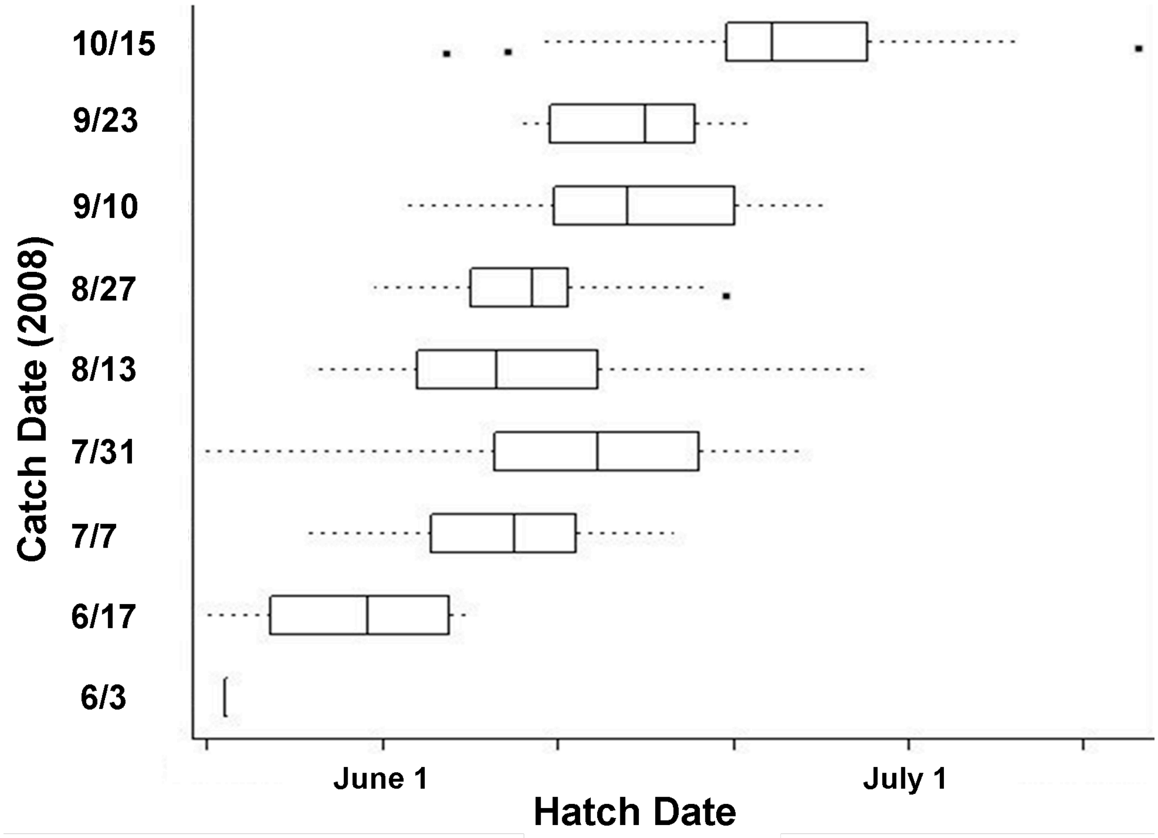
Fig. 3


Catch Date (2007)
10/4
9/13
8/27
8/14
7/23
7/5
6/18
June 1
July 1
August 1
Hatch Date

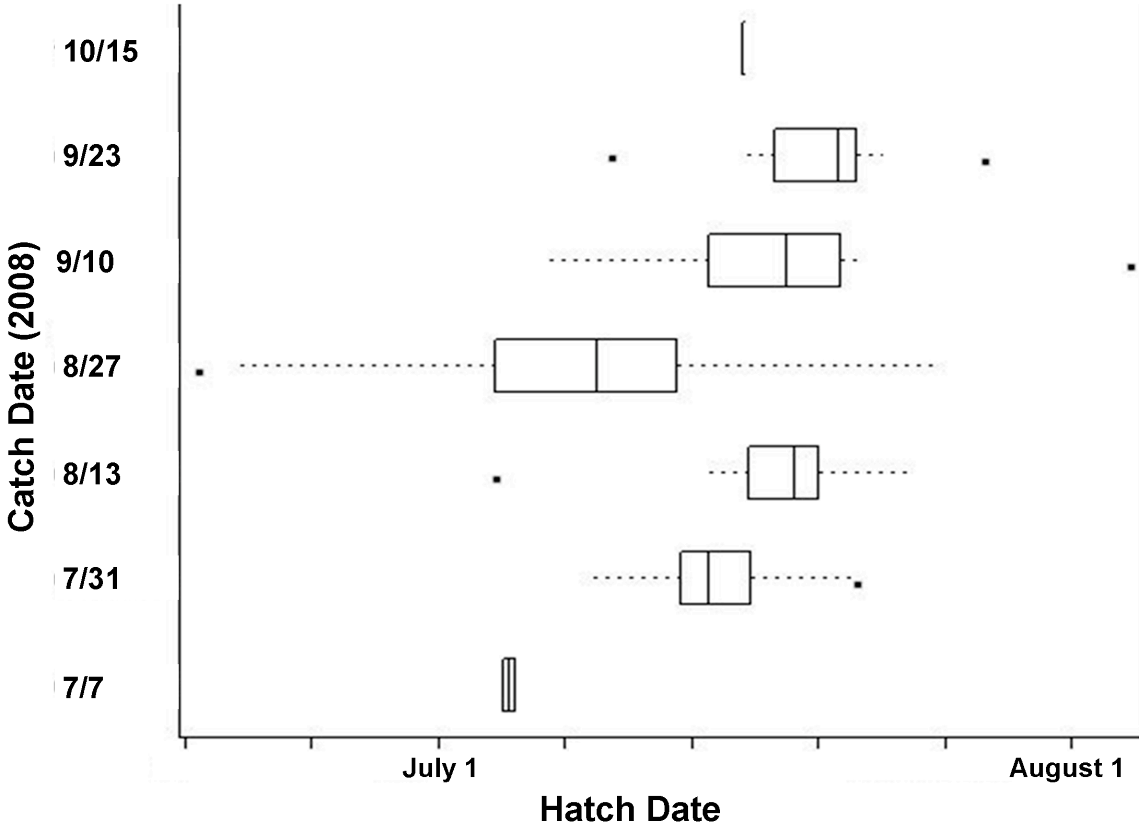
(a)


Catch Date (2007)
10/4
9/13
8/27
8/14
7/23
7/5
July 1
August 1
Hatch Date

(b)


10/15
9/23
9/10
8/27
8/13
7/31
7/7
6/17
6/3
Catch Date (2008)
June 1
July 1
Hatch Date

(c)


Catch Date (2008)
10/15
9/23
9/10
8/27
8/13
7/31
7/7
July 1
August 1
Hatch Date

(d)

Fig. 4

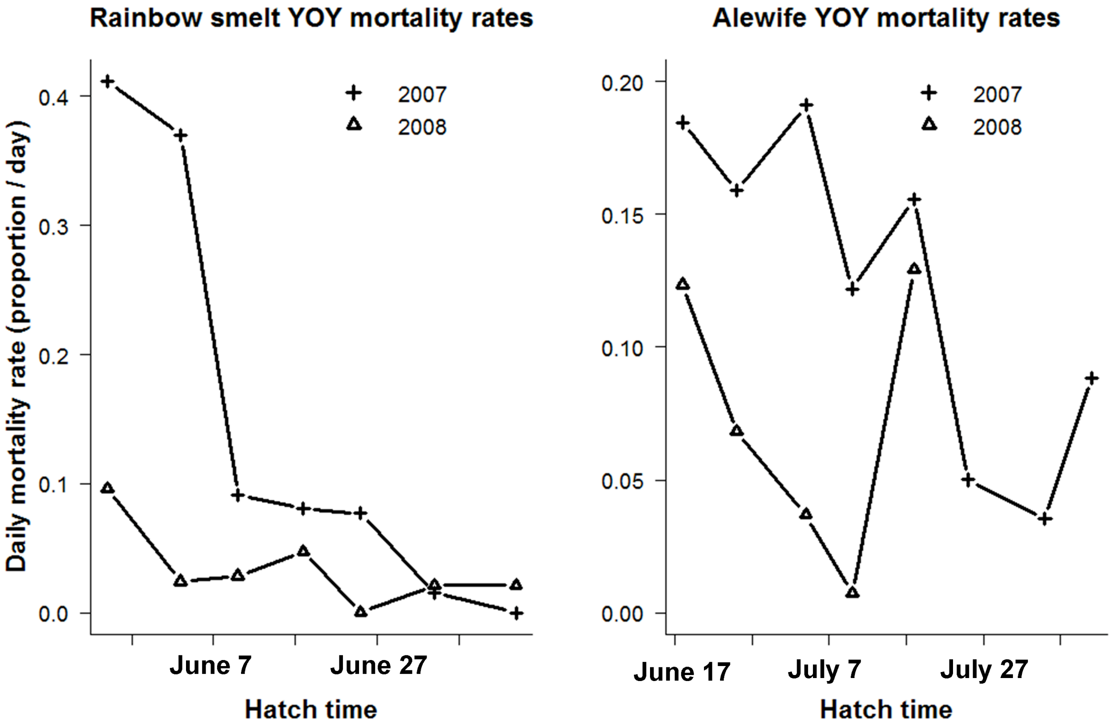

Rainbow smelt YOY mortality rates
Daily mortality rate (proportion / day)
0.4
0.3
0.2
0.1
0.0
+ 2007
Δ 2008
June 7
June 27
Hatch time
Alewife YOY mortality rates
0.20
0.15
0.10
0.05
0.00
+ 2007
Δ 2008
June 17
July 7
July 27
Hatch time

Fig. 5

CHAPTER 4:

RAINBOW SMELT AND ALEWIFE DISTRIBUTION RELATED TO TEMPERATURE AND LIGHT GRADIENTS IN LAKE CHAMPLAIN

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Abstract: Adult, and particularly age-0, native rainbow smelt (*Osmerus mordax*) and nonnative alewife (*Alosa pseudoharengus*) vertical distribution was studied in relation to physical habitat gradients in a large north-temperate lake (Lake Champlain). We used hydroacoustics, trawls, and gill nets to document vertical fish distribution, and recorded physical environmental data during 16 daytime-nighttime surveys over two years. Generalized additive mixed effects models and information criterion were used to describe distribution and determine factors related to vertical distribution. Adult rainbow smelt and age-0 rainbow smelt and alewife distributions were related to temperature, temperature gradient, and light. Adult alewife were 5-30 m shallower and age-0 alewife were 2-15 m shallower than their rainbow smelt counterparts. Adult rainbow smelt distribution overlapped with age-0 rainbow smelt and alewife near the thermocline (10-25 m), but adult alewife were shallower (0-6 m). Adult rainbow smelt were in water <10-12 °C, whereas age-0 rainbow smelt were in 10-20 °C, and adult and age-0 alewife were in 15-22 °C. If alewife remain abundant, differences in distributions of rainbow smelt and alewife may alter population dynamics and the trophic structure of the lake.

Running Head: Distribution of rainbow smelt and alewife

Nonnative species are powerful drivers of ecological change, and can complicate resource management, inflict economic costs, and reduce biodiversity (Wilcove et al. 1998; Sala et al. 2000; Perrings 2002; Pimentel et al. 2005; Hoagland and Jin 2006). Study of organism distribution is fundamental to ecology, and thus necessary to understand effects of nonnative species (Hutchinson 1953; Hardiman et al. 2004). Distribution can be a function of many factors, but often physical environmental gradients are influential (Ricklefs 2001).

Factors affecting or related to aquatic organism distribution have been studied for many years. Plankton distribution can be related to variables such as temperature, pH, light, and nutrient concentration (Reynolds 2006; Johnson et al. 2007). In the Great Lakes, vertical distribution of the invertebrate *Mysis diluviana* is related to light, temperature, and predator behavior (Gal et al. 2004; Boscarino et al. 2007). Early research found gradients of both dissolved oxygen (DO) and temperature influenced many species (Juday and Wagner 1908). Despite strong preferences for specific abiotic conditions however, fish occupy different habitat than would be dictated by abiotic preferences alone (Rudstam and Magnuson 1985). Instead, biotic characteristics such as predator or prey presence also influence fish distribution, which hints at ties between distributions and food webs.

In the Laurentian Great Lakes, alewife (*Alosa pseudoharengus*) were first noted in 1873, and likely entered Lake Ontario via canals or accidental introduction, whereas rainbow smelt (*Osmerus mordax*) were deliberately released in Crystal Lake Michigan in 1912, and subsequently spread throughout the Great Lakes (Mills et al. 1993). In Lake

Champlain, a large inland lake on the border of New York (USA),Vermont (USA), and Québec (Canada), rainbow smelt are presumed to be native (Moore 1929; Halnon 1963; Smith 1985), and the lake supports "giant" and smaller sized individuals. Alewife were first found in Lake Champlain in 2003, but their population did not expand rapidly until 2007. Rainbow smelt historically constituted up to 99% of pelagic trawl catches (Pientka and Parrish 2002), and were the dominant species occupying the central trophic level now shared with alewife.

Rainbow smelt and alewife are native only in Atlantic coastal systems, and their ecological role in freshwater systems is often viewed through the lens of their role as prey for larger sport-fish populations and avian predators (Stewart et al. 1981; Burness et al. 1994). This view may gloss over the uniqueness of these two cannibalistic species, especially in systems such as Lake Champlain, which is transitioning from one to two species at the mid-trophic level. Thus, there is need to understand more clearly the interaction of these two species in freshwater before making connections to other trophic levels. Specifically, distribution patterns of adult alewife and age-0 rainbow smelt and alewife are poorly understood, as are factors related to their distributions.

In 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 (Brandt et al. 1980; Heist and Swenson 1983). Age-0 fish, though, generally occupy warmer habitats (Dunstall 1984; Urban and Brandt 1993). In laboratory studies, adult alewife prefer temperatures from 16 to 21 °C from spring through fall, with maximum temperature preference occurring at the time of spring spawning, while during winter months adults prefer ~11 °C (Otto et al. 1976). Extreme cold temperatures can cause large-scale alewife die-offs (Lepak and Kraft 2007). In summer months, age-0 alewife preferred 25° C in the lab, and only decreased to 19 to 21° C by early winter (Otto et al. 1976). In lakes, though, alewife distribution patterns differ more than rainbow smelt, with fish in deep, colder water in some systems and warmer, surface water in others (Brandt 1980; Urban and Brandt 1993).

Light may also relate to distribution patterns. Eyes of clupeids and osmerids generally have peak spectral sensitivities around 500 – 520 nm (Bridges and Delisle 1974; Flamarique and Hawryshyn 1998), although some uncertainty remains regarding cone vs. rod spectral responses (Reckel et al. 2003). Both alewife and rainbow smelt are opportunistic visual feeders (Foltz and Norden 1977; Janssen 1978) and feeding rates are a function of light (Horppila et al. 2004). Thus, light could interact with temperature to affect distribution.

The goal of our study was to better understand the distribution of rainbow smelt and alewife in Lake Champlain. The specific objectives were to: (1) quantify rainbow smelt and alewife vertical distribution patterns, (2) identify physical environmental gradients that are related to distribution patterns, and (3) model distribution as a function of these gradients. We hypothesized that (1) young rainbow smelt and alewife adults and young would be in the same warm and shallow part of the water column, with adult rainbow smelt deeper, (2) distribution would be closely related to temperature, and (3) both rainbow smelt and alewife would undergo diel vertical migration. Results from this study will facilitate clearer predictions about population dynamics, and subsequent community and ecosystem inferences.

Materials and methods

To observe fish in a range of habitats, our primary survey site included several inshore-to-offshore transects, and one pelagic transect, in the Main Lake of Lake Champlain (Figure 1). The northern transect coincided with one of the Vermont Department of Fish and Wildlife's (VTFW) multi-year, lake-wide survey transects. Data collection ran from June to October of 2007 and 2008, with surveys (n=16) conducted every two to three weeks aboard the VTFW *Doré*. Surveys were conducted during daytime and nighttime, with daytime surveys ending at least one hour prior to sunset and nighttime surveys starting at least one hour after sunset (Parker Stetter et al. 2006).

To document fish distributions, we used both physical sampling and hydroacoustic techniques. A BioSonics DT-X split beam echosounder (120 kHz, 7.5° half – power beam width, 0.4 m·s pulse length, 2 pings/s) (BioSonics Inc., Seattle, WA USA) was used to collect hydroacoustic data. The transducer was mounted on a tow body and towed at ~2 m/s. The unit was calibrated at least once per month. Hydroacoustic data were recorded over the entire daytime and nighttime survey and also during dusk hours.

Fish were collected using 1m x 1m opening-closing (Tucker), and mid-water trawls. The Tucker trawl (1000 µm mesh) was used to target age-0 fish at specific depths, while the mid-water trawl (12.7 mm mesh) targeted larger fish. A depth sounder was attached to the headrope of each trawl to measure tow depth. Fish collected served to verify the identity of targets recorded acoustically, and samples were frozen in the field for preservation and workup in the lab. Lengths were measured for both adult (fresh, in field) and age-0 fish (thawed, in lab). No difference in length measurements was observed compared with unfrozen measurement using this freeze-thaw-measure process for YOY.

We also set two floating gill nets each nighttime during 2008 to sample the upper epilimnion. Gill nets were 6 m deep x 21 m long, with seven mesh sizes (6.25, 8, 10, 12, 15, 18, and 25 mm). Mesh sizes changed in the horizontal direction, with each panel 6 m deep x 3 m wide. Gill nets were suspended from the surface adjacent to our northern transect (Figure 1) with one closer to shore in 7-8 m of water and the second farther from shore in 30-32 m of water. Nets were set at sunset and pulled ~5 h later after the completion of our nighttime survey. We noted mesh size and vertical location of each fish caught in each net.

We collected abiotic environmental data during every survey as well. Temperature, DO, pH, and specific conductivity of water at 0.5-m depth intervals were measured at least three times per survey using a SeaBird SBE 19*plus* SEACAT Profiler (Sea-Bird Electronics Inc., Bellevue, WA USA). Continuous surface-water temperature was recorded using a logger (HOBO Water Temp Pro, Onset Computer Corporation, Pocasset, MA USA) attached to the acoustic towbody at a depth of 1 m.

Light intensity was recorded also at 0.5-m depth intervals, and continuously at the surface, using a high-sensitivity light meter recording wavelengths 460 to 580 nm (Mk9 archival tag, Wildlife Computers, Redmond, WA USA). We calculated extinction coefficients from these data. The Mk9 was calibrated to a Gamma Scientific light source, which has an accuracy of ±2% of the International Light calibration transfer standards (±2% for National Institute of Standards and Technology transfer). We recorded light in the range of 460 to 580 nm for several reasons. First, clupeids have a peak in light sensitivity around a wavelength of 500 nm (Flamarique and Hawryshyn 1998) and *Osmerus* around 512 – 541nm (Bridges and Delisle 1974). Second, light data were to be correlated with acoustic data collected deeper than 3-5 meters; depths at which the visible light spectrum falls well within our sensitivity range (Tam and Patel 1979).

Hydroacoustic data were processed using Myriax Software's *Echoview* program (Myriax Software Pty Ltd., Hobart, TAS Australia) and standard operating procedures for Great Lakes hydroacoustics (Rudstam et al. 2009). Plots were created of target strengths at all depths within each region, and frequency distribution data were exported for each date. Using these data and fish identification data from physical sampling at known depths, target strength ranges for age-0 and adult rainbow smelt and alewife, in decibels (dB), were identified and we confirmed yearling-and-older (YAO) rainbow smelt TS range was within the -60 to -35 dB range in previous studies (Parker Stetter et al. 2006).

Sawada's index (N_v), the average number of fish per acoustic reverberation volume, was calculated for each cell. Cells with N_v values greater than 0.10 were considered to have fish densities too high for accurate determination of *in situ* TS, and thus were given the value of surrounding cells (Rudstam et al. 2003).

Using mean *in situ* TS and Sv data, we calculated density (number per m^3) in each cell. The final step in determining fish densities was partitioning overall density for all specific organism groups present in the water column. The target identification process was done three different ways through the season, and was based both on physical samples and TS vs. depth plots. When adult and age-0 fish distribution overlapped, targets were separated based on known TS distributions for each age category (Parker Stetter et al. 2006). Despite increasing processing complexity as the season progressed, our analysis allowed the calculation of age-0 rainbow smelt, age-0 alewife, and YAO rainbow smelt density with high resolution.

With the objective of determining which environmental variables are related to observed rainbow smelt and alewife distribution patterns, and given the scope of our study, we proposed three working hypotheses that may explain distribution. These were:

Hypothesis 1: *Fish distribution is related to temperature only.*

Hypothesis 2: *Fish distribution is related to temperature and light.*

Hypothesis 3: *Fish distribution is related to temperature, temperature gradients, and light.*

These scientific hypotheses were transformed into statistical hypotheses stating fish distribution was best predicted by the variables outlined in each hypothesis. Based on the nature of our data, we used generalized additive mixed models (GAMMs). GAMMs were developed very recently for use when data are correlated and the study design includes clustered or spatially explicit sampling (Wood 2006). GAMMs account for correlation among observations using random effects, and use nonparametric regression to fit the flexible functional dependence of a variable on one or more covariates (Lin and Zhang 1999). Thus the general model layout is:

$$Y \sim \beta_0 + f(x_1 \ldots)$$

where fish distribution (*Y*) is a function of an intercept term (β_0) and a flexible function including one or several parameters $(x_1...)$ such as temperature, etc. Not shown in this formula is the random effects piece, which accounts for variability between, and correlation within, sample sites/profiles.

Thus, separate functions were written based on our hypotheses explaining fish distribution:

$$\text{Hypothesis 1: } Y \sim \beta_0 + f(temperature)$$

$$\text{Hypothesis 2: } Y \sim \beta_0 + f(temperature, light)$$

$$\text{Hypothesis 3: } Y \sim \beta_0 + f(temperature, \Delta temperature, light)$$

Each model was developed using the statistical program R (R Development Core Team 2009). Using log likelihood estimates we calculated Akaike's Information Criterion (*AIC*) and the Bayesian Information Criterion (BIC) for each model such that:

$$AIC = -2(\log(L)) + 2K$$
$$BIC = -2(\log(L)) + (\ln(n))K$$

where $\log(L)$ is the natural log of the maximum likelihood estimate, *K* is the number of parameters in the model, and *n* is the sample size (Anderson 2008). The difference between these criteria is that the *BIC* penalty for additional parameters is scaled by sample size, with larger sample sizes resulting in an increased penalty for a given number of parameters. Information criteria were used to rank the models and subsequently the strength of evidence in support of each hypothesis.

Results

Adult and age-0 rainbow smelt, and age-0 alewife distributions were related to temperature, temperature gradients, and light. Age-0 alewife were shallower than age-0 rainbow smelt. Both remained in the epilimnion for the entire diel cycle, but formed increasingly dense shoals as light level increased. Adult rainbow smelt migrated vertically in relation to light changes, while adult alewife were caught only in epilimnion gill nets.

A vertical temperature gradient existed in the main section of Lake Champlain on all survey dates, with warmer water near the lake surface, but until at least mid-July the transition to deeper cold water was gradual. This gradual temperature gradient is in contrast to the well-defined thermocline present from late-July through September. Surface-water temperature varied spatially and temporally < 2 °C during a given survey. Water temperature within the top 5 m ranged from 10.6°C on June 18, 2007 to 22.6°C on August 13, 2008. Hypolimnetic temperatures remained around 4-6°C. Light level at the surface varied over eight orders of magnitude (W/m^2, 460 to 540 nm), and extinction coefficients ranged from 0.20 W/m on 10 September 2008 to 0.94 W/m on 22 July 2008.

We did not collect any adult alewife in trawls. Given the susceptibility of adult alewife to mid-water trawls in other systems (e.g., Fabrizio et al. 1997), some should have been caught if present. Thus, we attributed no acoustic biomass to adult alewife at depths covered by the mid-water trawl.

In contrast to trawl catches, adult alewife were caught in surface gill nets every time gill nets were used, and generally were the most abundant adult species caught.

More adult alewife were caught inshore than offshore in June, whereas catches were equal or more were caught offshore in other months.

Adult rainbow smelt underwent diel vertical migration (DVM) and density at a given one meter depth interval ranged from 0 to 0.35 fish/m^3. Vertically, fish were dispersed most widely in June and October, with distribution contracted in the summer. During these summer periods, the lake was thermally stratified and adult rainbow smelt remained in 4 to 6 °C hypolimnion water during the daytime and migrated to thermocline depths at nighttime (Figure 3). Thus, at nighttime adults were observed at temperatures ranging from 4 to 20 °C and light levels ranging from $1 \cdot 10^{-8}$ to $1 \cdot 10^{-6}$ W/m^2, with most fish at depths cooler than 15 °C and light intensities of $1 \cdot 10^{-7}$ W/m^2 or less.

To test our hypotheses relating adult distribution to gradients of temperature, temperature change, and light, our three models were analyzed using data from all surveys. Based on AIC and BIC scores, the model including all three variables was the most parsimonious, followed by the model including temperature and light, then the model including only temperature (Table 1). Information criterion scores for models ranked second and third were much poorer and thus there is much less evidence in support of the corresponding hypotheses. The best fitting model described the highest relative density of rainbow smelt at temperatures less than 15 °C (Figure 3). If temperature change is constant, nighttime (i.e., post-DVM) density is predominantly a function of temperature and not light (Figure 3).

Age-0 alewife remained in relatively shallow epilimnetic water throughout spring, summer, and fall (Figure 4). Density ranged from 0 to 0.38 fish/m^3, with higher densities in shoals. Shoals formed at higher light levels, but diel vertical migration was not observed in response to light. Because age-0 alewife did not hatch until late June through July (Simonin et al. in prep.), few were present when the lake was isothermal. As the lake warmed, these fish continued to inhabit the warmest available water, and thus were found at temperatures ranging from about 15 to 23°C and light levels from $1.6 \cdot 10^{-7}$ to 1.91 W/m^2.

Based on AIC scores, age-0 alewife relative distribution is related to gradients of temperature, temperature change, and light, although the hypothesis that distribution is related to only temperature and light gradients received some support and was most parsimonious based on BIC scores (Table 2). The best fitting model describes highest relative density of age-0 alewife at temperatures around 20 °C (Figure 3).

Acoustic and physical sampling showed young rainbow smelt to occupy epi- and metalimnetic water throughout the main section of Lake Champlain from June through October. Specifically, from June through August they concentrated at depths corresponding to the top of the thermocline when it was present. In September and October, these fish began to distribute themselves predominantly at metalimnetic depths. Analyses revealed the acoustic detection limit for age-0 fish to range from 21 to 33 m, which was deeper than the maximum depth at which age-0 were present.

Age-0 rainbow smelt density ranged from 0 to about 1.47 fish per cubic meter, which is similar to that seen in hydroacoustic surveys of other systems (L.G. Rudstam, personal communication). Predators collected within the region containing age-0 rainbow smelt were only adult rainbow smelt and adult alewife, observed in densities of 0 to 0.022

fish per cubic meter. Temperatures where age-0 rainbow smelt were found ranged from 6°C to about 23°C, and light levels from approximately $2 \cdot 10^{-7}$ to $2 \cdot 10^{-5}$ W/m^2. As with age-0 alewife, age-0 rainbow smelt formed shoals during higher light levels, but little to no vertical migration was observed. Age-0 rainbow smelt models were analyzed, and the highest AIC scores were found to correspond to the model which included all three variables (Table 1). The model including temperature and light ranked second, but Δ_i values of this and the model including only temperature show very little to no evidence in support of their corresponding hypotheses.

Discussion

Our hypotheses that alewife would be shallower than adult rainbow smelt, and that distributions would be related to temperature, were generally supported. Rainbow smelt and at least age-0 alewife vertical distribution in Lake Champlain is related to gradients of temperature, temperature change, and light. Evidence supporting these relationships was quantified using information criterion. Nonnative alewife in Lake Champlain occupy shallower, warmer depths from spring through fall than native rainbow smelt. However, we did not expect adult alewife to be caught predominantly in depths of 6 m or less during daytime and nighttime. Differences between alewife and rainbow smelt distribution may alter the trophic structure and may affect alewife and rainbow smelt population dynamics.

Our results are in agreement with laboratory temperature preferences of adult alewife in the range of 16 to 21° C from spring to fall, with the maximum temperature preference occurring at the time of spring spawning. During winter months adults in the lab prefer ~11° C (Otto et al. 1976), and high alewife mortality in at least one recent winter (2008) support findings that temperature may in some way affect survival (Lepak and Kraft 2007). Vertical distributions of some alewife populations differ from these preferred temperatures, though, with adults in the Great Lakes often occupying cooler temperatures (Brandt 1980; Boscarino et al. 2007). For instance, in Lake Michigan, adult alewife remain on the bottom during the daytime at temperatures from 11 to 14° C, then remain at these temperatures but migrate to just below the thermocline at nighttime (Brandt 1980). However, in Lake Ontario, adult alewives occupy epilimnetic water with temperatures from 13 to 21° C (Olson et al. 1988). Thus, substantial variability in freshwater alewife distribution patterns and this variability may be a function of food availability and trophic relations in a given system (Boscarino et al. 2007). It is likely that adult alewife distribution in Lake Champlain is predominantly a function of food, within physiological constraints.

Young-of-year alewife in laboratory experiments prefer warmer temperatures than their adult counterparts (Otto et al. 1976). Age-0 alewife were in similar and sometimes cooler depths than adults, although age-0 sampling at surface depths may have been inadequate. Our study is thus in partial agreement with laboratory temperature studies, but other factors are influencing distribution as well.

Alewife temperature preferences are in contrast to the generally cooler water at which rainbow smelt occur (Ferguson 1965; Parker Stetter et al. 2006). For rainbow smelt, though, few laboratory preference studies have been done. Nonetheless, rainbow smelt physiology surely constrains individuals to specific habitats. Physiological responses are likely at play regarding fish entrance into regions of rapid temperature change, which is linked to sub-lethal and behavioral effects (Fry 1947; Donaldson et al. 2008). These effects are why the "temperature change" gradient was related to rainbow smelt distribution.

The balance between physiological constraints and complex bioenergetic and mortality tradeoffs ultimately dictate distribution. For example, alewife are effective planktivores (Brooks and Dodson 1965) and thus, in a system previously lacking this type of predator, may have an abundant food source in the upper water column. In contrast, the importance of thermocline habitat to rainbow smelt indicates the physiology-food balance of rainbow smelt in this system, because rainbow smelt feed on the invertebrate *Mysis diluviana*, which perform large-amplitude diel vertical migrations (Gal et al. 2006). Interaction with food resources may be the reason for the relationship between distribution and light for visual feeders like rainbow smelt, because light likely has fewer direct physiological ties (e.g., UV effects) at depths observed in our study (Williamson and Neale 2009).

The elusive nexus between physical gradients, distribution, trophic structure, and population dynamics is particularly intriguing. Historically, age-0 rainbow smelt were shielded from intense cannibalism during the summer months because of spatial separation from adults (Parker Stetter et al. 2006), but the presence of adult alewife predators may change seasonal predation rates. We now know that age-0 rainbow smelt and alewife, and adult alewife, have greater overlap in summer distribution than rainbow smelt young and adults did historically, but that adult alewife are currently shallower than age-0 of both species. If adult alewife distribution becomes deeper as mean zooplankton size decreases (Brooks and Dodson 1965), predation on age-0 fish could increase and destabilize the rainbow smelt population. Such changes in rainbow smelt population dynamics would influence other parts of the Lake Champlain ecosystem, as both lower and higher trophic levels are inherently tied to this central component of the food web.

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References

Anderson, D. R. 2008. Model based inference in the life sciences: a primer on evidence. Springer, New York, NY.

Boscarino, B. T., L. Rudstam, S. mata, G. Gal, O. E. Johannsson, and E. L. Mills. 2007. The effects of temperature and predator–prey interactions on the migration behavior and vertical distribution of *Mysis relicta*. Limnology and Oceanography 52:1599-1613.

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 109:469-478.

Brandt, S. B., J. Magnuson, and L. B. Crowder. 1980. Thermal habitat partitioning by fishes in Lake Michigan. Canadian Journal of Fisheries and Aquatic Sciences 37:1557-1564.

Bridges, C. D. B., and C. E. Delisle. 1974. Brief observations concerning the visual pigments of some selected fishes from Lake Heney, Quebec, a relict of glacial Lake Gatineau. Vision Research 14:187-193.

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

Burness, G. P., R. D. Morris, and J. P. Bruce. 1994. Seasonal and annual variation in brood attendance, prey type delivered to chicks, and foraging patterns of male common terns (*Sterna hirundo*). Canadian Journal of Zoology-Revue Canadienne De Zoologie 72:1243-1251.

Donaldson, M. R., S. J. Cooke, D. A. Patterson, and J. S. Macdonald. 2008. Cold shock and fish. Journal of Fish Biology 73:1491-1530.

Dunstall, T. G. 1984. Distribution of Rainbow Smelt and Alewife Larvae Along the North Shore of Lake-Ontario. Journal of Great Lakes Research 10:273-279.

Fabrizio, M. C., J. V. Adams, and G. L. Curtis. 1997. Assessing prey fish populations in Lake Michigan: comparison of simultaneous acoustic-midwater trawling with bottom trawling. Fisheries Research 33:37-54.

Ferguson, R. G. 1965. Bathymetric distribution of American smelt *Osmerus mordax* in Lake Erie. University of Michigan, Great Lakes Research Division Publication 13:47-60.

Flamarique, I. N., and C. W. Hawryshyn. 1998. Photoreceptor types and their relation to the spectral and polarization sensitivities of clupeid fishes. Journal of Comparative Physiology A: Neuroethology, Sensory, Neural, and Behavioral Physiology 182:793-803.

Foltz, J. W., and C. R. Norden. 1977. Food habits and feeding chronology of rainbow smelt, *Osmerus mordax*, in Lake Michigan. Fisheries Bulletin 75:637-640.

Fry, F. E. J. 1947. Effects of the environment on animal activity, volume 68. Publication of the Ontario Fisheries Research Laboratory, University of Toronto Studies in Biology, Toronto.

Gal, G., L. G. Rudstam, and O. E. Johannsson. 2004. Predicting *Mysis relicta* vertical distribution in Lake Ontario. Archiv Fur Hydrobiologie 159:1-23.

Gal, G., L. G. Rudstam, E. L. Mills, J. R. Lantry, O. E. Johannsson, and C. H. Greene. 2006. Mysid and fish zooplanktivory in Lake Ontario: quantification of direct and indirect effects. Canadian Journal of Fisheries and Aquatic Sciences 63:2734-2747.

Halnon, L. C. 1963. Historical survey of Lake Champlain's fishery. Vermont Fish and Game Department, F-1-R-10.

Hardiman, J. M., B. M. Johnson, and P. J. Martinez. 2004. Do predators influence the distribution of age-0 kokanee in a Colorado reservoir? Transactions of the American Fisheries Society 133:1366-1378.

Heist, B. G., and W. A. Swenson. 1983. Distribution and abundance of rainbow smelt in western Lake Superior as determined from acoustic sampling. Journal of Great Lakes Research 9:343-353.

Hoagland, P., and D. Jin. 2006. Science and economics in the management of an invasive species. BioScience 56:931-935.

Horppila, J., A. Liljendahl-Nurminen, and T. Malinen. 2004. Effects of clay turbidity and light on the predator-prey interaction between smelts and chaoborids. Canadian Journal of Fisheries and Aquatic Sciences 61:1862-1870.

Hutchinson, G. E. 1953. The concept of pattern in ecology. Proceedings of the Academy of Natural Sciences of Philadelphia 105:1-12.

Janssen, J. 1978. Feeding-behavior repertoire of the alewife, *Alosa pseudoharengus*, and the ciscos, *Coregonus hoyi* and *C. artedii*. Journal of the Fisheries Research Board of Canada 35:249-253.

Johnson, C. R., W. J. O'Brien, and S. MacIntyre. 2007. Vertical and temporal distribution of two copepod species, *Cyclops scutfier* and *Diaptomus pribilofensis*, in 24 h arctic daylight. Journal of Plankton Research 29:275-289.

Juday, C., and G. Wagner. 1908. Dissolved oxygen as a factor in the distribution of fishes. Transactions of the Wisconsin Acadamy of Science Arts and Letters 16:14-22.

Lepak, J., and C. Kraft. 2007. Alewife mortality, condition, and imune response to prolonged cold temperatures. Journal of Great Lakes Research.

Lin, X., and D. Zhang. 1999. Inference in generalized additive mixed models by using smoothing splines. Journal of the Royal Statistical Society. Series B (Statistical Methodology) 61:381-400.

Mills, E. L., J. H. Leach, J. T. Carlton, and C. L. Secor. 1993. Exotic species in the Great-Lakes - a history of biotic crises and anthropogenic introductions. Journal of Great Lakes Research 19:1-54.

Moore, E. 1929. A biological survey of the Champlain watershed. New York State Conservation Department, Albany, NY.

Olson, R. A., J. D. Winter, and D. C. Nettles. 1988. Resource partitioning in summer by salmonids in south-central Lake Ontario. Transactions of the American Fisheries Society 117:552-559.

Otto, R. G., M. A. Kitchel, and J. O. H. Rice. 1976. Lethal and preferred temperatures of the alewife (*Alosa pseudoharengus*) in Lake Michigan. Transactions of the American Fisheries Society 105:96-106.

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.

Perrings, C. 2002. Biological invasions in aquatic systems: The economic problem. Bulletin of Marine Science 70:541-552.

Pientka, B., and D. L. Parrish. 2002. Habitat selection of predator and prey: Atlantic salmon and rainbow smelt overlap, based on temperature and dissolved oxygen. Transactions of the American Fisheries Society 131:1180-1193.

Pimentel, D., R. Zuniga, and D. Morrison. 2005. Update on the environmental and economic costs associated with alien-invasive species in the United States. Ecological Economics 52:273-288.

R Development Core Team. 2009. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Reckel, F., B. Hoffmann, R. R. Melzer, J. Horppila, and U. Smola. 2003. Photoreceptors and cone patterns in the retina of the smelt Osmerus eperlanus (L.) (Osmeridae: Teleostei). Acta Zoologica 84:161-170.

Reynolds, C. 2006. Ecology of Phytoplankton. Cambridge University Press, Cambridge, UK.

Ricklefs, R. E. 2001. The Economy of Nature, 5th edition. W. H. Freeman and Company, New York.

Rudstam, L. G., and J. J. Magnuson. 1985. Predicting the vertical distribution of fish populations: analysis of cisco, *Coregonus artedii,* and yellow perch, *Perca flavescens*. Canadian Journal of Fisheries and Aquatic Sciences 42:1178-1188.

Rudstam, L. G., S. L. Parker, D. W. Einhouse, L. D. Witzel, D. M. Warner, J. L. Stritzel, D. L. Parrish, and P. J. Sullivan. 2003. Application of in situ target-strength estimations in lakes: examples from rainbow-smelt surveys in Lakes Erie and Champlain. Ices Journal of Marine Science 60:500-507.

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.

Sala, O. E., F. S. Chapin, J. J. Armesto, E. Berlow, J. Bloomfield, R. Dirzo, E. Huber-Sanwald, L. F. Huenneke, R. B. Jackson, A. Kinzig, R. Leemans, D. M. Lodge, H. A. Mooney, M. Oesterheld, N. L. Poff, M. T. Sykes, B. H. Walker, M. Walker, and D. H. Wall. 2000. Biodiversity - global biodiversity scenarios for the year 2100. Science 287:1770-1774.

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.

Tam, A. C., and C. K. N. Patel. 1979. Optical absorptions of light and heavy water by laser optoacoustic spectroscopy. Appl. Opt. 18:3348-3358.

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 36:359-372.

Wilcove, D. S., D. Rothstein, J. Dubow, A. Phillips, and E. Losos. 1998. Quantifying threats to imperiled species in the United States. BioScience 48:607-615.

Williamson, and Neale. 2009. UV light. Encyclopedia of Inland Waters. Elsevier.

Wood, S. N. 2006. Low-rank scale-invariant tensor product smooths for generalized additive mixed models. Biometrics 62:1025-1036.

Tables

Table 1. Hydroacoustic settings used in data collection and processing

Frequency (kHz)	**Beam width (◦)**	**Min. collect. thresh. (dB)**	**Transmitted pulse length (m·s)**	**Pulse rate (pulse / s)**	**Depth layer thickness (m)**	***In situ* TS settings**	**Noise at 1 m (S_v, dB)**
120 (BioSonics DtX)	7.5	-100	0.4	2	1	6 dB, 0.6	-115

Table 2. Comparison of models relating abiotic conditions to adult rainbow smelt, age-0 rainbow smelt, and age-0 alewife distribution. Models are ranked based on AIC scores.

Species and age class	Hypothesis	K	MLL (log($\mathcal{L}$))	AIC	BIC	Δ_i (AIC)	w_i (AIC)
Adult rainbow smelt	**Temperature, light, and temperature change**	13	3556	-7087	-7017	0	1
	Temperature and light	8	3481	-6947	-6904	140	0
	Temperature	5	3466	-6923	-6896	164	0
Age-0 rainbow smelt	**Temperature, light, and temperature change**	13	3128	-6229	-6159	0	1
	Temperature and light	8	2967	-5917	-5874	312	0
	Temperature	5	2861	-5713	-5685	516	0
Age-0 alewife	**Temperature, light, and temperature change**	13	3265	-6505	-6435	0	1
	Temperature and light	8	3256	-6497	-6454	8	0
	Temperature	5	3118	-6225	-6198	280	0

Figure captions

Figure 1. Lake Champlain (right panel), located between New York, Vermont, and Quebec. Location of surveys in the Main Lake (left) and Malletts Bay (right) regions of Lake Champlain. Contour lines represent 5-m depth intervals.

Figure 2. Example of adult rainbow smelt distribution during day and nighttime. Data from July 5, 2007.

Figure 3. Adult rainbow smelt (a), age-0 rainbow smelt (b), and age-0 alewife (c) relative density described by GAMMs in relation to temperature and light gradients. The "temperature change" variable is held constant at 0.0.

Figures

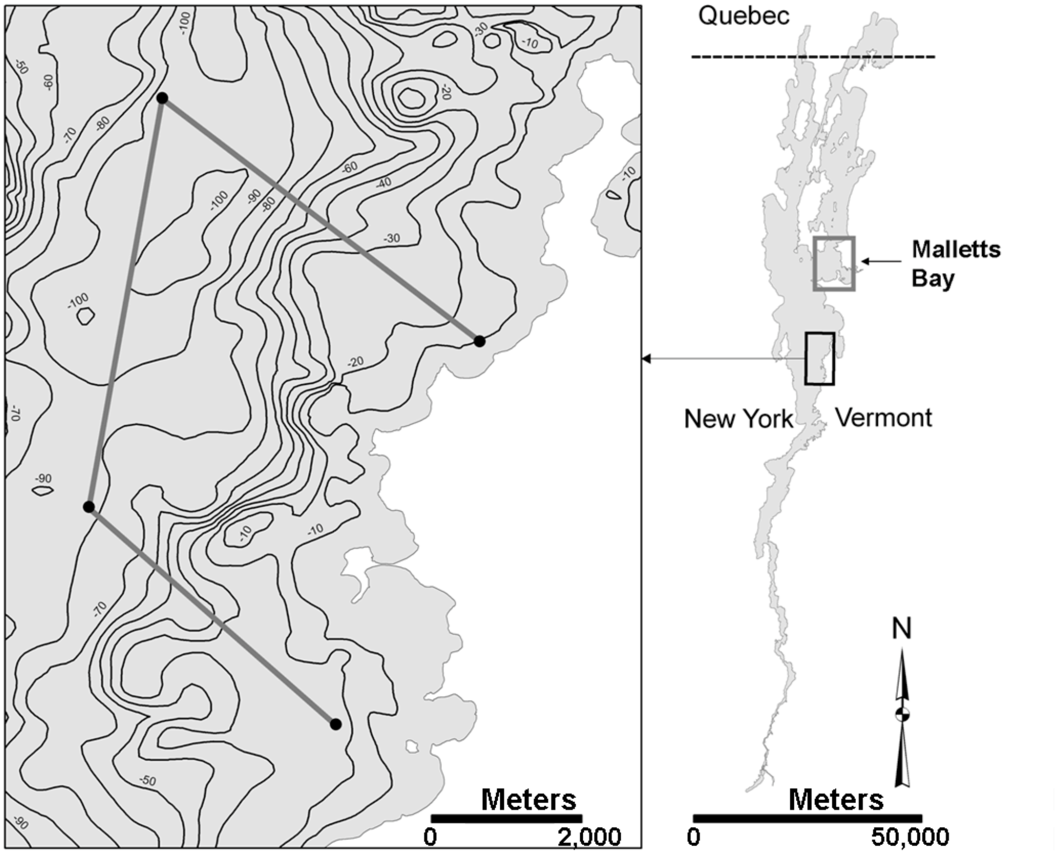


Figure 1

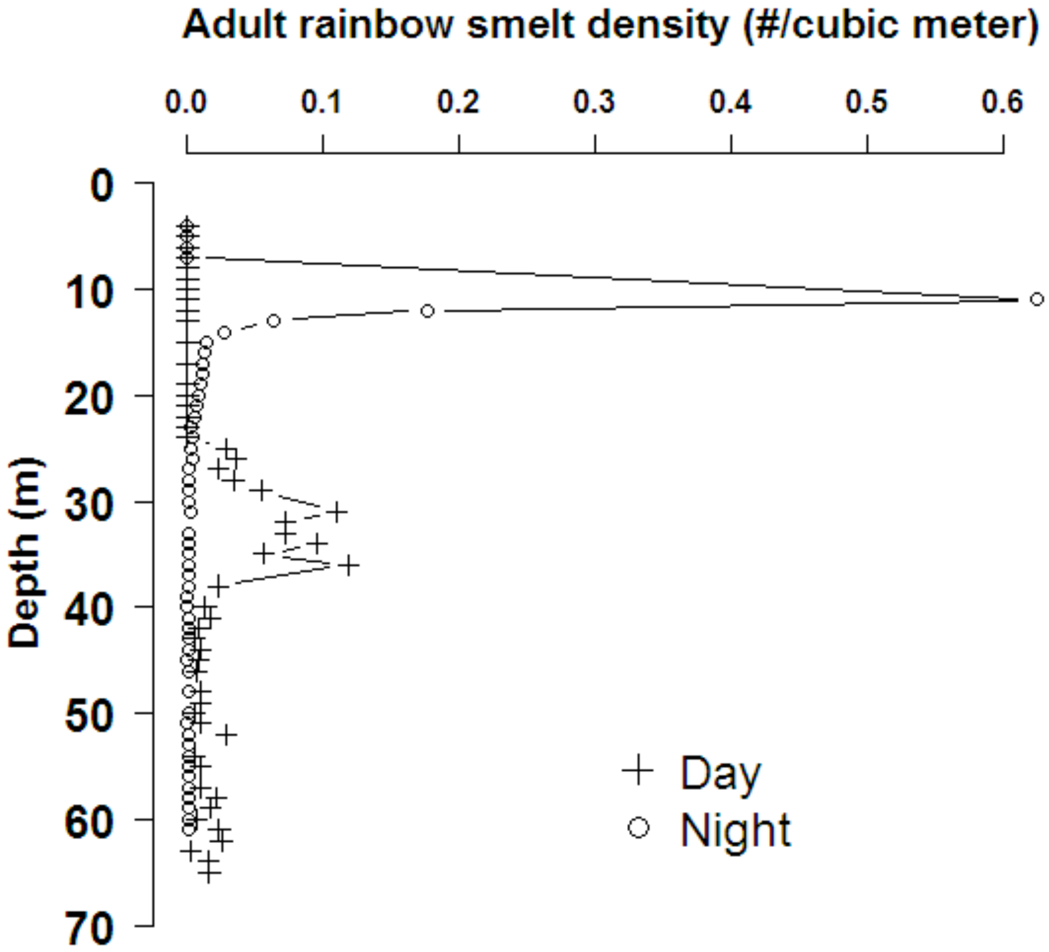
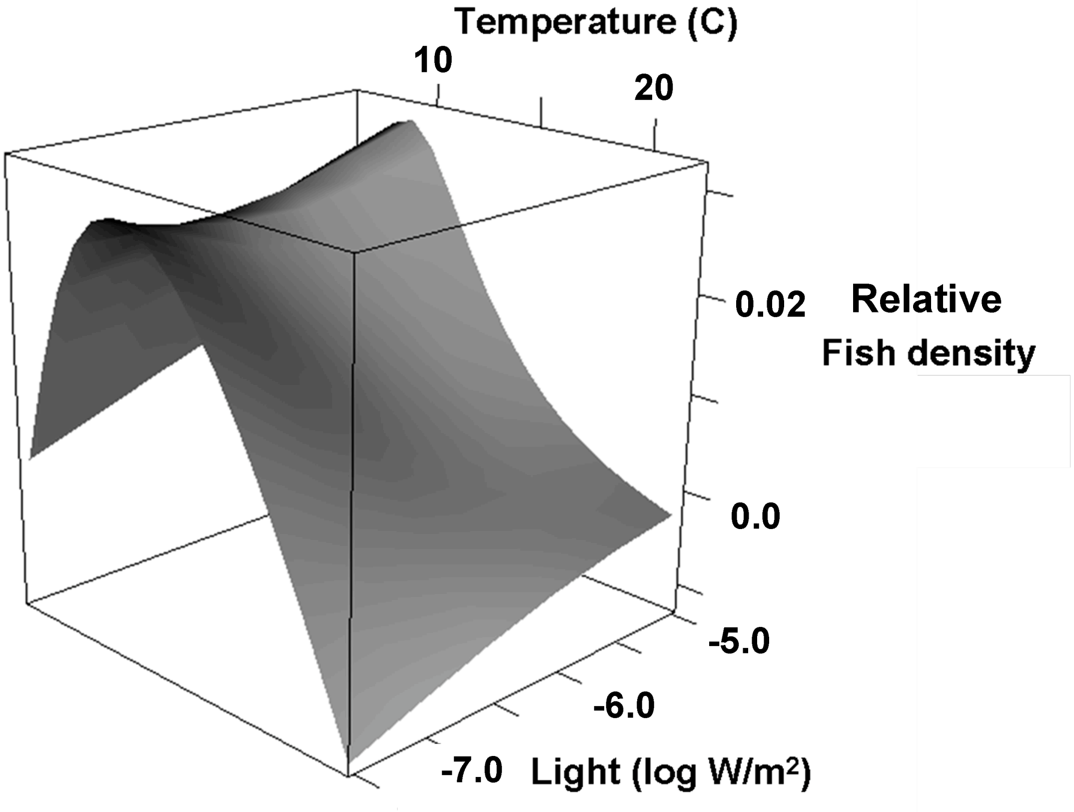
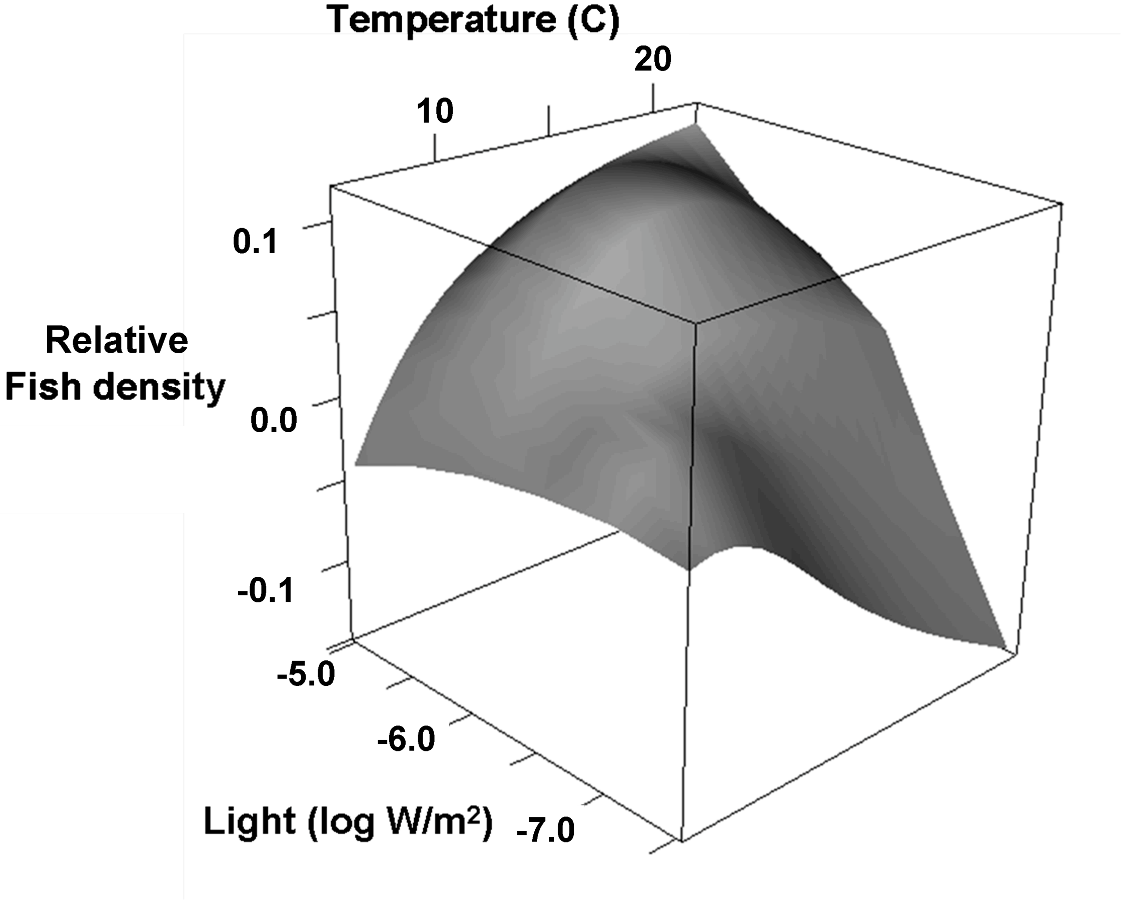

Adult rainbow smelt density (#/cubic meter)
0.0
0.1
0.2
0.3
0.4
0.5
0.6
Depth (m)
0
10
20
30
40
50
60
70
+ Day
○ Night

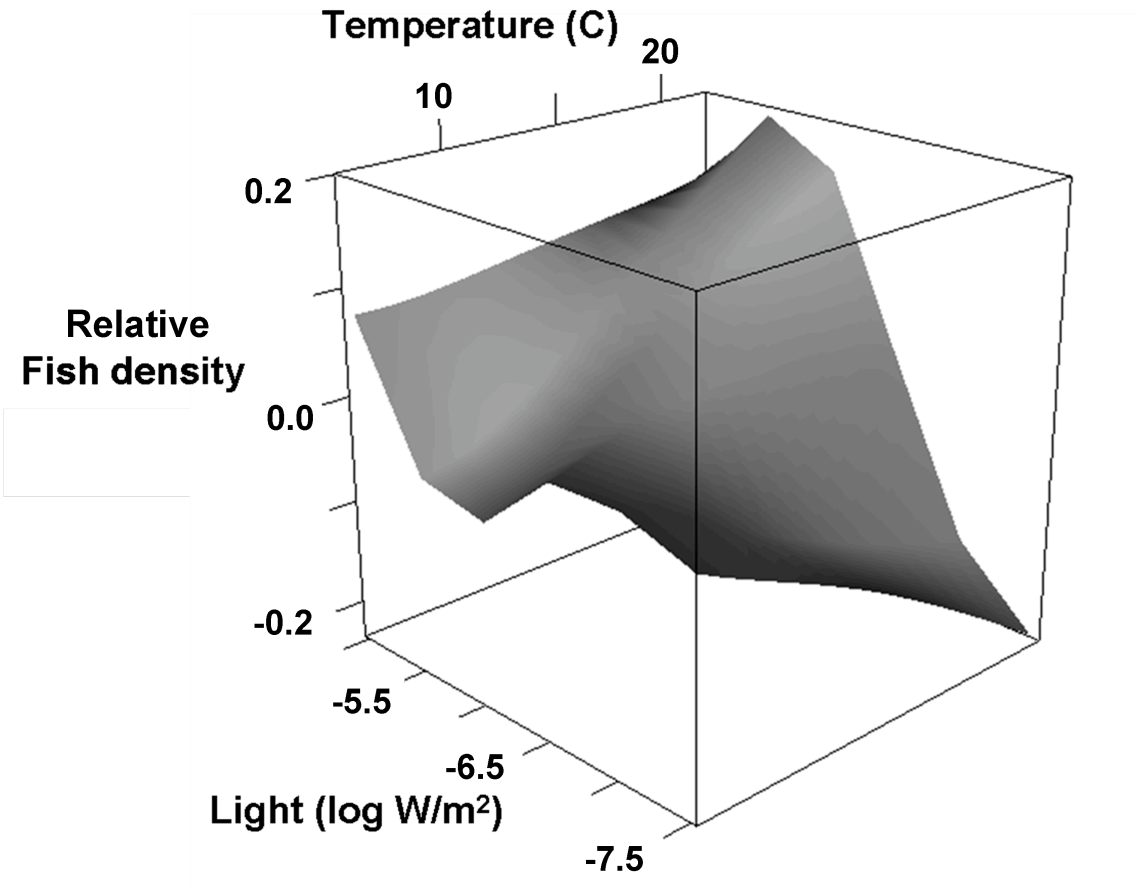
Figure 2


Temperature (C)
10
20
0.02
0.0
Relative Fish density
-5.0
-6.0
-7.0
Light (log W/m2)

(a)


Temperature (C)
10
20
Relative Fish density
0.1
0.0
-0.1
-5.0
-6.0
-7.0
Light (log W/m²)

(b)


Temperature (C)
20
10
0.2
Relative
Fish density
0.0
-0.2
-5.5
-6.5
Light (log W/m2)
-7.5

(c)
Figure 3

THESIS REFERENCES

Akielaszek, J. J., J. R. Moring, S. R. Chapman, and J. H. Dearborn. 1985. Experimental culture of young rainbow smelt, *Osmerus mordax*. Transactions of the American Fisheries Society **114**:596-603.

Anderson, D. R. 2008. Model based inference in the life sciences: a primer on evidence. Springer, New York, NY.

Appenzeller, A. R. and W. C. Leggett. 1992. Bias in Hydroacoustic Estimates of Fish Abundance Due to Acoustic Shadowing - Evidence from Day Night Surveys of Vertically Migrating Fish. Canadian Journal of Fisheries and Aquatic Sciences **49**:2179-2189.

Appenzeller, A. R. and W. C. Leggett. 1995. An Evaluation of Light-Mediated Vertical Migration of Fish Based on Hydroacoustic Analysis of the Diel Vertical Movements of Rainbow Smelt (Osmerus-Mordax). Canadian Journal of Fisheries and Aquatic Sciences **52**:504-511.

Appenzeller, A. R. and W. C. Leggett. 1996. Do diel changes in patchiness exhibited by schooling fishes influence the precision of estimates of fish abundance obtained from hydroacoustic transect surveys? Archiv Fur Hydrobiologie **135**:377-391.

Argyle, R. L. 1982. Alewives and Rainbow Smelt in Lake Huron - Midwater and Bottom Aggregations and Estimates of Standing Stocks. Transactions of the American Fisheries Society **111**:267-285.

Ayer, M. H., C. Benton, W. King, J. Kneebone, S. Elzey, M. Toran, K. Grange, and D. L. Berlinsky. 2005. Development of practical culture methods for rainbow smelt larvae. North American Journal of Aquaculture **67**:202-209.

Bernatchez, L. 1997. Mitochondrial DNA analysis confirms the existence of two glacial races of rainbow smelt Osmerus mordax and their reproductive isolation in the St Lawrence River estuary (Quebec, Canada). Molecular Ecology **6**:73-83.

Boscarino, B. T., L. Rudstam, S. mata, G. Gal, O. E. Johannsson, and E. L. Mills. 2007. The effects of temperature and predator–prey interactions on the migration behavior and vertical distribution of *Mysis relicta*. Limnology and Oceanography **52**:1599-1613.

Bozeman, E. L. and M. J. Van Den Avyle. 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.

Bradbury, I. R., K. Gardiner, P. V. R. Snelgrove, S. E. Campana, P. Bentzen, and L. Guan. 2006. Larval transport, vertical distributions and localized recruitment in anadromous rainbow smelt (Osmerus mordax). Canadian Journal of Fisheries and Aquatic Sciences **63**:2822-2836.

Brandt, S. B., J. Magnuson, and L. B. Crowder. 1980. Thermal habitat partitioning by fishes in Lake Michigan. Canadian Journal of Fisheries and Aquatic Sciences **37**:1557-1564.

Bridges, C. D. B. and C. E. Delisle. 1974. Brief observations concerning the visual pigments of some selected fishes from Lake Heney, Quebec, a relict of glacial Lake Gatineau. Vision Research **14**:187-193.

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 **19**:960-965.

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

Brown, S. B., M. T. Arts, L. R. Brown, M. Brown, K. Moore, M. Villella, J. D. Fitzsimons, D. C. Honeyfield, D. E. Tillitt, J. L. Zajicek, M. Wolgamood, and J. G. Hnath. 2005a. Can Diet-Dependent Factors Help Explain Fish-to-Fish Variation in Thiamine-Dependent Early Mortality Syndrome? Journal of Aquatic Animal Health **17**:36-47.

Brown, S. B., J. D. Fitzsimons, D. C. Honeyfield, and D. E. Tillitt. 2005b. Implications of Thiamine Deficiency in Great Lakes Salmonines. Journal of Aquatic Animal Health **17**:113-124.

Brown, S. B., D. C. Honeyfield, J. G. Hnath, M. Wolgamood, S. V. Marcquenski, J. D. Fitzsimons, and D. E. Tillitt. 2005c. Thiamine Status in Adult Salmonines in the Great Lakes. Journal of Aquatic Animal Health **17**:59-64.

Buckley, J. 1989a. 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.

Buckley, J. 1989b. Species profiles: life histories and environmental requirements of coastal fishes and invertebrates (North Atlantic) -- rainbow smelt. Page 11. U.S. Army Corps of Engineers.

Burczynski, J. J., P. H. Michaletz, and G. M. Marrone. 1987. Hydroacoustic assessment of the abundance and distribution of rainbow smelt in Lake Oahe. North American Journal of Fisheries Management **7**:106-116.

Burness, G. P., R. D. Morris, and J. P. Bruce. 1994. Seasonal and annual variation in brood attendance, prey type delivered to chicks, and foraging patterns of male common terns (*Sterna hirundo*). Canadian Journal of Zoology-Revue Canadienne De Zoologie **72**:1243-1251.

Carling, K. J., T. B. Mihuc, C. Siegfried, R. Bonham, and F. Dunlap. 2004. Where have all the rotifers gone? Zooplankton community patterns in Lake Champlain from 1992-2001. Pages 259-270 *in* T. O. Manley, P. Manley, and T. B. Mihuc, editors. Lake Champlain: partnership and research in the new millennium. Kluwer Academic/Plenum Publishers, New York.

Christie, W. 1974. Changes in the fish species composition of the Great Lakes. Journal of the Fisheries Research Board of Canada **31**: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.

Connell, J. H. 1961. The influence of interspecific competition and other factors on the distribution of the barnacle *Chthamalus stellatus*. Ecology **42**:710-723.

Connor, E. F. and D. Simberloff. 1986. Competition, scientific method, and null models in ecology. American Scientist **74**:155-162.

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*. Transactions of the American Fisheries Society **107**:56-62.

Crowder, L. B. 1980. Alewife, smelt and native fishes in Lake Michigan: competition or predation? Environmental Biology of Fishes **5**:225-233.

Dahlberg, M. D. 1981. Nearshore spatial distribution of fishes in gillnet samples, Cayuga Lake, New York. Journal of Great Lakes Research **7**:7-14.

Dong, Q. A. and D. L. DeAngelis. 1998. Consequences of cannibalism and competition for food in a smallmouth bass population: An individual-based modeling study. Transactions of the American Fisheries Society **127**:174-191.

Dryer, W. R. 1966. Bathymetric distribution of fish in the Apostle Islands region, Lake Superior. Transactions of the American Fisheries Society **95**:248-259.

Dunstall, T. G. 1984. Distribution of Rainbow Smelt and Alewife Larvae Along the North Shore of Lake-Ontario. Journal of Great Lakes Research **10**:273-279.

Errington, P. L. 1963. The phenomenon of predation. American Scientist **51**:180-192.

Evans, D. O. and D. H. Loftus. 1987. Colonization of inland lakes in the Great-Lakes region by rainbow smelt, Osmerus mordax - Their fresh-water niche and effects on indigenous fishes. Canadian Journal of Fisheries and Aquatic Sciences **44**:249-266.

Fabrizio, M. C., J. V. Adams, and G. L. Curtis. 1997. Assessing prey fish populations in Lake Michigan: comparison of simultaneous acoustic-midwater trawling with bottom trawling. Fisheries Research **33**:37-54.

Ferguson, R. G. 1965. Bathymetric distribution of American smelt *Osmerus mordax* in Lake Erie. University of Michigan, Great Lakes Research Division Publication **13**:47-60.

Fielder, D. G., J. S. Schaeffer, and M. V. Thomas. 2007. Environmental and ecological conditions surrounding the production of large year classes of walleye (Sander vitreus) in Saginaw Bay, Lake Huron. Journal of Great Lakes Research **33**:118-132.

Fisher, J. P., J. D. Fitzsimons, G. F. Combs, and J. M. Spitsbergen. 1996. Naturally occurring thiamine deficiency causing reproductive failure in Finger Lakes Atlantic salmon and great lakes lake trout. Transactions of the American Fisheries Society **125**:167-178.

Fitzsimons, J. D., B. Williston, G. Williston, L. Brown, A. El-Shaarawi, L. Vandenbyllaardt, D. Honeyfeld, D. Tillitt, M. Wolgamood, and S. B. Brown. 2007. Egg thiamine status of Lake Ontario salmonines 1995-2004 with emphasis on lake trout. Journal of Great Lakes Research **33**:93-103.

Fitzsimons, J. D., B. Williston, J. L. Zajicek, D. E. Tillitt, S. B. Brown, L. R. Brown, D. C. Honeyfield, D. M. Warner, L. G. Rudstam, and W. Pearsall. 2005. Thiamine Content and Thiaminase Activity of Ten Freshwater Stocks and One Marine Stock of Alewives. Journal of Aquatic Animal Health **17**:26-35.

Flamarique, I. N. and C. W. Hawryshyn. 1998. Photoreceptor types and their relation to the spectral and polarization sensitivities of clupeid fishes. Journal of Comparative Physiology A: Neuroethology, Sensory, Neural, and Behavioral Physiology **182**:793-803.

Foltz, J. W. and C. R. Norden. 1977. Food habits and feeding chronology of rainbow smelt, *Osmerus mordax*, in Lake Michigan. Fisheries Bulletin **75**:637-640.

Fry, F. E. J. 1937. The summer migration of the cisco, *Leuchtichtyus artedii*, in Lake Nipissing, Ontario. Publication of the Ontario Fish Research lab **55**:1-91.

Gal, G., E. R. Loew, L. G. Rudstam, and A. M. Mohammadian. 1999a. Light and diel vertical migration: spectral sensitivity and light avoidance by *Mysis relicta*. Canadian Journal of Fisheries and Aquatic Sciences **56**:311-322.

Gal, G., L. G. Rudstam, and C. H. Greene. 1999b. Acoustic characterization of *Mysis relicta*. Limnology and Oceanography **44**:371-381.

Gal, G., L. G. Rudstam, and O. E. Johannsson. 2004. Predicting *Mysis relicta* vertical distribution in Lake Ontario. Archiv Fur Hydrobiologie **159**:1-23.

Gal, G., L. G. Rudstam, E. L. Mills, J. R. Lantry, O. E. Johannsson, and C. H. Greene. 2006. Mysid and fish zooplanktivory in Lake Ontario: quantification of direct and indirect effects. Canadian Journal of Fisheries and Aquatic Sciences **63**:2734-2747.

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.

Gilbert, A. H. 2000. Lake Champlain angler survey 1997. Federal aid job performance report: Final Report.*in* V. Vermont Department of Fish and Wildlife: Waterbury, editor.

Gliwicz, Z. M. and A. Jachner. 1992. Diel Migrations of Juvenile Fish - a Ghost of Predation Past or Present. Archiv Fur Hydrobiologie **124**:385-410.

Gotelli, N. J. and A. M. Ellison. 2004. A Primer of Ecological Statistics. Sinauer Associates, Inc., Sunderland, MA.

Graham, J. J. 1956. Observations of the alewife (*Pomolobus pseudoharengus*) in fresh water., University of Toronto, Toronto.

Halnon, L. C. 1963. Historical survey of Lake Champlain's fishery. F-1-R-10, Vermont Fish and Game Department.

Hardiman, J. M., B. M. Johnson, and P. J. Martinez. 2004. Do predators influence the distribution of age-0 kokanee in a Colorado reservoir? Transactions of the American Fisheries Society **133**:1366-1378.

Hardin, G. 1960. The competitive exclusion principle. Science **131**:1292-1297.

Hart, J. L. and R. G. Ferguson. 1966. The American smelt. Trade news **18**:22-23.

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.

Heist, B. G. and W. A. Swenson. 1983. Distribution and abundance of rainbow smelt in western Lake Superior as determined from acoustic sampling. Journal of Great Lakes Research **9**:343-353.

Hendricks, M. L. 2003. Culture and transplant of alosines in North America. Pages 303-312 Biodiversity, status, and conservation of the world's shads.

Herbold, B. and P. B. Moyle. 1986. Introduced species and vacant niches. The American Naturalist **128**:751-760.

Hoagland, P. and D. Jin. 2006. Science and economics in the management of an invasive species. BioScience **56**:931-935.

Honeyfield, D. C., J. P. Hinterkopf, J. D. Fitzsimons, D. E. Tillitt, J. L. Zajicek, and S. B. Brown. 2005. Development of Thiamine Deficiencies and Early Mortality Syndrome in Lake Trout by Feeding Experimental and Feral Fish Diets Containing Thiaminase. Journal of Aquatic Animal Health **17**:4-12.

Hoover, E. E. 1936. The spawning activities of freshwater smelt, with special reference to the sex ratio. Copeia **2**:85-91.

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.

Hutchinson, G. E. 1953. The concept of pattern in ecology. Proceedings of the Academy of Natural Sciences of Philadelphia **105**:1-12.

Hutchinson, G. E. 1957. Concluding remarks. Cold Spring Harbor Symposium of Quantitative Biology **22**:415-427.

Hutchinson, G. E. 1961. The paradox of the plankton. The American Naturalist **95**:137-145.

Janssen, J. 1978. Feeding-behavior repertoire of the alewife, *Alosa pseudoharengus*, and the ciscos, *Coregonus hoyi* and *C. artedii*. Journal of the Fisheries Research Board of Canada **35**:249-253.

Johnson, B. M. and J. P. Goettl, Jr. 1999. Food web changes over fourteen years following introduction of rainbow smelt into a Colorado Reservior. North American Journal of Fisheries Management **19**:629-642.

Johnson, C. R., W. J. O'Brien, and S. MacIntyre. 2007. Vertical and temporal distribution of two copepod species, *Cyclops scutfier* and *Diaptomus pribilofensis*, in 24 h arctic daylight. Journal of Plankton Research **29**:275-289.

Jones, M. S., J. P. Goettl, Jr., and S. A. Flickinger. 1994. Changes in walleye food habits and growth following a rainbow smelt introduction. North American Journal of Fisheries Management **14**:409-414.

Juday, C. and G. Wagner. 1908. Dissolved oxygen as a factor in the distribution of fishes. Transactions of the Wisconsin Acadamy of Science Arts and Letters **16**:14-22.

Jude, D., B. A. Bachen, G. R. Henfelder, H. T. Tin, M. J. Winnell, F. J. Tesar, and J. A. Dorr. 1978. Adult and juvenile fish, ichthyoplankton and benthos populations in the vicinity of the J.H. Campbell Power Plant, Eastern Lake Michigan, 1977. University of Michigan, Great Lakes Research Division Special Report 65:639 p.

Kearney, M. 2006. Habitat, environment and niche: what are we modelling? Oikos **115**:186-191.

Kendall, W. 1927. The smelts. Bulletin of the United States Bureau of Fisheries **41**:217-375.

Kimura, K. 1929. On the detection of fish-groups by an acoustic method. Journal of the Imperial Fisheries Institute, Tokyo **24**:41-45.

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**:87-96.

Kitchell, J. F., S. P. Cox, C. J. Harvey, T. B. Johnson, D. M. Mason, K. K. Schoen, K. Aydin, C. Bronte, M. Ebener, M. Hansen, M. Hoff, S. Schram, D. Schreiner, and C. J. Walters. 2000. Sustainability of the Lake Superior fish community: Interactions in a food web context. Ecosystems **3**:545-560.

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.

Krueger, C. C., D. L. Perkins, E. L. Mills, and J. E. Marsden. 1995. Predation by alewives on lake trout fry in Lake Ontario: Role of an exotic species in preventing restoration of a native species. Journal of Great Lakes Research **21**:458-469.

Kubecka, J., J. Frouzova, M. Cech, J. Peterka, H. A. M. Ketelaars, A. J. Wagenwoort, and M. Papacek. 2000. Hydroacoustic assessment of pelagic stages of freshwater insects. Aquatic Living Resources **13**: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. Transactions of the American Fisheries Society **122**:942-950.

Langdon, R. W., M. T. Ferguson, and K. M. Cox. 2006. Fishes of Vermont. Vermont Fish and Wildlife Department, Montpelier, VT.

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**:1594-1606.

Lecomte, F. and J. J. Dodson. 2004. Role of early life-history constraints and resource polymorphism in the segregation of sympatric populations of an estuarine fish. Evolutionary Ecology Research **6**:631-658.

Lecomte, F. and J. J. Dodson. 2005. Distinguishing trophic and habitat partitioning among sympatric populations of the estuarine fish Osmerus mordax Mitchill. Journal of Fish Biology **66**:1601-1623.

Legault, R. and C. Delisle. 1968. The spawning of a population of giant smelt, *Osmerus eperlanus mordax*, in Lake Heney, Gatineau County, Quebec. Journal of the Fisheries Research Board of Canada **25**:1813-1830.

Lepak, J. and C. Kraft. 2007. Alewife mortality, condition, and imune response to prolonged cold temperatures. Journal of Great Lakes Research.

Levin, S. A. 1970. Community equilibria and stability, and extension of the competitive exclusion principle. The American Naturalist **104**:413-423.

Levine, S. N., M. A. Borchardt, A. D. Shambaugh, and M. Braner. 1999. Lower trophic level interactions in pelagic Lake Champlain. Pages 301-322 *in* T. O. Manley and P. Manley, editors. Lake Champlain in transition: from research toward restoration. American Geophysical Union, Washington, DC.

Lewis, J. M., K. V. Ewart, and W. R. Driedzic. 2004. Freeze resistance in rainbow smelt (*Osmerus mordax*): Seasonal pattern of glycerol and antifreeze protein levels and liver enzyme activity associated with glycerol production. Physiological and Biochemical Zoology **77**:415-422.

Locke, A. and S. C. Courtenay. 1995. Effects of Environmental-Factors on Ichthyoplankton Communities in the Miramichi Estuary, Gulf of St-Lawrence. Journal of Plankton Research **17**:333-349.

Madenjian, C. P., R. 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**:263-282.

Magnuson, J. J., L. B. Crowder, and P. A. Medvick. 1979. Temperature as an ecological resource. Amer. Zool. **19**:331-343.

Malinen, T. and A. Tuomaala. 2005. Comparison of day and night surveys in hydroacoustic assesment of smelt (*Osmerus eperlanus*) density in Lake Hiidenvesi. Advances in Limnology **59**:161-172.

Manley, T. O. and P. Manley. 1999. Lake Champlain in transition: from research toward restoration. American Geophysical Union, Washington, DC.

Marsden, J. E., B. J. Ellrott, R. M. Claramunt, J. L. Jonas, and J. D. Fitzsimons. 2005. A comparison of lake trout spawning, fry emergence, and habitat use in Lakes Michigan, Huron, and Champlain. Journal of Great Lakes Research **31**:492-508.

Mason, D. M., T. B. Johnson, C. S. Harvey, J. F. Kitchell, S. T. Schram, C. R. Bronte, M. H. Hoff, S. J. Lozano, A. S. Trebitz, D. R. Schreiner, E. C. Lamon, and T. Hrabik. 2005. Hydroacoustic estimates of abundance and spatial distribution of pelagic prey fishes in western Lake Superior. Journal of Great Lakes Research **31**:426-438.

May, R. M., J. R. Beddington, C. W. Clark, S. J. Holt, and R. M. Laws. 1979. Management of multispecies fisheries. Science **205**:267-277.

McKenna, J. E., B. M. Davis, M. C. Fabrizio, J. F. Savino, T. N. Todd, and M. Bur. 2008. Ichthyoplankton assemblages of coastal west-central Lake Erie and associated habitat characteristics. Journal of Great Lakes Research **34**:755-769.

Mercado-Silva, N., J. D. Olden, J. T Maxted, T. R. Hrabik, and M. J. Vander Zanden. 2006. Forecasting the spread of invasive rainbow smelt in the Laurentian Great Lakes region of North America. Conservation Biology **20**:1740-1749.

Miller, R. R. 1957. Origin and dispersal of the alewife, *Alosa pseudoharengus*, and the gizzard shad, *Dorosoma cepedianum*, in the Great Lakes. Transactions of the American Fisheries Society **86**:97-111.

Mills, E. L., J. M. Casselman, R. Dermott, J. D. Fitzsimons, G. Gal, K. T. Holeck, J. A. Hoyle, O. E. Johannsson, B. F. Lantry, J. C. Makarewicz, E. S. Millard, I. F. Munawar, M. Munawar, R. O'Gorman, R. W. Owens, L. G. Rudstam, T. Schaner, and T. J. Stewart. 2003. Lake Ontario: food web dynamics in a changing ecosystem (1970-2000). Canadian Journal of Fisheries and Aquatic Sciences **60**:471-490.

Mills, E. L., J. H. Leach, J. T. Carlton, and C. L. Secor. 1993. Exotic species in the Great-Lakes - a history of biotic crises and anthropogenic introductions. Journal of Great Lakes Research **19**:1-54.

Mills, E. L., J. H. Leach, J. T. Carlton, and C. L. Secor. 1994. Exotic species and the integrity of the Great Lakes - lessons from the past. BioScience **44**:666-676.

Mills, E. L., R. Ogorman, E. F. Roseman, C. Adams, and R. W. Owens. 1995. Planktivory by alewife (*Alosa pseudoharengus*) and rainbow smelt (*Osmerus mordax*) on microcrustacean zooplankton and dreissenid (Bivalvia, Dreissenidae) veligers in southern Lake-Ontario. Canadian Journal of Fisheries and Aquatic Sciences **52**:925-935.

Moore, E. 1929. A biological survey of the Champlain watershed. New York State Conservation Department, Albany, NY.

Nash, R. D. M. and A. J. Geffen. 1991. Spatial and temporal changes in the offshore larval fish assemblage in southeastern Lake Michigan. Journal of Great Lakes Research **17**:25-32.

O'Gorman, R. 1983. Distribution and abundance of larval fish in the nearshore waters of western Lake Huron. Journal of Great Lakes Research **9**:14-22.

O'Gorman, R., J. H. Elrod, R. W. Owens, C. P. Schneider, T. H. Eckert, and B. F. Lantry. 2000. Shifts in depth distributions of alewives, rainbow smelt, and age-2 lake trout in southern Lake Ontario following establishment of dreissenids. Transactions of the American Fisheries Society **129**:1096-1106.

Ogorman, R., E. L. Mills, and J. Degisi. 1991. Use of Zooplankton to Assess the Movement and Distribution of Alewife (Alosa-Pseudoharengus) in South-Central Lake-Ontario in Spring. Canadian Journal of Fisheries and Aquatic Sciences **48**:2250-2257.

Otto, R. G., M. A. Kitchel, and J. O. H. Rice. 1976. Lethal and preferred temperatures of the alewife (*Alosa pseudoharengus*) in Lake Michigan. Transactions of the American Fisheries Society **105**:96-106.

Oyadomari, J. K. and N. A. Auer. 2004. Inshore-offshore distribution of larval fishes in Lake Superior off the western coast of the Keweenaw Peninsula, Michigan. Journal of Great Lakes Research **30**:369-384.

Parker, S. L., L. G. Rudstam, E. L. Mills, and D. W. Einhouse. 2001. Retention of Bythotrephes spines in the stomachs of eastern Lake Erie rainbow smelt. Transactions of the American Fisheries Society **130**:988-994.

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.

Parker Stetter, S. L., L. D. Witzel, L. G. Rudstam, D. W. Einhouse, and E. L. Mills. 2005. Energetic consequences of diet shifts in Lake Erie rainbow smelt (*Osmerus mordax*). Canadian Journal of Fisheries and Aquatic Sciences **62**:145-152.

Perrings, C. 2002. Biological invasions in aquatic systems: The economic problem. Bulletin of Marine Science **70**:541-552.

Pientka, B. and D. L. Parrish. 2002. Habitat selection of predator and prey: Atlantic salmon and rainbow smelt overlap, based on temperature and dissolved oxygen. Transactions of the American Fisheries Society **131**:1180-1193.

Pigeon, D., J. J. Dodson, and L. Bernatchez. 1998. A mtDNA analysis of spatiotemporal distribution of two sympatric larval populations of rainbow smelt (Osmerus mordax) in the St. Lawrence River estuary, Quebec, Canada. Canadian Journal of Fisheries and Aquatic Sciences **55**:1739-1747.

Pimentel, D. 2005. Aquatic nuisance species in the New York State canal and Hudson River systems and the Great Lakes basin: An economic and environmental assessment. Environmental Management **35**:692-701.

Pimentel, D., S. McNair, J. Janecka, J. Wightman, C. Simmonds, C. O'Connell, E. Wong, L. Russel, J. Zern, T. Aquino, and T. Tsomondo. 2001. Economic and environmental threats of alien plant, animal, and microbe invasions. Agriculture Ecosystems & Environment **84**:1-20.

Pimentel, D., R. Zuniga, and D. Morrison. 2005. Update on the environmental and economic costs associated with alien-invasive species in the United States. Ecological Economics **52**:273-288.

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.

Power, M. and M. J. Attrill. 2007. Temperature-dependent temporal variation in the size and growth of Thames estuary smelt *Osmerus eperlanus*. Marine Ecology-Progress Series **330**:213-222.

R Development Core Team. 2009. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rand, P. S. and D. J. Stewart. 1998a. Dynamics of salmonine diets and foraging in Lake Ontario, 1983-1993: a test of a bioenergetic model prediction. Canadian Journal of Fisheries and Aquatic Sciences **55**:307-317.

Rand, P. S. and D. J. Stewart. 1998b. Prey fish exploitation, salmonine production, and pelagic food web efficiency in Lake Ontario. Canadian Journal of Fisheries and Aquatic Sciences **55**:318-327.

Ranta, E., V. Kaitala, and P. Lundberg. 1997. The spatial dimension in population fluctuations. Science **278**:1621-1623.

Reynolds, C. 2006. Ecology of Phytoplankton. Cambridge University Press, Cambridge, UK.

Ricklefs, R. E. 2001. The Economy of Nature. 5th edition. W. H. Freeman and Company, New York.

Rudstam, L. G. and J. J. Magnuson. 1985. Predicting the vertical distribution of fish populations: analysis of cisco, *Coregonus artedii,* and yellow perch, *Perca flavescens*. Canadian Journal of Fisheries and Aquatic Sciences **42**:1178-1188.

Rudstam, L. G., S. L. Parker, D. W. Einhouse, L. D. Witzel, D. M. Warner, J. L. Stritzel, D. L. Parrish, and P. J. Sullivan. 2003. Application of in situ target-strength estimations in lakes: examples from rainbow-smelt surveys in Lakes Erie and Champlain. Ices Journal of Marine Science **60**:500-507.

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**.

Rudstam, L. G., A. J. VanDeValk, and M. D. Scheuerell. 2002. Comparison of acoustic and Miller high-speed sampler estimates of larval fish abundance in Oneida Lake, New York. Fisheries Research **57**:145-154.

Rupp, R. S. 1965. Shore-spawning and survival of eggs of the American smelt. Transactions of the American Fisheries Society **94**:160-168.

Saint-Laurent, R., M. Legault, and L. Bernatchez. 2003. Divergent selection maintains adaptive differentiation despite high gene flow between sympatric rainbow smelt ecotypes (Osmerus mordax Mitchill). Molecular Ecology **12**:315-330.

Sala, O. E., F. S. Chapin, J. J. Armesto, E. Berlow, J. Bloomfield, R. Dirzo, E. Huber-Sanwald, L. F. Huenneke, R. B. Jackson, A. Kinzig, R. Leemans, D. M. Lodge, H. A. Mooney, M. Oesterheld, N. L. Poff, M. T. Sykes, B. H. Walker, M. Walker, and D. H. Wall. 2000. Biodiversity - global biodiversity scenarios for the year 2100. Science **287**:1770-1774.

Selgeby, J. H., W. R. MacCallum, and M. H. Hoff. 1994. Rainbow smelt - larval lake herring interactions: competitors of casual acquaintances? Page 9. U.S. National Biological Survey.

Shambaugh, A. D., A. Duchovnay, and A. Mcintosh. 1999. A survey of Lake Champlain's plankton. Pages 323-340 *in* T. O. Manley and P. Manley, editors. Lake Champlain in transition: from research toward restoration. American Geophysical Union, Washington, DC.

Simmonds, J. E. and D. MacLennan. 2005. Fisheries acoustics: theory and practice. 2nd edition. Blackwell Science Ltd, Oxford, UK.

Sirois, P. and J. J. Dodson. 2000. Critical periods and growth-dependent survival of larvae of an estuarine fish, the rainbow smelt Osmerus mordax. Marine Ecology-Progress Series **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.

Spiegelhalter, D., A. Thomas, N. Best, and D. Lunn. 2003. WinBUGS. MRC Biostatistics Unit, Cambridge, UK.

Stearns, S. C. 1976. Life-history tactics: a review of the ideas. The Quarterly Review of Biology **51**:3.

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.

Stickney, M., C. Hickey, and R. Hoerr. 2001. Lake Champlain Basin Program: working together today for tomorrow. Lakes & Reservoirs: Research & Management **6**:217-223.

Stockwell, J. D., D. L. Yule, T. R. Hrabik, J. V. Adams, O. T. Gorman, and B. V. Holbrook. 2007. Vertical distribution of fish biomass in Lake Superior: implications for day bottom trawl surveys. North American Journal of Fisheries Management **27**:735-749.

Tam, A. C. and C. K. N. Patel. 1979. Optical absorptions of light and heavy water by laser optoacoustic spectroscopy. Appl. Opt. **18**:3348-3358.

Taylor, E. B. 2001. Status of the sympatric smelt (Genus osmerus) populations of Lake Utopia, New Brunswick. Canadian Field-Naturalist **115**:131-137.

Taylor, E. B. and P. Bentzen. 1993. Evidence for Multiple Origins and Sympatric Divergence of Trophic Ecotypes of Smelt (Osmerus) in Northeastern North-America. Evolution **47**:813-832.

Tillitt, D. E., J. L. Zajicek, S. B. Brown, L. R. Brown, J. D. Fitzsimons, D. C. Honeyfield, M. E. Holey, and G. M. Wright. 2005. Thiamine and Thiaminase Status in Forage Fish of Salmonines from Lake Michigan. Journal of Aquatic Animal Health **17**:13-25.

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.

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**:359-372.

Urho, L. 1992. Morphological and Ecological Differences in the Development of Smelt and Herring Larvae in the Northern Baltic Sea. Sarsia **77**:1-10.

Urick, R. J. 1983. Principles of Underwater Sound. 3rd edition. Peninsula Publishing, Los Altos, California.

Waldman, J. R., C. Grunwald, and I. Wirgin. 2006. Evaluation of the native status of sea lampreys in Lake Champlain based on mitochondrial DNA sequencing analysis. Transactions of the American Fisheries Society **135**:1076-1085.

Wells, L. 1968. Seasonal depth distribution of fish in southeastern Lake Michigan. U.S. Fish and Wildlife Serice Fisheries Bulletin 67:15 p.

Wetzel, R. G. 2001. Limnology. 3rd edition. Elsevier Science, San Diego, California.

Wilcove, D. S., D. Rothstein, J. Dubow, A. Phillips, and E. Losos. 1998. Quantifying threats to imperiled species in the United States. BioScience **48**:607-615.

Wistbacka, S., A. Heinonen, and G. Bylund. 2002. Thiaminase activity of gastrointestinal contents of salmon and herring from the Baltic Sea. Journal of Fish Biology **60**:1031-1042.

Zaret, T. M. and A. S. Rand. 1971. Competition in tropical stream fishes: support for the competitive exclusion principle. Ecology **52**:336-342.