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Early mortality and freshwater forage fish recruitment: nonnative alewife and native rainbow smelt interactions in Lake Champlain

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Abstract: We studied the consequences of a nonnative species introduction and changes in temperature on early mortality and recruitment of native rainbow smelt (*Osmerus mordax*) and nonnative alewife (*Alosa pseudoharengus*) in Lake Champlain using a simulation model. Distribution patterns of adults and young-of-year (YOY) fish were predicted using a model based on observed distribution of different age groups as a function of temperature and light profiles simulated on a daily basis. Mortality rates averaged over the growing season were calculated as a function of fish densities and overlap between adults and YOY. Survival of YOY rainbow smelt and alewife depended on which predator was most abundant. Rainbow smelt YOY mortality rates are highest when rainbow smelt adults are abundant and alewife YOY mortality rates are highest when alewife adults are abundant, potentially allowing coexistence. August and September mortality rates were higher in the climate change scenario because of increased overlap of adults and YOY of both species. These results indicate that accounting for spatiotemporal fish distribution patterns can be important when forecasting the interacting effects of climate change and aquatic invasive species on fish recruitment.

Introduction

Environmental and biological mechanisms causing variable recruitment in fish populations have long been of interest to fisheries science (Cushing 1975; Wootton 1990; Diana 2004) and has received increased attention lately as we strive to predict effects of future climate change (e.g., Vert-pre et al. 2013; Feiner et al. 2015). Further, there is a continuing influx of nonnative species into many systems. Both climate change and new species are likely to affect recruitment and young-of-the-year (YOY) fish survival.

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

We are beginning to understand environment-driven recruitment dynamics in freshwater systems, with several recent studies conducted in the Laurentian Great Lakes of North America. In recent years, bloater (*Coregonus hoyi*) recruitment in Lake Huron has been predictable based on population demographics and alewife (*Alosa pseudoharengus*) abundance (Collingsworth et al. 2014). Alewife recruitment was more variable than bloater recruitment and affected by salmon predation and environmental factors. Temperature was influential in the production of strong alewife year classes in lakes Huron and Michigan, with more recruitment in warmer years (Madenjian et al. 2005; Collingsworth et al. 2014). These authors and others have correlated YOY survival with environmental factors in many freshwater systems, but the underlying

mechanisms behind these correlations are not well understood and these mechanisms may be species and system specific. Here we investigate the possible mechanisms regulating rainbow smelt and alewife recruitment in Lake Champlain, New York, Vermont and Quebec.

Rainbow smelt (*Osmerus mordax*) and alewife are pelagic fish species native to the Northwest Atlantic Ocean that are in many freshwater lakes in North America where they have invaded or been introduced as food for sportfish. These two species, in addition to native coregonids, are the forage fish base of valuable salmonid sport fisheries in the Laurentian Great Lakes and elsewhere in North America (e.g., Weidel et al. 2017). In Lake Champlain, a large freshwater lake on the border of New York (USA), Vermont (USA), and Quebec (Canada), rainbow smelt are native and alewife are not (Marsden and Hauser 2009). Alewife were first collected in 2003, and the population expanded rapidly in 2007 (Marsden and Hauser 2009). Both species prey on smaller fish including members of their own species (Brandt 1980; Henderson and Nepszy 1989; Moring and Mink 2002; Parker Stetter et al. 2007; O'Brien et al. 2014). In many systems, cannibalism is a primary driver of the population dynamics of the species, particularly of rainbow smelt (Rhodes et al. 1974; Lantry and Stewart 2000; Parker Stetter et al. 2007). Predation rates are a function of density of YOY and spatial overlap between adults and YOY (Parker Stetter et al. 2007). In most species, including alewife and rainbow smelt, YOY fish prefer higher temperatures than adults, which affect the depth distribution and spatial overlap between age groups (Ferguson 1958; Magnuson et al. 1979; Brandt et al. 1980; Crowder et al. 1981; Simonin et al. 2012).

Rainbow smelt recruitment is related to stock size more than to environmental variables in Lake Michigan, but accounting for non-stationarity in this relationship improves recruitment model fit and suggests there is a need to better understand environmental effects (Feiner et al. 2015). Environmental factors including spring precipitation are influential in the main basin of

Lake Huron, likely because of their influence on stream spawning habitat (O'Brien et al. 2014). Cannibalism was also influential in Lake Huron, with a negative relationship between adult spawning biomass and recruitment (O'Brien et al. 2014), as is also the case in lakes Erie and Champlain (Henderson and Nepszky 1989; Parker Stetter et al. 2007). In addition, rainbow smelt recruitment has been related to salmonid predation (Stewart et al. 1981), though the relationship is sometimes positive, with salmonid predation on age 1 and older rainbow smelt improving recruitment (O'Brien et al. 2014).

Here we develop a simulation model to explore the consequences of nonnative species introduction and changes in temperature on freshwater fish survival. We focused on the mortality pattern of YOY rainbow smelt and alewife over the first three to four months of life in Lake Champlain as affected by predation by adult rainbow smelt and alewife. To isolate the effects of cannibalism/predation, we did not include competitive interactions between YOY. The model estimates mortality of YOY fish of both species due to predation by the adults of both species while accounting for the spatial distribution of YOY and adults. Our objectives were to: 1) investigate the pattern of mortality of YOY rainbow smelt and YOY alewife through the first growing season with and without adult alewife present, 2) explore whether alewife are likely to replace rainbow smelt as a consequence of predation on YOY, and, 3) explore what effect climate-induced changes in temperature may have on mortality of YOY rainbow smelt and YOY alewife as a result of changing distributions of YOY and adults of both species.

Materials and methods

We created a model simulating YOY rainbow smelt and alewife mortality over the first four months of life in Lake Champlain. The model runs on a daily time step. Each day, the

vertical distribution of adult and YOY fish are predicted using age group and species-specific temperature and light preferences and the temperature and light profiles for that day. Fish distributions change daily as temperature and light profiles change through the season. Predation is a function of overlap between predator and prey, along with YOY growth and adult gape limitation. R (R Development Core Team 2018) is used for model fitting and all simulations.

Distribution simulation

We previously determined that rainbow smelt and alewife vertical distributions are predictable based on temperature and light gradients (Fig. 1; Simonin et al. 2012). For our new simulation model, we first developed temperature and light preference functions from the observed distributions and measured light and temperature profiles following Boscarino et al. (2010). The derivation of these functions is detailed in the Appendix.

The temperature and light preferences were then coupled with temperature and light vertical water column profiles to predict the proportion of the adult and YOY rainbow smelt and alewife populations at each 1-m depth interval each day of the growing season (Fig. 1). Daily water temperature and light profiles were obtained through linear interpolations between bi-weekly temperature profiles recorded by Vermont Department of Fish and Wildlife. Densities of all four fish groups were calculated for each depth by multiplying the expected proportion of the population at that depth with the total areal abundance (number per square meter) of each fish group. Thus, the density at each meter depth changes daily during the simulated time period as temperature and light changes, and is thus a function of temperature, light, and the simulated total population of each fish group (which is updated daily as the model progresses). The simulated time period was 1 June to 15 October (137 days). The initial densities of adult rainbow smelt and adult alewife were set to 0.05 fish/m^2 , and the initial density of YOY rainbow smelt and YOY alewife were set to 1 fish/m^2 . Rainbow smelt hatch about a month earlier than alewife

in Lake Champlain (Simonin et al. 2016), so rainbow smelt YOY enter the model on 1 June and alewife YOY enter on 1 July.

Predation simulation

Predation by adult individuals on YOY fish is a function of the density of YOY encountered by the average adult, also known as experienced density (YOY/m³; Tables 1 & 2; Parker Stetter et al. 2007). Experienced density is calculated for the average adult fish in the water column by summing over the vertical distribution of predator and prey (Table 2). Experienced density is related to predation rates through a functional response. The functional response was fit to previously-published empirical data relating rainbow smelt cannibalism rate to the average experienced density of YOY rainbow smelt calculated for adult rainbow smelt, and is linear relationship (Parker Stetter et al. 2007). Our relationship differs in that we do not first calculate a “proportion of cannibals” in the adult population as in Parker Stetter et al. (2007). We assume that all adult rainbow smelt and alewife can be piscivorous. The best fit to available data is (Fig. 2, $R^2 = 0.82$):

$$C = 1.93 * (ExDens) - 0.0217$$

where, C represents consumption per adult fish per day and $ExDens$ represents experienced density (Tables 1 & 2). The same relationship is used for adult alewife because no other information is available. The consumption rate is multiplied by the total population of adult fish to obtain the total number of each YOY species consumed by all adult rainbow smelt and all adult alewife in one day.

In addition to experienced density, predation is affected by the size of the YOY fish. Adult alewife are assumed to feed on fish less than 30 mm TL (e.g., Brooking et al. 1998). Adult rainbow smelt are assumed to feed on fish less than 80 mm TL (Stritzel Thompson 2011). Experienced density was therefore calculated only for YOY fish small enough to be eaten by

adults (<30 mm TL for alewife adults, <80 mm TL for rainbow smelt adults). YOY alewife and YOY rainbow smelt grow approximately linearly in Lake Champlain during June through September (Simonin 2015; Simonin et al. 2016). The growth rates obtained through daily ring counts and used in our model was 0.6 mm/d for rainbow smelt and alewife growth rate was 0.7 mm/d (Simonin et al. 2016, Table 2). The starting TL for YOY fish in the model is 5 mm.

Numbers of YOY of each species is decreased by the number consumed by adults each day. Mortality rates per day were calculated as the proportion consumed during the day divided by the population at the beginning of each day. In accordance with our objectives, the only source of mortality to YOY fish included in the simulation model was predation by adult rainbow smelt and alewife. Adult rainbow smelt and alewife daily mortality rate was also included in the model and was held at 0.002 throughout the simulation (Table 2).

Simulations included daytime and nighttime predation, using the same adult alewife distribution for day and night because our observations suggest they do not migrate vertically in Lake Champlain. We assumed daytime predation by adult rainbow smelt did not occur because they perform diel vertical migrations and do not overlap with YOY during the day (Simonin et al. 2012).

Alternative model runs

We modified the model to explore two additional questions. First, to compare the effects of predation by rainbow smelt vs. alewife, and to determine whether rainbow smelt will experience higher mortality because of alewife presence, we ran our simulation with varying proportions of rainbow smelt and alewife but keeping the initial total number of adult fish constant.

Second, in addition to running our simulation under normal Lake Champlain conditions, we ran the model using conditions representing a warmer climate. To do this, we by increasing

the epilimnion temperatures by 3 °C. All other starting conditions for this climate change scenario are the same as those used in previous model runs.

We compared the importance of estimating mortality using experienced density (which accounts for spatial overlap between predators and prey) vs. not accounting for differences in spatial overlap of predator and prey by setting temperature and light preferences to the same values for all fish groups. To do this, we set all fish groups to the same temperature and light values as those of YOY rainbow smelt and ran the model using these conditions. All other starting conditions were retained from previous model runs (e.g., areal densities of adults). Results from this additional simulation were used to explore the importance of accounting for vertical distributions of fish when estimating YOY mortality rates.

Results

Distributions and experienced density

Experienced density was highest in June and July for both adult fish group (Fig. 3). This is expected as YOY fish density is highest at that time, which was the case in part because simulated densities of YOY fish were highest in June and early July. Also, thermal stratification was less pronounced in June, allowing adult rainbow smelt distributions to partially overlap with YOY rainbow smelt at night. This was particularly true for YOY rainbow smelt because they hatch a month earlier than YOY alewife, and thus are exposed to predation for a longer period of time. In August, strong thermal stratification more effectively separated adult rainbow smelt from YOY of both species until September when YOY rainbow smelt moved into the thermocline because epilimnion temperatures increased above their preferred range. Rainbow smelt YOY outgrow predation by adult alewife in mid-July and YOY alewife outgrow adult

alewife predation in early August. Adult rainbow smelt consume YOY of both species until October.

YOY mortality pattern

If adult alewife are absent, our simulation shows that YOY rainbow smelt daily mortality rates were highest in June, then decreased steadily and increased again in September. The highest rainbow smelt daily mortality rates occurred in September (Fig. 4A). With alewife in the system, June mortality increased and is the month with the highest mortality rates, with rainbow smelt mortality in the June about twice as high as in September (Fig. 4B).

When comparing the effects of predation by rainbow smelt vs. alewife on YOY mortality, accounting for vertical dynamics is important. The model runs used in this comparison varied the proportion of the adult fish population composed of rainbow smelt vs. alewife (Figs. 4 & 5). When simulating recruitment and YOY mortality using only a density-dependent relationship, the highest overall mortality rates occurred when only rainbow smelt were in the system (Fig. 5A). Furthermore, rainbow smelt YOY experienced consistently higher mortality rates than alewife in this simulation because they grow slower and hatch earlier (Table 1; Simonin et al. 2016).

We explored the importance of the predator species by simulating YOY survival with different relative densities of the two predators. In these simulations, we compared survival rates of both YOY groups given an adult fish population of the same total abundance as in the standard run but consisting of all rainbow smelt, 75% rainbow smelt, 50% of both species, 25% rainbow smelt and all alewife. The relative survival of YOY rainbow smelt and alewife in the model did depend on which predator is most abundant. Rainbow smelt YOY mortality rates are highest when only rainbow smelt adults are present, and alewife YOY mortality rates are highest when only alewife adults are present (Fig. 5B). Both rainbow smelt YOY and alewife YOY are

included in the simulation independent of whether adults are present. When the abundance of rainbow smelt and alewife adults are the same, rainbow smelt YOY mortality rates are higher than those of YOY alewife (Fig. 5B).

Changes in temperature

We also compared YOY mortality rates under 2008 conditions in Lake Champlain with rates under a scenario of 3 °C higher epilimnetic temperature (after Livingstone 2003) while maintaining the same thermocline depth as in 2008 (Fig. 6). We found higher YOY June mortality rates under normal conditions, but also a slightly longer period of pre-stratification alewife predation in projected future conditions (Fig. 6). Mortality rates in late August and early September were also higher in our climate change scenario, though they decreased to a rate lower than the current rate by October.

Discussion

Distributions and experienced density

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

Adult alewife experienced density values are a function of YOY size and abundance to a greater extent than adult rainbow smelt experienced density values. Adult alewife overlap with YOY of both species throughout the year. However, later in the season, YOY fish become too large for alewife to consume and mortality from predation by adult alewife declines. This is in contrast to the importance of thermal separation for predictions of predation by adult rainbow smelt. Although alewife prefer warmer temperatures, the species is known to move into cooler depths to feed when necessary (Olson et al. 1988; Boscarino et al. 2009; Riha et al. 2017), and it is possible that alewife distributions currently observed in Lake Champlain could change with changes in zooplankton populations. This type of change, which would move alewife deeper in the epilimnion, would increase overlap between adult alewife and YOY rainbow smelt distribution and increase experienced density. June YOY mortality would be increased by this change in distribution, but YOY mortality later in the year would remain similar because adult alewife are gape limited at that time.

Patterns of YOY mortality

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

YOY, pushing YOY into the narrow thermocline and into closer proximity to adult rainbow smelt that reside in the thermocline. As temperatures decrease in the epilimnion in September and October, the spatial separation between YOY and adult rainbow smelt increases. This continues until autumn (September-October) when lake mixing increases overlap again.

Growth also influences YOY mortality. In our model, adult alewife can consume YOY up to 30 mm, but this is likely the upper limit of what is possible (Brooking et al. 1998). YOY alewife had relatively fast growth rates in Lake Champlain during our study period (Simonin 2015; Simonin et al. 2016), which reduces YOY alewife mortality by cannibalism. Rainbow smelt YOY have slower growth than alewife, and so are exposed to predation by alewife adults until 40-50 days post-hatching. Based on our observations in Lake Champlain, adult rainbow smelt consume YOY of both species for most of the period over which our model runs, so the model uses 80 mm TL as the maximum fish size consumed by adult rainbow smelt. However, it is likely that predation/cannibalism efficiency is reduced as YOY grow and become better able to escape adult predators, even if gape size is not limiting. Thus, it is possible our model over-predicts autumn mortality caused by adult rainbow smelt. YOY growth is also density dependent (Stritzel Thomson et al. 2011), and in years with particularly low YOY densities, YOY fish may grow more quickly and reach a larger size by October, such that adult rainbow smelt are less able to catch and consume them. If this happens, autumn mortality will again be lower than our model predicts.

The addition of alewife to this system increases June and early July mortality to levels not previously experienced by YOY rainbow smelt. YOY rainbow smelt in Lake Champlain were previously partially protected from cannibalism by thermal stratification from July through part of September (Parker Stetter et al. 2006, 2007; Overton et al. 2012). One primary way alewife affect native fish communities is through predation on larvae (Madenjian et al. 2008). Seasonal

inshore-offshore migrations of adult alewife in the Great Lakes (Madenjian et al. 2008) may affect which larvae are susceptible to adult alewife predation, but these migrations may be less important in Lake Champlain and smaller lakes.

Our model does not consider daytime predation by rainbow smelt adults as we expect predation occurs mainly during the night because adult rainbow smelt are deeper than YOY fish by day and do not interact with YOY individuals (Simonin et al. 2012). Alewife conversely are in the epilimnion of Lake Champlain during both day and night. Adult alewife school during the day in Lake Champlain (Simonin, unpublished data) and elsewhere (Olson et al. 1988; Riha et al. 2017), and we do not know the effect this has on their feeding behavior. Alewife are visual predators (Janssen 1980; Boscarino et al. 2010) and do feed in other systems during the day (e.g., Crowder et al. 1981), supporting our assumption that they feed during the day in Lake Champlain.

Invasibility

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

When alewife became well established in the Laurentian Great Lakes, relatively few larval fish predators were highly abundant, as rainbow smelt had already begun to decline somewhat in

abundance and native coregonids were not abundant (Smith 1972; Madenjian et al. 2008). Thus, YOY alewife mortality was likely low until cannibalism increased with higher abundance of adult alewife (Rhodes et al. 1974). In Lake Champlain, however, rainbow smelt are native and have been present in high abundances (Kirn and LaBar 1996; Stritzel Thomson et al. 2011). Despite this, alewife were able to become established. Our analysis suggests this is in part because YOY alewife distribution does not widely overlap with that of adult rainbow smelt.

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

Climate change scenario

The climate scenario we analyzed was only one of several possible future scenarios, but it suggests changes in climate may cause unexpected changes in YOY rainbow smelt and alewife mortality. In our simulation, June mortality decreased slightly because the thermocline formed more quickly, but mortality over the rest of the simulation increased somewhat. This is because the 3 °C increase in epilimnetic temperature caused the epilimnion to become warmer than what is preferred by YOY rainbow smelt and, to a lesser extent, YOY alewife. This will make them move deeper and into the metalimnion in closer proximity to adult rainbow smelt, thus increasing experienced density and predation. In contrast, during late August and September

under 2008 conditions, YOY preferred temperatures were found in or throughout the epilimnion, and YOY fish were spread more widely through this layer, thus decreasing experienced density and mortality.

These results suggest effects of climate and abiotic environmental change on recruitment relationships deserve attention, as has been suggested by Vert-pre et al. (2013) and Feiner et al. (2015), because these effects are complex and their direction and magnitude may differ, and even cancel each other out, as YOY fish progress through their first year of life. The primary effects of climate change on abiotic aspects of aquatic systems may include changes in mixing and stratification regimes, ice cover patterns, and hydrology (Nickus et al. 2010). Effects of these changes up food webs are not well understood. Our approach directly links abiotic conditions to fish distribution patterns and subsequent species interactions. Future work could expand on this approach by including additional nonlinearities in growth and variable abiotic conditions, including changes (most likely, increases) in YOY growth rates that may occur as a result of increasing temperatures.

Current climate and lake modeling efforts suggest changes in epilimnetic and thermocline structure may be expected if current climate trends continue. In stratified lakes, predictions are that the epilimnion will be warmer and stratification more stable (Livingstone 2003). These trends intuitively suggest conditions that may reduce YOY mortality, because thermal stratification separates adult rainbow smelt from YOY in Lake Champlain and other similar systems (Brandt et al. 1980; Crowder et al. 1981; Crowder and Magnuson 1982; Kirn and LaBar 1991; Simonin et al. 2012) and YOY typically prefer warmer conditions than adults (Magnuson et al. 1979, 1990). However, our simulation suggests that mortality rates could remain constant or even increase because adults and YOY temperature preferences may move them into closer proximity to each other compared with current conditions. We had expected lower overlap, and

therefore, lower cannibalism by rainbow smelt throughout the year. Our results illustrate that spatial distributions and temperature preferences of the species of interest are important components of predictions of aquatic species interactions in a warmer climate.

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Table 1. All parameters and parameter values used in our model simulation functions, with Table 2 symbols identified.

Symbol	Parameter description	Adult rainbow smelt	YOY rainbow smelt	Adult alewife	YOY alewife
<i>AD</i>	Starting areal density (#/m ²)	0.05	1	0.05	1
<i>VD</i>	Volumetric fish density	n/a	n/a	n/a	n/a
<i>B</i>	Simulated basin area (m ²)	10000	10000	10000	10000
<i>M</i>	Mortality rate (proportion of population not surviving per day)	0.002	Calculated in model	0.002	Calculated in model
<i>L</i>	Fish total length (mm)	n/a	Starting: 5	n/a	Starting: 5
<i>G</i>	Growth rate (mm/day)	n/a	0.6	n/a	0.7
<i>V</i>	Proportion of YOY fish vulnerable to adult alewife	n/a	n/a	n/a	n/a
<i>S</i>	Maximum fish size consumed (mm)	n/a	n/a	n/a	n/a
<i>ARS</i>	Adult rainbow smelt	n/a	n/a	n/a	n/a
<i>AAW</i>	Adult alewife	n/a	n/a	n/a	n/a
<i>YRS</i>	YOY rainbow smelt	n/a	n/a	n/a	n/a
<i>YAW</i>	YOY alewife	n/a	n/a	n/a	n/a
<i>P</i>	A vector of proportions of fish at each 1-m depth bin in the water column, based on fish preferences. Sums to 1 over all depths. Subscripts denote age category and species.	n/a	n/a	n/a	n/a
<i>ExDens</i>	Experienced density for a given adult species [sp] for a particular YOY species	n/a	n/a	n/a	n/a
<i>C</i>	Consumption of either YOY rainbow smelt or alewife by adults. YOY species noted in subscript, with adult predator in brackets.	n/a	n/a	n/a	n/a

Table 2. Functions used in simulation of alewife and rainbow smelt density and YOY mortality in Lake Champlain.

Model Stage	Equation
Density [of young rainbow smelt] vulnerable to adult predation	$VD_{YRS}[vulnerable] = AD * V * P$
Density [of young alewife] vulnerable to adult predation	$VD_{YAW}[vulnerable] = AD * V * P$
Experienced Density (sums over all depth bins (i) to obtain YOY/m ³ /adult)	$ExDens = \sum_{i=1}^n P_i * VD_i$
Predation by adults on YOY	$C_{YOY\ species\ of\ interest} = 1.93 * (ExDens) - 0.0217$
Total consumption by adults	$TC = C_{YRS-ARS} * (adult\ areal\ density) + C_{YRS-AAW} * (adult\ areal\ density)$
Density t+1 [young fish]	$AD[t + 1] = AD[t] - CYRS$
Density t+1 [adult fish]	$AD[t + 1] = AD[t] * (1 - M[n])$
Fish length	$L[t + 1] = L[t] + G$

Figure captions

Fig. 1. Adult rainbow smelt, YOY rainbow smelt, and YOY alewife vertical distributions in relation to light and temperature in the Main Lake of Lake Champlain during June, August, and October, 2008 (modified from Simonin et al. 2012). YOY alewife were not present until 1 July.

Fig. 2. Relationship between experienced density and number of YOY rainbow smelt consumed by adult rainbow smelt in Lake Champlain. We assumed that all adult rainbow smelt fed on YOY fish. Data are from Parker Stetter et al. (2007).

Fig. 3. Daily experienced density values from 1 June to 15 October for adults and YOY rainbow smelt (RS) and alewife (ALE) in Lake Champlain. YOY alewife do not appear until 1 July. Panels (A-D) are labeled as adults-YOY (RS or ALE) for each combination.

Fig. 4. Daily mortality rates (proportion of YOY rainbow smelt and alewife cohorts consumed per day) from 1 June through 15 October with (A) only adult rainbow smelt present, and (B) only adult alewife present. YOY alewife do not appear until 1 July.

Fig. 5. Mean YOY daily mortality rates (i.e., mean proportion of YOY cohort consumed per day over the modeled time period) shown with A) no differences in vertical distribution of adult and YOY fish and B) with differences in vertical distribution patterns included. The modeled time period is from 1 June through 15 October, but YOY alewife do not appear until 1 July.

Fig. 6. Mortality rates (proportion of YOY rainbow smelt and alewife cohorts consumed per day) from 1 June through 15 October under (A) normal conditions and (B) under a climate change

564 scenario in which epilimnion temperatures are 3 °C warmer than those during 2008 in Lake
565 Champlain. YOY alewife do not appear until 1 July.
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Fig. 1.

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573 **Fig. 2.**

Fig. 3.

Fig. 4.

Fig. 5.

Fig. 6.

Appendix: Calculation of temperature and light preferences

We previously determined that rainbow smelt and alewife vertical distributions are related to temperature and light gradients (Fig. 1; Simonin et al. 2012). To predict distributions in any temperature and light field, we developed temperature and light preference functions using the observed distributions from Simonin et al. (2012). Temperature preference functions used Thornton and Lessem curves, a relationship originally developed as an algorithm for modifying biological rates as a function of temperature (Thornton and Lessem 1978). The Thornton and Lessem curve is defined as,

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

And,

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

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

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

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

Where T is the observed temperature, P_1 , P_2 , P_3 and P_4 are fixed and identified in Appendix Table 1, and θ_3 is 2° C greater θ_2 . Thus, three temperature preference parameters (θ_1 , θ_2 and θ_4) were fit for each species/age category, with the upper and lower maximum preferences linked. A

normal distribution was assumed for the light preference function for adult rainbow smelt, YOY rainbow smelt, and YOY alewife as,

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

Where L is the observed light level in the 460-580 nm wavelength range (PAR, log W/m²), μ is the preferred light level (also in log W/m²) and σ is standard error of the light preference function. We used PAR values instead of lux or fishlux (see Boscarino et al. 2010) because that is the unit measured by our light meter. Temperature and light preferences were then multiplied together to calculate a final preference function as,

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

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

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

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

Where P_{spi} is the value of P_{sp} at depth i , B_i is the proportion of fish found at that depth, and $\sum P_{sp}$ is the sum of P_{sp} over all depths. Parameter optimization was done using the `optim` routine in R (R Development Core Team 2018) to minimize the sum of the squared difference between the proportion of fish present at an observed temperature-light combination, and the predicted proportion of fish present under those conditions. This fitting used all observed data from June through October, without assuming any changes in preference functions for that time period.

Table A.1. Parameters used to develop temperature preference.

Symbol	Parameter description	Adult rainbow smelt	YOY rainbow smelt	Adult alewife	YOY alewife
P_1	Value near lower threshold	0.4	0.4	0.4	0.4
P_2, P_3	Value near max. preference	0.98	0.98	0.98	0.98
P_4	Value near upper threshold	0.01	0.01	0.01	0.01
θ_1	Lower threshold temperature (°C)	6.1	5.8	20.1	9.1
θ_2	Lower max. preference (°C)	10.4	13.0	26.9	17.1
θ_3	Upper max. preference (°C)	12.4	15.0	28.9	19.1
θ_4	Upper threshold temperature (°C)	17.2	19.0	34.0	23.1
μ	Mean light preference (Log W/m^2)	-7.74	-6.25	n/a	-4.9

Reference

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