Rainbow smelt population responses to species invasions and change in environmental condition

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Abstract

Invasive species can cause major disruptions on native food webs, yet the impact of species introductions and whether they will become invasive appears to be context-dependent. Rainbow smelt and alewife co-exist as invasive species in the Laurentian Great Lakes and as native species on the Atlantic coast of North America, but in Lake Champlain rainbow smelt is the dominant native forage fish and alewife are invasive. Alewife became abundant by 2007, providing an opportunity to explore the dynamics of these two species in a system where only one is invasive. We used data from a 31-year forage fish survey to compare demographics of rainbow smelt populations in three basins of Lake Champlain with different volumes, nutrient levels, and predator abundances. Rainbow smelt catch-per-unit-effort (CPUE) remained constant in the large, deep Main Lake before and after alewife invaded, but decreased in the two smaller basins. Declines were primarily a result of increased age-0 and age-1 mortality. Predation by top piscivores, system productivity, and competition for resources alone could not explain the patterns in CPUE across the basins. The mechanisms that allow alewife and rainbow smelt to co-exist could be related to system volume and oxythermal habitat availability, and may explain why the two species do not negatively affect each other in the Great Lakes. Summer hypoxia in the smaller basins could force individuals into smaller habitat volumes with higher densities of competitors and cannibalistic adult rainbow smelt. Habitat availability may mediate the impact of invasive alewife on native rainbow smelt.

***Keywords**: alewife, demographics, resource competition, oxythermal habitat availability, predation*

Introduction

Effects of invasive species on ecosystems are difficult to predict based on the ecology of the invading species in their native range, or by their behavior as an invasive species in other systems (Mackie and Schloesser, 1996). Invasive species may have antagonistic or synergistic effects with other invasive species, although facilitation between invasive species (i.e., the invasion meltdown hypothesis) is most common (Braga et al., 2018; Glon et al., 2017; Simberloff and Von Holle 1999). Native species' responses to invasive species can range from improved fitness and survival to local extirpation (Jacobs et al., 2017; Madenjian et al., 2008). In aquatic systems, these responses can be related to system size, complexity of the native community, and disturbance history, including prior invasions and loss of native species, and habitat degradation (Brook et al., 2008; Ricciardi and Macisaac, 2010). Comparison of systems in which two species are both native, are both invasive, or one of each, can inform our understanding of the dynamics between native and invasive species.

Rainbow smelt (*Osmerus mordax*) and alewife (*Alosa pseudoharengus*) are native to and coexist along the Atlantic coast of North America (Bigelow and Schroeder, 2002). They also coexist in the Laurentian Great Lakes, where both species invaded in the early 1900s (Mills et al., 1993) and are now important prey for top predators, including lake trout (*Salvelinus namaycush*) and introduced Pacific salmonines (*Oncorhynchus* spp.; Happel et al., 2018; Ray et al., 2007; Stewart et al., 1981). Both species are pelagic planktivores and affect many native species in the Great Lakes because they feed on native larval fishes, compete with other planktivores, and are linked to thiamine deficiency in salmonine predators (Harder et al., 2018; Krueger et al., 1995; Madenjian et al., 2008; Myers et al., 2009). The two species typically coexist at unequal biomasses in the Great Lakes (e.g., Kao et al., 2016), but they do not appear to negatively affect each other, despite spatial overlap of larvae and age-0 life-stages (Madenjian et al., 2008). In some systems, however, alewife are invasive and rainbow smelt are native (e.g., Kircheis et al., 2004), and this context provides the opportunity to further examine their interactions . Here, we focus on the effects of a recent invasion of alewife on a native rainbow smelt population in Lake Champlain, USA.

Lake Champlain has a relatively intact biotic community, with only two species extinctions (lake trout and Atlantic salmon, but reintroduced by stocking), and a relatively small number of introduced species (51) relative to the Great Lakes (at least 188; Lake Champlain Basin Program, 2018; Marsden and Hauser, 2010; Marsden and Langdon, 2012; Ricciardi, 2006). The native coldwater prey fish community in Lake Champlain has low diversity, consisting primarily of rainbow smelt, trout-perch (*Percopsis omiscomaycus*), slimy sculpin (*Cottus cognatus*), and cisco (*Coregonus artedi*). Low diversity communities can be more vulnerable to species invasion under the biotic resistance hypothesis (Freestone et al., 2013; Elton, 1958), so the invasion of a prey fish in Lake Champlain may have important effects. The addition of alewife as an alternative prey could release rainbow smelt from predation and indirectly lead to increased rainbow smelt abundance. However, predatory release might eventually lead to higher rainbow smelt cannibalism, as 38-93% of age-0 rainbow smelt mortality in the lake prior to alewife invasion has been attributed to cannibalism (Parker Stetter et al., 2007).

Rainbow smelt in Lake Champlain supported native populations of landlocked Atlantic salmon (*Salmo salar*), lake trout and walleye (*Sander vitreus*) (Marsden and Langdon, 2012). Since the extirpation of the two salmonine species in the 1800s and the decline of walleye in the 1900s, rainbow smelt populations appeared to be regulated by cannibalism and intra-specific competition rather than predation by stocked salmonines (He and Labar, 1994; Kirn and Labar, 1996; Labar, 1993; Parker-Stetter et al., 2007; Stritzel-Thomson et al., 2011), in spite of sustained stocking of lake trout and Atlantic salmon that began in 1973. Lake trout stocking has been maintained at an average of 83,400 yearling equivalents since 1996 (Fisheries Technical Committee, 2016, 2008). Larger numbers of Atlantic salmon are stocked annually (an average of 278,000 yearling equivalents since 1987). Steelhead trout (*Oncorhynchus mykiss*) and brown trout (*Salmo trutta*) are also stocked at numbers similar to lake trout (B. Pientka, unpublished data). Walleye stocking in three tributaries started in the late 1980s.

Alewife were first discovered in Lake Champlain in 2003 and became abundant by 2007 (Marsden and Hauser, 2009), and have been incorporated into diets of walleye, Atlantic salmon, and to a lesser extent, lake trout (Simonin et al., 2018). Since the alewife invasion, body size of two zooplankton groups decreased to or below the size of alewife feeding preference (Mihuc et al., 2012), suggesting alewife could indirectly suppress rainbow smelt through competition for zooplankton (Kircheis et al., 2004, Urban and Brant 1993). Adult alewife could also directly suppress rainbow smelt through predation on larvae as the two life stages spatially overlap during summer (Simonin et al., 2012).

The general understanding of alewife invasions in large lakes is based on the Great Lakes, where both alewife and rainbow smelt replaced overfished coregonine planktivores and do not appear to impact each other (Madenjian et al., 2008). In Lake Champlain, we hypothesized that the presence of a relatively intact fish community would preclude invasive alewife from having a significant negative impact on the robust population of rainbow smelt. Alternatively, relatively low prey fish diversity in Lake Champlain could make rainbow selt susceptible to an alewife invasion. We tested these hypotheses using long-term survey data from three separate and semi-isolated basins of Lake Champlain (the Main Lake, Malletts

Bay, and Northeast Arm). The three basins differed in predator composition and abundance, productivity, size, and oxythermal conditions (Table 1). Rainbow smelt populations in the three basins have different demographic structures that indicate the populations are largely isolated from each other, although they are not genetically different (Euclide et al., 2020). Specifically, we speculated that after alewife invaded (1) higher abundance of predators in the Main Lake could suppress alewife populations and keep them at low levels, and favor rainbow smelt population stability (defined as an absence of trends in catches pre- and post-alewife invasion), compared to the two smaller basins where predators are less abundant. Alternatively, (2) based on basin size, rainbow smelt abundance could decrease the most in Malletts Bay, because small volume increases spatial overlap (Evans and Loftus 1987; Latta 1995), oxythermal habitat may be limited (Hrycik et al., 2017), and alewife:rainbow smelt interactions may include competition or predation. Furthermore, higher food availability would reduce competition, so (3) based on primary productivity, rainbow smelt abundance should remain stable in the Northeast Arm, where phosphorus levels are the highest; or (4) higher zooplankton densities in the Northeast Arm and Malletts Bay would be able to sustain rainbow smelt abundance after alewife invasion; and (5) the presence of *Mysis diluviana* in the Main Lake could serve as a resource subsidy and sustain rainbow smelt after invasion. Additionally, we speculated that (6) if alewife affect only age-0 rainbow smelt, then rainbow smelt mortality rate past age-1 would not change, because interspecific predation largely occurs during the larval stage (Simonin et al., 2019). Finally, (7) we also expected rainbow smelt condition and length to decline if competition between rainbow smelt and alewife is high. Overall, our objective was to determine whether and how invasive alewife affected native rainbow smelt across heterogeneous regions of a large lake with a fish community that is relatively intact and of low diversity.

Material and methods

Study system

Lake Champlain is a large lake (26 km^3 and 1,130 km^2) located among Vermont, New York (US), and Québec (CAN; Fig. 1). The Main Lake extends from Crown Point (NY) at the south to Rouses Point (NY) at the north, and contains the largest volume and the deepest areas of the lake (Table 1). Malletts Bay and the Northeast Arm are isolated from each other and the Main Lake by large islands and several causeways up to 5.2 km long between islands and the mainland. Water exchange and fish passage are possible but limited through shallow, narrow connections in each causeway (see Fig. 3 in Marsden and Langdon, 2012). The three basins differ in their nutrient levels and total volume (Table 1). The Northeast Arm is the most productive basin and has an extensive hypoxic zone that limits available summer habitat for lake trout. The Main Lake is the largest basin and has moderate to low productivity, and Malletts Bay is the smallest and least productive basin. Major fish predators in all three basins include Atlantic salmon, burbot (*Lota lota*), and walleye. Lake trout are present in all basins in winter but not in Malletts Bay and the Northeast Arm during summer (B. Pientka, unpublished data), as temperatures in the causeway passages exceed their thermal optima and required oxythermal habitat in the smaller basins is limited in summer.

Long-term survey data

The Vermont Fish and Wildlife Department conducted standardized assessment sampling of rainbow smelt from 1990 to 2015. The five standard stations included one in each of Malletts Bay and the Northeast Arm, and three in the Main Lake: north (Valcour Island), central (Juniper Island), and south (Barber Point; Figure 1). The most consistent sampling was conducted using stepped-oblique midwater trawling at night from late July through mid-August, when young-of-year (YOY) and yearling-and-older (YAO) fishes were vertically separated by thermal stratification (Table 1; Labar, 1998). The 5-m x 5-m midwater trawl had tapered mesh from 20.3 to 2.9 cm, stretch measure, with a 1.3-cm cod end mesh (Labar, 1998). Trawls began at 35-m depth or just above lake bottom (26 m in Malletts Bay and 29 m in the Northeast Arm) and were fished for 10 minutes, raised approximately 3 m and fished again for 5 min at that depth, continuing in a steplike fashion until the net reached 10 m below the surface (Labar, 1998). Four trawls were conducted at each of the five standard stations. Catch per unit effort (CPUE) was calculated as catch per 55 min of trawling. Fifty rainbow smelt were randomly sampled from each trawl and frozen on board, so up to 200 individuals were used each year per station to collect population demographics. In the laboratory, rainbow smelt were measured for total length (TL) and weight. Otoliths were extracted and stored in an ethanol/glycerol mixture (70:30) and age was estimated by counting annuli using whole otoliths under 10-45x magnification. Floating gillnets (6 m deep x 21 m long with 7 panels of 6.25, 8, 10, 12, 15, 18 and 25 mm mesh) were added in 2008 to focus on YOY and YAO alewife, which are undersampled in the midwater trawl. However, alewife < 50 mm are not well captured by the gillnets either (Warner et al., 2002). Nets were set at standard stations before dark and fished for 4 hours, and CPUE was calculated as catch per 4 hours.

We used vertical profile data from the Lake Champlain Long-Term Water Quality and Biological Monitoring Project to describe the oxythermal habitat in each basin (https://dec.vermont.gov/watershed/lakes-ponds/monitor/lake-champlain). We selected three stations, one in each basin, sampled fortnightly from late April to early November, to represent conditions in the Main Lake, Malletts Bay, and the Northeast Arm (Fig. 1). We also analyzed changes in mean summer (July-August) crustaceans zooplankton density collected by the Lake Champlain long-term monitoring program since 1992 at the same stations. Zooplankton samples were collected with whole water vertical tows taken monthly or bi-weekly using a 30-cm diameter, 153-um mesh net during the day (Mihuc et al., 2012). Zooplankton were identified to the lowest possible taxon. For the most abundant taxa (abundance > 5%) at the Main Lake and Northeast Arm stations, 7-10 individuals were measured per sample to estimate average length each year since 2001.

Data analysis

Annual data for rainbow smelt were pooled by basin and the resulting means were used for all the analyses. We tested for differences in CPUE among periods: 1987-2002 (before alewife invasion), 2003-2006 (invasion), and 2007-2015 (after invasion). We also tested for differences in average length (age-2+, because ages 0 and 1 were not well recruited into the gear) and Fulton's condition factor among periods for each basin using a Kruskal-Wallis pairwise comparison test. Fulton's condition, calculated for each individual, is the weight of a given individual divided by the cube of its length (Ricker, 1975). A scaling factor of 10^{-6} was applied to bring the condition close to 1. We pooled age-2 and age-3 fish for this analysis because condition cannot be compared across too many age classes due to allometric growth (Guy and Brown, 2007). We did not include weight comparisons because average length and weight were highly correlated (Pearson's product-moment correlation = 0.94).

We used longitudinal data (ages 2-5) of each cohort to calculate annual mortality rate (A). We estimated year-class CPUE in each year using the proportion of each year class in the annual subsamples of 200 individuals at each station, multiplied by the CPUE of that station that year. We calculated the instantaneous mortality rate Z as the slope of the linear relationship between age and the natural log of CPUE (Ogle, 2016):

$$\log(\mathrm{CPUE}) = Z * \mathrm{age} + \mathrm{intercept}.$$

We excluded age-0 and -1 because these ages were not fully recruited to the gear, and age-6 and older because none were collected after the alewife invasion. A is calculated as:

$$A = 1 - e^{-Z}$$

(Ogle, 2016). We compared annual mortality between the periods 1987-2002, before the arrival of alewife, and 2007-2015, after alewife became abundant. We used a Kruskal-Wallis pairwise comparison test for each of the three basins separately, and applied a Bonferroni correction of $\alpha/3$ for significance.

We calculated the maximum vertical habitat available for rainbow smelt using a sub-lethal threshold of 4.5 mg/l of dissolved oxygen (DO; Hrycik et al., 2017), and a temperature threshold of 16°C (Lantry and Stewart, 1993). Here, we used the extent of suitable oxythermal habitat in the vertical dimension as a proxy for habitat volume. For each sampling date, we extracted the shallowest depth for which temperature was below 16°C, and the deepest depth with DO concentration above 4.5 mg/l. The difference between these depths was used as an estimate of habitat availability for rainbow smelt.

Average densities of abundant zooplankton taxa each year were averaged before (1992-2002), during (2003-2006) and after (2007-2015) alewife invasion. Similarly, average length was estimated for 2001-2002, 2003-2006, and 2007-2015. For both zooplankton densities and lengths, we tested for differences among the three time periods using a Kruskal-Wallis pairwise comparison test.

All computational work and visualization was done using the packages *FSA* (Ogle, 2016), *ggplot2* (Wickham, 2016), and *PerformanceAnalytics* (Peterson and Carl, 2020), with R version 3.6.3 (R Core Team, 2020).

Results

Rainbow smelt CPUE was, on average, highest in the Northeast Arm (mean ± SD = 967 ± 1,095 fish per 55-min trawl), lowest in the Main Lake (265 ± 320), and intermediate in Malletts Bay (772 ±1,103) between 1987 and 2015 (Fig. 2A, Appendix A). CPUE in Malletts Bay and the Northeast Arm, however, were both lower in 2007-2015 than prior to and during alewife invasion ($p < 0.01$ for Malletts Bay and $p < 0.05$ for the Northeast Arm, Fig. 2A, Appendix B). CPUE increased significantly in Malletts Bay until 2002 (slope = 0.1, $p = 0.004$) and remained stable in the Northeast Arm (slope = 0.04, $p = 0.59$) until 2002, and decreased after 2003 ($p < 0.001$ in both basins, Figure 2B). CPUE remained unchanged in the Main Lake over the same time period (Figure 2). Overall, rainbow smelt CPUE declined 100-fold in the Northeast Arm and 30-fold in Malletts Bay after alewife became established in 2007. Alewife catches in floating gillnets were heterogeneous and the data should be treated with caution. However, the data support the field observation that alewife were consistently present in all basins (Fig. 3).

Average length of age-2+ rainbow smelt was not different between periods except in the Northeast Arm, where length increased between 1987-2002 and 2007-2015 ($p < 0.0001$, Fig. 4A, Appendix 1). Average length in 1987-2002 was highest in the Main Lake (147 ± 11.1 mm), lowest in Malletts Bay (127 ± 7.5 mm) and intermediate in the Northeast Arm (134 ± 9.1). In 2007-2012, after alewife became abundant, average length remained overall lowest in Malletts Bay (134 ± 14.2 mm), intermediate in the Main Lake (138 ± 13.8 mm) and highest in the Northeast Arm (153 ± 15.1 mm). Variability in length increased in all basins after alewife became established (Fig. 4). Condition was not significantly different between periods within each basin (Fig. 4B). Annual mortality differed in only one comparison, where it increased between 1987-2002 and 2003-2006 in Malletts Bay ($p = 0.007$, Fig. 4C, Appendix B).

The three basins stratify during the summer, with available oxythermal habitat more restricted in Malletts Bay and the Northeast Arm than in the Main Lake (Fig. 5, Appendix C). DO concentration remained above 5 mg/l between April and November at all depths in the Main Lake, but was below 4.5 mg/l every summer in Malletts Bay and the Northeast Arm (Fig. 5, Appendix C). The depth of the epilimnion increased during the summer in every basin, limiting the available near-surface habitat. Overall, habitat was most limited for rainbow smelt in the 1992-2002 period, during which the vertical habitat was restricted to 4 m or less for 73% of the days that were sampled between August 1st and October 31st in the Northeast Arm, and 52% of the time in Malletts Bay. The period of unfavorable conditions dropped to 36 and 41% in the Northeast Arm and Malletts Bay, respectively, during the 2007-2015 period (Fig. 6).

Zooplankton densities remained stable across the study periods at all three stations with the exception of declines in calanoid copepods and *Daphnia* sp. during the alewife colonization period (2003-2006) (Figure 7). Zooplankton body size did not change before and after the alewife invasion in the Main Lake and Northeast Arm, with the exception of *Daphnia retrocurva* which exhibited a decrease in body size after 2006 in the Main Lake (average length per period: 2001-2002 = 0.96 ± 0.04 mm, 2003-2006 = 1.03 ± 0.15 mm, 2007-2015 = 0.77 ± 0.11 mm; difference in means was between 2003-2006 and 2007-2015, $p = 0.05$; Figure 8).

Discussion

Our basic hypothesis that the rainbow smelt population of Lake Champlain would be resilient to the invasion of alewife was supported in one of our three study basins, in contrast with expectations drawn from the Great Lakes (Madenjian et al., 2008). Rainbow smelt CPUE remained stable in the Main Lake basin but declined sharply in Malletts Bay and the Northeast Arm. Based on the contrasting characteristics of the three basins in terms of habitat availability, productivity, food resources and predator abundance, we proposed several mechanisms to explain potential differences in how rainbow smelt might respond to alewife invasion. Our prediction that higher food availability would maintain rainbow smelt abundance in the face of competition with alewife was not supported. The decline in rainbow smelt CPUE was as severe in the relatively highly productive Northeast Arm as in the less productive Malletts Bay. Higher zooplankton densities in both of these basins did not prevent rainbow smelt population decline. Adult rainbow smelt mortality remained constant before and after alewife invasion, suggesting that the changes in CPUE were due to mortality at age-0 and age-1, which could be a consequence of predation, cannibalism, or competition. Average length and condition of rainbow smelt did not change before and after the invasion, suggesting that competition remained constant as rainbow smelt CPUE declined. The CPUE decline in the two smaller basins, compared to stable rainbow smelt CPUE in the larger Main Lake, suggests that presence of predators, habitat availability, and/or presence of *Mysis* as resource subsidies may mediate the impacts of alewife.

Top-down control by piscivores does not explain the patterns we observed. Predator abundance would need to have remained stable in the Main Lake and increased in the Northeast Arm and Malletts Bay to explain the patterns in rainbow smelt CPUE. In fact, predator abundance in the Main Lake likely decreased prior to the alewife invasion as lake trout annual stocking was reduced from an average of 185,900 to 83,400 yearling equivalents in 1996 while Atlantic salmon stocking remained constant. Although estimated survival and catches in annual assessments of both salmonines increased as a consequence of sea lamprey suppression in the mid-1990s, this increase likely did not fully compensate for the reduction in lake trout stocking (Marsden et al., 2003). Yet during 1987-2002, rainbow smelt CPUE remained relatively constant or increased in our three study basins, and only began to decline in the Northeast Arm and Malletts Bay in 2007, where lake trout are absent during the stratified period. Predation by adult alewife on young rainbow smelt is another possible mechanism to explain the apparent decline in age-0 and age-1 rainbow smelt in the Northeast Arm and Malletts Bay. A predation model based on seasonal vertical distributions of alewife and rainbow smelt, YOY growth rates, and gape-limitation of adult alewife predicted higher mortality of YOY rainbow smelt in the presence of invasive alewife in Lake Champlain (Simonin et al., 2019). However, predation by adult alewife as a driving force of rainbow smelt dynamics remains to be tested, as we found no evidence in the published literature that alewife consume YOY rainbow smelt (e.g., Brandt, 1980; Stewart and Binkowski, 1986 and references therein; Stewart et al., 2009).

The stability of rainbow smelt densities in the Main Lake before and after alewife invasion suggest that predators could facilitate coexistence between alewife and rainbow smelt. Predators may control the densities of both alewife and rainbow smelt, but the negative impact of predation on rainbow smelt is probably less than the positive impact of predation on alewife, i.e., reduced competition, predation and/or displacement pressure of alewife on rainbow smelt. Furthermore, the Main Lake is the only basin where alewife catches declined. Although the gillnet data must be viewed with caution, the apparent decline in alewife could be a sign of the functional response of predators to the invasion of alewife, and their switch to include more alewife in their diet (Simonin et al., 2018)

If bottom-up effects of system productivity could mitigate any possible impacts of competition from alewife (Power, 1992), we should have observed the most impact on rainbow smelt in the least productive basin, Malletts Bay, and the least impact in the most productive basin, the Northeast Arm. However, the patterns were not consistent with these expectations; rainbow smelt CPUE declined and average length and condition did not change before and after alewife invasion in these two basins. In fact, CPUE was lowest in the highly productive Northeast Arm after the invasion. In theory, the lower abundance of rainbow smelt and higher productivity in the Northeast Arm should have reduced intra-and inter-specific competition and increased growth and condition of rainbow smelt, compared to Malletts Bay, but we did not observe such patterns.

Alewife and rainbow smelt can be intense competitors for zooplankton (Evans and Loftus, 1987). System size, however, may mitigate or exacerbate competition. In small lake systems where habitat availability and heterogeneity may be limited, alewife appear to outcompete native rainbow smelt (Eaton and Kardos 1972; Kircheis et al., 2004; Kircheis and Stanley 1981). In the Great Lakes, rainbow smelt declines in the mid-1900s were associated with alewife increases (Smith, 1968), also suggesting competition. However, more recent evaluations of alewife effects on rainbow smelt in the Great Lakes led to the conclusion that alewife are likely to have negligible impacts on rainbow smelt (Madenjian et al., 2008). Larger, deeper systems may reduce spatial overlap of alewife and rainbow smelt due to thermal structure while providing greater or more diverse zooplankton resources (Amsinck et al., 2006; Dodson, 1992; Simonin et al., 2012). Additionally, *Mysis diluviana*, which is a major diet item of rainbow smelt in Lake Champlain and the Great Lakes (Labar, 1993; Gamble et al., 2011a,b) and also consumed by alewife (Madenjian et al., 2003), is abundant in the Main Lake but virtually absent in the two smaller basins (Ball et al., 2015; Hrycik et al., 2015; O'Malley and Stockwell, 2019; J.D. Stockwell, unpublished observations). Consequently, *Mysis* may serve as a buffer to reduce competition between rainbow smelt and alewife in the Main Lake but not in the two smaller basins.

Mysis densities in the Main Lake decreased slightly but not significantly after alewife invasion (Ball et al., 2015). In the absence of increased primary production (corroborated by stable TP levels), zooplankton production would likely have also remained stable. The absence of a decline in zooplankton densities suggests that rainbow smelt may have switched to a diet including less zooplankton after the alewife invasion, otherwise alewife or zooplankton abundance data would have shown a different pattern. The most likely resource subsidy is *Mysis*, which were already part of rainbow smelt diets (Labar 1993). The slight decline in *Mysis* densities would also reduce the predation pressure on zooplankton, making the surplus available to alewife.

System size and habitat availability may also interact with predation to negatively influence rainbow smelt following alewife invasion and contribute to the patterns we observed. Larger systems may provide greater temporal and spatial mis-match between spawning adult alewife moving inshore and post-hatch larval rainbow smelt dispersal into large volumes of water offshore (dilution effect) and also provide stronger thermal gradients that promote vertical segregation (Madenjian et al., 2008; Recksiek and McCleave, 1973; Simonin et al., 2019). In Lake Champlain, available oxythermal habitat volume was much smaller in the two smaller basins than in the Main Lake, where DO and temperature were suitable at all depths and years. Warm epilimnetic waters and the expansion of the hypoxic bottom layer during the warmest months (July to October) resulted in constriction of suitable rainbow smelt habitat in both Malletts Bay and the Northeast Arm. Prior to the alewife invasion, rainbow smelt could reside in suboptimal warm water during summer habitat constriction without competition from alewife. Post-invasion occupancy of shallower waters during habitat constriction likely increased their overlap with alewife (Simonin et al., 2019). However, in the absence of evidence that alewife prey on larval and YOY rainbow smelt, the effect of scale may only be relevant to cannibalism and predation by large piscivores. Cannibalism could contribute to the apparent increased mortality of age-0 and -1 rainbow smelt we observed in the Northeast Arm and Malletts Bay. Cannibalism was in fact higher in Malletts Bay and the Northeast Arm than the Main Lake prior to the alewife invasion (Stetter Parker et al., 2007), but this did not appear to negatively affect abundance compared with the Main Lake. Cannibalism could only explain the decrease in rainbow smelt abundance after alewife invasion if increased competition with alewife forced rainbow smelt to increase cannibalism. Therefore, habitat scale and physicochemical constraints may have indirectly contributed to driving population declines in the two smaller basins if individuals were forced into habitats with more predators or competitors in the two smaller basins (Costantini et al., 2008; Horppila et al., 2003, 2004).

Other changes in the Lake Champlain ecosystem may have influenced rainbow smelt or influenced the effects of alewife. Portions of the lake have become more eutrophic over the past few decades, but only in shallow bays not suitable for rainbow smelt (Smeltzer et al. 2012). Of the 51 species that have invaded the lake, most do not overlap ecologically or geographically with rainbow smelt; e.g., invasive macrophytes are confined to the southern lake and littoral waters. Two possible exceptions are white perch (*Morone americana*) and zebra mussels (*Dreissena polymorpha*) that invaded the southern lake in 1984 and 1993, respectively, and spread rapidly throughout the Main Lake (Marsden and Hauser 2009). White perch are omnivorous and consume fish (Couture and Watzin, 2008; Schaeffer and Margraf, 1986) and therefore represent a predation threat. However, we should have observed demographic changes prior to the alewife invasion if white perch had a negative impact on rainbow smelt. Zebra mussel filtration lowers phytoplankton density and increases water transparency, leading to zooplankton declines (MacIsaac, 1996); however, Secchi disk readings in Lake Champlain increased only slightly and only in the south lake region (Smeltzer et al., 2012) and adult densities remain too low in Malletts Bay and the Northeast Arm to expect an impact (Marsden et al., 2013; VTDEC, 2020). No other changes to the lake have occurred with a timeline and magnitude that are likely to explain the changes we observed in rainbow smelt populations.

The successful invasion and rapid expansion of alewife in Lake Champlain is surprising, given the relatively intact fish community and high predator abundance. In the Great Lakes, alewife expanded soon after large piscivore and plantivore populations collapsed (Applegate and Van Meter, 1970; Baldwin et al., 2009; Miller, 1957; Smith, 1970). Alewife populations subsequently declined following sustained stocking of salmonines in the 1960s (Stewart and Ibarra, 1991). However, salmonines have been stocked continuously in Lake Champlain since the 1970s and at higher densities than in the Great Lakes. Even after reductions in lake trout stocking in 1995, lake trout plus Atlantic salmon stocking densities were 3.6 - 6 times higher per unit volume in Lake Champlain than in lakes Michigan or Huron (Great Lakes Fish Stocking database, www.glfc.org/fishstocking/; Stewart and Ibarra, 1991; Wehse et al., 2017). Both species began to consume alewife at least by 2008, when anglers and state biologists noted alewife in salmonine stomachs (B. Pientka, unpublished observations). By 2011, stable isotope analysis confirmed that alewife were a major element in Atlantic salmon and walleye diets and to a lesser extent in lake trout diets (Simonin et al., 2018). The presence of a robust rainbow smelt population in Lake Champlain would also be expected to potentially suppress the invasion, as rainbow smelt are predators of age-0 and yearling alewife (Foltz and Norden 1977; O'Gorman, 1974). Alternatively, the relatively simple planktivore community may have had low invasion resistance and provided a resource opportunity for alewife (Shea et al., 2002).

To summarize, we investigated the specific situation where rainbow smelt is native and alewife invasive in a large and heterogeneous lake system. The native/introduced status of the two species was not a predictor of the impact of alewife on rainbow smelt. Instead, our results emphasize that the impact of alewife is context-dependent. Of the potential mechanisms to explain why rainbow smelt responded differently to an alewife invasion in the Main Lake than in the smaller basins, factors tied to habitat availability are best supported; low oxythermal habitat in the smaller basins may increase alewife and rainbow smelt overlap, while large habitat volume in the Main Lake supports the presence of predators and *Mysis*. Habitat availability is an important factor in the success or failure of species invasions (Tamayo and Olden, 2014; Vander Zanden et al., 2004). Our findings indicate that habitat availability may also play in an important role in the relative impact of invasive species. Consequently, managers must not only think about which systems are more vulnerable to invasion, but also which systems, once invaded, are the most likely to be impacted by the addition of invasive species.

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We thank George W. Labar who initiated the forage fish survey in the 1980s, and the captains and crews of the research vessels *Melosira* and *Doré* who conducted the surveys from 1984 to 1998 and from 1998 to 2015, respectively. We thank Angela Shambaugh and Pete Stangel at the VTDEC for providing us with the multiprobe data from the Lake Champlain long-term water quality and biological monitoring project. The project itself is supported by VTDEC, the NYDEC, and the Lake Champlain Basin Program. We thank the Marsden and Stockwell labs, as well as two anonymous reviewers and the Associate Editor David "Bo" Bunnell, for their comments on an earlier draft of this manuscript. This project was made possible by (1) fishing license sales and matching Dingell-Johnson/Wallop-Breaux funds, available through the Federal Aid in Sport Fish Restoration Act, (2) funds from Lake Champlain Sea Grant, Award NA18OAR4170099 from the National Oceanic and Atmospheric Administration National Sea Grant College Program, U.S. Department of Commerce, and (3) funds made available to Lake Champlain by Senator Patrick Leahy through the Great Lakes Fishery Commission.

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Table 1. Characteristics of the three major basins in Lake Champlain and variables that we hypothesized may affect rainbow smelt response to alewife invasion. Variables are numbered according to hypotheses outlined in the Introduction. Hypotheses 6-7 are not in the table because they relate to specific mechanisms of how alewife might impact rainbow smelt. Basin morphometry data from Myer and Gruendling (1979); total phosphorus (TP) data from Smeltzer et al., (2012); predator abundance data from B. Pientka (unpublished data). Asterisk (*) denotes variables calculated within this study. Grey shading means we expect the variable to support rainbow smelt populations stability in the specified basin. The metrics represent conditions during the study period (1987-2015).

	Main Lake	**Malletts Bay**	**Northeast Arm**	
Basin volume (km^3)	large (21.0)	small (0.72)	medium (3.45)	
Max basin depth (m)	122	32	49	
Avg basin depth (m)	30.8	13.3	12.8	
Variables				**Mechanism driving rainbow smelt stability**
(1) Predator abundance	high	low	low	Greater top-down control in the Main Lake
(2) Oxythermal habitat*	high	low	low	Greater habitat volume in the Main Lake
(3) Productivity (µg TP L^{-1})	low (10-15)	low (8-12)	high (20-25)	Higher productivity in the Northeast Arm may increase food availability
(4) Zooplankton densities*	lower	higher	higher	Higher food availability in the smaller basins
(5) *Mysis**	presence	absence	absence	Resource subsidies in the Main Lake

Figure captions

Figure 1 – Lake Champlain bathymetry and basins, with the five trawling sites and the two long-term monitoring stations. Stations in the Main Lake are, from north to south, Valcour Island, Juniper Island, and Barber Point. Grey lines show major tributaries.

Figure 2 – **(A)** Boxplot of average rainbow smelt CPUE and **(B)** changes in CPUE by period in for the Main Lake, Malletts Bay, and the Northeast Arm of Lake Champlain. Limits of each box represent the 25-75% quantiles, dark bars represent the median, lines show the 10-90 % limits of the CPUE, and dots represent outliers from the 10-90% distribution. The y-axis scale is logarithmic. Letters indicate groups that are significantly different (Kruskal-Wallis test with Bonferroni correction).

Figure 3 – **(A)** Boxplot of average alewife CPUE and **(B)** changes in alewife CPUE in the Main Lake, Malletts Bay, and the Northeast Arm of Lake Champlain. See Fig. 2 for description of boxplot. Horizontal dotted line represents average CPUE. YOY and YAO caught by floating gillnets were summed together. Striped area indicates period before alewife invasion.

Figure 4 – **(A)** Average total length of rainbow smelt (age-2+) in the Main Lake, Malletts Bay, and the Northeast Arm of Lake Champlain of Lake Champlain for three survey periods, **(B)** average condition for age 2 and 3 rainbow smelt, and **(C)** annual mortality per cohort. Letters indicate groups that are significantly different (Kruskal-Wallis test with Bonferroni correction).

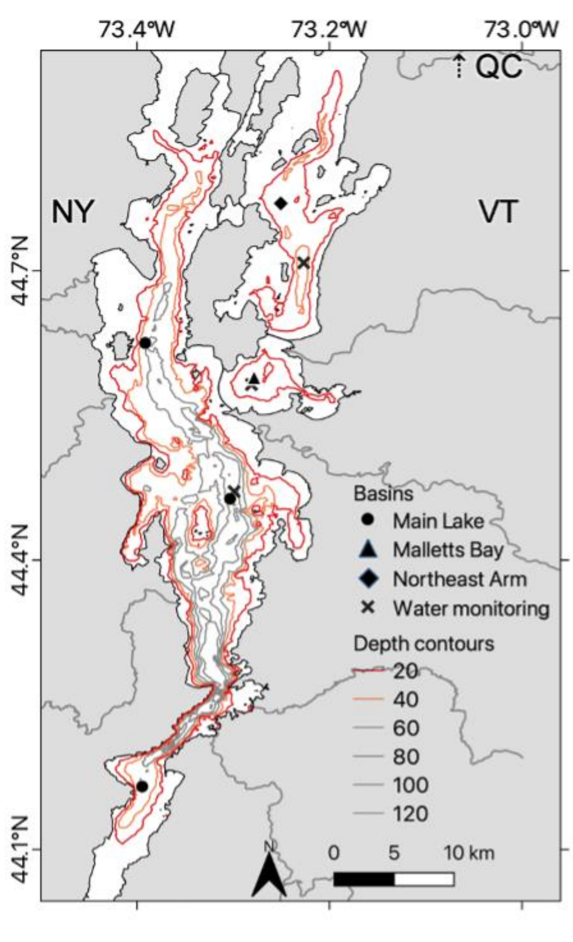
Figure 5 – Habitat available for rainbow smelt per month, and year, expressed by depths with oxygen > 4.5 mg/l and temperature < 16°C, for the Main Lake, Malletts Bay, and the Northeast Arm of Lake Champlain. Horizontal lines represent lake surface and bottom sediment (not visible for the Main Lake station because depth is 102 m). Lighter grey vertical lines indicate absence of data.

Figure 6 – Percentage of days in August-October per year and for which suitable water column habitat (defined by temperature below four possible thresholds and > 4.5 mg O_2/L) was between 2-4 m, 0-2 m, or unavailable, for the Main Lake, Malletts Bay, and the Northeast Arm of Lake Champlain. Dashed vertical lines indicate the separation between the periods used for Fig. 2-4.

Figure 7 – Mean summer density (#/m^3) of most abundant zooplankton groups, for the Main Lake, Malletts Bay, and the Northeast Arm of Lake Champlain. Grey background in plots indicate available length data (see Fig. 8).

Figure 8 – Mean length (mm) of most abundant zooplankton taxa in the Main Lake and Northeast Arm of Lake Champlain during pre-invasion (2001-2002), transitional (2003-2006), and post-invasion (2007-2015) of alewife.

Figure 1


73.4°W
73.2°W
73.0°W
QC
NY
VT
44.7°N
44.4°N
44.1°N
Basins
● Main Lake
▲ Malletts Bay
◆ Northeast Arm
× Water monitoring
Depth contours
20
40
60
80
100
120
N
0
5
10 km

666 **Figure 2**

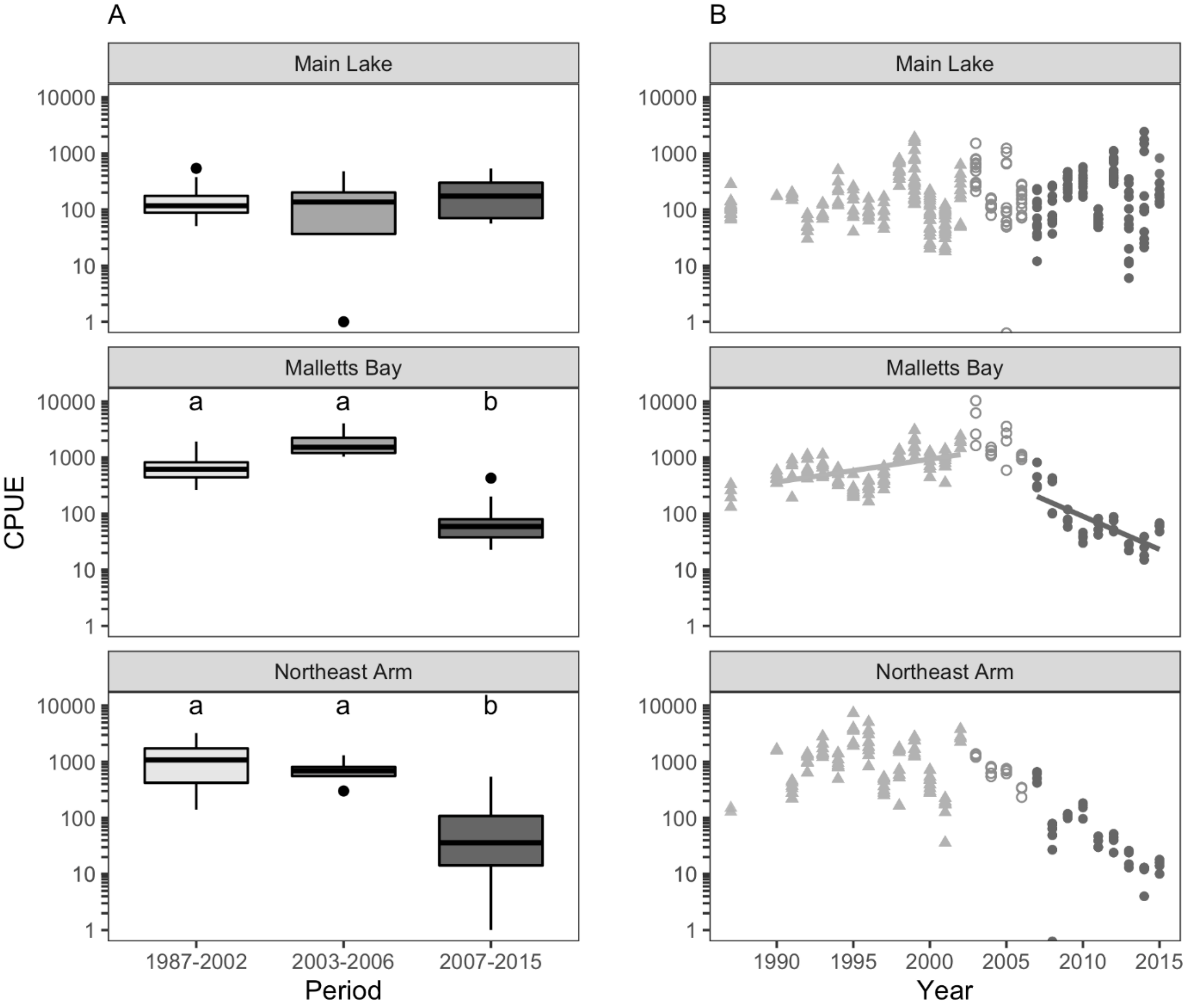


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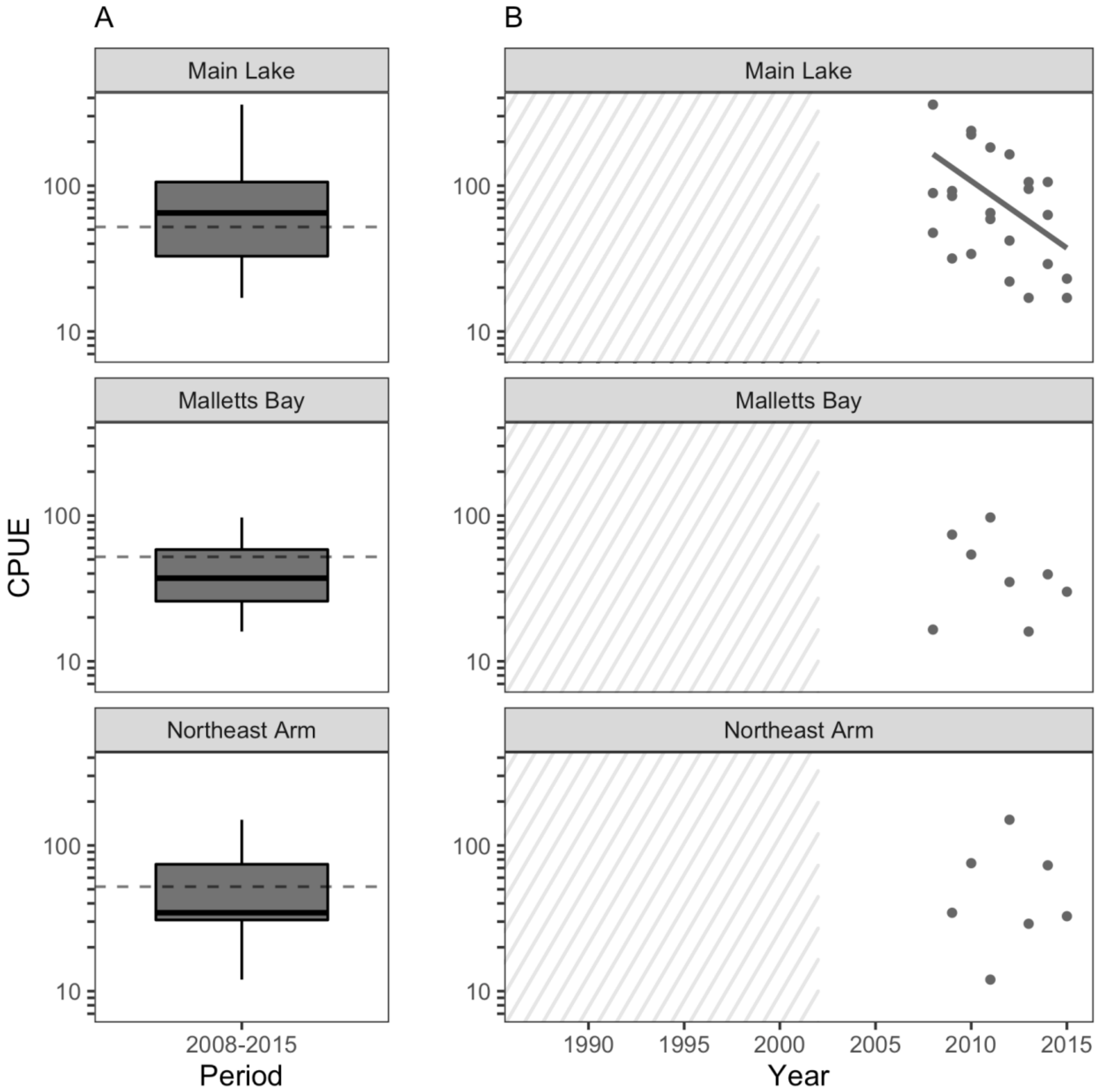
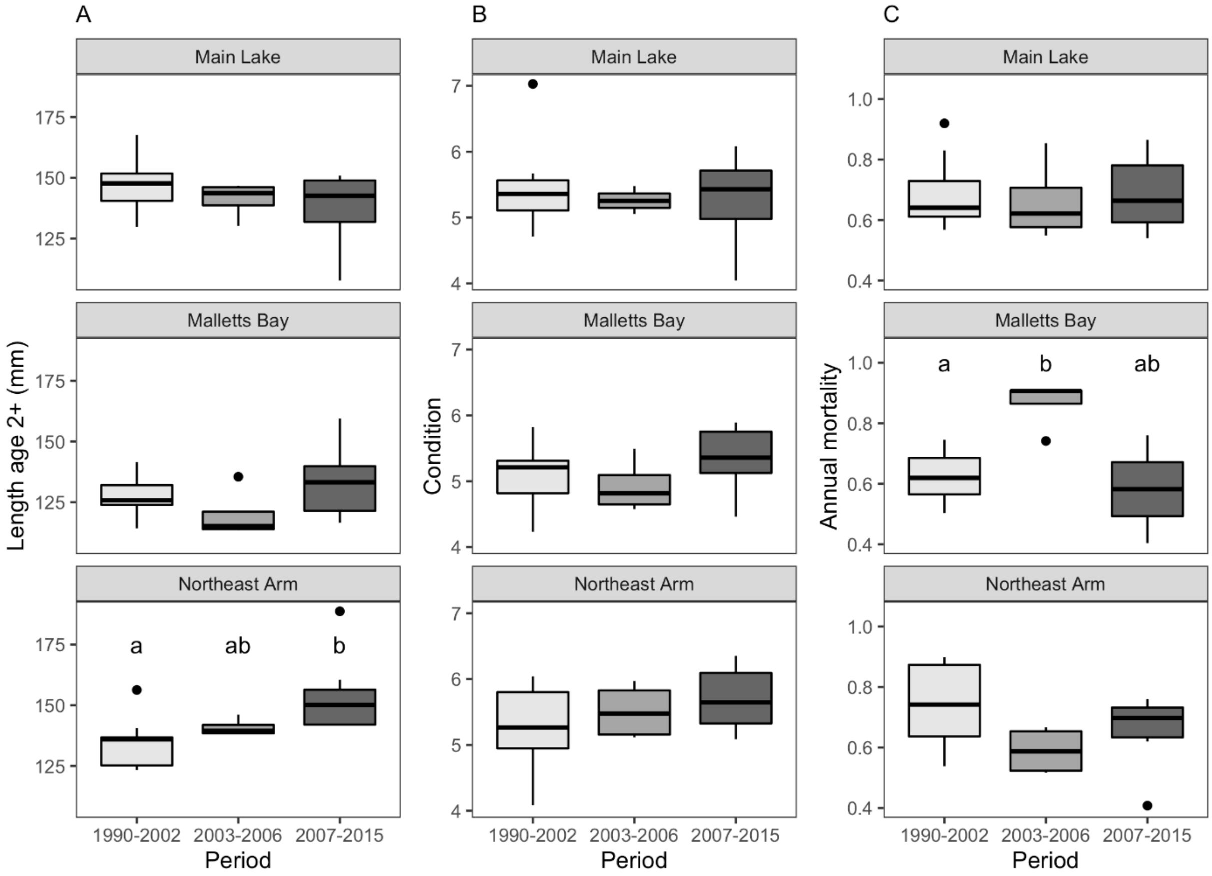
Figure 3



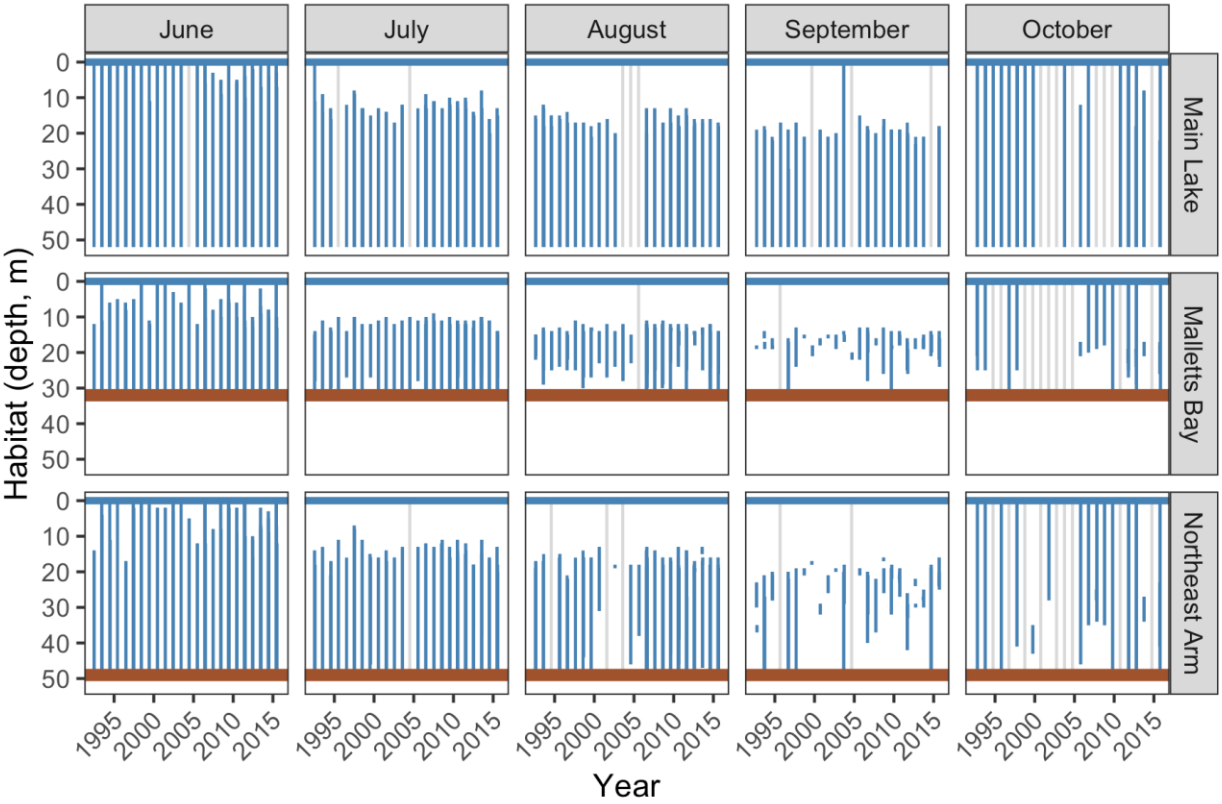
A
B
Main Lake
Malletts Bay
Northeast Arm
CPUE
10
100
2008-2015
Period
1990
1995
2000
2005
2010
2015
Year

670 **Figure 4**



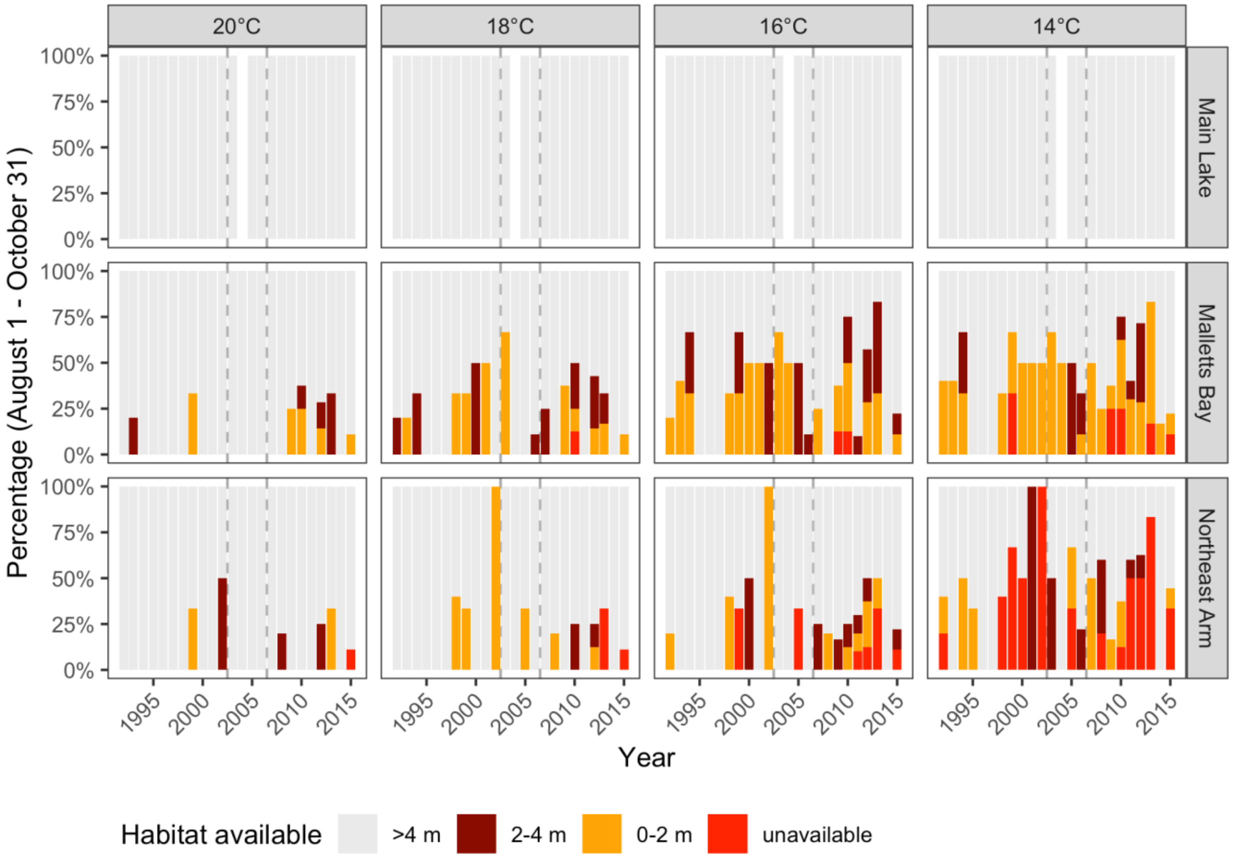
671
672

673 **Figure 5**

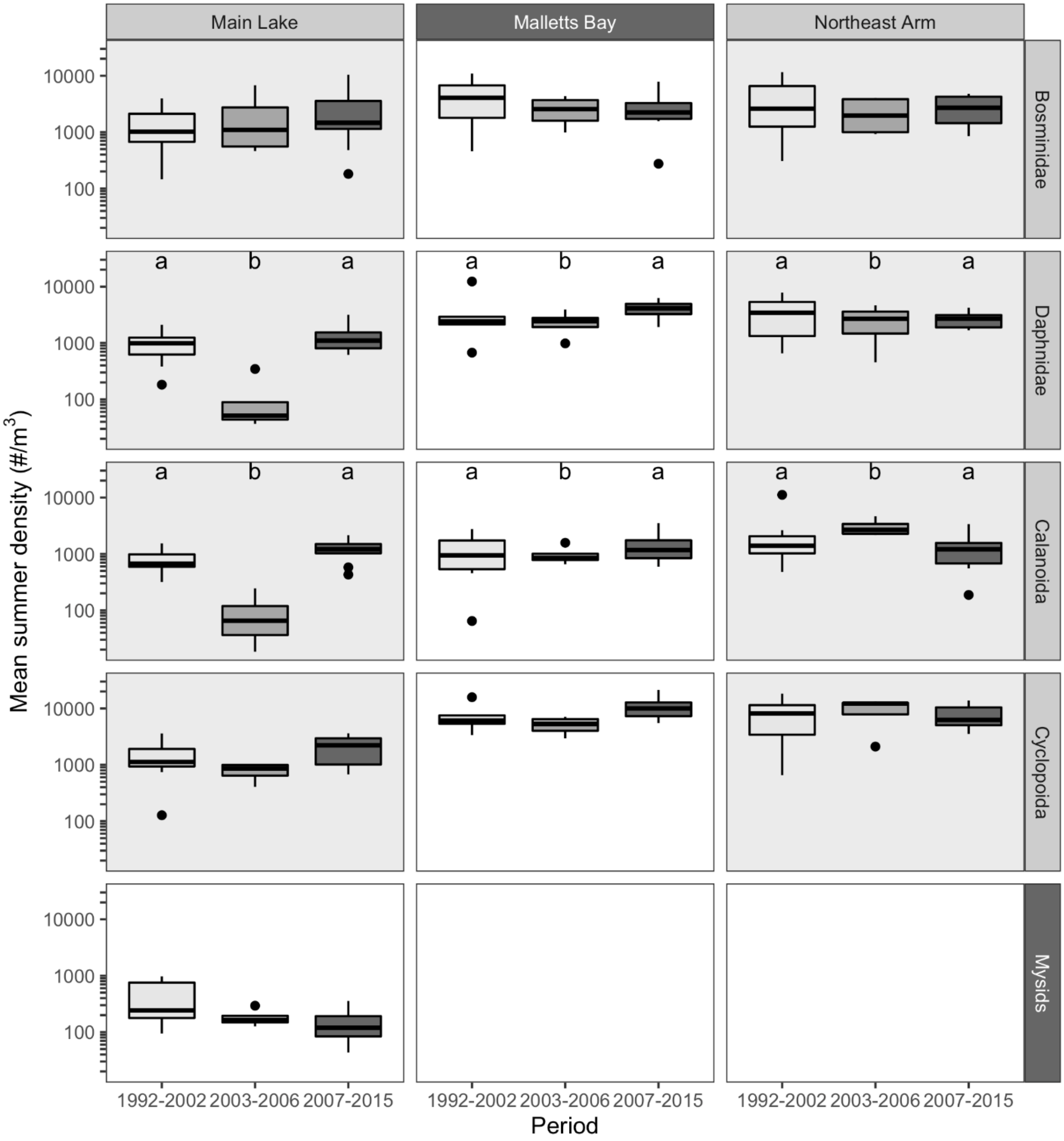


674

Figure 6

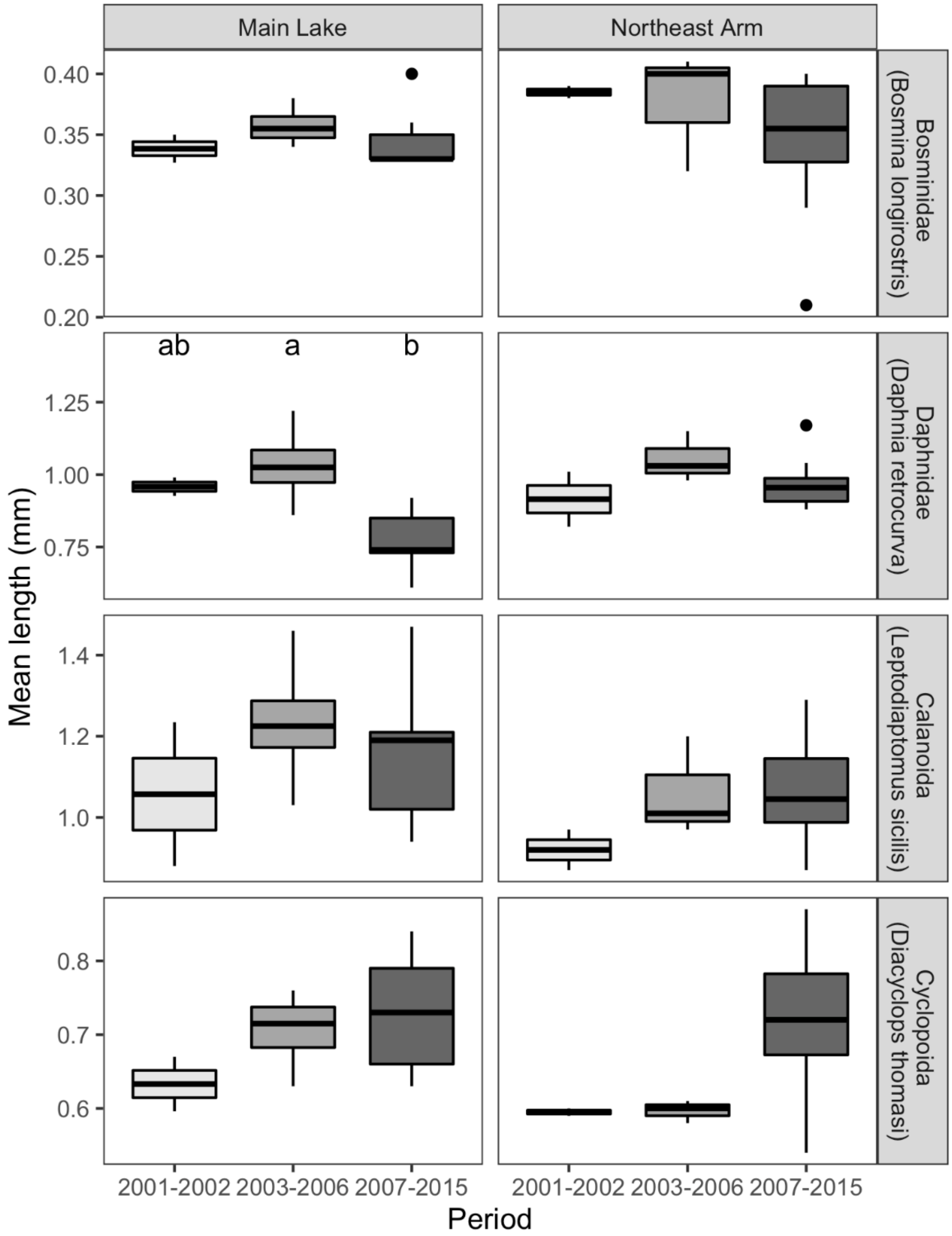

20°C
18°C
16°C
14°C
Main Lake
Malletts Bay
Northeast Arm
Percentage (August 1 - October 31)
100%
75%
50%
25%
0%
1995
2000
2005
2010
2015
Year
Habitat available
>4 m
2-4 m
0-2 m
unavailable

678 **Figure 7**



679

Figure 8


Main Lake
Northeast Arm
Bosminidae (Bosmina longirostris)
Daphnidae (Daphnia retrocurva)
Calanoida (Leptodiaptomus sicilis)
Cyclopoida (Diacyclops thomasi)
0.40
0.35
0.30
0.25
0.20
ab
a
b
1.25
1.00
0.75
1.4
1.2
1.0
0.8
0.7
0.6
Mean length (mm)
2001-2002
2003-2006
2007-2015
2001-2002
2003-2006
2007-2015
Period

Electronic Supplementary Material

Rainbow smelt population responses to species invasions and change in environmental condition

Rosalie Bruel[a], J. Ellen Marsden[a], Bernie Pientka[b], Nick Staats[c], Timothy Mihuc[d], Jason D. Stockwell[a]

1. Characteristics of sampling station

Table S1. Characteristics of sampling station (maximum depth, typical starting depth for trawling, and trawling time) in Lake Champlain with average catches of rainbow smelt standardized to 55 min trawl time at each station each year. Number in parentheses is the number individuals kept for biological analyses. A '-' indicates data or subsamples were not collected. No sampling was conducted in 1988-1989.

Basin	**Main Lake**				
Station	**Barber Point**	**Juniper Island**	**Valcour Island**	**Malletts Bay**	**Northeast Arm**
max depth (m)	50-60	70-90	56-62	22-32	22-40
starting depth (m)	35	35	35	26	29
trawling time (min)	55	55	55	40	45
Year			**mean CPUE**		
1987	139 (-)	110 (-)	-	231 (-)	139 (-)
1990	-	175 (119)	-	448 (199)	1,628 (125)
1991	-	173 (172)	-	614 (125)	324 (191)
1992	-	53 (176)	-	654 (199)	1,104 (192)
1993	93 (49)	-	-	654 (201)	1,674 (205)
1994	316 (284)	126 (101)	-	461 (203)	977 (100)
1995	202 (92)	72 (93)	-	278 (195)	3,553 (217)
1996	79 (100)	111 (100)	-	305 (200)	2,440 (200)
1997	124 (57)	66 (-)	-	465 (202)	398 (199)
1998	-	572 (303)	-	1,127 (196)	1,069 (208)
1999	317 (200)	146 (200)	1,288 (200)	1,696 (200)	1,814 (200)
2000	65 (175)	55 (199)	155 (198)	864 (200)	440 (195)
2001	63 (100)	84 (201)	35 (138)	864 (198)	158 (183)
2002	247 (203)	51 (168)	374 (200)	1,957 (200)	2,869 (196)
2003	587 (200)	825 (200)	285 (200)	5,193 (200)	1,304 (200)
2004	138 (203)	113 (200)	-	1,276 (200)	690 (200)
2005	902 (200)	50 (194)	78 (198)	2,226 (199)	693 (200)
2006	256 (201)	131 (196)	121 (199)	1,037 (200)	306 (179)
2007	152 (162)	77 (172)	56 (210)	470 (200)	551go (200)
2008	209 (202)	67 (194)	64 (210)	252 (224)	49 (201)
2009	300 (206)	400 (197)	248 (198)	82 (224)	108 (199)
2010	459 (199)	305 (200)	185 (201)	38 (104)	150 (202)
2011	66 (199)	67 (214)	71 (187)	61 (164)	36 (114)
2012	811 (205)	388 (201)	595 (205)	66 (235)	40 (155)
2013	12 (48)	254 (197)	68 (200)	25 (69)	20 (63)
2014	1,697 (193)	117 (160)	29 (115)	24 (67)	10 (32)
2015	630 (200)	223 (200)	153 (199)	60 (162)	14 (45)

2. Results of Kruskal-Wallis

Table S2. Results of Kruskal-Wallis pairwise comparison test between periods for the three basins and the four variables of interest. *p* is the overall p-value, *p.adj* is the p-value with Bonferroni correction to account for multiple comparison. *p.signif* indicates the level of significance: ns (p.adj > 0.05); * (p.adj > 0.01); ** (p.adj > 0.001); *** (p.adj > 0.0001); **** (p.adj ≤ 0.0001).

variable	Basin	Period 1	Period 2	p	p.adj	p.signif
log(CPUE)	Main Lake	1987-2002	2003-2006	0.362	1.000	ns
		1987-2002	2007-2015	0.688	1.000	ns
		2003-2006	2007-2015	0.727	1.000	ns
	Malletts Bay	1987-2002	2003-2006	0.018	0.053	ns
		1987-2002	2007-2015	0.000	0.000	****
		2003-2006	2007-2015	0.003	0.008	**
	Northeast Arm	1987-2002	2003-2006	0.442	1.000	ns
		1987-2002	2007-2015	0.000	0.001	***
		2003-2006	2007-2015	0.008	0.024	*
Average length age-2+ (mm)	Main Lake	1987-2002	2003-2006	0.412	1.000	ns
		1987-2002	2007-2015	0.209	0.630	ns
		2003-2006	2007-2015	1.000	1.000	ns
	Malletts Bay	1987-2002	2003-2006	0.130	0.390	ns
		1987-2002	2007-2015	0.324	0.970	ns
		2003-2006	2007-2015	0.050	0.150	ns
	Northeast Arm	1987-2002	2003-2006	0.060	0.180	ns
		1987-2002	2007-2015	0.000	0.000	***
		2003-2006	2007-2015	0.034	0.100	ns
Average condition (age 2-3)	Main Lake	1987-2002	2003-2006	0.549	1.000	ns
		1987-2002	2007-2015	0.896	1.000	ns
		2003-2006	2007-2015	1.000	1.000	ns
	Malletts Bay	1987-2002	2003-2006	0.477	1.000	ns
		1987-2002	2007-2015	0.357	1.000	ns
		2003-2006	2007-2015	0.260	0.780	ns
	Northeast Arm	1987-2002	2003-2006	0.871	1.000	ns
		1987-2002	2007-2015	0.126	0.380	ns
		2003-2006	2007-2015	0.503	1.000	ns
Annual mortality	Main Lake	1987-2002	2003-2006	0.839	1.000	ns
		1987-2002	2007-2015	0.635	1.000	ns
		2003-2006	2007-2015	0.762	1.000	ns
	Malletts Bay	1987-2002	2003-2006	0.002	0.007	**
		1987-2002	2007-2015	0.945	1.000	ns
		2003-2006	2007-2015	0.114	0.340	ns
	Northeast Arm	1987-2002	2003-2006	0.102	0.310	ns
		1987-2002	2007-2015	0.521	1.000	ns
		2003-2006	2007-2015	0.257	0.770	ns

Table S3. Results of Kruskal-Wallis pairwise comparison test between periods for the three basins and the zooplankton taxa of interest. *p* is the overall p-value, *p.adj* is the p-value with Bonferroni correction. *p.signif* indicates the level of significance: ns, p>0.05; *, p>0.01; **, p>0.001; ***, p>0.0001; ****: p≤0.0001

variable	Taxa	Basin	Period 1	Period 2	p	p.adj	p.signif
Mean summer density (#/ m^3)	Cyclopoida	Main Lake	1992-2002	2003-2006	0.104	0.310	ns
			1992-2002	2007-2015	0.230	0.690	ns
			2003-2006	2007-2015	0.050	0.150	ns
		Malletts Bay	1992-2002	2003-2006	0.476	1.000	ns
			1992-2002	2007-2015	0.067	0.200	ns
			2003-2006	2007-2015	0.020	0.059	*
		Northeast Arm	1992-2002	2003-2006	0.661	1.000	ns
			1992-2002	2007-2015	0.976	1.000	ns
			2003-2006	2007-2015	0.446	1.000	ns
	Calanoida	Main Lake	1992-2002	2003-2006	0.001	0.004	**
			1992-2002	2007-2015	0.056	0.170	ns
			2003-2006	2007-2015	0.003	0.008	**
		Malletts Bay	1992-2002	2003-2006	0.762	1.000	ns
			1992-2002	2007-2015	0.616	1.000	ns
			2003-2006	2007-2015	0.446	1.000	ns
		Northeast Arm	1992-2002	2003-2006	0.056	0.170	ns
			1992-2002	2007-2015	0.413	1.000	ns
			2003-2006	2007-2015	0.030	0.089	ns
	Bosminidae	Main Lake	1992-2002	2003-2006	0.851	1.000	ns
			1992-2002	2007-2015	0.295	0.880	ns
			2003-2006	2007-2015	0.825	1.000	ns
		Malletts Bay	1992-2002	2003-2006	0.610	1.000	ns
			1992-2002	2007-2015	0.682	1.000	ns
			2003-2006	2007-2015	1.000	1.000	ns
		Northeast Arm	1992-2002	2003-2006	0.753	1.000	ns
			1992-2002	2007-2015	0.740	1.000	ns
			2003-2006	2007-2015	0.446	1.000	ns
	Daphnidae	Main Lake	1992-2002	2003-2006	0.003	0.009	**
			1992-2002	2007-2015	0.412	1.000	ns
			2003-2006	2007-2015	0.003	0.008	**
		Malletts Bay	1992-2002	2003-2006	1.000	1.000	ns
			1992-2002	2007-2015	0.102	0.310	ns
			2003-2006	2007-2015	0.030	0.089	ns
		Northeast Arm	1992-2002	2003-2006	0.489	1.000	ns
			1992-2002	2007-2015	0.566	1.000	ns
			2003-2006	2007-2015	0.862	1.000	ns
	Rotifera	Main Lake	1992-2002	2003-2006	0.343	1.000	ns
			1992-2002	2007-2015	0.080	0.240	ns
			2003-2006	2007-2015	0.604	1.000	ns
	Mysids	Main Lake	1992-2002	2003-2006	0.280	0.840	ns
			1992-2002	2007-2015	0.020	0.060	ns
			2003-2006	2007-2015	0.503	1.000	ns
Mean length (mm)	*Diacyclops thomasi*	Main Lake	2001-2002	2003-2006	0.267	0.800	ns
			2001-2002	2007-2015	0.288	0.860	ns

		2003-2006	2007-2015	0.588	1.000	ns
	Northeast Arm	2001-2002	2003-2006	1.000	1.000	ns
		2001-2002	2007-2015	0.178	0.530	ns
		2003-2006	2007-2015	0.085	0.250	ns
Daphnia retrocurva	Main Lake	2001-2002	2003-2006	0.533	1.000	ns
		2001-2002	2007-2015	0.045	0.130	ns
		2003-2006	2007-2015	0.017	0.050	*
	Northeast Arm	2001-2002	2003-2006	0.400	1.000	ns
		2001-2002	2007-2015	0.694	1.000	ns
		2003-2006	2007-2015	0.184	0.550	ns
Leptodiaptomus sicilis	Main Lake	2001-2002	2003-2006	0.800	1.000	ns
		2001-2002	2007-2015	0.723	1.000	ns
		2003-2006	2007-2015	0.315	0.950	ns
	Northeast Arm	2001-2002	2003-2006	0.236	0.710	ns
		2001-2002	2007-2015	0.190	0.570	ns
		2003-2006	2007-2015	1.000	1.000	ns
Bosmina longirostris	Main Lake	2001-2002	2003-2006	0.348	1.000	ns
		2001-2002	2007-2015	0.532	1.000	ns
		2003-2006	2007-2015	0.201	0.600	ns
	Northeast Arm	2001-2002	2003-2006	0.800	1.000	ns
		2001-2002	2007-2015	0.507	1.000	ns
		2003-2006	2007-2015	0.304	0.910	ns

3. Temperature and DO profile

We used vertical profile data obtained with a multiprobes sensor by the Vermont Department of Environmental Conservation (DEC), as part of the Lake Champlain long-term monitoring program initiated in 1992 (https://dec.vermont.gov/watershed/lakes-ponds/monitor/lake-champlain). The program is carried on jointly with the New York DEC with fundings from Lake Champlain Basin Program and the two states. Fifteen stations are sampled fortnightly from late April to early November, and we selected stations 19, 25 and 34 to represent conditions in the Main Lake, Malletts Bay, and the Northeast Arm respectively (Fig. 1 main text).

We rounded the depths to the closest meter and built heatmaps using the function *filled.contour()* in R (Fig. S1, S2) (Read et al., 2011).

References

Read, J.S., Hamilton, D.P., Jones, I.D., Muraoka, K., Winslow, L.A., Kroiss, R., Wu, C.H., Gaiser, E., 2011. Derivation of lake mixing and stratification indices from high-resolution lake buoy data. Environ. Model. Softw. 26, 1325–1336.

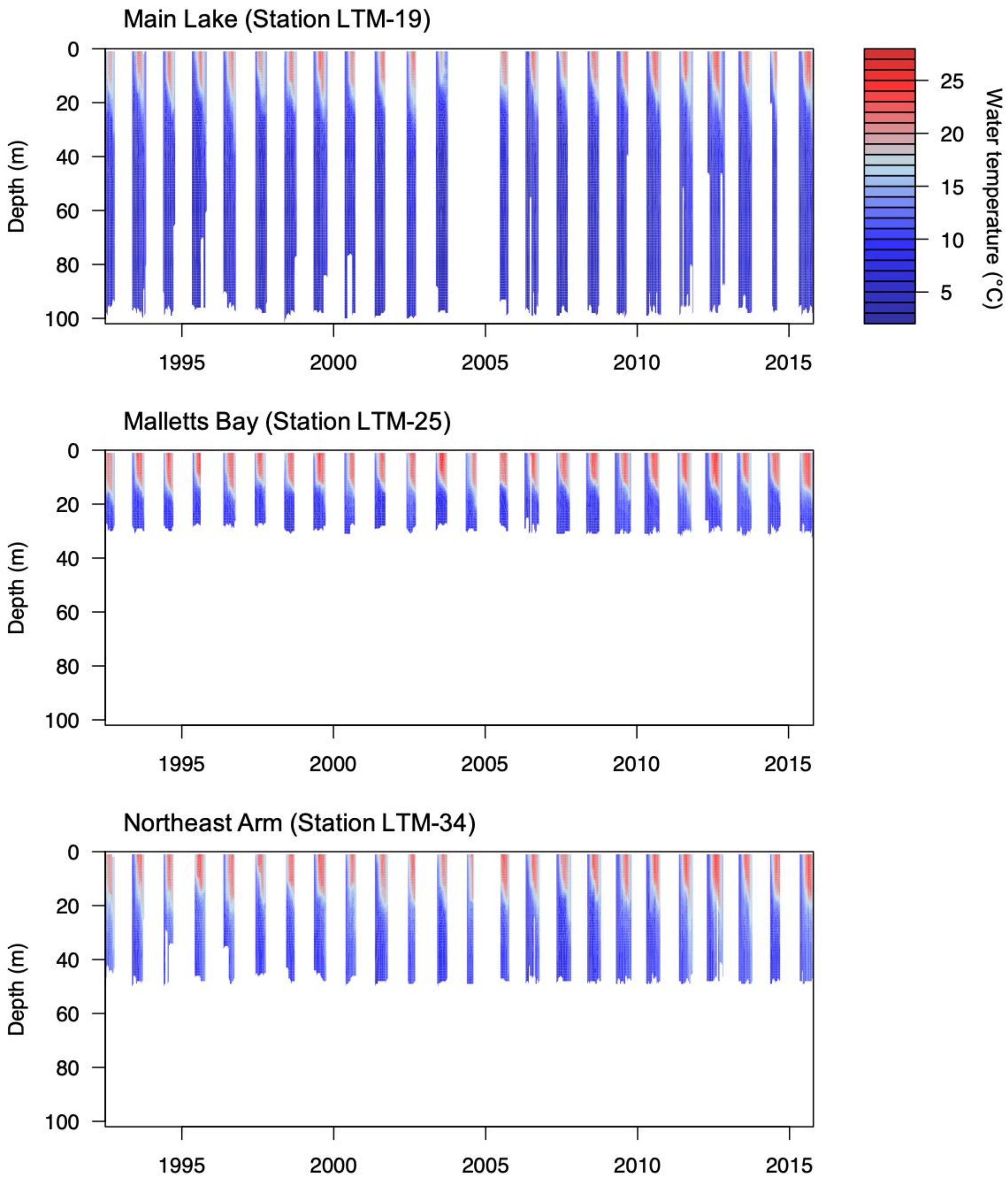


Figure S1. Water temperature (°C) in three basins of Lake Champlain each summer between 1992 and 2015.

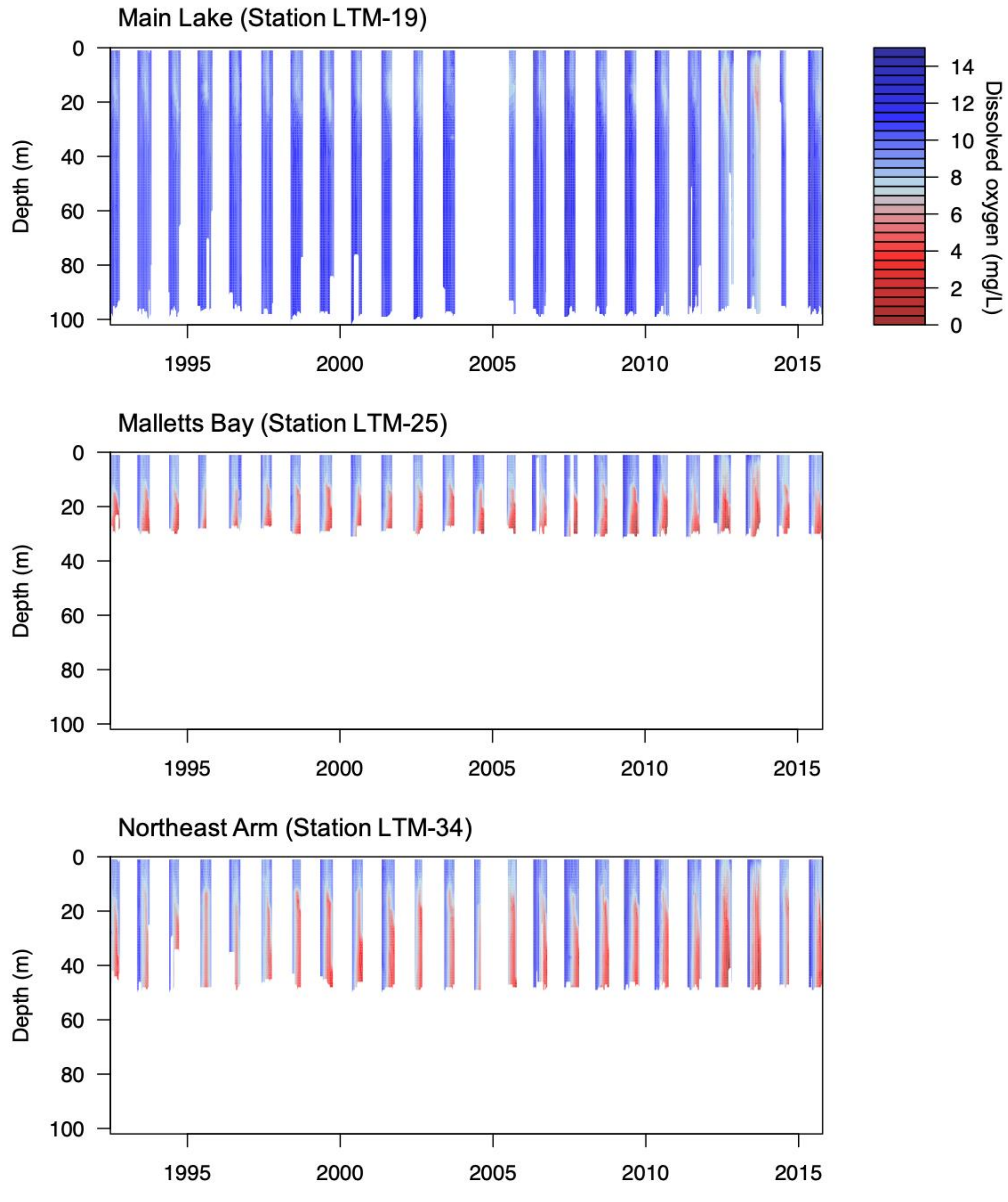


Figure S2. Dissolved oxygen (mg/l) in three basins of Lake Champlain each summer between 1992 and 2015.