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Larval Northern Pike (Esox lucius) Ecology in Natural and Restored Coastal Wetlands of the Upper St. Lawrence River

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LARVAL NORTHERN PIKE (*ESOX LUCIUS*) ECOLOGY IN NATURAL AND RESTORED COASTAL WETLANDS OF THE UPPER ST. LAWRENCE RIVER

by

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A thesis
submitted in partial fulfillment
of the requirements for the
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Department of Environmental and Forest Biology

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Abstract

E. A. Augustyn. Larval Northern Pike (*Esox lucius*) Ecology in Natural and Restored Coastal Wetlands of the Upper St. Lawrence River. 117 pages, 8 tables, 23 figures, 2 appendices, 2017.

We explored several aspects of the northern pike larval period including the abiotic and biotic dynamics of spring nursery marshes, prey selection in two common nursery habitats, and physical conditions, diet, and survival rates in enhanced wetlands. These findings highlight the importance of physical conditions of nursery marshes on the development of eggs and larvae and production of abundant zooplankton prey. In laboratory experiments, larvae displayed greater prey selection for zooplankton originating in flooded wetlands than nearshore bays. A greater proportion of large cladocerans were selected by larvae given a wetland assemblage. In a mark and recapture study, larval pike survival rates were higher in enhancement sites when compared with those in existing sites, possibly due to more suitable environmental conditions. This research on pike ecology in coastal wetlands may help managers and researchers to better understand larval requirements and devise effective solutions to environmental problems affecting their recruitment.

Key Words: Northern pike, St. Lawrence River, nursery marsh, larval ecology, zooplankton prey, wetland enhancement

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Preface

The northern pike (*Esox lucius*) is a large, piscivorous, apex predator in the St. Lawrence River and plays a significant role in aquatic food web structure, contributing to overall ecosystem function (Skov et al., 2002). Declines in adult northern pike abundance in the St. Lawrence River have been observed in recent decades (Smith et al., 2007; McCullough & Gordon, 2015), and are hypothesized to be related to reduced reproductive success linked to disruptions of the natural hydrologic regime and associated wetland vegetation changes (Farrell, 2001; Farrell et al., 2006). In the St. Lawrence River, the spawning period is spatially and temporally protracted, and begins in flooded wet meadows in early spring, transitions to nearshore areas of bays, and is completed in offshore, deep sites in late spring (Farrell, 2001; Farrell et al., 1996, 2006). Reductions in water level fluctuation are thought to alter pike spawning distributions by eliminating spring flood pulses that allow access to shallow, productive floodplains (Farrell, 2001). Diminished seasonal high and low water fluctuations may also promote expansion of invasive robust forms of *Typha* (cattail) in the spawning and nursery grounds that tend to be avoided by northern pike (Franklin & Smith, 1963; Farrell, 2001), and crowd out beneficial native wet meadow vegetation (Cooper et al. 2008; Wilcox et al. 2008, Farrell et al. 2010). Larval pike are believed to remain near the spawning sites (Raat, 1988), therefore the nursery habitat is indirectly determined by the egg distribution. Early spawners yield higher survival from egg fertilization to hatching (Murry et al., 2008) and experience a longer growing season, resulting in a greater potential for growth and production of juveniles than nearshore bay and especially offshore spawners (Farrell et al., 2006).

Interactions between larvae and their environment may influence the year class strength of fish populations (Cushing, 1990; Mertz & Myers, 1994). Northern pike are gape-limited and depend on zooplankton prey during the first few weeks of exogenous feeding (Devries et al., 1998; Nilsson & Bronmark, 2000), until they reach approximately 28 mm and begin feeding on fish larvae (Cooper, 2000). Available prey and the ability to capture and ingest prey are critical for survival of many larval fishes (Cushing, 1990; Mayer & Wahl, 1997), including the northern pike (Skov et al., 2003; Ljunggren et al., 2010). Zooplankton assemblage composition and overall abundance are influenced by several environmental factors, including water level, temperature, and primary productivity, that are dynamic in large river systems (Pace et al., 1992; Thorp et al., 1994; Basu & Pick, 1996; Goździejewska et al., 2016), a characteristic that may have implications on the ability of larval pike to procure abundant, suitable prey during the critical larval stage.

The overall goal of this thesis was to study the physical habitats, diets, and survival responses of northern pike larvae in upper St. Lawrence River nursery sites related to two spawning strategies (bay and wetland tributary spawning) and in sites where habitat restoration occurred. Chapter 1 examined the temporal patterns of zooplankton and phytoplankton productivity, water temperature, and dissolved oxygen in relation to spring flooding and larval development during the nursery period. Chapter 2 examined prey selection of larvae exposed to seasonally-flooded wetland and nearshore bay zooplankton assemblages during an early (first feeding) and more advanced larval stage, to look at the effects of nursery habitat changes on diets of larval pike. Chapter 3 investigated the effects of wetland enhancement techniques on larval pike survival, and described differences in the overall physical environments, zooplankton prey abundance, and prey selection by larvae, occurring at spawning pool enhancement, channel connectivity enhancement, and reference nursery marshes. This study aimed to discern the impacts of wetland habitat changes and enhancements on larval northern pike in the St.

Lawrence River by investigating several aspects of the larval nursery conditions. We hope that this work will add to the knowledge base surrounding larval pike ecology and promote future wetland enhancements to increase their productivity.

Format of the chapters

Each chapter was prepared as a separate manuscript for publication. Chapters 1 and 2 were prepared for submission to *Freshwater Biology* (Wiley) and Chapter 3 was prepared for submission to *Hydrobiologia* (Springer).

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Chapter 1: Flood pulse timing and physical and biotic conditions for larval northern pike (*Esox lucius*) in a large river-floodplain system

Abstract

Physical and biological variables including water temperature, water level, dissolved oxygen, chlorophyll a, and zooplankton, were monitored in floodplain wetlands of a large river system, during the northern pike spawning and nursery periods. Catch per unit effort (CPUE) from spring adult spawning runs was used to estimate temporal patterns in egg deposition, and equations to predict demersal egg and yolk-sac-larvae developmental rates from ambient water temperatures, were used to project dates of larval swim-up and likely onset of exogenous feeding. Daily CPUE of 2016 northern pike spawners identified two separate peaks on March 29-30 and April 12. Site level temporal projections of larval development indicated the time differential to swim-up was reduced by an average of four days between early spawners and later spawners, due to warming following a prolonged early cool period. Minimum temperature, chlorophyll a concentration, and zooplankton abundance coincided with peak spring water level, suggesting flushing and dilution effects by oligotrophic, flood waters derived from the main river. Zooplankton abundance peaked two weeks following highest spring water levels (April 22) and prior to projected exogenous feeding by larval pike, suggesting a match in timing with abundant prey availability. All physical and biological variables examined in this study appeared to respond to peak spring water levels and subsequent warming. These data suggest that spring water level and water temperature play a major role in shaping the nursery marsh conditions available for northern pike larvae.

Introduction

Physical and biological interactions of large river-floodplain systems are strongly influenced by flow regime (Junk *et al.*, 1989; Poff *et al.*, 1997; Tockner *et al.,* 1999; Bunn & Arthington, 2002). Temperate rivers typically reach flood stage in spring, following periods of snow melt and heavy rainfall, and channel-floodplain connectivity is typically established during this time. Seasonally-flooded wetlands and floodplains serve as spawning and nursery sites for many species of resident and migratory fishes (Baber *et al.*, 2002), and spawners gain access to floodplains during high water events (King *et al.*, 2009; van de Wolfshaar *et al.*, 2011). The flow regime may also alter the environmental conditions for other aquatic biota (Tockner *et al.*, 1999; Thomaz *et al.*, 2007), and is a primary determinant of zooplankton dynamics in river-floodplain systems (Basu & Pick, 1996; Gozdziejewska *et al.*, 2016). Flood waters may flush out zooplankton, returning the assemblage to an earlier successional phase (Baranyi *et al.*, 2002). As flood waters recede, organic matter accumulates (Jones *et al.*, 2014), and zooplankton biomass and crustacean species richness increases (Baranyi *et al.*, 2002; Scholl *et al.*, 2012; Gorski *et al.*, 2013, 2016). The timing and duration of flooding also affects recruitment of juvenile fish (Gutreuter *et al.*, 1999; King *et al.*, 2003). Seasonally-flooded wetlands are ideal larval rearing habitats (Gorski *et al.*, 2016) because they are shallow and warm quickly, fostering high productivity of zooplankton prey (Bass *et al.*, 1997).

The northern pike (*Esox lucius*) is an important top predator in the St. Lawrence River that briefly occupies seasonally-flooded wetlands as spawning and nursery grounds. Northern pike spawn in early spring following ice-melt between 4.4°C and 11.1°C (Scott & Crossman, 1973), and temperature influences the development, growth, and survival of eggs and larvae (Kipling 1983; Doyon *et al*., 1988; Farrell *et al.*, 2006; Mingelbier *et al.*, 2008). Eggs hatch in 6-

14 days in water temperatures of 10.9-15°C, and yolk absorption occurs in 14-17 days at water temperatures greater than 11°C (Cooper *et al.*, 2008). Hatched larvae remain in the shallow spawning marshes (Franklin & Smith, 1963; Holland & Huston, 1985; Massé *et al.*, 1991) and exhibit a brief planktivorous stage at the onset of exogenous feeding (Bry *et al.*, 1995). Hjort (1914) postulated that larvae need to procure suitable prey shortly after yolk absorption to survive. Cushing (1974, 1990) expanded upon Hjort's hypothesis by positing that spawning and larval periods must coincide with peaks in suitable prey, such as zooplankton. Variability in the timing of zooplankton hatches lead to variability in larval mortality (Cushing 1974, 1990), which may determine year class strength (Mertz & Myers, 1994).

Ecological dynamics in river-floodplain systems are structured by natural flow regime (Heiler *et al.*, 1995; Poff *et al.*, 1997), and water level management may disrupt underlying hydrodynamic patterns. Reduction of natural flood periodicity reduces connectivity between rivers and their floodplains, and may alter timing of flooding events. Habitat connectivity is vital for exchange of water, nutrients, and biota (Junk *et al.*, 1989; Heiler *et al.*, 1995; Tockner *et al.*, 1999), and positively influences both fish species richness and piscivore richness (Bouvier *et al.*, 2009). Water level regulation in the St. Lawrence River for example, is thought to decrease available spawning habitat for northern pike, forcing adults to spawn in deeper, offshore sites and later in the season to allow water temperatures to warm (Farrell, 2001; Farrell *et al.*, 2006; Smith *et al.*, 2007). This spawning protraction leads to lower production of juvenile pike (Farrell *et al.*, 2006), and may contribute to overall population declines through lost recruitment potential (McCullough & Gordon, 2015). Additionally changes in spatial and temporal patterns due to protracted spawning may lead to a loss of access to productive foraging areas and mismatches of prey for larvae (Cushing 1974, 1990). Floodplain wetlands typically have greater zooplankton densities than their associated main channels (Bass *et al.*, 1997; Spaink *et al.*, 1998; Nunn *et al.*, 2007; Gorski *et al.*, 2013), creating an ideal environment for larval fish growth. Flood pulse linkages to zooplankton and larval fish ecology have been studied in several large, regulated river systems (Baranyi *et al.*, 2002; Schramm & Eggleton, 2006; Gutreuter *et al.*, 1999; van de Wolfshaar *et al.*, 2011; Scholl *et al.*, 2012; Gorski *et al.*, 2013), but many regulated rivers lack even basic descriptive relationships.

The St. Lawrence River is the only natural outlet of the Great Lakes and runs 1197 kilometers from Lake Ontario to the Gulf of St. Lawrence. Water levels in the St. Lawrence River are managed at the Moses-Saunders Power dam in Massena, NY, and regulation has diminished cyclical patterns of flooding and reduced seasonal water level fluctuations throughout the St. Lawrence River (Farrell *et al*., 2010b). The St. Lawrence River has the lowest suspended sediment load of the world's large rivers (Gleick, 1993), which affects the distribution of primary producers and consumers. The St. Lawrence River also supports a diverse and abundant fishery (McCullough & Gordon, 2015). Our aim was to assess the effects of spring flood pulses on seasonally-flooded wetlands with regard to physical factors, and phytoplankton and zooplankton abundance. Interactions between the timing of pike spawning and subsequent larval pike ontogeny were examined in relation to the spring flood pulse and resulting environmental changes by posing these specific questions: (1) how do physical and biological environmental conditions change during the spring flood pulse in relation to northern pike spawning and larval development, and (2) do peaks in temperature and phytoplankton and zooplankton abundance coincide with the onset of exogenous feeding for larvae?

Methods

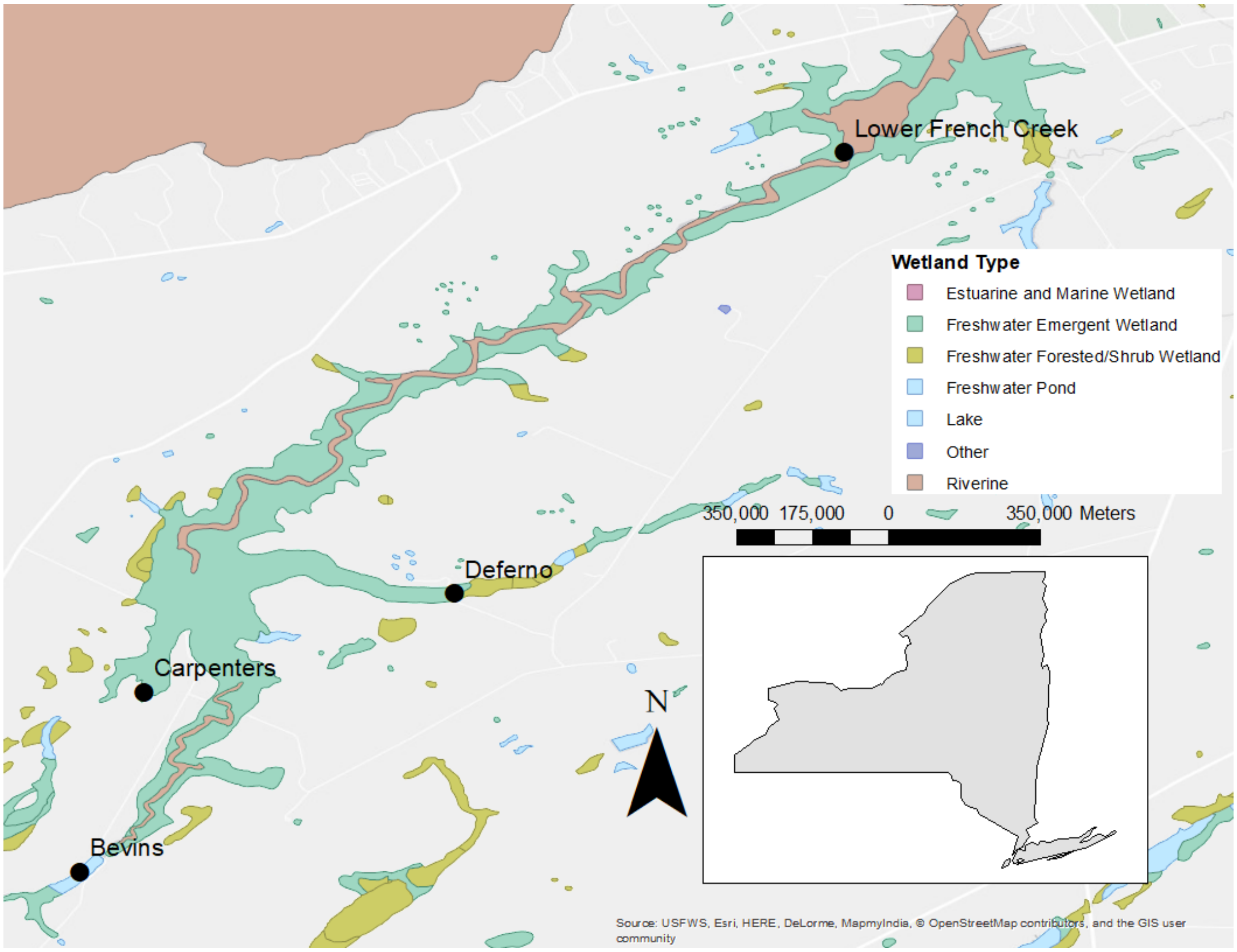
Study area

The Thousand Islands region begins at the confluence between Lake Ontario and the St. Lawrence River, and runs for approximately 80 river kilometers. The region consists of over 1800 islands and hundreds of coastal wetlands, which serve as habitats for aquatic biota. French Creek is located within the Thousand Islands region, near Clayton, NY, and is a low gradient, drowned river mouth tributary to the St. Lawrence River, with a vast floodplain made up of primarily emergent wetland vegetation. Water levels in French Creek mimic those of the St. Lawrence River (Farrell *et al.*, 2014). French Creek represents one of the upper St. Lawrence River's larger undeveloped drowned river mouth wetland systems and sustains a population of northern pike and other important sport fishes (NYSDEC, 1993).

Physical conditions

Four sampling sites within the French Creek watershed were visited on April 1, 8, 15, 22, and 29, 2016 (Figure 1). Sites were selected based on their historical importance as northern pike spawning and nursery sites (Marean, 1976), and to sample throughout the entire watershed. Three sites were chosen in the headwaters of three branches of French Creek: Bevins, Deferno, and Carpenters. The fourth site, lower French Creek, is located downstream of the other three sites. Bevins and Deferno represent unregulated branches of the watershed, and lower French Creek is an unregulated wide section near its confluence with the St. Lawrence River. Carpenters branch possesses a water control structure for the purposes of creating an inundated marsh for a longer period of time (Farrell *et al.,* 2014). All sampling sites had a water depth of 0.2-1.0 m. Water level data from Alexandria Bay, NY (NOAA buoy station ID: 8311062, http://tidesandcurrents.noaa.gov) was used to identify peak water level in the river during April, 2016. Water level trends were plotted using a locally-weighted scatterplot smoothing (loess) curve which uses “nearest neighbor” algorithms to smooth data points into an overall model.

A HOBO Pro v2 temperature logger model U22-001 (Onset Computer Corporation, Bourne, Massachusetts, U.S.A.) was deployed during the first sampling event at each site and recorded temperature (°C) at 1-hour intervals. Differences in temperature among sites were tested with a one-way ANOVA ($\alpha=0.05$). Dissolved oxygen (mg/L) and conductivity (µS/cm) were measured using a YSI ProDSS multiprobe (YSI Incorporated, Yellow Springs, Ohio, U.S.A.) at the surface, mid-column, and near bottom substrate of the flooded marshes. Differences in mean dissolved oxygen throughout the water column were tested with a one-way ANOVA ($\alpha=0.05$) and differences throughout the sampling period were tested with a repeated measures ANOVA ($\alpha=0.05$). Relationships between temperature and dissolved oxygen were examined using a linear regression model.



Source: USFWS, Esri, HERE, DeLorme, MapmyIndia, © OpenStreetMap contributors, and the GIS user community

Figure 1: French Creek flood pulse monitoring sites and their associated wetland types. Mapping sources include U.S. Fish and Wildlife Service National Wetlands Inventory and ESRI.

Biological variables

Water samples were taken each visit to examine patterns in phytoplankton and zooplankton biomass throughout the sampling period. Duplicate 1-liter grab samples were taken for chlorophyll a analysis and duplicate 3-liter zooplankton grab samples were taken, sieved through 53-μm mesh, and preserved in 95% ethanol (Black & Dodson, 2003). During processing, water samples for chlorophyll a analysis were homogenized, subsampled (75-400-mL), and filtered through a 0.7-μm, Whatman GF/F glass fiber filter (GE Healthcare Bio-Sciences, Pittsburgh, Pennsylvania, U.S.A.). Chlorophyll a concentrations were analyzed using the acetone extraction method with a Turner Designs 10 AU fluorometer (Turner Designs, San Jose, California, U.S.A.). Concentrations from duplicate samples were averaged, and differences among sampling dates were tested for using a repeated measures ANOVA (α=0.05) with site included as a random effect. Zooplankton samples were sieved using 53-μm mesh and rinsed with filtered water. All individuals were counted and identified under a Leica MZ dissecting microscope (Leica Microsystems, Wetzlar, Germany) at 10x magnification. Cladocerans were identified to lowest taxonomic group and copepods were identified to order using Ward & Whipple (1959) and Thorp & Covich (2001). Zooplankton densities from duplicate samples were calculated and averaged. Differences in zooplankton densities among sampling dates were tested for using a repeated measures ANOVA (α=0.05) with site included as a random effect.

Egg and larval development

Timing of northern pike egg and larval development was estimated with water temperature data using relationships defined by Farrell *et al.* (2006):

$$\text{Egg to hatch (days): } y = 1489.5x^{-2.0275}$$

$$\text{Hatch to swim-up (days): } y = 7494.6x^{-2.3838}$$

where x was the mean observed water temperature (°C). The start date of egg and larval development was estimated using data from adult northern pike spawner surveys at Bevins and Carpenters in French Creek. Catch per unit effort (CPUE) was calculated using catch data and number of net nights fished, and dates with the greatest CPUE were selected for egg and larval development projections. The majority of adults (males and females) observed during 2016 spring spawning surveys were of ripe condition (89%), determined through manual extrusion of gametes, with the exception of two post-spawn females caught on April 15 and two pre-spawn females caught on March 30 and March 31. We assumed the date that spawners were caught represented the onset of egg development, because the majority of adults were capable of spawning on that date. Egg and larval development projections were calculated for each site using mean water temperatures collected using temperature loggers. The date of egg hatch was determined, and days required to swim-up were calculated using only water temperatures following that date. Temporal patterns of zooplankton abundance sampled during April 2016 were compared to the estimated period for northern pike egg and larval development, to examine prey availability for larvae at swim-up.

Results

Physical conditions

Water level height during the sampling period displayed two flood peaks. Water level was relatively low prior to flooding, experiencing a minimum on April 4 (74.84 m; Figure 2). Water level increased to a peak on April 8 (75.0 m) and a second peak on April 12 (75.0 m; Figure 2). After these flood pulses, water level generally declined for the remainder of the month. Water temperatures declined substantially during flooding and began to rise following peak water level (Figure 3). Lowest mean water temperature occurred at Bevins on April 6 (1.9°C) and highest water temperature occurred at lower French Creek on April 22 (15.3°C). Patterns in mean water temperatures were not significantly different among sampling sites ($F_{3,112}$=0.88, *p*=0.46) and dropped from ~9°C on April 1 to ~3°C around April 6 before increasing to the monthly maximum of ~14°C on April 22. After the maximum, water temperatures generally declined for the remainder of the month.

Mean dissolved oxygen was lowest on April 22 and highest on April 8 (Figure 4). There were no significant differences in oxygen at surface, middle, or bottom depth in the water column ($F_{2,57}$=0.26, *p*=0.77), suggesting mixing. Oxygen readings throughout the water column were then treated as replicates for the analysis of dissolved oxygen and sampling date. Repeated measures ANOVA indicated significant differences in dissolved oxygen among sampling dates ($F_{4,52}$=27.78, *p*<0.001), and post hoc Tukey HSD comparisons specified April 22 (mean=5.44 mg/L), as having lower dissolved oxygen than any other date (Figure 4). Dissolved oxygen was significantly greater on April 8 (mean=9.86 mg/L) than April 1 (mean=8.03 mg/L), suggesting a response to flooding. Regression analyses indicate that dissolved oxygen was inversely related to water temperature (y=12-0.36*x, R^2=0.19, p<0.001, n=60). Conductivity ranged from 59.2 to 529 µS/cm and there were no apparent trends in values observed throughout the survey or among sampling sites.

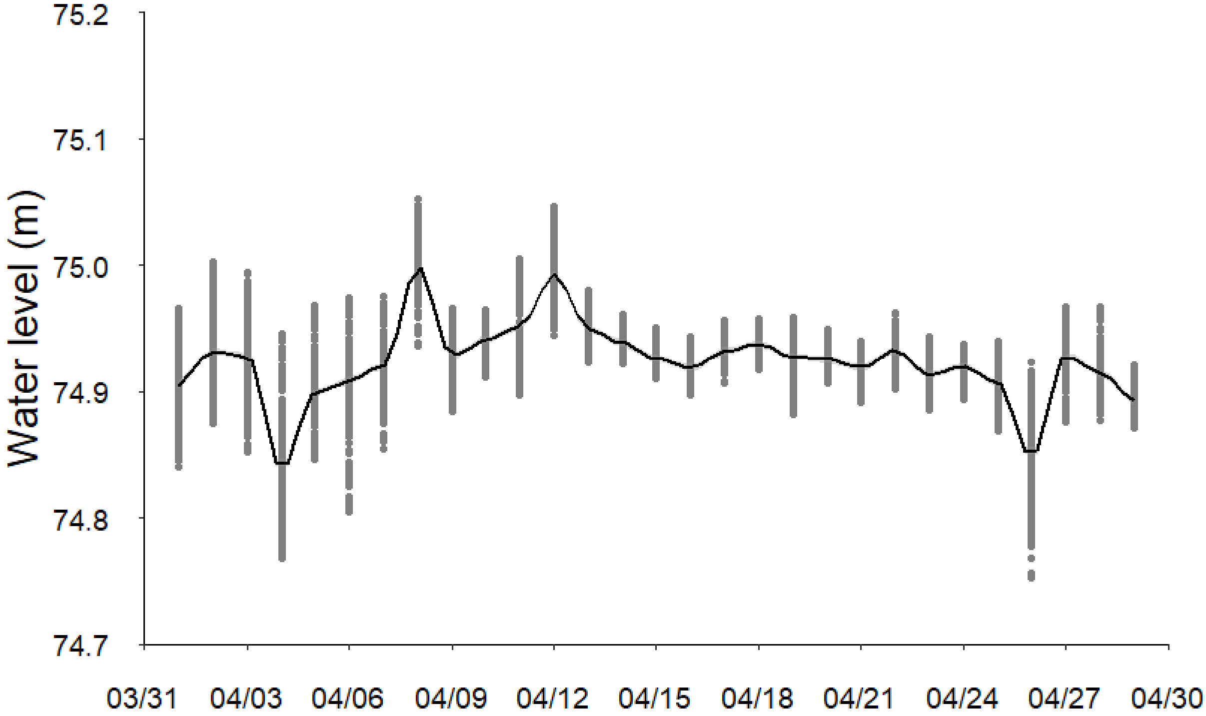


Figure 2. Observed daily water-levels (m) during April 2016 at Alexandria Bay, NY (NOAA buoy station ID: 8311062, http://tidesandcurrents.noaa.gov). Points represent recordings taken every 6 minutes for the 24 hour period. The locally-weighted scatterplot smoothed trendline describes the overall water level patterns. Peak water levels occurred on April 8 and April 12 with recorded heights of ~75 m.

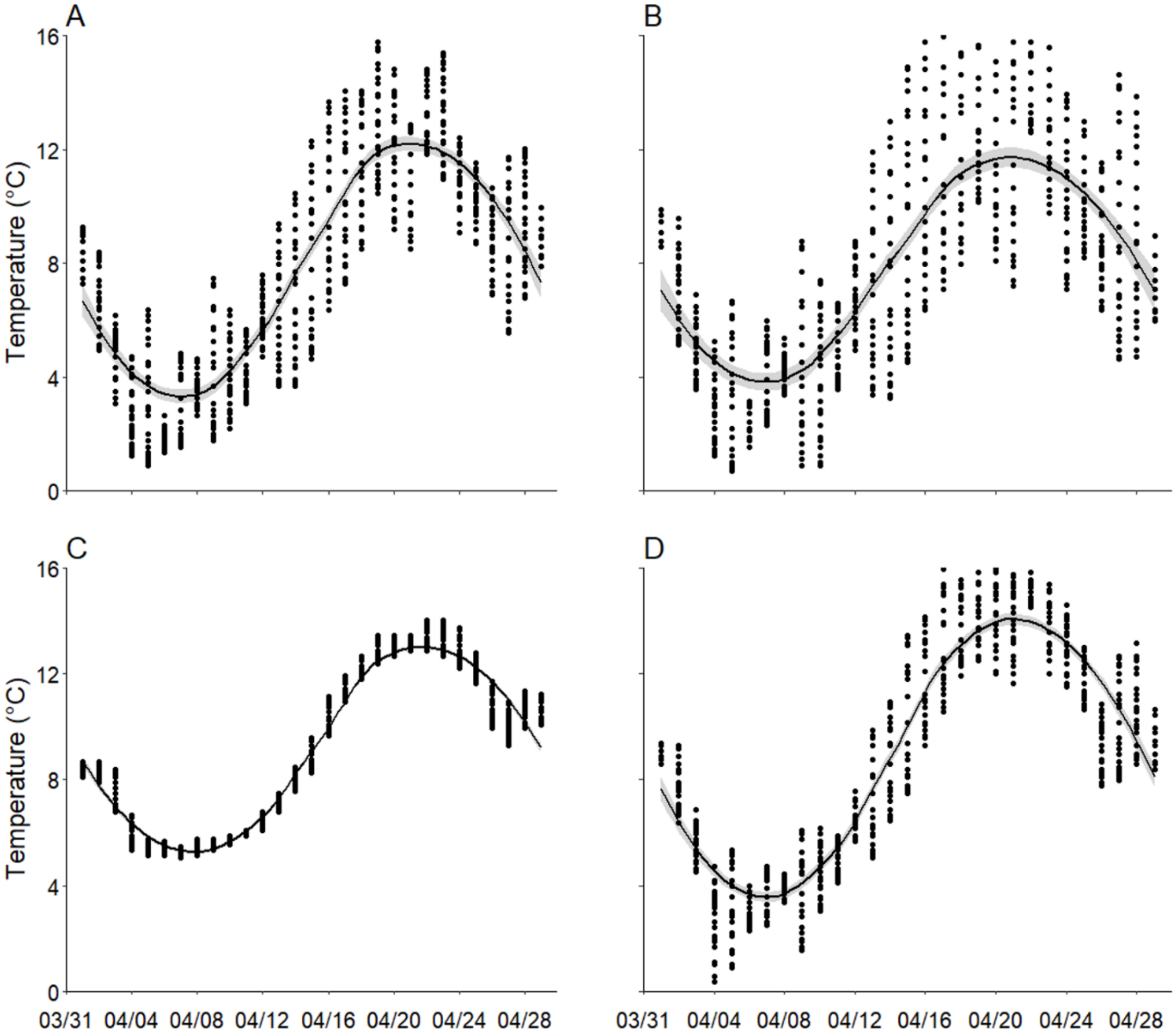


Figure 3. Daily temperature data (°C) recorded using HOBO temperature loggers at mid-water column of Bevins (A), Deferno (B), Carpenters (C), and lower French Creek (D) during April 2016. Points represent temperature recorded at hourly intervals. The locally weighted scatterplot smoothing trendline describes overall temperature patterns during the monitoring period.

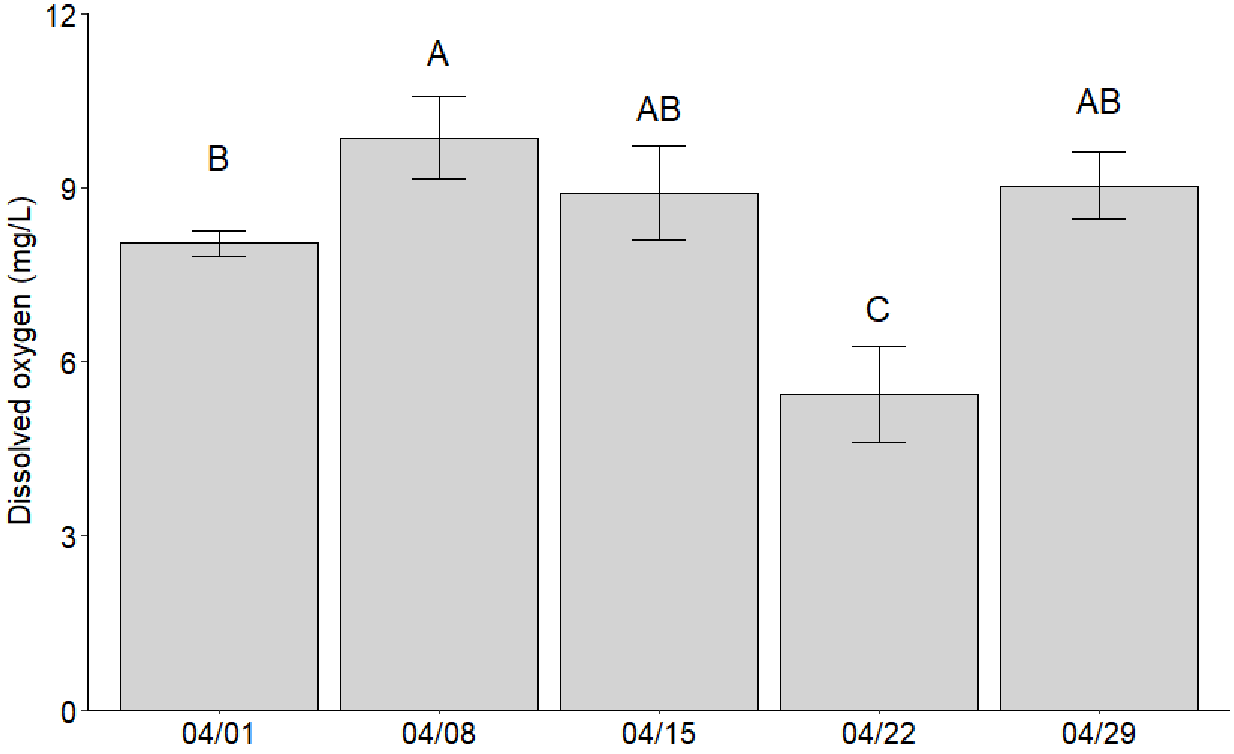


Figure 4. Mean daily dissolved oxygen (mg/L; SE) recorded during April 1, 8, 15, 22, and 29 sampling events using an YSI multiprobe at sampling sites. Sampling occurred between 09:00 and 17:00. Dates are labelled with distinct letters assigned by post hoc comparisons using Tukey's HSD test.

Biological variables

Chlorophyll a concentrations were higher at the beginning of the sampling period, declined during flooding, and began to rise following flooding (Figure 5). Concentrations ranged from 0.42 to 10.95 μg/L throughout the sampling period. Repeated measures ANOVA revealed there was a significant difference in chlorophyll a among sampling dates ($F_{4,32}$=3.69, p=0.01) and post hoc Tukey HSD comparisons indicated concentrations were significantly higher on April 1 than on April 8 and 15 (Figure 5).

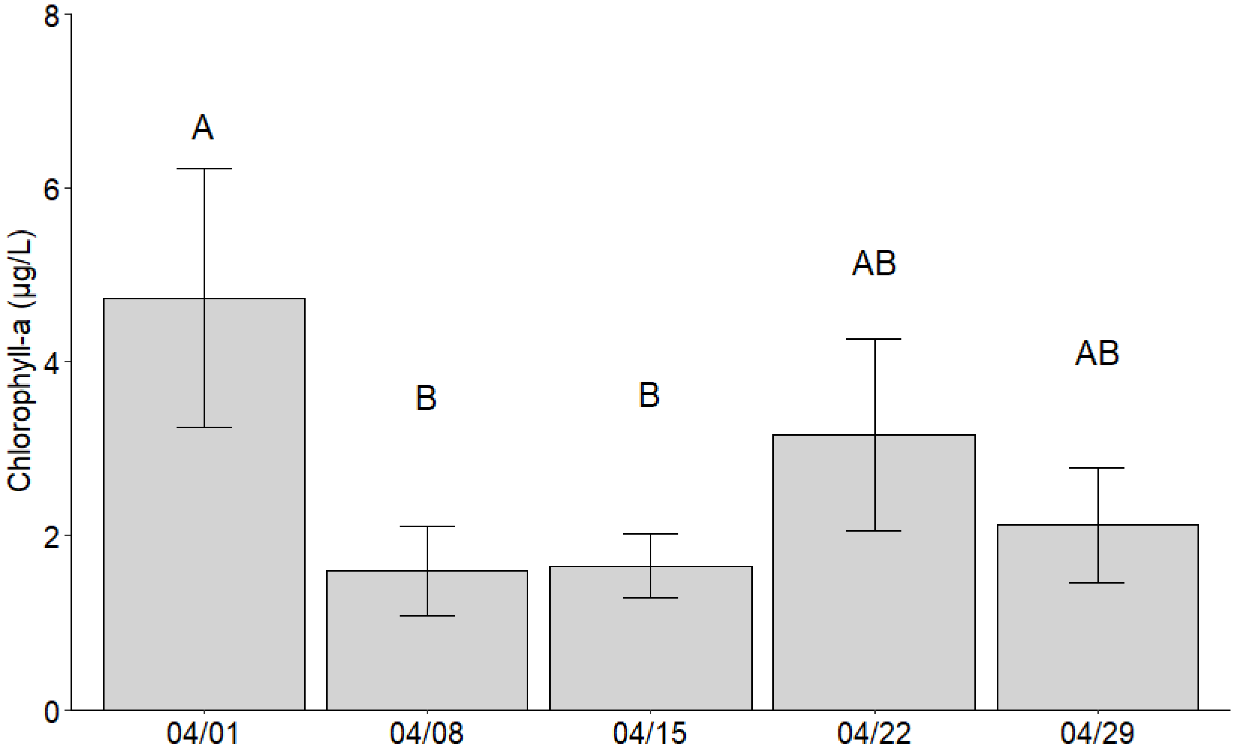


Figure 5. Mean chlorophyll a concentrations (µg/L; SE) from 3-L grab samples at Bevins, Carpenters, Deferno, and lower French Creek on April 1, 8, 15, 22, 29. Dates are labelled with a distinct letter assigned by post hoc comparisons using Tukey's HSD test.

Zooplankton abundances displayed distinct changes during the sampling period, with lowest densities occurring during flooding, and greatest densities occurring two weeks following flooding. Mean total zooplankton densities ranged from 0.33 to 55.67 per liter. Repeated measures ANOVA indicated significant differences occurred between sampling dates ($F_{4,32}$=4.41, *p*=0.01) and post hoc Tukey HSD comparisons indicated densities were significantly higher on April 22 and significantly lower on April 8, than on other sampling dates (Figure 6). Sixteen zooplankton taxonomic groups (order to species) were observed (Appendix 1). The major zooplankton groups were pooled, and densities estimated for major groups indicated copepods dominated the assemblage at all sites from April 1 to April 22 with the exception of the Deferno site on April 15 and 22, where rotifers dominated (Table 1). Peaks in cyclopoids occurred 1-2 weeks following flooding and declined for the remainder of the survey (Appendix 1). Cladocerans began to dominate the assemblage on April 29 at Bevins, Carpenters, and Deferno, following the retreat of flood waters and periods of warm water temperatures, while ostracods dominated at lower French Creek. Densities of the large cladocerans, *Daphnia* spp., *Ceriodaphnia* spp., and *Simocephalus* spp., were low in the beginning of the monitoring period but increased throughout, with highest abundances occurring 3-4 weeks following flooding (Appendix 1).

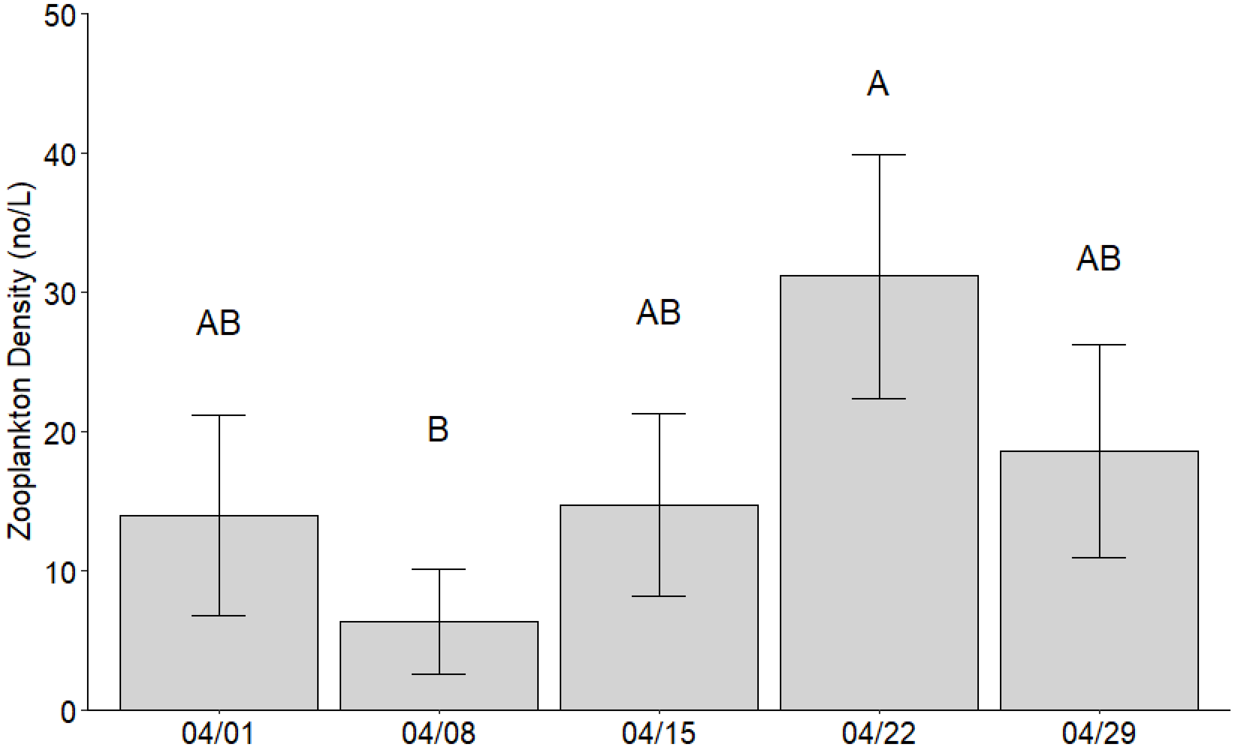


Figure 6. Mean zooplankton density (no/L; SE) of grab samples taken at Bevins, Deferno, Carpenters, and lower French Creek on April 1, 8, 15, 22, 29. Dates are labelled with distinct letter codes assigned using a post hoc Tukey HSD test.

Table 1: Mean densities (no/L; SE) of major zooplankton groups identified from grab samples taken on April 1, 8, 15, 22, and 29, 2016 at Bevins, Carpenters, Deferno, and lower French Creek. Means were calculated by averaging duplicate samples. Means that are not followed by a standard error indicate the density of the taxa was identical in both samples.

		Density (no L^{-1}; SE)			
Date	Site	Copepoda	Cladocera	Rotifera	Ostracoda
4/1	Bevins	3(2)	0.33	0.67	-
	Carpenters	44.3 (3.33)	2.17 (1.5)	0.33	-
	Deferno	0.67 (0.33)	0.33	0.67(0.33)	-
	Lower French Creek	2.5 (0.5)	0.33	1	0.33
4/8	Bevins	0.67	-	0.33	0.33
	Carpenters	23 (2)	1	-	-
	Deferno	0.67	-	-	0.33
	Lower French Creek	0.33	-	-	-
4/15	Bevins	0.5 (0.17)	0.33	-	-
	Carpenters	40 (2.67)	3 (0.67)	-	1
	Deferno	0.33	0.33	0.83 (0.17)	0.33
	Lower French Creek	8.67 (0.67)	0.83 (0.5)	6.67	0.67
4/22	Bevins	17.2 (11.5)	2.83 (0.17)	1.83 (0.17)	-
	Carpenters	27 (1.33)	15.5 (3.83)	-	-
	Deferno	1	-	2.67 (0.33)	1
	Lower French Creek	52.8 (19.8)	1.33 (0.33)	1.17 (0.5)	-
4/29	Bevins	2 (1)	10.8 (6.8)	0.33	0.83 (0.5)
	Carpenters	6 (0.67)	44.5 (11.8)	-	-
	Deferno	1.5 (0.5)	1.83 (1.17)	0.67	-
	Lower French Creek	2.5 (0.83)	1.17 (0.83)	0.5 (0.17)	4

Spawning and egg and larval development

A total of 39 adult spawners were caught in French Creek from March 29 to April 15. Sixteen adults were caught at Bevins: 9 females, 6 males, and 1 unknown, and 23 adults were caught at Carpenters: 10 females, 12 males, and 1 unknown. Spawning adult northern pike CPUE for 2016 was greatest on March 29-30 and April 12, reaching 2.5 spawners · net night $^{-1}$ on both dates (Figure 7). Bimodal peaks observed in catch combined for Bevins and Carpenters, suggested two distinct runs within French Creek, nearly two weeks apart and separated by a mean water temperature drop of 7.5°C at Bevins and 5.6°C at Carpenters (Figure 7). The first spawning run peak began at a water temperature of 6.4-8.2°C, and spawning resumed when temperature rebounded to 7.2°C degrees.

Egg and larval development projections were calculated for spawning start dates of March 29 and April 12. Fewer total development days for eggs and larvae were estimated for April 12 spawners (31-45 days) versus March 29 spawners (36-50 days) due to greater exposure to warmer temperatures and therefore more rapid development experienced by the second cohort of spawners (Table 2). Predictions for date of swim-up ranged from May 4 to May 18 for the March 29 cohort and from May 13 to May 27 for April 12 cohort (Table 2). Peak zooplankton abundances occurred on April 22 at Bevins, Deferno, and lower French Creek and on April 29 at Carpenters, suggesting that zooplankton numbers displayed a relative peak prior to the projected swim-up of pike larvae.

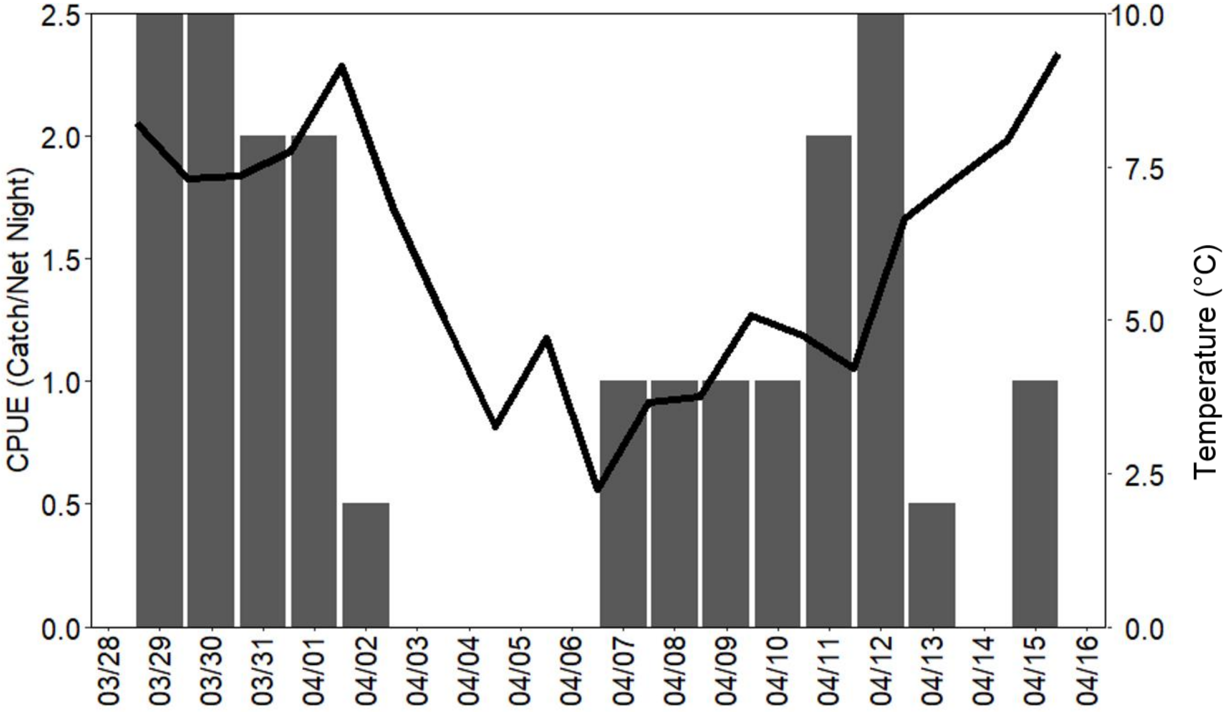


Figure 7. Mean CPUE of adult northern pike spawners (spawners · net night $^{-1}$; bar plot) and mean water temperature (°C; line graph) observed during the month of April, 2016.

Table 2: Days of development for northern pike larvae estimated from temperature-based equations in Farrell *et al.*, (2006). Development of eggs and larvae resulting from March 29 and April 12 spawners were estimated due to greatest adult CPUE observed on those dates.

Site	Mean temperature (°C)	Egg to hatch (days)	Hatch to swim-up (days)	Total development days	Date of swim-up
March 29 spawning projection					
Carpenters	9.1	17	21	38	May 6
Bevins	7.8	23	27	50	May 18
Deferno	8.2	21	24	45	May 13
Lower French Creek	8.9	18	18	36	May 4
April 12 spawning projection					
Carpenters	10.9	12	24	36	May 18
Bevins	10.0	14	31	45	May 27
Deferno	10.4	13	28	41	May 23
Lower French Creek	11.6	10	21	31	May 13

Discussion

Synchrony of spring flooding and water temperatures play a major role in shaping the physical and biological nursery marsh conditions linked to timing of critical needs and ontogeny of northern pike larvae. These results corroborate modelling efforts by Farrell *et al.* (2006) and Smith *et al.* (2007), which highlight the linkages between environmental processes occurring in spawning and nursery habitats and northern pike reproductive success. The influence of hydrologic connectivity is known to be of critical importance to plankton dynamics occurring in seasonally-flooded wetlands (Tockner *et al.*, 1999; Baranyi *et al.*, 2002; Górski *et al.*, 2013). Our results also suggest warming temperatures were crucial to support increasing zooplankton abundances, especially cladocerans, and hastened the development of northern pike eggs and larvae. Slow egg and larval development due to cold temperatures may lead to larvae hatching “mis-matched” to the optimal environment and abundant prey. The interaction between water temperature and water level, and timing relative to larval development and food availability (e.g., Cushing’s hypothesis), was of particular importance to the spring-spawning northern pike. Both spring water levels and spring water temperatures are considered master variables that positively influence year class strength of St. Lawrence River pike, and fluctuations of both factors were likely the origin of historical cyclic patterns in strong year classes (Smith *et al.*, 2007). Water level regulation of the St. Lawrence River has disrupted these natural processes, reducing the northern pike population and steadily lowering year class strength of juveniles (Smith *et al.*, 2007).

Temperature may be the most influential factor affecting northern pike during their spawning and larval stages (Fortin *et al.*, 1982; Casselman, 2002; Farrell *et al.*, 2006; Mingelbier *et al.*, 2008). Adults actively select the warmest areas of the spawning marshes to deposit eggs (Mingelbier *et al.*, 2008), and evidence exists that temperature thresholds trigger adults to begin spawning (Pauwels *et al.*, 2014). In the present study, temperatures prior to flooding were near the optimal range of 6-12°C for egg incubation and high quality larvae (Cooper, 2000; Bondarenko *et al.*, 2015), but declined to as low as 1°C when peak water level was observed. Cold air temperatures (-11 to -1 °C) were also observed immediately prior to flooding on April 4-6, therefore, projections of days required for egg incubation and swim-up were much longer than those observed in other studies on pike egg and larval development (Cooper, 2000; Farrell *et al.*, 2006; Cooper *et al.*, 2008). The cold temperatures observed prior to and during flooding increased the length of development, and may have resulted in high mortalities of eggs and larvae in the field. Temperatures lower than 3°C result in low fertilization and hatching rates because egg development ceases (Bondarenko *et al.*, 2015) and in one study, pike larvae maintained at a constant temperature of 4.7°C did not develop to the swim-up stage (Cooper *et al.*, 2008). The optimum temperature for juvenile pike growth ranges from 19 to 21°C

(Casselman, 1978). Temperatures rarely exceeded 15°C during this study, but increased to greater than 20°C during the juvenile emigration period (Augustyn, 2017, Chapter 3).

Daily dissolved oxygen concentrations were consistently above the incipient lethal oxygen concentration of 0.5-1.5 mg/L (Casselman, 1978) during the sampling period. Dissolved oxygen was negatively influenced by temperature and experienced a minimum on April 22 (mean=5.4 mg/L), when the highest temperatures were observed. Dissolved oxygen was highest during flooding, suggesting that flood waters brought oxygen-rich waters from the main river to the nursery marshes. Dissolved oxygen did not appear to be of concern in French Creek during the larval period, although concentrations are known to decline to below the incipient lethal concentration during the juvenile emigration period in early summer (Augustyn, 2017, Chapter 3).

Chlorophyll a concentrations were highest prior to flooding, and decreased with increased connectivity between to the main channel of French Creek, similar to observations by Knowlton & Jones (1997) in Missouri River floodplains and Ahearn *et al.*, (2006), in a restored floodplain of the Cosumnes River, California. Chlorophyll a minima have been observed to occur during periods of high discharge (Tockner *et al.*, 1999), and phytoplankton were likely flushed from the marsh and diluted during flooding. Concentrations began to increase following flooding at all sites coinciding with increases in temperature. Chlorophyll a concentrations in the main St. Lawrence River typically do not exceed 5 µg/liter (Farrell *et al.*, 2010a), and concentrations observed in this study were comparable to those in the main river, but did increase above 10 µg/liter at Carpenters prior to flooding, and above 8 µg/liter at lower French Creek following flooding. Mean chlorophyll a can increase to 20 µg/liter in wetlands of the upper St. Lawrence

River throughout the growing season (Farrell *et al.*, 2014), but sampling for this study was limited to early spring.

Nutrient and algal productivity originating in floodplain and slackwater habitats are thought to be extremely important to large, oligotrophic rivers, such as the St. Lawrence River (Thorp *et al.*, 1998; Thorp & Delong, 2002). The seasonal fluctuation of floodplain/main channel connectivity allows for the concentration of high phytoplankton biomass during periods of disconnection, which is then transferred to the main channel during flooding (Tockner *et al.*, 1999; Ahearn *et al.*, 2006). Nutrients and phytoplankton derived from the floodplain are thought to be essential to biota in the main channels (Junk *et al.*, 1989) and reductions in flooding not only prevent biota from entering the productive floodplain, but also prevent the exchange of vital nutrients, algae, and zooplankton to the main river (Ahearn *et al.*, 2006; Gorski *et al.*, 2013). Lower French Creek, the furthest downstream site in this study, was the only site where the highest chlorophyll a concentrations were observed following flooding, suggesting algae and/or nutrients were transferred downstream as flood waters receded. Both watershed and main river derived waters may have been sources of observed flooding, although depressions in phytoplankton and zooplankton biomass observed during flooding suggest the bulk of the water was derived from overflow of the main river. Flow reversal was also observed on April 15 and April 29, which further suggests water moved into French Creek from the main river. Watershed derived flooding typically results in a release of nutrients (Tockner *et al.*, 1999) although no significant release of spring nutrients has been detected in wetlands of the upper St. Lawrence River (Farrell *et al.*, 2014). Water level regulation occurring in the system may inhibit the complete understanding of the natural patterns.

Highest zooplankton densities occurred two weeks following flooding on April 22, which has been observed in other temperate river-floodplain systems (Gorski *et al.*, 2013). Despite the detection of statistical differences, changes in density were modest, ranging from a minimum abundance of 6.29/liter to a maximum abundance of 31.13/liter. Cold temperatures observed during the sampling period may have inhibited cues that many cladoceran species require for hatching (Vandekerkhove *et al.*, 2005), suggesting warm temperatures should coincide with spring flooding for extensive zooplankton productivity to occur. Copepods were the dominant group at the beginning of the sampling period but cladocerans began to dominate the assemblage at the end of the sampling period. Zooplankton biomass is positively related to the residence time of water, and large-bodied zooplankton typically dominate following a spring flooding event (Baranyi *et al.*, 2002; Casper & Thorp, 2007). Carpenters had higher zooplankton densities than the other sites examined in this study and also displayed the least water temperature fluctuation. The water control structure maintains high water levels throughout the spring (Farrell *et al.*, 2014), and fosters a shallow, warm, flooded habitat where zooplankton thrived. The assemblage of the main St. Lawrence River consists of primarily cyclopoid copepods, nauplii, and *Bosmina longirostris* (Casper & Thorp, 2007; Farrell *et al.*, 2010a). Copepods display relatively fast swimming speeds when compared with cladocerans (Kerfoot, 1978) and *Bosmina longirostris* are small in size, which might make them unfavorable for larval fish that are trying to grow as quickly as possible. Seasonally-flooded wetlands provide a plethora of large, nutritious zooplankton prey, which promotes fast growth rates of juvenile fish (Gutreuter *et al.*, 1999; Phelps *et al.*, 2015) and access to abundant, large zooplankton prey is an advantage of larval fish inhabitation of floodplains. Lateral connectivity may transfer zooplankton from the floodplain to the main channel, enhancing overall biological productivity of large river systems (Gorski *et al.*, 2013).

Spring flooding triggers short potadromous fish migrations, including those of pike, into the tributary wetlands. Water level regulation diminishes natural fluctuations and reduces flooding, potentially disrupting environmental cues required by floodplain spawners. Protracted spawning of northern pike in the St. Lawrence River is thought to be directly related to water level regulation (Farrell, 2001), because muted flood pulses reduce the availability of tributary floodplain wetlands, forcing pike to spawn in deeper, less suitable habitats, and later in time due to temperature thresholds (Farrell *et al.*, 2006). Late spawning results in lower egg survival (Farrell 2001, Murry *et al.*, 2008) and YOY production (Farrell *et al.*, 2006) when compared with early, tributary spawning. Late-spawned larvae experience a shorter growing season and may be exposed to lower prey abundances in offshore habitats then early-spawned larvae (Farrell *et al.*, 2006). The 2016 YOY production in French Creek was extremely low (Augustyn, 2017, Chapter 3) when compared with that in prior years (Farrell *et al.*, 2017). Precipitation in the upper St. Lawrence River between April and June was below average during 2016, ranking as the 7th driest year in recorded history (NOAA NCEI). Low rainfall coupled with water level regulation and cold spring temperatures could have contributed to overall low production. Northern pike abundances indexed by the New York State Department of Environmental Conservation have been in decline since the 1980s (McCullough & Gordon, 2015), and reductions in natural water level fluctuations and resulting loss of spawning habitats are thought to be the main drivers of these declines (Farrell, 2001; Farrell *et al.*, 1996, 2006; Smith *et al.*, 2007).

This study provides evidence that seasonal flooding helps govern the environmental conditions and biotic dynamics in floodplain habitats of the St. Lawrence River. The life cycles of many fish species have evolved in regard to these patterns (Junk *et al.*, 1989), and the northern pike is one such species in which reproduction is linked to spring flooding (Smith *et al.*, 2007; Lee *et al.*, 2015). Seasonal flooding maintains connectivity between the main channel and floodplain, and reinforces advantageous life history strategies. We suggest that maintaining naturally fluctuating water levels and a diversity of wetland habitats will likely promote northern pike juvenile production, and buffer the population against deleterious environmental events, such as the cold water temperatures and drought observed in this study.

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Chapter 2: Prey selection by larval northern pike (*Esox lucius*) exposed to different zooplankton assemblages representing seasonally-flooded wetland and nearshore bay habitats

Abstract

We designed a prey selection study to investigate whether northern pike larvae select similar prey taxa in seasonally-flooded wetlands and nearshore bays that represent primary northern pike spawning habitats, and are affected by habitat changes. At first exogenous feeding, swim-up larvae exposed to bay and wetland assemblages were generalist consumers, feeding primarily on cyclopoid copepods and small cladocerans. Consistent with random feeding, no positive selection was observed for any prey taxa. Advanced larvae selected the large cladoceran *Simocephalus* spp., neutrally in both bays and wetlands, while *Ceriodaphnia* spp., the other large cladoceran, was selected positively by larvae offered a wetland assemblage and neutrally by larvae in a bay assemblage. Larger-sized prey were consumed by wetland larvae than by bay larvae at the advanced stage. Large cladocerans made up a greater proportion of the zooplankton assemblage in seasonally-flooded wetlands versus nearshore bay habitats, and may explain the difference in size selectivity. This laboratory study suggests larvae hatched in wetland environments have greater access to large cladoceran prey during this critical period, and differences in spatial and temporal spawning distributions may have important implications on zooplankton consumption during the larval period.

Introduction

Prey availability and the ability to capture and ingest prey are critical for survival of larval fish during the first stages (Cushing 1990; Mayer & Wahl, 1997). Often larval fishes, including piscivores, are gape-limited, and dependent on zooplankton prey during the first few weeks of exogenous feeding (Devries *et al.*, 1998; Nilsson & Bronmark, 2000). The northern pike (*Esox lucius*) is a voracious, apex predator in the St. Lawrence River that consumes zooplankton during its first life stages (Raat, 1988), and abundant prey is critical for larval survival (Skov *et al.*, 2003; Ljunggren *et al.*, 2010). Reported larval pike diets are comprised primarily of cyclopoid copepods and cladocerans (Desvilettes *et al.*, 1994; Lehtiniemi *et al.*, 2007; Salonen *et al.*, 2009), which typify the assemblage of the upper St. Lawrence River (Farrell *et al.*, 2010). Zooplankton assemblage composition is influenced by several environmental factors including flow, temperature, and turbidity (Rossaro, 1988; Pace *et al.*, 1992; Thorp *et al.*, 1994), and changes in the species composition can affect the growth and recruitment of juvenile fish (Miller *et al.*, 1990).

The spawning period for northern pike in the St. Lawrence River is protracted, occurring over many weeks (Farrell, 2001; Chizinski *et al.*, 2016), and along a spatial gradient from shallow (<30 cm) seasonally-flooded wetlands of tributaries to deep (>6 m) offshore areas (Farrell *et al.*, 1996, 2006; Farrell 2001), and because of this behavior, larvae may have access to different zooplankton forage depending on their nursery habitat type. The protracted spawning behavior is thought to occur in response to water level regulation and associated wetland vegetation changes that occur in the St. Lawrence River (Farrell, 2001; Farrell *et al.*, 2006). Offshore spawning occurs later in the spring, after cooler spring water temperatures reach suitable levels (Farrell *et al.*, 2006). Spatial and temporal variation in spawning has direct effects on young-of-year (YOY) production (Farrell *et al.*, 2006) and year class strength (Smith *et al.*, 2007). Laboratory and modelling work indicates early tributary spawners yield higher egg survival (Murry *et al.*, 2008), and a greater potential for growth and YOY production (Farrell *et al.*, 2006) than nearshore bay or offshore spawners, due to a longer growing season.

Hatched larvae remain in the spawning grounds and are nourished by their yolk-sac until exogenous feeding begins (Raat, 1988). Swim-up larvae begin feeding on zooplankton, and must encounter appropriate and abundant prey soon after yolk-sac absorption to survive (Hjort, 1914; Cushing, 1974, 1990). Northern pike larvae prefer large prey types (Lehtiniemi *et al.*, 2007; Salonen *et al.*, 2009), and exhibit a progression in the zooplankton taxa they consume, beginning with copepods and later switching to large cladocerans and insect larvae (Raat 1988; Desvilettes *et al.*, 1994, 1997; Bry *et al.*, 1995). Copepods display much faster swimming speeds than cladocerans (Kerfoot, 1978) and this dietary switch may be due to difficulties in capturing large copepods.

Gape limitations (Nilsson & Brönmark, 2000) and low abundances of suitably-sized fish larvae may explain the dominance of zooplankton in diets of larval piscivores (Persson & Brönmark, 2002). Specifically, northern pike larvae may rely on zooplankton until they are approximately 28 mm (Cooper, 2000), and able to consume fish. Suitable and abundant zooplankton prey presence after swim-up is critical for larval pike survival, and despite this, few studies have focused on zooplankton assemblage differences and their suitability as prey in relation to nursery habitats.

This study was designed to examine the prey selection of northern pike larvae at two developmental stages exposed to zooplankton assemblages, originating from two distinct habitats that represent different spawning strategies. We used laboratory experiments to address two questions involving larval northern pike prey selection: (1) do seasonally-flooded wetlands or nearshore bays support a greater proportion of zooplankton taxa preferred by larvae, and (2) do changes in larval preference of specific zooplankton types occur from swim-up to advanced stages?

Methods

Prey selection experiments- swim-up larvae

Salisbury and Flynn Bays, known northern pike spawning habitats both located on Grindstone Island in the upper St. Lawrence River (Figure 1), were selected as zooplankton collection sites and were treated as replicates. Both locations include backwater spawning habitats consisting of a seasonally-flooded emergent wetland with connecting channels and nearshore littoral habitat associated with the bays. Zooplankton were collected in areas that best represented habitat categories on May 18, 2016, with funnel traps designed by Bruce Smith of Ithaca College, NY and described in Brown *et al.* (2017). Funnel traps were assembled from PVC cylinders, 20 cm long and 10 cm in diameter. The exterior of the cylinder was painted black and a clear, inverted funnel with a 2 cm opening was attached to one end of the cylinder so aquatic organisms can enter the trap, but cannot easily exit. The opposite end of the cylinder was capped and a hole was drilled into the cap to fit a waterproof LED flashlight. The flashlight directs light out of the funnel, attracting phototactic organisms. Funnel traps were set after dark at bay and wetland locations and illuminated with a battery-powered bulb. Zooplankton were collected after 1 hour and stored in coolers overnight. All large insects, tadpoles, and fish that might prey on smaller zooplankton were removed immediately after collection.

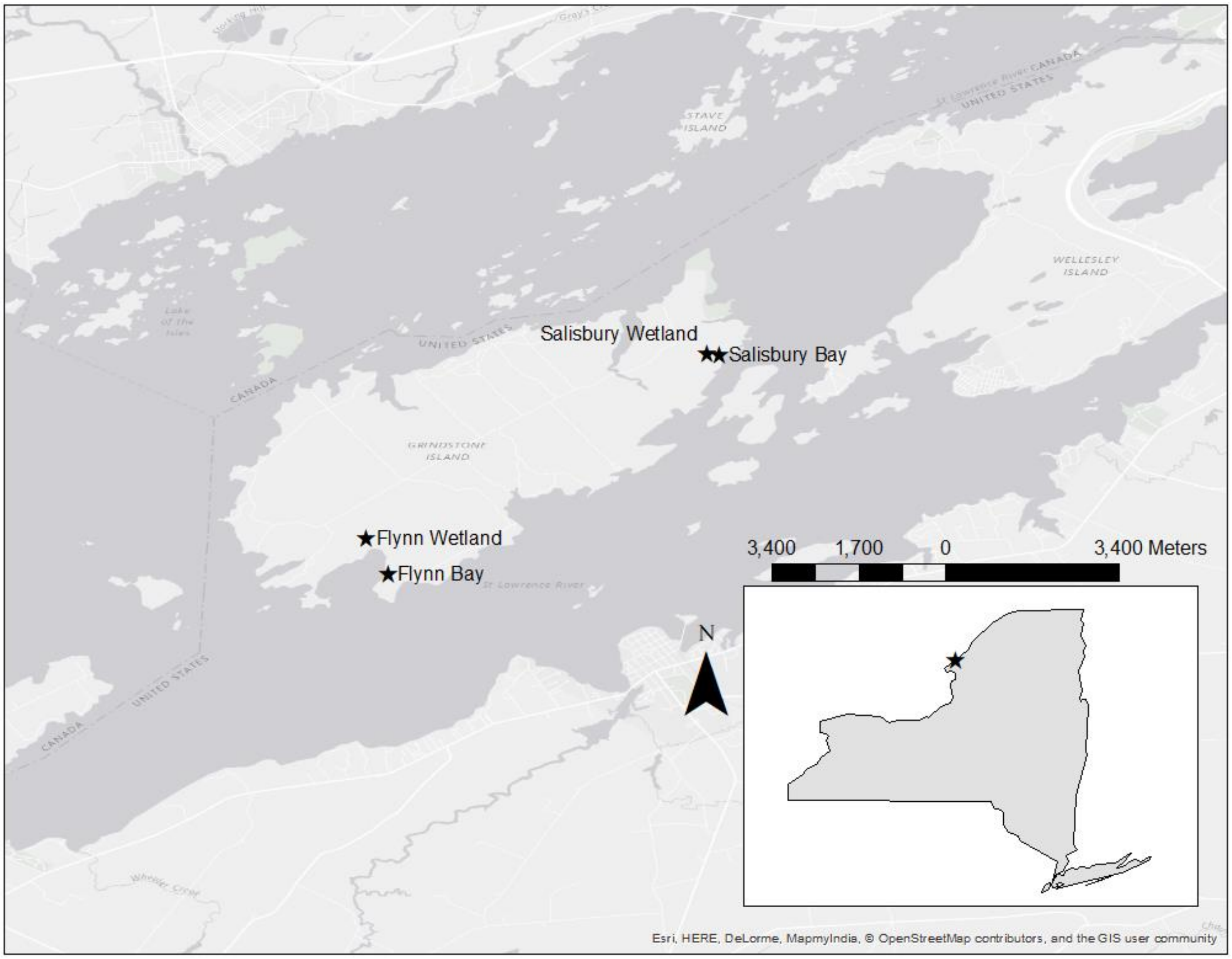

Figure 1. Locations of light trap deployment in Flynn and Salisbury bays, Grindstone Island, NY. Mapping sources include ESRI.

Light traps were used to sample common taxa occurring in the sites. Light traps typically collect fewer zooplankton types than plankton nets but survival of the organisms is improved. Live zooplankton were imperative for the experiment, and for this reason light traps were selected as a zooplankton capture method. Mean densities from each assemblage were estimated by counting number of zooplankton in three 10-mL aliquots taken from the sample. Room temperature river water was added volumetrically so resulting densities were similar from each site and water temperature was not affected. The entire sample of each treatment was homogenized in storage coolers, and 1500-mL of sample was extracted and distributed into 44 randomly selected 1.89-L glass containers. Water temperature was 12.5°C. Each zooplankton assemblage (bay vs. wetland) was replicated twenty times. Containers were placed in random order in 37.5-L rectangular glass aquaria and were isolated from one another with white dividers.

Larvae used in the experiment were cultured in the laboratory as progeny from a one male to one female pairing to reduce genetic diversity as a potential driver of prey selection. Adult spawning northern pike were captured in French Bay on April 17, 2016 in Oneida trapnets. Eggs were stripped from the female and fertilized with milt from the male using the dry method (Sorenson *et al.*, 1966; Klingbiel, 1986). Fertilized eggs were incubated in hatching jars for two weeks and received a continuous flow of well water. After hatch, yolk-sac fry were transferred to 75-L glass aquaria housed on a three rack shelf where yolk-absorption occurred in approximately one week. Northern pike egg and larval development are influenced by water temperature (Farrell *et al.*, 2006), and previous work conducted in Flynn Bay indicated larvae begin feeding three weeks following egg deposition at naturally occurring water temperatures (Cooper, 2000). The first trial of experiments for this study was carried out exactly three weeks following egg fertilization.

The first experimental trial was conducted at first exogenous feeding (mean length = 13.2 mm, SE = 0.04), meaning larvae had not encountered or consumed any prey prior to the trial. Five northern pike larvae were randomly selected and distributed into each container. Wetland and bay treatments were replicated (n=2) using zooplankton assemblages from Flynn and Salisbury Bays. Time until first prey strike was measured (seconds) and averaged for the first ten containers to calculate a mean orientation time (four minute). Larvae were allowed to feed for an additional hour, similar to other larval prey selection experiments, because digestion is minimal and prey items in the gut are easily identified (Graham & Sprules, 1992; Mayer & Wahl, 1997). Following the trial, zooplankton were sieved through 53-μm mesh. Larvae were removed with forceps and preserved in 95% ethanol. The remaining zooplankton were also preserved in 95% ethanol. During processing, larvae were measured (mm) and rinsed with well water prior to processing. The entire gut was dissected and all prey items were counted, identified, and measured using a Leica MZ dissecting microscope (Leica Microsystems, Wetzlar, Germany) at 10x magnification. Only larvae that consumed zooplankton were included in the selection analysis which included 123 of 200 (61.5%) during this trial. Of the 77 larvae that did not consume zooplankton, 27 were given the bay assemblage and 50 were given the wetland assemblage. Cladocerans were identified to lowest taxonomic group and copepods were identified to order using Ward & Whipple (1959) and Thorp & Covich (2001), and the proportion of each prey taxon in the diet was calculated. Differences in the lengths of prey consumed were tested using a 2-sample *t*-test ($\alpha=0.05$). The remaining zooplankton assemblage that was not consumed was filtered, rinsed, and all prey items were counted and identified.

Prey selection experiments- advanced larvae

The selection experiment was repeated with larger larvae (mean length = 17.7 mm, SE = 0.08) of the same genetic strain as the first trial. The advanced trial was repeated with methods described for the swim-up trial, but following swim-up, larvae were fed *Artemia* spp. for three weeks. Prior to the experiment, larvae were starved for six hours to allow for gut passage of *Artemia* spp. through the intestinal tract. Water temperature was 19.1°C. Zooplankton abundances were substantially greater during the advanced larvae trial, so the remaining assemblage was subsampled during processing. The entire sample was suspended in 30-mL of water and homogenized. Aliquots of 1-mL were taken using a pipette and counted until at least 300 individuals (Górski *et al.*, 2013) were identified or the entire remaining assemblage was sorted.

Larval feeding strategy

A modified Costello diagram (Figure 2) was used to evaluate feeding patterns of larvae for each treatment (Costello, 1990; Amundsen *et al.*, 1996). This technique uses the prey-specific abundance as the percentage of a prey taxon's occurrence relative to all prey consumed by an individual predator where the prey taxon occurs:

$$P_i = \left(\sum S_i / \sum S_{t_i}\right) \times 100$$

where P_i = the prey-specific abundance of prey type i, S_i = number of prey type i in all stomachs, and S_{t_i} = the total number of prey items in the stomachs of predators with prey i in their stomach. Prey-specific abundance is plotted against the frequency of occurrence:

$$O_i = \frac{J_i}{P}$$

where O_i = the frequency of occurrence of prey type i, J_i = the number of fish containing prey type i, and P = the number of fish with food in their stomachs (Bowen 1996).

Amundsen *et al.* (1996) modified the original diagram by including three axes for interpreting feeding patterns (Figure 2). The axis increasing from the lower left to the upper right indicates prey importance. The axis increasing from the lower right to the upper left indicates niche width contribution. High between-phenotype component (BPC) occurs when individuals within a population specialize on different prey items, whereas high within-phenotype component (WPC) occurs when most individuals within a population use many prey items concurrently. The vertical axis represents feeding strategy.

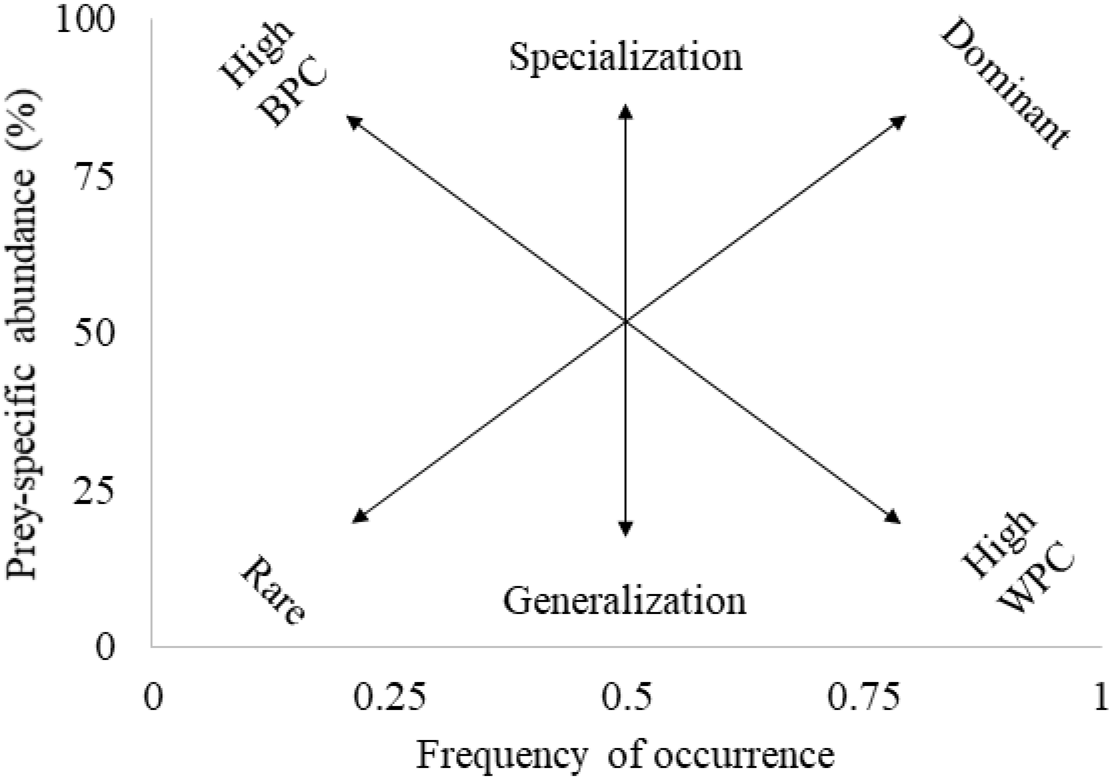

Figure 2. Modified Costello feeding diagram (Amundsen *et al.*, 1996) with 3 axes: feeding strategy, prey importance, and niche width contribution.

Important assemblages

A hierarchical agglomerative cluster analysis was performed using the BOOTCLUS program (McKenna, 2003) to identify significant assemblages present in the larval pike diets and environment (α=0.05). Raw abundance data were analyzed using the Bray-Curtis coefficient and the Unweighted Pair Group Method with Arithmetic Mean (UPGMA) linkage with 1000 bootstrap samples to test each linkage. The analysis was used to generate a dendrogram classifying zooplankton assemblage relationships within the experimental treatments and each cluster classified by the analysis represents a significantly distinct assemblage. This analysis allowed for the examination of the proximity of the diets and environmental assemblages.

Prey selection

Vanderploeg & Scavia's (1979) relativized electivity index was used to evaluate prey selection by larvae given wetland and bay zooplankton assemblages. An index value was calculated for each prey item:

$$E_i^* = \frac{[W_i - (1/n)]}{[W_i + (1/n)]}, \text{where } W_i = \frac{r_i/p_i}{\sum r_i/p_i}$$

where r_i is the relative abundance of prey type i in the stomach, p_i is the relative abundance of this prey in the environment, and n is the number of prey types. Values range from -1 to +1. Negative values indicate rejection of the prey type, values near zero indicate random or neutral feeding, and positive values indicate selection of the prey type. Larvae from each jar were pooled and proportions of prey items consumed were averaged for each treatment. This index was selected because prey were not replaced during the experiment and individuals from some prey types were consumed entirely, eliminating the use of other indices (Manly, 1974; Chesson, 1978). The relativized electivity index ($E*$) is the best electivity index when compared with similar indices because it corrects for the number of prey types among samples, making treatments comparable (Lechowicz, 1982; Confer & Moore, 1987). The E* index values were arcsine transformed (arcsine $\sqrt{[(E_i^* + 1)/2]}$ to improve normality and homogenize variances (Alcaraz & Garcia-Berthou, 2007; Almeida *et al.*, 2012). A Student's t-test was used to test if E* values significantly differed from 0.

A series of Kruskal-Wallis non-parametric tests were performed to test for significant differences in prey selectivity among habitat type and time frame. All tests were done using raw E* values for each prey taxa. The first set of comparisons identified the effect of habitat on prey selectivity for each developmental stage (swim-up or advanced larvae). Selectivity of wetland prey taxa by swim-up larvae were compared to selectivity of the same taxa originating from a bay. This test was repeated for prey taxa consumed by advanced larvae. The second set of comparisons identified changes in selectivity over time, but within the same habitat. Selectivity of individual wetland prey taxa by swim-up larvae were compared to the wetland taxa's selectivity by advanced larvae. This test was repeated for prey taxa originating from bays. All statistical testing were performed using R version 3.3.1 (R Core Team, 2016) and Minitab 17 statistical software (Minitab, 2010) unless otherwise noted.

Results

Larval feeding strategy

Swim-up wetland larvae primarily consumed cyclopoids (Frequency of Occurrence (O) =100%; Table 1). Cladocerans (<0.7 mm), such as small *Ceriodaphnia* spp. (O=13.3%), *C. sphaericus* (O=20%), *Scapholeberis* spp. (O=26.7%), and small *Simocephalus* spp. (O=13.3%), and ostracods (O=46.7%) were also commonly found in the diet. Swim-up bay larvae also consumed cyclopoids (O=90%), but *C. sphaericus* was the most frequently consumed taxon (O=95%). There were no significant differences in the lengths of prey consumed by swim-up larvae (t_{248}=1.21, *p*=0.23) in wetlands (mean=0.68 mm, SE=0.03) versus bays (mean=0.64 mm, SE=0.02).

Advanced wetland larvae continued to feed on cyclopoids (O=100%), but large cladocerans (>0.8 mm) became increasingly more represented in the diet. Large *Simocephalus* spp. occurred in 100% of the diets and *Ceriodaphnia* spp. occurred in 95%. Advanced bay larvae continued to consume both cyclopoids (O=100%) and small *C. sphaericus* (<0.4 mm; O=94.7%) in similar proportions to bay larvae at swim-up. Ostracods (O=94.7%) and small *Scapholeberis* spp. (<0.6 mm; O=94.7%) occurred more frequently in advanced larval diets. Significant differences in the length of prey consumed by advanced larvae due to habitat type were detected (t_{2218}=6.88, *p*<0.001), with wetland larvae consuming larger prey (mean=0.83 mm, SE=0.01) than bay larvae (mean=0.74 mm, SE=0.01).

Table 1: Frequency of occurrence (%) of the prey taxa represented in the diets of experimental larvae. Prey taxa not found in either trial for a specific treatment are indicated with a dash (-).

	Wetland		Bay	
Prey	Swim-up	Advanced	Swim-up	Advanced
Amphipoda	0	5	-	-
Acroperus spp.	0	5	0	63.2
B. longirostris	0	10	0	42.1
Calanoida	-	-	0	31.6
Ceriodaphnia spp.	13.3	95	5	26.3
Chironomidae	0	15	0	47.4
Chydoridae	6.7	35	5	47.4
C. sphaericus	20	85	95	94.7
Cyclopoida	100	100	90	100
Diaphanosoma spp.	0	10	0	10.5
Harpacticoida	-	-	0	5.3
Macrothricidae	-	-	0	10.5
Ostracoda	46.7	50	60	94.7
P. pediculus	-	-	0	26.3
Scapholeberis spp.	26.7	15	25	94.7
Sida crystallina	-	-	0	5.3
Simocephalus spp.	13.3	100	0	47.4

Examination of the Costello-Amundsen plots revealed few differences in the feeding strategies of northern pike larvae exposed to the four treatments (Figure 3). Swim-up wetland larvae were generalists, although there was a slight specialization on cyclopoid copepods (Figure 3). Swim-up bay larvae, advanced wetland larvae, and advanced bay larvae also exhibited generalized feeding strategies. Advanced larvae began to incorporate more taxa into the diet and advanced bay larvae consumed the most prey types, totaling seventeen.

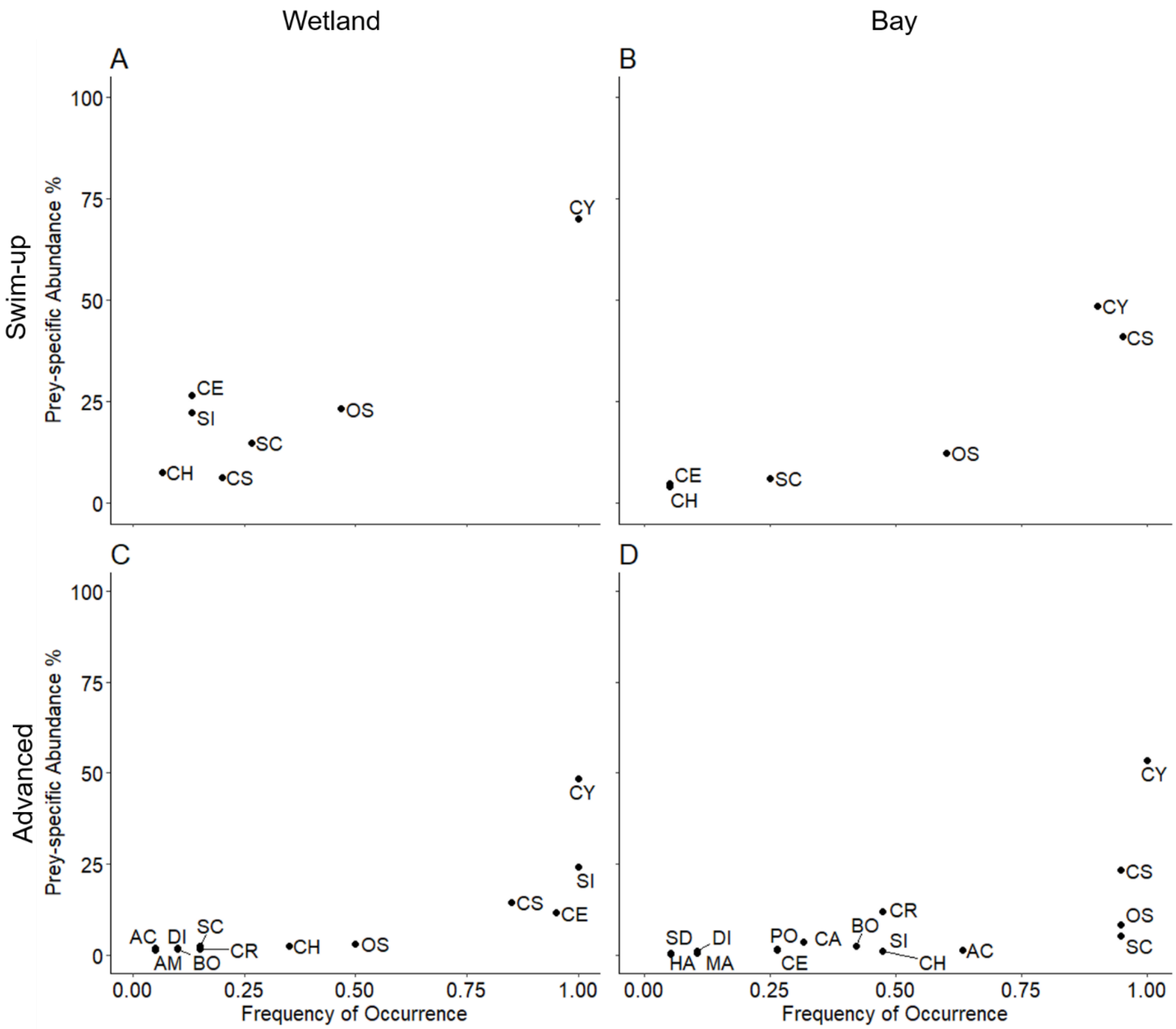

Figure 3. Amundsen-Costello diagrams showing feeding strategy of swim-up larvae given a wetland (A) or bay assemblage (B) and advanced larvae given a wetland (C) or bay (D) assemblage. Zooplankton taxa codes are as follows: AC, *Acroperus* spp.; AM, Amphipoda; BO, *B. longirostris*; CA, Calanoida; CE, *Ceriodaphnia* spp.; CR, Chironomidae; CH, Chydoridae; CS, *C. sphaericus*; CY, Cyclopoida; DI, *Diaphanosoma* spp.; HA, Harpacticoida; MA, Macrothricidae; OS, Ostracoda; PO, *P. pediculus*; SC, *Scapholeberis* spp.; SD, *S. crystallina*; SI, *Simocephalus* spp.

Important assemblages

Analysis of raw abundance data identified eight distinct clusters (Appendix 2), meaning each environmental and diet assemblage had unique characteristics (Figure 4). Assemblage A was dominated by cyclopoids and ostracods from the diets of swim-up wetland larvae (Figure 5). Assemblage B was dominated by cyclopoids and *C. sphaericus* from the diets of swim-up bay larvae. Assemblage C included wetland zooplankton from the first trial and was also dominated by cyclopoids and ostracods. Assemblage C was significantly different than Assemblage A despite similar dominant taxa, suggesting larvae did not select prey in proportion to their quantities in the environment and positive or negative selection occurred. Assemblage D was dominated by cyclopoids and *C. sphaericus* from the diets of advanced bay larvae. Chironomids and *Scapholeberis* spp. also represented a large part of the Assemblage D, which was not observed in other assemblages. Cyclopoids were the dominant taxa of Assemblage E, the diets of advanced wetland larvae, but *Simocephalus* spp. was the second most dominant, making up ~25% of the assemblage and *Ceriodaphnia* spp. made up ~10% of the assemblage. Assemblage F included bay zooplankton from the first trial and was significantly different than Assemblage B, suggesting prey selection. Assemblage G was dominated by *Simocephalus* spp. and *C. sphaericus* from the wetland environment during the advanced trial. *Simocephalus* spp. represented ~25% of the assemblage, which is the similar to the proportion in the advanced wetland larval diets (Assemblage E). Assemblage H was dominated by *C. sphaericus* and cyclopoids from the bay environment during the advanced trial, with amphipods making up ~10% of the assemblage.

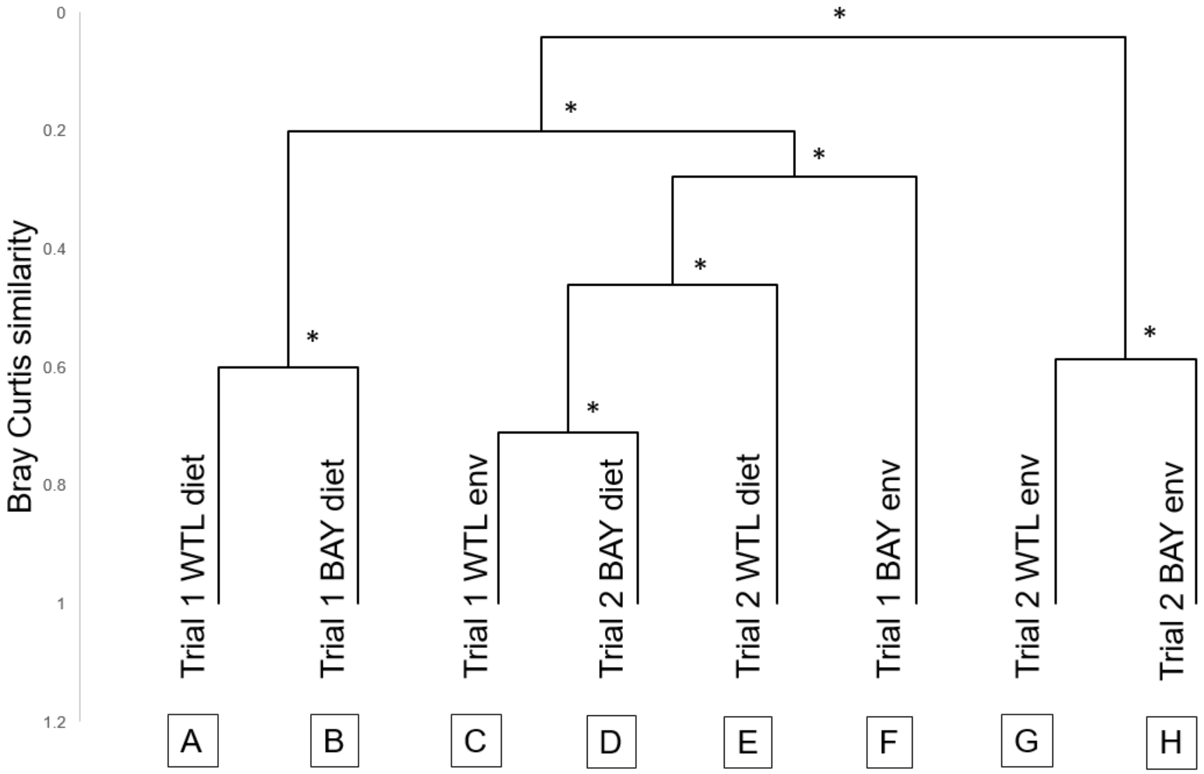

Figure 4. Zooplankton assemblages identified by the analysis of raw abundance data using the Bray-Curtis similarity index and the UPGMA linkage method, and 1000 bootstrap samples with the BOOTCLUS package. The dendrogram displays the structure of the diet and environment assemblages sampled in wetland and bay habitats for swim-up and advanced larval selection experiments. Significantly different assemblages are represented with a distinct letter and an asterisk (*).

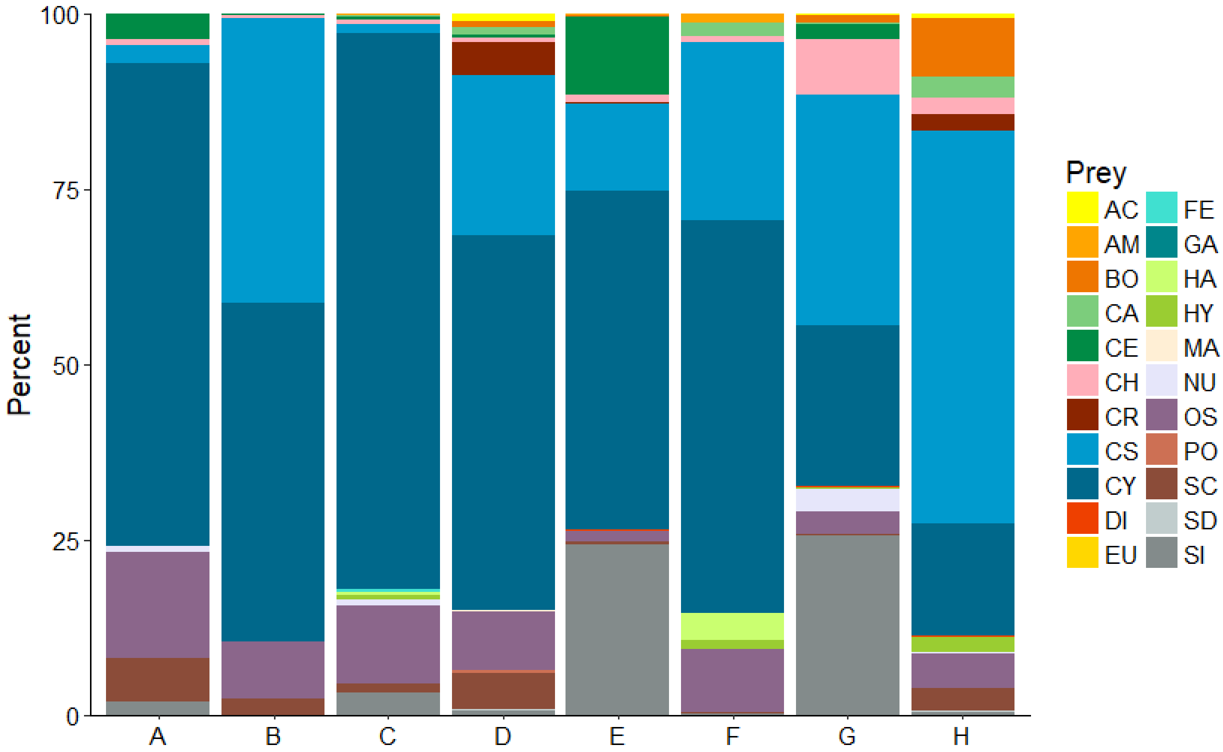

Figure 5. Stacked bar chart displaying the percent composition of each significant zooplankton assemblage resulting from the cluster analysis. Each significant assemblage is labelled with the letter assigned during the cluster analysis on the x-axis. Prey taxa codes are as follows: AC, *Acroperus* spp.; AM, Amphipoda; BO, *B. longirostris*; CA, Calanoida; CE, *Ceriodaphnia* spp.; CR, Chironomidae; CH, Chydoridae; CS, *C. sphaericus*; CY, Cyclopoida; DI, *Diaphanosoma* spp.; EU, *Eubosmina coregoni*; FE, fish egg; GA, Gastropoda; HA, Harpacticoida; HY, Hydrachnida; MA, Macrothricidae; NU, nauplii; OS, Ostracoda; PO, *P. pediculus*; SC, *Scapholeberis* spp.; SD, *S. crystallina*; SI, *Simocephalus* spp..

Prey selection

Swim-up larvae displayed significant negative selection (*t*-tests, $p<0.05$) of *C. sphaericus*, nauplii, ostracods, and *Simocephalus* spp. when given a wetland assemblage, and of chydorids when given a bay assemblage (Figure 6). Selection of the other taxa (e.g., *Ceriodaphnia* spp., chydorids, cyclopoids, and *Scapholeberis* spp. for wetland larvae, and *Ceriodaphnia* spp., *C. sphaericus*, cyclopoids, ostracods, and *Scapholeberis* spp. for bay larvae) was not significantly different than 0 (*t*-tests, $p>0.05$), indicating these prey were eaten in proportion to their quantities in the environment and neutral selection occurred.

Advanced larvae displayed significant negative selection (*t*-tests, $p<0.05$) of *Acroperus* spp., amphipods, *B. longirostris*, chydorids, *C. sphaericus*, ostracods, and *Scapholeberis* spp. given a wetland assemblage, and for *Acroperus* spp., *B. longirostris*, calanoid copepods, chydorids, *C. sphaericus*, *Diaphanosoma* spp., ostracods, *Scapholeberis* spp., and *S. crystallina* given a bay assemblage (Figure 6). Significant positive selection ($t=4.83$, df=19, $p<0.001$) occurred for *Ceriodaphnia* spp. by wetland larvae, but *Ceriodaphnia* spp. were neutrally selected by bay larvae ($t=0.88$, df=5, $p=0.42$). Selection of cyclopoids, *Simocephalus* spp., and chironomids was neutral for both wetland and bay larvae (*t*-tests, $p>0.05$). Additionally, *Diaphanosoma* spp. were neutrally selected by wetland larvae, whereas macrothricids and *P. pediculus* were neutrally selected by bay larvae (*t*-tests, $p>0.05$).

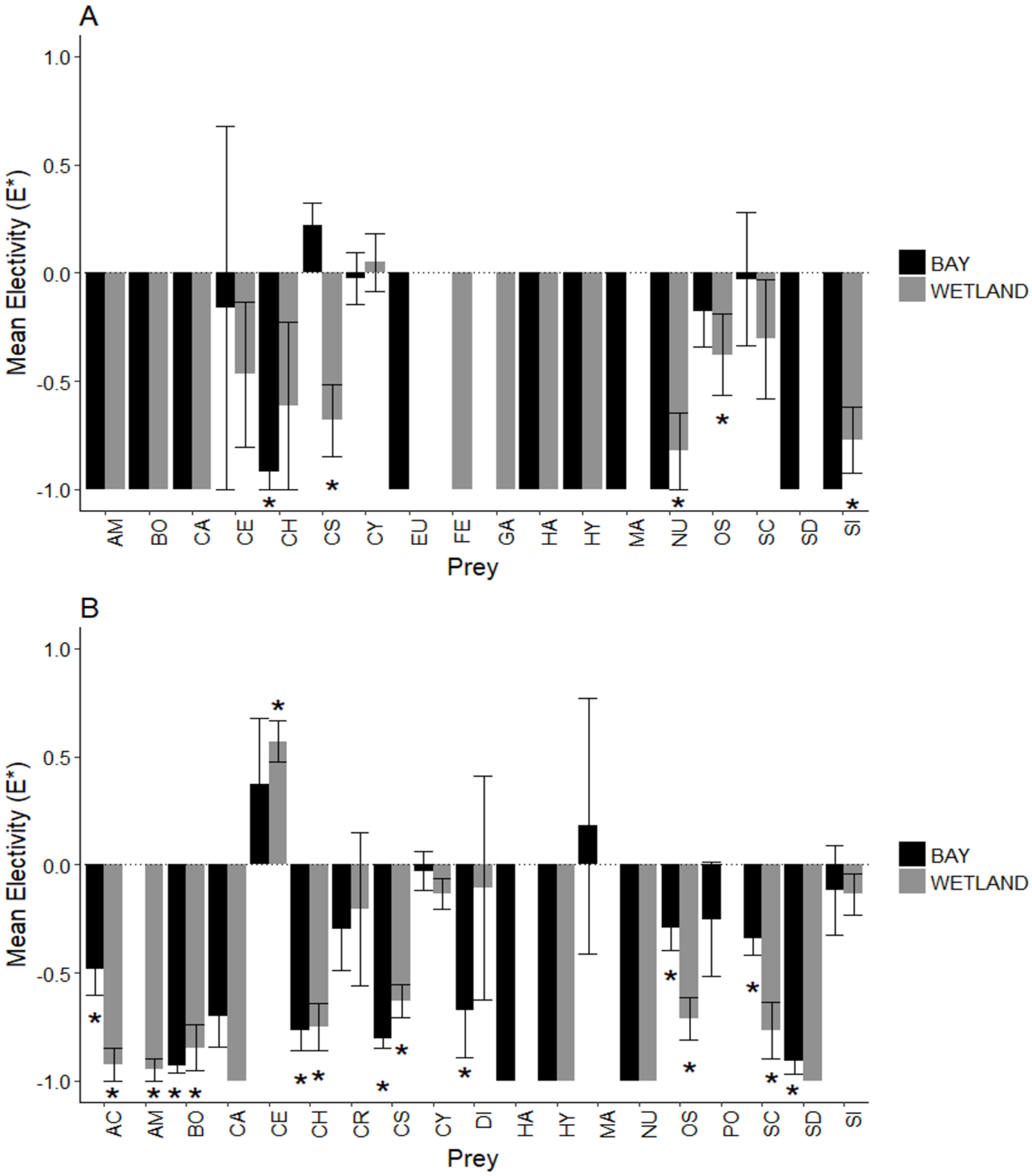

Figure 6. Mean relativized electivity (SE) for (A) swim-up and (B) advanced larvae selection experiments given a bay (black) or wetland (gray) zooplankton assemblage. Index values significantly different from 0 are denoted with an asterisk (*). Prey taxa codes are as follows: AC, *Acroperus* spp.; AM, Amphipoda; BO, *B. longirostris*; CA, Calanoida; CE, *Ceriodaphnia* spp.; CR, Chironomidae; CH, Chydoridae; CS, *C. sphaericus*; CY, Cyclopoida; DI, *Diaphanosoma* spp.; EU, *Eubosmina coregoni*; FE, fish egg; GA, Gastropoda; HA, Harpacticoida; HY, Hydrachnida; MA, Macrothricidae; NU, nauplii; OS, Ostracoda; PO, *P. pediculus*; SC, *Scapholeberis* spp.; SD, *S. crystallina*; SI, *Simocephalus* spp.

Swim-up larvae neutrally selected *Ceriodaphnia* spp., cyclopoids, ostracods, and *Scapholeberis* spp., and avoided chydorids and *Simocephalus* species. Selection of all of the above prey did not significantly differ between habitats (Kruskal Wallis tests, *p*>0.05; Table 2). Selection of *C*. *sphaericus* by swim-up larvae was significantly different between habitat types (*H*=11.42, df=1, *p*=0.001). *C. sphaericus* was neutrally selected by swim-up larvae given a bay assemblage ($\overline{E^{*}}$= 0.22) and avoided by swim-up larvae given a wetland assemblage ($\overline{E^{*}}$= -0.68).

Advanced larvae neutrally selected cyclopoids, chironomids, and *Simocephalus* spp., and avoided calanoids, chydorids, *C*. *sphaericus*, *Diaphanosoma* spp., and ostracods. Selection for the above prey did not differ between habitats (Kruskal Wallis tests, *p*>0.05; Table 2). Advanced larvae showed greater selection for *Acroperus* spp. (*H*=9.2, df=1, *p*=0.002), ostracods (*H*=9.95, df=1, *p*=0.002), and *Scapholeberis* spp. (*H*=10.02, df=1, *p*=0.002) when offered a bay assemblage versus a wetland assemblage, and for *B*. *longirostris* (*H*=6.35, df=1, *p*=0.01) when offered a wetland assemblage versus a bay assemblage, although all of the above prey types were avoided.

Table 2: Differences in mean prey electivity (SE) due to habitat assemblage (wetland or bay) for swim-up and advanced larvae. Significant differences (α=0.05) detected using Kruskal Wallis tests are bolded.

	Prey taxa	Bay E*	Wetland E*
Swim-up	*Ceriodaphnia* spp.	-0.16 (0.84)	-0.47 (0.34)
	Chydoridae	-0.92 (0.08)	-0.61 (0.39)
	C. sphaericus	**0.22 (0.11)**	**-0.68 (0.17)**
	Cyclopoida	-0.03 (0.12)	0.05 (0.13)
	nauplii	-1	-0.82 (0.18)
	Ostracoda	-0.18 (0.16)	-0.38 (0.19)
	Scapholeberis spp.	-0.03 (0.31)	-0.30 (0.28)
	Simocephalus spp.	-1	-0.77 (0.15)
Advanced	***Acroperus* spp.**	**-0.48 (0.10)**	**-0.92 (0.08)**
	B. longirostris	**-0.93 (0.03)**	**-0.85 (0.11)**
	Calanoida	-0.70 (0.14)	-1
	Ceriodaphnia spp.	0.37 (0.30)	0.57 (0.10)
	Chironomidae	-0.30 (0.19)	-0.21 (0.36)
	Chydoridae	-0.77 (0.09)	-0.75 (0.11)
	C. sphaericus	-0.80 (0.05)	-0.63 (0.08)
	Cyclopoida	-0.03 (0.09)	-0.13 (0.07)
	Diaphanosoma spp.	-0.68 (0.22)	-0.11 (0.52)
	Ostracoda	**-0.29 (0.11)**	**-0.71 (0.10)**
	***Scapholeberis* spp.**	**-0.34 (0.07)**	**-0.77 (0.13)**
	Simocephalus spp.	-0.12 (0.21)	-0.14 (0.10)

Selection of *Ceriodaphnia* spp., cyclopoids, macrothricids, ostracods, and *Scapholeberis* spp. by bay larvae did not differ significantly between trials (Kruskal Wallis tests, p>0.05; Table 3). Bay larvae showed greater selection for *B. longirostris* (H=4.99, df=1, p=0.03), calanoids (H=5, df=1, p=0.03), and chydorids (H=7.15, df=1, p=0.007) as advanced larvae than as swim-up larvae, although all electivity values were negative. Bay larvae also displayed greater selection for *Simocephalus* spp. (H=8.35, df=1, p=0.004) as advanced larvae ($\overline{E^*}$= -0.12) than as swim-up larvae ($\overline{E^*}$= -1), shifting from negative selection to neutral. Selection of *C. sphaericus* by bay larvae significantly declined from the first trial to the second trial (H=22.56, df=1, p<0.001), switching from neutral selection ($\overline{E^*}$= 0.22) to avoidance ($\overline{E^*}$= -0.8).

Selection of *B. longirostris*, chydorids, *C. sphaericus*, cyclopoids, nauplii, ostracods, and *Scapholeberis* spp. by wetland larvae did not differ significantly between trials (Kruskal Wallis tests, *p*>0.05; Table 3). Wetland larvae displayed greater selection for *Ceriodaphnia* spp. (*H*=7.55, df=1, *p*=0.007) and *Simocephalus* spp. (*H*=9.66, df=1, *p*=0.002) as advanced larvae than as swim-up larvae. Selection of *Ceriodaphnia* spp. shifted from neutral ($\overline{E^*}$= -0.16) to positive ($\overline{E^*}$= 0.37) whereas selection of *Simocephalus* spp. shifted from negative ($\overline{E^*}$= -0.78) to neutral ($\overline{E^*}$= -0.14).

Table 3: Differences in mean prey electivity (SE) due to timing (swim-up vs advanced) for wetland and bay larvae. Significant differences (α=0.05) detected using Kruskal Wallis tests are bolded.

	Prey taxa	Swim-up E*	Advanced E*
Bay	***B. longirostris***	**-1**	**-0.93 (0.03)**
	Calanoida	**-1**	**-0.70 (0.14)**
	Ceriodaphnia spp.	-0.16 (0.84)	0.37 (0.30)
	Chydoridae	**-0.92 (0.08)**	**-0.77 (0.09)**
	C. sphaericus	**0.22 (0.11)**	**-0.80 (0.05)**
	Cyclopoida	-0.03 (0.12)	-0.03 (0.09)
	Macrothricidae	-1	0.18 (0.59)
	Ostracoda	-0.18 (0.16)	-0.29 (0.11)
	Scapholeberis spp.	-0.03 (0.31)	-0.34 (0.07)
	***Simocephalus* spp.**	**-1**	**-0.12 (0.21)**
Wetland	*B. longirostris*	-1	-0.85 (0.11)
	***Ceriodaphnia* spp.**	**-0.47 (0.34)**	**0.57 (0.10)**
	Chydoridae	-0.61 (0.39)	-0.75 (0.11)
	C. sphaericus	-0.68 (0.17)	-0.63 (0.08)
	Cyclopoida	0.05 (0.13)	-0.13 (0.07)
	nauplii	-0.82 (0.18)	-1
	Ostracoda	-0.38 (0.19)	-0.71 (0.10)
	Scapholeberis spp.	-0.30 (0.28)	-0.77 (0.13)
	***Simocephalus* spp.**	**-0.78 (0.15)**	**-0.14 (0.10)**

Discussion

Selection experiments revealed larval pike were generalist consumers when exposed to both wetland and bay zooplankton assemblages during the swim-up and advanced larvae trials. Pike seemed to display plasticity in the size and species of the prey they consume during the larval stage, although patterns did emerge. Larvae from both habitats consumed primarily cyclopoid copepods and small cladocerans at swim-up larval stages, but began to select for larger cladocerans during the advanced larval stage. Copepods dominate spring assemblages in the Great Lakes, whereas cladocerans are more abundant later in the summer (Evans *et al.*, 1980), due to temperature and photoperiod cues required for hatching and differing life history strategies (Vandekerkhove *et al.*, 2005). Analogous patterns in assemblage composition were observed during spring zooplankton sampling in a tributary to the St. Lawrence River, with copepods representing 90% of the assemblage on April 1 versus 16% on April 29, and cladocerans representing 5% of the assemblage on April 1 versus 78% on April 29 (Augustyn, 2017, Chapter 1).

The cluster analysis revealed differences in larval diets relative to the assemblage available in the environment, suggesting selection and avoidance. The diets of swim-up larvae in wetlands and bays were statistically different, but the two clusters were close in proximity, suggesting larvae from each habitat consume similar prey at first feeding. Furthermore, the first set of prey selection comparisons indicated there were no ecologically important differences in selection due to habitat, with the exception of *C. sphaericus*, which bay larvae neutrally selected and wetland larvae avoided during the swim-up stage. This provides evidence that larvae feed similarly despite habitat differences. The difference in selection of *C. sphaericus,* may have occurred because of their greater proportions in the bay habitats (~25%) versus the wetland habitats (<5%). In the Baltic Sea, pike larvae in the inner and outer habitats also displayed similar prey selection despite differences in the zooplankton assemblages among habitats (Salonen *et al.*, 2009). The second major cluster included both wetland and bay advanced larval diets and wetland and bay environmental assemblages during the swim-up trial, suggesting that although the environmental assemblage may change, the larvae continue to feed on similar prey taxa present throughout the entire larval period. The cluster analysis revealed that different assemblages existed among habitat types and time periods, providing evidence that spatial and temporal distributions of larvae have implications on the zooplankton assemblage available for consumption.

Many of the prey available during selection experiments were avoided by larvae despite high abundances in the environment such as the cladocerans, *C. sphaericus* and *Scapholeberis* spp., and ostracods. These prey types did occur frequently in the diets of bay larvae, but were not selected relative to their abundances in the environment. Lengths in this study averaged 0.29 mm for *C. sphaericus,* 0.43 mm for *Scapholeberis* spp., and 0.46 mm for ostracods, which were smaller than *Simocephalus* spp. (mean=0.99 mm), *Ceriodaphnia* spp. (mean=0.5 mm), and cyclopoids (mean=0.98 mm). Abundant prey types may have been avoided simply due to their small sizes. Northern pike are limited by their gape which increases linearly with total length (Nilsson & Bronmark, 2000), but prefer large prey to small prey when given the choice (Lehtiniemi *et al.*, 2007). Our results were consistent with this established pattern and showed advanced larvae selecting for larger prey than swim-up larvae in both habitats. Larger-sized fish have better vision than smaller fish, which enables them to better search out prey (Breck & Gitter, 1983; Li *et al.*, 1985; Walton *et al.*, 1994), and under-developed visual abilities may prevent smaller fish from selecting preferred prey (Li *et al.*, 1985). Additionally, prey encounter rates for piscovores are thought to increase with prey size because larger prey create more disturbance, which is easier to detect (Breck, 1993). Of interest, advanced larvae consumed larger prey in wetlands relative to bay habitats, and large cladocerans made up a greater percentage of the wetland assemblage than the bay assemblage during both the swim-up and advanced trials. Optimal foraging theory predicts increases in specialist feeding strategies to occur when preferred prey types are abundant in the environment (Pyke *et al.*, 1977). Prey abundance was shown to have an effect the selection of plankton by fish larvae in one study, with large plankton selected for when their abundances were high, but when large plankton were scarce, small plankton were selected (Rajasilta & Vuorinen, 1983).The presence of seventeen prey types in the diets of advanced bay larvae may have been due to the low abundances of large cladocerans, causing larvae to consume a greater diversity of prey.

Farrell *et al.* (2010) documented the nearshore bay zooplankton assemblage of the St. Lawrence River as consisting primarily of small cladocerans (*B. longirostris* and *C. sphaericus*), and copepod nauplii and adults. The nearshore bay assemblage described during this study was similar to that of Farrell *et al.* (2010), with *C. sphaericus* and cyclopoid copepods comprising the greatest proportions of the assemblage. *Ceriodaphnia* spp. are known to be associated with productive, vegetated zones (Amoros, 1984), and made up about 20% of the nearshore bay assemblage in the St. Lawrence River during the 1970s (Farrell *et al.,* 2010). Declines in *Ceriodaphnia* observed from the 1970s to the 2000s are believed to be a result of decreases in productivity of the main river associated with phosphorus reductions and the invasion of dreissenid mussels (Farrell *et al.*, 2010). Dreissenid mussels are effective filter feeders and have been the source of widespread declines in chlorophyll a concentrations observed throughout the Great Lakes (Howell *et al.*, 1996; Cha *et al.*, 2013). Tributary wetland habitats have remained predominantly resistant to dreissenid mussel invasions observed in the main river, possibly due to shallow depths, fluctuating water levels, and open, exposed conditions in winter (Zanatta *et al.*, 2002). The absence of dreissenids may explain the presence of *Ceriodaphnia* spp. in these habitats. Seasonal wetlands may act as strongholds of these large cladocerans as primary productivity declines to natural, oligotrophic levels in the main St. Lawrence River. Our results suggest that pike larvae hatched in seasonally-flooded wetlands will have greater access to abundant, large cladoceran prey, specifically *Ceriodaphnia* spp. and *Simocephalus* spp., than larvae hatched in nearshore areas of bays.

The observed temporal progression from copepods to large cladocerans is consistent with results from other studies on larval pike diets (Raat, 1988; Desvilettes *et al.*, 1994, 1997; Bry *et al.*, 1995). Both copepods and cladocerans meet nutritional requirements of larval pike (Desvilettes *et al.*, 1997), although there are some differences in the amounts of specific essential fatty acids. Cladocerans have lower levels of docosahexaenoic acid (DHA) than copepods but higher levels of eicosapentaenoic acid (EPA; Persson & Vrede, 2006; Smyntek *et al.*, 2008). A bioconversion of EPA to DHA by pike larvae could be possible (Desvilettes *et al.*, 1994, 1997), which has been shown in daphnids (von Elert, 2002). Furthermore, it is thought DHA is retained and deposited by the fish (Henderson & Tocher, 1987). Our experimental findings, which showed pike larvae consuming primarily copepods at first feed in both wetlands and bay assemblage treatments, would be consistent with the general requirement for DHA immediately after yolk sac absorption.

Larvae from all treatments consumed cyclopoids neutrally, suggesting cyclopoids are an extremely important prey type. Copepods may be nutritious but they are also difficult to catch. *Cyclops* spp. adults have relatively fast swimming speeds (0.9 mm/s-3.0 mm/s; Li & Li, 1979) when compared with *Simocephalus vetulus* (0.1 mm/s; Cooper *et al.*, 1985), and adult female cyclopoids can display even greater swimming speeds (2-4 mm/s; Gerritsen, 1978). Optimal foraging theory postulates larvae will select prey on the basis of maximizing energetic gains and minimizing energetic costs of capture, consumption, and digestion (Schoener, 1971; Pyke *et al.*, 1977). Many species of larval fish consume cladocerans because they are relatively easy to catch despite the caloric advantages of copepods (Nunn *et al.*, 2012) and pike larvae may use large cladocerans as prey to conserve energy after nutritional requirements have been met. Our results suggest reduced nutrition may be less important to larval pike than successful prey capture, and larvae may benefit from consuming large cladocerans based on their ease of capture.

Selection experiment results highlighted the potential importance of habitat type on the zooplankton assemblage available to larval fishes but may not be entirely applicable in the natural environment. Zooplankton behaviors occurring in a natural setting, such as diel migration or occupying highly vegetated areas (Bollens & Frost, 1991; Burks *et al.*, 2002), may affect the ability of larval fish to procure prey. Zooplankton used in this study were distributed into glass containers, eliminating structure for predator avoidance. Zooplankton could have occupied different levels in the water column, although this behavior was not observed during the experiment. The use of light traps as a zooplankton capture method was done for the purposes of collecting common organisms and was not intended to quantify densities. Light traps may select organisms with a positive phototactic response and typically collect fewer taxonomic groups when compared to plankton nets and grab samples, missing rare taxa (Choat *et al.*, 1993; Hickford & Schiel 1999). Conversely, grab sampling may not effectively sample the assemblage due to vertical diel migration of several types of zooplankton (Zaret & Suffern, 1976). We did attempt to collect zooplankton using a combination of plankton nets and grab sampling with the aforementioned biases in mind, but were unsuccessful due to shallow depths of the seasonally-flooded wetlands.

Spring temperature is one of the primary determining factors of northern pike year class strength (Casselman 2002; Smith *et al.*, 2007), and tributary wetlands warm quicker and are more productive than bays and deep littoral zones (Farrell *et al.*, 2014). In the Baltic Sea, low zooplankton abundance is a major cause of recruitment failure for northern pike. (Ljunggren *et al.*, 2010). Inner habitats have greater abundances of cladocerans and copepods (Salonen *et al.*, 2009), and act as sources of pike larvae, whereas deep, outer habitats act as sinks (Lappalainen *et al.*, 2008; Kallasvuo *et al.*, 2010). We argue that similar patterns are applicable in the St. Lawrence River. Seasonal wetlands in tributaries provide higher abundances of zooplankton prey (Nunn *et al.*, 2012; Spaink *et al.*, 1998), greater cladoceran species richness (Nunn *et al.*, 2007), and zooplankton remain viable longer (Bass *et al.*, 1997) when compared with open water areas of large river systems. Larvae resulting from spawners utilizing nearshore bay or offshore habitats may experience difficulties in procuring suitable zooplankton prey following swim-up, further indicating the disadvantages of protracted spawning. Survival and recruitment of juvenile fishes is a complex matter that cannot be explained solely by forage. Other factors including physical environment (Casselman, 1978), predation (Skov *et al.*, 2003; Grønkjær *et al.*, 2004; Nilsson, 2006), and competition (Polis, 1988) are important for juvenile pike survival and must be considered in understanding overarching patterns. Nevertheless high mortality does occur at the onset of exogenous feeding (Bry *et al.*, 1995), and changes in larval prey should be examined in the context of habitat alterations.

Many life history strategies of fish have evolved in response to seasonal patterns in water level and temperature (Junk *et al.*, 1989; Schramm & Eggleton, 2006). Northern pike are broadcast spawners, providing no parental care for eggs and larvae, and most likely exhibit potadromy for the advantages of refuge from predators, abundant prey, and warm conditions conducive for fast growth of larvae. In the spring, connectivity between rivers and their floodplains is established during flooding, allowing for the exchange of nutrients and organisms (Thomaz *et al.*, 2007; Gorski *et al.*, 2013). Water level regulation disrupts natural seasonal fluctuations and prevents extreme flooding that may be vital to spring floodplain spawners. Eggs are demersal and adhesive, remaining close to areas where they were deposited (Casselman & Lewis, 1996), and thus, there is little opportunity for larvae to move to a more favorable environment. Abundant, high-quality habitats with adequate forage must be available during all stages of development for northern pike populations to persist (Lehtiniemi, 2005), and survival of northern pike from egg to juvenile is greatest in tributary wetlands when compared to nearshore areas of bays and deep littoral habitats (Farrell *et al.*, 2006).

Changes in spawning and nursery habitats due to water level regulation and *Typha* (cattail) expansion have sparked concerns for larval northern pike survival and recruitment to the population (Farrell, 2001; Cooper *et al.*, 2008). In the Thousand Islands region, emergent vegetation in many seasonally-flooded wetlands has been converted to cattail or access to these areas has been blocked, forcing northern pike adults to spawn in less suitable habitats. In the past decade, several enhancement projects were completed in the Thousand Islands region to reconnect remnant sedge meadows with their main channels. Enhanced marshes display higher larval survival (Augustyn, 2017, Chapter 3) and overall catch of juvenile northern pike (Brown *et al.*, in prep) when compared with reference marshes (Augustyn, 2017, Chapter 3). Our experimental findings illustrate the importance of shallow, seasonally-flooded wetlands as nursery grounds for larval pike and clearly demonstrate that larvae hatching in nearshore bays and offshore will have less access to preferred, large bodied zooplankton prey during the critical larval period. We hope that this research on zooplankton selection by larval northern pike will contribute to the knowledge base surrounding impacts of *Typha* expansion on northern pike populations and provide scientific support for reconnecting the main St. Lawrence River to its floodplain wetlands.

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Chapter 3: Larval northern pike (*Esox lucius*) abiotic environmental conditions, zooplanktivory, and survival to emigration following connectivity restoration in a *Typha* dominated wetland

Abstract

Declines in young of year (YOY) northern pike (*Esox lucius*) abundance in coastal wetlands of the St. Lawrence River are thought to be a result of wetland vegetation change, disruption of natural water level fluctuations, and habitat degradation. Connectivity enhancements and spawning pool excavations are two restoration methods that were recently implemented in a tributary to the St. Lawrence River, with the goal of increasing YOY pike production. We examined northern pike survival rates (from stocked advanced larvae to summer emigration), abiotic environmental factors (e.g., water temperature and dissolved oxygen), and larval diets in channel connectivity, spawning pool, and reference nursery habitats, to determine if wetland enhancements successfully improve conditions for YOY pike development and survival. Stocked pike emigrated at a similar temporal distribution and at similar lengths when compared with wild fish. Survival of larvae stocked in channel and spawning pool enhancements was identical (1.5%) and significantly greater than survival of larvae stocked in reference marshes (0.08%). Mean water temperatures throughout the sampling period were highest in spawning pools followed by channels and reference sites, whereas dissolved oxygen was greatest in pools, followed by reference sites, and channels. Diets of larvae stocked in spawning pools and reference sites were similar, whereas larvae in channels consumed different taxa. Differences in diet among study sites did not reflect differences in survival, suggesting that larvae were not limited by zooplankton prey. Highest survival rates observed in spawning pool and channel enhancement sites suggest temperature and the presence of preferred vegetation were critical to

larval pike. This study showed excavation enhancement to be a feasible method of increasing YOY pike survival and production in coastal wetlands of the Great Lakes if springtime water levels are sufficient to periodically flood spawning and nursery sites.

Introduction

Coastal wetlands of the Laurentian Great Lakes serve as crucial habitats for many fishes during their spawning and nursery periods (Jude & Pappas, 1992). Wetlands are typically warmer and more productive than their associated main channels, and provide young of year (YOY) fishes ample forage, protection from predation, and ideal, warm conditions for rapid growth (Bass et al., 1997; Spaink et al., 1998; Gutreuter et al., 1999; Nunn et al., 2007). Physical and biological dynamics occurring during the larval and juvenile stages may influence the year class strength of fish populations (Cushing, 1990; Houde, 1994) and larval survival is influenced by several processes (Letcher et al., 1996), including environmental factors (e.g. temperature, water level, and dissolved oxygen; Clady, 1976; Uphoff Jr., 1989), abundant and suitable prey items (Mayer & Wahl, 1997; Burrow et al., 2011), predation (Houde, 1987; Letcher et al., 1996; Skov et al., 2003), and growth (Houde, 1987; Letcher et al., 1996).

Northern pike (*Esox lucius*) is an apex predator that uses seasonally-flooded wetlands during the spawning and nursery periods (Bry, 1996; Casselman & Lewis, 1996). In the St. Lawrence River, the spawning period is protracted, and begins in flooded wet meadows in early spring, transitions to nearshore areas of bays, and is completed in offshore deeper sites in late spring (Farrell, 2001; Farrell et al., 2006). Water level management is thought to prevent access of tributary spawning grounds and has altered wetland plant communities in freshwater coastal wetland systems (Farrell et al., 2010b). The invasive *Typha* x. *glauca* (a hybrid of *T. angustifolia* and *T. latifolia*) is a robust cattail form that has expanded in the upper St. Lawrence River following the construction of the Moses Saunders Power Dam (Cooper et al., 2008; Wilcox et al., 2008; Farrell et al., 2010b; Rippke et al., 2010). Spawning northern pike prefer flooded sedge and grass vegetation (Franklin & Smith, 1963; McCarraher & Thomas, 1972; Bry, 1996), and tend to avoid *Typha* (Franklin & Smith, 1963; Farrell, 2001). The conversion of sedge meadows to *Typha* along with changes in the hydroperiod creating lower spring water levels (Farrell et al. 2010b), are thought to have altered spawning distributions (Farrell, 2001; Farrell et al., 2006).

Northern pike eggs are demersal and newly hatched larvae attach to vegetation via adhesive papillae. Egg hatch is temperature dependent (Farrell et al., 2006), and occurs as early as 7 days in warming springtime water temperatures (Scott & Crossman, 1973; Cooper et al., 2008). Hatched larvae feed off of their yolk sac until exogenous feeding begins. Larval diets consist primarily of copepods and cladocerans (Desvilettes et al., 1994; Lehtiniemi et al. 2007; Salonen et al., 2009; Augustyn, 2017, Chapter 2), and the coincidence of exogenous feeding and abundant zooplankton prey is crucial during the larval period (Cushing 1974, 1990; Burrow et al., 2011). Larvae remain in shallow nurseries for several weeks before emigrating to nearby areas (Raat, 1988). Declining water levels throughout the growing season force juveniles to exist in higher densities (Massé et al., 1991), and results in increased cannibalism (Skov et al., 2003; Nilsson et al. 2014) and lower dissolved oxygen concentrations (Casselman, 1978), which are thought to contribute to the emigration behavior.

Declines in the catches of YOY northern pike have been observed in tributaries of the St. Lawrence River over the past decade (Smith et al., 2007; Farrell et al., 2017), and adult stocks have experienced a significant decline thought to be associated with poor population recruitment (McCullough & Gordon, 2015). Efforts to restore populations have focused on habitat improvements to enhance northern pike spawning and nursery grounds in tributaries. Restoring connectivity helps increase opportunities for northern pike entry into seasonally-flooded wetlands impacted by *Typha* expansion. Wetlands with greater connection to other surface waters have higher species diversity and more abundant biota contributing to overall greater ecosystem function (Jude & Pappas, 1992).

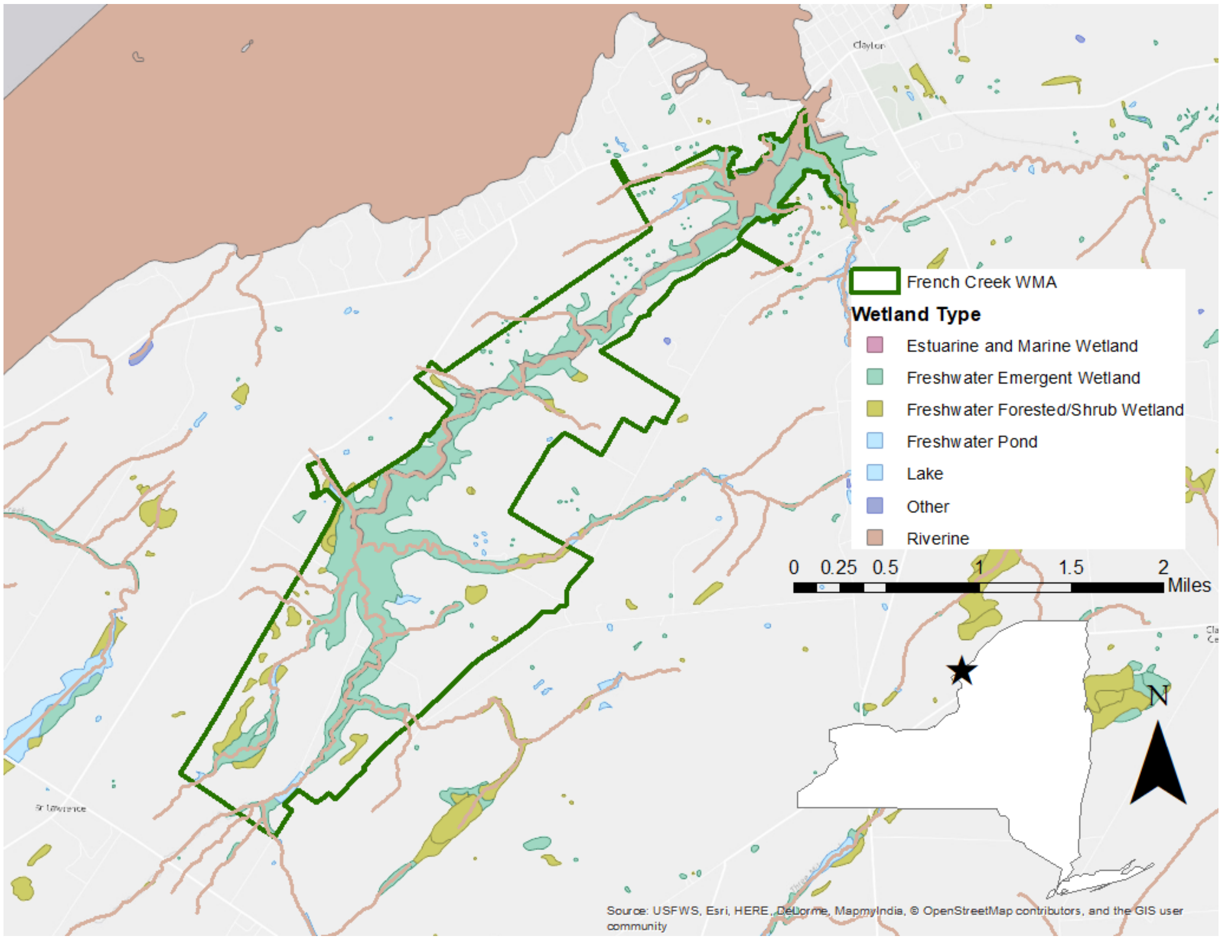
Excavation within dense stands of cattail is a technique that has been implemented in the Great Lakes (Mathers & Hartley, 1995; Vincent, 1995). Excavations are designed to create an interspersion of open water and vegetated habitats, and have higher marsh bird and plant species richness and greater abundances of aquatic macroinvertebrates than natural ponds or dense cattail areas (Schummer et al., 2012). Channel connectivity enhancements reconnect main channels of rivers with their floodplain marshes and allow fauna access to these productive habitats (McKenna, 2003b; Brown et al., in prep).

Evaluation and monitoring is a critical step in determining project success, and helps develop and advance effective strategies for sustaining fish populations. Mark and recapture techniques are fundamental to estimating fish survival rates and population abundances, and have been used extensively to evaluate restoration effects (Henning et al., 2006; Ogston et al., 2014). The purpose of this study was to test whether restored connectivity and excavation nursery marshes can mimic existing, functioning sites and are viable as critical habitats for northern pike in the context of specific early life requirements. We evaluated these objectives by (1) measuring physical conditions, and key larval prey selection and availability in restored versus functioning reference sites, (2) comparing relative abundance and size of wild and stocked northern pike as an indicator of site suitability, and (3) evaluating survival outcomes of stocked larvae to test if differences among sites exist from time of release to emigration of juveniles.

Methods

Study area

French Creek is a meandering, drowned river mouth tributary of the St. Lawrence River, approximately 8 kilometers long and located near Clayton, NY (Figure 1). The watershed is largely undeveloped, and French Creek possesses a broad floodplain including over 280 hectares of extensive wetland habitat. A 930 hectare section of the watershed is protected and managed as a New York State Department of Environmental Conservation (NYSDEC) Wildlife Management Area (WMA). Large areas of submerged and emergent aquatic vegetation exist for fish spawning and nursery habitats, including seasonally-flooded sedge meadows which are preferred by northern pike (Bry, 1996).



Source: USFWS, Esri, HERE, DeLorme, MapmyIndia, © OpenStreetMap contributors, and the GIS user community

Figure 1. Wetland types within the French Creek watershed, Clayton, NY. The NYSDEC WMA (outlined in green) encompasses the majority of the drainage. Mapping sources include U.S. Fish and Wildlife Service National Wetlands Inventory, NYSDEC, and ESRI.

Enhancement work

Beginning in 2008, two types of wetland enhancements were designed and implemented in French Creek with the restoration goals of increasing YOY northern pike production. The enhancement work was planned in fulfillment of the Fish Habitat Conservation Strategy in partnership with the U.S. Fish and Wildlife Service. Channel excavation methods for connectivity enhancements are outlined in Brown et al. (in prep). Spawning pool enhancements were completed by Ducks Unlimited via the Great Lakes Restoration Initiative. Excavations were created using a long-arm excavator during the winters of 2012 and 2013. The excavator removed sediment and vegetation, and created complexes of connected channels and pools within monotypic *Typha* stands, constructing new and novel habitat for northern pike to occupy. The complexes were designed to create connectivity to remnant sedge meadows and increase diversity of emergent and submerged aquatic vegetation, beneficial to an array of wildlife.

Sampling sites

Sixteen spawning/nursery sites within French Creek were selected for this study, including eight sites where enhancement work was completed and eight reference sites (Figure 2). Reference sites were defined as existing side channels within *Typha* stands due to the lack of remnant sedge meadow marshes that did not receive restoration. Reference and enhanced marshes occurred in close proximity to one another throughout the entire French Creek drainage. Five spawning pool and three channel enhancements were represented within the eight enhanced sites.

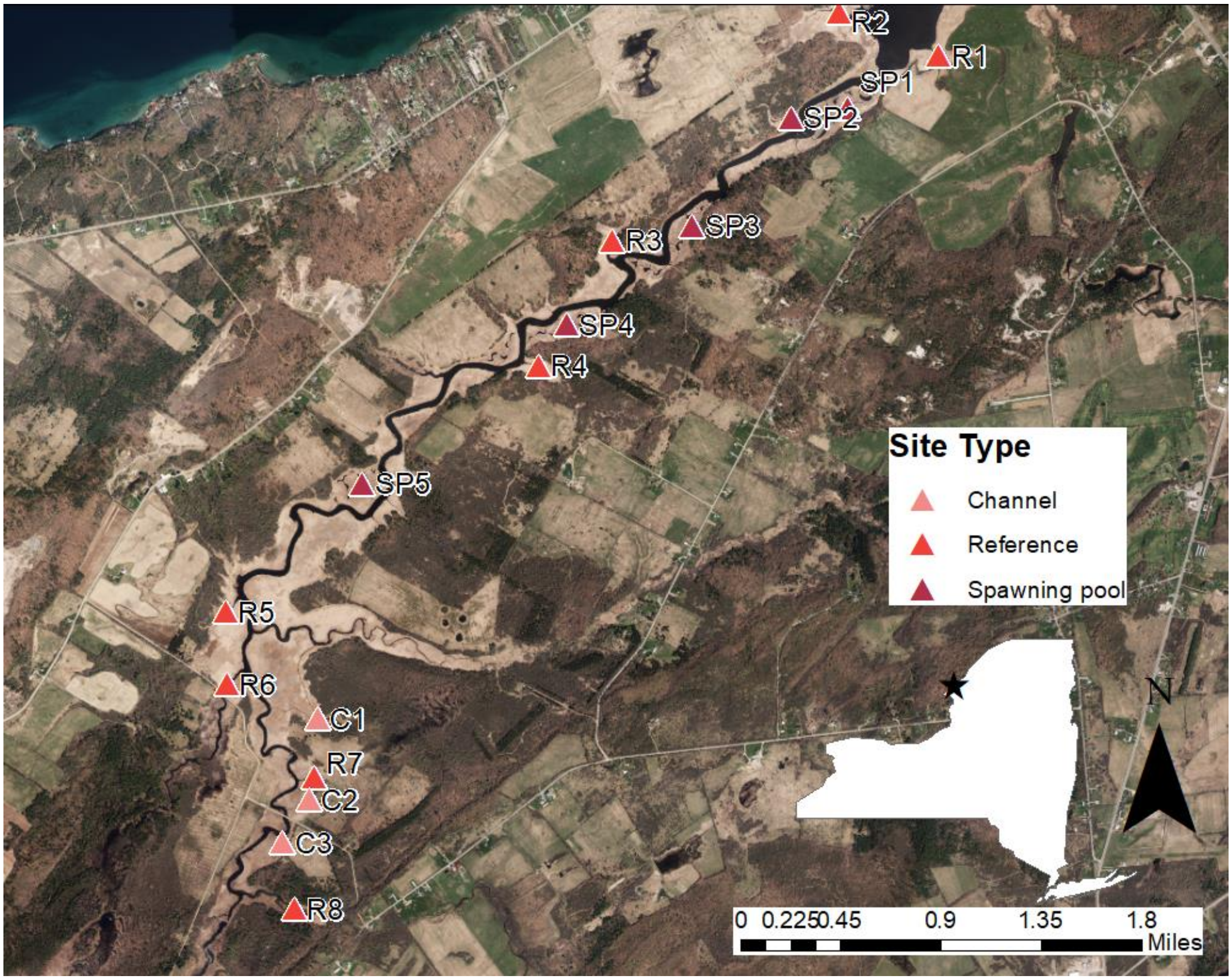


Figure 2. Northern pike swim-up larvae stocking and trapping locations in French Creek, Clayton, NY in 2016. Existing reference habitats (n=8) were compared to excavated spawning pool complexes (n=5) and channel excavations (n=3). Orthoimagery was downloaded from New York State GIS Clearinghouse (http://gis.ny.gov/).

Larvae propagation and marking

Adult spawning northern pike were caught at the mouth of French Creek between April 14 and April 17, 2016 in Oneida-type trapnets, and brought to the Thousand Islands Biological Station. Eggs were stripped from females and fertilized with milt from males using the dry method (Sorenson et al., 1966; Klingbiel, 1986). Fertilized eggs were incubated in hatching jars. Freshwater flowed into the jars continuously for two weeks and dead eggs were removed by siphoning. After hatch, yolk-sac larvae were transferred to raceways and were fed *Artemia* spp.

for two weeks. Ten days after hatching, larvae were marked with oxytetracycline (OTC) using the methods described by Fielder (2002). The OTC leaves a visible fluorescent ring on the otolith when removed, sectioned, and viewed under a transmitted ultraviolet light microscope under 100-400x magnification (Farrell & Werner, 1999). Twenty control larvae sampled from the OTC batch immersion for released pike were sacrificed, and dissected otoliths were viewed prior to stocking to validate mark success.

Larvae stocking

Larvae were stocked at all sixteen locations on May 17 and 18, 2016 at a mean length of 13.8 mm (sd=0.65). Marsh areas were estimated using Google Earth Pro by measuring the wetted area, and stocking occurred at a rate of 3000 larvae per hectare of marsh (Table 1). Larvae were acclimated to marsh water by the slow addition of water from the site to transport coolers, while monitoring temperature and oxygen levels with an YSI ProDSS multiprobe. Once temperatures in the transport coolers mimicked the temperatures of the marsh, larvae were distributed evenly throughout the site. Onset HOBO U26 dissolved oxygen data loggers were placed in the middle of the water column at each site, and logged temperature (°C) and dissolved oxygen (mg/L) every 15 minutes for the entire sampling period. The logger deployed in channel site C1 was determined to have malfunctioned during the survey and did not collect dissolved oxygen data. This logger was omitted from the analysis.

Emigration trapping

Peak emigration of juvenile northern pike in upper St. Lawrence River tributaries occurs from June 1 to July 1 (Farrell, unpublished data), and trapping for this study occurred from June 13 to July 1, 2016. Two types of traps were used to capture juveniles emigrating downstream;

modified minnow traps and mini-mesh hoop nets. The minnow traps had a 2.54-cm throat and were wrapped with 0.8-mm nylon mesh. Each trap was centered and sewn to the top of 0.8-mm nylon mesh wings, 200-cm in length on each side, and 122-cm in height. These traps are fished similar to hoop nets, and are buoyed with floats on top line and weighted with lead core line on the bottom, to span the entire water column. The trap is staked with a reinforcing rod attached on the downstream end. Mini-mesh hoop nets are made of four connected hoops, 60-cm in diameter, with 2.54-cm throats, wrapped with 1.6-mm mesh, and outfitted with the same wing design as the modified minnow traps. Larger mesh size encouraged water flow through the trap to help maintain higher oxygen levels and protect fish. All possible outlet channels for both reference and channel marshes were blocked for this study. The large number of outlet channels (n=21) from spawning pool marshes prevented the complete coverage of these sites, so channels set with traps were selected using a random number generator. The decision to use two sampling gears was based on the goal of sampling all study sites, and each trap type was deployed at random in order to minimize any potential gear bias. Both types of traps blocked channels entirely and were assumed to catch pike at similar rates (Brown et al., in prep). Traps were checked daily and all fish were identified to species and enumerated. All juvenile northern pike were measured for total length (mm), and a sample of the catch was retained in 95% ethanol for origin determination with otolith examination. Total catch of stocked versus wild was examined, and total length and date at emigration were compared using *t*-tests at $\alpha=0.05$ to determine if differences in behavior existed based on origin.

Otolith mark determination

To determine northern pike origin (wild or stocked), otoliths were dissected from pike captured during emigration and examined for presence of OTC marks indicative of stocked larvae. Otoliths were removed by splitting the head laterally at the caudad portion of the braincase with scissors, to access the semi-circular canals. Otoliths were extracted with a fine insect-pin probe and secured to a pre-heated clear glass microscope slide with a thermo-polymer. Once dried, otoliths were hand sanded on both sides with 600 or 1000 grit sandpaper until daily rings were visible, and viewed with an epi-fluorescent microscope. The sagittal otolith was used for the mark inspection. An Amscope B600 compound microscope with 4x-100x objectives (40x-1000x total magnification), outfitted with an EPI Fluorescence microscopy kit (510-nm dichroic mirror, 350-580-nm exciting filter, and 530-nm barrier filter), and a 100-watt mercury UV light source was used for all viewing. All otoliths were viewed by two observers. Marked otoliths displayed a gold ring that followed a daily growth ring near the center of the otolith. Wild northern pike were assumed to be those observed without an OTC mark. Each observer decided whether the otolith was marked or not and revealed the decision after viewing was completed. If observers disagreed, a second otolith was prepared and viewed using this same protocol.

Survival estimation

Survival estimates were done using similar methods as Farrell & Werner (1999) and Farrell (2001). Using the results from OTC mark determination via the otolith viewing, the proportion of stocked individuals was calculated for each site by dividing the total number of fish determined to be of stocked origin by the total fish retained during sampling. This resulted in a proportion of stocked origin fish at each site which was then multiplied by the total released fish to estimate the number of stocked origin fish that were released during the survey. These two numbers were added together to estimate the minimum number of survivors:

(1) Estimate 1 = (# of stocked origin/retained · released) + # of stocked origin

Juvenile northern pike were assumed to emigrate equally from all outlet channels. Estimate 1 was then multiplied by the total number of outlet channels and divided by the number of blocked outlet channels to estimate the total number of surviving stocked pike emigrating from all outlet channels as:

(2) Estimate 2 = Estimate 1 · total channels/blocked channels

This only applied to spawning pool sites where all outlet channels were not blocked. The temporal distribution of historic emigration occurring over the entire growing season (May-August) was examined prior to this study to isolate peak emigration activity (Farrell, unpublished data). This examination guided the sampling period selected for this study. Percent emigration occurring during the sampling period was calculated to be 38% (φ). Estimate 2 was then multiplied by $1-\varphi$, to represent the number of emigrants missed, and added to Estimate 2 for the final survivor estimate:

(3) Estimate 3 = (Estimate 2 · (1- φ)) + Estimate 2

Estimated survivors were divided by the number of larvae stocked at each site and multiplied by 100 (Farrell & Werner, 1999; Farrell, 2001). Survival estimates were pooled for each site type and a two-sample *t*-test was done to test for differences in survival between the pool and channel sites ($\alpha=0.05$). Afterwards, survival estimates for pool and channel sites were combined to test for differences between enhanced and reference marshes ($\alpha=0.05$).

Physical environmental factors

During the emigration survey, daily water temperatures and dissolved oxygen concentrations were collected using a YSI ProDSS multiprobe at the surface, mid-water column, and depth between 08:30 and 18:00. To verify accuracy, field data were used to compare with temperature and oxygen data collected with Onset HOBO U26 dissolved oxygen data loggers deployed at all study sites. Mean water temperature and mean dissolved oxygen were calculated for both logger and multiprobe data for each site, and were compared for differences. Mean water temperature and dissolved oxygen from both instruments were pooled for site type (reference, pool, and channel), and tested for differences using one-way ANOVA (α=0.05).

Larval diet analysis

Duplicate 3-liter zooplankton grab samples were taken at each site during stocking to investigate the available prey assemblage during the larval period. Zooplankton were anesthetized with effervescent tablets, filtered through a 53-µm sieve, and preserved in 95% ethanol (Black & Dodson, 2003). In the laboratory, zooplankton were filtered through a 53-µm sieve and rinsed with well water. All individuals were counted using a Leica MZ 10x dissecting microscope. Cladocerans were identified to lowest taxonomic group and copepods were identified to order. Zooplankton densities from duplicate samples were averaged and differences in densities between site type were tested for using a one-way ANOVA at α=0.05.

Each site was revisited six days following stocking to recapture larvae for diet analysis. Netters worked from canoes and focused their efforts on shallow, vegetated areas of the marsh. Each site was visited and dip-netting took place until at least ten pike larvae were captured or until approximately one hour had passed. Larvae were measured for length and preserved in 95%

ethanol. In the laboratory, larvae were dissected for their stomach under a Leica MZ 10x dissecting microscope. Stomach contents were rinsed with well water and all prey items were counted. Cladocerans were identified to lowest possible taxonomic group and copepods were identified to order. Ward & Whipple (1959) and Thorp & Covich (2001) were used as references for identification of all zooplankton. A total of 56 northern pike larvae were captured for diet analysis, 25 from reference marshes, 11 from channel enhancements, and 20 from spawning pools.

Prey availability and selection

A hierarchical agglomerative cluster analysis was performed using the BOOTCLUS program (McKenna, 2003a) to assess the presence of significantly distinct assemblages of available zooplankton that may contribute to larval diets. Raw abundance data were analyzed using the Bray-Curtis similarity index and Unweighted Pair Group Method with Arithmetic Mean (UPGMA) linkage method with 1000 bootstrap samples to test each linkage (α=0.05). The cluster analysis was used to create a dendrogram that identified and arranged the significant assemblages.

Prey selection was estimated using the Chesson index (Manly, 1974; Chesson, 1978, 1983). Selectivity coefficients (α) were calculated for prey items from each individual larvae:

$$\alpha i = \frac{ri / p_i}{\sum_{i=1}^{m} (ri / p_i)}$$

where r = the proportion of items of food type i in the diet, p = the proportion of items of food type i in the environment, and m = the number of prey items in the environment (Manly, 1974; Chesson, 1978, 1983). Selectivity coefficients range from 0 to 1 where α < 1/m indicates avoidance and $\alpha > 1/m$ indicates preference. When $\alpha = 1/m$, prey are consumed in proportion to the abundance in the environment. The Chesson index allows for comparisons in selectivity across spatial scales when the available prey items vary. Selectivity coefficients were calculated for each individual larvae and averaged for site type (reference, pool, and channel). Selectivity coefficients were compared with random feeding (1/m) to test for significance using a one sample t-test at $\alpha=0.05$.

Results

Emigration trapping

A total of 148 juvenile pike were caught over the sampling period. Of the 148 caught, 121 were retained for origin determination via otolith viewing. Sixty of the 121 (~50%) retained were of stocked origin (Table 1). Length at emigration was not significantly different between stocked and wild fish ($t(107)=0.66$, $p=0.51$), and averaged 84.8-mm (sd=14.6) across all sites (Figure 3). Date of emigration was not significantly different between stocked and wild fish ($t(110)=0.21$, $p=0.83$), and peak emigration occurred on June 20 with 18 individuals caught that day (Figure 4). The CPUE was significantly different between site type ($F(2,276)=9.13$, $p<0.001$; Figure 5). Post hoc Tukey comparisons indicated CPUE at reference sites (mean=0.13±0.07) was significantly lower than at pools or channels (Table 1). The CPUE was not significantly different at pools (mean=0.43±0.18) and channels (mean=0.51±0.2; Table 1).

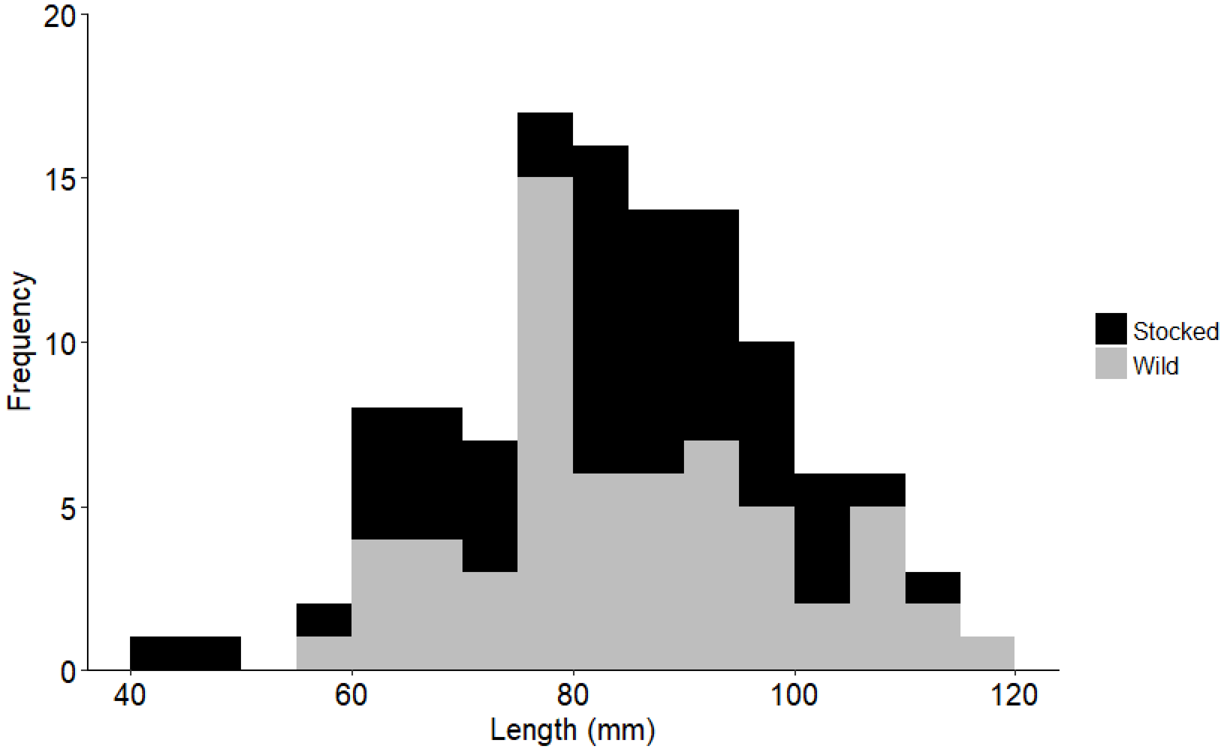


Figure 3. Length frequency histogram of stocked (black) and wild (gray) northern pike at time of capture during the emigration survey.

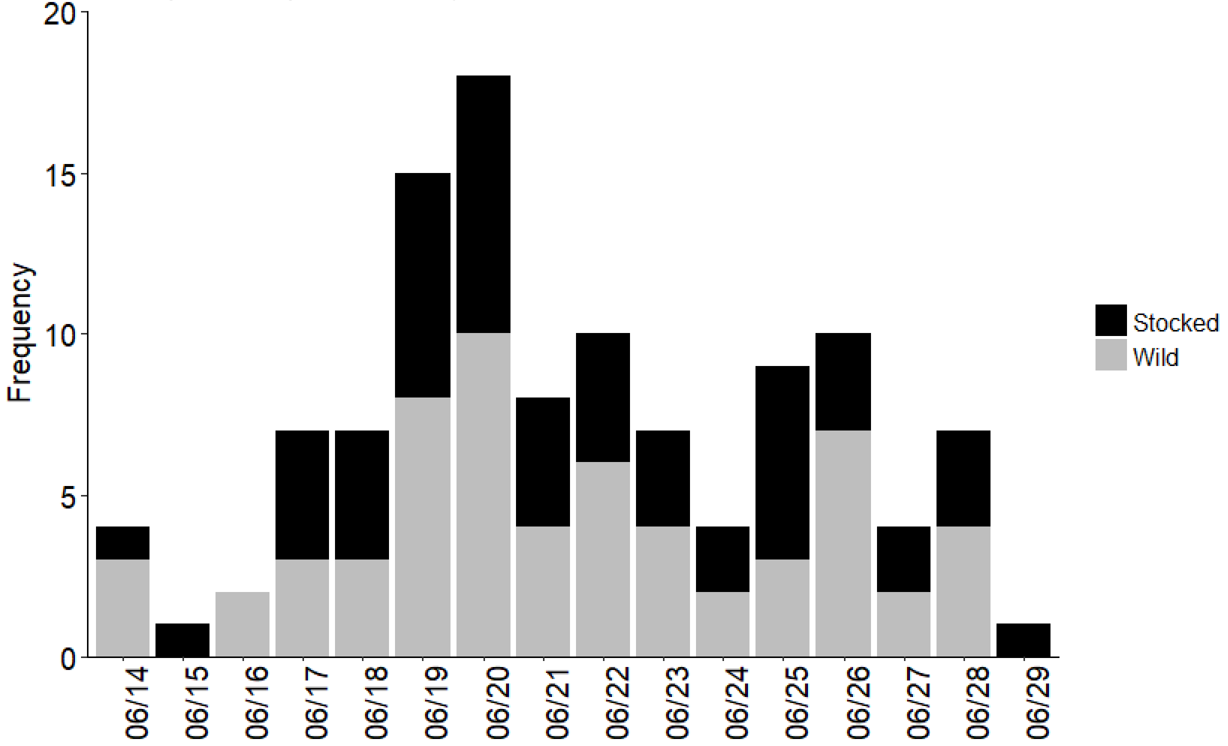


Figure 4. Frequency of emigration occurring at each date during the emigration survey for stocked (black) or wild (gray) northern pike.

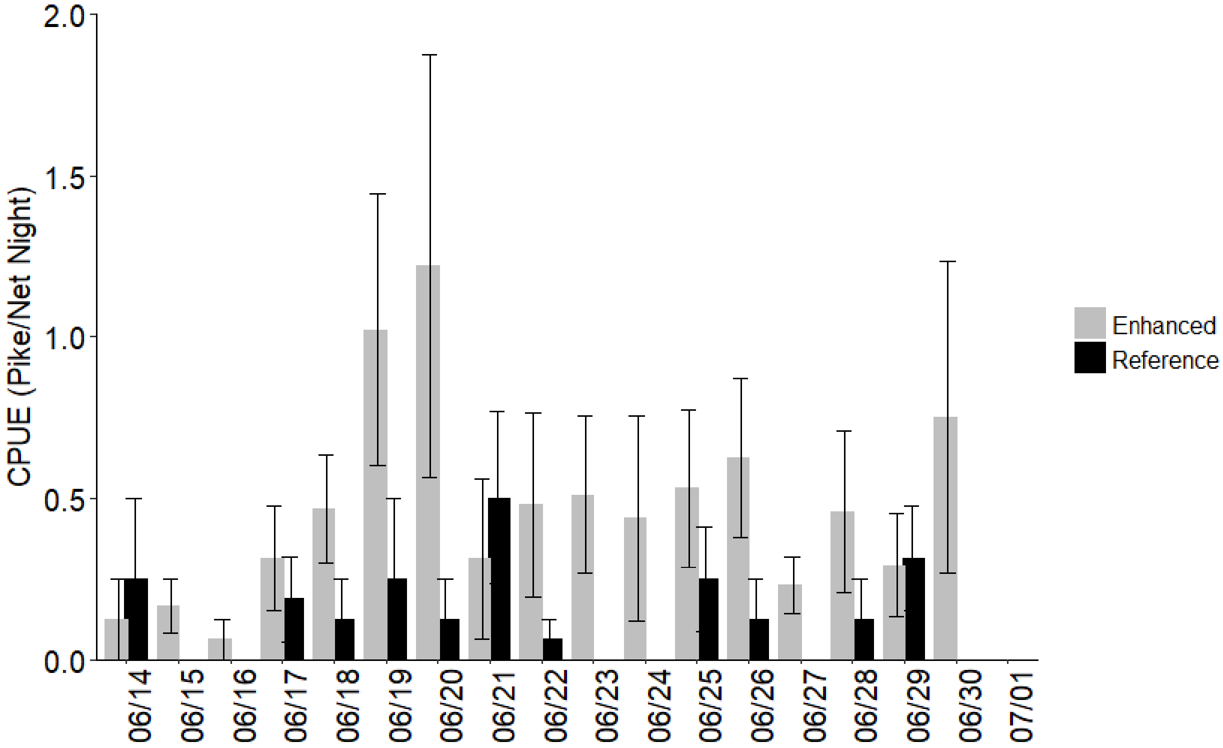


Figure 5. Mean catch per unit effort (pike/net night; SE) of enhanced (gray) and reference (black) sites during the emigration survey. There was no difference in CPUE of pike at channel and spawning pool sites so results were pooled for visual interpretation.

Table 1: Numbers of northern pike stocked, captured (catch), and marked with set dates and CPUE (pike/net night) observed during juvenile emigration survey at reference, spawning pool, and channel excavations in French Creek.

Location	Set Date (m/d/y)	End Date (m/d/y)	Net Nights	# Stocked	NP Catch	# Marked/ # Retained	CPUE
REFERENCE							
R1	6/13/2016	7/1/2016	18	810	3	0/1	0.17
R2	6/13/2016	7/1/2016	34	3720	3	1/2	0.09
R3	6/13/2016	6/30/2016	17	1830	1	0/1	0.06
R4	6/14/2016	6/30/2016	16	1110	1	1/1	0.06
R5	6/13/2016	6/30/2016	17	1710	0	0/0	0
R6	6/13/2016	7/1/2016	18	780	4	1/4	0.22
R7	6/13/2016	7/1/2016	18	690	0	0/0	0
R8	6/13/2016	6/29/2016	16	4200	10	6/10	0.63
TOTAL			154	14850	22	9/19	0.13
SPAWNING POOL							
SP1	6/13/2016	7/1/2016	69	1950	11	3/9	0.16
SP2	6/13/2016	7/1/2016	18	480	3	2/3	0.17
SP3	6/13/2016	6/30/2016	50	1650	8	4/7	0.16
SP4	6/14/2016	6/30/2016	32	2460	47	22/38	1.47
SP5	6/14/2016	6/30/2016	30	3840	10	5/9	0.33
TOTAL			199	10380	79	36/66	0.43
CHANNEL							
C1	6/13/2016	6/29/2016	33	3540	8	3/8	0.24
C2	6/13/2016	7/1/2016	36	630	32	9/22	0.89
C3	6/13/2016	6/30/2016	17	660	7	3/6	0.41
TOTAL			86	4830	47	15/36	0.51
OVERALL TOTALS			439	30060	148	60/121	0.30

Survival estimates

No significant difference in the mean percent survival of northern pike larvae was observed for larvae stocked in channel (1.49%±1.88) versus spawning pool (1.51%±1.48) sites (*t*(4)=0.02, *p*=0.986; Figure 6). When survival estimates from channels and spawning pools were pooled, significantly higher survival occurred for larvae stocked in enhanced (1.5±1.08) versus reference (0.084±0.07) sites (*t*(7)=2.57, *p*=0.04; Figure 6).

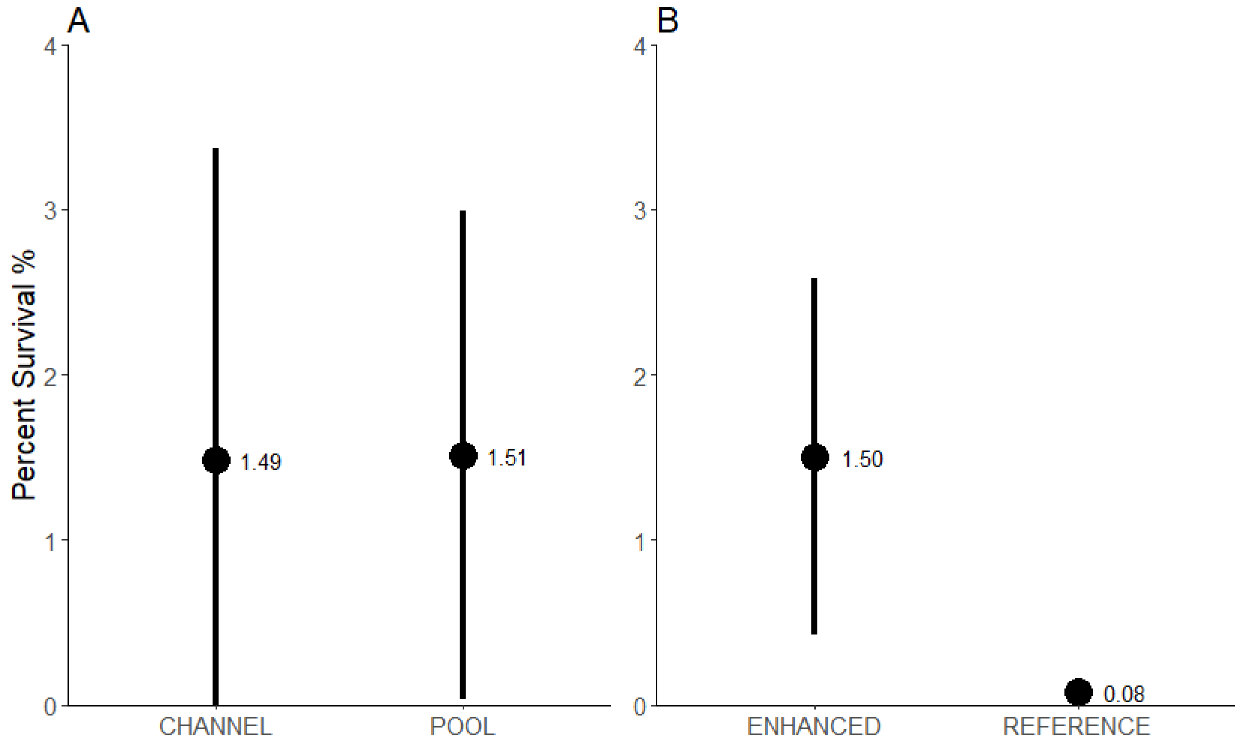


Figure 6. Mean percent survival plotted with 95% confidence intervals for (A) channel versus spawning pool marshes and (B) pooled enhanced versus reference marshes.

Physical environmental factors

Mean daily water temperature readings collected using the YSI multiprobe displayed the same patterns as HOBO U26 loggers (Figure 7). Data recorded using the loggers was further analyzed for differences, and significant differences in mean water temperature were detected among site types ($F(2,941)=139.6$, $p<0.001$). Post-hoc Tukey comparisons revealed that mean water temperatures were significantly higher in spawning pools (mean=21.7°C ± 0.29) compared to other sites and mean water temperatures were significantly higher in channels (mean=19.9°C ± 0.37) than in reference sites (mean=17.8°C ± 0.27).

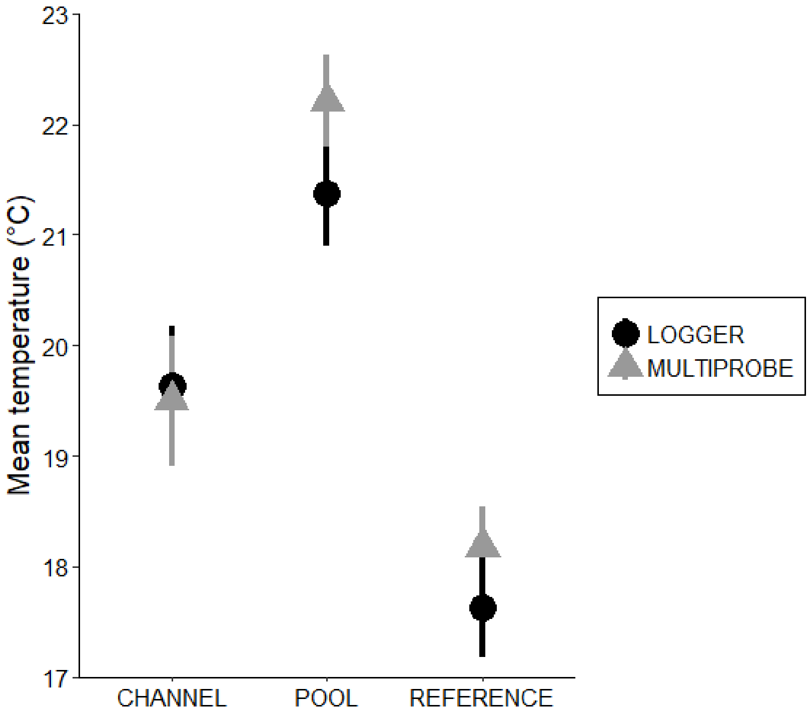


Figure 7. Mean water temperature (°C) plotted with 95% confidence intervals at channel, spawning pool, and reference marshes recorded using HOBO U26 loggers (black circle) and a YSI ProDSS multiprobe (gray triangle).

Mean daily dissolved oxygen readings collected using the YSI multiprobe and loggers displayed similar patterns at spawning pools and reference sites, but not at channels (Figure 8). Multiprobe readings for channel sites were much higher than those recorded using the loggers. Logger readings were significantly different between site types (*F*(2,258)=147.5, *p*<0.001), and post-hoc Tukey tests revealed that mean dissolved oxygen concentrations were significantly higher in spawning pools (mean=6.15 mg/L ± 0.36) than other site types and mean dissolved oxygen was significantly higher in reference sites (mean=4.36 mg/L ± 0.35) than in channel sites (mean=1.15 mg/L ± 0.33). Multiprobe dissolved oxygen readings were significantly different between site types (*F*(2,266)=42.19, *p*<0.001). A post-hoc Tukey test reported mean dissolved oxygen concentrations were significantly higher in spawning pools (mean=7.47 mg/L ± 0.45) than other sites and there was no significant difference in mean dissolved oxygen between reference (mean=4.53 mg/L ± 0.44) and channel sites (mean= 4.67 mg/L ± 0.67).

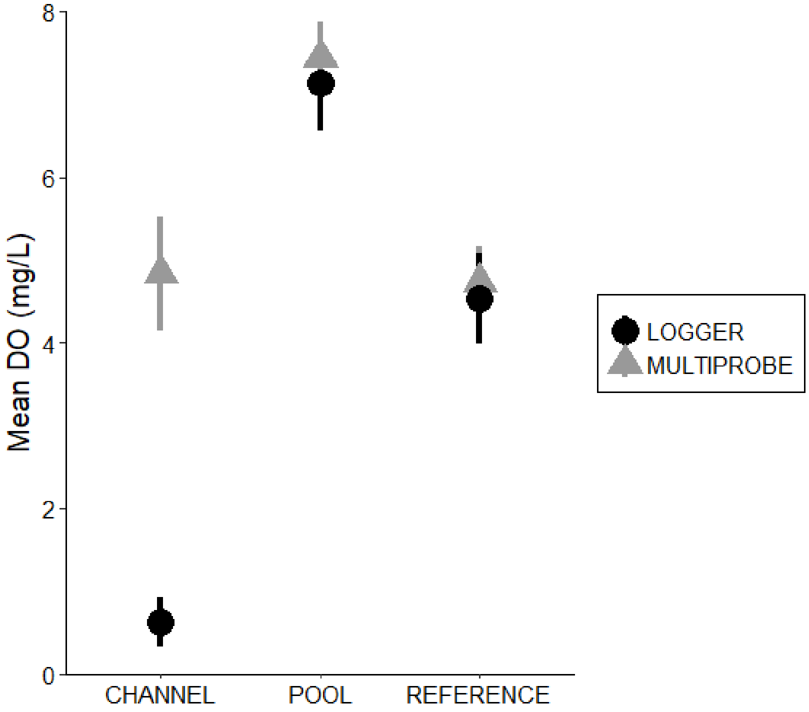


Figure 8. Mean dissolved oxygen (mg/L) readings plotted with 95% confidence intervals at channel, spawning pool, and reference marshes using HOBO U26 loggers (black circle) and a YSI ProDSS multiprobe (gray triangle).

Larval diets and prey selection

Zooplankton densities (#/L) were not significantly different between site types (*F*(2,29)=0.71, *p*=0.50), but densities were greater in channels (mean=121.6/L ± 39.6) than pools (mean=77.6/L ± 30.5) or reference sites (mean=100.0/L ± 43.9). The cluster analysis based on available zooplankton and larval diets identified three distinct assemblages (Figure 9). Cluster A included the zooplankton resulting from grab sampling at reference, pool, and channel sites. The inclusion of all 3 site types suggests there was no significant difference in the assemblage available to the larvae at any of the sites. Cluster A was dominated by *Bosmina longirostris* and nauplii, and also included a smaller percentage of cyclopoids and *Chydorus sphaericus* (Figure 9). Cluster B included the diets of larvae recovered in reference and pool sites, and was dominated by *Simocephalus* spp. and cyclopoids, and to a lesser extent *Diaphanosoma* spp., *Ceriodaphnia* spp., and chydorids (Figure 9). Cluster C included the diets of larvae recovered in channel sites. Over 50% of the assemblage was comprised of *Ceriodaphnia* spp., with cyclopoids, chydorids, and *Simocephalus* spp. making up a smaller percentage (Figure 9).

Differences in the composition of Cluster A versus Clusters B and C suggest prey selection (positive or negative) occurred. Larvae from reference sites selected against *B. longirostris*, *C. sphaericus*, and cyclopoids ($p<0.05$) when compared with the neutral selection ($1/m=0.0667$; Table 2). Selection of *Diaphanosoma* spp., *Scapholeberis* spp., and *Simocephalus* spp. by reference larvae did not significantly differ from neutral selection ($p>0.05$). Mean selection of *Simocephalus* spp. by reference larvae was high (0.15; sd=0.05), but a significant difference from random feeding was not detected. Negative selection by pool larvae occurred for *B. longirostris*, *C. sphaericus*, and cyclopoids ($p<0.05$) when compared with the neutral selection ($1/m=0.0769$), whereas positive selection occurred for *Simocephalus* spp. ($t(9)=3.49$, $p=0.008$; Table 2). Larvae from channel sites selected against chydorids, cyclopoids, and *Polyphemus pediculus* ($p<0.05$) when compared with neutral selection ($1/m=0.0667$; Table 2). Mean selection of *Ceriodaphnia* spp. was positive (0.076; sd=0.03), but did not differ from neutral selection ($p>0.05$).

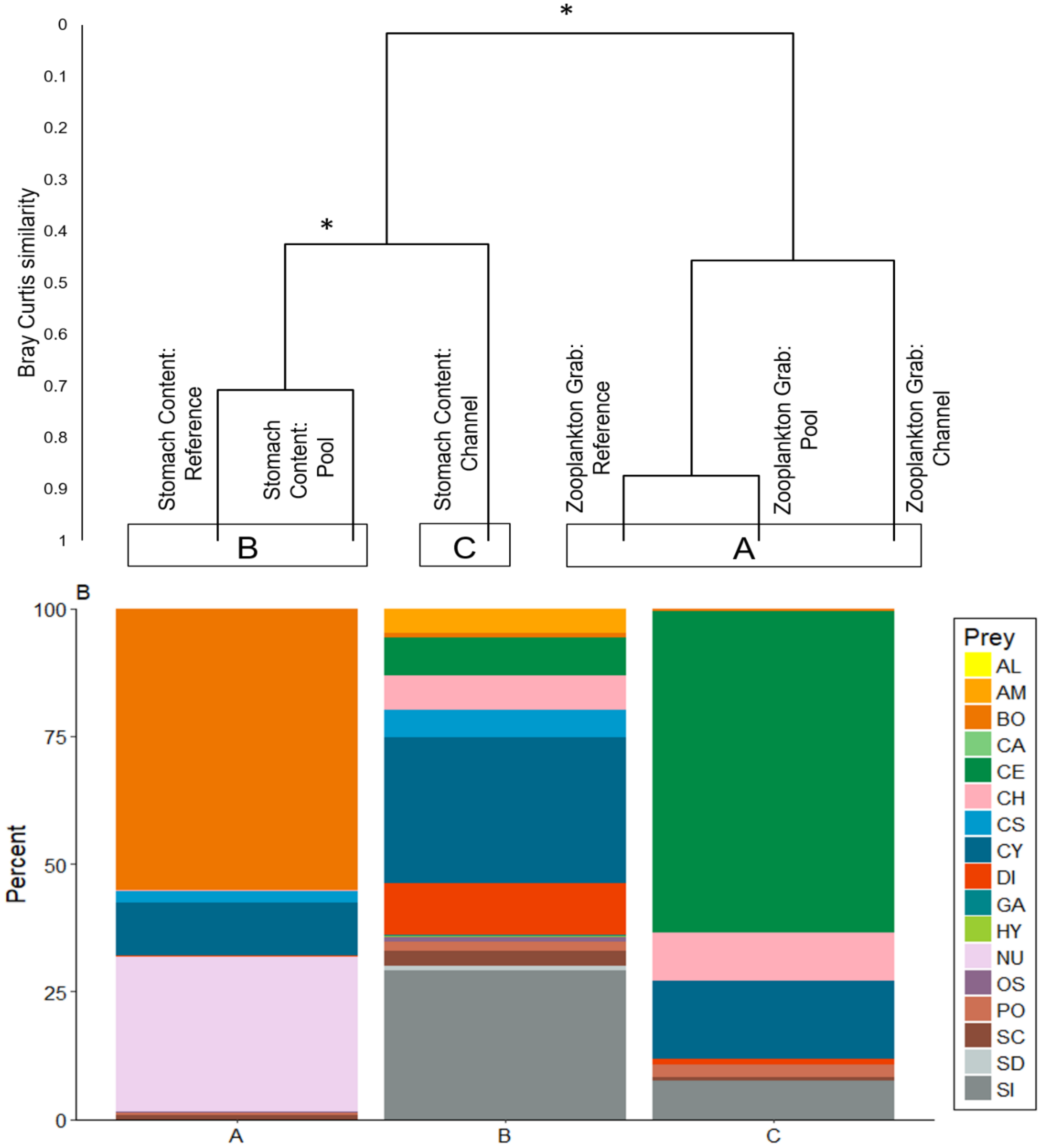


Figure 9. Significant assemblages from zooplankton sampling and larval diets identified using the Bray-Curtis similarity index and UPGMA linkage method with 1000 random bootstrap samples. The dendrogram (A) displays the classification of significant assemblages, which are indicated with a unique letter and an asterisk (*). The stacked bar chart (B) displays the percent contribution of each prey taxa. Prey taxa codes are as follows: AL, *Alonella* spp.; AM, Amphipoda; BO, *B. longirostris*; CA, Calanoida; CE, *Ceriodaphnia* spp.; CH, Chydoridae; CS, *C. sphaericus*; CY, Cyclopoida; DI, *Diaphanosoma* spp.; GA, Gastropoda; HY, Hydrachnida; NU, nauplii; OS, Ostracoda; PO, *P. pediculus*; SC, *Scapholeberis* spp.; SD, *S. crystallina*; SI, *Simocephalus* spp.

Table 2: Mean prey selectivity ($\bar{\alpha}_i$; SD) for larval northern pike collected from reference, spawning pool, and channel nursery marshes in French Creek, NY, May 2016. Index values significantly different (p<0.05) from 1/m are labelled with an asterisk and either a "+" indicating positive selection or a "-" indicating negative selection.

Site type	1/m	Prey type	$\bar{\alpha}_i$	
Reference	0.0667	*B. longirostris*	-0.0006 (0.0004)	*
		C. sphaericus	-0.0017 (0.0007)	*
		Cyclopoida	-0.0094 (0.0088)	*
		Diaphanosoma spp.	0.0661 (0.0171)	
		P. pediculus	0.0011 (NA)	
		Scapholeberis spp.	0.0633 (0.0478)	
		Simocephalus spp.	0.1500 (0.0542)	
Pool	0.0769	*B. longirostris*	-0.001 (0.000003)	*
		C. sphaericus	-0.0026 (0.002)	*
		Cyclopoida	-0.006 (0.0002)	*
		Simocephalus spp.	+0.1098 (0.0283)	*
Channel	0.0667	*B. longirostris*	0.0001 (NA)	
		Ceriodaphnia spp.	0.0764 (0.0291)	
		Chydoridae	-0.0169 (0.0058)	*
		Cyclopoida	-0.0251 (0.0168)	*
		P. pediculus	-0.0027 (0.0012)	*
		Scapholeberis spp.	0.0017 (NA)	

Discussion

Connectivity enhancements implemented in Great Lakes wetlands are a viable technique to enhance ecosystem function (Mathers & Hartley, 1995; Vincent, 1995). A rapid response of northern pike use of connectivity enhancements has been observed (Brown et al., in prep), and results from our study indicate high suitability exists for larvae to fulfill early life requirements in enhanced marshes because pike were able to successfully develop from larvae to juvenile emigrants at several sites. Spawning pool and channel excavation enhancements increased YOY northern pike survival, and the presence of wild fish at emigration indicated successful natural reproduction. Differences in environmental conditions of the nursery marshes may in part explain the variation in success (Table 3), and were clearly highlighted in this study. Connectivity enhancement promoted a rapid colonization opportunity for spawning pike, and natural reproduction observed suggests enhancements may have fulfilled habitat requirements for spawning, although that was not a focus of the study. Zooplankton also displayed rapid responses to enhancements as assemblages were similar at existing and enhanced sites. Zooplankton assemblages have been documented to exhibit rapid recovery following restoration projects (Dodson & Lillie, 2001; Badosa *et al.*, 2010), and their value as indicator groups has been recommended (Lougheed &Chow-Fraser, 2002). Increased nutrient availability through sediment disturbance and the rapid evolution of the plant community following excavation may have created opportunities for specific zooplankton to colonize.

Enhancements fostered favorable conditions for larval pike survival, but northern pike entry onto the spawning and nursery grounds is water level dependent. Reference marshes, which have not been completely blocked with *Typha* and maintained connectivity during the study, might be maintained by ground water hydrology. This would explain the significantly lower temperatures observed and the lack of *Typha* encroachment. Spring flooding creates connectivity between main channels and floodplain wetlands, allowing access for spawning fishes (Baber et al., 2002), and naturally occurring water level fluctuations enhance the abundance and quality of pike spawning habitat (Mingelbier et al., 2008). High spring water levels are positively associated with pike year class strength (Johnson, 1957; Smith et al., 2007) and YOY pike densities in nursery sites, with the greatest abundances occurring in marshes with highest water height (Vuorinen et al., 1998; Cucherousset et al., 2009). The 2016 YOY production in French Creek was extremely low when compared with prior years (Farrell *et al*., 2017). Water levels measured at the Alexandria Bay, NY gauging station (NOAA buoy station ID: 8311062, http://tidesandcurrents.noaa.gov) indicated 2016 as an extremely low water level year compared to yearly averages, which may have contributed to overall low production (Farrell et al., 2017). Northern pike abundances have been in decline since the 1980s (McCullough &

Gordon, 2015), and reductions in natural water level fluctuations and resulting loss of spawning habitats are thought to be the main drivers of these declines (Farrell, 2001; Farrell *et al.*, 2006; Smith *et al.*, 2007). Water level regulation in the St. Lawrence River has altered the hydroperiod, reducing seasonal variability and fostering the expansion of *Typha* (Farrell et al., 2010b; Rippke et al., 2010). More natural fluctuations, including high levels in spring for flooding of spawning habitats and low levels to reduce *Typha*, coupled with implementation of wetland excavation enhancements would provide the necessary environment for YOY northern pike production to increase.

Table 3: Summary of northern pike CPUE and percent survival (%) and environmental conditions measured in French Creek nursery marshes during this study. Means and 95% confidence intervals are reported. Significantly different means identified using *t*-tests are labelled with an asterisk (*). Significantly different means identified using ANOVA are labelled with corresponding letters resulting from post-hoc Tukey tests.

	CPUE	Percent survival (%)	Temperature (°C)	Dissolved oxygen (mg/L)	Zooplankton density (no/L)
Enhanced	-	1.50 ± 1.08*	-	-	-
Channel	0.51 ± 0.20^a	1.49 ± 1.88	19.9 ± 0.37^b	1.15 ± 0.33^c	121.6 ± 39.6
Pool	0.43 ± 0.18^a	1.51 ± 1.48	21.7 ± 0.29^a	6.15 ± 0.36^a	77.6 ± 30.5
Reference	0.13 ± 0.07^b	0.08 ± 0.07*	17.8 ± 0.27^c	4.36 ± 0.35^b	100.0 ± 43.9

Mean water temperature throughout the larval period was highest in spawning pools, followed by channels, and lastly reference sites, whereas mean dissolved oxygen was greatest in spawning pools, followed by reference, and lastly channels. Interestingly, percent survival was identical in channel and pool sites, despite the lower temperatures and dissolved oxygen at channel sites. In channel sites, mean daily dissolved oxygen readings recorded using the YSI multiprobe were much higher than readings collected using loggers. This may be because dissolved oxygen in shallow, flooded meadows is quickly depleted after nightfall, when photosynthesis is no longer occurring and respiration continues. Further investigation of daily fluctuations revealed dissolved oxygen levels reaching as low as 0 mg/L in channel sites during the night (Figure 10). Dissolved oxygen also steadily lowered throughout the entire deployment period but did increase during the daytime (Figure 10). Northern pike are extremely tolerant of low oxygen conditions, surviving in concentrations as low as 0.3 mg/L for short periods of time (Casselman, 1978), but consumption, conversion efficiency, and growth rates are reduced in low oxygen environments (Adelman & Smith, 1970; Casselman, 1978). Some St. Lawrence River wetlands are known to be devoid of oxygen by early summer (Farrell et al., 2014), and some sites in this study approached anoxia during the sampling season. Five northern pike juveniles recovered in traps were dead upon arrival with no signs of predation or disease, suggesting mortality occurred due to low oxygen. It is possible that pike in channels located a refugia during low dissolved oxygen periods as loggers were only set at single locations.

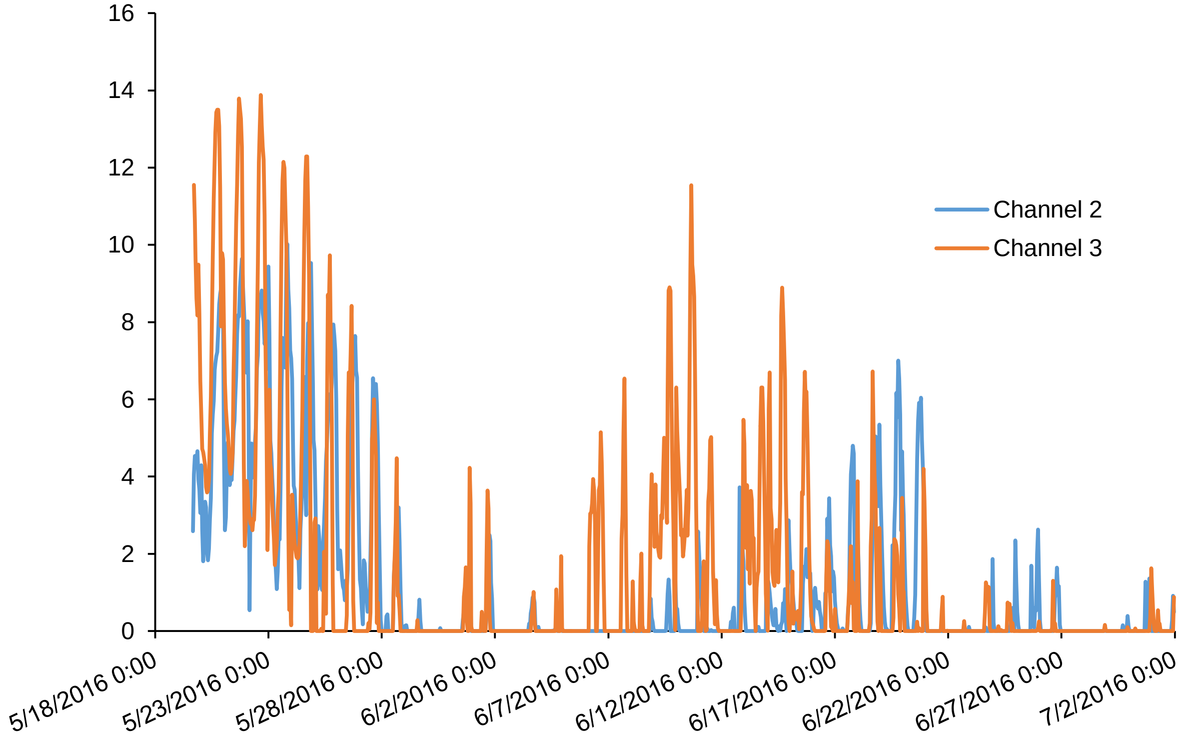


Figure 10. Dissolved oxygen (mg/L) measured at hourly intervals throughout the deployment period (5/19/16-7/1/16) in channel sites C2 and C3.

Temperature is one of the most important factors controlling growth of northern pike during the early stages (Franklin & Smith, 1963; Bry et al., 1991), and physiological growth optima are range between 19 and 21°C (Casselman, 1978). Warm temperatures occurring in spawning pools and channels likely promoted faster growth of larvae than in reference sites. Predator size and larval growth explained 67% of the variation in larval survival in one study (Letcher et al., 1996), and both factors have long been recognized as important determinants of survival of young fish (Houde, 1987). One potential rationale for similar survival rates in spawning pool and channel sites is the presence of sedge vegetation in channels, although vegetation was not a focus of our study. Channel connectivity enhancements were designed to reconnect the mainstem of French Creek to remnant sedge meadows. Sedge vegetation was only dominant at channel enhancements although small patches were observed at the edges of some spawning pools (Farrell et al., 2015). Vegetation is well known to be critical to northern pike especially during the larval and juvenile stages (Bry, 1996; Casselman & Lewis, 1996), and larvae have been shown to distribute themselves to sedge vegetation following hatch (Nilsson et al., 2014). Zooplankton typically are more abundant in vegetated versus non-vegetated environments (Watkins et al., 1983; Nilsson et al., 2014), and their densities in this study were greatest in channel sites, although differences in density due to site were not significant. Densities of zooplankton collected in the grab samples could have been affected by the vegetation present where the sample was collected, although efforts were focused on sampling the entire water column in representative habitats of the site. Juvenile pike also use vegetation for protection against predation (Werner et al., 1977; Skov & Berg, 1999). Potential tradeoffs between channels with greater vegetation and zooplankton abundances versus spawning pools with optimal physical conditions may occur, however in this study, both scenarios resulted in similar percent survival of larvae.

Northern pike larvae displayed positive or negative prey selection in all of the site types. Of interest was the discrepancy in the diets of larvae originating from different sites. Reference and pool larvae primarily selected *Simocephalus* spp., whereas channel larvae selected *Ceriodaphnia* spp., although significant positive selection was only detected for pool larvae. Due to the nature of the index, selectivity coefficients could not be calculated for prey taxa that were not present in the grab samples. *Simocephalus* spp. was found in the diet of some channel larvae, but was not represented in the grab sample. *Simocephalus* spp. are typically found in or around vegetated areas (Thorp & Covich, 2001) which may have provided shelter from the grab sample. Positive selection for *Simocephalus* spp. by channel larvae may have occurred but we were unable to detect it. *Simocephalus* spp. and *Ceriodaphnia* spp. were the dominant taxa in all of the larval diets and possess several similarities. Both belong to Daphnidae family, inhabit littoral zones, and display similar feeding and movement behaviors (Amoros, 1984). *Simocephalus* spp. are larger than *Ceriodaphnia* spp., which would have implications on the number of prey items a larvae would need to procure to equate to the same nutrition value. Despite size differences, these species are essentially analogous in terms of their functional role as food for larval fish.

Zooplankton food limitation is thought to contribute to recruitment failure of YOY northern pike in the Baltic Sea (Ljunggren et al., 2010). Zooplankton densities, however were not significantly different between site types, similar to previous findings in French Creek (Farrell et al., 2014). Zooplankton limitation to pike is more likely to occur in deeper offshore sites associated with protracted spawning (Farrell 2001).Wetlands in the upper St. Lawrence River do not appear to be nutrient limited and are much more productive than the main river (Farrell et al., 2010a, 2014). Discrepancies in taxa consumed at channel versus spawning pool and reference sites did not mimic differences in survival, suggesting larvae in French Creek were not limited by zooplankton prey at any of the sites.

Farrell (2001) estimated survival of pike to be 0.00008-0.0001% from egg to fall juvenile in a St. Lawrence River bay. Survival from spawning to egg hatch was 84.1% (Farrell, 2001), which is within the 60-96% range observed in other studies (Pliszka, 1954; Franklin & Smith, 1963). Estimates completed by Farrell (2001) used eggs collected in nearshore areas of bays versus the tributary wetlands examined in this study. Larvae in this study were stocked following the transition to exogenous feeding, whereas Farrell (2001) observed naturally spawned eggs and larvae over the entire developmental period. Greater survival was detected during this study than that of Farrell (2001), suggesting higher mortalities may occur following yolk sac absorption and in bay versus tributary wetland sites. Variability in timing and spatial distribution of zooplankton hatches could also add to the overall variability of larval survival (Burrow et al., 2011). Bry et al. (1995) did not detect a single critical period but mortality occurring throughout the entire larval period, although highest mortality did occur at the onset of exogenous feeding. One weakness of the survival estimates in the present study is the lack of complete coverage of all of the exit channels present at spawning pools. Blockades could have been set at the outlet channels that were not trapped, but the complex structure of the spawning pools and long lengths of outlet channels may have confused out-migrating juveniles and we did not want to them to become stranded.

Cannibalism is one of the major causes of mortality during the juvenile stages of northern pike (Bry & Gillet, 1980; Wright & Giles, 1987; Skov et al., 2003; Grønkjær et al., 2004). While our study did not specifically examine cannibalism as a factor in the survival analysis, we did attempt to control for it by stocking at a similar rate and dispersing the fry throughout the entire site. These actions should have allowed stocked pike to exist in similar densities to other stocked pike at all sites. Several studies have suggested that stocking of northern pike where natural reproduction occurs is not successful (Skov & Nilsson, 2007; Hühn et al., 2014), potentially because of low genetic fitness of stocked fish and prevailing effects of hatchery rearing (Skov et al., 2011). This study used adult spawners recovered from the French Creek drainage, therefore progeny would have been spawned somewhere within the watershed where they were stocked. The northern pike population in French Creek exhibits some local genetic differences from other spawning sites in the St. Lawrence River, possibly due to well-suited habitat and spatial isolation from other locations (Bosworth & Farrell, 2006). Pike in this study were stocked early in the juvenile stage and at comparable sizes (~13 mm), which would allow for imprinting if natal homing occurs, and results in higher overall survival (Grimm & Klinge, 1996; Grønkjær et al., 2004). Early stocking allows for a longer period of growth and therefore lowers the risk of predation from larger, naturally spawned pike (Grønkjær et al., 2004). Stocked pike in this study emigrated at the same mean length and with the same temporal distribution as wild pike suggesting that residual effects of hatchery life did not affect survival to emigration. Stocking of northern pike fry at locations without a sustaining population has shown success (Vuorinen et al., 1998; Sutela et al., 2004), and our study demonstrated that stocking pike larvae is a feasible manipulation tool following restoration efforts that aim to develop a self-sustaining population. However, the presence of wild fish in traps during the emigration survey indicated natural reproduction occurred in enhancement sites and northern pike spawners can potentially rapidly colonize newly-created spawning habitats.

This study showed wetland enhancement marshes to increase the survival of northern pike during their critical, larval stages. Future work should focus on identifying which environmental mechanisms have the greatest effect on larval survival in both types of wetland enhancement (e.g., channel connectivity and spawning pool) and investigate whether similar mechanisms influence survival in reference marshes.

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Conclusion

Understanding the requirements of fish species at each life stage is imperative to managing populations. Throughout this thesis, we highlighted several aspects of larval northern pike ecology in coastal wetlands of the upper St. Lawrence River. In the context of fisheries management, this work added understanding of the fundamental biotic and abiotic interactions affecting northern pike during their larval stages. In chapter 1 we estimated egg and larval development and showed spring water temperatures and water levels to be critical for temporal and spatial patterns in spawning and egg and larval development. We found zooplankton prey to be flushed from the spawning and nursery marshes during flooding but abundances quickly rebound as flood waters began to recede, peaking prior to projected exogenous feeding of pike larvae. In chapter 2 we highlighted the importance of seasonally-flooded wetlands as producers of abundant, large cladocerans that pike selected during their advanced larval stages. Selection has been shown to increase as the abundance of preferred prey increase, and larvae given a wetland assemblage had access to a greater abundance of these prey. Nearshore bay and offshore spawning are known to be less advantageous than early, tributary spawning, and lead to lower egg survival and young of the year production. This work showed another disadvantage to the protracted spawning behavior, as larvae in nearshore bays will have less access to abundant, large cladoceran prey during the critical larval stage. In chapter 3 we showed larval survival to be significantly greater in spawning pool and channel connectivity enhancement marshes than in reference marshes. Enhancements displayed warmer water temperatures than reference sites, likely promoting fast growth of larvae. Excavation designs should focus on creating shallow marshes, to foster warm temperatures for abundant food production and fast larval growth, with increased connectivity to sedge and grass meadows. No one to our knowledge has highlighted the survival differences of northern pike larvae in enhancement and reference marshes, and future work should try to isolate the mechanisms that have the greatest influence on larval survival. Understanding the requirements of northern pike larvae can help researchers and managers devise effective strategies for increasing recruitment and bolstering the population.

This thesis also highlighted several important patterns in zooplankton abundances with regard to spring wetland conditions. Phytoplankton and zooplankton biomass were greatest prior to spring flooding for April of 2016, and both declined at the time of flooding, suggesting dilution effects. Phytoplankton biomass and zooplankton abundance began to increase with warming temperatures, and cladoceran hatch was likely cued during this time. In chapter 2 we showed wetlands to have significantly larger-bodied zooplankton than nearshore areas of bays, and future work could attempt to describe differences in abundances and taxa by sampling thoroughly and repeatedly throughout the spring and summer. Chapter 3 documented the rapid colonization of zooplankton in the enhancement marshes by the inclusion of zooplankton assemblages from all three site types in the same cluster. Future work should look at the mechanisms allowing for the dispersal of zooplankton into newly created habitats and whether water movement, excavation activities, or other methods allow for the colonization of these organisms.

Appendices

Appendix 1: Mean density (no/L; SE) of zooplankton taxa (identified to lowest taxonomic resolution feasible) collected by grab sampling on April 1, 8, 15, 22, and 29, 2016 at Bevins, Carpenters, Deferno, and lower French Creek. Means were calculated by averaging duplicate samples. Means that are not followed by a standard error indicate the density of the taxa was identical in both samples.

4/1				
Taxa	Bevins	Carpenters	Deferno	Lower French Creek
Cyclopoida	0.33	24.5 (4.83)	-	0.67
nauplii	2.83 (1.83)	19.83 (1.5)	0.67 (0.33)	1.83 (0.5)
Bosmina longirostris	-	1	-	-
Chydorus sphaericus	-	0.33	-	0.33
Chydoridae	0.33	0.33	-	-
Daphnia spp.	-	1.5 (0.83)	-	-
Macrothricidae	-	-	0.33	-
Ostracoda	-	-	-	0.33
Rotifera	0.67	0.33	1.33 (0.33)	1
4/8				
Cyclopoida	-	4.17 (1.17)	0.33	-
nauplii	0.67	18.83 (0.83)	0.33	0.33
Daphnia spp.	-	1	-	-
Ostracoda	0.33	-	0.33	-
Rotifera	0.33	-	-	-
4/15				
Cyclopoida	-	27 (14.33)	0.33	2.5 (0.83)
Harpacticoida	-	0.5 (0.17)	-	-
nauplii	0.5 (0.17)	12.5 (4.83)	0.33	6.17 (0.17)
B. longirostris	-	0.33	-	0.33
Ceriodaphnia spp.	-	0.67 (0.33)	-	0.33
C. sphaericus	0.33	1.33	0.33	0.33
Chydoridae	-	0.33	-	-
Daphnia spp.	-	0.33	-	0.33
Scapholeberis spp.	-	0.33	-	-
Ostracoda	-	1	0.33	0.67
Rotifera	-	-	0.83 (0.17)	6.67
4/22				
Calanoida	-	1.17 (0.17)	-	-
Cyclopoida	0.67	14.5 (1.5)	0.67	2.5 (1.5)
nauplii	16.83 (11.17)	11.33 (0.33)	0.33	50.33 (18.33)

B. longirostris	-	0.33	-	-
Ceriodaphnia spp.	-	4 (1)	-	0.67
C. sphaericus	2.67	1.67 (0.33)	-	1
Chydoridae	0.33	1 (0.67)	-	-
Daphnia spp.	-	1.67	-	-
Polyphemus pediculus	-	6.83 (3.83)	-	-
Ostracoda	1.67	-	1	0.67
Rotifera	1.83 (0.17)	-	2.67 (0.33)	1.17
		4/29		
Calanoida	-	0.33	-	0.33
Cyclopoida	0.33	5.5 (0.83)	-	1.67
nauplii	1.83 (1.17)	0.67	1.5 (0.5)	2.5 (1.17)
B. longirostris	-	18.5 (2.17)	-	-
Ceriodaphnia spp.	-	9 (3.33)	-	-
C. sphaericus	10.67 (6.67)	10.83 (7.17)	1.5 (0.83)	1.17 (0.83)
Chydoridae	0.33	1	0.33	-
Daphnia spp.	-	0.33	-	-
Diaphanosoma spp.	-	0.67	-	-
P. pediculus	-	5 (1)	0.33	-
Simocephalus spp.	-	0.33	-	-
Ostracoda	0.83 (0.5)	-	-	0.33
Rotifera	0.33	-	0.67	0.5 (0.17)

Appendix 2: Probability values of each assemblage linkage resulting from cluster analysis performed using the BOOTCLUS software package.

Linkage	Probability value, *p*(0.05)
1	0.002 S
2	0.002 S
3	0 S
4	*
5	*
6	*
7	*

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