

ARTICLE

Varying Effects of Common Reed Invasion on Early Life History of Northern Pike

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Abstract

The invasion of North American wetlands by the Eurasian subspecies of common reed *Phragmites australis australis* is well documented, but very few studies have been conducted on its effects on freshwater fish communities. Northern Pike *Esox lucius* is one of several fish species using wetlands for reproduction and early development that could be affected by the spread of common reed. The effects of vegetation type (common reed stands, other reference plant assemblages) were evaluated on four aspects (egg deposition, abundance, growth, and feeding) of the early life history of Northern Pike in two St. Lawrence River wetlands in Quebec. During high water levels in 2009, the relative abundance of Northern Pike eggs was three times higher in the reference plant assemblages than in the common reed stands at the two study sites. In 2010, when water levels were extremely low and few other plant assemblages were accessible by fish, the relative abundance of eggs was two times higher in the common reed stands than in other plant assemblages within the only site available for sampling. In 2009, the relative abundance, length, and weight of age-0 Northern Pike did not differ significantly between common reed stands and reference assemblages. Growth rate, condition, prey type, and relationship between digestive tract dry weight and total fish dry weight suggested slightly more favorable conditions in common reed stands in some cases or in reference assemblages in other cases (no consistent pattern between the vegetation types). Although common reed is still in the early invasion process in St. Lawrence River freshwater marshes, it does not seem to have any negative effects on Northern Pike early life history. However, little is known about the magnitude of common reed biomass accumulation, making it impossible to predict whether these stands, which are part of an ongoing invasion, will provide long-term quality habitat.

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Wetlands are important ecosystems for many fish species. They provide reproductive, growth, and feeding habitats for at least 19 families of freshwater fish in Canada and the USA (Dibble et al. 1996). These ecosystems are characterized by the presence of submerged and emergent aquatic vegetation, which are important components of fish habitat (Venable 1986). The use of freshwater wetlands by fish is closely associated with the hydrological fluctuations of rivers and lakes (Carpenter et al. 1992), especially when spring flooding increases wetland area and allows access to floodplains (Massé et al. 1988; Junk et al. 1989). Despite their critical importance to the life cycle of many fish species, North American wetlands have suffered disturbances from agricultural, urban, and industrial development, which have severely reduced their extent (Groupe de Travail National sur les Terres Humides 1988; USEPA 2013). Invasive exotic plant species are also simultaneously eroding the ecological integrity of wetlands and, indirectly, the quality of fish habitat (Zedler and Kercher 2004).

A well-documented example of wetland transformation by an invasive plant is the introduction and expansion of the Eurasian subspecies of common reed *Phragmites australis australis* (family Poaceae; Saltonstall 2002) in intertidal marshes along the eastern coast of North America (Chambers et al. 1999). This genotype of common reed (haplotype M), probably introduced to New England in the early 19th century, is now widespread in North America (Saltonstall et al. 2004). Common reed forms vast stands that exhibit low plant diversity (Lambert and Casagrande 2006; Meadows and Saltonstall 2007; Chambers et al. 2008). The establishment and expansion of common reed in wetlands is generally driven by disturbances, such as shoreline development and low water levels, which create seed beds for the plant or contribute to nitrogen pollution, increasing the competitiveness of this invasive species (Silliman and Bertness 2004; King et al. 2007; Mozdzer and Ziemann 2010; Tulbure and Johnston 2010; Kettenring et al. 2011; Wilcox 2012).

The effects of common reed invasion on intertidal marsh fishes have been extensively studied. The biomass produced each year by common reed stands (Windham and Lathrop 1999; Warren et al. 2001) contributes to marsh surface elevation above sea level and eliminates surface pools, thereby modifying the hydrological regime (Lathrop et al. 2003; Osgood et al. 2003; Hunter et al. 2006). Some littoral fishes are particularly affected by these habitat changes, such as the Mummichog *Fundulus heteroclitus*, a dominant species in intertidal marshes. The recruitment of Mummichog, which plays a key role in the food web of these marshes, may be compromised by the invasion of common reed since the abundance of larvae and juveniles of this species, as well as their potential larval prey, are particularly low in common reed stands (Able and Hagan 2000, 2003; Fell et al. 2003; Osgood et al. 2003; Raichel et al. 2003; Hunter et al. 2006; Hagan

et al. 2007). Moreover, Mummichog populations that reside in common reed stands have a higher incidence of parasitism and the fish without parasites exhibit lower lipid reserves than the fish residing in marshes that have not been hydrologically altered by common reed invasion (Dibble and Meyerson 2012). White Perch *Morone americana*, a dominant predator of oligohaline marshes, also seems to avoid common reed stands, possibly because of reduced food abundance (Jones et al. 2014).

Currently, one of the largest information gaps regarding the relationship between common reed and wetlands concerns the effects of common reed on freshwater marshes. Common reed is proliferating throughout freshwater wetlands of the Great Lakes and St. Lawrence River watersheds (Bourgeau-Chavez et al. 2013; Tougas-Tellier 2013). The trend toward decreasing Great Lakes water levels over the past few decades is largely responsible for the establishment (via seed germination) and subsequent vegetative expansion (via rhizomes and stolons) of common reed (Trebitz and Taylor 2007; Whyte et al. 2008; Tulbure and Johnston 2010; Wilcox 2012). A similar phenomenon has also been observed along the St. Lawrence River (Hudon et al. 2005), where water levels have been decreasing for at least 30 years (Hudon et al. 2009).

The spread of common reed in freshwater marshes could have profound effects on fish communities. However, very few studies have addressed this concern in freshwater. Two studies suggested that the richness and abundance of fish species (mainly sunfishes of the genus *Lepomis*) do not differ significantly between common reed stands and marshes dominated by narrowleaf cattail *Typha angustifolia* (Aday 2007; Kulesza et al. 2008). However, these studies were based on a low fishing effort.

In the St. Lawrence River, Northern Pike *Esox lucius* could be one of the freshwater fish species most affected by common reed expansion in wetlands because it is highly dependent on submerged wetland vegetation to complete its life cycle (Bry 1996). Northern Pike are nonguarding, open-substrate phytophil spawners (Balon 1975). Both males and females swim through and over the vegetation in shallow water, and eggs and milt are released simultaneously (Fabricius and Gustafson 1958; Scott and Crossman 1973). Eggs are adhesive and remain attached to the spawning ground vegetation. They usually hatch within 2 weeks. At hatching, yolk sac larvae (6–8 mm in length) remain attached to the vegetation during a period of 6–10 d by using the adhesive glands on their heads (Scott and Crossman 1973; Bry 1996). Age-0 Northern Pike remain close to the spawning site for several weeks and gradually disperse to adjacent areas after they reach a length of 20 mm (Franklin and Smith 1963; Fortin et al. 1982; Cucherousset et al. 2009). During spring floods, Northern Pike use the submerged vegetation of marshes, lakes, and river floodplains as spawning substrate (Fortin et al. 1982; Massé et al. 1991, 1993; Casselman and Lewis 1996). However,

floodplains are also good habitats for the establishment and development of common reed stands (Hudon et al. 2005). The proliferation of common reed in Northern Pike spawning areas is of particular concern because this predatory species, which plays a regulatory role in fish communities (Casselman and Lewis 1996), is also an important sport fish that has been declining in abundance over the last decades along the St. Lawrence River (Lake Ontario Management Unit 2014; Ministère des Forêts, de la Faune et des Parcs du Québec, unpublished data).

The main objective of this study was to assess whether common reed stands are suitable reproductive freshwater habitats for Northern Pike along the St. Lawrence River. More specifically, we addressed the effects of common reed on (1) egg deposition, as well as on the (2) abundance, (3) growth, and (4) feeding habits of age-0 Northern Pike. In a context where the expansion of common reed in the St. Lawrence floodplain decreases plant diversity (Lavoie et al. 2003), and possibly the extent and duration of flooding, the general hypothesis tested in this study is that the invasion of freshwater marshes by common reed has an overall negative effect on Northern Pike reproduction and early life history stages.

METHODS

Study Sites

This study was conducted in two wetlands located along the St. Lawrence River, Quebec (Figure 1). The first site (45°22'N, 73°46'W) was located in the Lafleur Creek floodplain (area = 37 ha), which drains into the Saint-Jean Creek and subsequently into Lake Saint-Louis, a large fluvial lake of the St. Lawrence River near Montreal. In the 1980s, the Saint-Jean Creek spawning ground, comprising the Lafleur Creek floodplain, was the largest Northern Pike spawning ground of Lake Saint-Louis. The spawning ground was used by about 6,000 Northern Pike and produced 2,000 age-0 fish/ha (Dubé and Gravel 1989). Plant assemblages of the marsh were once dominated by cattails *Typha* spp., flowering rush *Butomus umbellatus*, and reed canarygrass *Phalaris arundinacea* (Létourneau and Jean 2006). The presence of common reed appears to be quite recent; small reed stands covered 4 ha in 2010 (Environment Canada, unpublished data).

The second site (45°36'N, 73°29'W) was located in the Boucherville Islands archipelago (total area = 1,253 ha), which includes the most extensive marshes of the Montreal region (Hudon 2004). Until the late 1970s, the common reed was absent from plant surveys (Hudon 2004) and aquatic plant composition was dominated by cattails, flowering rush, reed canarygrass, and river bulrush *Bolboschoenus fluviatilis*, as well as by other various bulrush species *Schoenoplectus* spp. (Pilon et al. 1980). Afterwards, the site was colonized by the common reed. Stands of the species increased from 1 to 33 ha between 1980 and 2002 (Hudon et al. 2005). Presently, the Boucherville Islands archipelago is the most extensive wetland

area colonized by the common reed in the St. Lawrence River (Hudon et al. 2005); the most recent estimate (2010) reports about 86 ha of common reed stands (Tougas-Tellier 2013).

Spring floods play a major role in the ecology of both study sites, as flooded areas are important spawning grounds for Northern Pike and many other fish species (Massé et al. 1988). In 2009, from the beginning of April to the end of June, the period during which most of the sampling was conducted, water levels measured at Lake Saint-Louis (Pointe-Claire) and Boucherville Islands (Montréal Harbour) were higher than historical means. In contrast, the spring flood amplitude in 2010 was very small. The water level of Lake Saint-Louis was not high enough to flood the Lafleur Creek plain. At Boucherville Islands, water levels reached their maximum in March and then dropped below reference levels by the beginning of May.

Fish Sampling

The basic assumptions of our sampling design were that Northern Pike spawning generally lasts 2 or 3 weeks between the beginning of April and the beginning of May in southern Quebec (depending on the temperature and flood period) and that eggs and yolk sac larvae remained attached to the vegetation structure on which they were deposited for the duration of the sampling period (Fortin et al. 1982; Massé et al. 1988). Yolk sac larvae were considered equivalent to eggs because they are usually still attached to vegetation or have a very limited mobility since their fins are not yet fully developed at this life stage (Raat 1988; Yeager 1990). In all plant assemblages studied, the current velocity was very weak during the study period. The mean radial distance over which age-0 Northern Pike move during their first weeks of life is only about 14 m (Cucherousset et al. 2009), and sampling plots in a particular plant assemblage were separated by a distance well beyond this value from the other vegetation types located nearby.

Northern Pike egg deposition.—A split-plot sampling design was used for the entire sampling period. At both study sites, three sectors, each composed of two plots (about 2,000 m² each; one colonized by the common reed and the other by a reference plant assemblage), were delineated along the shoreline or in the floodplain (Figure 1B, C). The locations of sectors and plots were determined by the availability of spawning areas, which depended on the extent of the current spring flood (which was greater in 2009 than in 2010), and by Northern Pike spawning habitat preferences with regard to water depth and temperature. Spawning occurs after the onset of spring floods in warming waters above 5–6°C, and maximal egg deposition is observed in shallow water (generally less than 70 cm) in the 8–12°C water temperature range (Fortin et al. 1982; Casselman and Lewis 1996; Farrell 2001). Both plots in each sector were located at similar depths in shallow water (0.5–1.5 m) to prevent the loss of sampling sites in case of rapid water level drop and to avoid the possible confounding effects of water temperature.

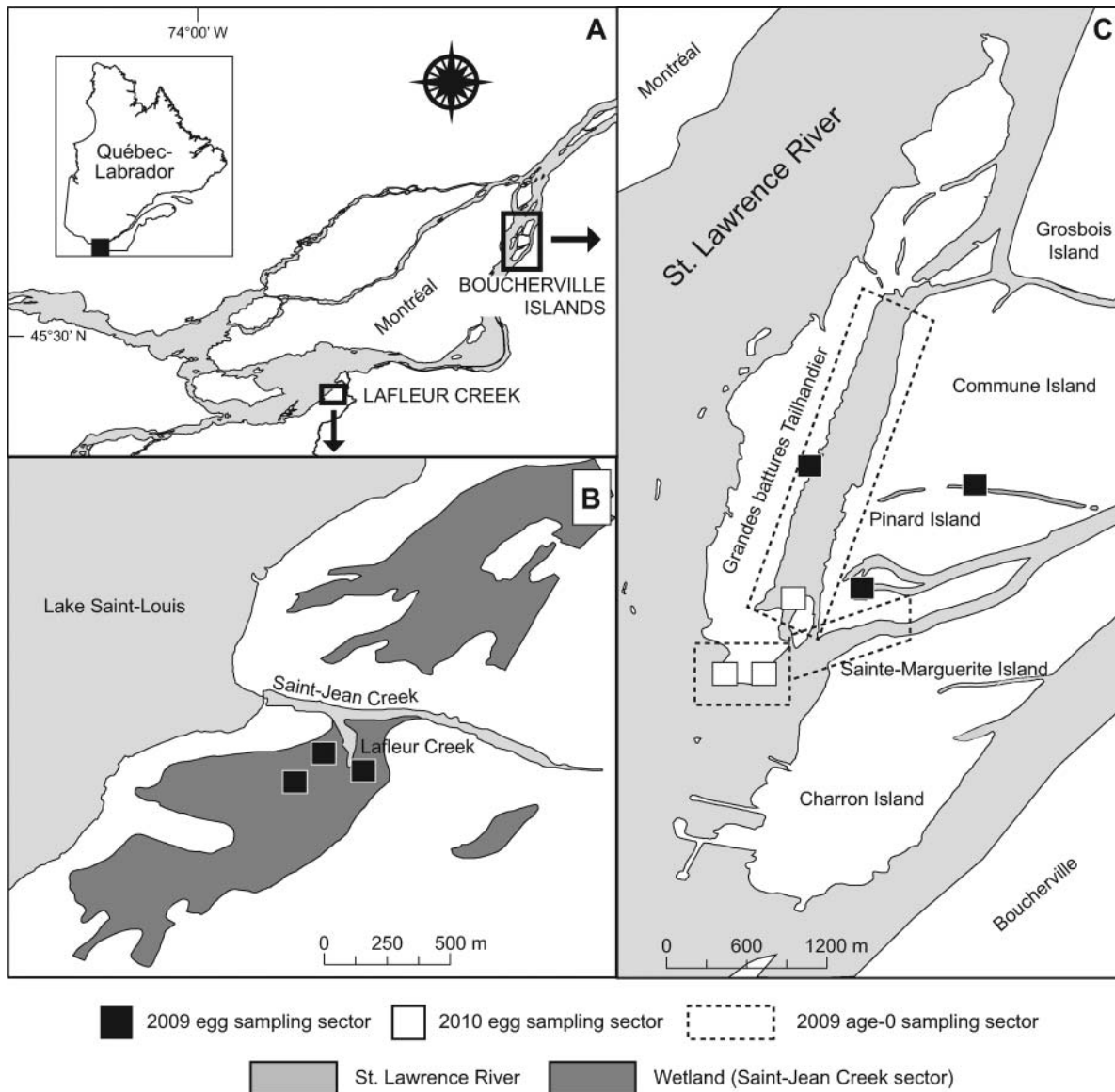


FIGURE 1. Location of (A) study sites and sampling sectors of eggs, yolk sac larvae, and age-0 Northern Pike in Quebec at (B) Lafleur Creek in 2009 and (C) Boucherville Islands in 2009 and 2010.

In all the invaded plots, common reed was the only plant species encountered. At Lafleur Creek, the mean common reed density in the invaded plots was 79–106 stems/m² and the plant assemblages of the reference plots were dominated by flowering rush, cattails, river bulrush, and broadfruit bur-reed *Sparganium eurycarpum*. At Boucherville Islands, the mean common reed density was 84–111 stems/m² and the reference plant assemblages were in 2009 dominated by reed canary-grass, often associated with river bulrush. In 2010, the egg deposition study was conducted only at Boucherville Islands because the water level was not high enough to flood the Lafleur Creek plain. Marshes sampled in 2010 were colonized mostly by common reed (72–81 stems/m²) or by cattails and river bulrush. Apart from a few other common reed stands,

these plant assemblages were the only vegetation stands flooded during the spring of 2010.

In 2009, Northern Pike eggs and yolk sac larvae were sampled twice a week for 4 weeks at 20 stations in each plot (spaced 10 m apart and not overlapping) using a rectangular kick net (0.36 m wide × 0.28 m long × 0.3 m deep) swiped along the marsh bed over a distance of 1 m (0.36 m²) between April 15 and May 8. The egg deposition sampling started when gill-net fishing confirmed the presence of running, ripe Northern Pike close to the plot. Since egg incubation lasts 10–20 d (Fortin et al. 1982; Massé et al. 1988), this ensured the capture of most of the shed eggs. A total of 720 kick-net swipes was made at Lafleur Creek (360 in each vegetation type) and 514 were made at Boucherville Islands (258 in

common reed stands and 256 in reference plant assemblages). In 2010, 720 swipes (360 in each vegetation type) were made during April 6–23 at Boucherville Islands only, because the water level was not high enough to flood the Lafleur Creek plain. The orientation of the swipes varied systematically between sample dates to ensure that no area around the station was sampled twice. Northern Pike eggs and yolk sac larvae were preserved in 10% formaldehyde. Egg and larva identification was subsequently confirmed in the laboratory based on criteria defined by Fuiman (1982) and Yeager (1990). Finally, water depth and temperature were noted at each sampling station. Hourly water temperatures were also continuously recorded during the sampling period using temperature data loggers (Minilog-T, Vemco; accuracy $\pm 0.1^\circ\text{C}$) set in the middle of each plot.

Age-0 Northern Pike abundance.—The relative abundance of age-0 Northern Pike in each vegetation type was evaluated in 2009 only. In 2010, the water level was not high enough to flood the Lafleur Creek plain and at Boucherville Islands most of the floodplains were quickly drained by the rapid water level drop. In 2009, the sampling protocol was adjusted to take into account the decreasing water levels occurring at both study sites. At Lafleur Creek, water levels decreased gradually throughout the sectors used for sampling and fishing gear was moved very little over the entire period. Age-0 Northern Pike were sampled at 36 stations (18 in each vegetation type) using small unbaited hoop nets (2 m long \times 0.46 m high, with a stretched mesh size of 2.5 mm) set four times per week for a 24-h period between May 12 and June 19. The total sampling effort was 120 net-days (60 in each vegetation type) over a 6-week period.

At Boucherville Islands, the high spring flood amplitude necessitated adjustments to the sampling protocol. New sectors (common reed density in the invaded plots = 87–113 stems/m²) had to be delineated for age-0 fish sampling (Figure 1C). Fishing gear was sometimes moved within sectors to keep adequate water levels (0.25–0.65 m) for setting hoop nets. A total of 58 stations (29 in each vegetation type) was sampled between May 12 and July 3, 2009. Nets were lifted four times weekly. The total fishing effort was 176 net-days (88 in each vegetation type) over a period of 8 weeks. The wet meadows and marshes that were selected as reference sites were dominated by reed canarygrass, often associated with river bulrush and cattails. Age-0 Northern Pike were preserved in 10% formaldehyde. Water depth and water temperature were noted at each hoop-net sampling station, and water temperatures were also continuously recorded during the sampling period using temperature data loggers.

Age-0 Northern Pike growth and feeding.—In the laboratory, total length (TL) and wet weight (measured to the nearest 0.01 g) were determined for all age-0 Northern Pike collected in 2009. The digestive tracts (oesophagus, stomach, and intestine) of fish captured were examined. Prey types found in the digestive tracts were identified and grouped into

the following three categories: (1) crustacean, (2) insect, and (3) fish. These groups were chosen as they generally correspond to the sequence of food preferences of age-0 Northern Pike as they grow (Hunt and Carbine 1951; Frost 1954; Mongeau 1955; Dumont and Fortin 1977; Fago 1977). Diet was quantified using the frequency of occurrence (the proportion of nonempty digestive tracts containing a given prey category). All age-0 Northern Pike and their digestive tracts (empty or not) were also oven dried at 60°C for 24 h and weighed (Lantry and O’Gorman 2007). We used the ratio of digestive tract dry weight to total dry weight of the fish as an indirect indicator of feeding activity in each vegetation type.

Data Analysis

Age-0 Northern Pike growth.—For all plots, total length (mm) growth rate of age-0 Northern Pike was determined by calculating the slope of the linear relationship between total length and capture date. Weight (g) growth rate was calculated as an instantaneous rate (Ricker 1975), corresponding to the slope of the relationship between the natural logarithm of wet weight values and the date of capture. Weight–length relationships were calculated using log₁₀ values. The Fulton’s condition factor (*K*; Ricker 1975) was also computed. Relationships between condition factor and length were analyzed using linear regressions. Finally, the relationship between digestive tract dry weight and total dry fish weight was characterized by linear regressions after log₁₀ data transformation.

Statistical analyses.—Northern Pike eggs and yolk sac larvae (TL = 7–22 mm) data were pooled to compare data from common reed stands to reference plant assemblages. Within a plot, for a given date, egg and larva counts from each kick-net sampling station were not independent. Accordingly, mean values of the number of eggs and yolk sac larvae (log₁₀ transformation) as well as the mean proportion of stations with at least one egg or yolk sac larva (PSP) collected per plot (arcsine transformation), for the 20 sampling stations and for a given sampling date, were chosen as sampling units for statistical analysis and compared using a repeated-measures split-plot analysis of variance (ANOVA). Site (Lafleur Creek and Boucherville Islands), vegetation type (common reed stands and reference plant assemblages), and the interaction between site and vegetation type were considered fixed-effects variables, whereas sectors (three per site) were treated as random-effects variables.

Comparisons of mean catch per unit of effort (CPUE) of age-0 Northern Pike between vegetation types were performed using repeated-measures nonparametric analyses, as described by Brunner et al. (2002). The same procedure was also used to compare the length and weight of age-0 Northern Pike and the mean water temperatures between vegetation types. This procedure was used since the assumptions of normality and homogeneity of variance were not met.

TABLE 1. Sampling effort and the number and relative abundance (CPUE) of Northern Pike eggs and yolk sac larvae and the proportion of sampling stations with the presence of eggs or larvae (PSP) in common reed stands and reference plant assemblages at Lafleur Creek in 2009 and Boucherville Islands in 2009 and 2010.

Site	Year	Vegetation	Sampling days (<i>n</i>)	Kick-net stations (<i>n</i>)	Eggs and larvae (<i>n</i>)	CPUE		Stations with presence (<i>n</i>)	PSP (%)	
						Mean	SD		Mean	SD
Lafleur Creek	2009	Common reed	18	360	23	0.06	0.08	18	5	7
		Reference assemblage	18	360	85	0.24	0.23	56	16	13
Boucherville Islands	2009	Common reed	13	258	61	0.24	0.25	28	11	8
		Reference assemblage	13	256	186	0.72	0.93	69	27	23
	2010	Common reed	18	360	523	1.45	1.03	157	44	16
		Reference assemblage	18	360	222	0.62	0.54	97	27	16

The slopes and intercepts of regressions comparing length and weight over time were compared using a random coefficient model procedure. For a given parameter, this type of model takes into account the result found within each sector in the overall comparison between vegetation types (Jacqmin-Gadda et al. 2007). The same procedure was performed for the relationships between weight and length of age-0 Northern Pike, as well as between digestive tract dry weight and total dry weight. These descriptors were analyzed separately by site since the sampling periods differed.

The occurrence of prey items in stomach contents was compared between vegetation types using a log-linear analysis. This test allows for comparisons, using baseline values, when there are more than two categorical variables and when the contingency table is complex (Field 2005). In our case, site contingency tables included three categorical variables: (1) vegetation type, (2) prey type, and (3) the presence or absence of a prey type. Multiple comparisons (using Fisher's protected

least-significant-difference test) were performed to determine which of the three prey types were more prevalent.

Finally, to ensure that variations in water depth between sampling stations did not create site biases, mean water depths registered at each station (kick net and hoop net) during reproduction and growth periods were compared between vegetation types using ANOVAs, for which vegetation type was considered a fixed-effect and the sector, interactions between sectors, vegetation types, and sampling dates were considered random-effects. All analyses were performed using mixed procedure (PROC MIXED) in SAS software (SAS Institute 2008).

RESULTS

Northern Pike Egg Deposition

In 2009, at all sites (Lafleur Creek and Boucherville Islands) combined, both mean CPUE and mean proportion of

TABLE 2. Results of the ANOVAs comparing the relative abundance (CPUE) of Northern Pike eggs and yolk sac larvae and the proportion of sampling stations with the presence of eggs or larvae (PSP) in common reed stands and reference plant assemblages at Lafleur Creek in 2009 and Boucherville Islands in 2009 and 2010.

Site	Year	Variable	Effect	<i>F</i>	df	<i>P</i>
All sites	2009	CPUE	Site	3.98		0.0707
			Vegetation type	6.12	1, 11	0.0304
			Site × vegetation	0.02		0.8966
	2009	PSP	Site	2.54		0.1395
			Vegetation type	7.43	1, 11	0.0199
			Site × vegetation	0.01		0.9050
Boucherville Islands	2010	CPUE	Vegetation type	8.91	1, 7	0.0224
	2010	PSP	Vegetation type	5.95	1, 3	0.0839

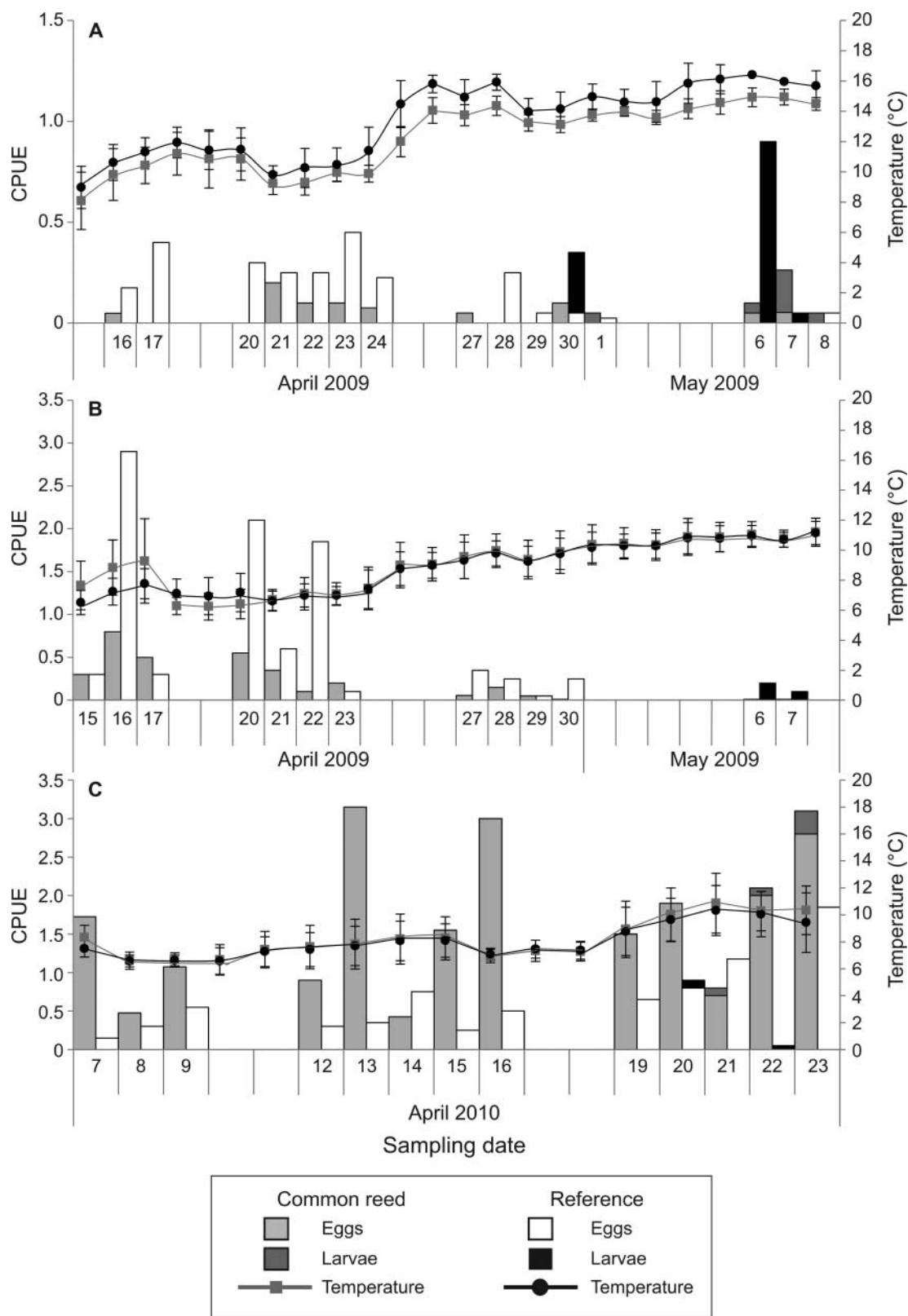


FIGURE 2. Temporal trends of the relative abundance (CPUE) of Northern Pike eggs and yolk sac larvae and mean \pm SD daily water temperature in common reed stands and reference plant assemblages at (A) Lafleur Creek in 2009 and Boucherville Islands in (B) 2009 and (C) 2010. Only sampling dates are shown.

stations with the presence of eggs or larvae (PSP) were significantly lower in common reed stands (CPUE = 0.14 ± 0.07 [mean \pm SD], PSP = $7 \pm 8\%$) than in reference plant assemblages (CPUE = 0.44 ± 0.18 , PSP = $20 \pm 18\%$), and no site effect was detected (Tables 1, 2).

At Lafleur Creek in 2009, common reed stands were used less for spawning than were reference plant assemblages (Table 1; Figure 2A); CPUE and PSP were four and three times lower in common reed stands than in reference assemblages, respectively. Mean water temperatures were not significantly different ($F_{1, 1} = 137.24$, $P = 0.0542$) between common reed stands (mean \pm SD, $12.5 \pm 2.2^\circ\text{C}$) and reference assemblages ($13.6 \pm 2.5^\circ\text{C}$; Figure 2A). Moreover, mean water depths in common reed stands (56 ± 12 cm) and reference assemblages (61 ± 12 cm) were not significantly different ($F_{1, 34} = 1.67$, $P = 0.2055$).

At Boucherville Islands in 2009, common reed was also used less for spawning than were reference assemblages (Table 1; Figure 2B); CPUE and PSP were three and two times lower in common reed stands than in reference assemblages, respectively. Mean water temperatures were not significantly different ($F_{1, 2} = 5.85$, $P = 0.1367$) between common reed (mean \pm SD, $9.1 \pm 2.0^\circ\text{C}$) and reference assemblages ($8.7 \pm 1.8^\circ\text{C}$; Figure 2B). Mean water depths of common reed stands (67 ± 27 cm) and reference assemblages (78 ± 27 cm) measured at each kick-net sampling station were also not significantly different ($F_{1, 22} = 3.70$, $P = 0.0674$).

Northern Pike egg deposition in 2010 was different than in 2009. The CPUE was two times higher in common reed stands than in reference assemblages, and the observed difference was significant (Tables 1, 2; Figure 2C). However, no significant difference was found for the PSP (Tables 1, 2). Mean water temperatures recorded in 2010 in common reed stands (mean \pm SD, $8.2 \pm 2.0^\circ\text{C}$) and reference assemblages ($8.0 \pm 1.8^\circ\text{C}$) were not significantly different ($F_{1, 2} = 0.15$, $P = 0.7390$) during the spawning period (Figure 2C). As in 2009, mean water depths measured in common reed stands (37 ± 13 cm) and reference assemblages (40 ± 14 cm) were not significantly different ($F_{1, 32} = 0.88$, $P = 0.3559$).

Abundance and Growth of Age-0 Northern Pike

At Lafleur Creek in 2009, CPUE of age-0 Northern Pike was not significantly different between vegetation types ($F_{1, 2} = 1.12$, $P = 0.4009$; Table 3; Figure 3A). No significant difference was detected regarding mean TL ($F_{1, 2} = 0.28$, $P = 0.6516$) and mean weight ($F_{1, 2} = 0.03$, $P = 0.8750$) of age-0 Northern Pike caught in common reed stands and reference assemblages (Table 4). However, the weight-length relationship of age-0 Northern Pike (Table 5) was significantly different between vegetation types in regards to both slopes ($F_{1, 4} = 45.73$, $P = 0.0025$) and intercepts ($F_{1, 2} = 48.40$, $P = 0.0020$). The differences between vegetation types are highlighted by the relationship between the Fulton's condition factor and the TL of the age-0 Northern Pike (Figure 4A): the condition factor did not vary with length in common reed stands ($n = 202$, $r^2 = 0.00$, $P = 0.6574$), while it increased in reference assemblages ($n = 258$, $r^2 = 0.25$, $P < 0.0001$).

Daily length growth rates showed no significant difference between common reed stands and reference assemblages ($F_{1, 131} = 0.30$, $P = 0.5824$). However, instantaneous weight growth rates were significantly different ($F_{1, 420} = 3.87$, $P = 0.0498$) between vegetation types. Growth rates were 1.53 mm/d ($n = 214$, $r^2 = 0.75$, $P < 0.0001$) and 0.09 g/d ($n = 202$, $r^2 = 0.77$, $P < 0.0001$) in common reed stands and 1.36 mm/d ($n = 269$, $r^2 = 0.48$, $P < 0.0001$) and 0.08 g/d ($n = 258$, $r^2 = 0.48$, $P < 0.0001$) in reference assemblages.

Mean daily water temperatures recorded during the sampling period of age-0 fish were not significantly different ($F_{1, 1} = 3.33$, $P = 0.3191$) between common reed stands (mean \pm SD, $15.7 \pm 2.2^\circ\text{C}$) and reference assemblages ($17.1 \pm 2.7^\circ\text{C}$; Figure 3A). A significant difference ($F_{1, 117} = 4.90$, $P = 0.0288$) was found in mean depths of hoop-net fishing stations between common reed (40 ± 11 cm) and reference assemblages (45 ± 12 cm).

At Boucherville Islands in 2009, CPUE of age-0 Northern Pike was not significantly different between vegetation types ($F_{1, 2} = 0.01$, $P = 0.9152$; Table 3; Figure 3B). No significant difference was observed with respect to mean length ($F_{1, 2} = 2.47$, $P = 0.2566$) or mean weight ($F_{1, 2} = 4.77$, $P = 0.1607$) of fish between vegetation types (Table 4). Similarly, no

TABLE 3. Sampling effort, total catches, and mean relative abundance (CPUE) of age-0 Northern Pike collected in hoop nets in common reed stands and reference plant assemblages at Lafleur Creek and Boucherville Islands in 2009.

Site	Vegetation	Total catch (<i>n</i>)	Sampling effort (net-day)	CPUE		
				Mean	SD	Range
Lafleur Creek	Common reed	218	59	3.7	4.5	0–19
	Reference assemblage	272	60	4.5	7.4	0–38
Boucherville Islands	Common reed	115	88	1.3	3.3	0–27
	Reference assemblage	122	88	1.4	3.1	0–18

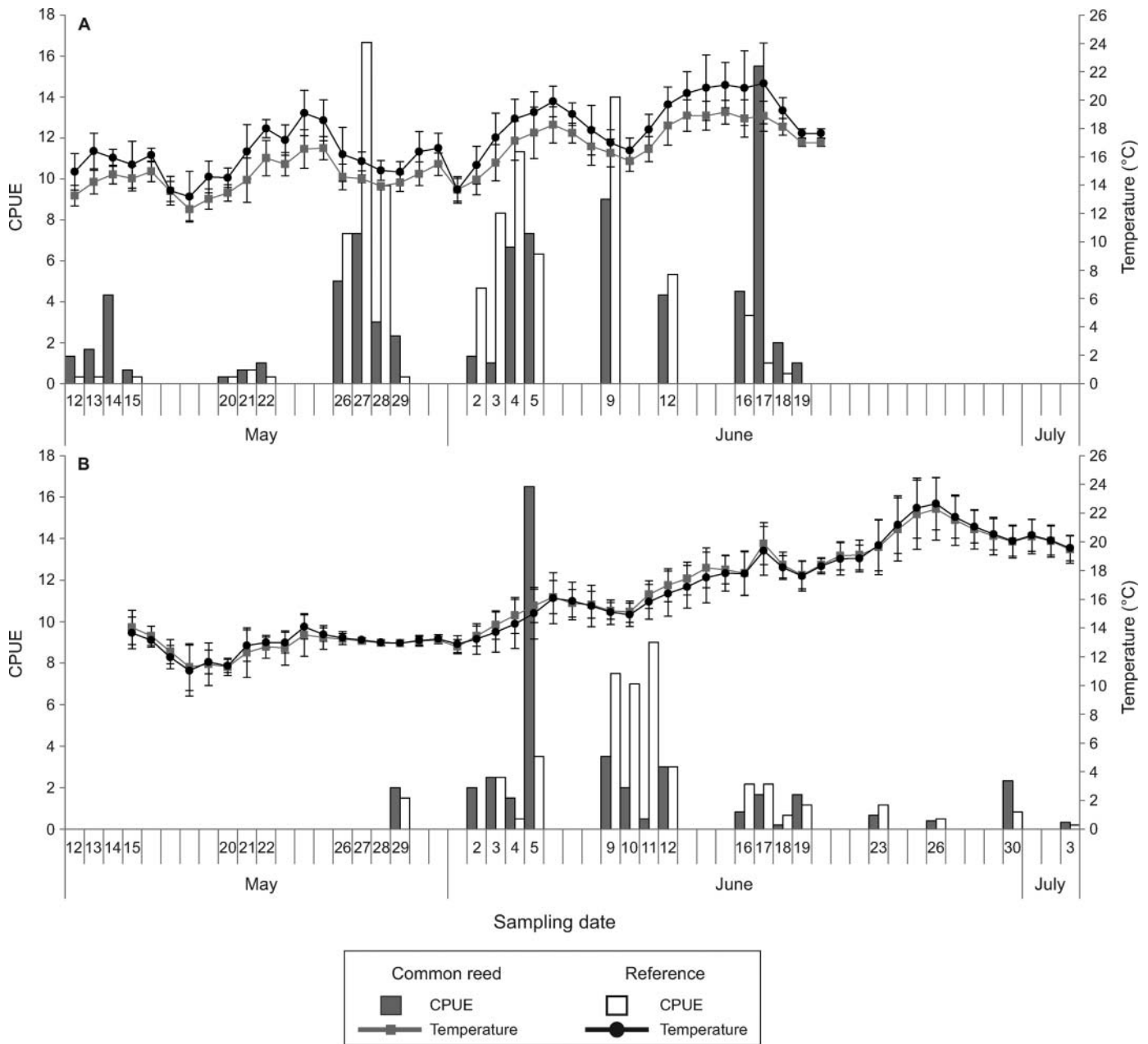


FIGURE 3. Temporal trends of the relative abundance (CPUE) of age-0 Northern Pike and mean \pm SD daily water temperature in common reed stands and reference plant assemblages at (A) Lafleur Creek and (B) Boucherville Islands in 2009. Only sampling dates are shown.

significant difference was found in the weight-length relationship (Table 5) between vegetation types for both slopes ($F_{1, 2} = 0.59$, $P = 0.5220$) and intercepts ($F_{1, 1} = 0.48$, $P = 0.6137$).

The condition factor remained essentially stable when age-0 Northern Pike grew in length in both common reed stands ($n = 111$, $r^2 = 0.02$, $P = 0.1649$) and reference assemblages ($n = 120$, $r^2 = 0.03$, $P = 0.0733$) (Figure 4B). Daily growth rates for length ($F_{1, 232} = 1.82$, $P = 0.1782$) and weight ($F_{1, 3} = 0.93$, $P = 0.4024$) were not significantly different between vegetation types. These rates were 1.24 mm/d ($n = 115$, $r^2 =$

0.75, $P < 0.0001$) and 0.09 g/d ($n = 111$, $r^2 = 0.75$, $P < 0.0001$) in common reed stands and 1.15 mm/d ($n = 121$, $r^2 = 0.57$, $P < 0.0001$) and 0.09 g/d ($n = 120$, $r^2 = 0.58$, $P < 0.0001$) in reference assemblages. Mean water temperatures in common reed stands (mean \pm SD, $16.2 \pm 3.4^\circ\text{C}$) did not differ significantly ($F_{1, 3} = 0.19$, $P = 0.6932$) from those in reference assemblages ($16.1 \pm 3.5^\circ\text{C}$; Figure 3B). Slight differences ($F_{1, 108} = 6.38$, $P = 0.0130$) in mean water depths were found between common reed stands (48 ± 15 cm) and reference assemblages (54 ± 17 cm).

TABLE 4. Mean length and weight of age-0 Northern Pike captured in common reed stands and reference plant assemblages at Lafleur Creek and Boucherville Islands in 2009.

Site	Vegetation	Total length (mm)				Weight (g)			
		<i>n</i>	Mean	SD	Range	<i>n</i>	Mean	SD	Range
Lafleur Creek	Common reed	214	58	19	17–110	202	1.64	1.27	0.07–6.65
	Reference assemblage	269	59	13	21–96	258	1.50	1.08	0.07–6.66
Boucherville Islands	Common reed	115	39	14	19–76	111	0.55	0.59	0.06–2.70
	Reference assemblage	121	39	11	20–71	120	0.48	0.44	0.06–2.66

Feeding of Age-0 Northern Pike

The digestive tract contents of 458 age-0 Northern Pike collected at Lafleur Creek in 2009 were examined for food items. Of these, 175 had an empty stomach (64 in common reed stands, 111 in reference assemblages). The occurrence of prey items was significantly different between vegetation types ($\chi^2 = 16.21$, $P = 0.0003$). Although crustaceans (amphipods, cladocerans, copepods, and isopods) were the main prey items consumed by age-0 fish in all vegetation types, their occurrence was significantly higher ($\chi^2 = 4.82$, $P = 0.0282$) in fish caught in common reed stands (80%) than in reference assemblages (59%). However, the occurrence of insects (Chironomidae, Ephemeroptera, and Odonata) did not differ significantly ($\chi^2 = 2.61$, $P = 0.1061$) between vegetation types (common reed = 13%, reference assemblages = 7%). The occurrence of fish in reference assemblages (17%) was not significantly different ($\chi^2 = 3.31$, $P = 0.0687$) from their occurrence in common reed stands (9%).

Relationships between \log_{10} values of digestive tract dry weight and total body dry weight of age-0 Northern Pike (Table 5) were significantly different between common reed stands and reference assemblages, both for slopes ($F_{1, 278} = 11.05$, $P = 0.0010$) and intercepts ($F_{1, 14} = 11.41$, $P = 0.0047$). Differences observed between vegetation types slightly increased with fish weight. For example, digestive tract weight with contents averaged 12.4% of a 0.2-g fish

captured in common reed stands and 13.6% for a same size fish caught in reference assemblages. For a heavier fish (0.8 g), values were 9.9% and 12.3%, respectively.

At Boucherville Islands in 2009, the digestive tract contents of 231 age-0 Northern Pike were examined for food items. Of these, 41 had empty stomachs (30 in common reed stands, 11 in reference assemblages). The occurrence of prey items was not significantly different between vegetation types ($\chi^2 = 0.84$, $P = 0.6554$). The occurrence of crustaceans consumed by age-0 Northern Pike was 70% in common reed stands and 79% in reference assemblages. The occurrence of insects was 57% in common reed stands and 66% in reference assemblages. The occurrence of fish as food items was 10% in common reed stands and 9% in reference assemblages. Finally, no significant difference was found between common reed stands and reference assemblages for the relationship between digestive tract weight and total body dry weight of age-0 Northern Pike (Table 5), in regards to both slopes ($F_{1, 186} = 3.51$, $P = 0.0625$) and intercepts ($F_{1, 186} = 2.19$, $P = 0.1402$).

DISCUSSION

Northern Pike Egg Deposition

Data collected in this study do not support the general hypothesis tested, i.e., that the early invasion of freshwater

TABLE 5. Regression equations describing the relationships between wet body weight (*W*) and total length (TL) and between digestive tract dry weight (*Wt*) and total body dry weight (*Wb*) of age-0 Northern Pike sampled at Lafleur Creek and Boucherville Islands in 2009.

Site	Vegetation	Regression equation	<i>n</i>	<i>P</i>	<i>r</i> ²
<i>W</i> – <i>TL</i>					
Lafleur Creek	Common reed	$\log_{10}W = 2.9942 \log_{10}TL - 5.1848$	202	< 0.0001	0.99
	Reference assemblage	$\log_{10}W = 3.2267 \log_{10}TL - 5.6071$	258	< 0.0001	0.98
Boucherville Islands	Common reed	$\log_{10}W = 2.9613 \log_{10}TL - 5.1174$	111	< 0.0001	0.99
	Reference assemblage	$\log_{10}W = 2.9186 \log_{10}TL - 5.0570$	120	< 0.0001	0.98
<i>Wt</i> – <i>Wb</i>					
Lafleur Creek	Common reed	$\log_{10}Wt = 0.8399 \log_{10}Wb - 1.0186$	138	< 0.0001	0.97
	Reference assemblage	$\log_{10}Wt = 0.9244 \log_{10}Wb - 0.9189$	145	< 0.0001	0.93
Boucherville Islands	Common reed	$\log_{10}Wt = 0.8052 \log_{10}Wb - 0.9953$	81	< 0.0001	0.93
	Reference assemblage	$\log_{10}Wt = 0.8719 \log_{10}Wb - 0.9212$	109	< 0.0001	0.91

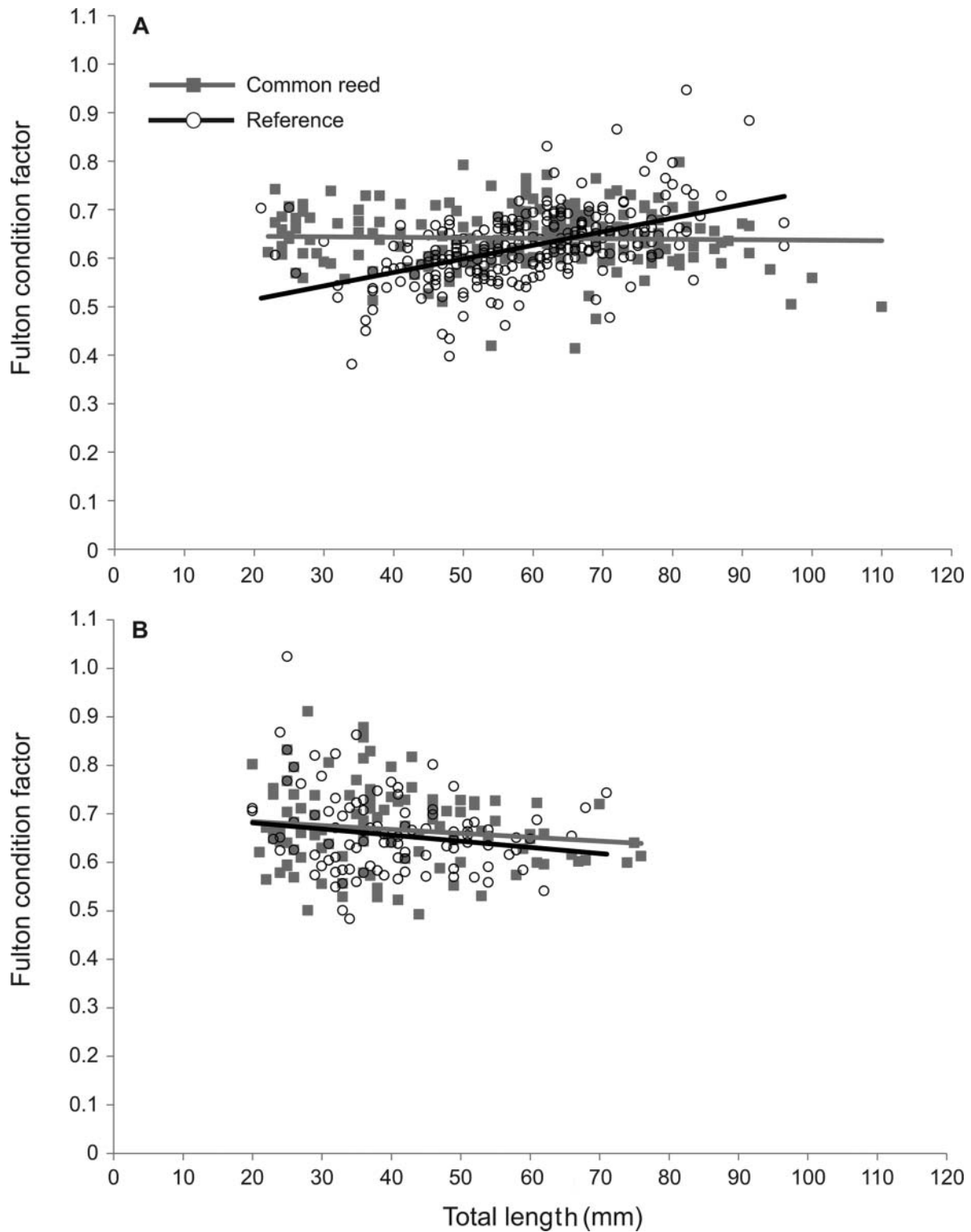


FIGURE 4. Relationship of Fulton condition factor to total length for age-0 Northern Pike captured in common reed stands and reference plant assemblages at (A) Lafleur Creek and (B) Boucherville Islands in 2009.

marshes by common reed has an overall negative effect on Northern Pike reproduction and early life history stages. In the St. Lawrence River floodplain, the presence of common reed, even in dense and homogeneous stands, does not prevent Northern Pike from spawning. The use of a particular vegetation type may depend on water level variations that control the access to the different plant assemblages during the spawning period.

Several studies have shown that Northern Pike use a variety of plant assemblages for spawning. At least 25 plant species are known to be used as spawning substrate by this fish (Fortin et al. 1982; Raat 1988; Bry 1996). However, many studies also indicate that plants with narrow leaves (e.g., grasses and sedges), which form short, dense vegetation mats, are the most suitable substrates, while tougher, robust plants (e.g., cattails) are generally seldom or not used (Fabricius and Gustafson 1958; Franklin and Smith 1963; Forney 1968; Bry 1996; Caselman and Lewis 1996; Farrell 2001; Cooper et al. 2008). Studies conducted in Quebec have shown that the egg density of Northern Pike is particularly high in wet meadows dominated by reed canarygrass. It is only when access to wet meadows is restricted by low water levels that other emergent aquatic vegetation types (common reed, bulrushes, cattails) are more frequently used (Fortin et al. 1982; Massé et al. 1988).

During the two study years, we observed two different situations with regards to Northern Pike spawning habitat use in freshwater marshes invaded by common reed. The year with high water levels (2009) resulted in a higher use of reed canarygrass wet meadows or flowering rush marshes for egg deposition while the year with low water levels (2010), which severely restricted fish access to wet meadow vegetation, resulted in a higher use of common reeds stands as spawning substrate. This suggests that common reed stands are non-preferred habitats but are nevertheless used as spawning substrates for Northern Pike when other grasses and sedges are not available.

In 2010, common reed and cattail stands with river bulrush were essentially the only vegetation types available during the Northern Pike spawning period. A possible hypothesis to explain the higher use of common reed stands by spawning Northern Pike is that the shorter leaves of this plant tend to break off and accumulate on the marsh floor, thus building up a relatively suitable spawning substrate, at least compared with the long, tougher leaves of cattails. Common reed stands probably offer a lower quality spawning ground than Northern Pike preferred vegetation but are better in this respect than plant assemblages dominated by cattails and river bulrush.

In the oligohaline waters of the estuaries and bays in the northern Baltic Sea in Finland, sheltered, soft-bottomed littoral shores covered by common reed stands are known to be important spawning and nursery habitat for Northern Pike. However, during the spring period they essentially form the only available vegetated littoral habitat of the Baltic coast, since the

breaking ice removes other perennial littoral vegetation (Kallavuo et al. 2011).

Besides vegetation type, it is generally accepted that spawning site selection by Northern Pike is also conditioned by water depth and temperature (Clark 1950; Fabricius and Gustafson 1958; Kennedy 1969; Fortin et al. 1982; Massé et al. 1991; Farrell et al. 2006; Mingelbier et al. 2008). Northern Pike have a strong preference for spawning sites in shallow water, which warms up quickly (Fortin et al. 1982; Raat 1988). To avoid the confounding effects of temperature, sampling sectors with similar water depths were chosen for all vegetation types. Nevertheless, one would expect that, for a similar time period and water depth, water temperatures in common reed stands would be somewhat cooler than in the other reference plant assemblages since less incident light reaches the water surface (Hudon 2004). However, our results do not support this assumption. Water depth and temperature were therefore not considered as contributing factors to the observed differences in egg abundance between vegetation types.

Abundance, Growth, and Feeding of Age-0 Northern Pike

The invasion of wetlands by common reed does not seem to have a major effect on the relative abundance, growth, or feeding of age-0 Northern Pike. At both sites, most of the variables monitored or used to characterize early development of age-0 Northern Pike did not differ significantly between vegetation types. At Lafleur Creek in 2009, length and weight growth rates were somewhat higher in common reed stands, although differences were slight or nonsignificant. However for fish caught in common reed stands at Lafleur Creek, the condition factor remained stable as they grew in length, whereas it increased for fish caught in the reference plant assemblages.

For the relationship between the digestive tract dry weight and the dry body weight, differences between vegetation types were observed at Lafleur Creek, suggesting that the digestive tract contents were getting comparatively heavier as the age-0 Northern Pike grew in the reference plant assemblage. Dietary changes that occur as age-0 Northern Pike get older may explain some of the differences. Active feeding starts when they reach 12–15 mm in length (Franklin and Smith 1963; Dumont and Fortin 1977; Raat 1988; Bry 1996). At first, they depend on small crustacean prey, which are gradually abandoned in favor of amphipods, isopods, aquatic insect larvae (chironomids), and fish when they reach about 25–30 mm in length. They become essentially piscivorous when they exceed 80 mm in length (Hunt and Carbine 1951; Frost 1954; Dumont and Fortin 1977). During the period when the fish diet was composed mainly of invertebrates, age-0 Northern Pike seem to have found enough food in common reed stands to maintain length and weight growth rates comparable to those of reference plant assemblages. However, as the fish grew their better

condition in the reference plant assemblages suggests higher food availability or quality in that habitat.

CONCLUSION

The results of this study on Northern Pike egg deposition, as well as those of other projects conducted in the same area (Fortin et al. 1982; Massé et al. 1988, 1991), indicate that Northern Pike first use wet prairie marshes with plant assemblages that offer good spawning substrates, such as reed canarygrass, when they are available. However, common reed stands are also used as spawning substrate by Northern Pike, especially when low water levels restrict fish habitat use to the lower part of the marshes.

Common reed stands are not barren zones devoid of fish; they are used by Northern Pike, as well as by various North American freshwater fish species also found in brackish intertidal marshes, such as Banded Killifish *Fundulus diaphanus*, Brown Bullhead *Ameiurus nebulosus*, Pumpkinseed *Lepomis gibbosus*, and Spottail Shiner *Notropis hudsonius* (Meyer et al. 2001; Warren et al. 2001; Fell et al. 2003; Kimball et al. 2010). In Lake Erie, similar abundances of sunfish *Lepomis* spp. have been observed in common reed stands and in marshes dominated by cattails (Aday 2007; Kulesza et al. 2008). As part of fieldwork for this study, 21 different fish species were identified in common reed stands. Eggs and age-0 individuals of Burbot *Lota lota* and Central Mudminnow *Umbra limi*, as well as nests of Bowfin *Amia calva* and Largemouth Bass *Micropterus salmoides*, were observed (M. Larochelle, unpublished data). These observations show that common reed stands are used by various fish species for reproduction and juvenile development. This is also the case for amphibian and bird species; there has been little or no observed impact from the common reed invasion on bird and amphibian abundance and reproduction in southern Quebec wetlands (Mazerolle et al. 2014; Gagnon Lupien et al., in press). These studies on the effects of common reed on fish and wildlife were conducted during the early invasion process in St. Lawrence River freshwater marshes. However, little is known about the magnitude of common reed biomass accumulation, making it impossible to predict whether these stands, which are part of an ongoing invasion, will provide long-term quality habitat.

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