

What do the empty stomachs of northern pike (*Esox lucius*) reveal? Insights from carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) stable isotopes

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Received: 22 October 2007 / Accepted: 5 May 2008 / Published online: 30 May 2008

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Abstract The frequency of individuals with empty stomachs (FES) can vary greatly among northern pike populations. However, the FES has only seldom been analyzed in this species and its meaning is still not fully understood. It has been suggested that a high FES may reflect a strongly piscivorous behaviour while low FES could reflect a higher utilization of invertebrates. We compared the stomach contents and the trophic position of northern pike in 16 populations of individuals feeding mainly on fish or benthic invertebrates. We tested the hypothesis that northern pike with empty stomachs or with fish in their stomachs have a higher trophic position than individuals feeding on invertebrates. Carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) stable isotope signatures were used to estimate the trophic position of individuals. We found no significant difference in the trophic position among piscivores, invertebrate feeders, and northern pike with empty stomachs. The average trophic position of northern pike was high (mean \pm SD = 4.3 ± 0.4 , $n=66$) and was correlated with total length. These results indicate that, although invertebrates could be an important part of the diet of northern pike in Canadian Shield lakes, fish are still the dominant prey. Hence, feeding on invertebrates in our study lakes would reflect an opportunistic rather than a specialized feeding strategy.

Keywords Invertebrates · Piscivory · Diet · Trophic position · Stomach contents

Introduction

Stomach content analysis has proven to be a useful tool to understand fish feeding ecology. This approach has allowed researchers to highlight the importance of inter-specific competition as a potential determinant of morphological variation (Bourke et al. 1999) as well as emphasize the role of trophic bottlenecks as a key factor in lake fish communities (Persson and Greenberg 1990). However, one of its limitations is the difficulty of interpreting data from individuals with empty stomachs. It has been suggested that such individuals should be considered as part of the feeding population and not as sampling errors or as uninformative data. For example, Huey et al. (2001) found that several top predator lizards have a higher frequency of empty stomachs (FES) than do species that feed at lower trophic levels. These authors argued that individuals occupying high trophic levels are more likely to have empty stomachs than those at lower levels because prey density is relatively low for most top predators. In a study of 254 fish species with different foraging behaviours, Arrington et al. (2002) found that the average FES was 16.2%, with piscivorous fishes being the only trophic group with a high proportion of empty stomachs. Species feeding on whole fish prey, a behaviour often associated with reduced foraging, had the highest proportions of empty stomachs (Arrington et al. 2002).

The proportion of individuals with empty stomachs can vary largely in northern pike populations (Chapman

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et al. 1989). However, the FES of this species has only seldom been analyzed (Diana 1979; Chapman et al. 1989; Beaudoin et al. 1999; Soupir et al. 2000) and its meaning is still not fully understood. Chapman et al. (1989) and Chapman and Mackay (1990) suggested that a high FES may reflect a mainly piscivorous feeding behaviour whereas a low FES would reflect a higher utilization of invertebrates because individuals must feed on higher numbers of small prey to meet their energy requirements. Such a hypothesis is not easy to test with stomach content data because they provide only a snapshot of an organism's diet and therefore do not reveal long-term feeding habits.

Naturally occurring stable isotopes of carbon and nitrogen have been used to describe the long-term trophic relationships among organisms in food webs (Peterson and Fry 1987). Furthermore, stable isotopes can give available insight into the long-term feeding behaviour of consumers because they integrate the feeding history over longer periods of time (Peterson and Fry 1987). Even though the isotopic composition of fish muscle can change following the production of new tissues, the complete turnover of their isotopic composition in response to a change in food could take years in slow-growing populations (Hesslein et al. 1993). Thus, the stable isotope composition of muscles represents a reliable long-term average of the food sources of a predator. Because there is only a limited increase in the fraction (0–1‰) of ^{13}C in a predator relative to its prey, ratios of $^{13}\text{C}/^{12}\text{C}$ ($\delta^{13}\text{C}$) in organisms generally reflect the isotopic composition of their diet (Hesslein et al. 1993). Thus, $\delta^{13}\text{C}$ signatures provide information on the source of carbon at the base of the food web. Phytoplankton and benthic algae in freshwater lakes often have distinct $\delta^{13}\text{C}$ signatures due to different fractionation rates during carbon fixation. Consequently, the $\delta^{13}\text{C}$ of pelagic lacustrine organisms tends to be lower than that of littoral organisms (Vander Zanden and Rasmussen 1999). Since $\delta^{13}\text{C}$ signatures are stable through the food chain, the $\delta^{13}\text{C}$ of aquatic consumers can be used to discriminate between littoral and pelagic consumers (Hecky and Hesslein 1995). In contrast, because organisms preferentially excrete the lighter nitrogen isotope (Vander Zanden and Rasmussen 1999), ^{15}N is consistently enriched in organisms up through the food web (Minagawa and Wada 1984; Peterson and Fry 1987). Although it can vary among taxa and tissues, the enrichment in $^{15}\text{N}/^{14}\text{N}$ ($\delta^{15}\text{N}$) from prey to predator

is consistent across food webs, averaging $3.4\pm 0.3\text{‰}$ (Post 2002). Hence, $\delta^{15}\text{N}$ provides an integrative measure of an organism's trophic position based on its long-term diet (Minagawa and Wada 1984). It is thus possible to investigate the relationship between the short-term diet (as revealed by stomach contents) and the long-term integrated trophic position (as revealed by $\delta^{15}\text{N}$ signatures) of a consumer. By revealing the trophic position of individuals, stable isotopes could give insight into the ecological meaning of FES.

The goal of this paper is to test the hypothesis of Chapman et al. (1989), which states that individuals with empty stomachs or with fish in their stomachs have a higher trophic position than individuals feeding on invertebrates. We classified northern pike from 16 populations on the basis of their stomach contents (piscivore, invertebrate feeder, or empty stomach) and compared their trophic positions on the basis of their $\delta^{15}\text{N}$ signatures.

Materials and methods

Study site

The study was conducted in 16 headwater lakes of the Canadian Shield within a 50,000 km² area around Réservoir Gouin in Haute-Mauricie, Québec, Canada (48°50' N, 75°00' W, Appendix). Of these lakes, nine had an undisturbed watersheds (N35, N43, N55, N56, N70, N88, N89, N107, N122), three had their catchments burned in 1995 (FP2, FP24, FP30), three had their catchments logged in 1995 (C2, C9, C23), and one was logged in 1996 (P25; see Carignan et al. 2000 for a more complete description and a map of the study site). The $\delta^{13}\text{C}$ signatures of benthic organisms were not affected by these watershed perturbations while their $\delta^{15}\text{N}$ signatures were slightly affected (Garcia 2001). Despite this, we used the $\delta^{15}\text{N}$ signature of primary consumers (benthic organisms) to estimate the trophic position of northern pike since the effect of these perturbations does not change the estimation of their trophic position (Garcia and Carignan 2000).

Sample collection

All the lakes were sampled during the summers of 1996, 1997, and 1998 with experimental monofilament gillnets of 102.3 m long \times 2.7 m deep, with

stretched mesh of 20, 24, 33, 36, 50, 60, 76, 90, and 100 mm (filament diameter of 0.17, 0.20, 0.20, 0.20, 0.20, 0.32, 0.32, 0.32, and 0.32 mm, respectively). Gillnets were set perpendicular to the shore, with small and large meshes alternating from the shore among gillnets. Fishing effort was six nets per night for lakes <50 ha, eight nets per night for lakes 50–100 ha, ten nets per night for lakes 100–150 ha, and 12 nets per night for lakes >150 ha. The nets fished for 18 to 19 h, always covering the period between 16:00 and 10:30. The fish communities of the study lakes were mainly composed of yellow perch *Perca flavescens*, walleye *Sander vitreus*, white sucker *Catostomus commersoni*, lake whitefish *Coregonus clupeaformis*, and cyprinid fishes (Appendix). Northern pike was the only species sampled in lake N122. For each fish caught, total length (± 1 mm) and weight (± 0.1 g) were noted. Northern pike stomachs were removed and preserved in a 10% formalin solution for diet analysis. A boneless, skinless fillet of dorsal muscle was removed from each northern pike, frozen, and freeze-dried for further isotopic analysis. Due to logistic constraints, it was not possible to collect samples for all fish species.

Stomach content analysis

Northern pike were classified on the basis of their stomach contents into three categories: piscivorous, invertebrate feeder, or empty stomach. Here we defined the stomach as that section of the alimentary canal between the pyloric and the intestinal narrowings (Bucke 1971). Stomachs were considered empty when there was an absence of any measurable organic material (Arrington et al. 2002). We classified individuals in the piscivorous group based on the presence of fish in their stomachs. Hence, northern pike with prey fish and other prey types in their stomachs were considered as piscivores. Each prey category was dried for 12 h at 60°C and then weighed (± 0.0001 g).

Isotopic analysis

Bertolo et al. (2005) showed that benthic organisms constitute the appropriate baseline for the stable isotope analyses in our study lakes. Therefore, we sampled benthic organisms for stable isotope analysis with dip nets in the littoral zone (<2 m deep) of each study lake. Invertebrates were sorted, identified to the

level of suborder or family, counted, and kept frozen until freeze-dried. Only non-predatory organisms (primary consumers) were considered. The organisms were divided into four taxonomic groups: Amphipoda, Trichoptera, Ephemeroptera, and Chironomidae. Stable C and N analyses were performed on 0.7 mg of dried fish muscle or dried invertebrates (Garcia and Carignan 2000). The analyses were performed using a continuous-flow Isoprime isotope ratio mass spectrometer coupled with an elementary analyser (N 1500). Stable isotope values are expressed in δ notation as parts per thousand deviation from a standard reference:

$$\delta^{13}\text{C} \text{ or } \delta^{15}\text{N} = \left[\left(\frac{R_{\text{sample}}}{R_{\text{standard}}} \right) - 1 \right] \bullet 1000 \quad (1)$$

where R is $^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$. Standard references were Pee Dee Belemnite limestone for $\delta^{13}\text{C}$ and atmospheric nitrogen for $\delta^{15}\text{N}$. We assumed that $\delta^{15}\text{N}$ increases by 3.4‰ on average per trophic level (Post 2002). Variations in baseline $\delta^{15}\text{N}$ values from lake to lake need to be corrected for cross-system comparisons; we did this using the method proposed by Vander Zanden and Rasmussen (1999). These authors expressed the relationship between the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of primary consumers (pcon) as:

$$\delta^{15}\text{N}_{\text{pcon}} = \frac{6.34}{1 + \exp[9.67 + (0.356 \bullet \delta^{13}\text{C}_{\text{pcon}})]} \quad (2)$$

The residuals calculated on the basis of Eq. 2 (U_{res}) were then used to correct the fish trophic position by the following procedure. For each primary consumer, the U_{res} is calculated by subtracting the value given by the equation from its measured $\delta^{15}\text{N}$. For each lake, an average residual (\bar{U}_{res}) of all primary consumers is then computed. Next, the measured $\delta^{13}\text{C}$ of each fish from a given lake is entered into Eq. 2 to obtain an estimate of $\delta^{15}\text{N}$. The \bar{U}_{res} for that lake is then added to the estimated $\delta^{15}\text{N}$. The value thus obtained is the lake-corrected baseline $\delta^{15}\text{N}$ ($\delta^{15}\text{N}_{\text{corrected}}$), which is specific for each individual fish. Finally, the corrected trophic position of the fish is given by the equation:

$$\Lambda_{\text{pike}} = \left[\frac{(\delta^{15}\text{N}_{\text{pike}} - \delta^{15}\text{N}_{\text{corrected}})}{3.4} \right] + 2 \quad (3)$$

where Λ_{pike} is the northern pike trophic position and $\delta^{15}\text{N}_{\text{pike}}$ is the $\delta^{15}\text{N}$ measured for each individual fish.

The constant 3.4 is the $\delta^{15}\text{N}$ increment per unit of trophic level, and the constant 2 corresponds to the trophic level of primary consumers. To correct for the inter-lake variation in the $\delta^{13}\text{C}$ baseline, we corrected the $\delta^{13}\text{C}$ value of northern pike by subtracting the $\delta^{13}\text{C}$ signal of zoobenthos from the $\delta^{13}\text{C}$ signal of northern pike within each lake (Post 2002). Benthic organisms were chosen for the carbon baseline correction because the carbon signature of northern pike is known to be more closely related to benthic invertebrates than to zooplankton in our study lakes (Bertolo et al. 2005).

Results

Among the study lakes, the FES of northern pike ranged from 0% to 100% for an average of 36.3% (SD±28.6%), stomachs with invertebrates ranged from 0% to 77.8% for an average of 24.8% (SD±23.1%), and stomachs of fish with fish prey ranged from 0% to 100% for an average of 38.9% (SD±24.4%; Table 1). No significant relationships were found between the frequency of piscivory and the FES (Spearman's coefficient of rank correlation: $n=16$, $\rho=0.30$, $P=0.258$) nor between the frequency of invertebrate feeders and the FES (Spearman's coefficient of rank correlation: $n=16$, $\rho=-0.38$, $P=0.169$).

Among the northern pike classified as piscivores, 72% were pure piscivores while 28% had a mixed diet of fish and invertebrates in their stomach. Swimming insects were overwhelmingly the dominant prey for pike classified as invertebrate feeders. Yellow perch and cyprinids were the two dominant prey eaten by piscivorous individuals.

The mean trophic position and carbon ($\delta^{13}\text{C}$) signature of northern pike with invertebrates and prey fish in their stomachs were comparable (Fig. 1). Invertebrate feeders and piscivorous individuals clearly overlap, showing that their long-term integrated trophic position and carbon sources were similar and not related to prey items found in their stomachs at the time of capture (Fig. 1). Both the mean trophic position and the carbon signature ($\delta^{13}\text{C}$) of northern pike with empty stomachs largely overlapped with those of the two other groups (Fig. 1). It is noteworthy that the carbon-corrected signatures of northern pike (i.e., $\delta^{13}\text{C}$ of northern pike – the $\delta^{13}\text{C}$ of zoobenthos) were slightly positive for the three groups (Fig. 1). This result indicates similar $\delta^{13}\text{C}$ values between zoobenthic prey and northern pike, with some $\delta^{13}\text{C}$ fractionation possibly occurring up the food web. The trophic position of northern pike was high in the study lakes (mean=4.3±0.4, $n=66$) and was correlated with the total length of individuals (General Linear

Table 1 Stomach content analysis: frequency of occurrence of invertebrates, prey fish, and empty stomachs of northern pike in the study lakes

Lake	Northern pike (n)	Total length mean ± SD	Occurrence of invertebrates %	Occurrence of fish %	Occurrence of empty stomachs %
C2	11	569±118	9.1	54.5	36.4
C23*	13	551±97	7.7	53.8	38.5
C9	10	652±144	40.0	50.0	10.0
FP2	2	509±69	0.0	0.0	100.0
FP24	9	627±65	22.2	55.6	22.2
FP30	4	503±131	25.0	0.0	75.0
N107	3	602±31	0.0	100.0	0.0
N122	9	573±58	77.8	11.1	11.1
N35*	6	464±300	0.0	33.3	66.7
N43	11	504±106	36.4	45.5	18.2
N55	4	566±30	25.0	50.0	25.0
N56	4	562±13	25.0	25.0	50.0
N70*	9	598±195	0.0	33.3	66.7
N88	3	563±45	33.3	33.3	33.3
N89	3	562±71	66.7	33.3	0.0
P25*	7	553±104	28.6	42.9	28.6

*Lakes with no isotopic data

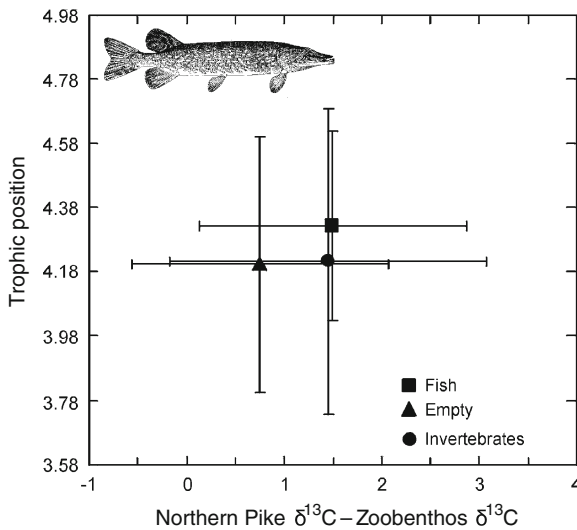


Fig. 1 Trophic position and $\delta^{13}\text{C}$ signal of the three northern pike categories: piscivorous ($n=28$), invertebrate feeders ($n=20$), and individuals with empty stomachs ($n=18$). Trophic positions are based on $\delta^{15}\text{N}$ values corrected for inter-lake variability (see “Materials and methods”). To avoid the confounding effect of inter-lake variation, we corrected the $\delta^{13}\text{C}$ value of northern pike by subtracting the $\delta^{13}\text{C}$ signal of zoobenthos from that of the individuals within each lake. Error bars indicate standard deviation

Model (GLM) $n=65$, $t=6.719$, $P<0.0001$, $R^2=0.417$, Fig. 2) as:

$$\text{TP northern pike} = 2.973 + 0.002 \bullet L_{t(\text{mm})} \text{ northern pike}$$

When the total length of individuals was accounted for, trophic position was not significantly different among feeding groups (GLM, feeding group: $F=0.801$, $P=0.454$; feeding group $\bullet L_t$: $F=0.619$, $P=0.542$). Furthermore, no significant differences were found between the total lengths of invertebrate feeders, piscivores, and northern pike with empty stomachs (analysis of variance; $F=0.583$; $P=0.561$; Fig. 2).

Discussion

Our study confirms that the FES can be relatively high in northern pike. Diana (1979) suggested that, within a population, northern pike are asynchronous feeders and that the time between their meals exceeds the digestion time. Hence, any northern pike population should have some individuals representing each

of the foraging sequences (i.e., searching, digesting, satiated). The feeding intervals of fishes are known to be related to the energy content, conversion efficiency, and particle size of their food (Arrington et al. 2002). The consumption of high-quality food items allows individuals to rely on stored energy and forgo foraging for longer periods (Bowen 1996). Empty stomachs are not necessarily related to a negative energy balance but may rather reflect the high energy content of a previously assimilated prey (Arrington et al. 2002).

Chapman et al. (1989) suggested that the proportion of empty stomachs in northern pike is directly related to the proportion of piscivorous individuals in the population. The frequency of individuals with empty stomachs was highly variable in our study lakes and was not related to the proportion of piscivores in the populations. Moreover, individuals with empty stomachs had both a trophic level and size similar to those found with invertebrates or prey fish in their stomachs. Our results indicate that northern pike is primarily a piscivorous species and that individuals also use benthic invertebrates in their diet. Furthermore, there is no evidence that some individuals specialize on benthic invertebrates.

In the absence of prey fish, invertebrate feeding could be important for northern pike with potential

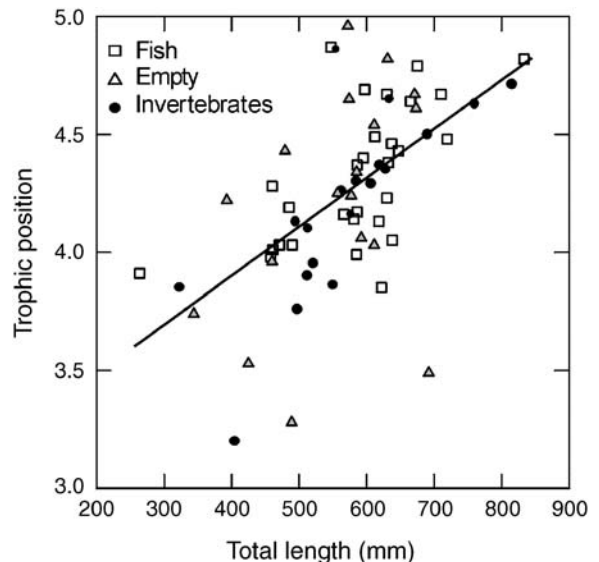


Fig. 2 Relationship between trophic position (based on $\delta^{15}\text{N}$ value) and the total length of northern pike. Piscivorous ($n=28$), invertebrate feeders ($n=20$), and individuals with empty stomachs ($n=18$) are shown. The regression line was computed using pooled data (see text)

consequences for the structure of macroinvertebrate communities (Venturelli and Tonn 2005). This feeding behaviour has been considered sub-optimal (Venturelli and Tonn 2006) and interpreted as a trophic adaptation to a low abundance of prey fish in unproductive ecosystems (Chapman et al. 1989; Chapman and Mackay 1990; Beaudoin et al. 1999). Feeding at more than one trophic level can be a trade-off, where proteins from scarce prey are complemented by energy from abundant food sources (Beaudoin et al. 1999). Predation on invertebrates is known to be most prevalent among northern pike in allopatric populations (Beaudoin et al. 1999; Venturelli and Tonn 2006). In our study, northern pike of different sizes were found to feed largely on invertebrates even in the presence of prey fish, as revealed by stomach content analysis. However, no isotopic differences were observed between invertebrate feeders, piscivores and northern pike with empty stomachs. The isotopic signatures of slow-growing adult northern pike likely reflect diets integrated over a period of one year (Hesslein et al. 1993). It is thus possible that a seasonal peak of invertebrate feeding by northern pike was underestimated by the current analysis. Such seasonality would have been easier to reveal if only fast-growing age-0 northern pike had been analyzed: this developmental stage rapidly integrates the isotopic composition of its food (Vander Zanden et al. 1998).

The carbon signature ($\delta^{13}\text{C}$) of northern pike was very similar to that of invertebrate prey sampled in the littoral zone. However, stable isotope analysis revealed that the trophic positions of northern pike feeding on invertebrates were high and comparable to those of piscivorous individuals. This result suggests that although invertebrates could be an important part of the diet of northern pike in Canadian Shield lakes, prey fish are still the dominant prey over the long term. Thus, prey fish are likely to be the main trophic link between northern pike and the littoral habitat in our study lakes. The $\delta^{13}\text{C}$ signature of northern pike could be mostly due to the consumption of littoral prey fish, which depend on benthic invertebrates. Bertolo et al. (2005) showed a strong similarity between the $\delta^{13}\text{C}$ signatures of both piscivorous and prey fish species in our lakes and the $\delta^{13}\text{C}$ signature of benthic invertebrates. The high contribution of littoral zone organisms to the diets of piscivorous species is consistent with the findings of Vander Zanden and Vadeboncoeur (2002) and Vadeboncoeur et al. (2002), who showed that

benthic production plays a central role in supporting higher trophic level production in temperate lakes.

The positive correlation between northern pike length and its trophic position suggests that individuals forage on prey with a higher trophic position as they grow. Trophic position often increases with body size within a given food web, although exceptions exist (Layman et al. 2005 and references therein). Such a shift in prey type and size during ontogeny has been observed in many fish species (Frost 1954; Lawler 1965; Hart and Hamrin 1988; Mittelbach and Persson 1998). This foraging behaviour is associated with an increase in gape width and swimming speed (Hart and Hamrin 1988). Such a positive body length–trophic position relationship has important implications for fisheries, since it could affect toxic contaminant bioaccumulation. Mercury concentrations of northern pike in our study area have been shown to be positively correlated to trophic position, with larger individuals having mercury concentrations that exceed the recommended limit for human consumption (Garcia and Carignan 2005).

Only a few studies have compared short-term (as revealed by stomach contents) and long-term (as revealed by $\delta^{15}\text{N}$ stable isotopes) fish diets (Beaudoin et al. 1999; Beaudoin et al. 2001; Venturelli and Tonn 2006). These two approaches are highly informative when used jointly. Stomach contents give a high taxonomic resolution of the feeding habits but are limited to food items recently acquired. In contrast, stable isotope analysis allows the discrimination of prey from different trophic levels on a longer time scale. Our study is a further example of the value of integrating conventional dietary analysis techniques with stable isotope analysis. These two approaches should be seen to be complementary and used jointly when possible.

Acknowledgments We are grateful to the many summer assistants from the Université du Québec à Trois-Rivières, Université de Montréal, and Université du Québec à Montréal who participated in the field work. We thank Véronique Boily for her help in the database assemblage. R. Carignan and E. Garcia provided data on lake morphometry and northern pike stable isotope data. Y. Paradis was supported by post-graduate fellowships from *le Fonds d'Action Québécois en Développement Durable*, the *Fondation Héritage Faune*, and the *Saint-Laurent Fednav* fellowship, and A. Bertolo by the Canada Research Chair in Freshwater Ecology. This project was funded by grants from Sustainable Forest Management Network Centre of Excellence, the Natural Sciences and Engineering Research Council of Canada, and the Canada Research Chair program to P. Magnan.

Appendix

Physical characteristics and mean biomass per unit effort (BPUE; g·net⁻¹·night⁻¹) of the dominant fish species in the study lakes

Lake	Lake area (km ²)	Maximum depth (m)	Secchi depth (m)	Species richness (n)	Biomass per unit effort					
					Northern pike	Yellow perch	Walleye	White sucker	Lake whitefish	Others
C2	0.37	12	1.8	4	3,446	234	0	19	0	59
C23	0.29	6	1.4	4	2,390	99	2,622	0	3,169	0
C9	0.66	19	3.6	4	4,382	57	0	306	0	0
FP2	0.35	10	2.2	5	2,343	140	0	59	571	97
FP24	0.17	13	4.6	2	2,378	113	0	0	0	0
FP30	0.34	13	2.4	6	4,290	74	3,659	432	7,344	2
N107	0.46	23	4.1	6	2,282	129	0	673	0	32
N122	0.20	10	3.4	1	784	0	0	0	0	0
N35	0.15	8	3.5	4	1,502	423	0	132	0	8
N43	0.29	9	2.2	5	3,086	14	0	2	1,413	5
N55	0.27	7	3.2	7	3,722	171	0	25	0	164
N56	0.27	10	3.1	3	4,113	0	0	414	0	71
N70	0.65	21	4.3	7	2,259	599	3,866	660	2,356	840
N88	0.57	13	3.7	3	2,190	0	0	8213	0	43
N89	0.67	13	5.0	6	2,259	116	1,578	1,298	3,495	39
P25	0.33	11	4.3	5	1,094	43	4,979	450	6,596	0

The biomass of “others” mainly consisted of cyprinid species

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