

Catherine P. Beaudoin · William M. Tonn
Ellie E. Prepas · Leonard I. Wassenaar

Individual specialization and trophic adaptability of northern pike (*Esox lucius*): an isotope and dietary analysis

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Abstract Northern pike (*Esox lucius*) are often considered to be specialist piscivores, but under some circumstances will continue to eat invertebrates as adults. To examine effects of fish assemblage composition on the trophic ecology of pike, we combined stable isotope analysis (SIA) of carbon and nitrogen and stomach content analysis (SCA) on pike from five lakes in northern Alberta, three of which contain only pike (“pike-only”) and two that also contain yellow perch (*Perca flavescens*) or white sucker (*Catostomus commersoni*) (“pike-other”). Fish were more important as prey and empty stomachs, which often characterize piscivores, were significantly more frequent in pike-other than in pike-only lakes. However, even though invertebrates were more important for pike in pike-only lakes, SIA and SCA indicated that invertebrates were also an important component of pike diets in pike-other lakes. SIA and SCA also revealed considerable intrapopulation variation in trophic ecology, with individuals in some populations differing by as much as two trophic levels. Comparisons of stomach contents and isotope signatures of the same fish suggested that within these variable populations, specialization on invertebrates or fish was a long-term trait of some individuals. SIA indicated that trophic position increased and diets shifted to a greater importance of littoral prey as pike grew in pike-only lakes, but not in lakes with other fish present. Trophic adaptability in northern pike is expressed at both the population level, where the trophic ecology is sensitive to differences in prey regimes, and at the organismal level, in

the form of intrapopulation variation and individual specialization.

Key words *Esox lucius* · Individual variation · Stable isotope analysis · Stomach content analysis · Trophic adaptability

Introduction

The foraging behavior and feeding ecology of fish are generally characterized by adaptive flexibility and trophic adaptability (Dill 1983; Gerking 1994). More than for many other groups of animals, the trophic ecology of many fish species allows them to feed on a variety of prey and shift among prey types as circumstances change. This generalist, or opportunistic, strategy should be particularly advantageous in cold-temperate lakes, where productivity tends to be lower, the availability of temperatures that are favorable for foraging is temporally limited, and strong seasonality is associated with different prey peaking in availability at different times (Keast 1979). In fact, Keast (1979) found that over half of the fishes in Lake Opinicon, Ontario are generalist feeders. In addition, the relative isolation of lake ecosystems in glaciated landscapes can contribute to among-lake differences in the composition of fish communities (Magnuson et al. 1998); resulting lake-to-lake differences in biotic conditions (prey communities, presence or absence of competitors or predators) should promote diet flexibility and variability among populations (Lacasse and Magnan 1992).

This high degree of feeding plasticity is often associated with species at low or intermediate trophic levels (Lowe-McConnell 1975; Gu et al. 1997), whose prey are often smaller and less mobile than those of piscivorous fish. Because the tactics required to strike and capture fish prey are more demanding than those needed for feeding on many invertebrates and are closely linked to morphological features such as body form and mouth size (Webb 1984), piscivorous fishes could be expected to

C.P. Beaudoin · W.M. Tonn (✉) · E.E. Prepas
Department of Biological Sciences,
University of Alberta,
Edmonton, AB,
T6G 2E9, Canada
e-mail: bill.tonn@ualberta.ca, Fax: +1-780-4929234

L.I. Wassenaar
Environment Canada,
National Water Research Institute,
11 Innovation Blvd, Saskatoon, SK,
S7N 3H5, Canada

have more specialized and less flexible diets than other species. Indeed, Webb (1984; Webb and Skadsen 1980) found that the body and fin form of esocids allow them to achieve apparently optimal strike tactics, compared with other teleost predators, and northern pike (*Esox lucius*) are often considered to be specialist piscivores (e.g., Keast 1978). After pike attain lengths of 20–35 mm, fish constitute more of the diet and become the dominant, if not the sole, prey of pike > 85 mm (Hunt and Carbine 1951; Frost 1954; Lawler 1965; Mittelbach and Persson 1998). Among 28 species or year-classes of fishes whose diets were examined by Keast (1979), pike had the lowest diet diversity. In the most intensive studies of pike diets reviewed by Vander Zanden et al. (1997), the percentage of fish prey ranged from 99.1% to 99.9%.

Still, occasional studies suggest that adult pike are not always specialist piscivores as they are generally portrayed. In their recent review, Vander Zanden et al. (1997) found that over all studies, the among-lake variation in trophic position of *Esox* (northern pike plus chain pickerel, *E. niger*) was comparable to that of the other fishes examined. Although this could, in part, have resulted from variation in the trophic positions of their fish prey among the study lakes (as well as their combining the two species of *Esox*), some studies report that adult pike will continue to eat invertebrates opportunistically (e.g., Stephenson and Momot 1991). Going further, Chapman et al. (1989) suggested that pike diets remain flexible throughout their lives. However, their study was limited to analyzing the frequencies of occurrence of vertebrates and invertebrates in pike stomachs among lakes, and thus could not quantify the importance of different prey types, nor address what factors, such as predator size and prey composition or availability, influenced prey importance within and among lakes. A more detailed assessment of the trophic ecology of pike is required to examine this species' trophic adaptability and investigate factors that might influence its expression.

The trophic ecology of animals can be studied using stomach content (SCA) and stable isotope (SIA) analyses. Traditionally, dietary studies quantify stomach contents of a predator, revealing directly and specifically the taxa being consumed, but only during the time immediately preceding capture. More recently, analyses of naturally occurring stable isotopes, especially those of carbon (^{13}C and ^{12}C) and nitrogen (^{15}N and ^{14}N), have been used in ecology to describe trophic relationships. Because there is only limited fractionation (0–1‰ enrichment) of ^{13}C in a predator relative to its prey (DeNiro and Epstein 1978), ratios of ^{13}C ($\delta^{13}\text{C}$) in organisms generally reflect the isotopic composition of their diet, providing information on the original source of carbon to the food web. In contrast, ^{15}N is consistently enriched in organisms up through the food web (Hesslein et al. 1991) because organisms preferentially excrete the lighter nitrogen isotope (Minagawa and Wada 1984; Peterson and Fry 1987). The enrichment in

$\delta^{15}\text{N}$ from prey to predator is consistent across different food webs, averaging 3.40‰ (Minagawa and Wada 1984; Peterson and Fry 1987; Cabana and Rasmussen 1996). Thus, $\delta^{15}\text{N}$ provides a measure of an organism's trophic position based on its long-term assimilated diet (Gearing 1991). SIA should be particularly useful in studies of piscivorous fish, such as pike, where empty stomachs can be common (e.g., Frost 1954; Diana 1979; Chapman et al. 1989) and large but rare prey can be under-represented in analyses based solely on SCA. However, although the use of SIA has a number of advantages over SCA in food web studies by providing information about a fish's long-term assimilated diet, such studies are enhanced through complementary use of SIA and SCA. SCA can provide a taxonomic resolution of prey that may be difficult to achieve by SIA, particularly in complex food webs, such as those of littoral zones of lakes where pike reside (Hecky and Hesslein 1995; Vander Zanden et al. 1997).

To investigate dietary flexibility in northern pike (e.g., continued invertebrate feeding in fish > 85 mm), and to examine factors that influence such flexibility within and among populations, we used SIA and SCA on pike from a series of lakes that differ in the richness and composition of their fish assemblages, including lakes that contained only pike. Due to the absence of other prey fish species, we hypothesized that invertebrates would be a large component of pike diets in lakes that contained only pike ("pike-only" lakes), compared with lakes where other prey fish are present ("pike-other" lakes). We also predicted that cannibalism would be more important in pike-only lakes because this feeding strategy tends to occur in fish when food quality and/or quantity is low (Smith and Reay 1991). A second, related set of objectives was to examine individual variation in diets within lakes and to test whether, and how, food habits of pike changed as they grew in pike-only lakes compared with lakes that contained other fish species. Few studies have compared dietary and isotope studies in the same lakes, indeed on the same fish, and none that we know of have made comparisons of the two methods over a series of lakes that span a range of prey availability. As well, although Gu et al. (1997) recently used SIA to examine intrapopulation variation in diets in blue tilapia (*Oreochromis aureus*), we know of no studies that have compared SIA and SCA for the same fish to investigate individual differences in trophic ecology.

Materials and methods

Study lakes

Fish assemblages in small lakes of north-central Alberta are relatively depauperate (Robinson and Tonn 1989). The low numbers of fish species in these lakes can be explained not only by their small sizes, shallow depths, and the relatively severe climate of the region, but also by the region's great distance from major glacial refugia (Nelson and Paetz 1992). Due to the effectiveness of northern pike as a piscivore, small-bodied fishes are generally absent in the presence of pike, further impoverishing pike-dominated assem-

blages (Robinson and Tonn 1989). Finally, because northern pike is more tolerant than other large-bodied species of the hypoxic waters that frequently characterize these lakes during winter (Magnuson and Karlen 1970), it can sometimes be the only fish species present. This allows for the ultimate comparison of dietary patterns of pike in different assemblages, pike as the only fish species present (pike-only) versus pike in the presence of other fish (pike-other).

Our five study lakes are located in roadless areas of the mixed-wood boreal forest of northern Alberta (Table 1). Three lakes, C17, R4, and SPH200, contained only northern pike, although when an upstream beaver dam was breached in spring 1996, a few individuals of brook stickleback (*Culaea inconstans*) were introduced briefly into the last lake, but subsequently disappeared in summer 1996. In two lakes, pike co-occurred with other larger-bodied fishes. LLB20 contained northern pike and yellow perch (*Perca flavescens*), whereas SPH20 contained northern pike, yellow perch, and white sucker (*Catostomus commersoni*). The study lakes are all small and shallow, and range from mesotrophic to eutrophic (based on total phosphorus, Wetzel 1983) (Table 1).

Methods

At SPH200, northern pike and potential prey were collected in May, June and August 1996, whereas in the other four study lakes, sampling occurred once, in August or September 1996. Five to ten multi-mesh gillnets (depending on lake size) were set overnight in each lake for 8- to 10-h sets, inshore and offshore. Gillnets were 1.5 × 30 m, with the following barmesh sizes: 5, 6.25, 8, 10, 12.5, 15.5, 19.5, 24, 29, 35, 43, and 55 mm. For each captured fish, total length (TL) was recorded and muscle tissue and the digestive tract were removed and frozen for later SIA and SCA, respectively. Due to budget constraints and because of the integrative nature of SIA, not all pike used for SCA were subjected to SIA. For all analyses, pike were separated into two size-classes: large (>85 mm TL) and small (<85 mm TL), based conservatively on the length at which pike begin eating only fish (Frost 1954; Hunt and Carbine 1951; Lawler 1965).

Aquatic invertebrates were collected as potential prey from several locations during fish samplings in SPH200, LLB20, and SPH20. Macroinvertebrates were sampled with a pond net from at least six sites in the littoral zones (two to three sweeps per site). Additional samples of snails, leeches, and other epiphytic invertebrates were collected by hand. Benthic invertebrates in the profundal zone were sampled at three or four sites with an Ekman grab. Live individuals were separated from the detrital fraction and sorted to order or family. All trichopterans and mollusks were removed from their cases or shells. Zooplankton (mostly Cladocera, Copepoda and Diptera larvae) were obtained from vertical hauls of a 243-µm tow net, beginning from 1 m above the bottom throughout each lake. Samples from three to four sites were pooled to ensure sufficient biomass for SIA. Zooplankton samples were separated through a series of graded sieves (500 and 243 µm), and further sorted by hand into three groups, Daphnidae (a representative herbivore), Chaoboridae (a representative carnivore), and other zooplankton. Samples were held in water for at least 24 h to

allow the invertebrates to void their guts. Because of logistical constraints (access was limited to float plane only), invertebrates were not sampled from C17 and R4.

Because lipids may be depleted in ¹³C and affect ecological interpretations (Kling et al. 1992), they were removed prior to SIA; samples were washed in a 1:1 methanol:chloroform solution for three 10-min intervals and then freeze-dried. Before freeze-drying, invertebrates were sorted, held in water for ≥24 h to allow voiding of guts, and carbonates were removed with 1 M HCl (Boutton 1991). To homogenize samples, the cleaned, treated, and freeze-dried tissues were ground with a mortar and pestle.

Samples were analyzed for stable carbon and nitrogen ratios with a Micromass Optima continuous flow isotope ratio mass spectrometer (CF-IRMS) directly coupled to a Carlo Erba NA1500 elemental analyzer (EA) and autosampler at the National Hydrology Research Institute (Saskatoon, Sask., Canada). For each invertebrate sample and individual fish, 1 mg of freeze-dried, pulverized, and powdered tissue was loaded into 5 × 8 mm tin capsules, which were then folded, crushed into a cube, and loaded onto the autosampler of the EA. Samples were flash combusted at 1100°C, followed by on-line removal of water and on-line chromatographic separation of N₂ and CO₂. The N₂ and CO₂ were introduced directly into the mass spectrometer via helium carrier gas. A pulse of N₂ reference gas was introduced into the mass spectrometer with an automated gas injection system, followed by the N₂ sample gas peak. After integration of the N₂ sample and reference isotopic ratios, the mass spectrometer peak jumps to CO₂ tuning and then integrates the sample CO₂ pulse, followed by an injection of CO₂ from the reference gas box. A laboratory working standard of urea was run every 10 samples for the CF-IRMS. External reproducibility of the CF-IRMS instrument for both carbon and nitrogen isotope analysis was better than ±0.6‰.

Stable isotope data are presented as the relative difference between ratios of a sample and standards. A differential notation known as the delta (δ) notation is used to express these relative differences: $\delta R(\text{‰}) = [(R_{\text{sample}}/R_{\text{standard}})/R_{\text{standard}}] \times 10^3$, where $R = {}^{13}\text{C}/{}^{12}\text{C}$ or ${}^{15}\text{N}/{}^{14}\text{N}$; δ¹³C or δ¹⁵N is the permil (‰) deviation of that sample from the recognized isotope standard, PeeDee Bel-emnite (PDB) limestone for δ¹³C and atmospheric N₂ for δ¹⁵N (Gearing 1991).

Stomach contents were sorted taxonomically, counted, and, for large pike, weighed. In one case, the mass of a large pike that had recently been cannibalized was calculated using a lake-specific length-mass regression. For pike in the large size-class, frequency of occurrence and the percentage composition of prey taxa by number (percent number) and by mass (percent mass) were calculated. The relative importance index, RI (George and Hadley 1979), is essentially a mean of the three diet measures for each prey taxon and reduces the amount of bias that may occur if any one is used separately (Wallace 1981). For a given population, the RI of prey taxon *i* is calculated as:

$$RI_i = 100 AI_i / \sum_{i=1}^n AI_i$$

where AI_{*i*} (absolute importance of prey taxon *i*) = frequency of occurrence + percent number + percent mass of the prey taxon *i*;

Table 1 Physical, chemical, and biological characteristics of the five study lakes during summer 1996 (fish species: np northern pike, yp yellow perch, ws white sucker)

Lake	Location (N, W)	Fish assemblage	Fish species	Surface area (km ²)	Depth (m) maximum (mean)	Mean (±SE) summer ^a total phosphorus (µg l ⁻¹)
LLB20	55°8', 111°45'	Pike-other	np, yp	0.62	5.8 (2.1)	47 ± 5
SPH20	55°25', 113°42'	Pike-other	np, yp, ws	1.57	8.5 (4.4)	22 ± 1
SPH200	55°23', 113°38'	Pike-only	np ^b	0.56	9.5 (4.1)	40 ± 5
C17	55°39', 111°55'	Pike-only	np	0.51	7.6 (1.8)	19 ± 1
R4	55°43', 110°43'	Pike-only	np	0.18	5.5 (1.0)	29 ± 6

^aIncludes values from June, July and August 1996

^bA few brook stickleback (*Culaea inconstans*) were caught in June 1996

n is the number of different prey types; frequency of occurrence is the percentage of all non-empty stomachs containing food in which prey taxon i was found, percent number is the percentage that prey taxon i contributes to the total number of food items in all stomachs, and percent mass is the percentage that prey taxon i contributes to the total mass of food in all stomachs (Bowen 1996). For small pike (≤ 85 mm TL), only frequency of occurrence and percent number were determined and used in RI calculations. Digested remains of fish prey, such as scales, pharyngeal arches or other bones, were used to identify ingested prey items when possible. However, these prey items and unidentifiable organic matter or macrophytes that could not be quantified were not included in the above calculations.

Differences in dietary and isotopic measures between pike in pike-only and pike-other assemblages, or between large and small pike, were examined using t -tests when variances were homogeneous and separate-variance t -tests when variances were heterogeneous. Frequency and proportional data were transformed prior to analyses with the angular transformation (Sokal and Rohlf 1981). All statistical analyses were conducted using SPSS (Norusis 1997).

Results

Pike-other lakes

In LLB20, only large (> 85 mm) pike were captured. $\delta^{15}\text{N}$ signatures of pike ranged over 6‰ (Table 2), indicating considerable individual variation that spanned approximately two trophic levels. SIA indicated that many pike relied heavily on littoral invertebrates, such as odonates, but that others ate pike and perch as well (Fig. 1a). Variation in carbon isotopic signatures was also quite large (Table 2), which suggests that some pike consumed food sources that were likely pelagic (or had eaten pelagic prey). Among pike that had eaten recently (almost two-thirds had empty stomachs), half had consumed invertebrates and half had eaten fish, but only one had eaten both types of prey. Although invertebrates (primarily amphipods) were consumed in considerably higher numbers than fish, most of the prey mass was fish (Table 3). Based on the RI, the most important prey were amphipods and pike (Table 3).

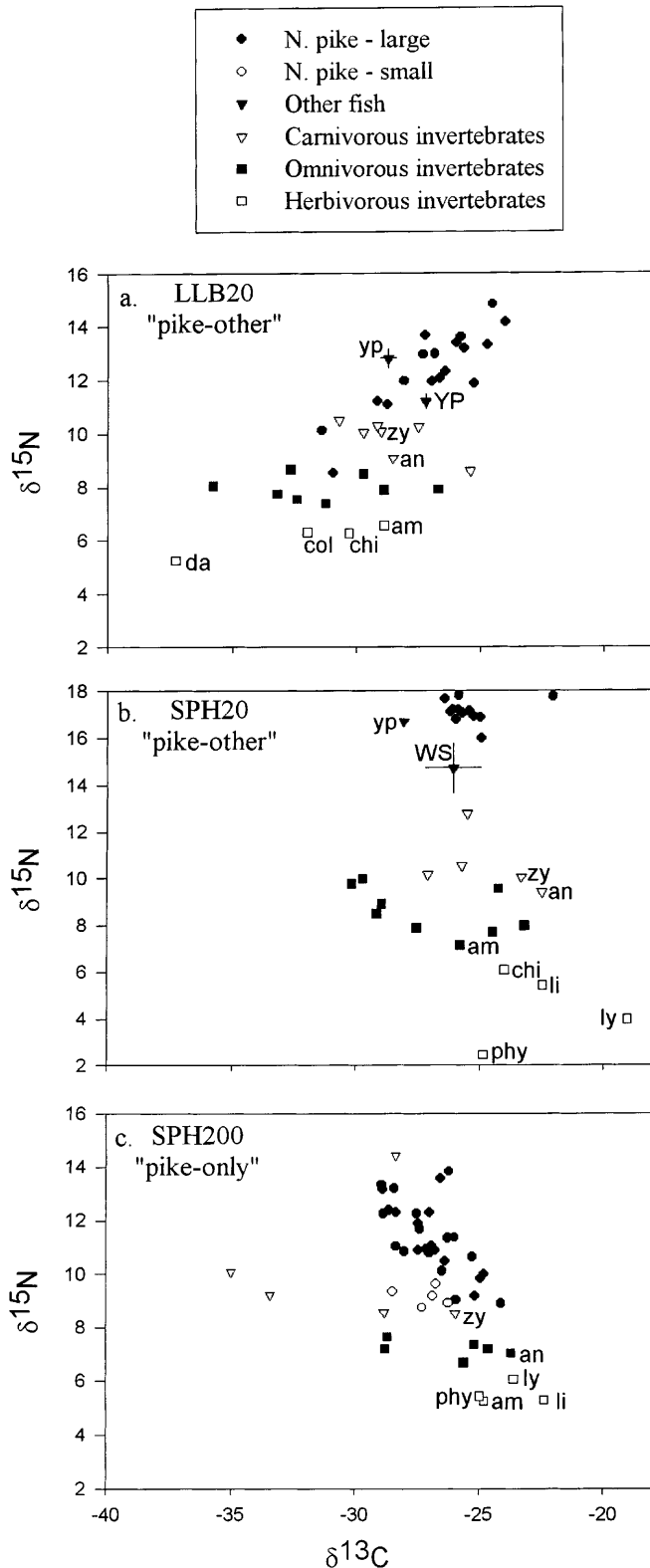
In contrast to LLB20, the $\delta^{15}\text{N}$ signatures of large pike in SPH20 varied little among individual pike (Table 2). These signatures were at least 3–4‰ higher than the signatures of most pike in other lakes (Table 2), despite comparable among-lake signatures of basal consumers (Fig. 1), suggesting that there was an additional (fifth) trophic level. The isotopic signatures of large pike in SPH20 were consistent with a piscivorous diet primarily of white sucker, and possibly smaller pike (Fig. 1b). SCA confirmed that fish dominated the prey biomass, although invertebrates were present in more stomachs, and in higher numbers (Table 3). The most important prey fish were yellow perch (Table 3), in contrast to the SIA results. However, we were unable to capture large perch, thus none were available for SIA. Odonates (Anisoptera larvae) and amphipods were the most important of a rather diverse invertebrate prey assemblage (Table 3), although most taxa were represented in only a single stomach. Similar to LLB20, more than half of the pike examined had empty stomachs (Table 3).

Pike-only lakes

In SPH200, $\delta^{15}\text{N}$ signatures of large pike spanned 5‰ (Table 2), indicating that individual variation within this population, as in LLB20, bridged nearly two full trophic levels. SIA suggested that large pike had diets consisting primarily of littoral invertebrates, such as odonates, and smaller northern pike (Fig. 1c). In contrast to the pike-other lakes, only 12% of the large pike had empty stomachs. Of those with prey, almost all contained invertebrates, usually exclusively so, and relatively few had eaten fish (primarily pike; Table 3). Still, a single large pike dominated the total mass of prey (Table 3). Odonates and amphipods were the most important invertebrates consumed, and smaller pike were the dominant prey fish.

Table 2 Means (\pm SE) and ranges of total lengths (TL, mm), $\delta^{13}\text{C}$, and $\delta^{15}\text{N}$ signatures of large (> 85 mm) and small (≤ 85 mm) northern pike in the five study lakes during summer 1996

Fish assemblage Lake	Size-class n	TL Mean \pm SE (Range)	$\delta^{13}\text{C}$ (‰)		$\delta^{15}\text{N}$ (‰)	
			Mean \pm SE	Range	Mean \pm SE	Range
Pike-other						
LLB20	18	Large 355 \pm 46 (109–768)	-27.0 \pm 0.5	-31.4 to -24.0	12.4 \pm 0.4	8.5 to 14.8
SPH20	14	Large 512 \pm 28 (261–651)	-25.4 \pm 0.3	-26.4 to -22.0	17.1 \pm 0.1	16.0 to 17.8
Pike-only						
SPH200	28	Large 339 \pm 40 (113–930)	-26.9 \pm 0.3	-28.9 to -26.7	11.4 \pm 0.3	8.9 to 13.8
	5	Small 54 \pm 2 (49–60)	-27.1 \pm 0.4	-28.5 to -26.2	9.2 \pm 0.2	8.7 to 9.6
C17	19	Large 291 \pm 42 (99–570)	-27.3 \pm 0.2	-28.6 to -25.0	12.8 \pm 0.1	11.0 to 13.9
R4	10	Large 367 \pm 31 (140–531)	-31.9 \pm 0.4	-34.4 to -30.2	10.2 \pm 0.2	9.0 to 10.8



The isotopic signatures of pike in C17 and R4 (all > 85 mm) were comparable to, although less variable than, those in SPH200 (Table 2). However, since stable isotope signatures of potential prey items were not available for C17 and R4, we could not fully assess diets

Fig. 1 Scatter plot of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures (‰) of northern pike and potential prey in **a** LLB20, **b** SPH20, and **c** SPH200 during summer 1996. Plots include points for individual pike and when possible, mean (\pm SE) values of prey taxa. Trophic categorization of invertebrates were based on Merritt and Cummins (1978) and Clifford (1991), modified by $\delta^{15}\text{N}$ signatures. Important prey items for northern pike and herbivorous invertebrates that indicate the basal $\delta^{15}\text{N}$ signals are labeled: yellow perch (*YP/yp*), white sucker (*WS*), Zygotera (*zy*), Anisoptera (*an*), Amphipoda (*am*), Daphnidae (*da*), Coleoptera (*col*), Chironomidae (*chi*), Limnephilidae (*li*), Lymnaeidae (*ly*), and Physidae (*phy*). For yellow perch, *upper-* and *lowercase* letters indicate large (> 150 mm) and small (\leq 150 mm) size-classes, respectively

of pike using SIA. As in SPH200, but unlike the two pike-other lakes, few (\leq 10%) pike in these two lakes had empty stomachs. Unlike SPH200, however, no cannibalism was detected by SCA in either R4 or C17, i.e., invertebrates were the only prey items consumed by the pike sampled (Table 3). Odonates and amphipods, and even chaoborid larvae in C17, were the most important taxa identified by SCA (Table 3).

Thus, although consumption of invertebrates was not uncommon in the two pike-other lakes, it was nearly ubiquitous in the pike-only lakes (Table 3). Indeed, the frequency of occurrence of invertebrate feeding among large (> 85 mm) pike was higher, on average, in pike-only (98.2%) than in pike-other lakes (55.8%; *t*-test, $P = 0.007$). Large pike in the two lake types also differed in the proportion of individuals with empty stomachs. More than half ($\bar{x} = 59.5\%$) of the pike captured in lakes containing other fishes were empty, which is characteristic of piscivore populations, whereas only 9–12% of the large pike in pike-only lakes were empty (separate-variance *t*-test, $P = 0.048$).

Individual specialization

In addition to these clear interpopulation differences between lake types, considerable variation existed among individual pike in stomach contents and isotopic signatures, both within lakes and between lake types. Most frequently, SCA indicated that an individual pike had recently consumed only invertebrates, or only fish, but not both. To assess if such snapshot differences may represent longer-term individual specialization that would be reflected in isotopic signatures, we identified large pike subjected to both SCA and SIA and that were either purely piscivorous or purely invertebrate feeders (based on SCA). Across all lakes, pike that had been purely piscivorous at the time of their capture had significantly higher $\delta^{15}\text{N}$ signatures ($13.1 \pm 0.9\text{‰}$, $n = 9$) than pike that had recently eaten only invertebrates ($11.3 \pm 0.4\text{‰}$, $n = 22$) (*t*-test, $P = 0.045$). Interestingly, pike with empty stomachs had $\delta^{15}\text{N}$ signatures that were nearly identical to the piscivorous pike ($13.0 \pm 0.7\text{‰}$, $n = 15$).

Table 3 Frequency of occurrence (%FO), percentage by number and by mass, and index of relative importance (RI) of prey taxa in the diets of large (> 85 mm) and small (≤85 mm) northern pike in the five study lakes during summer 1996. Sample sizes (*n*) refer to

the total number of fish stomachs examined; also given under size-class are the means (±SE) and ranges of total lengths of pike containing food items, and the percentages of stomachs that were empty

Lake	Size-class	Item	%FO	%Number	%Mass	RI
LLB20	Large <i>n</i> = 33 418 ± 20 (250–496) 64% empty	Total invertebrates	50.0	97.8	24.4	60.7
		Amphipoda	41.7	95.9	22.2	49.2
		Anisoptera larvae	16.7	0.7	2.2	6.0
		Chironomidae larvae	8.3	0.7	0	2.8
		Unidentified invertebrate	8.3	0.4	0	2.7
		Total fish	50.0	2.2	75.5	39.3
		Yellow perch	8.3	0.4	2.3	3.4
		Northern pike	25.0	1.1	71.1	29.9
		Unidentified fish	16.7	0.7	2.1	6.0
		Other				
		Scales	8.3			
		Macrophytes	16.7			
		Organic matter	16.7			
		SPH20	Large <i>n</i> = 29 503 ± 24 (250–577) 55% empty	Total invertebrates	61.5	83.9
Amphipoda	7.7			38.7	0.6	14.2
Anisoptera larvae	30.8			12.9	22.8	20.1
Chironomidae larvae	7.7			3.2	0.1	3.3
Coleoptera	7.7			3.2	3.4	4.3
Diptera	7.7			3.2	0	3.3
Gastropoda	7.7			3.2	0	3.3
Hirudinea	7.7			3.2	0.2	3.4
Pelyceopoda	7.7			12.9	0.3	6.3
Trichoptera larvae	7.7			3.2	0.8	3.5
Total fish	23.1			16.1	71.7	38.2
Yellow perch	23.1			9.7	60.5	28.2
Northern pike	7.7			3.2	4.5	4.7
Unidentified fish	7.7			3.2	6.7	5.3
Other						
Spruce needles	15.4					
<i>Nostoc</i>	7.7					
Organic matter	7.7					
SPH200	Large <i>n</i> = 43 382 ± 35 (113–850) 12% empty	Total invertebrates	94.7	98.4	15.4	73.6
		Amphipoda	71.1	80.3	4.2	38.4
		Anisoptera larvae	47.4	6.1	8.4	15.3
		Chaoboridae larvae	2.6	0.1	0	0.7
		Rotifera	2.6	0.1	0	0.7
		Trichoptera larvae	13.2	0.6	0.1	3.4
		Unidentified invertebrate	7.9	0.4	1.1	2.3
		Zygoptera larvae	39.5	10.8	1.6	12.8
		Total fish	21.1	1.5	84.5	26.4
		Northern pike	10.5	0.6	84.2	23.5
		Brook stickleback	10.5	0.9	0.3	2.9
		Other				
		Macrophytes	10.5			
		Organic matter	5.3			
SPH200	Small <i>n</i> = 7 54 ± 2 (49–60) 0% empty	Total invertebrates	100	100	100	100
		Amphipoda	75.0	50.0	na	55.5
		Chaoboridae larvae	25.0	42.3	na	29.9
		Chironomidae larvae	25.0	7.7	na	14.5
		Other				
		Filamentous algae	12.5	1.9		
C17	Large <i>n</i> = 10 115 ± 4 (99–130) 10% empty	Total invertebrates	100	100	100	100
		Amphipoda	88.9	88.7	90.8	12.7
		Chaoboridae larvae	33.3	8.1	5.0	73.2
		Gastropoda	11.1	0.8	0.7	3.4
C17	Large	Notonectidae	11.1	0.8	0.7	3.5
		Pelyceopoda	11.1	0.8	0	3.3
		Zygoptera larvae	11.1	0.8	2.8	4.0
		Other				
Organic matter	44.4					

Table 3 (Contd.)

Lake	Size-class	Item	%FO	%Number	%Mass	RI
R4	Large <i>n</i> = 11 370 ± 35 (140–531) 9% empty	Total invertebrates	100	100	100	100
		Amphipoda	60.0	51.0	14.3	46.5
		Anisoptera larvae	90.0	26.9	83.0	6.0
		Chaoboridae larvae	10.0	15.9	0.1	2.8
		Coleoptera	10.0	2.1	0.3	29.2
		Gastropoda	20.0	1.4	0.3	5.1
		Hirudinea	10.0	0.7	0.3	2.6
		Nematomorpha	10.0	0.7	0.4	2.6
		Trichoptera larvae	10.0	0.7	1	2.5
		Unidentified invertebrate	10.0	0.7	0	2.7
		Other				
		Organic matter	10.0			

Relations between pike size and trophic ecology

We attempted to collect small pike (≤ 85 mm) in all lakes, but were successful only in SPH200. These small pike had significantly lower $\delta^{15}\text{N}$ signatures than large pike in SPH200 (separate-variance *t*-test, $P < 0.0001$; Table 2, Fig. 1c), indicating that they occupied a lower trophic level. SIA suggested that their diets consisted of a combination of omnivorous invertebrates from the littoral zone (Fig. 1c). There was no detectable difference between the carbon isotope signatures of large and small pike (*t*-test, $P = 0.7$), suggesting that their diets could be traced to similar (littoral) carbon sources. Consistent with SIA, all of the prey in stomachs of small pike were invertebrates, with amphipods being most important (Table 3). Chaoborids, which occurred in stomachs of a few large pike in SPH200, were also relatively important in the diet of small pike.

Although direct comparisons between small and large pike could not be done in all study lakes, there were indications that $\delta^{15}\text{N}$ and/or $\delta^{13}\text{C}$ of pike increased with increasing total length of pike, depending on the fish assemblage present. $\delta^{15}\text{N}$ and total length of northern pike were positively correlated in all three pike-only lakes but not in the two lakes that contained other fish species (Table 4). Similarly, correlations between $\delta^{13}\text{C}$ signatures and pike length in SPH20 and LLB20 (pike-other) were not significant, nor was the relation significant in SPH200, where considerable cannibalism was detected. However, $\delta^{13}\text{C}$ and total length were positively correlated in the other two pike-only lakes, R4 and C17 (Table 4), which suggested an increase in the importance of littoral relative to pelagic prey as pike grew.

Discussion

Our analyses of the trophic ecology of northern pike in small lakes of Alberta's boreal forest revealed that populations were significantly affected by a lakes' fish assemblage, but populations were also characterized by large individual variation in diet, e.g., stomach contents ranging from pure invertebrate feeding to pure piscivory, and isotope signatures differing by $> 6\%$ for both $\delta^{15}\text{N}$

Table 4 Correlation coefficients between total length of northern pike and their $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ signatures for the five study lakes

Lake	$\delta^{15}\text{N}$			$\delta^{13}\text{C}$		
	<i>r</i>	<i>n</i>	<i>P</i>	<i>r</i>	<i>n</i>	<i>P</i>
Pike-other						
LLB20	-0.1	18	0.6	-0.1	18	0.8
SPH20	0.5	14	0.1	0.001	14	1.0
Pike-only						
SPH200	0.7	33	< 0.0001	0.2	33	0.2
C17	0.5	19	0.05	0.7	19	< 0.0001
R4	0.9	10	< 0.0001	0.9	10	< 0.0001

and $\delta^{13}\text{C}$, even within a single lake. The intrapopulation variation in $\delta^{15}\text{N}$ signatures for a species usually considered to be a specialist piscivore (e.g., Keast 1978) was surprisingly comparable to that measured for the omnivorous blue tilapia in a Florida lake (Gu et al. 1997).

Effects of fish assemblage composition

Despite within-lake variation, which contributed to among-lake similarities regardless of the fish assemblage present, our SIA and SCA also revealed assemblage-level differences in the consumption patterns of northern pike. Thus, although some individuals within all study lakes consumed invertebrates, invertebrate feeding was nearly ubiquitous in pike-only lakes but much less common in lakes with other prey fishes. When pike with empty stomachs are included, only one-third of the pike in pike-other assemblages had eaten invertebrates shortly before capture, but nearly 90% of all individuals examined in pike-only lakes had done so.

Although such a difference in the frequency of invertebrate feeding does not necessarily translate into a corresponding difference in the importance of piscivory, we suggest that it does for these and other populations of pike. Chapman et al. (1989) had earlier documented a negative correlation between the frequency of occurrence of invertebrates in the diet of pike and the proportion of empty stomachs, consistent with our results. They also documented the reverse: a

positive relationship between empty stomachs and the frequency of occurrence of fish in the diet. Although not noted in the study itself, these data also revealed a strong negative relationship between the frequencies of occurrence of vertebrates and invertebrates in the diets of pike.

Chapman et al. (1989) proposed that the differences in the feeding strategies of pike that they observed were related to the presence or availability of different prey types among the different lakes, but were unable to demonstrate this relationship. Thus, the differences in the frequencies of occurrence of both invertebrate prey and in the frequencies of empty stomachs that we found between pike-only and pike-other lakes is the first empirical demonstration of such a relationship. SIA further pointed to the long-term importance of fish, and unimportance of invertebrates, in the diet of many of the pike analyzed in LLB20 and all in SPH20. Indeed, in SPH20, where yellow perch and white suckers were both present as potential prey, SIA revealed that pike occupied a trophic level that was, on average, one full position higher than that of most pike in the other lakes.

SIA also detected assemblage-related differences in the occurrence of a relationship between isotope signatures and body size in larger (> 85 mm) pike. There were positive relationships between $\delta^{15}\text{N}$ signatures and size of pike in SPH200, R4, and C17 (all pike-only lakes), but not in LLB20 or SPH20 (pike-other lakes). This indicates that pike generally increase their trophic position as they grow in pike-only lakes, but do not (over the range of sizes examined) in the lakes that contain pike and other prey fish. In contrast, Hesslein and Ramlal (1993) found a general trend of increasing $\delta^{15}\text{N}$ signatures with increasing size of northern pike in the Athabasca River, which has several fish species, and suggested that larger pike occupied a higher trophic level than smaller pike. Similarly, Hobson and Welch (1995) showed a strong relationship between $\delta^{15}\text{N}$ and length for a cannibalistic population of Arctic char (*Salvelinus arcticus*). However, similar to our results, Kiriluk et al. (1995) found no such relationship for lake trout (*Salvelinus namaycush*) in Lake Ontario, suggesting that the lake trout's opportunistic diet accounted for both the large range of $\delta^{15}\text{N}$ signatures among individual fish and the similar values among different age-classes.

Individual variation, resulting from trophic flexibility and opportunism, likely also accounts for the lack of relationship between $\delta^{15}\text{N}$ and size for pike in SPH20 and especially in LLB20, where the large range in $\delta^{15}\text{N}$ signatures spanned two trophic levels independent of fish length. Our SIA in pike-other lakes thus support the results of Chapman et al. (1989), also working in pike-other lakes, who found no differences in length between piscivorous pike and pike that had recently eaten only invertebrates. In contrast, smaller pike in our pike-only lakes tended to occupy lower trophic positions than larger pike, suggesting more size-dependent opportunities for trophic flexibility in these lakes.

Cannibalism was not evident in two of the pike-only lakes, R4 and C17. Instead, SCA indicated that these two pike populations were maintained on diets of invertebrates. Although isotope signatures were lacking for invertebrates in these two lakes, the relatively limited variation in $\delta^{15}\text{N}$ in pike did not indicate any individuals occupied a higher trophic position. Perhaps smaller pike, more vulnerable to predation, were less available due to the extensive macrophytes present in these lakes, which could serve as refuges (Wright 1990). The small number of stomachs analyzed may have reduced our ability to detect cannibalism in R4 and C17; however, empty stomachs, which are common in piscivorous pike populations (e.g., Diana 1979; Chapman et al. 1989; this study), were rare in these two lakes, suggesting that cannibalism was not common. Taking our data as a whole, it appears likely that the prevalence of cannibalism in pike reflected the availability of both conspecific and heterospecific prey.

There was also no relationship between $\delta^{15}\text{C}$ and size of pike in LLB20 and SPH20 (pike-other lakes) but a positive relationship between $\delta^{13}\text{C}$ signatures and size in R4 and C17 (pike-only lakes). The positive relationships in the pike-only lakes may be due to a shift from pelagic to littoral feeding habits. Based on SCA, only pike under 140 mm in these lakes consumed Chaoboridae, which typically have more depleted $\delta^{13}\text{C}$ signatures, due to a pelagic food base (France 1995). Kiriluk et al. (1995) also found a correlation between $\delta^{13}\text{C}$ and fish size in lake trout, which also reflected a habitat-related switch in feeding, from benthic to pelagic prey, as the fish matured.

The lack of a relationship between total length and $\delta^{13}\text{C}$ in SPH200 (pike-only) indicated that although large and small pike were at different trophic levels in this lake, they all consumed organisms that use the same, primarily littoral, carbon source. SCA did reveal that some of the small pike consumed chaoborids, but SIA suggested that this was likely a recent, seasonal phenomenon, perhaps related to chaoborid emergence. Similar seasonality of feeding on invertebrates has been documented for pike in Tucker Lake, Alberta (Chapman et al. 1989) and for a nearby boreal population of fathead minnows (*Pimephales promelas*) (Price et al. 1991). As well, chaoborids were also consumed by large pike in SPH200, minimizing size-related impacts on $\delta^{13}\text{C}$ signatures. If cannibalism was the major contributor to the relationship between $\delta^{15}\text{N}$ and size in SPH200, cannibalism would not have contributed to any corresponding relationship with $\delta^{13}\text{C}$.

Individual specialization

As noted, there was considerable individual variation in both the longer-term trophic ecology (SIA) and short-term diets (SCA) of pike within assemblage types (pike-only and pike-other) and even within individual assemblages. The short-term diet variation was partic-

ularly characterized by individual specialization, i.e., some pike that had only fish in their stomachs and others that had only invertebrates. Due to the long-term, integrative nature of SIA (Hesslein et al. 1993), there is no direct cause-and-effect relationship between a fish's immediate diet, documented by SCA, and its isotope signature; it is therefore interesting that individuals that had recently eaten only invertebrates had lower $\delta^{15}\text{N}$ signatures than the recently piscivorous pike. This integration of short- and long-term assessment of an individual's trophic ecology is a potentially important advantage of combining SIA and SCA techniques in the study of individual variation within populations. Our results suggest that individual differences in short-term diets at least partially reflect longer-term trophic differences, i.e., many of the pike in these lakes were not simply consuming invertebrates opportunistically, but were long-term invertebrate specialists. Such individual specialization may be similar to the food specialization of individual trout observed by Bryan and Larkin (1972). Long-term specialization on invertebrates could have important bioenergetic consequences for such pike, given the higher costs and lower rewards of feeding on small prey (e.g., Hart and Connellan 1984; but see Werner et al. 1981). Overall, it appears that pike in pike-only lakes grow more slowly than those in pike-other assemblages (P. Aku and W. Tonn, unpublished work) but whether the intrapopulation specialization on invertebrates or fish have similar growth consequences is not known.

Similarities between pike-only and pike-other assemblages

The widespread within-lake variation in the trophic ecology of individual pike resulted in a number of population-level similarities between pike in pike-only and pike-other assemblages. SIA indicated that prey of pike comprised both invertebrates and fish in two of three lakes for which SIA of prey was performed. The range of isotope signatures of pike and their positions relative to those of basal consumers were similar in LLB20 (pike-other) and SPH200 (pike-only), suggesting that the average trophic position of pike in these two lakes was comparable and represented a gradient of individuals that spanned two trophic levels. SCA confirmed the use of invertebrate prey in all five study lakes, regardless of the presence or absence of other species of fish. Indeed, the RI indicated that invertebrates had greater dietary importance than fish in all five study lakes. However, whenever piscivory was documented by SCA (LLB20, SPH20, and SPH200), fish always contributed more to the percent mass of prey, and most likely to the high $\delta^{15}\text{N}$ of some (LLB20, SPH200) or all (SPH20) individuals.

We expected that cannibalism would be more important in pike-only lakes, compared with the pike-other lakes, because it is thought to occur mainly when

other food is scarce or unavailable (Frost 1954; Smith and Reay 1991; Hobson and Welch 1995). Based on SIA and SCA, cannibalism by pike was indeed evident in the pike-only SPH200. Surprisingly, however, cannibalism was also important in LLB20 (pike-other), indeed, was more important than feeding on perch. The prevalence of cannibalism in LLB20 might be explained by the size distribution and numbers of prey fish in the lake. Compared with the second pike-other lake, SPH20, the catch per unit effort (CPUE) of pike in LLB20 was similar (0.4 and 0.5 fish $\text{net}^{-1} \text{h}^{-1}$ in LLB20 and SPH20, respectively) but the CPUE of perch was much lower in LLB20 (0.4 fish $\text{net}^{-1} \text{h}^{-1}$) than in SPH20 (3.0 fish $\text{net}^{-1} \text{h}^{-1}$) (W.M. Tonn, unpublished work). Therefore, it appears that there were considerably fewer alternative fish prey for pike in LLB20 compared with SPH20. As well, perch were larger in LLB20 (W.M. Tonn, unpublished work) and may have been more difficult for pike to capture and consume (Hart and Hamrin 1988).

Complementarity of SIA and SCA

Our study is one of the few to present comparative data on dietary and isotopic analyses of the trophic ecology of a consumer species, using data from the same ecosystems. Fewer still are comparative studies in ecosystems that span a wide range of prey assemblage composition, or that could compare SIA and SCA from the same individuals. SIA and SCA supplied us with different, but complementary, information on the diets of pike. Isotopic signatures of adult pike likely reflect diets integrated over the past year or so (Hesslein et al. 1993), whereas SCA indicated what pike consumed just prior to being captured. Integrating the two approaches allowed us to document convincingly interpopulation differences, individual variation, and even individual specialization in the trophic ecology, extending our knowledge and understanding of trophic adaptability in northern pike. Chapman et al. (1989) had previously documented the existence (and sometimes the frequent occurrence) of invertebrate feeding by pike. Unfortunately, their stomach content data were limited to frequency of occurrence and thus they could not assess the relative importance of invertebrate prey. However, our complete SIAs (LLB20, SPH20, SPH200) showed clearly that many pike in SPH200 (pike-only), and even some individuals in LLB20 (pike-other), had isotope signatures consistent with a diet based primarily on invertebrates. SCA generally, but not always, supported SIA and vice versa. Discrepancies between the two approaches primarily involved the importance of specific invertebrate or fish taxa, e.g., the importance of yellow perch versus white suckers in SPH20. Such mismatches were likely due to short-term, seasonal opportunism in feeding, another facet of trophic adaptability that has been documented previously in pike (e.g., Lawler 1965).

Conclusions

Winter hypoxia is a common feature in the naturally productive lakes of boreal Alberta (Nelson and Paetz 1992); the isolation of the lakes and the high tolerance of pike to this stress relative to other large-bodied species can result in the occurrence of pike-only fish "assemblages" in this region. The trophic adaptability (*sensu* Gerking 1994) that we have documented for pike should contribute to their ability to maintain populations in such lakes. However, the bioenergetic costs and resulting effects on growth, reproduction, and population dynamics in such biotically challenging environments are unknown. Given the assemblage-level effects on the trophic ecology of pike that we have documented, and the potential occurrence of invertebrate-feeding specialists suggested by our data, a valuable next step would be to relate mechanistically the performances of both individual pike and pike populations to resource availability, and identify the behavioral and/or bioenergetic strategies (e.g., Diana 1983) employed by pike across this disturbance-induced biotic gradient. Although the mechanistic details of the tactics (e.g., thrust and strike) of pike piscivory are known (e.g., Webb and Skadsen 1980), behavioral studies are needed to help us identify how pike can alter these tactics to allow them to succeed, if not thrive, on a diet of invertebrates. Such studies would allow us to better understand the opportunities and consequences of trophic flexibility in pike, and ultimately understand and predict how the food webs in small lakes in the mixed-wood boreal forest are affected by, and recover from, winter hypoxia or other disturbances in these ecosystems.

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