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[Article]

Diet and Growth of Northern Pike in the Absence of Prey Fishes: Initial Consequences for Persisting in Disturbance-Prone Lakes

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Abstract.—The northern pike *Esox lucius* is a renowned piscivore, but will prey opportunistically on invertebrates (e.g., in small lakes of boreal Alberta, where winterkill can unexpectedly reduce or eliminate prey fishes). We emulated such a disturbance by stocking a fishless lake with northern pike and then monitored their diet and growth over two summers. Stomach content analysis revealed that stocked adults responded to the sudden absence of prey fishes by specializing on energy-rich leeches (families Glossiphoniidae and Erpobdellidae), whereas juvenile offspring consumed a broader mix of invertebrates. Stable isotope analysis supported these results and indicated a relatively rapid drop in the trophic position of stocked adults. Compared with growth of northern pike in regional lakes containing prey fishes, growth of adults in the experimental lake was apparently compromised by a diet of invertebrates but growth of juveniles was high. Although long-term dynamics of northern pike in these disturbance-prone lakes are undocumented, our results suggest that northern pike are capable of adapting rapidly to the absence of prey fishes; however, such a diet imposes a trophic bottleneck that can lead to stunting.

The northern pike *Esox lucius* is considered to be piscivorous throughout most of its circumpolar range (Casselman 1996). Indeed, the morphology and behavior of northern pike are specialized for ambushing fish prey from the cover of vegetation (Keast and Webb 1966; Webb 1984; Bry 1996). Not surprisingly, numerous studies have shown northern pike to specialize on fish prey (Frost 1954; Franklin and Smith 1963; Vander Zanden et al. 1997; and references therein). Consumption of large fishes is particularly important for growth (Hart and Connellan 1984; Diana 1987; Margenau 1995).

Despite the piscivorous nature of northern pike and the advantage of piscivory for growth, predation on invertebrates (invertivory) has been documented, particularly in naturally productive systems in northwestern North America. Periodic bouts of invertivory among otherwise piscivorous northern pike up to 600 mm in length (Chapman et al. 1989; Chapman and Mackay 1990; Sammons et al. 1994; Lorenzoni et al. 2002) have been attributed to differences in the seasonal availability of vertebrate and invertebrate prey. In other systems, predation on macroinvertebrates appears more consistent (e.g., Beaudoin et al. [1999] identified invertebrate specialists in two populations of otherwise piscivorous northern pike on the basis of complementary stomach content analysis [SCA] and stable isotope analysis [SIA]). Such trophic flexibility (Gerking 1994) is probably advantageous because of dynamic prey environments (Dill 1983). Disturbances (e.g., winterkills) are common in many small, naturally productive boreal lakes (Danylchuk and Tonn 2003). However, because northern pike are more tolerant of winter hypoxia than other large-bodied fishes on which they feed (Magnuson and Karlen 1970; Casselman 1996), northern pike can be found in lakes void of forage fishes (Robinson and Tonn 1989). Populations of northern pike in these lakes probably persist, in part, because of an opportunistic feeding strategy (Chapman and Mackay 1990; Beaudoin et al. 1999). Indeed, invertivory is most prevalent among adult northern pike in allopatric lakes (lakes in which northern pike occur in the absence of prey fishes; Beaudoin et al. 1999).

Unclear, however, is the initial dietary response of northern pike to sudden allopatry, as would occur after a major winterkill (Tonn et al. 2004). Also unknown is the energetic cost of the response and how this cost affects growth. Northern pike are opportunists, but they are also relatively poor learners (Coble et al. 1985). An abrupt dietary switch from large to small prey (e.g., from piscivory to invertivory) might reduce net energy intake per unit time, at least initially (Schoener 1971; Werner et al. 1981; Gerking 1994; Pazzia et al. 2002), and translate into lower growth.

In this study, we emulated sudden allopatry caused by winterkill by stocking piscivorous northern pike into a fishless lake, while simultaneously monitoring other populations in lakes containing prey fishes, to

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determine the (1) initial dietary response of the stocked northern pike and their juvenile offspring and (2) consequences for growth of adult northern pike and their offspring. This research is particularly relevant, given the increasing prevalence of anthropogenic disturbances (e.g., forestry and oil and gas exploration) in the boreal region (Timoney 2003). These disturbances not only increase the accessibility of small, remote lakes to fishers and other recreational users but might also affect the frequency or severity of winterkill (Devito et al. 2000; Schindler 2001) and, therefore, the dynamics of both predators and prey (Tonn et al. 2004; Venturelli and Tonn 2005). Effective management of these developing fisheries requires, in part, that we understand how disturbance-mediated patterns in diet and growth affect the dynamics of populations of northern pike.

Methods

Experimental design.—Our experiment was conducted in three small, shallow, naturally eutrophic lakes in a remote region of the mixed-wood boreal forest of northeast Alberta (Figure 1). The two reference lakes in this study, R1 (103.5 ha in area, 8 m in maximum depth) and R2 (61.6 ha, 4.5 m), were dominated by northern pike and yellow perch *Perca flavescens*. The experimental lake (EXP; 13 ha, 5.2 m) had been fishless for at least 6 years after a suspected winterkill (W.M.T. and coworkers, unpublished data). During summer 2000 (May–August), we conducted monthly monitoring of (1) diet and growth of northern pike (in the reference lakes only, details below) and (2) abundance and biomass of macroinvertebrates in the 1.0–1.5-m depth zone of each lake (see Venturelli and Tonn 2005 for details). In May 2001, we collected northern pike ($N = 355$; mean total length [TL] $\pm$ SE $=$ 587 $\pm$ 2.5 mm; mean mass $\pm$ SE $=$ 1,148 $\pm$ 12 g) from nearby Piche Lake (518 ha, 18 m), which also contained the following species: yellow perch, walleye *Sander vitreus*, white sucker *Catostomus commersoni*, brook stickleback *Culaea inconstans*, and various cyprinids; we then introduced northern pike from this lake into EXP to achieve a biomass density of approximately 35 kg/ha. Northern pike were individually tagged with plastic anchor tags. Sampling continued in the three study lakes throughout 2001 and 2002. To prevent winterkill of northern pike in EXP, we visited the lake twice per month (December 2001–March 2002) to clear the ice of snow and aerate the water with compressed air (Venturelli and Tonn 2005).

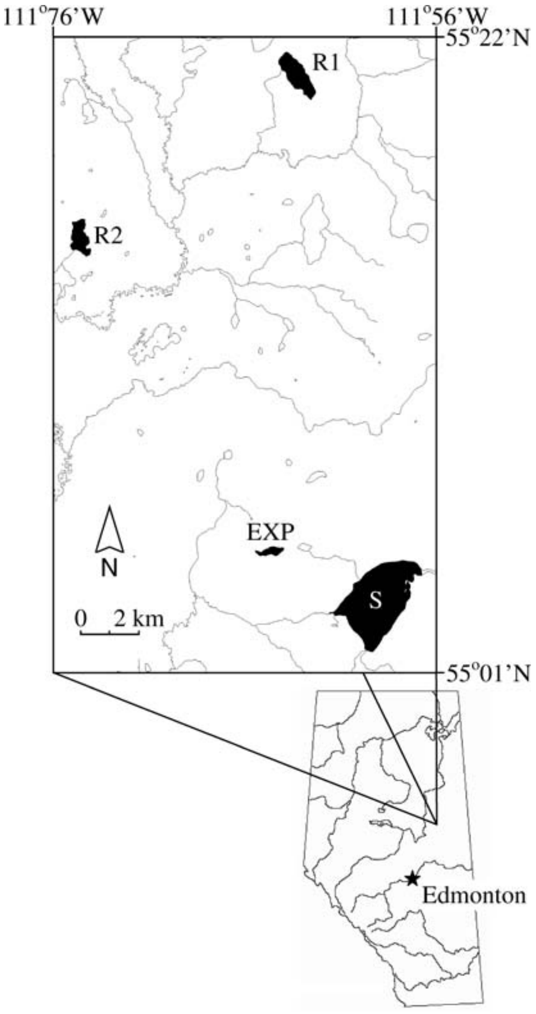

FIGURE 1.—Map of Alberta, showing location of study lakes (inset): Reference Lake 1 (R1; 55°20′N, 111°64′W); Reference Lake 2 (R2; 55°15′N, 111°76′W); Experimental Lake (EXP; 55°05′N, 111°65′W); and Piche Lake (source [S] lake; 55°03′N, 111°60′W).

Stable isotope analysis.—Stable isotope analysis is a means of describing the trophic structure of food webs by comparing isotopic signatures of constituent organisms (Post 2002). In this study, we used stable isotopic ratios of carbon ($^{13}C/^{12}C$) and nitrogen ($^{15}N/^{14}N$) to compare the trophic positions of northern pike in EXP and the source lake.

Samples for SIA were collected in 2002 from EXP (late July) and Piche Lake (early August). Lymnaeid snails, amphipods (*Gammarus lacustris* and *Hyallela azteca*), and erpobdellid leeches (hereafter, "leeches") were handpicked or netted from littoral habitats and kept alive for 24 h to allow for evacuation of gut contents. We captured northern pike and yellow perch with gill nets and hook and line. Blood was collected from the caudal vein of adults. White muscle tissue was used in SIA of yellow perch and young-of-the-year (age-0) northern pike. Samples were frozen in the field and transported to the laboratory. We removed inorganic carbon from thawed macroinvertebrate samples by soaking them in 1 M HCl for 24 h (or until bubbles no longer appeared). Each specimen was then air dried for approximately 48 h, homogenized with a mortar and pestle, weighed to 1.0 ± 0.1 mg, and sealed in a 5- × 8-mm tin capsule. We used composite, taxon-within-lake samples when individual specimens did not meet the target mass.

Up to five replicate samples of each taxon were analyzed at the National Water Research Institute, Saskatoon, by means of an online, continuous-flow, isotope-ratio mass spectrometer calibrated to reference standards (Pee Dee belemnite limestone and atmospheric nitrogen). Isotope ratios are expressed in delta (δ) notation as parts per thousand (‰) deviation from standard with the formula

$$\delta^{13}\mathrm{C} \text{ or } \delta^{15}\mathrm{N} = [(R_{\mathrm{sample}} - R_{\mathrm{standard}})/R_{\mathrm{standard}}] \times 1{,}000,$$

where $R = {}^{13}\mathrm{C}/{}^{12}\mathrm{C}$ or ${}^{15}\mathrm{N}/{}^{14}\mathrm{N}$ (Gearing 1991).

Trophic position (λ) of northern pike in Piche Lake was calculated as

$$\lambda_p = \lambda_s + (\delta^{15}\mathrm{N}_p - \delta^{15}\mathrm{N}_s)/3.4,$$

following Post (2002), where subscripts p and s refer to northern pike and a baseline invertebrate herbivore (here, snails), respectively. We calculated trophic position of northern pike in EXP by means of a modified version of this equation (a two-end-member mixing model; Post 2002) to account for ambiguity in the baseline nitrogen in this system, vegetative (snails) versus detrital (amphipods).

Stomach content analysis.—We used multimesh gill nets (45.5 m long × 1.5 m deep; bar mesh sizes of 6.25, 8, 10, 12.5, 16.5, 22, 25, 30, 33, 43, 50, 60, and 75 mm) to collect up to 20 stomach samples per month (May–August of 2000–2002) from northern pike in the littoral zones of R1 and R2. Samples were collected in late morning or early afternoon and limited to recently captured northern pike to minimize errors associated with the digestion or regurgitation of prey. Using a nonlethal flushing technique similar to Light et al. (1983), a maximum of 20 stomach samples per month were also obtained from adult northern pike angled in EXP (2001 and 2002). The better than 97% efficiency of prey removal reported by Light et al. (1983) was supported in this study by preliminary data on northern pike from the reference lakes. Age-0 northern pike were captured in EXP in 2002 with overnight and daytime sets of Gee minnow traps and fyke nets. Due to the difficulty in applying the flushing technique to small fish (Hyslop 1980), age-0 northern pike were sacrificed and their stomachs dissected. Diet samples were preserved in a 10% solution of formalin, and prey were later identified to the lowest practical taxonomic level. Each taxon was then enumerated, individuals were measured, and their dry mass was estimated by means of length–dry mass regressions (see Venturelli and Tonn 2005 for details).

TABLE 1.—Caloric density of prey taxa consumed by adult and juvenile northern pike in northeast Alberta lakes. Values represent the mean of a range in some cases. The caloric density of fish prey was calculated by averaging values for adult and juvenile yellow perch.

Prey taxon	Energy density (cal/mg dry mass)
Hirudinids	5.67[a]
Snails	4.34[a]
Amphipods	4.07[a]
Ephemeropterans	5.69[a]
Anisopterans	4.07[b]
Zygopterans	5.35[b]
Hemipterans	4.82[b]
Trichopterans	5.00[b]
Coleopterans	5.37[b]
Dipterans	4.93[a]
Cladocerans	5.46[a]
Anurans	1.64[b]
Fishes	4.86[a]

[a] Hanson et al. (1997).

[b] Cummins and Wuychuck (1971).

Stomach content analyses were limited to those prey taxa that occurred in more than one stomach sample from any lake over the duration of the study. Frequency of occurrence and percentage composition of prey taxa by number and dry mass were used to determine the relative importance (George and Hadley 1979) of prey taxa to adult (>450 mm TL) and juvenile (<330 mm TL) northern pike in each lake and year. Relative importance for R1 and R2 was averaged further to obtain overall reference means against which to compare results from EXP.

The average energy content (EC) of adult and juvenile diets was calculated as

$$\mathrm{EC} = \sum_{j=1}^{n} \left(m_j \times e_j\right),$$

where m_j = the proportion, by dry mass, of prey type j in the diet and e_j = the energy density of prey type j (Table 1). To estimate the potential for within-lake competition between adults and juveniles and to compare diets between lakes, we measured diet overlap by means of the simplified Morisita index (C_H; Krebs 1989):

$$C_{\mathrm{H}} = \left(2 \times \sum_{i=1}^{n} p_{ij} \times p_{ik}\right) \Big/ \left(\sum_{i=1}^{\mathrm{n}} p_{ij}^2 + \sum_{i=1}^{n} p_{ik}^2 \right),$$

where p_{ij} and p_{ik} = the proportion of prey type i in diet j and k, respectively. We estimated diet breadth (DB; macroinvertebrate prey only) in the experimental and reference lakes as

$$\mathrm{DB} = \sum_{j=1}^{n} \sqrt{(p_j \times a_j)},$$

where p_j = the proportion of prey type j in the diet and a_j = the proportion of prey type j in the environment (Krebs 1989). The frequencies of empty adult and juvenile stomachs were averaged for each year according to lake type (EXP or reference). We employed the two-tailed Fisher's exact test to test the null hypothesis that empty stomachs were equally frequent in EXP and the reference lakes.

Estimated and observed growth of northern pike.— Cleithra collected from up to 100 northern pike per lake in July of each year (2000–2002) from gill-net surveys conducted in R1 and R2 were used by Dr. Peter Aku (Alberta Conservation Association) to develop lake-specific regression equations relating length of cleithra (anterior radius [AR]) to TL of northern pike. For R1,

$$\mathrm{TL} = 10.627 \times \mathrm{AR} - 0.159 (R^2 = 0.9831; n = 141),$$

and for R2,

$$\mathrm{TL} = 10.842 \times \mathrm{AR} - 0.472 (R^2 = 0.9792; n = 111).$$

Radius length was measured from the origin to the posterior edge of each annulus (A) along the AR with a digital caliper interfaced with a computer. Back-calculated length at age for individual fish was obtained by substituting A for AR in the regression equations. We combined these data with similar data from R1 and R2 in 1996 and 1997 (P. Aku and W.M.T., unpublished data) to determine a length-at-age profile for the reference lakes. For each age in this profile, we then calculated the percentage increase in TL. Age-specific growth rates were similarly developed from approximately 300 northern pike from three allopatric populations sampled in this region in 1996 and 1997 (P. Aku and W.M.T., unpublished data).

Based on the length-at-age profile of northern pike from the reference lakes, we estimated that northern pike introduced into EXP ranged in age from 4 to 8 years. Growth of these individuals 1 year after introduction was measured directly with recapture data from May 2002 (n = 54) and was expressed as percentage increase in TL. We then compared annual growth in EXP to the average growth increment of northern pike of ages 4–8 in regional lakes with and without prey fishes. Length at age 1 for juveniles in EXP (measured in early July 2003) was similarly compared with estimated length at age 1 for juveniles in reference and allopatric lakes. Statistical tests were not used in either comparison because values were obtained with dissimilar methods (i.e., measured from individuals in EXP, but estimated from populations in other lakes).

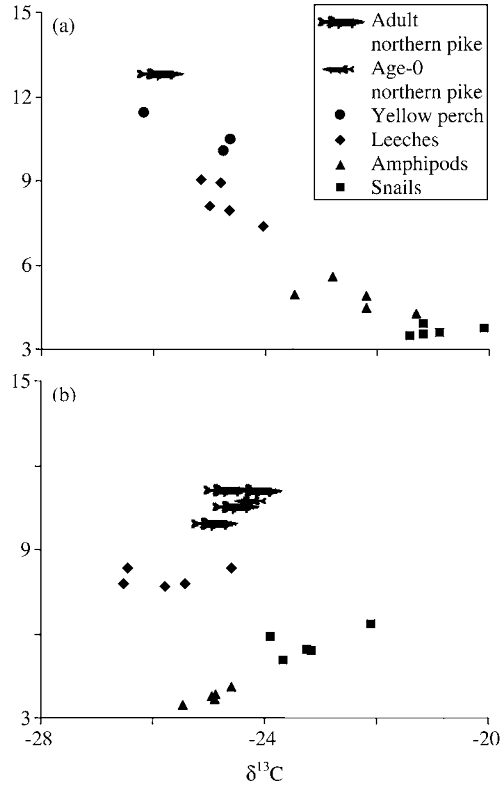

FIGURE 2.—Scatterplots of stable carbon ($\delta^{13}C$; ‰) and stable nitrogen ($\delta^{15}N$; ‰) isotopic signatures of northern pike, yellow perch, and macroinvertebrates in northeast Alberta lakes, **(a)** Piche Lake and **(b)** the experimental lake, sampled during late July and early August 2002.

Results

Diets of Northern Pike

Based on SIA, adult northern pike in Piche Lake were positioned at the top of the food web (Figure 2a). The long-term diet of these northern pike consisted of yellow perch and, given their low $\delta^{13}C$ signature, probably other unsampled pelagic fishes (see France 1995). This diet corresponded to a trophic position of 4.7. In EXP, isotopic signatures of adult and age-0 northern pike were similar (Figure 2b) and suggested that these northern pike were also the top predators in this food web. The trophic position of northern pike in EXP was estimated at only 3.9.

Stomach content analysis identified leeches (Erpob-

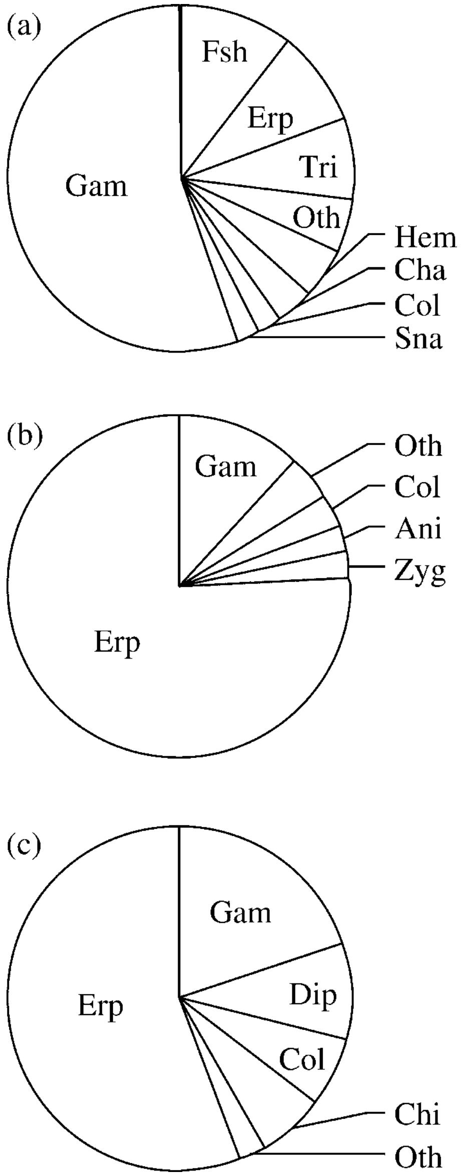

FIGURE 3.—Relative importance of prey taxa in diets of adult northern pike (>450 mm TL) collected from northeast Alberta lakes (see Figure 1): **(a)** two reference lakes (average of years and lakes), **(b)** the experimental lake in 2001, and **(c)** the experimental lake in 2002. Sample size information appears in Table 3. Taxa include anisopterans (Ani), *Chaoborus* spp. (Cha), chironomids (Chi), coleopterans (Col), dipteran pupae (Dip), erpobdellid leeches (Erp), fishes (Fsh), gammarids (Gam), hemipterans (Hem), snails (Sna), trichopterans (Tri), and "zygopterans (Zyg). Other (Oth) indicates prey taxa with a relative importance less than 2.00 (reference lakes: adult frogs, anisopterans, chironomids, dipteran pupae, and zygopterans; experimental lake 2001: chironomids, dipteran pupae, and trichopterans; experimental lake 2002: adult frogs, *Chaoborus* spp., and larval frogs).

dellidae) as the dominant prey of adult northern pike from EXP in 2001 and 2002 (Figure 3). Of secondary importance was the amphipod *G. lacustris*, along with coleopterans and dipterans. Although *G. lacustris* became more important (and leeches less so) in 2002, both EC (Table 2) and overlap (Table 3) of the 2001 and 2002 diets were high. In 2002, diets of age-0 northern pike in EXP were dominated by *G. lacustris*; secondary prey were zygopterans, chironomids, and two families of leeches (Glossiphoniidae and Erpobdellidae; Figure 4). These diets contained less energy per unit mass and were broader than diets of adults (Table 2). Overlap of juvenile and adult diets in EXP in 2002 was moderate (Table 3).

The amphipod, *G. lacustris*, was the dominant prey in the reference lakes; fishes, leeches, and larval trichopterans were of secondary importance (Figure 3). This diet contrasted sharply with that of adults in EXP in 2001, but less so in EXP in 2002 (Table 3). Diets of adult northern pike from the reference lakes contained consistently less energy but were broader than those from EXP, although the latter broadened their diet in 2002 (Table 2). The mean annual frequency of empty stomachs of adult northern pike in EXP (13 of 43) was not significantly different than that in the reference lakes (1 of 9; Fisher's exact test: $P = 0.415$). Diets of juveniles from the reference lakes were similar to reference lake adults and EXP juveniles in terms of composition of prey (Figure 4), EC and DB (Table 2), and overlap (Table 3). The mean annual frequency of empty stomachs of juvenile northern pike in EXP (0 of 13) and the reference lakes (2 of 13) did not differ ($P = 0.481$).

Growth of Northern Pike

Annual percentage increase in TL of adult northern pike in boreal Alberta lakes that contained prey fishes was estimated from back-calculated length-at-age data as being nearly 2.5 times as great as in regional allopatric lakes (Figure 5a). Observed growth of adults in EXP was only slightly higher than back-calculated growth in allopatric lakes (5% versus 4%). Back-calculated length at age of juvenile northern pike after 1 year in lakes with prey fishes (220 mm) was greater than that in lakes without prey fishes (160 mm; Figure 5b). The largest first-year growth increment, however, was the observed growth among juveniles in EXP, which increased in length to almost 320 mm.

Discussion

Dietary Responses of Northern Pike to Invertebrate Prey

The trophic level and $\delta^{13}C$ and $\delta^{15}N$ signatures of the northern pike in Piche Lake were similar to those

TABLE 2.—Mean sample size, total length (TL; mm), and diet characteristics of adult (>450 mm TL) and juvenile (<330 mm TL) northern pike from the two reference lakes (REF; average of years [2001–2002] and lakes) and the experimental lake (EXP) in northeast Alberta.

Lake	Sample size (mean/year)	TL Mean ± SE	TL Range	Diet energy (cal/mg dry mass)	Frequency of empty stomachs/year	Diet breadth
Adults						
REF	9	516 ± 18.41	451–694	4.34	1	0.81
EXP (2001)	36	615 ± 11.43	490–798	5.55	9	0.30
EXP (2002)	50	619 ± 6.57	534–705	5.30	17	0.45
Juveniles						
REF	13	273 ± 6.36	147–329	4.34	2	0.90
EXP (2002)	13	123 ± 11.23	73–195	4.85	0	0.79

reported for other large, piscivorous northern pike in boreal Alberta (Beaudoin et al. 1999, 2001; Paszkowski et al. 2004). This trophic level was, however, 0.8 positions higher than that of the northern pike from Piche Lake after their introduction into the fishless EXP. This change is consistent with results of Vander Zanden et al. (1997) and Beaudoin et al. (2001), which suggest that invertivorous populations of northern pike feed 0.5–1.5 trophic positions below piscivorous conspecifics (our calculations). Similarly, lake trout *Salvelinus namaycush* dropped 0.6 trophic positions over 10 years as they became planktivorous in response to introduced competitors (Vander Zanden et al. 1999).

A potential source of error in our estimate of trophic change was a difference in sources of energy as a function of lake size. As lake size increases, external (littoral) production becomes less important and internal (pelagic) production more so (France 1995; Post 2002). The lighter $\delta^{13}C$ signature of northern pike relative to littoral consumers in Piche Lake is typical of large lakes and suggests an additional unsampled source of pelagic carbon. Since the $\delta^{15}N$ of primary consumers increases with decreasing $\delta^{13}C$ (Vander Zanden and Rasmussen 1999), our use of a littoral $\delta^{15}N$ baseline might have overestimated the trophic position of northern pike in Piche Lake. To correct for this, we assumed a −4.6‰ $\delta^{13}C$ and +1.6‰ $\delta^{15}N$ difference for a pelagic baseline relative to a littoral baseline (Vander Zanden and Rasmussen 1999) and assumed that both habitats were represented equally in diets of northern pike (but see Vadeboncoeur et al. 2002). We incorporated this pelagic baseline into our estimate of trophic position by means of a two-end-member mixing model (Post 2002). Results suggest that northern pike in EXP might have dropped only 0.3 positions. On the other hand, rates of isotopic turnover in the blood and muscle of fishes can be as long as 450 d (Herzka 2005) and are highly dependent on growth (Harvey et al. 2002). Given that we sampled adult northern pike in EXP roughly 400 d after introduction, 0.3 might represent a conservative estimate of change in trophic position. Regardless, a 0.3–0.8 change is substantial given the duration of our experiment, and suggests that isotopic signatures of adults can respond relatively rapidly to dramatic changes in diet, as would result from disturbance events.

According to SCA, adult northern pike adjusted to allopatry by preying heavily on large leeches. Leeches are not usually important in diets of northern pike (Chapman and Mackay 1990; Sammons et al. 1994; Beaudoin et al. 1999, 2001), probably owing to a combination of their small size relative to prey fishes and low availability in systems with fish. Leeches, however, represent a large, easily digested, high-energy alternative to other macroinvertebrates (Table 1). Given that these leeches were abundant in EXP (Venturelli and Tonn 2005), probably owing to the prolonged absence of fish predators, the importance of leeches in

TABLE 3.—Matrix of dietary overlap (Morisita index) between adult (>450 mm) and juvenile (<330 mm) northern pike from two reference lakes (REF; average of years [2001–2002] and lakes) and the experimental lake (EXP) in northeast Alberta.

Life stage	Lake	Adults REF	Adults EXP (2001)	Adults EXP (2002)	Juveniles REF	Juveniles EXP (2002)
Adults	REF	1.000				
	EXP (2001)	0.23	1.000			
	EXP (2002)	0.40	0.93	1.000		
Juveniles	REF	0.95	0.12	0.21	1.000	
	EXP (2002)	0.84	0.24	0.44	0.91	1.000

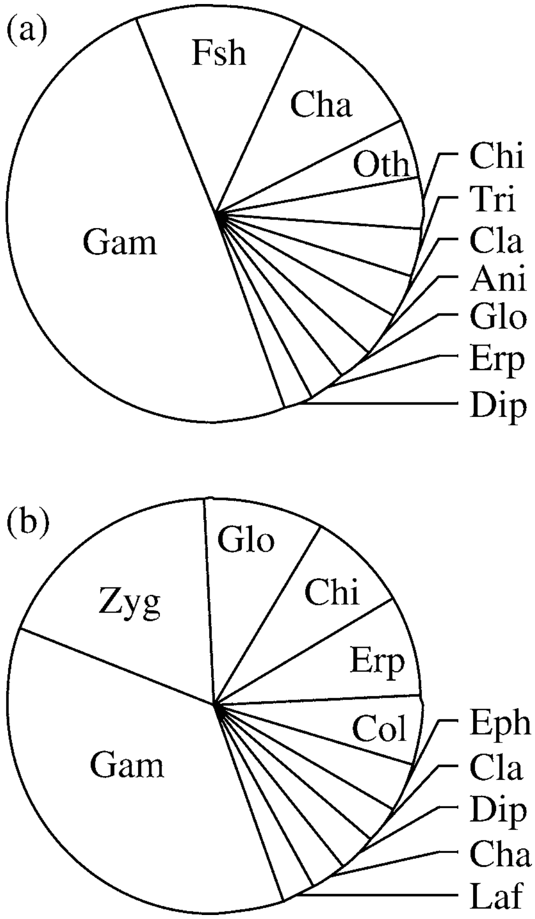

FIGURE 4.—Relative importance of prey taxa in diets of juvenile northern pike (<330 mm TL) collected from northeast Alberta lakes (see Figure 1): **(a)** two reference lakes (average of years and lakes) and **(b)** the experimental lake in 2002. Sample size information appears in Table 3. Taxa include anisopterans (Ani), *Chaoborus* spp. (Cha), chironomids (Chi), cladocerans (Cla), coleopterans (Col), dipteran pupae (Dip), ephemeropterans (Eph), erpobdellid leeches (Erp), fishes (Fsh), gammarids (Gam), glossiphoniid leeches (Glo), larval frogs (Laf), trichopterans (Tri), and zygopterans (Zyg). Other (Oth) indicates prey taxa with a relative importance less than 2.00 (reference lakes: coleopterans, ephemeropterans, snails, and zygopterans).

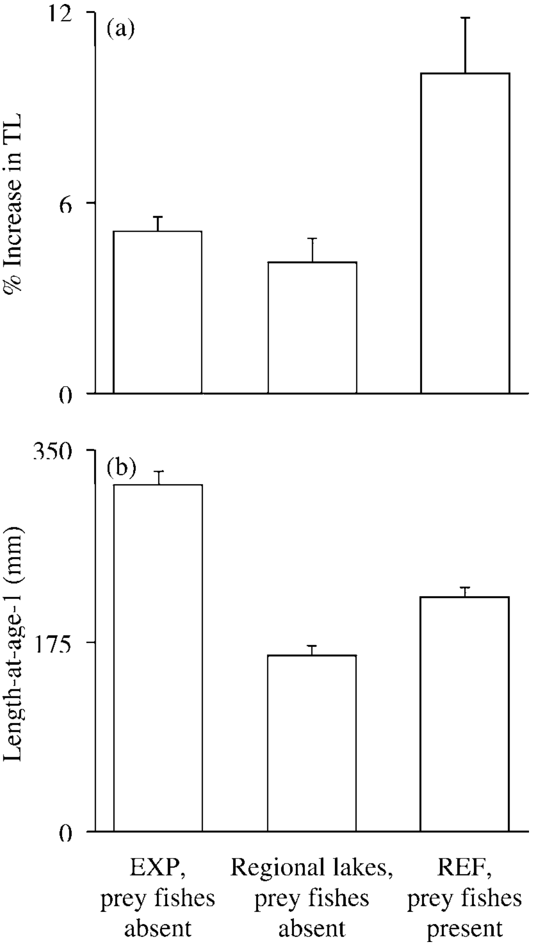

FIGURE 5.—Observed (experimental lake; EXP) and back-calculated growth in TL of **(a)** 4–8-year-old adult (>450 mm) northern pike (mean percentage increase in TL) and **(b)** juvenile northern pike (length at age 1). Growth is from individuals for EXP, populations for regional lakes, and lake-years for reference lakes (REF). Back-calculated growth in regional lakes and REF includes data from P. Aku and W. M. Tonn (unpublished; see Methods for details). Standard error bars are for illustrative purposes only. Data were not used in statistical analyses.

diets of northern pike in 2001 and 2002 further indicates that the stocked population adjusted rapidly to allopatry with a diet that optimized energy intake per unit time (Gerking 1994).

Examining the diet of northern pike in the two reference lakes (both containing prey fishes) was intended as a comparison of foraging strategies of piscivorous and invertivorous northern pike. Surprisingly, however, SCA indicated that adult northern pike in R1 and R2 were largely invertivorous; they preyed mostly on *G. lacustris* but also consumed other macroinvertebrates and some fish. Diet data from reference lakes were, nonetheless, valuable in evaluating the dietary response of northern pike in EXP. For example, given that predators are predicted to become specialists when high-ranking prey are abundant (Schoener 1971; Werner and Hall 1974), the narrow breadth of diet of adult northern pike in EXP relative to the reference lakes further indicated that leeches were a high-ranking, abundant prey in EXP. The relatively broad diets of northern pike in the reference lakes suggests that leeches in these systems were relatively unavailable, probably a result of predation. Indeed, diets of northern pike in EXP in 2002 began to broaden and converge upon the reference lake diet in response to a reduced abundance and biomass of leeches (Venturelli and Tonn 2005).

Interestingly, the frequency of northern pike with empty stomachs in the reference lakes was not significantly different from that in EXP, but was more than half of that observed previously in these systems (Beaudoin et al. 1999). The proportion of empty stomachs in a population of northern pike is inversely related to the importance of invertivory (Diana 1979; Chapman et al. 1989; Beaudoin et al. 1999), as northern pike must consume small invertebrate prey more frequently to meet their energy requirements (Chapman et al. 1989). The prevalence of invertivory and the corresponding low frequency of empty stomachs among adult northern pike in both reference lakes suggest that the availability of fish prey was limited. Although age-0 yellow perch appeared to be abundant (P.A.V., unpublished data), this might have been only a recent phenomenon because of winterkill events in R1 (“L800” in Tonn et al. 2004) and R2 (W.M.T. and coworkers, unpublished data). Alternatively, areas of dense macrophytes in these systems might have provided refuge for yellow perch while supplying adult northern pike with an abundance of invertebrates (Diehl 1993).

Unlike adult northern pike, age-0 northern pike in EXP did not specialize on leeches but exhibited a more diverse diet that included the amphipod *H. azteca*, zygopterans, and glossiphoniid leeches. This diet was, however, similar to that of juveniles in another nearby allopatric lake ($C_H = 0.9$; Beaudoin et al. 1999; our calculation) and our reference lakes. Juveniles in the reference lakes might not have consumed more leeches and fishes for the same reasons as adult northern pike (see above). Equally plausible is that age-0 northern pike were selecting from a larger range of prey types and sizes than adults because (1) invertebrate taxa are more likely to be detected by age-0 northern pike, (2) net energy gain for small predators tends to vary less with size of prey (Mittelbach 1981), and (3) age-0 northern pike selected shallow, densely vegetated (and invertebrate-rich) habitats to avoid cannibalism (Grimm and Klinge 1996).

Growth Response of Northern Pike to Invertebrate Prey

Based on EC, diets of adult northern pike in EXP in 2001 and 2002 should have produced more growth than the reference diet, which consisted primarily of *G. lacustris* and to a lesser extent, fish and other macroinvertebrates. However, the observed growth rate of adult northern pike in EXP was low relative to the reference lakes, suggesting that the sudden switch from piscivory to invertivory had a negative effect on growth and that invertivory is not ideal. Indeed, the annual increase in TL of adult northern pike in the reference lakes was about 10%, which compares favorably with a mean of 8% using data from 82 circumpolar water bodies on three continents (Casselman 1996; our calculation). In contrast, annual growth of adults was 4% in our regional allopatric lakes and 5% in EXP . Stunted northern pike have been observed after a prolonged absence of suitably sized prey (Goeman and Spencer 1992; Margenau 1995); our results suggest that invertivory compromises growth of adults in as little as 1 year.

Given the prevalence of invertivory in the reference lakes, it is curious that their adult northern pike exhibited growth that was more indicative of a piscivorous diet. Since piscivory is associated with a relatively low percent daily ration and perhaps lower costs associated with decreased activity (Pazzia et al. 2002), the net energy gained by consuming the occasional prey fish might be greater than expected from a simple measure of the EC of a diet. Furthermore, piscivory was more common in these populations before recent winterkills (Beaudoin et al. 1999; Tonn et al. 2004; W.M.T. and coworkers, unpublished data); thus, our estimated growth from back-calculated length-at-age profiles would have partly reflected this earlier, more-piscivorous diet (P.A.V., unpublished data). In addition, northern pike in these lakes might have preyed more heavily on fishes during the fall and winter, when densities of macrophytes (and, therefore, prey refugia) would be low relative to our sampling period (May–August). Growth of northern pike during winter is possible (Diana and Mackay 1979), but the relative importance of prey fishes in diets during this period has yet to be determined.

Similar to adults, estimated annual growth of juveniles in the reference lakes (about 220 mm) was comparable with the circumpolar average (about 200 mm; Casselman 1996), while the relatively slow growth in regional allopatric lakes suggests that elevated rates of growth are associated with an ontogenetic transition to piscivory (Hunt and Carbine 1951). Surprisingly, observed growth in EXP exceeded both the circumpolar average and reference estimates. The exceptional growth of age-0 northern pike in EXP might reflect a lower degree of intraspecific competition relative to the reference lakes, a higher degree of cannibalism than was indicated by our data, or both.

Conclusion

Winterkill is common in Alberta's Boreal Plains lakes (Danylchuk and Tonn 2003), and the sudden reduction or elimination of prey fishes probably contributes to the prevalence of invertivory by northern pike in these systems (Beaudoin et al. 1999). After their introduction into EXP, northern pike dropped in trophic position and specialized on leeches, which were abundant, relatively large, energy-rich prey. Foraging lower in the food web can mean higher energetic costs and slower rates of growth (Pazzia et al. 2002), however. Invertivory was more than adequate to meet the energy requirements for juvenile growth but limited the growth of adults. Therefore, disturbance-induced invertivory will probably stunt populations in small, boreal lakes by failing to support continued growth of adults, despite high levels of primary production in these habitats. Higher competition with juvenile northern pike for a shared food resource probably exacerbates the stunting of adults (Diana 1987). Data from the regional allopatric lakes suggested that such populations might remain chronically stunted, perhaps as a result of a simple negative feedback in which maximum achievable size is eroded by an increasing scarcity of preferred invertebrate prey. Chronic stunting as a result of competition for food has even been observed in dense populations of piscivorous northern pike and is difficult to reverse (Goeman and Spencer 1992; Margenau 1995).

Effects of food web disturbances, such as winterkill, on growth rates of northern pike can be complex. By reducing the local population of invertivorous fish, winterkill can eliminate optimal (fish) prey but can also allow preferred macroinvertebrate prey taxa to recover from predation (Tonn et al. 2004). These opposing effects demonstrate the need for further research into the relationship between invertivory and growth and how this relationship varies with prolonged or periodic disturbance and allopatry. For example, the paucity of intercohort and intracohort cannibalism among invertivorous northern pike in small, boreal lakes (Beaudoin et al. 1999; this study) is inconsistent with data from other systems (Smith and Reay 1991). Research is also needed to address effects of invertivory and stunting on the reproductive ecology and life history of northern pike (Ylikarjula et al. 1999; Claessen et al. 2002).

Populations of northern pike in these small, once-remote lakes were of little concern to managers 30 years ago. The increased (and increasing) prevalence of local (e.g., resource exploration and extraction) and regional (e.g., climate) disturbances (Schindler 2001; Timoney 2003) has made effective management strategies necessary. Developing and implementing strategies that complement a lake's natural disturbance regime remains a challenge, however, because natural disturbances are by nature unpredictable in both time and space and because the long-term population dynamics of northern pike in these systems have yet to be determined. Until these issues are addressed, we recommend that resource managers err on the side of caution when implementing policies that will affect directly populations of northern pike or their prey or that will otherwise alter a lake's natural disturbance regime via changes in land use (Tonn et al. 2003) or the quality and quantity of lake water (Danylchuk and Tonn 2003).

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