

Invertivory by northern pike (*Esox lucius*) structures communities of littoral macroinvertebrates in small boreal lakes

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Abstract. Recent comparative studies suggest that macroinvertebrates in small Boreal Plains lakes respond to large fluctuations in fish densities caused by winterkill and subsequent recovery even when such fluctuations involve the normally piscivorous northern pike (*Esox lucius*). We introduced pike into a boreal lake made fishless by a past winterkill to isolate experimentally the effects of pike on littoral macroinvertebrates. We compared postmanipulation macroinvertebrate data from the experimental lake (EXP) to premanipulation data from the same lake, to parallel data from 2 unmanipulated reference lakes (R1 and R2) containing pike, and to data from mesocosms within EXP. Pike in all 3 lakes preyed heavily upon macroinvertebrates; diets consisted predominantly of the amphipod *Gammarus lacustris* in R1 and R2 and erpobdellid leeches in EXP. Principal components analysis (PCA) of macroinvertebrate communities distinguished between systems with and without fish and detected a shift in the macroinvertebrate community of EXP and predator-exposed control mesocosms away from large conspicuous taxa (e.g., odonates, coleopterans, and leeches) toward less-conspicuous taxa such as dipterans and trichopterans following manipulation. Responses of individual taxa were generally in agreement with PCA; erpobdellid leeches and odonates showed consistent negative responses to pike. Our study provides experimental evidence at the whole-lake scale that northern pike can affect littoral macroinvertebrates in small boreal lakes, and demonstrates the sensitivity that littoral food webs in these systems can have to changes in the density of fish.

Key words: disturbance, whole lake, mesocosm, predation, Erpobdellidae, *Gammarus*, Alberta, principal components analysis, randomized intervention analysis.

Research into the effects of predation by fish on macroinvertebrate communities has produced conflicting or inconsistent results. Thorp (1986) suggested that these inconsistencies were caused, in part, by the failure of studies to distinguish between 2 distinct roles of predators. Comparative studies of systems with and without fish (e.g., Carlisle and Hawkins 1998) and experiments in which fish were introduced into fishless systems (e.g., Post and Cucin 1984, Stoks and McPeck 2003) tend to identify predators as a cause (*sensu* Thorp 1986) of community structure. Such results are not surprising because they involved invertebrate communities that were assembled and structured in the absence of native fish predators (Wellborn et al. 1996). On the other hand, studies that manipulate densities of native predators typically establish predation as a mechanism that contributes to the regulation (*sensu* Thorp 1986) of community structure (reviewed in Wellborn et al. 1996).

Many of these latter studies, however, are conducted at small scales, e.g., in mesocosms, that have been criticized for having limited relevance at larger scales (Carpenter 1996). Simple comparisons of lakes with fish vs fishless lakes can be misleading because lakes supporting or lacking fish undoubtedly differ in other respects. Studies of dynamic whole-lake systems in which the densities (or presence) of fish predators fluctuate frequently would be more informative. Winterkill and subsequent recovery in lakes of Canada's Boreal Plains can cause annual densities of fish to vary by more than an order of magnitude (Danylchuk and Tonn 2003), and fish might all but disappear for a period of time (Tonn et al. 2004). Based on the results of a natural trajectory experiment (*sensu* Diamond 1986), Tonn et al. (2004) suggested that littoral macroinvertebrates responded strongly to winterkill-induced fluctuations in fish density in lakes dominated by northern pike (*Esox lucius*) and yellow perch (*Perca flavescens*).

Perch are well-known invertivores (e.g., Post and Cucin 1984), but pike are considered specialized piscivores once they reach 80 to 120 mm total length (TL) (Hunt and Carbine 1951, Frost

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1954, Eklöv and Hamrin 1989). However, predation on macroinvertebrates by pike up to 600 mm can be substantial in some systems in western North America. For example, Beaudoin et al. (1999) reported invertivory by adult pike in pike-only lakes in north-central Alberta. Reports of extensive invertivory by adult pike in lakes containing prey fish (Chapman et al. 1989, Chapman and Mackay 1990, Sammons et al. 1994) and the identification of invertebrate specialists within an otherwise piscivorous population (Beaudoin et al. 1999) are more surprising.

Can pike predation structure macroinvertebrate communities in small Boreal Plains lakes? To date, most research on trophic interactions involving northern pike has focused on their role as piscivores (He and Wright 1992, Eklöv and Persson 1996). Eklöv and VanKooten (2001) observed a reduction in macroinvertebrates in mesocosm treatments with pike but ultimately attributed this reduction to a habitat shift by roach (*Rutilus rutilus*). We are not aware of any manipulative study that examined explicitly the relationship between northern pike and their macroinvertebrate prey. The combination of naturally occurring pike-only lakes (Beaudoin et al. 1999) and responses of littoral invertebrates to winterkill and subsequent repopulation of fish predators (Tonn et al. 2004) suggested an experimental approach. We added pike to a lake in the Boreal Plains of Alberta to examine experimentally the effect of invertivory by northern pike on 1) the overall structure of the littoral macroinvertebrate community, and 2) the abundance, biomass, and mean individual size of littoral macroinvertebrate taxa. We compared the results of the manipulation to premanipulation baseline data and to parallel observations in 2 unmanipulated fish-bearing reference lakes. We also conducted a complementary mesocosm experiment in the experimental lake. Our objective was to provide insight into the relationship between pike and macroinvertebrates that could, in turn, identify potential impacts of natural or anthropogenic fluctuations in populations of pike on boreal lake food webs.

Methods

Description of study lakes

We conducted our study in 3 small, shallow, and naturally eutrophic lakes in the mixed-

wood boreal forest of north-central Alberta (Table 1, Fig. 1). Access to all 3 lakes was limited to all-terrain vehicles. The smallest of these lakes, the experimental lake (EXP), had been fishless for ~6 y because of an apparent winterkill (WMT, unpublished data). A discriminant analysis of northern Alberta lakes misclassified EXP as a pike-dominated lake based on a suite of limnological traits (Tonn et al. 2003, WMT, unpublished data). The absence of fish and its manageable size and isolation from other surface waters made EXP an ideal candidate for a whole-lake manipulation. We used 2 nearby lakes, R1 and R2, as unmanipulated reference lakes. Similar populations of yellow perch and northern pike dominated both lakes, and the size structure of pike in these lakes was similar (Table 1). R1 had recovered from a severe winterkill 4 y earlier (Tonn et al. 2004), whereas recent winterkill events in R2 were small or mitigated by immigration of fishes from connecting surface waters (WMT, unpublished data).

Experimental design

We used a before-after-control-impact (BACI) approach in which effects of introduced pike in EXP (summer 2001 and 2002) were compared to baseline data (2000) and to data from the 2 unmanipulated reference lakes (2000–2002). Data in all summers consisted of monthly (May–August) observations of water chemistry, macroinvertebrates, and pike diets (see below). We collected all samples in a given month in ≤ 7 d to minimize temporal variability. We did not sample R1 and R2 in June 2002 because of logistical constraints.

In mid-May 2001, we collected 355 northern pike with gill nets and hook-and-line from a neighboring lake. Pike were transported to the experimental lake, lightly anesthetized with tricaine, weighed, measured (TL), and fitted with numbered anchor tags. Fish were monitored for ~30 min before release into EXP at a biomass density of ~35 kg/ha, which is reasonable for allopatric pike in small, productive, and unexploited lakes in boreal Alberta (C. Davis, Alberta Sustainable Resource Development, personal communication). To prevent winterkill of pike in EXP between postmanipulation summers (2001 and 2002), we visited EXP bimonthly from early December to late March to clear the ice of snow and to aerate the water using compressed air.

TABLE 1. Geographic locations, and physical, chemical, and biological characteristics of the 3 study lakes. Physical data are from Prepas et al. (2001), except surface area of the experimental lake and maximum depth of all lakes (our study). Mean (± 1 SE) total N (TN), total P (TP), and chlorophyll *a* (Chl-*a*) were averaged from monthly samples (May–August) over all summers (2000–2002). Biological data are from our study, except macrophyte dry mass (Tonn et al. 2004). Size structure of pike was calculated from pooled data (2000–2002) in both reference lakes and stocking data in the experimental lake. TL = total length, na = not available, np = northern pike (*Esox lucius*), yp = yellow perch (*Perca flavescens*), ws = white sucker (*Catostomus commersoni*), bs = brook stickleback (*Culaea inconstans*). Species in parentheses were uncommon.

	Lake		
	Experimental	Reference 1	Reference 2
Location (lat, long)	55°05'N, 111°65'W	55°20'N, 111°64'W	55°15'N, 111°76'W
Surface area (ha)	11.5	106.5	61.6
Maximum depth (m)	5.2	7.5	4.0
Mean depth (m)	2.5	na	2.0
TN ($\mu\text{g/L}$)	1747.9 \pm 109.4	1371.6 \pm 189.2	1806 \pm 50.9
TP ($\mu\text{g/L}$)	51.6 \pm 4.1	37.6 \pm 5.1	99.0 \pm 7.1
Chl- <i>a</i> ($\mu\text{g/L}$)	14.0 \pm 4.4	18.7 \pm 6.4	63.4 \pm 9.5
Macrophyte dry mass (g/m^2)	na	2	77
Fish species	np ^a	np, yp, (bs)	np, yp, (ws), (bs)
Pike size structure			
TL (mm)	587 \pm 2.5	361 \pm 6.4	365 \pm 8.3
Range (mm)	475–764	208–841	238–685
<i>n</i>	355 ^b	227	98

^a The experimental lake was fishless in 2000, but contained stocked np in 2001 and 2002
^b Values do not include recruitment that occurred in summer 2002

We conducted a 2-y (2001–2002) mesocosm experiment in EXP to address the lack of replication common in whole-lake experiments (Carpenter 1989). This experiment compared the responses of macroinvertebrates in 4 fishless enclosures to responses in 2 control mesocosms accessible to pike. Fishless enclosures were 3 m wide and extended ~7 m from shore to encompass the 0- to 1-m depth zone. Walls consisted of a vinyl curtain anchored in the sediment and supported above the water surface by a wooden frame. We installed two 30 × 28-cm windows, covered with 1.6-mm bar-mesh screening, in each fishless enclosure to accommodate fluctuating water levels. Control mesocosms were identical in design to fishless enclosures except that 50% of each wall was open to the lake and to pike.

Sample collection

We collected an average of 5 stomachs/mo from adult pike in R1 and R2 (except June 2002) using multimesh gill nets (45.5 m long and 1.5 m deep with bar-mesh sizes 6.25, 8, 10, 12.5, 16.5, 22, 25, 30, 33, 43, 50, 60, and 75 mm). We

set nets perpendicular to shore in 1 to 3 m of water from midmorning to early afternoon (~3.5 h). To minimize errors associated with the digestion or regurgitation of prey, we collected stomachs only from pike that were not showing rigor mortis. We estimate conservatively that our sampling corresponded to an insignificant exploitation rate of 1 to 2%/y (PAV and WMT, unpublished data).

We also obtained an average of 11 samples of stomach contents monthly from adult pike captured by hook and line in EXP in 2001 and 2002. We anaesthetized these pike lightly with tricaine before measuring their length and flushing their stomachs using a nonlethal technique similar to one used by Light et al. (1983); these fish were returned to the lake after recovery. We also applied this flushing procedure to 3 pike gill-netted in R1 and subsequently dissected their stomachs. Efficiency of removal of consumed prey was comparable to the >97% efficiency reported by Light et al. (1983), suggesting that comparisons of diets determined by dissection and flushing were appropriate. We preserved all stomach samples in the field with 10% formalin.

We sampled macroinvertebrates in the littoral

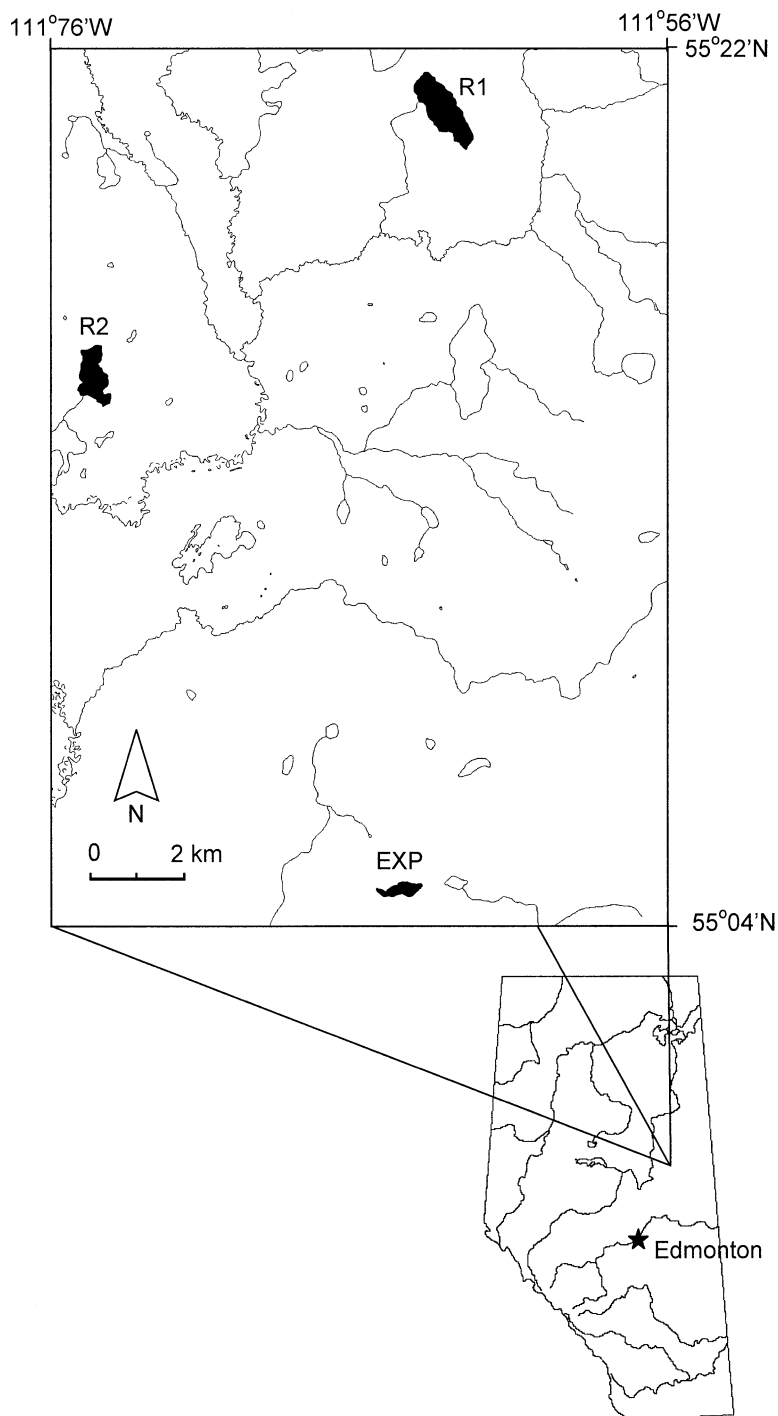


FIG. 1. Locations of the 3 study lakes in Alberta, Canada. R1 = reference lake 1, R2 = reference lake 2, EXP = experimental lake.

zone (1.0–1.5 m in depth) monthly (May–August) at 6 (2000), 12 (2001), and 8 (2002) randomly chosen sites in each lake using a triangular sweep net (30.5 × 30.5 × 30.5 cm, bar-mesh size = 800 × 900 μm, U-shaped surface–bottom–surface sweep). We sampled the same general location using an Ekman grab (225 cm²) and sieved the contents of the grab through a 243-μm-mesh wash bag. The number and frequency of samples in all years was sufficient to capture seasonal variation in boreal Alberta lakes (based on Hanson et al. 1989). We also collected grab and sweep samples from 2 sites in each fishless enclosure and control mesocosm monthly (May–August) in 2001 and 2002. We hand-picked live invertebrates >1 mm (anterior of head to posterior of abdomen) within 24 h of collection using sugar flotation (Lind 1974) and preserved the invertebrates in 70% ethanol.

We collected epilimnetic water monthly with an opaque 1-L sample bottle from a depth of ~0.5 m over the deepest part of each lake and from the centre of each mesocosm. We refrigerated these samples for later analysis.

Laboratory work

Macroinvertebrates in grab and sweep samples and organisms in stomach samples were identified to the lowest practical taxonomic level (usually genus) (Clifford 1991, Nelson and Paetz 1992, Russell and Bauer 2000), enumerated, and measured. If an invertebrate taxon was abundant in a stomach sample or in a given lake-month (grab and sweep samples), we calculated its mean length from a subsample of 40 individuals. We estimated dry mass of invertebrates using published (e.g., Wrona 1982, Burgherr and Meyer 1997, Poepperl 1998, Wilhelm and Lasenby 1998, Benke et al. 1999) and unpublished (G. G. Mittlebach, Michigan State University, personal communication) length–dry mass regressions.

We estimated dry mass of vertebrate prey found in stomach samples using a combination of locally derived length–wet mass regressions (WMT, unpublished data, C. Paszkowski and B. Eaton, University of Alberta, personal communication) and wet mass–dry mass conversions (Ahokas and Duerr 1975, Diana and Mackay 1979, Brown et al. 1988, Churchill and Storey 1994, Hayes and Taylor 1994). We used regression equations of backbone length to TL (Knight

et al. 1984) and operculum length to TL (P. Aku, University of Louisiana at Monroe, personal communication) to estimate lengths of partially digested fishes.

We analyzed water samples for total N (TN), total P (TP), and chlorophyll *a* (Chl-*a*) at the Limnology Services Laboratory, Department of Biological Sciences, University of Alberta, following protocols described in Prepas et al. (2001).

Statistical analysis

Stomach content analysis (SCA).—We restricted SCA in all lakes to pike >450 mm TL for consistency with the sizes of individuals stocked into EXP. We excluded empty stomachs from SCA. We calculated frequency of occurrence and % composition of each prey taxon by number and dry mass (Bowen 1996). We summarized these results by calculating the relative importance (RI) of each prey taxon as

$$RI_a = \frac{100AI_a}{\sum_{a=1}^n AI_a}$$

where *n* is the number of different prey taxa and AI_a = % frequency of occurrence + % total numbers + % total mass of prey taxon *a* (George and Hadley 1979). We used a linear index of food selection (Ready et al. 1985) to compare the relative abundances and masses of prey taxa in diets of pike to the relative abundances and masses of available prey. We calculated the latter as average monthly proportions in grab (benthic) and sweep (macrophytic and water column) samples. We limited calculations of availability to prey taxa occurring in >1 stomach sample from any lake over the duration of the study. Therefore, estimates of selectivity were conservative. We excluded vertebrate prey because their abundance in the lakes either was not estimated or was estimated using dissimilar methods. We calculated both RI and selectivity as monthly means averaged by year in each lake. We further averaged annual means for R1 and R2 to obtain a value (the reference diet) against which to compare results from EXP.

Community structure and responses.—We averaged grab and sweep samples in each month and year to produce composite values of macroinvertebrate abundance and biomass of each

taxon in each system (lake or mesocosm). We then explored the overall structure of the macroinvertebrate prey community in EXP relative to the other systems before and after introduction of pike using ordination analysis. Lengths of the 1st axes in preliminary detrended correspondence analyses (DCA) were always <2.0 standard deviation units, indicating an incomplete turnover in taxa among the study systems. Therefore, an analysis assuming linear responses of organisms to any underlying environmental gradient was appropriate (ter Braak 1987). We used principal components analysis (PCA) on the correlation matrix to examine patterns in mean abundance (number/sample) and mean biomass (mg/sample) among systems and years. Data matrices were $\log(x + 1)$ transformed to linearize curvilinear relationships between taxa. We used the broken-stick method of component analysis (Legendre and Legendre 1998) to determine how many ordination axes were nontrivial and interpretable. Because this approach helps to distinguish between signal and noise in PCA, parallel trajectories of experimental and reference systems in ordination space imply year effects, whereas differences in trajectories suggest a treatment effect. We tested the null hypothesis of no concordance (association) between matrices of abundance and biomass using Procrustes analyses (Jackson 1995). Significant results from this analysis would suggest that the 2 matrices exhibit similar patterns across systems.

We used randomized intervention analyses (RIA) (Carpenter et al. 1989) to test the null hypothesis of no change in mean abundance, biomass, and individual size of macroinvertebrate taxa in EXP relative to reference lakes. We compared monthly means in EXP to reference monthly means (an average of R1 and R2 in each month) before ($n = 4$) and after ($n = 7$) manipulation. We also used RIA to test for natural or treatment-related trends in TN, TP, and Chl-*a* over the duration of the study. Including multiple reference systems increased the likelihood of incorporating intersystem variation, an advantage usually lacking in RIA (Murtaugh 2002).

Mesocosms.—We lacked premanipulation data for the mesocosm experiment, so we analyzed treatment effects using linear regression. We regressed mean abundance, biomass, and size of individual macroinvertebrate taxa against

month (May = 1, June = 2, etc.) for fishless enclosures and control mesocosms. We assumed that effects of predation by pike increased with time. Therefore, we focused on results from 2002 when qualitatively comparing these regression results to the RIAs. We excluded 1 fishless enclosure and 1 control mesocosm from our analysis because they were damaged by beavers. Thus, sample sizes were 12 and 4 mo, respectively. We tested for differences in slope between treatments in each year using *t*-tests. A positive effect of predation by pike (i.e., an increase in mean abundance, biomass, or individual size of a macroinvertebrate taxon) occurred when the slope of the regression from the control mesocosms was significantly ($p < 0.05$) greater than the slope of the regression from the fishless enclosures. Conversely, a negative effect occurred when the slope of the regression from the control mesocosms was significantly less than the slope of the regression from the fishless enclosures. We regarded values of p between 0.20 and 0.05 as indicative of nonsignificant trends, and we treated values of $p > 0.20$ as indicating neutral responses. We $\log(x)$ or $\log(x + 1)$ transformed non-normal data sets and removed outliers before analysis.

Results

SCA

Erpobdellid leeches were important in diets of pike from EXP in 2001 and, to a lesser degree, in 2002 (Fig. 2). *Gammarus*, coleopterans, and dipterans all increased in importance in 2002. In contrast, *Gammarus* was important in diets of northern pike from the reference lakes, whereas fishes, leeches, and larval trichopterans were of secondary importance (Fig. 2). *Hyalella* were rarely consumed, despite their high abundance in EXP and R2. Pike in EXP showed strong positive selection for leeches and strong negative selection for *Gammarus* based on both abundance and biomass; selection for dipterans was negative in 2002 (Table 2). In contrast, pike in the reference lakes showed positive selection for *Gammarus* and leeches, but negative selection for dipterans (Table 2). Other taxa in EXP and reference lakes were consumed in proportions similar to their observed abundance (or biomass).

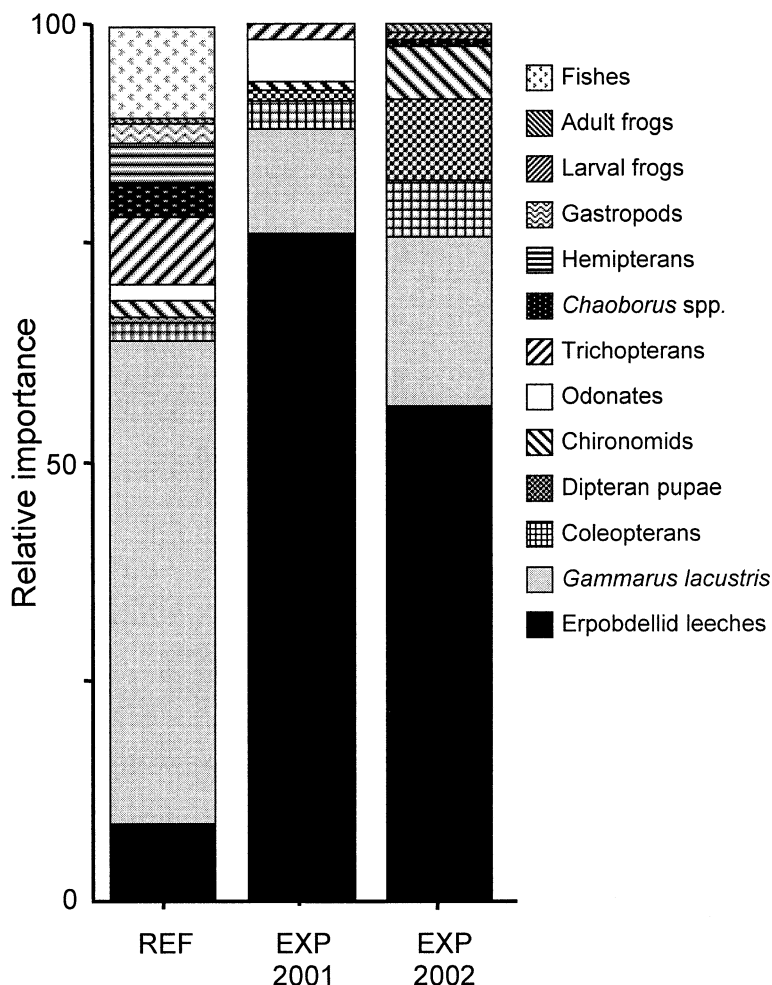


FIG. 2. Relative importance of prey taxa in diets of northern pike from the reference lakes (REF) averaged across all lakes and years ($n = 46$, mean ± 1 SE total length of northern pike = 516 ± 18 mm) and the experimental lake (EXP) in 2001 ($n = 27$, mean total length of northern pike = 615 ± 11 mm) and 2002 ($n = 33$, mean total length of northern pike = 619 ± 7 mm).

Macroinvertebrate communities in unmanipulated lakes

The short axis length in the preliminary DCA ordinations indicated that macroinvertebrate communities in the 3 study lakes were broadly similar in composition (at the taxonomic resolution of our analyses) despite the fishless state of EXP at the start of our study. Prior to manipulation of EXP, macroinvertebrate communities in all 3 lakes were dominated by amphipods and dipterans (Table 3). *Gammarus lacustris* tended to be more abundant in R2 than in EXP

and R1, whereas the smaller *Hyaella azteca* was more abundant in EXP and R1 than in R2. Large taxa such as erpobdellid leeches, odonates, and coleopterans were relatively rare in all lakes, but they were up to 4 \times more abundant in EXP than in the reference lakes. These taxa also tended to be much larger in EXP than in the reference lakes. Biomass in EXP was dominated by these large taxa and the 2 amphipod taxa, whereas biomass in the reference lakes was dominated overwhelmingly by *Gammarus* and, to a lesser degree, *Hyaella* and dipterans (Table 3).

TABLE 2. Positive (+), negative (–), and neutral (o) selection by pike >450 mm total length for abundance and biomass of selected macroinvertebrate prey taxa using the linear index of food selection. Pike exhibited neutral selection for all other prey taxa (Gastropoda, Odonata, Hemiptera, Trichoptera, Coleoptera, and dipteran pupae). The index could not be calculated for vertebrate prey (see text). REF = reference lakes, EXP = experimental lake.

Prey taxa	REF	EXP 2001	EXP 2002
Erpobdellidae	+	+	+
<i>Gammarus lacustris</i>	+	–	–
<i>Chaoborus</i> spp.	–	o	–
Chironomidae	–	–	–

Community-level responses

The broken-stick method indicated that only the first 2 ordination axes were important in interpreting patterns of macroinvertebrate abundance and biomass. Axes 1 and 2 together summarized 56% of the variance among lake-years (Table 4). Despite the absence of turnover in taxonomic composition, the PCA based on abundance discriminated between fishless systems (EXP in 2000 and fishless enclosures in 2001 and 2002) and systems with fish (Fig. 3A). Following addition of pike, the abundance trajectories in EXP and the control mesocosms were parallel and converged on R1. In contrast, abundance trajectories in the reference lakes and fishless enclosures appeared haphazard and independent. Community-level patterns for macroinvertebrate biomass (not shown) were strongly concordant with those for abundance (Procrustes analysis; $p = 0.001$), although the biomass trajectories of EXP and R1 were more similar in direction (suggesting a modest year effect) than the abundance trajectories.

We developed a qualitative a posteriori classification of macroinvertebrates in relation to their vulnerability to predation by pike (PAV, WMT, H. Proctor, University of Alberta, and G. Scrimgeour, Alberta Conservation Association, unpublished data). We ranked invertebrate taxa according to their size, degree of activity, and habitat preference. PCA suggested that community-level responses to addition of pike were driven by a reduction in the abundance and biomass of large, active, or conspicuous taxa classified as vulnerable to pike (e.g., odonates, coleopterans, and, to a lesser extent, leeches) (Fig.

3B). As the vulnerable taxa decreased, the abundance and biomass of small, inactive, or inconspicuous taxa typically associated with the presence of fish (e.g., dipterans and trichopterans) increased.

Responses of individual taxa

RIA generally supported the community-level ordinations. Abundance, biomass, or individual size of large and active erpobdellid leeches and odonates followed a negative trend in EXP relative to the reference lakes following the addition of northern pike (Table 5). However, other taxa, particularly taxa that were small, inactive, or inconspicuous to pike, tended to show weak or neutral responses to the addition of pike. Responses of invertebrate taxa in mesocosms were not statistically significant, but the trends in the mesocosms generally supported the whole-lake results. RIA did not detect any unique temporal trend in TN, TP, or Chl-*a* concentrations in EXP relative to the reference lakes ($p > 0.20$).

Discussion

The potential for northern pike to influence macroinvertebrates in the littoral zone of boreal mixed-wood lakes was indicated by pike diets in the reference lakes. These diets consisted mostly of large macroinvertebrates despite the presence of prey fish. Invertivory by pike up to 600 mm TL has been observed occasionally in lakes containing prey fish, particularly in naturally productive systems in western North America (Chapman et al. 1989, Sammons et al. 1994, Beaudoin et al. 1999), and might reflect a relative scarcity of vertebrate prey (Chapman and Mackay 1990). Foodweb theory suggests that omnivory by top predators, and the presence of refugia for prey, can stabilize communities in small lakes (McCann et al. 2005). Thus, although gill-net surveys in both reference lakes showed that juvenile yellow perch were abundant (PAV, unpublished data), shallow areas with dense macrophyte cover might have provided sufficient refuge to prevent heavy predation on juvenile yellow perch (Eklöv 1997) while supplying pike with an abundance of invertebrates (Diehl 1993a).

TABLE 3. Composition (mean [± 1 SE] annual abundance and biomass) of invertebrate prey communities (for grabs and sweeps combined) and mean individual dry mass of common macroinvertebrate taxa in EXP (prior to manipulation) and in R1 and R2 (mean from 2000–2002).

Taxon	Abundance (no./sample)			Biomass (mg dry mass/sample)		
	EXP	R1	R2	EXP	R1	R2
Erpobdellidae	2.4 \pm 1.0	0.6 \pm <0.1	0.8 \pm 0.2	12.1 \pm 5.6	5.0 \pm 1.0	5.9 \pm 1.7
Gastropoda	1.0 \pm 0.1	1.5 \pm <0.1	3.5 \pm 0.1	3.2 \pm 1.0	3.2 \pm 0.5	6.0 \pm 1.2
<i>Gammarus lacustris</i>	7.6 \pm 3.1	15.8 \pm 1.8	64.2 \pm 3.6	16.7 \pm 5.3	58.8 \pm 13.0	236.0 \pm 33.6
<i>Hyalella azteca</i>	39.5 \pm 14.3	37.4 \pm 5.6	28.5 \pm 5.3	13.8 \pm 1.6	9.2 \pm 2.0	8.8 \pm 1.4
Odonata	1.0 \pm 0.1	0.5 \pm 0.2	1.0 \pm 0.5	4.8 \pm 1.8	2.0 \pm 0.8	1.3 \pm 0.8
Hemiptera	1.1 \pm 0.6	1.2 \pm 0.4	1.6 \pm 0.6	1.9 \pm 0.9	1.8 \pm 0.2	4.9 \pm 1.2
Trichoptera	0.6 \pm 0.3	2.4 \pm 0.5	0.5 \pm 0.2	1.6 \pm 0.9	7.5 \pm 2.9	2.5 \pm 0.1
Coleoptera	0.5 \pm 0.1	0.4 \pm 0.1	0.4 \pm 0.2	40.0 \pm 17.9	2.2 \pm 1.5	5.1 \pm 2.8
<i>Chaoborus</i> spp.	10.5 \pm 4.2	27.1 \pm 19.1	0.3 \pm 0.2	2.0 \pm 0.6	6.4 \pm 4.6	0.2 \pm 0.2
Chironomidae	13.8 \pm 6.5	21.3 \pm 5.2	47.5 \pm 21.2	2.4 \pm 0.9	7.0 \pm 2.0	27.3 \pm 18.5
Dipteran pupae	0.2 \pm 0.1	1.3 \pm 0.2	0.4 \pm 0.4	<0.1 \pm <0.1	0.3 \pm 0.2	0.2 \pm 0.2
Other	1.8 \pm 1.2	4.1 \pm 1.3	3.8 \pm 1.0	2.8 \pm 0.8	3.1 \pm 0.8	3.6 \pm 0.7

Community-level responses

Our ordinations suggested that the addition of pike affected the macroinvertebrate community in EXP. The tendency for these fish to feed both extensively and selectively on macroinvertebrates in productive boreal lakes probably explains why ordinations of the invertebrate communities differed between systems with and without fish. In general, lakes with pike had macroinvertebrate communities in which inconspicuous taxa such as dipterans and trichopterans were abundant and had high biomass. This pattern is consistent with those observed in studies comparing communities in lakes with and without fish, and it suggests that selective consumption of large taxa and large individuals by native fish predators is an important mechanism shaping macroinvertebrate communities in lakes (Carlisle and Hawkins 1998, Wong et al. 1998, Knapp et al. 2001, Tonn et al. 2004). However, the relatively high abundance and biomass of *Gammarus* in R2 was anomalous, given the importance of this species in the diets of pike in reference lakes. This result suggests that predation by fish on amphipod predators, such as leeches, odonates, and coleopterans (reviewed in Clifford 1991 and MacNeil et al. 1999), might have an indirect, positive effect on amphipods. On the other hand, the biomass density of macrophytes in R2 was >35 \times higher than in R1 and might have had a positive effect on the amphipods in the form of habitat and cover (Tolonen

et al. 2003). The high biomass density of macrophytes also might explain why gastropods were more abundant in R2 than in EXP or R1.

Addition of pike to EXP coincided with a shift in the macroinvertebrate community away from conspicuous taxa (odonates, coleopterans, and leeches) toward taxa that were relatively inconspicuous. Given: 1) the consistency of this trajectory with that seen in the control mesocosms (with a 1-y lag), 2) the convergence of trajectories in both EXP and the control mesocosms toward R1, 3) the consistency of these patterns in the ordinations of both abundance and biomass, and 4) the inconsistency of these trajectories with the trajectory of the fishless enclosures, we conclude that most changes observed in EXP were caused by the addition of pike and were not simply year effects. Our results also show that differences between systems with and without fish and responses of macroinvertebrates to the winterkill of fishes in Boreal Plains lakes (Tonn et al. 2004) were not a consequence only, or even primarily, of predation by yellow perch; northern pike alone can produce the same effects.

Responses of individual taxa

Pike in EXP fed selectively on 2 species of erpobdellid leeches: *Erpobdella punctata* and *Nepheleopsis obscura*. In addition, we observed trends toward lower abundance and biomass,

TABLE 3. Extended.

Individual dry mass (mg)		
EXP	R2	R2
41.2 ± 30.6	6.8 ± 1.2	4.6 ± 0.4
3.0 ± 3.0	4.5 ± 1.7	2.1 ± 0.3
3.4 ± 1.9	5.4 ± 0.9	6.3 ± 0.5
0.5 ± <0.1	0.4 ± <0.1	0.3 ± <0.1
10.9 ± 3.4	4.7 ± 1.7	1.4 ± 0.5
6.7 ± 5.4	2.4 ± 0.7	5.3 ± 1.5
2.8 ± 1.8	4.5 ± 1.8	6.8 ± 2.4
108.7 ± 55.9	5.9 ± 2.5	18.1 ± 14.3
0.2 ± <0.1	0.2 ± <0.1	0.3 ± <0.1
0.2 ± <0.1	0.3 ± 0.1	0.3 ± 0.1
0.3 ± 0.1	0.2 ± 0.1	0.5 ± 0.2
—	—	—

and smaller sizes, of erpobdellids in EXP. These trends were consistent between the whole-lake and mesocosm experiments, suggesting a direct causal relationship between the presence of fish and negative effects on erpobdellids. However, not all trends in the leech population in EXP were statistically significant; effects of predation by pike might have been muted by flexible life-history strategies that buffered populations of erpobdellid leeches from environmental variation (Baird et al. 1987). Nevertheless, treatment responses shown by leeches in the absence of environmental changes (e.g., water chemistry) suggest a strong direct interaction between leeches and northern pike (see also Tonn et al. 2004).

To our knowledge, ours is the first study to identify impacts of invertivory by northern pike on macroinvertebrate communities. The trends that we observed were consistent with results of earlier studies showing effects of other fishes on macroinvertebrates. For example, Blumenshine et al. (2000) also identified size-selective predation on leeches and odonates by largemouth bass (*Micropterus salmoides*) as a major factor structuring the size distribution of a macroinvertebrate community. Predation by fishes on large odonates tends to favour small cryptic macrophyte-dwelling taxa (Blois-Heulin et al. 1990, Stoks and McPeck 2003). The negative (albeit weak) response of coleopteran abundance and biomass to the manipulation of pike in our study was also consistent with earlier work in-

TABLE 4. Percentage of variance explained by, and eigenvectors of prey taxa for, the first 3 axes in a principal components (PC) analysis of macroinvertebrate abundance. c = conspicuous prey taxon, i = inconspicuous prey taxon.

Prey taxon	PC axis		
	1	2	3
% of variance	31.6	24.4	14.0
Eigenvectors			
Erpobdellidae (c)	0.2316	-0.2385	-0.4334
Gastropoda (i)	0.5002	0.1794	0.1859
<i>Gammarus lacustris</i> (c)	0.4819	0.2371	0.1939
Odonata (c)	0.0884	-0.5288	0.1218
Hemiptera (c)	0.3171	0.0922	-0.5181
Trichoptera (i)	-0.1287	0.3319	-0.0298
Coleoptera (c)	0.1002	-0.4147	-0.4211
<i>Chaoborus</i> spp. (i)	-0.4940	-0.0750	-0.1565
Chironomidae (i)	0.0629	0.3696	-0.4617
Dipteran pupae (i)	-0.2844	0.3772	-0.2023

volving the presence vs absence of small fishes (Fairchild et al. 2000).

Gammarus and smaller larval insects dominated pike diets in the reference lakes, but these taxa were preyed upon less intensely by pike in EXP. This trend was particularly evident for *Gammarus*, which was positively selected in the reference lakes, but negatively selected in EXP. This trend was probably caused by the higher relative abundance of leeches in EXP than in the reference lakes. Any responses of *Gammarus* and smaller larval insects in EXP to the predator were probably indirect and, thus, more difficult to interpret because of a myriad of potential foodweb linkages. For example, the diets of erpobdellid leeches can include amphipods and larval chironomids, odonates, and trichopterans (Davies et al. 1981, Wrona 1982, Cywinska and Davies 1989). On the other hand, amphipods are predators of erpobdellid cocoons and juveniles (Cywinska and Davies 1989). Moreover, dense stands of macrophytes might serve as a refuge for conspicuous taxa (Tolonen et al. 2003). Thus, net changes in abundance, biomass, or size of invertebrates would depend on interaction strengths as well as habitat heterogeneity, illustrating the difficulty in resolving responses of many individual taxa at the whole-lake (or even mesocosm) scale.

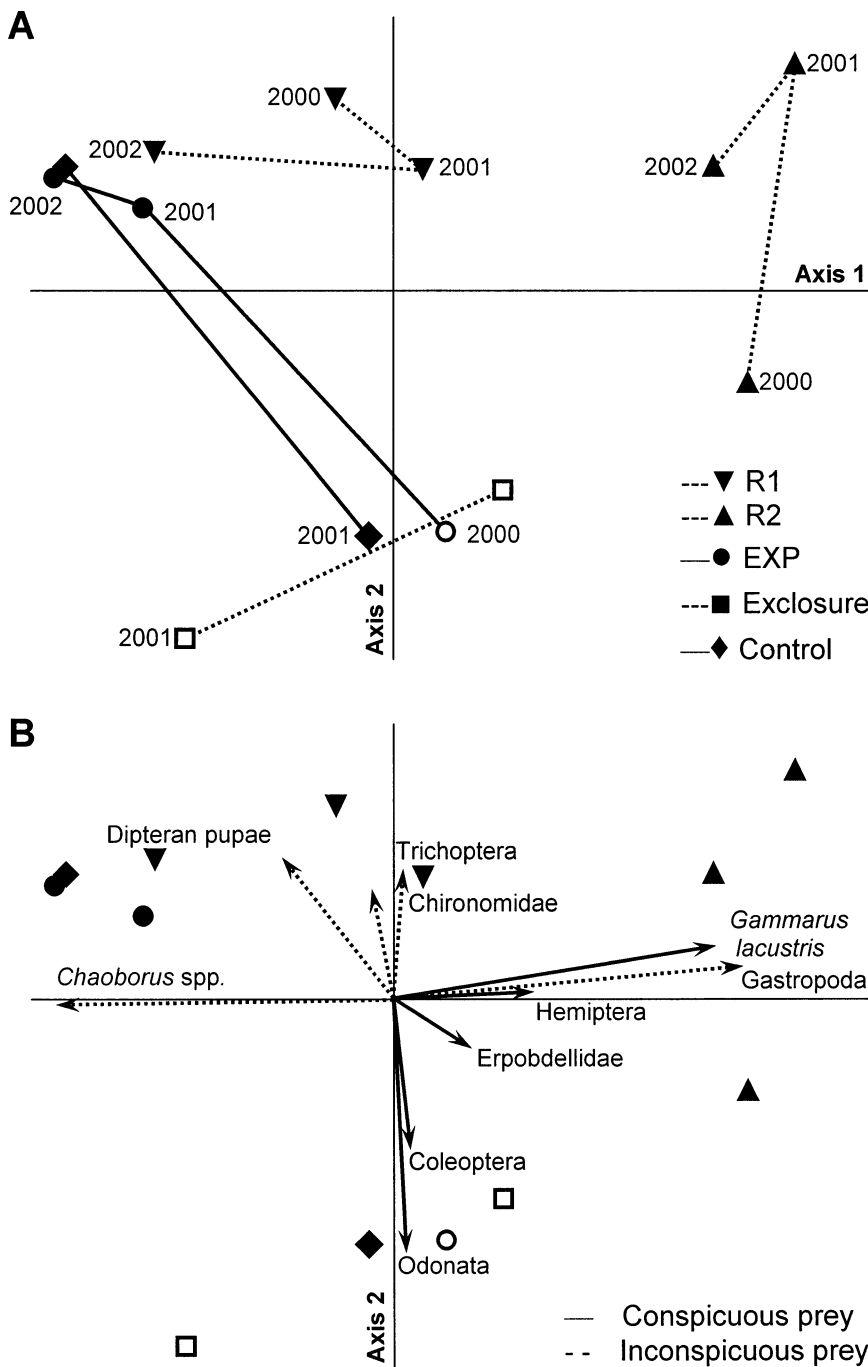


FIG. 3. Standardized and centered principal components analysis of macroinvertebrate abundance (number/sample) showing trajectories of reference (R1 and R2) and experimental (EXP) lakes and fishless exclosures and control mesocosms from 2000 to 2002 (A) and the relationship between these trajectories and conspicuous and inconspicuous macroinvertebrate prey taxa (B). Filled and open symbols refer to experimental units (lakes and mesocosms) with and without pike, respectively. EXP was fishless in 2000 but contained stocked pike in 2001 and 2002.

TABLE 5. Directions of effects of northern pike on the mean summer abundance, biomass, and size of individual macroinvertebrate prey taxa in the experimental lake vs the reference lakes before ($n = 4$) and after ($n = 7$) manipulation as indicated by random intervention analysis (RIA). * = significant ($p < 0.05$) negative effect of pike, + = positive trend ($0.20 \geq p \geq 0.05$), - = negative trend ($0.20 \geq p \geq 0.05$), o = neutral effect ($p > 0.20$). Blank cells indicate insufficient data to perform analyses.

Prey taxon	Abundance	Biomass	Size
Erpobdellidae	-	o	*
Gastropoda	o	o	
<i>Gammarus lacustris</i>	o	o	+
Odonata	o	*	*
Hemiptera	o	o	o
Trichoptera	o	-	o
Coleoptera	o	-	o
<i>Chaoborus</i> spp.	o	o	o
Chironomidae	o	o	+
Dipteran pupae	+	o	

Pike structure macroinvertebrate communities

Littoral food webs are inherently complex because of a multiplicity of direct and indirect interactions, including omnivory, multiple predators, complex or variable life histories, ontogenetic resource shifts, flexible behavior, and prey refugia (Crowder and Cooper 1982, Gilinsky 1984, Blois-Heulin et al. 1990, Diehl 1993b, Wellborn et al. 1996, Wisenden et al. 1997, Eklöv and VanKooten 2001). Such complexities tend to attenuate top-down effects in littoral food webs relative to those observed in pelagic systems (Carpenter et al. 1985). Demonstrating clear top-down effects of predation by native fish on the structure of littoral macroinvertebrate communities often requires large, sometimes unrealistic, changes in predator density, artificial mesocosms, or a combination of these approaches.

Our experiment was more realistic than most top-down studies because it was conducted at the whole-lake scale, used natural densities of fish, and focused on systems in which the densities of native fish predators fluctuate frequently because of winterkill events. A complementary mesocosm experiment corroborated our whole-lake results, demonstrating at 2 spatial scales that predation by native northern pike can strongly affect littoral macroinvertebrate

communities in small lakes of Alberta's Boreal Plains. Specifically, the community of littoral macroinvertebrates in EXP and the control mesocosms showed a clear change following addition of pike, largely because of responses of conspicuous prey taxa such as erpobdellid leeches and odonates. Given the results of our PCA and the absence of any environmental trend or a similar change in the invertebrates of the fishless enclosures, we think it unlikely that these changes occurred in response to year effects. Furthermore, data from R1 and R2, in which populations of invertivorous pike have been established for ≥ 5 y, suggest that observed effects of pike on abundance and biomass are not temporary.

Limited sample sizes prevented us from examining effects of pike on the richness or evenness of the littoral macroinvertebrates community (see Thorp 1986). However, given that EXP contained $2\times$ as many unique taxa as either reference lake (PAV, unpublished data), a carefully designed, long-term study would probably show a more direct relationship between the presence/absence of native fish predators and community diversity. Additional research also is needed to determine how the size structure of populations of pike, which can be influenced, in part, by the timing or severity of winterkill, may differentially affect macroinvertebrates. Juvenile pike require particular attention in this regard because they: 1) are more likely to survive (Casselman and Harvey 1975) or recolonize following winterkill events, 2) occupy macroinvertebrate-rich habitats normally too shallow or densely vegetated for large conspecifics (Eklöv 1997), and 3) are smaller than adults and can, therefore, include in their diets macroinvertebrates that are too small or inconspicuous for adults (Werner and Gilliam 1984).

In a serendipitous natural experiment, Tonn et al. (2004) identified winterkill-induced changes in the density of fishes as an important mechanism structuring macroinvertebrate communities in small lakes of Alberta's Boreal Plains. Our study provides experimental support for this relationship, and demonstrates the importance of predation by northern pike in littoral food webs. Our results are consistent with theoretical and empirical studies identifying the importance of large predators in small lakes (McCann et al. 2005) and should be taken into account when considering the possible consequences of an-

thropogenic disturbances on pike. For example, invertivorous pike appear capable of decreasing populations of preferred prey quickly. Thus, stocking pike in these small western boreal lakes would probably exacerbate competition for food. Fisheries managers might want to consider increased harvest pressure as a means of alleviating such density-dependent competition. Similarly, resource managers should be concerned about impacts that can alter disturbance regimes, such as winterkill, via changes in land use in lake catchments (Tonn et al. 2003) or climate (Danylchuk and Tonn 2003).

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