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# Responses of northern pike and their macroinvertebrate prey to manipulation: a study of predation, winterkill, and food web dynamics in boreal lakes

by

Paul Anthony Venturelli

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partial fulfillment of the requirements for the degree of
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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled **Responses of northern pike and their macroinvertebrate prey to manipulation: a study of predation, winterkill, and food web dynamics in boreal lakes** submitted by **Paul Anthony Venturelli** in partial fulfillment of the requirements for the degree of **Master of Science**.

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This thesis is dedicated to the memory of my grandfather,
O’Dino Venturelli

*Grazie, Nonno. Riposa in pace*

# ABSTRACT

Winterkill in small lakes of boreal Alberta often forces northern pike (Esox lucius) to prey on invertebrates. Multi-lake, comparative studies suggest that this affects both macroinvertebrate communities and growth of pike. My objective was to examine experimentally the consequences of invertebrate predation by pike on a) littoral macroinvertebrate communities, and (b) the growth of pike. In May 2001, I stocked a small, fishless lake with individually tagged pike. During two subsequent summers, leeches dominated diets of adult pike, whereas juveniles consumed amphipods and other macroinvertebrates. Pike caused a reduction in the abundance, size, and biomass of leeches, and a shift in community structure towards small, inconspicuous taxa. Growth of pike suggests that a diet of macroinvertebrates will ultimately lead to stunting. These results suggest that food webs in Alberta's boreal lakes are sensitive to disturbance. Long-term effects of disturbance on these food webs, however, have yet to be determined.

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# Chapter 1. GENERAL INTRODUCTION (DISTURBANCE AS A MECHANISM FOR UNDERSTANDING FOOD WEBS IN BOREAL LAKES)

Communities of fishes, and lake food webs in general, are products of biotic and abiotic factors operating at various spatial and temporal scales. A given assemblage of fishes, for example, is influenced by geological and evolutionary history, regional climate and geography, lake characteristics, and a suite of biotic interactions (Tonn 1990, Jackson et al. 2001). Multi-lake comparative studies suggest that natural disturbances, particularly the mortality caused by depletion of dissolved oxygen in winter (winterkill), are major factors controlling species composition of fish assemblages in north-temperate lakes (Tonn and Magnuson 1982, Robinson and Tonn 1989, Tonn et al. 1995). During winter, a cover of snow and ice limits atmospheric inputs and reduces photosynthetic production of oxygen in lakes; simultaneously, stored oxygen in the lake water is consumed by decomposing organic matter (Greenbank 1945, Fast 1994), which also produces gases (e.g., methane; Molongoski and Klug 1980) that can augment consumption of oxygen and are toxic to fish (Fast 1994). In general, winterkill occurs when concentrations of dissolved oxygen drop below a critical threshold (e.g. < 0.5 mg/l for northern pike, *Esox lucius*, although this value tends to vary according to temperature; Magnuson and Karlen 1970, Petrosky and Magnuson 1973, Casselman 1996).

In small (< 100 ha) lakes of north-central Alberta, winterkill combines with predation and the isolation of lakes to produce a dichotomy of fish assemblages (Robinson and Tonn 1989). Small-bodied fishes tend to dominate in lakes where large-bodied piscivores are excluded by severe winterkill and/or relative isolation. Predation by northern pike, on the other hand, excludes small-bodied species from lakes less prone to winterkill and/or where winterkill is ameliorated by surface connections. Although pike in these lakes typically co-occur with other large-bodied fishes like yellow perch (*Perca flavescens*) and white sucker (*Catostomus commersoni*), pike are relatively tolerant of winterkill conditions (Magnuson and Karlen 1970, Casselman 1996) and therefore sometimes occur alone (Robinson and Tonn 1989).

How winterkill and predation interact to structure food webs within these assemblage types, however, is less clear owing to a lack of temporal (multi-year) studies. In the absence of winterkill, predation by pike can have a strong influence on fish communities. Size-biased predation, for example, can alter the size structure of prey populations (Frost 1954). Indeed, pike are such effective piscivores that they are commonly used in biomanipulation experiments as a means of forcing trophic cascades via predator-induced reductions in densities of planktivorous fishes (e.g. Søndergaard et al. 1997, Elser et al. 2000, Lathrop et al. 2002). Predation by pike may also indirectly affect the feeding ecology, behaviour, growth, and life history of the fishes on which they prey (Persson et al. 1996, Jackson et al. 2001 and reference therein).

Winterkill, however, frequently causes single-season declines in fish density of 50 – 90% in Alberta's small boreal lakes (Danylchuk & Tonn 2003), and therefore serves to mediate predator-prey interactions. An obvious consequence is the sudden, albeit temporary, release of prey from predation by pike. Winterkill can also affect food webs by modifying the structure and dynamics of remnant populations of pike and/or prey fishes (Casselman and Harvey 1975). Furthermore, pike will adjust their feeding ecology to include macroinvertebrate prey when prey fishes are unavailable (Chapman and Mackay 1990, Beaudoin et al. 1999). Although winterkill-induced fluctuations in densities of pike and perch may affect benthic macroinvertebrates in the littoral (inshore) zone (Langlois 2000), little is known about the consequences of predation by pike on macroinvertebrate communities when prey fishes become unavailable due to winterkill.

Equally unclear is the dietary response of pike to sudden, forced invertivory (as would occur following a winterkill), and how this cost affects growth. Invertivorous pike in north-central Alberta tend to grow slowly (P. Aku and W. Tonn, unpublished data). While this pattern is consistent with bioenergetics simulations (Diana 1987) and lab experiments (Hart and Connellan

1984) that suggest pike become stunted in the absence of suitably sized prey, growth of pike can also be compromised by competition (Diana 1987), changes in maturation rate due to size-selective mortality (Diana 1983) age- or size-dependent interactions (Ylikarjula et al. 1999), and the very time frame over which these mechanisms operate. Further study is therefore required to determine the relative importance of invertivory for growth of pike in these systems.

Despite being relatively frequent in Boreal Plains lakes (Danylchuk and Tonn 2003), winterkill remains unpredictable in time and space and is therefore difficult to study within the framework of realistic monitoring designs. A more practical and no less relevant approach is controlled manipulation. To date, however, many micro- and mesocosm experiments have produced results that are inconsistent with patterns observed at larger scales. For example, mesocosm studies suggest that predation by fish on littoral macroinvertebrates is important only seasonally (Gilinsky 1984), if at all (Pierce & Hinrichs 1997; Cobb & Watzin 1998). Similarly, models developed from micro- or mesocosm-level observations inaccurately predict growth (Diana 1996) or prey-size selection by pike (Nilsson and Brönmark 1999) under natural conditions.

Given the unpredictability of winterkill and the fact that small-scale experiments are often criticized for having limited relevance at the spatial and temporal scales at which resources are usually managed or organisms such as pike operate (Carpenter 1996), I examined potential consequences of winterkill on predator-prey interactions in Alberta's boreal lake food webs by conducting a whole-lake manipulation. To address challenges of large-scale experiments, i.e., replication and the strength and duration of manipulation (Carpenter 1989), I collected one year of baseline data before introducing northern pike into a small, fishless lake at a high yet realistic biomass density. Results of the manipulation over a two-year period were then compared to baseline data and parallel observations in two unmanipulated reference systems. In Chapter 2, I examine effects of predation by pike on littoral macroinvertebrates using data from the whole-lake experiment and a complementary 2-year, within-lake mesocosm experiment. Chapter 3 addresses the dietary response of both adult and juvenile pike to invertivory, and the effect this diet has on growth. I base the latter primarily on data from this study, but also make use of longer-term regional data sets that serve to increase the temporal perspective of my results.

Determining the relationship between pike and macroinvertebrates in Alberta's boreal lakes while assessing the importance of natural phenomena (i.e., winterkill) in modifying this relationship is necessary for management strategies that incorporate natural disturbance. This information can also put into perspective potential effects of anthropogenic disturbances on aquatic food webs, such as increased access of once remote lakes to commercial, recreational, and subsistence fisheries as a result of industrial activities. In addition, the propensity of a lake to winterkill is a function of its morphometry, nutrient status, and surface-water connections (Babin and Prepas 1985, Tonn et al. 2003). Although their effects may depend on landscape position (Devito et al. 2000, Prepas et al. 2001), anthropogenic disturbances such as climate change (McCarthy et al. 2001) and forestry (Rask et al. 1993, Buttle et al. 2000) can alter these features of lakes and therefore the severity and frequency of winterkill. The potential, therefore, for these and other disturbances to affect aquatic ecosystems is real. Accurately addressing these impacts requires that we develop a better understanding of how disturbance affects food webs in Alberta's small, boreal lakes.

## Literature cited

Babin, J. and Prepas, E.E. 1985. Modelling winter oxygen depletion rates in ice-covered temperate zone lakes in Canada. Can. J. Fish. Aquat. Sci. **42** : 239-249.

Beaudoin, C.P., Tonn, W.M., Prepas, E.E., and Wassenaar, L.I. 1999. Individual specialization and trophic adaptability of northern pike (*Esox lucius*): an isotope and dietary analysis. Oecologia **120**: 386-396.

Buttle, J.M., Creed, I.F., Pomeroy, J.W. 2000. Advances in Canadian forest hydrology, 1995 – 1998. Hydrol. Process. **14**: 1551-1578.

Carpenter, S.R. 1989. Replication and treatment strength in whole-lake experiments. Ecology **70**: 453-463.

Carpenter, S.R. 1996. Microcosm experiments have limited relevance for community and ecosystem ecology. Ecology **77**: 677-680.

Casselman, J.M. 1996. Age, growth and environmental requirements of pike. *In* Pike: biology and exploitation. *Edited by* J.F. Craig. Chapman and Hall, Dunscore. pp. 69-101.

Casselman, J.M. and Harvey, H.H. 1975. Selective fish mortality resulting from low winter oxygen. Verg. Internat. Verein. Limnol. **19**: 2418-2429.

Chapman, L.J. and Mackay, W.C. 1990. Ecological correlations of feeding flexibility in northern pike (*Esox lucius*). J. Fresh. Ecol. **5**: 313-322.

Cobb, S.E. and Watzin, M.C. 1998. Trophic interactions between yellow perch (*Perca flavescens*) and their benthic prey in a littoral zone community. Can. J. Fish. Aquat. Sci. **55**: 28-36.

Danylchuk, A.J. and Tonn, W.M. 2003. Natural disturbances and fish: local and regional influences on winterkill of fathead minnows on boreal lakes. Trans. Am. Fish. Soc. **132**: 289-298.

Devito, K.J., Creed, I.D., Rothwell, R.L., and Prepas, E.E. 2000. Landscape controls on phosphorous loading to boreal lake: implications for the potential impacts of forest harvesting. Can. J. Fish. Aquat. Sci. **57**: 1977-1984.

Diana, J.S. 1983. Growth, maturation, and production of northern pike in three

Michigan lakes. Trans. Am. Fish. Soc. **112**: 38-46.

Diana, J.S. 1987. Simulation of mechanisms causing stunting in northern pike populations. Trans. Am. Fish. Soc. **116**: 612-617.

Elser, J.J., Sterner, R.W., Galford, A.E., Chrzanowski, T.H., Findlay, D.L., Mills, K.H., Paterson, M.J., Stainton, M.P., Schindler, D.W. 2000. Pelagic C:N:P stoichiometry in a eutrophied lake: responses to a whole-lake food-web manipulation. Ecosystems. **3**: 293-307.

Fast, A.W. 1994. Winterkill prevention in lakes and ponds using artificial aeration. Rev. Fish. Sci. **2**: 23-77.

Frost, W.E. 1954. The food of pike, *Esox lucius* L., in Windermere. J. Anim. Ecol. **23**: 339-360.

Gilinsky, E. 1984. The role of fish predation and spatial heterogeneity in determining benthic community structure. Ecology **65**: 455-468.

Greenbank, J. 1945. Limnological conditions in ice-covered lakes, especially related to winter-kill of fish. Ecol. Mono. **15**: 343-392.

Hart, P.J.B. and Connellan, B. 1984. Cost of prey capture, growth rate and ration size in pike, *Esox lucius* L., as functions of prey weight. J. Fish. Biol. **25**: 279-292.

Jackson, D.A., Peres-Neto, P.R., and Olden, J.D. 2001. What controls who is where in freshwater fish communities – the roles of biotic, abiotic, and spatial factors. Can. J. Fish. Aquat. Sci. **58**: 157-170.

Langlois, P.W. 2000. The influence of trophic state, thermal structure and winterkill on littoral macroinvertebrate communities in Boreal Plain lakes. MSc. Thesis, Univeristy of Alberta, Edmonton, Canada.

Lathrop, R.C., Johnson, B.M., Johnson, T.B., Vogelsang, M.T., Carpenter, S.R., Hrabik, T.R., Kitchell, J.F., Magnuson, J.J., Rudstam, L.G., and Steward, R.S. 2002. Stocking piscivores to improve fishing and water clarity: a synthesis of the Lake Mendota biomanipulation project. Freshwater Biol. **47**: 2410-2424.

Magnuson, J.J. and Karlen, D.J. 1970. Visual observations of fish beneath the ice in a winterkill lake. J. Fish. Res. Board Can. **27**: 1059-1068.

McCarthy, J.J., Canziani, O.F., Leary, N.A., Dokken, D.J., and White, K.S. 2001. Climate Change 2001: impacts, adaptation and vulnerability. Contributions of working group II to the third assessment report of the intergovernmental panel on climate change. Cambridge University Press, Cambridge.

Molongoski, J.J., and Klug, M.J. 1980. Anaerobic metabolism of particulate organic matter in the sediments of a hypereutrophic lake. Freshwater Biol. 10: 507-518.

Nilsson, P.A. and Brönmark, C. 1999. Foraging among cannibals and kleptoparasites: effects of prey size on pike behavior. Behav. Ecol. **10**: 557-566.

Persson, L., Andersson, J., Wahlstrom, E., and Eklöv, P. 1996. Size-specific interactions in lake systems: predator gape limitation and prey growth rate and mortality. Ecology **77**: 900-911.

Petrosky, B.R., and Magnuson, J.J. 1973. Behavioral responses of northern pike, yellow perch and bluegill to oxygen concentrations under simulated winterkill conditions. Copeia **1973**: 125-35.

Pierce, C.L., and Hinrichs, B.D. 1997. Response of littoral invertebrates to reduction of fish density: Simultaneous experiments in ponds with different fish assemblages. Freshwater Biol. **37**: 397-408.

Prepas, E.E., Pinel-Alloul, B., Planas, B., Methot, G., Paquet, S., and Reddyk, S. 2001. Forest harvest impacts on water quality and aquatic biota on the Boreal Plain: introduction to the TROLS lake program. Can. J. Fish. Aquat. Sci. **58**: 421-436.

Rask, M., Arvola, L., and Salonen, K. 1993. Effects of deforestation and burning on the limnology of a small forest lake in southern Finland. Verh. Internat. Ver. Limnol. **25**: 525-528.

Robinson, C.L. and Tonn, W.M. 1989. Influence of environmental factors and piscivory in structuring fish assemblages of small Alberta lakes. Can. J. Fish. Aquat. Sci. **46**: 81-89.

Søndergaard, M., Jeppesen, E., and Berg, S. 1997. Pike (*Esox lucius* L.) stocking as a biomanipulation tool 2. Effects on lower trophic levels in Lake Lyng, Denmark. Hydrobiologia **342/343**: 319-325.

Tonn, W.M. 1990. Climate change and fish communities: a conceptual framework. Trans. Am. Fish. Soc. **119**: 337-352.

Tonn, W.M., and Magnuson, J.J. 1982. Patterns in the species composition and richness of fish assemblages in northern Wisconsin lakes. Ecology **63**: 1149-1166.

Tonn, W.M., Vandenbos, R.E., and Paszkowski, C.A. 1995. Habitat on a broad scale: relative importance of immigration and extinction for small fish assemblages. Bull. Fr. Peche Piscic. **337/338/339/**: 47-61.

Tonn, W.M., Paszkowski, C.A., Scrimgeour, G.J., Aku, P.K.M., Lange, M., Prepas, E.E., and Westcott, K.M. 2003. Effects of forest harvesting and fire on fish assemblages in boreal plains lake: a reference condition approach. Trans. Am. Fish. Soc. **132**: 514-523.

Ylikarjula, J., Heino, M., and Dieckmann, U. 1999. Ecology and adaptation of stunted growth in fish. Evol. Ecol. **13**: 433-453.

# Chapter 2. RESPONSE OF LITTORAL MACROINVERTEBRATES IN A FISHLESS BOREAL LAKE TO THE INTRODUCTION OF NORTHERN PIKE, *ESOX LUCIUS*

## Introduction

Effects of predation by fish on pelagic invertebrates are well documented. Early studies establishing relationships between planktivorous fish and the size and abundance of zooplankton (Hrbáček et al. 1961, Brooks and Dodson 1965) have led to developments in food-web theory (Carpenter et al. 1985, McQueen et al. 1986) and the use of biomanipulation as a technique for rehabilitating culturally eutrophied lakes (Shapiro et al. 1975, Kairesalo et al. 1999, Kasprzak et al. 2002, Lathrop et al. 2002). In contrast, effects of fish on littoral macroinvertebrates are less clear. Over 50 years ago, Ball and Hayne (1952) observed a two-fold increase in the abundance and biomass of benthic macroinvertebrates following the removal of fish, but subsequent experiments have produced conflicting results (Post and Cucin 1984, Thorp 1986, Hanson and Butler 1994, Pierce and Hinrichs 1997, Svensson et al. 1999, Blumenshine et al. 2000).

Small-scale manipulations of fish densities suggest that responses of the littoral macroinvertebrate community vary from strong (Crowder and Cooper 1982) to weak (Thorp and Bergey 1981) and are often limited to certain taxa or guilds (Gilinsky 1984, Diehl 1992, Mancinelli et al. 1992). In addition to direct effects, these mesocosm manipulations indicate that fish can influence macroinvertebrates indirectly by modifying habitat (Wilcox and Hornbach 1991) and species interactions (Diehl 1995, Batzer et al. 2000). Mesocosm experiments also suggest that direct and indirect effects of fish can be mediated by a suite of factors, including habitat heterogeneity (Crowder and Cooper 1982, Gilinsky 1984, Diehl 1992), omnivory (Diehl 1993b), seasonality (Gilinsky 1984), and behaviour of prey (Wisenden et al. 1997). Small-scale experiments, however, are often criticized for having limited realism due to spatial and temporal scales that fail to incorporate natural variation (Carpenter 1996), leaving the question of the significance of fish predation on littoral macroinvertebrates unresolved. Despite the inconsistencies or limited relevance of small-scale experiments, comparative studies of lakes with and without fish routinely report differences in assemblages of littoral macroinvertebrates (Carlisle and Hawkins 1998, Wong et al. 1998, Stoks and McPeek 2003).

Since lakes supporting or lacking fish undoubtedly differ in other respects, ascribing among-lake differences in macroinvertebrates assemblages to fish predation is problematic. More informative comparisons would involve systems in which densities of fish vary significantly over time, e.g., due to disturbances. Recently, for example, Danylchuk and Tonn (2003) showed that fish populations in Alberta's Boreal Plains lakes frequently experience single-season declines in density of 50-90% as a result of winterkill, then recover almost as quickly. Similarly severe, albeit temporary declines in fish density have been observed in lakes dominated by northern pike (*Esox lucius*, W. Tonn, unpublished data; Langlois 2000). The question I address in this study is: could such fluctuations in fish density affect littoral macroinvertebrates?

Invertebrates are typically important prey only for juvenile pike up to 80 – 120 mm total length (TL; Hunt and Carbine 1951, Frost 1954, Franklin and Smith 1963, Eklöv and Hamrin 1989), above which pike are generally considered to be specialized piscivores (Frost 1954, Wolfert and Miller 1978, Diana and Mackay 1979, Eklöv and Hamrin 1989). In some systems in western North America, however, predation on macroinvertebrates by pike up to 600 mm can be substantial. Beaudoin et al. (1999), for example, reported invertivory among adult pike in pike-only lakes that are common in north-central Alberta. More surprising is the high incidence of 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).

To date, most research on trophic interactions involving northern pike has examined predator-prey dynamics of piscivorous pike (Savino and Stein 1989, He and Wright 1992, Eklöv and Persson 1996). Given their penchant for predation on macroinvertebrates in small, Boreal Plains lakes, however, is it possible that pike can structure macroinvertebrates communities? Eklöv and VanKooten (2001) conducted a pond experiment in which predation by pike reduced the biomass of macroinvertebrates, but ultimately attributed this pattern to a habitat shift of roach (*Rutilus rutilus*). In a serendipitous natural experiment, Langlois (2000) suggested that winterkill-induced fluctuations in fish density affected benthic macroinvertebrates in lakes dominated by pike and yellow perch (*Perca flavescens*). I am aware of no manipulative study, however, that examines explicitly the relationship between densities of northern pike and their macroinvertebrate prey.

In this study, I added pike to a fishless lake in the Boreal Plains of Alberta to examine experimentally the effect of invertivory by northern pike on 1) the abundance, biomass, and mean individual size of littoral macroinvertebrate taxa and 2) the overall structure of the littoral macroinvertebrate community. I also compared effects of this manipulation to two reference lakes and conducted a complementary mesocosm experiment within the experimental lake. My objective was to provide insight into the relationship between pike and their macroinvertebrate prey that could, in turn, identify potential impacts on the structure of boreal lake food webs of natural or anthropogenic fluctuations in populations of pike.

## Methods

### a) Description of study lakes

The study was conducted in three small, shallow, naturally eutrophic lakes in the mixed-wood boreal forest of north-central Alberta (Figure 2-1; Table 2-1). The smallest of these lakes, the experimental lake (EXP), had been fishless for at least 6 years due to a suspected winterkill (W. Tonn and co-workers, unpublished data). The prolonged absence of fish in EXP, together with its manageable size and isolation from other surface waters, made it an ideal candidate for a whole-lake manipulation. Two nearby lakes, R1 and R2, were dominated by yellow perch and northern pike. R1 was recovering from a severe winterkill 4 years earlier (Langlois 2000), whereas any past winterkills in R2 were likely small and mitigated by immigration of fishes from connecting surface waters (W. Tonn, and co-workers, unpublished data). R1 and R2 served as unmanipulated reference systems in this study.

### b) Experimental design

I used a BACI (before-after-control-impact) approach in which effects of introduced pike (summer 2001 and 2002) in EXP were compared to baseline data (summer 2000) and to the two unmanipulated reference systems (summer 2000 – 2002). Data in all summers consisted of monthly (May – August) samples of water chemistry, macroinvertebrates, and diets of pike, and a mid-summer estimate of relative densities of fishes (see below for detailed procedures). All samples in a given month were collected over a maximum of 7 days to minimize temporal variability. R1 and R2 were not sampled in June 2002 due to logistical constraints.

Northern pike (N = 355, mean TL 587 ± 2.5 mm, mean mass 1148 ± 12 g) were collected in mid-May 2001 from a neighbouring lake with gill nets and hook-and-line. Pike were transported to the experimental lake, lightly anesthetized with tricaine, weighed, measured (TL), and fitted with numbered anchor tags. Fish were monitored for ca. 30 minutes before release into the experimental lake, at a biomass density of ~35 kg/ha. As a precaution to prevent winterkill of the experimental population of pike between post-manipulation summers (2001 and 2002), I visited EXP every other week from early December to late March to clear the ice of snow (to increase light penetration and stimulate photosynthesis) and artificially aerate the water using compressed air.

To address the lack of replication common in whole-lake experiments (Carpenter 1989), I also conducted a 2-year (2001 – 2002) mesocosm experiment in EXP that compared the responses of macroinvertebrates in four fishless exclosures to two control structures accessible to pike. Exclosures were 3 m wide and extended approximately 7 m from shore to encompass the 0 – 1 m depth-zone. Walls consisted of a vinyl curtain anchored into the sediment and supported above the surface by a wooden frame. Two windows, 30 x 28 cm, covered with screening (0.16 cm bar mesh), were installed in each exclosure to accommodate fluctuating water levels. Controls were identical in design, except that 50% of each wall was open to the lake (and therefore to pike).

### c) Collection of samples

I determined the relative densities of northern pike and yellow perch in the reference lakes in July of each year as biomass-per-unit-effort (BPUE, mean biomass/hr/net) by setting, over two consecutive nights, multi-mesh gillnets (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). Three nets were set in shallow water (0 – 2 m) and one in the 2 – 4 m zone. For a given night, the location and orientation of nets within each zone were determined randomly. Netted fish were identified to species, and their length (TL, mm) and wet mass (g) measured. To avoid netting mortality in the stocked population, I did not estimate BPUE of northern pike in EXP.

Stomach contents were obtained from a subsample of 20 pike during each biomass survey of R1 and R2. I also collected up to 20 stomachs from the reference lakes in May, June (2000 and 2001 only), and August using morning sets of multi-mesh gill nets; the location, orientation, and depth of nets were selected to maximize capture of pike. Stomachs were collected from individuals across the range of available size classes. To minimize errors associated with the digestion or regurgitation of prey, stomachs were only collected from freshly dead pike.

A maximum of 20 stomach samples per month were obtained from adult pike in EXP captured by hook and line in 2001 and 2002. I lightly anaesthetized these pike with tricaine before measuring their length and flushing their stomachs using a non-lethal technique similar to one used by Light et al. (1983); these fish were then returned to the lake. I applied this procedure to three pike gillnetted in R1 and subsequently dissected their stomachs. Efficiency of removal of consumed prey was qualitatively comparable to the > 97% efficiency reported by Light et al. (1983) using similar methods, suggesting that comparisons of diets determined by dissection and flushing are appropriate. All stomach samples were preserved in the field with 10% formalin.

Macroinvertebrates in the littoral zone (1.0 – 1.5 m in depth) were sampled monthly (May – August) at six (2000), 12 (2001), and eight (2002) randomly chosen sites in each lake using a sweep net (930 $cm^2$, bar mesh size 800 x 900 μm) and an Ekman grab (225 $cm^2$) fitted with a top screen (500 μm bar mesh). Grab samples were further sieved through a 243 μm wash bag. Based on Hanson et al. (1989), the number and frequency of samples in all years was sufficient to capture seasonal variation in boreal Alberta lakes. I also collected grab and sweep samples monthly (May – August) from two sites within each mesocosm in 2001 and 2002. Invertebrates > 1 mm (anterior of head to posterior of abdomen) were hand picked live within 24 hr using sugar flotation (Lind 1974) and preserved in 70% ethanol.

Finally, monthly samples of epilimnetic water were collected with a sample bottle from a depth of ca. 0.5 m over the deepest part of each lake, and from the centre of each mesocosm. These samples were refrigerated for later analysis.

### d) Laboratory work

Macroinvertebrates in grab and sweep samples, and organisms in stomach samples, were identified to the lowest practical taxonomic level (usually genus) following Clifford (1991), Nelson and Paetz (1992), and Russell and Bauer (2000), and enumerated. Dry mass of invertebrates was estimated using published (Lewis 1975, Dumont and Balvay 1979, Wrona 1982, Kabbe and Meyer 1991, Burgherr and Meyer 1997, Poepperl 1998, Wilhelm and Lasenby 1998, Benke et al. 1999, Sabo et al. 2002) and unpublished (G. Mittlebach, personal communication) length-dry mass regressions. If an invertebrate taxon was abundant in a stomach sample (or in a given lake-month, in the case of grab and sweep samples), I estimated its average per capita mass from a subsample of 40 individuals.

Dry mass of vertebrate prey was estimated using a combination of locally derived length-wet mass regressions (W. Tonn, unpublished data, C. Paszkowski and B. Eaton, unpublished data) and wet mass-dry mass conversions (Talyor and Kollros 1946, Adhoka and Duerr 1975, Diana and Mackay 1979, Brown et al. 1988, Churchill and Storey 1994, Hayes and Taylor 1994). Regression equations of backbone length to TL (Knight et al. 1995) and operculum length to TL (P. Aku, unpublished data) were also used to estimate the lengths of partially digested fishes.

Water samples were analysed for total phosphorous (TP) at the Limnology Services Laboratory, Department of Biological Sciences, University of Alberta using the modified potassium persulphate technique (Prepas and Rigler 1982).

### e) Statistical analysis

Stomach content analysis (SCA) was restricted to pike > 450 mm TL to reflect the size of individuals stocked into the experimental lake. I calculated the frequency of occurrence and percentage composition of each prey taxon by number and dry mass (Bowen 1996). The relative importance (Ri) of each prey taxon was calculated as $Ri_a = 100Ai_a/\Sigma Ai_a$, where $Ai_a$ = frequency of occurrence + percent number + percent mass of prey taxon *a* (George and Hadley 1979). I employed a linear index of food selection (Ready et al. 1985) to compare the relative abundance and mass of invertebrate prey in diets of pike to the relative abundance and mass of available prey. The latter were calculated as the average proportions in grab (benthic) and sweep (macrophytic and water column) samples. Availability was limited to prey taxa occurring in more than one stomach sample from any lake over the duration of the study, and therefore resulted in conservative estimates of selectivity. I excluded vertebrate prey from calculations of selectivity because their abundance in the lakes was either not estimated, or estimated using dissimilar methods. All values were calculated as monthly means and averaged by year in each lake. Annual means for R1 and R2 were further averaged to obtain a value (termed the reference diet) against which to qualitatively compare results from EXP. Empty stomachs were recorded but excluded from SCA.

The overall structure of the macroinvertebrate community in EXP before and after introduction of pike was investigated using ordination analysis. Lengths of the first axes in preliminary detrended correspondence analyses (1.2 – 1.8 standard deviations) indicated that analysis assuming linear responses of organisms to the environmental gradient was appropriate (ter Braak 1987). I therefore used principal components analysis (PCA) to examine patterns in mean abundance (number/sample) and mean biomass (mg/sample) among systems (lakes and mesocosms) and years from grab and sweep samples separately. Taxa that, on average, made up $< 0.1\%$ of the mean annual total abundance or biomass of macroinvertebrates in a matrix were pooled to create an "other" category. Matrix rows were relativised by rank (McCune and Mefford 1995). Parallel trajectories in PCA would imply that systems responded similarly to year effects, whereas differences in trajectories of experimental and reference systems would suggest a treatment effect. I tested the null hypothesis of no concordance (association) between pairs of matrices (e.g. biomass in grabs vs. abundance in sweeps) using Procrustes analyses (Jackson 1995). Significant results from these analyses suggest that compared matrices exhibit similar patterns across systems.

Randomized intervention analysis (RIA; Carpenter et al. 1989) tested the null hypothesis of no change in mean abundance, biomass, and individual size of macroinvertebrate taxa in grab or sweep samples in EXP relative to reference lakes. I 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. Including multiple reference systems increased the likelihood of incorporating intersystem variation, an advantage usually lacking in RIA (Murtaugh 2002).

Because I lacked pre-manipulation data for the mesocosm experiment, I analysed for treatment effects using linear regression. Mean abundance, biomass, and size of individual macroinvertebrate taxa were regressed against month (May = 1, June = 2, etc.) for exclosures and controls, with a resultant sample size in

2001 of 16 and 8 months, respectively. One of each treatment exclosure was excluded from analysis in 2002 due to damage by beavers. Sample size for exclosures and controls in 2002 was therefore 12 and 4 months, respectively. Differences in slope between treatments in each year were detected using a *t*-test (Zar 1999). A significant ($P < 0.05$) difference was interpreted as a positive treatment effect (i.e., an increase in mean abundance, biomass, or individual size of a macroinvertebrate taxon) when a control regression was positive and/or an exclosure regression was negative. Similarly, a negative effect was said to occur when control regressions were negative and/or exclosure regressions were positive. Non-significant results were considered neutral responses. Non-normal data sets were log (x) or log (x + 1) transformed and outliers removed before analysis. Given that treatment effects probably increased with time, I focused on results of regression for 2002 when qualitatively comparing to results of RIA.

## Results

### a) Macroinvertebrate communities in study lakes

Macroinvertebrate communities in all 3 study lakes were dominated by amphipods and dipterans (Table 2-2). *Gammarus lacustris* tended to dominate R2, whereas the smaller *H. azteca* was most abundant in EXP (prior to stocking) and in R1. Accordingly, relative biomass of amphipods in R2 was high, especially when compared to EXP. Hemipterans, odonates, dytiscid coleopterans, glossiphoniid leeches, and trichopterans characterized the remainder of the macroinvertebrate community in EXP, and biomass was distributed relatively evenly among amphipods, erpobdellid leeches, odonates, and dytiscid coleopterans (Table 2-2). In addition to amphipods and dipterans, macroinvertebrate communities in both reference lakes were dominated by trichopterans and hemipterans, while dytiscid coleopterans were rare. Glossiphoniid leeches and odonates, however, were relatively common in R2. Unlike EXP, biomass in reference lakes was overwhelmingly dominated by amphipods and dipterans (Table 2-2). Erpobdellid leeches, odonates, and dytiscid coleopterans tended to be much larger in EXP than in the reference lakes.

### b) Stomach content analysis

Diets of northern pike from the reference lakes were dominated by amphipods (Figure 2-2). Fishes, erpobdellid leeches, and larval trichopterans were of secondary importance. In contrast, leeches dominated diets of pike from EXP in 2001 and, to a lesser degree, in 2002. Less important were amphipods, coleopterans, and dipterans, all of which became more important in diets of pike in EXP in 2002.

For both abundance and biomass, pike in the reference lakes displayed positive selection for amphipods and leeches but negative selection for dipterans (Figure 2-2). In contrast, pike in EXP demonstrated strong positive selection for leeches, but strong negative selection for amphipods and dipterans. Other taxa in EXP and reference lakes were consumed in proportion to their observed abundance (or biomass).

### c) Community response

PCA of macroinvertebrate data delineated fishless systems (EXP in 2000 and exclosures in 2001 and 2002) from those with fish. Following addition of pike, the trajectories of EXP and the control exclosures paralleled each other and converged on the reference lakes (especially R1), each of which had independent trajectories. These patterns were best illustrated by PCA of macroinvertebrate abundance in grab samples (Figure 2-3a), which were concordant with patterns of biomass (Procrustes analysis; $P = 0.001$) and abundance ($P < 0.01$) in grab and sweep samples, respectively. Cumulative variance explained by axis 1 and 2 ranged from 50 to 62% in these ordinations.

Response of fishless systems to addition of pike was driven by a reduction in the abundance and biomass of large, active, and/or non-cryptic (i.e., conspicuous) taxa such as coleopterans, zygopteran odonates, and, to a lesser extent, leeches (Figure 2-3b) and an increase in the abundance and biomass of small, inactive, and/or cryptic (i.e., inconspicuous taxa) typically associated with the presence of fish (e.g., dipterans, and trichopterans). Community-level patterns based on macroinvertebrate biomass in sweep samples, however, were not concordant with other ordinations (*P*>0.1) in that the trajectories of EXP and the controls were largely parallel to, but not convergent with, the reference lakes and exhibited no clear relationship to conspicuousness of taxa.

### d) Response of individual taxa

RIA and regression analysis indicated that erpobdellid leeches in EXP (and mesocosm controls) declined consistently in abundance, biomass, and individual size in response to the addition of northern pike, relative to unmanipulated systems (R1, R2, and exclosures; Figure 2-4, Table 2-3). There were also suggestions of a negative response by larval coleopterans to addition of pike, especially from sweep samples, whereas amphipods tended to display an overall increase (Table 2-3). In addition, results for larval odonates suggested a negative response in benthic habitats (grab samples) while showing an opposite trend in vegetative habitats (sweep samples). Other taxa exhibited weak or inconsistent responses to manipulation. RIA (whole lake) and regression (mesocosm) analyses were generally in agreement for grab samples, however, sweeps samples were somewhat contradictory in that gammarids and dipteran pupae responded positively in the whole lake experiment but negatively in mesocosms (Table 2-3).

## Discussion

### a) Community response

The potential for northern pike to influence macroinvertebrates in the littoral zone of boreal mixed wood lakes is demonstrated by diets in the reference lakes, which were dominated by large macroinvertebrates despite the presence of prey fish. Invertivory by pike in lakes containing prey fish has been observed occasionally, particularly in naturally productive systems in western North America (Chapman et al. 1989, Sammons et al. 1994, Beaudoin et al. 1999) and may reflect a relative scarcity of vertebrate prey (Chapman and Mackay 1990). Although gill net surveys revealed an abundance of young-of-the-year (YOY) perch in both reference lakes (P. Venturelli, unpublished data), macrophytes may have been sufficiently dense to provide refuge for YOY perch, while supplying pike with an abundance of invertebrates (Diehl 1993a).

The tendency for pike to feed selectively on macroinvertebrates in productive boreal lakes likely explains why ordinations of the invertebrate communities differed between systems with and without fish. In general, the former exhibited macroinvertebrate communities dominated by inconspicuous taxa, e.g., dipterans and trichopterans, consistent with comparative studies that suggest that the selective removal of large taxa and large individuals by fish predators is an important causal mechanism shaping macroinvertebrate communities (Carlisle and Hawkins 1998, Langlois 2000, Knapp et al. 2001). Indeed, despite the relative importance of gammarids in reference diets, the higher average abundance and biomass of the amphipod *G. lacustris* in the reference lakes, relative to the pre-manipulated EXP, suggests an indirect, positive effect of predation by fish via their consumption of predators of amphipods (e.g., leeches, odonates, and coleopterans).

Addition of pike to EXP coincided with a shift in its macroinvertebrate community from one dominated by conspicuous taxa, e.g., coleopterans, zygopterans, and leeches, towards one dominated by inconspicuous taxa. Given a) the consistency of this trajectory with that of the control mesocosms, b) its convergence towards the reference systems, and c) the consistency of these relationships in three of the four ordinations, I contend that changes observed in EXP resulted from the manipulation and were not simply year effects. The generally parallel trajectories of EXP and reference systems in the one anomalous ordination (macroinvertebrate biomass in sweep samples) suggest a strong year effect for this matrix.

### b) Response of individual taxa

Diets of pike in EXP were dominated by two species of erpobdellid leeches, *Erpobdella punctata* and *Nephelopsis obscura*. Simultaneously, I observed a reduction in the abundance, biomass, and size of erpobdellids that was consistent between whole-lake and mesocosm experiments, suggesting a causal relationship.

*N. obscura* can breed 12, 15, or 19 months after hatching (Davies and Everett 1977, Baird et al. 1987) and switch from semelparous to interoparous modes of reproduction in different environments to increase fitness (Linton et al. 1983). This flexible life history strategy buffers erpobdellid populations from environmental variation and may have muted effects of predation by pike. That leeches nonetheless exhibited a treatment response therefore suggests a strong, direct interaction between leeches and northern pike.

Although dominating diets in the reference lakes, amphipods and larval insects were preyed upon less intensely by pike in EXP. Any responses of these taxa to manipulation, therefore, were likely indirect and thus more difficult to interpret, due to a myriad of potential food web linkages. Erpobdellid leeches, for example, can include amphipods and larval chironomids, odonates, and trichopterans in their diet (Davies and Everett 1975, Davies et al. 1981, Wrona 1982, Cywinska and Davies 1988). Conversely, amphipods and larvae of both coleopterans and odonates are known predators of erpobdellid cocoons and juveniles (Cywinska and Davies 1988). Thus, a reduction in the abundance of erpobdellids could cause either a reduction or an increase in the abundance of amphipods and larval coleopterans and odonates, illustrating the difficulty in resolving responses of individual taxa.

The inconsistency of results between sweep samples in the whole-lake and mesocosm experiments may reflect effects of exclosures. For example, macrophytes in exclosures tended to be denser and more sheltered from waves than macrophytes in control structures (P. Venturelli, personal observation) and may have subsequently supported higher abundance and biomass of macroinvertebrates (Crowder and Cooper 1982, Gilinsky 1984). In addition, both the substrate provided by exclosure walls and the warmer water in these structures (by ca. $1^{o}$C) than in EXP (P. Venturelli, unpublished data), may have also positively affected the abundance of biomass of macroinvertebrates. Given that analyses were conducted assuming that effects of exclosures were negligible, these differences could be interpreted as a pike-induced reduction in control mesocosms. Equally plausible, however, is that pike were attracted to these control structures (Eklöv 1997) such that predation pressure on macroinvertebrates was high relative to other areas of EXP.

Despite the potential for indirect effects and effects of exclosures to confound responses of individual taxa, some trends I observed were consistent with earlier results. The negative (albeit weak) response of larval coleopterans to manipulation, for example, is consistent with the negative association between fish and the biomass and size of coleopterans observed by Fairchild et al. (2000). Predation by fishes on large taxa, particularly benthic anisopterans, can be sufficiently high to favour the dominance of small, cryptic, macrophyte-dwelling taxa (including zygopterans) in the presence of fish (Blois-Heulin et al. 1990, Stoks and McPeek 2003). Such a mechanism would be consistent with the weak, negative response of odonate naiads in the benthos while they were displaying a concurrent positive trend in sweep samples. The low frequency of odonates in my samples, however, prevented analysis of the data at lower taxonomic levels. I also detected a weak, positive response of *G. lacustris* to stocking of pike that may have indirectly resulted from effects of pike on conspicuous macroinvertebrates (e.g., leeches, odonates, and coleopterans) that typically prey on amphipods (reviewed in Clifford 1991, and MacNeil et al. 1999).

## Conclusions

This study demonstrates experimentally that northern pike can affect littoral macroinvertebrates in Alberta's Boreal Plains lakes. The effect was strongest and most consistently documented at the level of overall community composition; significant responses of individual taxa were documented only for a few groups. This conclusion is similar to that reached by Langlois (2000), who employed a natural experiment approach involving winterkill of fish. Specifically, selective predation by pike in my experiment contributed directly to an observed reduction in the abundance, biomass, and size of erpobdellid leeches in EXP and control mesocosms. Responses among less common prey taxa were weak, indirect, or difficult to detect. Nonetheless, the cumulative responses of the macroinvertebrate communities of both experimental systems to the introduction of pike were distinct involving reductions in the relative abundance and biomass of conspicuous taxa and simultaneous increases in the abundance and biomass of inconspicuous taxa.

Littoral food webs are inherently complex owing to a multiplicity of direct and indirect interactions, including omnivory, multiple predators, complex and/or variable life histories, ontogenetic resource shifts, flexible behaviour, 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 (Yodzis 1988, Cardinale et al. 2002). Thus, the significant response of even a few taxa to manipulation and the community trajectories in EXP and control mesocosms in 2 years indicate the importance of pike as invertebrate predators in productive boreal lake food webs. Furthermore, data from R1 and R2, in which populations of invertivorous pike have been established for 5 or more years, suggest that observed effects are not transitory.

Research focusing on the long-term consequences of predation by pike on littoral macroinvertebrates is nonetheless necessary because effects of size-structured populations of pike may differ given the efficiency of small pike as predators in the littoral zone (Eklöv 1997) and the relative absence of size refugia for macroinvertebrate prey (Werner and Gilliam 1984, Persson et al. 1996). Pike in EXP also demonstrated size- and taxon-biased predation, which can affect the structure of prey communities (Wong et al. 1998, Blumenshine et al. 2000). I was unable to test for such responses, however, due to limited statistical power and the limited duration of the field experiment. Results of my experiment nonetheless suggest that littoral food webs in Alberta's Boreal Plains lakes are sensitive to changes in the density of fishes, and that such sensitivity should be taken into account when implementing management strategies that directly affect pike (e.g. harvest limits and stocking) or potentially alter disturbance regimes, such as winterkill, via changes in land-use in lake catchments (Tonn et al. 2003).

**Table 2-1**. Geographical location, physical, chemical, and biological characteristics of the study lakes. Physical data from Prepas et al. (2000) except surface area of the experimental lake and maximum depth of all lakes, which were collected in this study. Total phosphorous was averaged from monthly samples (May – August) over all summers (2000 - 2002). np = northern pike (*E. lucius*); yp = yellow perch (*P. favescens*); ws = white sucker (*Catastomus commersoni*); bs = brook stickleback (*Culaea inconstans*). Species in parentheses were uncommon.

| **Lake** | **Location (N,W)** | **Surface area (ha)** | **Maximum depth (m)** | **Mean depth (m)** | **Total phosphorous (µg/L) ± SE** | **Fish species** |
|---|---|---|---|---|---|---|
| Experimental | 55°03', 111°39' | 11.5 | 5.25 | 2.53 | 51.59 ± 4.10 | * |
| Reference 1 | 55°12', 111°38' | 106.5 | 7.50 | na | 37.59 ± 5.11 | np, yp, (bs) |
| Reference 2 | 55°09', 111°46' | 61.6 | 4.00 | 2.05 | 98.99 ± 7.10 | np, yp, (ws), (bs) |

* the experimental lake was fishless in 2000, but contained stocked np in 2001 and 2002

**Table 2-2**. Average composition (by abundance and biomass) of invertebrate assemblages and mean individual dry mass of common macroinvertebrate taxa in the experimental (EXP; 2000) and reference lakes (R1 and R2; 2000 – 2003). Values were calculated separately for grab and sweep samples and averaged.

| | *Mean annual relative abundance* **(number/total) x 100%** | | | *Mean annual relative biomass* **(mg dry mass/total) x 100%** | | | *Mean individual dry* **mass (mg)** | | |
|---|---|---|---|---|---|---|---|---|---|
| **Taxon** | **EXP** | **R1** | **R2** | **EXP** | **R1** | **R2** | **EXP** | **R1** | **R2** |
| Hirudinae (Glossiphoniidae) | 0.72 | 0.48 | 1.04 | 1.25 | 0.63 | 0.90 | 7.41 | 2.56 | 1.29 |
| Hirudinae (Erpobdellidae) | 0.18 | 0.30 | 0.28 | 10.8 | 3.91 | 2.70 | 64.6 | 9.09 | 11.5 |
| Amphipoda (*Gammarus lacustris*) | 13.5 | 13.5 | 51.8 | 15.6 | 58.0 | 75.4 | 3.36 | 5.37 | 6.27 |
| Amphipoda (*Hyallela azteca*) | 41.0 | 27.5 | 15.2 | 12.5 | 7.45 | 3.80 | 0.51 | 0.38 | 0.35 |
| Odonata | 1.52 | 0.60 | 1.38 | 12.3 | 2.21 | 0.36 | 29.2 | 20.8 | 1.72 |
| Hemiptera | 2.39 | 1.57 | 2.20 | 1.79 | 2.44 | 1.39 | 6.73 | 2.44 | 5.35 |
| Trichoptera | 0.64 | 2.10 | 0.39 | 1.47 | 6.94 | 1.08 | 2.81 | 4.54 | 6.85 |
| Coleoptera (Dytiscidae) | 0.87 | 0.31 | 0.41 | 39.1 | 2.31 | 1.37 | 206 | 5.50 | 31.3 |
| Diptera | 38.6 | 53.5 | 27.3 | 4.79 | 15.4 | 12.9 | 0.40 | 0.37 | 0.70 |
| Other | 0.65 | 0.27 | 0.06 | 0.29 | 0.72 | 0.07 | - | - | - |

**Table 2-3**. Effects of northern pike on the mean monthly abundance, biomass, and size of individual macroinvertebrate taxa in grab and sweep samples using a) randomized intervention analysis [experimental lake vs. reference lakes before (n = 4) and after (n = 7) manipulation] and b) linear regression exclosures (n = 12) vs. controls (n = 4) in 2002]. See text for details. “+” and “-” refer to positive and negative trends (0.2 > P > 0.05), respectively. “++” and “--” denote significant (P < 0.05) positive and negative effects of pike, respectively. “o” refers to neutral effects (P > 0.25). Blank cells occur where there were insufficient data to perform analyses.

**a) Whole-lake effects**

| **Sample** | **Response** | **Taxon** | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| **Type** | **Variable** | **Erpobdellidae** | ***G. lacustris*** | **Odonata** | **Trichoptera** | **Coleoptera** | ***Chaoborus*** | **Chironomidae** | **Dipt. Pupae** |
| **Grab** | **Abundance** | o | + | -- | - | o | o | o | o |
| | **Biomass** | - | o | -- | - | - | o | o | o |
| | **Size** | | + | ++ | o | | | ++ | |
| **Sweep** | **Abundance** | - | | | o | - | o | o | + |
| | **Biomass** | -- | + | o | o | -- | o | o | o |
| | **Size** | -- | o | | | | | | |

**b) Mesocosm effects**

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| **Grab** | **Abundance** | o | o | - | o | o | o | o | o |
| | **Biomass** | - | o | o | o | o | o | - | - |
| | **Size** | -- | o | | o | o | | + | |
| **Sweep** | **Abundance** | | - | o | - | | - | o | -- |
| | **Biomass** | | o | o | o | o | - | o | -- |
| | **Size** | | | | | | o | | |

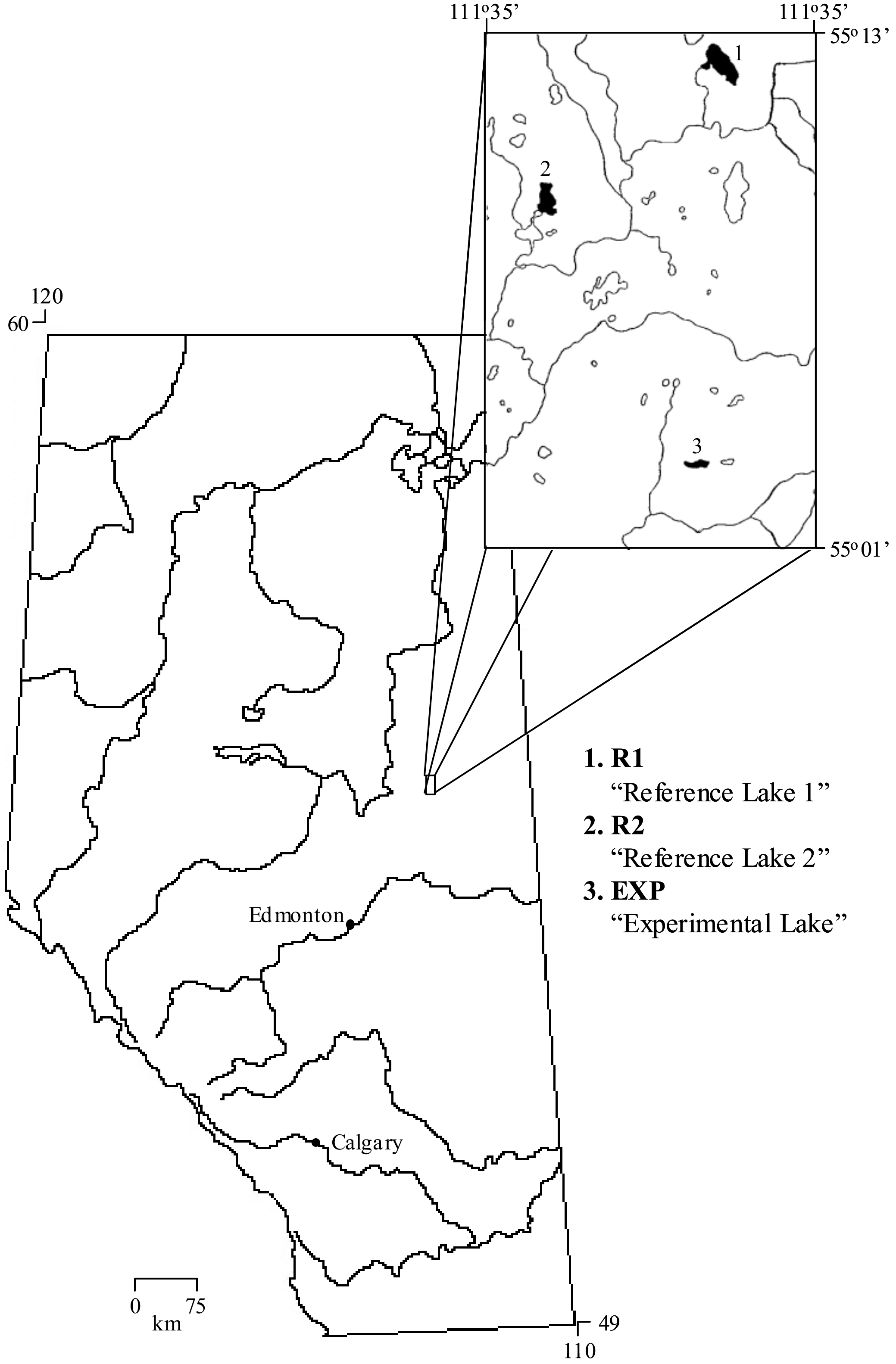

**Figure 2-1**. Map of Alberta showing location of study lakes

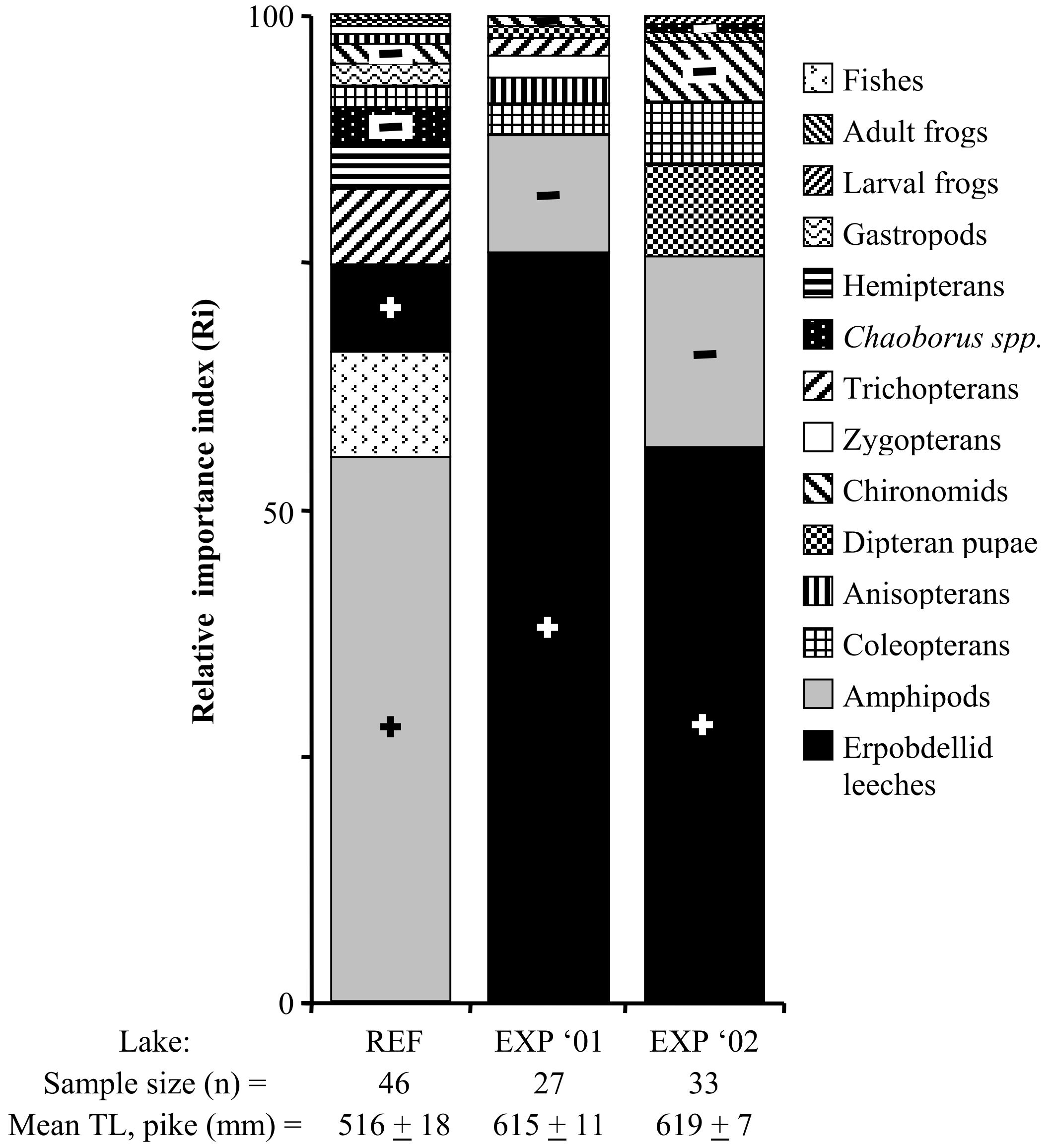

**Figure 2-2**. Relative importance index of prey taxa in diets of northern pike from the reference lakes (REF; average of all lakes and years) and the experimental lake (EXP) in the first and second summers following addition of pike. "+" and "–" symbols indicate positive and negative selection, respectively, for abundance and biomass of invertebrate prey using the linear index of food selection; the index could not be calculated for fish prey (see text).

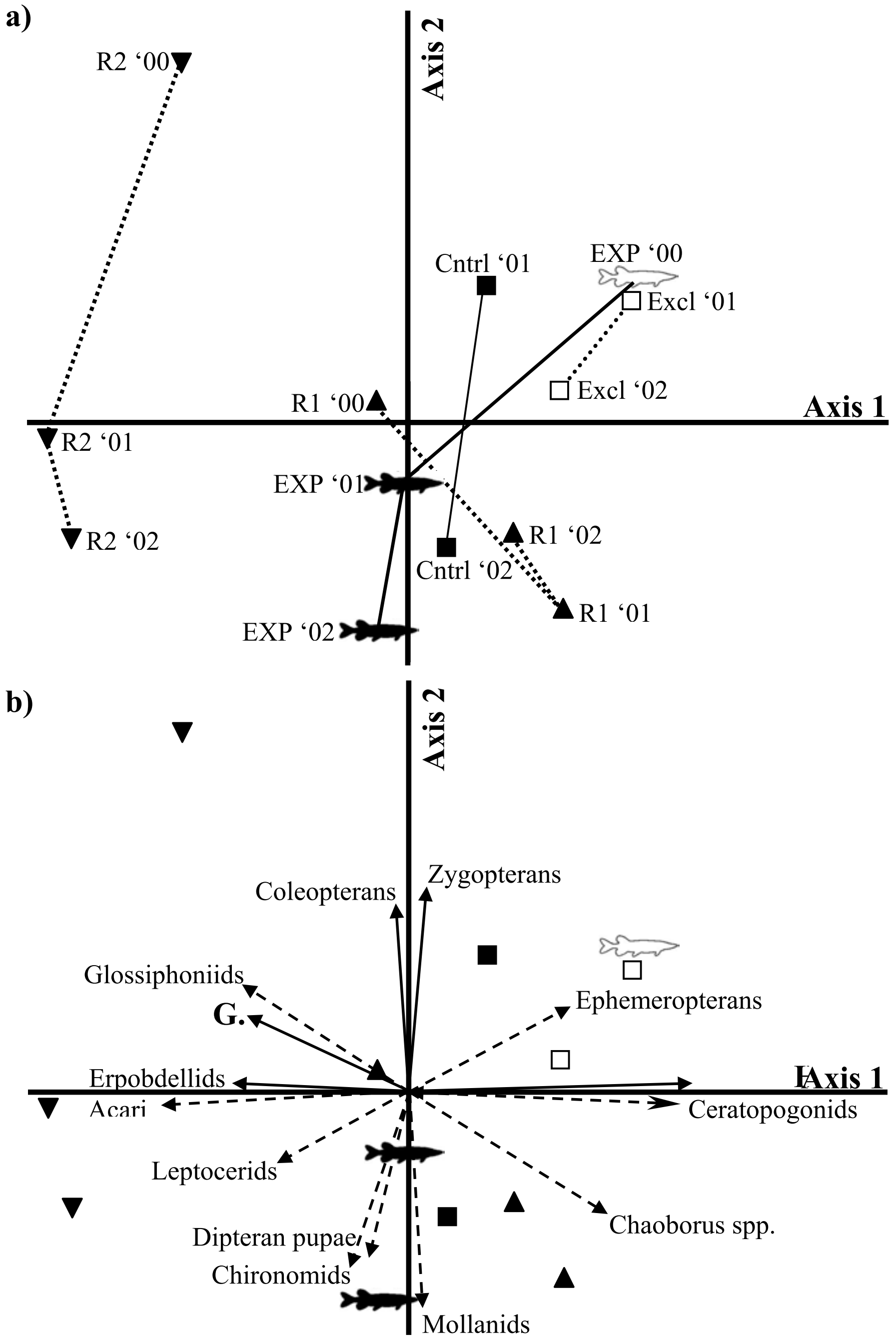

**Figure 2-3**. Standardized and centered principal components analysis of macroinvertebrate abundance (number/sample) in grab samples showing a) trajectories of the reference lakes (R1 and R2), the experimental lake (EXP), exclosures (Excl) and control exclosures (Cntrl), and b) the relationship between these trajectories and conspicuous (---) and inconspicuous (—) macroinvertebrate taxa. Shaded and open symbols refer to experimental systems with and without pike, respectively.

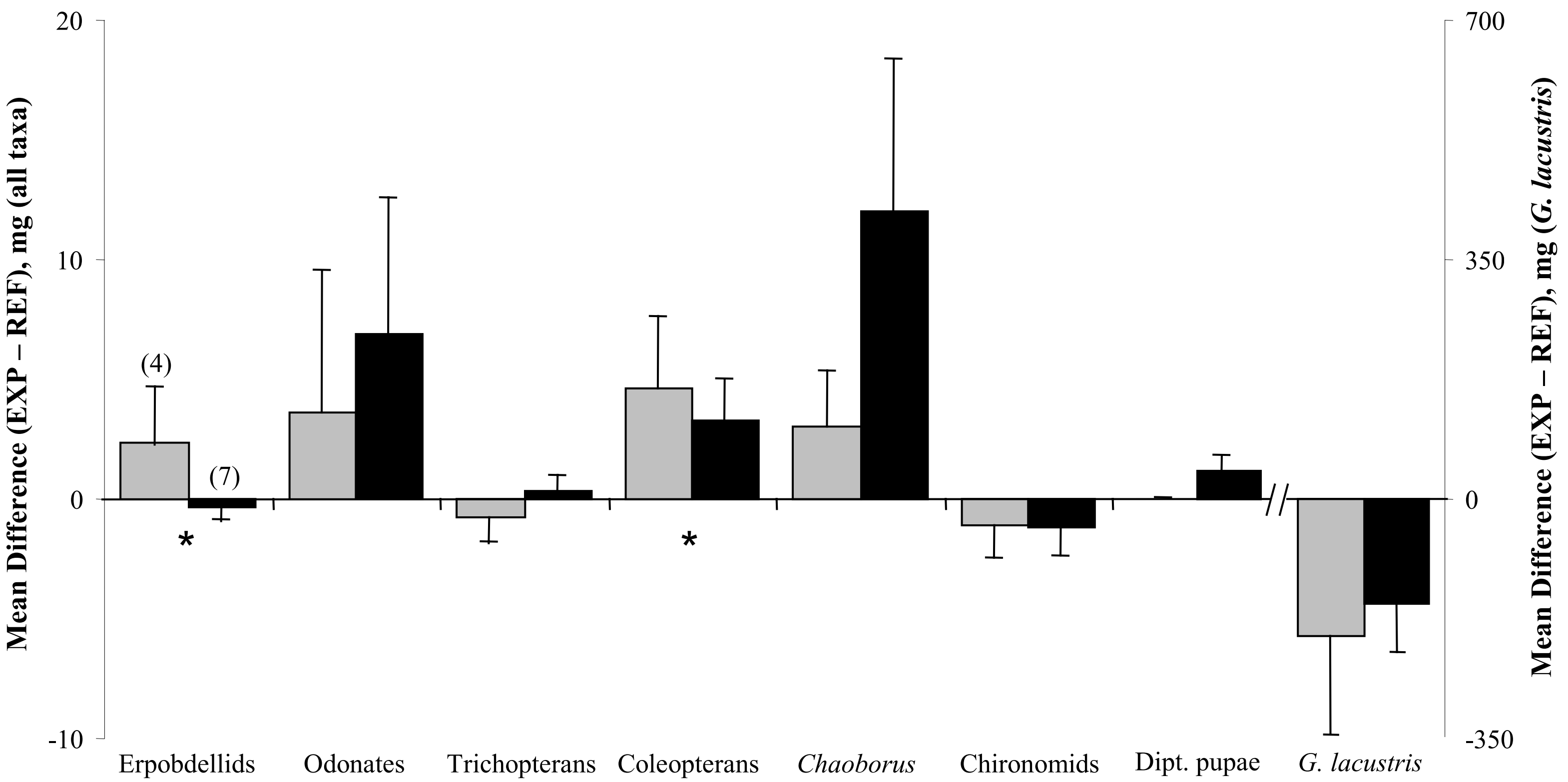

**Figure 2-4**. Mean differences in macroinvertebrate biomass in sweep samples between the experimental lake (EXP) and reference lakes (REF) before (grey) and after (black) stocking of pike. Positive values indicate higher biomass of a given taxon in the experimental lake; negative values indicate lower biomass. * $P < 0.05$ using randomized intervention analysis. Numbers in parenthesis apply to all taxa and refer to the number of paired comparisons before and after manipulation. Standard error bars are for illustrative purposes only and were not used in statistical analyses.

## Literature cited

Ahokas, R.A. and Duerr, F.G. 1975. Tissue water and intracellular osmoregulation in two species of euryhalie teloests, *Culaea inconstans* and *Fundulus diaphanus*. Comp. Biochem. Physiol. A, **52**: 449-454.

Baird, D.J., Linton, L.R., and Davies, R.W. 1987. Life-history flexibility as a strategy for survival in a variable environment. Funct. Ecol. **1**: 45-48.

Ball, R.C. and Hayne, D.W. 1952. Effects of the removal of fish population on the fish-food organisms of a lake. Ecology **33**: 41-48.

Batzer, D.P., Pusateri, C.R., and Vetter, R. 2000. Impacts of fish predation on marsh invertebrates: direct and indirect effects. Wetlands **20**: 307-312.

Beaudoin, C.P., Tonn, W.M., Prepas, E.E., and Wassenaar, L.I. 1999. Individual specialization and trophic adaptability of northern pike (*Esox lucius*): an isotope and dietary analysis. Oecologia **120**: 386-396.

Benke, A.C., Huryn, A.D., Smock, L.A., and Wallace, B.J. 1999. Length-mass relationships for freshwater invertebrates in North American with particular reference to the southeastern United States. J. N. Am. Benthol. Soc. **18**: 308-343.

Blois-Heulin, C., Crowley, P.H., Arrignton, M., and Johnson, D.M. 1990. Direct and indirect effects of predators on the dominant invertebrates of two freshwater littoral communities. Oecologia **84**: 295-306.

Blumenshine, S.C., Lodge, D.M., and Hodgson, J.R. 2000. Gradient of fish predation alters body size distributions of lake benthos. Ecology **81**: 374-386.

Bowen, S.R. 1996. Quantitative description of the diet. *In* Fisheries Techniques, 2nd ed. *Edited by* B.R. Murphy, and D.W. Willis. American Fisheries Society, Bethesda. pp. 513-532.

Brooks, J.L. and Dodson, S.I. 1965. Predation, body size, and composition of plankton. Science **150**: 28-35.

Brown, P.S., Barry, B., and Brown, S.C. 1988. Changes in absolute and proportional water content during growth and metamorphosis of *Rana sylvatica*. Comp. Biochem. Physiol. A, **91**: 189-194.

Burgherr, P. and Meyer, E.I. 1997. Regression analysis of linear body dimensions vs. dry mass in stream macroinvertebrates. Arch. Hyrdobiol. **139**: 1101-1112.

Cardinale, B.J., Palmer, M.A., and Collins, S.L. 2002. Species diversity enhances ecosystem functioning through interspecific facilitation. Nature **415**: 426-429.

Carlisle, D.M. and Hawkins, C.P. 1998. Relationships between invertebrate assemblage structure, 2 trout species, and habitat structure in Utah mountain lakes. J. N. Am. Benthol. Soc. **17**: 286-300.

Carpenter, S.R. 1989. Replication and treatment strength in whole-lake experiments. Ecology **70**: 453-463.

Carpenter, S.R. 1996. Microcosm experiments have limited relevance for community and ecosystem ecology. Ecology **77**: 677-680.

Carpenter, S.R., Kitchell, J.F., and Hodgson, J.R. 1985. Cascading trophic interactions and lake productivity. BioScience **35**: 634-639.

Carpenter, S.R., Frost, T.M., Heisey D., and Kratz, T.K. 1989. Randomized intervention analysis and the interpretation of whole-ecosystem experiments. Ecology **70**: 1142-1152.

Chapman, L.J., Mackay, W.C., and Wilkinson, C.W. 1989. Feeding flexibility in northern pike (*Esox lucius*): fish versus invertebrate prey. Can. J. Fish. Aquat. Sci. **46**: 666-669.

Chapman, L.J. and Mackay, W.C. 1990. Ecological correlations of feeding flexibility in northern pike (*Esox lucius*). J. Fresh. Ecol. **5**: 313-322.

Clifford, H.F. 1991. Aquatic Invertebrates of Alberta. University of Alberta Press, Edmonton.

Crowder, L.B. and Cooper, W.E. 1982. Habitat structural complexity and the interaction between bluegills and their prey. Ecology **63**: 1802-1813.

Churchill, T.A. and Storey, K.B. 1994. Metabolic responses to dehydration by liver of the wood frog, *Rana sylvatica*. Can. J. Zool. **72**: 1420-1425.

Cywinska, A. and Davies, R.W. 1989. Predation on the erpobdellid leech *Nephelopsis obscura* in the labaratory. Can. J. Zool. **67**: 2689-2693.

Danylchuk, A.J. and Tonn, W.M. 2003. Natural disturbances and fish: local and regional influences on winterkill of fathead minnows on boreal lakes. Trans. Am. Fish. Soc. **132**: 289-298.

Davies, R.W. and Everett, R.P. 1975. The feeding of four species of freshwater Hirudinoidea in Southern Alberta. Verh. Internat. Verein. Limnol. **19**: 2816-2827.

Davies, R.W. and Everett, R.P. 1977. The life history, growth, and age structure of *Nephelopsis obscura* Verill, 1892 (Hirudinoidea) in Alberta. Can. J. Zool. **55**: 620-627.

Davies, R.W., Wrona, F.J., Linton, L., and Wilkialis, J. 1981. Inter- and intra-specific analyses of the food niches of two sympatric species of Erpobdellidae (Hirudinoidea) in Alberta, Canada. Oikos **37**: 105-111.

Diana, J.S. and Mackay, W.C. 1979. Timing and magnitude of energy depostion and loss in the body, liver, and gonads of northern pike (*Esox lucius*). J. Fish. Res. Board Can. **36**: 481-487.

Diehl, S. 1992. Fish predation and benthic community structure: the role of omnivory and habitat complexity. Ecology **73**: 1646-1661.

Diehl, S. 1993a. Effects of habitat structure on resource availability, diet and growth of benthivorous perch, *Perca fluviatilis*. Oikos **67**: 403-414.

Diehl, S. 1993b. Relative consumer sizes and the strengths of direct and indirect interactions in omnivorous feeding relationships. Oikos **68**: 151-157.

Diehl, S. 1995. Direct and indirect effects of omnivory in a littoral lake community. Ecology **76**: 1727-1740.

Dumont, H.J. and Balvay, G. 1979. The dry weight estimation of *Chaoborus flavicans* (Meigen) as a function of length and instars. Hydrobiologia **64**: 139-145.

Eklöv, P. 1997. Effects of habitat complexity and prey abundance on the spatial and temporal distributions of perch (*Perca fluviatilis*) and pike (*Esox lucius*). Can. J. Fish. Aquat. Sci. **54**: 1520-1531.

Eklöv, P. and Hamrin, S.F. 1989. Predatory efficiency and prey selection: interactions between pike *Esox lucius*, perch *Perca fluviatilis* and rudd

*Scardinus erythrophthalmus*. Oikos **56**: 149-156.

Eklöv, P., and Persson, L. 1996. The response of prey to the risk of predation: proximate cues for refuging juvenile fish. Anim. Behav. **51**: 105-115.

Eklöv, P. and VanKooten, T. 2001. Facilitation among piscivorous predators: effects of prey habitat use. Ecology **82**: 2486-2494.

Fairchild, G.W., Faulds, A.M., and Matta, J.F. 2000. Beetle assemblages in ponds: effects of habitat and site age. Freshwater Biol. **44**: 523-534.

Franklin, D.R. and Smith, L.L. 1963. Early life history of the northern pike, *Esox lucius* L., with special reference to the factors influencing the numerical strength of year classes. Trans. Am. Fish. Soc. **92**: 91-110.

Frost, W.E. 1954. The food of pike, *Esox lucius* L., in Windermere. J. Anim. Ecol. **23**: 339-360.

George, E.L. and Hadley, W.F. 1979. Food and habitat partitioning between rock bass (*Ambloplites rupestris*) and smallmouth bass (*Mciropterus dolomieui*) yound of the year. Trans. Am. Fish. Soc. **108**: 253-261.

Gilinsky, E. 1984. The role of fish predation and spatial heterogeneity in determining benthic community structure. Ecology **65**: 455-468.

Hanson, J.M., Prepas, E.E., and Mackay, W.C. 1989. Size distribution of the macroinvertebrate community in a freshwater lake. Can. J. Fish. Aquat. Sci. **46**: 1510-1519.

Hanson, M.A. and Butler, M.G. 1994. Responses of food web manipulation in a shallow waterfowl lake. Hydrobiologia **279/280**: 457-466.

Hayes, D.B. and Taylor, W.W. 1994. Changes in the composition of somatic and gonadal tissues of yellow perch following white sucker removal. Trans. Am. Fish. Soc. **123**: 204-216.

He, X. and Wright, R.A. 1992. An experimental study of piscivore-planktivore interactions: population and community responses to predation. Can. J. Fish. Aquat. Sci. **49**: 1176-1183.

Hrbáček, J., Dvořakova, M., Kořinek, V., and Prochánzkóva, L. 1961.

Demonstration of the effect of fish stock on the species composition of zooplankton and the intensity of metabolism of the whole plankton association. Verh. Internat. Verein. Limnol. **14**: 192-195.

Hunt, B.P. and Carbine, W.F. 1951. Food of young pike, *Esox lucius* L., and associated fishes in Peterson's ditches, Houghton Lake, Michigan. Trans. Am. Fish. Soc. **80**: 67-83.

Jackson, D. 1995. PROTEST: A PROcrustean Randomization TEST of community environmental concordance. EcoScience 2: 297-303.

Kabbe, K. and Meyer, E. 1991. Biomass studies of water mites of the genera *Limnocharees* Latreille and *Hydrodroma* Koch (Hydrachnidia). *In* The Acari. *Edited by* R. Schuster and P.W. Murphy. Chapman & Hall, New York.

Kairesalo, T., Laine, S., Loukkanen, E., Malinen, T., and Keto, J. 1999. Direct and indirect mechanisms behind successful biomanipulation. Hydrobiologia **395/396**: 99-106.

Kasprzak, P., Lathrop, R.C., Mehner, T., and Koschel, R. 2002. Biomanipulation of lake ecosystems: an introduction. Freshwater Biol. **47**: 2277-2281.

Knapp, R.A., Matthews, K.R., and Sarnelle, O. 2001. Resistance and resilience of alpine lake fauna to fish introductions. Ecol. Monograph. **71**: 401-421.

Knight, R.L., Margraf, J.F., and Carline, R.F. 1984. Piscivory by walleyes and yellow perch in western Lake Erie. Trans. Am. Fish. Soc. **113**: 677-693.

Langlois, P.W. 2000. The influence of trophic state, thermal structure and winterkill on littoral macroinvertebrate communities in Boreal Plain lakes. MSc. Thesis, Univeristy of Alberta, Edmonton, Canada.

Lathrop, R.C., Johnson, B.M., Johnson, T.B., Vogelsang, M.T., Carpenter, S.R., Hrabik, T.R., Kitchell, J.F., Magnuson, J.J., Rudstam, L.G., and Steward, R.S. 2002. Stocking piscivores to improve fishing and water clarity: a synthesis of the Lake Mendota biomanipulation project. Freshwater Biol. **47**: 2410-2424.

Lewis, W.M. 1975. Distribution and feeding habits of a tropical *Chaoborus* population. Verh. Internat. Verein. Limnol. **19**: 3106-3119.

Light, R.W., Adler, P.H., and Arnold, D.E. 1983. Evaluation of gastric lavage for stomach analysis. N. Am. J. Fish. Manage. **3**: 81-85.

Lind, O.T. 1974. Handbook of common methods in limnology. The C.V. Mosby Company, St. Louis.

Linton, L.R., Davies, R.W., and Wrona, F.J. 1983. The effects of water temperature, ionic content and total dissolved solids on *Nephelopsis obscura* and *Erpobdella punctata* (Hirudinoidea, Erpobdellidae). Holarctic Ecology **6**: 64-68.

MacNeil, C., Dick, J. T.A., Elwood, R.W. 1999. The dynamics of predation on *Gammarus* spp. (Crustacea: Amphipoda). Biol. Rev. **74**: 375-395.

Mancinelli, G., Costantini, M.L., and Rossi, L. 2002. Cascading effects of predatory fish exclusion on the detritus-based food web of a lake littoral zone (Lake Vico, central Italy). Oecologia **133**: 402-411.

McCune, B., and Mefford, M.J. 1995. PC-ORD. Multivariate analysis of ecological data, version 2.0. MjM Software design, Glendeden Beach.

McQueen, D.J., Post, S.R., Mills, E. L. 1986. Trophic relationships in freshwater ecosystems. Can. J. Fish. Aquat. Sci. **43**: 1571-1581.

Murtaugh, P.A. 2002. On rejection rates of paired intervention analysis. Ecology **83**: 1752-1761.

Nelson, J. S. and M. J. Paetz. 1992. The fishes of Alberta. The University of Alberta Press, Edmonton; The University of Calgary Press, Calgary.

Persson, L., Andersson, J., Wahlstrom, E., and Eklöv, P. 1996. Size-specific interactions in lake systems: predator gape limitation and prey growth rate and mortality. Ecology **77**: 900-911.

Pierce, C.L. and Hinrichs, B.D. 1997. Response of littoral invertebrates to reduction of fish density: Simultaneous experiments in ponds with different fish assemblages. Freshwater Biol. **37**: 397-408.

Poepperl, R. 1998. Biomass determination of aquatic invertebrates in the northern German lowland using the relationship between body length and dry mass. Faun. Okol. Mitt. **7**: 379-386.

Post, J.R. and Cucin, D. 1984. Changes in the benthic community of a small precambrian lake following the introduction of yellow perch, *Perca flavescens*. Can. J. Fish. Aquat. Sci. **41**: 1496-1501.

Prepas, E.E., and Rigler, F.H. 1982. Improvements in quantifying the phosphorous concentration in lake water. Can. J. Fish. Aquat. Sci. **39**: 822-829.

Ready, R.C., Mills, E.L., and Confer, J.L. 1985. A new estimator of, and factors influencing, the sampling variance of the linear index of food selection. Trans. Am. Fish. Soc. **114**: 258-266.

Russell, A. P., and A. M. Bauer. 2000. The amphibians and reptiles of Alberta: a field guide and primer of boreal herpetology. University of Calgary Press, Calgary.

Sabo, J.L., Bastow, J.L., and Power, M.A. 2002. Length-mass relationships for adult aquatic and terrestrial invertebrates in a California watershed. J. N. Am. Benthol. Soc. **21**: 336-343.

Sammons, S.M., Scalet, C.G., and Neumann, R.M. 1994. Seasonal and size-related changes in the diet of northern pike from a shallow prairie lake. J. Fresh. Ecol. **9**: 321-329.

Savino, J.F. and Stein, R.A. 1989. Behavioural interactions between fish predators and their prey: effects of plant density. Anim. Behav. **37**: 311-321.

Shapiro, J., Lamarra, V., and Lynch, M. 1975. Biomanipulation: an ecosystem approach to lake restoration. *In* Water quality management through biological control. *Edited by* P.L. Brezonik, and J.L. Fox. Department of Environmental Engineering Sciences, University of Florida, Gainesville. pp. 85-96.

Stoks, R., and McPeek, M.A. 2003. Predators and life histories shape *Lestes* damselfly assemblages along a freshwater habitat gradient. Ecology **84**: 1576-1587.

Svensson, J.M., Bergman, E., and Gunnar, A. 1999. Impact of cyprinid reduction on the benthic macroinvertebrate community and implications for increased nitrogen retention. Hydrobiologia **404**: 99-112.

Taylor, C.A. and Kollros, J.J. 1946. Stages in the normal development of *Rana* *pipiens* larvae. Anat. Rec. **94**: 2-23.

ter Braak, C.J.F. 1987. CANOCO – a FORTRAN program for canonical community ordination by partial detrended canonical correspondence analysis, principal components analysis and redundancy analysis, version 2.1. Agricultural Mathematic Group, Wageningen.

Thorp, J.H. 1986. Two distinct roles for predators in freshwater assemblages. Oikos **47**: 75-82.

Thorp, J.H., and Bergey, E.A. 1981. Field experiments on responses of a freshwater, benthic macroinvertebrate community to vertebrate predators. Ecology **62**: 365-375.

Tonn, W.M., Paszkowski, C.A., Scrimgeour, G.J., Aku, P.K.M., Lange, M., Prepas, E.E., and Westcott, K.M. 2003. Effects of forest harvesting and fire on fish assemblages in boreal plains lake: a reference condition approach. Trans. Am. Fish. Soc. **132**: 514-523.

Wellborn, G.A., Skelly, D.K., and Werner, E.E. 1996. Mechanisms creating community structure across a freshwater gradient. An. Rev. Ecol. System. **27**: 337-63.

Werner, E.E. and Gilliam, J.F. 1984. The ontogenetic niche and species interactions in size-structured populations. An. Rev. Ecol. System. **15**: 393-425.

Wilcox, T.P. and Hornbach, D.J. 1991. Macrobenthic community response to carp (*Cyprinus carpio L.*) foraging. J. Fresh. Ecol. **6**: 171-183.

Wilhelm, F.M. and Lasenby, D.C. 1998. Seasonal trends in the head capsule length and body length/weight relationships of two amphipod species. Crustaceana **71**: 399-410.

Wisenden, B.D., Chivers, D.P., and Smith, R.J.F. 1997. Learned recognition of predation risk by *Enallamga* damselfly larvae (Odonata, Zygoptera) on the basis of chemical cues. J. Chem. Ecol. **23**: 137-151.

Wong, A.H.K., Williams, D.D., McQueen, D.J., Demers, E., and Ramcharan, C.W. 1998. Macroinvertebrate abundance in two lakes with contrasting fish communities. Arch. Hydrobiol. **141**: 283-302.

Wrona, F.J. The influence of biotic and abiotic parameters on the distribution and abundance of two sympatric species of Hirudinoidea. PhD. thesis, University of Calgary, Calgary, Canada.

Yodzis, P. 1988. The indeterminacy of ecological interactions as perceived through perturbation experiments. Ecology **69**: 508-515.

Zar, J.H. 1999. Biostatistical Analysis, 4th ed. Prentice Hall, Upper Saddle River.

# Chapter 3. INTRODUCTION OF PISCIVOROUS NORTHERN PIKE, *ESOX LUCIUS*, INTO A FISHLESS LAKE: EFFECTS OF ALLOPATRY ON DIET AND GROWTH OF ADULTS AND JUVENILES

## Introduction

The northern pike (*Esox lucius*) has a well-earned reputation throughout most of its circumpolar range as a large, voracious piscivore (Scott and Crossman 1973, Casselman 1996). Indeed, the morphology and behaviour of pike appear specialized for foraging on other fishes. Camouflage, large teeth, powerful jaws, an elongate body form, and a posterior arrangement of fins all contribute to the success of pike at ambushing prey from the cover of vegetation (Keast and Webb 1966, Webb 1984, Bry 1996). Not surprisingly, therefore, numerous studies have identified adult pike as specialized piscivores (Frost 1954, Franklin and Smith 1963, Vander Zanden et al. 1997, and references therein).

Pike do not generally select the largest prey fish consumable (Hart and Hamrin 1988, Nilsson and Brönmark 1999), but choose instead to consume prey 1/4 – 1/3 their length (Nursall 1973) such that size of prey tends to increase with size of pike (Frost 1954, Diana 1979). Bioenergetic simulations (Diana 1987) and lab experiments (Hart and Connellan 1984) suggest that large prey fish are important to the growth of pike. This relationship is supported by field studies in which the abundance of large pike was attributed, in part, to the availability of large prey (Makoweki 1973, Diana 1979, Owens and Pronin 2000). Similarly, an absence of large prey can result in stunted pike (Margenau 1995, Diana 1987).

Despite the piscivorous nature of northern pike and the advantage of this diet for growth, predation on invertebrates (invertivory) is fairly common, particularly in naturally productive systems in western North America. The most obvious example is from Beaudoin et al. (1999), who reported invertivory among adult pike in allopatric lakes (lakes in which pike are geographically isolated from prey fishes), which are common in boreal Alberta (Robinson and Tonn 1989). Periodic bouts of invertivory, however, have also been observed among otherwise piscivorous pike up to 600 mm in length (Chapman et al. 1989, Chapman and Mackay 1990, Sammons et al. 1994). These dietary shifts were attributed to relative differences in the seasonal availability of vertebrate and invertebrate prey. Predation on macroinvertebrates may be more consistent, however, as Beaudoin et al. (1999) identified invertebrate specialists in two populations of otherwise piscivorous pike on the basis of complementary stomach-content and stable isotope analysis.

The ability of adult northern pike to exploit macroinvertebrates in response to spatial and temporal variation in availability is indicative of trophic flexibility (Gerking 1994), which may serve to increase fitness in a dynamic environment (Dill 1983). Disturbance in the form of depletion of dissolved oxygen in winter (winterkill) is common in many small, naturally productive lakes in the western boreal region that can result in single-season declines in fish density of 50-90% (Danylchuk and Tonn 2003). However, because northern pike posses a higher tolerance for winter hypoxia than the large-bodied fishes on which they feed (Magnuson and Karlen 1970, Casselman 1996), such winterkill events can leave pike stranded in lakes void of forage fish (Robinson & Tonn 1989). Populations of pike in these lakes likely persist, in part, because pike can employ an opportunistic feeding strategy (Chapman and Mackay 1990, Beaudoin et al. 1999).

Unclear, however, is the dietary response of pike to sudden allopatry (as would occur following a winterkill), the bioenergetic costs of having to make this adjustment, and, ultimately, how this cost affects growth. Pike are opportunists, but they are also relatively poor learners (Coble et al. 1985). According to optimal foraging theory (Schoener 1971), an abrupt dietary switch from large to small prey, e.g., from piscivory to invertivory, would reduce net energy intake per unit time, and thus translate into reduced growth. Although growth of pike in boreal Alberta's allopatric lakes is typically low relative to lakes in which prey fishes are present, presumably as a result of prolonged invertivory (P. Aku and W. Tonn, unpublished data), the growth response of piscivorous pike immediately following sudden allopatry has never been quantified.

In this study, I stocked a fishless lake with piscivorous pike while monitoring pike in lakes containing prey fish to determine a) the dietary response of adult and juvenile pike to sudden allopatry, b) the bioenergetic costs of an invertebrate diet, and c) the consequences of these costs for growth of pike and their offspring. My purpose was to assess the consequences of winterkill for growth of pike and thereby contribute to the effective management of pike in variable environments. This research will also improve our understanding of how food webs in small, boreal lakes may be affected by disturbances, both natural and anthropogenic.

## Methods

### a) Description of study lakes

This experiment was conducted in three small, shallow, naturally eutrophic lakes in the mixed-wood boreal forest of east-central Alberta (Figure 3-1). Two lakes in this study, R1 (103.5 ha in area, 8 m maximum depth) and R2 (61.6 ha, 4.5 m) served as reference lakes. Yellow perch (*Perca flavescens*) and northern pike dominated both lakes. The experimental lake (EXP; 13 ha, 5.2 m) had been fishless for at least 6 years due to a suspected winterkill (Tonn and co-workers, unpublished data). In May 2001, after a 1-year pre-treatment period, I collected northern pike (N = 355, mean TL 587 ± 2.5 mm SE, mean mass 1148 ± 12 g SE) from nearby Piche Lake (518 ha, 18 m, containing pike, perch, walleye; *Stizostedion vitreum*, white sucker; *Catostomus commersoni*, brook stickleback; *Culaea inconstans*, and various cyprinids) and introduced them into EXP to achieve a biomass density of ca. 35 kg/ha (see Chapter 2). Sampling continued in the three study lakes throughout 2001 and 2002.

### b) Stable isotope analysis

Stable isotope analysis (SIA) is a means of estimating the trophic structure of aquatic food webs by comparing the isotopic signatures of constituent organisms (Vander Zanden et al. 1999). In this study, I used isotopic ratios of carbon

($^{13}C/^{12}C$) and nitrogen ($^{15}N/^{14}N$) to categorize where in the food web pike were feeding (i.e., their trophic position) before and after imposed allopatry.

Samples for use in 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 were handpicked or netted from littoral habitats and kept alive for 24 hours to allow for evacuation of gut contents. I captured pike and yellow perch using gill nets and hook and line. Blood was collected from the caudal vein of adult pike while white muscle tissue was used in SIA of yellow perch and young-of-the-year pike (YOY). Samples were frozen in the field and transported to the University of Alberta. I removed inorganic carbon from thawed macroinvertebrate samples by soaking them in 1 N HCL for 24 hours (or until bubbles no longer appeared). Invertebrate and fish specimens were then air dried for ca. 48 hours, homogenized with a mortar and pestle, weighed out to $1.0 \pm 0.1$ mg, and sealed in a 5 x 8 mm tin capsule. I used a composite taxon-within-lake sample when individual specimens did not meet the target mass.

Up to 5 replicate samples of each taxon were analysed at the National Water Research Institute, Saskatoon, Canada using 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 part per thousand (‰) deviation from standard using the formula $\delta^{13}C$ or $\delta^{15}N = [(R_{sample} - R_{standard})/R_{standard}] \times 1000$ where $R = {}^{13}C/^{12}C$ or $^{15}N/^{14}N$.

Trophic position (TP) of pike in Piche Lake was calculated as $TP = \lambda + (\delta^{15}N_{pike} - \delta^{15}N_{snails})/3.4$ following Post (2002), where $\lambda$ is the trophic position of snails. I calculated trophic position of pike in EXP using a modified version of this equation, termed a two-end-member-mixing model (Post 2002), to account for ambiguity in the baseline for isotopic nitrogen ratio in this system, i.e., vegetative (snails) vs. detrital (amphipods).

### c) Stomach content analysis

I used multi-mesh gill nets to collect up to 20 stomach samples per month (May – August, 2000 – 2002) from pike in the littoral zone of R1 and R2. Samples were collected in late morning or early afternoon and limited to recently dead pike to minimize errors associated with the digestion or regurgitation of prey. A maximum of 20 stomach samples per month were also obtained from adult pike angled in EXP (2000 – 2002) using a non-lethal flushing technique similar to Light et al. (1983). The > 97% efficiency of prey removal reported by Light et al. (1983) was supported in this study by qualitative observations made while practicing this technique on pike from the reference lakes. YOY were captured in EXP in 2002 using overnight and daytime sets of Gee minnow traps and fyke nets. These fish were sacrificed and their stomachs dissected due to the difficulty in applying the flushing technique to small fish (Hyslop 1980). Diet samples were preserved in 10% formalin and prey were later identified to the lowest practical taxonomic level. Each taxon was then enumerated, measured, and dry-mass estimated using length-dry mass regressions (see Chapter 2).

From the stomach content analysis (SCA), frequency of occurrence and percent composition of prey taxa by number and dry mass (Bowen 1996) were used to determine the relative importance index (Ri; George and Hadley 1979) for prey taxa of adult (> 450 mm TL) and juvenile (< 330 mm TL) pike in each lake-year. I calculated selectivity of pike for macroinvertebrate prey following Ready et al. (1985; see Chapter 2). Empty stomachs sampled in a given lake-month were expressed as a percentage of total stomachs collected in that month and averaged over the year. Index of relative importance, selectivity, and percent empty stomachs for R1 and R2 were further averaged to obtain overall reference means against which to compare results from EXP. I used contingency analysis (Zar 1999) to test the null hypothesis that the proportion of pike with empty stomachs was the same in EXP (average of both years) and the reference lakes.

Breadth of experimental and reference diets (BD; macroinvertebrate prey only) was calculated as $BD = \Sigma \sqrt{(p_j a_j)}$ (Krebs 1989), where $p_j$ = the proportion of prey type $j$ in the diet and $a_j$ = the proportion prey type $j$ in the environment.

Likewise, I measured the degree of overlap between diets using the Simplified Morisita Index ($C_H$; Krebs 1989) calculated as: $C_H = (2 \Sigma^n_i p_{ij}p_{ik})/(\Sigma^n_i p^2_{ij} + \Sigma^n_i p^2_{ik})$, where $p_{ij}$ and $p_{ik}$ = the proportion of prey type $i$ in diet $j$ and $k$, respectively.

### d) Simulated growth of pike

A fish bioenergetics model (Hanson et al. 1997) was used to compare the energy content of each diet and its effects on growth. Model parameters are summarized in Table 1. I defined length of simulation period as 123 days, based on the availability of data on diets and growth of pike (May to August, inclusive). Records of water temperature in EXP during this same period were incomplete owing to a malfunctioning data logger. Simulations were therefore based on a mean regional water temperature derived from data logger readings taken in the littoral zone of each lake at 30-minute intervals throughout each summer. The proportion of prey in diets was determined using SCA (see above). Energy densities (j/g wet mass) of these prey were from Hanson et al. (1997) and Cummins and Wuychuck (1971). I used mean values if a range of energy density was available. Where necessary, I also converted energy densities based on dry mass to wet mass assuming dry:wet ratios of 15% for insects (Cummins and Wuychuck 1971) and 20% for frogs (Churchill and Storey 1994). The remaining parameters, consumption and percent daily ration (amount of prey consumed per day expressed as the percent of a fish's mass), were estimated iterively by fitting observed growth of pike in EXP to their diet during the same period (May to September 2001).

I then held model parameters constant to predict how pike would grow under different diet scenarios: the diet of pike EXP in 2002, the reference-lake diet, and a hypothetical all-fish diet. I employed the same procedure to predict growth of juvenile pike on a reference-lake and all-fish diet. Because growth of juveniles in EXP was measured from late June 2002 to early July 2003 (K. Norris, unpublished data), I multiplied observed growth by 0.65 to correct for growth during the winter (Diana and Mackay 1979). Given that diet was the only manipulated variable in these simulations, predicted growth was essentially a surrogate for energy content that allowed me to quantify the relative benefits of each diet in terms of contribution to growth. This approach was not designed, however, to allow quantitative comparisons of predicted and observed growth because the simulation assumed unrealistically that consumption and ration did not vary with diet, and that water temperature remained constant throughout the summer.

### e) Observed and estimated growth of pike

Cleithra collected from up to 100 pike per lake-year from R1 and R2 in July of 2000, 2001, and 2002 (see Chapter 2) were used by Dr. Peter Aku, University of Louisiana at Monroe, to develop lake-specific regression equations relating length of cleithra to total length (TL) of pike. Equations were then used to back-calculate the length-at-age (in years) for individual fish. I combined these data with similar data from R1 and R2 in 1996 and 1997 (P. Aku and W. Tonn, unpublished data) to determine a length-at-age profile for the reference systems. A similar profile developed from ca. 300 northern pike from 4 small (19 - 115 ha) allopatric lakes sampled in this region in 1996 and 1997 was also made available (P. Aku and W. Tonn, unpublished data). I then calculated age-specific growth, expressed as percentage annual increase in total length (%TL), for each age class in each profile. Annual growth of adult pike in EXP was measured directly using recapture data from May 2002. Based on the length of these recaptured individuals at time of introduction (May 2001) and the length-at-age profile for reference lakes, I estimated that pike in EXP at introduction ranged in age from 4-8 years. I therefore qualitatively compared the observed annual growth of adult pike in EXP to the average growth of 4 to 8 year-old pike in reference and allopatric lakes. Similarly, length at age-1 of juvenile pike in EXP (measured in early July 2003) was compared to estimated length at age-1 of juveniles in reference and allopatric lakes. I did not compare growth or length-at-age between lake types statistically because values were obtained using dissimilar methods (i.e. measured from individuals in EXP but estimated from populations in other lakes).

## Results

### a) Diets of pike

Based on SIA, pike in Piche Lake were positioned at the top of the food web (Figure 3-2a). The long-term diet of pike probably consists of yellow perch and other (unsampled) fishes, corresponding to a trophic position of 5.4. In EXP, isotopic signatures of adult and YOY pike were similar (Figure 3-2b) and suggested that, as in Piche, these pike were the top predators in this food web. According to SIA, however, pike in EXP likely fed on a combination of amphipods and erpobdellid leeches that corresponded to a trophic position of 3.9, 1.5 trophic levels below the pike in Piche.

SCA confirmed this latter diet by identifying erpobdellid leeches as the dominant prey of adult pike from EXP in 2001 and 2002 (Figure 3-3). Secondarily important were amphipods, coleopterans, and dipterans. Although amphipods became more important (and leeches less so) in 2002, overlap of these diets was high (Table 3-2). According to the linear index of food selection for both abundance and biomass, adults in EXP demonstrated strong selection for leeches, while amphipods and dipterans were avoided (or unavailable). Diets of YOY in EXP in 2002 were broader than diets of adults, and were dominated by amphipods, with zygopterans, chironomids, and two orders of leeches being secondary prey (Figure 3-4). Selection was positive for amphipod abundance, but negative for amphipod biomass (i.e. YOY were preying selectively on small amphipods). Selection was also positive for zygopterans and glossiphoniid leeches, whereas dipterans were avoided (or unavailable). Other taxa in EXP and reference lakes were consumed in proportion to their observed abundance (or biomass). Overlap of juvenile and adult diets in EXP in 2002 was low (Table 3-2).

Amphipods were the dominant prey type in the reference lakes, with fishes, erpobdellid leeches, and larval trichopterans as secondary prey (Figure 3-3). This diet contrasted sharply with that of adults in EXP in 2001, but less so with diets in EXP in 2002 ($C_H = 0.2$ and 0.4, respectively; Table 3-2). Adult pike from the reference lakes consistently had a greater breadth of diet than pike from

EXP, although the latter broadened their diet in 2002 (Table 3-3). Frequency of empty stomachs of adult pike in EXP was almost twice high as in the reference lakes but this difference was not significant ($P > 0.05$). Diets of juveniles from the reference lakes were similar to adult pike, although dipterans were more important and erpobdellid leeches less so (Figure 3-4). Selection among adults and juveniles was for amphipods (and leeches, in the case of adults) while dipterans were avoided (or unavailable). Diets of juveniles from both experimental and reference systems exhibited a high degree of overlap. The difference in frequency of empty stomachs of juvenile pike in EXP and the reference lakes (0% and 18%, respectively) was not significant ($P > 0.05$).

**b) Simulated growth of pike in mass**

On average, the leech-rich diet of adult pike in EXP contributed to a 35% increase in mass by the end of summer 2001 (Figure 3-5). According to the bioenergetics model, this growth was realized with a 1.27% daily ration (Table 3-1). Had pike been feeding at this ration but with the diet observed in EXP in summer 2002 (fewer leeches, more amphipods), growth would have been only 18%. Similarly, the diet of adults from reference lakes, which was dominated by amphipods but also contained fishes, would have resulted in an increase in mass of only 15%. Predicted growth at a 1.27% ration was highest (59%) with the hypothetical diet of adult perch, nearly 4 times greater than growth predicted under the diets in EXP in 2002 and in the reference lakes. In terms of energy content, therefore, diets were ranked accordingly: all-fish > EXP ’01 > EXP ’02 > Ref.

Growth of YOY in EXP in 2002 was estimated at 4264% (Figure 3-6) and corresponded to a 7% daily ration (Table 3-1). Using the same parameters, the reference-lake diet of juveniles would result in a comparable increase, while a hypothetical all-fish diet would support growth 5-6 times greater than that realized on diets of invertebrates. Energetically, therefore, diets could be ranked as all-fish > EXP ’03 ≈ Ref.

### c) Observed and estimated growth of pike in length

Annual percent increase in TL of adult pike in lakes with prey fish was estimated from back-calculated length-at-age data as being nearly 2.5 times greater than in allopatric lakes (Figure 3-7). Observed growth of adults in EXP was only slightly higher than back-calculated growth in allopatric lakes (5% versus 4%). Estimated length-at age of juvenile pike after 1 year in lakes with prey fish (220 mm) was greater than back-calculated growth in lakes without (160 mm; Figure 3-8). The largest first-year growth increment, however, was the observed growth among juveniles in EXP, which increased in length almost 320 mm in one year.

## Discussion

### a) Dietary responses of pike to invertebrate prey

Although results of SIA in Piche Lake were based on a single adult pike, the $\delta^{13}C$ and $\delta^{15}N$ signatures of this individual, and its trophic level, were similar to those reported for other large, piscivorous pike in east-central Alberta (Beaudoin 1998, Beaudoin et al. 1999, Paskowski et al. in review). According to Vander Zanden et al. (1997), trophic position among populations of piscivorous pike can vary by one trophic level as a result of variation in the availability and trophic position of prey. Trophic position of adult pike in Piche (5.4) was therefore in general agreement with Vander Zanden et al. (1997), whose data would put piscivorous *Esox* (northern pike and chain pickerel, *E. niger*, consuming $\geq$ 95% fish by volume) at an average trophic position of 4.4 (my calculation).

Adults from Piche dropped 1.5 trophic positions following introduction into the fishless EXP. This change was consistent with Vander Zanden et al. (1997) and Beaudoin (1998), whose data suggest that invertivorous populations of pike feed 0.5 – 1.5 trophic positions below piscivorous conspecifics (my calculations). Likewise, lake trout (*Salvelinus namaycush*) have been reported to drop in trophic position (0.6), as they became planktivorous in response to introduced competitors (Vander Zanden et al. 1999).

According to SCA, adult pike adjusted to allopatry by preying selectively on large erpobdellid leeches. Leeches are not usually important in diets of pike

(Lawler 1965, Chapman and Mackay 1990, Sammons et al. 1994, Beaudoin et al. 1999), likely due in part to their small size relative to prey fish, and low availability in systems with fish. Leeches, however, represent a large, easily digested, high-energy alternative to other macroinvertebrates. Given also that these leeches were abundant in EXP (see Chapter 2), likely due to the prolonged absence of fish predators, the continued importance of leeches in diets of pike throughout the summers of 2001 and 2002 further suggested that pike selected a diet that optimized energy intake per unit time (Gerking 1994), and signaled a relatively rapid adjustment to allopatry.

The diet of pike in two lakes containing prey fish was intended to serve as a reference with which to compare foraging strategies of piscivorous and invertivorous pike. Surprisingly, however, SCA and SIA indicated that adult pike in R1 and R2 were largely invertivorous, preying selectively on amphipods but also consuming erpobdellid leeches, other macroinvertebrates, and some fish. Diet data from reference lakes were nonetheless valuable in evaluating the response of pike in EXP to invertebrate prey. 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 pike in EXP relative to the reference lakes was further evidence that erpobdellid leeches were a high-ranking, abundant prey in EXP. That pike in the reference lakes were also selecting leeches, but exhibited relatively broad diets that included low- and high-ranking alternatives, suggests that leeches in this system were relatively unavailable, perhaps as a result of predation. Indeed, diets of pike in EXP in 2002 broadened and began to converge upon the reference-lake diet in response to a reduction in the abundance and biomass of leeches (see Chapter 2). Pike in the reference lakes may have therefore consumed more amphipods than leeches because the latter were relatively scarce due to heavy predation pressure.

Interestingly, the frequency of empty stomachs in the reference lakes (28%) was not significantly different from EXP (14%), and was much less than the ca. 60% frequency observed previously in these systems (Beaudoin et al. 1999). The proportion of empty stomachs in a population of pike is directly related to the importance of piscivory (Diana 1979, Chapman et al. 1989, Beaudoin et al. 1999). Chapman et al. (1989) explained this relationship in terms of the relative difference in size of fish and invertebrates as prey, purporting that pike must consume small, invertebrate prey more frequently to meet their energy requirements and are therefore less apt to have empty stomachs. The prevalence of invertivory and correspondingly low frequency of empty stomachs among adult pike in both reference lakes, despite an apparent abundance of YOY yellow perch (P. Venturelli, unpublished data), may reflect the fact that macrophytes in these systems were dense and therefore provided refuge for prey fishes while supplying adult pike with an abundance of invertebrates (Diehl 1993). Dense macrophytes could also truncate the visual field of these sit-and-wait predators, thereby limiting pike to prey in their immediate vicinity. The proportion of small invertebrates in diets of pike may be high under such a scenario due to local depletion of preferred invertebrate prey (Wetterer and Bishop 1985). Whether or not pike increase their activity when preying on invertebrates, and how increased activity may affect net energy gain per unit time, however, is unknown.

Unlike adult pike, YOY in EXP did not specialize on erpobdellid leeches, but preyed instead on amphipods, zygopterans, and glossiphoniid leeches. Concordantly, the diet of YOY exhibited only modest overlap with those of adults and was relatively broad. On the other hand, this diet was similar to that of juveniles in another regional allopatric lake ($C_H = 0.9$; Beaudoin et al. 1999, my calculation) and the reference lakes. The later may not have included more erpobdellids or fishes in their diet due to predation and the density of macrophytes in these systems, respectively (see above). It is equally plausible that YOY were less discriminating in their diet than adults because a) the body size ratio of YOY predators to invertebrate prey was relatively small, and b) net energy gain for small predators tends to vary less with size of prey (Mittelbach 1981). Thus, juveniles in all systems were likely selecting from a larger range of highly-ranked prey types and sizes than adults, and may explain why YOY in EXP selected for small amphipods.

### b) Growth response of pike to invertebrate prey

According to the bioenergetics model, diets exhibited by adult pike in EXP were energetically superior to reference diets, which consisted primarily of amphipods and the occasional fish. Nonetheless, the EXP diet of leeches and other large invertebrates were consistently less rewarding than the hypothetical diet of prey fishes, suggesting invertivory is not ideal. This was supported by the growth of adult pike in EXP, which revealed that the sudden switch from piscivory to invertivory had a negative effect on growth. In reference lakes with prey fish, annual percent increase in TL of adult pike was ca. 10%. This compares favourably to the 8% documented for 4 to 8 year old pike, using data from 82 circumpolar water bodies on 3 continents (Casselman 1996; my calculation). In contrast, annual growth of adults in regional alloptaric lakes and EXP was 4 and 5%, respectively. Stunted pike have been observed following prolonged absence of suitably sized prey (Goeman and Spence 1992, Margenau 1995); my results suggest invertivory compromises growth of adults in as little as 1 year.

Given the prevalence of invertivory in the reference lakes, it is curious that adult pike exhibited growth that was more indicative of a piscivorous diet. Three factors may have contributed to this discrepancy. Firstly, a simple calculation based on values from Table 3-1 suggests that a pike must eat 300 large amphipods ca. 0.04 g wet mass each (12 g total) to gain the energy equivalent of 1 10g perch. Given that piscivory is therefore associated with a relatively low percent daily ration (and perhaps costs associated with activity; Pazzia et al. 2002), the occasional inclusion of prey fishes in the diet of pike may thus be more important than suggested by the bioenergetics model. Secondly, Beaudoin (1998) and Beaudoin et al. (1999) suggest that piscivory was more common in these populations before R1 suffered a severe winterkill in 1996 (Langlois 2000), and R2 partially winterkilled in 1999 (N. Kalef, personal communication). Estimated growth of adult pike in these lakes was determined from back-calculated length-at-age profiles and thus likely reflected, in part, this earlier more-piscivorous diet. Although this hypothesis was weakly supported by a *post-hoc* analysis of data constrained to years following winterkill, sample size was limited to 5 relatively young individuals. Finally, pike in these lakes may have preyed more heavily on fishes during the fall and winter, when densities of macrophytes (and therefore prey refugia) were low relative to my sampling period (May – August).

Similar to adults, estimated annual growth of juveniles in the reference lakes (ca. 220 mm) was comparable to the circumpolar average (ca. 200 mm; Casselman 1996), while the relatively slow growth of juveniles in regional allopatric lakes was consistent with Hunt and Carbine (1951), who identified availability of prey fishes as an important determinant of growth in juveniles. YOY in EXP, however, reached an average TL of 319 mm in the absence of prey fishes. This growth appears inconsistent with bioenergetic simulations, which suggest that invertebrate diets are inferior to diets composed of fish. Based on my results, however, prey fishes are relatively unimportant in reference-lake diets, suggesting that comparisons to a hypothetical all-fish diet are unrealistic. The disparity between simulated and observed growth may also reflect the fact that juveniles in the reference and allopatric lakes did not actually feed at the 7% daily ration assumed by the model. Optimum ration for piscivorous, 20 g (~140 mm) pike at 15$^{o}$C, for example, is 3.2% (reviewed by Casselman 1996), whereas juveniles in the reference lakes may have fed at a lower ration due to a low availability of preferred prey. Thus, rapid growth of juvenile pike in EXP probably reflects not only the fact that large, energy-rich invertebrates were present, but that they were also abundant.

## Conclusion

Winterkill is common in Alberta's Boreal Plains lakes (Robinson and Tonn 1989), and the sudden reduction or elimination of prey fishes likely contributes to the prevalence of invertivory in these systems (Beaudoin et al. 1999). Following their introduction, northern pike in EXP responded to sudden, imposed invertivory by taking advantage of an abundance of large, energy-rich prey. According to growth data, this foraging strategy was adequate in meeting the energy requirements of juvenile pike, but was relatively poor in compensating for the metabolic costs of foraging and other activities in adults. These results are in line with a body of literature that suggests truncated prey fields, particularly the absence of prey fishes, are inadequate for growth of large piscivores, and therefore result in stunted populations (Kerr 1971, Werner and Gilliam 1984, Diana 1987, Pazzia et al. 2002, Sherwood et al. 2002). Therefore, despite the fact that pike are trophically adaptable, disturbance-induced invertivory can compromise growth of adults, and may ultimately contribute to stunted populations in small, boreal lakes.

Invertivory may also intensify competition between large and small pike for common prey, and thus exacerbate stunting (Diana 1987). Juvenile pike, for example, tend to be more efficient at feeding on invertebrates abundant in habitats normally too shallow or densely vegetated for large conspecifics (Casselman 1996, Eklöv 1997). While my study certainly implies that different age classes of invertivorous pike consume similar resources (e.g., in the reference lakes), research quantifying competitive interactions among size-classes and their effects on growth would be valuable. Indeed, relative to the abundance of studies on piscivorous populations (reviewed by Bry 1996, Casselman 1996, Grimm and Klinge 1996), ecological interactions between size classes of invertivorous pike have received little attention. Large pike, for example, commonly cannibalize small conspecifics (Smith and Reay 1991), whereas inter-cohort cannibalism among invertivorous pike in small, Boreal Plains lakes is relatively rare (Beaudoin et al. 1999, this study).

Although invertebrates dominated the diet of pike in the reference lakes, pike in these systems did not appear stunted. Conversely, growth of pike in EXP was compromised on a diet superior to, but apparently converging on, the reference-lake diet. Resolving this apparent contradiction requires further research into the relationship between invertivory and growth, and how this relationship varies with prolonged allopatry. Nonetheless, my results suggest that the potential exists for populations of pike in disturbance-prone, Boreal Plains lakes to become stunted, despite high levels of primary production in these habitats. Given that stunting may also be difficult to reverse (Geoman and Spencer 1992, Margenau 1995), care should be taken when implementing management strategies that directly affect pike (e.g. harvest limits and stocking), or potentially alter disturbance regimes via changes in land use (Tonn et al. 2003) or the quality and quantity of lake water (McCarthy et al. 2001).

**Table 3-1**. Input parameters used to model growth of adult and juvenile pike under different diet scenarios.

| **Model Parameter** | | **Input Value** |
|---|---|---|
| Duration of simulation (days) | | 123[a] |
| Temperature (°C) | | 18.83[a] |
| Initial mass (g) | adults | 1148[a] |
| | juveniles | 3.84[a] |
| Final mass (g) | adults | 1552[a] |
| | juveniles | 167.57[a] |
| Daily ration (%) | adults | 1.27[b] |
| | juveniles | 6.95[b] |
| Consumption (g) | adults | 2095.46[b] |
| | juveniles | 356.95[b] |
| Prey energy density (J/g wet mass) | hirudinids | 4745[d] |
| | gastropods | 2182[d] |
| | amphipods | 4429[c] |
| | ephemeropterans | 4705[c] |
| | anisopterans | 2253[e] |
| | zygopterans | 3360[e] |
| | hemipterans | 3178[e] |
| | trichopterans | 3139[e] |
| | coleopterans | 3373[e] |
| | dipterans | 1762[c] |
| | cladocerans | 2514[c] |
| | anurans | 1372[f] |
| | fishes | 5201[c] |

[a] This study

[b] Model estimate based on data from this study

[c] Hanson et al. (1997)

[d] Hanson et al. (1997) assuming a dry:wet mass ratio of 15% (Cummins and Wuychuck 1971)

[e] Cummins and Wuychuck (1971)

[f] Cummins and Wuychuck (1971) assuming a dry:wet mass ratio of 20% (Churchill and Storey 1994)

**Table 3-2**. Paired matrix showing degree of dietary overlap between adult (> 450 mm) and juvenile (< 330 mm) northern pike from the reference lakes (REF) and the experimental lake (EXP).

| | | **Adults** | | | **Juveniles** | |
|---|---|---|---|---|---|---|
| | | **REF** | **EXP ’01** | **EXP ’02** | **REF** | **EXP ’02** |
| **Adults** | **REF** | 1.000 | | | | |
| | **EXP ’01** | 0.23 | 1.000 | | | |
| | **EXP ’02** | 0.40 | 0.93 | 1.000 | | |
| **Juveniles** | **REF** | 0.95 | 0.12 | 0.21 | 1.000 | |
| | **EXP ’02** | 0.84 | 0.24 | 0.44 | 0.91 | 1.000 |

**Table 3-3**. Sample size, mean total length (TL), and range in TL of a) adult, and b) juvenile northern pike from the reference lakes (average of all lakes and years) and the experimental lake (EXP) used to calculate breadth of diet and percent frequency of empty stomachs.

**a) Adults (> 450 mm TL)**

| Lake | Sample size (n) | Mean TL mm (± SE) | Range TL (mm) | Percent empty | Breadth of diet |
|---|---|---|---|---|---|
| **Reference** | 46 | 516 (18.41) | 451 – 694 | 14.1 | 0.81 |
| **EXP ‘01** | 27 | 615 (11.43) | 490 – 798 | 28.1 | 0.30 |
| **EXP ‘02** | 33 | 619 (6.57) | 534 – 705 | 27.6 | 0.45 |

**b) Juveniles (< 330 mm TL)**

| Lake | Sample size (n) | Mean TL mm (± SE) | Range TL (mm) | Percent empty | Breadth of diet |
|---|---|---|---|---|---|
| **Reference** | 77 | 273 (6.36) | 147 – 329 | 18.3 | 0.90 |
| **EXP ‘02** | 13 | 123 (11.23) | 73 – 195 | 0 | 0.79 |

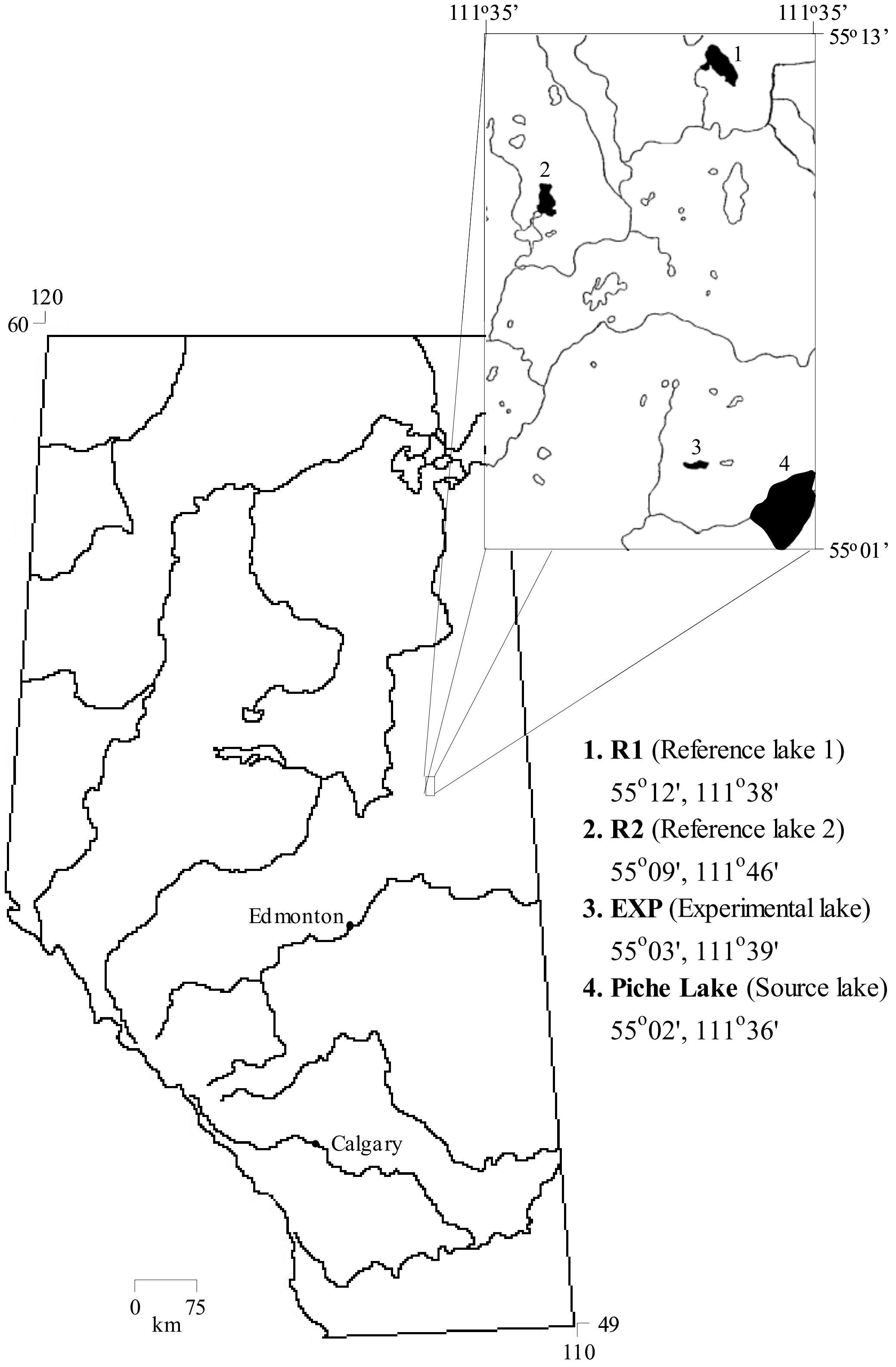

**Figure 3-1**. Map of Alberta showing location of study lakes

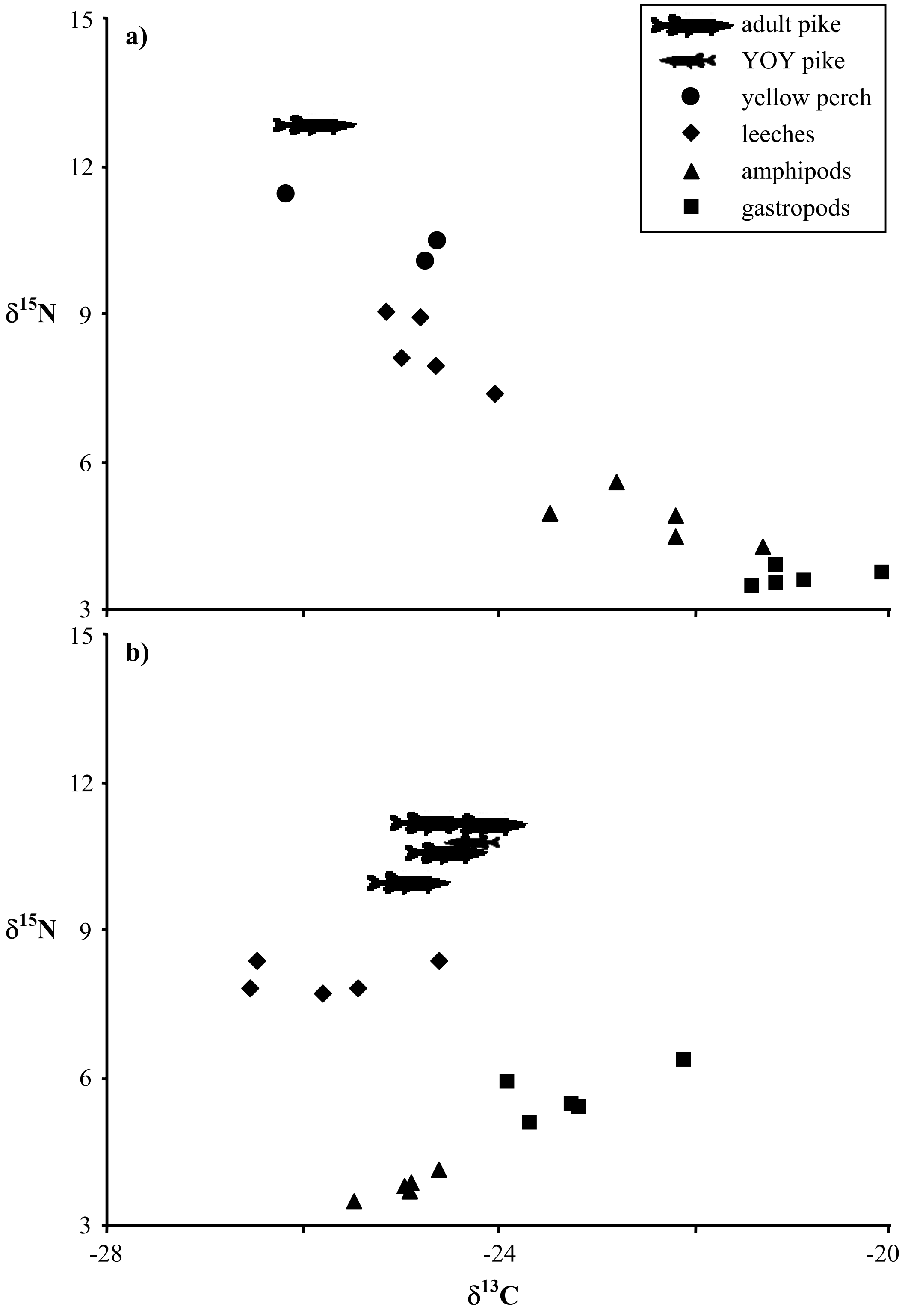

**Figure 3-2**. Scatter plot of $\delta^{13}$C and $\delta^{15}$N signatures (‰) of northern pike, yellow perch, and macroinvertebrates in a) Piche Lake and b) the experimental lake in late July and early August 2002.

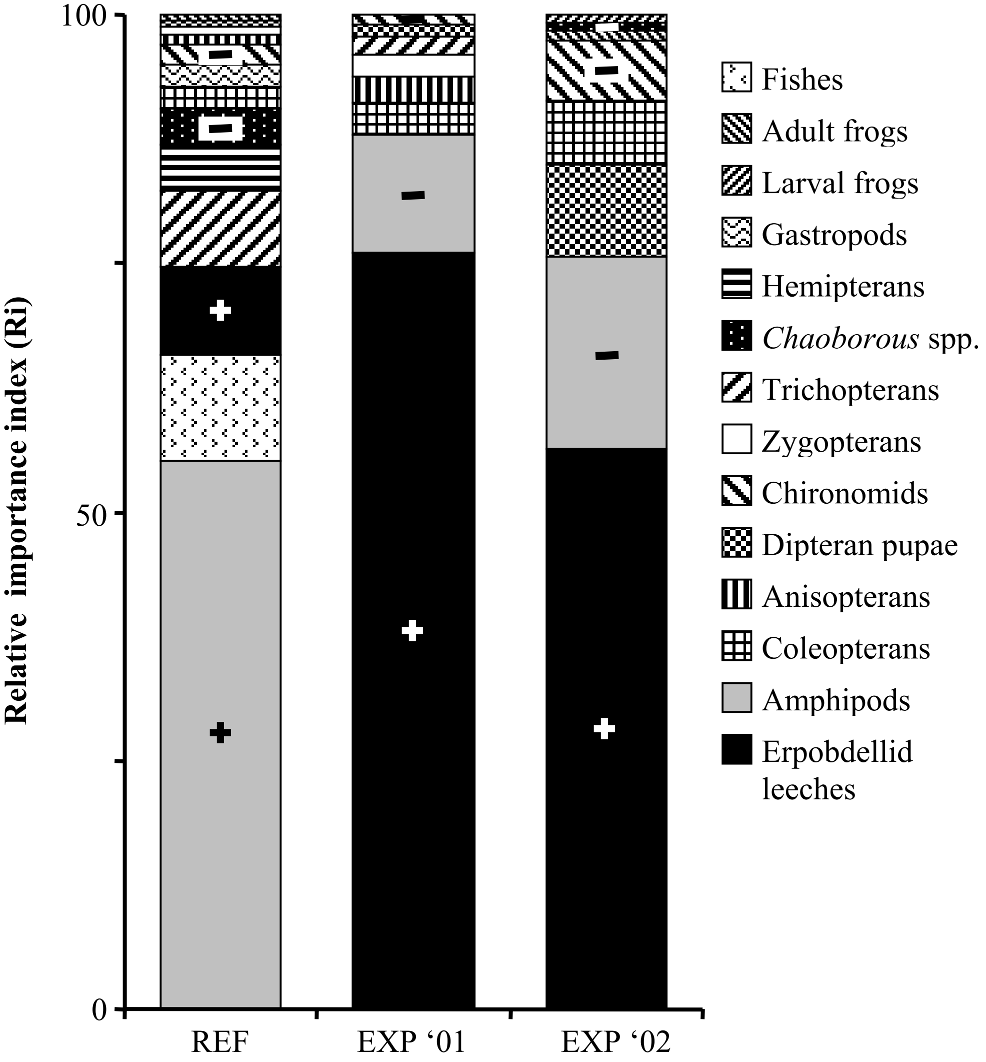

**Figure 3-3**. Relative importance index of prey taxa in diets of adult northern pike (> 450 mm) from the reference lakes (REF; average of all lakes and years) and the experimental lake (EXP) in the first and second summers following addition of pike. "+" and "–" symbols indicate positive and negative selection, respectively, for abundance and biomass of invertebrate prey using the linear index of food selection; the index could not be calculated for fish prey (see text). Size and description of samples are found in Table 3-3.

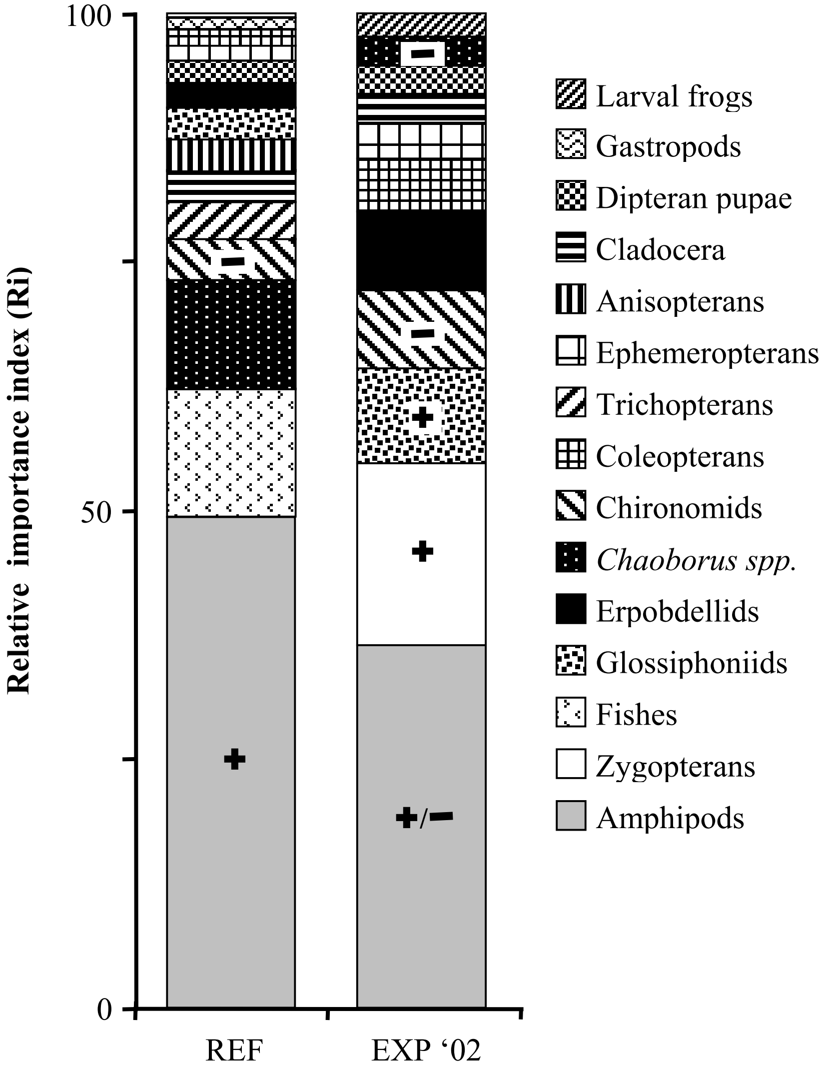

**Figure 3-4**. Relative importance index of prey taxa in diets of juvenile northern pike (< 330 mm) from the reference lakes (REF; average of all lakes and years) and the experimental lake (EXP) in 2002. "+" and "–" symbols indicate positive and negative selection, respectively, for abundance and biomass of invertebrate prey using the linear index of food selection; the index could not be calculated for fish prey (see text). "+/-" symbol indicates that selection was positive for abundance and negative for biomass. Size and description of samples are found in Table 3-3.

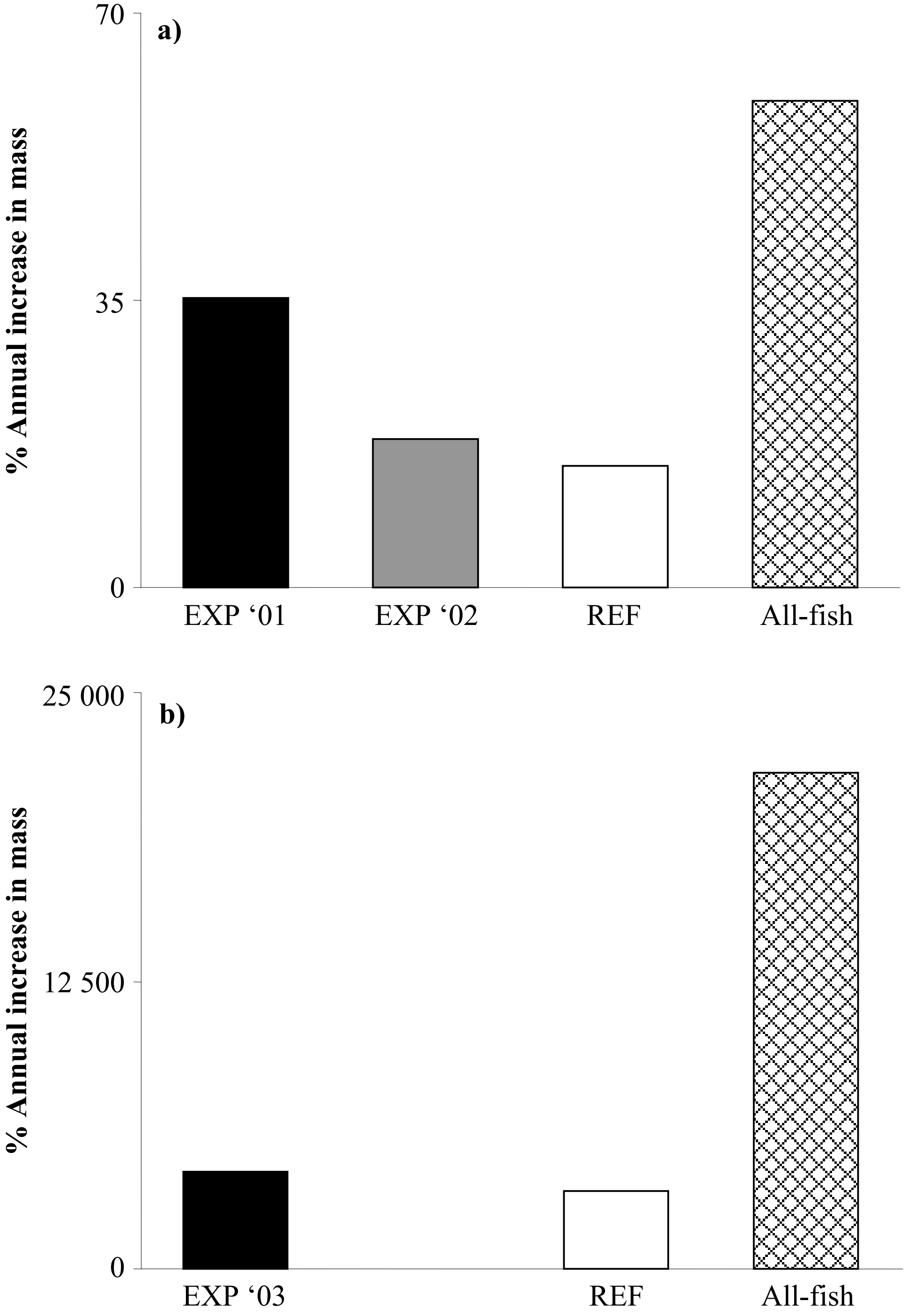

**Figure 3-5**. Growth in mass of a) adult (> 450 mm) and b) juvenile (<330 mm) pike observed in the experimental lake (EXP; black), and simulated growth of pike based on diets from EXP in 2002 (grey), the reference lakes (REF; white), and a hypothetical all-fish diet (crosshatching). See text for details.

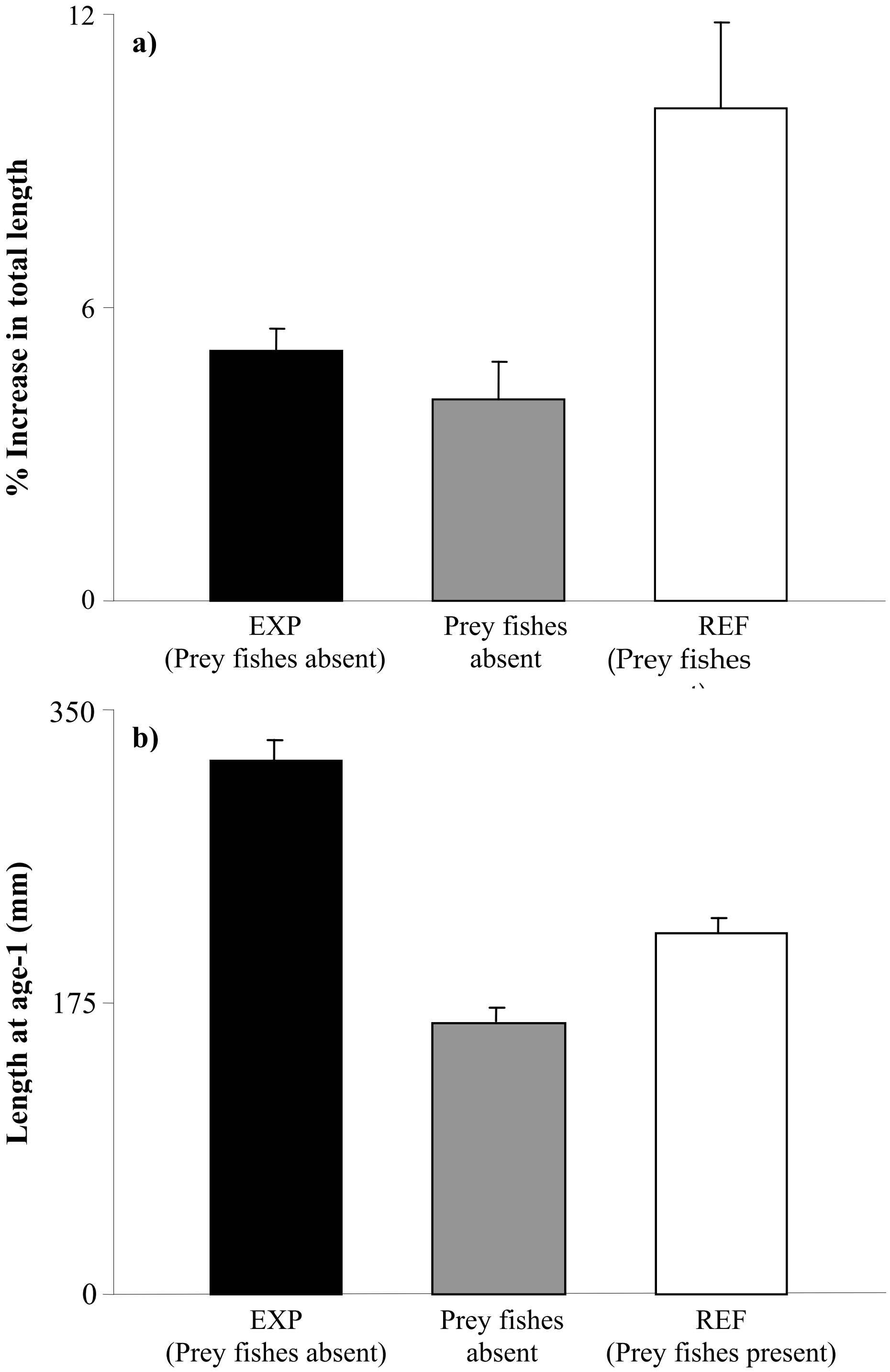

**Figure 3-6**. Observed (experimental lake; EXP) and back-calculated (lakes with and without prey fish) growth in total length of a) adult (> 450 mm) pike 4 to 8 years of age, and b) juvenile (age-1) pike. Growth in lakes with prey fishes (reference lakes; REF) and without prey fishes includes data from P. Aku and W. Tonn (unpublished data; see text for details). Standard error bars are for illustrative purposes only and were not used in statistical analyses.

## Literature cited

Beaudoin, C.P. 1998. Stable isotope study of food webs in lakes of Alberta's Boreal forest. MSc. Thesis, Univeristy of Alberta, Edmonton, Canada.

Beaudoin, C.P., Tonn, W.M., Prepas, E.E., and Wassenaar, L.I. 1999. Individual specialization and trophic adaptability of northern pike (*Esox lucius*): an isotope and dietary analysis. Oecologia **120**: 386-396.

Bowen, S.R. 1996. Quantitative description of the diet. *In* Fisheries Techniques, 2nd ed. *Edited by* B.R. Murphy, and D.W. Willis. American Fisheries Society, Bethesda. pp. 513-532.

Bry, C. 1996. Role of vegetation in the life cycle of pike. *In* Pike: biology and exploitation. *Edited by* J.F. Craig. Chapman and Hall, Dunscore. pp. 45-67.

Casselman, J.M. 1996. Age, growth and environmental requirements of pike. *In* Pike: biology and exploitation. *Edited by* J.F. Craig. Chapman and Hall, Dunscore. pp. 69-101.

Chapman, L.J., Mackay, W.C., and Wilkinson, C.W. 1989. Feeding flexibility in northern pike (*Esox lucius*): fish versus invertebrate prey. Can. J. Fish. Aquat. Sci. **46**: 666-669.

Chapman, L.J. and Mackay, W.C. 1990. Ecological correlations of feeding flexibility in northern pike (*Esox lucius*). J. Fresh. Ecol. **5**: 313-322.

Churchill, T.A. and Storey, K.B. 1994. Metabolic responses to dehydration by liver of the wood frog, *Rana sylvatica*. Can. J. Zool. **72**: 1420-1425.

Coble, D.W., Farabee, G.B., and Anderson, R.O. 1985. Comparative learning ability of selected fishes. Can. J. of Fish. Aquat. Sci. **42**: 791-796.

Cummins, K.W. and Wuycheck, J.C. 1971. Caloric equivalents for investigations in ecological energetics. Mitt. int. Ver. Limnol. **18**: 1-1588.

Danylchuk, A.J. and Tonn, W.M. 2003. Natural disturbances and fish: local and regional influences on winterkill of fathead minnows on boreal lakes. Trans. Am. Fish. Soc. **132**: 289-298.

Diana, J.S. 1979. The feeding pattern and daily ration of a top carnivore, the northern pike (*Esox lucius*). Can. J. Zool. **57**: 2121-2127.

Diana, J.S. 1987. Simulation of mechanisms causing stunting in northern pike populations. Trans. Am. Fish. Soc. **116**: 612-617.

Diana, J.S. 1996. Energetics. *In* Pike: biology and exploitation. *Edited by* J.F. Craig. Chapman and Hall, Dunscore. pp. 103-124.

Diana, J.S. and Mackay, W.C. 1979. Timing and magnitude of energy depostion and loss in the body, liver, and gonads of northern pike (*Esox lucius*). J. Fish. Res. Board Can. **36**: 481-487.

Diehl, S. 1993. Relative consumer sizes and the strengths of direct and indirect interactions in omnivorous feeding relationships. Oikos **68**: 151-157.

Dill, L.M. 1983. Adaptive flexibility in the foraging behavior of fishes. Can. J. Fish. Aquat. Sci. **40**: 398-408.

Eklöv, P. 1997. Effects of habitat complexity and prey abundance on the spatial and temporal distributions of perch (*Perca fluviatilis*) and pike (*Esox lucius*). Can. J. Fish. Aquat. Sci. **54**: 1520-1531.

Franklin, D.R. and Smith, L.L. 1963. Early life history of the northern pike, *Esox lucius* L., with special reference to the factors influencing the numerical strength of year classes. Trans. Am. Fish. Soc. **92**: 91-110.

Frost, W.E. 1954. The food of pike, *Esox lucius* L., in Windermere. J. Anim. Ecol. **23**: 339-360.

George, E.L. and Hadley, W.F. 1979. Food and habitat partitioning between rock bass (*Ambloplites rupestris*) and smallmouth bass (*Mciropterus dolomieui*) yound of the year. Trans. Am. Fish. Soc. **108**: 253-261.

Gerking, S.D. 1994. Feeding ecology of fish. Academic Press, San Diego.

Goeman, T.J., and Spencer, P.D. 1992. Fish community responses to manipulation of northern pike and yellow perch densities in a Minnesota centrarchid lake. Minnesota Department of Natural Resources Investigational Report No. 416.

Grimm, M.P. and Klinge, M. 1996. Pike and some aspects of its dependence on vegetation. *In* Pike: biology and exploitation. *Edited by* J.F. Craig. Chapman and Hall, Dunscore. pp. 125-156.

Hanson, P.C., T.B. Johnson, D.E. Schindler, and J.F. Kitchell. 1997. Fish bioenergetics 3.0. University of Wisconsin Sea Grant Institute, Madison.

Hart, P.J.B. and Connellan, B. 1984. Cost of prey capture, growth rate and ration size in pike, *Esox lucius* L., as functions of prey weight. J. Fish. Biol. **25**: 279-292.

Hart, P. and Hamrin, S.F. 1988. Pike as a selective predator. Effects of prey size, availability, cover and pike jaw dimensions. Oikos **51**: 220-226.

Hunt, B.P. and Carbine, W.F. 1951. Food of young pike, *Esox lucius* L., and associated fishes in Peterson's ditches, Houghton Lake, Michigan. Trans. Am. Fish. Soc. **80**: 67-83.

Hyslop, E.J. 1980. Stomach contents analysis: a review of methods and their application. J. Fish Biol. **17**: 411-429.

Keast, A. and Webb, D. 1966. Mouth and body form relative to feeding ecology of the fish fauna of a small lake, Lake Opinicon, Onario. J. Fish. Res. Board Can. **23**: 1845-1874.

Kerr, S.R. 1971. Prediction of growth efficiency in nature. J. Fish. Res. Board Can. **28**: 809-814.

Krebs, C.J. 1989. Ecological Methodology. Harper Collins Publishers, New York.

Langlois, P.W. 2000. The influence of trophic state, thermal structure and winterkill on littoral macroinvertebrate communities in Boreal Plain lakes. MSc. Thesis, Univeristy of Alberta, Edmonton, Canada.

Lawler, G.H. 1965. The food of pike, *Esox lucius*, in Heming Lake, Manitoba. J. Fish. Res. Board of Can. **22** : 1357-1377.

Light, R.W., Adler, P.H., and Arnold, D.E. 1983. Evaluation of gastric lavage for stomach analysis. N. Am. J. Fish. Manage. **3**: 81-85.

Magnuson, J.J. and Karlen, D.J. 1970. Visual observations of fish beneath the ice in a winterkill lake. J. Fish. Res. Board Can. **27**: 1059-1068.

Makowecki, R. 1973. The trophy pike, Esox lucius, of Seiber Lake. MSc. Thesis, Univeristy of Alberta, Edmonton, Canada.

Margenau, T.L. 1995. Stunted northern pike: a case history of community manipulations and field transfer. Wisconsin Department of Natural Resources Research Report No. 169.

McCarthy, J.J., Canziani, O.F., Leary, N.A., Dokken, D.J., and White, K.S. 2001. Climate Change 2001: impacts, adaptation and vulnerability. Contributions of working group II to the third assessment report of the intergovernmental panel on climate change. Cambridge University Press, Cambridge.

Mittelbach, G.G. 1981. Foraging efficiency and body size: a study of optimal diet and habitat use by bluegills. Ecology **62**: 1370-1386.

Nilsson, P.A. and Brönmark, C. 1999. Foraging among cannibals and kleptoparasites: effects of prey size on pike behavior. Behav. Ecol. **10**: 557-566.

Nursall, J.R. 1973. Some behavioural interactions of spottail shinters (*Notropis hudsonius*), yellow perch (*Perca flavescens*), and northern pike (*Esox lucius*). J. Fish. Res. Board. Can. **30**: 1161-1178.

Owens, R.W. and Pronin, N.M. 2000. Age and growth of pike (*Esox lucius*) in Chivyrkui Bay, Lake Baikal. Journal of Great Lakes Research **26**: 164-173.

Pazzia, I., Trudel, M., Ridgway, M., and Rasmussen, J.B. 2002. Influence of food web structure on the growth and bioenergetics of lake trout (*Salvelinus namaycush*). Can. J. Fish. Aquat. Sci. **59**: 1593-1605.

Post, D.M. 2002. Using stable isotopes to estimate trophic position: models, methods, and assumptions. Ecology **83**: 703-718.

Ready, R.C., Mills, E.L., and Confer, J.L. 1985. A new estimator of, and factors influencing, the sampling variance of the linear index of food selection. Trans. Am. Fish. Soc. **114**: 258-266.

Robinson, C.L. and Tonn, W.M. 1989. Influence of environmental factors and piscivory in structuring fish assemblages of small Alberta lakes. Can. J. Fish. Aquat. Sci. **46**: 81-89.

Sammons, S.M., Scalet, C.G., and Neumann, R.M. 1994. Seasonal and size-related changes in the diet of northern pike from a shallow prairie lake. J. Fresh. Ecol. **9**: 321-329.

Scott, W. B., and E. J. Crossman. 1973. Freshwater Fishes of Canada. Fish. Res.

Board Can. Bulletin No. 184.

Schoener, T.W. 1971. Theory of feeding strategies. Ann. Rev. Ecol. Syst. **2**: 369-404.

Sherwood, G.D., Pazzia, I., Moeser, A., Hontela, A., and Rasmussen, J.B. 2002. Shifting gears: enzymatic evidence for the energetic advantage of switching diet in wild-living fish. Can. J. Fish. Aquat. Sci. **59**: 229-241.

Smith, C., and Reay, R. 1991. Cannibalism in teleost fish. Rev. Fish Biol. Fish. **1**: 41-64.

Tonn, W.M., Paszkowski, C.A., Scrimgeour, G.J., Aku, P.K.M., Lange, M., Prepas, E.E., and Westcott, K.M. 2003. Effects of forest harvesting and fire on fish assemblages in boreal plains lake: a reference condition approach. Trans. Am. Fish. Soc. **132**: 514-523

Vander Zanden, M.J., Cabana, G., and Rasmussen, J.B. 1997. Comparing trophic position of freshwater fish calculated using stable nitrogen isotope ratios ($\delta^{15}N$) and literature dietary data. Can. J. Fish. Aquat. Sci. **54**: 1142-1158.

Vander Zanden, M.J. and Rasmussen, J.B. 1999. Primary consumer $\delta^{13}C$ and $\delta^{15}N$ and the trophic position of aquatic consumers. Ecology **80**: 1395-1404.

Webb, P.W. 1984. Body and fin form and strike tactics of four teleost predators attacking fathead minnow (Pimephales promelas) prey. Can J. Fish. Aquat. Sci. **41**: 157-165.

Werner, E.E. and Hall, D.J. 1974. Optimal foraging and the size selection of prey by the bluegill sunfish (*Lepomis macrochirus*). Ecology **55**: 1042-1052.

Werner, E.E. and Gilliam, J.F. 1984. The ontogenetic niche and species interactions in size-structured populations. An. Rev. Ecol. System. **15**: 393-425.

Wetterer, J.K. and Bishop, C.J. 1985. Planktivore prey selection: the reactive field volume model vs. the apparent size model. Ecology **66**: 457-464.

# Chapter 4. GENERAL DISCUSSION AND CONCLUSIONS

The degree to which Alberta's boreal lakes are threatened by both direct (resource extraction) and indirect (climate change) disturbances has made paramount the need for effective management strategies. To address potential effects of anthropogenic disturbance on boreal lakes, however, we must first improve our understanding of ecological processes within these highly variable systems, especially impacts of and responses to natural disturbance. Previous work using multi-lake comparative studies suggests that populations of northern pike (*Esox lucius*) in small lakes of north-central Alberta prey opportunistically on macroinvertebrates (Chapman and Mackay 1990, Beaudoin et al. 1999), with possible consequences for both macroinvertebrate communities (Langlois 2000) and growth of pike (P. Aku and W. Tonn, unpublished data). The objectives of this study were to examine these possibilities experimentally, provide a mechanistic understanding of these patterns, and relate them to disturbance.

Stable isotope analysis, together with stomach content analysis, revealed that piscivorous pike adjusted quickly to the absence of prey fishes by adopting a specialized diet of energy-rich leeches and other conspicuous macroinvertebrates. While the persistence of invertivorous pike in these systems (Beaudoin et al. 1999) appears paradoxical given the piscivorous nature of pike (Keast and Webb 1966, Vander Zanden et al. 1997), phenotypic specialization does not necessarily rule out an opportunistic feeding strategy (Robinson and Wilson 1998). Indeed, opportunism is common among most fishes as a means of increasing fitness in variable environments (Gerking 1994). While my study certainly suggests that invertivory did not negatively affect growth of juvenile pike, growth of adults was compromised. Invertebrates may therefore represent a trophic bottleneck that imposes an upper limit on size of pike. Furthermore, pike affected littoral macroinvertebrates by reducing the abundance and biomass of conspicuous taxa, especially leeches, which coincided with a broadening of the diet of pike to include energetically less rewarding prey. Given that diets of pike and macroinvertebrates present in the reference lakes exhibited similar characteristics as in EXP despite the presences of prey fishes, invertivorous pike appear capable of quickly exhausting their preferred prey base.

Together, these results suggest a scenario in which populations of invertivorous pike in small, naturally eutrophic boreal lakes become chronically stunted due to a simple negative feedback in which maximum achievable size is eroded by an increasing scarcity of preferred prey. Although winterkill likely exacerbates this cycle via size- and species-selective mortality (Magnuson and Karlen 1970, Casselman and Harvey 1975), it is equally conceivable that such disturbances mitigate stunting by allowing macroinvertebrates to periodically recover from predation. For instance, pike in the experimental lake probably benefited somewhat from an unexploited community of macroinvertebrates.

Determining the long-term consequences of invertivory in these variable systems, however, requires further study. The ecology of invertivorous pike, for example, remains virtually unknown, particularly with respect to the role of young pike, both in terms of their effects on macroinvertebrates and their relationship to older, larger conspecifics. Research is also needed to address effects of invertivory and stunting on the reproductive ecology of pike. According to research on Eurasian perch (*Perca fluviatilis*), stunting can affect life-history characteristics (e.g., size at maturation), and therefore the dynamics and size structure of populations (Ylikarjula et al. 1999, Claessen et al. 2002). Pike are also capable of intra- and inter-cohort cannibalism (reviewed by Grimm and Klinge 1996). While evidence of cannibalism in these systems was generally weak (Beaudoin et al. 1999, this study), research examining explicitly the development, prevalence, and importance of cannibalism in terms of individual growth and population dynamics of pike would nonetheless be valuable.

Despite the need for additional research, my study clearly demonstrates the sensitivity of boreal lake food webs to disturbance. Given that responses developed quickly and are potentially persistent (Goeman and Spencer 1992, Margenau 1995), resource managers should err on the side of caution when implementing policies that affect aquatic resources. Harvest limits for pike, for example, should account for natural variability in population (e.g., winterkill) by allowing ample time for recovery. Although the opposite is equally valid, i.e., that limits could be relaxed in anticipation of winterkill, applying this strategy would be difficult given the unpredictability of winterkill in time and space. Size limits should also be sensitive to situations where growth may be compromised in the absence of forage fish species. Similarly, resource managers should strive to limit local (e.g., resource exploration and extraction) and regional (e.g., climate) disturbances that can interact with a lake's natural disturbance regime.

## Literature cited

Beaudoin, C.P., Tonn, W.M., Prepas, E.E., and Wassenaar, L.I. 1999. Individual specialization and trophic adaptability of northern pike (*Esox lucius*): an isotope and dietary analysis. Oecologia **120**: 386-396.

Casselman, J.M. and Harvey, H.H. 1975. Selective fish mortality resulting from low winter oxygen. Verg. Internat. Verein. Limnol. **19**: 2418-2429.

Chapman, L.J., Mackay, W.C., and Wilkinson, C.W. 1989. Feeding flexibility in northern pike (*Esox lucius*): fish versus invertebrate prey. Can. J. Fish. Aquat. Sci. **46**: 666-669.

Claessen, D., Van Oss, C., de Roos, A.M., and Persson, L. 2002. The impact of size-dependant predation on population dynamics and individual life history. Ecology **83**: 1660-1675.

Gerking, S.D. 1994. Feeding ecology of fish. Academic Press, San Diego.

Goeman, T.J., and Spencer, P.D. 1992. Fish community responses to manipulation of northern pike and yellow perch densities in a Minnesota centrarchid lake. Minnesota Department of Natural Resources Investigational Report No. 416.

Keast, A. and Webb, D. 1966. Mouth and body form relative to feeding ecology of the fish fauna of a small lake, Lake Opinicon, Ontario. J. Fish. Res. Board Can. **23**: 1845-1874.

Langlois, P.W. 2000. The influence of trophic state, thermal structure and winterkill on littoral macroinvertebrate communities in Boreal Plain lakes. MSc. Thesis, Univeristy of Alberta, Edmonton, Canada.

Magnuson, J.J. and Karlen, D.J. 1970. Visual observations of fish beneath the ice in a winterkill lake. J. Fish. Res. Board Can. **27**: 1059-1068.

Margenau, T.L. 1995. Stunted northern pike: a case history of community manipulations and field transfer. Wisconsin Department of Natural Resources Research Report No. 169.

Robinson, B.W. and Wilson, D.S. 1998. Optimal foraging, specialization, and a solution to Liem's paradox. Amer. Nat. **151**: 223-235.

Vander Zanden, M.J., Cabana, G., and Rasmussen, J.B. 1997. Comparing trophic position of freshwater fish calculated using stable nitrogen isotope ratios ($\delta^{15}$N) and literature dietary data. Can. J. Fish. Aquat. Sci. **54**: 1142-1158.

Ylikarjula, J., Heino, M., and Dieckmann, U. 2000. Ecology and adaptation of stunted growth in fish. Evol. Ecol. **13**: 433-453.

# Appendix A:
# Isotopic signatures of biota used in stable isotope analysis

**Table A-1**. Isotopic signatures of carbon ($\delta^{13}$C) and nitrogen ($\delta^{15}$N) expressed as parts per thousand (‰) of organisms in the experimental lake (EXP; 29 July) and Piche Lake (4 August) in 2002. Composite samples are expressed as mean ± SE (n).

| | **EXP** | | **Piche Lake** | |
|---|---|---|---|---|
| **Organisms** | **$\delta^{13}$C** | **$\delta^{15}$N** | **$\delta^{13}$C** | **$\delta^{15}$N** |
| Gastropoda (Lymnaedae) | -23.2 ± 0.3 (5) | 5.6 ± 0.2 (5) | -20.9 ± 0.2 (5) | 3.6 ± 0.1 (5) |
| Amphipoda | -24.9 ± 0.1 (5) | 3.8 ± 0.1 (5) | -22.4 ± 0.3 (5) | 4.8 ± 0.2 (5) |
| Hirudinae (Erpobdellidae) | -25.8 ± 0.3 (5) | 8.0 ± 0.1 (5) | -24.7 ± 0.2 (5) | 8.3 ± 0.3 (5) |
| Yellow perch (juvenile) | na | na | -24.7 ± 0.1 (2) | 10.2 ± 0.2 (2) |
| Yellow perch (adult) | na | na | -26.2 | 11.4 |
| Northern pike (juvenile) | -24.2 | 10.6 | na | na |
| Northern pike (adult) | -24.5 ± 0.1 (5) | 10.7 ± 0.2 (5) | -25.9 | 12.8 |

# Appendix B:

# Diets of northern pike from experimental and reference lakes used in stomach content analysis and bioenergetics modeling

**Table B-1**. Percentage by number (%N) and mass (%M), frequency of occurrence (%FO), and relative importance index (Ri) of prey taxa in diets of adult (> 450 mm) northern pike in the experimental lake (EXP) and the reference lakes (Ref; average of all lakes and years). All insect prey were larval, with the exception of hemipterans, which were represented by juvenile and adult instars.

| **Lake (year)** | **Item** | **% N** | **% M** | **% FO** | **Ri** |
|---|---|---|---|---|---|
| EXP (2001) | Hirudinae (Erpobdellidea) | 82.6 | 92.1 | 100 | 76.1 |
| | Amphipoda | 9.3 | 7.2 | 25.9 | 11.7 |
| | Odonata (Anisoptera) | 3.0 | < 0.0 | 5.9 | 2.5 |
| | Odonata (Zygoptera) | 1.6 | < 0.0 | 6.3 | 2.2 |
| | Trichoptera | 1.1 | < 0.0 | 5.9 | 2.0 |
| | Coleoptera | 1.8 | 0.7 | 9.8 | 3.4 |
| | Diptera (Chironomidae) | 0.1 | < 0.0 | 3.6 | 1.0 |
| | Diptera (pupae) | 0.5 | < 0.0 | 3.6 | 1.1 |
| EXP (2002) | Hirudinae (Erpobdellidea) | 58.4 | 67.2 | 78.3 | 56.2 |
| | Amphipoda | 19.1 | 13.9 | 37.6 | 19.5 |
| | Coleoptera | 7.5 | 8.2 | 8.3 | 6.6 |
| | Diptera (*Chaoborus* spp.) | < 0.0 | < 0.0 | 3.1 | 0.9 |
| | Diptera (Chironomidae) | 4.8 | 1.1 | 15.8 | 6.0 |
| | Diptera (pupae) | 9.7 | 8.4 | 14.9 | 9.1 |
| | Anura (*Rana sylvatica* adults) | 0.4 | 1.3 | 1.6 | 0.9 |
| | Anura (*Rana sylvatica* larvae) | 0.1 | < 0.0 | 2.8 | 0.8 |
| Ref (2000-2002) | Hirudinae (Erpobdellidea) | 7.0 | 5.0 | 23.2 | 9.0 |
| | Gastropoda | 0.5 | < 0.0 | 8.2 | 2.2 |
| | Amphipoda | 74.5 | 68.4 | 73.9 | 55.2 |
| | Odonata (Anisoptera) | 0.1 | 0.2 | 4.2 | 1.1 |
| | Odonata (Zygoptera) | < 0.0 | < 0.0 | 2.8 | 0.7 |
| | Hemiptera | 2.7 | 0.6 | 14.7 | 4.6 |
| | Trichoptera | 5.9 | 5.6 | 18.5 | 7.7 |
| | Coleoptera | 0.1 | 1.2 | 7.8 | 2.3 |
| | Diptera (*Chaoborus* spp.) | 0.1 | < 0.0 | 13.7 | 3.5 |
| | Diptera (Chironomidae) | 1.2 | 1.7 | 4.7 | 1.9 |
| | Diptera (pupae) | < 0.0 | < 0.0 | 2.5 | 0.6 |
| | Anura (*Rana sylvatica* adults) | 7.8 | 16.1 | 17.2 | 10.5 |
| | Fishes | < 0.0 | 1.0 | 1.2 | 0.6 |

**Table B-2**. Percentage by number (%N) and mass (%M), frequency of occurrence (%FO), and relative importance index (Ri) of prey taxa in diets of juvenile (< 330 mm) northern pike in the experimental lake (EXP) and the reference lakes (Ref; average of all lakes and years). All insect prey were larval, with the exception of hemipterans, which were represented by juvenile and adult instars.

| **Lake (year)** | **Item** | **% N** | **% M** | **% FO** | **Ri** |
|---|---|---|---|---|---|
| EXP (2002) | Hirudinae (Erpobdellidea) | 2.8 | 14.7 | 16.7 | 7.9 |
| | Hirudinae (Glossiphoniidea) | 8.3 | 15.7 | 16.7 | 9.5 |
| | Amphipoda | 50.9 | 32.4 | 73.3 | 36.4 |
| | Ephemeroptera | 3.3 | 2.8 | 10.0 | 3.7 |
| | Odonata (Zygoptera) | 12.9 | 13.8 | 51.7 | 18.2 |
| | Coleoptera | 2.9 | 9.3 | 10.0 | 5.2 |
| | Diptera (*Chaoborus* spp.) | 3.6 | 3.2 | 5.0 | 2.7 |
| | Diptera (Chironomidae) | 10.5 | 2.4 | 21.7 | 8.0 |
| | Diptera (pupae) | 1.7 | 0.7 | 10.0 | 2.9 |
| | Daphniidae | 2.1 | 0.5 | 10.0 | 2.9 |
| | Anura (*Rana sylvatica* larvae) | 1.0 | 4.5 | 5.0 | 2.4 |
| Ref (2000-2002) | Hirudinae (Erpobdellidea) | 0.3 | 0.4 | 10.4 | 2.7 |
| | Hirudinae (Glossiphoniidea) | 2.4 | 2.4 | 7.1 | 2.9 |
| | Gastropoda | 1.0 | 0.1 | 4.2 | 1.3 |
| | Amphipoda | 58.0 | 68.0 | 77.2 | 49.3 |
| | Ephemeroptera | 0.1 | 0.2 | 6.3 | 1.6 |
| | Odonata (Anisoptera) | 2.3 | 2.7 | 8.3 | 3.2 |
| | Odonata (Zygoptera) | 0.1 | < 0.0 | 1.5 | 2.4 |
| | Trichoptera | 0.2 | 0.1 | 14.6 | 3.6 |
| | Coleoptera | 0.3 | 1.8 | 4.2 | 1.5 |
| | Diptera (*Chaoborus* spp.) | 17.3 | 6.3 | 21.0 | 10.8 |
| | Diptera (Chironomidae) | 0.3 | 0.1 | 17.1 | 4.2 |
| | Diptera (pupae) | 2.0 | 2.1 | 5.2 | 2.3 |
| | Daphniidae | 0.2 | < 0.0 | 13.4 | 3.3 |
| | Fishes | 15.4 | 15.8 | 21.6 | 12.8 |

# Appendix C:
# Principal Components Analysis: matrices and results

**Table C-1**. Abbreviations of invertebrate taxa and groupings used in Principal Components Analysis. The "other" category refers to a pooling of taxa that, on average, made up < 0.1% of the mean annual total abundance or biomass of macroinvertebrates in a given matrix (see individual matrices for more detail).

| Class | Sublcass | Order | Suborder | Family | Subfamily | Genus | Species | Code |
|---|---|---|---|---|---|---|---|---|
| CLITELLATA | Hirudinae | Rhynchobdellida |  | Glossiphoniidae |  |  |  | RGL |
|  |  | Pharyngobdellida |  | Erpobdellidae |  |  |  | PER |
| GASTROPODA | Pulmonata |  |  |  |  |  |  | GPU |
| ARACHNIDA |  | Acarina |  |  |  |  |  | AAC |
| CRUSTACEA | Malacostraca | Amphipoda |  |  |  | *Gammarus* | *lacustris* | GLA |
|  |  |  |  |  |  | *Hyallela* | *azteca* | HAZ |
| INSECTA |  | Ephemeroptera |  |  |  |  |  | EPH |
|  |  | Odonata | Anisoptera |  |  |  |  | OAN |
|  |  |  | Zygoptera |  |  |  |  | OZY |
|  |  | Hemiptera |  | Corixidae |  |  |  | HCO |
|  |  |  |  | Notonectidae |  |  |  | HNO |
|  |  |  |  | "Total" |  |  |  | HTO |
|  |  |  |  | "Others" |  |  |  | HOT |
|  |  | Megaloptera |  | Sialidae |  | *Sialis* |  | MSI |
|  |  | Lepidoptera |  |  |  |  |  | LEP |
|  |  | Trichoptera |  | Leptoceridae |  |  |  | TLE |
|  |  |  |  | Limnephilidae |  |  |  | TLI |
|  |  |  |  | Molannidae |  |  |  | TMO |
|  |  |  |  | Phryganeidae |  |  |  | TPH |
|  |  |  |  | Polycentropodidae |  |  |  | TPO |
|  |  |  |  | "Others" |  |  |  | TOT |
|  |  | Coleoptera |  | "Total larvae" |  |  |  | CTL |
|  |  |  |  | "Total adults" |  |  |  | CTA |
|  |  |  |  | Dytiscidae | Dytiscinae |  |  | CDY |
|  |  |  |  | "Other larvae" |  |  |  | COL |

**Table C-1**. (continued)

| Class | Sublcass | Order | Suborder | Family | Subfamily | Genus | Species | Code |
|---|---|---|---|---|---|---|---|---|
| | | Diptera | Nematocera | Ceratopogonidae | | | | DCE |
| | | | | Chaoboridae | | *Chaoborus* | | DCA |
| | | | | Chironomidae | | | | DCH |
| | | | | “All pupae” | | | | DPU |
| | | | | “Others” | | | | DOT |
| “OTHER” | | | | | | | | OTH |

**Table C-2**. Original data matrix used in Principal Components Analysis of mean annual abundance (number/sample) in grab samples from study lakes and mesocosm treatments. Table C-1 lists taxonomic codes. OTH = HTO, CTA, DOT.

| System and year | RGL | PER | AAC | GLA | HAZ | EPH | OAN | OZY | TLE | TMO | TPH | TOT | CTL | DCE | DCA | DCH | DPU | OTH |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| EXP ‘00 | 1.42 | 0.25 | 0.04 | 5.13 | 72.0 | 0.29 | 1.04 | 0.25 | 0.04 | 0.17 | 0.17 | 0.50 | 0.13 | 1.58 | 0.29 | 24.8 | 0.13 | 0.25 |
| R1 ‘00 | 1.75 | 0.71 | 0.13 | 23.0 | 63.6 | 0.13 | 0.04 | 0.38 | 1.63 | 1.33 | 0.25 | 0.00 | 0.21 | 3.21 | 0.58 | 29.9 | 0.04 | 0.17 |
| R2 ‘00 | 1.63 | 0.50 | 0.08 | 41.4 | 31.0 | 0.04 | 0.00 | 0.25 | 0.21 | 0.00 | 0.13 | 0.04 | 0.25 | 0.92 | 0.04 | 2.25 | 0.00 | 0.08 |
| EXP ‘01 | 2.02 | 0.79 | 0.10 | 21.4 | 87.5 | 0.13 | 0.10 | 0.06 | 0.23 | 0.17 | 0.27 | 0.21 | 0.15 | 2.25 | 0.98 | 54.6 | 0.31 | 0.21 |
| R1 ‘01 | 1.00 | 0.58 | 0.23 | 26.6 | 54.3 | 0.08 | 0.02 | 0.33 | 1.10 | 1.52 | 0.50 | 0.85 | 0.50 | 2.35 | 1.88 | 45.7 | 0.60 | 0.94 |
| R2 ‘01 | 5.28 | 1.15 | 0.32 | 51.8 | 48.0 | 0.00 | 0.00 | 0.02 | 0.46 | 0.23 | 0.00 | 0.04 | 0.33 | 1.56 | 0.02 | 133 | 2.02 | 0.15 |
| Excl ‘01 | 2.22 | 0.88 | 0.22 | 13.6 | 44.6 | 0.91 | 0.03 | 0.94 | 0.06 | 0.31 | 0.06 | 0.38 | 0.84 | 14.4 | 6.28 | 16.3 | 0.09 | 0.56 |
| Cntrl ‘01 | 1.42 | 1.08 | 0.08 | 12.4 | 92.3 | 0.17 | 0.25 | 0.42 | 0.17 | 0.33 | 0.08 | 0.08 | 1.67 | 5.5 | 0.25 | 35 | 0.25 | 0.33 |
| EXP ‘02 | 0.66 | 0.69 | 0.16 | 12.0 | 83.3 | 0.03 | 0.09 | 0.22 | 0.22 | 0.34 | 0.19 | 0.03 | 0.00 | 4.31 | 1.38 | 90.1 | 1.41 | 0.22 |
| R1 ‘02 | 1.21 | 0.92 | 0.25 | 21.0 | 92.0 | 0.46 | 0.08 | 0.17 | 1.83 | 1.00 | 0.17 | 0.29 | 0.17 | 9.38 | 6.83 | 32.8 | 0.25 | 0.38 |
| R2 ‘02 | 4.58 | 1.50 | 0.88 | 26.5 | 75.3 | 0.00 | 0.00 | 0.00 | 0.79 | 0.42 | 0.17 | 0.08 | 0.08 | 0.63 | 0.42 | 138 | 0.17 | 0.29 |
| Excl ‘02 | 1.46 | 1.88 | 0.13 | 25.7 | 58.5 | 0.54 | 0.67 | 0.38 | 0.04 | 1.08 | 0.08 | 0.08 | 0.92 | 12.5 | 2.79 | 50.2 | 0.33 | 0.71 |
| Cntrl ‘02 | 1.38 | 0.50 | 0.00 | 8.75 | 55.9 | 0.00 | 0.38 | 0.00 | 0.38 | 1.75 | 0.25 | 0.00 | 0.13 | 6.38 | 1.13 | 50.3 | 0.38 | 0.25 |

**Table C-3**. Original data matrix used in Principal Components Analysis of mean annual biomass (mg/sample) in grab samples from study lakes and mesocosm treatments. Table C-1 lists taxonomic codes. OTH = AAC, EPH, TOT, DOT.

| System and year | RGL | PER | GLA | HAZ | OAN | OZY | HTO | TLE | TLI | TMO | TPH | TPO | CDY | COL | CTA | DCE | DCA | DCH | DPU | OTH |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| EXP ‘00 | 1.97 | 21.7 | 20.5 | 23.4 | 19.9 | 0.26 | 2.02 | 0.01 | 0.62 | 0.10 | 1.89 | 0.45 | 13.7 | 0.05 | 0.00 | 1.45 | 0.05 | 4.20 | 0.02 | 0.82 |
| R1 ‘00 | 1.83 | 11.6 | 94.8 | 11.1 | 0.00 | 0.25 | 0.03 | 0.61 | 0.00 | 1.45 | 1.20 | 0.00 | 0.38 | 0.00 | 0.00 | 1.96 | 0.13 | 20.5 | 0.00 | 1.31 |
| R2 ‘00 | 2.71 | 6.31 | 3.64 | 16.3 | 0.00 | 0.66 | 0.08 | 2.38 | 0.00 | 0.00 | 20.8 | 1.34 | 0.59 | 0.00 | 0.22 | 2.39 | 0.01 | 1.24 | 0.00 | 0.07 |
| EXP ‘01 | 1.25 | 9.84 | 56.1 | 31.8 | 0.53 | 0.12 | 0.09 | 0.04 | 0.00 | 0.17 | 3.17 | 0.58 | 0.00 | 1.20 | 0.52 | 1.31 | 0.26 | 32.4 | 0.07 | 0.55 |
| R1 ‘01 | 0.99 | 5.23 | 64.2 | 15.6 | 0.58 | 0.14 | 0.48 | 0.77 | 2.66 | 5.19 | 4.10 | 0.24 | 0.53 | 0.13 | 0.10 | 1.06 | 0.43 | 9.70 | 0.18 | 0.55 |
| R2 ‘01 | 4.15 | 11.0 | 93.6 | 12.1 | 0.00 | 0.04 | 0.41 | 0.18 | 3.01 | 0.69 | 0.00 | 0.00 | 0.53 | 0.00 | 0.31 | 2.24 | 0.01 | 31.9 | 0.88 | 0.16 |
| Excl ‘01 | 1.05 | 17.0 | 26.4 | 13.1 | 0.45 | 0.37 | 0.73 | 0.01 | 0.20 | 0.33 | 0.67 | 0.37 | 2.42 | 2.14 | 0.28 | 5.23 | 0.37 | 1.60 | 0.01 | 2.11 |
| Cntrl ‘01 | 1.07 | 13.6 | 13.9 | 14.2 | 4.65 | 0.78 | 0.01 | 0.07 | 0.00 | 1.01 | 0.01 | 0.01 | 0.00 | 4.83 | 0.00 | 3.76 | 0.06 | 4.57 | 0.01 | 3.16 |
| EXP ‘02 | 0.73 | 16.7 | 23.7 | 29.2 | 1.48 | 0.09 | 0.73 | 0.17 | 0.01 | 0.53 | 1.73 | 0.00 | 0.00 | 0.00 | 0.00 | 3.06 | 0.45 | 37.8 | 0.88 | 0.04 |
| R1 ‘02 | 1.52 | 11.2 | 64.5 | 24.4 | 4.35 | 0.16 | 0.04 | 0.26 | 0.50 | 5.81 | 9.98 | 0.00 | 0.09 | 0.28 | 0.21 | 3.76 | 1.56 | 6.20 | 0.69 | 0.16 |
| R2 ‘02 | 4.76 | 17.9 | 137 | 16.5 | 0.00 | 0.00 | 1.64 | 0.27 | 0.17 | 0.56 | 3.64 | 0.00 | 0.07 | 0.00 | 0.42 | 1.59 | 0.19 | 127 | 0.15 | 0.26 |
| Excl ‘02 | 0.88 | 53.9 | 50.7 | 17.0 | 6.14 | 0.13 | 0.15 | 0.01 | 0.00 | 1.91 | 0.06 | 0.07 | 0.00 | 2.28 | 1.16 | 8.62 | 0.64 | 5.23 | 0.21 | 2.67 |
| Cntrl ‘02 | 1.34 | 11.6 | 6.06 | 23.8 | 10.7 | 0.00 | 0.09 | 0.15 | 0.00 | 2.52 | 1.29 | 0.00 | 0.01 | 0.00 | 0.00 | 4.12 | 0.19 | 11.8 | 0.09 | 1.57 |

**Table C-4**. Original data matrix used in Principal Components Analysis of mean annual abundance (number/sample) in sweep samples from study lakes and mesocosm treatments. Table C-1 lists taxonomic codes. OTH = HGL, HER, OAN, HOT, MSI, LEP, TOT, DCE.

| System and year | GPU | AAC | GLA | HAZ | EPH | OZY | HCO | HNO | TLE | TLI | TPH | CDY | COL | CTA | DCA | DCH | DPU | OTH |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| EXP ‘00 | 1.90 | 0.67 | 10.1 | 6.98 | 0.24 | 0.83 | 1.39 | 0.73 | 0.00 | 0.00 | 0.00 | 0.78 | 0.12 | 0.07 | 20.7 | 3.09 | 0.22 | 0.43 |
| R1 ‘00 | 3.14 | 0.74 | 10.8 | 2.59 | 0.00 | 0.30 | 2.34 | 0.46 | 0.10 | 0.63 | 0.05 | 0.56 | 0.00 | 0.00 | 0.55 | 0.55 | 3.00 | 0.00 |
| R2 ‘00 | 7.22 | 0.80 | 87.3 | 10.9 | 0.00 | 3.28 | 0.83 | 1.67 | 0.11 | 0.00 | 0.10 | 0.10 | 0.00 | 0.08 | 0.00 | 8.03 | 0.08 | 0.00 |
| EXP ‘01 | 0.81 | 1.48 | 7.31 | 6.96 | 0.25 | 1.27 | 0.81 | 0.90 | 0.02 | 0.08 | 0.27 | 0.35 | 0.04 | 0.29 | 82.0 | 4.31 | 3.6 | 0.35 |
| R1 ‘01 | 2.85 | 0.98 | 9.73 | 7.13 | 0.10 | 1.31 | 1.94 | 0.92 | 1.71 | 0.58 | 0.42 | 0.29 | 0.17 | 0.08 | 19.9 | 17.6 | 2.65 | 0.27 |
| R2 ‘01 | 6.73 | 2.98 | 89.0 | 3.58 | 0.02 | 0.35 | 3.65 | 1.98 | 0.02 | 0.02 | 0.29 | 1.10 | 0.00 | 0.04 | 0.38 | 2.44 | 0.31 | 0.04 |
| Excl ‘01 | 0.72 | 0.22 | 0.41 | 5.78 | 0.75 | 3.13 | 0.13 | 3.00 | 0.03 | 0.19 | 0.00 | 0.44 | 0.44 | 0.81 | 31.8 | 1.44 | 0.38 | 0.53 |
| Cntrl ‘01 | 0.92 | 5.5 | 0.83 | 23.2 | 0.17 | 3.00 | 2.67 | 1.00 | 0.00 | 0.42 | 0.08 | 0.92 | 0.00 | 0.17 | 15.1 | 5.00 | 0.42 | 0.25 |
| EXP ‘02 | 0.63 | 1.59 | 0.38 | 3.44 | 0.16 | 1.81 | 0.59 | 0.78 | 0.16 | 0.19 | 0.22 | 0.03 | 0.03 | 0.03 | 65.8 | 0.69 | 2.94 | 0.16 |
| R1 ‘02 | 2.96 | 0.92 | 3.54 | 4.83 | 0.46 | 0.58 | 0.54 | 0.33 | 0.33 | 0.04 | 0.00 | 0.08 | 0.00 | 0.04 | 124 | 1.29 | 1.46 | 0.42 |
| R2 ‘02 | 7.33 | 2.83 | 89.4 | 2.13 | 0.04 | 2.25 | 1.04 | 0.29 | 0.17 | 0.00 | 0.00 | 0.08 | 0.00 | 0.17 | 1.08 | 0.88 | 0.00 | 0.13 |
| Excl ‘02 | 2.54 | 0.92 | 1.58 | 6.83 | 7.13 | 3.42 | 0.67 | 4.38 | 0.00 | 0.46 | 0.04 | 0.13 | 0.75 | 0.19 | 35.8 | 1.08 | 0.04 | 0.19 |
| Cntrl ‘02 | 0.13 | 0.25 | 0.88 | 0.38 | 0.00 | 0.00 | 0.00 | 1.50 | 0.00 | 0.13 | 0.00 | 0.13 | 0.00 | 0.00 | 27.4 | 0.13 | 1.00 | 0.00 |

**Table C-5**. Original data matrix used in Principal Components Analysis of mean annual biomass (mg/sample) in sweep samples from study lakes and mesocosm treatments. Table C-1 lists taxonomic codes. OTH = RGL, HOT, MSI, LEP, DCE.

| System and year | PER | GPU | AAC | GLA | HAZ | EPH | OAN | OZY | HCO | HNO | TLI | TPH | TOT | CDY | COL | CTA | DCA | DCH | DPU | OTH |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| EXP ‘00 | 2.35 | 6.39 | 0.50 | 13.0 | 4.21 | 0.11 | 4.84 | 1.88 | 1.06 | 0.71 | 0.00 | 0.00 | 0.21 | 66.0 | 0.19 | 0.02 | 3.90 | 0.57 | 0.09 | 0.77 |
| R1 ‘00 | 0.00 | 5.76 | 0.46 | 74.0 | 0.74 | 0.00 | 0.00 | 0.74 | 2.37 | 1.38 | 0.16 | 0.03 | 0.06 | 1.02 | 0.00 | 0.00 | 2.08 | 0.15 | 0.06 | 0.00 |
| R2 ‘00 | 0.00 | 16.9 | 0.6 | 396 | 6.34 | 0.00 | 0.00 | 5.18 | 0.47 | 14.1 | 0.00 | 0.90 | 0.06 | 18.7 | 0.00 | 0.89 | 0.00 | 3.14 | 0.03 | 0.00 |
| EXP ‘01 | 0.67 | 1.55 | 1.91 | 25.8 | 3.18 | 2.13 | 7.64 | 1.24 | 0.28 | 1.37 | 0.07 | 0.03 | 0.45 | 23.2 | 0.03 | 3.56 | 19.1 | 0.80 | 1.41 | 0.02 |
| R1 ‘01 | 0.55 | 5.25 | 1.21 | 36.0 | 2.00 | 0.09 | 0.00 | 5.14 | 1.59 | 2.25 | 2.20 | 6.85 | 0.53 | 7.63 | 1.55 | 0.28 | 4.75 | 5.15 | 0.91 | 0.00 |
| R2 ‘01 | 0.00 | 10.4 | 2.94 | 244 | 1.04 | 0.01 | 0.00 | 0.48 | 1.90 | 5.73 | 0.01 | 0.73 | 0.03 | 7.12 | 0.00 | 0.34 | 0.28 | 0.55 | 0.15 | 0.05 |
| Excl ‘01 | 0.00 | 2.09 | 0.07 | 7.58 | 1.87 | 0.77 | 1.17 | 2.03 | 0.07 | 4.90 | 0.98 | 0.00 | 0.07 | 34.6 | 0.17 | 2.64 | 4.86 | 0.17 | 0.15 | 0.12 |
| Cntrl ‘01 | 0.00 | 1.39 | 2.04 | 6.06 | 4.97 | 0.01 | 0.00 | 6.00 | 1.00 | 1.91 | 0.05 | 2.34 | 0.37 | 57.6 | 0.00 | 0.06 | 3.35 | 0.73 | 0.05 | 0.13 |
| EXP ‘02 | 0.00 | 1.58 | 0.83 | 5.46 | 1.73 | 0.10 | 6.12 | 1.00 | 0.74 | 2.61 | 0.82 | 0.01 | 0.04 | 1.50 | 0.17 | 0.18 | 15.8 | 0.13 | 1.40 | 0.04 |
| R1 ‘02 | 0.98 | 8.32 | 0.88 | 19.1 | 1.44 | 0.69 | 0.00 | 0.73 | 0.54 | 2.21 | 2.22 | 0.00 | 0.06 | 0.43 | 0.00 | 0.50 | 29.4 | 0.42 | 0.56 | 1.71 |
| R2 ‘02 | 0.02 | 8.73 | 0.71 | 400 | 0.56 | 0.02 | 0.00 | 1.23 | 0.97 | 4.16 | 0.00 | 0.00 | 0.14 | 0.15 | 0.00 | 0.70 | 0.47 | 0.14 | 0.00 | 0.11 |
| Excl ‘02 | 3.06 | 12.4 | 0.24 | 23.1 | 1.55 | 3.87 | 0.00 | 1.89 | 0.39 | 4.66 | 1.29 | 0.01 | 0.00 | 0.65 | 0.77 | 0.47 | 6.04 | 0.09 | 0.00 | 0.10 |
| Cntrl ‘02 | 0.00 | 0.60 | 0.18 | 15.4 | 0.09 | 0.00 | 0.00 | 0.00 | 0.00 | 2.16 | 0.36 | 0.00 | 0.00 | 17.3 | 0.00 | 0.00 | 7.92 | 0.01 | 0.37 | 0.00 |

**Table C-6**. Eigenvectors from principal components analysis of macroinvertebrate abundance (number/sample) and biomass (mg/samples) in grab (benthic) and sweep (water and vegetation) samples. Conspicuous taxa were defined as taxa that were large, active, and/or non-cryptic. Inconspicuous taxa were defined as taxa that were small, inactive, and/or cryptic. "na" denotes taxa not included in a given matrix. Blanks occur for taxa that had a relatively low coefficient of determination.

| | **Eigenvectors** | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | **Grabs** | | | | **Sweeps** | | | |
| | **Abundance** | | **Biomass** | | **Abundance** | | **Biomass** | |
| **Conspicuous taxa** | **Axis1** | **Axis 2** | **Axis 1** | **Axis 2** | **Axis 1** | **Axis 2** | **Axis 1** | **Axis 2** |
| Erpobdellids | -0.286 | 0.080 | 0.311 | -0.073 | na | na | 0.135 | -0.294 |
| *G. lacustris* | -0.274 | 0.232 | | | -0.295 | -0.179 | -0.221 | -0.217 |
| *H. azteca* | 0.368 | -0.001 | | | | | | |
| Anisopterans | | | 0.175 | -0.345 | na | na | 0.195 | 0.346 |
| Zygopterans | 0.092 | 0.379 | 0.264 | 0.185 | 0.231 | -0.328 | | |
| Hemipterans | na | na | -0.030 | 0.282 | na | na | na | na |
| Corixids | na | na | na | na | -0.296 | -0.265 | -0.301 | -0.200 |
| Notonectids | na | na | na | na | 0.206 | 0.225 | | |
| Dytiscid coleopterans | na | na | 0.082 | 0.337 | | | -0.153 | 0.380 |
| Other coleopterans | -0.057 | 0.361 | 0.341 | -0.182 | 0.314 | 0.079 | | |
| Adult coleopterans | na | na | | | 0.260 | -0.214 | | |
| **Inconspicuous taxa** | | | | | | | | |
| Glossiphoniids | -0.277 | 0.276 | -0.160 | 0.399 | na | na | | |
| Acari | -0.351 | -0.024 | na | na | -0.224 | 0.053 | | |
| Gastropods | na | na | na | na | -0.230 | -0.289 | -0.093 | -0.438 |
| Ephemeropterans | 0.275 | 0.247 | na | na | 0.338 | 0.007 | 0.304 | -0.102 |
| Leptocerids | -0.245 | -0.218 | -0.228 | 0.122 | -0.240 | -0.127 | na | na |
| Limnephilids | na | na | -0.311 | 0.113 | -0.098 | 0.496 | 0.251 | -0.172 |
| Phryganeids | | | | | -0.259 | 0.050 | -0.314 | 0.016 |
| Polycentropids | na | na | 0.275 | 0.243 | na | na | na | na |
| Molannids | 0.083 | -0.389 | -0.291 | -0.302 | na | na | na | na |
| Other trichopterans | | | na | na | na | na | -0.358 | 0.089 |
| Ceratopogonids | 0.362 | 0.057 | | | na | na | na | na |
| *Chaoborus spp.* | 0.302 | -0.287 | -0.052 | -0.396 | 0.230 | 0.241 | 0.343 | 0.041 |
| Chironimids | -0.164 | -0.345 | -0.340 | -0.125 | | | -0.342 | 0.074 |
| Dipteran pupae | 0.173 | -0.033 | -0.291 | -0.211 | -0.179 | 0.383 | 0.120 | 0.318 |
| Other taxa | na | na | -0.293 | -0.109 | 0.302 | -0.188 | | |

**Table C-7**. System coordinates from principal components analysis of macroinvertebrate abundance (number/sample) and biomass (mg/samples) in grab (benthic) and sweep (water and vegetation) samples from the experimental lake (EXP) and reference lakes in 2000 – 2002, and exclosures and control exclosures (2001 and 2002).

| | **System Coordinates** | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | **Grabs** | | | | **Sweeps** | | | |
| | **Abundance** | | **Biomass** | | **Abundance** | | **Biomass** | |
| **System (and year)** | **Axis1** | **Axis 2** | **Axis 1** | **Axis 2** | **Axis 1** | **Axis 2** | **Axis 1** | **Axis 2** |
| EXP (2000) | 2.837 | 1.803 | -1.801 | 2.083 | 0.943 | -1.516 | 0.115 | 0.386 |
| Reference 1 (2000) | -0.381 | 0.298 | -0.828 | 0.652 | -3.809 | 1.619 | -1.815 | -1.090 |
| Reference 2 (2000) | -2.768 | 4.422 | 1.510 | 3.980 | -1.887 | -2.306 | -3.397 | 0.337 |
| EXP (2001) | -0.042 | -0.748 | 0.999 | 0.025 | 0.403 | 0.087 | 1.539 | 3.256 |
| Reference 1 (2001) | 1.926 | -2.292 | -2.327 | 0.148 | -2.126 | 0.109 | -1.600 | -0.607 |
| Reference 2 (2001) | -4.428 | -0.197 | -3.219 | 1.664 | -2.444 | -1.273 | -2.786 | -0.305 |
| Exclosures (2001) | 2.732 | 1.498 | 3.687 | 0.968 | 5.920 | -0.428 | 2.534 | 0.719 |
| Control Excl. (2001) | 0.953 | 1.670 | 2.353 | -1.665 | 0.670 | 0.137 | -2.282 | 1.877 |
| EXP (2002) | -0.341 | -2.548 | -1.750 | -1.192 | -0.067 | 1.651 | 2.614 | 2.201 |
| Reference 1 (2002) | 1.300 | -1.353 | -1.784 | -2.829 | -0.008 | -0.686 | 2.832 | -2.353 |
| Reference 2 (2002) | -4.125 | -1.440 | -2.652 | 1.434 | -0.715 | -2.270 | -2.192 | -2.154 |
| Exclosures (2002) | 1.8556 | 0.398 | 2.568 | -2.873 | 3.475 | 0.781 | 3.058 | -3.531 |
| Control Excl. (2002) | 0.480 | -1.511 | -0.356 | -2.394 | -0.356 | 4.094 | 1.380 | 1.263 |

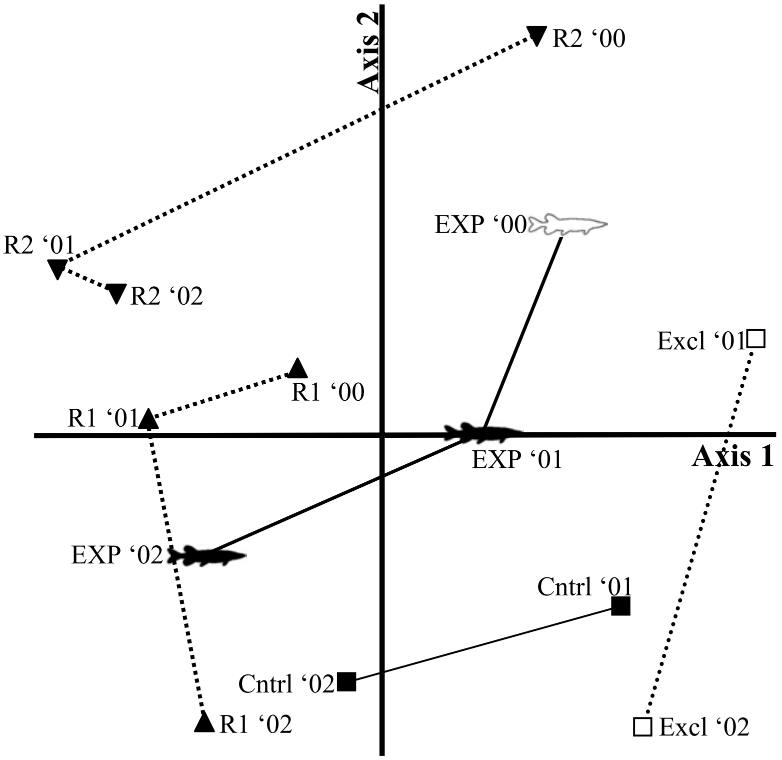

**Figure C-1**. Standardized and centered principal components analysis of macroinvertebrate biomass (mg/sample) in vegetated habitats showing trajectories of the reference lakes (R1 and R2), the experimental lake (EXP), exclosures (Excl) and control exclosures (Cntrl). Shaded and open refer to experimental systems with and without fish, respectively.

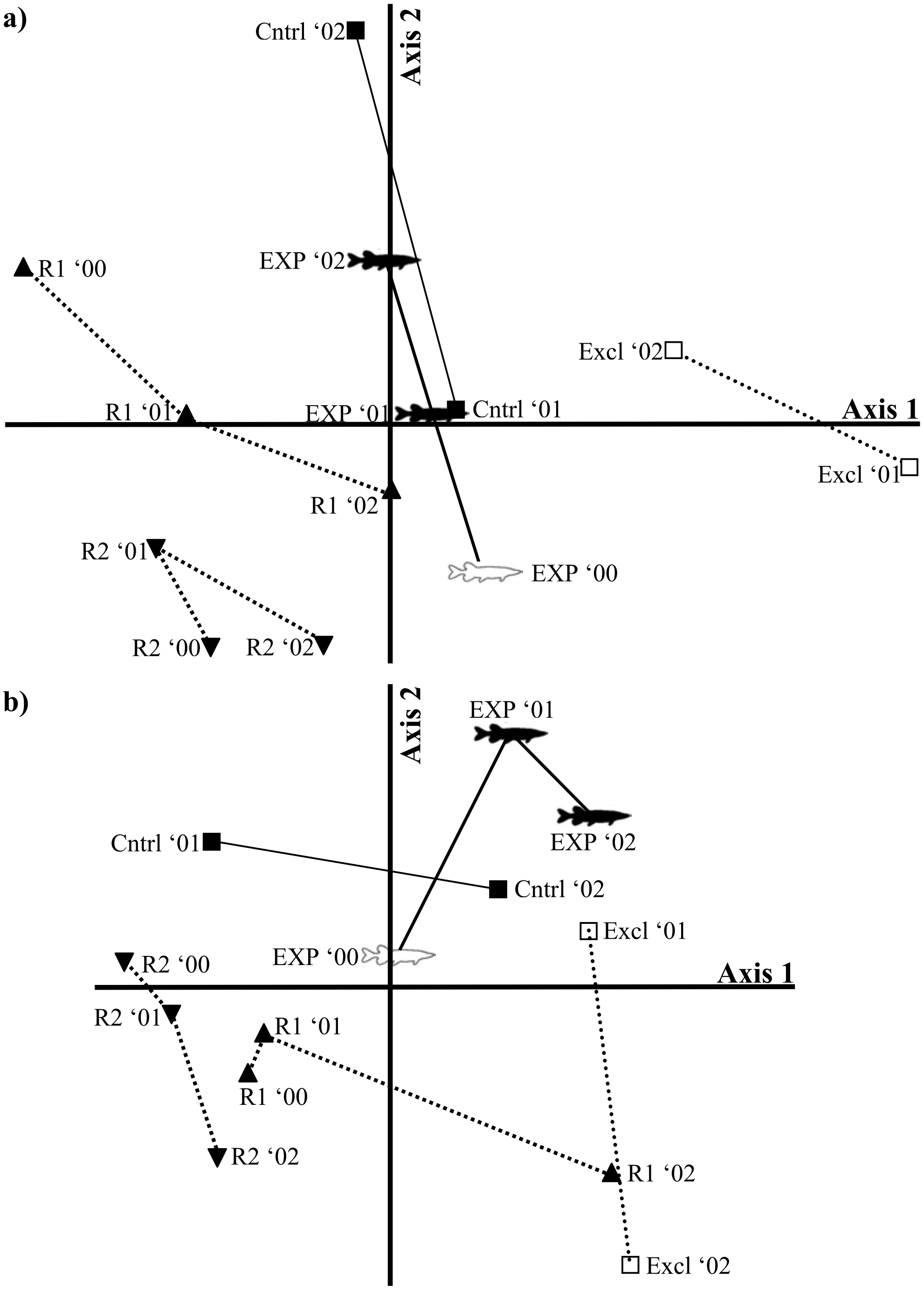

**Figure C-2**. Standardized and centered principal components analysis of a) macroinvertebrate abundance (number/sample); and b) macroinvertebrate biomass (mg/sample) in vegetated habitats showing trajectories of the reference lakes (R1 and R2), the experimental lake (EXP), exclosures (Excl) and control exclosures (Cntrl). Shaded and open symbols refer to experimental systems with and without fish, respectively.

# Appendix D:
# Results of regression analysis, 2001

**Table D-1**. Effects of northern pike on the mean monthly abundance, biomass, and size of individual macroinvertebrate taxa in grab and sweep samples using a) randomized intervention analysis [experimental lake vs. reference lakes before (n = 4) and after (n = 7) manipulation] and b) linear regression exclosures (n = 12) vs. controls (n = 4) in 2001]. See text for details. "+" and "-" refer to positive and negative trends (0.2 > P > 0.05), respectively. "++" and "--" denote significant (P < 0.05) positive and negative effects of pike, respectively. "o" refers to neutral effects (P > 0.25). Blank cells occur where there were insufficient data to perform analyses.

| Sample | Response | Taxon | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| Type | Variable | Erpobdellidae | *G. lacustris* | Odonata | Trichoptera | Coleoptera | *Chaoborus* | Chironomidae | Dipt. Pupae |
| Grab | Abundance | - | - | o | o | o | -- | -- | - |
| | Biomass | - | - | o | o | o | -- | - | - |
| | Size | o | o | | | | | ++ | |
| Sweep | Abundance | | -- | - | o | o | -- | o | - |
| | Biomass | | - | o | o | o | -- | o | - |
| | Size | | | | | | o | | |