

Indirect effects of metal contamination on energetics of yellow perch (*Perca flavescens*) resulting from food web simplification

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SUMMARY

1. Benthic invertebrate community composition and yellow perch (*Perca flavescens*) diet, growth and activity levels from lakes along a metal-contamination gradient were used to assess the importance of a naturally diverse prey base for maintaining energy transfer to growing fish, and how this transfer is disrupted by metal contamination.
2. Zoobenthic communities had lower diversity in metal-contaminated lakes, with a notable absence of large bodied invertebrate taxa.
3. The average mass of non-zooplankton prey items was significantly greater for 2+ and 3+ perch from the reference lake, and increased significantly with age in all except the most contaminated lakes where prey choice was limited.
4. Benthivorous perch from all contaminated lakes exhibited slowed growth. Perch from one of the contaminated lakes exhibited faster growth during piscivory, indicating slowed growth only while benthivorous.
5. Estimates of fish activity, using the activity of the glycolytic enzyme Lactate dehydrogenase in perch white muscle tissue as a proxy, suggested that shifts in diet to larger prey (in reference and intermediately contaminated lakes) lowered activity costs, which may explain how diet shifts maintain growth efficiency as perch grow larger.

Keywords: energetic bottleneck, energetics, fish growth, lake food web, metal contamination, *Perca flavescens*, stunting, Sudbury, yellow perch

Introduction

Freshwater zoobenthos are particularly vulnerable to environmental change because of the transmission of contaminants from surrounding catchments to lake sediments (Lake *et al.*, 2000). In particular, atmospheric deposition of metal ore smelting emissions concentrates in lake sediments (Luoma, 1989), drastically altering species composition, reducing overall

biodiversity and reducing the average body size of invertebrate fauna. Metal-sensitive macroinvertebrates, such as molluscs, crustaceans and mayflies, tend to disappear and the community becomes dominated by metal-tolerant invertebrates, such as chironomids, caddis flies and oligochaetes (Johnson, Eriksson & Wiederholm, 1992; Gower *et al.*, 1994; Kovacs, Rasmussen & Sherwood, 2004).

The loss of zoobenthic diversity because of metal contamination may have important consequences for ecosystem processes (Lake *et al.*, 2000). In particular, loss of the larger benthic invertebrates may compromise the efficiency of energy transfer to fish. Sherwood *et al.* (2002b) showed the importance of a naturally diverse prey base, particularly the presence of large invertebrates, for maintaining energy transfer to growing fish. If activity costs of foraging for many,

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small prey become too high, growth rates will slow down or, in the most extreme cases, stop altogether (Pazzia *et al.*, 2002; Sherwood *et al.*, 2002a,b). Foraging efficiency may also decrease below the optimal prey size as a result of reduced manoeuvrability of larger fish, reduced ability to retain small prey in the mouth and even reduced ability to see small prey (Persson, 1987). Yellow perch (*Perca flavescens*, Mitchill), periodically switch to larger prey as they grow. Perch move from feeding on zooplankton in their first year to zoobenthos by their second year and continue periodically to switch to larger benthic invertebrates, such as odonates and crayfish, until they grow large enough to switch to piscivory (Boisclair & Leggett, 1989a). The loss of benthic community diversity in metal-contaminated lakes, particularly the absence of large invertebrates, means that perch can not benefit from the energetic advantages of switching prey as the appropriate prey is lacking, and thus their growth is stunted (Sherwood *et al.*, 2002a).

Sudbury, Ontario, Canada (latitude 46°37', longitude 80°48'), is one region where lakes have been subject to extensive acidification and high metal deposition from industry emissions. Implementation of improved recovery methods (Keller, 1992) have led to a decline in concentrations of metals such as copper, nickel and cadmium, although they still remain high relative to estimates of probable effects levels on aquatic life. The continuing metal contamination of lake sediments undoubtedly still affects lake communities. Low species diversity at all trophic levels is characteristic of Sudbury lakes, notably the absence or scarcity of large benthic invertebrates such as molluscs, amphipods and crayfish (Keller, Henberry & Gunn, 1999). Grazers, such as these, play an important role in energy transfer and their absence

may have important implications for top trophic levels such as fish (Henberry, 1997).

We studied five lakes from the Sudbury region that encompassed a large range of metal contamination, in order to assess food web effects of metal pollution on the efficiency of energy transfer to fish. We predicted that lakes with higher metal contamination will exhibit the following trends:

1 reduced diversity and average size of benthic invertebrates;

2 reliance on small prey by adult perch populations;

3 stunted perch populations wherever adult perch continue to rely on smaller prey; and

4 lowered activity costs following well-defined diet shifts from planktivory to benthivory and from benthivory to piscivory.

Methods

Study site

The five lakes chosen for this study were selected from a survey of 15 lakes in the Sudbury region conducted in June 2001. Table 1 shows the available chemical and physical characteristics of the five study lakes. The lakes chosen are at various distances from the Sudbury smelters and encompass the range of metal contamination present in the region (Table 2). None of the lakes have significant fisheries on them and all lakes except Crowley Lake have some shoreline houses, but no significant development. All sampling took place on five consecutive days in late June 2002.

Hannah and Middle Lakes are located in the same catchment, 6 km south of one of Sudbury's largest smelting plants. Both lakes were highly acidified and

Table 1 Physical and chemical characteristics of the study lakes and approximate distances from Sudbury

Lake	pH	Alk. (mg L ⁻¹ CaCO ₃)	DOC (mg L ⁻¹)	Ca (µg L ⁻¹)	Area (ha)	Max depth (m)	Mean depth (m)	Distance fm Sudbury (km)
Hannah	7.2*	14.9*	4.9*	11 060.7*	27.2 [†]	8.5 [†]	4.0 [†]	6
Middle [‡]	6.8	7.2	3.2	11 100.0	28.0	15.0	2.0	6
Richard [‡]	7.1	18.2	2.1	11 900.0	79.4	9.5	3.9	9
Crowley	6.4*	5.1*	4.2*	2509.8*	42.1 [†]	16.0 [†]	6.4 [†]	12
Geneva	6.6*	8.2*	7.2*	3022.2*	356.4 [‡]	25.3	6.3 [‡]	53

*Data from: P. Couture, Laurentian University, Department of Biology, Sudbury, Ontario, Canada (personal communication).

[†]Data from: OMOEE (Ontario Ministry of Environment and Energy). 1990. An inventory of the water chemistry and invertebrate fauna in Sudbury urban lakes: A progress report of the 1990 Urban Lakes Survey.

[‡]Data from: (Carbone, Keller & Griffiths, 1998).

Table 2 Metal concentrations in the water, sediment and perch livers (dry weight) of the study lakes and the Canadian government's probable effect levels (PEL) for aquatic life

Lake	Water ($\mu\text{g L}^{-1}$)			Sediment ($\mu\text{g g}^{-1}$)			Perch livers ($\mu\text{g g}^{-1} \pm \text{SD}$)*		
	Cd	Cu	Ni	Cd	Cu	Ni	Cd	Cu	Ni
Hannah [†]	0.5	74.8	174.8	2.7	1051.2	1092.5	15.03 \pm 4.46	671.79 \pm 624.81	6.15 \pm 4.28
Middle [‡]	0.3	21.0	250.0	–	–	–	18.95 \pm 4.98	257.13 \pm 238.37	4.44 \pm 3.75
Richard [‡]	0.2	14.0	120.0	–	–	–	9.72 \pm 2.99	31.09 \pm 17.83	4.57 \pm 3.22
Crowley [†]	0.2	15.6	73.2	1.9	568.8	550.0	23.22 \pm 13.16	48.98 \pm 43.10	2.38 \pm 3.44
Geneva [†]	0.0	1.1	4.5	1.6	49.4	98.9	2.84 \pm 3.74	13.92 \pm 2.48	1.33 \pm 3.26
PEL [§]	0.017	2–4	25–150	3.5	197	–	–	–	–

*Data from: A. Gagnon & A. Hontela, Université du Québec à Montréal, Département des Sciences Biologiques, Montréal, Québec, Canada (personal communication).

[†]Data from: P. Couture, Laurentian University, Department of Biology, Sudbury, Ontario, Canada (personal communication).

[‡]Data from: OMOEE (Ontario Ministry of Environment and Energy). 1990. An inventory of the water chemistry and invertebrate fauna in Sudbury urban lakes: A progress report of the 1990 Urban Lakes Survey.

[§]Data from: CCME. 1999. Canadian Environmental Quality Guidelines. Canadian Council of Ministers of the Environment. Winnipeg, Manitoba.

–, Data not available.

metal-contaminated by the 1950s, but have been recovering since being limed in the 1970s, which successfully raised the pH to circumneutral levels and lowered the metal concentrations in the water column. Nevertheless, metal concentrations in the sediment remain very high (Table 2), so these lakes are categorised as 'highly contaminated' in the present study. Yellow perch in both lakes comprise 99.9% of fish biomass with small populations of brown bullhead (*Ameiurus nebulosus*, Lesueur) and Iowa darters (*Etheostoma exile*, Girard). Small populations of golden shiners (*Notemigonus crysoleucas*, Mitchill) and northern redbelly dace (*Phoxinus eos*, Cope) are also present in Middle Lake (Wright, 1995).

Richard and Crowley Lakes are categorised as 'intermediately contaminated' lakes. Water and sediment metal concentrations are higher than Canadian government standards for aquatic life; however, they are not so high as in the highly contaminated lakes (Table 2). The fish community of Crowley Lake is similar to the most contaminated lakes, dominated by yellow perch with a small population of Iowa darters. Richard Lake is considerably more diverse, with additional populations of largemouth bass (*Micropterus salmoides*, Lacepède), smallmouth bass (*Micropterus dolomieu*, Lacepède), northern pike (*Esox lucius*, Linnaeus), pumpkinseed (*Lepomis gibbosus*, Linnaeus), white suckers (*Catostomus commersonii*, Lacepède), golden shiners and central mudminnows (*Umbra limi*, Kirtland).

Geneva Lake is located upwind from industry emissions and was never acidified or heavily contaminated with metals. Concentrations of metals in the water and the sediment are well below government standards (Table 2), making Geneva Lake a reference lake for the present study. Geneva Lake is considerably larger than all the other lakes; however, only the southern bay was sampled, which is of comparable size to the rest of the lakes and is only connected to the rest of the lake by a very narrow channel (approximately 5 m wide). In addition to yellow perch, Geneva Lake has a very diverse fish community including: walleye (*Sander vitreus*, Mitchill), largemouth bass, smallmouth bass, northern pike, brook trout (*Salvelinus fontinalis*, Mitchill), lake trout (*Salvelinus namaycush*, Walbaum), pumpkinseeds, white suckers, brown bullhead, burbot (*Lota lota*, Linnaeus) and a few species of darters (*Etheostoma*) and shiners (*Notemigonus*).

Fish collection

Each lake was sampled over 1 day in the last week of June 2002. Yellow perch were caught using gill nets, and 1.5 cm mesh minnow nets and by angling. No attempt was made to sample young-of-the-year. Nets were set during the afternoon and evening, and were checked for fish every 30–45 min. From each lake, approximately 120 perch were taken from as wide a range of body sizes as possible. Perch were sacrificed

after capture, immediately placed on ice and were later frozen at -20°C for subsequent diet and enzyme analysis. Both total frozen length (to the nearest millimetre) and frozen mass (to the nearest gram) were measured. Perch were aged using opercula. Fulton's condition factor (FCF), an indicator of energetic performance, was calculated as:

$$\text{FCF} = 100 \times \frac{\text{Weight}_{(\text{g})}}{[\text{Length}_{(\text{cm})}]^3} \quad (1)$$

Invertebrate collection

From five to nine benthic samples were taken from the study lakes at the same time and location as the fish. Samples were taken at different depths in and around macrophyte beds in order to encompass a variety of microhabitats. Kicknet samples (area of 0.2 m^2) were taken at 0.5 m depths, and Ekman grabs (0.0225 m^2) were used for 1 and 2 m depths. A 10 – 15 min horizontal plankton tow was conducted in the open-water epilimnion of each lake using a zooplankton net of mesh size $250\text{ }\mu\text{m}$. All samples were stored for a few hours on ice prior to being frozen at -20°C .

Benthic samples were sorted using a dissecting microscope and invertebrates were identified to order, counted, measured and dried at 55°C for 48 h to obtain a dry weight measurement and to estimate the abundance and the per cent weight that each invertebrate order accounted for per square meter. The Shannon–Weiner Index of Diversity (H' ; Magurran, 1988) was used to compare average invertebrate diversity of benthic samples between lakes:

$$H' = -\sum p_i \ln p_i \quad (2)$$

Where p_i is n_i/N , n_i is the number of individuals in the i th order and N is the total number of individuals in the sample. The benthic invertebrates were also classified into size classes based on individual dry weight. The limits defining the eleven size classes were the same as those chosen by Boisclair & Leggett (1989b).

Perch diet composition

Perch diet was determined from the thawed stomach contents of 45 fish per lake. If there were many empty stomachs, additional fish stomach contents were

analysed to characterise better the diet of the population. Individual prey items were identified to order, counted, measured and dried at 55°C for 48 h to obtain a dry weight estimate of each order. The per cent occurrence of each prey taxon (percentage of fish with that prey taxon in their stomach) and the per cent weight of each prey taxon (percentage of total stomach contents dry weight that prey taxon accounted for) were determined for each age class per lake. Those prey taxa with both a high per cent occurrence (a common prey) and a high per cent weight (a profitable prey), were deemed to be the most important prey for that age class in that lake.

Lactate dehydrogenase analysis

Lactate dehydrogenase (LDH) activity was measured for the same fish used for diet analysis and chosen to encompass the whole range of perch sizes caught from each lake. Sample preparation and analysis methods closely followed the protocol described by kit specifications (LDH-optimised, Sigma-Aldrich®, Oakville, Canada) and the slight modifications of Sherwood *et al.* (2002a). The only change to these procedures was that protein analysis was carried out on sample preparations according to Sigma-Aldrich® Bradford Reagent specifications. All samples were run in duplicate and the average coefficient of variation for all LDH assays was $<5\%$.

Statistical analyses

Yellow perch and invertebrate weights were log transformed in order to meet requirements of normality and homoscedasticity for the valid application of all parametric analyses. Mean perch, prey and invertebrate weights were compared using one-way ANOVA followed by Tukey–Kramer multiple comparison tests ($\alpha = 0.05$). The significance of diet shifts for resetting perch LDH activity was determined using ANCOVA with body weight as the continuous variable and diet categorised with two dummy variables defining the shifts from planktivory to benthivory and from benthivory to piscivory. ANCOVA models were compared with simple linear models with F -ratio tests to determine if the inclusion of diet categories accounted for a significant proportion of the variation in the data. Diet categories were assigned based on stomach contents. If any plankton were present in stomach

contents the fish was categorised as a planktivore, despite any presence of benthos. Similarly, if fish were present it was categorised as a piscivore. Otherwise, if only benthos were present it was categorised as a benthivore. Perch with empty stomachs were not included in the ANCOVA analyses.

Results

Benthic invertebrate community analysis

The mean diversities of the benthic invertebrate communities for Geneva Lake and Richard Lake were significantly higher than those for Crowley Lake and Hannah Lake; Middle Lake was not significantly different from any other lake (Table 3). There were no significant differences detected between lakes in the abundance of each order, as sample sizes were insufficient. Many benthic invertebrate taxa, such as gastropods, molluscs, leeches, amphipods and odonates, were not present in most of the contaminated lakes. No special effort was made to sample for crayfish *Malacostraca*; however, a regional survey on crayfish distribution (J.H. Heneberry, K. Errulat, M. Robitaille, L. Whitmore & J.R.M. Morris 1992, unpublished data, Laurentian University, Sudbury, ON, Canada) found crayfish present in only one of the intermediately contaminated lakes, Crowley Lake. Crayfish are present in the reference lake, Geneva Lake, as many were found in perch stomach contents.

Dipterans and trichopterans made up most of the invertebrate biomass in Hannah, Middle and Crowley

Lakes (Fig. 1). These taxa were also important in the other contaminated lake, Richard Lake, although, amphipods and coleopterans also accounted for a large proportion of the total biomass. In the reference lake, Geneva Lake, odonates made up most of the per cent weight, followed by trichopterans and ephemeropterans. The size distribution of benthic invertebrates from sediment samples differed between lakes (Fig. 2). The reference lake, Geneva Lake, was the only lake with invertebrates in all eleven size classes, although abundances in the largest size classes were low. The intermediate and the highly contaminated lakes had reduced size structures of benthic invertebrates.

Perch diet analysis

Age 1+ perch fed primarily on zooplankton in all lakes but Richard Lake, in which dipterans were the dominant prey item (Table 4). The most important prey item for 2+ perch was consistently zoobenthos although the dominant invertebrate order differed between lakes. In the reference lake, Geneva Lake, 2+ perch were feeding predominantly on the mayfly *Hexagenia* (approximately 30 mm in length). In Crowley Lake, an intermediately contaminated lake, chironomids (approximately 7 mm) had a high per cent occurrence for 2+ perch; however most of the per cent weight was dominated by a few large odonates (approximately 17 mm). Age 2+ perch in the other intermediately contaminated lake, Richard Lake, had a similar diet that was dominated by chironomids

Table 3 The mean density (\pm SE of the mean) of benthic invertebrate orders and mean Shannon–Weiner's index of diversity (H') for the sediment samples of the five study lakes. Numbers in brackets are the sediment sample sizes. Numbers followed by the same letter (a, b) are not significantly different from each other (one-way ANOVA among lakes followed by a Tukey–Kramer multiple comparison test, $F_{4,28} = 9.2$, $P < 0.0001$).

Order	Geneva	Crowley	Richard	Middle	Hannah
Amphipoda	110 \pm 24	0.0	588 \pm 296	65.0 \pm 5.0	0.0
Coleoptera	8.6 \pm 1.8	5.0 \pm 0.0	24.7 \pm 8.8	18.2 \pm 13.2	0.0
Diptera	709 \pm 255	2238 \pm 1199	1816 \pm 1168	1756 \pm 932	1538 \pm 570
Ephemeroptera	93.2 \pm 27.2	5.0 \pm 0.0	222 \pm 133	127 \pm 6.67	0.0
Gastropoda	107 \pm 41	0.0	64.4 \pm 36.3	0.0	0.0
Hirudinea	12.5 \pm 2.5	0.0	0.0	0.0	0.0
Hydrachnidia	37.1 \pm 12.7	24.7 \pm 19.7	71.2 \pm 21.6	0.0	0.0
Nematoda	148 \pm 74	16.7 \pm 7.3	49.4 \pm 21.5	133 \pm 0.0	79 \pm 50
Odonata	14.9 \pm 6.5	0.0	34.6 \pm 9.9	13.9 \pm 7.7	0.0
Pelecypoda	59.3 \pm 14.8	0.0	31.3 \pm 13.2	0.0	0.0
Trichoptera	32.6 \pm 7.6	19.8 \pm 8.0	112 \pm 44	189 \pm 113	151 \pm 44
H'	0.88 \pm 0.10 (9) a	0.10 \pm 0.12 (6) b	0.84 \pm 0.12 (6) a	0.54 \pm 0.13 (5) ab	0.35 \pm 0.11 (7) b

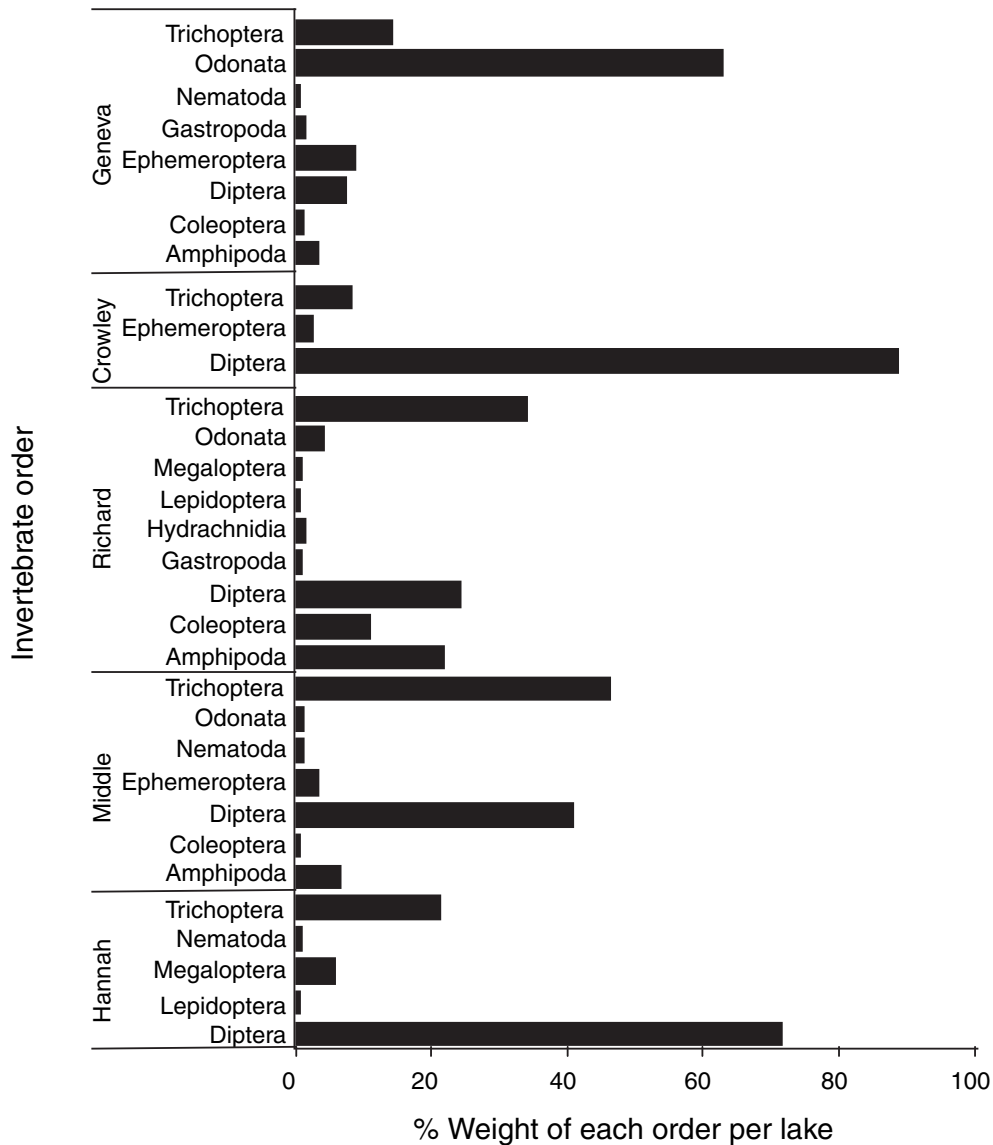


Fig. 1 Percentage of the total dry weight (mg) comprised by each invertebrate order in benthic samples from each lake.

(approximately 5 mm) followed closely by odonates (approximately 10 mm) and amphipods (approximately 4 mm). Age 2+ perch in both the contaminated lakes relied on small benthic invertebrates: trichopterans (approximately 5 mm) in Middle Lake and chironomids (approximately 5 mm) in Hannah Lake. There did not appear to be any further diet shifts to large bodied invertebrates or fish in the contaminated lakes, as older perch in Middle and Hannah continued to rely on these small benthic invertebrates. In the reference lake, Geneva Lake, the most important prey for 3+ perch was crayfish (approximately 30–50 mm). Perch older than 3+ were not caught in Geneva Lake.

In Crowley Lake, 3+ and 4+ perch relied primarily on odonates (approximately 20 mm) and became largely piscivorous (approximately 70 mm) by age 5+. For Richard Lake, the most important prey for 3+ perch was fish (approximately 40 mm), which became even more important for 4+ and 5+ perch.

Overall, the average mass of individual non-zooplankton prey items (i.e. prey size) was significantly different between lakes (Fig. 3; Table 5). However, within each age class, prey size differed between lakes only for ages 2+ and 3+ (Table 5). For 2+ perch, prey items of Geneva Lake perch had a mean weight about three times higher than all the

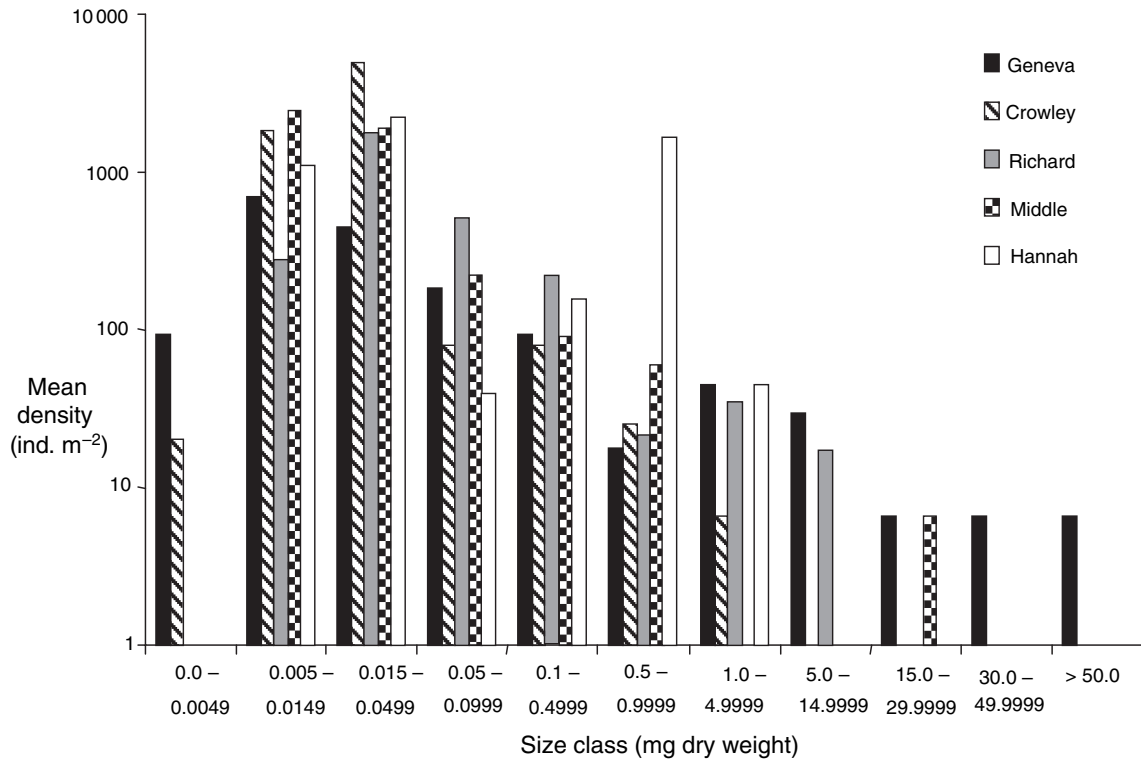


Fig. 2 Mean density of each benthic invertebrate size class in each lake. Size class limits (mg dry weight) are defined on the *x*-axis and follow (Boisclair & Leggett, 1989b).

other lakes, but only significantly higher than Crowley Lake, one of the intermediately contaminated lakes (Table 5). Mean prey size of age 3+ Geneva perch was two to eight times greater than the rest of the lakes, but only significantly different from Hannah Lake, one of the contaminated lakes (Table 5). If only benthic prey items are included in the analysis, prey items of age 3+ Geneva Lake perch are significantly larger than prey for Crowley, Middle and Hannah Lakes perch ($F_{4,48} = 7.03$, $P = 0.0002$). The average mass of individual prey items did not differ between lakes for 1+ perch or for 4+ perch, although sample sizes for 4+ perch were limited and no 4+ fish from Geneva Lake were caught (Table 5).

Non-zooplankton prey size increased with perch age in the reference lake, Geneva Lake, and in the two intermediate lakes, Crowley and Richard Lakes (Table 5). In Geneva Lake, mean individual prey weight increased significantly between all three age classes. However, in the intermediate lakes, mean prey size was only significantly higher by age 5+. When fish prey items were omitted from the analysis, there was no significant increase in prey size with age

in either Crowley ($F_{4,35} = 2.08$, $P = 0.10$) or Richard ($F_{3,26} = 0.99$, $P = 0.41$) Lakes. There was no significant increase in prey size with age in either of the contaminated lakes, Middle Lake and Hannah Lake (Table 5).

Perch growth analysis

Yellow perch comprised about 95% of the number of fish caught in all lakes. In order to gain an indication of the difference between lakes in how large perch tended to grow, the mean weights of the largest 15% of perch caught from each lake were compared. The mean weights of the largest perch from the reference lake, Geneva Lake, and one of the intermediate lakes, Crowley Lake, were two to three times higher than the other intermediate lake, Richard Lake. Additionally, the mean weights of the largest perch from Geneva, Crowley and Richard Lakes were two to six times higher than the contaminated lakes, Hannah and Middle (Table 6).

Comparing average perch weight across lakes at each age, 1+ perch from Geneva Lake were about 1.5

Table 4 Summary of yellow perch diet transition. Included are the most important prey taxa for each age class from each perch population. Prey taxa were deemed 'most important' by having the highest combined per cent occurrence in perch stomach contents and per cent weight (mg dry) of total stomach contents. The number of perch with each prey taxa present is indicated by *n*.

Lake	Age class	Prey taxa	% Occurrence	% Dry weight	<i>n</i>
Hannah	1+	Zooplankton	54.5	63.8	11
	2+	Diptera	63.6	18.3	3
	3+	Diptera	76.9	20.0	10
	4-5+	Trichoptera	53.8	10.9	
		Diptera	85.7	56.6	7
Middle	1+	Zooplankton	83.3	86.4	18
	2+	Trichoptera	71.4	22.9	7
	3-4+	Odonata	28.6	69.8	
		Trichoptera	80.0	46.5	5
Richard	1+	Diptera	66.7	75.9	6
	2+	Zooplankton	50.0	16.4	
		Diptera	66.7	37.1	12
		Amphipoda	41.7	28.6	
	3+	Odonata	33.3	31.7	
4-5+	Fish	42.8	78.9	7	
Crowley	1+	Fish	66.7	96.0	3
	1+	Zooplankton	100.0	90.7	7
	2+	Diptera	77.8	9.4	11
	3-4+	Odonata	22.2	82.0	
		Fish	83.3	96.2	6
Geneva	1+	Fish	83.3	85.9	6
	2+	Zooplankton	83.3	85.9	6
	3+	Ephemeroptera	38.5	43.6	13
	3+	Malacostraca	35.3	81.2	17

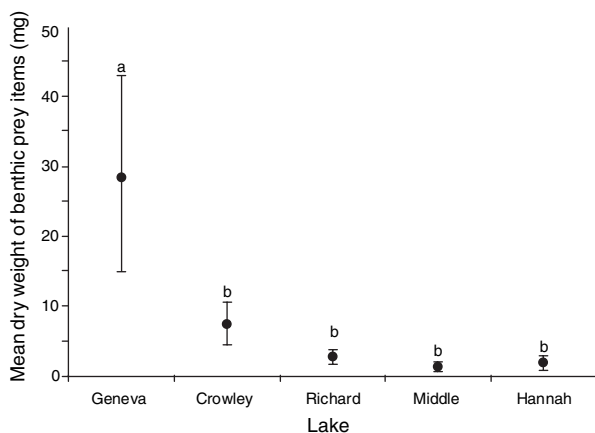


Fig. 3 Mean dry weight of individual benthic invertebrates from yellow perch stomach contents (milligram dry weight; mean \pm SE of the mean). Lakes with the same letter are not significantly different from each other based on one-way ANOVA followed by Tukey-Kramer multiple comparison test.

times heavier than 1+ perch in Richard and Hannah Lakes (Fig. 4; Table 6). Mean weight in Geneva Lake was twice as high as perch in all the other lakes by age 2+ and two to four times higher by age 3+ (Table 6). Perch in the intermediate and contaminated lakes were not significantly different from each other at age 1+ or age 2+. By age 3+, mean body weights of perch in the intermediate lake, Richard Lake, were two times higher than perch in both the contaminated lakes; although perch in the other intermediate lake, Crowley Lake, were only significantly larger than Hannah Lake perch. By age 4+, perch in both intermediate lakes were about two to three times heavier than perch in both contaminated lakes (Table 6).

Comparing size at age within each lake, 1+ perch were significantly smaller than 2+ perch and 2+ perch were significantly smaller than 3+ perch in all lakes, although the degree by which they differed was different for each lake (Table 6). In Hannah, Middle and Richard Lakes perch were stunted, as there were no significant differences between the mean weights of the older age classes. However, in Crowley Lake, 4-7+ perch were significantly larger than 3+ perch (Table 6).

Comparing perch condition across lakes at each age shows that age 1+ perch from all lakes had a similar condition except for Crowley Lake where condition was significantly lower than all the other lakes ($F_{4,62} = 11.71$, $P < 0.0001$). At age 2+, Geneva Lake perch had significantly higher condition than perch in Crowley, Middle and Hannah Lakes, and Richard Lake perch had significantly higher condition than perch from Crowley and Middle Lakes ($F_{4,70} = 20.87$, $P < 0.0001$). Differences were even greater at age 3+, where Geneva Lake perch had significantly higher condition than perch from all the other lakes and Richard Lake perch were still significantly higher than perch from Crowley and Middle Lakes ($F_{4,49} = 24.44$, $P < 0.0001$).

Lactate dehydrogenase activity analysis

Individual white muscle LDH activity was plotted as a function of body size (Fig. 5). Although both simple linear regressions and ANCOVA models, which incorporate diet shifts into the analysis, were significant, the ANCOVA models accounted for more of the variation in the data (i.e. higher adjusted R^2

Table 5 The average mass of non-zooplankton, individual prey items (mean milligram dry weight \pm SE of the mean; sample size in brackets) from perch stomach contents compared across lakes including all ages (first row) and across lakes within the first four age classes. Reading horizontally for these comparisons, entries followed by the same letter in bold type (a, b) are not significantly different from each other and the *F*-ratios and *P*-values are found in the right hand columns. Mean weight of prey items are also compared across ages within each lake. Reading vertically for these comparisons, entries followed by the same letter in normal type (a, b, c) are not significantly different from each other (*F*-ratios and *P*-values are in the bottom two rows of the table). One-way ANOVA, followed by a Tukey–Kramer multiple comparison test.

Age	Geneva	Crowley	Richard	Middle	Hannah	<i>F</i> -ratio	<i>P</i> -value
All	26.9 \pm 12.6 (59) a	56.9 \pm 24.7 (46) a	4.9 \pm 4.3 (35) ab	1.3 \pm 0.6 (32) b	12.4 \pm 3.1 (15) b	$F_{4,212} = 5.7$	0.0002
1+	0.3 \pm 0.1 (12) a	0.06 \pm 0.02 (3) ab	0.4 \pm 0.2 (5) a	0.2 \pm 0.03 (15)	0.5 \pm 0.3 (11)	$F_{4,75} = 1.6$	0.18
2+	9.0 \pm 3.0 (28) b/a	2.9 \pm 2.3 (17) a/b	2.5 \pm 1.3 (17) ab/ab	2.5 \pm 1.9 (9) ab	0.08 \pm 0.03 (4) ab	$F_{4,85} = 3.4$	0.013
3+	66.7 \pm 35.8 (20) c/a	8.6 \pm 8.5 (6) ab/ab	25.0 \pm 10.8 (10) ab/ab	2.2 \pm 1.3 (7) ab	9.0 \pm 8.5 (16) b	$F_{4,55} = 4.1$	0.006
4+	NA	21.3 \pm 12.3 (9) ab	27.4 \pm 27.1 (2) ab	0.8 (1)	3.7 \pm 3.1 (11)	$F_{3,19} = 0.95$	0.44
5+	NA	79.2 \pm 42.9 (8) b	83.6 (1) b	NA	9.6 \pm 9.3 (3)		
6–7+	NA	564.0 \pm 217.8 (3) c	NA	NA	NA		
<i>F</i> -ratio	$F_{2,57} = 10.7$	$F_{5,40} = 10.2$	$F_{4,30} = 4.4$	$F_{3,28} = 2.1$	$F_{4,40} = 0.9$		
<i>P</i> -value	0.0001	<0.0001	0.007	0.12	0.47		

NA, not applicable.

Table 6 Mean body weight (mean gram wet weight \pm standard error of the mean; sample sizes in brackets) of the largest 15% of perch caught and of the first four age classes are compared across lakes. Reading horizontally for these comparisons, entries followed by the same letter in bold type (a, b, c, d) are not significantly different from each other (the *F*-ratios and *P*-values are in the right hand columns). Mean perch body weight is also compared between ages within each lake. Reading vertically for these comparisons, entries followed by the same letter in normal type (a, b, c, d, e) are not significantly different from each other (the *F*-ratios and *P*-values are in the bottom rows). One-way ANOVA followed by a Tukey–Kramer multiple comparison test.

Age	Geneva	Crowley	Richard	Middle	Hannah	<i>F</i> -ratio	<i>P</i> -value
Top 15%	77.4 \pm 4.4 (19) a	91.7 \pm 15.3 (27) a	37.3 \pm 2.7 (18) b	21.0 \pm 0.8 (15) c	15.9 \pm 0.3 (27) c	$F_{4,101} = 80.6$	<0.0001
1+	6.5 \pm 0.9 (7) a/a	4.2 \pm 0.4 (9) a/ab	3.4 \pm 0.4 (16) a/b	4.4 \pm 0.3 (18) a/ab	4.0 \pm 0.3 (17) a/b	$F_{4,62} = 4.6$	0.0024
2+	22.3 \pm 2.4 (17) b/a	10.7 \pm 0.7 (16) b/b	11.0 \pm 0.7 (17) b/b	10.9 \pm 0.8 (18) b/b	7.9 \pm 1.0 (7) b/b	$F_{4,70} = 17.1$	<0.0001
3+	67.9 \pm 5.9 (16) c/a	24.9 \pm 3.5 (8) c/bc	33.0 \pm 5.1 (9) c/b	15.1 \pm 0.9 (8) c/cd	13.5 \pm 0.9 (13) c/c	$F_{4,49} = 46.2$	<0.0001
4+	NA	53.6 \pm 11.1 (7) d/a	39.9 \pm 6.3 (4) c/a	21.5 \pm 0.9 (10) d/b	15.8 \pm 1.2 (8) c/b	$F_{3,25} = 25.7$	<0.0001
5+	NA	84.5 \pm 17.4 (3) de	44.7 \pm 2.9 (2) c	27.1 (1) cd	13.0 (1) bc		
6+	NA	230.1 (1) e	42.6 (1) c	NA	NA		
7+	NA	198.9 \pm 66.7 (4) e	NA	NA	NA		
<i>F</i> -ratio	$F_{2,37} = 88.5$	$F_{6,41} = 69.5$	$F_{5,43} = 66.4$	$F_{4,50} = 74.4$	$F_{4,41} = 56.7$		
<i>P</i> -value	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001		

NA, not applicable.

values; Table 7). In the ANCOVA model for Geneva Lake, including the shift from planktivory (mostly *daphnia* 1–2 mm in length) to benthivory (many kinds of insect larvae and crustaceans from 5 to 50 mm in length) resulted in a significant increase in fit over a simple linear regression (*F*-ratio test, $F_{11,28} = 2.88$, $P < 0.05$). For the intermediate lake, Crowley, the first diet shift from planktivory to benthivory was not a significant component in the ANCOVA model. Only the shift from benthivory (mainly dipterans and odonates about 7 and 17 mm in length, respectively) to piscivory (mainly perch from 50 to 80 mm in length) at about 100 g resulted in a significant

downshift in LDH for perch in Crowley Lake. However, because many fish in Crowley Lake had empty stomachs, the sample size for the ANCOVA model was considerably less than the linear model and was not a significantly better fit (*F*-ratio test, $F_{22,25} = 1.30$, $P > 0.5$). The linear regression for Richard Lake was significant; however too many sampled fish had empty stomachs to perform an ANCOVA. Perch in Middle Lake switch from planktivory (*Daphnia* of 1 mm) to benthivory (dipterans of 4 mm and trichopterans of 5 mm) at about 6 g and do not make a further switch to piscivory. Incorporating the shift to benthivory in an ANCOVA model

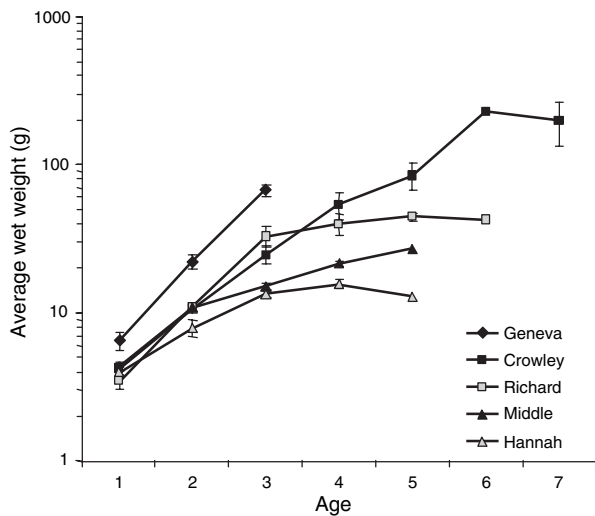


Fig. 4 Mean weights of different age classes of perch from each lake. Error bars represent the standard error of the mean. Symbols are triangles for the most contaminated lakes, squares for the intermediately contaminated lakes and diamonds for the reference lake.

for Middle Lake did improve the adjusted R^2 over the simple linear regression (Table 7), but it was not a significantly better fit (F -ratio test, $F_{24,28} = 0.85$, $P > 0.5$). Neither the linear regression nor the ANCOVA model were significant for Hannah Lake, the other contaminated lake (Table 7).

Discussion

Large size classes of benthic invertebrates are absent in metal-contaminated lakes

In Sudbury, benthic invertebrate diversity was reduced in metal-contaminated lakes. More importantly, metal-sensitive large invertebrates, such as molluscs, crustaceans, gastropods, odonates and large ephemeropterans, were absent or accounted for a low percentage of zoobenthic biomass, and the community was dominated by metal-tolerant taxa such as chironomids and trichopterans. These results are consistent with previous research in Rouyn-Noranda, Québec, Canada (Kovacs *et al.*, 2004) and from many other studies on the effects of metal contamination on invertebrate assemblages in lakes (Johnson *et al.*, 1992; Gower *et al.*, 1994), streams (Clements *et al.*, 2000) and estuaries (Gaston *et al.*, 1998).

An important consequence of having a less diverse, small-bodied benthic invertebrate community is the

manner in which the functional role these invertebrates play in lake food webs is affected. Zoobenthos are important food for fish, transferring energy from algal production and detritus, which would otherwise accumulate in the sediment. Diversity in the zoobenthos is important for energy transfer as each group specialises on a particular food source (Covich, Palmer & Crowl, 1999). The loss of a particular species, or a functional group of species, may result in the loss of an energetic pathway leading to fish. In a study comparing the diets of 15 species of North American freshwater fish, an average of 65% of fish diet originated either directly or indirectly from zoobenthic production (Vadeboncoeur *et al.*, 2002). Therefore, the importance of a naturally diverse benthic prey base may not be trivial. In the present study, metal contamination shifts the zoobenthic species composition towards smaller bodied invertebrates. The absence of the top four size classes of benthic invertebrates in most of our contaminated lakes, may have important energetic consequences for visual fish predators, such as yellow perch.

Limited prey choice for yellow perch in metal contaminated lakes

The stomach contents analysis supported our second prediction that perch from more metal-contaminated lakes are forced to rely more heavily on smaller prey, a result that is consistent with Rouyn-Noranda lakes (Kovacs *et al.*, 2004). The diet transition for Geneva Lake perch was to significantly larger zoobenthic prey, whereas in the intermediate and contaminated lakes there was no significant difference in the average size of zoobenthic prey items as perch aged. Perch in the intermediate lakes eventually became piscivorous by age 5+, which accounts for the drastic and significant increase in prey size for older perch in these lakes.

Perch diet composition in Sudbury lakes generally reflected what was available to them based on the benthic community analysis. In Geneva Lake and Crowley Lake, however, stomach contents of larger perch showed preferential selection of large ephemeropterans (*Hexagenia*) and malacostracans (crayfish) in Geneva and large odonates in Crowley, of which we found few or none in our benthic samples. Furthermore, prey taxa preferentially selected by perch in the reference lake (*Hexagenia* for 2+ perch and crayfish for

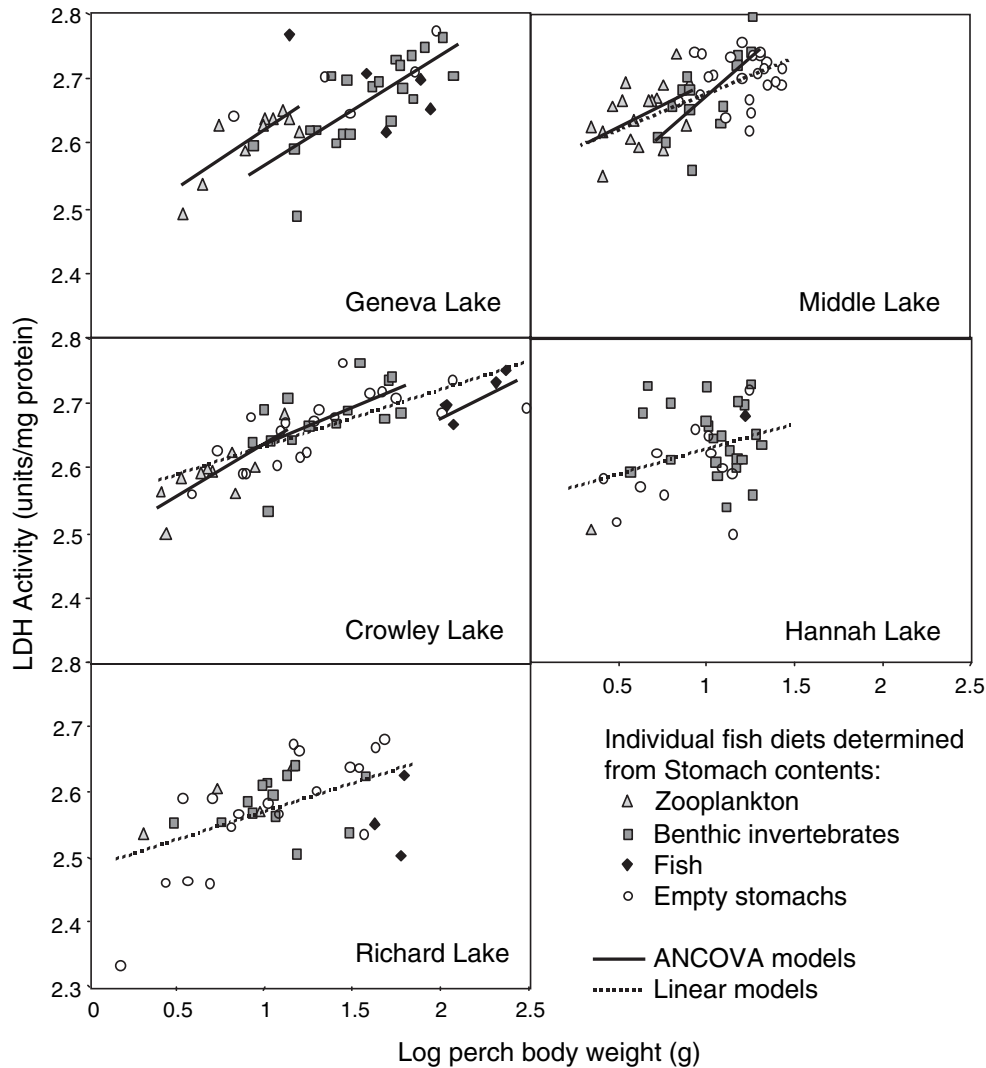


Fig. 5 Log white muscle lactate dehydrogenase (LDH) activity (units per milligram protein) versus body size for yellow perch from all five study lakes. All lines are based on models from Table 7.

3+ perch), were those considered sensitive to metal contamination and were not found in any of the other lakes.

Failure to switch to large prey leads to stunted growth

In accordance with our third prediction and consistent with Rouyn-Noranda lakes, perch in the two highly contaminated Sudbury lakes exhibited slow growth at a certain body weight. Furthermore, slow growth occurred near the typical size where a shift to larger benthic prey is expected. Perch in all the contaminated and intermediate lakes did not grow as large as perch in the reference lake at each age (Fig. 4).

Diet shifts lower energetic costs

Consistent with previous studies that used the activity of LDH in fish white skeletal muscle to estimate anaerobic glycolytic potential, the results show that glycolytic potential is highly variable but generally scales positively to body size (Childress & Somero, 1990; Sherwood *et al.*, 2002b). The results also support previous findings on the effect of diet ontogeny on LDH activity (Sherwood *et al.*, 2002a,b). LDH activity tended to increase rapidly with body size in each lake, and *complete* diet shifts resulted in a downshift of LDH activity. This downshift, or resetting of LDH to a lower level, is attributed to a lower need for glycolytic

Table 7 Summary of results for lactate dehydrogenase activity analysis

Lake	Model	Equation parameters				Adj. R^2	F -ratio	$P > F$	n
		a	b	c	d				
Geneva	Linear	2.50	0.11	NA	NA	0.45	$F_{1,39} = 34.13$	<0.0001	41
	ANCOVA	2.42	0.18	0.03	NA	0.65	$F_{2,28} = 29.26$	<0.0001	31
Crowley	Linear	2.54	0.09	NA	NA	0.59	$F_{1,47} = 71.09$	<0.0001	49
	ANCOVA	2.46	0.13	NA	0.04	0.70	$F_{2,25} = 32.53$	<0.0001	28
Richard	Linear	2.48	0.06	NA	NA	0.27	$F_{1,36} = 14.47$	0.0005	38
	ANCOVA	Insufficient diet data							
Middle	Linear	2.58	0.10	NA	NA	0.32	$F_{1,52} = 26.20$	<0.0001	54
	ANCOVA*	2.51	0.18	0.02	NA	0.34	$F_{2,28} = 8.82$	0.001	31
Hannah	Linear	2.56	0.07	NA	NA	0.07	$F_{1,35} = 3.62$	0.07	37
	ANCOVA	Insufficient diet data							

Polynomial equations are $\log\text{LDH} = a + b \times \log W$ for linear regression, and $\log\text{LDH} = a + b \times \log W - c - d$ for ANCOVA where c and d are dummy variables coding for diet shifts from planktivory to benthivory, and benthivory to piscivory, respectively.

NA, not applicable.

*ANCOVA model is not a significantly better fit over linear model.

potential because of the sharp decline in the number of burst swimming prey attacks required once prey size becomes much larger. By increasing prey size, the number of prey needed to be captured by a perch decreases and therefore glycolytic potential is down-regulated because of lower anaerobic demands (Sherwood *et al.*, 2002a,b).

In Middle Lake, one of the most contaminated lakes, LDH scaled significantly with body size; however, categorising the perch in terms of diet did not significantly reduce the variation in the data, possibly because of an absence of a complete diet shift from planktivory to benthivory. Middle Lake is somewhat similar to one of the most contaminated lakes from Rouyn-Noranda where both diet and stable isotopes indicated a shift to small benthic invertebrates (mainly chironomids), but without resulting in a significant resetting of LDH activity (Sherwood *et al.*, 2002a). In the other highly contaminated lake, Hannah Lake, perch of all sizes were eating mostly chironomids and trichoptera, making it impossible to categorise the perch into diet categories. However, it may be precisely the lack of complete diet shifts in these highly contaminated lakes that explain why there is no clear resetting of activity levels and why these populations are stunted.

For the intermediately contaminated lake, Crowley Lake, only the shift to piscivory significantly reduced the variability in the scaling of LDH with body weight. The shift from planktivory to benthivory was not a significant parameter in the ANCOVA

model, indicating that the perch are not benefiting energetically, in terms of significantly reducing their activity costs, from switching to benthic prey. The absence of the largest benthic invertebrate size classes may reduce the profitability of switching to benthivory as small benthic prey are not much larger than zooplankton. Benthic resources do not appear to be so limited that growth stops altogether (as in the highly contaminated lakes) as the perch eventually grow through benthivory to become piscivorous. This explanation is also supported by the fact that the most important prey items for benthivorous perch include both small taxa (dipterans and amphipods) and large taxa (odonates), instead of only large taxa as in the reference lake (mayfly larvae and crayfish), or only small taxa (dipterans and trichoptera) as in the highly contaminated lakes. In Richard Lake, almost half of the fish selected for LDH analysis had empty stomachs. Thus, there was insufficient diet data to perform the ANCOVA.

Like perch populations from the uncontaminated lakes in Rouyn-Noranda (Sherwood *et al.*, 2002a) and the lakes in the Eastern Townships of Quebec, Canada (Sherwood *et al.*, 2002b), perch from Geneva Lake showed significant resetting of LDH following the shift from planktivory to benthivory. The lack of a significant shift to piscivory is expected as stomach contents data indicated that 3+ perch (the oldest perch we caught) had not yet become exclusively piscivorous. Geneva Lake was the only lake where LDH activity was significantly reset following the shift to

benthivory, it was the only lake where perch maintained high growth rates throughout benthivory and it was the only lake where there was an increase in the size of benthivorous prey between ages. This evidence supports our fourth prediction, suggesting that the availability of a large size range of benthic invertebrates is important for lowering fish activity costs and ultimately maintaining high growth rates.

Energy available for growth depends on activity costs

Stunting in perch populations is a well-documented phenomenon that is often attributed to resource limitation because of low zoobenthic production (Persson, 1987; Diehl, 1993; Heath & Roff, 1996) or high perch densities (Hansson, 1985). However, there is evidence that energy expenditure for active metabolism may also be related to stunting in perch populations. It has been suggested that activity costs are highest when fish spend most of their time attacking many, small prey (mostly anaerobic activity) than when they spend most of their time searching for a few, large prey (mostly aerobic activity), and that high activity costs compromise the amount of energy available for growth (Krohn & Boisclair, 1994; Sherwood *et al.*, 2002a). This hypothesis is supported by the fact that the quantity of food consumed is not always related to perch growth rates (Boisclair & Leggett, 1989a; Sherwood *et al.*, 2000), that perch have higher growth rates following diet shifts (Boisclair & Leggett, 1989c; Sherwood *et al.*, 2002a) despite the lower abundance of larger invertebrates (Rasmussen, 1993), and that growth rates of perch decrease as the proportion of small prey items in the diet simultaneously increases (Diehl, 1993; Boisclair & Rasmussen, 1996; Lott, Willis & Lucchesi, 1996; Hjelm, Persson & Christensen, 2000). Furthermore, Sherwood *et al.* (2000) showed that age 4+ perch from reference and contaminated lakes in Rouyn-Noranda did not differ in rates of prey consumption, but did differ in conversion efficiencies. Thus, the difference between fast growing and stunted perch populations may also occur at the level of active metabolism, not only at the level of consumption.

Ideally, perch will maximise their growth efficiency by switching their diet to optimal sized prey as they grow, thus maintaining high growth rates. Under this scenario, if a perch outgrows its prey, its growth rate will slow down until it is large enough to exploit the

next size class of prey, when growth should return to normal. This period of slow growth constitutes what is known as a growth bottleneck (Heath & Roff, 1996; Hjelm *et al.*, 2000; Sherwood *et al.*, 2002a,b). Stunted perch populations result from a gap in the prey size structure, which is so large that the perch stop growing, and never become large enough to utilise the next size class of prey.

We suggest that metal contamination of lakes creates gaps in the prey size structure, producing the patterns in perch growth as described above. Only the perch population from the reference lake showed a significant resetting of LDH activity following the shift to benthivory. Piscivory was low in Geneva Lake, despite the fact that the perch were larger than some of the piscivorous perch from the intermediate lakes. The presence of large invertebrate prey in Geneva Lake would increase the optimal size for switching to piscivory. It has previously been noted that piscivory is not necessary for high perch growth rates where there is an invertebrate prey base of good size (Lott *et al.*, 1996). Perch in the intermediate lakes experienced reduced growth through the size range in which perch are typically benthivorous. We suggest that the absence of large bodied invertebrates, such as crayfish and mayfly larvae, is the cause of the reduced growth. These perch appear to eventually make it through the slow growing benthivorous stage to become piscivorous. The resetting of LDH activity and the increase in growth rates in Crowley Lake may be because of lower activity costs after the shift to piscivory. In the most contaminated lakes where perch were extremely stunted, there was an absence or low abundance of intermediately sized prey in addition to the absence of large invertebrates. The perch in these systems would quickly outgrow any energetic benefits of switching to small benthic prey, which are not much larger than zooplankton, as evidenced by their slow growth and lack of a significant lowering of activity costs. Given the variation in the LDH data, a small resetting of LDH activity may not be evident. It is also possible that the apparent shift to benthivory in the contaminated lakes was not a complete shift and that the perch continued to periodically rely on plankton. Stable isotope ratios for perch from Hannah Lake and Middle Lake suggest a mixed pelagic and benthic diet and when Hannah Lake was sampled the previous year, at the same time of the

season, perch of all sizes were eating zooplankton (A.C. Iles, personal observation).

These patterns of indirect, food web mediated effects on the energetics of yellow perch are not restricted to metal-contaminated lakes. Similar growth effects have been described for other anthropogenic disturbances that alter food web structure, such as eutrophication and species introductions. Schaeffer, Diana & Haas (2000) suggested that eutrophic conditions in Saginaw Bay, Lake Huron, caused increased zooplankton and chironomid production and improved feeding conditions for age 0+ and age 1+ perch. However, the loss of mayfly larvae and other large benthic invertebrates caused stunting of older perch (Schaeffer *et al.*, 2000). The loss of large-bodied prey in eutrophic lakes in the Eastern Townships of Quebec was linked to increased activity rates and low growth rates in perch (Boisclair & Rasmussen, 1996). Hayward & Margraf (1987) observed low growth rates among perch inhabiting the eutrophic western basin of Lake Erie, coinciding with a heavier reliance on small prey. Interestingly, the food web effects of eutrophication have often been reversed. For example, the introduction of the exotic zebra mussel (*Dreissena polymorpha*) to Lake Erie caused a decline in phytoplankton, an increase in zoobenthic abundance and diversity (particularly the return of mayfly larvae) and an increase in growth rates of yellow perch (Tyson & Knight, 2001). Introduced bass were shown to reduce densities of forage fish, forcing lake trout to feed on zooplankton and benthic invertebrates to the point where the trout exhibited reduced growth (Vander Zanden, Casselman & Rasmussen, 1999).

Direct versus indirect effects of metal contamination on fish

The environmental conditions in which an organism lives are crucial for its ability to deal with exposure to any contaminant (Beyers, Rice & Clements, 1999). For instance, with metal contamination, diets that cause higher growth rates result in lower tissue metal concentrations, even when metal exposure is the same (a dilution effect of growth) (Kamunde & Wood, 2003). Consequently, the stunted perch from our contaminated lakes may be suffering not only from high activity costs, but from high body concentrations of metals as well. High body concentrations of metals may also explain why perch in the intermediately

contaminated lakes managed to grow through the energetic bottleneck of benthivory despite poor prey choice, whereas in the highly contaminated lakes they did not. Perch from metal-contaminated lakes in Sudbury and Rouyn-Noranda have an impaired cortisol stress response, an indication of chronic, sublethal contaminant stress, and exhibit increased concentrations of metallothionein, a metal binding and detoxifying protein, in their livers and kidneys (Brodeur *et al.*, 1997; Laflamme *et al.*, 2000; Rajotte & Couture, 2002; Audet & Couture, 2003).

Because of the many variables that can affect growth rates of wild fish (e.g. size, water temperature, activity, prey quantity/quality, contaminant stressors) it can be difficult to determine which variable is responsible for observed growth patterns (Beyers *et al.*, 1999; Campbell *et al.*, 2003). Using a fish bioenergetics model to isolate the influence of dieldrin exposure on the growth of largemouth bass, Beyers *et al.* (1999) found that the effects were insignificant relative to the natural variation in food quantity and temperature. In a study examining the effects of stream metal contamination on the metal bioaccumulation of brown trout, food availability and temperature were the most important factors affecting trout growth rates and condition (Clements & Rees, 1997). Furthermore, only differences in the available sizes of prey and possibly perch density, could explain differences in yellow perch growth between the two intermediate lakes from Rouyn-Noranda, as perch in both lakes had similar levels of metal bioaccumulation (Kovecses *et al.*, 2004).

Although the relative influence of metal contamination on fish through direct, physiological effects and indirect, food web mediated effects has not yet been quantified, we might be able to assess the relative effects to some degree, by comparing mean condition factors in metal-contaminated and clean lakes at age 1+, when all are planktivorous and there should be minimal indirect effects of prey size but possible physiological effects of metal exposure, versus at age 3+, when both should have an effect. The results showed that age 1+ perch from all the lakes had similar condition factors, except for Crowley Lake where condition was significantly lower. By age 3+, the differences between lakes were greater as Geneva Lake perch had a significantly higher mean condition than perch from all the other lakes (higher *F*-value despite the smaller sample size). This pattern

implies that indirect, food web mediated effects of metal contamination may be more important for determining perch growth rates than direct, physiological effects, although physiological effects such as cortisol impairment and gill histopathology, would also be expected to have some energetic costs, and thus probably exacerbate growth reductions in adult fish (Campbell *et al.*, 2003). However, differences between lakes in fish community structure, zooplankton size or zooplankton availability may also play a role here in determining condition of age 1+ perch; although, the vast majority of fish caught in all lakes were yellow perch and results show that there was no significant difference of age 1+ perch prey size between lakes.

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