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**Indirect effects of metal-contamination on energetics of yellow perch (*Perca flavescens*) in Sudbury area lakes, resulting from food web simplification**

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## Abstract

Metal-contamination of lakes simplifies food webs and reduces the efficiency of energy transfer to top trophic organisms, such as yellow perch (*Perca flavescens*). Benthic invertebrate community composition and yellow perch 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 is disrupted by metal-contamination. As perch grow larger, they shift their diet to larger prey; otherwise, the activity costs of foraging for many, small prey, instead of a few large prey, become too high and the fish stop growing. Metal-contaminated lakes have less diverse zoobenthic communities, particularly the lack of large bodied invertebrate taxa, forcing perch to rely on smaller benthic prey. Perch from metal-contaminated lakes display slow growth and poor condition during benthivory. Estimates of fish activity, using the activity of the glycolytic enzyme Lactate dehydrogenase in perch white muscle tissue as a proxy, suggest that diet shifts to larger prey lower activity costs and may explain how diet shifts maintain growth efficiency as perch grow larger. Perch from metal-contaminated lakes cannot benefit from the energetic advantages of switching to larger prey and thus exhibit poor growth.

## Résumé

La contamination des lacs par les métaux simplifie les réseaux trophiques et réduit l'efficacité du transfert énergétique aux niveaux trophiques les plus élevés. Durant leur croissance, les perchaudes (*Perca flavescens*) consomment des proies de plus en plus grosses; autrement le coût énergétique de chasser plusieurs petites proies devient trop élevé, ce qui limite la croissance des poissons prédateurs. La composition des communautés d'invertébrés benthiques, et la diète, croissance et activité des perchaudes ont été utilisés pour évaluer l'importance d'une communauté de proies diversifiée pour maintenir un transfert énergétique suffisant pour la croissance des perchaudes afin d'établir l'impact des métaux sur ces communautés. Les communautés d'invertébrés benthiques provenant de lacs contaminés démontrent une réduction de diversité, en particulier un manque de gros invertébrés, forçant les perchaudes à consommer de plus petites proies. Les perchaudes dans les lacs contaminés démontrent une croissance lente et un facteur de condition réduit lorsqu'elles se nourrissent d'invertébrés benthiques. Les évaluations de l'activité de poissons, procuré à partir du niveau d'activité de lactate déhydrogénase dans le muscle blanc, suggèrent qu'une consommation de proies de plus en plus grosses diminue les coûts d'activité, et explique donc pourquoi les perchaudes provenant de lacs références maintiennent une croissance plus élevée. Les perchaudes provenant de lacs contaminés par les métaux ne peuvent donc pas bénéficier des avantages énergétiques suivant la consommation de grosses proies, et par conséquent démontrent une croissance réduite.

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represents the results of my own independent research and has been co-authored by my thesis supervisor, Dr. Joseph B. Rasmussen. Dr. Rasmussen, as my supervisor, has contributed to the design, execution, analysis and presentation of the results presented herein.

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## Introduction

Human alterations of the global environment, through land use change, modification of global biogeochemistry and biotic additions and losses, are having dire consequences for biodiversity on Earth (e.g. Lake *et al.* 2000). Estimations of current rates of human induced species extinction are 100-1000 times greater than natural rates (Chapin *et al.* 2000). Declines in biodiversity may affect ecosystem function, as simplified ecosystems become less resilient to natural and human induced environmental fluctuations (Chapin *et al.* 2000, McCann 2000). Complex food webs, involving many, weakly interacting species, stabilize trophic dynamics by backing up and buffering strong consumer-resource interactions within an ecosystem (McCann 2000). Without this greater complexity driving community and ecosystem stability, a food web consisting of a few strong interacting species would be prone to destabilizing dynamics and collapses and thus a loss of ecosystem function (McCann 2000). A less understood component of food web theory is how a decrease in the number of energetic pathways, due to species loss, affects energy transfer to top trophic compartments. A reduction in biodiversity could compromise the amount of energy transferred to higher trophic levels or the efficiency with which this energy is transferred.

Freshwater sediment biota are particularly vulnerable to environmental change because of the transmission of impacts from the surrounding watershed (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 mollusks, crustaceans and mayflies, tend to disappear and the community becomes dominated by metal-tolerant invertebrates, such as chironomids, caddis flies and oligochaetes (Kraft & Sypniewski 1981, Rygg 1985, Hare 1992, Johnson *et al.* 1992, Gower *et al.* 1994, Clements *et al.* 2000, Kovacs and Rasmussen, in prep.). This shift towards a dominance by subsurface-deposit feeders in metal-contaminated habitats has also been well documented for estuaries (Gaston *et al.* 1998) and for streams draining mining areas (Beltman *et al.* 1998, Malmqvist & Hoffsten 1999).

Freshwater benthic invertebrate communities are an important functional component of lake ecosystems. These communities are very diverse and provide many valuable ecosystem services such as aeration of the sediment, enhancing decomposition of organic matter and recycling nutrients for primary producers to take up. Zoobenthos also play a large role in freshwater food webs, transferring energy and nutrients from primary producer and detrital pathways to top trophic levels (Covich *et al.* 1999). Although the zoobenthos is typically a very diverse community, benthic invertebrate taxa are unlikely to be interchangeable components in ecosystem processes (Covich *et al.* 1999). Each species has specific preferences for particular temperatures, pH, current velocities, plant presence, type of substrata and exposure, so true species redundancy is likely to be low, especially in temperate regions where species richness is relatively low (Rasmussen 1993, Covich *et al.* 1999).

The loss of zoobenthic diversity due to metal-contamination may have important consequences for the ecosystem processes in which invertebrates play a role (Lake *et al.* 2000). Particularly, the loss of the larger benthic invertebrates may compromise the efficiency of energy transfer to fish. Recent research by Sherwood *et al.* (2002b) shows the importance of a naturally diverse prey base for maintaining energy transfer to growing fish. Visually feeding fish (those that locate and attack each prey item as opposed to 'blind' filter feeders or deposit feeders) have a maximal foraging efficiency within a certain range of prey sizes. Above this range a greater swimming capacity or gape size is required to capture prey. Below this range foraging efficiency decreases from the need to capture more prey, as it is more energetically efficient for fish to catch a few large prey items rather than hundreds of small ones (Persson 1987, Diehl 1993, Heath & Roff 1996, Tyson & Knight 2001). If activity costs of foraging for many, 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, 2002b). Foraging efficiency may also decrease below the optimal prey size as a result of reduced maneuverability of larger fish, reduced ability to retain small prey in the mouth and reduced ability to even see small prey (Persson 1987). Consequently, visually feeding fish, such as yellow perch (*Perca flavescens*), 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 to periodically switch

to larger benthic invertebrates, such as odonates and crayfish, until they grow large enough to switch to piscivory (Boisclair & Leggett 1989a). However, 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).

The energetic basis of prey-size selection, with regards to activity costs, was recently explored by Sherwood *et al.* (2002b). Activity costs were quantified by estimating white muscle glycolytic potential through measuring the activity of the glycolytic enzyme lactate dehydrogenase (LDH; Sherwood *et al.* 2002a, 2002b). White muscle anaerobic metabolism is thought to be involved in supplying energy to spontaneous burst movements, such as those used for attacking prey or escaping predators (Somero & Childress 1980). The flexibility of glycolytic enzymes, allows fish to acclimatize themselves to higher anaerobic needs; however, the tradeoff for higher glycolytic potential is the energetic cost of anaerobic metabolism, which is much higher than aerobic metabolism and leaves less energy available for growth (Goolish 1991, Jayne & Lauder 1994). Diet shifts to larger prey in yellow perch populations were accompanied by lowered LDH activity, indicating reduced fish activity costs and providing evidence for how diet shifts are important for growth efficiency (Sherwood *et al.* 2002b). In perch populations from metal-contaminated lakes where choice of benthic invertebrate prey was limited, LDH levels remained elevated and fish activity costs were implicated as the cause of the reduced growth rates of these populations (Sherwood *et al.* 2002a).

For centuries, metal smelting industries have had severe effects on aquatic and terrestrial ecosystems worldwide (e.g. Ek *et al.* 2001). Sudbury, Ontario (latitude 46° 37', longitude 80° 48'), is one such region where lakes have been subject to extensive acidification and high levels of metal deposition from industry emissions. Over time though, initially crude smelting processes were replaced by more efficient recovery methods (Keller 1992). Concentrations of metals such as copper, nickel and cadmium have declined, although they still remain high relative to estimates of probable effects levels for aquatic life. Nriagu *et al.* (1998) suggest that this is because lake watersheds

are saturated with metal deposits from the past 100 years of industry emissions. Mobilization of these metals during precipitation events sustains the high metal concentrations in the waters and sediments of lakes (Nriagu *et al.* 1998). Due to emission controls, average pH in most lakes has risen (Keller *et al.* 1999). Increasing pH generally improves water quality and has been thought to reduce metal exposure to aquatic organisms, as most metals are insoluble in neutral water, sorbing quickly to particles which sediment out of the water column (Schindler 1988). However, despite lower aqueous metal concentrations, an increase in pH may lead to an increase in metal *bioavailability* for aquatic organisms (Croteau *et al.* 2002). This is because hydrogen ions and some free metal ions compete for biological uptake sites; with increasing pH, the influence of declining hydrogen ion concentrations on organismal metal concentrations is greater than the influence of declining metal concentrations in the water (Croteau *et al.* 2002).

Continuing metal-contamination of lake sediments and waters is a concern as this undoubtedly still affects lake communities. Low species diversity at all trophic levels is characteristic of Sudbury lakes (Keller *et al.* 1999). Even at near neutral pH, lakes within about 20-30km of the Sudbury smelters have unusually simplified biological communities, notably the absence or scarcity of large benthic invertebrates such as molluscs, amphipods and crayfish (Keller *et al.* 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 (Heneberry 1997).

Our research explores lakes ranging in metal contamination from the Sudbury region in order to assess food web effects of metal pollution on the efficiency of energy transfer to fish. We predict that lakes with a higher degree of 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.
4. Resetting of LDH activities following well-defined diet shifts from planktivory to benthivory and from benthivory to piscivory.

This study will also assess whether results are consistent with what has been shown previously from another metal-contaminated region, Rouyn-Noranda, Quebec (latitude, longitude; Sherwood *et al.* 2002a, Kovecses & Rasmussen, in prep). If so, results may be generalized to other systems.

## Methods

### Study site

The five lakes chosen for this study were selected from a 15 lake survey of the Sudbury region conducted in the summer of 2001 (figure 1). Listed in table 1 are the chemical and physical characteristics of the five study lakes available from the literature. The lakes chosen are at various distances from the Sudbury smelters and encompass the range of metal contamination present in the region (table 2). All sampling took place in late June 2002.

Hannah and Middle Lakes are two of the most contaminated lakes in the Sudbury area, located only 6km south of one of Sudbury's largest smelting plants, Copper Cliff (figure 1). Both are part of the same watershed and have some shoreline houses and cottages on them. Both lakes were highly acidified and metal contaminated by the 1950's although they have been recovering since being limed in the 1970's, which successfully raised the pH to circumneutral levels and lowered the metal concentrations in the water column, although metal concentrations in the sediment remain very high (table 2). Because of the close proximity of Hannah and Middle Lakes to the smelting plants and the high sediment metal concentrations, these lakes are categorized 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*) and Iowa darters (*Etheostoma exile*). Small populations of golden shiners (*Notemigonus crysoleucas*) and northern red belly dace (*Phoxinus eos*) are also present in Middle Lake (Wright 1995).

Richard and Crowley Lakes are categorized here as intermediately contaminated lakes. Water metal concentrations are higher than government standards for aquatic life; however, they are not as high as in the highly contaminated lakes (table 2). Richard Lake is located on the outskirts of Sudbury and has some shoreline houses and cottages on it, whereas Crowley Lake is in a more remote area, but is still close to Sudbury (figure 1). The fish community in Richard Lake is considerably more diverse than Crowley Lake. Richard Lake has populations of largemouth bass (*Micropterus salmoides*), smallmouth bass (*Micropterus dolomieu*), northern pike (*Esox lucius*), pumpkinseeds (*Lepomis gibbosus*), white suckers (*Catostomus commersoni*), golden shiners and mudminnows



(*Umbra limi*) in addition to yellow perch. The fish community in Crowley Lake is similar to the most contaminated lakes, dominated by yellow perch with a small population of Iowa darters.

Geneva Lake, is located about 50 km northwest of Sudbury, upwind from industry emissions (figure 1), 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. In addition to yellow perch, Geneva Lake has a very diverse fish community including: walleye (*Stizostedion vitreum*), largemouth bass, smallmouth bass, northern pike, brook trout (*Salvelinus fontinalis*), lake trout (*Salvelinus namaycush*), pumpkinseeds, white suckers, brown bullhead, burbot (*Lota lota*) and a few species of darters and shiners.

### **Fish collection**

Each lake was sampled over one day. Yellow perch were caught using experimental gill nets, 1.5cm mesh minnow nets and rod and reel. Nets were set during the afternoon and evening, and were periodically checked for fish every 30-45 minutes. 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 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 (Le Cren 1947). Fulton's condition factor, a common bioenergetic performance indicator for fish, was calculated for all fish caught in each lake:

$$(1) \quad FCF = 100 * \text{weight}_{(g)} / (\text{length}_{(cm)})^3$$

Lake Memphemagog, an uncontaminated lake in the Eastern Townships of Quebec, is included in the condition factor analysis to provide another example of an unstressed perch population.

## **Invertebrate collection**

Benthic samples (~5-9) were taken from study lakes at the same time and location as the capture of fish. Samples were taken at different depths in and around macrophyte beds in order to encompass a variety of microhabitats. Kicknet samples were taken at 0.5m depths, and Ekman grabs were used for 1m and 2m depths. Kicknet samples were taken by one person holding the kicknet at one arms length and pulling it towards her toe. Kicknet samples encompassed an area of 0.50m by 0.40m and Ekman samples encompassed an area of 0.15m by 0.15m. A 10-15 minute horizontal plankton tow was conducted in the epilimnion of each lake, on the same day the fish were caught, using a zooplankton net (mesh size: 250  $\mu$ m). All samples were stored a few hours on ice prior to being frozen.

To characterize the benthic community composition of each lake, benthic samples were sorted using a dissecting microscope. Invertebrates were identified to order, counted, measured and dried in a drying oven at 55°C for 48 hours to obtain a dry weight measurement and to estimate the abundance and the percent weight that each invertebrate order accounts 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:

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

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 each size class were the same as those chosen by Boisclair & Leggett (1989b), which split the invertebrates into eleven size classes.

## **Perch diet composition**

Perch diet was determined from the thawed stomach contents of the same fish used for enzyme analysis. Individual prey items were identified to order, counted, measured and dried in a drying oven at 55°C for 48 hours to obtain a dry weight estimate of each order. If there were many empty stomachs, additional fish stomach contents were analysed in order to better characterize the diet of the population. The percent occurrence

of each prey taxa (percentage of fish with that prey taxa in their stomach) and the percent weight of each prey taxa (percentage of total stomach contents dry weight that prey taxa accounted for) were determined for each age class per lake. Those prey taxa with both a high percent occurrence (a highly common prey for perch) and a high percent weight (a highly profitable prey for perch), were deemed to be the most important prey for that age class in that lake (Costello 1990).

### **Stable isotope analyses**

Carbon ( $\delta^{13}\text{C}$ ) and nitrogen ( $\delta^{15}\text{N}$ ) stable isotope analysis, of the same fish selected for enzyme analysis, was performed to establish a more integrated characterization of diet. Isotopes were measured on dorsal white muscle tissue (just posterior to the dorsal fin) and also for pooled zooplankton and selected benthic invertebrates from benthic samples. All samples were dried in a drying oven at 55°C for 48 hours and ground into fine powder using a mortar and pestle. Samples were analysed using a mass spectrometer (G.G. Hatch Laboratories, University of Ottawa, ON). Stable carbon ( $\delta^{13}\text{C}$ ) and nitrogen ( $\delta^{15}\text{N}$ ) signatures are reported relative to a standard of Pee Dee belemnite and Atmospheric nitrogen, respectively, and are expressed as the parts per thousand (‰) deviation from the standard (Peterson & Fry 1987):

$$(3) \quad \delta^{13}\text{C} \text{ or } \delta^{15}\text{N} = ((R_{\text{sample}}/R_{\text{standard}})-1)*1000; R = {}^{13}\text{C}/{}^{12}\text{C} \text{ or } {}^{15}\text{N}/{}^{14}\text{N}$$

### **Lactate dehydrogenase (LDH) analysis**

Lactate dehydrogenase (LDH) activity was measured for ~45 fish 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-Optimized, Sigma Diagnostics®) 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 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 ( $X' = \log(X + 1)$ ) in order to meet requirements of normality and homoscedasticity for the valid application of all parametric analyses (Zar 1996). Mean perch, prey and invertebrate weights were compared using One-Way Analysis of Variance (ANOVA) followed by Tukey-Kramer multiple comparison tests ( $\alpha = 0.05$ ). Condition factor patterns were fit with both linear and polynomial models. Polynomial models were kept if including extra parameters produced a significantly better fit ( $F$  ratio test), given the cost of an extra degree of freedom (i.e. not simply if they produced a higher  $R^2$  value).

The significance of diet shifts for resetting perch LDH activity was determined using Analysis of Covariance (ANCOVA) with body weight as the continuous variable and diet categorized with two dummy variables defining the shifts from planktivory to benthivory and from benthivory to piscivory. ANCOVA models were compared to 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 plankton were present in stomach contents the perch was categorized as a planktivore, and if fish were present it was categorized as a piscivore. Perch with empty stomachs were not included in the ANCOVA analysis except for those from Crowley Lake and Richard Lake. For these lakes, perch with empty stomachs were assigned a diet category based on the similarity of their carbon isotope signature to those of perch with known stomach contents. This was not done for the remaining three lakes, as there was no clear pattern in the isotopic signatures of the fish. In these lakes, fish had signatures in between the pelagic and benthic signals, making it difficult to distinguish which fish were eating from the pelagic food chain and which from the benthic food chain.

## Results

### Benthic Invertebrate Community analysis

The mean diversity of the benthic invertebrate community for Geneva Lake and Richard Lake was significantly higher than Crowley Lake and Hannah Lake (table 3). There were no significant differences detected between lakes in the abundance of each order as the sample sizes were not sufficiently large enough given the high variability of the samples. Many benthic invertebrate taxa, such as gastropods, molluscs, leeches, amphipods and odonates, are not present in most of the contaminated lakes. No special effort was made to sample for crayfish (order Malacostraca); however, a survey on crayfish distribution in the Sudbury region (Errulat *et al.* 1992) found crayfish present in one of the intermediately contaminated lakes, Crowley Lake, but absent in the rest of the contaminated lakes, Richard, Middle and Hannah Lakes. Crayfish are present in the reference lake, Geneva Lake, as many were found in perch stomach contents in the present study.

Dipterans and trichopterans make up most of the invertebrate biomass in Hannah, Middle and Crowley Lakes (figure 2). These taxa are also important for the other contaminated lake, Richard Lake, however, amphipods and coleopterans also account for a large proportion of the total biomass. In the reference lake, Geneva Lake, odonates make up most of the percent weight, followed by trichopterans and ephemeropterans.

The distribution of benthic invertebrates from sediment samples among size classes differed between lakes (figure 3). The reference lake, Geneva Lake, was the only lake with invertebrates in all eleven size classes, although abundances of the largest size classes were low. The intermediate and the highly contaminated lakes had reduced size structure of benthic invertebrates. Crowley Lake's benthic community was composed of invertebrates from the first seven size classes and invertebrates from Richard Lake spanned size classes 2 through 8. Hannah Lake's invertebrates spanned size classes 2 through 7 and Middle Lake's were mostly between 2 and 6 with one large trichopteran falling into size class 9. Size classes 2, 3, 4 and 5 contained the majority of benthic invertebrates for all lakes, except Hannah Lake where the distribution of benthic invertebrates was bimodal with size classes 2, 3 and 6 having the highest abundances, a pattern driven by the presence of littoral and profundal dipterans, respectively.

## 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* (~30mm in length). In Crowley Lake, an intermediately contaminated lake, chironomids (~7mm) had a high percent occurrence for 2+ perch but did not make up much of the percent weight as this was dominated by a few large odonates (~17mm). Age 2+ perch in the other intermediately contaminated lake, Richard Lake, had a similar diet that was dominated by chironomids (~5mm) followed closely by odonates (~10mm) and amphipods (~4mm). Age 2+ perch in both the contaminated lakes rely on small benthic invertebrates, trichopterans (~5mm) in Middle Lake and chironomids (~5mm) in Hannah Lake. There do 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 continue to rely on these small benthic invertebrates. In the reference lake, Geneva Lake, the most important prey for 3+ perch is crayfish (~30-50mm). Perch older than 3+ were not caught in Geneva Lake. In Crowley Lake, 3+ and 4+ perch rely primarily on odonates (~20mm) and become largely piscivorous (~70mm) by age 5+. For Richard Lake, the most important prey for 3+ perch is fish (~40mm), which become even more important for 4+ and 5+ perch in this lake.

Overall, the average mass of individual non-zooplankton prey items (i.e. prey size) was significantly different between lakes (figure 4, table 5). Within each age class though, 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 that was about 3 times higher than all the 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 about 2-8 times greater than the rest of the lakes, but only significantly different from Hannah Lake, one of the contaminated lakes (table 5). The lack of significance between most lakes is due to the large range in prey size for all lakes. 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 increases 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 increases significantly between all three age classes. However, in the intermediate lakes, mean prey size is only significantly higher by age 5+ and when fish prey items are left out of the analysis, there is no significant increase in prey size with age in either Crowley ( $F_{4, 35} = 2.08, p = 0.10$ ) or Richard ( $F_{3, 26} = 0.99, p = 0.41$ ). There is no significant increase in prey size with age in both the contaminated lakes, Middle Lake and Hannah Lake (table 5).

### **Perch growth analysis**

The mean weights of the largest 15% of perch caught from the reference lake, Geneva Lake, and one of the intermediate lakes, Crowley Lake, are 2-3 times higher than perch from the other intermediate lake, Richard Lake. Additionally, the mean weights of the largest perch from Geneva, Crowley and Richard Lakes are 2-6 times higher than the largest perch from the contaminated lakes, Hannah Lake and Middle Lake (table 6).

Comparing the average perch weights across lakes at each age, 1+ perch from Geneva Lake are about 1.5 times heavier than 1+ perch in Richard and Hannah Lakes (figure 5, table 6). Mean weight in Geneva Lake is twice as high as perch in all the other lakes by age 2+ and 2-4 times higher by age 3+ (table 6). Perch in the intermediate and contaminated lakes are not significantly different from each other at age 1+ or age 2+. By age 3+ though, mean body weights of perch in the intermediate lake, Richard Lake, are 2 times higher than perch in both the contaminated lakes; although perch in the other intermediate lake, Crowley Lake, are only significantly larger than Hannah Lake perch. By age 4+, perch in both intermediate lakes are about 2-3 times heavier than perch in both contaminated lakes (table 6).

Comparing size at age within each lake, 1+ perch are significantly smaller than 2+ perch and 2+ perch are significantly smaller than 3+ perch in all lakes, although the

degree with which they differ is different for each lake (table 6). In Hannah, Middle and Richard Lakes perch are stunted, as there are no significant differences between the mean weights of the older age classes. In Crowley Lake though, 4-7+ perch are significantly larger than 3+ perch (table 6).

Perch from both Lake Memphemagog and the reference lake from Sudbury, Geneva Lake, show a general increase in condition factor with size (figure 6). In contrast, perch from the most heavily contaminated lakes, Hannah Lake and Middle Lake, show an overall decrease in condition as the perch get larger. Cubic models provided a significantly better fit than linear equations only for the intermediately contaminated lakes (using an  $F$  ratio test, not simply an observed increase in the  $R^2$  value; Crowley Lake  $F_{2, 173} = 10.10, p < 0.0001$ ; Richard Lake  $F_{2, 115} = 4.27, p = 0.05$ ). Comparing condition across lakes at each age shows that age 1+ perch from all lakes have a similar condition except for Crowley Lake where condition is significantly lower than all the other lakes ( $F_{4, 62} = 11.71, p < 0.0001$ ). At age 2+, Geneva Lake perch have significantly higher condition than perch in Crowley, Middle and Hannah Lakes, and Richard Lake perch have significantly higher condition than perch from Crowley and Middle Lakes ( $F_{4, 70} = 20.87, p < 0.0001$ ). Differences are even greater at age 3+, where Geneva Lake perch have significantly higher condition than perch from all the other lakes and Richard Lake perch condition remains significantly higher than perch from Crowley and Middle Lakes ( $F_{4, 49} = 24.44, p < 0.0001$ ).

### **Lactate dehydrogenase activity analysis**

Individual white muscle Lactate dehydrogenase (LDH) activity was plotted as a function of body size (figure 7). Fish were coded as either being planktivorous, benthivorous or piscivorous based on their stomach contents. 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  $R^2$  values; table 7). In the ANCOVA model for Geneva Lake, including the shift from planktivory (mostly daphnia 1-2mm in length) to benthivory (many kinds of insect larvae and crustaceans from 5-50mm 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 both the intermediate lakes, Crowley and Richard, the first diet shift from planktivory to benthivory was not a significant component in either ANCOVA model. Only the shift from benthivory (mainly dipterans and odonates about 7 and 17 mm in length, respectively) to piscivory (mainly perch from 50-80mm in length) at about 100g resulted in a significant downshift in LDH for perch in Crowley Lake ( $F$  ratio test,  $F_{1,46} = 7.14, p < 0.05$ ). Perch in Richard Lake become benthivorous (mostly dipterans, amphipods and odonates about 5, 4 and 10mm in length, respectively) starting at about 5g and switch to piscivory (darters about 40mm in length) at about 40g. The ANCOVA model for Richard Lake, including both diet shifts, was a significant improvement in fit over a simple linear regression ( $F$  ratio test,  $F_{2,34} = 6.71, p < 0.01$ ), however, the individual parameter coding for the shift to benthivory was not significant ( $T$  test, Prob.  $> |t| = 0.66$ ). Perch in Middle Lake switch from planktivory (daphnia of 1mm) to benthivory (dipterans of 4mm and trichopterans of 5mm) at about 6g and do not make a further switch to piscivory. Incorporating the shift to benthivory in an ANCOVA model 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 those from previous research in Rouyn-Noranda (Kovecses & Rasmussen, in prep.) and from many other studies on the effects of metal-contamination on invertebrate assemblages in lakes (Kraft & Sypniewski 1981, Rygg 1985, Hare 1992, Johnson *et al.* 1992, Gower *et al.* 1994, Clements *et al.* 2000), streams (Gaston *et al.* 1998) and estuaries (Beltman *et al.* 1998, Malmqvist & Hoffsten 1999).

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 are inedible for fish and would otherwise accumulate in the sediment. Diversity in the zoobenthos is important for energy transfer as each group specializes on a particular food source (i.e. shredders, algae grazers, deposit feeders, filterers...etc.; Covich *et al.* 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. On average, about 65% of fish diet originates either directly or indirectly from zoobenthic production, and zoobenthos averages 77% of total prey consumption by perch (Vadeboncoeur *et al.* 2002, Vander Zanden & Vadeboncoeur 2002). Therefore, the importance of a naturally diverse benthic prey base, particularly the availability of many size classes of benthic invertebrates, may not be trivial. The noted shift in zoobenthic species composition due to metal contamination is accompanied by a reduction in the size structure of available prey for fish. Figure 3 illustrates the absence of the top four size classes of benthic invertebrates in most of the contaminated lakes, whereas all four are present in the reference lake, Geneva Lake. We argue that this gap in prey size structure may have important energetic consequences for visual fish predators, such as yellow perch.

### **Limited prey choice for yellow perch in metal contaminated lakes**

Perch diet composition in polluted Sudbury lakes generally reflects what is available to them based on the benthic community analysis. In Geneva Lake and Crowley Lake, however, stomach contents of larger perch showed that the perch were preferentially selecting large ephemeropterans (*Hexagenia*) and malacostracans (crayfish) in Geneva and large odonates in Crowley, of which we found few or none in our benthic samples. This is because larger invertebrates tend to have lower abundance (Rasmussen 1993) and perch are most likely better at finding these invertebrates than are humans with kicknets or ekmans. Furthermore, prey taxa preferentially selected by perch in the reference lake (*Hexagenia* for 2+ perch and crayfish for 3+ perch), are those that are typically considered sensitive to metal contamination and were not found in either stomach contents or benthic samples from any of the other lakes.

Stomach contents analysis supports the second hypothesis that perch from more metal-contaminated lakes are forced to rely more heavily on smaller prey. The diet transition for Geneva Lake perch is to significantly larger zoobenthic prey, whereas in the intermediate and contaminated lakes there is no significant difference in the average size of zoobenthic prey items as perch age. Perch in the intermediate lakes eventually become piscivorous by age 5+, which accounts for the drastic and significant increase in prey size for older perch in these lakes.

The changes to diet transition patterns caused by metal contamination are remarkably consistent between Sudbury and Rouyn-Noranda lakes (Kovecses and Rasmussen *in prep*). Diet transition in reference lakes was very similar with perch switching from a zooplankton/dipteran diet at age 1+ to a diet dominated by large benthic invertebrates from ages 2+ to 4+ (mainly odonates and crayfish). Perch in these reference lakes become piscivorous at age 5+. A high taxonomic richness of zoobenthic prey was present here as it was for the Sudbury reference lake. The polluted lakes from Rouyn-Noranda were also remarkably similar to the most contaminated lakes in Sudbury. Perch would switch from zooplankton to feeding on dipterans and trichopterans but could not shift to large-bodied benthic invertebrates. Perch from one of the Rouyn-Noranda intermediate lakes, Bousquet Lake, had a similar diet transition to the reference lakes in

both regions, despite moderate concentrations of heavy metals. Perch from the other intermediate lake, Vaudray, had *Hexagenia* available to them and were eating little else. Unlike Sudbury though, perch from the intermediate lakes in Rouyn-Noranda did not appear to become piscivorous.

### **Failure to switch to large prey leads to stunted growth**

In accordance with hypothesis 3 and consistent with Rouyn-Noranda lakes, perch in the two highly contaminated Sudbury lakes are stunted. Furthermore, stunting occurs at the typical size where a shift to larger benthic prey or piscivory is expected. Interestingly, perch from the two intermediate lakes exhibit poor growth through this benthivorous size range as well. Comparing size at age, perch in all the contaminated and intermediate lakes are growing much slower than perch in the reference lake, Geneva Lake.

The decreasing trend in condition factor over the entire perch size spectrum in the contaminated lakes implies that smaller perch are better able to meet energy requirements than larger perch. This is most likely because available prey in these lakes (zooplankton and small dipterans and trichopterans) are suitable for small perch, but as the perch increase in size, there is no opportunity to exploit increasingly larger prey in order to compensate for increasingly higher energetic demands. This result is consistent with previous studies that have found how perch growth rate decreases as the proportion of small prey items in the diet simultaneously increases (Deihl 1993, Lott *et al.* 1996, Boisclair & Rasmussen 1996, Hjelm *et al.* 2000).

For the intermediate lakes, Richard and Crowley, the best model describing how condition factor changes with size was a cubic model. This suggests that over some parts of the perch size spectrum, conditions are such that perch grow in a manner resembling what occurs in the reference lakes. However, unlike the reference lakes, over some parts of the size spectrum, condition factor decreases. Between total lengths of about 7 to 13 cm, the size range where perch are typically benthivorous, condition factor declines but then increases again beyond this stage. This decline is similar to what occurs over this size range in the contaminated lakes and is most likely due to the unavailability of large benthic prey for perch to switch to and maintain a high foraging efficiency. Perch stop

growing after this size range in the most contaminated lakes, however, in Crowley Lake perch growth just slows down until they become piscivorous, when size at age and condition factor increase dramatically. In Richard Lake, size at age increases after the switch to piscivory at age 3+, but does not appear to have as fast rate of growth as in Crowley Lake. This may be due to differences in the availability of forage fish. Benthic resources in the intermediate lakes do not have as wide a size spectrum as in Geneva Lake, where perch are preferentially feeding on large bodied invertebrates (mayfly larvae and crayfish) and have large increases in size at age. Like perch in the highly contaminated lakes, perch in the intermediate lakes do experience a reduced net energy return rate from foraging on small benthos, but zoobenthic prey are not as limited as in the highly contaminated lakes, so perch eventually reach piscivory.

### **Perch benefit energetically from switching to larger prey**

In accordance with previous studies that use the activity of lactate dehydrogenase (LDH) in fish white skeletal muscle to estimate anaerobic glycolytic potential, the results of the present study show that glycolytic potential is highly variable but generally scales positively to body size (Childress & Somero 1990, Sherwood *et al.* 2002b). White muscle, an anaerobic tissue (Jayne & Lauder 1994) which accounts for about 95% of Percid muscle mass (Goolish 1991), powers the spontaneous burst of energy required for a fish to pursue, attack and capture prey or to escape predators (Somero & Childress 1980). Anaerobic metabolism is an inefficient way to meet energetic demands and is only invoked when the energy demand cannot be supplied aerobically (Goolish 1991).

Many studies have attributed the positive scaling of LDH with body size to the need for increased muscle *power* in order to accelerate a larger fish against higher drag forces (Somero & Childress 1980, Sullivan & Somero 1980, Childress & Somero 1990, Goolish 1991). However, the results of the present LDH analysis also support previous findings on the effect of diet ontogeny on LDH activity (Sherwood *et al.* 2002a, 2002b). Although LDH activity tended to increase rapidly with body size in each lake, complete diet shifts resulted in a decrease in LDH activity, effectively resetting the energy demands of feeding. This resetting of LDH is attributed to a lower need for glycolytic potential due to the sharp decline in the number of burst swimming prey attacks required once prey

size becomes much larger. It is more energetically profitable for a large fish to capture a few large prey items rather than 100's of small actively-mobile ones, as it minimizes the number of costly, anaerobic burst swimming attacks (Sherwood *et al.* 2002a, 2002b). Therefore, the positive allometry of LDH activity may be due to the need for increased burst swimming *frequency* rather than the need for increased muscle *power*. This is simply because larger fish require more food to meet higher metabolic costs, and if prey size cannot be increased then the number of prey captured must increase and therefore glycolytic potential must increase to meet rising anaerobic demands.

In Middle Lake, one of the most contaminated lakes, LDH scaled significantly with body size; however, categorizing 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. Additionally, fish of all sizes have similar isotopic signatures, suggesting that that even the largest perch in Middle Lake continue to rely on plankton for at least part of the year. This 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). The LDH pattern for the other contaminated lake, Hannah Lake, does appear to scale positively with body size until the perch reach 10 grams where it becomes quite variable. Perch carbon isotopic signatures also become quite variable above 10 grams, implicating diet as the cause for the sudden variability in the LDH; however, the exact reasons for this are unclear as perch of all sizes were eating mostly chironomids and trichopterans, making it impossible to categorize the perch into diet categories. The lack of complete diet shifts in these highly contaminated lakes may explain why there is no clear resetting of activity levels, the steady decline in condition factor as the perch grow larger and, ultimately, why these populations are stunted. Like perch populations from the reference lakes in Rouyn-Noranda (Sherwood *et al.* 2002a) and the lakes in the Eastern Townships of Quebec (Sherwood *et al.* 2002b), perch from Geneva Lake showed significant resetting of LDH following diet shifts. However, only the shift from planktivory to benthivory significantly reset LDH activities. This is as expected since stomach contents data indicated that 3+ perch (the oldest perch we caught) had not yet become exclusively

piscivorous. For both the intermediate lakes, Richard and Crowley, 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 models for both these lakes, 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 (like in the highly contaminated lakes) as the perch eventually grow through this stage and reach piscivory. This explanation is also supported by the decrease in condition factor in these lakes during benthivory and 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 trichopterans) as in the highly contaminated lakes.

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 and an increase in condition factor through benthivory and it was the only lake where there was an increase in the size of benthivorous prey between ages. This suggests that the availability of a large size range of benthic invertebrates (especially the large bodied mayfly larvae and crayfish) is important for resetting fish activity costs and ultimately maintaining high rates of fish growth.

### **Energy available for growth depends on activity costs**

Stunting in perch populations is a well-documented phenomenon that is often attributed to resource limitation due to low zoobenthic production (Persson 1987, Rask 1993, Diehl 1993, Heath & Roff 1996) or high perch densities (Hansson 1985). However, there is evidence that the mechanism that causes stunting in perch may be related to how much energy is expended for activity metabolism rather than simply a reduced daily ration.

Fish foraging costs have previously been thought to be incurred at two distinct stages: the search for prey (relating to prey abundance) and prey handling (relating to

prey size) (Boisclair & Leggett 1989b). Steady, routine swimming, such as what a fish would use to search for prey, is an aerobic activity using exclusively red muscle fibers (Jayne & Lauder 1994). The manipulation and the digestion of prey are also considered aerobic activities (Goolish 1991). However, unsteady, burst swimming, such as that which fish use to attack prey or to escape from predators, is an anaerobic activity, which is much more costly than aerobic activity as it uses energy obtained from the inefficient, but quick, glycolytic pathway (Goolish 1991, Jayne & Lauder 1994). There is evidence to suggest 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 this compromises the amount of energy left over 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 the growth rate of perch decreases as the proportion of small prey items in the diet simultaneously increases (Deihl 1993, Lott *et al.* 1996, Boisclair & Rasmussen 1996, Hjelm *et al.* 2000). Furthermore, Boisclair & Leggett (1989c) found that although perch growth rates declined as fish density increased, there was no relationship between the quantity of food consumed and fish density. They suggested that as fish density rose, non-exploitative (interference) interactions decreased perch growth through increased activity costs, and that this was a more plausible explanation than exploitative competition reducing the quantity and quality of food consumed. 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. The difference between fast growing and stunted perch populations occurs at the level of active metabolism, not at the level of consumption.

Figure 8 illustrates the idea that perch will have a maximal foraging efficiency on a particular prey size at a certain body size. Foraging efficiency refers to the energy from consumption left over for growth once all other metabolic costs (e.g. standard metabolic rate, activity costs, excretion, etc.) have been met. If all other metabolic costs, including



the activity costs of foraging, equal 100% of the amount of energy consumed, then there will be no energy left over for growth and the perch will stop growing (stunt). Below the optimal body size for feeding on a particular prey size, foraging efficiency is thought to be low due to the need for a greater swimming capacity or gape size to capture prey (Persson 1987). Above the optimal body size for feeding on a particular prey size, the amount of energy left over for growth decreases as a result of increased activity costs due to the need to capture a greater number of prey. Ideally, when many, different sized prey are present in a lake, perch will optimize their energy available for growth by switching their diet to larger and larger prey items as they grow (figure 8a). In this way, perch maintain high growth rates throughout their lives and quickly become large as they only experience small and short declines in the percent of energy left over for growth. A gap in the available size classes of benthic prey, will slow the rate of growth down through the shift to piscivory until the perch reach the normal size that perch become piscivorous, when growth should return to normal (figure 8b). This period of slow growth constitutes what is known as a growth bottleneck (Heath & Roff 1996, Hjelm *et al.* 2000, Sherwood *et al.* 2002a, 2002b). Stunted perch populations result from a gap in the prey size structure that is large enough that perch activity costs leave no energy left over for growth (figure 8c).

Metal contamination of lakes creates gaps in the prey size structure, producing the patterns in perch growth as described above. The perch in the intermediate lakes experience reduced growth and a decline in condition through the size range in which perch are typically benthivorous. The absence of large bodied invertebrates, such as crayfish and mayfly larvae, in these intermediately contaminated lakes, may be the cause of this growth bottleneck. In addition to the large invertebrates, there was also an absence or low abundance of intermediately sized prey, such as amphipods and odonates in the most contaminated lakes. Perch in these lakes stunted after experiencing very low growth rates and a sharp decline in condition factor.

Relative to perch from the reference lake, perch from metal contaminated lakes do not benefit as much energetically from switching to benthic prey (in terms of lowering activity costs), thus their growth is slow. Only the perch population from the reference lake showed a significant resetting of LDH activity following the shift to benthivory.

This may be because the absence of large benthic invertebrates in the contaminated lakes causes perch to quickly outgrow any lowering of activity costs switching to small benthic prey which are not much larger than zooplankton. Given the variation in the LDH data, a small resetting of LDH activity may not be evident. It is also possible, at least for the highly contaminated lakes, that the apparent shift to benthivory was not a complete shift and that the perch continue to periodically rely on plankton. Stable isotope ratios for perch from Hannah Lake and Middle Lake suggest a combined pelagic and benthic influence and when Hannah Lake was sampled the previous year, at the same time of the season, perch of all sizes were eating zooplankton (personal observation).

Perch from the intermediately contaminated lakes appear to eventually make it through the slow growing benthivorous stage and become piscivorous. This diet change is accompanied by a simultaneous lowering of LDH activity and an increase in growth rate, possibly because of lower activity costs. Perch caught from the reference lake had not yet switched to piscivory despite the fact that they reached sizes larger than some of the piscivorous perch from the intermediate lakes. This may be because the presence of large invertebrate prey increases the optimal size at which perch should switch to piscivory ( $S_p$ , figure 8a,b). 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).

### **Direct vs. indirect effects of metal contamination on fish**

The reduced growth rates at our contaminated sites could also be the result of allocating energy to remedy any direct effects of metals on physiological functions. Wild caught perch from metal-impacted lakes in Rouyn-Noranda have impaired cortisol stress response to capture, an indication of chronic, sublethal contaminant stress (Brodeur *et al.* 1997). Perch from these same lakes also have increased concentrations of metallothioneine, a metal binding and detoxifying protein, in their livers and kidneys (Laflamme *et al.* 2000). Recent laboratory studies on yellow perch caught in indicate that perch in Sudbury lakes also suffer the same metabolic costs of heavy metal exposure (Rajotte & Couture 2002, Audet & Couture 2003, Gagnon & Hontela pers. comm.).

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). Furthermore, knowledge of mechanisms is incomplete and some mechanisms may not yet be discovered (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 & Rasmussen, in prep.).

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 no indirect effects of prey size yet, versus at age 3+, when the differences in food web structure 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 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, results show that there was no significant difference of age 1+ perch prey size between lakes.

The environmental conditions in which an organism lives are crucial for its ability to deal with exposure to any contaminant (Beyers *et al.* 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 not only be suffering from high activity costs, but also from high body concentrations of metals. This may be an alternative explanation for 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 perch did not.

### **Food web mediated effects of other anthropogenic disturbances**

These patterns of indirect, food web mediated effects on the energetics of yellow perch are not restricted to metal-contaminated lakes. Similar patterns have been described for perch populations subject to other forms of anthropogenic disturbance that simplify food web structure such as eutrophication, species introductions and acidification.

The increased inputs of detritus to sediments following eutrophication often cause deoxygenation of the sediments and the invertebrate community to become dominated by small, anoxia tolerant chironomids and oligochaetes. Furthermore, the base of the food web leading to top trophic level fish switches from being dominated by benthic periphyton and macrophytes in oligotrophic lakes to being dominated by pelagic phytoplankton in eutrophic lakes (Vadeboncoeur *et al.* 2001). Benthic algal production provides crucial food and refuges for benthic invertebrates so a shift to pelagic production may also explain why small deposit feeders dominate the invertebrate community in eutrophic lakes as opposed to large-bodied grazers, shredders and scrapers (Vadeboncoeur *et al.* 2001). Hayward and Margraf (1987) noted lower growth rates of perch inhabiting the eutrophic western basin of Lake Erie, coinciding with a heavier reliance on small prey. The loss of the large-bodied prey in eutrophic lakes in the Eastern

Townships of Quebec was linked to increased activity rates in perch, leaving less energy for growth (Boisclair & Rasmussen 1996). Schaeffer *et al.* (2000) suggested that eutrophic conditions in Saginaw Bay, Lake Huron, shifted the lake food web from being benthic to pelagic-based, 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 in Saginaw Bay caused stunting of older perch, which reached a size threshold of 15-18cm (Schaeffer *et al.* 2000). In a study on fish communities among small, shallow Danish lakes, Jeppesen *et al.* (2000) found increased abundances of planktivorous fish as lakes become richer and macrophyte beds disappear. As adult perch are forced to rely more heavily on plankton in these lakes, they progressively become less abundant as they tend to lose out in competition with cyprinids, which are much more efficient at pelagic foraging (Jeppesen *et al.* 2000).

Species introductions can also modify energy flows through food webs with consequences for top trophic levels. For example, introduced bass reduce densities of forage fish, forcing lake trout to feed on zooplankton and benthic invertebrates to the point where the trout exhibit reduced growth (Vander Zanden *et al.* 1999). Interestingly, the food web effects of eutrophication have often been reversed (i.e. switched back to a benthic-based food web) following invasions of bivalves. For example, after the introduction of the exotic zebra mussel (*Dreissena polymorpha*) to Lake Erie, there was 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). Other studies have noted increases in zoobenthic abundance and diversity in response to enhanced benthic habitat complexity and biodeposition by introduced bivalves (Ricciardi *et al.* 1997) and the resultant increase in top trophic level production (both fish and birds) (Phelps 1994, Thayer *et al.* 1997).

Although much less studied, the growth response of yellow perch to lake acidification shows a similar pattern. Acidification causes the loss of several benthic invertebrate taxa that are important for perch dietary development, particularly amphipods, crayfish and mayfly larvae (Schindler *et al.* 1991, Lonergan & Rasmussen 1996). As such, littoral benthic invertebrate communities in acidified lakes are largely dominated by acid-tolerant chironomid species. In 1980, Ryan and Harvey documented

stunted perch populations in many of the acidified La Cloche Mountain lakes of Killarney Park, Ontario. Since then, some lakes have recovered to approximately their pre-industrial pH levels due to atmospheric pollution reductions (Snucins *et al.* 2001). Despite apparent chemical recovery, many of these lakes still support only large populations of stunted perch, as the zoobenthic community has not yet recovered.

## Conclusions

Many forms of anthropogenic disturbances are transmitted to lake sediments and directly or indirectly affect freshwater food webs (Lake *et al.* 2000). Exacerbating this problem is the observation that benthic biota have a low resistance to disturbance and communities take a long time to recover (Palmer *et al.* 1997). Some of the most sensitive species to a variety of contaminants are those that are vital to the growth of perch. Thus, indirect, food web mediated effects causing stunting of perch populations is a widespread and common occurrence. The results of the present study on metal-contaminated lakes in the Sudbury region are consistent with what has been shown previously for metal-contaminated lakes in Rouyn-Noranda (Sherwood *et al.* 2002a, b, Kovecses & Rasmussen in prep.). As these regions differ in history, geology, climatology, and have been impacted by slightly different emissions, the possibility exists that results may be generalized to other systems.

Clearly, simplification of the benthic invertebrate community affects ecosystem processes. The present study has focused on the functional role that benthic biodiversity plays in transferring energy from detritus and primary producers to top trophic levels, and how this function is disturbed by metal contamination. The loss of benthic biodiversity may have also compromised other ecosystem processes such as nutrient cycling, bioturbation of the sediment and the decomposition of organic matter. Indeed, Schultheis *et al.* (1997) showed that copper contamination in a stream altered the abundance and the taxonomic composition of the invertebrate community, ultimately causing reduced leaf decomposition rates. Benthic biota are a vital part of freshwater ecosystems and management aimed towards protecting benthic community structure will also protect the processes that help maintain the quality of surface waters and the production of fisheries.

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

Lake	pH	Alk. (mg/L CaCO <sub>3</sub> )	DOC (mg/L)	Ca (µg/L)	Area (ha)	Max depth (m)	Mean depth (m)	Distance fm Sudbury (km)
Hannah	7.2 <sup>2</sup>	14.9 <sup>2</sup>	4.9 <sup>2</sup>	11060.7 <sup>2</sup>	27.2 <sup>3</sup>	8.5 <sup>3</sup>	4.0 <sup>3</sup>	6
Middle <sup>3</sup>	6.8	7.2	3.2	11100.0	28.0	15.0	2.0	6
Richard <sup>3</sup>	7.1	18.2	2.1	11900.0	79.4	9.5	3.9	9
Crowley	6.4 <sup>2</sup>	5.1 <sup>2</sup>	4.2 <sup>2</sup>	2509.8 <sup>2</sup>	42.1 <sup>3</sup>	16.0 <sup>3</sup>	6.4 <sup>3</sup>	12
Geneva	6.6 <sup>2</sup>	8.2 <sup>2</sup>	7.2 <sup>2</sup>	3022.2 <sup>2</sup>	356.4 <sup>1</sup>	25.3	6.3 <sup>1</sup>	53

<sup>1</sup>Data from: Carbone *et al.* 1998

<sup>2</sup>Data from: Couture pers. Comm.

<sup>3</sup>Data from: OMOEE 1990-1991

**Table 2:** Metal concentrations in the water and sediment of the study lakes and the Canadian government's probable effect levels (PEL) for aquatic life.

Lake	Water ( $\mu\text{g/L}$ )				Sediment ( $\mu\text{g/g}$ )		
	Al	Cd	Cu	Ni	Cd	Cu	Ni
Hannah <sup>1</sup>	210.5	0.5	74.8	174.8	2.7	1051.2	1092.5
Middle <sup>2</sup>	10.0	0.3	21.0	250.0	-	-	-
Richard <sup>2</sup>	28.0	0.2	14.0	120.0	-	-	-
Crowley <sup>1</sup>	52.5	0.2	15.6	73.2	1.9	568.8	550.0
Geneva <sup>1</sup>	18.5	0.0	1.1	4.5	1.6	49.4	98.9
PEL <sup>3</sup>	100	0.017	2-4	25-150	3.5	197	-

<sup>1</sup>Data from: Couture pers. comm.

<sup>2</sup>Data from: OMOEE 1990-1991

<sup>3</sup>Data from: Canadian Council of Ministers of the Environment. 1999. Canadian Environmental Quality Guidelines

- Data not available

**Table 3:** The Mean abundance per square meter ( $\pm$  standard error of the mean) of benthic invertebrate orders and mean Shannon-Weiner's index of diversity ( $H'$ ) for the sediment samples. Numbers in brackets are the 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	109.9 $\pm$ 24.2	0.0	588.1 $\pm$ 295.6	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	708.5 $\pm$ 254.9	2237.8 $\pm$ 1198.5	1816.0 $\pm$ 1168.0	1755.5 $\pm$ 931.8	1537.7 $\pm$ 569.7
Ephemeroptera	93.2 $\pm$ 27.2	5.0 $\pm$ 0.0	222.2 $\pm$ 133.3	126.7 $\pm$ 6.67	0.0
Gastropoda	106.9 $\pm$ 40.8	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	147.5 $\pm$ 73.8	16.7 $\pm$ 7.3	49.4 $\pm$ 21.5	133.3 $\pm$ 0.0	79.1 $\pm$ 50.08
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	111.6 $\pm$ 44.2	188.7 $\pm$ 112.7	151.0 $\pm$ 43.7
$H'$	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

**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 percent occurrence in perch stomach contents and percent weight (mg dry) of total stomach contents.

Lake	Age class	Prey taxa	% Occurrence	% Dry weight	n
Hannah	1+	Zooplankton	54.5	63.8	11
	2+	Diptera	63.6	18.3	3
	3+	Diptera	76.9	20.0	10
		Trichoptera	53.8	10.9	
		Diptera	85.7	56.6	
	4-5+	Trichoptera	57.1	9.3	7
Middle	1+	Zooplankton	83.3	86.4	18
	2+	Trichoptera	71.4	22.9	7
		Odonata	28.6	69.8	
	3-4+	Trichoptera	80.0	46.5	5
Richard	1+	Diptera	66.7	75.9	6
		Zooplankton	50.0	16.4	
	2+	Diptera	66.7	37.1	12
		Amphipoda	41.7	28.6	
		Odonata	33.3	31.7	
		Fish	42.8	78.9	
	3+	Fish	42.8	78.9	7
	4-5+	Fish	66.7	96.0	3
Crowley	1+	Zooplankton	100.0	90.7	7
	2+	Diptera	77.8	9.4	11
		Odonata	22.2	82.0	
	3-4+	Odonata	57.1	66.8	7
	5-7+	Fish	83.3	96.2	6
Geneva	1+	Zooplankton	83.3	85.9	6
	2+	Ephemeroptera	38.5	43.6	13
	3+	Malacostraca	35.3	81.2	17

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

Age	Geneva	Crowley	Richard	Middle	Hannah	$F$ ratio	$p$
All	26.89 $\pm$ 12.60 (59) <b>a</b>	56.93 $\pm$ 24.70 (46) <b>a</b>	4.86 $\pm$ 4.29 (35) <b>ab</b>	1.28 $\pm$ 0.61 (32) <b>b</b>	12.40 $\pm$ 3.15 (15) <b>b</b>	$F_{4,212} = 5.65$	0.0002
1+	0.31 $\pm$ 0.13 (12) <b>a</b>	0.06 $\pm$ 0.02 (3) <b>ab</b>	0.42 $\pm$ 0.21 (5) <b>a</b>	0.16 $\pm$ 0.03 (15)	0.49 $\pm$ 0.34 (11)	$F_{4,75} = 1.62$	0.18
2+	8.96 $\pm$ 3.07 (28) <b>b / a</b>	2.90 $\pm$ 2.29 (17) <b>a / b</b>	2.52 $\pm$ 1.31 (17) <b>ab / ab</b>	2.52 $\pm$ 1.91 (9) <b>ab</b>	0.08 $\pm$ 0.03 (4) <b>ab</b>	$F_{4,85} = 3.38$	0.013
3+	66.66 $\pm$ 35.81 (20) <b>c / a</b>	8.57 $\pm$ 8.45 (6) <b>ab / ab</b>	25.01 $\pm$ 10.79 (10) <b>ab / ab</b>	2.18 $\pm$ 1.31 (7) <b>ab</b>	8.97 $\pm$ 8.51 (16) <b>b</b>	$F_{4,55} = 4.09$	0.006
4+	NA	21.32 $\pm$ 12.25 (9) <b>ab</b>	27.39 $\pm$ 27.10 (2) <b>ab</b>	0.80 (1)	3.72 $\pm$ 3.07 (11)	$F_{3,19} = 0.95$	0.44
5+	NA	79.22 $\pm$ 42.93 (8) <b>b</b>	83.64 (1) <b>b</b>	NA	9.58 $\pm$ 9.31 (3)		
6 -7+	NA	564.02 $\pm$ 217.80 (3) <b>c</b>	NA	NA	NA		
$F$ ratio	$F_{2,57} = 10.66$	$F_{5,40} = 10.15$	$F_{4,30} = 4.35$	$F_{3,28} = 2.11$	$F_{4,40} = 0.90$		
$p$	0.0001	< 0.0001	0.007	0.12	0.47		

NA - Not Applicable

**Table 6:** Mean body weight (mean g wet weight  $\pm$  standard error of the mean; sample sizes in brackets) of the largest 15% of perch caught and the mean body weights of the first four age classes are compared across lakes. The  $F$  ratios and  $p$  values for these comparisons are in the two right hand columns. Entries followed by the same letter in bold type (**a**, **b**, **c**, **d**) are not significantly different from each other (one-way ANOVA within row followed by a Tukey-Kramer multiple comparison test). Mean perch body weight is also compared between ages within each lake. The  $F$  ratios and  $p$  values for this comparison is in the bottom two rows of the table. Entries followed by the same letter in normal type (a, b, c, d, e) are not significantly different from each other (one-way ANOVA within column followed by a Tukey-Kramer multiple comparison test).

Age	Geneva	Crowley	Richard	Middle	Hannah	$F$ ratio	$p$
Top 15%	77.36 $\pm$ 4.41 (19) <b>a</b>	91.67 $\pm$ 15.27 (27) <b>a</b>	37.29 $\pm$ 2.72 (18) <b>b</b>	20.97 $\pm$ 0.84 (15) <b>c</b>	15.94 $\pm$ 0.32 (27) <b>c</b>	$F_{4, 101} = 80.61$	< 0.0001
1+	6.49 $\pm$ 0.87 (7) a / <b>a</b>	4.20 $\pm$ 0.42 (9) a / <b>ab</b>	3.44 $\pm$ 0.37 (16) a / <b>b</b>	4.37 $\pm$ 0.33 (18) a / <b>ab</b>	4.00 $\pm$ 0.26 (17) a / <b>b</b>	$F_{4, 62} = 4.64$	0.0024
2+	22.25 $\pm$ 2.42 (17) b / <b>a</b>	10.66 $\pm$ 0.67 (16) b / <b>b</b>	10.96 $\pm$ 0.73 (17) b / <b>b</b>	10.86 $\pm$ 0.82 (18) b / <b>b</b>	7.90 $\pm$ 0.98 (7) b / <b>b</b>	$F_{4, 70} = 17.12$	< 0.0001
3+	67.88 $\pm$ 5.89 (16) c / <b>a</b>	24.88 $\pm$ 3.51 (8) c / <b>bc</b>	32.95 $\pm$ 5.07 (9) c / <b>b</b>	15.13 $\pm$ 0.92 (8) c / <b>cd</b>	13.51 $\pm$ 0.90 (13) c / <b>c</b>	$F_{4, 49} = 46.23$	< 0.0001
4+	NA	53.64 $\pm$ 11.08 (7) d / <b>a</b>	39.90 $\pm$ 6.30 (4) c / <b>a</b>	21.50 $\pm$ 0.92 (10) d / <b>b</b>	15.79 $\pm$ 1.17 (8) c / <b>b</b>	$F_{3, 25} = 25.69$	< 0.0001
5+	NA	84.53 $\pm$ 17.39 (3) de	44.70 $\pm$ 2.90 (2) c	27.10 (1) cd	13.00 (1) bc		
6+	NA	230.10 (1) e	42.60 (1) c	NA	NA		
7+	NA	198.93 $\pm$ 66.66 (4) e	NA	NA	NA		
$F$ ratio	$F_{2, 37} = 88.46$	$F_{6, 41} = 69.48$	$F_{5, 43} = 66.35$	$F_{4, 50} = 74.35$	$F_{4, 41} = 56.72$		
$p$	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001		

NA - Not Applicable

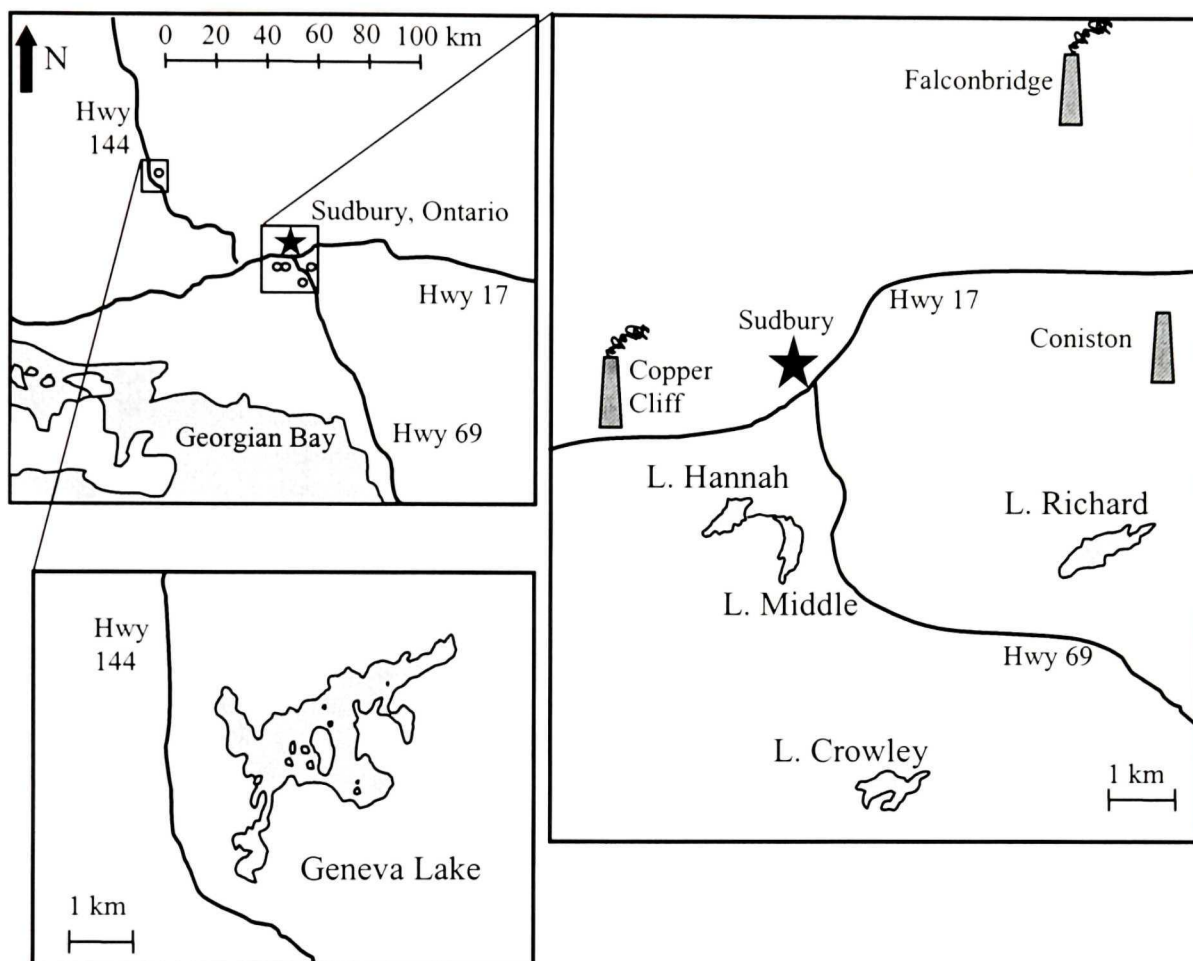
**Table 7:** Summary of results for lactate dehydrogenase activity analysis.

Lake	Model	Equation parameters				Adj. R <sup>2</sup>	F ratio	Prob.>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	2.48	0.12	NA	0.03	0.64	$F_{2,46} = 43.75$	<0.0001	49
Richard	Linear	2.48	0.06	NA	NA	0.27	$F_{1,36} = 14.47$	0.0005	38
	ANCOVA	2.40	0.13	-0.01 <sup>ns</sup>	0.05	0.44	$F_{3,34} = 10.89$	<0.0001	38
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							

NA - Not Applicable

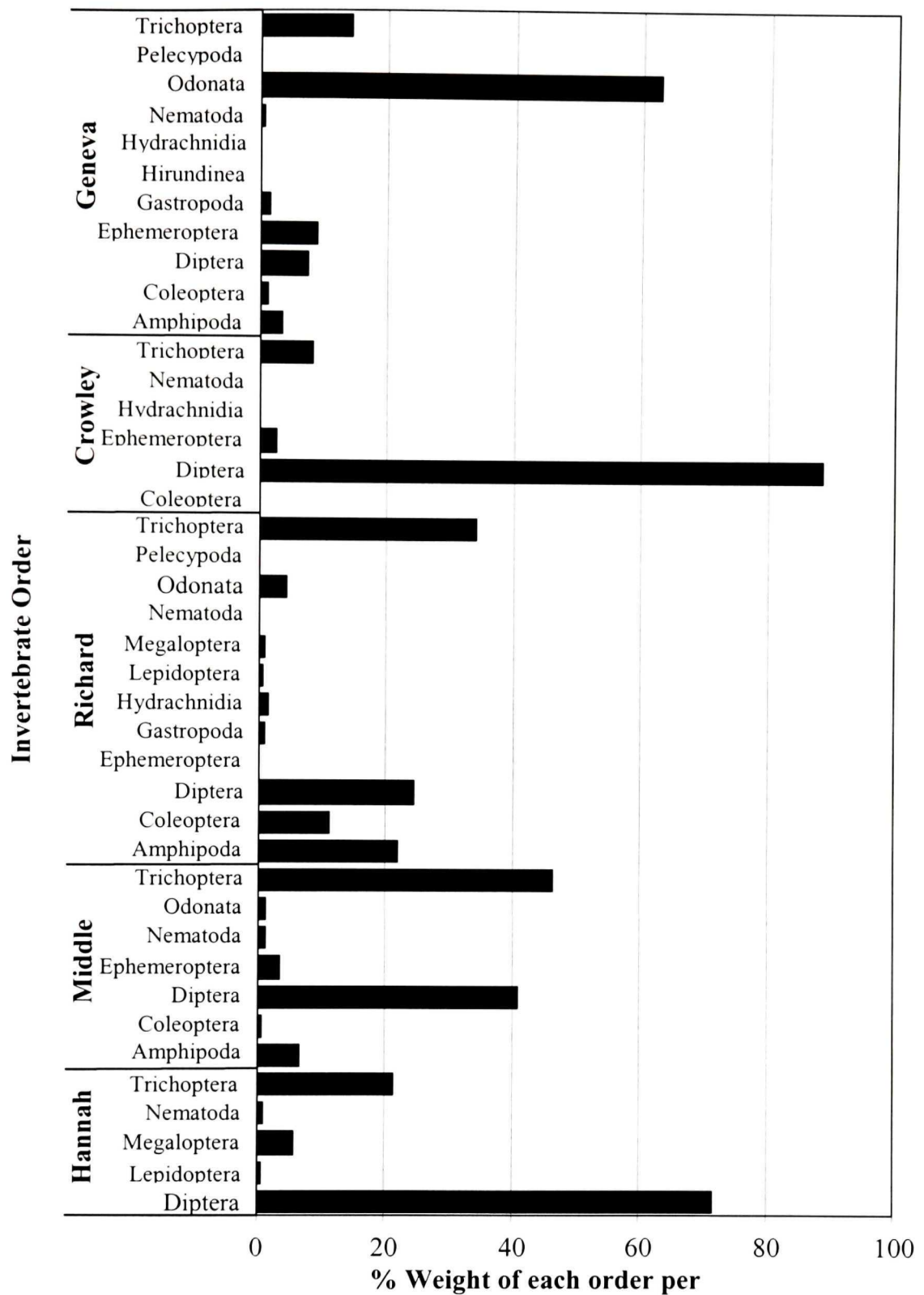
Polynomial equations are  $\log\text{LDH} = a + b \cdot \log W$  for linear regression, and  $\log\text{LDH} = a + b \cdot \log W - c - d$  for ANCOVA where  $c$  and  $d$  are dummy variables coding for diet shifts from planktivory to benthivory, and benthivory to piscivory, respectively.

ns - model term is not significant



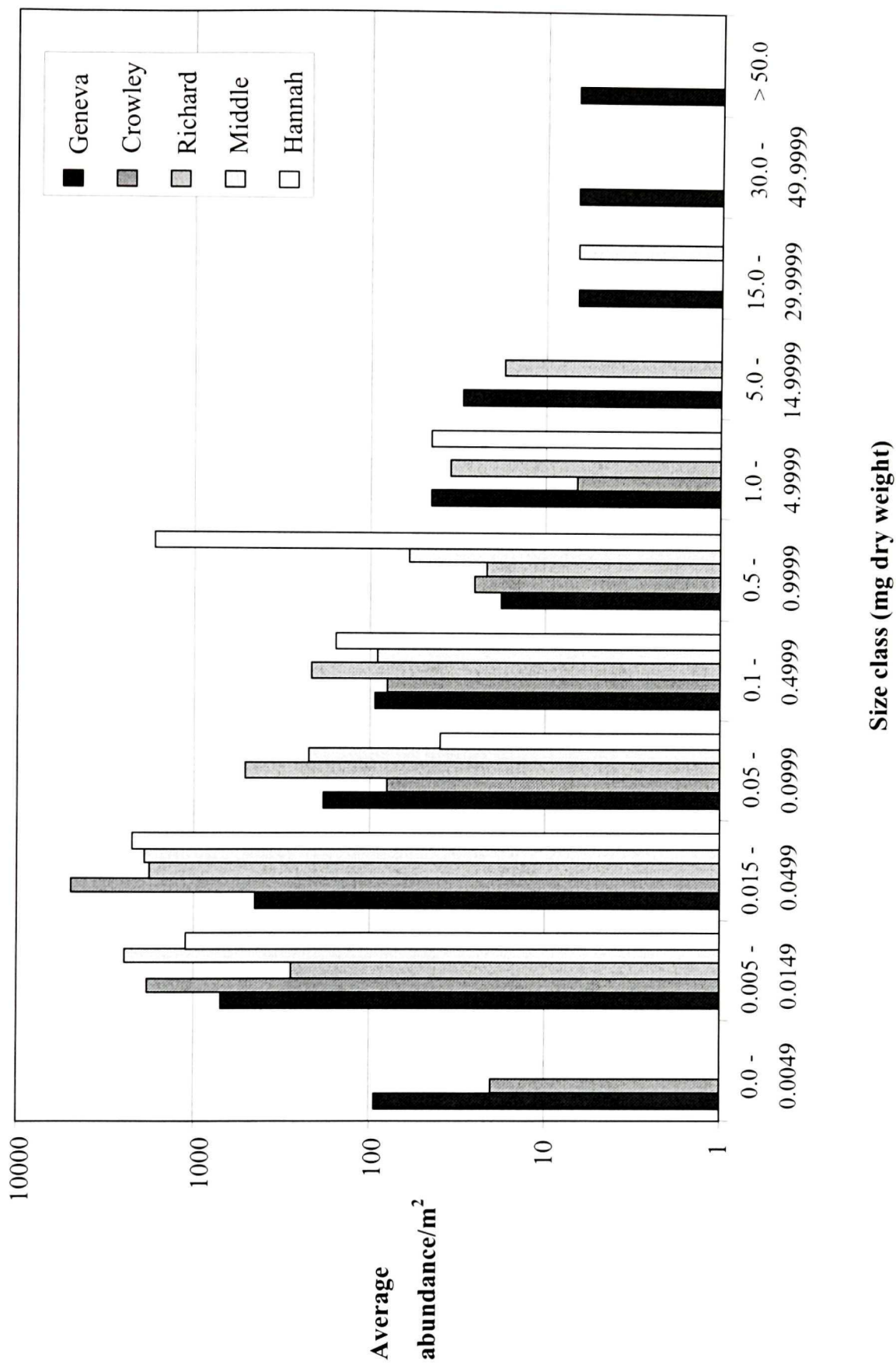
**Figure 1:** Location of the five study lakes in relation to the city of Sudbury and the main smelting centers, Copper Cliff, Falconbridge and Coniston. The most frequent wind directions are from north to south through the winter months (December till April), from southwest to northeast during the summer (May till September) and from south to north in the fall (October and November).

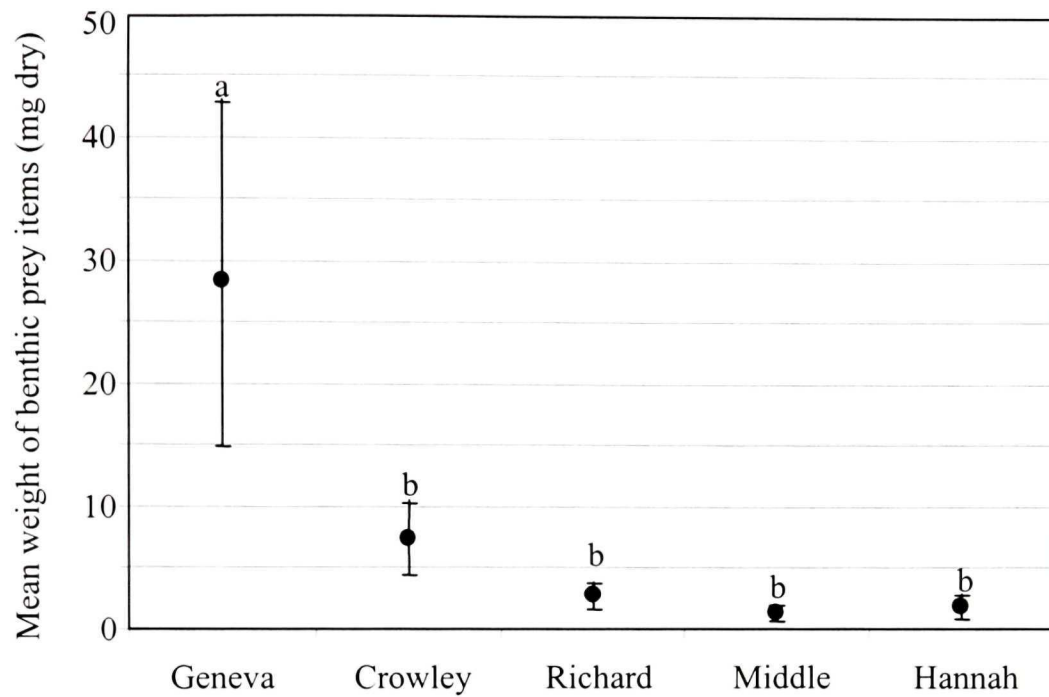




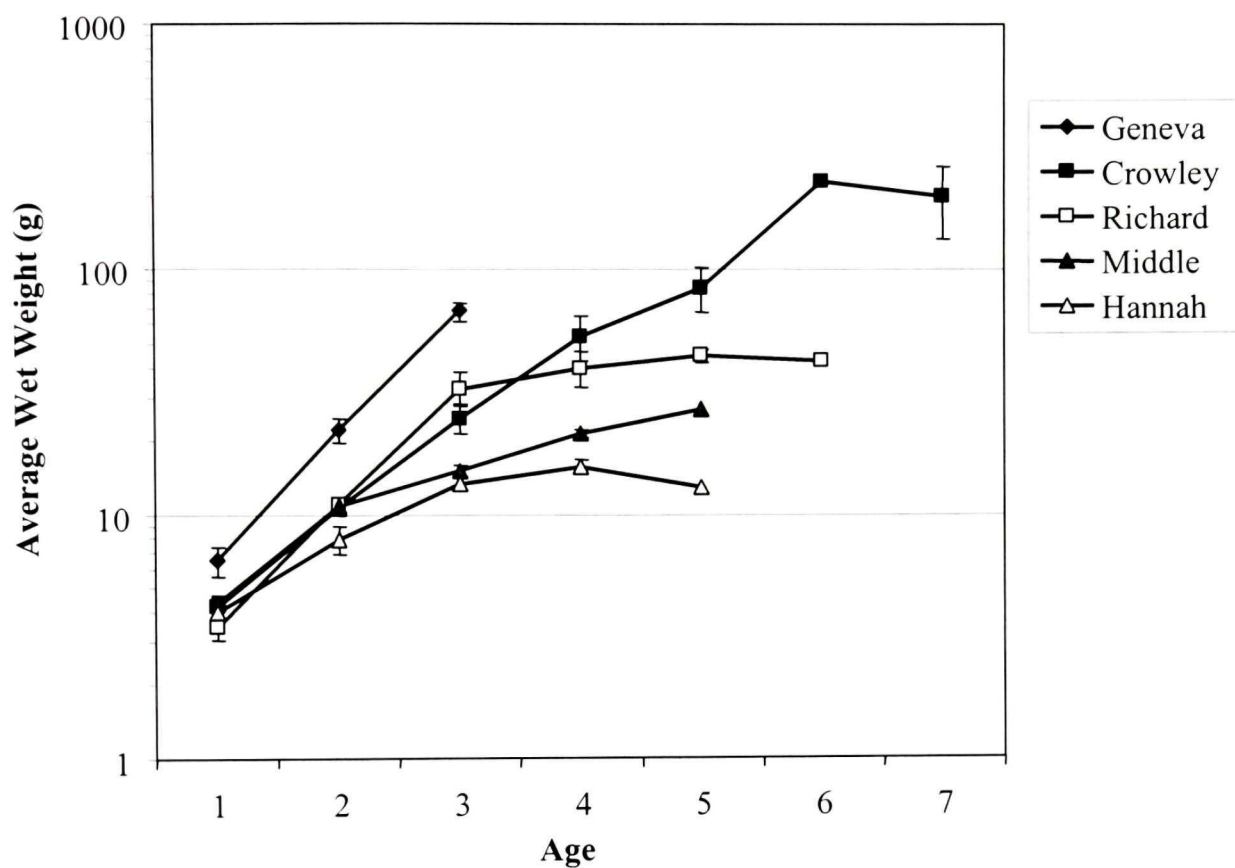
**Figure 2:** Percent of the total dry weight (mg) comprised by each invertebrate order in benthic samples from each lake.

**Figure 3:** Mean abundance per square meter 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).

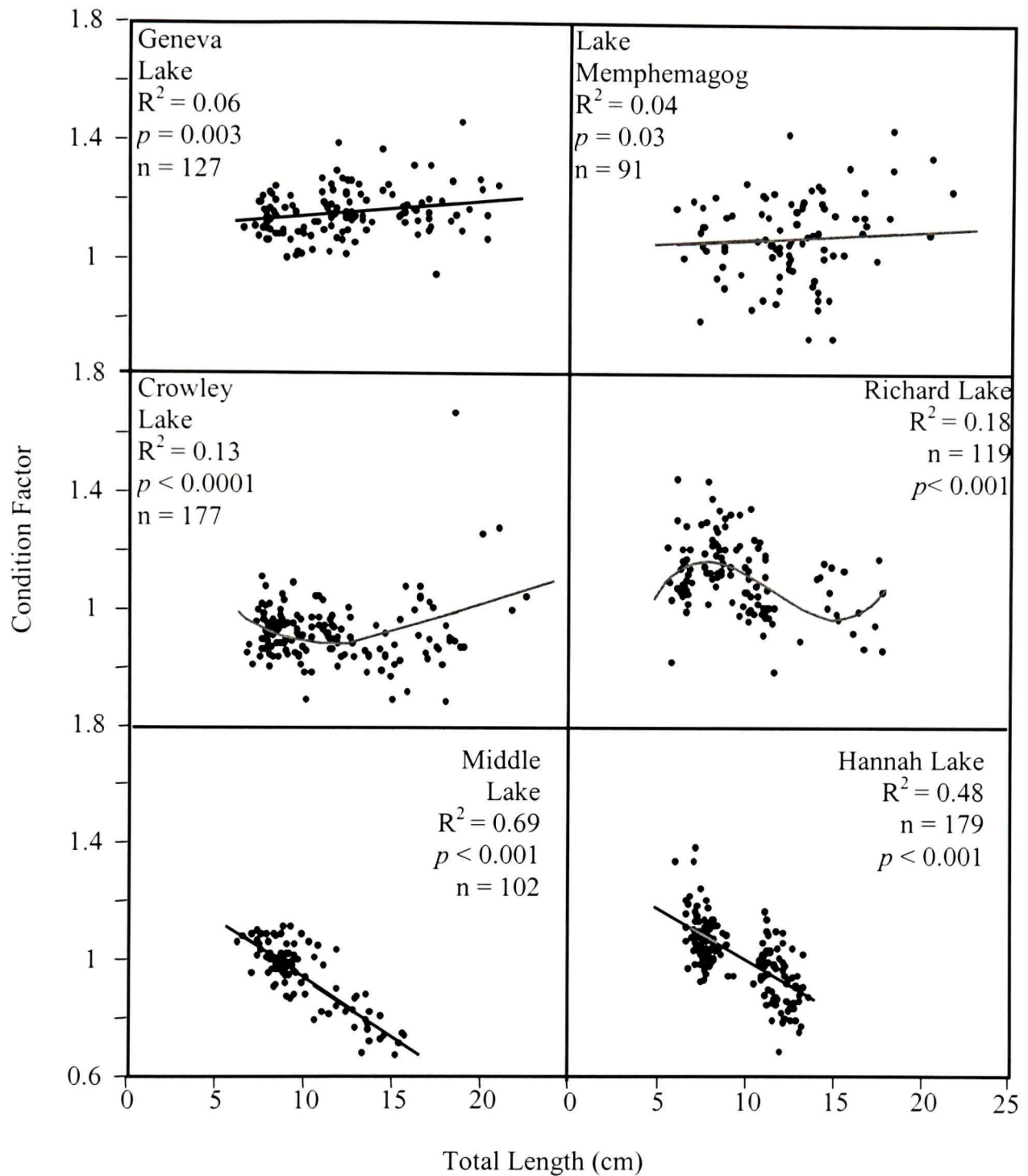




**Figure 4:** Mean weight of individual benthic invertebrates from yellow perch stomach contents (mg dry weight; mean  $\pm$  standard error of the mean). Lakes with the same letter are not significantly different from each other based on one-way ANOVA followed by Tukey-Kramer multiple comparison test.

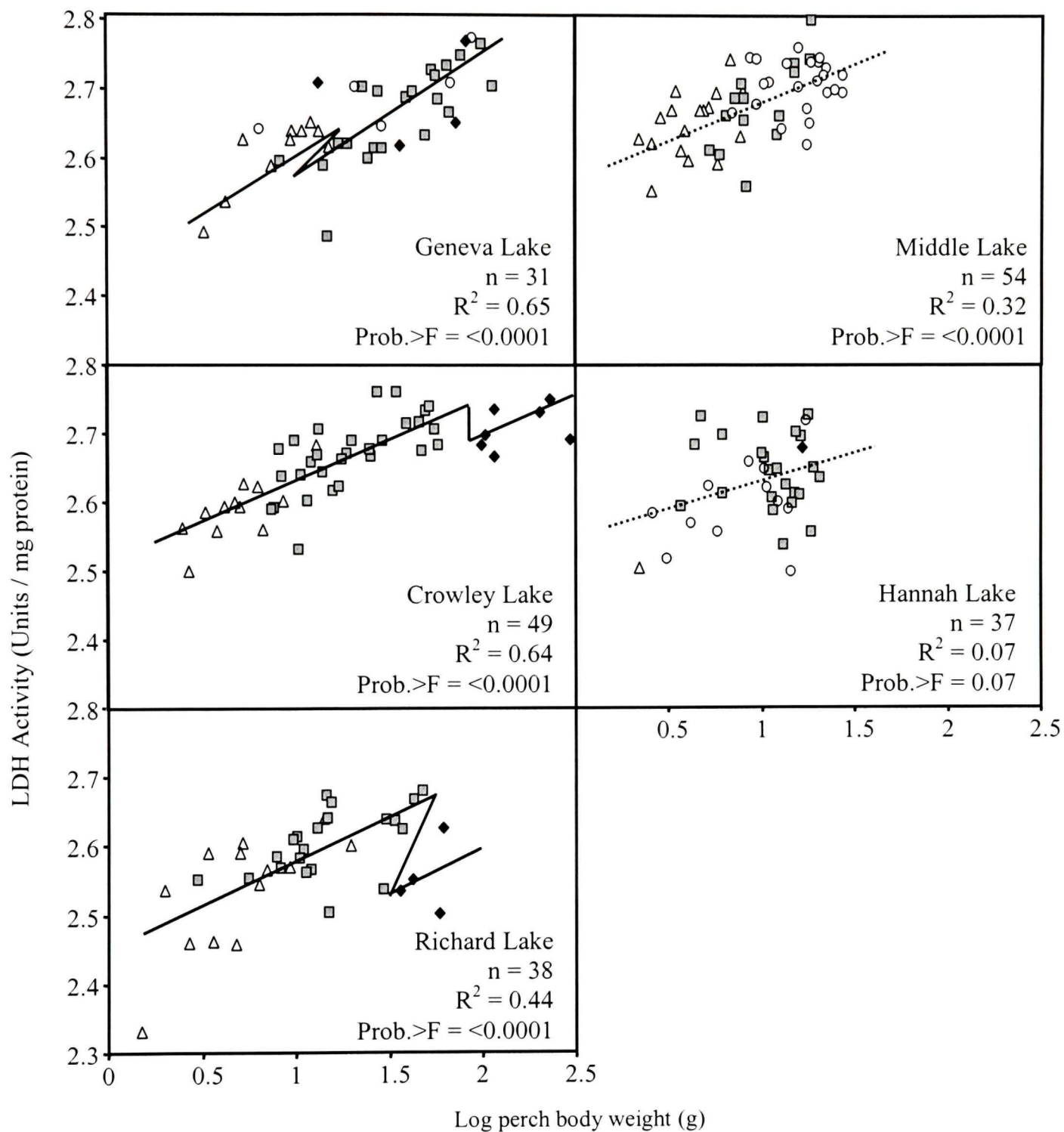


**Figure 5:** Mean weights of different age classes of perch from each lake. Error bars represent the standard error of the mean. Symbols are triangles for the most contaminated lakes, squares for the intermediately contaminated lakes and diamonds for the reference lake.



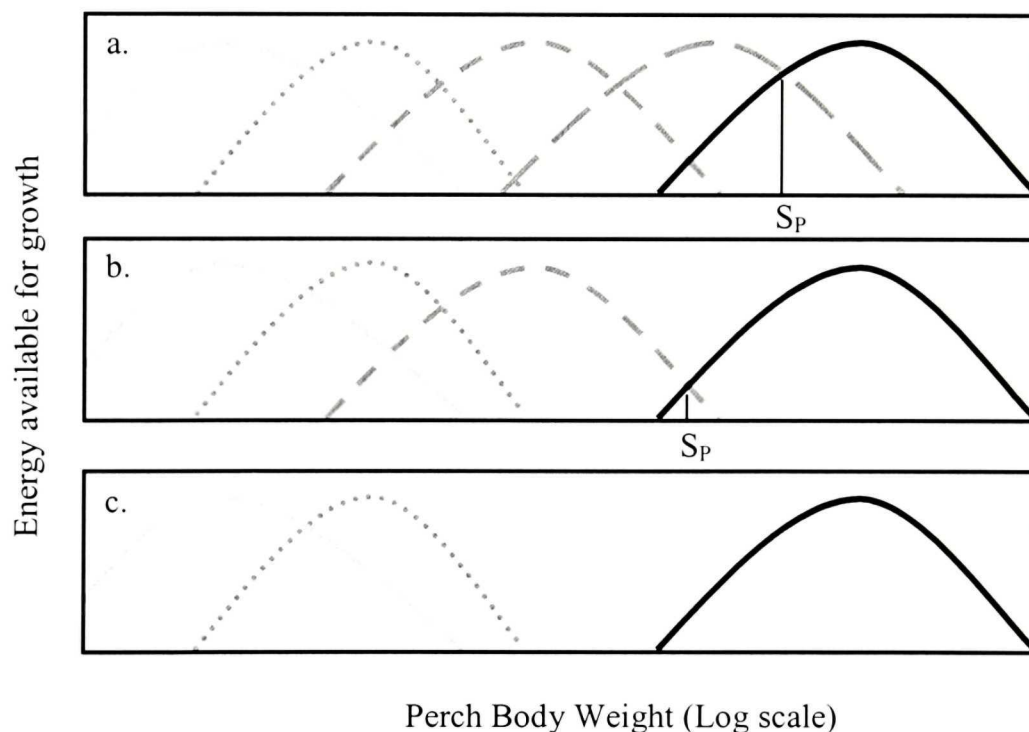
**Figure 6:** Fulton's condition factor relative to total length for all fish caught from each lake, including an additional reference lake, Lake Memphemagog, from the Eastern Townships of Quebec. Refer to Methods section for the explanation of line fitting techniques

**Figure 7:** Log white muscle lactate dehydrogenase (LDH) activity (units per mg protein) versus body size for yellow perch from all five study lakes. Line fits are ANCOVA (solid lines) for Geneva, Crowley and Richard Lakes, and linear regression (dotted lines) for Hannah and Middle Lakes. All lines are based on models from table 7. Individual perch diet, determined from stomach contents, is indicated by the symbols: shaded triangles for zooplankton, shaded squares for benthic invertebrates, solid diamonds for fish, and open circles for empty stomachs. Because of the clarity of the stable isotope results for Crowley and Richard Lakes (see Appendix D), fish with empty stomachs from these lakes were classified as either planktivorous, benthivorous or piscivorous based on the similarity of their isotopic signatures to those of fish with known stomach contents.





**Figure 8:** Predicted effects of missing size classes of benthic invertebrates on final fish size and growth efficiency of yellow perch. Energy left over for growth in relation to body weight for perch feeding on zooplankton (solid gray line), small benthic invertebrates (dotted line), medium benthic invertebrates (dashed line), large benthic invertebrates (wide dashed line) and fish (solid black line), in (a) lakes where all size classes of benthic invertebrates are available, (b) lakes where large benthic invertebrates are missing, and (c) lakes where only small benthic invertebrates are available. Note that the presence of large benthic invertebrates increases the optimal size for switching to piscivory ( $S_p$ ), and that in (b), perch experienced reduced energy available for growth, and hence reduced growth rates, during the period when they become piscivorous (i.e. an energetic bottleneck). Note also that in (c), the absence of both large and medium sized benthic invertebrates means that the energy available for growth drops to zero and the perch stop growing at an intermediate size (i.e. a stunted population).



## Appendices

### Appendix A: Benthic sample descriptions

Sample	Type	Depth (m)	Sediment	Vegetation
Gen 1	Kicknet	0.5	sm-med rocks	none
Gen 2	Kicknet	0.5	sm-med rocks	none
Gen 3	Eckman	1.5	logs	grassy bottom some macrophytes
Gen 4	Eckman	1	logs	grassy bottom some macrophytes
Gen 5	Eckman	2	mud	none
Gen 6	Eckman	0.5	mud	none
Gen 7	Kicknet	0.25	sand & sm rocks	none
Gen 8	Eckman	1.5	mud	none
Gen 9	Eckman	0.5	organic debris	none
Cro 1	Kicknet	0.5	sand & wood debris	none
Cro 2	Kicknet	0.5	sand & loose gravel & rocks	none
Cro 3	Kicknet	0.5	sand & sm rocks & logs	none
Cro 4	Kicknet	0.5	rocks med & lg	none
Cro 5	Eckman	2	mud	none
Cro 6	Eckman	2	mud	none
Cro 7	Eckman	2	mud	none
Cro 8	Eckman	2	mud & some clay & sand	none
Ric 1	Kicknet	0.5	sand. clay. sm wood debris	none
Ric 2	Eckman	1.5	mud & clay	none
Ric 3	Eckman	1	mud	emergent weed bed w/ lily pads
Ric 4	Eckman	1.5	mud	emergent weed bed w/ lily pads
Ric 5	Kicknet	0.5	clay & woody debris	emergent reeds
Ric 6	Eckman	2	clay & woody debris	none
Mid 1	Eckman	1	clay	bay surrounded by emergent grassy macrophytes
Mid 2	Kicknet	0.5	fine org debris	edge of grassy emergent macrophytes
Mid 3	Eckman	0.5	fine org debris & some clay	grassy weed bed. lots of benthic algae
Mid 4	Eckman	0.5	fine org debris & some clay	grassy weed bed. lots of benthic algae
Mid 5	Eckman	1	fine org debris	none
Mid 6	Eckman	0.5	fine org debris	close to reeds
Mid 7	Kicknet	0.5	fine org debris	grassy veg. some lily pads
Han 1	Kicknet	0.5	clay & bits of woody debris	none
Han 2	Kicknet	0.5	clay & bits of woody debris	none
Han 3	Kicknet	0.5	clay & sm rocks	some reedy emergent macrophytes
Han 4	Kicknet	0.5	clay & sm rocks	some reedy emergent macrophytes
Han 5	Kicknet	0.25	clay & sm rocks	some reedy emergent macrophytes
Han 6	Eckman	2	mud	none
Han 7	Eckman	0.5	mud	emergent macrophytes and grassy bottom
Han 8	Eckman	2	mud	emergent macrophytes and grassy bottom
Han 9	Eckman	3	mud & clay	none
Han 10	Eckman	1.5	mud & clay	none

## Appendix B: Benthic invertebrate data

Sample	Contents	Number	Abundance /m <sup>2</sup>	Dry weight (mg)	Individual dry weight (mg)	Size class
<b>Lake Geneva</b>						
Gen 1	Amphipoda	16	106.67	2.47	0.1544	SC5
	Coleoptera	1	6.67	0.03	0.0300	SC3
	Coleoptera	1	6.67	0.08	0.0800	SC4
	Coleoptera	2	13.33	1.84	0.9200	SC6
	Diptera	3	20.00	0.90	0.3000	SC5
	Diptera	5	33.33	0.24	0.0480	SC3
	Diptera	141	940.00	1.85	0.0131	SC2
	Ephemeroptera	4	26.67	1.18	0.2950	SC5
	Gastropoda	3	20.00	0.19	0.0633	SC4
	Hydrachnidia	1	6.67	0.32	0.3200	SC5
	Odonata	1	6.67	41.24	41.2400	SC10
	Odonata	1	6.67	81.71	81.7100	SC11
	Odonata	1	6.67	0.87	0.8700	SC6
	Tricoptera	6	40.00	0.14	0.0233	SC3
Gen 2	Amphipoda	35	233.33	4.39	0.1254	SC5
	Coleoptera	1	6.67	0.09	0.0900	SC4
	Coleoptera	1	6.67	0.92	0.9200	SC6
	Coleoptera	3	20.00	0.09	0.0300	SC3
	Diptera	8	53.33	0.15	0.0188	SC3
	Diptera	166	1106.67	2.64	0.0159	SC3
	Ephemeroptera	39	260.00	9.65	0.2474	SC5
	Gastropoda	13	86.67	1.08	0.0831	SC4
	Hirundinea	3	20.00	0.17	0.0567	SC4
	Hydrachnidia	1	6.67	0.12	0.1200	SC5
	Hydrachnidia	3	20.00	0.57	0.1900	SC5
	Nematoda	3	20.00	0.71	0.2367	SC5
	Odonata	1	6.67	57.96	57.9600	SC11
	Odonata	1	6.67	0.16	0.1600	SC5
	Odonata	1	6.67	11.24	11.2400	SC8
	Tricoptera	1	6.67	28.44	28.4400	SC9
	Tricoptera	11	73.33	1.20	0.1091	SC5
Gen 3	Diptera	1	44.44	0.04	0.0400	SC3
	Diptera	11	488.89	0.31	0.0282	SC3
	Ephemeroptera	1	44.44	0.19	0.1943	SC5
	Ephemeroptera	1	44.44	12.84	12.8400	SC8
Gen 4	Amphipoda	2	88.89	0.05	0.0250	SC3
	Diptera	1	44.44	2.44	2.4400	SC7
	Diptera	10	444.44	0.10	0.0100	SC2
	Diptera	131	5822.22	3.83	0.0292	SC3
	Ephemeroptera	3	133.33	0.93	0.3100	SC5
	Gastropoda	8	355.56	1.86	0.2325	SC5
	Hydrachnidia	1	44.44	0.12	0.1200	SC5

Gen 5	Nematoda	13	577.78	0.60	0.0462	SC3
	Pelecypoda	2	88.89	0.08	0.0400	SC3
	Tricoptera	1	44.44	8.50	8.5045	SC8
	Tricoptera	1	44.44	13.85	13.8500	SC8
	Diptera	3	133.33	0.12	0.0400	SC3
	Diptera	8	355.56	0.86	0.1075	SC5
	Ephemeroptera	1	44.44	0.19	0.1900	SC5
	Ephemeroptera	2	88.89	0.22	0.1100	SC5
	Gastropoda	1	44.44	0.12	0.1247	SC5
	Gastropoda	3	133.33	0.80	0.2667	SC5
Gen 6	Nematoda	2	88.89	0.12	0.0606	SC4
	Pelecypoda	1	44.44	0.04	0.0400	SC3
	Amphipoda	1	44.44	0.15	0.1500	SC5
	Diptera	1	44.44	0.04	0.0400	SC3
	Diptera	33	1466.67	0.76	0.0230	SC3
	Ephemeroptera	7	311.11	0.66	0.0943	SC4
	Gastropoda	4	177.78	0.09	0.0225	SC3
	Hydrachnidia	2	88.89	0.10	0.0500	SC4
	Nematoda	3	133.33	0.01	0.0033	SC1
	Amphipoda	14	93.33	2.20	0.1571	SC5
Gen 7	Coleoptera	3	20.00	0.10	0.0333	SC3
	Diptera	1	6.67	0.09	0.0900	SC4
	Diptera	2	13.33	0.08	0.0400	SC3
	Diptera	177	1180.00	1.81	0.0102	SC2
	Ephemeroptera	2	13.33	0.06	0.0300	SC3
	Gastropoda	4	26.67	0.32	0.0800	SC4
	Hirundinea	2	13.33	0.09	0.0450	SC3
	Hydrachnidia	1	6.67	0.12	0.1200	SC5
	Nematoda	8	53.33	0.03	0.0038	SC1
	Tricoptera	1	6.67	8.50	8.5045	SC8
Gen 8	Amphipoda	2	88.89	0.30	0.1500	SC5
	Diptera	2	88.89	0.04	0.0200	SC3
	Diptera	3	133.33	0.03	0.0100	SC2
	Diptera	36	1600.00	1.63	0.0453	SC3
	Diptera	45	2000.00	0.59	0.0131	SC2
	Ephemeroptera	1	44.44	0.05	0.0480	SC3
	Gastropoda	1	44.44	0.12	0.1200	SC5
	Hydrachnidia	1	44.44	0.01	0.0100	SC2
	Hydrachnidia	2	88.89	0.06	0.0300	SC3
	Nematoda	1	44.44	0.06	0.0606	SC4
Gen 9	Odonata	1	44.44	0.07	0.0700	SC4
	Odonata	1	44.44	0.76	0.7600	SC6
	Amphipoda	5	222.22	1.38	0.2760	SC5
	Diptera	1	44.44	0.17	0.1700	SC5
	Diptera	3	133.33	0.12	0.0400	SC3
	Diptera	37	1644.44	3.24	0.0876	SC4
	Ephemeroptera	2	88.89	0.84	0.4200	SC5

	Nematoda	3	133.33	0.04	0.0133	SC2
	Pelecypoda	1	44.44	0.04	0.0400	SC3
	Tricoptera	1	44.44	0.10	0.1000	SC5
<b>Lake Crowley</b>						
Cro 1	Coleoptera	1	6.67	0.09	0.0900	SC4
	Diptera	4	26.67	0.92	0.2300	SC5
	Diptera	278	1853.33	6.50	0.0234	SC3
Cro 2	Nematoda	3	20.00	0.01	0.0033	SC1
	Diptera	1	6.67	0.01	0.0100	SC2
	Diptera	1	6.67	0.01	0.0100	SC2
	Diptera	2	13.33	0.45	0.2250	SC5
	Diptera	258	1720.00	3.54	0.0137	SC2
	Nematoda	1	6.67	0.01	0.0108	SC2
	Tricoptera	1	6.67	0.83	0.8300	SC6
Cro 3	Tricoptera	3	20.00	1.42	0.4733	SC5
	Coleoptera	1	6.67	0.05	0.0500	SC4
	Diptera	4	26.67	0.46	0.1150	SC5
	Diptera	7	46.67	0.67	0.0957	SC4
	Diptera	1382	9213.33	8.88	0.0064	SC2
	Nematoda	6	40.00	0.11	0.0183	SC3
	Tricoptera	1	6.67	0.49	0.4947	SC5
Cro 4	Diptera	4	26.67	0.23	0.0575	SC4
	Diptera	41	273.33	0.84	0.0205	SC3
	Ephemeroptera	1	6.67	1.17	1.1700	SC7
	Hydrachnidia	1	6.67	0.04	0.0400	SC3
	Tricoptera	1	6.67	0.30	0.3000	SC5
Cro 5	Diptera	3	133.33	1.00	0.3333	SC5
	Diptera	6	266.67	1.32	0.2200	SC5
	Diptera	187	8311.11	6.13	0.0328	SC3
Cro 7	Diptera	6	266.67	2.32	0.3867	SC5
	Diptera	7	311.11	0.50	0.0714	SC4
	Diptera	424	18844.44	8.90	0.0210	SC3
	Hydrachnidia	1	44.44	0.01	0.0100	SC2
	Tricoptera	1	44.44	0.20	0.2000	SC5
	Tricoptera	1	44.44	0.67	0.6700	SC6
<b>Lake Richard</b>						
Ric 1	Amphipoda	27	180.00	5.76	0.2133	SC5
	Coleoptera	1	6.67	0.01	0.0100	SC2
	Coleoptera	1	6.67	0.10	0.1000	SC5
	Diptera	3	20.00	0.09	0.0300	SC3
	Diptera	202	1346.67	10.35	0.0512	SC4
	Diptera	304	2026.67	5.84	0.0192	SC3
	Gastropoda	2	13.33	0.04	0.0200	SC3
	Hydrachnidia	3	20.00	0.18	0.0600	SC4
	Lepidoptera	1	6.67	0.87	0.8700	SC6
	Megaloptera	1	6.67	1.19	1.1900	SC7
	Tricoptera	15	100.00	0.57	0.0380	SC3

Ric 2	Amphipoda	1	44.44	0.19	0.1900	SC5
	Amphipoda	44	1955.56	16.12	0.3664	SC5
	Coleoptera	1	44.44	0.74	0.7400	SC6
	Coleoptera	1	44.44	9.86	9.8600	SC8
	Diptera	6	266.67	0.44	0.0733	SC4
	Diptera	379	16844.44	6.52	0.0172	SC3
	Gastropoda	3	133.33	0.38	0.1267	SC5
	Hydrachnidia	2	88.89	0.34	0.1700	SC5
	Odonata	1	44.44	1.27	1.2700	SC7
	Odonata	1	44.44	2.87	2.8700	SC7
	Pelecypoda	1	44.44	0.25	0.2500	SC5
	Tricoptera	1	44.44	0.19	0.1900	SC5
	Tricoptera	1	44.44	0.54	0.5400	SC6
	Tricoptera	6	266.67	0.20	0.0333	SC3
Ric 3	Amphipoda	33	1466.67	2.75	0.0833	SC4
	Diptera	1	44.44	0.01	0.0100	SC2
	Diptera	27	1200.00	0.25	0.0093	SC2
	Ephemeroptera	8	355.56	0.26	0.0325	SC3
	Hydrachnidia	3	133.33	0.07	0.0233	SC3
	Nematoda	2	88.89	0.01	0.0050	SC2
	Pelecypoda	1	44.44	0.25	0.2500	SC5
	Tricoptera	3	133.33	0.05	0.0167	SC3
Ric 4	Amphipoda	5	222.22	0.57	0.1140	SC5
	Coleoptera	1	44.44	0.12	0.1200	SC5
	Diptera	19	844.44	0.91	0.0479	SC3
	Ephemeroptera	2	88.89	0.21	0.1050	SC5
	Tricoptera	1	44.44	0.01	0.0100	SC2
Ric 5	Amphipoda	23	153.33	5.88	0.2557	SC5
	Coleoptera	1	6.67	5.23	5.2300	SC8
	Diptera	1	6.67	0.33	0.3300	SC5
	Diptera	6	40.00	0.28	0.0467	SC3
	Diptera	311	2073.33	6.10	0.0196	SC3
	Gastropoda	10	66.67	0.68	0.0680	SC4
	Hydrachnidia	6	40.00	1.21	0.2017	SC5
	Nematoda	3	20.00	0.35	0.1167	SC5
	Odonata	1	6.67	0.62	0.6200	SC6
	Pelecypoda	1	6.67	0.25	0.2500	SC5
	Tricoptera	1	5.00	12.02	12.0200	SC8
	Tricoptera	1	6.67	0.84	0.8400	SC6
	Tricoptera	2	13.33	27.75	13.8750	SC8
	Tricoptera	22	146.67	1.62	0.0736	SC4
Ric 6	Amphipoda	4	177.78	0.35	0.0875	SC4
	Diptera	1	44.44	0.05	0.0500	SC4
	Diptera	10	444.44	1.07	0.1070	SC5
	Diptera	36	1600.00	3.13	0.0869	SC4
	Hydrachnidia	2	88.89	0.08	0.0400	SC3
	Nematoda	1	44.44	0.07	0.0700	SC4

	Odonata	1	44.44	1.39	1.3900	SC7
	Tricoptera	11	488.89	5.37	0.4882	SC5
<b>Lake Middle</b>						
Mid 2	Amphipoda	14	93.33	2.64	0.1886	SC5
	Coleoptera	1	6.67	0.14	0.1400	SC5
	Diptera	2	13.33	0.14	0.0700	SC4
	Diptera	109	726.67	3.34	0.0306	SC3
	Odonata	1	6.67	0.06	0.0600	SC4
	Odonata	1	6.67	0.10	0.1000	SC5
	Odonata	2	13.33	0.18	0.0900	SC4
	Tricoptera	1	6.67	20.82	20.8200	SC9
	Tricoptera	3	20.00	1.13	0.3767	SC5
	Tricoptera	6	40.00	0.54	0.0900	SC4
Mid 3	Diptera	1	44.44	0.65	0.6500	SC6
	Diptera	2	88.89	1.23	0.6150	SC6
	Diptera	20	100.00	0.36	0.0180	SC3
	Ephemeroptera	3	133.33	0.30	0.1000	SC5
	Tricoptera	1	44.44	0.04	0.0400	SC3
Mid 4	Diptera	4	177.78	0.06	0.0150	SC3
	Diptera	4	177.78	0.10	0.0250	SC3
	Diptera	6	266.67	0.22	0.0367	SC3
	Diptera	128	5688.89	1.78	0.0139	SC2
	Diptera	298	13244.44	8.84	0.0297	SC3
	Tricoptera	2	88.89	0.99	0.4950	SC5
	Tricoptera	6	266.67	0.31	0.0517	SC4
	Tricoptera	29	1288.89	2.60	0.0897	SC4
Mid 5	Coleoptera	1	44.44	0.04	0.0400	SC3
	Diptera	2	88.89	0.07	0.0350	SC3
	Diptera	10	444.44	3.58	0.3580	SC5
	Diptera	98	4355.56	1.51	0.0154	SC3
	Nematoda	3	133.33	0.63	0.2100	SC5
	Odonata	1	44.44	0.23	0.2300	SC5
	Tricoptera	1	44.44	0.55	0.5500	SC6
	Tricoptera	4	177.78	0.45	0.1125	SC5
Mid 7	Amphipoda	12	80.00	1.39	0.1158	SC5
	Coleoptera	1	6.67	0.10	0.1000	SC5
	Diptera	4	26.67	1.28	0.3200	SC5
	Diptera	216	1440.00	1.62	0.0075	SC2
	Ephemeroptera	24	160.00	1.70	0.0708	SC4
	Odonata	1	6.67	0.06	0.0600	SC4
	Tricoptera	1	6.67	0.36	0.3600	SC5
	Tricoptera	22	146.67	0.26	0.0118	SC2
<b>Lake Hannah</b>						
Han 1	Diptera	1	6.67	0.08	0.0800	SC4
	Diptera	10	66.67	0.36	0.0360	SC3
	Nematoda	3	20.00	0.21	0.0700	SC4
	Tricoptera	6	40.00	2.14	0.3567	SC5

Han 3	Diptera	19	126.67	0.22	0.0116	SC2
	Tricoptera	1	6.67	0.41	0.4100	SC5
Han 6	Diptera	5	222.22	1.47	0.2940	SC5
	Diptera	20	888.89	0.92	0.0460	SC3
	Tricoptera	4	177.78	1.13	0.2825	SC5
Han 7	Diptera	68	3022.22	0.77	0.0113	SC2
	Lepidoptera	1	44.44	0.25	0.2500	SC5
	Tricoptera	2	88.89	0.12	0.0600	SC4
	Tricoptera	6	266.67	2.13	0.3550	SC5
Han 8	Diptera	76	3377.78	1.16	0.0153	SC3
	Nematoda	4	177.78	0.02	0.0050	SC2
Han 9	Diptera	37	1644.44	19.91	0.5381	SC6
	Diptera	102	4533.33	2.26	0.0222	SC3
	Megaloptera	1	44.44	2.12	2.1200	SC7
	Nematoda	1	44.44	0.06	0.0600	SC4
	Tricoptera	7	311.11	1.40	0.2000	SC5
Han 10	Tricoptera	4	177.78	0.71	0.1775	SC5

### Appendix C: Yellow perch body size and diet data

Yellow perch data:						Stomach contents data:			
Fish #	TL (cm)	W (g)	LDHP	Sex	Age	Prey Taxa	#	L (mm)	W (mg)
<b>Lake Geneva</b>									
Ge02-1	9.6	10.2							
Ge02-2	8.0	5.9							
Ge02-3	8.2	6.4							
Ge02-4	8.9	7.6	387.15	TS	1	Daphnia	10	1	0.28
						Hemiptera	1	2	0.14
						unknown insect	1	10	1.64
Ge02-5	7.6	5.2							
Ge02-6	8.0	5.7							
Ge02-7	9.0	8.5	393.64	TS	1	Diptera	1	5	0.26
						Trichoptera	5	4	2.59
						Hydrachnidia	2	1	0.25
						Amphipoda	1	3	0.32
Ge02-8	7.3	4.3	344.55	TS	1	Diptera	2	3	0.09
						unknown insect	1	0.5	0.04
						Daphnia	30	1	1.59
Ge02-9	7.9	5.7							
Ge02-10	7.5	4.5							
Ge02-11	8.2	6.0							
Ge02-12	8.7	7.1							
Ge02-13	8.1	5.6							
Ge02-14	8.0	5.6							
Ge02-15	8.2	6.2							



Ge02-16	7.8	5.7							
Ge02-17	8.1	6.0							
Ge02-18	7.7	5.4							
Ge02-19	8.4	6.8							
Ge02-20	6.7	3.3	310.32	?	1	Daphnia	30	1	1.51
						Amphipoda	1	3	0.17
						Nematoda	1	1	0
Ge02-21	7.8	5.2							
Ge02-22	8.4	6.8							
Ge02-23	8.0	5.4	424.01	F	1	Trichoptera	10	5	0.01
						Diptera	1	11	0.37
						Daphnia	10	1	1.04
Ge02-24	8.5	7.0							
Ge02-25	8.0	5.8							
Ge02-26	8.5	7.6							
Ge02-27	10.1	11.3							
Ge02-28	10.6	12.2							
Ge02-29	8.2	6.7							
Ge02-30	8.3	6.9							
Ge02-31	9.1	7.5							
Ge02-32	8.5	7.3							
Ge02-33	10.1	11.1	434.60	?	2	Daphnia	172	2	8.99
Ge02-34	11.2	15.1	306.95	?	2	Hexagenia	1	30	26.98
Ge02-35	12.5	19.4							
Ge02-36	12.4	23.1							
Ge02-37	12.6	25.2	397.10	F	3	Trichoptera	1	30	0.67
						Hexagenia	1	50	64.59
Ge02-38	11.9	17.9							
Ge02-39	10.9	14.5	388.79	M	2	Odonata	1	10	4.24
						Amphipod	1	7	0.64
						Trichoptera	7	5	1.91
						Daphnia	1	2	0.1
Ge02-40	8.5	6.6	437.26	M	1	empty			
Ge02-41	9.9	9.8	434.49	?		Coleoptera	1	9	4.4
						Daphnia	74	1.5	4.82
Ge02-42	10.5	12.4	447.94	M	2	Trichoptera	10	5	3.97
						Zoop.	26	1	1.31
						Diptera	1	5	0.09
						Diptera	1	5	0.07
Ge02-43	9.7	9.9							
Ge02-44	10.7	13.7	435.06	M	2	Daphnia	20	2	1.29
						Diptera	3	3	0.3
						Odonata	1	15	13.3
						Trichoptera	16	8	6.65
Ge02-45	11.6	19.4	416.42	M	2	Trichoptera	6	15	10.89
						Amphipod	3	2	1.71
						Odonata	1	10	3.51
Ge02-46	12.8	23.8							

Ge02-47	12.4	21.8							
Ge02-48	12.2	19.7							
Ge02-49	13.4	27.3	410.09	M	2	Hemiptera	1	10	6.84
						Hexagenia	3	30	93.62
Ge02-50	11.9	19.6							
Ge02-51	12.7	23.3							
Ge02-52	13.4	27.1							
Ge02-53	15.8	43.6	495.60	F	3	Hirudinea	1	4	71.44
Ge02-54	17.2	54.9							
Ge02-55	15.5	42.4							
Ge02-56	17.6	51.3							
Ge02-57	16.7	55.2	532.67	M	3	Hirudinea	1	4	29.27
Ge02-58	17.3	56.6							
Ge02-59	19.0	74.6							
Ge02-60	20.5	98.5							
Ge02-61	9.4	9.7							
Ge02-62	11.1	17.3							
Ge02-63	11.3	17.0							
Ge02-64	12.4	21.5	502.10	M	2	empty			
Ge02-65	15.7	45.4							
Ge02-66	11.5	15.4	413.56	M	2	Daphnia	136	2	9.86
						Ephemeroptera	1	10	8.53
Ge02-67	11.6	18.4							
Ge02-68	13.6	29.9	410.25	F	2	Odonata	1	25	80.61
						Hexagenia	1	20	16.97
Ge02-69	16.3	56.6							
Ge02-70	16.5	48.5							
Ge02-71	17.1	59.8	482.98	M	3	Odonata	1	15	1.05
						Daphnia	1	2	0.04
Ge02-72	9.3	9.7	423.69	F	1	Hemiptera	7	2	0.49
						Daphnia	1216	1.5	24.32
Ge02-73	11.4	17.2							
Ge02-74	11.6	17.2							
Ge02-75	11.7	19.6							
Ge02-76	11.9	21.7							
Ge02-77	12.8	26.4							
Ge02-78	12.4	21.9							
Ge02-79	12.8	23.5	503.10	F	2	Odonata	1	10	2.76
						Hemiptera	1	2	0.13
						Daphnia	6	1.5	0.31
Ge02-80	15.6	43.3							
Ge02-81	16.4	51.1	429.57	F	3	Plecoptera	1	10	3.55
Ge02-82	11.1	16.6							
Ge02-83	12.4	23.2							
Ge02-84	17.1	56.5							
Ge02-85	15.8	45.3							
Ge02-86	13.6	27.4							
Ge02-87	17.9	68.4	464.61	F	3	Malacostraca	1	25	154.8

						Hemiptera	1	10	5.95
						Hexagenia	1	25	5.53
Ge02-88	17.2	66.5	540.43	M	3	Adult Dipteran	1	5	0.28
Ge02-89	17.1	57.4	523.84	F	3	Malacostraca	1	10	4.82
Ge02-90	20.0	101.3							
Ge02-91	21.1	116.5	504.75	F	3	Malacostraca	1	55	715.44
Ge02-92	11.6	17.6	416.82	M	2	Coleoptera	1	12	1.02
Ge02-93	11.8	18.8							
Ge02-94	12.2	19.2							
Ge02-95	8.9	7.7							
Ge02-96	9.7	9.3							
Ge02-97	11.6	17.8							
Ge02-98	12.7	24.2							
Ge02-99	13.3	28.5	496.81	F	2	Hexagenia	1	20	7.39
Ge02-100	12.9	24.2							
Ge02-101	15.0	40.9							
Ge02-102	18.7	74.8	500.05	F	3	Malacostraca	1	20	39.13
						fish	1	15	1.48
Ge02-103	14.5	41.5							
Ge02-104	9.6	8.9							
Ge02-105	9.3	8.5							
Ge02-106	11.2	16.6							
Ge02-107	12.2	22.9							
Ge02-108	13.0	23.1							
Ge02-109	14.8	40.2	486.13	F	3	Malacostraca	1	33	160.9
Ge02-110	18.5	79.5	558.15	F	3	Odonata	2	20	46.63
						Malacostraca	1	30	45.94
Ge02-111	19.4	84.8	449.04	F	3	Diptera	1	8	0.54
						fish	1	10	4.35
Ge02-112	20.5	91.8	592.41	F	3	empty			0
Ge02-113	10.7	13.7	585.81	F	2	Diptera	5	2	30.12
						Hemiptera	1	3	0.27
						fish	2	15	2.94
						Hexagenia	1	25	14.09
Ge02-114	11.7	18.3							
Ge02-115	12.5	21.3							
Ge02-116	13.0	25.0							
Ge02-117	12.0	23.9							
Ge02-118	14.5	37.2	509.70	F	2	fish	1	20	12.58
Ge02-119	13.2	28.6							
Ge02-120	13.9	30.0	441.02	F	2	empty			
Ge02-121	16.3	50.4							
Ge02-122	15.9	47.4	414.48	F	2	fish	1	15	8.68
Ge02-123	12.8	23.8							
Ge02-124	16.5	50.5							
Ge02-126	18.4	70.0	511.14	F	3	empty			
Ge02-127	20.2	101.3	580.03	F	3	Diptera	1	4	0.18
Ge02-128	19.0	99.8							

**Lake Crowley**

Cr02-1	10.0	6.7	363.71	TS	2	Daphnia	12	1	0.37
						Diptera	1	1	0.11
						Chironimids	4	5	0.3
						Chironomids	6	5	0.89
Cr02-2	8.0	4.6							
Cr02-3	9.6	7.2							
Cr02-4	8.5	5.0	392.71	TS	1	Daphnia	100	2	1.25
						fish	1	20	0.12
Cr02-5	6.8	2.7	316.28	TS	1	Daphnia	100	2	0.62
Cr02-7	9.9	7.4	389.30	F	2	unknown insect	1	5	0.36
						unknown insect	1	7	0.36
Cr02-8	8.2	4.5							
Cr02-9	8.0	4.2							
Cr02-10	8.3	5.3							
Cr02-11	9.0	6.4							
Cr02-12	7.6	3.7							
Cr02-13	7.7	4.0							
Cr02-14	8.8	5.9							
Cr02-15	8.0	4.2							
Cr02-16	8.0	4.2							
Cr02-17	9.0	6.0							
Cr02-18	8.3	5.3							
Cr02-19	7.5	3.7							
Cr02-20	11.5	14.5							
Cr02-21	9.5	7.7							
Cr02-22	9.2	6.8							
Cr02-23	8.3	5.3	423.12	TS	1	empty			
Cr02-24	9.4	6.9							
Cr02-25	8.0	4.6							
Cr02-26	8.2	5.1							
Cr02-27	8.2	5.0							
Cr02-28	7.5	4.2							
Cr02-29	8.3	5.2							
Cr02-30	9.0	6.8							
Cr02-31	8.2	4.9							
Cr02-32	8.4	5.1							
Cr02-33	7.8	4.3							
Cr02-34	11.0	12.2	454.49	F	2	empty			
Cr02-35	11.3	12.7							
Cr02-36	8.6	5.5							
Cr02-37	8.6	5.5							
Cr02-38	10.4	10.3	339.92	F	2	Chironomids	8	5	3.07
						Fish	1	7	1.11
						Chironomids	1	10	0.57
Cr02-39	8.3	5.2							
Cr02-40	7.8	5.0							
Cr02-41	11.7	14.0	439.68	M	2	Chironomids	1	7	0.32

						Daphnia	1	1	-0.06
						Tricoptera	18	4	6.1
Cr02-42	8.8	6.3	420.19	TS	1	Daphnia	8	1	0.05
Cr02-43	11.8	14.2							
Cr02-44	9.5	7.8							
Cr02-45	7.4	3.3	384.55	F	1	Daphnia	28	1	0.09
Cr02-46	8.2	5.0							
Cr02-47	7.9	4.2							
Cr02-48	10.4	9.9	489.32	M	2	Diptera	1	1	0.01
						Diptera	1	4	0.02
Cr02-49	7.8	4.7	397.75	TS	1	Daphnia	400	0.5	1.09
Cr02-50	10.4	10.7	437.10	F	2	Chironomid	17	7	2.35
						Chironimids	10	7	1.91
						Odonata	1	15	8.15
Cr02-51	9.5	7.7	389.74	F	2	unknown insect	1	15	3.07
Cr02-52	11.4	13.0	466.78	F	2				
Cr02-53	11.4	14.0							
Cr02-54	11.0	12.1							
Cr02-55	10.0	8.4	435.02	?	2	Plecoptera	1	5	0.01
Cr02-56	8.7	6.2							
Cr02-57	9.0	6.4							
Cr02-58	8.5	5.7							
Cr02-59	8.0	4.7							
Cr02-60	8.0	4.0							
Cr02-61	8.2	4.9							
Cr02-62	7.2	3.5							
Cr02-63	7.9	4.4							
Cr02-64	7.3	3.8	361.90	TS	1	unknown			2.77
Cr02-65	9.7	8.6							
Cr02-66	11.2	12.6							
Cr02-67	8.1	4.9							
Cr02-68	7.8	4.0							
Cr02-69	7.9	4.2	391.88	TS	1	Daphnia	60	1	2.22
						Chironomid	5	5	0.47
						Diptera	3	3	0.12
Cr02-70	8.9	6.2							
Cr02-71	9.6	7.9							
Cr02-72	11.5	12.8	483.23	F	2	Daphnia	120	21	2.28
						Chironomid	1	10	0.01
Cr02-73	12.5	17.2	420.59	M	3	empty			
Cr02-74	11.6	14.3							
Cr02-75	8.9	5.9							
Cr02-76	7.9	4.3							
Cr02-77	7.9	4.5							
Cr02-78	9.3	7.5							
Cr02-79	7.7	4.4							
Cr02-80	8.6	6.2							
Cr02-81	12.7	17.7	460.44	F	3	Diptera adult	1	5	0.01

						Chironomid	1	5	0.01
						unknown	1	15	1.01
						Diptera	1	5	0.11
Cr02-82	11.1	12.6							
Cr02-83	9.6	7.3							
Cr02-84	11.3	12.9							
Cr02-85	9.3	8.6	399.71	F	2	Diptera	1	5	-0.06
						Daphnia	50	2	0.2
						Diptera	3	5	0.12
Cr02-86	8.4	5.5							
Cr02-87	8.6	6.1							
Cr02-88	10.4	8.6							
Cr02-89	8.2	5.2							
Cr02-90	10.8	11.6	400.80	F	2	empty			
Cr02-91	7.7	4.4							
Cr02-92	9.7	7.2							
Cr02-93	8.4	5.4							
Cr02-94	7.9	4.3							
Cr02-95	6.7	2.5	365.60	TS	1	Tricoptera	1	5	0.05
						Daphnia	116	2	0.9
Cr02-96	7.0	2.7							
Cr02-97	11.5	13.3							
Cr02-98	15.8	27.5	575.24	F	3	empty			
Cr02-99	11.5	14.0							
Cr02-100	12.0	14.1							
Cr02-101	7.7	4.3							
Cr02-102	12.5	18.6							
Cr02-103	14.0	25.4	464.13	F	3	Chironomids	33	7	5.83
						Tricoptera	3	5	0.38
						Diptera	1	7	0.29
Cr02-104	7.5	4.6							
Cr02-105	10.8	12.0							
Cr02-106	8.8	6.9							
Cr02-107	8.5	5.6							
Cr02-108	12.0	15.7	412.88	F	2	empty			
Cr02-109	16.5	47.5	473.46	F	3	Odonate	4	25	203.22
Cr02-110	20.0	99.2	483.21	F	5				
Cr02-111	21.0	116.1	464.21	F	4	fish	1	60	291.5
						Coleoptera	1	10	1.13
						Odonata	1	15	0.58
Cr02-112	14.5	24.8	475.84	M	3	empty			
Cr02-113	16.5	45.9							
Cr02-114	17.0	49.3							
Cr02-115	13.6	20.5							
Cr02-116	19.0	58.3	482.77	F	4	Odonate	1	15	16.8
Cr02-117	17.2	49.9	541.15	F	5	Coleoptera	3	10	46.38
						Odonata	2	15	17.02
Cr02-118	16.4	39.2	518.17	F	4	empty			

Cr02-119	16.5	45.8	520.50	M	4	empty			
Cr02-120	15.4	29.3	488.29	F	4	Chironomid	9	5	1.02
						Tricoptera	2	7	0.62
Cr02-121	10.8	12.9							
Cr02-122	13.4	20.1	490.10	M	3	empty			
Cr02-123	13.5	18.8	468.31	M	3	empty			
Cr02-124	18.5	104.5	497.94	F	5	Lepodoptera	1	35	59.93
						fish	1	70	254.06
						Coleoptera	1	5	2.6
Cr02-125	8.0	5.1							
Cr02-126	9.8	8.0							
Cr02-127	7.8	4.7							
Cr02-128	9.8	8.4							
Cr02-129	8.1	4.5							
Cr02-130	10.6	12.2							
Cr02-131	9.5	8.2	476.02	F	2	unknown insect	1	5	
Cr02-132	11.0	13.4	508.48	F	2	Odonate	2	20	77.38
Cr02-133	7.9	4.6							
Cr02-134	8.7	6.8							
Cr02-135	17.4	44.9							
Cr02-136	17.5	45.2							
Cr02-137	18.8	56.7							
Cr02-138	18.5	55.2	507.81	M	7	empty			
Cr02-139	11.4	12.5							
Cr02-140	15.0	26.7							
Cr02-141	17.8	44.7							
Cr02-142	14.3	22.5							
Cr02-143	14.8	24.4							
Cr02-144	14.9	22.2							
Cr02-145	11.8	14.5							
Cr02-146	21.7	99.5							
Cr02-147	18.3	53.7							
Cr02-148	15.1	29.6							
Cr02-149	17.0	43.1							
Cr02-150	11.8	12.9							
Cr02-151	22.5	116.6	542.74	F	7	empty			
Cr02-152	28.5	230.1	563.61	F	6	fish	1	70	522.58
Cr02-153	25.5	203.1	538.92	F		fish	2	65	1920.52
Cr02-154	14.2	24.2							
Cr02-155	16.2	41.6							
Cr02-156	18.0	38.7							
Cr02-157	13.6	20.7							
Cr02-158	14.5	25.1							
Cr02-159	15.7	41.0							
Cr02-160	14.5	27.3							
Cr02-161	18.2	52.3	549.96	F	4	fish	2	50	175.19
						Odonate	2	20	166.54
						Coleoptera	1	5	1.44

Cr02-162	18.0	53.8							
Cr02-163	12.8	17.1							
Cr02-164	33.4	298.9	492.39	F	7	empty			
Cr02-165	29.8	325.0	545.26	F	7	fish	1	80	209.21
Cr02-166	12.4	18.7							
Cr02-167	18.2	53.3							
Cr02-168	16.8	39.4							
Cr02-169	15.4	34.5	577.27	M	4	Chironomids	35	1	8.25
						Plecoptera	2	15	0.94
						Odonate	2	1	3.25
Cr02-170	12.2	15.0							
Cr02-171	16.9	39.0							
<b>Lake Richard</b>									
Ri02-1	5.6	1.9		TS	1	empty			
Ri02-2	6.3	2.9		TS	1	Chironomids	25	2	1.99
Ri02-3	6.0	2.8		F	1	empty			
Ri02-4	6.2	2.5							
Ri02-5	6.0	2.3							
Ri02-6	6.5	3.0							
Ri02-7	6.3	2.7							
Ri02-8	6.0	3.1							
Ri02-9	6.5	3.2							
Ri02-10	7.3	5.0							
Ri02-11	8.2	6.5							
Ri02-12	8.6	7.3							
Ri02-13	8.7	8.6							
Ri02-14	9.9	10.2	410.69	F	2	Daphnia	1	2	0.13
						Odonata	2	11	22.48
Ri02-15	10.7	15.0	319.22	F	2	Chironomids	80	5	23.27
						Amphipods	30	3	9.74
						Odonata	2	11	9.71
Ri02-16	6.5	3.5							
Ri02-17	6.4	2.8							
Ri02-18	6.7	3.6	289.35	?	1	empty			
Ri02-19	8.4	7.9	384.37	?	2	Chironomid	1	5	0.16
Ri02-20	7.9	5.5							
Ri02-21	7.7	5.1							
Ri02-22	7.8	6.8							
Ri02-23	8.2	7.0							
Ri02-24	8.0	6.2							
Ri02-25	6.3	2.6		TS	1	Daphnia	30	1.5	1.37
Ri02-26	8.7	8.4							
Ri02-27	8.3	6.9							
Ri02-28	8.3	6.4							
Ri02-29	7.7	5.9							
Ri02-30	9.0	9.6							
Ri02-31	6.2	2.5							
Ri02-32	5.5	2.0	344.28	?	1	Daphnia	20	1.5	0.63



Ri02-33	6.6	3.0				Odonata	2	6	2.29
Ri02-34	6.6	3.0	356.27	TS	1	Chironomid	5	5	1.54
Ri02-35	6.5	2.9		F	1	empty			
Ri02-36	6.6	3.2		M	1	empty			
Ri02-37	8.0	5.6	357.72	TS	1	Diptera stomach parasites	1	920	15.65
Ri02-38	8.2	6.7							
Ri02-39	7.6	5.2	403.13	TS	1	Daphnia	30	1	2.86
						Chironomid	6	8	3.37
Ri02-40	8.5	6.8							
Ri02-41	8.3	7.2							
Ri02-42	8.0	7.0	367.76	?	1	empty			
Ri02-43	9.0	8.3	368.99	?	2	Hyaella	70	3	20.24
						Chironomids	2	2	0.96
Ri02-44	10.6	14.3							
Ri02-45	10.2	14.2							
Ri02-46	6.8	3.4	388.86	TS	1	empty			
Ri02-47	6.3	3.0							
Ri02-48	5.7	1.9							
Ri02-49	5.7	1.5	214.53	TS	1	empty			
Ri02-50	6.3	2.7							
Ri02-51	6.5	3.0							
Ri02-52	6.2	2.7							
Ri02-53	6.7	3.4							
Ri02-54	6.5	2.7	288.21	TS	1	empty			
Ri02-55	8.5	6.9							
Ri02-56	8.4	7.1							
Ri02-57	8.7	7.9							
Ri02-58	8.2	5.9							
Ri02-59	8.3	6.3							
Ri02-60	9.0	8.1							
Ri02-61	11.0	14.7	437.39	M	2	Diptera	21	8	10.32
Ri02-62	6.4	3.0							
Ri02-63	6.6	2.9							
Ri02-64	7.8	4.8	286.92	?	1	empty			
Ri02-65	8.0	6.3	351.32	F	2	empty			
Ri02-66	7.6	5.0	390.20	F	2	empty			
Ri02-67	8.5	7.2							
Ri02-68	11.2	14.0	435.86	F	2	Daphnia	80	1	3.8
						unknown insect	2	10	7.02
Ri02-69	14.2	14.4	472.23	F	2	empty			
Ri02-70	11.5	15.2							
Ri02-71	10.9	12.9							
Ri02-72	11.0	13.1	422.11	F	2	Odonata	1	10	2.09
Ri02-73	10.9	11.7							
Ri02-74	11.2	13.5							
Ri02-75	10.8	12.3							

Ri02-76	11.2	13.5							
Ri02-77	10.0	9.5							
Ri02-78	10.1	12.0	367.86	M	2	empty			
Ri02-79	11.0	12.8							
Ri02-80	10.5	12.4							
Ri02-81	11.1	13.6							
Ri02-82	11.0	15.5	460.20	M	3	empty			
Ri02-83	13.0	19.4	398.74	F	3	empty			
Ri02-84	9.3	9.6	407.43	M	2	Chironomids	160	5	25.42
						Amphipods	1	5	0.64
Ri02-85	9.5	11.3	364.40	M	2	Chironomids	3	3	0.19
						Amphipods	19	3	7.28
Ri02-86	9.8	10.7							
Ri02-87	10.1	11.6							
Ri02-88	10.0	11.0	392.43	M	2	Chironomids	11	5	2.53
						unknown insect	1	10	2.1
Ri02-89	10.4	13.8							
Ri02-90	9.5	10.4	381.97	F	2	empty			
Ri02-91	14.3	33.6		F	F	fish	1	40	46.15
Ri02-92	13.9	29.4	343.94	F	3	Odonata	1	20	22.56
Ri02-93	15.2	33.7	433.53	M	4	empty			
Ri02-94	14.5	30.3	434.66	M	4	empty			
Ri02-95	15.5	41.8	354.96	F	5	fish	3	40	250.93
Ri02-96	14.7	36.1	342.85	F	3	empty			
Ri02-97	16.0	37.3	419.40	F	4	Chironomids	44	5	12.92
Ri02-98	16.3	42.6	465.73	M	6	empty			
Ri02-99	17.2	47.6	478.15	F	5	empty			
Ri02-100	17.7	58.3	317.00	F	4	fish	1	40	54.49
Ri02-R1	15.1	33.7							
Ri02-R2	14.2	31.3							
Ri02-R3	9.5	8.3							
Ri02-R4	10.6	12.0							
Ri02-R5	9.8	9.9							
Ri02-R6	17.4	61.3	422.53	?	3	chironomids	2	2	0.24
						fish	1	40	82.96
Ri02-R7	11.4	14.0		?	2	empty			
Ri02-R8	10.2	11.0							
Ri02-R9	10.6	12.2							
Ri02-R10	9.7	9.2	370.74	F	2	Daphnia	10	1	0.52
						Chironomids	10	3	1.3
						Amphipods	25	4	11.42
Ri02-R11	14.6	32.6		F	3	fish (darters)	2	45	169.04
Ri02-R12	16.7	39.5		F	3	Amphipod	64	3	19.49
						Odonata	2	15	16.12
Ri02-R13	11.5	11.8							
Ri02-R14	17.7	47.1		F	3	Trichoptera	2	15	10.33
Ri02-R15	11.0	15.7		F	3	Amphipods	18	3	9.92
						Chironomids	3	3	0.85

Ri02-R16	10.1	10.0							
Ri02-R17	10.2	10.4							
Ri02-R18	10.4	10.8							
Ri02-R19	9.1	7.7							
Ri02-R20	11.0	14.3		?	2	Odonata	1	30	20.5
<b>Lake Middle</b>									
Mi02-1	8.8	6.8	546.63	M	1	Ostracod	1	3	0.13
Mi02-2	8.3	5.8	389.30	TS	1	Daphnia	13	2	0.17
Mi02-3	8.8	6.5	454.43	F	1	Tricoptera	5	3	0.61
Mi02-4	11.5	15.9	569.16	M	2	empty			
Mi02-5	8.6	6.1							
Mi02-6	8.4	6.0	398.76	M	1	Ephemeroptera	4	5	1.49
						Chironomid	1	4	0.05
						unknown	3	10	0.04
Mi02-7	7.8	4.8							
Mi02-8	9.9	10.4	505.20	F	2	unknown	1.5	15	0.06
						unknown	3	5	0.16
Mi02-9	9.7	8.1	480.33	M	2	Tricoptera head	1	5	0.22
						unknown	?	?	1.86
Mi02-10	7.9	4.8							
Mi02-11	9.2	7.5							
Mi02-12	8.5	6.9							
Mi02-13	10.5	12.2	426.28	F	2	Tricoptera	17	4	7.13
Mi02-14	10.8	12.5	454.77	F	3	Tricoptera	3	3	1.14
						Orthoptera	1	2	4.46
Mi02-15	7.8	4.8							
Mi02-16	8.3	5.7	490.18	TS	1	Chironomid	1	2	0.35
						Daphnia	80	2	2.96
Mi02-17	8.1	5.3							
Mi02-18	9.3	8.1	446.96	M	2	unknown insect	1	4	0.23
Mi02-19	8.5	6.3							
Mi02-20	9.0	7.2							
Mi02-21	7.0	3.8							
Mi02-22	7.5	4.3							
Mi02-23	8.5	6.0							
Mi02-24	7.1	3.8							
Mi02-25	8.1	5.8							
Mi02-26	8.9	7.9							
Mi02-27	7.7	4.4							
Mi02-28	9.5	8.0							
Mi02-29	8.1	5.2	467.48	F	1	Nematod	1	5	0.29
						Diptera larvae	1	4	0.16
						Daphnia	100	2	2.4
Mi02-30	7.0	3.5	493.75	TS	1	Ostracod	1	3	0.15
						Daphnia	140	2	2.02
Mi02-31	7.7	4.9	462.59	TS	1	Chironomid	2	3	0.28
						Daphnia	180	2	2.69
Mi02-32	11.5	13.8	538.64	M	3	empty			

Mi02-33	8.7	6.8							
Mi02-34	8.7	5.8							
Mi02-35	8.5	6.2							
Mi02-36	8.0	5.2							
Mi02-37	7.0	3.7	405.58	TS	1	Daphnia	680	0.8	2.32
						Chironomid	2	2	0.13
Mi02-38	8.5	6.2							
Mi02-39	8.2	5.4							
Mi02-40	8.4	5.9							
Mi02-41	9.5	9.4	472.16	F	2	empty			
Mi02-42	8.0	5.6							
Mi02-43	8.8	6.5							
Mi02-44	10.3	11.1	507.15	F	2	unknown	1	5	4.78
Mi02-45	6.7	3.3	462.84	TS	1	Daphnia	1440	2	2.29
						Chironomid	1	2	0.01
Mi02-46	8.6	5.9							
Mi02-47	7.9	4.8							
Mi02-48	9.1	6.7							
Mi02-49	8.7	7.0							
Mi02-50	7.2	4.1	392.71	TS	1	Daphnia	440	2	1.5
Mi02-51	9.7	8.7	548.35	M	2	empty			
Mi02-52	8.9	6.2							
Mi02-53	8.6	6.1							
Mi02-54	8.8	7.0	459.49	?	2	empty			
Mi02-55	8.2	5.4							
Mi02-56	9.2	7.5							
Mi02-57	7.5	4.3	406.12	TS	1	Tricoptera	1	2	0.09
						Daphnia	2	2	0.19
						Chironomid	1	10	0.07
						Ephemeroptera	1	5	0.23
Mi02-58	8.5	5.9							
Mi02-59	8.4	6.1							
Mi02-60	8.6	6.2							
Mi02-61	9.1	7.3	480.86	M	2	unknown	56	5	1.01
Mi02-62	9.0	7.3							
Mi02-63	8.6	6.4							
Mi02-64	6.2	2.6	414.56	TS	1	Daphnia	864	2	1.6
						Dipteran	1	1	0.11
Mi02-65	9.1	7.7	424.97	M	2	Lepidoptera	1	9	0.32
						Daphnia	20	2	1.07
Mi02-66	8.4	6.5							
Mi02-67	8.3	5.7							
Mi02-68	6.7	2.9	452.85	TS	1	Daphnia	600	2	1.33
Mi02-69	7.6	4.8							
Mi02-70	7.2	3.9	433.32	TS	1	Daphnia	200	2	0.93
Mi02-71	5.9	2.2	422.00	TS	1	Daphnia	1920	2	2.05
Mi02-72	9.1	8.0	493.78	M	2	Daphnia	52	2	2.51
Mi02-73	8.0	4.7	462.41	M	1	Daphnia	440	2	1.99

Mi02-74	8.3	5.6							
Mi02-75	8.6	6.1							
Mi02-76	8.6	5.9							
Mi02-77	8.1	4.9							
Mi02-78	6.2	2.6	354.64	TS	1	Daphnia	560	2	1.97
Mi02-79	7.8	4.9							
Mi02-80	15.3	27.1	490.86	M	5	empty			
Mi02-81	15.4	27.3	519.72	F	4	empty			
Mi02-82	12.5	15.2	540.23	M	3	Lepidoptera	1	10	9.18
Mi02-83	10.7	10.2	503.99	M	2	Chironomid	1	4	0.09
						Trichopterans	8	3	2.72
Mi02-84	14.0	22.5	490.20	M	4	empty			
Mi02-85	11.1	11.3	547.11	M	3	empty			
Mi02-86	13.0	15.1	524.58	F	2	Odonata	2	20	35.27
						Trichoptera	5	5	1.78
Mi02-87	11.5	12.9	435.61	F	2	empty			
Mi02-88	12.4	15.9	499.33	M	2	empty			
Mi02-89	10.3	8.8	360.63	M	2	Trichoptera	2	8	0.68
						Odonata	1	8	2.95
Mi02-90	13.4	19.9	509.33	M	4	empty			
Mi02-91	13.3	18.1	443.39	M	3	empty			
Mi02-93	12.6	17.6	413.77	M	3	empty			
Mi02-94	13.3	18.6	541.21	M	2	empty			
Mi02-95	14.2	21.5	518.20	F	4	empty			
Mi02-96	12.7	18.1	548.06	F	3	Trichoptera	14	6	8.63
						Amphipod	1	5	0.4
Mi02-97	13.2	20.5	549.91	M	4	empty			
Mi02-98	15.1	24.8	494.60	M	4	empty			
Mi02-99	12.0	14.4		F	3	black fly	1	2	0.1
						Trichoptera	1	2	0.11
Mi02-100	14.8	22.2	531.95	M	4	empty			
Mi02-101	13.4	17.6	465.77	F	4	empty			
Mi02-102	14.0	20.3	541.62	M	4	empty			
Mi02-103	13.2	18.4	623.05	M	4	Trichoptera	3	5	2.4
<b>Lake Hannah</b>									
Ha02-1	6.6	3.3		TS	1	Zoop.	232	1	5.31
Ha02-2	6.8	3.2		TS	1	Chironomid	1	2	0.08
Ha02-3	7.3	4.2		F	1	Zoop.	40	1	2.32
						Chironomids	7	4	0.43
Ha02-4	7.8	5.3		TS	1	empty			
Ha02-5	7.7	4.7		TS	1	Trichoptera	2	5	1.59
Ha02-7	6.4	2.7							
Ha02-8	7.1	3.8							
Ha02-9	6.9	3.4							
Ha02-10	6.2	2.9							
Ha02-11	6.7	3.3		TS	1	empty			
Ha02-12	6.6	3.4							
Ha02-13	7.6	4.9		F	1	Trichoptera	1	3	0.02

Ha02-14	6.6	3.1	TS	1	Chironomids	13	4	2.6
Ha02-15	6.5	2.9			empty			
Ha02-16	6.9	3.3						
Ha02-17	7.0	3.5						
Ha02-18	6.8	2.9	F	1	Daphnia	1	1	0.03
Ha02-19	7.1	3.9						
Ha02-20	7.0	3.5						
Ha02-21	7.0	3.8						
Ha02-22	6.9	3.6	F	2	empty			
Ha02-23	8.1	5.8						
Ha02-24	7.6	4.4			Odonata	1	15	3.82
Ha02-25	6.5	3.2						
Ha02-26	7.3	4.3	TS	2				
Ha02-27	7.6	4.6						
Ha02-28	7.2	4.0						
Ha02-29	6.4	3.5						
Ha02-30	7.6	4.7						
Ha02-31	6.8	3.1						
Ha02-32	7.3	4.3						
Ha02-33	8.0	5.2			empty			
Ha02-34	7.1	3.4						
Ha02-35	6.6	3.0						
Ha02-36	7.2	3.8						
Ha02-37	8.7	6.2						
			M	2	Chironomid	12	4	1.58
					unknown	1	6	0.13
Ha02-38	7.2	4.0						
Ha02-39	7.1	4.3						
Ha02-40	7.1	3.5	M	1				
Ha02-41	6.7	3.1						
Ha02-42	6.4	2.9						
Ha02-43	7.4	4.3						
Ha02-44	6.5	3.1						
Ha02-45	7.9	5.1			empty			
Ha02-46	6.0	2.3						
Ha02-47	7.4	4.6						
Ha02-48	6.7	3.1						
Ha02-49	7.6	4.9			Daphnia	132	1	3.53
					Diptera	2	3	0.44
Ha02-50	7.5	4.7						
Ha02-51	6.5	3.8						
Ha02-52	6.8	3.9						
Ha02-53	7.6	4.9						
Ha02-54	6.8	3.4						
Ha02-55	7.6	4.9						
Ha02-56	6.2	2.9						
Ha02-57	6.5	3.2						
Ha02-58	7.3	4.0						

Ha02-59	6.8	3.3						
Ha02-60	6.7	3.1						
Ha02-61	6.2	2.9						
Ha02-62	6.0	2.6	TS	1				
Ha02-63	6.5	2.7						
Ha02-64	7.4	4.0						
Ha02-65	6.2	2.9						
Ha02-66	6.6	3.1						
Ha02-67	6.0	2.5						
Ha02-68	6.0	2.5						
Ha02-69	6.0	2.4						
Ha02-70	6.2	2.9						
Ha02-71	7.7	5.1						
Ha02-72	7.2	4.2						
Ha02-73	6.8	3.3						
Ha02-74	6.9	3.5						
Ha02-75	7.4	4.2						
Ha02-76	6.1	2.7						
Ha02-77	6.7	3.1						
Ha02-78	7.0	3.7	TS	1	Chironomids	68	2	1.31
					Diptera	1	2	0.11
Ha02-79	7.2	4.4						
Ha02-80	6.3	2.7						
Ha02-81	6.7	3.4						
Ha02-82	6.8	3.4						
Ha02-83	7.0	3.3						
Ha02-84	5.4	2.1						
Ha02-85	6.5	3.1						
Ha02-86	6.8	3.2						
Ha02-87	7.3	3.8						
Ha02-88	6.4	2.7						
Ha02-89	7.1	3.5						
Ha02-90	7.6	5.0						
Ha02-91	7.5	4.2						
Ha02-92	7.0	3.9						
Ha02-93	6.8	3.1						
Ha02-94	6.5	3.0						
Ha02-95	7.6	4.9						
Ha02-96	7.1	3.7						
Ha02-97	6.7	3.4						
Ha02-98	8.4	5.6						
Ha02-99	7.1	3.6						
Ha02-100	6.9	3.5						
Ha02-101	6.1	2.2	TS	1	Zoop.	344	0.8	3.79
					Diptera	1	1	0.01
Ha02-102	6.0	2.4						
Ha02-103	7.0	3.2						
Ha02-104	7.2	4.2	F	1	empty			

Ha02-105	8.3	6.0	M	1	Daphnia	140	1	4.4
					Chironomids	6	3	0.58
Ha02-106	8.3	6.2	TS	2	Chironomid	1	3	0.04
					Trichoptera	1	3	0.03
Ha02-108	10.6	12.3	F	3	empty			
Ha02-107	10.4	10.5						
Ha02-109	10.4	11.4						
Ha02-110	10.4	11.3	M	3	Trichoptera	23	3	8.34
Ha02-111	10.5	13.5	M	3	Trichoptera	11	3	2.5
					Chironomid	1	10	0.22
Ha02-112	10.7	12.1						
Ha02-113	10.2	10.4	F	3	Diptera	3	5	0.6
					Chironomids	70	10	9.92
Ha02-114	11.1	15.0	F	4	Chironomids	26	6	8.6
					Diptera	2	7	0.94
Ha02-115	10.4	11.0						
Ha02-116	10.2	10.6						
Ha02-117	10.4	11.9						
Ha02-118	10.3	10.7						
Ha02-119	10.9	11.5						
Ha02-120	9.8	8.6	M	4	empty			
Ha02-121	10.3	10.2	F	3	Diptera	2	3	0.3
Ha02-122	10.2	10.6	M	2	empty			
Ha02-123	10.3	11.0	F	2	Chironomids	56	6	6.45
Ha02-124	10.8	13.0	F	5	Chironomids	1	6	0.09
					Trichopterans	3	5	1.34
					Odonata	2	15	56.42
Ha02-125	10.5	10.9						
Ha02-126	10.5	11.8						
Ha02-127	11.1	13.3						
Ha02-128	12.0	17.9	F	4	Diptera	160	7	40.64
Ha02-129	11.6	15.2						
Ha02-130	12.2	16.4	F	4	Chironomids	1	8	0.28
					Trichoptera	10	5	1.43
Ha02-131	11.0	13.1						
Ha02-132	10.7	13.3						
Ha02-133	12.7	18.5	F	4	Trichoptera	10	4	9.17
Ha02-134	11.5	16.1	F	4	Diptera	80	8	23.19
Ha02-135	10.8	12.9						
Ha02-136	11.5	14.7	F	4	Diptera	80	8	19.88
					Trichoptera	1	3	3.52
Ha02-137	12.2	16.5						
Ha02-138	12.3	17.5	F	3	empty			
Ha02-139	11.5	16.6	F	3	fish (darter)	1	50	136.66
					Diptera	4	8	1.87
Ha02-140	10.5	11.3						



Ha02-141	11.2	14.6						
Ha02-142	11.0	13.0						
Ha02-143	11.5	15.1						
Ha02-144	12.7	20.8	F	3	Trichoptera	30	3	8.32
Ha02-145	10.6	13.1						
Ha02-146	11.0	13.1						
Ha02-147	11.6	14.7						
Ha02-148	10.3	10.3	?	2	empty			
Ha02-149	10.7	11.6	F	3	Diptera	136	8	13.23
					Trichoptera	5	3	0.39
Ha02-150	10.6	13.5						
Ha02-H1	10.6	10.1						
Ha02-H2	11.6	12.1	F	3	Odonata	1	15	2.45
					Diptera	124	8	12.95
Ha02-H3	11.4	14.6						
Ha02-H4	10.9	11.0						
Ha02-H5	11.1	11.5						
Ha02-H6	10.7	11.0						
Ha02-H7	11.1	11.7						
Ha02-H8	10.5	10.0	?	3	Diptera	5	6	1.54
					Trichoptera	5	3	2.16
Ha02-H9	11.7	14.7						
Ha02-H10	10.3	10.2						
Ha02-H11	11.0	11.5						
Ha02-H12	11.7	13.8						
Ha02-H13	12.1	14.8						
Ha02-H14	12.0	16.1						
Ha02-H15	12.2	14.3						
Ha02-H16	10.9	10.1						
Ha02-H17	11.4	10.0						
Ha02-H18	11.8	13.6						
Ha02-H19	11.9	14.0	M	3	empty			
Ha02-H20	11.6	12.4						
Ha02-H21	11.2	12.1						
Ha02-H22	11.8	15.3	F	3	Trichoptera	1	6	1.27
Ha02-H23	11.5	12.3						
Ha02-H24	12.1	15.1						
Ha02-H25	12.5	15.1						
Ha02-H26	12.4	14.3	F		empty			
Ha02-H27	11.9	13.4						
Ha02-H28	12.5	16.5						
Ha02-H29	12.4	16.8						
Ha02-H30	13.0	19.2	F	4	Tricoptera	2	3	0.36
					Odonata	1	20	34.27

## Appendix D: Stable Isotope Data

Fish #	%C	%N	Delta 13C	Delta 15N
<b>Lake Geneva</b>				
Ge02-109	38.86	12.18	-28.18	7.73
Ge02-110	46.08	14.33	-27.68	7.53
Ge02-127	46.81	14.63	-27.9	7.26
Ge02-34	25.46	7.84	-28.77	8.24
Ge02-37	0	0	-28.46	6.65
Ge02-39	54.91	17.11	-28.59	7.94
Ge02-42	43.29	13.33	-28.14	6.95
Ge02-44	45.16	13.97	-28.7	8.01
Ge02-45	46.34	14.35	-28.62	7.53
Ge02-49	45.95	14.26	-27.71	7.33
Ge02-53	43.6	13.42	-27.72	7.59
Ge02-57	44.31	13.77	-26.25	6.62
Ge02-68	44.02	13.62	-27.7	7.56
Ge02-7	48.51	14.95	-28.2	7.38
Ge02-71	43.85	13.57	-27.99	7.95
Ge02-79	40.64	12.45	-29.39	7.74
Ge02-81	41.79	12.9	-30.18	7.95
Ge02-87	45.85	14.23	-29.11	8.21
Ge02-88	44.77	13.86	-27.64	8.09
Ge02-89	47.43	14.69	-28.55	6.71
Ge02-91	43.63	13.5	-28.65	7.96
Ge02-92	45.42	14.23	-27.81	7.67
Ge02-99	40.98	12.7	-28.93	6.6
Ge02-112	48.79	14.62	-27.73	7.91
Ge02-120	44.27	13.55	-28.7	7.42
Ge02-126	47.76	14.73	-28.88	7.77
Ge02-40	46.86	14.57	-28.37	8.01
Ge02-64	42.87	13.28	-27.1	6.83
Ge02-102	41.89	13.03	-28.57	7.38
Ge02-111	43.79	40.79	-28.55	7.39
Ge02-113	46.71	14.59	-29.2	7.35
Ge02-118	52.5	16.06	-29.34	7.58
Ge02-122	49.17	15.04	-27.68	7.46
Ge02-20	36.36	11.15	-28.81	8.52
Ge02-23	40.81	12.26	-27.08	6.8
Ge02-33	56.07	17.45	-27.61	7.48
Ge02-4	36.62	11.2	-32.46	5.14
Ge02-41	36.98	11.36	-26.76	6.99
Ge02-66	42.03	13.12	-27.24	8.49
Ge02-72	47.01	14.63	-29.26	8.49
Ge02-8	52.87	16.41	-27.56	6.84
Ge02-40 duplicate	47.52	14.6	-27.94	7.38
Ge02-68 duplicate	47.62	14.61	-28.19	7.44
Ge02-99 duplicate	46.85	14.48	-28.36	7.16
Ge02-126 duplicate	54.18	16.75	-28.85	7.38

**Lake Crowley**

Cr02-109	41.63	12.82	-27.63	6.79
Cr02-116	46.96	14.49	-30.39	6
Cr02-117	46.59	14.5	-30.67	6.25
Cr02-132	49.22	15.05	-28.42	7.5
Cr02-161	48.47	15.15	-29.38	7.94
Cr02-169	46.86	14.45	-32.39	7.19
Cr02-50	39.55	11.98	-27.14	8.33
Cr02-103	46.58	14.2	-30.63	7.44
Cr02-120	47	14.58	-25.34	6.48
Cr02-38	40.14	12.15	-28.14	7.97
Cr02-41	46.59	14.36	-29.19	8.34
Cr02-48	44.4	13.32	-27.51	5.69
Cr02-55	45.81	13.6	-27.57	8.97
Cr02-81	46.56	14.29	-28.35	7.22
Cr02-108	48.08	14.61	-27.38	6.37
Cr02-110	47.97	14.37	-28.09	8.58
Cr02-112	49.72	15.3	-28.28	8.01
Cr02-118	48.09	14.9	-28.64	7.57
Cr02-119	45.3	13.22	-30.78	7.8
Cr02-122	42.44	12.96	-26.85	8.48
Cr02-123	46.46	14.2	-28.63	8.12
Cr02-131	46.66	14.32	-27.66	7.37
Cr02-138	48.43	14.65	-29.78	9.02
Cr02-151	40.28	12.22	-28.08	9.33
Cr02-164	55.05	16.78	-26.88	10.01
Cr02-23	42.3	12.83	-25.09	7.56
Cr02-34	41.86	12.53	-28.87	8.08
Cr02-51	47.24	14.15	-26.99	8.61
Cr02-52	44.27	13.69	-30.09	6.81
Cr02-64	28.2	8.39	-26.61	6.34
Cr02-7	41.42	12.63	-28.68	8.36
Cr02-73	44.21	13.45	-31.39	7.56
Cr02-90	44.01	13.56	-29.07	7.6
Cr02-98	45.33	13.82	-30.31	6.42
Cr02-111	48.08	14.72	-25.66	8.87
Cr02-124	44.95	13.47	-28.09	7.77
Cr02-152	48.58	14.17	-26.56	9.31
Cr02-153	47.84	14.13	-28.01	7.86
Cr02-165	57.81	17.35	-27.09	9.41
Cr02-1	33.75	10.27	-26.92	8.58
Cr02-4	40.3	12.18	-27.53	7
Cr02-42	44.91	13.62	-26.38	8.34
Cr02-45	39.73	11.92	-25.67	6.66
Cr02-49	42.56	12.84	-27.31	6.72
Cr02-5	37.48	11.41	-26.08	7.32
Cr02-69	45.44	13.32	-25.36	7.31
Cr02-72	44.94	13.7	-29.1	8.16
Cr02-85	47.54	14.07	-26.25	6.53
Cr02-95	46.03	13.91	-27.67	8.69

**Lake Richard**

Ri02-43	43.43	13.29	-23.51	6.77
Ri02-R10	46.59	14.52	-25.25	7.66
Ri02-84	44.89	14.08	-25.52	8.38
Ri02-14	43.32	13.63	-25.69	8.26
Ri02-85	45.93	14.15	-25.92	6.11
Ri02-72	47.48	14.83	-32.22	6.08
Ri02-15	40.6	12.57	-22.64	7.17
Ri02-92	45.53	14.16	-33.3	6.29
Ri02-49	42.68	13.31	-28.42	9.64
Ri02-54	47.04	14.3	-29.01	9.2
Ri02-46	38.2	11.82	-28.94	9.26
Ri02-18	50.36	15.11	-29.44	10.11
Ri02-64	43	13.14	-29.58	9.61
Ri02-66	45.96	14.31	-30.58	10.07
Ri02-65	46.55	14.17	-30.1	10.7
Ri02-42	46.45	14.34	-31.71	9.04
Ri02-90	44.64	13.89	-25.7	8.93
Ri02-78	47.73	14.81	-25.21	7.48
Ri02-69	46.62	13.82	-27.83	7.85
Ri02-82	41.92	13.01	-27.83	6.12
Ri02-83	47.15	14.84	-30.73	6.94
Ri02-94	45.9	14.2	-31.94	6.67
Ri02-93	47.68	14.55	-30.56	7.97
Ri02-96	47.25	14.33	-22.98	6.98
Ri02-98	47.53	14.13	-30.96	6.89
Ri02-99	46.63	14.07	-30.59	7.79
Ri02-95	36.4	11.17	-24.62	9.97
Ri02-100	43.39	13.56	-25.5	11.14
Ri02-R6	45.91	14.37	-23.98	10
Ri02-32	44.45	13.3	-27.95	8.31
Ri02-39	46.16	14.12	-30.72	10.07
Ri02-68	44.92	13.77	-29.73	5.86
Ri02-34	48.19	14.64	-28.13	8.93
Ri02-37	46.01	13.98	-29.46	9.78
Ri02-19	48.06	14.94	-32.06	8.66
Ri02-88	47.41	14.42	-23.37	7.05
Ri02-61	49.6	15.37	-32.14	9.71
Ri02-97	47.61	14.82	-30.8	6.89
Ri02-43 duplicate	45.94	14.17	-22.94	7.12
Ri02-72 duplicate	44.3	13.88	-32.29	5.57
Ri02-94 duplicate	46.24	14.59	-32.61	7.02

**Lake Middle**

Mi02-82	44.82	14.47	-25.63	9.57
Mi02-89	36.48	11.01	-25.2	8.16
Mi02-96	48.25	15.03	-23.79	8.7
Mi02-103	44.89	14.02	-27.67	8.8
Mi02-4	51.62	16.36	-26.29	9.41
Mi02-8	42.14	13.31	-27.12	10.3
Mi02-32	44.82	14.36	-26.47	8.72

Mi02-41	45.12	14.54	-26.23	9.01
Mi02-51	45.75	14.72	-26.53	9.82
Mi02-54	46.36	14.94	-24.95	9.57
Mi02-80	44.58	14.13	-25.52	10.09
Mi02-81	37.95	12.23	-26.95	9.65
Mi02-84	45.22	14.4	-26.19	9.78
Mi02-85	38.83	12.38	-26.76	8.52
Mi02-88	43.01	13.31	-26.26	8.29
Mi02-90	41.01	12.48	-27.64	9.17
Mi02-91	50.74	15.47	-27.04	8.43
Mi02-93	60.35	18.44	-26.59	8.65
Mi02-94	41.72	12.98	-27.97	8.33
Mi02-95	36.33	11.23	-23.62	8.7
Mi02-97	61.73	19.33	-26.46	8.72
Mi02-98	43.17	13.53	-27.39	8.8
Mi02-100	52.66	16.37	-27.39	8.45
Mi02-101	44.79	14.08	-26.96	8.87
Mi02-102	54.36	17.06	-26.77	9.46
Mi02-1	38.97	12.29	-24.3	9.4
Mi02-2	44.95	14.32	-26.43	8.62
Mi02-29	44.76	14.31	-26.43	9.87
Mi02-30	40.71	12.79	-25.52	6.88
Mi02-31	46.83	15.17	-26.16	7.99
Mi02-37	33.43	10.64	-24.85	8.97
Mi02-45	45.76	14.47	-25.66	9.53
Mi02-50	39.53	12.77	-25.88	10.26
Mi02-64	47.6	15	-24.91	9.46
Mi02-65	45.31	14.49	-26.11	8.79
Mi02-68	46.42	14.75	-26.31	9.28
Mi02-70	47.35	15.08	-27.45	8.14
Mi02-71	45.85	14.58	-25.41	9.89
Mi02-72	43.6	13.76	-26.98	8.91
Mi02-73	44.94	14.34	-26.79	10.84
Mi02-78	47.05	14.84	-26.06	9.02
Mi02-3	43.46	13.75	-26.38	8.25
Mi02-6	45.24	14.41	-25.7	7.76
Mi02-9	46.59	14.81	-26.95	9.11
Mi02-13	30.8	9.88	-25.07	9.38
Mi02-14	41.05	13.25	-23.02	9.14
Mi02-16	43.94	13.87	-26.04	8.86
Mi02-18	42.55	13.58	-27.76	9.07
Mi02-44	42.75	13.57	-26.34	9.59
Mi02-57	46.17	14.72	-24.7	9.24
Mi02-61	46.74	14.88	-26.61	9.4
Mi02-83	44.31	14.1	-26.25	8.37
0+ Perch	32.67	10.11	-28.15	7.83
Mi02-16 duplicate	48.4	15.13	-26.18	7.97
Mi02-50 duplicate	35.03	11.12	-26.44	8.41
Mi02-72 duplicate	42.26	13.17	-27.08	8.63
Mi02-87 duplicate	54.24	17.38	-25.22	8.54

Mi02-98 duplicate	38.41	12.23	-27.14	8.18
<b>Lake Hannah</b>				
Ha02-24	43.42	13.26	-23.3	8.99
Ha02-H2	38.85	11.92	-27.62	8.2
Ha02-124	46.64	14.32	-23.55	8.06
Ha02-130	45.3	13.99	-26.96	8.26
Ha02-128	37.39	11.46	-25.98	8.48
Ha02-H30	44.1	13.86	-27	8.32
Ha02-62	37.67	11.32	-26.52	9.18
Ha02-14	40.45	12.26	-26.62	7.28
Ha02-104	48.44	15.03	-25.37	8.92
Ha02-33	45.66	14	-26.16	7.87
Ha02-23	50.47	15.46	-24.3	8.03
Ha02-120	47.24	14.57	-27.69	8.08
Ha02-148	47.83	14.84	-24.68	7.49
Ha02-122	46.85	14.49	-27.64	7.99
Ha02-108	49.18	15.47	-26.67	7.47
Ha02-H19	44.66	13.67	-27.1	8.33
Ha02-H26	42.84	13.36	-26.05	8.42
Ha02-138	45.25	14.17	-24.28	7.76
Ha02-139	44.33	13.79	-26.76	7.38
Ha02-101	41.87	12.87	-25.82	8.44
Ha02-78	44.51	13.49	-27	7.55
Ha02-5	38.18	11.55	-25.61	7.56
Ha02-106	49.56	15.09	-26.76	7.39
Ha02-37	41.23	12.57	-26.2	7.64
Ha02-H8	37.53	11.58	-28.31	10.93
Ha02-121	45.98	14.33	-26.94	8.47
Ha02-113	46.85	14.49	-27.49	8.42
Ha02-123	46.76	14.37	-27.46	7.49
Ha02-110	45.56	14.07	-27.48	8.16
Ha02-149	42.8	13.26	-27.22	7.85
Ha02-111	45.94	14.02	-28.34	7.21
Ha02-136	43.28	13.12	-29.05	6.51
Ha02-114	45.8	14.27	-27.42	7.97
Ha02-H22	45.36	14.02	-26.69	8.35
Ha02-134	45.28	14.04	-27.52	8.53
Ha02-133	43.1	13.32	-24.26	8.12
Ha02-144	49	15.15	-25.86	8.73
Ha02-14 duplicate	44.97	14.05	-27.02	9.17
Ha02-108 duplicate	43.19	13.9	-26.59	8.65
Ha02-128 duplicate	48.28	15.06	-25.73	8.61
Ha02-H2 duplicate	45.78	14.37	-27.31	7.05
Ha02-H30 duplicate	48.69	15.5	-27.31	8.6
<b>Invertebrate taxa</b>	<b>%C</b>	<b>%N</b>	<b>Delta 13C</b>	<b>Delta 15N</b>
<b>Lake Geneva</b>				
Zooplankton	50.31	7.70	-30.46	4.25
Diptera	46.29	10.91	-34.16	2.10
Trichoptera	58.73	7.65	-31.26	0.75
Coleoptera	50.72	10.25	-26.95	0.05

Hyallela	28.35	5.46	-22.34	-1.51
Gastropoda	48.33	13.10	-26.47	0.56
Ephemeroptera	51.28	10.88	-28.54	0.34
Hemiptera	52.67	12.76	-27.64	5.20
Megaloptera	52.19	9.37	-28.96	2.61
Zygoptera	49.19	14.33	-27.16	4.08
Gomphidae	53.54	6.66	-28.32	0.40
Trichoptera	51.57	11.76	-25.59	2.82
Hexagenia	52.07	10.34	-29.63	2.27
Hexagenia duplicate	51.33	10.29	-29.65	0.80
<b>Lake Crowley</b>				
Zooplankton	45.7	7	-27.46	10.02
Chironomids	40.57	10.45	-31.512	4.111
Chironomids duplicate	40.3	10.37	-31.663	3.782
Red Chironomids	47.85	12.28	-34.867	3.508
Chaoborus	41.58	16.96	-28.593	5.087
Ephemeroptera	38.82	10.31	-26.087	1.284
<b>Lake Richard</b>				
Chironomids	40.71	7.95	-27.289	3.441
Trichoptera	38.33	9.16	-26.874	3.484
Amphipoda	30.99	7.64	-24.701	3.033
Odonata	36.63	9	-26.423	4.49
Odonata duplicate	31.77	7.77	-26.691	4.578
<b>Lake Middle</b>				
Chironomids	40.39	9.9	-22.206	3.698
Red Chironomids	47.64	11.98	-29.264	3.836
Amphipoda	38.34	8.83	-26.279	2.798
Leptoceridae	43.67	11.24	-22.313	4.399
Ephemeroptera	41.23	9.54	-26.132	1.243
<b>Lake Hannah</b>				
Chironomids	49.96	11.62	-23.741	2.862
Polycentropodidae	38.24	9.9	-27.127	5.079
Leptoceridae	41.08	9.47	-22.127	4.787

