

Bioenergetic costs of heavy metal exposure in yellow perch (*Perca flavescens*): in situ estimates with a radiotracer (^{137}Cs) technique

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Abstract: While the flow of energy is understood to determine the growth of organisms and the productivity of ecosystems, little is known about the sublethal effect of pollutants on the energetic efficiency of wild populations. We used field estimates of fish growth coupled to in situ estimates of food consumption rates obtained from the mass balance of a globally dispersed, trophically transferred radiotracer (^{137}Cs) to demonstrate the bioenergetic impairment of yellow perch (*Perca flavescens*) from lakes polluted by heavy metals (Cd, Cu, and Zn). Annual growth increment relative to the total energy budget (conversion efficiency) was about three times lower in cortisol-impaired yellow perch from metal-polluted lakes relative to yellow perch from reference lakes (4.2% compared with 10.8%), suggesting that fish exposed to pollutants experienced greater total energetic costs. In addition, metal-polluted lakes were dominated by adult yellow perch populations and simplified prey bases, suggesting that effects are occurring at multiple levels of biological organization. Our in situ bioenergetic approach to toxicity assessment provides a measurable and ecologically relevant endpoint for assessing the sublethal effects of pollutants on fish communities.

Résumé : Bien qu'on sache que le flux d'énergie détermine la croissance des organismes et la productivité des écosystèmes, on sait peu de choses de l'effet subléthal des polluants sur l'efficacité énergétique des populations sauvages. Nous avons utilisé des estimations de la croissance des poissons dans la nature couplées à des estimations des taux d'alimentation in situ obtenues à partir du bilan massique d'un radiotracteur présent partout sur la Terre et transmis par voie trophique (^{137}Cs) pour déterminer la perturbation bioénergétique de la perchaude (*Perca flavescens*) de lacs pollués par des métaux lourds (Cd, Cu et Zn). L'incrément annuel de croissance en rapport avec le bilan énergétique global (efficacité de conversion) était environ 3 fois plus bas chez les perchaudes des lacs pollués par les métaux, dont le métabolisme du cortisol était perturbé, que chez les perchaudes de lacs témoins (4,2% comparativement à 10,8%), ce qui indique que les coûts énergétiques totaux sont plus élevés chez les poissons exposés aux polluants. De plus, dans les lacs pollués par les métaux, les populations de perchaudes adultes étaient dominantes et la diversité des proies était faible, ce qui laisse penser que les effets des polluants se font sentir à divers niveaux du biote. Notre approche bioénergétique in situ en matière d'évaluation de la toxicité offre un paramètre mesurable et écologiquement pertinent pour évaluer les effets sublétaux des polluants sur les communautés de poissons.

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Introduction

Wild fisheries comprise about one quarter of the animal protein consumed by humans, and an increasing fraction of this resource is being degraded by pollutants resulting in

contaminated flesh and toxic stress to populations and the ecosystems that support them (Abramovitz 1996). Aquatic biota is especially impacted in freshwater systems; as many as 37% of fish species, 67% of mussels, and 65% of crayfish are considered endangered in North America (Brown 1997). The extent to which toxic stress from low-level exposure to pollutants such as heavy metals and organic contaminants may be a factor in this loss of ecological integrity is unknown and difficult to assess with conventional toxicological techniques.

Toxicologists generally measure toxicity with death or morbidity of living organisms (Sprague 1973). While death is a finite endpoint and easily measured in controlled laboratory conditions, the measurement of survival in wild organisms is inherently difficult (Heath 1995). Equally problematic is the use of biomarkers of sublethal toxicity because most are biomarkers of exposure rather than of effect (i.e., measures of health or ecological performance; McCarthy and Munkittrick 1996). A potentially promising measure of performance is the thermodynamic parameter energy. En-

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ergy metabolism has long been the currency of performance preferred by both physiological (Bartholomew 1982) and ecosystem scientists (Lindeman 1942). Thus, to assess the impact of a chronic exposure to sublethal concentrations of a pollutant in a field setting, energy metabolism used as a performance response would seem to be a reasonable physiological and ecological approach to toxicity assessment.

Despite this logic, energetic approaches have gained little favour in ecotoxicology for reasons related to interpretability and practicality. For example, the most widely reported index of bioenergetic performance in fish is growth (e.g., Munkittrick and Dixon 1989). Growth is easily measured, and in bioenergetic budgets of the form

$$(1) \quad C = G + (SMR \cdot A) + SDA + F + U$$

where C is specific consumption rate (grams food per gram body mass per day), G is specific growth rate (somatic and gonadal) (grams per gram per day), SMR is standard metabolic rate (grams per gram per day), A is activity (dimensionless), SDA is specific dynamic action (grams per gram per day), F is egestion (grams per gram per day), and U is excretion (grams per gram per day) (Kitchell et al. 1977), growth is what remains after all other metabolic costs have been met. Any changes in metabolic rate (usually standard metabolic rate) brought about by a toxicological response should also affect growth. Indeed, laboratory studies have consistently demonstrated reduced growth in pollutant-exposed fish (e.g., Cope et al. 1994). However, if one were to attempt to evaluate the bioenergetic performance of a wild fish by measuring growth rate alone, interpretability would be confounded because a wild fish's growth is as much an expression of food intake as energy metabolism. Given that feeding levels for fish can vary considerably among populations, both naturally (Boisclair and Leggett 1989a) and as a possible consequence of pollution (Munkittrick and Dixon 1989), it becomes clear that growth, as an index of bioenergetic performance, would be interpretable only if scaled to the feeding rate of the fish; in other words, we need to measure conversion efficiency (the efficiency at which food energy is converted to growth). Reliable, in situ estimates of feeding rates are then required. Unfortunately, in order to accurately measure the feeding rates of wild fish, conventional techniques, based on gut content analysis (Elliot and Persson 1978), require large numbers of fish and extensive sampling effort (Trudel and Boisclair 1993), making such estimates logistically impractical. To overcome this logistical constraint, a more practical method of estimating consumption rates is required. Rowan and Rasmussen (1996) have recently employed a radiotracer (^{137}Cs) mass-balance technique to produce annually and seasonally integrated estimates of the feeding rates of wild fish. Their method requires considerably less field sampling effort, making it ideally suited to multilake comparisons.

The primary objective of this study was to apply the ^{137}Cs method of Rowan and Rasmussen (1996) to compare the bioenergetic performance (growth rate, consumption rate, and conversion efficiency) of yellow perch (*Perca flavescens*) from lakes of varying degrees of heavy metal pollution in Quebec. Previous studies (Brodeur et al. 1997) have shown that yellow perch from metal-polluted lakes are chronically stressed; they exhibit an impaired cortisol stress

response, a general bioindicator of chronic contaminant stress in fish (Hontela 1997). We hypothesized that such physiological impairment should have negative effects on the bioenergetic performance in yellow perch and that such effects may also be accompanied by changes at higher levels of biological organization such as changes in population and community characteristics.

Methods

Study sites

This study was conducted primarily in the mining region of Abitibi, northwestern Quebec, and includes five lakes along a metal contamination gradient (Couillard et al. 1995). Relative metal pollution of these lakes is indicated in Fig. 1 (also see Table 1) and is determined primarily by proximity to smelting operations in the city of Rouyn-Noranda and wind direction (Couillard et al. 1995). Lakes Dasserat and Opatatica are remote headwater lakes with no point sources of pollution and are classified as reference lakes. Lakes Osisko and Dufault are subject to point-source and atmospheric metal inputs and are classified as metal-polluted lakes. Finally, Lake Vaudray has been polluted by metals via atmospheric transport and is classified here as an intermediate lake.

In addition to the five Abitibi lakes, three other lakes were included in our sampling and analyses. Lake Memphremagog, located in the Eastern Townships (approximately 125 km east of Montreal) and remote from any industrial activity (Girard et al. 1998), was sampled and included in the set of reference lakes. Lake St. Louis, a fluvial lake in the St. Lawrence River immediately west of the island of Montreal, receives pollutant loading from multiple sources (Hontela et al. 1992). Although published Cd levels for this lake (situated near Beauharnois) are comparatively low (see Table 1), it was included in the intermediate set because yellow perch here have been shown to exhibit impaired cortisol stress response (Hontela et al. 1992; Girard et al. 1998), probably the result of high contamination by polycyclic aromatic hydrocarbons, polychlorinated biphenyls, and Hg. Finally, published bioenergetic data for yellow perch from the middle reaches of the Ottawa River near Pembroke, Ontario (Rowan and Rasmussen 1996), was included in our analyses to further complement the reference set. Reported levels for heavy metals in unionid bivalves (Metcalf-Smith et al. 1992) from the Ottawa River near this site indicate that metal pollution is minimal (Table 1). Other sources of pollution are unlikely to be problematic; upper reaches of the Ottawa River have been sampled by others as reference sites in ecotoxicological studies involving fish and amphibians (Branchaud et al. 1995; Gendron et al. 1997). Very little industry and agriculture exist between those sites and the middle reaches considered here (Primeau 1996). Table 1 is a summary of all the available metal data for all lakes considered as well as some limnological characteristics.

Sample collection and preparation

Yellow perch were collected in the fall of 1994 and 1995 from all lakes with multimesh experimental gill nets, hook and line, and seine. Blood samples were taken for cortisol analysis; a detailed discussion of methods and results is provided in Brodeur et al. (1997). Wet weight was recorded, opercular bones were removed for age determination, and stomach contents were isolated for determination of diet composition (individual prey items were identified to order) and ^{137}Cs analysis. Whole fish and pooled stomach contents (pooling of samples allowed for more precise ^{137}Cs determination and integrated the diet variability) were ashed at 450°C for 48 h and ^{137}Cs concentration was analysed by gamma spec-

Fig. 1. Map showing location, in relation to the copper smelting centre of Rouyn-Noranda, of the five lakes sampled in Abitibi, north-western Quebec (enlarged area, approximately 48°00'N, 79°00'W; average relative wind directions at Rouyn-Noranda are indicated by the vector diagram, modified from Couillard et al. 1995), and of three additional sites in southern Quebec (approximately 45°00'N, 73°00'W).

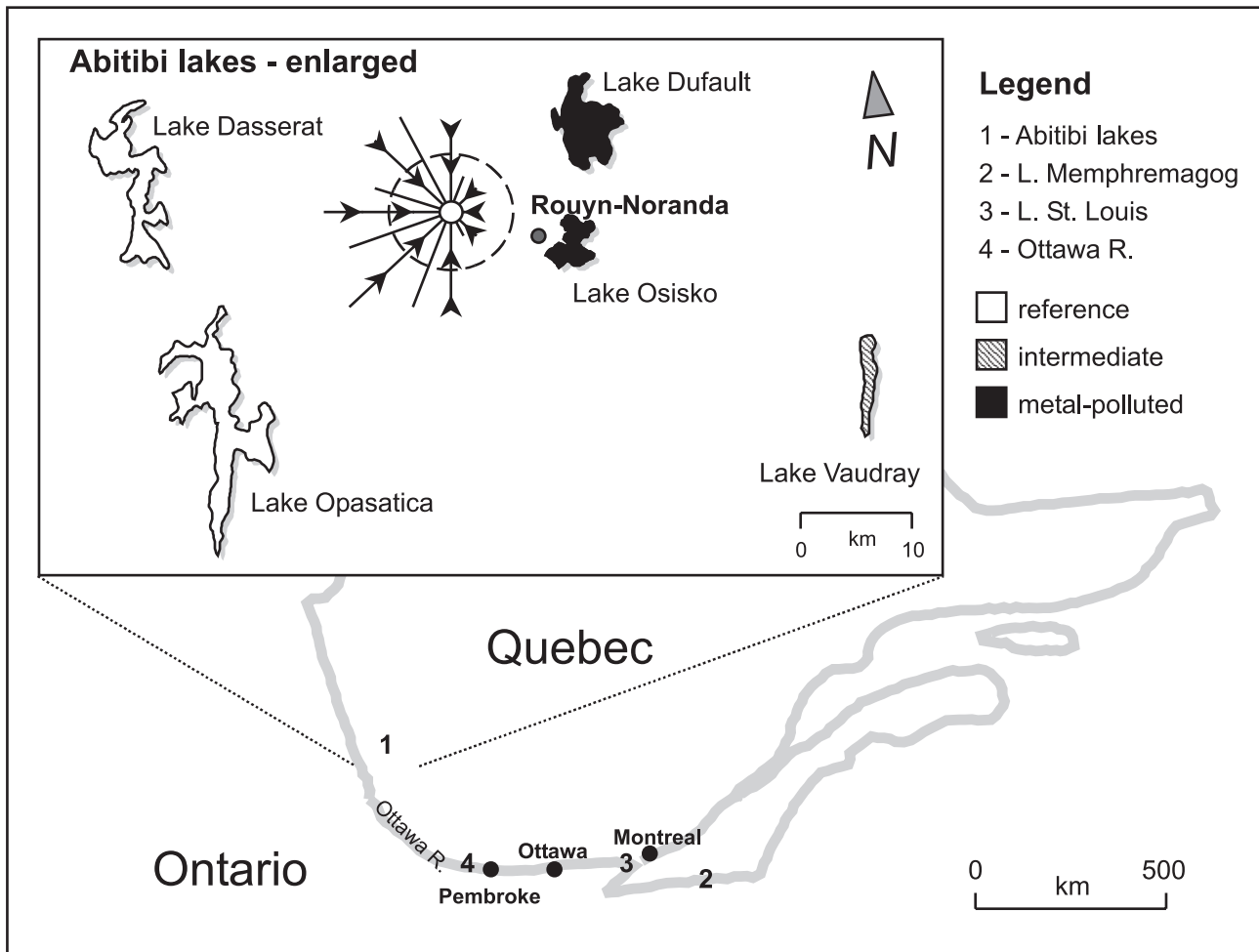


Table 1. Metal contamination profile for representative biota and limnological characteristics of the study sites.

	Group							
	Reference				Intermediate		Metal-polluted	
	Dasserat	Opasatica	Memphremagog	Ottawa River	St. Louis	Vaudray	Dufault	Osisko
Yellow perch liver metal concentrations ($\mu\text{g}\cdot\text{g dry weight}^{-1}$)^a								
Cd	5.3±0.6	2.9±0.4	<0.01 ^c		1.1 ^c	25.1±1.7	61.3±5.3	45.7±3.2
Cu	10.8±0.9	10.4±1.8				12.9±0.7	148.5±11.1	246.5±29.8
Zn	98.6±4.2	92.4±3.6				108.9±1.6	151.1±3.7	177.2±9.0
Unionid metal concentrations ($\mu\text{g}\cdot\text{g dry weight whole organism}^{-1}$)^b								
Cd		19.9	7.5	4.0–15.0	3	152		
Limnological characteristics								
pH	7.3	7.4	6.4–8.4 ^c	6.8 ^d	8.3 ^c	7.1	7.4	7.9
Secchi depth (m)	2.5	2	3.6–5.3 ^e			2.5	1.8	2.3
Conductivity ($\mu\text{S}\cdot\text{cm}^{-1}$)	72	88	130–158 ^c	42 ^d	226–300 ^c	48	173	300

Note: See the Methods section for explanation of the grouping scheme.

^aData obtained from Laflamme (1999).

^bData obtained from Tessier et al. (1993) for *Anodonta grandis* and from Metcalfe-Smith et al. (1992) and Metcalfe-Smith (1994) for *Elliptio complanata* and *Lampsilis radiata*.

^cData obtained from Girard et al. (1998).

^dData obtained from Gendron et al. (1997).

^eData obtained from Rasmussen (1988).

Table 2. ^{137}Cs concentration and assimilation efficiency (input data for eq. 3) of age 4+ yellow perch diets.

	$[^{137}\text{Cs}]_d$	α	Diet
Dasserat	3.32	0.32	78% ephemeropterans, 17% YOY, 5% crustaceans
Memphremagog	1.08	0.6	79% YOY, 12% crustaceans, 9% various insects
Opasatica	0.57	0.46	48% YOY, 44% various insects, 8% crustaceans
Ottawa River ^a	3.63	0.68	83% YOY, 14% various insects and crustaceans, 3% gastropods
Dufault	1.6	0.82	100% copepods
Osisko	2.09	0.55	100% chironomids
St. Louis	0.38	0.39	64% gammarids, 36% various insects
Vaudray	9.99	0.29	75% ephemeropterans, 25% gammarids

Note: Diets are represented by % volumetric prey contribution from pooled stomach contents by lake. YOY is predominantly young-of-the-year yellow perch and spottail shiner.

^aData obtained from Rowan and Rasmussen (1996), where YOY is predominantly young-of-the-year yellow perch.

trometry with a germanium coaxial well detector (model GCW 1521, Canberra Industries Inc.).

Bioenergetic analysis

We chose to compare the bioenergetic performance (growth rate, consumption rate, and conversion efficiency) of yellow perch between the ages of 3+ and 4+ primarily because this cohort, over the 2 years of sampling, was the only cohort sufficiently represented for among-lake comparisons (making up almost 40% of all fish captured). Specific daily growth rate (G , grams per gram per day) was calculated as

$$(2) \quad G = \ln \left(\frac{w_t}{w_0} \right) / 365$$

where w_t is the body mass (grams) of age 4+ fish in 1995 (time t) and w_0 is the body mass (grams) of age 3+ fish in 1994 (initial). Specific daily consumption rate (C , grams per gram per day) was estimated from an independently validated (Forseth et al. 1992) ^{137}Cs mass-balance model (Rowan and Rasmussen 1996):

$$(3) \quad C = \frac{(Q_t - Q_0 e^{-(E+D)t} + Q_g)(G + E + D)}{\alpha [^{137}\text{Cs}]_d w_0 (e^{Gt} - e^{-(E+D)t})}$$

where Q_t is the ^{137}Cs body burden (the product of ^{137}Cs concentration, $[^{137}\text{Cs}]_t$, and body mass, w_t) (becquerels) at time t (days), Q_0 is the initial ^{137}Cs body burden (becquerels), Q_g is the gonadal ^{137}Cs burden (becquerels) released at spawning (omission of Q_g results in model outcome changes of less than 5% in this case), G is the specific growth rate (grams per gram per day), E is the elimination rate of ^{137}Cs (becquerels per becquerel per day), D is the radioactive decay of ^{137}Cs (becquerels per becquerel per day), $[^{137}\text{Cs}]_d$ is the concentration of ^{137}Cs in the diet (becquerels per kilogram), w_0 is the initial body mass (kilograms), and α is the assimilation efficiency of ^{137}Cs from the diet (fraction); α varies according to prey type, as stated in Forseth et al. (1992): Chironomidae larvae, 0.55; Gammaridae (crustaceans), 0.48; Ephemeroptera larvae, 0.23 (assumed to represent various insects); zooplankton, 0.82; fish muscle, 0.66. Lake-specific ^{137}Cs assimilation efficiency values were given as

$$(4) \quad \alpha = \sum_{i=1}^n p_i \alpha_i$$

where p_i is the percent contribution of the i th prey item to the diet of age 4+ yellow perch (by volume) and α_i is the assimilation efficiency of the i th prey item and are shown in Table 2. The model (eq. 3) was integrated over 1 year assuming water temperature to follow a sin function similar to that published for another north temperate water body (Rowan et al. 1997). Thus, both growth and

consumption rates represent the annual mean. Finally, conversion efficiency ($K1$, percent), also on an annual basis, was calculated by

$$(5) \quad K1 = \frac{G}{C} \times 100.$$

Data handling, error estimation, and statistical analysis

To characterize and compare yellow perch populations, age data were transformed into percentage of total within-lake catch (from all sources of capture) for ages 2+ to 9+ (entire observed range). The effect of age and pollution category (POLL, grouped and coded: reference = 0, intermediate = 1, and metal-polluted = 2) on catch percentage (combined from both years) was analysed by two-way analysis of variance (ANOVA). Yellow perch diet was used as a descriptor of the community. Because yellow perch are generalist feeders (Keast 1977), we assumed that the diet integrated over all age-classes for a given population would be a good representation of the available prey base in that community. Diet was presented as percent occurrence of the 12 most important (present at least 1% of the time) invertebrate prey items (identified to order or subclass) and of fish (primarily young-of-the-year (YOY) yellow perch or spottail shiner (*Notropis hudsonius*)) in the diets of age 2+ to 9+ yellow perch.

The mean and the 95% confidence interval associated with growth rate, consumption rate, and conversion efficiency (from eqs. 2, 3, and 5, respectively) were estimated by Monte Carlo simulations, which allowed us to account simultaneously for error in a number of measured parameters based on randomly generated pseudo-values (Trudel and Boisclair 1993). The pseudo-value (P^*) for a given parameter (P) is given by

$$(6) \quad P^* = P + (\text{SE}_P \text{RN})$$

where SE_P is the standard error of P and RN is a normally distributed random number with a mean of 0 and a standard deviation of 1. In this manner, a population of 1000 pseudo-values was generated for each measured parameter. One thousand replicates should provide more than adequate results, as normally, there is little to be gained by performing more than 100 Monte Carlo replicates (Efron and Tibshirani 1986). One thousand estimates for growth, consumption, and conversion efficiency were computed by solving eqs. 2, 3, and 5 with pseudo-values of their respective parameters (w_t , w_0 , $[^{137}\text{Cs}]_t$, $[^{137}\text{Cs}]_0$, $[^{137}\text{Cs}]_d$). The mean and the 95% confidence interval associated with G , C , and $K1$ estimates were defined respectively by the 50th percentile and by the 2.5th and 97.5th percentiles of the 1000 estimates of G , C , and $K1$.

The difference in mean estimated growth rate, mean estimated consumption rate, and mean estimated conversion efficiency among POLLS (reference versus intermediate + metal-polluted) and sexes was examined by two-way ANOVA. Negative conversion efficiency results are biologically irrelevant and were thus converted to zero values where applicable. The relationship between

growth rate, consumption rate, POLL, and sex was analysed by analysis of covariance (ANCOVA) with growth rate as the dependent variable, POLL (coded: reference = 0 and intermediate + metal-polluted = 1) and sex as the independent variables, and consumption rate as the covariate.

Results

Yellow perch bioenergetics

Specific daily growth rate was estimated for age 4+ yellow perch (Table 3). Estimated growth rate varied from negative values in Osisko yellow perch (an artifact of loss in condition factor over the sampling period) to $0.0021 \text{ g}\cdot\text{g}^{-1}\cdot\text{day}^{-1}$ in Opasatica females and was significantly related to POLL; yellow perch from metal-polluted lakes (including intermediate) exhibited, on average, three times lower specific growth rates than yellow perch from reference lakes ($F_{1,15} = 21.93$, $p < 0.001$). No effect of sex, or of the interaction between sex and POLL, was observed on growth rate (Table 4).

Using the ^{137}Cs mass-balance approach (eq. 3), we estimated specific daily consumption rates for the same age 4+ yellow perch. Consumption rates varied over an order of magnitude from 0.0033 to $0.0255 \text{ g}\cdot\text{g}^{-1}\cdot\text{day}^{-1}$ but were significantly related to neither POLL nor sex (Table 4). A relationship between growth and consumption is shown in Fig. 2; overall, ANCOVA revealed a significant effect of consumption rate ($F_{1,15} = 19.75$, $p < 0.001$) and of the categorical variable for POLL ($F_{1,15} = 43.10$, $p < 0.0001$) on growth rate (entire model: $F_{4,15} = 19.49$, adjusted $r^2 = 0.83$, $p < 0.0001$, $n = 16$). There was no significant effect of sex ($F_{1,15} = 0.21$, $p > 0.60$), or of the interaction between POLL and sex ($F_{1,15} = 0.23$, $p > 0.60$), in the ANCOVA. Finally, as a corollary to the above results, conversion efficiency was found to be significantly lower ($F_{1,15} = 30.10$, $p < 0.0001$) (Table 4) in metal-polluted lakes (4.2%) than in reference lakes (10.8%) (Table 3).

Yellow perch age structure and prey community

Age structures for yellow perch populations from all lakes sampled are presented in Fig. 3. In the reference lakes, the youngest age-class (age 2+) constituted, on average, about 40% of the total catch with a gradual decline in percent age representation thereafter. Conversely, in the metal-polluted lakes, age 2+ yellow perch made up only about 10% of the total catch; instead, there existed a peak in age representation at age 4+ (Lake Osisko was made up almost entirely of this one age-class). A two-way ANOVA revealed a significant effect of the interaction between POLL and age ($F_{14,63} = 3.27$, $p < 0.005$) on catch percentage. Driving this result was the fact that age 2+ yellow perch were significantly underrepresented in metal-polluted lakes compared with reference lakes (Student's t test, $p < 0.05$). The age structure of yellow perch in intermediate lakes was between the two previous extremes, with age 2+ yellow perch making up approximately 20% of the total catch and with peaks in age representation at ages 3+ and 4+.

Yellow perch diet, in terms of percent occurrence of various prey items for each lake, is presented in Fig. 4. It is important to note that this representation of diet differs from that shown in Table 2 (which was used for bioenergetic analysis of age 4+ yellow perch only) in that it includes stomach

contents from all age-classes. In general, feeding habits (assumed to reflect available prey base) tended to exhibit qualitative differences among lakes. In reference lakes, diet richness (in terms of number of prey items represented) was relatively high, with a number of important groups being represented in the diet, fish being the most frequent prey item. In the metal-polluted lakes, however, diet richness was relatively low, with zooplankton and dipterans (chironomids) dominating the diet; absent were many important prey groups such as ephemeropterans, odonates, and fish. In the intermediate lakes, diet richness may have been high, and important prey items such as amphipods and trichopterans may have been present. However, in these lakes, too, piscivory remained virtually nonexistent.

Discussion

Our data show that yellow perch from metal-polluted lakes exhibited, on average, almost three times lower specific growth rates than yellow perch from reference lakes. In fact, yellow perch from one of the most contaminated lakes (Osisko) even displayed negative growth (Table 3). Although this pattern in growth reduction in contaminated lakes is statistically significant, the biological meaning of this result remains unclear. It is only with feeding rates, estimated from the ^{137}Cs mass balance, that these growth data become more readily interpretable. First, and most striking, slower growing yellow perch populations from all but one of the polluted lakes had consumption rates that were similar to those from reference lakes (Table 3). This means that the growth reduction that we observed involves a reduced conversion efficiency of the fish (i.e., growth is affected at the level of energy metabolism, presumably standard metabolism, active metabolism, or both) and not simply a reduced food intake, as has been a possible interpretation in previous studies (Munkittrick and Dixon 1989). Second, statistically, the inclusion of food consumption rate as a covariate in our analysis (Fig. 2) led to a much clearer distinction in growth rates between lakes than did the use of the categorical variable for lake contamination alone. This in fact helped to explain some of the error overlap in estimates of growth rate among lakes of varying contamination (Table 3) as well as the extremely low growth rate for Osisko yellow perch.

Thus, we observed that for a given amount of food consumed, the percent allocation to growth (conversion efficiency) in metal-polluted yellow perch was only one third that achieved by yellow perch from unpolluted reference lakes (4.2% compared with 10.8%), representing a significant increase in total energetic costs. Others, too, have documented increased energetic costs in wild poikilotherms due to pollutant exposure. Hopkins et al. (1997) reported an increase in maintenance costs (standard metabolic rate measured as O_2 consumption at rest) of banded water snakes (*Nerodia fasciata*) collected from lakes exposed to coal ash wastes. Similarly, Rowe et al. (1998) documented increased standard metabolic rate (also measured as O_2 consumption at rest) in bullfrog tadpoles (*Rana catesbeiana*) from lakes, again, polluted by coal ash wastes. These studies have isolated standard metabolic rate (SMR in eq. 1) as being affected by pollutant exposure. There is little doubt that the decrease in conversion efficiency that we observed in metal-

Table 3. ^{137}Cs concentrations, body mass (W), and growth (G) (input data for eq. 3), estimates of consumption (C) and conversion efficiency (KI), and cortisol stress response data for age 4+ yellow perch from reference, intermediate, and metal-polluted sites (values in parentheses are SE except for those for G , C , and KI , which are the 95% confidence interval).

	Sex	n_t	n_0	$[^{137}\text{Cs}]_t$ (Bq·kg ⁻¹)	$[^{137}\text{Cs}]_0$ (Bq·kg ⁻¹)	W_t (g)	W_0 (g)	G (g·g ⁻¹ ·day ⁻¹)	C (g·g ⁻¹ ·day ⁻¹)	KI (%)	[Plasma cortisol] (ng·mL ⁻¹)
Reference (age 4+)											
Dasserat	♀	2	3	2.70 (0.37)	3.09 (0.74)	72.2 (12.7)	42.9 (5.7)	0.0014 (0.0012)	0.0119 (0.0029)	11.7 (9.4)	324 (62)
Dasserat	♂	9	2	2.81 (0.22)	3.09 (0.74)	57.7 (3.0)	33.0 (5.0)	0.0016 (0.0010)	0.0113 (0.0026)	13.7 (5.6)	224 (21)
Memphremagog	♀	3	8	2.60 (0.41)	2.26 (0.67)	132.4 (18.7)	62.4 (3.6)	0.0020 (0.0008)	0.0215 (0.0046)	9.6 (4.4)	318 (34)
Memphremagog	♂	4	9	1.96 (0.43)	1.74 (0.21)	78.8 (5.5)	43.3 (3.3)	0.0016 (0.0006)	0.0136 (0.0062)	12.8 (8.0)	260 (19)
Opasatica	♀	7	3	1.20 (0.10)	1.20 (0.14)	78.7 (5.2)	36.3 (4.1)	0.0021 (0.0008)	0.0255 (0.0064)	8.5 (3.4)	353 (28)
Opasatica	♂	4	6	0.94 (0.06)	1.20 (0.14)	43.5 (4.1)	25.3 (4.1)	0.0015 (0.0010)	0.0149 (0.0044)	10.1 (6.0)	415 (42)
Ottawa River ^a	♂	5		9.45 (na)	6.42 (na)	74.7 (na)	28.0 (na)	0.0027 (na)	0.0229 (na)	11.8 (na)	na
Ottawa River ^a	♂	3		9.67 (na)	8.28 (na)	95.7 (na)	53.1 (na)	0.0016 (na)	0.0187 (na)	8.6 (na)	na
Mean (±SE)								0.0018 (0.0002)	0.0175 (0.0019)	10.8 (0.7)	316 (28)
Intermediate and metal-polluted (age 4+)											
Dufault	♀	2	9	6.64 (1.24)	3.31 (0.30)	24.0 (4.0)	20.1 (1.2)	0.005 (0.0010)	0.0233 (0.0078)	2.0 (4.5)	183 (23)
Dufault	♂	7	19	4.82 (0.48)	4.13 (0.26)	16.8 (0.5)	15.6 (0.5)	0.0002 (0.0002)	0.0129 (0.0027)	1.6 (2.0)	223 (32)
Osisko	♀	52	44	1.38 (0.10)	1.21 (0.26)	91.3 (2.0)	99.7 (2.3)	-0.0002 (0.0002)	0.0038 (0.0004)	-ve	159 (8)
Osisko	♂	25	14	1.51 (0.14)	1.18 (0.16)	59.3 (1.9)	73.4 (2.7)	-0.0006 (0.0002)	0.0033 (0.0004)	-ve	232 (17)
St. Louis	♀	2	2	0.60 (0.11)	0.54 (0.07)	72.4 (7.2)	50.3 (6.9)	0.0010 (0.0010)	0.0184 (0.0082)	5.8 (5.9)	266 (72)
St. Louis	♂	7	7	0.56 (0.10)	0.54 (0.07)	62.8 (2.6)	42.4 (2.2)	0.0011 (0.0004)	0.0150 (0.0070)	7.7 (5.1)	156 (19)
Vaudray	♀	4	4	14.70 (0.23)	18.10 (0.28)	40.6 (1.1)	29.0 (1.1)	0.0009 (0.0002)	0.0223 (0.0093)	4.4 (2.4)	na
Vaudray	♂	5	5	19.50 (0.31)	23.40 (0.37)	29.5 (0.6)	22.0 (0.6)	0.0008 (0.0002)	0.0253 (0.0106)	3.4 (1.8)	na
Mean (±SE)								0.0005 (0.0002)**	0.0155 (0.0030)	4.2 (0.8)***	203 (18)*

Note: na, not available; -ve, negative value. Significantly different from reference (ANOVA): * $p < 0.01$, ** $p < 0.001$, *** $p < 0.0001$.

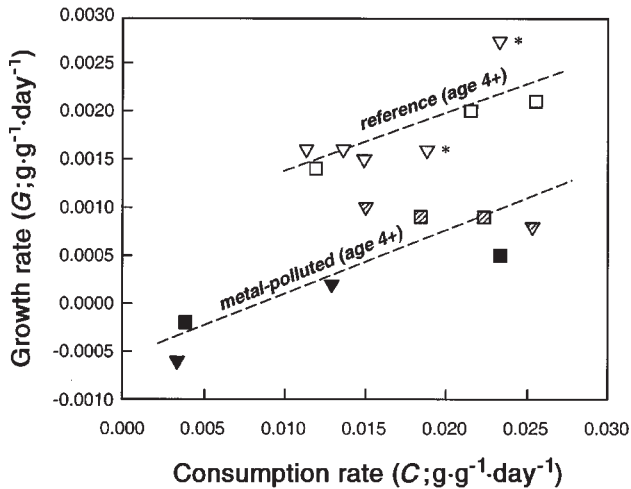
^aData from Rowan and Rasmussen (1996); cortisol data from Brodeur et al. (1997).

Table 4. ANOVA results for the effects of pollution category (POLL) and sex on yellow perch growth rate (*G*), consumption rate (*C*), and conversion efficiency (*K1*).

Effect	<i>G</i>		<i>C</i>		<i>K1</i>	
	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>
POLL	21.93	<0.001	0.406	>0.50	30.1	<0.0001
Sex	0.13	>0.70	0.662	>0.40	1.1	>0.30
POLL × sex	0.06	>0.80	0.005	>0.90	0.01	>0.90

Note: Degrees of freedom (df) associated with main effects and interaction is 1; total df = 15.

Fig. 2. Relationship between specific daily growth rate and specific daily consumption rate in female (squares) and male (triangles) age 4+ yellow perch from reference and metal-polluted lakes (shading scheme as in Fig. 1). Asterisks indicate data published for age 4+ Ottawa River yellow perch (Rowan and Rasmussen 1996). Plotted lines for reference and metal-polluted lakes (includes intermediate) were obtained by least squares regression.



polluted yellow perch is caused, at least in part, by a similar effect.

It is important to note that the energetic costs that we observed may also include increases in activity (*A* in eq. 1). For instance, it is possible that the food base may be impoverished in metal-polluted lakes to the point where either prey abundance or prey type affects the activity expended in maintaining a given level of consumption. We have no data to indicate whether prey abundance is affected. However, lower than normal feeding rates for Osisko yellow perch, compared with the range of yellow perch feeding rates found by Boisclair and Leggett (1989a), may have resulted from limited food supply. However, it is apparent from diet analysis (Fig. 4) that prey type was indeed altered; in general, diets shifted from diverse and predominantly piscivorous in reference lakes towards less diverse, chironomid and zooplankton dominated in metal-polluted lakes. This is consistent with others who have reported similar shifts in invertebrate prey communities exposed to mixtures of heavy metals (Cu, Cd, and Zn) towards metal-tolerant species (e.g., Gower et al. 1994). Regardless of abundance, chironomids and zooplankton in the diet of adult yellow perch and the

Fig. 3. Yellow perch age structures among lakes of varying metal pollution in terms of percentage of total catch by age-class. Open circles and the dotted line refer to reference populations, hatched squares and the dashed line refer to intermediate populations, and solid triangles and the solid line refer to metal-polluted populations. Data are from all sources of capture for all lakes from both years (experimental gill net, seine, and hook and line; sample sizes range from 30 to 171). Plotted lines represent averages. Asterisks indicate data obtained from Rowan and Rasmussen (1996).

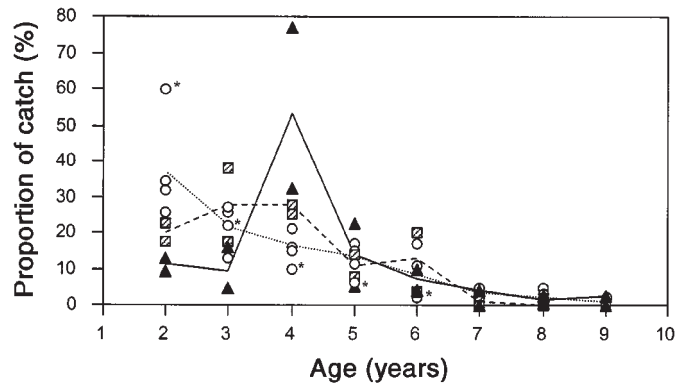
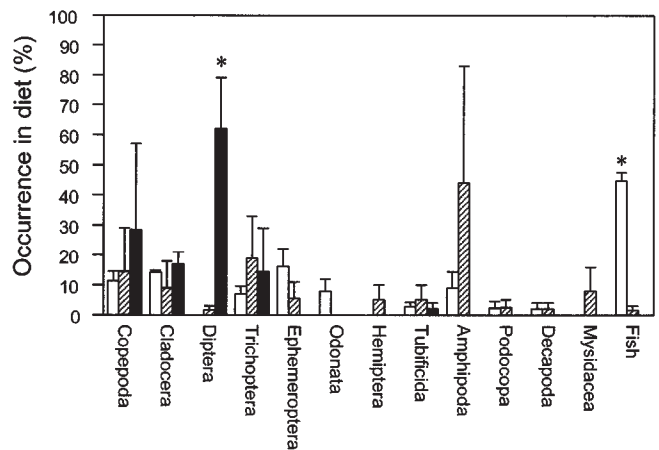


Fig. 4. Frequency of occurrence of the 13 most important prey items in the diets of yellow perch from lakes of varying metal pollution. Open bars are for reference lakes, hatched bars are for intermediate lakes, and solid bars are for metal-polluted lakes. Error bars represent SE. Data include diets from all age-classes (sample sizes range from 30 to 171). Asterisks indicate that the mean occurrence of that prey item in the diet differs significantly among reference and metal-polluted lakes (Student's *t* test, *p* < 0.05). "Diptera" is exclusively chironomids, and "fish" is roughly equal parts of YOY yellow perch and spottail shiner.



absence of piscivory may be negatively affecting bioenergetic performance in metal-polluted lakes; when consumption rates are adjusted for variable caloric content of different prey types (Cummins and Wuycheck 1971), the same patterns in bioenergetic impairment are evident. Boisclair and Leggett (1989b) showed that a predominance of zooplankton in the diets of age 2+ yellow perch was negatively correlated with conversion efficiency. Their interpretation of these results was that younger, smaller yellow

perch (age 1+) graze more efficiently on zooplankton. As a corollary, older, larger fish should feed more efficiently on larger prey such as small fish and large invertebrates. Thus, it is possible that a large difference in prey type and prey size among lakes altered the amount of activity expended in foraging, thereby affecting bioenergetic performance.

The observed shift in prey community is one possible explanation for low conversion efficiencies in age 4+ yellow perch from metal-polluted lakes. However, we have not accounted for other factors such as water temperature, expected growth trajectories, fish community, and other limnological characteristics. With respect to water temperature, the largest difference among lakes (in terms of the length of the growing season) was no doubt between Lake Memphremagog and the Abitibi lakes. Lake Memphremagog is further south and undergoes earlier stratification and later fall turnover. In spite of this geographic difference, bioenergetic results for Lake Memphremagog yellow perch (on a relative basis) were very similar to those for Abitibi reference lakes (see Table 3). It is therefore unlikely that water temperature differences among lakes (especially among Abitibi lakes) were a significant factor. Similarly, it is improbable that variable growth trajectories and developmental stage influenced our overall findings. All fish sampled for bioenergetic analysis were sexually mature and most appeared to have considerable growth potential. In the case of Lake Osisko, the fact that yellow perch did not grow over the interval sampled suggests that this particular cohort may have reached an asymptotic size. However, larger, older yellow perch from this population were observed, suggesting that there exists no fixed size constraint for Osisko yellow perch. Perhaps food limitation became more problematic in this lake as this cohort progressed in time. Indeed, chironomid density and average gut fullness of yellow perch (predominantly chironomids) in Lake Osisko dropped drastically from 1994 to 1995 (personal observation). With regard to the possible influence of fish community, Boisclair and Leggett (1989c) found that the average density of cyprinids explained 97 and 44% of the among-population variability in conversion efficiency of age 2+ and 3+ yellow perch, respectively (i.e., average cyprinid density negatively affected yellow perch growth). We do not have density estimates for fish community. However, cyprinids were not present in Lake Osisko (nor was any other species of fish), and through casual observation, we saw comparatively fewer cyprinids in Lake Dufault seine hauls than in reference lakes. Thus, the poor bioenergetic performance of yellow perch in the two most metal-polluted lakes was probably not due to fish community interactions (particularly from cyprinids; centrarchid density was also very low in all Abitibi lakes). It does remain possible, however, that average yellow perch density, which may have been higher in metal-polluted lakes, contributed to the poor performance through increased activity (Boisclair and Leggett 1989c).

Included in Table 1 are some limnological characteristics of the study lakes (pH, conductivity, and Secchi depth). Variation in pH was quite small and well within the range of preference for many fish species including yellow perch (Peterson et al. 1989). Conductivity, although generally higher in metal-polluted lakes, should not have affected our results. Boisclair and Rasmussen (1996) have reported a wide range

of values for bioenergetic performance in several nonpolluted yellow perch populations. When these are compared with published conductivity values for the same lakes (Rasmussen 1988) covering a similar range in values as encountered here, no pattern is evident. Finally, Secchi depth, which has been related to yellow perch activity rates elsewhere (Boisclair and Rasmussen 1996), varied little among lakes (Table 1) and therefore should have little bearing on our results.

Low conversion efficiency is a direct measure of performance impairment, but it was not the only indicator of poor biological integrity that we observed in metal-polluted yellow perch populations. Along with energetic impairment, we observed a drastic shift in age composition of yellow perch from metal-polluted lakes (Fig. 3); in particular, young yellow perch were underrepresented in metal-polluted lakes. This would suggest that recruitment was lower in metal-polluted populations, which is consistent with our knowledge of life history toxicity in fish where embryo and larval stages are most susceptible to lethal effects of toxicants (McKim 1977). Perhaps younger fish are less able to cope with increased energy demands associated with increased metabolism. Investigations are presently underway to examine the possible effects of in situ metal exposure on the energy requirements of young yellow perch. At the other end of the spectrum, impaired cortisol stress response has been reported in yellow perch from the same metal-polluted lakes (Brodeur et al. 1997). The existence of this hormonal biomarker of pollutant stress is notable in two ways. First, it provides us with an independent measure of the health status of the yellow perch; cortisol is a gluconeogenic and lipolytic hormone and cortisol-impaired fish can be considered unhealthy in terms of normal endocrine function (Hontela 1997). Second, it may also provide us with a possible mechanism for the decline in energetic performance that we observe. Cortisol impairment has been hypothesized (Hontela 1997) to be the result of chronically elevated basal cortisol secretion, which would tend to increase catabolic processes, thereby creating an energetic sink. Alternatively, this endocrine dysfunction may simply reflect the chronic toxicity of metals to the interrenal (cortisol producing) tissue (Hontela et al. 1992) and disrupted cortisol secretion may cause metabolic anomalies. It was also shown that liver and interrenal metallothioneins, detoxifying metal-binding proteins, are higher in yellow perch from metal-polluted lakes in Abitibi (Laflamme 1999), thus providing an independent measure of exposure. In addition, the synthesis of metallothioneins may directly or indirectly involve a significant metabolic expenditure (Felts and Heath 1984), and this, too, could be linked to the energetic impairment that we observe. Taken as a whole, elevated metallothionein levels, impaired cortisol stress response, and skewed age structures in yellow perch from metal-polluted lakes lend support to our assertion that these yellow perch are exposed to levels of pollution that are eliciting toxic responses at multiple levels of biological organization within individuals and ultimately affecting the energetic performance and survival of wild fish populations.

Conclusions

Our study demonstrates a significant bioenergetic cost as-

sociated with living in an environment subject to chronic sublethal exposure to heavy metal pollution. Such levels of exposure may not be uncommon, and this, combined with our strong global dependence on wild fish stocks (Abramovitz 1996), may constitute a substantial economic loss. In fact, the economic value of food production and recreation services provided by global aquatic resources (the majority of which are presumably fisheries related) has been estimated to be in the range of US\$1 trillion per year (Costanza et al. 1997). In addition, our study stresses an avenue for ecotoxicology, away from its traditional focus on death (and (or) birth) of organisms, which works well in the laboratory, towards a bioenergetic approach more suited to field situations. The application of the radiocesium mass-balance technique to bioenergetics makes this shift practical and efficient. Because energy flow is central to most physiological and ecosystem processes and because it lends itself to a workable performance measure (conversion efficiency), even under noncontrolled field settings, we conclude that our approach to the assessment of toxicity contributes a significant advancement in our ability to quantify performance-related effects of pollutants on wild-living organisms which may ultimately be extended to whole ecosystems.

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