A comparison of methods for estimating activity costs of wild fish populations: more active fish observed to grow slower[1]

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Abstract: Activity costs can account for a major proportion of fish energy budgets and may trade off against observed growth rates in wild fish populations. Recent approaches to estimating activity costs in situ have used a contaminant–bioenergetic mass balance modelling approach, allowing for a broader examination of activity costs among populations compared with time-consuming alternative approaches. We report the results of this contaminant–bioenergetic modelling approach to estimating in situ activity costs compared with two alternative independent methods of assessing in situ activity costs. Comparisons were made between a fast- and slow-growing yellow perch (*Perca flavescens*) population. Contaminant–bioenergetic estimates of activity costs in the fast-growing population were 39% lower than those in the slow-growing population. Activity estimated from recorded swimming behaviours was 37% lower in the fast-growing population and 22%–29% lower in the fast-growing population based on published relationships between activity costs and axial white muscle glycolytic enzyme capacities. Consumption rates were actually 32% lower in the fast-growing population, implying that lower activity costs more than compensated for lower food intake. The agreement among the three independent measures of activity costs strongly support the idea that activity costs, rather than food intake, are a major determinant of growth differences in these two wild fish populations.

Résumé : Les coûts des activités peuvent représenter une fraction importante des bilans énergétiques des poissons, ce qui peut se faire au détriment des taux de croissance dans les populations sauvages de poissons. Les méthodes récentes d'estimation des coûts des activités in situ utilisent une modélisation énergétique de bilan de masse avec un contaminant, ce qui permet un examen plus étendu des coûts des activités chez les populations que les méthodes de rechange qui requièrent plus de temps. Nous comparons les résultats d'une telle méthode bioénergétique avec contaminant pour mesurer les coûts des activités in situ à ceux de deux méthodes de rechange indépendantes d'estimation des coûts des activités in situ. Nous avons comparé des populations de perchaudes (*Perca flavescens*) à croissance rapide et à croissance lente. Par la méthode bioénergétique avec contaminant, les estimations des coûts des activités sont 39 % plus basses dans la population à croissance rapide que dans celle à croissance basse. L'activité estimée d'après l'enregistrement des comportements de nage est de 37 % plus basse dans la population à croissance rapide; elle est de 22–29 % plus basse dans la population à croissance rapide lorsqu'elle est calculée à partir des relations publiées entre les coûts des activités et les capacités des enzymes glycolytiques des muscles blancs axiaux. Les taux de consommation sont en fait 32 % plus bas dans la population à croissance rapide, ce qui implique que les coûts réduits des activités compensent amplement l'ingestion plus faible de nourriture. La concordance entre les trois mesures indépendantes des coûts des activités vient appuyer fortement l'hypothèse selon laquelle ce sont les coûts des activités, plutôt que l'ingestion de nourriture, qui sont les facteurs explicatifs principaux des différences de croissance entre ces deux populations sauvages de poissons.

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Introduction

Growth rate is a tremendously plastic characteristic of fish and can vary widely both within and among populations (Boisclair and Leggett 1989*a*). Over large north–south environmental gradients, cumulative growing degree-days often correlate with variation in growth (Power and van den Heuvel 1999). As well, annual or seasonal variations in climate and (or) water temperature may also correlate significantly with variation in growth (e.g., Claramunt and Wahl 2000; Fechhelm et al. 1992; King et al. 1999). However, these relationships can rarely account for more than 50% of the variation in growth rates observed (but see Fechhelm et al. 1992). Furthermore, if one narrows the geographic scale of comparison amongst populations of a particular fish species, effectively eliminating climatic variation between environments, wide variation in growth may still be observed among populations (Boisclair and Leggett 1989*a*). Additionally, growth in fish is optimized for a given set of environmental and ecological conditions and can trade off against increased energy allocation in behaviours such as predator avoidance (Billerbeck et al. 2001; Lankford et al. 2001). As such, it is likely that at least some component of this observed plasticity in growth is due to differences in energy allocation to active metabolism between populations. However, active metabolism remains a difficult metric to quantify in the field; a variety of methods have been employed to measure it, but almost all have come under criticism, and few of these methods have been compared with one another to judge their consistency.

Activity costs have long been hypothesized to contribute significantly to fish energy budgets (Weatherly 1966). Individual growth rate can be seen as the by-product of an optimization process that trades off the levels of energy acquisition and predation risk — associated with activities such as foraging and predator avoidance — to maximize the production of offspring (Ware 1980). Thus, the cost of activity is a primary component in the system of trade-offs that determines the life history of an animal. Understanding the role of activity in this system is an important step in identifying the factors that determine the life histories of fish.

Early models of fish bioenergetics represented activity as a small component of energy budgets (Kitchell et al. 1977). However, a number of studies in the past 15 years have shown that activity costs can be a major determinant of growth, reproduction, and survival (Boisclair and Leggett 1989*b*; Trudel et al. 2001; Pazzia et al. 2002). In particular, studies describing large-scale differences in activity (i.e., between populations over long time series, such as in Pazzia et al. 2002) and queries as to the ultimate reasons for these differences (food intake versus activity, as in Trudel et al. 2001) are beginning to surface. Answering these questions adequately requires reliable methods for quantifying activity differences in wild populations over long time scales.

Among the variety of approaches used to address the role of activity costs on the growth of organisms, some have examined trade-offs between an organism's physiological capacity for activity (Arendt 2003) and its scope for growth. Capacity for activity can be measured in the laboratory using forced swimming experiments. However, an organism's physiological scope for activity may not necessarily reflect actual activity levels observed in the field, particularly if highly variable ecological characteristics, such as food distribution and availability or the presence of predators, affect the activity of an organism. Direct behavioural observations can be used to estimate activity costs (Boisclair and Sirois 1993; Aubin-Horth et al. 1999), but this approach is extremely time consuming and expensive and difficult to apply to large-bodied or cold-water species of fish that occur outside of the littoral zone. Additionally, without a large sampling effort, observation-based methods cannot offer long-term average estimates of activity costs for populations of fish.

Another method that has been used to estimate activity in the field is the examination of lactate dehydrogenase (LDH) activities in the axial musculature of fish. Higher LDH activity indicates enhancement of anaerobic capacity and may therefore reflect recent activity levels in fish (Sherwood et al. 2002*a*, 2002*b*). Increased levels of this enzyme support activities such as burst swimming, which can account for a large proportion of activity-based metabolic costs associated with the pursuit of prey or escape from predators.

Long-term activity costs in wild fish populations may also be estimated as a function of the difference between consumption and growth estimates using bioenergetics models (Boisclair and Leggett 1989*b*; Aubin-Horth et al. 1999; Trudel et al. 2001). This approach is convenient because of the ease with which it can be applied to both current and archived data compared with other methods of estimating activity costs currently in use (Trudel et al. 2001). However, this approach has also come under criticism for a number of reasons. First, predictions made by bioenergetics models depend on the accuracy of submodels used to describe metabolic rates of fish in the field (Krohn and Boisclair 1994; Aubin-Horth et al. 1999). As a result, the error surrounding predictions derived from bioenergetics models can be greatly magnified and difficult to accurately estimate. Second, field estimates of consumption based on stomach contents can also be difficult and time consuming to estimate and are based on submodels that are subject to their own assumptions and criticisms (Grant and Kott 1999; Whitledge and Hayward 2000; Bochdansky and Deibel 2001). Third, consumption estimates that are based on contaminant accumulation models do not model contaminant elimination as a function of active metabolism, which is an assumption that has been criticized as unrealistic and one that may result in overestimates of activity rates (He and Stewart 1997). Additionally, because activity rates calculated from bioenergetic models are in part dependent on growth, activity rates estimated using this approach are not entirely independent of the growth of the fish being modelled, making it difficult to examine statistical relationships between these terms (Boisclair and Leggett 1989*b*). The sum of these criticisms has cast some doubt on estimates of active metabolism acquired using bioenergetics models. Therefore, a comparison between activity levels using this method against others would be helpful in determining the degree of consistency and (or) reliability amongst methods.

This study had two primary objectives. The first objective was to assess the validity of field-based activity costs esti-

mated using contaminant accumulation–bioenergetics models against two other methods of estimating activity in situ (field-based observations of individual fish and LDH activity) between two populations of fish with very different growth rates and trajectories. The second objective was to add to the small set of measurements of the importance of activity relative to consumption in determining observed differences in fish growth.

Methods

Description of contaminant–bioenergetics model

The model we used is a slightly modified version from that reported by Trudel and Rasmussen (2001). The model combines the mass balance formulations for contaminants and fish mass on a daily basis using the mercury (Hg) mass balance model (MMBM, Trudel and Rasmussen 2001), with the mass balance of fish energy budgets using a traditional bioenergetics model (BM; Kitchell et al. 1977; Hewett and Johnson 1992). The MMBM models the balance of methylmercury (MeHg) in the tissues of fish, as this is the form of Hg that is most readily bioaccumulated (Mason et al. 1995; Lawson and Mason 1998; Lawrence et al. 1999). If fish total mercury (THg) and MeHg concentrations are equivalent, as they were for the fish captured in this study (Rennie 2003), then one can use fish THg as an estimate of MeHg.

The uptake of MeHg in fish is mediated via uptake through the gills (Norstrom et al. 1976; Post et al. 1996) and through absorption in the gut from diet (Leaner and Mason 2002). A number of studies have shown convincingly that in uncontaminated waterbodies (i.e., those that do not receive point-source inputs of Hg), the primary mode of uptake of MeHg in adult fish is through food, and less than 0.1% of assimilated MeHg is taken up through the gills (Lock 1975; Hall et al. 1997; Lawson and Mason 1998). Therefore, uptake through the gills in adult fish from uncontaminated waterbodies can be considered negligible. The concentration of Hg in muscle and the whole body can be assumed to be equivalent (Becker and Bigham 1995; Trudel et al. 2000; Trudel and Rasmussen 2001). One can therefore model the accumulation of MeHg in fish as

$$(1)\qquad \frac{\mathrm{dHg}}{\mathrm{d}t} = (\alpha C_{\mathrm{d}} C_t) - (E + G + K)\mathrm{Hg}$$

where Hg is the MeHg concentration of the fish (μg Hg·g^{-1} wet weight); α is the assimilation efficiency of MeHg from food; C_{d} is the concentration of MeHg in food (μg Hg·g^{-1} wet weight); C_t is the mass-specific food consumption rate (day^{-1}) at time t; E is a function describing the instantaneous elimination rate of Hg (day^{-1}); G is the mass-specific growth rate (day^{-1}), and K is a function describing the instantaneous loss rate of MeHg to gonads (day^{-1}). If modelled over small (i.e., 1 day) time steps, daily differences in parameter values such as E and K will be small and can be considered constants over short time increments. This allows for the integration of eq. 1 to yield

$$(2)\qquad \mathrm{Hg}_t = \mathrm{Hg}_0\, \mathrm{e}^{-(E+G+K)t} + \frac{\alpha C_t C_{\mathrm{d}}}{(E+G+K)}[1 - \mathrm{e}^{-(E+G+K)t}]$$

where Hg_0 and Hg_t are the MeHg concentration in fish at time 0 and time t, respectively. Rearranging to solve for consumption rate yields the following equation:

$$(3)\qquad C_t = \frac{\mathrm{Hg}_t - \mathrm{Hg}_0\, \mathrm{e}^{-(E+G+K)t}}{\alpha C_{\mathrm{d}}[1 - \mathrm{e}^{-(E+G+K)t}]}(E + G + K)$$

The MMBM (eq. 3) is solved over a daily time step and combined with the BM through the common term, C_t (C_t can be converted from units of day^{-1} to J·day^{-1} by multiplying C_t by the product of the energy density of the prey and fish weight). The BM can be expressed on a daily time step as

$$(4)\qquad W_t = W_0 + [(C_t \cdot \mathrm{ED}_{\mathrm{prey}}) - (F + U + N + R_{\mathrm{T}})]/\mathrm{ED}_{\mathrm{fish}}$$

where W_t is the fish weight (g) at time t; W_0 is the initial fish weight (g), C_t is ingestion rate (J·day^{-1}) at time t, $\mathrm{ED}_{\mathrm{prey}}$ is the energy density of prey (J·g^{-1}), $\mathrm{ED}_{\mathrm{fish}}$ is the energy density of fish (J·g^{-1}), F is losses due to egestion (J·day^{-1}); U is losses due to excretion (J·day^{-1}); N is losses due to reproduction (J·day^{-1}), and R_{T} is losses due to metabolism (J·day^{-1}). Egestion and excretion losses are functions of temperature, body size, and consumption (eq. 2 in Hewett and Johnson 1992), and all parameters for the BM are from Kitchell et al. (1977), reported in Hewett and Johnson (1992).

Consumption rate in the BM is expressed as

$$(5)\qquad C_t = C_{\max} \cdot p \cdot f(T)$$

where C_t is ingestion (J·day^{-1}) at time t, $C_{\max}$ is the maximum consumption of a fish (J·day^{-1}), described by an allometric function based on laboratory experiments, $f(T)$ is a temperature function that defines the reduction in consumption above and below the optimal feeding temperature, and p is the proportion of maximum consumption realized by a fish, a value that reflects other constraints on feeding rate.

Losses from metabolism, R_{T} from eq. 4, can be further subdivided into three components:

$$(6)\qquad R_{\mathrm{T}} = \mathrm{ACT} \cdot R_{\mathrm{s}} + R_{\mathrm{d}}$$

where R_{d} is specific dynamic action (J·day^{-1}), or heat increment, R_{s} represents losses due to standard metabolism (J·day^{-1}), and ACT represents energy lost to active metabolism as a multiple of standard metabolism (unitless), where $1 < \mathrm{ACT} < \infty$. Alternatively, ACT may also be further decomposed as $1+(R_{\mathrm{a}}/R_{\mathrm{s}})$, where activity costs ($R_{\mathrm{a}}$) are expressed in energetic units (J·day^{-1}).

Equations 3 and 4 are both mass balance equations. As such, C_t in eq. 3 is constrained by the balance of MeHg over the time period being modelled. This was set to equal C_t from eq. 4, which is constrained by balancing mass over the time period being modelled. By iterating both equations on a daily basis, the unique solution of p and ACT that achieve the observed final weight and MeHg concentration for the particular cohort of fish being modelled was obtained through an optimization routine. The optimization minimized the error between observed W_t and Hg_t, and modelled W_t and Hg_t, such that the average difference between observed and modelled W_t and Hg_t was less than 0.01%.

Table 1. Input parameters of the Hg mass balance model and bioenergetics model.

Symbol	Parameter description	Value	Source
α	Assimilation efficiency	0.8	1
φ	Coefficient of Hg elimination	0.0029	2
β	Allometric exponent of Hg elimination	–0.20	2
γ	Temperature coefficient of Hg elimination	0.066	2
GSI_m	Gonadosomatic index, males	0.05	3, 4, 5, 6, 11
GSI_f	Gonadosomatic index, females	0.17	3, 6, 7, 8, 9
ED_{FX}	Ratio of energy density of ovaries to energy density of the whole fish	1.2	7, 10
ED_{FY}	Ratio of energy density of testes to energy density of the whole fish	0.85	11
ED_{prey}	Energy density of fish stomach contents	3517 $J \cdot g^{-1}$	11

Note: Source references are as follows: 1, Norstrom et al. (1976); 2, Trudel and Rasmussen (1997); 3, Norton (1997); 4, Sulistyo et al. (2000); 5, Vuorinen et al.(1992); 6, B.A. Henderson, University of Toronto at Mississauga, 3349 Mississauga Road N., Mississauga, ON L5L 1C6, unpublished data; 7, Henderson et al. (2000); 8, Nelson and Magnuson (1992); 9, Heibo and Vøllestad (2002); 10, Diana (1983); 11, Rennie (2003).

Parameterization of the model

Daily elimination of MeHg (E in eq. 3) was modelled as a function of fish size (W) and temperature (T), as described in Trudel and Rasmussen (1997):

$$E = \varphi W^{\beta} e^{\gamma T} \quad (7)$$

where φ, β, and γ are empirically derived constants (Table 1). Assimilation of MeHg from the diet (α in eq. 3) is assumed to be 80% (Table 1). Daily losses due to spawning (K in eq. 3) are

$$K = \frac{Q \cdot \mathrm{GSI}}{365} \quad (8)$$

where Q is the ratio of MeHg in the gonads (C_g, $\mu g\ Hg \cdot g^{-1}$ wet weight) to Hg in perch (C_f, $\mu g\ Hg \cdot g^{-1}$ wet weight), GSI is the gonadosomatic index at spawning (Table 1), and 365 is the number of days in a year. In contrast with previous models, we estimated Q on a daily basis, following relationships determined between yellow perch (*Perca flavescens*) Hg in flesh and in the gonads. Separate equations were used for both female (Hammerschmidt et al. 1999) and male yellow perch (Rennie 2003):

$$\text{Females: } (C_g = 7.656 \times 1.002^{C_f})\,0.15 \quad (9)$$

$$\text{Males: } (C_g = 21.498 \times 1.001^{C_f})\,0.168 \quad (10)$$

Values 0.15 and 0.168 above convert concentrations from Hg per unit dry weight into Hg per unit wet weight. Losses in weight due to reproduction are modelled as a one-time loss on an arbitrary day (30 April in this model) as

$$W_t = W_{t-1} - W_{t-1}(\mathrm{GSI} \cdot \mathrm{ED}_{F(X,Y)}) \quad (11)$$

where W_t is the weight of the fish after spawning, W_{t-1} is the weight of fish the day before spawning, and $ED_{F(X,Y)}$ is the ratio of the energy density of the gonads to energy density of the whole fish (Table 1). Because we are interested in the mass balance to yield endpoints of this modelling exercise, differences in the modelled losses for gonads between energetic (BM) and contaminant (MMBM) processes — necessary to remain compatible with the structure of each model — will have little impact on the predictions of average accumulation and loss rates over the modelled time period, which are the primary, useful outputs of both models.

Seasonal bioenergetic estimates of C and R_a were obtained using fish Hg_0 and W_0 for a particular cohort in June and using Hg_t and W_t for the same cohort collected in August of the same year. C_d was calculated as the cohort-specific average over the two time periods. Lake temperature data was obtained from temperature loggers deployed over the growing season. Energy densities of fish were estimated from the literature at 4184 $J \cdot g^{-1}$ (Hewett and Johnson 1992). Caloric density of prey (stomach contents) and testes were measured directly by bomb calorimetry. Energy densities of ovaries were estimated from Henderson et al. (2000).

Error estimation

To reflect sampling error from model inputs in our bioenergetics estimates, we used Monte Carlo simulations to estimate standard errors (Trudel et al. 2000). For a particular cohort, 1000 pseudo-values of initial and final weight or Hg concentration were calculated from the sample means and standard errors, assuming a normal distribution around the mean. A suite of bioenergetic estimates was calculated for each pseudo-value. Reported bioenergetics estimates are averages of these pseudo-values; standard errors are reported for comparison (Appendix A). Many studies that model contaminant accumulation and bioenergetics choose not to estimate error around their bioenergetics estimates at all (Essington and Houser 2003; Henderson et al. 2003). Though our method of error estimation represents an overall underestimate of error propagated through the model, it is consistent with methodologies employed in contaminant models reported elsewhere (Tucker and Rasmussen 1999; Trudel et al. 2000; Trudel and Rasmussen 2001).

Species and lakes studied

Yellow perch were sampled from Plastic Lake and Shoe Lake in the Dorset region of Ontario, Canada. Shoe Lake is about 7.5 km northwest of Plastic Lake and is similar in size, bathymetry, and climate (Table 2). Shoe Lake has a slightly higher pH and is also home to piscivorous fish species, such as smallmouth bass (*Micropterus dolomieu*) and lake trout (*Salvelinus namaycush*). Importantly, yellow perch from Shoe Lake have been shown to grow faster than fish

Table 2. Comparison of the two lakes under study.

Attribute	Plastic Lake	Shoe Lake
Latitude (°N)	45°10′830″	45°12′450″
Longitude (°W)	78°49′200″	78°54′600″
pH	5.6	6.6
DOC ($mg \cdot L^{-1}$)[a]	2.05	3.24
Mean depth (m)	8.1	5.5
Surface area (km^2)	32.6	38.6
Fish community[b]	Yellow perch, rainbow smelt, white sucker, northern redbelly dace, golden shiner, creek chub, pearl dace, brown bullhead, rock bass, pumpkinseed	Yellow perch, lake trout, smallmouth bass, rock bass, pumpkinseed, golden shiner
Average invertebrate density ($g \cdot m^{-2}$)	19.3±8.9	37.9±7.1

[a]Dissolved organic carbon.
[b]Based on data provided by the Ontario Ministry of Natural Resources (D. Flowers, Minden Office, Hwy 35 By-Pass, Minden, Ontario, Canada, personal communiation) and on species encountered during the course of the study.

from Plastic Lake (Rennie 2003). Fish were collected a total of five times from both lakes over 2 years: in late June and late August in 2001 and in early May, late June, and late August in 2002. A combination of gill nets set for short periods (3 h or less), minnow traps, 4-foot trap nets (1 foot = 0.3048 m), Kushneriuk traps (Kushneriuk and Paloheimo 1984), and a 40-foot beach seine were all used to catch a wide size range of perch while minimizing mortality to incidentally captured fish. Lake temperatures were monitored throughout the growing season using temperature loggers deployed in littoral and epilimnetic habitats occupied by yellow perch.

Sampling

Fish

Captured fish were euthanized, placed in new, Hg-free Ziploc™ plastic freezer bags (Rennie 2003), and stored on ice in coolers. Fish were returned to the lab and either immediately processed or frozen at –20 °C for later processing. Fork length, total length, weight, and sex were determined for each fish collected. Otoliths and scales were collected for ageing, of which the former were used as the primary ageing structure.

White muscle for Hg analysis was dissected from the predorsal area on the left-hand side of the fish just above the lateral line, using a stainless steel scalpel blade. Fish were sampled from smallest to largest within a given catch to minimize the possibility of cross-contamination, since Hg concentration in fish tissue is correlated with body size (Somers and Jackson 1993; Gorski et al. 1999; Rennie 2003). Scalpel blades were cleaned between samples using a combination rinse of 20% HCl, clean deionized water, and wiped dry with an ultra-low Hg Kimwipe™. Tissue samples were stored in preweighed, Hg-free (Rennie 2003), 1.7-mL polyethylene microcentrifuge tubes (VWR International, Mississauga, Ontario) and frozen at –20 °C. Stomach fullness was subjectively rated on a scale of 0 to 4 (0 being empty, 4 being full). Stomachs were cut from the carcass, and contents were removed and placed individually into acid-washed glass scintillation vials that were sealed and frozen at –20 °C. The proportion of empty stomachs in each sampling period was used to help determine the feeding status of perch in our two lakes.

Invertebrates

Benthic invertebrates were the primary constituents of perch diets in our lakes (Rennie 2003). To help determine how prey density — and thus availability to perch — might affect differences in activity costs and consumption between lakes, we compared the total weight of invertebrates collected in each lake during three separate collection periods. Eight benthic invertebrate samples were collected from each lake at each sampling period, using equal sampling effort. Samples were taken with D-shaped kicknets, representing an approximate sampling area of 0.5 m^2.

Laboratory analysis

THg determination of fish muscle

Approximately 250–500 mg of wet muscle was weighed, dried overnight at 60 °C, and reweighed. A known amount of dry tissue was then transferred to clean, acid-washed test tubes, digested in 2 mL of 4:1 H_2SO_4:HNO_3 at 250 °C for 4–6 h, and allowed to cool overnight. Clean, acid-washed glass marbles were placed over the openings of digestion tubes to limit atmospheric contamination and sample loss during digestion. Digests were diluted with 10 mL of Hg-free deionized water and allowed to cool for approximately 2 hours. Two hundred µL of concentrated BrCl (Bloom and Crecelius 1983) was added to preserve samples, which were sealed with parafilm and refrigerated. Samples were analyzed within 5 days of preservation, but were typically analyzed the day following preservation. Immediately before analysis, samples were treated with 20 µL of 30% $NH_2OH \cdot HCl$ to reduce halogens and nitrogen oxides present in the sample, which can interfere with detection. THg was determined using cold vapour atomic fluorescence spectrometry (Tekran model 2600 analyzer, Tekran Inc., Toronto, Ontario) in a class-100 clean room, compliant with US–EPA method 1631. Reagent and analytical blanks were run alongside all samples, the values for which were subtracted from all tissues and standard reference materials.

MeHg determination of fish tissues and diet

The organic Hg fraction in both fish and invertebrates occupying lower trophic levels is typically less that 100% of THg concentrations (Lasorsa and Allengil 1995; Tremblay and Lucotte 1997; Bowles et al. 2002). Therefore, we determined organic Hg of fish stomach contents to estimate MeHg in fish diets used in this study. Because the majority of organically bound Hg in animal tissues is in the form of MeHg (Paterson et al. 1998), fish tissues and stomach contents were analyzed for organic Hg content to estimate MeHg.

Whole fish (young of the year) or fish tissues (muscle or testes) were homogenized using a stainless steel Polytron homogenizer–sonicator (Brinkman Instruments Inc., Rexdale, Ontario). Samples were homogenized for 10-s intervals and kept on ice between homogenizations to avoid excessive heating. The process was repeated until homogenization was complete. To avoid cross-contamination, we rinsed the blades of the homogenizer thoroughly between samples with a combination of metal-specific detergent (Citranox™) and Hg-free deionized water and then wiped them dry with a clean Kimwipe™. Subsamples of fish tissue homogenates were added to preweighed, acid-washed, 20-mL scintillation vials and weighed (a second set of subsamples of these tissues were also taken for dry-weight and THg determinations). Five millilitres of Hg-free deionized water was added, and samples were again homogenized using clean techniques to avoid cross-contamination.

Wet stomach contents were transferred to 20-mL, preweighed, acid-washed glass scintillation vials, weighed, dried at 50 °C overnight, reweighed, and pulverized with an acid-washed glass rod. To avoid cross-contamination, we rinsed glass rods with a combination of concentrated H_2SO_4 and deionized water and then wiped dry with an Hg-free Kimwipe™. Five millilitres of Hg-free deionized water was added to the ground stomach contents.

After receiving 5 mL of Hg-free deionized water, all samples received 3 mL of 0.65 mol·L^{-1} $CuSO_4$, and 4 mL of 3 mol·L^{-1} KBr. Samples were shaken for 30 min, after which 5 mL of a 3:2 mixture (*v*/*v*) of methylene chloride – hexane was added to extract organically bound Hg from the sample and shaken for 24 h. Samples were allowed to settle overnight. Four millilitres of the organic layer was then removed and added to clean, acid washed digestion tubes. Samples were digested and analyzed for THg as previously described.

Analytical quality assurance and control

National Research Council (NRC) certified biological reference standards DORM-2 and DOLT-2 (http://inms-ienm.nrc-cnrc.gc.ca/calserv/crm_e.htm#data) were analyzed concurrently with tissues for MeHg and THg determinations and corrected for by blank subtraction. Mean raw values of THg for DORM-2 and DOLT -2 over the course of the study (21 replicate digests) were 4.70 μg Hg·g^{-1} dry weight and 2.26 μg Hg·g^{-1} dry weight, respectively, (standard errors: DORM-2, 0.17 μg·g^{-1}; DOLT-2, 0.09 μg·g^{-1}). These values fall within 10% of the reported NRC THg concentrations and within 95% confidence limits reported by NRC (DORM-2 = 4.64 ± 0.26 μg·g^{-1}; DOLT-2 = 2.14 ± 0.28 μg·g^{-1}). Average recoveries for uncorrected DORM-2 and DOLT-2 over the course of the study were 101% and 106%, respectively. Analytical spike recoveries averaged 109%, with one–five spikes run in each analysis over 14 analytical runs. The average value for DORM-2 over all organic Hg analyses over the course of the study (17 replicate digests) was also within 10% of the nominal MeHg concentration reported by NRC (DORM-2 = 4.47 ± 0.32 μg·g^{-1}).

Considerable deviation from the nominal values in NRC standards occurred in 7 of the 21 THg digest runs performed during the study. For analyses where DORM-2 values deviated by more than 15% of nominal values, corrections of fish Hg concentration were made by dividing the observed concentration by a specific run bias correction factor, equal to the ratio of the average observed DORM-2 value in a digest to nominal values reported by NRC. We validated this correction with use of a power analysis, which determined that flesh tissues taken from the same fish run in different digests were indistinguishable from one another after correction (Rennie 2003).

Table 3. Swimming behaviours and associated swimming speeds observed using data collected from both Plastic Lake and Shoe Lake yellow perch (*Perca flavescens*), July 2001.

Behaviour observed	Swimming speed[a]	*N*
Swimming	1.46±0.13	22
Slow-swimming	0.73±0.06	21
Darting	5.25±1.15	6
Hovering (stationary)	0	na

Note: Numbers reported are averages based on data collected from both lakes. na, not applicable.
[a]Body lengths·s^{-1} ± 1 SE.

Observed swimming behaviour

Direct observations of fish were performed between 31 July and 15 August 2001 and between 26 July and 1 August 2002. 2001 data were collected in the morning (0600–1000, local time), afternoon (1000–1700), and evening (1700–2000) from both lakes, whereas 2002 data were collected in late morning – early afternoon only. Lakes were sampled on alternate dates so as to control for potential seasonal or lunar differences between lakes over the sampling period.

A snorkelling observer remained motionless while visually tracking a particular fish. Before timing began, the observer estimated the total length of a chosen fish. The activities of the fish were then documented over a 5-min period of observation. Seven activities for fish were documented; swimming, slow-swimming, chasing, escaping, darting, flashing, and hovering (stationary). Swimming speeds (in body lengths per second) were estimated for swimming, slow-swimming, and darting behaviours from both lakes in 2001 (Table 3). Five to fifteen observations of individual fish were taken from three–four sites around each lake during each time period recorded, as time and daylight permitted. Swimming and slow-swimming were differentiated by the relative speed with which fish were moving; chasing and escaping were characterized by the pursuit of one fish by another, at speeds approximating those observed for "swimming"; darting was noted as a very fast sudden movement, often the result of a startle response or escape from predation. Flashing was noted as a quick change in direction,

during which fish appeared to scrape up against objects in the water. The swimming speed for flashing was assigned the same value as that for darting.

For each individual fish, we summed the total time spent performing a given behaviour over the 5-min period of observation. Active behaviours were summed to estimate the total amount of time in a 5-min period spent active for an individual fish. Observers also quantified the number of feeding behaviours observed over the 5-min period. Feeding behaviours were classified as fish actively pecking at substrates or at open water (presumably zooplankton). Frequency of feeding behaviours were $\log_{10}(x+1)$-transformed to normalize distributions before analyses.

Energetics calculations using field swimming observations

Hourly energetics of fish were calculated using equations modified from Trudel and Boisclair (1996):

$$E_{\mathrm{h}} = 12 \cdot E_{5\,\mathrm{min}} \tag{12}$$

$$E_{5\,\mathrm{min}} = \sum_{n}^{i} E\mathrm{b}_i 13.56 \tag{13}$$

where E_{h} is the hourly energetic investment of an observed fish ($E{\cdot}\mathrm{h}^{-1}$), $E_{5\ \mathrm{min}}$ is the energetic investment in activity of the fish per 5-min period ($\mathrm{J}{\cdot}5\ \mathrm{min}^{-1}$), $\sum_n^i E\mathrm{b}_i$ is the sum of energetics for each (ith) behaviour over n behaviours observed, and 13.56 is an oxycaloric value ($\mathrm{J}{\cdot}\mathrm{mg}\ \mathrm{O_2}^{-1}$; Elliott and Davidson 1975). Energetics for individual fish behaviours, $E\mathrm{b}_i$ ($\mathrm{mg}\ \mathrm{O_2}{\cdot}\mathrm{min}^{-1}$), was calculated as

$$E\mathrm{b}_i = O_{\mathrm{min}(i)} T\mathrm{s}_i \tag{14}$$

where $O_{\mathrm{min}(i)}$ is the cost of a particular activity ($\mathrm{mg}\ \mathrm{O_2}{\cdot}\mathrm{min}^{-1}$), and $T\mathrm{s}_i$ is the number of swimming seconds observed for that activity ($\mathrm{min}{\cdot}5\ \mathrm{min}^{-1}$). Swimming cost was estimated using an empirical relationship of oxygen consumption with mean fish weight (W; g wet) and spontaneous swimming speed (S, $\mathrm{cm}{\cdot}\mathrm{s}^{-1}$; Boisclair and Tang 1993):

$$O_{\mathrm{h}} = 0.117\, W^{0.54}\, S^{1.09} \tag{15}$$

Swimming costs per hour (O_{h}) were calculated, and specific swimming speeds (in body lengths$\cdot\mathrm{s}^{-1}$; Table 3) were converted to absolute swimming speeds ($\mathrm{cm}{\cdot}\mathrm{s}^{-1}$) through multiplication of specific swimming speeds by the estimated size of the fish (cm) under observation.

Daily energetic investment ($\mathrm{J}{\cdot}\mathrm{day}^{-1}$) was estimated by calculating average weight-specific hourly estimates of active energetic investment ($\mathrm{J}{\cdot}\mathrm{g}^{-1}{\cdot}\mathrm{day}^{-1}$) for morning, afternoon, and evening samples in 2001. Weight was estimated from length–weight relationships in the lakes under study. Daily estimates were weighted according to the number of hours defined by each sampling period, and the total was used to estimate weight-specific averages of energetic investment. Night activity in yellow perch was assumed to account for a negligible component of fish activity based on recorded observations using infrared cameras (N.C. Collins, University of Toronto at Mississauga, 3359 Mississauga Road N., Mississauga, ON L5L 1C6, unpublished data).

LDH and protein analyses

Fish carcasses were kept frozen at –20 °C for 6 months immediately prior to analysis; preservation of tissues at –20 °C immediately after capture has been shown to adequately preserve the LDH enzyme (Sherwood et al. 2002*b*). Muscle samples from fish collected in 2002 were prepared and analyzed for both LDH and protein concentrations as described in Rajotte and Couture (2002).

Estimation of growth rate and life history parameters

Specific growth rates were estimated as described by Ricker (1975):

$$G = \frac{1}{\Delta t} \ln\left(\frac{W_t}{W_0}\right) \tag{16}$$

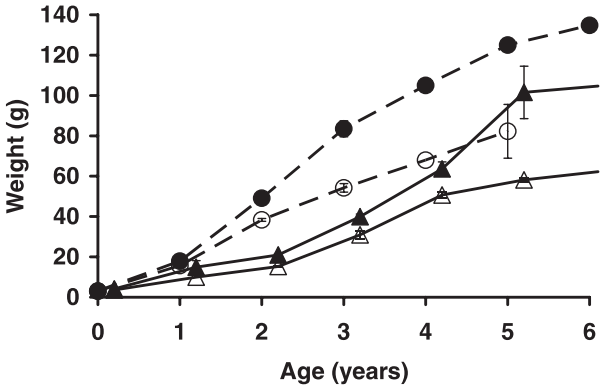
Collections of female fish in early May 2002 were used to determine age and size at maturity of female yellow perch by estimating the inflection point in a logistic regression between maturity status against age or size at maturity. Samples of male fish under 3 years of age were insufficient to calculate age at maturity and were assigned a value of 2 years of age in both lakes for bioenergetic modelling purposes. This value reflects the provincial average for male yellow perch age at maturity in Ontario (Purchase 2003). Instantaneous mortality rates for each population were estimated from catch curves as the slope of the right-hand tail of the distribution of log abundance versus age, using all fish in each lake collected over 2001 and 2002.

Statistical analyses

Comparisons between lakes of log absolute consumption estimates (C; $\mathrm{g}{\cdot}\mathrm{day}^{-1}$) and log activity costs (R_{a}, $\mathrm{kJ}{\cdot}\mathrm{day}^{-1}$) obtained from mass balance models were made using the log average body size over the time period modelled as a covariate. This analysis was repeated for both seasonal and annual models of fish C and R_{a}. This approach allowed simple comparisons of slopes and intercepts (using analysis of covariance, ANCOVA) between the populations investigated. A posteriori comparisons were performed to determine significant differences between lakes, and critical p values were corrected for the number of comparisons performed using sequential Bonferroni corrections where appropriate. All statistical procedures were carried out with SAS (Version 6.12, 1989, SAS Institute Inc., Cary, North Carolina). These relationships were used to estimate C and R_{a} for a 40-g fish, as this size approximates the median size of fish encountered in our experiment and allowed relevant comparisons between lakes from ANCOVA models. Maintenance ration was estimated as the intercept of the relationship between specific consumption rate (day^{-1}) and growth rate (day^{-1}) and can be interpreted as the energy intake required to maintain basic bodily functions without growth or mass loss. Differences between lakes were determined using ANCOVA, after verifying that slopes were not significantly different.

Time spent active, feeding behaviours, and hourly energetic estimates from 2001 swimming observations were compared between lakes across three sampling periods (morning, afternoon, and evening) using analysis of variance (ANOVA). A posteriori comparisons were made using effect coding and hypothesis testing in SAS (SAS Institute Inc.).

Fig. 1. Yellow perch (*Perca flavescens*) growth (represented by size-at-age of fish collected in August–September 2001–2002) in Plastic Lake (triangles, solid lines) and Shoe Lake (circles, broken lines). Plastic Lake data are offset in time slightly for clarity. Males are open symbols, females are closed symbols. Error bars are ±1 standard error. Projections of lines to age 6 are based on small (N = 1) sample sizes or estimated from catch data in May and July.



Observed activity rates for 2002 samples were compared using Student's t test. The relationship of muscle LDH activity with body weight was compared between lakes using a test for heterogeneity of slopes.

Results

Growth and life history traits

Size at age was typically greater for Shoe Lake fish for both males and females (Fig. 1). Specific growth rates of perch from Plastic Lake were almost half of those observed in Shoe Lake (t test, t_{13} = 2.87, p = 0.013; Table 4). Female perch from Plastic Lake matured later and were larger than Shoe Lake perch (Table 4). Instantaneous mortality rates were slightly higher in Shoe Lake, but not significantly (test for heterogeneity of slopes, $F_{[1,5]}$ = 1.01, p = 0.36; Table 4).

Prey availability

The total density of benthic invertebrates collected in Shoe Lake was consistently higher over three sample periods than that in Plastic Lake (Table 2). However, this difference was nonsignificant on average because of high interseasonal variation within a lake and a small sample size (paired t test, t_2 = –2.6; p = 0.12). In contrast, we observed no consistency in differences of the proportion of perch collected with empty stomachs between Shoe and Plastic lakes over the four sampling periods examined, and differences between lakes were not significant (paired t test, t_4 = 0.76, p = 0.5; Table 4).

Bioenergetics estimates

Slopes of log activity costs against log body weight were not significantly different between lakes (test for heterogeneity of slopes: $F_{[1,15]}$ = 0.6689, p = 0.43). Differences in activity costs between lakes bordered on significant (p = 0.097). Activity was generally higher in Plastic Lake perch compared with those in Shoe Lake at small and large body sizes, with considerable overlap for intermediate-sized fish (Fig. 2*a*; Table 5). Residuals from relationships between activity multipliers with body weight were compared between sexes, but no significant difference was detected (t_{15} = 1.026, p = 0.327).

Table 4. Comparison of yellow perch (*Perca flavescens*) growth, proportion of empty stomachs, and life history traits from the two lakes under study.

Attribute	Plastic Lake	Shoe Lake
Average % of empty stomachs	45.7±10.3	39.2±5.6
Specific growth rate (day^{-1})	0.00248*±0.0007	0.00492±0.0004
Female age at maturity (years)	4.4	3.0
Female size at maturity (mm)	176	166
Maximum age (years)	7	6
Survivorship (year^{-1})	0.47	0.54

Note: Significant differences between lakes are marked with an asterisk.

Slopes of log relative consumption against log body weight were not significantly different between lakes (test for heterogeneity of slopes: $F_{[1,15]}$ = 1.36, p = 0.26). Estimates of consumption rates were significantly higher in Plastic Lake perch than those in Shoe Lake (Fig. 2*b*; Table 5). Residuals from relationships between consumption and body weight were compared between sexes, but no significant difference was found (t_{15} = 0.841, p = 0.414). Maintenance ration was estimated to be slightly higher for Plastic Lake perch (0.0458 day^{-1}) than for Shoe Lake perch (0.0352 day^{-1}), though these differences between lakes were not significant ($F_{[1,14]}$ = 1.14, p = 0.3; Fig. 2*c*).

Swimming observations

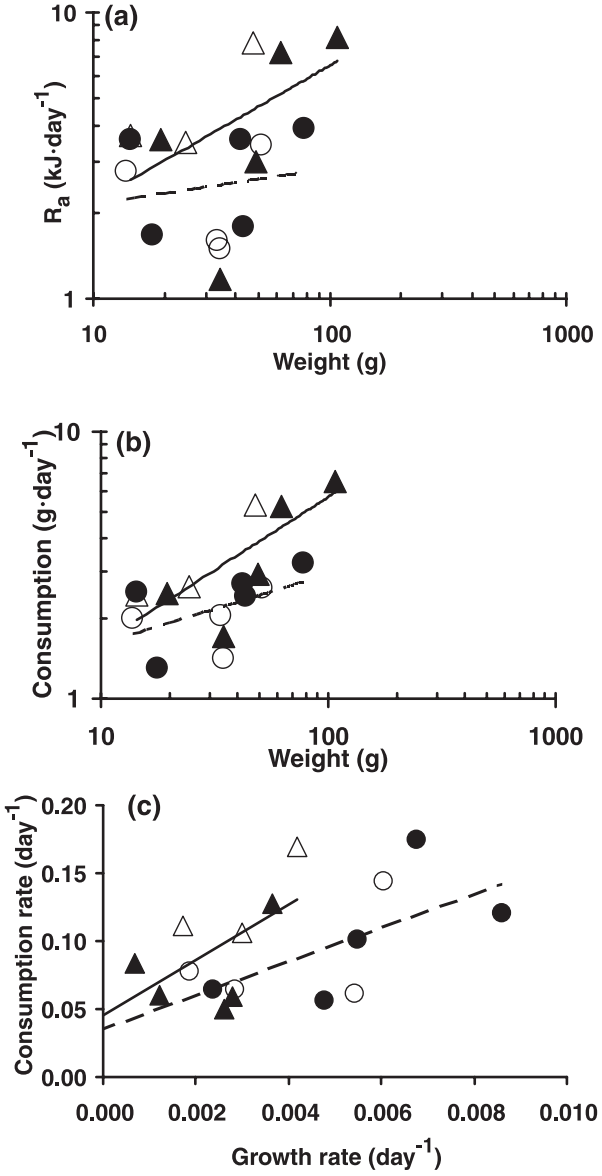
Perch in Plastic Lake were typically more active than perch in Shoe Lake (Figs. 3*a*, 3*b*). For 2001 samples, both energetic estimates (joules per gram per hour) and the time spent active over a 5-min period were higher for perch from Plastic Lake than from Shoe Lake (Table 5). Differences between time of collection were also significant ($F_{[2,87]}$ = 14.16, p = 0.0001). A posteriori comparisons revealed that differences between lakes were significant for morning and afternoon samples, but not for evening samples (morning: $F_{[1,87]}$ = 10.75, p = 0.0001; afternoon: $F_{[1,87]}$ = 8.77, p = 0.0015; evening: $F_{[1,87]}$ = 1.96, p = 0.17; p_{crit} = 0.01). Differences between lakes were also observed in 2002 (t test, t_{60} = 4.24, p = 0.0001). Daily energetic estimates (joules per day) based on observed swimming were on average 51% of activity rates calculated from bioenergetics models.

Frequency of perch feeding behaviours observed in a 5-min period was significantly higher for Plastic Lake than for Shoe Lake perch (Fig. 3*c*) and differed by time of sampling ($F_{[2,87]}$ = 4.22, p = 0.0178). Frequency of perch feeding behaviours in 2002 was not significantly different between lakes (t_{60} = 0.79, p = 0.43).

Muscle LDH activity

Because LDH is often found to scale positively with body size (Childress and Somero 1990), we selected a narrow range (34–67 g) of body sizes for comparison between lakes

Fig. 2. Bioenergetics of yellow perch (*Perca flavescens*) from Shoe Lake (circles) and Plastic Lake (triangles). Male fish are open symbols, females are solid symbols. Activity costs (R_a) against size (*a*), absolute consumption rates against body size (*b*), and relationships of specific consumption rate with specific growth rate (*c*) are shown.



across both sexes. This size range represents a large proportion (30%–45%) of fish caught in both lakes over the duration of the experiment. Within this size range, Plastic Lake perch had significantly higher muscle LDH activity than Shoe Lake perch (Table 5). We further examined the relationship between enzyme activity and body size for each lake. Shoe Lake muscle LDH activities scaled positively with body size, whereas no relationship was detected in Plastic Lake perch (Fig. 4). A test for heterogeneity of slopes between lakes revealed a significant interaction between perch size and muscle LDH activity (Table 5). The gender of perch did not explain any of the variation in muscle LDH activity.

Sherwood et al. (2002*a*) reported a strong positive relationship between muscle LDH activity and activity expressed as a multiple of standard metabolism. Using means of muscle LDH activity for Plastic Lake and Shoe Lake perch from the 34- to 67-g size range and the equation reported by Sherwood et al. (2002*a*), Shoe Lake perch were estimated to have activity costs 22%–29% lower than Plastic Lake perch. This estimated difference is only slightly lower than differences based on bioenergetics calculations and observed swimming behaviour (Table 5).

Discussion

Multiple independent methods of assessment agree that both activity levels and consumption rates are higher in Plastic Lake than in Shoe Lake. For activity level, two tests show significant differences at the 5% level and one at the 10% level; consumption rates were different at the 5% and 0.1% level. Since these are independent data testing the same scientific hypothesis (i.e., that slow-growing Plastic Lake fish act and feed differently than Shoe Lake fish), we combined these probabilities to determine the overall significance across all experiments (Sokal and Rohlf 1995). Activity differences between the two lakes were highly significant when p values were combined across all three methods (χ^2_6 = 28.04, $p < 0.0001$). Consumption rates were also highly significant across both methods of estimation (χ^2_4 = 20.69, p = 0.0004). Therefore, we conclude that the evidence for differences in both activity and consumption between the lakes is very strong, with both activity and consumption being significantly higher in Plastic Lake.

Our data illustrate that slow growth in Plastic Lake perch is a direct consequence of higher activity rates in this population, despite much higher rates of energy uptake (consumption) in Plastic Lake perch compared with Shoe Lake perch. Averaging across all methods of estimation, feeding rates of fast-growing Shoe Lake perch were 45% lower than slow-growing Plastic Lake perch, and activity costs were 28% lower in Shoe Lake perch compared with the slow-growing population of Plastic Lake. How lower activity and consumption combine to result in faster growth may at first seem counterintuitive. It may be that this demonstrates a greater effect of activity levels over consumption in determining overall growth rates; the energy saved by Shoe Lake perch by not allocating to activity may more than make up for reduced feeding rates. This pattern is also perhaps a reflection of the design of the BM, since the allometric exponent for metabolic activity (0.8) is greater than the allometric exponent for C_{max} for perch (0.72, Kitchell et al. 1977; Hewett and Johnson 1992). Thus, for the same size of fish, a decrease in active metabolism will result in a greater amount of excess energy (and thus growth, as it is defined in the BM) than would an equal proportional increase in consumption. Clearly, more data is required to address these possibilities directly. Regardless, the clear implication from our findings is that Plastic Lake fish are left with a lower rate of net energy available for growth because of higher activity costs, despite higher feeding rates.

The general agreement among these three independent estimates of activity costs helps support the use of bioenergetics approaches to determining activity costs in the

Table 5. Statistical summary of various consumption and activity estimation methods between Shoe Lake and Plastic Lake yellow perch (*Perca flavescens*).

Variable	Estimation method	Test statistic	*p*	% difference	Figure
Consumption	Bioenergetics	$F_{[1,141]} = 5.67$*	0.0321*	33.1[a]	2*b*
	Observed feeding behaviour	$F_{[1,871]} = 11.60$*	0.001*	57.7[b]	3*c*
Activity (R_a)	Bioenergetics	$F_{[1,141]} = 3.16$	0.097	39.7[a]	2*a*
	Observed swimming behaviour	$F_{[1,871]} = 14.31$*	0.0003*	37.1[b]	3*b*
Activity (physiological anaerobic capacity)	Differences in LDH activity for fish 34–67 g	$t_{40} = 2.04$*	0.028*	10.2	4
	LDH activity across observed size range of fish	Lake×weight interaction: $F_{[1,81]} = 9.57$*	0.0027*	na	4

Note: Significant statistical results are marked with an asterisk. Percent difference is calculated as the difference between lakes divided by the value observed in Plastic Lake, expressed as a percentage. LDH, lactate dehydrogenase, na, not applicable.

[a]At 40 g.

[b]Average of four time periods.

Fig. 3. Time spent active over a 5-min period of observation (*a*), estimates of relative energy expenditure per hour calculated from observed behaviour of individual yellow perch (*Perca flavescens*) over a 5-min period (*b*), and comparison of feeding behaviour (*c*) for yellow perch in Plastic Lake (triangles, solid line) and Shoe Lake (circles, broken line). Solid symbols are 2001 data, open symbols are 2002. 2002 samples were collected over late morning – early afternoon. Error bars are ±1 standard error.

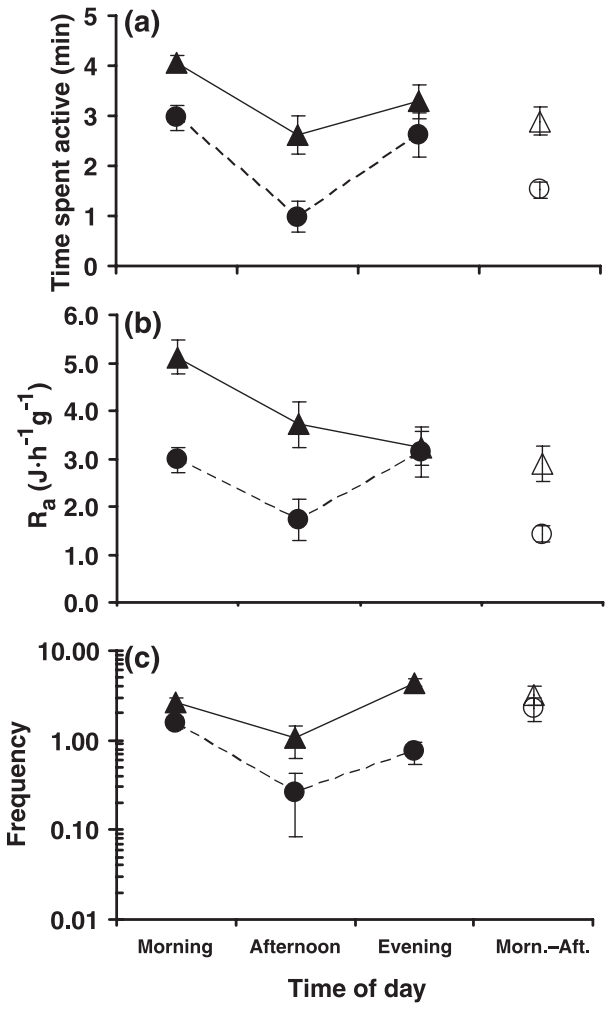
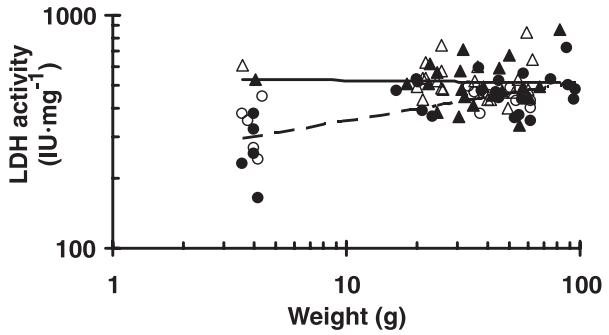


Fig. 4. Relationship between lactate dehydrogenase (LDH) activity and body size for yellow perch (*Perca flavescens*) collected in Plastic Lake (triangles, solid line; $F_{[1,43]} = 0.06$, $p = 0.81$) and Shoe Lake (circles, broken line; $F_{[1,38]} = 33.22$, $r^2 = 0.47$, $p < 0.0001$). Males are open symbols, females are solid symbols.



field. A number of studies have used contaminant–bioenergetic approaches to determine that activity costs were important determinants of growth and life history of fish (Trudel et al. 2001; Pazzia et al. 2002). These studies use field-validated contaminant bioaccumulation models to estimate fish consumption (Rowan and Rasmussen 1996; Trudel et al. 2000). However, activity costs determined using this approach have not been compared with alternate methods in wild populations. Though the results in this paper do not truly constitute a validation of the contaminant–bioenergetics approach, as none of the methods can be said to represent an absolute measure of activity in our populations, the close convergence of three independent methods argues that the pattern observed is very likely real and not simply an artefact of our estimation methods. Given that the qualitative differences between populations are real, as the combined statistical assessments clearly demonstrate, then an additional finding of our study is that the statistical power of the contaminant–bioenergetics approach to detect differences in activity is low compared with the two other methods we employed; only relatively large differences in activity derived from the contaminant–bioenergetics approach are likely to be detectable. A necessary corollary of this finding suggests that when statistically significant differences between populations are detected using this method, then the true effect is likely to be much stronger than the statistical probability indicates,

relative to the other methodologies employed in this study. This demonstration of the relatively conservative nature of the contaminant–bioenergetics approach in estimating differences in activity costs should lend additional support to studies employing this methodology that do report significant (or close to significant) differences in field-based activity costs between populations.

The trade-off between realized growth rates and activity in fish has long been recognized (Weatherly 1966; Boisclair and Leggett 1989*b*), but to our knowledge, only one other study has formally examined this relationship between natural populations in their native habitat using multiple independent methods for determination of activity costs. Aubin-Horth et al. (1999) reported that young-of-the-year perch from a fast-growing lake allocated a lower percentage of their total energy budget to activity than those in a lake with slower growth. However, the generality of the findings from this study are unclear, as the fish examined were limited to body sizes less than 10 g and differences in activity were low relative to the range of growth observed between the two populations under study. Our study independently supports the suggestion of Aubin-Horth et al. (1999) of a negative relationship between growth and activity in yellow perch, using multiple independent methods of assessing activity costs. Additionally, our study demonstrates that this relationship also applies to fish of larger body sizes and that the observed differences in activity costs between our populations are as large as has been observed elsewhere in nature (Boisclair and Leggett 1989*b*).

Neither of the populations considered in this study appear to suffer from starvation, given that the number of empty stomachs between lakes was roughly equivalent. As well, food availability (based on consistently higher patterns of benthic invertebrate density) appears to be higher overall in Shoe Lake. Perch in Plastic Lake may therefore need to increase their level of activity to seek out sufficient energy for growth and reproduction. It is possible that the absence of predators in Plastic Lake allows these perch to allocate a greater amount of energy to foraging activities than one might observe otherwise, since the risk of predation is much lower in Plastic Lake than in Shoe Lake. Similarly, one could argue that activity levels are essentially capped in Shoe Lake because of the presence of large-bodied piscivores. If food sources were to become limiting in this lake, an increase in activity might lead to a greater exposure of perch to large-bodied predators and thus reduce the number of active individuals. From this perspective, a trait-mediated "positive" effect of predator presence (Abrams 1984) may be contributing to higher growth rates in Shoe Lake perch. Positive trait-mediated effects of predators on prey have been well documented experimentally (Peacor 2002).

Given a fixed mortality rate, life history models (Roff 1984; Lester et al. 2004; Shuter et al. 2005) predict that slower growth will be associated with later maturity. This prediction is consistent with our observations, since both populations exhibited similar mortality rates and yet the slower-growing population (Plastic Lake) matured 1 year later than the faster-growing population. A similar result is predicted when maturity is assumed to occur at constant size, which does not appear to be the case for yellow perch. Though size at maturity is not dramatically different between our two populations, recent studies of yellow perch in Ontario have demonstrated two- to three-fold differences among populations in mean female size at maturity and age at maturity (Purchase et al. 2005), concluding that females of this species do not mature at a fixed size or age. In contrast with our findings, other studies (Ridgway and Chapleau 1994; Jansen 1996; Claramunt and Wahl 2000) have found that slower growing or stunted populations tended to mature earlier than faster-growing populations. However, in these studies it was either estimated or assumed that slow growth was associated with higher mortality (Jansen 1996; Claramunt and Wahl 2000; Trudel et al. 2001), thus leading to a decline in age at maturity (Roff 1984). This is in contrast with our two populations, where estimated moralities were similar.

Sexual dimorphism in growth was also observed in these lakes. Owing to their smaller size at age, one might also expect male perch to either eat less or be more active. However, there appeared to be no consistent or systematic variation between sexes in either consumption or active metabolism that could explain between-sex differences in growth in our two populations. This is in contrast with recent work that detected significant differences between activity and consumption rates in sexually dimorphic walleye from Ontario (Henderson et al. 2003). Because differences in size and Hg concentrations between populations (lakes) at a given age in this study are much larger than those between sexes within a population, we may not have had adequate statistical power to resolve between-sex differences in consumption and activity.

Overall, our results support the validity of the contaminant–bioenergetic approach to estimating activity and add to the small body of literature suggesting that among-lake variation in activity costs are at least as important as variation in food consumption in determining the growth rates of freshwater fish populations. The contaminant–bioenergetic approach, though perhaps conservative relative to other methods, is easy to employ in the field and to apply to archived data. We hope this study encourages further use of the contaminant–bioenergetics approach in studies of activity levels and their variation across fish populations.

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Appendix A

Appendix appears on the following page.

Table A1. Summary of body weight (W), Hg concentrations in fish (Hg), methylmercury (MeHg) concentrations in food (C_d), consumption rates (C), activity cost (R_a), and activity multipliers (ACT) for fish calculated using the Hg mass balance model combined with a bioenergetics model.

Year modelled	Age	Sex	Maturity	W_0 (g)	W_t (g)	Hg_0 ($\mu g \cdot g^{-1}$)	Hg_t ($\mu g \cdot g^{-1}$)	C_d ($\mu g \cdot g^{-1}$)	C (day^{-1})	R_a ($kJ \cdot day^{-1}$)	ACT
Plastic Lake											
2001	2	1	1	11.72	15.26	0.150	0.149	0.013	0.169	3.70	4.57
				(0.32, 20)	(0.41, 34)	(0.006, 20)	(0.011, 26)	(0.004, 43)	(0.024)	(0.60)	(0.56)
2002	3	1	1	22.16	26.76	0.211	0.177	0.017	0.106	3.53	3.14
				(0.67, 33)	(1.20, 27)	(0.024, 10)	(0.012, 10)	(0.002, 22)	(0.031)	(1.47)	(0.88)
2002	4	1	1	44.97	50.11	0.219	0.196	0.015	0.112	7.80	3.77
				(1.08, 6)	(2.26, 7)	(0.012, 6)	(0.012, 6)	(0.002, 18)	(0.029)	(2.48)	(0.87)
2001	2	2	0	16.39	20.63	0.137	0.129	0.013	0.128	3.61	3.74
				(0.27, 139)	(0.72, 60)	(0.005, 39)	(0.007, 42)	(0.004, 43)	(0.018)	(0.68)	(0.49)
2001	3	2	0	43.79	52.22	0.156	0.190	0.043	0.060	3.01	2.09
				(1.78, 40)	(3.21, 12)	(0.007, 26)	(0.020, 10)	(0.023, 28)	(0.013)	(1.29)	(0.46)
2002	3	2	0	31.63	37.29	0.177	0.130	0.017	0.050	1.16	1.54
				(0.77, 63)	(1.19, 55)	(0.013, 10)	(0.006, 12)	(0.002, 22)	(0.017)	(1.19)	(0.55)
2002	4	2	1	60.84	63.48	0.177	0.165	0.015	0.084	7.25	3.08
				(1.75, 19)	(4.02, 6)	(0.012, 10)	(0.016, 6)	(0.002, 18)	(0.035)	(4.06)	(1.15)
2001	5	2	1	101.30	109.30	0.215	0.254	0.044	0.060	8.20	2.58
				(6.58, 5)	(12.35, 6)	(0.027, 5)	(0.106, 2)	(0.032, 3)	(0.041)	(7.95)	(1.51)
Shoe Lake											
2001	1	1	0	10.70	15.67	0.091	0.097	0.012	0.144	2.77	3.70
				(0.55, 25)	(0.51, 16)	(0.006, 16)	(0.012, 16)	(0.002, 28)	(0.030)	(0.18)	(0.73)
2001	2	1	1	27.30	38.47	0.123	0.116	0.027	0.061	1.59	1.77
				(1.18, 5)	(0.76, 46)	(0.009, 5)	(0.004, 27)	(0.011, 38)	(0.008)	(0.11)	(0.23)
2002	2	1	1	31.17	37.32	0.118	0.114	0.019	0.064	1.49	2.12
				(0.93, 13)	(1.28, 5)	(0.006, 10)	(0.004, 5)	(0.002, 15)	(0.009)	(0.09)	(0.28)
2002	3	1	1	48.16	54.23	0.151	0.168	0.024	0.078	3.44	2.86
				(2.61, 15)	(2.09, 8)	(0.006, 10)	(0.012, 8)	(0.003, 29)	(0.015)	(0.22)	(0.50)
2001	1	2	0	10.78	16.52	0.089	0.106	0.012	0.175	3.59	4.39
				(0.46, 28)	(0.63, 19)	(0.005, 14)	(0.019, 13)	(0.002, 28)	(0.038)	(0.22)	(0.84)
2002	1	2	0	13.00	22.37	0.068	0.104	0.019	0.120	1.66	3.23
				(0.72, 10)	(2.25, 6)	(0.004, 10)	(0.011, 6)	(0.001, 16)	(0.019)	(0.99)	(0.53)
2001	2	2	0	36.30	49.07	0.124	0.116	0.027	0.056	1.79	1.70
				(1.98, 26)	(1.15, 82)	(0.005, 19)	(0.004, 57)	(0.011, 38)	(0.007)	(0.11)	(0.19)
2002	2	2	0	35.01	49.48	0.101	0.122	0.019	0.101	3.59	3.33
				(1.58, 10)	(3.04, 12)	(0.006, 9)	(0.004, 9)	(0.002, 15)	(0.010)	(0.11)	(0.30)
2002	3	2	1	71.81	83.46	0.127	0.140	0.024	0.065	3.92	2.53
				(4.36, 8)	(3.96, 24)	(0.006, 8)	(0.012, 10)	(0.003, 29)	(0.014)	(0.32)	(0.52)

Note: Values in parentheses are standard errors and the number of observations used to calculate means, respectively. For sex, 1 is male, 2 is female. For maturity, 0 is immature, 1 is mature.