Bioenergetics and mercury dynamics in fish

by

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SUMMARY

This research focuses on the development, evaluation, and application of a mercury (Hg) mass balance model for predicting the accumulation of Hg in fish. This model requires accurate estimates of Hg elimination rate by fish and feeding rates to adequately predict Hg concentration in fish. An empirical model was developed to estimate Hg elimination by fish using data obtained from published experiments. This analysis showed that Hg elimination rate was overestimated in short-term experiments, positively correlated to water temperature, negatively correlated to body size, and that the elimination rate of inorganic Hg was faster than that of methylmercury. This empirical model was then incorporated in a Hg mass balance model to predict the concentration of Hg in fish. The Hg mass balance model accurately predicted Hg concentration in fish when it was combined with food consumption rates that were determined using a radioisotopic method. This analysis suggested that the parameters of the Hg mass balance model were adequate for predicting Hg concentration in fish. I also showed that Hg concentration tended to be underestimated by the Hg mass balance model when it was combined with feeding rates determined with a laboratory-derived bioenergetic model, probably because activity costs derived in the laboratory do not reflect activity costs of fish in the field. Beside predicting Hg concentration in fish, I showed that this mass balance model could also be used to estimate feeding rates of fish in the field by measuring the concentration of Hg in fish. This approach was validated using data obtained from a published experiment. It was also successfully tested using independent estimates of feeding rates obtained with a radioisotopic method. I applied this Hg mass balance model to compare the energy budget of sympatric populations of dwarf and normal whitefish (*Coregonus clupeaformis*). This analysis showed that dwarf whitefish consumed 40-50% more food than normal whitefish. Conversion efficiency of dwarf whitefish were two to three times lower than normal whitefish. Thus, the low growth of dwarf fish can be more readily explained in terms of high energy allocation to metabolism rather than by a low rate of food consumption.

RÉSUMÉ

Cette étude porte sur le développement, l'évaluation, et l'application d'un bilan massique du mercure (Hg) afin de prédire l'accumulation du Hg chez les poissons. Ce modèle nécessite des estimations justes des taux d'élimination du Hg et des taux de consommation des poissons pour prédire la teneur en Hg des poissons. Un modèle empirique a été développé à partir de données publiées pour estimer le taux d'élimination du Hg des poissons. Cette analyse a démontré que les taux d'élimination du Hg étaient surestimés dans les expériences de courte durée, positivement corrélés à la température de l'eau, négativement corrélés à la masse des poissons, et que l'élimination du Hg inorganique était plus rapide que celle du méthylmercure. Ce modèle empirique a ensuite été incorporé dans le bilan massique du Hg afin de prédire la teneur en Hg des poissons. Le bilan massique du Hg a correctement prédit la concentration en Hg des poissons lorsqu'il était combiné à des taux de consommation déterminés par une méthode radioisotopique. Cette analyses suggère que les paramètres du bilan massique du Hg sont adéquats pour prédire la teneur en Hg des poissons. J'ai également démontré que la teneur en Hg était sous-estimée lorsque le bilan massique était combiné à des taux de consommation déterminés par un modèle bioénergétique, probablement parce que les coûts d'activité estimés en laboratoire ne réflètent pas les coûts d'activité des poissons en milieu naturel. En plus de prédire la teneur en Hg des poissons, j'ai démontré que ce bilan massique pouvait également être utilisé pour estimer les taux de consommation des poissons en milieu naturel en mesurant la teneur en Hg chez les poissons. Cette approche a été validée à l'aide de données provenant de la litérature. Elle a également été testée à l'aide de taux de consommation obtenus de façon indépendante. J'ai appliqué ce bilan massique pour comparer le budget énergétique de grands corégones (*Coregonus clupeaformis*) nains et normaux vivant en sympatrie. Cette analyse a démontré que les corégones nains consommaient 40-50% plus de nourriture que les corégones normaux. L'efficacité de croissance des corégones nains était deux à trois fois plus petite que celle des corégones normaux. Ces résultats indiquent que la faible croissance des corégones nains est reliée à des pertes métaboliques élevées plutôt qu'à un faible taux de consommation.

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PREFACE

The Faculty of Graduate Studies and Research of McGill University requires that the following statements be made in order to inform the reader of Faculty regulations:

"Candidates have the option of including, as part of the thesis, the text of one or more papers submitted or to be submitted for publication, or the clearly-duplicated text of one or more published papers. These texts must be bound as an integral part of the thesis.

If this option is chosen, ***connecting texts that provide logical bridges between the different papers are mandatory.*** *The thesis must be written in such a way that it is more than a mere collection of manuscripts; in other words, results of a series of papers must be integrated.*

The thesis must still conform to all other requirements of the "Guidelines for Thesis Preparation". ***The thesis must include:*** *a Table of Contents, an abstract in English and French, an introduction which clearly states the rationale and objectives of the study, a review of the literature, a final conclusion and summary, and a thorough bibliography or reference list.*

Additional material must be provided where appropriate (e.g. in appendices) and in sufficient detail to allow a clear and precise judgement to be made of the importance and the originality of the research reported in the thesis.

In the case of manuscripts co-authored by the candidate and others, ***the candidate is required to make an explicit statement in the thesis as to who contributed to such work and to what extent.*** *Supervisors must attest to the accuracy of such statements at the doctoral oral defense. Since the task of the examiners is made more difficult in these cases, it is in the candidate's interest to make perfectly clear the responsibilities of all the authors of the co-authored papers."*

This thesis consists of four chapters. Each of these chapters represent a distinct manuscript that was or will be submitted for publication in peer-reviewed scientific journals. All the work presented in this thesis was designed and executed by myself in close collaboration with my supervisor, Dr. J.B. Rasmussen (Department of Biology,

McGill University). All the chapters of the thesis were written by myself, and were co-authored by my supervisor who, in addition to providing technical advice and editorial comments, contributed to the development of the ideas presented in these chapters. Chapter 3 and 4 were also co-authored by R. Schetagne and Dr. A. Tremblay (Hydro-Québec) who provided most of the data that were used in these chapters. Chapter 1 has been published in *Environmental Science and Technology*. Chapter 3 is in press in *Canadian Journal of Fisheries and Aquatic Sciences* and should appear in the January or February issue of the year 2000. Chapter 2 is in press in *Ecological Applications*. Finally, chapter 4 has been submitted for publication to *Canadian Journal of Fisheries and Aquatic Sciences*.

CONTRIBUTIONS TO KNOWLEDGE

This thesis focuses on the bioenergetics of mercury accumulation in fish. I developed a mercury mass balance that could not only be used to accurately predict the concentration of mercury in fish, but also to assess the energy budget of fish under natural conditions.

Chapter 1

This is the first study to demonstrate that elimination rates of mercury by fish have been biased (overestimated) in short-term experiments. This bias has prevented previous studies from demonstrating that mercury elimination rates were positively correlated to water temperature in fish. As a consequence, this study is also the first to incorporate both fish size and water temperature as predictors of mercury elimination rate by fish in an empirical model.

Chapter 2

Although several mass balance models of mercury dynamics have been developed during the last 25 years, the parameters of these models have generally been adjusted *post hoc* to produce a close fit between observed and predicted mercury concentration. Moreover, the validity of the feeding rates used in these previous studies is questionable. In this study, I showed that mercury concentration was accurately predicted in fish using a mercury mass balance model when it was combined with food consumption rates estimated with a radioisotopic method using parameters derived *a priori* from laboratory experiments and field surveys. I also showed that mercury concentration tended to be underestimated when food consumption rates were estimated with a carbon-based bioenergetic model, probably because activity costs were not adequately represented in the bioenergetic model. Finally, I showed that mercury concentration was adequately estimated by the mass balance model when it was combined with a bioenergetic model that was implemented with site-specific activity costs. This analysis demonstrates the importance of adequately estimating food consumption rates of fish to accurately predict mercury concentration in fish using a mercury mass balance model.

Chapter 3

This is the first study that demonstrates that the mercury mass balance model used to predict mercury concentration in fish can also be used to accurately estimate food consumption rates of fish under natural conditions. This mercury mass balance model was validated using data obtained from a published experiment. I also showed that food consumption rates determined by a mercury and a radiocesium mass balance models were not significantly different.

Chapter 4

This is the first study that compared the energy budget of sympatric populations of dwarf and normally growing fish. I showed that the slow growth of dwarf fish was not due to an unusually low feeding rate. Instead, the analysis performed in this study showed that food consumption rates of dwarf fish determined with the mercury mass balance model were even higher than those of normally growing fish. I showed that dwarf fish allocated a larger fraction of their energy budget to metabolism than normally growing fish. The results obtained in this study also suggest that age at maturity may be inversely correlated to metabolic rates in fish.

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To the memory of H. André Trudel

"Animals are not always struggling for existence, but when they do begin, they spend the greater part of their lives eating. Feeding is such a universal and commonplace business that we are inclined to forget its importance. The primary force of all animals is the necessity of finding the right kind of food and enough of it."

Elton (1927)

"It is also apparent that studies of the behavior of methylmercury in nature must be intimately linked with bioenergetic studies."

Andren and Nriagu (1979)

GENERAL INTRODUCTION

Mercury (Hg) and its derivatives have been utilized extensively for more than three millennia (Nriagu 1979). Early uses of Hg included the extraction of gold and the formation of the vermilion pigment, a bright red color that was highly valued by the Romans. Mercury has also been used in medicine for the treatment of several diseases including syphilis, in chloralkali plants to produce caustic soda and chlorine gas, and in seed dressing to control fungal infections (Nriagu 1979). Mercury is currently used in dentistry (e.g. amalgam tooth filling), anti-fouling paints, laboratory and electrical instruments (e.g. thermometer, incandescent lamps and batteries), and gold mining activities (Malm et al. 1990; WHO 1990). More than 10^7 kg of Hg are produced annually by human activities, and an important fraction of this production is released directly into the aquatic and terrestrial environments, as well as in the atmosphere (Nriagu 1979; Watson 1979; Nriagu and Pacyna 1988).

Mercury is a persistent contaminant in the environment that can cause severe neurological damage to humans (e.g. Minamata disease), retard mental development of children, and may sometimes even lead to death (Hunter et al. 1940; Bakir et al. 1973; Takizawa 1979; WHO 1990). Furthermore, Hg can be transferred to the human fetus during pregnancy and might interfere with the brain development of the embryo (see review in WHO 1990). Mercury also represents a threat to wildlife because it can be accumulated in high concentrations in both aquatic and terrestrial animals (Berg et al. 1966; Johnels et al. 1967; Fimreiti et al. 1971; Wren et al. 1983; Wren 1986; Muir et al. 1992; Scheuhammer et al. 1998; Wolfe et al. 1998). For instance, the reduction of seed-

eating bird populations in Sweden in the 1950-60s was partly attributed to the massive use of seed treated with Hg fungicides (Borg et al. 1969).

The toxicity of Hg depends on its chemical speciation with organic compounds. The most toxic form of Hg is methylmercury, which was also detected in high concentration in the victims of the Minamata disease and in their food (see reviews in Takizawa 1979; WHO 1990). It is generally recognized that fish represent the most important source of methylmercury to human populations (Lindberg et al. 1987; WHO 1989, 1990; Lindqvist et al. 1991) and to fish-eating wildlife such as loons, herons and mink (Wren 1986; Scheuhammer et al. 1998). Although Hg is principally released in the environment as inorganic Hg, more than 95% of the total Hg in fish is methylmercury (Bloom 1989, 1992; Grieb et al. 1990; Wiener et al. 1990). Consequently, the risk of Hg poisoning in humans and wildlife is likely to be related to their diet. Fitzgerald and Clarkson (1991) estimated that the tolerable human intake of methylmercury (200 $\mu g \cdot wk^{-1}$; WHO 1976) was exceeded by more than 250,000 fish consumers in the United States alone. Even though industrial emissions of Hg to the aquatic environment have been considerably reduced during the last 30 years due to effective legislation and improved technology (Lindqvist et al. 1991), Hg concentration in fish will remain elevated for decades in polluted aquatic ecosystems due to the long half-life of Hg in the environment (Lodenius 1991; Verdon et al. 1991; Parks et al. 1994; Håkanson 1996).

The potential hazards associated with Hg toxicity on human health and wildlife are not restricted to directly polluted lakes and rivers. Elevated Hg concentrations in fish have often been reported in lakes that are remote from direct sources of Hg pollution in several countries, including Canada (Wren and MacCrimmon 1983; McMurthy et al. 1989; Wren et al. 1991; Cabana et al. 1994), the United States (Grieb et al. 1990; Sorensen et al. 1990; Wiener et al. 1990; Lathrop et al. 1991; Lange et al. 1993), Sweden (Johnels et al. 1967; Håkanson 1980; Håkanson et al. 1988), and Finland (Turunen and Alm 1990). For instance, more than 80% of the lakes listed in the Ontario Hg database include fish with Hg concentration higher than the admissible limit of 0.5 $\mu g \cdot g^{-1}$ set by the WHO (1976). Håkanson et al. (1988) estimated that Hg concentration of fish exceeds 0.5 $\mu g \cdot g^{-1}$ in more than 40 000 lakes in Sweden. This represents about 50% of the lakes in Sweden (Håkanson 1996). Consequently, the health risk associated with Hg intoxication

to humans and wildlife together with the global Hg contamination of ecosystems requires the development and evaluation of models to understand and predict Hg accumulation in fish.

Dynamics of mercury concentration in fish

Mercury concentration generally increases with age or size in fish (Bache et al. 1971; Scott and Armstrong 1972; Cutshall et al. 1978; MacCrimmon et al. 1983; Mathers and Johansen 1985; Borgmann and Whittle 1992; and many others). Mercury is accumulated in fish by direct uptake of contaminated water through the gills and absorption of contaminated food through the intestinal wall (Olson et al. 1973; Pentreath 1976a, 1976b, 1976c; Phillips and Buhler 1978; Boudou et al. 1991). Laboratory studies also indicate that the accumulation rate of Hg is influenced by fish feeding and metabolic rates, as well as Hg concentration in water and in food, and that the uptake of Hg from water and food sources are additive (Reinert et al. 1974; Lock et al. 1975; Phillips and Buhler 1978; Ribeyre et al. 1980; Rodgers and Beamish 1981, 1982, 1983). Early models developed to predict the accumulation of Hg in fish generally suggested that water was the dominant source of Hg to fish (Fagërstrom et al. 1974). This interpretation is not supported by recent studies. Mercury is biomagnified in fish and aquatic food chains suggesting that food is the dominant pathway of Hg in fish (Biddinger and Gloss 1984; Watras and Bloom 1992; Cabana et al. 1994; Suedel et al. 1994; Becker and Bigham 1995; Hill et al. 1996). Furthermore, the importance of direct uptake of Hg from water was probably overestimated in these early studies. The values of methylmercury concentration in water obtained prior to 1980 were about one to three orders of magnitude higher than recent estimates, probably due to analytical difficulties and potential contamination of the water samples (Gill and Bruland 1990). In addition, a fraction of the dissolved pool of methylmercury is associated with dissolved organic carbon (DOC) and is not available for direct uptake (Hintelman et al. 1995). Finally, fish exposed only to Hg contaminated water accumulate 1000-times less Hg than fish exposed to both Hg contaminated water and food (Lock et al. 1975; McKim et al. 1976; Pentreath 1976a, 1976b, 1976c; Cember et al. 1978; Gill and Bruland 1990; Porcella 1994; Becker

and Bigham 1995; Hill et al. 1996). This suggests that Hg uptake from water represents less than 0.1% of the Hg accumulated in fish, and may be considered negligible.

Several theoretical models have been developed to describe the dynamics of Hg in fish during the last 25 years (Fagerström et al. 1974; Norstrom et al. 1976; Braune 1987; Jensen 1988; Harris and Snodgrass 1993; Rodgers 1994; Korhonen et al. 1995; Post et al. 1996; Harris and Bodaly 1998). Most of these models have been developed to describe the dynamics of the total quantity of Hg (also known as body burden) in fish. However, toxicologists are generally concerned with the concentration of Hg in the edible portion of fish, rather than by the total quantity of Hg in fish, since advisory guidelines are based on Hg concentration measured in skinless filets. Thomann (1981) derived a general mass balance model that can be used to describe the dynamics of contaminant concentration in fish. Assuming that Hg uptake from water is negligible and that Hg concentration in skinless filets and in the whole fish are equal, the mass balance model of Hg concentration (C; $\mu g \cdot g^{-1}$) may be written as (Thomann 1981; Appendix I);

$$(1) \qquad \frac{dC}{dt} = (\alpha \cdot C_d \cdot I) - (E + G + K) \cdot C$$

where α is the assimilation efficiency of Hg from food, C_d is the concentration of Hg in fish diet ($\mu g \cdot g^{-1}$), I is the food consumption rate of fish ($g \cdot g^{-1} \cdot d^{1}$ or d^{-1}), E is the elimination rate of Hg ($\mu g \cdot \mu g^{-1} \cdot d^{-1}$ or d^{-1}), G is the specific growth rate ($g \cdot g^{-1} \cdot d^{1}$ or d^{-1}), and K is the loss rate of Hg due to spawning ($\mu g \cdot \mu g^{-1} \cdot d^{-1}$ or d^{-1}). Integrating this equation gives (Appendix I);

$$(2) \qquad C_t = C_o \cdot e^{-(E+G+K)t} + \frac{(\alpha \cdot C_d \cdot I)}{(E+G+K)} \cdot \left[1 - e^{-(E+G+K)t}\right]$$

where C_o is the initial concentration of Hg in fish ($\mu g \cdot g^{-1}$), C_t is the concentration of Hg in fish at time t ($\mu g \cdot g^{-1}$). In immature fish, K is equal to zero. Thus, the accumulation of Hg could be adequately predicted in fish if accurate estimates of C_o, E, G, K, α, C_d, and I were obtained.

The objectives of this thesis were to (1) estimate the parameters of this mass balance model, (2) evaluate the accuracy of the predictions of this model, (3) determine the effects of metabolic parameters on Hg accumulation in fish, and (4) demonstrate that this model can also be applied to assess the energy budget of fish.

Modeling the elimination rate of mercury by fish

The elimination rate of Hg is quite variable in fish and appears to be influenced by fish size and water temperature (Ruohtula and Miettinen 1975; Sharpe et al. 1977). Few studies have attempted to develop a general empirical model that could be used to estimate the elimination rate of Hg by fish and usually incorporated only body size as the independent variable. However, the general applicability of these models for estimating Hg elimination rate in fish is questionable. Norstrom et al. (1976) presented the first empirical model of Hg elimination by fish. His model was constructed using data mostly obtained on goldfish (*Carassius auratus*) and covered a relatively small range of body size (1-300g). Most of the data used by Norstrom et al. (1976) were also obtained from short-term experiments. Rowan and Rasmussen (1995) showed that the elimination rate of radioactive cesium (^{137}Cs), another persistent contaminant in fish, was overestimated in short-term experiments. Thus, Norstrom's model may be inadequate for estimating the elimination rate of Hg by fish. Hendriks' (1995) model has very low predictive power (r^2=0.24). Furthermore, his model was built using both inorganic Hg and methylmercury elimination rate, and also included data from mammals to increase the range of body size. Inorganic Hg is generally eliminated faster than methylmercury in fish (de Freitas et al. 1974; Pentreath 1976a, 1976b, 1976c, 1976d), while methylmercury is excreted faster in mammals than in fish (Fagerström et al. 1974; Magos 1987), suggesting that his model might also be biased. Therefore, there is a need to develop a reliable model to estimate the elimination rate of Hg by fish.

In chapter 1, I developed a simple empirical model to estimate the elimination rate of Hg by fish. I showed that Hg elimination could be accurately estimated using fish size and water temperature, and that Hg elimination rate was overestimated in short-term experiments.

Predicting mercury concentration with a mass balance model

Mercury mass balance models are sensitive to uncertainty associated with food consumption rates (Harris and Snodgrass 1993; Rodgers 1994), indicating the importance of accurately estimating this parameter for predicting Hg concentration in fish using this approach. Feeding rates used in Hg mass balance models have generally been estimated with laboratory-derived bioenergetic models. In these studies, there has usually been a close fit between observed and predicted Hg concentration in fish. However, the apparent success of these Hg mass balance models may be somewhat artificial. The assimilation efficiency and the elimination rate of Hg have often been adjusted until a good fit was produced between observed and predicted Hg concentrations. The validity of these *post hoc* adjustments for other species and other populations is unknown. The validity of the feeding rates used in these mass balance models is also questionable. Several studies have shown that bioenergetic models often underestimate the quantity of food consumed by fish, presumably because activity costs are not adequately represented in these models (Boisclair and Leggett 1989a; Post 1990; Fox 1991; Wahl and Stein 1991; Madon and Culver 1993; Rowan and Rasmussen 1996). Activity costs are generally derived from laboratory experiments and assumed constant for a given species. However, activity costs have been shown to vary four-fold among populations of the same species (Boisclair and Leggett 1989b). Activity costs are also generally higher in adult than in juvenile fish (Rowan and Rasmussen 1996). Thus, the activity costs derived from one population or age-class may not be applicable to other situations. Because bioenergetic models are sensitive to uncertainty associated with activity costs, accurate estimates of activity costs are required for predicting Hg concentration in fish using Hg mass balance models and bioenergetic models. Unfortunately, it is extremely difficult to estimate activity costs of fish in the field with accuracy (Trudel and Boisclair 1996).

In the second chapter of the thesis, I tested this Hg mass balance model using food consumption rates obtained using a radioisotopic method recently refined by Rowan and Rasmussen (1996, 1997) and a carbon-based bioenergetic model. I showed that the Hg mass balance model accurately predicted Hg concentration in fish when it was combined with food consumption rates determined with this radioisotopic method, but tended to underestimate the accumulation of Hg when it was combined with food consumption

rates that were estimated with the bioenergetic model. Therefore, this mass balance model may be useful for predicting Hg concentration in fish.

Estimating food consumption rates with a mercury mass balance model

In addition to providing a theoretical framework for understanding the process of Hg accumulation in fish, mass balance models of Hg dynamics could also be used to estimate feeding rates of fish in the field (Rodgers and Beamish 1982). In principle, it is possible to estimate food consumption rates of fish by rearranging eq. (2) as;

$$(3) \qquad I = \frac{C_{t+\Delta t} - C_t e^{-(E+G+K)\Delta t}}{\alpha \cdot C_d \cdot \left[1 - e^{-(E+G+K)\Delta t}\right]}(E+G+K)$$

Considering that fish age and weight and that Hg concentration of fish and their prey can be determined relatively easily, Hg would be a useful tracer for estimating food consumption rates of fish in the field. Although mass balance models of persistent contaminants such as ^{137}Cs and PCB have been developed during the last three decades for estimating food consumption rates of fish (e.g. Kevern 1966; Kolehmainen 1974; Norstrom et al. 1976; Niimi 1981; Borgmann and Whittle 1992; Forseth et al. 1992; Rodgers 1994; Rowan and Rasmussen 1996, 1997; Tucker and Rasmussen 1999), these models have rarely been used compared to traditional methods based on stomach contents or bioenergetic models. This may be because (1) fish ecologists have been under the impression that this approach could only be used in highly contaminated sites, (2) measuring these chemicals in fish and their prey is difficult, or (3) few empirical models are available to estimate the elimination rate of these chemicals. In the third chapter of the thesis, I developed a Hg mass balance model to estimate food consumption rates of fish. The model was validated using data obtained from a published experiment. It was also tested using independent estimates obtained with a radioisotopic method (i.e. Rowan and Rasmussen 1996, 1997).

To further illustrate the utility of this approach for studying fish bioenergetics, I applied the Hg mass balance model to compare the energy budget of sympatric populations of dwarf and normally growing fish in the fourth chapter of the thesis.

Sympatric populations of dwarf and normal morphs of the same species have frequently been observed in north temperate and subarctic lakes (Fenderson 1964; Mann and McCart 1981; Hindar and Jonsson 1982; Jonsson et al. 1988). Dwarf fish have a much lower growth rate, reach maturity earlier, and have a shorter lifespan than normal fish (Fenderson 1964; Jonsson and Hindar 1982; Jonsson et al. 1988). To achieve a lower growth rate than the normal phenotype, dwarf fish must consume less food and/or allocate a larger fraction of their energy budget to metabolism. I tested the hypotheses that dwarf fish have a lower feeding rate and/or higher metabolic rate than normally growing fish. In this study, feeding rates were determined using a Hg mass balance model. It would have been extremely difficult to perform this analysis using conventional methods based on stomach contents. Thus, chemical tracers like Hg provide a promising alternative to stomach contents for studying the bioenergetics of fish.

In summary, I will develop a simple Hg mass balance model to predict the accumulation of Hg in fish. Before this model can be applied, I have to derive an empirical model to estimate the elimination rate of Hg by fish that will subsequently be used in the Hg mass balance model. I will test this Hg mass balance model by combining it with feeding rates estimated with a radioisotopic method. I will then demonstrate that this mass balance model can also be used to estimate food consumption rates of fish in the field. Finally, I will apply this model to estimate the energy budget of sympatric populations of dwarf and normally growing fish to illustrate the utility of this method.

CHAPTER 1

MODELING THE ELIMINATION OF MERCURY BY FISH

Abstract

Mass balance models can be used to predict mercury accumulation in fish. However, factors influencing mercury elimination, an essential parameter of the mass balance model, are poorly understood. We developed a general model of mercury elimination from fish using literature data. Our analysis showed that short-term experiments (<90 days) overestimated the elimination rate of mercury and that inorganic mercury was excreted 3-fold faster than methylmercury. Both inorganic mercury and methylmercury excretion were negatively correlated to body size, but only methylmercury elimination was significantly correlated to water temperature. A general model of methylmercury excretion was developed using temperature, body size, and a dummy variable representing exposure time (acute vs chronic) as independent variables (r^2 = 0.77). Methylmercury depuration rate was independent of mercury burden and concentration, indicating that it is a first order process. Methylmercury elimination tended to be overestimated by a factor of 2 to 6 by empirical models that were published prior to this study. A field test showed that our model adequately estimated the elimination rate of methylmercury under natural conditions.

Introduction

Mercury (Hg) is a persistent contaminant that can cause severe neurological damage to humans and wildlife (*1-6*). Furthermore, Hg can be transferred to the human fetus during pregnancy and might interfere with the brain development of the embryo (*3*). It is generally recognized that fish represent the most important source of Hg to human populations (*3*). However, the potential hazards associated with Hg poisoning are not restricted to polluted lakes and rivers. Elevated Hg concentrations in fish have often been reported in lakes far from direct sources of Hg pollution in several countries, including Canada (*6-8*), the United States (*9-11*), and Sweden (*12*). The health risk associated with Hg intoxication to humans together with the global Hg contamination of aquatic ecosystems necessitates the development of models to predict Hg dynamics in fish.

Mass balance models are particularly useful for predicting Hg concentration in fish (*13-15*). Bioenergetics-based models describe the concentration of Hg in a fish by the balance between Hg uptake from food and water, and Hg elimination from fish tissues (*16-20*). Hg uptake from food and water is determined by the energy requirements of the fish and is estimated using a carbon-based bioenergetic model. The elimination rate of Hg in mass balance models is assumed to be a first order process and has usually been described by an allometric relationship (*16-23*). The elimination of Hg by fish acutely exposed to Hg contaminated water is generally biphasic: the fast component has a half-life of days to weeks, while the slow component has a half-life of months to years (*24-26*). For fish that receive a single dose of Hg, 20-30% of the initial Hg burden is eliminated by the fast component (*24-25*). However, it has been suggested that chronically exposed fish excrete persistent contaminants almost exclusively from the slow component (*27-29*). This implies that, for the purpose of predicting fish Hg dynamics with bioenergetic models, the elimination rate of Hg can be described only by the slow component, and that the fast component may be ignored. Despite the sensitivity of bioenergetics-based models to Hg elimination (*20*), few empirical models have been developed to predict Hg elimination from the slow component by fish.

Elimination rates of persistent contaminants are generally negatively correlated with body size (*30-33*), and positively correlated with water temperature (*32-34*). The

elimination rate of Hg is negatively correlated with body size, with an allometric exponent ranging from -0.58 (*16*) to -0.22 (*35*). The general applicability of these models for predicting Hg concentration in fish is, however, questionable. For instance, Norstrom's (*16*) model was developed using experiments performed almost exclusively on goldfish (*Carassius auratus*), and covered a relatively small range of fish size (1-300 g). Hendriks' (*35*) model has very low predictive power (r^2=0.24). In addition, his model was built using both inorganic Hg and methylmercury (MeHg) elimination rates and also included elimination data from mammals to increase the range of body size. Inorganic Hg is generally eliminated faster than MeHg in fish (*37-41*), while MeHg is excreted faster in mammals than in fish (*17,42*), suggesting that his model might be biased.

The evidence supporting the effect of water temperature on Hg elimination rate is conflicting. Ruohtula and Miettinen (*24*) showed that Hg excretion rate of rainbow trout (*Oncorhyncush mykiss*) increased with water temperature (Q_{10}=1.5). Similarly, Ribeyre et al. (*43*) showed that Hg contaminated rainbow trout maintained in clean water tended to retain more Hg at low temperature. In contrast, other studies have found no significant effect of water temperature on Hg elimination rate in goldfish between 4 and 24 °C (*37,44*). Therefore, there remains considerable uncertainty regarding the coefficients for body size and temperature effects on Hg excretion.

The objective of this work was to develop a general model of Hg elimination rate from fish. The hypotheses tested during this study were: (I) inorganic Hg is excreted faster than MeHg in fish, (II) Hg elimination rate is negatively correlated to body size and (III) positively correlated to water temperature. We also examined the influence of Hg burden and concentration on the excretion rate of Hg, to test the assumption that Hg excretion rate is a first order process.

Methods

We used published estimates of MeHg and inorganic elimination rates by fish from the slow component to develop a Hg elimination model. The experimental procedure commonly used for estimating MeHg and inorganic Hg elimination rates consisted of exposing fish to water or food contaminated with ^{203}Hg or $CH_3{}^{203}Hg$. The contaminated

fish were then transferred to clean water where fish ^{203}Hg burden was measured periodically. In acutely exposed fish, the elimination of ^{203}Hg is biphasic (*24-25*). The excretion rate of Hg from the slow compartment can be estimated using the slope of log Hg burden as a function of time during the linear phase of the elimination. This approach requires that the experiment last long enough to achieve this linear phase. It has been shown that short-term experiments overestimate the elimination rate of contaminants from the slow components (*32,45*). However, the effect of the duration of the experiment on the elimination rate of Hg is not known.

We examined the influence of the duration of the experiment, body size, water temperature, Hg burden and concentration on both MeHg and inorganic Hg elimination rate using correlation and regression analyses (*46*). All variables except water temperature were log transformed (natural logarithm) to linearize the relationship between the dependent and independent variables and to stabilize the variance (*46*). Finally, since MeHg is the predominant (>95%) form of Hg in fish (*47-50*), we developed a general model of MeHg excretion rate by fish using multiple regression analyses (*46*).

Results and Discussion

Statistical analyses

A total of ninety six estimates of Hg elimination rate from the slow compartment covering sixteen fish species were obtained from the literature (Table 1). The elimination rate of inorganic Hg ($r = -0.88$; $p<0.0001$) and MeHg ($r = -0.64$; $p<0.0001$) were both negatively correlated to the duration of the experiment. These data were therefore separated into two groups according to the duration of the experiment for the remainder of the analyses (<90 days and >90 days). These time intervals were chosen because Rowan and Rasmussen (*32*) showed that an experiment needed to last at least 90 days to adequately distinguish the fast and slow components of ^{137}Cs elimination. Short-term experiments (i.e. <90 days) tended to overestimate the elimination rate of inorganic Hg and MeHg by a factor of 7.6 on average (Figure 1). The elimination rate of inorganic Hg was on average 1.8-fold faster than MeHg (Figure 1). A two-way ANOVA indicated that Hg elimination rate varied significantly with the duration of the experiment ($F_{1,92}=40.6$;

Table 1. Body size, water temperature, mercury excretion rate (E) and half-life, mercury concentration ([Hg]) and burden, and duration of the experiment of various fish species reported in the literature.

Species	Size (g)	Temperature (°C)	E (d^{-1})	Half-life (d)	[Hg] ($mg \cdot g^{-1}$)	Burden (mg)	Duration (d)	Source
			Inorganic mercury					
Carassius auratus	1.3	13	0.087	8			28	(36)
Carassius auratus	15	13	0.046	15			60	
Carassius auratus	10		0.029	24			60	(51)
Esox lucius	62	13	0.01	69			59	(36)
Esox lucius	208	13	0.0081	86			59	
Gambusia affinis	0.3	20	0.53	1.3			6	(52)
Ictalurus nebulosus	62	13	0.01	69			70	(36)
Ictalurus nebulosus	208	13	0.0081	86			70	
Ictalurus nebulosus	320	13	0.0039	178			70	
Ictalurus punctatus	250	21	0.00096	723	0.0064	1.6	155	(53)
Perca flavescens	15	13	0.046	15			60	(36)
*Pleuronectes platessa**	42	10	0.0051	135			141	(38)
Pleuronectes platessa	70	10	0.021	33			41	(39)
*Raja clavata**	18	10	0.0029	242			165	(41)
Raja clavata	59	10	0.011	62			43	
			Methylmercury					
Anguilla vulgaris	100	10	0.00076	910	0.018	1.8	130	(26)
Anguilla vulgaris	100	10	0.00067	1030	0.018	1.8	130	
Anguilla vulgaris	100	10	0.00067	1030	0.018	1.8	130	

Table 1. (continue)

Carassius auratus	1	13	0.042	17			60	(36)
Carassius auratus	7	13	0.017	41			60	
Carassius auratus	17	13	0.008	87			60	
Carassius auratus	1	20	0.035	20			60	(37)
Carassius auratus	7	20	0.023	30			60	
Carassius auratus	8	10	0.021	33			60	
Carassius auratus	9	5	0.021	33			60	
Carassius auratus	10	20	0.02	35			60	
Carassius auratus	10	20	0.023	30			60	
Carassius auratus	43	24	0.019	36			60	
Carassius auratus	1	22	0.02	35	0.72	0.72	43	(44)
Carassius auratus	5	24	0.013	53			45	
Carassius auratus	7.4	22	0.008	87	0.85	6.29	59	
Carassius auratus	7.4	24	0.013	53	0.15	1.11	41	
Carassius auratus	8.1	10	0.006	116	0.51	4.131	59	
Carassius auratus	9.2	5	0.006	116	0.23	2.116	59	
Carassius auratus	10.2	20	0.006	116	0.4	4.08	59	
Carassius auratus	15.4	24	0.006	116	0.71	10.934	59	
Carassius auratus	42.9	24	0.004	173	0.25	10.725	59	
*Esox lucius**	16160	4	0.0011	680	8.7	140592	180	(54)
*Esox lucius**	18500	10	0.00072	967	7.9	146150	270	
*Esox lucius**	3920	10	0.00095	728	8.3	32536	365	
*Esox lucius**	1000	10	0.00094	737	8.4	8400	365	
Esox lucius	300	10	0.00092	750	0.0058	1.74	130	(26)
Esox lucius	300	10	0.0011	640	0.0058	1.74	130	
Esox lucius	300	10	0.00089	780	0.0058	1.74	130	
Esox lucius	75	13	0.005	139			59	(36)

Table 1. (continue)

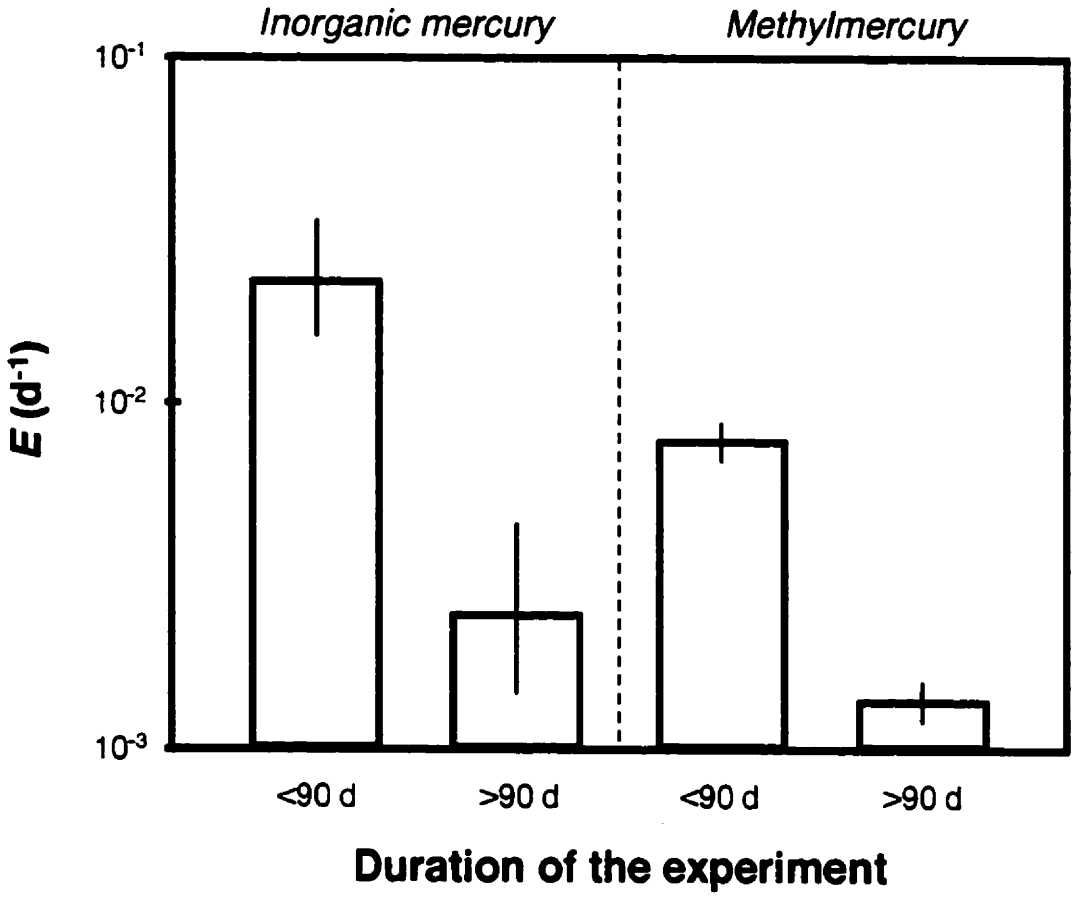
Esox lucius	150	13	0.004	173			59	
Esox lucius	85	9	0.0018	385			60	(37)
Ictalurus nebulosus	7	13	0.017	41			61	(36)
Ictalurus nebulosus	75	13	0.005	139			61	
Ictalurus nebulosus	150	13	0.004	173			61	
Ictalurus nebulosus	300	13	0.0075	92			61	
Ictalurus nebulosus	8	14	0.03	23			60	(37)
Ictalurus nebulosus	280	19	0.002	347			60	
Lepomis macrochirus	8	24	0.0053	130	0.04	8.25	95	(25)
Lota lota	350	13	0.0016	433			60	(36)
Lota lota	680	13	0.00098	707			60	
Lota lota	270	10	0.003	231			60	(37)
Lota lota	390	10	0.002	347			60	
Oncorhynchus mykiss	33	17	0.0034	204	3	99	111	(24)
Oncorhynchus mykiss	33	17	0.0022	316	0.4	13.2	124	
Oncorhynchus mykiss	33	17	0.0022	319	0.3	9.9	124	
Oncorhynchus mykiss	33	17	0.0022	320	0.4	13.2	124	
Oncorhynchus mykiss	33	17	0.0026	268	0.11	3.63	115	
Oncorhynchus mykiss	33	17	0.0019	348	0.06	1.98	125	
Oncorhynchus mykiss	33	4	0.0013	516	0.08	2.64	126	
Oncorhynchus mykiss	6.3	10.5	0.0065	107			28	(55)
Oncorhynchus mykiss	7.3	10.5	0.0052	134			56	
Oncorhynchus mykiss	10.2	10.5	0.0065	107			84	
Oncorhynchus mykiss	5.5	10.5	0.0083	83	4.8	26.4	28	
Oncorhynchus mykiss	6.6	10.5	0.006	116	7.6	50.16	56	
Oncorhynchus mykiss	8.2	10.5	0.0065	106	7.8	63.96	84	
Oncorhynchus mykiss	5.1	10.5	0.0101	69	12.6	64.26	28	

Table 1. (continue)

Oncorhynchus mykiss	6.1	10.5	0.0068	102	19.9	121.39	56	
Oncorhynchus mykiss	7.3	10.5	0.0073	95	29.2	213.16	84	
Oncorhynchus mykiss	6.8	10.5	0.0094	74			28	
Oncorhynchus mykiss	10.6	10.5	0.0062	112			56	
Oncorhynchus mykiss	17.1	10.5	0.0065	107			84	
Oncorhynchus mykiss	5.4	10.5	0.0122	57	5.9	31.86	28	
Oncorhynchus mykiss	7.7	10.5	0.0091	77	8.9	68.53	56	
Oncorhynchus mykiss	12.3	10.5	0.0073	95	8.8	108.24	84	
Oncorhynchus mykiss	5.7	10.5	0.0127	55	12.9	73.53	28	
Oncorhynchus mykiss	8.7	10.5	0.0088	79	28.9	251.43	56	
Oncorhynchus mykiss	13.3	10.5	0.0072	97	35.3	469.49	84	
Perca flavescens	9	15	0.01	69			60	(36)
Perca flavescens	17	13	0.008	87			60	
Perca flavescens	9	15	0.01	69			60	(37)
Perca flavescens	47	11	0.014	50			60	
Pleuronectes flevus	180	10	0.00089	780	0.0097	1.746	100	(26)
Pleuronectes flevus	180	10	0.00099	700	0.0097	1.746	100	
*Pleuronectes platessa**	61	10	0.0025	275	0.012	0.732	146	(40)
Pleuronectes platessa	60	10	0.0048	163			44	(39)
Poecilla reticulata	0.17	25	0.0063	110			30	(56)
Raja clavata	107	10	0.0022	323			45	(41)
Serranus criba	10	20	0.0026	267			60	(57)
Stizostedion vitreum	12	13	0.0081	86			60	(36)
Stizostedion vitreum	12	13	0.022	32			60	

* Chronically exposed fish

Figure 1. The elimination rate (E) of methylmercury and inorganic mercury in relation to the duration of the experiment. Standard errors are represented by the vertical bars.


Inorganic mercury
Methylmercury
10^{-1}
10^{-2}
10^{-3}
E (d^{-1})
<90 d
>90 d
<90 d
>90 d
Duration of the experiment

$p<0.0001$) and with the form of Hg (MeHg or inorganic Hg) administered to the fish ($F_{1,92}=7.9$; $p<0.01$).

MeHg and inorganic Hg elimination rates from fish were both negatively correlated to body size (Table 2; Figure 2). The allometric exponent was smaller in short-term experiments, and smaller in inorganic Hg than MeHg (Figure 2). When Hg elimination rates were adjusted for differences in body size, Hg elimination rates obtained in short-term experiments were 3.1-fold higher than those obtained in long-term experiments. Adjusted Hg elimination rates were 2.8-fold slower for MeHg than inorganic Hg. MeHg elimination rate from fish was positively correlated to water temperature only in long-term experiments (Table 2; Figure 3). The excretion rate of inorganic Hg was also positively correlated to water temperature (Table 2). This relationship was, however, driven by the single experiment that was performed at 20 ºC with inorganic Hg. The significant effect of water temperature on the clearance rate of inorganic Hg could be due to the small size of the fish used in that experiment (0.3 g), since small fish tend to excrete inorganic Hg faster (Table 2; Figure 2). The elimination rate of MeHg was not correlated to Hg burden or concentration in either short- or long-term experiments (Table 2).

Multiple regression analysis was used to develop a general model of MeHg elimination rate. This analysis was performed only with data from long-term experiments, since it appears that short-term experiments overestimated the slow component of MeHg elimination (Figure 1-3). Stepwise multiple regression only retained water temperature as the best predictor of MeHg excretion rate. An examination of the relationship between MeHg elimination rate and body size suggested that chronically exposed fish excreted MeHg at a faster rate than acutely exposed fish (Figure 2). A multiple regression analysis (SE in parentheses) was therefore performed using temperature (T; ºC), fish weight (W; g), and a dummy variable for chronic (D=1) and acute (D=0) exposures;

(1) $\log_e E = 0.066(0.019)\cdot T - 0.20(0.06)\cdot \log_e W + 0.73(0.24)\cdot D - 6.56(0.45)$

$R^2 = 0.77$; SE = 0.31; $P<0.0001$; n = 21

Table 2. Pearson correlation between the elimination rate of mercury from fish and weight, water temperature, mercury burden and concentration. All the variables, except water temperature, were log transformed (natural logarithm).

Variable	*r*	*p*	*n*
Inorganic mercury: duration <90 days			
Weight	-0.93	<0.0001	12
Temperature	0.67	<0.05	11
Methylmercury: duration <90 days			
Weight	-0.67	<0.0001	60
Temperature	0.18	>0.15	60
Burden	-0.12	>0.6	20
Concentration	0.18	>0.4	20
Methylmercury: duration >90 days			
Weight	-0.65	<0.002	21
Temperature	0.77	<0.0001	21
Burden	-0.18	>0.4	21
Concentration	0.10	>0.6	21

Figure 2. The elimination rate (E) of methylmercury and inorganic mercury from fish plotted in relation to body size. ●, methylmercury elimination rate obtained in long-term experiments (>90 d); ○, methylmercury elimination rate obtained in short-term experiments (<90 d); ■, inorganic mercury elimination rate obtained in short-term experiments.

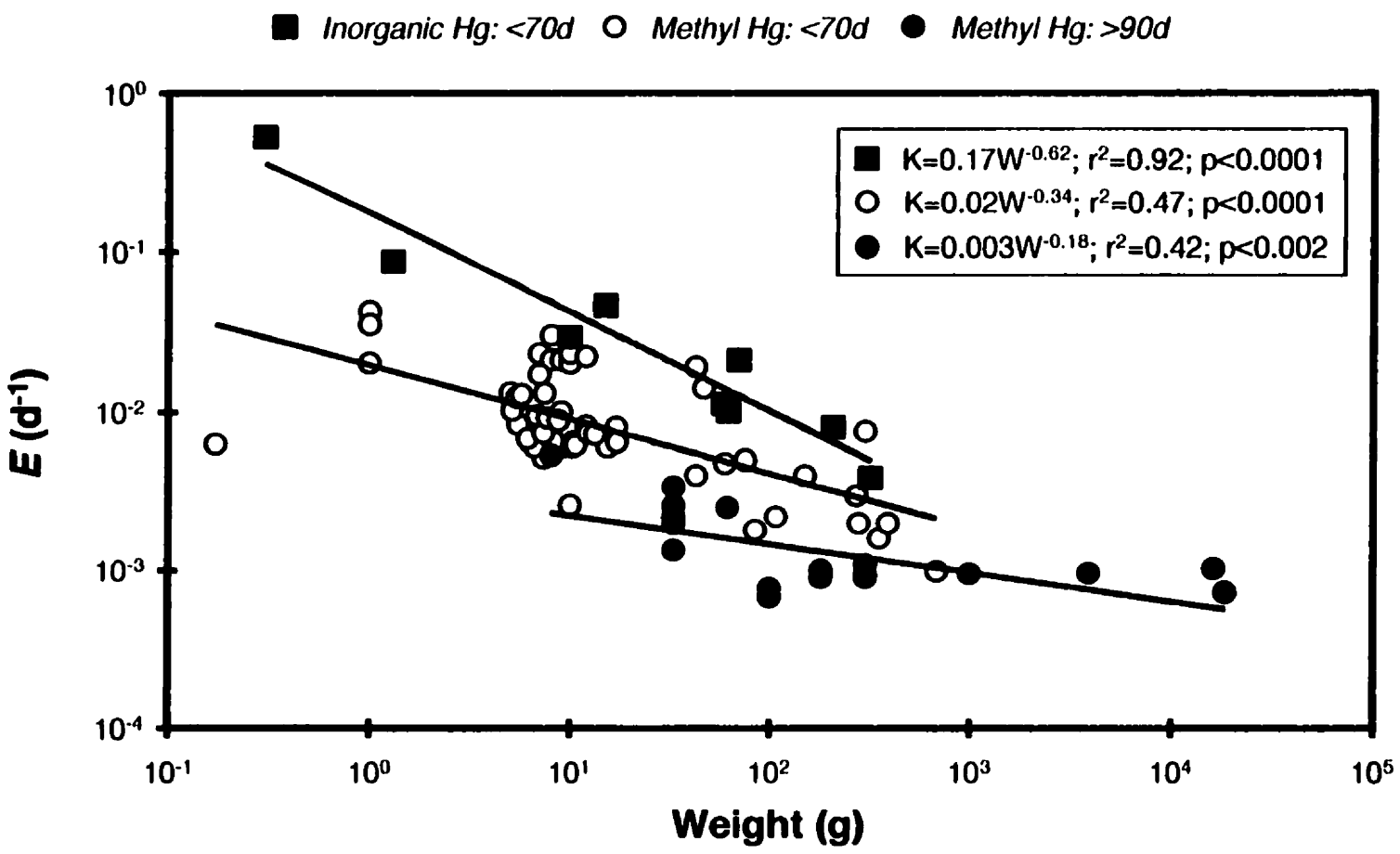
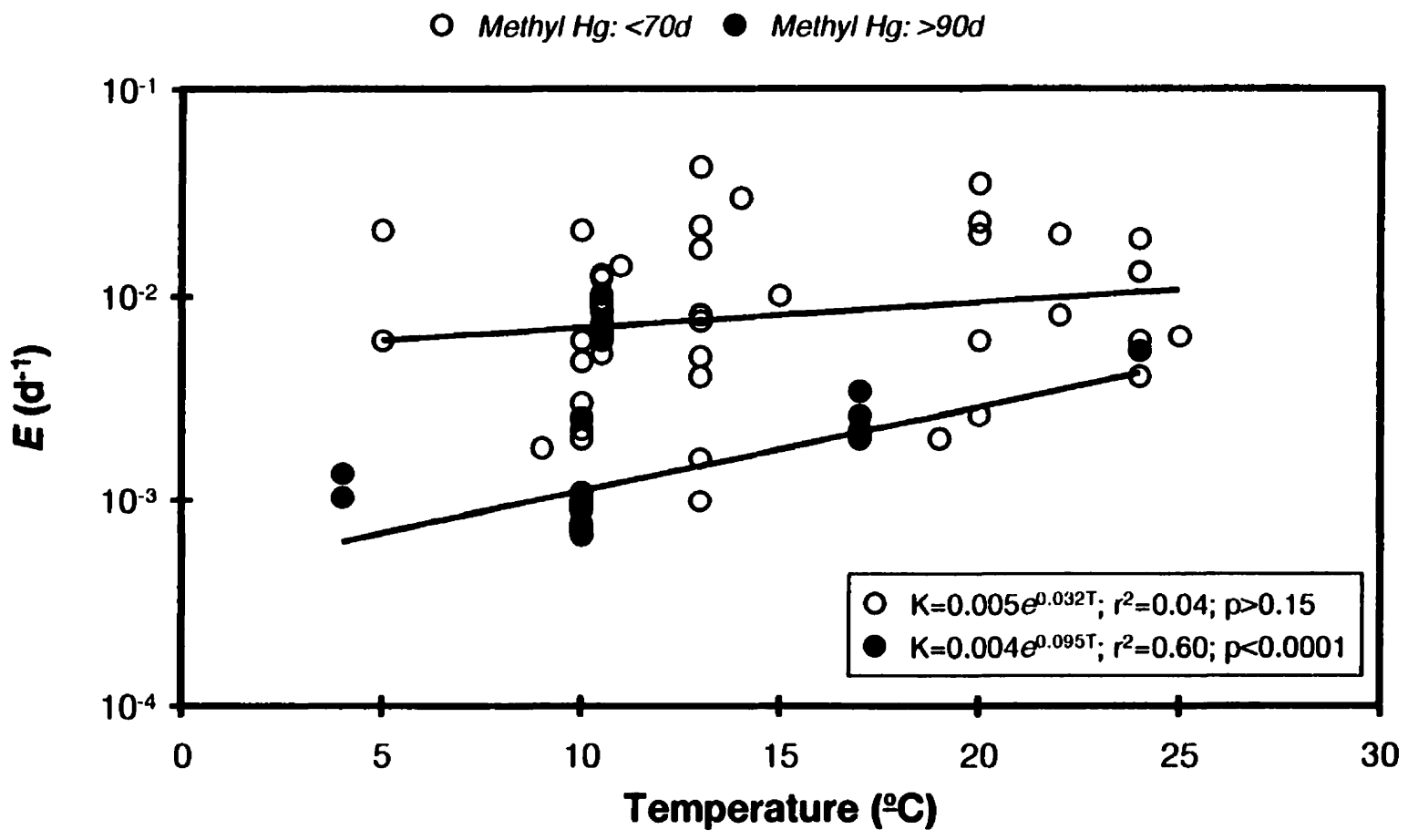

Inorganic Hg: <70d
Methyl Hg: <70d
Methyl Hg: >90d
K=0.17W-0.62; r2=0.92; p<0.0001
K=0.02W-0.34; r2=0.47; p<0.0001
K=0.003W-0.18; r2=0.42; p<0.002
E (d-1)
Weight (g)
10^0
10^-1
10^-2
10^-3
10^-4
10^-1
10^0
10^1
10^2
10^3
10^4
10^5

Figure 3. The elimination rate (E) of methylmercury from fish plotted in relation to water temperature. Legend as in Figure 1.2.


Methyl Hg: <70d
Methyl Hg: >90d
10^{-1}
10^{-2}
10^{-3}
10^{-4}
E (d^{-1})
0
5
10
15
20
25
30
Temperature (ºC)
K=0.005$e^{0.032T}$; r^2=0.04; p>0.15
K=0.004$e^{0.095T}$; r^2=0.60; p<0.0001

where E is the elimination rate (d^{-1}). This model indicates that the Q_{10} of MeHg elimination rate is 1.9 and that chronically exposed fish excreted MeHg 2.1-fold faster than acutely exposed fish.

Differentiation of the fast and slow components

The statistical analyses performed in this study showed that estimates of the slow component of MeHg and inorganic Hg elimination were influenced by the duration of the experiment. The elimination rates of MeHg and inorganic Hg from fish were overestimated by a factor of 3.1 in short-term experiments. Similar results have been obtained for ^{137}Cs and PCBs (*32,45*). Rowan and Rasmussen (*32*) suggested that 60 days was not sufficiently long to properly discriminate the fast and slow components of persistent contaminants. To examine the effect of the duration of the experiment on the apparent elimination rate of the slow component of MeHg, we used MeHg burden measured by Järvenpää *et al.* (*26*; their Figure 1) and by Ruohtula and Miettinen (*24*; their Figure 3) on contaminated flounder (*Pleuronectes flevus*) and rainbow trout, respectively, when these fish were maintained in Hg free water. We compared the elimination rates of the slow component of MeHg using 60 and 100 days of data. We estimated the elimination rate of the slow component of MeHg using the "stripping method" (*58*). The apparent elimination rate of the slow component of MeHg was 2- to 4-fold higher when 60 days of data were used, which is in agreement with the 3-fold difference observed in this study between the elimination rate obtained in short- and long-term experiments.

Inorganic mercury vs methylmercury excretion

Our analysis supports the hypothesis that inorganic Hg is eliminated faster than MeHg. This result is consistent with those of de Freitas *et al.* (*36*) and Pentreath (*38-41*) who also showed that inorganic Hg was eliminated faster than MeHg in fish. Since virtually all the Hg in fish is MeHg (>95%) (*47-50*), Hg mass balance models should rely only on the clearance rate of MeHg from fish. Hendriks (*35*) has recently developed an empirical model of MeHg elimination using both inorganic Hg and MeHg excretion rate estimates. His model is therefore likely to overestimate the clearance rate of MeHg from

fish. Furthermore, mass balance models based on his MeHg clearance model are likely to underestimate Hg concentration in fish.

The predominance of MeHg over inorganic Hg in fish has generally been attributed to the higher assimilation efficiency of MeHg from food than inorganic Hg (*59-60*). The assimilation efficiency of MeHg from food is 5- to 10-fold higher than inorganic Hg (*36,39,61*). The 3-fold difference observed between the excretion rate of these two substances suggests that both the higher assimilation efficiency of MeHg from food and the lower clearance rate of MeHg from fish are responsible for the predominance of MeHg in fish.

Influence of body size

Excretion rates of persistent contaminants are generally negatively correlated with body size (*16,31-33,35,44*). The negative correlation observed between MeHg excretion rate and body size in our study is thus consistent with the literature. Inorganic Hg and MeHg elimination rates obtained in short term experiments were also negatively correlated to body size, but with much steeper slopes than in long-term experiments. The allometric exponent of MeHg clearance rate obtained in our study was equal to -0.20 (SE=0.06), which is identical to the value assumed by Fagerström *et al.* (*17*). The steeper slope obtained by Norstrom *et al.* (*16*), -0.58, could be attributed to the overestimation of MeHg elimination rate from the small fish (1-45 g). The experiments that they performed on small fish were generally too short (<60 days) to properly discriminate the fast and slow components of MeHg elimination. Norstrom's model tended to overestimate MeHg excretion rate obtained in long-term experiment by a factor of 1.8 within the size range of their model (1-300 g). This model has frequently been applied beyond the range of body size valid for the model (e.g. *19-22*). For fish larger than 300 g, Norstrom's model tended to underestimate the elimination rate of MeHg.

Although Hendriks (*35*) used short-term experiments and elimination rate of inorganic Hg to develop his empirical model of MeHg elimination, he obtained an allometric exponent almost identical (-0.22) to our value. This probably occurred because he included the elimination rate of MeHg from mammals to expand the size range of his

model (0.002-80 kg). MeHg is generally excreted faster in mammals than in fish: the half-life of MeHg usually ranges between 5 and 130 days in mammals (*42*), while it ranged between 130 and 1030 days in long-term experiments on fish (Table 1). We reanalyzed the data reported by Hendriks (*35*) without the elimination rate of MeHg from mammals. The allometric exponent was then equal to -0.47 ($r = -0.77$; $p<0.005$) and was closer to the value we derived for short-term experiments (Figure 2). The empirical model of Hendriks (*35*) systematically overestimated MeHg excretion rate of fish by 6.1-fold on average. These results suggest that both the Norstrom's and Hendriks' models are not appropriate for estimating MeHg elimination rate of fish.

MeHg elimination rate has usually been described by an allometric equation in Hg mass balance models. The value of this exponent has often been assumed, taking values between 0.06 and -0.87 (*17-19,22*). The assumed values were probably selected *ad hoc* to increase the fit between observed Hg concentration of fish in the field and predicted Hg concentration from the model. Mass balance models should rely on experimentally or empirically derived parameters, and not on assumed values.

Influence of water temperature

There are surprisingly few studies that have attempted to evaluate the effect of temperature on contaminant elimination rate in poikilothermic animals. The elimination rates of contaminants are generally positively correlated to water temperature (*24,32-34,62*). In our study, there was a strong positive correlation between the elimination rate of MeHg in fish and water temperature. The Q_{10} calculated from the regression model (eq. 4) was equal to 1.9 and was not significantly different from the Q_{10} of 2.0 assumed by Rodgers (*20*). Ribeyre *et al.* (*43*) also reported that rainbow trout retained less MeHg at higher temperature. The Q_{10} calculated from their experiments was equal to 1.6, which is similar to our value and to the value of 1.5 calculated from Ruohtula and Miettinen (*24*). Sharpe *et al.* (*44*) did not find a significant effect of temperature on MeHg elimination rate in goldfish between 4 and 24 °C. This discrepancy might be due to the inadequate differentiation of the fast and slow components of MeHg elimination by the later study, since their experiments lasted less than 60 days. The lack of significant correlation

observed in our study between MeHg elimination rate and water temperature in short-term experiments supports this interpretation.

Influence of Hg burden and concentration

Mass balance models usually assume that the elimination rates of contaminants are a first order kinetic process, that is the proportion of the contaminant that is eliminated during a time interval is constant, irrespective of the contamination level in the organism (*14,16*). This assumption has rarely been tested. A lack of independence between Hg elimination rate and Hg concentration would indicate that Hg elimination is not a first order process. This would imply that every estimates of Hg elimination are biased, since they were determined using a model that assumes a first order kinetic. de Freitas *et al.* (*37*) reported that MeHg elimination rate was positively correlated with MeHg burden in goldfish. However, their excretion rate estimates might be biased because the short duration of their experiments (<60 days) did not allow a proper discrimination of the fast and slow components of MeHg elimination. Ruohtula and Miettinen (*26*) showed that the excretion rate of MeHg was positively correlated to MeHg concentration in individual rainbow trout. MeHg excretion rate of rainbow trout increased by 15-20% for each increment of 1 $\mu g \cdot g^{-1}$ in MeHg concentration. In contrast, the lack of correlation observed between MeHg elimination rate and initial Hg burden or concentration in our study suggests that the excretion rate of MeHg in fish is a first order process. Nonetheless, the assumption that MeHg elimination is a first order process may require further testing.

Influence of exposure time

The influence of exposure time on the elimination rate of persistent contaminants has rarely been assessed. Our analysis showed that chronically exposed fish excreted MeHg 2.1-fold faster than acutely exposed fish. In contrast, inorganic Hg was excreted at a slower rate in chronically exposed fish (*38,41*). However, this result could also be attributed to the short duration of the experiment in acutely exposed fish (60 vs 150 days), since Hg elimination is generally overestimated in short-term experiments. McKim *et al.* (*63*) showed that MeHg elimination in chronically exposed brook trout (*Salvelinus*

fontinalis) was negligible. However, the confidence interval associated with the initial and final MeHg concentration were large, since they only used 2-3 fish for each of these two periods. This suggests that the statistical power of their analysis was not high enough to detect a significant difference between initial and final MeHg concentration. Similarly, Laarman *et al.* (*64*) showed that MeHg elimination was negligible in yellow perch (*Perca flavescens*) and rock bass (*Ambloplites rupestris*) that were transferred from a contaminated lake to "clean ponds". These results are however questionable since MeHg burden of yellow perch and rock bass increased during their study, suggesting that the fish were exposed to MeHg contaminated food or water. Finally, Pentreath (*41*) was unable to measure MeHg elimination in chronically exposed thornback ray (*Raja clavata*). The reason for the discrepancy observed between his results and our study is unknown and remains to be clarified by further studies.

Field-test of the elimination model

A mass balance model can be evaluated by comparing predicted values from the model with independent observations. A close correspondence between predicted and observed values suggests that the parameters of the mass balance model are adequate to describe the process under investigation. Therefore, we evaluated the accuracy of the Hg excretion model derived in this study by comparing feeding rates generated by a Hg mass balance model with independent observations. Assuming that Hg uptake from water is negligible (*23*,*65*), the mass balance model of fish Hg concentration can be written as;

$$\frac{dC}{dt} = \alpha \cdot C_d \cdot I - (G + E) \cdot C \qquad (2)$$

where C and C_d are Hg concentration in fish and their prey ($\mu g \cdot g^{-1}$), respectively, α is the assimilation efficiency of Hg from food, I is the ingestion rate (d^{-1}), and G is the specific growth rate (d^{-1}). Integrating this differential equation, and solving it for ingestion rate, we obtain the following equation;

$$(3) \qquad I = \frac{C_{t+\Delta t} - C_t \cdot e^{-(G+E)\Delta t}}{\alpha \cdot C_d \cdot \left[1 - e^{-(G+E)\Delta t}\right]} \cdot (G+E)$$

where C_t and $C_{t+\Delta t}$ are fish Hg concentration at time t and $t+\Delta t$ ($\mu g \cdot g^{-1}$), respectively, and Δt is the time interval (d). This equation indicates that fish ingestion rates can be determined using Hg concentration in fish and their prey, fish size and growth, Hg assimilation efficiency from food and elimination rate.

Feeding rates of northern pike (*Esox lucius*) and walleye (*Stizostedion vitreum*) from Lake Simcoe (Ontario, Canada) were estimated using the Hg mass balance model and were compared with published estimates of ingestion rates for these species. Hg concentration of walleye, northern pike and their prey, fish age and size, and water temperature were obtained from Mathers and Johansen (*61*). In these calculations, we assumed that the assimilation efficiency of MeHg from food was equal to 80% (16).

Consumption rates obtained using the Hg mass balance model (eq. 3) in conjunction with the elimination rate derived in this study (eq. 1) ranged from 0.007 to 0.027 $g \cdot g^{-1} \cdot d^{-1}$ (Table 3). These values are in agreement with the feeding rates obtained by Rowan and Rasmussen (*67*) for northern pike and walleye from the Ottawa River and Great Slave Lake (Table 3). Feeding rates derived using Norstrom (*16*) and Hendriks (*35*) excretion models were generally lower and higher than those obtained by Rowan and Rasmussen (Table 3), respectively. These results suggest that the empirical model of MeHg elimination obtained in our study (eq. 1) provides reliable estimates of MeHg excretion rate from fish in the field.

Recommendations for future studies

The main objective of Hg mass balance models is to predict *in situ* Hg dynamics in fish. To be applicable to natural conditions, both Hg uptake and elimination estimates must reflect *in situ* processes. Unfortunately, too few estimates of Hg elimination have been determined directly in the field. Lockhart et al. (*54*) and Laarman et al. (*64*) transferred fish from a Hg contaminated site to a Hg "clean" lake to estimate the elimination rate of Hg by fish. This approach has also been applied with ^{137}Cs (*29*) and PCBs (*45*). This

Table 3. Comparison between feeding rates ($g \cdot g^{-1} \cdot d^{-1}$) of northern pike (*Esox lucius*) and walleye (*Stizostedion vitreum*) from Lake Simcoe estimated using a mercury mass balance model with three methylmercury excretion models and independent estimates obtained by Rowan and Rasmussen (*67*) using a mass balance model of ^{137}Cs.

Excretion model	Average	Range
	Northern pike	
Norstrom (16)	0.0064	0.0035 - 0.011
Hendriks (30)	0.025	0.018 - 0.031
equation 1	0.010	0.0071 - 0.013
^{137}Cs method*	0.016	0.0075 - 0.026
	Walleye	
Norstrom (16)	0.0082	0.0045 - 0.012
Hendriks (30)	0.068	0.049 - 0.087
equation 1	0.021	0.015 - 0.027
^{137}Cs method*	0.018	0.013 - 0.025

*Ottawa River and Great Slave Lake

approach offers several advantages over laboratory estimates of Hg elimination. First, it reflects the conditions experienced by the fish in the field such as exposure time (generally chronic exposure) and fish Hg concentration. Second, it can be used to estimate simultaneously the elimination rate of other persistent contaminants, such as PCBs and DDT. However, prey contamination should be sufficiently low in the clean environment to make sure that Hg elimination is not compensated by the uptake of Hg from food.

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CONNECTING STATEMENT

In the first chapter of the thesis, I developed an empirical model to estimate the elimination rate of Hg by fish. I showed that the elimination rate of Hg was overestimated in short-term experiments, that inorganic Hg was eliminated at a faster rate than methylmercury, and that Hg elimination rate was positively correlated to water temperature and negatively correlated to body size. In the next chapter, I developed a Hg mass balance model to predict Hg concentration in fish. The elimination rate of Hg by fish, a required parameter of the mass balance model, was estimated using the empirical model derived in chapter 1. The Hg mass balance model was tested using food consumption rates determined with a radioisotopic method. The performance of this mass balance modeling approach was also compared to that obtained using laboratory-based bioenergetic models.

CHAPTER 2

PREDICTING MERCURY CONCENTRATION IN FISH USING A MASS BALANCE MODEL: THE IMPORTANCE OF FOOD CONSUMPTION RATES

Abstract

Mass balance models have frequently been used with laboratory-derived bioenergetic models to examine the accumulation of mercury (Hg) in fish. The accumulation of Hg in fish has usually been successfully described by these models. However, this has generally been achieved by adjusting the parameters of these models until there was a close fit between observed and predicted values. In this study, we developed and tested a simple Hg mass balance model (MMBM) to predict Hg concentration in fish. This MMBM requires the estimation of Hg concentration in food, the assimilation efficiency of Hg from food, the elimination rate of Hg by fish, and the feeding rates of fish. The MMBM accurately predicted the accumulation of Hg in the three fish species examined in this study when it was combined with food consumption rates that were determined with a radioisotopic method. This shows that the parameters of the MMBM are useful for predicting Hg concentration in fish. The MMBM tended to underestimate Hg concentration in fish when it was combined with food consumption rates determined using laboratory-derived bioenergetic models, possibly because activity costs derived under laboratory conditions do not adequately represent activity costs of fish in the field. When feeding rates were estimated with a bioenergetic model implemented with site-specific estimates of activity costs, the MMBM accurately predicted the concentration of Hg in fish. Therefore, until activity costs can be accurately estimated *in situ*, predictions obtained with MMBM implemented with a laboratory-derived bioenergetic model should be interpreted cautiously.

Introduction

Since the tragic episode of mercury (Hg) poisoning that occurred in Minamata during the 1950's, there has been a growing concern about the fate of Hg in biota. Fish are of special concern since they generally represent the most important source of Hg to humans (WHO 1990), and to fish-eating wildlife such as loons, herons, and mink (Wren 1986; Scheuhammer et al. 1998). Elevated concentrations of Hg have often been reported in fish located in areas remote from human activities (Håkanson et al. 1988; McMurtry et al. 1989; Sorensen et al. 1990; Lathrop et al. 1991; Cabana et al. 1994). Thus, there is a need to develop models that can accurately predict Hg concentration in fish.

Mass balance models have frequently been used in conjunction with laboratory-derived bioenergetic models to describe the accumulation of Hg in fish with age (Norstrom et al. 1976; Braune 1987; Jensen 1988; Harris and Snodgrass 1993; Rodgers 1994; Korhonen et al. 1995; Post et al. 1996; Harris and Bodaly 1998). Mass balance modeling requires the determination of Hg concentration in food and water, the absorption efficiency of Hg from food and water, the elimination rate of Hg from fish, and the feeding and respiration rates of fish. Accurate estimates of Hg concentration in food, absorption efficiency of Hg from food, elimination rate of Hg from fish, and feeding rates are especially important due to the sensitivity of Hg mass balance models (MMBM) to these parameters (Norstrom et al. 1976; Rodgers 1994; Post et al. 1996).

Mercury concentrations predicted with MMBM have usually been in close agreement with observed values (Norstrom et al. 1976; Braune 1987; Borgmann and Whittle 1992; Harris and Snodgrass 1993; Korhonen et al. 1995; Post et al. 1996). The apparent success of MMBM may be somewhat artificial though. The close fit obtained between observed and predicted values has usually been achieved by adjusting the parameters of the MMBM such as absorption efficiency of Hg from food and the elimination rate of Hg from fish, until there was a close correspondence between observed and predicted Hg concentration (e.g. Braune 1987; Borgmann and Whittle 1992; Harris and Snodgrass 1993; Korhonen et al. 1995; Post et al. 1996). Thus, these studies do not represent a true test of the accuracy of MMBM, but rather represent a calibration of these models.

The validity of these *post hoc* adjustments may also be questionable, and may not be applicable to other situations. For instance, the elimination rate of Hg from fish has generally been modeled with an allometric equation, using an allometric exponent typically ranging between –0.58 and –0.80 (Norstom et al. 1976; Harris and Snodgrass 1993; Korhonen et al. 1995). However, these values are about three to four times lower (i.e. more negative) than the value that was obtained empirically by Trudel and Rasmussen (1997).

These adjustments also assumed that the feeding rates estimated with laboratory-derived bioenergetic models were accurate. This assumption is also questionable, as several studies have shown that bioenergetic models tend to underestimate the quantity of food consumed by fish in the field, presumably because activity costs are not adequately represented (Boisclair and Leggett 1989a; Post 1990; Fox 1991; Madon and Culver 1993; Rowan and Rasmussen 1996). Activity costs are generally derived from laboratory experiments, and are usually assumed constant across populations. In contrast, Boisclair and Leggett (1989a) showed that activity costs could vary four-fold among populations of the same species. More recently, Rowan and Rasmussen (1996) showed that activity costs were generally higher for adult than juvenile fish, and tended to be higher than the values typically assumed in bioenergetic models. This suggests that predictions based on food consumption rates and activity costs estimated from laboratory-derived bioenergetic models are inadequate.

The importance of adequately estimating food consumption rates to accurately predicting Hg concentration in fish with mass balance models is generally not well appreciated in the toxicological literature. For a given size of fish, food consumption rates of fish can vary substantially (more than 10-fold) among populations and among species (Boisclair and Leggett 1989b; Trudel et al. 2000). Hence, food consumption rates may also be an important determinant of the observed variability of Hg concentrations in fish.

The objective of this study was to present and test a MMBM that was based on system-specific estimates of food consumption rates of fish determined in the field. The MMBM was tested on lake trout (*Salvelinus namaycush*), yellow perch (*Perca flavescens*), and walleye (*Stizostedion vitreum*). Food consumption rates of fish were estimated using a radiocesium (^{137}Cs) mass balance model. This approach is not labor

intensive in the field (Rowan and Rasmussen 1996), and provides feeding rates similar to those obtained with traditional methods based on stomach contents (Forseth et al. 1992, 1994). The performance of this mass balance modeling approach was compared to that of laboratory-based bioenergetic models. Finally, we examined the effects of activity costs on the accumulation of Hg in fish.

Mercury mass balance model

Derivation of a mercury mass balance model

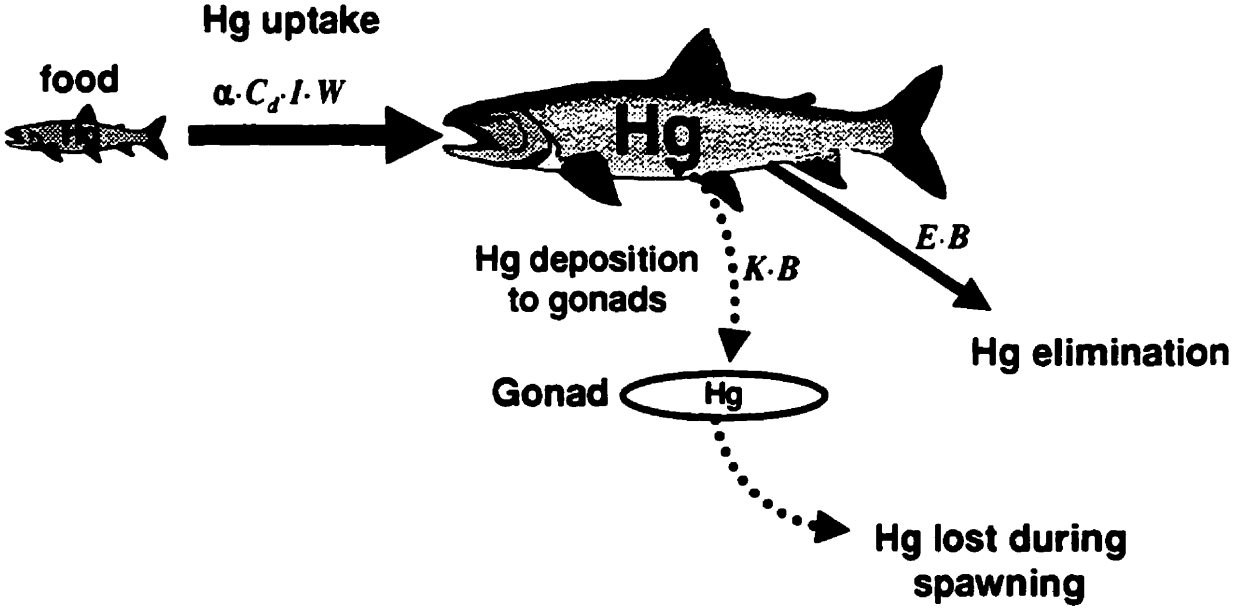
In fish, Hg is accumulated by direct uptake of contaminated water through the gills and absorption of contaminated food through the gastrointestinal tract. However, fish exposed only to Hg contaminated water accumulate 1000-times less Hg than fish exposed to Hg contaminated water and food (McKim et al. 1976; Cember et al. 1978; Porcella 1994; Becker and Bigham 1995; Hill et al. 1996). This suggests that Hg uptake from water represents less than 0.1% of the Hg accumulated in fish, and may be considered negligible. Thus, the accumulation of Hg in fish can be expressed as (Fig. 1: Thomann 1981):

$$(1) \qquad \frac{dB}{dt} = (\alpha \cdot C_d \cdot I \cdot W) - (E + K) \cdot B$$

where B is the total quantity of Hg in fish (further referred to as Hg burden; μg), α is the assimilation efficiency of Hg from food (dimensionless), C_d is the concentration of Hg in food (μg/g), I is the ingestion rate of fish (d^{-1}), W is the mass of the fish (g), E is the elimination rate of Hg from fish (d^{-1}), and K is the daily loss of Hg to the gonads (d^{-1}). This model assumes that a constant fraction of Hg is lost from the body to the gonads each day without any exchange back to fish (Fig. 1; Rowan and Rasmussen 1997).

Since most of the Hg (>95%) in fish is methylmercury (Bloom 1989, 1992), this MMBM assumes that there is no conversion of inorganic Hg potentially contained in the ingested prey to methylmercury in the intestine of fish. This assumption is supported by the work of Pennacchioni et al. (1976), Pentreath (1976), Huckabee et al. (1978) who showed that fish did not methylate inorganic Hg. Rudd et al. (1980) reported that fish

Fig. 1. Diagram representing the pathway of mercury intake and losses in fish. α; assimilation efficiency of Hg; C_d: concentration of Hg in food ; I: ingestion rate of fish; W: fish mass; B: total quantity of Hg in fish; E: elimination rate of Hg from fish; K: daily loss of Hg to the gonads.


Hg uptake
food
$\alpha \cdot C_d \cdot I \cdot W$
Hg
$E \cdot B$
Hg deposition
to gonads
$K \cdot B$
Hg elimination
Gonad
Hg
Hg lost during
spawning

intestinal contents could methylate inorganic Hg *in vitro*, though the fraction of inorganic Hg that was methylated was fairly small (0.005-0.4%/d) and can be assumed negligible in fish.

Toxicologists generally measure the concentration of Hg in the edible portion of fish (i.e. skinless fillets), rather than the total quantity of Hg in fish. Assuming that the concentration of Hg in muscle tissue and in the whole body are equal in fish (Lockhart al. 1972; Becker and Bigham 1995; Post et al. 1996), the mass balance model of Hg concentration (C; µg/g) can be written as:

$$(2) \qquad \frac{dC}{dt} = \frac{d\left(B/W\right)}{dt} = \frac{W \cdot dB - B \cdot dW}{W^2 \cdot dt} = \frac{1}{W} \cdot \frac{dB}{dt} - C \cdot \frac{dW}{W \cdot dt}$$

Therefore, the mass balance model of Hg concentration requires a mass balance model for Hg burden as well as a mass balance model for fish size. Assuming that fish mass is growing exponentially during the time interval, the mass balance of fish size is (Ricker 1979):

$$(3) \qquad \frac{dW}{W \cdot dt} = G$$

where G is the specific growth rate (d^{-1}). Thus, combining eqs. 1, 2 and 3 gives:

$$(4) \qquad \frac{dC}{dt} = (\alpha \cdot C_d \cdot I) - (E + G + K) \cdot C$$

Integrating this equation gives:

$$(5) \qquad C_{t+\Delta t} = C_t \cdot e^{-(E+G+K)\Delta t} + \frac{(\alpha \cdot C_d \cdot I)}{(E+G+K)} \cdot \left[1 - e^{-(E+G+K)\Delta t}\right]$$

where C_t and $C_{t+\Delta t}$ are concentration of Hg in fish (μg/g) at time t and $t+\Delta t$ (d). In juvenile fish, eq. (5) can be simplified by setting K=0, as these fish do not spawn.

Eq. (5) was used to predict the accumulation of Hg in fish through time (i.e. with age) using site-specific and age-specific estimates of I, G, and C_d. The value of α, E, and K were derived *a priori* from published experiments (see next section). C_t was set to the concentration of Hg observed in the youngest age-class available for a given population. The MMBM was then used to predict the concentration of Hg in the subsequent age-classes. The accuracy of the MMBM was assessed by comparing the predicted and observed accumulation of Hg with age.

Parameterization of the mercury mass balance model

The assimilation efficiency of Hg of fish fed with prey fish typically ranges between 0.6 and 0.95, with a modal value around 0.8 (Norstrom et al. 1976; de Freitas et al. 1977; Suzuki and Hatanaka 1975; Ribeyre et al. 1980). Because methylmercury is covalently bonded to sulfur in protein, α should be correlated with protein assimilation efficiency (Trudel et al. 2000). In general, about 80% of organic material is assimilated by carnivorous fish (Brett and Groves 1979), which is similar to the mode of laboratory-derived α values. Thus, we assumed that α was equal to 0.8 in fish (Table 1).

The elimination rate of Hg from fish can be modeled as a function of body size and water temperature (T; °C) as (Trudel and Rasmussen 1997):

$$E = \varphi \cdot W^{\beta} \cdot e^{\gamma T} \quad (6)$$

where φ, β, γ are empirically derived constants (Table 1).

Specific growth rate can be estimated as (Ricker 1979):

$$G = \frac{1}{\Delta t} \cdot \ln\left(\frac{W_{t+\Delta t}}{W_t}\right) \quad (7)$$

Table 1. Parameters of the mercury mass balance model.

Symbol	Parameter description	Value	Source
α	Assimilation efficiency	0.80	1
φ	Coefficient of mercury elimination	0.0029	2
β	Allometric exponent of mercury elimination	-0.20	2
γ	Temperature coefficient of mercury elimination	0.066	2
Q_m	Ratio of mercury concentration in the gonads and whole fish for males	0.59	3
Q_f	Ratio of mercury concentration in the gonads and whole fish for females	0.12	3

1. Norstrom et al. (1976); 2. Trudel and Rasmussen (1997); 3. Trudel et al. (*in press*)

where W_t and $W_{t+\Delta t}$ are fish mass (g) at time t and $t+\Delta t$. Growth rate can be estimated for each age-classes using the mass of two consecutive age-classes.

The daily loss rate of Hg from the body to the gonads can be estimated as (Appendix 1):

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

where Q is the ratio of Hg concentration in the gonads to Hg concentration in fish, and GSI is the gonadosomatic index (dimensionless).

Method

Size and mercury concentration

The MMBM was applied to Lake Memphremagog lake trout (Quebec-Vermont) and yellow perch and walleye from the Ottawa River (Quebec-Ontario). Lake trout were collected from Lake Memphremagog prior to spawning during the fall of 1994 with multi-mesh experimental gill nets. Fish mass was determined with an electronic balance (±0.1 g). Gonads were removed from adult fish and weighed (±0.1 g) to determine the *GSI* of male and female lake trout (Trudel et al. 2000). The age of lake trout was determined using otoliths. Stomach contents were examined to determine lake trout diet. Rainbow smelt (*Osmerus mordax*) was the dominant prey (96%) in the diet of these fish. These results were confirmed with stable isotopes of carbon and nitrogen (Vander Zanden and Rasmussen 1996). Hg concentration in lake trout and rainbow smelt were determined using cold-vapor atomic absorption spectroscopy. Approximately 1 g wet weight of skinless dorsal muscle tissue was digested overnight at 80°C in 5.0 ml of concentrated HNO_3 and 0.5 ml of concentrated HCl (trace metal grade). After the digestion was complete, the samples were cooled to room temperature. One drop of a saturated $KMnO_4$ solution was then added to stabilize Hg^{2+} ions in the acid solution. This solution was further diluted to 15 ml with nanopure water. Hg concentration in the muscle tissue was determined using a Perkin Elmer 5100 Spectrophotometer equipped

with an auto-sampler. Sodium borohydride was used as the reducing agent during the Hg analyses.

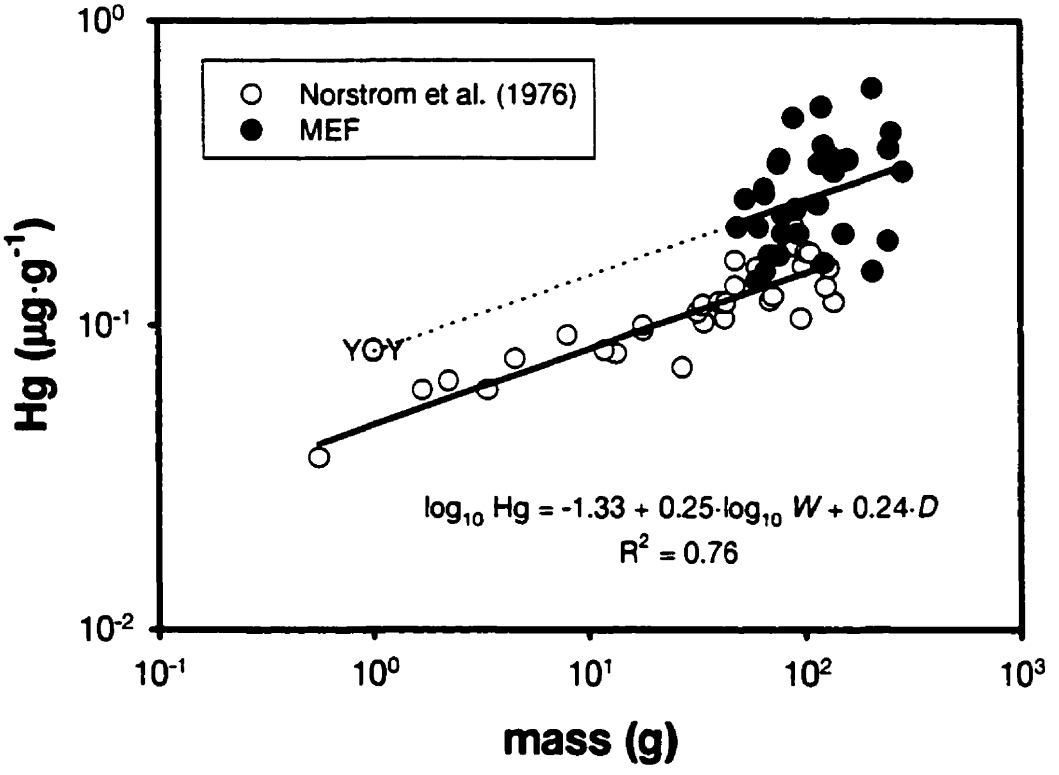
The age and size of yellow perch from the Ottawa River were taken from Rowan and Rasmussen (1996). We used the values for fish that were caught during spring. These values differed from the growth curve derived by Norstrom et al. (1976) probably because their curve was fitted on fish that were caught mostly during fall. Hg concentrations of yellow perch were extracted from Norstrom et al. (1976) using a digitizer and modeled as a function of size. C_d of the prey consumed by yellow perch was equal to 0.033 µg/g (Norstrom et al. 1976).

The age and size of walleye from the Ottawa River were obtained from Rowan and Rasmussen (1996), while Hg concentrations of these fish were obtained from the databases of the Ministère de l'Environnement et de la Faune of Quebec (MEF). The diet of walleye from the Ottawa River consisted primarily (97%) of young-of-the-year (YOY) yellow perch (Rowan and Rasmussen 1996). We estimated the concentration of YOY yellow perch from the regression between Hg concentration and fish size ($\log_{10}$ transformed data), assuming that YOY perch weighed 1 g. Unfortunately, the MEF have measured Hg concentration only in large perch from this river (Fig. 2). Furthermore, these values differ significantly from those obtained by Norstrom et al. (1976) for yellow perch from the Ottawa River (Fig. 2; $F_{1,61}=42.2$; $p<0.0001$), possibly because their method of Hg analysis differed or because they sampled at a different place or time in the river. Thus, the concentration of Hg in YOY perch consumed by walleye was estimated by extrapolating Hg concentration of yellow perch measured by the MEF with a multiple regression model developed using body size and a categorical variable representing the source of data as independent variables (Fig. 1). Hg concentration in YOY perch determined with this model was 0.082 µg/g. The *GSI* of yellow perch and walleye from the Ottawa River were taken from Rowan and Rasmussen (1996).

Food consumption rates

Food consumption rates of yellow perch, walleye and lake trout were determined using the ^{137}Cs method recently refined by Rowan and Rasmussen (1996, 1997). This method requires the determination of ^{137}Cs concentration in fish and their food, the

Fig. 2. Mercury concentration of yellow perch from the Ottawa River determined by Norstrom et al. (1976) and by the Ministère de l'Environnement et de la Faune of Quebec (MEF) as a function of body size. The solid lines represent Hg concentration of yellow perch predicted with a multiple regression model that used body size (W) and a categorical variable representing the source of data (D=0: Norstrom; D=1: MEF) as independent variables. The dotted line indicates how the concentration of Hg in young-of-the-year (YOY) yellow perch consumed by walleye from the Ottawa River was extrapolated from the multiple regression equation.


Norstrom et al. (1976)
MEF
YOY
$\log_{10}$ Hg = -1.33 + 0.25·$\log_{10}$ *W* + 0.24·*D*
R^2 = 0.76
Hg (µg·g^{-1})
mass (g)
10^0
10^{-1}
10^{-2}
10^{-1}
10^0
10^1
10^2
10^3

assimilation efficiency of ^{137}Cs from food, the elimination rate of ^{137}Cs by fish, and water temperature. ^{137}Cs concentration in yellow perch, walleye and their food were obtained from Rowan and Rasmussen (1996) and modeled as a function of age using linear regression. ^{137}Cs concentration in lake trout and rainbow smelt were determined using a gamma spectrometer equipped with a germanium coaxial detector (Canberra Industries Inc.). Fifteen fish were pooled to determine ^{137}Cs concentration in rainbow smelt. All samples were reduced to ashes in an oven at 450°C for 24 hours before they were analyzed to concentrate ^{137}Cs in a small volume. The assimilation efficiency of ^{137}Cs from food was taken from Rowan and Rasmussen (1996). The elimination rate of ^{137}Cs was determined using body mass and water temperature following Rowan and Rasmussen (1995). Daily water temperature was modeled with a Gaussian function (Table 2). We assumed that the maximum temperature experienced by lake trout was 10°C (Stewart et al. 1983).

Evaluation of the mercury mass balance model

Eq. (5) was used to predict the accumulation of Hg in lake trout, yellow perch and walleye combined with feeding rates determined using the ^{137}Cs method. The accuracy of the MMBM was evaluated by comparing observed and predicted Hg concentrations. For lake trout, we used the average Hg concentration determined on each age-class as observed values. Observed Hg concentrations of yellow perch and walleye were determined for each age-class from the relationship between Hg concentration and body size because the ages of the fish used to determine Hg concentration were not available. A geometric mean regression was used to model the structural relationship between Hg concentration and fish size (Sokal and Rohlf 1995). C_t was set to the average Hg concentration determined on the youngest age-class available for these populations. C_t was excluded from the comparisons because it was used as the starting point in the MMBM.

The integration of eq. (4) implicitly assumes that the parameters of the MMBM are constant through time. This assumption is probably not valid over an extended period of time (e.g. month, year) as food consumption rates, growth rates, and Hg elimination rates vary as a function of body size and water temperature (Trudel and Rasmussen 1997,

Table 2. Water temperature (°C) curve of Lake Memphremagog and the Ottawa River (T: temperature; J: day of the year).

Lake or River	Temperature
Lake Memphremagog	$T = 3.8 + 14.7 \cdot e^{-(J-219)^2/72^2}$
Ottawa River[1]	$T = 3.2 + 18.5 \cdot e^{-(J-225)^2/71^2}$

[1]Rowan et al. (1997)

Trudel et al. 2000). To circumvent this problem, we applied the mass balance on a daily basis by interpolating fish size between age-classes and by modeling temperature on a daily basis using a Gaussian function (Forseth et al. 1992; Rowan et al. 1997; Trudel et al. 2000). The concentration of Hg in fish achieved at the end of each year was used as the predicted value.

Two procedures were used to evaluate the MMBM implemented with food consumption rates estimated with the ^{137}Cs method. First, the degree and sources of error in the model predictions were determined by partitioning the mean squared error (MSE) between predicted and observed values (Rice and Cochran 1984). The mean component (MC) indicates the bias due to the difference between the predicted and observed means. The slope component (SC) indicates the bias that results from the deviation of the slope of the relationship between observed and predicted values from one. The residual component (RC) indicates the proportion of the MSE that represents random error. Thus, the errors of the model are not systematic when MC and SC are close to zero and when RC is close to 1. Second, the reliability index (K_s) of Leggett and Williams (1981) was calculated. This index indicates that ≈68% of the observed values are within a factor of K_s of predicted values. The closer the index is to one, the better the fit between the predicted and observed values. The two procedures outlined above thus evaluate the bias and precision of the model.

The ^{137}Cs method was chosen to test the MMBM because it has been shown to produce food consumption rates similar to those obtained with traditional methods based on stomach contents but with considerably less sampling effort (Forseth et al. 1992, 1994). It may be argued though that the ^{137}Cs method may accurately predict Hg concentration in fish simply because the ^{137}Cs mass balance model used to estimate food consumption rates of fish has the same mathematical structure as the MMBM. Similar equations have been used to describe Hg and ^{137}Cs dynamics in fish because both chemicals are trophically transferred (Biddinger and Gloss 1984; Cabana et al. 1994; Rowan and Rasmussen 1994; Suedel et al. 1994). In addition, the elimination rate of these chemicals seems to follow a first-order kinetics. However, it is important to note that all the parameters of the Hg and ^{137}Cs models, with the exception of body size, water temperature and *GSI*, have been derived totally independently using different studies and

experiments. Moreover, the value of these parameters differed for Hg and ^{137}Cs. Finally, these chemicals were measured independently using different methods, and were usually measured on different individual fish as well. Thus, the MMBM presented in this study can be evaluated using food consumption rates determined with the ^{137}Cs method.

Accuracy of bioenergetic models

The ability of bioenergetic models to predict Hg concentration in fish with the MMBM was also evaluated in this study using the two procedures outlined in the previous section. The parameters of the bioenergetic model were taken from Stewart et al. (1983) for lake trout, and from Kitchell et al. (1977) for yellow perch and walleye. The energy density of lake trout was estimated from fish size using the empirical model of Stewart et al. (1983). We assumed that the energy densities of walleye and yellow perch were equal to 5020 and 4185 J/g (wet weight), respectively (Kelso 1973; Boisclair and Leggett 1989a). We assumed that the energy density of the rainbow smelt consumed by lake trout was 6650 J/g (Rottiers and Tucker 1982). The energy density of the prey consumed by yellow perch was set to 3350 J/g (Cummins and Wuycheck 1971). The energy density of the gonads was assumed to be 20% higher than the value of the soma (Diana 1983). Respiration rates were converted to energy units using an oxycalorific equivalent of 13.56 J/mg O_2 (Elliott and Davison 1975).

Activity costs are generally expressed as a multiple of standard metabolic rate in bioenergetic models (hereafter referred to as activity multipliers). Two sets of activity multipliers were used to estimate food consumption rates with the bioenergetic models. First, we used the laboratory-derived activity multipliers assumed in these models. Second, we used the activity multipliers determined in the field by Rowan and Rasmussen (1996) specifically for yellow perch and walleye from the Ottawa River. No site-specific estimates of activity costs were available for Lake Memphremagog lake trout. We therefore used the activity multipliers of lake trout from Great Slave Lake derived in the field by Rowan and Rasmussen (1996) to determine if the values obtained in their study are valid for other populations. Activity multipliers determined in the field by Rowan and Rasmussen (1996) were modeled as a function of body size or age using linear and non-linear regressions (Table 3).

Table 3. Empirical models describing the relationship between activity multipliers (*ACT*) determined in the field and fish mass (*W*; g) or age (years). *ACT* were obtained from Rowan and Rasmussen (1996).

Species	Equation	r^2	SE_{est}	n
Lake trout[1]	$ACT = 7.74 \cdot 10^{-4} \cdot W + 1.18$	0.60	1.16	16
Yellow perch[2]	$ACT = 0.88 \cdot e^{0.24 \cdot Age}$	0.95	0.13	7
Walleye[2]	$ACT = 0.21 \cdot Age + 1.47$	0.56[a]	0.56	7

[1]Great Slave Lake; [2]Ottawa River

[a]p=0.052

Effects of activity costs on mercury accumulation in fish

Given that bioenergetic models are sensitive to activity costs (Kitchell et al. 1977; Stewart et al. 1983), Hg concentrations predicted with the MMBM are likely to be influenced by the activity multiplier used to estimate food consumption rates of fish. Activity costs are known to vary at least four-fold across populations of yellow perch (Boisclair and Leggett 1989a). Therefore, we estimated how much variation in Hg concentration can be produced by using different activity costs in yellow perch. Activity multipliers of yellow perch vary between 1.0 and 4.0 in the field and tend to increase with fish size (Boisclair and Leggett 1989a; Boisclair and Rasmussen 1996; Rowan and Rasmussen 1996). We used four sets of activity costs to predict Hg concentration in yellow perch (Fig. 2). First, we assumed that the activity multiplier was equal to 1.0 for every age-class (Hewett and Johnson 1992). Second, we modeled the activity multiplier of yellow perch with an allometric equation. In this analysis, we assumed that the activity multiplier of a 1 g perch was equal to 1.0, and allowed it to increase to 2.0, 3.0, and 4.0 in perch weighing 100 g (Fig. 3). Allometric exponents of 0.15, 0.24, and 0.30 were required to produce these activity multipliers.

Results

Mercury concentration

Mercury concentrations in yellow perch and lake trout tended to be lower than the safety limit of 0.5 µg/g set by the World Health Organization (WHO 1976) for the consumption of Hg contaminated fish by humans (Fig. 4-5). In walleye, 65% of the fish analyzed by the MEF had a Hg concentration higher than this safety limit (Fig. 6). Hg concentration increased with size in yellow perch ($F_{1,29}$=112.8; p<0.0001) and walleye ($F_{1,53}$=92.1; p<0.0001), but seemed to have reached a steady state in lake trout (Fig. 4-6). Hg concentration in the prey consumed by lake trout averaged 0.13 µg/g (S_x=0.02; n=9).

Food consumption rates

^{137}Cs concentration averaged 1.68 Bq/kg (S_x=0.45; n=57) in Lake Memphremagog lake trout and did not vary significantly with fish age ($F_{6,50}$=0.3; p>0.9). It increased significantly with size in yellow perch ($F_{1,6}$=224.4; p<0.0001) and walleye

Fig. 3. Models describing the relationship between activity multiplier and body size used to examine the effects of activity costs on mercury accumulation in yellow perch.

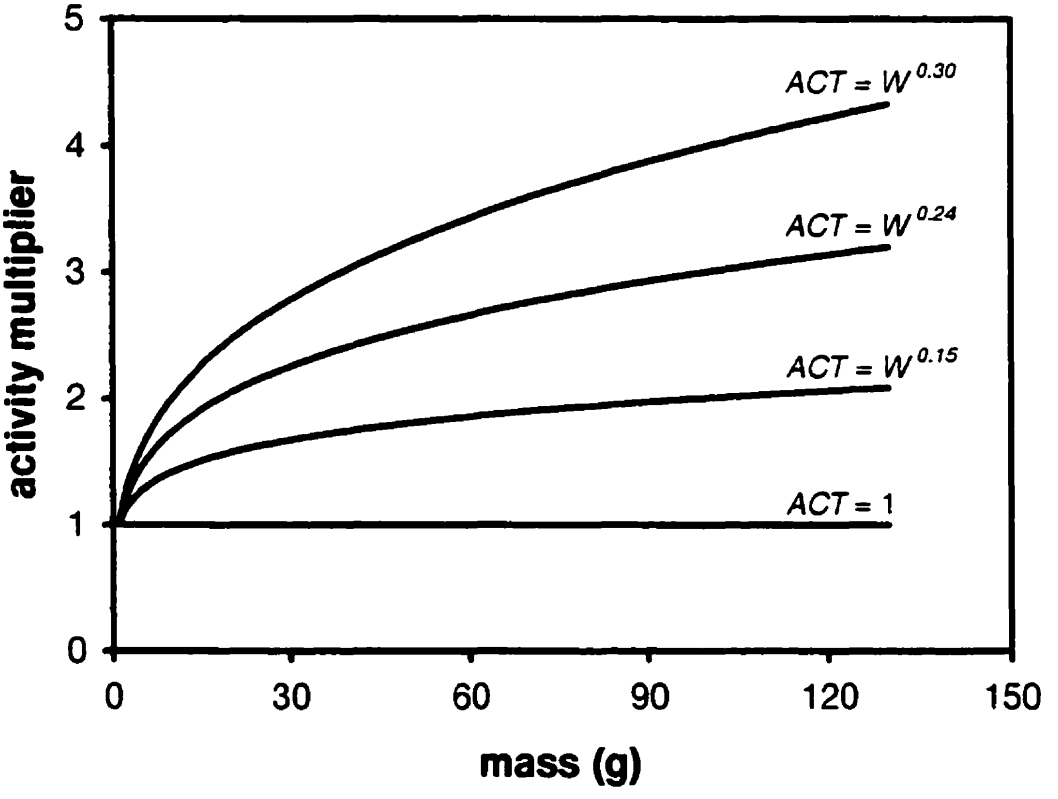

5
4
3
2
1
0
activity multiplier
ACT = W 0.30
ACT = W 0.24
ACT = W 0.15
ACT = 1
0
30
60
90
120
150
mass (g)

Fig. 4. Mercury concentration in Lake Memphremagog lake trout as a function of age. The open circles represent the average concentration of mercury in fish. The vertical bars represent ± 1·SE. The numbers above the error bars represent the sample size of that age-class. The solid lines represent the concentration of mercury predicted with the mercury mass balance model. Food consumption rates were estimated with (1) the ^{137}Cs method (●). (2) a bioenergetic model using laboratory-derived activity costs (■), and (3) a bioenergetic model using field-derived activity costs (▲).

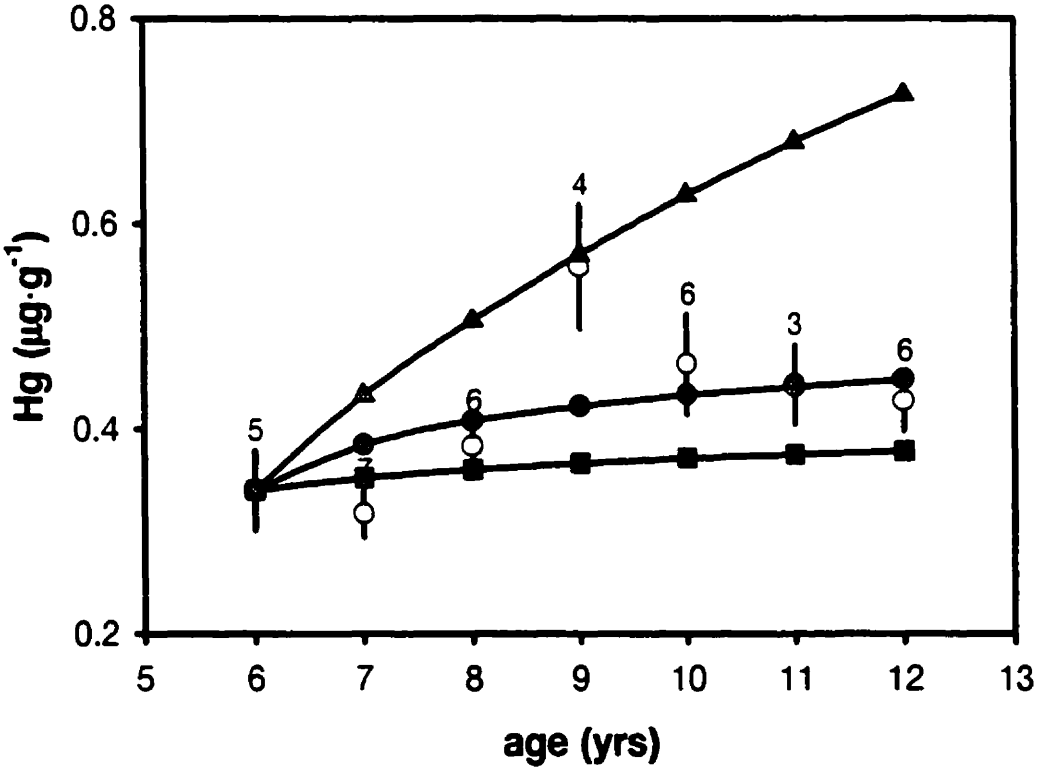

0.8
0.6
0.4
0.2
Hg (µg·g-1)
5
6
7
8
9
10
11
12
13
age (yrs)
5
6
4
6
3
6

Fig. 5. Mercury concentration of yellow perch from the Ottawa River as a function of fish size. The dotted line represents the regression equation (model II) obtained between $\log_{10}$ Hg concentration and $\log_{10}$ fish size. The solid lines represent the concentration of mercury predicted with the mass balance model. Open circles represent mercury concentrations determined on individual fish. The other symbols are as in Fig. 4.

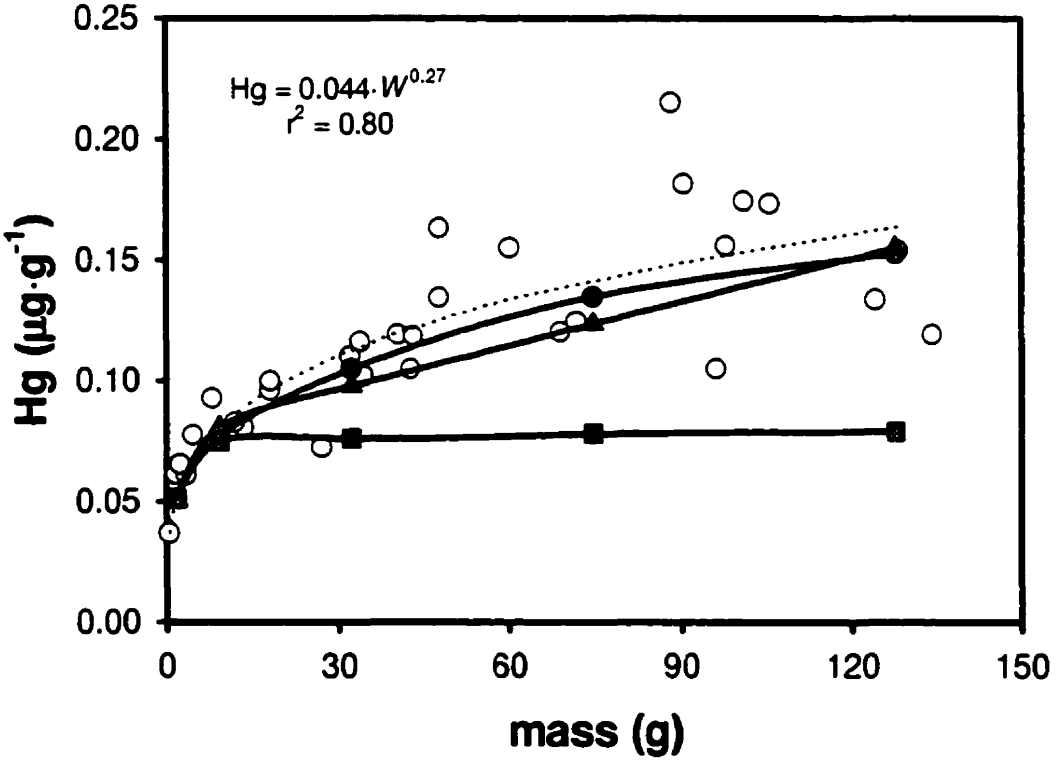
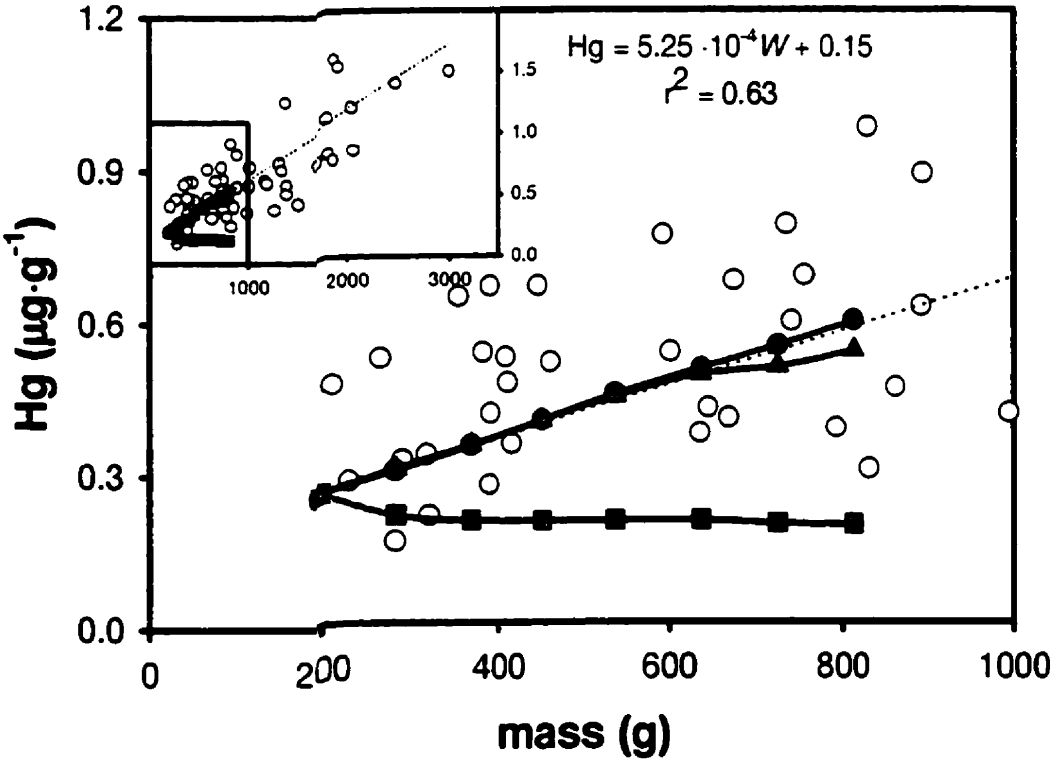

Hg = 0.044·W^0.27
r^2 = 0.80
Hg (µg·g^-1)
0.25
0.20
0.15
0.10
0.05
0.00
0
30
60
90
120
150
mass (g)

Fig. 6. Mercury concentration of walleye from the Ottawa River as a function of fish size. Legend as in Fig. 4.


Hg = 5.25 ·10⁻⁴W + 0.15
r² = 0.63
Hg (µg·g⁻¹)
mass (g)
1.2
0.9
0.6
0.3
0.0
0
200
400
600
800
1000
1.5
1.0
0.5
0.0
1000
2000
3000

($F_{1,6}$=78.0; p<0.0002) from the Ottawa River. The concentration of ^{137}Cs in the prey consumed by lake trout and walleye was 0.70 and 3.95 Bq/kg, respectively (Table 4). ^{137}Cs concentration in the food consumed by yellow perch increased from 2.50 Bq/kg in juveniles to 3.63 Bq/kg in adults (Table 4).

Food consumption rates estimated with the ^{137}Cs method ranged from 0.0061 to 0.029 $g \cdot g^{-1} \cdot d^{-1}$ (Table 5) and differed significantly among species ($F_{2,14}$=135.8; p<0.0001). Food consumption rates tended to be lower in lake trout and higher in yellow perch (Table 5). Specific feeding rates varied only slightly among age-classes of these species (Table 5). The largest difference observed between two age-classes of a given species was 28% in lake trout, 13% in yellow perch, and 39% in walleye. Except for yellow perch, these differences were larger than the 15-25% error typically associated with feeding rates.

Evaluation of the mercury mass balance model

The MMBM predicted the concentration of Hg in lake trout, yellow perch, and walleye fairly well when it was combined with food consumption rates determined with the ^{137}Cs method (Fig. 4-6). The reliability index was close to one (Table 6), indicating that predicted and observed values were quite similar. Partitioning of the MSE indicated that almost all of the error was associated with the random component in lake trout (Table 6), indicating that the errors associated with the predictions were not due to a systematic bias. However, partitioning of the MSE indicated that most of the error was associated with the mean component in yellow perch and walleye (Table 6), probably because predicted Hg concentrations tended to be lower than observed values in yellow perch, but higher than observed values in walleye (Fig. 5-6). Nevertheless, predicted Hg concentrations were usually within 20% of the observed values (Fig. 4-6).

Accuracy of bioenergetic models

Laboratory-derived bioenergetic models tended to underestimate food consumption rates determined with the ^{137}Cs method by a factor of 1.7 and 2.3 in yellow perch and walleye, respectively (Table 5). In lake trout, food consumption rates determined with the laboratory-derived bioenergetic model were only 10% lower than

Table 4. Size (W) and ^{137}Cs concentration in fish ($[^{137}Cs]$), and ^{137}Cs concentration in the food ($[^{137}Cs]_d$) of fish from Lake Memphremagog and the Ottawa River. Fish size was estimated by linear and non-linear regression analyses.

Species	Age (years)	W (g)	$[^{137}Cs]$ (Bq/kg)	$[^{137}Cs]_d$ (Bq/kg)
LAKE MEMPHREMAGOG				
Lake trout (*Salvelinus namaycush*)				
	6 m	2164.7	1.68	0.70
	7 m	2778.8	1.68	0.70
	8 m	3341.8	1.68	0.70
	9 m	3838.7	1.68	0.70
	10 m	4265.5	1.68	0.70
	11 m	4625.0	1.68	0.70
	12 m	4923.2	1.68	0.70
OTTAWA RIVER[a]				
Walleye (*Stizostedion vitreum*)				
	2 i	197.0	10.20	3.95
	3 i	282.2	11.81	3.95
	4 i	367.5	13.42	3.95
	5 i	452.8	15.04	3.95
	6 m	538.0	16.65	3.95
	7 m	636.9	18.26	3.95
	8 m	725.1	19.87	3.95
	9 m	813.3	21.49	3.95
Yellow perch (*Perca flavescens*)				
	1 i	1.7	4.85	2.50[b]
	2 i	9.2	5.35	2.50[b]
	3 i	32.2	6.90	2.93
	4 m	74.7	9.75	3.63
	5 m	127.7	13.30	3.63

Note: i, immature; m, mature

[a] Data from Rowan and Rasmussen (1996)

[b] Modified from Rowan and Rasmussen (1996) assuming that the ^{137}Cs concentration in the diet of 1-2$^+$ perch is 15% lower than 3$^+$ fish. This correction was performed because Rowan and Rasmussen (1996) incorrectly assumed that the diet of these fish was dominated by young-of-the-year perch rather than by benthic invertebrates (Qadri and Rubec 1974; Rodgers and Qadri 1982).

Table 5. Food consumption rates ($g \cdot g^{-1} \cdot d^{-1}$) of three fish species estimated with a radiocesium mass balance model, and a bioenergetic model implemented with laboratory- and field-based activity costs.

Species	Age	Radiocesium	Bioenergetic model	
			Laboratory	Field
Lake trout	6	0.0081	0.0075	0.0107
	7	0.0074	0.0068	0.0108
	8	0.0069	0.0063	0.0110
	9	0.0066	0.0059	0.0112
	10	0.0063	0.0057	0.0114
	11	0.0061	0.0055	0.0115
Yellow perch	1	0.0282	0.0214	0.0232
	2	0.0290	0.0209	0.0222
	3	0.0284	0.0140	0.0225
	4	0.0247	0.0120	0.0244
Walleye	2	0.0136	0.0085	0.0146
	3	0.0139	0.0077	0.0149
	4	0.0145	0.0072	0.0155
	5	0.0152	0.0068	0.0162
	6	0.0163	0.0066	0.0170
	7	0.0190	0.0067	0.0179
	8	0.0201	0.0065	0.0187

Table 6. Field test of a mercury mass balance model using food consumption rates estimated with the ^{137}Cs method. The mean squared difference between observed and predicted values was partitioned into mean, slopes, and error components. The reliability index (K_s) of Leggett and Williams (1981) was also computed. The ability of bioenergetic models implemented with either laboratory- or field-derived activity costs to predict mercury concentration with the mass balance model was also evaluated.

Species and method	Source of error			K_s
	Mean	Slope	Residual	
Lake trout				
^{137}Cs	0.02	0.06	0.92	1.15
Laboratory[1]	0.42	0.10	0.48	1.24
Field[2]	0.62	0.19	0.19	1.36
Yellow perch				
^{137}Cs	0.82	0.13	0.05	1.06
Laboratory[3]	0.66	0.33	0.01	1.67
Field[2]	0.61	0.05	0.34	1.11
Walleye				
^{137}Cs	0.64	0.28	0.08	1.02
Laboratory[3]	0.83	0.13	0.04	2.24
Field[2]	0.12	0.37	0.51	1.04

[1]Stewart et al. (1983); [2]Rowan and Rasmussen (1996); [3]Hewett and Johnson (1992)

those derived with the ^{137}Cs method (Table 5). Bioenergetic models implemented with site-specific estimates of activity costs provided food consumption rates similar to those obtained with the ^{137}Cs method in yellow perch and walleye (Table 5). The bioenergetic model overestimated food consumption rates of Lake Memphremagog lake trout determined with the ^{137}Cs method by a factor of 1.3-1.8 when it was implemented with activity costs derived in the field for lake trout from Great Slave Lake (Table 5).

The accumulation of Hg in Lake Memphremagog lake trout with age was adequately predicted by the MMBM when it was combined with food consumption rates determined with a laboratory-derived bioenergetic model (Fig. 4; Table 6). However, these predictions were slightly less accurate than those obtained using the MMBM implemented with food consumption rates estimated with the ^{137}Cs method (Fig. 4; Table 6). The MMBM tended to underestimate the concentration of Hg in yellow perch and walleye when it was combined with laboratory-derived bioenergetic models (Fig. 5-6; Table 6). The final concentrations of Hg predicted in this situation were 2-3 times lower than observed values (Fig. 5-6).

The MMBM accurately predicted Hg concentration in yellow perch and walleye when it was combined with food consumption rates that were determined using a bioenergetic model and site-specific estimates of activity costs (Fig. 5-6; Table 6). The accumulation of Hg in Lake Memphremagog lake trout was overestimated by the MMBM when it was combined with food consumption rates that were estimated using a bioenergetic model implemented with the activity costs derived for lake trout from Great Slave Lake. In this situation, the final concentration was overestimated by 64% (Table 6).

Effects of activity costs on mercury accumulation in fish

Food consumption rates of yellow perch determined with the bioenergetic model of Kitchell et al. (1977) varied in relation to the simulated activity costs: food consumption rates increased with activity costs (Table 7). The relationship between food consumption rates and age (or size) also varied with the simulated change of activity costs with body size. Food consumption rates of yellow perch estimated with the bioenergetic model tended to decrease with body size when the activity multiplier was

Table 7. Food consumption rates ($g \cdot g^{-1} \cdot d^{-1}$) of yellow perch determined with the bioenergetic model of Kitchell et al. (1977) in relation to activity costs (*ACT*: activity multiplier; *W*: mass).

Age	$ACT = 1$	$ACT = W^{0.15}$	$ACT = W^{0.24}$	$ACT = W^{0.30}$
1	0.021	0.025	0.029	0.031
2	0.021	0.024	0.030	0.036
3	0.014	0.022	0.030	0.041
4	0.012	0.022	0.032	0.046

assumed constant for every age-classes, but tended to increase with fish size when activity costs were scaled to $W^{0.30}$ (Table 7).

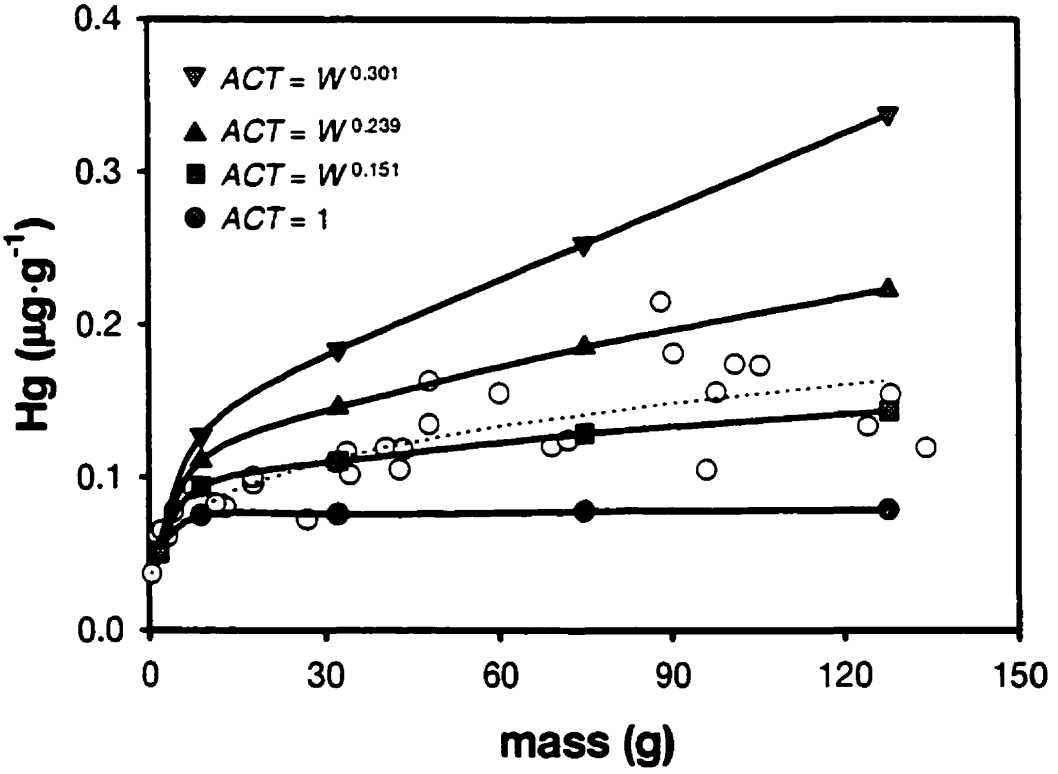
The accumulation of Hg predicted with the MMBM was strongly influenced by the simulated activity costs in yellow perch (Fig. 7). The MMBM predicted that Hg concentration in 100 g perch could vary 3.8-fold depending on the activity costs used in the bioenergetic model to estimate fish feeding rates (Fig. 7). The relationship between Hg concentration and fish size also varied as a function of activity costs. The MMBM predicted that Hg concentration would reach a steady-state if a constant activity multiplier was used to estimate food consumption rates of yellow perch (Fig. 7). This MMBM also predicted that Hg concentration would increase rapidly with age or size if the allometric exponent of activity costs was large (Fig. 7).

Discussion

Our analysis showed that the MMBM presented in this study accurately predicted the accumulation of Hg in fish when it was combined with food consumption rates determined using the ^{137}Cs method. Predicted Hg concentrations obtained with this MMBM were usually within 20% of observed values in the three species examined in this study. Given that the MMBM is sensitive to food consumption rates and that the uncertainty associated with the estimation of fish feeding rates is typically on the order of ±15-25% (Boisclair and Leggett 1988; Trudel and Boisclair 1993; Trudel et al. 2000), a difference of only 20% between observed and predicted Hg concentration could be considered within the measurement error of feeding rate estimates. This suggests that the parameters of the MMBM presented in this study may be accurate for predicting the concentration of Hg in fish in the field.

Accurate estimates of food consumption rates are required to adequately predict Hg concentration in fish using a MMBM. The analyses performed in this study suggest that laboratory-derived bioenergetic models may not be appropriate for estimating food consumption rates of fish in the field, because activity costs derived under laboratory conditions do not reflect activity costs of fish in the field. These analyses also showed that the concentration of Hg in fish predicted with a MMBM was strongly influenced by the choice of activity cost used to estimate food consumption rates with the bioenergetic

Fig. 7. Effects of activity costs on mercury concentration predicted with a mercury mass balance model for yellow perch from the Ottawa River. Activity multipliers (*ACT*) used in the bioenergetic model of Kitchell et al. (1977) were modeled as a function of body mass (*W*). Open circles represent observed mercury concentrations. The doted line represents the regression equation (model II) obtained between $\log_{10}$ Hg concentration and $\log_{10}$ fish size.


0.4
0.3
0.2
0.1
0.0
Hg (µg·g-1)
ACT = W 0.301
ACT = W 0.239
ACT = W 0.151
ACT = 1
0
30
60
90
120
150
mass (g)

model. Bioenergetic models may sometimes accurately estimate feeding rates of fish using laboratory-derived activity costs. However, we presently cannot predict when these laboratory-derived bioenergetic models will work. Therefore, unless site-specific estimates of activity costs are available from direct measurements or empirical models developed using field-derived activity costs, predictions obtained with a contaminant mass balance model implemented with a laboratory-derived bioenergetic model should be interpreted cautiously.

Accurate estimates of C_d, α, and E are also required for adequately predicting Hg concentration in fish with a MMBM due to the sensitivity of MMBM to these parameters. The main difficulty of estimating C_d with accuracy resides in obtaining an accurate description of fish diet. The diet of fish is typically determined by the examination of stomach contents. However, to accurately describe fish diet with stomach contents, fish must be collected on several sampling dates, since fish diet can vary within a year in relation to prey availability (Winemiller 1990). This approach requires considerable sampling effort in the field. Alternatively, an integrated description of fish diet may be assessed using stable isotopes of carbon and nitrogen, but with a much lower sampling effort (Vander Zanden and Rasmussen 1996; Vander Zanden et al. 1997). Hence, stable isotopes may help to accurately determine C_d.

In this study, we assumed that α was equal to 80% and constant for every age-class and species. This assumption was based on the modal value of α published in the literature for fish fed with prey fish, and on the assumption that α depends on the assimilation efficiency of proteins (Trudel et al. 2000). Furthermore, because Hg is biomagnified in fish (Cabana and Rasmussen 1994; Cabana et al. 1994; Vander Zanden and Rasmussen 1996), it was expected that the transfer efficiency of Hg from food would be elevated in fish. While about 80% of the organic matter is usually assimilated by carnivorous fish, the assimilation efficiency of organic matter may vary with prey type and gut morphology (e.g. stomachless vs fish with a well defined stomach). Thus, the assumed value of α appears reasonable for most carnivorous fish, but more effort is needed to quantify α for stomachless fish and herbivorous fish.

The elimination rate of Hg was estimated with the empirical model we recently developed using data obtained from published experiments performed in the laboratory

and in the field (Trudel and Rasmussen 1997). This model explains a large proportion of the variance associated with Hg elimination rate (77%), and can be applied to fish weighing between 8 g and 18.5 kg. Furthermore, we showed that the elimination rate of Hg was independent of Hg concentration in fish, indicating that Hg elimination is a first-order kinetic process. To our knowledge, only two empirical models of Hg elimination rate by fish have been published prior to our study. The model of Hendriks (1995) systematically overestimates the elimination rate of Hg by fish by a factor of about six, while the model of Norstrom et al. (1976) overestimates Hg elimination for fish smaller than 300 g, but underestimates Hg elimination rate for fish larger than 300 g (Trudel and Rasmussen 1997). Thus, these two empirical models should not be used to estimate the elimination rate of Hg by fish in MMBM.

A theoretical model based on thermodynamic principles has been developed by Borgmann and Whittle (1992) to estimate the elimination rate of Hg and hydrophobic organic contaminants (HOC) by fish. They assumed that the elimination rate of these chemicals was influenced by α and by food consumption rates of fish, and that α varied in relation to food consumption rates and with the concentration of these chemicals in fish. These assumptions are not supported though for Hg and HOC. The elimination rate of Hg is similar in well fed fish and fasted fish (Burrows and Krenkel 1973). Dabrowska et al. (1996) and Fisk et al. (1998) showed that the α of HOC was independent of HOC concentration in fish. Thus, the validity of the elimination model proposed by Borgmann and Whittle (1992) is disputable.

Accumulation of mercury with age

The MMBM proposed in this study offers a theoretical framework that may help to understand how the accumulation of Hg through time is regulated in fish. Mercury concentration generally increases with age or size in fish (Bache et al. 1971; Scott and Armstrong 1972; Cutshall et al. 1978; and others). This is commonly believed to result from the longer exposure time of older fish to Hg. Clearly, older fish can only accumulate Hg if they are continually exposed to it. However, this explanation is not sufficient by itself to explain this pattern. First, Hg concentration does not always increases with fish size (Scott and Armstrong 1972; Meili 1991). Thus, older fish do not necessarily

accumulate more Hg, even if they are exposed to Hg for a longer time. Second, the concentration of Hg in fish exposed to a constant source of Hg under laboratory condition generally reach steady-state within a few months (McKim et al. 1976; Cember et al. 1978). This suggests that Hg concentration increases with fish age because the intake of Hg from food relative to Hg elimination and growth also increases as fish gets older. This may occur if older fish are feeding on more contaminated prey and/or if food conversion efficiency (i.e.$CE = G/I$) decreases with body size (Borgmann and Whittle 1992). This interpretation may be examined with the MMBM derived in this study.

To illustrate the potential effect of prey contamination and CE on Hg concentration in fish, we have set eq. (5) to steady state, and assumed that K is small compared to E and G:

$$C = \frac{\alpha \cdot C_d \cdot I}{E+G} \tag{9}$$

Thus, if all the parameters on the right hand size of the equation remain constant through time, Hg concentration will reach an asymptote (i.e. steady-state). The time required to reach this asymptote will be determined by $[1-e^{-(E+G)\cdot\Delta t}]$; if the sum of E and G is large, Hg concentration will quickly reach a steady state. However, Hg concentration will increase with fish age if C_d increases with fish age. Hg concentration may also increase with size if I increases faster with body size than the sum of E and G. Because both I and E tend to scale to body size with an allometric exponent close to –0.2 (Trudel and Rasmussen 1997; Trudel et al. 2000), Hg concentration will increase with body size if specific growth rate decreases faster with body size than specific feeding rates. In other words, Hg concentration will increase with body size if CE decreases with body size. A reduction in CE with fish age can occur if metabolic costs are larger in older fish. This interpretation is supported by the simulations we performed in this study: Hg concentration reached a steady state when activity costs were constant for every age-class, but increased with age when activity costs increased with age or size. This suggests that the concentration of Hg in fish depends not only on the quantity of food consumed by fish, but also on how fish allocate the consumed energy to activity costs and growth.

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CONNECTING STATEMENT

In the second chapter, I developed and tested a Hg mass balance model to predict the accumulation of Hg in fish. I showed that Hg concentration was adequately predicted by the model when it was combined with food consumption rates that were estimated with a radioisotopic method, but tended to be underestimated when it was combined with food consumption rates that were estimated with a bioenergetic model, probably because metabolic costs were not adequately represented in bioenergetic models. In the following chapter, I demonstrate that, in addition to predicting Hg concentration in fish, this Hg mass balance model can also be used to estimate food consumption rates of fish when the concentration of Hg in fish is known. This approach was validated using data obtained from a published experiment. It was also tested *in situ* using independent estimates of fish feeding rates obtained using the radioisotopic method. This approach is not labor intensive and can be applied to determine the energy budget in situations that would be logistically difficult for established methods based on stomach contents.

CHAPTER 3

ESTIMATING FOOD CONSUMPTION RATES OF FISH USING A MERCURY MASS BALANCE MODEL

Abstract

We present a simple method for estimating food consumption rates of fish in the field based on a mercury mass balance model. This method requires the determination of fish age, size and growth, and mercury concentration in fish and its food. The model was validated using data obtained from a previously published laboratory experiment. A field test of the model showed that food consumption rates determined with the mercury mass balance model differed from independent estimates obtained with the ^{137}Cs method by only 0.6-16.1%. The model was applied to fish from various lakes in Quebec and Ontario. Food consumption rates estimated with the mercury mass balance model varied significantly both among species and populations. Furthermore, female fish tended to eat 30-40% more food than male, probably to meet the larger energy requirement associated with egg production. A sensitivity analysis indicated that the mercury mass balance model was mostly responsive to variables that can be easily measured in the field, such as fish size, and mercury concentration in fish and its food. By providing a low-effort approach to quantifying food consumption rates of fish in the field, this method may helps to refine our understanding of the environmental factors that influence the quantity of food consumed by fish.

Introduction

The ingestion of food is a central process in fish ecology. Fish must acquire a minimum quantity of energy in order to survive and maintain physiological integrity. Once this minimal energy is exceeded, fish can use the surplus energy for somatic growth and the production of gonads (Kitchell et al. 1977). At the population and community levels, food consumption rates can influence the intensity of intra- and interspecific competition (Hanson and Leggett 1986), the impact of predators on prey communities (Stewart and Ibarra 1991), and the recycling of nutrients through waste production (Kraft 1992). However, despite its ecological importance, few studies have attempted to examine the effects of environmental conditions on the quantity of food consumed by fish, probably due to the extensive effort required to estimate long-term (e.g. season, year) consumption rates for a large number of populations using traditional methods based on stomach contents.

Simple models based on the mass balance of persistent contaminants such as radioactive cesium (^{137}Cs), PCB, and DDE have been developed during the last three decades to estimate the quantity of food consumed by fish in the field (Kevern 1966; Kolehmainen 1974; Borgmann and Whittle 1992; Forseth et al. 1992; Rowan and Rasmussen 1996, 1997; Tucker and Rasmussen 1999). These models require the determination of the concentration of the chemical in fish and their prey, as well as the chemical absorption efficiency from food and the elimination rate of the chemical by fish. This approach has traditionally been applied to highly polluted systems (Kolehmainen 1974; Borgmann and Whittle 1992; Forseth et al. 1992,1994). However, it has recently been shown that these models could be used even at ambient or low level of contamination (Rowan and Rasmussen 1996, 1997; Tucker and Rasmussen 1999). Furthermore, this approach can provide food consumption rates similar to those derived with stomach contents (Forseth et al. 1992, 1994), but with considerably less sampling effort. Yet, mass balance models of chemical tracers have rarely been used compared to methods based on stomach contents or bioenergetic models even though they were developed during the same period. This may be because (1) fish ecologists were not exposed to this toxicological literature, (2) fish ecologists were under the impression that it could only be

used in highly contaminated system, (3) measuring these chemicals in fish and their prey is difficult, or (4) no adequate empirical models were available until recently (e.g. Rowan and Rasmussen 1995; Trudel and Rasmussen 1997) to estimate the elimination rate of these chemicals. Thus, this approach would be more practical if we could use a chemical tracer that could be easily determined in fish and their food at any level of contamination and if the elimination rate of that chemical from fish could be accurately estimated.

Mercury (Hg), like ^{137}Cs, is mainly absorbed from food by fish (Trudel and Rasmussen, *submitted*). It is globally distributed in the environment due to natural processes and human activities, and can be easily determined in the biota with atomic absorption spectroscopy even when Hg concentration in fish and their food are low. Accurate measurements of Hg concentration can be obtained in fish with less than 1 g wet weight of muscle tissue. It can also be determined on biopsy (Lockhart et al. 1972), allowing for the release of the fish once the muscle sample is taken. Furthermore, the elimination rate of Hg by fish can be accurately determined using only fish size and water temperature (Trudel and Rasmussen 1997). This suggests that Hg may be a useful chemical tracer for estimating the quantity of food consumed by fish *in situ* (Rodgers and Beamish 1982). Moreover, because Hg is routinely measured by several agencies and laboratories around the world, there is a potentially large database that could be used to quantify food consumption rates of fish in the field.

The objective of this study was to present and validate a simple method for estimating food consumption rates of fish in the field based on the mass balance of Hg. The Hg mass balance model was also tested with independent estimates of food consumption rates obtained with the ^{137}Cs method. Finally, to illustrate the utility of this approach, we used Hg concentration of fish published in the literature and obtained from Hydro-Quebec databases to estimate the feeding rates of four fish species from one reservoir and five lakes located in Quebec and Ontario. Food consumption rates were compared among species, populations, and sex, and also with published values obtained using stomach contents and the ^{137}Cs method.

Materials and methods

Mercury mass balance model

The mass balance model of Hg concentration (C; $\mu g \cdot g^{-1}$) can be expressed as (Appendix II);

$$(1) \qquad \frac{dC}{dt} = (\alpha \cdot C_d \cdot I) - (E + G + K) \cdot C$$

where α is the assimilation efficiency of Hg from food, C_d is the concentration of Hg in fish diet ($\mu g \cdot g^{-1}$), I is the food consumption rate of fish ($g \cdot g^{-1} \cdot d^{1}$ or d^{-1}), E is the elimination rate of Hg ($\mu g \cdot \mu g^{-1} \cdot d^{-1}$ or d^{-1}), G is the specific growth rate ($g \cdot g^{-1} \cdot d^{1}$ or d^{-1}), and K is the loss rate of Hg due to spawning ($\mu g \cdot \mu g^{-1} \cdot d^{-1}$ or d^{-1}). Several forms of Hg can be found in the environment. In fish, most of the Hg (>95%) is methylmercury (Bloom 1992). Hence, Hg and methylmercury will be used as synonyms in this study. Integrating this differential equation, and solving it for food consumption rate, we obtain the following equation (Appendix II);

$$(2) \qquad I = \frac{C_{t+\Delta t} - C_t e^{-(E+G+K)\Delta t}}{\alpha \cdot C_d \cdot \left[1 - e^{-(E+G+K)\Delta t}\right]} (E + G + K)$$

where C_t and $C_{t+\Delta t}$ are the concentration of Hg in fish at time t and $t+\Delta t$ ($\mu g \cdot g^{-1}$), respectively, and Δt is the time interval (d). Eq. (2) indicates that fish ingestion rates can be determined using Hg concentration in fish and their prey, fish size and growth, Hg assimilation efficiency from food and Hg elimination rate from fish. This model assumes that consumption, growth and Hg elimination rates are constant during the time interval Δt. This assumption is probably not valid over an extended period of time (e.g. month, year) because these variables can be influenced by fish size and water temperature. Forseth et al. (1992) recommended to interpolate fish size, chemical concentration, and water temperature on a daily basis between sampling dates to estimate food consumption rates of fish with mass balance models of chemical tracers. Seasonal or yearly consumption rate

can then be obtained by summing the daily ration values obtained during these intervals (Forseth et al. 1992).

The α of Hg for prey fish typically ranges between 60 and 95% (de Freitas et al. 1977; Ribeyre et al. 1980). Because methylmercury forms covalent bounds with proteins (Carty and Malone 1979), α is expected to vary with protein assimilation, which is generally equal to 80% in carnivorous fish (Brett and Groves 1979). Therefore, we assumed that α was equal to 0.8 in fish, which correspond to the mode of laboratory-derived α values for fish fed with natural prey items (Table 1).

We recently reviewed the literature to develop an empirical model of Hg elimination by fish (Trudel and Rasmussen 1997). We showed that Hg elimination was independent of Hg burden or concentration, indicating that Hg dynamics can be expressed by a first order kinetic model. We also showed that Hg elimination of fish could be accurately estimated using fish size (W; g) and water temperature (T; °C);

$$(3) \qquad E = \varphi \cdot W^{\beta} \cdot e^{\gamma T}$$

where φ, β, γ are empirically derived constants (Table 1). The loss rate of Hg due to spawning can be determined using the gonadosomatic index (GSI; $g \cdot g^{-1}$) and Hg concentration in the gonads (C_g; $\mu g \cdot g^{-1}$) and in fish (C_f; $\mu g \cdot g^{-1}$);

$$(4) \qquad K = \frac{Q \cdot GSI}{365}$$

where Q is the ratio of Hg concentration in the gonads to fish and 365 represent the number of days in a year (Appendix I). A review of the literature indicated that Q was equal to 0.12 (SE=0.03) and 0.59 (SE=0.01) in females and males, respectively (Table 1). Assuming a sex ratio of 1:1, Q may be estimated as;

$$(5) \qquad Q = \frac{(Q_m \cdot GSI_m + Q_f \cdot GSI_f)}{(GSI_m + GSI_f)}$$

Table 1. Parameters of the mercury mass balance model.

Symbol	Parameter description	Value	Source
α	Assimilation efficiency	0.80	1
φ	Coefficient of mercury elimination	0.0029	2
β	Allometric exponent of mercury elimination	-0.20	2
γ	Temperature coefficient of mercury elimination	0.066	2
Q_m	Ratio of mercury concentration in the gonads and whole fish for males	0.59	3, 4
Q_f	Ratio of mercury concentration in the gonads and whole fish for females	0.12	4-6

1. Norstrom et al. (1976); 2. Trudel and Rasmussen (1997); 3. Lockhart et al. (1972); 4. Doyon et al. (1996); 5. Niimi (1983); 6. Lange et al. (1994)

where the subscripts *m* and *f* represent males and females, respectively.

Validation of the mercury mass balance model

We used the laboratory experiment performed by Rodgers and Beamish (1982) to validate the Hg mass balance model presented in this study. In their study, rainbow trout (*Oncorhynchus mykiss*) were raised at 10.5 °C and were fed with Hg contaminated food (23.2±1.0 and 76.5±1.3 $\mu g \cdot g^{-1}$) for a period of 84 days. Only fish that consumed 1% of their body weight per day were retained for this analysis, because fish that consumed larger meals had a significantly lower growth rate than control fish, probably because of Hg poisoning. The size and the concentration of Hg in rainbow trout during the 84 days were extracted from their Fig. 2 and 4, respectively (Table 2). The assimilation efficiency of Hg from food and Hg elimination by fish were also determined in their study. On average, α was equal to 0.72 (SE=0.05) in their study. This value is 10% lower than the value that we assumed in Table 1, probably because they used artificial food rather than natural prey items. The elimination rate of Hg by rainbow trout averaged 0.0070 d^{-1} (SE=0.0004 d^{-1}); this value is about two-fold larger than the value predicted by our empirical model. This difference was expected as the elimination rate of Hg is biphasic in short-term experiments; the fast component has a half-life of days to weeks, while the slow component has a half-life of months to years (Ruohtula and Miettinen 1975). We used eq. (2) with the parameters derived in their study to validate the Hg mass balance model. Monte Carlo simulations were used to assess the error associated with the estimation of food consumption rates (Manly 1997).

Field test of the mercury mass balance model

We tested the Hg mass balance model with independent estimates of food consumption rates obtained in the field using the ^{137}Cs method recently refined by Rowan and Rasmussen (1996, 1997). The ^{137}Cs method was used to test the Hg mass balance model because it provides food consumption rates similar to those obtained with a benchmark method based on stomach contents (Forset et al. 1992, 1994), but with considerably less sampling effort. This analysis was performed with lake trout (*Salvelinus*

Table 2. Mass (W_t; g) and mercury concentration (C_t; $\mu g \cdot g^{-1}$) of rainbow trout fed with Hg contaminated food during a period of 84 days. The concentration of Hg in the food was 23.2±1.0 (Group A) and 76.5±1.3 $\mu g \cdot g^{-1}$ (Group B). Data from Rodgers and Beamish (1982).

day	Group A		Group B	
	W_t	C_t	W_t	C_t
0	5.19		4.96	
14	6.12	1.71	5.66	9.10
28	6.72	4.71	6.35	12.56
42	7.36		6.81	
56	8.43	5.17	7.73	19.49
70	9.35		8.66	
84	10.18	7.90	9.58	29.19

namaycush) from Lake Memphremagog (Quebec-Vermont), and walleye (*Stizostedion vitreum*) and yellow perch (*Perca flavescens*) from the Ottawa River (Quebec-Ontario). Fish size, water temperature, Hg concentration in fish and their food, and ^{137}Cs concentration in fish and their food, and ^{137}Cs concentration in fish and their food were obtained from Trudel and Rasmussen (*submitted*). We used the equations and parameters provided by Rowan and Rasmussen (1995, 1996) to estimate the ingestion rates of lake trout, walleye, and yellow perch with the ^{137}Cs method. Daily water temperature was estimated with a Gaussian function of Julian date (Table 3). For lake trout, we assumed that they would maintain their position in the water column where the temperature is not exceeding 10°C (Stewart et al. 1983). Fish size, Hg and ^{137}Cs concentrations in fish were modeled as a function of age using linear and non-linear regressions. Growth rates were estimated using mean fish weight determined on adjacent age-classes with the regression models. Specific growth rate was estimated as (Ricker 1979);

$$(6) \qquad G = \frac{1}{\Delta t} \cdot \ln\left(\frac{W_{t+\Delta t}}{W_t}\right)$$

where W_t and $W_{t+\Delta t}$ are fish mass at time t and $t+\Delta t$ (g). With the exception of Lake Memphremagog lake trout, the *GSI* of the species used in this study were taken from Rowan and Rasmussen (1996). For Lake Memphremagog lake trout, the *GSI* was determined directly and was equal to 5 and 15% for male and female fish, respectively. Monte Carlo simulations were performed to assess the uncertainty associated with the estimation of food consumption rates with the Hg and ^{137}Cs mass balance models (Manly 1997). Food consumption rates obtained with these two models were compared with an Analysis of Covariance (ANCOVA), using body mass as a covariate. Both food consumption rates and fish mass were $\log_{10}$ transformed for the statistical analyses to linearize the relationship between these variables and to stabilize the variance (Zar 1996). We also used the reliability index (K_r) of Leggett and Williams (1981) to compare these two methods. The closer the index is to one, the better the fit is between these two methods.

Table 3. Water temperature (°C) curves of four lakes (L), one river and one reservoir (R) located in Quebec and Ontario. (temperature: T; day of the year: J)

Lakes, Rivers, and Reservoirs	Temperature
L. Ontario[a], L. Memphremagog	$T = 3.8 + 14.7 \cdot e^{-(J-219)^2/72^2}$
Ottawa River[b]	$T = 3.2 + 18.5 \cdot e^{-(J-225)^2/71^2}$
Caniapiscau R.[c], L. Serigny[c], L. Rond-de-Poêle[c]	$T = 3.8 + 9.5 \cdot e^{-(J-223)^2/61^2}$
L. Simcoe[d]	$T = 4.0 + 18.5 \cdot e^{-(J-207)^2/70^2}$

[a]Data from Kwiatkowski (1982)
[b]Data from Rowan et al. (1997)
[c]Data from Hydro-Quebec
[d]Data from Mathers and Johansen (1985)

Application of the mercury mass balance model

The Hg mass balance model was also used to estimate food consumption rates of lake whitefish (*Coregonus clupeaformis*), northern pike (*Esox lucius*), walleye, and lake trout from four lakes and one reservoir located in Quebec and Ontario (Appendix III). For these populations, fish age and size, Hg concentration in fish and their food, and water temperature were obtained from Kwiatkowski (1982), Mathers and Johansen (1985), Borgmann and Whittle (1992), Madenjian et al. (1995), Doyon et al. (1996), Doyon et al. (1998), and Hydro-Quebec databases (Table 3, Appendix III). In these studies, C_d was either determined directly on stomach contents of fish (e.g. Mathers and Johansen 1985) or was estimated as the weighted average Hg concentration of the different prey items found in the diet of the fish as;

$$(7) \qquad C_d = \sum p_i \cdot C_i$$

where p_i represents the proportion of the i^{th} prey in the diet, and C_i is the concentration of Hg of that prey ($\mu g \cdot g^{-1}$). Food consumption rates were compared among species, population and sex with an ANCOVA using fish mass as a covariate. Food consumption rates and fish mass were $\log_{10}$ transformed for the statistical analyses to linearize the relationship between these variables and to stabilize the variance (Zar 1996).

We also indirectly evaluated the Hg mass balance model by comparing food consumption rates obtained in this study with published values determined with stomach contents and with the ^{137}Cs mass balance model for a similar range of body size. Published values obtained with stomach contents covered 46 freshwater and marine fish species that were collected from various lakes located in North America and Europe, as well as from several seas and oceans (Appendix IV). Published values derived with the ^{137}Cs mass balance model covered 15 freshwater species that were collected mostly (91 %) from the Ottawa River and Great Slave Lake. Food consumption rates of fish have been expressed both on an absolute and relative (to mass) basis using various units (e.g., g dry, g wet, J, cal). In this study, all ingestion rates were converted in g wet$\cdot d^{-1}$. Dry mass was assumed to represent 10%, 14%, and 25% of the wet mass in zooplankton, benthic invertebrates,

and fish, respectively. Food consumption rates expressed in energy units (J or cal) were converted into g wet weight using the energy density of the different prey items found in the diet of the fish. Stepwise multiple regression was used to compare food consumption rates determined with stomach contents, the Hg and ^{137}Cs mass balance models (Zar 1996). Body size, water temperature, and a categorical variable representing the method used to estimate fish feeding rate were used as independent variables in the multiple regression analysis.

Sensitivity analysis

A sensitivity analysis was also performed to evaluate the robustness of the Hg mass balance model to uncertainty in eq. (2). This analysis was performed on the lowest and highest feeding rate (relative to mass) estimated with the Hg mass balance model. Each parameter in eq. (2) was increased and decreased by 10%, and the resultant change in consumption rates was calculated.

Results

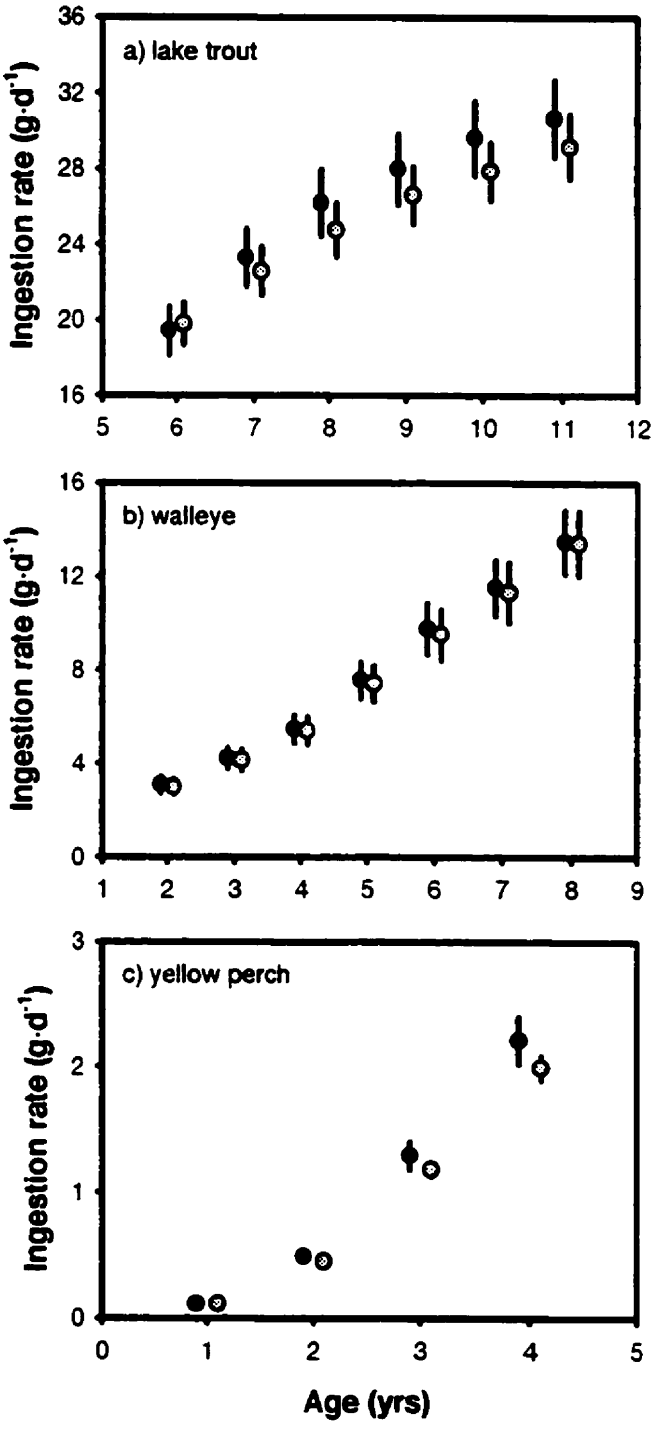
Validation of the Hg mass balance model

Food consumption rates of rainbow trout determined with the Hg mass balance model were equal to 0.99 (SE=0.08) and 0.98 $\%\cdot d^{-1}$ (SE=0.07) for fish that were fed with food containing 23.2 and 76.5 μg of Hg per g of food, respectively. These values differed by only 1-2 % of the actual feeding rates of these fish. Thus, there was an excellent agreement between the actual feeding rates and the values estimated with the Hg mass balance model.

Field test of the Hg mass balance model

Food consumption rates estimated with the Hg mass balance model ranged from 19.4 to 30.7 $g\cdot d^{-1}$ in lake trout, 3.1 to 13.5 $g\cdot d^{-1}$ in walleye, and 0.1 to 2.2 $g\cdot d^{-1}$ in yellow perch, and were similar to those obtained with the ^{137}Cs mass balance (Fig. 1). On average, food consumption rates determined with the Hg mass balance model differed from those obtained with the ^{137}Cs method by 4.5% in lake trout, 1.9% in walleye, and

Figure 1. Comparison of Lake Memphremagog lake trout consumption rate determined with the mercury mass balance model (●) and with the ^{137}Cs method (⊙). The error bars represent ± 1·SE and were determined by Monte Carlo simulations.


a) lake trout
Ingestion rate (g·d⁻¹)
36
32
28
24
20
16
5
6
7
8
9
10
11
12
b) walleye
Ingestion rate (g·d⁻¹)
16
12
8
4
0
1
2
3
4
5
6
7
8
9
c) yellow perch
Ingestion rate (g·d⁻¹)
3
2
1
0
0
1
2
3
4
5
Age (yrs)

12.0% in yellow perch (Fig. 1). These differences were always within two standard error of the estimates. There was no significant difference in the food consumption rates determined with the Hg and ^{137}Cs mass balance models (slope: $F_{1,30}$=0.3, p>0.5; intercept: $F_{1,30}$=0.1, p>0.7). Furthermore, the reliability index was close to one (K_r=1.07), indicating that the ingestion rates obtained with these two methods were quite similar.

Application of the Hg mass balance model

Food consumption rates were highly variable among age-classes and species, and tended to increase with body size (Fig. 2). For a given size, food consumption rates tended to be higher for lake whitefish from the Caniapiscau Reservoir, and lower for Lake Memphremagog lake trout and male northern pike from the Caniapiscau Reservoir (Fig. 2). The allometric exponent of food consumption rates ranged from 0.62 in lake trout to 1.06 in northern pike (Table 4) and varied significantly among species ($F_{4,87}$=6.1, p<0.0005). Food consumption rates varied significantly among populations in lake whitefish ($F_{2,33}$=7.6, p<0.005), northern pike ($F_{2,18}$=8.1, p<0.005), lake trout ($F_{1,10}$=73.5, p<0.0001), and walleye ($F_{2,17}$=11.5, p<0.001). On average, females tended to eat 30-40% more food than males (Fig. 2a,c). Food consumption rates varied significantly between sexes in lake whitefish ($F_{1,8}$=224.3, p<0.0001) and northern pike ($F_{1,7}$=19.1, p<0.005).

Food consumption rates estimated with the Hg mass balance model were similar to published values obtained from other populations and species using stomach contents and the ^{137}Cs mass balance model (Fig. 3). The relationship between food consumption rates and body mass was similar for these three methods (Fig. 3; Table 5). The best empirical model of food consumption rates included only body size and water temperature as independent variables (SE in parentheses):

(8) $$\log_{10} DR = -1.38(0.06) + 0.80(0.02)\cdot\log_{10} W + 0.014(0.003)\cdot T$$

$R^2 = 0.88$; $SE_{est} = 0.24$; p<0.0001; n=377

Once the effects of body size and water temperature were accounted for, the categorical variables representing the method used to estimate food consumption rates

Figure 2. Relationship between consumption rate and mass for a) lake whitefish, b) lake trout, c) northern pike, and d) walleye. ●, L. Memphremagog; ○, L. Ontario; ▼, L. Rond-de-Poêle; ▽, L. Simcoe; △, L. Serigny; □, Caniapiscau R. (juvenile); ■, Caniapiscau R. (female); ▩, Caniapiscau R. (male).

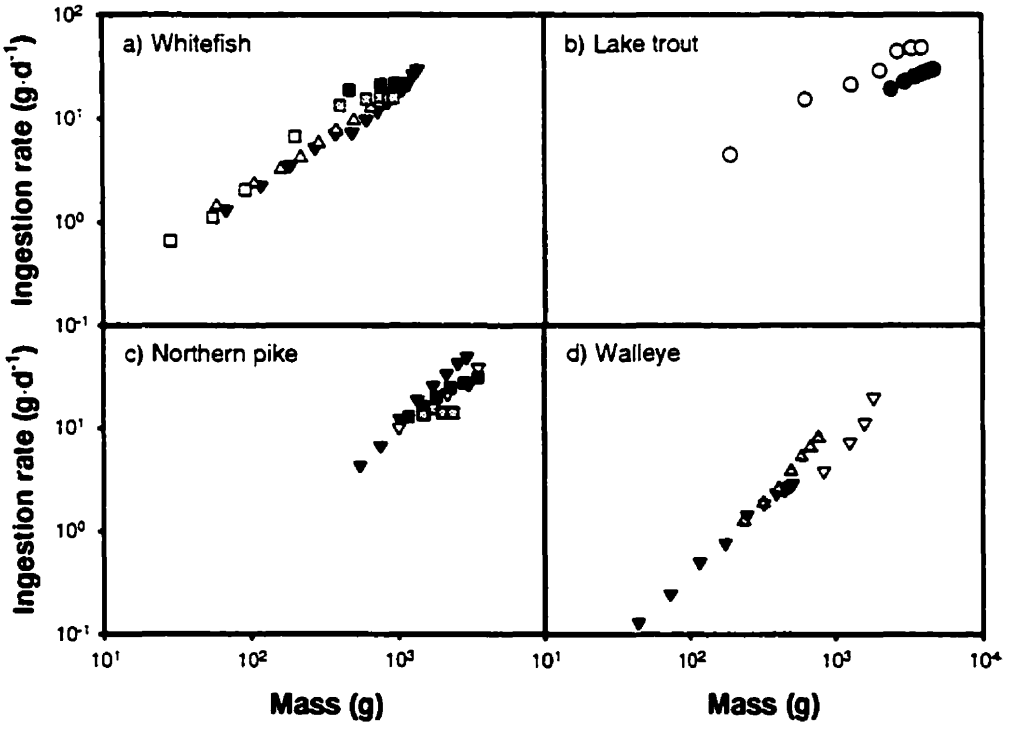

a) Whitefish
b) Lake trout
c) Northern pike
d) Walleye
Ingestion rate (g·d⁻¹)
Ingestion rate (g·d⁻¹)
Mass (g)
Mass (g)

Table 4. Allometric relationships of food consumption rates (*DR*; $g \cdot d^{-1}$) determined on five freshwater fish species. The data used to develop these models are plotted in Fig. 2. Standard error of the coefficients are in parenthesis. *W*: body size (g); SE_{est}: standard error of the estimate.

Species	Model	*n*	SE_{est}	r^2
Lake whitefish	$\log_{10} DR = -1.59(0.08) + 0.96(0.03) \cdot \log_{10} W$	37	0.09	0.96
Northern pike	$\log_{10} DR = -2.16(0.41) + 1.06(0.13) \cdot \log_{10} W$	22	0.12	0.77
Walleye	$\log_{10} DR = -1.91(0.11) + 1.01(0.04) \cdot \log_{10} W$	21	0.07	0.97
Yellow perch	$\log_{10} DR = -1.50(0.05) + 0.94(0.03) \cdot \log_{10} W$	4	0.04	0.99
Lake trout	$\log_{10} DR = -0.65(0.28) + 0.62(0.08) \cdot \log_{10} W$	13	0.12	0.78

Figure 3. Comparison of food consumption rates determined using the mercury mass balance model (●) presented in this study, with those obtained using a) stomach contents (○), and b) a radiocesium mass balance model (△). Food consumption rates determined with stomach contents and the cesium mass balance model were obtained from the literature.

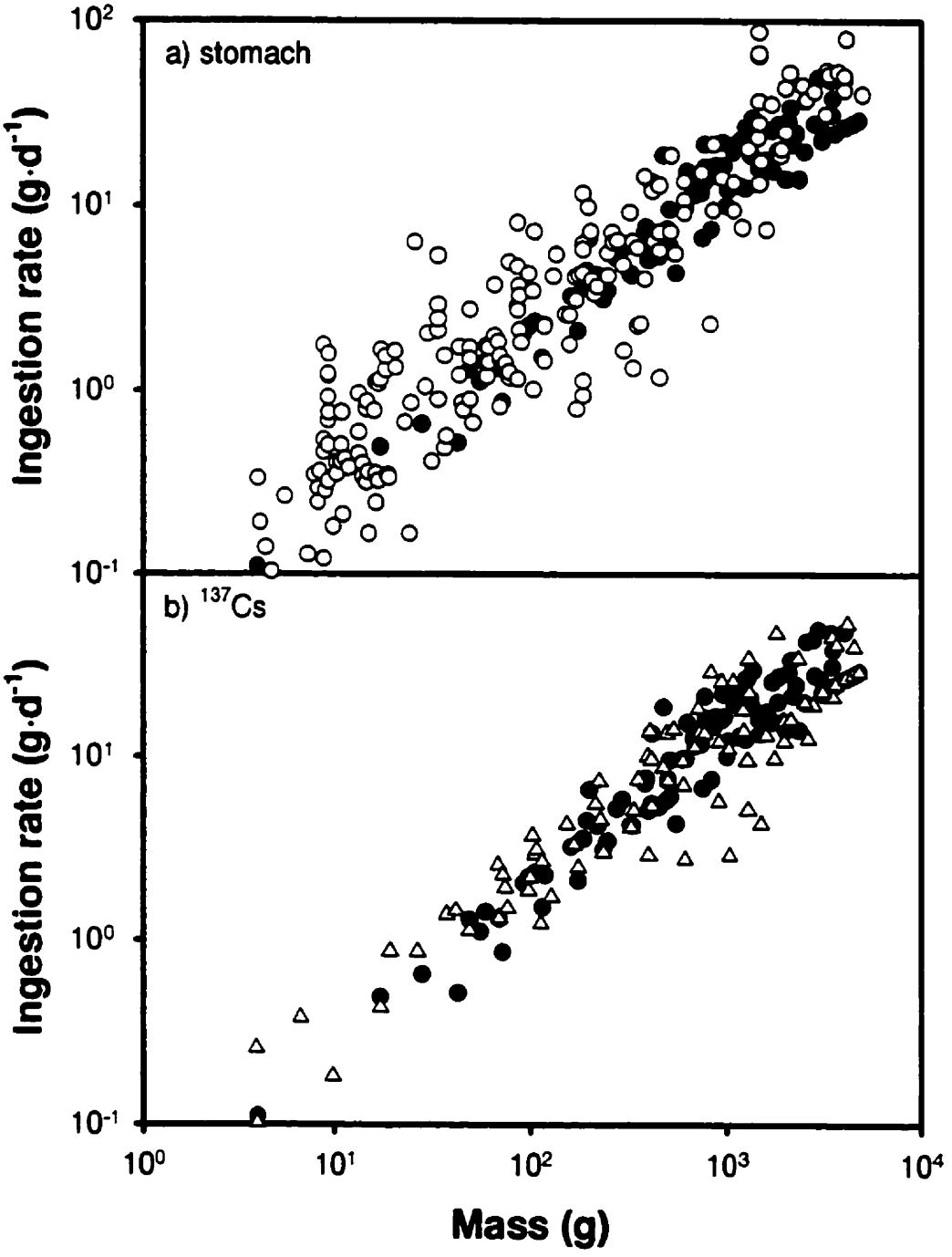

a) stomach
b) ^{137}Cs
Ingestion rate (g·d^{-1})
Ingestion rate (g·d^{-1})
Mass (g)
10^{2}
10^{1}
10^{0}
10^{-1}
10^{0}
10^{1}
10^{2}
10^{3}
10^{4}

Table 5. Allometric relationships of food consumption rates (*DR*; $g \cdot d^{-1}$) determined with various methods. The data used to develop these models are plotted in Fig. 3. Standard error of the coefficients are in parenthesis. MMBM: Mercury mass balance model; Stom: Stomach contents; CMBM: ^{137}Cs mass balance model; *W*: body size (g); SE_{est}: standard error of the estimate.

Method	Model	*n*	SE_{est}	r^2
MMBM	$\log_{10} DR = -1.37(0.07) + 0.84(0.03) \cdot \log_{10} W$	97	0.14	0.92
Stom	$\log_{10} DR = -1.17(0.10) + 0.78(0.04) \cdot \log_{10} W$	194	0.29	0.83
CMBM	$\log_{10} DR = -1.11(0.09) + 0.73(0.03) \cdot \log_{10} W$	86	0.22	0.86

were not significant. This indicates that the stomach contents approach, the Hg and ^{137}Cs mass balance models provide similar estimates of food consumption rates of fish, and that there is no systematic bias associated with the Hg mass balance model presented in this study.

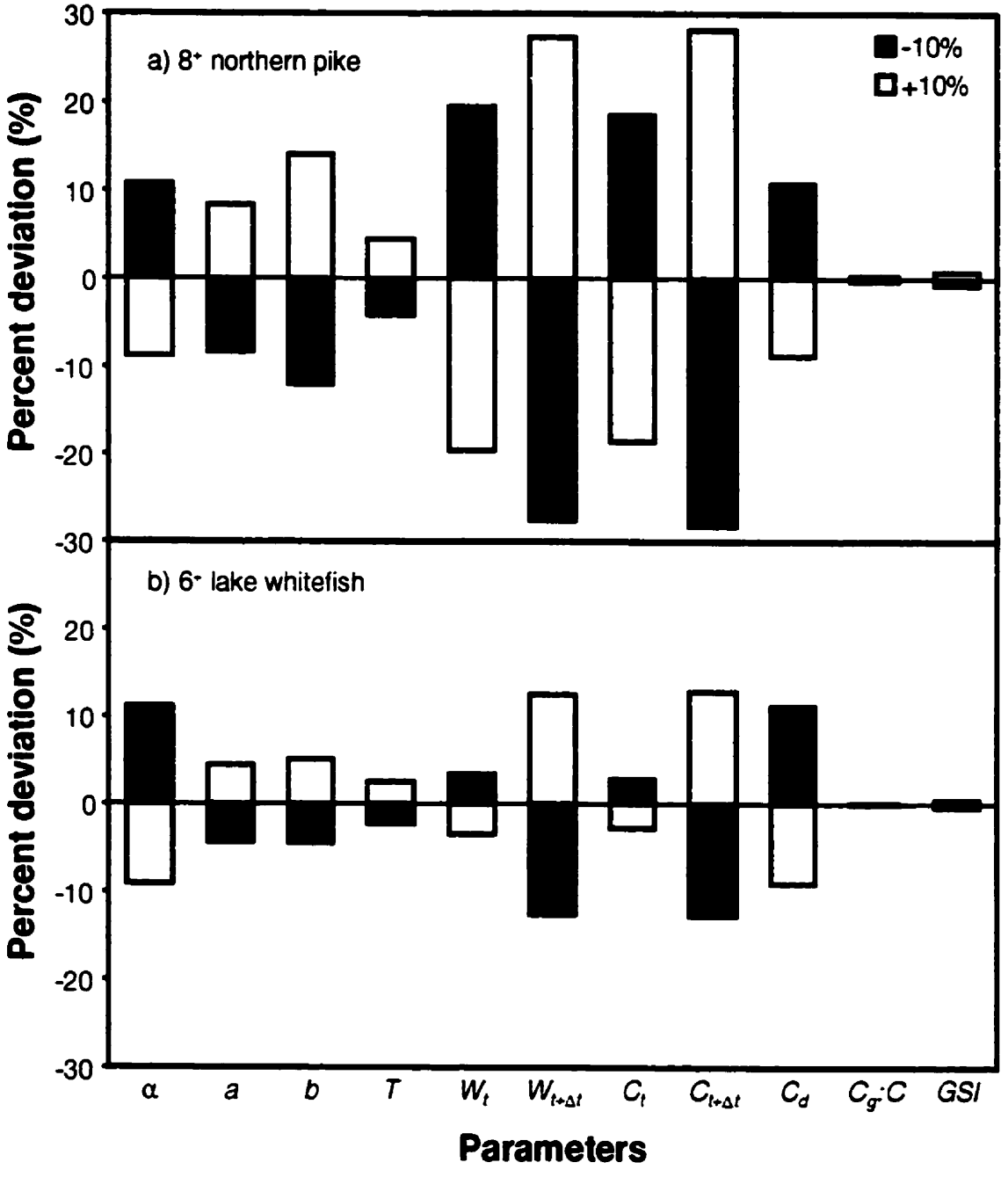
Sensitivity analysis

The sensitivity analysis showed that the Hg mass balance model was not sensitive to uncertainty associated with fish *GSI* and Hg concentration in the gonads, but was moderately sensitive to the parameters of the Hg elimination model, and water temperature (Fig. 4). For instance, a 10% change in the *GSI* produced only a 0.3-0.7% change in food consumption rates. Food consumption rates were most sensitive to final fish size and final Hg concentration, followed by Hg concentration in the food, Hg assimilation efficiency, and initial fish size and initial Hg concentration (Fig. 4). For example, a 10% change in the final fish size produced a 12.5-27.5% change in fish food consumption rates.

Discussion

We presented a simple method for estimating food consumption rates of fish in the field based on a Hg mass balance model. This method requires the determination of Hg concentration in fish and its food, fish age and size, fish growth, water temperature, Hg elimination from fish, and Hg assimilation efficiency from food. The method presented in this study was validated using data from a previously published laboratory experiment performed by Rodgers and Beamish (1982) where feeding rates were monitored throughout the experiment. This analysis showed that the predicted and observed food consumption rates of fish differed by only 1-2%, indicating that the Hg mass balance model provides accurate and reliable estimates of fish feeding rates. This method was also tested in the field with independent estimates of food consumption rates obtained with a ^{137}Cs mass balance model on three fish species covering a total of 17 age-classes. Except for yellow perch, fish feeding rates determined with the Hg and ^{137}Cs mass balance models differed by 6% or less. In yellow perch, food consumption rates determined with these two

Figure 4. Sensitivity of feeding rate estimates to a 10% change in the parameters of eq. 2. (α: assimilation efficiency; a: mass coefficient of the Hg elimination model; b: mass exponent of the Hg elimination model; T: water temperature; W_t and $W_{t+\Delta t}$: initial and final fish mass; C_t and $C_{t+\Delta t}$: initial and final Hg concentration in fish; C_d: Hg concentration in the diet; $C_{g:f}$: ratio of Hg concentration in the gonad and in fish; GSI: gonadosomatic index).


a) 8+ northern pike
-10%
+10%
Percent deviation (%)
30
20
10
0
-10
-20
-30
b) 6- lake whitefish
Percent deviation (%)
α
a
b
T
W_t
$W_{t+\Delta t}$
C_t
$C_{t+\Delta t}$
C_d
C_g:C
GSI
Parameters

methods differed by 7-16%. However, these differences were well within the error associated with these estimates. The Hg mass balance model was also indirectly tested with independent estimates of food consumption rates obtained from the literature on different populations and usually on different species. The relationship between food consumption rates and body size obtained with the Hg mass balance model was similar to the one derived with published values obtained with stomach contents and with a ^{137}Cs mass balance model. This indicates that there was no systematic bias associated with food consumption rates obtained with the Hg mass balance model. The close correspondence obtained between these estimates does not indicate that the values of parameters of the Hg mass balance model presented in this study are valid per se because two estimates were compared. Nevertheless, the success of this direct and indirect corroboration increases the likelihood that the parameters we presented in this study are accurate. Taken together, these analyses suggest that the Hg mass balance model presented in this study provides adequate estimates of fish food consumption rates in the field.

It is generally recommended to use food consumption rates determined with stomach contents to directly test methods for estimating fish feeding rates in the field, probably because fish ecologists are under the impression that such estimates constitute direct observations of feeding rates. The Eggers (1977) and the Elliott and Persson (1978) model are the most widely used methods to estimate food consumption rates of fish with stomach contents. Although these methods involve direct measurements of the quantity of food in the stomachs of fish collected in the field, these measurements are converted to food consumption rates using an estimate of the clearance rate of food from the stomach and a mass balance model somewhat similar to those used to describe the dynamics of Hg and ^{137}Cs concentrations. Thus, it should be emphasized that feeding rates determined from stomach contents approaches are not really more "direct" observations than rates inferred from tracer mass balance models.

In this study, we used food consumption rates determined with a ^{137}Cs mass balance model, instead of stomach contents, to directly test the Hg mass balance model in the field because the ^{137}Cs is not labor intensive in the field and because it provides long-term feeding rates comparable to those obtained with stomach contents (Forseth et al.

1992, 1994). Moreover, long-term food consumption rates determined with stomach contents are not necessarily always more reliable than those obtained with the ^{137}Cs method. The Elliott and Persson (1978) model is the only method based on stomach or whole digestive tract contents that has been validated to date. This method assumes that the evacuation rate of food from the stomach is exponential and only provides estimates of daily consumption rates. Long-term feeding rates are usually obtained by integrating a time series of daily ration determined at 2-4 week intervals. This approach assumes that there is no important day-to-day variation in the quantity of food consumed by fish. This assumption is supported by the work of Trudel and Boisclair (1993) on dace (*Phoxinus* sp.). However, large day-to-day variations in daily food consumption rates have also been observed in the field in pumpkinseed sunfish (*Lepomis gibbosus*) and yellow perch (J.B. Rasmussen, *unpublished data*). These variations appeared to be related to short-term fluctuations of the meteorological conditions. Thus, long-term feeding rates obtained with stomach contents may not always be adequate. The accuracy of the Elliott and Persson (1978) model also depends on our ability to accurately estimate the evacuation rate of food from the stomach and to accurately describe the feeding cycle during a 24-h period. Negative estimation of feeding rates frequently occurs with this model for some periods of the day, usually when there is a sharp decrease in the stomach contents between two consecutive sampling intervals (Cochran and Adelman 1982). This may result either because the evacuation rate of food is underestimated or because the feeding cycle is not adequately described (Cochran and Adelman 1982; Trudel and Boisclair 1994). The magnitude of the bias introduced by these negative feeding rates is unknown at present. The Elliott and Persson (1978) model is also generally not recommended for piscivorous fish, because they tend to consume a single large meal during a day rather than feeding continuously. Moreover, the evacuation rate of food in piscivorous fish is often linear rather than exponential (Hall et al. 1995). Several methods based on stomach contents have been proposed for piscivorous fish (e.g. Diana 1979; Hall et al. 1995), but none of these methods has been validated yet. Finally, the Elliott and Persson (1978) model assumes that the evacuation rate of food is independent of the feeding rate. The evacuation rate of the whole digestive tract appears to be correlated with feeding rates in

tadpoles (Wassersug 1975). While tadpoles are not fish, their digestive tract is similar to that of stomachless fish. This assumption has yet to be tested in fish. Thus, there is little reason to believe that the stomach contents approach is more reliable than the ^{137}Cs mass balance model to estimate food consumption rates of fish in the field.

Although ^{137}Cs mass balance models have been developed more than three decades ago to estimate food consumption rates of fish in the field (e.g. a decade before the Elliott and Persson model), this approach has been largely and unduly ignored by fish biologists. When Mann (1978) reviewed the methods to quantify food consumption rates of fish in the field, he did not even mention that mass balance models of ^{137}Cs had been developed to estimate fish feeding rates in the field. Elliott and Persson (1978) briefly stated that ^{137}Cs could be used to estimate long-term feeding rates of fish, but without giving any further details on this method. It took a tragic accident like Chernobyl to resurrect some interests for mass balance models of ^{137}Cs dynamics in fish. This may be because the few fish biologists that were aware of this method probably had the impression that it could only be used in systems that were highly contaminated with ^{137}Cs. This chemical is globally dispersed in the environment because of nuclear weapon testing (and occasional accidents like Chernobyl) and can be accurately measured with modern gamma spectroscopy even at low level of contamination. Thus ^{137}Cs can be used to estimate food consumption rates of fish in almost any aquatic ecosystem without adding any ^{137}Cs to the system. Because this method provides similar food consumption rates to those obtained with stomach contents (Forseth et al. 1992, 1994), it can also be used as an alternative to stomach contents to directly test other methods for estimating fish feeding rate in the field like the Hg mass balance model presented in this study.

It may be argued that the Hg and ^{137}Cs mass balance models provided similar estimates of food consumption rates only because they have the same mathematical structure. Similar equations have been used to describe the dynamics of Hg and ^{137}Cs in fish because they are both trophically transferred contaminants (Cabana et al. 1994; Rowan and Rasmussen 1994) whose elimination seems to follow a first-order kinetics in spite of different biochemical mode of bioaccumulation. However, it is important to note that, except for body size, water temperature and *GSI*, all the parameters of the Hg and

^{137}Cs models have been derived totally independently using different studies and experiments, and that the values of these parameters differed for Hg and ^{137}Cs. Furthermore, these chemicals have been measured independently using different methods (i.e. atomic absorption vs gamma spectroscopy) and generally on different individual fish. Given the number of parameters that have to be estimated (i.e. nine for each model, plus fish size and water temperature), it is rather improbable that these mass balance models would provide similar estimates of feeding rates by chance alone even if they have the same mathematical structure. Thus, the similarity of mathematical structure of the Hg and ^{137}Cs mass balance models can not, by itself, be responsible for the similarity of the feeding rates obtained with these two models.

The generic parameters of the Hg mass balance model presented in Table 1 provided reasonable estimates of fish feeding rates in the field. There is presently no empirical evidence that indicates that these parameters differ systematically among species (Trudel and Rasmussen 1997), suggesting that they may be used to estimate the feeding rates of other species or populations. However, it may be necessary to further estimate these parameters to determine if these values are appropriate for other fish species. In particular, more effort should be directed to estimate the assimilation efficiency of Hg from food under field conditions, as the Hg mass balance model is quite sensitive to uncertainty associated with this parameter. The assimilation efficiency of Hg from food is expected to be correlated with protein assimilation efficiency, because Hg is covalently bound to protein (Carty and Malone 1979). Thus, it may vary with prey type and gut morphology (e.g. stomachless vs fish with well defined stomach). It may be possible to use the approach recently developed by Tucker and Rasmussen (1999) for ^{137}Cs to estimate the assimilation efficiency of Hg in the field. This would require the determination of the concentration of Hg and the content of acid insoluble ash in the foregut and hindgut of fish. However, this method will have to be validated under controlled conditions before it is applied in the field.

The Hg mass balance proposed in this study offers several advantages over currently used methods for estimating food consumption rates of fish in the field (i.e. stomach contents, bioenergetic models, ^{137}Cs mass balance model). First, the Hg mass

balance model is substantially less labor intensive than the stomach contents approach. In contrast to the stomach contents approach, the Hg mass balance model does not require that fish are collected every 3-6 hours during a 24-h period to estimate fish feeding rates. Furthermore, despite the effort of Hayward et al. (1991) to develop a low-effort regression approach to quantify food consumption rates with stomach contents, their method still requires a calibration with fish collected every 3-6 hours over several 24-h periods. Their method also requires that the feeding cycle is stable through time, and may not be appropriate for fish that shift their feeding peak from day to night during the summer such as dace (*Phoxinus sp.*; M. Trudel, *unpublished data*). Furthermore, the calibration may not be valid among years and populations (Hayward et al. 1991). The stomach contents approach is especially difficult to apply in the field for piscivorous fish because the abundance of these fish is usually low. In addition, these fish are usually dispersed rather than aggregated. Thus, only few fish (if any) may be captured in a single net, especially if fish are collected every 3-6 hours. Finally, these fish are generally quite valuable for sport fishery (e.g. lake trout, walleye). This often limit the number of fish that can be sacrificed to avoid upsetting the public. The Hg mass balance model presented in this study is well suited for piscivorous fish even when sample size is low because mean fish size and Hg concentration of fish in each age-class can be determined using a regression model developed with relatively few fish (20-30 fish). This approach may also help to reduce the error associated with the estimation of these parameters, even when sample size is low.

Second, bioenergetic models require accurate estimates of standard metabolic rates and activity costs to estimate food consumption rates of fish, because these models are acutely sensitive to uncertainty associated with these parameters (Kitchell et al. 1977; Stewart et al. 1983). However, it is presently difficult to accurately estimate fish activity costs *in situ* (Trudel and Boisclair 1996). In contrast to bioenergetic models, the Hg mass balance model does not require the estimation of fish metabolic rate for estimating fish ingestion rates, as the elimination rate of Hg is independent of activity rates (Östlund 1969).

Thirdly, while it is possible to accurately measure ^{137}Cs in biological samples with modern gamma spectroscopy (Rowan and Rasmussen 1996), these analyses generally require large amount of fish and prey tissues (>20 g), and it typically requires 6-24 hours to perform only one ^{137}Cs analysis for populations that did not receive large inputs of ^{137}Cs from the Chernobyl fallout or that are not in regions of high clay content soils (Rowan and Rasmussen 1994). This may be problematic for fish feeding on invertebrates, because of the difficulty of obtaining enough food to perform the ^{137}Cs analysis. In contrast, Hg can be analyzed accurately on small samples (<1 g) even when Hg concentration in fish is particularly low (<0.01 $\mu g \cdot g^{-1}$). Furthermore, with modern atomic absorption spectroscopy, approximately 150 samples can be analyzed in 6 hours. However, for fish feeding on invertebrates, it is necessary to measure methylmercury in the diet rather than total Hg, as a fraction of the total Hg in invertebrates may be inorganic Hg. Methylmercury concentration in invertebrate samples can be easily determined by atomic fluorescence spectroscopy (Bloom 1992). This analysis also requires less than 1 g of samples, but only 20 samples can be analyzed for methylmercury in 8 hours. Nevertheless, this is far more samples that can be analyzed per unit of time than ^{137}Cs. In fish, methylmercury concentration and total Hg concentration are equivalent because almost all of the Hg is methylmercury in fish (Bloom 1992). Since its faster and cheaper to measure total Hg than methylmercury, total Hg should be determined in fish instead of methylmercury concentration.

In addition to ^{137}Cs and Hg, PCB and DDE have been proposed as chemical tracers for estimating food consumption rates of fish (Borgmann and Whittle 1992). However, no empirical models are presently available to accurately estimate the elimination rates of these chemicals. Despite this difficulty, Borgmann and Whittle (1992) used DDE to estimate the quantity of food consumed by Lake Ontario lake trout. Food consumption rates of Lake Ontario lake trout estimated with DDE by these authors were similar to those obtained with Hg in this study for the first two age-classes, but tended to be 1.6-fold higher with DDE afterward. This difference probably occurred because these authors used a more negative allometric exponent for DDE elimination than the value we used for Hg (-0.59 vs –0.20). However, unlike the Hg elimination model used in this

study, the allometric exponent of DDE elimination was assumed rather than empirically derived. Furthermore, the assimilation efficiency of PCB and DDE from food is poorly known for natural prey items, as most values have been determined on fish fed with an artificial diet (e.g. Trout Chow, TetraMin flakes). This suggests that PCB and DDE are presently not appropriate chemical tracers for quantifying food consumption rates of fish in the field.

The main disadvantage of the Hg mass balance model is its sensitivity to Hg concentration in food. Hence, this method requires either an accurate description of fish diet or that Hg concentration in the food is determined directly on stomach contents, and may require that fish are sampled more frequently than once a year if prey contamination varies seasonally. Furthermore, Hg concentration in the diet may vary with fish size, since larger fish tend to feed on larger prey, and hence, on more contaminated prey (Borgmann and Whittle 1992). However, this does not always occur, since Hg concentration in walleye and northern pike diet did not vary systematically with fish size for fish older than 1 year old in Lake Simcoe (Mathers and Johansen 1985).

Variation of food consumption rates among species and populations

Food consumption rates varied both among species and populations in this study. For instance, whitefish tended to eat 2.1-fold more food than walleye. Food consumption rates varied 1.8-fold between lake trout populations. The variation of food consumption rates observed among species and populations probably reflects differences in physiological requirement (e.g. standard metabolic rate), caloric content of food, prey availability and fish abundance. Feeding is believed to play an important role in fish ecology, and may influence numerous processes in an ecosystem such as competition, predation, and nutrient dynamics (Hanson and Leggett 1986; Stewart and Ibarra 1991; Kraft 1992). Although food consumption rates have been estimated for several fish populations (see Fig. 3), few studies have attempted to examine the effects of environmental conditions on the quantity of food consumed by fish. This is probably due to the difficulty of accurately estimating long-term food consumption rates of fish in the field. Due to the low-effort required to quantify ingestion rates of fish in the field with the

Hg mass balance model, the approach proposed in this study may therefore help to refine our understanding of the factors that influence long-term food consumption rates of fish in the field. In particular, the Hg mass balance model proposed in this study may be useful for quantifying the feeding rates of archived fish. Hg concentration of fish is also routinely measured by several agencies and laboratories to determine if fish are edible for human consumption or to determine the effects of environmental conditions on the accumulation of Hg in fish. These values are generally stored in large databases and could be used to estimate the consumption rates of numerous fish populations. Hg databases and literature data were quite useful in this study, as they allowed us to estimate the feeding rate of six fish species for a total of 91 age-classes. Thus, the Hg mass balance proposed in this study can allow us to do bioenergetic work over a broader ecological context than traditional approaches.

Energy allocation in male and female fish

Female fish typically invest more energy into the production of gonads than males due to their higher *GSI*. To produce these gonads, females must either consume more food or have a lower metabolic rate than males (Diana 1983a). The higher food consumption rates of females observed in this study support the former hypothesis. Similarly, food consumption rates of northern pike and lake trout from Great Slave Lake were larger in females than males by about 30-40% (Rowan and Rasmussen 1996). Diana (1979) also observed that female northern pike ate more food than male in lac Ste. Anne. However, Adams et al. (1982) showed that male largemouth bass (*Micropterus salmoides*) tended to consume more food than females during the summer, autumn, and winter months. This difference may be related to the breeding behavior of bass. The fish that were used in this study exhibit little parental care of the eggs and young. In contrast, male bass build and guard the nest until the young fish leave the nest. Therefore, these male fish must consume large quantities of food to meet the energy requirement associated with their breeding behavior.

To test the hypothesis that female fish spend less energy in metabolism, we estimated the total respiration rate of fish by difference between food consumption rates

determined with the Hg mass balance model and growth rates in conjunction with a bioenergetic model. The energy budget of fish can be written as;

$$(9) \qquad DR = P_s + P_g + R_T + F + U$$

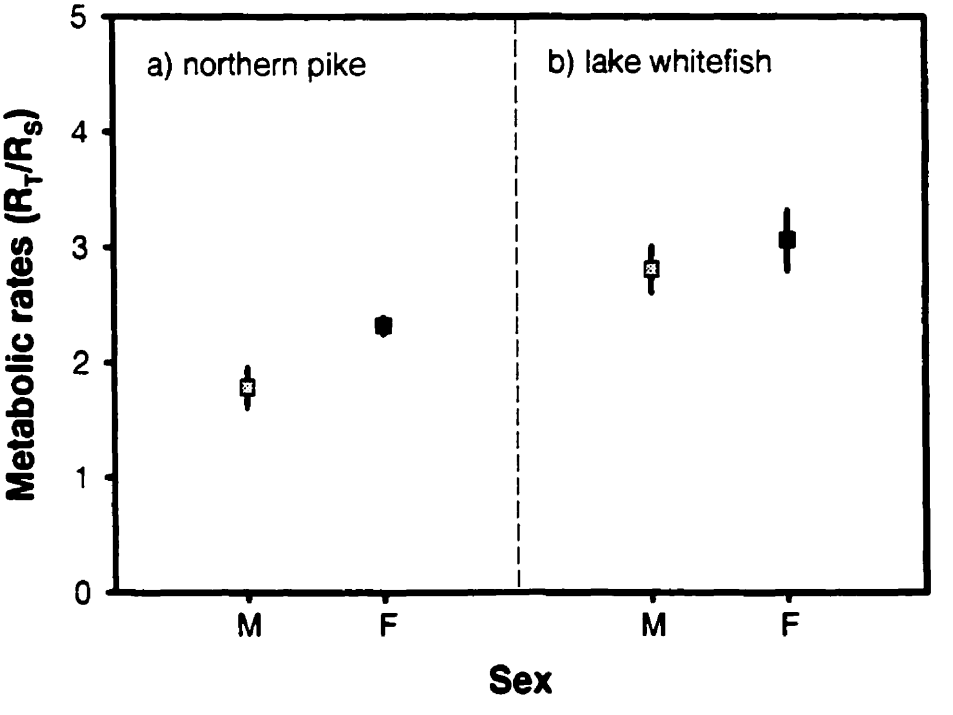
where DR is the quantity of food consumed by fish, P_s and P_g are respectively the production of the soma and gonads, R_T is the total respiration rate, and F and U are the fecal and urinary losses, respectively (all the parameters are in $J \cdot d^{-1}$). R_T can be determined by difference, provided that the other parameters are known;

$$(10) \qquad R_T = DR - (P_s + P_g + F + U)$$

To estimate the R_T of male and female fish from the Caniapiscau Reservoir, F and U were taken from Bevelhimer et al. (1985) for northern pike, and Rudstam et al. (1994) for whitefish. We assumed that the energy density of invertebrates and prey fish were 3350 and 4185 $J \cdot g^{-1}$ (wet mass), respectively. We assumed an energy density of 5020 $J \cdot g^{-1}$ for northern pike (Diana 1983a). The energy density of whitefish was modeled as a function of body size (Rudstam et al. 1994). Finally, the energy density of testis and ovary were assumed to be 20% higher than the energy density of the soma (Diana 1983b).

Total metabolic rates tended to be lower in northern pike than in lake whitefish (Fig. 5). This probably reflects differences in the feeding behavior of these fish, as northern pike are a sit-and-wait predator while lake whitefish actively forage for their prey. Metabolic costs tended to be higher in females than males (Fig. 5). Total metabolic rates varied significantly between species ($F_{1,16}$=21.7, $p<0.0005$) but not between sex ($F_{1,16}$=4.4, $p>0.05$). The interaction between species and sex was also not significant ($F_{1,16}$=0.6, $p>0.4$). This analysis thus suggests that the higher energy demand of female for the production of gonads is met by increasing their food consumption rates, rather than by reducing their metabolic rates.

Figure 5. Metabolic rates of northern pike and lake whitefish in relation to sex (M: male; F: female). Total respiration rates (R_T) were divided by standard metabolic rates (R_S) to control for body size differences. The error bars represent ± 1·SE.


a) northern pike
b) lake whitefish
Metabolic rates (R_T/R_S)
5
4
3
2
1
0
M
F
M
F
Sex

Management implications

The Hg mass balance presented in this study may be useful for fisheries managers to determine how many fish can be stocked in a lake without reducing its forage base. Predator demand (i.e. feeding rate) and its impact on forage fish have traditionally been determined with bioenergetic models (Stewart and Ibarra 1991). However, these models often tend to underestimate food consumption rates of fish obtained with either stomach contents or with ^{137}Cs mass balance model, probably because field metabolic rates are not adequately represented in bioenergetic models (Boisclair and Leggett 1989; Rowan and Rasmussen 1996). This may be problematic, because stocking programs based on bioenergetic model estimates may eventually lead to the collapse of the food base, and also of the stocked fish. For instance, lake trout is stocked in both Lake Memphremagog and Lake Ontario to support sport fisheries. In these populations, food consumption rates determined with the bioenergetic model of Stewart et al. (1983) are about 1.2-2.2 times lower than values determined with the Hg mass balance model in this study. This suggests that bioenergetic models may not be an appropriate tool for assessing the potential impacts of predators on their forage base, and that stocking programs should be based on food consumption rates determined with a mass balance model of chemical tracers like Hg or ^{137}Cs instead of those obtained with a bioenergetic model.

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CONNECTING STATEMENT

In chapter 3, I demonstrated that the Hg mass balance model could also be used to estimate the feeding rates of fish. The model was validated using data obtained from a published experiment. I also successfully tested this model using food consumption rates determined with a radioisotopic method. In the fourth chapter of the thesis, I applied this mass balance model to compare the energy budget of sympatric populations dwarf and normally growing fish. I tested the hypothesis that dwarf fish consume less food than normal fish. This analysis would have been extremely tedious and labor intensive if food consumption rates had been estimated using stomach contents. It also illustrates the utility of the Hg mass balance model for studying bioenergetics of fish under natural conditions.

CHAPTER 4

WHY IS THE GROWTH OF DWARF FISH SO LOW? AN ENERGETIC ANALYSIS OF DWARFISM IN LAKE WHITEFISH (*COREGONUS CLUPEAFORMIS*)

Abstract

Sympatric populations of dwarf and normal lake whitefish (*Coregonus clupeaformis*) commonly occur in north temperate and subarctic lakes. Dwarf lake whitefish have a much lower growth rate, mature earlier, and have a shorter lifespan than normal lake whitefish. Furthermore, they are not found when cisco (*C. artedi*) are present, possibly due to competitive exclusion. In this study, we compared the energy budget of dwarf and normal lake whitefish, and cisco using food consumption rates estimated with mass balance models of chemical tracers (i.e. mercury and radiocesium). These chemicals are globally distributed due to their long-range transport and can be easily detected in the biota. Our analysis showed that the energy budget of dwarf lake whitefish and cisco were similar. Dwarf lake whitefish and cisco consumed about 40-50% more food than normal lake whitefish. The conversion efficiency of dwarf lake whitefish and cisco were two to three times lower than normal lake whitefish. These results suggest that dwarf lake whitefish and cisco allocate a larger fraction of their energy budget to metabolism than normal lake whitefish. Our analysis also suggests that the earlier maturation and shorter lifespan of dwarf lake whitefish and cisco may be due to their higher metabolic rates.

Introduction

Growth is a thermodynamic process that results from the balance between the energy consumed and the energetic costs associated with metabolism, and fecal and waste products. When energy intake exceeds the energetic costs, the surplus energy can be channeled to growth and reproduction (Ware 1982). Once sexual maturity is reached, growth rate usually decreases in fish, as they allocate a fraction of their surplus energy to produce gonads and to fuel the behavioral activities associated with reproduction such as migration, courtship, building and guarding nest (Roff 1983).

Growth is highly flexible in fish and varies tremendously both within and among populations (Boisclair and Leggett 1989). Sympatric populations of dwarf and normal forms of the same species have been frequently observed in north temperate and subarctic lakes (Fenderson 1964; Hindar and Jonsson 1982; Jonsson et al. 1988). Dwarf fish are characterized by a much lower growth rate than normal fish. They reach maturity earlier and at a smaller size, and also tend to have a much shorter lifespan than normally growing fish. In addition, dwarf and normal phenotypes usually forage on different prey items and in different habitats (pelagic vs benthic diet) (Robinson and Wilson 1994; Wimberger 1994).

To achieve a lower growth rate than the normal phenotype, dwarf fish must consume less food and/or allocate a larger fraction of their energy budget to metabolism. The energy budget of dwarf fish has never been determined under natural conditions, probably due to the difficulty of estimating food consumption rates of fish using traditional methods based on stomach contents. These methods require the sacrificing of a large number of fish and necessitate a tremendous sampling effort in the field (Trudel et al. 2000), and may not be suited to compare the energy budget of dwarf and normal fish.

The objectives of this study were compare the energy budget of dwarf and normal fish. We tested the hypotheses that (1) dwarf fish have lower food consumption rates and (2) higher metabolic rates than normal individuals. This study was performed on two sympatric populations of dwarf and normal lake whitefish (*Coregonus clupeaformis*) located in northern Quebec. Sympatric populations of dwarf and normal lake whitefish have been observed in several lakes in North America and Europe (Fenderson 1964; Svärdson 1970; Fortin and Gendron 1990; Bodaly et al. 1991; Doyon et al. 1998a).

Dwarf lake whitefish rarely exceed 250 mm, and mature at a smaller size and at an earlier age than normal lake whitefish (Fenderson 1964; Bodaly 1979; Fortin and Gendron 1990; Bodaly et al. 1991). Normal lake whitefish feed on zooplankton when they are small and shift to benthic invertebrates when they reach a size of about 200-250 mm, while dwarf lake whitefish mainly consume zooplankton throughout their life (Rekahn 1970; Scott and Crossman 1973; Doyon et al. 1998b).

Dwarf lake whitefish are usually not found when cisco are present, suggesting that these fish may occupy the same ecological niche (Fortin and Gendron 1990; Bodaly et al. 1991; Chouinard et al. 1996; Pigeon et al. 1997; Doyon et al. 1998a). Similarly to dwarf lake whitefish, the diet of cisco mainly consists of zooplankton (Scott and Crossman 1973). Cisco also tend to be smaller and mature earlier than normal lake whitefish (Scott and Crossman 1973). Moreover, the growth of cisco is reduced when they are raised with lake whitefish (Davis and Todd 1998). Hence, we also compared the energy budget of two sympatric populations of cisco (*Coregonus artedi*) and normal lake whitefish in this study. Although dwarf lake whitefish and cisco are genetically distinct (Sajdak and Phillips 1997), they were classified in the same functional group (i.e. dwarf phenotype) for the purpose of this study.

Food consumption rates of dwarf and normal lake whitefish, and cisco were estimated using a mercury (Hg) mass balance model that we recently developed (Trudel et al. 2000), as well as a radioactive cesium (^{137}Cs) mass balance model refined by Rowan and Rasmussen (1996, 1997). Mass balance models of chemical tracers like Hg and ^{137}Cs offer an alternative to stomach contents for accurately estimating food consumption rates of fish (Forseth et al. 1992; Rowan and Rasmussen 1996; Trudel et al. 2000). This approach requires considerably less sampling effort than stomach contents, and has recently been validated for Hg by Trudel et al. (2000).

Methods

Species and study sites

This study was conducted on lake whitefish from the Caniapiscau Reservoir, Lake Serigny, Lake Rond-de-Poēle, and the Ottawa River, and on cisco from Lake Rond-de-Poēle and the Ottawa River. Normal lake whitefish are present in these four systems,

while dwarf lake whitefish are only present in the Caniapiscau Reservoir and Lake Serigny. The Caniapiscau Reservoir is located in northern Quebec (54°00'N 69°52'W) and was impounded between 1981 and 1984 (Doyon et al. 1998a). It is the largest reservoir of the hydroelectric complex of La Grande River. Lake Serigny (55°18'N 69°42'W) and Lake Rond-de-Poële (52°26'N 77°00'W) are also located in Northern Quebec and served as reference sites to evaluate the effects of the impoundment of the La Grande Complex. Finally, the Ottawa River is located on the border of Quebec and Ontario and flows into the St-Lawrence River near Montreal (Quebec).

Food consumption and growth rates

Food consumption rates (I; $g \cdot g^{-1} \cdot d^{-1}$) of dwarf and normal lake whitefish and cisco from the reservoir and the two lakes located in Northern Quebec were estimated with a Hg mass balance model as (Trudel et al. 2000; Appendix II):

$$(1) \qquad I = \frac{C_{t+\Delta t} - C_t e^{-(E+G+K)\Delta t}}{\alpha \cdot C_d \cdot \left[1 - e^{-(E+G+K)\Delta t}\right]} (E + G + K)$$

where C_t and $C_{t+\Delta t}$ are the concentration of Hg in fish at time t and $t+\Delta t$ ($\mu g \cdot g^{-1}$), respectively, Δt is the time interval (d), α is the assimilation efficiency of Hg from food (dimensionless), C_d is the concentration of Hg in food ($\mu g \cdot g^{-1}$), E is the elimination rate of Hg ($\mu g \cdot \mu g^{-1} \cdot d^{-1}$), G is the specific growth rate ($g \cdot g^{-1} \cdot d^{-1}$), and K is the loss of Hg due to spawning ($\mu g \cdot \mu g^{-1} \cdot d^{-1}$). This model has been successfully validated and provides food consumption rates similar to those obtained using stomach contents and a mass balance model of radiocesium (Trudel et al. 2000).

The assimilation efficiency of Hg from food was set to 0.8 (Norstrom et al. 1976; Table 1). The elimination rate of Hg from fish was estimated using fish size (W; g) and water temperature (T; °C) as (Trudel and Rasmussen 1997):

$$(2) \qquad E = \varphi \cdot W^{\beta} \cdot e^{\gamma T}$$

Table 1. Parameters of the mercury mass balance model.

Symbol	Parameter description	Value	Source
α	Assimilation efficiency	0.80	1
φ	Coefficient of mercury elimination	0.0029	2
β	Allometric exponent of mercury elimination	-0.20	2
γ	Temperature coefficient of mercury elimination	0.066	2
Q_m	Ratio of mercury concentration in the gonads and whole fish for males	0.59	3
Q_f	Ratio of mercury concentration in the gonads and whole fish for females	0.12	3

1. Norstrom et al. (1976); 2. Trudel and Rasmussen (1997); 3. Trudel et al. (2000)

where φ, β, γ are empirically derived constants (Table 1).

The loss rate of Hg due to spawning was estimated as (Trudel et al. 2000):

$$(3) \qquad K = \frac{Q \cdot GSI}{365}$$

where Q is the ratio of Hg concentration in the gonads to fish, GSI is the gonadosomatic index, and 365 represent the number of days in a year.

To estimate the feeding rate of whitefish and cisco with the Hg mass balance model, we obtained the age, mass, and Hg concentration of lake whitefish and cisco, and Hg concentration of their food from Doyon et al. (1996, 1998b) and Hydro-Quebec databases (Appendix V). The GSI of lake whitefish and cisco were taken from Rowan and Rasmussen (1996). Hg concentration and fish size were modeled as a function of age using linear and non-linear regressions (Trudel et al. 2000). Daily water temperature of the Caniapiscau Reservoir, Lake Serigny and Lake Rond-de-Poële was modeled with a Gaussian function as:

$$(4) \qquad T = 3.8 + 9.5 \cdot e^{\frac{-(JD-223)^2}{61^2}}$$

where JD is the Julian day. Specific growth rate was estimated as (Ricker 1979):

$$(5) \qquad G = \frac{1}{\Delta t} \cdot \ln\left(\frac{W_{t+\Delta t}}{W_t}\right)$$

where W_t and $W_{t+\Delta t}$ are fish mass at time t and $t+\Delta t$ (g). Specific growth rate was estimated for each age-class using the mass of two consecutive age-classes. Food consumption rates were estimated on a daily basis by interpolating fish size and Hg concentration between two adjacent age-classes (Forseth et al. 1992; Trudel et al. 2000). Annual food consumption rates were then determined by summing the daily ration values obtained during these intervals.

Food consumption rates of lake whitefish and cisco from the Ottawa River were estimated using the ^{137}Cs mass balance model outlined in Rowan and Rasmussen (1996, 1997). Fish age and mass, ^{137}Cs concentration in fish and their food, and water temperature were obtained from Rowan and Rasmussen (1996) and Rowan et al. (1997) (Appendix VI). Fish mass and ^{137}Cs concentration were modeled as a function of fish age using linear and non-linear regressions. The elimination rate of ^{137}Cs from fish was estimated using fish size and water temperature (Rowan and Rasmussen 1995).

Allocation of energy to growth

The relationship between growth and consumption rates was examined using simple and multiple regression analyses (Sokal and Rohlf 1995). In this study, growth rates represented the sum of somatic (P_s; $J \cdot d^{-1}$) and gonad growth (P_g; $J \cdot d^{-1}$). Somatic growth was estimated as:

$$(6) \qquad P_s = G \cdot W \cdot E_f$$

where E_f is the energy density of fish ($J \cdot g^{-1}$). Gonad growth was estimated in adult fish as:

$$(7) \qquad P_g = GSI \cdot W \cdot E_g$$

where E_g is the energy density of the gonads ($J \cdot g^{-1}$). The energy densities of lake whitefish and cisco were modeled as a function of fish size (Rudstam et al. 1994). The energy densities of testis and ovary were assumed to be 20% higher than the energy density of the soma (Diana 1983).

The proportion of the energy budget allocated to growth (both somatic and gonad growth) was estimated for each age-class as:

$$(8) \qquad CE = \frac{P_s + P_g}{DR}$$

where *CE* is the gross conversion efficiency and *DR* is daily ration of fish ($J \cdot d^{-1}$). *DR* was obtained by converting food consumption rate estimated with eq. (1) in $g \cdot g^{-1} \cdot d^{-1}$ to $J \cdot d^{-1}$ assuming that the energy density of the food consumed by lake whitefish and cisco was equal to 3350 $J \cdot g^{-1}$ (wet mass) (Trudel et al. 2000).

Allocation of energy to metabolism

The energy budget of a fish can be written as:

(9) $$DR = P_s + P_g + R_T + F + U$$

where R_T is the total respiration or metabolic rate ($J \cdot d^{-1}$). and F and U are the feces and excretory products ($J \cdot d^{-1}$), respectively. Thus, R_T can be determined by difference, provided that the other parameters of the budget are known as:

(10) $$R_T = DR - (P_s + P_g + F + U)$$

F and U were derived from the bioenergetic model of Rudstam et al. (1994) to estimate R_T of dwarf and normal lake whitefish and cisco. The proportion of the energy budget allocated to R_T was estimated by dividing R_T by *DR*.

Statistical analyses

Food consumption rates, conversion efficiency, and metabolic rates were compared between dwarf lake whitefish, cisco, and normal lake whitefish using a 2X4 ANOVA (Sokal and Rohlf 1995), where 2 is the number of phenotypes (dwarf and normal) and 4 is the number of sites being compared. For these analyses, dwarf lake whitefish and cisco were assigned to the dwarf phenotype, while normal like whitefish were assigned to the normal phenotype. Food consumption rates were compared between fish on a relative basis (i.e. $g \cdot g^{-1} \cdot d^{-1}$) in this study, as body size varied between phenotypes. However, the use of specific feeding rates to compare the energy budget of fish has been criticized as food consumption rates tend to scale to body size with an allometric exponent around to 0.8 (Hewett and Kraft 1993). It has been suggested that

feeding rates could be appropriately compared between fish of different size if they were divided by $W^{0.8}$ instead of $W^{1.0}$ (Hewett and Kraft 1993). However, this rule of thumb is only valid if the allometric exponent of food consumption rates is equal to 0.8, and should not be applied without first examining if this exponent is valid for the species under investigation. The allometric exponent of food consumption rates is not significantly different from isometry in lake whitefish (Trudel et al. 2000). Thus, food consumption rates of lake whitefish can be appropriately compared across size if they are divided by $W^{1.0}$ and not by $W^{0.8}$. This indicates that specific feeding rates can be used to compare the energy budget of dwarf lake whitefish, cisco, and normal lake whitefish.

Results

Food consumption and growth rates

At a given age, normal lake whitefish were larger than both dwarf lake whitefish and cisco in the sites examined in this study (Fig. 1). Dwarf lake whitefish and cisco matured earlier and at a smaller size, and had a shorter lifespan than normal lake whitefish in these sites (Table 2).

Food consumption rates estimated with the Hg and ^{137}Cs mass balance models averaged 0.032 $g \cdot g^{-1} \cdot d^{-1}$ in dwarf lake whitefish, 0.021 $g \cdot g^{-1} \cdot d^{-1}$ in normal lake whitefish, and 0.028 $g \cdot g^{-1} \cdot d^{-1}$ in cisco (Fig. 2). Despite their lower growth rate, dwarf lake whitefish and cisco tended to consume approximately 40-50% more food than normal lake whitefish (Fig. 2). However, the difference between food consumption rates of cisco and normal lake whitefish varied between sites: on average, cisco consumed 69% and 16% more food than normal lake whitefish in Lake Rond-de-Poële and in the Ottawa River, respectively (Fig. 2). Food consumption rates varied significantly between phenotypes and among sites (Table 3). The interaction between phenotype and site was also significant (Table 3). Independent linear contrasts were used to interpret the significant interaction between phenotype and site (Sokal and Rohlf 1995). This analysis indicated that the difference between cisco and normal lake whitefish was not constant between sites ($F_{1,45}$=6.8; $p<0.02$). It also indicated that the difference between dwarf and normal lake whitefish was not significantly different from the difference between cisco and normal lake whitefish ($F_{1,45}$=0.2; $p>0.6$).

Fig. 1. Total length (mm) of dwarf lake whitefish (○), normal lake whitefish (●), and cisco (△) as a function of fish age. The solid line represent the von Bertalanffy growth curve and was fitted by non-linear regression. For the Ottawa River, a power equation was used to model fish length.

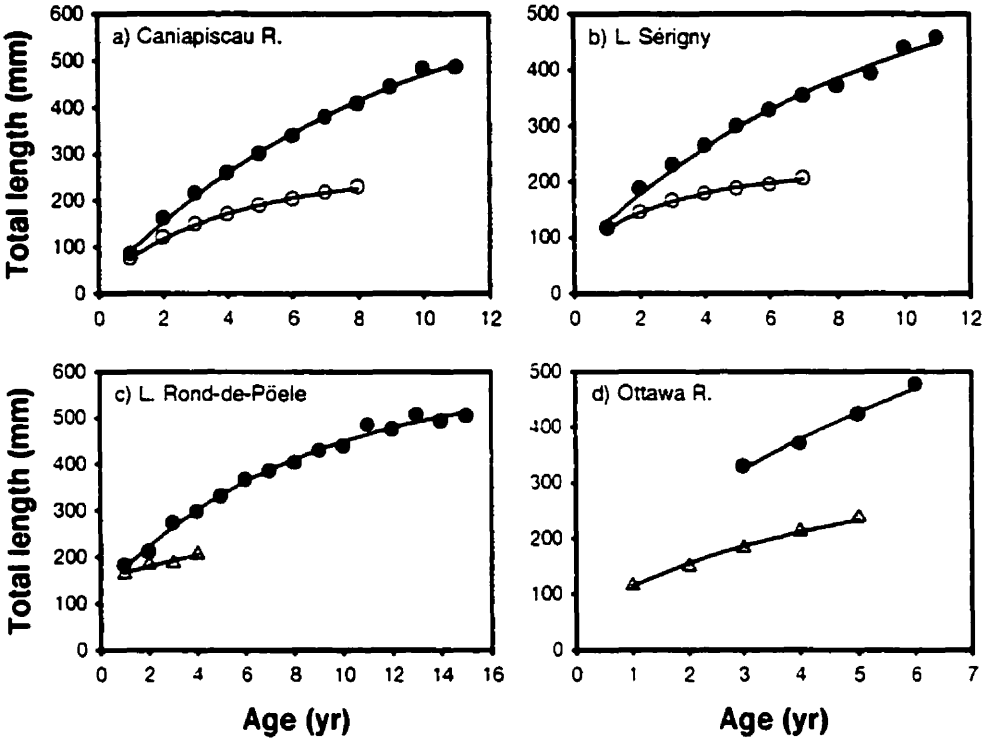

a) Caniapiscau R.
b) L. Sérigny
c) L. Rond-de-Pöele
d) Ottawa R.
Total length (mm)
Total length (mm)
Age (yr)
Age (yr)

Table 2. Life history parameters of dwarf lake whitefish, normal lake whitefish and cisco from four aquatic ecosystems. α_m: age at maturity; L_α: length at maturity.

Population	α_m (yr)	L_α (mm)	Longevity (yr)
Caniapiscau Reservoir			
Dwarf lake whitefish	2-3	148	<10
Normal lake whitefish	6	345	>15
Lake Serigny			
Dwarf lake whitefish	3	165	<10
Normal lake whitefish	6-7	329	>15
Lake Rond-de-Poële			
Cisco	2	180	<10
Normal lake whitefish	7	388	>15
Ottawa River			
Cisco	2	155	n.a.
Normal lake whitefish	4	378	n.a.

n.a.: not available

Fig. 2. Average food consumption rates of dwarf lake whitefish (black bars), normal lake whitefish (white bars), and cisco (gray bars) from four sites. The error bars represent 1 SE.

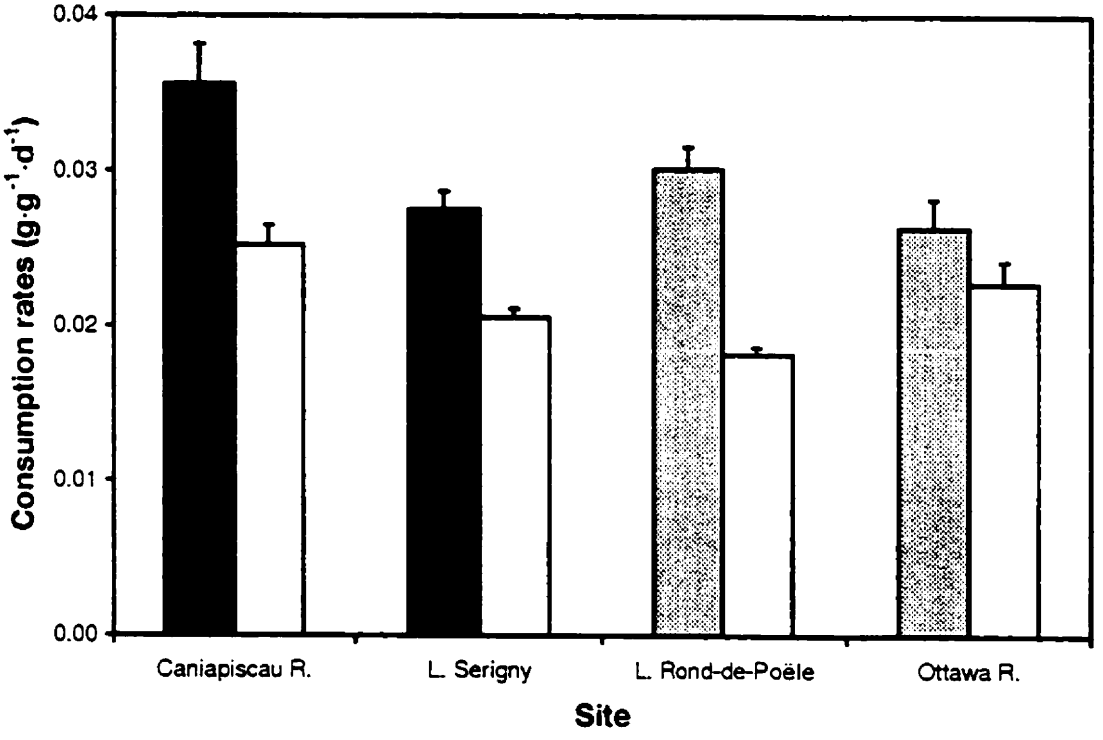

0.04
0.03
0.02
0.01
0.00
Consumption rates (g·g⁻¹·d⁻¹)
Caniapiscau R.
L. Serigny
L. Rond-de-Poële
Ottawa R.
Site

Table 3. Statistical comparison of the energy budget of dwarf lake whitefish, normal lake whitefish, and cisco (two-way ANOVA).

	F	*df*	*p*
Consumption rates ($g \cdot g^{-1} \cdot d^{-1}$)			
phenotype	64.9	1,45	<0.0001
site	11.8	3,45	<0.0001
phenotype*site	2.9	3,45	<0.05
Conversion efficiency			
phenotype	97.6	1,45	<0.0001
site	6.2	3,45	<0.002
phenotype*site	1.0	3,45	>0.4
Metabolic rates (% of feeding rates)			
phenotype	97.1	1,45	<0.0001
site	6.2	3,45	<0.002
phenotype*site	1.0	3,45	>0.4

Allocation of energy to growth

Growth rates tended to increase with the quantity of food consumed by fish in lake whitefish and in cisco (Fig. 3). At a given consumption rate, growth rates tended to be higher in normal whitefish, lower in dwarf lake whitefish, and intermediate in cisco (Fig. 3). The best empirical model predicting the growth rate (P; $J \cdot d^{-1}$) of coregonids in these systems was (SE in parentheses);

$$(11) \quad \log_{10} P = -0.58(0.22) + 0.94(0.06) \cdot \log_{10} DR - 0.56(0.07) \cdot DW - 0.28(0.07) \cdot CIS$$
$$R^2 = 0.94;\ SE_{est} = 0.158;\ n = 53\ ;\ p<0.0001$$

where DW is a binary variable that takes the value of one for dwarf lake whitefish and zero for normal lake whitefish and cisco, and CIS is a binary variable that takes the value of one for cisco and zero for the other species. This model indicates that dwarf lake whitefish and cisco allocated 3.6-fold and 1.9-fold less energy to growth than normal lake whitefish, respectively. Cisco tended to allocate a larger fraction of their energy budget than dwarf lake whitefish probably because fish from the Ottawa River had a higher conversion efficiency (Fig. 4).

Conversion efficiency averaged 4.8% in dwarf lake whitefish, 16.0% in normal lake whitefish, and 9.5% in cisco (Fig. 4). Conversion efficiency tended to be higher in fish from the Ottawa River than from the sites located in northern Quebec (Fig. 4). Conversion efficiency varied significantly between phenotypes and among sites (Table 3). The interaction between phenotype and site was not significant (Table 3).

Allocation of energy to metabolism

Dwarf lake whitefish and cisco tended to spend more energy in respiration than normal lake whitefish (Fig. 5). The proportion of the energy budget allocated to R_T averaged 62.7% in dwarf lake whitefish, 51.5% in normal lake whitefish, and 58.0% in cisco (Fig. 5). Coregonids from the Ottawa River tended to allocate a lower fraction of their energy budget to R_T than fish from northern Quebec (Fig. 5). R_T varied significantly between phenotypes and among sites (Table 3). The interaction between phenotype and site was not significant (Table 3).

Fig. 3. Relationship between fish growth ($J \cdot d^{-1}$) and consumption rates ($J \cdot d^{-1}$) in dwarf lake whitefish (○), normal lake whitefish (●), and cisco (△).

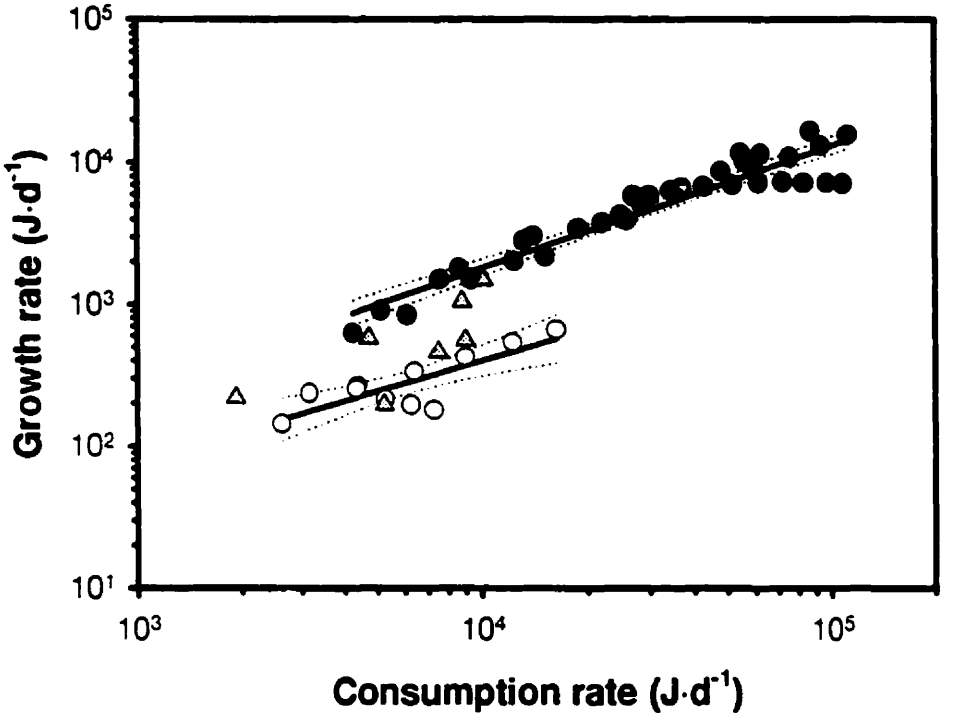

10^5
10^4
10^3
10^2
10^1
Growth rate (J·d^{-1})
10^3
10^4
10^5
Consumption rate (J·d^{-1})

Fig. 4. Proportion of the energy budget allocated to growth in dwarf lake whitefish (black bars), normal lake whitefish (white bars), and cisco (gray bars). The error bars represent 1 SE.

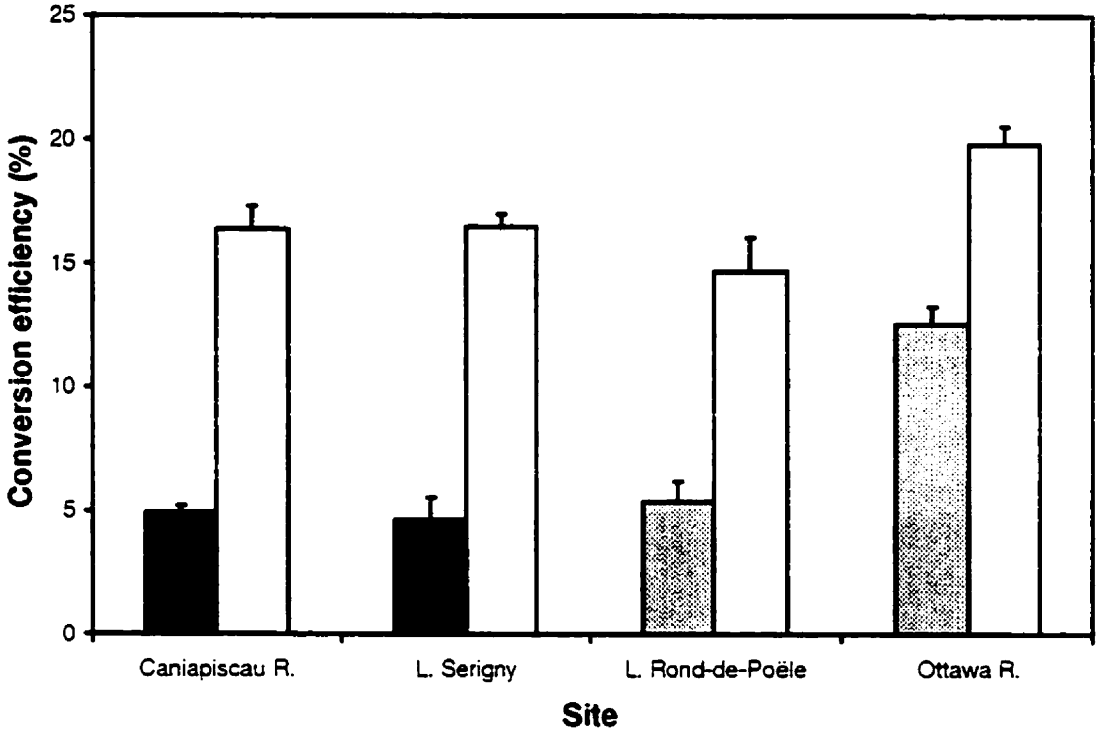
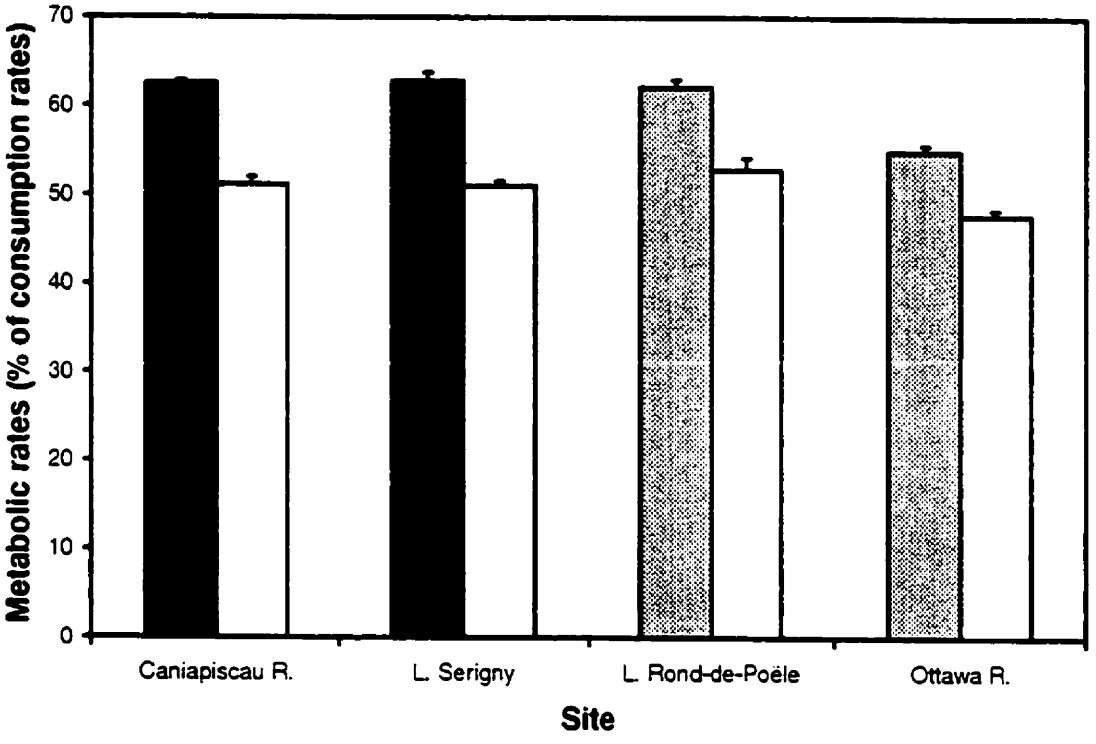

25
20
15
10
5
0
Conversion efficiency (%)
Caniapiscau R.
L. Serigny
L. Rond-de-Poële
Ottawa R.
Site

Fig. 5. Proportion of the energy budget allocated to respiration (R_T) in normal lake whitefish, dwarf lake whitefish, and cisco. Legend as in Fig. 4.


Metabolic rates (% of consumption rates)
70
60
50
40
30
20
10
0
Caniapiscau R.
L. Serigny
L. Rond-de-Poële
Ottawa R.
Site

Discussion

Bioenergetics and dwarfism

The analyses performed in this study showed that specific feeding rates of dwarf lake whitefish and cisco were about 40-50% higher than those of normal lake whitefish. Furthermore, we showed that the conversion efficiency of dwarf lake whitefish and cisco were 2-3 times lower than in normal lake whitefish. Therefore, the low growth of dwarf fish can be more readily explained in terms of high energy allocation to metabolism rather than by a low rate of food consumption. In this study, dwarf and normal lake whitefish allocated about 60 and 50% of their energy budget to metabolism, respectively. Although this difference appears to be small, fish growth is quite sensitive to small variation associated with metabolic rates (Kitchell et al. 1977). Thus, even if only a small fraction of the energy budget is diverted to metabolism, it can have large effects on growth.

The proportion of the energy budget allocated to metabolism differed between the dwarf and normal phenotypes either because standard metabolic rates (SMR), activity costs, or both were higher in dwarf lake whitefish and cisco than in normal lake whitefish. Activity costs tend to be positively correlated to feeding rates in actively foraging fish (Kerr 1982; Boisclair 1992). Thus, since dwarf lake whitefish and cisco eat about 40-50% more food than normal lake whitefish, they are also likely to be more active. We may ask though why would dwarf lake whitefish and cisco consume more food and spend more energy in foraging activity if they cannot grow as fast or even faster than normal lake whitefish? The most parsimonious interpretation is that dwarf lake whitefish and cisco also have higher SMR than normal lake whitefish. Hence, if SMR were higher in dwarf lake whitefish and cisco, they would need to consume more food to meet their energy requirement, and would also need to spend more energy to acquire this food. Thus, both SMR and activity costs are expected to be higher in dwarf lake whitefish and in cisco.

SMR of fish are generally estimated using the intercept of the relationship between swimming costs and swimming speed (Brett 1964; Beamish 1970). SMR have not yet been determined in dwarf lake whitefish, but have been estimated in normal lake whitefish and a variety of cisco species. In general, the intercept of the relationship

between swimming costs and swimming speed is 30-80% higher in cisco than in normal lake whitefish (Rudstam et al. 1994), which supports our interpretation that the SMR of cisco are higher than that of normal lake whitefish. In contrast though, Bernatchez and Dodson (1985) compared swimming costs of cisco and normal lake whitefish, and concluded that SMR were lower in cisco. However, their interpretation is not supported by their data. They measured swimming costs of cisco and normal lake whitefish swimming at speeds ranging from 20 to 55 $cm \cdot s^{-1}$ and from 20 to 40 $cm \cdot s^{-1}$, respectively. These experiments were performed at 5, 12, and 17 °C in normal lake whitefish, and only at 12 °C in cisco. Swimming costs of normal lake whitefish swimming at speeds exceeding 40 $cm \cdot s^{-1}$ were estimated from the relationship between swimming costs and swimming speed derived for rainbow trout (*Oncorhynchus mykiss*) by Rao (1968). We reanalyzed the data presented by Bernatchez and Dodson (1985) in their Fig. 1 by excluding the values that were estimated with the trout model. From their data, it is apparent that there is an interaction between swimming speed and water temperature, as the slope of the relationship between swimming costs and swimming speed was lower for fish maintained at 17 °C. Also, the swimming costs of cisco and normal lake whitefish maintained at 12 °C were quite similar. The best empirical model predicting swimming costs explained about 96% of the variance and included swimming speed, water temperature, and the interaction between swimming speed and water temperature as independent variables. There was no significant difference between the swimming costs of cisco and normal lake whitefish ($F_{1,12}$=0.01; p>0.9), suggesting that the SMR of cisco and normal lake whitefish are similar. Thus, the laboratory evidence supporting the hypothesis that cisco have higher SMR than normal lake whitefish is equivocal at present, and further work will be required to test this hypothesis in the laboratory.

It has been suggested that the biochemical activity of some enzymes involved in cell respiration and glycolysis could be used as surrogates of metabolic rates of fish *in situ*. In particular, Goolish and Adelman (1987) showed that the biochemical activity of cytochrome *c* oxidase (CCO) was independent of swimming costs, while Sullivan and Somero (1980) showed that the biochemical activity of lactate dehydrogenase (LDH) was higher in more active fish. Thus, the biochemical activity of CCO and LDH may be used as a surrogate of fish SMR and swimming costs, respectively (G. Sherwood, *personal*

communication). Guderley et al. (1986) and Couture and Guderley (1990) showed that the biochemical activity of CCO and LDH were both higher in cisco than in normal lake whitefish. This suggests that SMR and swimming costs are higher in cisco, which is consistent with our interpretation.

Competition between dwarf and normal lake whitefish

Resource polymorphism commonly occur in species-poor environments with well-defined benthic and pelagic habitats such as north temperate and subarctic lakes, and may represent a response to reduce intraspecific competition (Robinson and Wilson 1994; Wimberger 1994). Although adult dwarf and normal lake whitefish exploit different resources (pelagic vs benthic niches), juvenile dwarf and normal lake whitefish both consume zooplankton (Reckahn 1970; Scott and Crossman 1973; Doyon et al. 1998b). However, since growth rates and conversion efficiencies of normal lake whitefish are higher than dwarf lake whitefish (and cisco) when they both feed on zooplankton, the former should drive the latter to extinction. Yet, these phenotypes have been coexisting for thousands of years (Bernatchez and Dodson 1990), suggesting that the resources exploited by dwarf and normal lake whitefish are sufficiently different to allow coexistence.

We hypothesize that dwarf and normal lake whitefish coexist by feeding on small and large zooplankton, respectively, and that this niche differentiation is achieved by using different feeding behavior. Planktivorous fish can feed on zooplankton either by particulate feeding or by suspension (or filter) feeding (Ehlinger 1989; Sanderson and Cech 1992). Particulate feeders consume each prey individually, and tend to select large prey (James and Findley 1989). Suspension feeders filter large volume of water and retain plankton in their oral cavity possibly by using gill rakers as a sieve (but see Sanderson et al. 1991). Suspension feeders also tend to have a large number of long and closely spaced gill rakers, and are relatively non selective compared to particulate feeders (Sanderson and Cech 1992). Thus, the average size of the prey consumed by particulate feeders should be somewhat larger than that of suspension feeders (James and Findley 1989). Since the metabolic cost of suspension feeding is about 2.5 times higher than particulate feeding (Sanderson and Cech 1992), and that normal lake whitefish have

lower metabolic rates than dwarf lake whitefish, it suggests that juvenile lake whitefish consume large zooplankton by particulate feeding and that dwarf lake whitefish consume smaller zooplankton by suspension feeding. Because suspension feeders usually do not use this feeding mode until they have reached a size of 2-3 cm standard length (Sanderson and Cech 1992), we do not expect that diet will differ greatly between dwarf and normal lake whitefish at the larval stage. This interpretation is supported by the recent work of Chouinard and Bernatchez (1998) who showed that the diet of dwarf and normal lake whitefish was fairly similar at the larval stage, as the diet overlap index ranged from 85.2 to 95.6% between sampling dates. Unfortunately, dietary data of dwarf and normal lake whitefish are not sufficiently detailed at present to adequately test this hypothesis.

Competition between cisco and dwarf lake whitefish

Several studies have shown that dwarf lake whitefish usually do not co-occur with cisco (Fortin and Gendron 1990; Bodaly et al. 1991; Chouinard et al. 1996; Pigeon et al. 1997; Doyon et al. 1998a). Because dwarf lake whitefish and cisco have similar diet, morphology and life-histories, they may occupy the same ecological niche, and hence, may compete for limited resources (Pigeon et al. 1997). In this study, we provide further evidence that dwarf lake whitefish and cisco play the same functional role in aquatic ecosystems. Food consumption rates of dwarf lake whitefish and cisco were similar. In addition, the lack of a significant interaction between phenotype and site for conversion efficiency indicates that the response of dwarf lake whitefish and cisco to the presence of normal lake whitefish was similar. These results indicate that dwarf lake whitefish and cisco are unlikely to coexist due to the similarity of their diet, life-history, and bioenergetics.

Metabolic rates and life-history

Life-history models have been developed to understand and predict the extent of life-history variation in animals and plants (e.g. Roff 1984; Stearns and Koella 1986). These models attempt to maximize fitness of organisms, often defined as the life-time production of offspring, by optimizing trade-offs between growth, reproduction, and

mortality. As mortality rates generally increase with growth rates in fish (Roff 1984), life-history theory predicts that fast growing individuals will mature earlier. In contrast to these predictions, dwarf lake whitefish and cisco, despite their lower growth rate, mature earlier than the normal lake whitefish (Fenderson 1964; Fortin and Gendron 1990; Bodaly et al. 1991; this study).

Roff (1992) argued that slow growing fish could mature earlier than fast growing fish if their mortality rates were higher. Since the lifespan of dwarf lake whitefish tend to be shorter than normal individuals (Fenderson 1964; Fortin and Gendron 1990; Bodaly et al. 1991), it suggests that their mortality rates are also higher. This supports Roff's interpretation that the earlier maturation of dwarf fish may be due to their higher mortality rates. The mortality rate of dwarf lake whitefish and cisco could be higher if small fish were preferentially selected by piscivorous fish. This is unlikely though, as juvenile lake whitefish, cisco, and dwarf lake whitefish are in the same size range (<250 mm), suggesting that mortality due to predation should be similar for dwarf and normal lake whitefish that live in sympatry. This also suggests that the lower survival of dwarf lake whitefish and cisco may represent a cost of reproduction, as the energy devoted to reproduction is drained away from the soma (Bertschy and Fox 1999).

An alternative explanation for the earlier maturation of dwarf lake whitefish and cisco is that the gain in fecundity that can be obtained by delaying maturation is smaller than the risk of dying before reproducing in dwarf fish. Since fecundity generally increases with body size in fish, there may be an advantage to delay maturation, as more offspring will be produced if fish reach larger sizes. However, when metabolic rates are elevated (or conversion efficiency is low), fish may not be able to fuel enough energy into growth. Thus, if growth levels-off, like in dwarf lake whitefish and cisco, the small gain that can be obtained in fecundity by delaying maturation may be offset by a greater risk of mortality. In this situation, fish should mature and reproduce earlier. This interpretation is supported by our data, as fish that matured earlier in this study also had higher metabolic rates. Similar results were also obtained by Forseth et al. (1994) and Tucker and Rasmussen (1999): fish that had higher metabolic rates and lower conversion efficiencies within a cohort also matured earlier. This interpretation is also consistent with the life-history model of Hutchins (1993) who suggested that fish would mature

earlier if the growth of adult fish was small relative to the growth of juvenile fish (i.e. if growth levels-off).

Few studies have attempted to link life-history strategy of fish with patterns of energy acquisition and energy allocation. This is probably due to the difficulty of estimating food consumption rates of fish under natural conditions using traditional methods based on stomach contents. The analyses performed in this study were based on feeding rates of fish that were estimated using a Hg mass balance model that we recently developed and validated (Trudel et al. 2000) as well as a ^{137}Cs mass balance model that was recently refined by Rowan and Rasmussen (1996, 1997). Mercury and ^{137}Cs are globally dispersed due to their long residence time in the atmosphere and can be readily detected in the biota with modern instruments. Mass balance models of chemical tracers require considerably less sampling effort in the field than methods based on stomach contents. In addition, these mass balance models can be applied on archived fish. Thus, mass balance models of chemical tracers offer a promising alternative to stomach contents for studying the bioenergetics of fish under natural conditions and for examining the influence of energy allocation on life-history strategies of fish.

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GENERAL CONCLUSIONS

This thesis focused on the bioenergetics of Hg accumulation in fish. In particular, I developed a simple Hg balance model that can be used to accurately predict Hg concentration in fish, as well as estimating food consumption rates of fish. This mass balance model assumes that Hg elimination is a first order process, and requires accurate estimates of Hg elimination by fish. Since empirical models published prior to this study overestimated the elimination rate of Hg by a factor of 2-6 (Trudel and Rasmussen 1997), I developed an empirical model of Hg elimination rate by fish using data obtained from published laboratory and field experiments. This analysis showed that Hg elimination was overestimated in short-term experiments, probably because it is not possible to properly discriminate the fast and slow components of Hg elimination in short-term experiments. I also showed the elimination rate of inorganic Hg was about three times faster than methylmercury. The elimination rate of Hg was positively correlated with water temperature and negatively correlated with body size. As the elimination rate of Hg was independent of Hg concentration in fish, I concluded that Hg elimination was a first order process in fish.

The ability of the Hg mass balance model presented in this thesis to accurately predict Hg concentration depends on the accuracy of the parameters used in this model. Accurate estimates of food consumption rates are especially important due to the sensitivity of the Hg mass balance model to this parameter. The validity of this mass balance model was assessed by comparing observed and predicted values using parameters that were derived *a priori* from laboratory experiments and from field surveys. Predicted values were within 20% of observed values when the Hg mass balance model was combined with food consumption rates that were determined with a radioisotopic method. This suggests that the parameters of the Hg mass balance model that were determined in this thesis are adequate for predicting Hg concentration in fish.

In the past, Hg mass balance models were used with food consumption rates determined with laboratory-derived bioenergetic models to predict Hg concentration in fish. The validity of bioenergetic models have often been questioned, as they tend to underestimate the quantity of food consumed by fish in the field, probably because activity costs derived in the laboratory may not reflect activity costs of fish in the field

(Boisclair and Leggett 1989a; Post 1990; Fox 1991; Wahl and Stein 1991; Madon and Culver 1993; Rowan and Rasmussen 1996). In this study, I showed that the Hg concentration in fish tended to be underestimated when the Hg mass balance model was used with laboratory-derived bioenergetic models. I also showed that the Hg mass balance model accurately predicted Hg concentration in fish when it was combined with food consumption rates that were determined using a bioenergetic model that used field-derived activity costs. Thus, unless site-specific estimates of activity costs are available, predictions obtained with a bioenergetic model should be interpreted cautiously.

Bioenergetic models are quite sensitive to errors associated with activity costs. Because activity costs can vary at least four-fold among populations of the same species, accurate estimates of activity costs are required in bioenergetic models to predict Hg concentration with a Hg mass balance model. In this thesis, I showed that predicted Hg concentration in fish with the Hg mass balance model could vary four-fold depending on the assumed activity costs. These simulations also indicated that Hg concentration increased with size (or age) when activity costs also increased with size. These analyses suggests that Hg concentration in fish could increase with size if conversion efficiency decreases with fish size.

The Hg mass balance model derived in this thesis requires accurate estimates of food consumption rates to predict Hg concentration in fish. However, these estimates are far more difficult to obtain than the values we are trying to predict with the Hg mass balance. The concentration of Hg in fish can be easily and accurately measured on small quantities (<1 g wet) of fish tissues with modern atomic absorption spectroscopy. In this thesis, I suggested that feeding rates of fish could be estimated under natural conditions with the Hg mass balance derived in this study if Hg concentration in fish and their food were known. The validity of this approach was examined using data obtained from a previously published experiment performed by Rodgers and Beamish (1982). Feeding rates predicted with the Hg mass balance model developed in this study were within 1-2 % of the actual feeding regime imposed by Rodgers and Beamish (1982) in their experiment. This approach was also tested in the field with independent estimates of food consumption rates obtained using a radioisotopic method. These two estimates differed by only 0.6-16.1% in the three species examined in this study. This difference was within

the error associated with these estimates. Taken together, these analyses indicate that the Hg mass balance model derived in this thesis can be used to accurately estimate food consumption rates of fish under natural conditions.

I applied this Hg mass balance model to compare the energy budget of two sympatric populations of dwarf and normal lake whitefish (*Coregonus clupeaformis*) and two sympatric populations of cisco (*Coregonus artedi*) and normal lake whitefish. This analysis showed that food consumption rates dwarf lake whitefish and cisco were 40-50% higher than normal lake whitefish. In addition, conversion efficiency of dwarf lake whitefish and cisco were two to three times lower than normal lake whitefish. These results suggest that the lower growth rate of dwarf lake whitefish and cisco cannot be attributed to a reduced feeding rate, but suggest instead that they allocated a larger fraction of their energy budget. I hypothesized that both standard metabolic rates and activity costs of dwarf lake whitefish and cisco were higher than those of normal lake whitefish. I also hypothesized that dwarf and normal lake whitefish coexist by feeding on different size-classes of zooplankton, and that this niche differentiation is achieved by using different feeding behavior. I argued that juvenile lake whitefish feed on large zooplankton by particulate feeding, and that dwarf lake whitefish feed on smaller zooplankton by suspension feeding, as the later mode of feeding is more costly. Finally, I argued that the earlier maturation of dwarf lake whitefish and cisco was a consequence of their higher metabolic rates and lower conversion efficiency. When metabolic rates are high, such as in dwarf lake whitefish and cisco, growth levels-off. In this situation, I argued that fish should mature earlier as the small gain in fecundity that can be obtained by delaying maturity is probably offset by a greater risk of dying before reproducing.

The Hg mass balance model developed in this thesis represents a framework that can be used to understand how the accumulation of Hg is regulated in fish. It can also provides reliable estimates of food consumption rates of fish under natural conditions. Although feeding rates of fish have been determined in a large number of studies (over 100 published articles), little is known about the factors that influence the quantity of food consumed by fish, probably due to the difficulty of obtaining these estimates with traditional methods based on stomach contents (but see Boisclair and Rasmussen 1996). By providing a low-effort approach to quantifying food consumption rates of fish in the

field, this Hg mass balance model may help to refine our understanding of the environmental factors that influence the quantity of food consumed by fish.

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LIST OF APPENDICES

APPENDIX I. Mercury mass balance model

Several forms of Hg can be found in the environment. In fish, most of the Hg (>95%) is methylmercury (Bloom 1989, 1992). Thus, Hg and methylmercury will be used as synonyms throughout this study. In fish, Hg is accumulated by uptake of contaminated water through the gills and absorption of contaminated food through the gastrointestinal tract. However, fish exposed only to Hg contaminated water accumulate 1000-times less Hg than fish exposed to Hg contaminated water and food (McKim et al. 1976; Cember et al. 1978; Porcella 1994; Becker and Bigham 1995; Hill et al. 1996). This suggests that Hg uptake from water represents less than 0.1% of the Hg accumulated in fish, and may be considered negligible. Thus, the accumulation of Hg in fish can be expressed as:

$$\text{(A1)} \quad \frac{dB}{dt} = (\alpha \cdot C_d \cdot I \cdot W) - E \cdot B$$

where B is the total quantity of Hg in fish (further referred to as Hg burden; μg), α is the assimilation efficiency of Hg from food (dimensionless), C_d is the concentration of Hg in food ($\mu g \cdot g^{-1}$), I is the ingestion rate of fish (d^{-1}), W is the mass of the fish (g), and E is the elimination rate of Hg from fish (d^{-1}). This mass balance model assumes that there is no methylation of inorganic Hg to methylmercury in the intestine of fish. The importance of this process is still debated in the literature. Several studies have not been able to detect any methylation of inorganic Hg in fish (Pennacchioni et al. 1976; Pentreath 1976; Huckabee et al. 1978). Rudd et al. (1980) reported that fish intestinal contents could methylate inorganic Hg *in vitro*, but the fraction of inorganic Hg that was methylated was fairly small ($0.005\text{-}0.4\% \cdot d^{-1}$). Thus, methylation of inorganic Hg in fish intestine is unlikely to represent an important source of methylmercury to fish.

Toxicologists generally measure the concentration of Hg in the edible portion of fish (i.e. skinless fillets), rather than the total quantity of Hg in fish. The concentration of Hg in muscle tissue and in the whole body are generally equal in fish (Lockhart al. 1972; Becker and Bigham 1995; Post et al. 1996). Thus, the mass balance model of Hg concentration (C; $\mu g \cdot g^{-1}$) can be written as;

$$\text{(A2)}\quad \frac{dC}{dt}=\frac{d\left(B/W\right)}{dt}=\frac{W\cdot dB-B\cdot dW}{W^2\cdot dt}=\frac{1}{W}\cdot\frac{dB}{dt}-C\cdot\frac{dW}{W\cdot dt}$$

Therefore, the mass balance model of Hg concentration requires a mass balance model for Hg burden as well as a mass balance model for fish size. Assuming that fish mass is growing exponentially during the time interval, the mass balance of fish size is (Ricker 1979);

$$\text{(A3)}\quad \frac{dW}{W\cdot dt}=G$$

where G is the specific growth rate (d^{-1}). Thus, combining eqs. A1, A2 and A3 gives;

$$\text{(A4)}\quad \frac{dC}{dt}=(\alpha\cdot C_d\cdot I)-(E+G)\cdot C$$

In sexually mature fish, Hg accumulated in the gonads can also be eliminated during spawning (Niimi 1983), indicating that this route of elimination should be taken into account in the mass balance model. Gonads may be considered as a separate compartment that receives a continuous input of Hg from the body (Rowan and Rasmussen 1997). Thus, assuming that a constant fraction of Hg is lost from the body to the gonads each day (K; d^{-1}) without any exchange back to fish (Rowan and Rasmussen 1997), eq. A1 becomes;

$$\text{(A5)}\quad \frac{dB}{dt}=(\alpha\cdot C_d\cdot I\cdot W)-(E+K)\cdot B$$

Therefore, for mature fish, eq. A4 becomes;

$$\text{(A6)}\quad \frac{dC}{dt}=(\alpha\cdot C_d\cdot I)-(E+G+K)\cdot C$$

Integrating this equation gives;

$$(A7) \quad C_t = C_o \cdot e^{-(E+G+K)t} + \frac{(\alpha \cdot C_d \cdot I)}{(E+G+K)} \cdot \left[1 - e^{-(E+G+K)t}\right]$$

where C_o is the initial concentration of Hg in fish ($\mu g \cdot g^{-1}$), C_t is the concentration of Hg in fish at time t ($\mu g \cdot g^{-1}$). In immature fish, K is equal to zero. Note also that if the concentration of Hg in muscle and in the whole fish are not equal, this model can still be applied if C_o and C_t are divided by the ratio of Hg concentration in muscle to that in the whole fish.

The assimilation efficiency of Hg of fish fed with prey fish typically ranges between 0.6 and 0.95, with a modal value around 0.8 (Norstrom et al. 1976; de Freitas et al. 1977: Suzuki and Hatanaka 1975; Ribeyre et al. 1980). We recently argued that, because methylmercury is covalently bonded to sulfur in protein, α should be correlated with protein assimilation efficiency (Trudel et al. 2000). In general, about 80% of the organic material is assimilated by carnivorous fish (Brett and Groves 1979), which is similar to the mode of laboratory-derived α values. Thus, we assumed that α was equal to 0.8 in fish.

The elimination rate of Hg from fish can be modeled as a function of body size and water temperature (T; °C) as:

$$(A8) \quad E = \varphi \cdot W^{\beta} \cdot e^{\gamma \cdot T}$$

where φ, β, γ are empirically derived constants (Trudel and Rasmussen 1997).

Specific growth rate can be estimated as (Ricker 1979);

$$(A9) \quad G = \frac{1}{\Delta t} \cdot \ln\left(\frac{W_{t+\Delta t}}{W_t}\right)$$

where W_t and $W_{t+\Delta t}$ are fish mass (g) at time t and $t+\Delta t$.

The daily loss rate of Hg from the body to the gonads is equal to the quantity of Hg in the gonads at spawning (B_g; μg) divided by the quantity of Hg in fish (B_f; μg) and by the number of days in a year (365 d), such that;

$$(A10) \quad K = \frac{1}{365} \cdot \frac{B_g}{B_f}$$

The quantity of Hg in the gonads is equal to the product of Hg concentration in the gonads (C_g; $\mu g \cdot g^{-1}$) and the mass of the gonads (W_g; g);

$$(A11) \quad B_g = C_g \cdot W_g$$

Similarly, the quantity of methylmercury in a fish is equal to the product of methylmercury concentration in fish (C_f; $\mu g \cdot g^{-1}$) and fish mass (W_f; g);

$$(A12) \quad B_f = C_f \cdot W_f$$

Substituting eq. 11 and 12 into eq. 10 and simplifying;

$$(A13) \quad K = \frac{Q \cdot GSI}{365}$$

where Q is the ratio of Hg concentration in the gonads to Hg concentration in fish (i.e. $\frac{C_g}{C_f}$), and GSI is the gonadosomatic index (dimensionless). For Hg, the value of Q differs between male and female fish (Niimi 1983; Lange et al. 1994; Doyon et al. 1998; Hammerschmidt et al. 1999). Assuming a sex ratio of 1:1, Q may be estimated as;

(A14) $$Q = \frac{(Q_m \cdot GSI_m + Q_f \cdot GSI_f)}{(GSI_m + GSI_f)}$$

where the subscripts m and f represent males and females, respectively.

Appendix II. Estimating food consumption rates of fish with a mercury mass balance model

Assuming that Hg uptake from water is negligible, the mass balance model of Hg concentration (C; $\mu g \cdot g^{-1}$) can be written as (Trudel et al. 2000);

$$\text{(B1)} \quad \frac{dC}{dt} = (\alpha \cdot C_d \cdot I) - (E + G + K) \cdot C$$

where α is the assimilation efficiency of Hg from food, C_d is the concentration of Hg in food ($\mu g \cdot g^{-1}$), E is the elimination rate of Hg ($\mu g \cdot \mu g^{-1} \cdot d^{-1}$ or d^{-1}), G is the specific growth rate ($g \cdot g^{-1} \cdot d^{1}$ or d^{-1}), and K is the loss rate of Hg due to spawning ($\mu g \cdot \mu g^{-1} \cdot d^{-1}$ or d^{-1}). Integrating this equation gives;

$$\text{(B2)} \quad C_{t+\Delta t} = C_t \cdot e^{-(E+G+K)\Delta t} + \frac{(\alpha \cdot C_d \cdot I)}{(E+G+K)} \cdot \left[1 - e^{-(E+G+K)\Delta t}\right]$$

where C_t and $C_{t+\Delta t}$ are the concentration of Hg in fish at time t and $t+\Delta t$ ($\mu g \cdot g^{-1}$), respectively, and Δt is the time interval (d). Solving eq. (A2) for food consumption rates, we obtain:

$$\text{(B3)} \quad I = \frac{C_{t+\Delta t} - C_t e^{-(E+G+K)\Delta t}}{\alpha \cdot C_d \cdot \left[1 - e^{-(E+G+K)\Delta t}\right]} (E + G + K)$$

Appendix III. Body mass, mercury concentration in fish and in their food, and food consumption rates of fish determined from a mercury mass balance model.

Species	*n*	Age (years)	W_t (g)	$W_{t+\Delta t}$ (g)	C_t ($\mu g \cdot g^{-1}$)	$C_{t+\Delta t}$ ($\mu g \cdot g^{-1}$)	C_d ($\mu g \cdot g^{-1}$)	I ($g \cdot g^{-1} \cdot d^{-1}$)
Caniapiscau Reservoir[a]								
Lake whitefish (*Coregonus clupeaformis*)								
	2	2 i	17.2	39.6	0.32	0.32	0.060	0.023
	4	3 i	39.6	71.6	0.32	0.32	0.060	0.020
	5	4 i	71.6	113.4	0.32	0.32	0.050	0.022
	4	5 i	113.4	289.0	0.32	0.32	0.040	0.033
	2	6 fm	289.0	648.6	0.32	0.32	0.032	0.040
	2	6 mm	289.0	526.3	0.32	0.32	0.032	0.033
	7	7 fm	648.6	890.6	0.32	0.32	0.032	0.028
	7	7 mm	526.3	708.3	0.32	0.32	0.032	0.025
	16	8 fm	890.6	1028.2	0.32	0.32	0.032	0.023
	14	8 mm	708.3	837.5	0.32	0.32	0.032	0.021
	17	9 fm	1028.2	1096.4	0.32	0.32	0.032	0.020
	14	9 mm	837.5	920.5	0.32	0.32	0.032	0.018
	12	10 fm	1096.4	1129.6	0.32	0.32	0.032	0.019
	8	10 mm	920.5	970.8	0.32	0.32	0.032	0.017
Northern pike (*Esox lucius*)								
	3	4 fm	1048.7	1301.5	1.54	1.79	0.46	0.011
	7	5 fm	1301.5	1615.4	1.79	1.95	0.46	0.011
	7	5 mm	1373.9	1596.3	1.70	2.00	0.46	0.009
	20	6 fm	1615.4	2004.8	1.95	2.03	0.46	0.011
	12	6 mm	1596.3	1854.6	2.00	2.12	0.46	0.009
	22	7 fm	2004.8	2488.2	2.03	2.02	0.46	0.011
	14	7 mm	1854.6	2154.8	2.12	2.05	0.46	0.007
	15	8 fm	2488.2	3088.1	2.02	1.93	0.46	0.010
	9	8 mm	2154.8	2503.5	2.05	1.81	0.46	0.006
	10	9 fm	3088.1	3832.6	1.93	1.75	0.46	0.009
Lake Memphremagog								
Lake trout (*Salvelinus namaycush*)								
	5	6 m	2174.4	2778.8	0.34	0.39	0.13	0.008
	7	7 m	2778.8	3341.8	0.39	0.42	0.13	0.007
	6	8 m	3341.8	3838.7	0.42	0.45	0.13	0.007
	4	9 m	3838.7	4265.5	0.45	0.47	0.13	0.007
	6	10 m	4265.5	4625.0	0.47	0.48	0.13	0.006
	3	11 m	4625.0	4932.2	0.48	0.49	0.13	0.006
Lake Ontario[b]								
Lake trout (*Salvelinus namaycush*)								
		1 i	68.0	322.0	0.03	0.06	0.021	0.023
		2 i	322.0	939.0	0.06	0.10	0.025	0.024
		3 i	939.0	1690.0	0.10	0.12	0.029	0.016
		4 i	1690.0	2414.0	0.12	0.15	0.032	0.014
		5 i	2414.0	3090.0	0.15	0.18	0.035	0.016
		6 m	3090.0	3723.0	0.18	0.20	0.038	0.014
		7 m	3723.0	4320.0	0.20	0.21	0.041	0.012

Lac Rond-de-Poêle[a]

Lake whitefish (*Coregonus clupeaformis*)							
3	1 i	48.5	89.4	0.06	0.07	0.015	0.019
6	2 i	89.4	148.7	0.07	0.08	0.015	0.019
7	3 i	148.7	227.0	0.08	0.08	0.015	0.019
8	4 i	227.0	322.8	0.08	0.09	0.015	0.019
8	5 i	322.8	432.7	0.09	0.10	0.021	0.019
2	6 m	432.7	552.1	0.10	0.11	0.021	0.015
7	7 m	552.1	676.2	0.11	0.12	0.021	0.016
7	8 m	676.2	800.5	0.12	0.13	0.021	0.016
5	9 m	800.5	921.1	0.13	0.15	0.021	0.017
3	10 m	921.1	1035.2	0.15	0.16	0.021	0.017
2	11 m	1035.2	1140.8	0.16	0.18	0.021	0.018
3	12 m	1140.8	1236.8	0.18	0.19	0.021	0.019
3	13 m	1236.8	1322.8	0.19	0.21	0.021	0.021
4	14 m	1322.8	1398.8	0.21	0.23	0.021	0.022
Northern pike (*Esox lucius*)							
9	2 i	452.8	633.1	0.23	0.30	0.11	0.008
9	3 i	633.1	868.9	0.30	0.37	0.11	0.009
7	4 m	868.9	1164.7	0.37	0.46	0.11	0.012
11	5 m	1164.7	1516.7	0.46	0.56	0.11	0.014
8	6 m	1516.7	1910.4	0.56	0.67	0.11	0.015
13	7 m	1910.4	2321.2	0.67	0.78	0.11	0.016
9	8 m	2321.2	2720.1	0.78	0.90	0.11	0.017
4	9 m	2720.1	3081.0	0.90	1.01	0.11	0.017
Walleye (*Stizostedion vitreum*)							
8	2 i	31.8	54.3	0.13	0.19	0.09	0.012
3	3 i	54.3	89.8	0.19	0.23	0.09	0.012
3	4 i	89.8	141.9	0.23	0.26	0.09	0.013
6	5 i	141.9	210.2	0.26	0.30	0.09	0.012
4	6 m	210.2	287.5	0.30	0.32	0.09	0.014
2	7 m	287.5	362.2	0.32	0.35	0.09	0.013
2	8 m	362.2	423.9	0.35	0.38	0.09	0.013
3	9 m	423.9	468.5	0.38	0.40	0.09	0.012
10	10 m	468.5	497.9	0.40	0.42	0.09	0.012
5	11 m	497.9	516.0	0.42	0.44	0.09	0.012

Lac Serigny[a]

Lake whitefish (*Coregonus clupeaformis*)							
9	2 i	38.8	79.9	0.16	0.18	0.03	0.024
1	3 i	79.9	133.3	0.18	0.19	0.03	0.022
2	4 i	133.3	191.0	0.19	0.19	0.03	0.020
2	5 i	191.0	251.5	0.19	0.20	0.03	0.019
3	6 m	251.5	331.1	0.20	0.21	0.03	0.020
3	7 m	331.1	435.9	0.21	0.21	0.03	0.020
2	8 m	435.9	573.9	0.21	0.22	0.03	0.019
2	9 m	573.9	755.5	0.22	0.22	0.03	0.019
1	10 m	755.5	994.7	0.22	0.22	0.03	0.019

Lake Simcoe[c]

Northern pike (*Esox lucius*)							
12	2 i	446.0	1561.0	0.15	0.20	0.10	0.010
2	3 m	1561.0	2760.0	0.20	0.26	0.10	0.010
4	4 m	2760.0	3206.0	0.26	0.33	0.10	0.009

6	5 m	3206.0	3735.0	0.33	0.43	0.10	0.011
Walleye (*Stizostedion vitreum*)							
10	2 i	613.0	1059.0	0.25	0.32	0.15	0.009
7	3 i	1059.0	1449.0	0.32	0.42	0.15	0.010
8	4 i	1449.0	1756.0	0.42	0.55	0.15	0.011
5	5 m	1756.0	1923.0	0.55	0.71	0.15	0.015
		Ottawa River[d]					
Walleye (*Stizostedion vitreum*)							
	2 i	197.0	282.2	0.21	0.26	0.082	0.013
	3 i	282.2	367.5	0.26	0.30	0.082	0.013
	4 i	367.5	452.8	0.30	0.35	0.082	0.014
	5 m	452.8	538.0	0.35	0.39	0.082	0.017
	6 m	538.0	636.9	0.39	0.49	0.082	0.017
	7 m	636.9	725.1	0.49	0.53	0.082	0.017
	8 m	725.1	813.3	0.53	0.58	0.082	0.018
Yellow perch (*Perca flavescens*)							
	1 i	1.7	9.2	0.05	0.08	0.033	0.028
	2 i	9.2	32.2	0.08	0.11	0.033	0.029
	3 i	32.2	74.7	0.11	0.14	0.033	0.026
	4 i	74.7	127.7	0.14	0.16	0.033	0.023

Note: i, immature; m, mature; fm, female mature, mm male mature

[a] Data from Hydro-Quebec

[b] Data from Borgmann and Whittle (1992) and Madenjian et al. (1995)

[c] Data from Mathers and Johansen (1985)

[d] Data from Norstrom et al. (1976), Rowan and Rasmussen (1996)

Appendix IV. Body size, water temperature, consumption (C), habitat (F:freshwater; M:marine), life stage (A: adult; J: juvenile), diet (B: benthic invertebrate; F: fish; Z: zooplankton) and method used to estimate consumption rate (^{137}Cs: radioactive cesium mass balance model; Stom: stomach contents) of various fish species obtained from the literature.

Species	Location	Size (g)	Temp (°C)	C ($g \cdot d^{-1}$)	Habitat	Stage	Diet	Method	Source
CLUPEIFORMES									
Clupeidae									
Alosa pseudoharengus (Wilson)	Atlantic Ocean	118.6	7.2	1.45	M	A	Z	Stom	1
Alosa pseudoharengus	Atlantic Ocean	118.6	7.4	2.23	M	A	Z	Stom	1
Engraulidae									
Engraulis encrasicolus L.	Mediterranean Sea	10.3	20.7	0.40	M	A	Z	Stom	2
CYPRINIFORMES									
Catastomidae									
Catastomus commersoni (Lacépède)	Ottawa R.	41.9	12.0	1.45	F	J	B	^{137}Cs	3
Catastomus commersoni	Ottawa R.	1088	12.0	26.00	F	A	B	^{137}Cs	3
Moxostoma erythrurum (Rafinesque)	Vermillion R.	360	20.0	2.30	F	A	B	Stom	4
Moxostoma macropiledatum (Lesueur)	Ottawa R.	485.4	12.0	13.45	F	A	B	^{137}Cs	3
Moxostoma macropiledatum	Ottawa R.	825	12.0	29.04	F	A	B	^{137}Cs	3
Moxostoma macropiledatum	Ottawa R.	1290	12.0	34.06	F	A	B	^{137}Cs	3
Cyprinidae									
Cyprinus carpio L.	Vermillion R.	1592	20.0	7.48	F	A	B	Stom	4
Cyprinus carpio	Mississippi R.	1262	9.0	24.48	F	A	B	Stom	5
Cyprinus carpio	Mississippi R.	1497	14.0	33.23	F	A	B	Stom	5
Notropis atherionoides Rafinesque	Ottawa R.	0.9	12.0	0.082	F	A	Z	^{137}Cs	3
Notropis atherionoides	Ottawa R.	2.3	12.0	0.15	F	A	Z	^{137}Cs	3
Notropis atherionoides	Ottawa R.	3.9	12.0	0.26	F	A	Z	^{137}Cs	3
Notropis atherionoides	Ottawa R.	6.65	12.0	0.38	F	A	Z	^{137}Cs	3
Notropis heterolepis Eigenmann & Eigenmann	Ottawa R.	2.15	12.0	0.086	F	A	Z	^{137}Cs	3
Notropis hudsonius (Clinton)	Ottawa R.	2.95	12.0	0.14	F	A	Z	^{137}Cs	3
Phoxinus eos x *P. neogaeus* (Cope)	L. Triton	1.3	20.0	0.11	F	A	B	Stom	6
Plagopterus argentissimus Cope	Virgin R.	2.1	20.0	0.17	F	A	B	Stom	7
Rutilus rutilus L.	L. Sövdeborgssjön	16.8	19.2	1.08	F	A	Z	Stom	8

ESOCIFORMES									
Esocidae									
Esox lucius L.	Great Slave L.	1026	8.5	11.08	F	A	F	^{137}Cs	3
Esox lucius	Great Slave L.	1231	8.5	13.79	F	A	F	^{137}Cs	3
Esox lucius	Great Slave L.	1281	8.5	9.61	F	A	F	^{137}Cs	3
Esox lucius	Great Slave L.	1306	8.5	22.46	F	A	F	^{137}Cs	3
Esox lucius	Great Slave L.	1582	8.5	13.13	F	A	F	^{137}Cs	3
Esox lucius	Great Slave L.	1907	8.5	15.64	F	A	F	^{137}Cs	3
Esox lucius	Great Slave L.	1957	8.5	15.66	F	A	F	^{137}Cs	3
Esox lucius	Great Slave L.	3623	8.5	40.94	F	A	F	^{137}Cs	3
Esox lucius	Ottawa R.	389.5	12.0	10.09	F	A	F	^{137}Cs	3
Esox lucius	Ottawa R.	709.6	12.0	18.38	F	A	F	^{137}Cs	3
Esox lucius	Ottawa R.	1299	12.0	34.55	F	A	F	^{137}Cs	3
GADIFORMES									
Gadidae									
Gadus macrocephalus Tilesius	Bering Sea	1095	3.1	9.53	M	A	F	Stom	9
Gadus macrocephalus	Bering Sea	1217	2.3	7.57	M	A	F	Stom	9
Gadus macrocephalus	Bering Sea	4994	3.1	39.95	M	A	F	Stom	9
Gadus macrocephalus	Bering Sea	5383	2.3	25.30	M	A	F	Stom	9
Gadus morhua L.	Atlantic Ocean	90.5	8.5	1.82	M	A	B	Stom	10
Gadus morhua	Atlantic Ocean	104.5	5.7	1.00	M	A	B	Stom	10
Gadus morhua	Atlantic Ocean	3243	9.3	53.83	M	A	F	Stom	10
Gadus morhua	Atlantic Ocean	3732	5.8	52.99	M	A	B	Stom	10
Gadus morhua	Faroe Plateau	600	8.0	13.62	M	A	B	Stom	11
Gadus morhua	Faroe Plateau	2000	8.0	43.40	M	A	B	Stom	11
Gadus morhua	Faroe Plateau	4000	8.0	42.00	M	A	B	Stom	11
Gadus morhua	L. Torridon	3.6	11.1	0.18	M	J	B	Stom	12
Gadus morhua	L. Torridon	37.8	11.7	0.56	M	J	B	Stom	12
Gadus morhua	L. Torridon	61.5	7.1	1.71	M	J	B	Stom	12
Gadus morhua	L. Torridon	66.1	7.9	1.97	M	J	B	Stom	12
Gadus morhua	L. Torridon	136.6	11.1	5.46	M	J	B	Stom	12
Gadus morhua	L. Torridon	204.3	11.7	7.23	M	A	B	Stom	12
Gadus morhua	L. Torridon	261.1	7.9	7.21	M	A	B	Stom	12
Gadus morhua	L. Torridon	277.6	7.1	6.52	M	A	B	Stom	12
Gadus morhua	L. Torridon	412.7	11.1	12.09	M	A	B	Stom	12
Gadus morhua	L. Torridon	514.7	11.7	18.79	M	A	B	Stom	12

Gadus morhua	North Sea	180	8.0	4.21	M	J	B	Stom	11
Gadus morhua	North Sea	330	8.0	6.37	M	A	B	Stom	11
Gadus morhua	North Sea	950	8.0	14.25	M	A	B	Stom	11
Gadus morhua	North Sea	1300	8.0	20.41	M	A	B	Stom	11
Gadus morhua	North Sea	1700	8.0	35.36	M	A	B	Stom	11
Gadus morhua	North Sea	2100	8.0	52.08	M	A	B	Stom	11
Gadus morhua	North Sea	2800	8.0	41.44	M	A	B	Stom	11
Gadus morhua	North Sea	3300	8.0	51.15	M	A	B	Stom	11
Gadus morhua	North Sea	4000	8.0	50.40	M	A	B	Stom	11
Gadus morhua	North Sea	5000	8.0	83.50	M	A	B	Stom	11
Gadus morhua	North Sea	6000	8.0	102.60	M	A	B	Stom	11
Melanogrammus aeglefinus (L.)	Faroe Plateau	14	8.0	0.40	M	J	B	Stom	11
Melanogrammus aeglefinus	Faroe Plateau	37	8.0	0.48	M	J	B	Stom	11
Melanogrammus aeglefinus	Faroe Plateau	70	8.0	1.53	M	J	B	Stom	11
Melanogrammus aeglefinus	Faroe Plateau	160	8.0	2.56	M	A	B	Stom	11
Melanogrammus aeglefinus	Faroe Plateau	250	8.0	4.18	M	A	B	Stom	11
Melanogrammus aeglefinus	Faroe Plateau	450	8.0	7.20	M	A	B	Stom	11
Melanogrammus aeglefinus	Faroe Plateau	600	8.0	10.74	M	A	B	Stom	11
Melanogrammus aeglefinus	Faroe Plateau	850	8.0	9.52	M	A	B	Stom	11
Melanogrammus aeglefinus	Faroe Plateau	1100	8.0	13.42	M	A	B	Stom	11
Melanogrammus aeglefinus	Faroe Plateau	1500	8.0	17.40	M	A	B	Stom	11
Melanogrammus aeglefinus	Faroe Plateau	2000	8.0	25.20	M	A	B	Stom	11
Melanogrammus aeglefinus	Faroe Plateau	2500	8.0	37.00	M	A	B	Stom	11
Melanogrammus aeglefinus	Faroe Plateau	3200	8.0	31.36	M	A	B	Stom	11
Melanogrammus aeglefinus	North Sea	14	8.0	0.34	M	J	B	Stom	11
Melanogrammus aeglefinus	North Sea	37	8.0	1.54	M	J	B	Stom	11
Melanogrammus aeglefinus	North Sea	70	8.0	1.48	M	J	B	Stom	11
Melanogrammus aeglefinus	North Sea	160	8.0	1.79	M	A	B	Stom	11
Melanogrammus aeglefinus	North Sea	250	8.0	5.55	M	A	B	Stom	11
Melanogrammus aeglefinus	North Sea	450	8.0	5.76	M	A	B	Stom	11
Melanogrammus aeglefinus	North Sea	600	8.0	9.18	M	A	B	Stom	11
Melanogrammus aeglefinus	SW Norway	86.1	7.0	2.84	M	J	B	Stom	13
Merlangius merlangus L.	Baltic Sea	75	7.8	1.40	M	J	F	Stom	14
Merlangius merlangus	Baltic Sea	153	7.8	2.59	M	J	F	Stom	14
Merlangius merlangus	Baltic Sea	221	7.8	3.69	M	J	F	Stom	14
Merlangius merlangus	Baltic Sea	295	7.8	4.84	M	J	F	Stom	14
Merlangius merlangus	Baltic Sea	348	7.8	5.95	M	J	F	Stom	14

Merlangius merlangus	Baltic Sea	422	7.8	6.41	M	J	F	Stom	14
Merlangius merlangus	Irish Sea	61.4	9.0	1.42	M	J	F	Stom	15
Merlangius merlangus	Irish Sea	213.5	9.0	3.35	M	A	F	Stom	15
Merlangius merlangus	Irish Sea	511.1	9.0	7.26	M	A	F	Stom	15
Theragra chalcogramma[1] (Pallas)	Bering Sea	187.3	1.9	1.12	M	A	Z	Stom	16
Theragra chalcogramma[1]	Bering Sea	187.3	2.2	5.81	M	A	Z	Stom	16
Theragra chalcogramma[1]	Bering Sea	187.3	2.3	6.20	M	A	Z	Stom	16
Theragra chalcogramma[1]	Bering Sea	187.3	2.2	0.94	M	A	Z	Stom	16
Theragra chalcogramma[1]	Bering Sea	187.3	2.4	4.31	M	A	Z	Stom	16
Theragra chalcogramma[1]	Bering Sea	187.3	3.6	11.61	M	A	Z	Stom	16
Theragra chalcogramma[1]	Bering Sea	1474	1.9	13.27	M	A	Z	Stom	16
Theragra chalcogramma[1]	Bering Sea	1474	2.2	64.87	M	A	Z	Stom	16
Theragra chalcogramma[1]	Bering Sea	1474	2.3	28.01	M	A	Z	Stom	16
Theragra chalcogramma[1]	Bering Sea	1474	2.2	36.85	M	A	Z	Stom	16
Theragra chalcogramma[1]	Bering Sea	1474	2.4	28.01	M	A	Z	Stom	16
Theragra chalcogramma[1]	Bering Sea	1474	3.6	66.33	M	A	Z	Stom	16
Theragra chalcogramma[1]	Bering Sea	1474	2.6	86.97	M	A	Z	Stom	16
Trisopterus esmarki Nilsson	Atlantic Ocean	15	7.0	0.17	M	A	Z	Stom	13
Merlucciidae									
Merluccius bilinearis (Mitchill)	Atlantic Ocean	4.1	11.9	0.19	M	A	B	Stom	10
Merluccius bilinearis	Atlantic Ocean	9.9	7.6	0.18	M	A	B	Stom	10
Merluccius bilinearis	Atlantic Ocean	207.7	11.8	3.99	M	A	F	Stom	10
Merluccius bilinearis	Atlantic Ocean	265.3	8.5	6.37	M	A	F	Stom	10
Merluccius productus (Ayres)	Pacific Ocean	860	8.2	21.50	M	A	Z	Stom	17
GASTEROSTEIFORMES									
Gasterosteidae									
Gasterosteus aculeatus L.	Llyn Frongoch	0.28	10.0	0.013	F	A	Z	Stom	18
PERCIFORMES									
Centrarchidae									
Ambloplites rupestris (Rafinesque)	Ottawa R.	26.7	12.0	0.87	F	J	B	^{137}Cs	3
Ambloplites rupestris	Ottawa R.	68.2	12.0	2.57	F	A	B	^{137}Cs	3
Ambloplites rupestris	Ottawa R.	72.1	12.0	2.27	F	A	B	^{137}Cs	3
Ambloplites rupestris	Ottawa R.	102.6	12.0	3.70	F	A	B	^{137}Cs	3
Ambloplites rupestris	Ottawa R.	115	12.0	2.68	F	A	B	^{137}Cs	3

Ambloplites rupestris	Ottawa R.	154.1	12.0	4.28	F	A	B	^{137}Cs	3
Ambloplites rupestris	Ottawa R.	168.1	12.0	3.31	F	A	B	^{137}Cs	3
Ambloplites rupestris	Ottawa R.	224.5	12.0	7.39	F	A	B	^{137}Cs	3
Lepomis gibbosus (L.)	L. Croche	8.8	21.0	0.54	F	J	B	Stom	19
Lepomis gibbosus	L. Memphremagog	8.8	22.0	1.75	F	J	B	Stom	19
Lepomis macrochirus Rafinesque	L. Opinicon	8.8	22.9	0.12	F	J	B	Stom	20
Lepomis macrochirus	L. Mendota	4.7	23.1	0.10	F	J	B	Stom	21
Lepomis macrochirus	L. Mendota	14.9	22.1	0.36	F	J	B	Stom	21
Lepomis macrochirus	L. Mendota	43.8	22.7	1.21	F	J	B	Stom	21
Lepomis macrochirus	L. Wingra	16.4	22.2	0.24	F	J	B	Stom	21
Lepomis macrochirus	L. Wingra	31.7	22.2	0.41	F	J	B	Stom	21
Lepomis macrochirus	L. Wingra	51.4	22.2	0.66	F	J	B	Stom	21
Lepomis macrochirus	White Oak L.	99.9	19.3	2.21	F	A	B	^{137}Cs	3
Lepomis megalotis (Rafinesque)	Vermillion R.	23	20.0	0.67	F	A	B	Stom	2
Micropterus dolomieui Lacépède	Ottawa R.	69.1	12.0	1.33	F	J	B	^{137}Cs	3
Micropterus dolomieui	Ottawa R.	76.5	12.0	1.49	F	J	B	^{137}Cs	3
Micropterus dolomieui	Ottawa R.	113.3	12.0	1.23	F	J	B	^{137}Cs	3
Micropterus dolomieui	Ottawa R.	128.2	12.0	1.72	F	J	B	^{137}Cs	3
Micropterus dolomieui	Ottawa R.	228.2	12.0	4.54	F	A	B	^{137}Cs	3
Micropterus dolomieui	Ottawa R.	332.6	12.0	5.09	F	A	B	^{137}Cs	3
Micropterus dolomieui	Ottawa R.	400.1	12.0	13.80	F	A	B	^{137}Cs	3
Micropterus dolomieui	Ottawa R.	466.4	12.0	8.77	F	A	B	^{137}Cs	3
Micropterus dolomieui	Ottawa R.	526.7	12.0	14.12	F	A	B	^{137}Cs	3
Micropterus dolomieui	Ottawa R.	591.4	12.0	6.98	F	A	B	^{137}Cs	3
Micropterus dolomieui	Ottawa R.	722.3	12.0	13.58	F	A	B	^{137}Cs	3
Micropterus dolomieui	Ottawa R.	913.3	12.0	12.06	F	A	B	^{137}Cs	3
Micropterus dolomieui	Ottawa R.	1219	12.0	18.04	F	A	B	^{137}Cs	3
Micropterus dolomieui	Vermillion R.	199	20.0	9.89	F	A	B	Stom	4
Micropterus salmoides (Lacépède)	L. Rebecca	171.6	20.0	4.12	F	A	F	Stom	22
Gobiidae									
Pomatoschistus lozanoi de Buen	Zwin saltmarsh	0.11	17.5	0.0012	M	J	Z	Stom	23
Pomatoschistus lozanoi	Zwin saltmarsh	0.11	18.0	0.0059	M	J	Z	Stom	23
Pomatoschistus microps Kroyer	Wadden Sea	0.16	18.5	0.050	M	J	Z	Stom	24
Pomatoschistus minutus Pallas	Wadden Sea	0.86	18.5	0.11	M	J	Z	Stom	24

Moronidae									
Morone americana[2] (Gmelin)	L. Erie	34.3	18.5	2.90	F	A	B	Stom	25
Morone americana[2]	L. Erie	34.3	17.9	5.36	F	A	B	Stom	25
Morone americana[2]	L. Erie	34.3	16.0	2.11	F	A	B	Stom	25
Morone americana[2]	L. Erie	34.3	9.4	0.89	F	A	B	Stom	25
Morone americana[2]	L. Erie	34.3	17.0	2.44	F	A	B	Stom	25
Pentacerotidae									
Pseudopentaceros wheeleri Hardy	Hancock Seamont	450	15.0	1.17	M	A	Z	Stom	26
Pseudopentaceros wheeleri	Hancock Seamont	450	15.0	12.87	M	A	Z	Stom	26
Percidae									
Etheostoma nigrum Rafinesque	Ottawa R.	0.45	12.0	0.023	F	A	B	^{137}Cs	3
Gymnocephalus cernuus (L.)	Krautsand Reede Elbe	4.4	19.7	0.14	M	J	B	Stom	27
Gymnocephalus cernuus	Krautsand Reede Elbe	172.7	19.7	3.11	M	A	B	Stom	27
Perca flavescens (Mitchill)	Baptiste L.	43.8	18.5	1.72	F	A	B	Stom	28
Perca flavescens	L. Brome	9.3	22.0	1.20	F	J	B	Stom	29
Perca flavescens	L. Brome	17.4	19.2	1.66	F	J	B	Stom	29
Perca flavescens	L. Brome	86.7	24.0	4.67	F	J	B	Stom	29
Perca flavescens	L. Bromont	8.2	21.2	0.29	F	J	B	Stom	29
Perca flavescens	L. Brompton	9.4	19.2	0.76	F	J	B	Stom	29
Perca flavescens	L. D'Argent	9.3	22.0	0.68	F	J	B	Stom	29
Perca flavescens	L. D'Argent	11.4	18.7	0.43	F	J	B	Stom	29
Perca flavescens	L. Drolet	14.7	17.4	0.87	F	J	B	Stom	29
Perca flavescens	L. Erie	13.4	19.6	0.59	F	J	B	Stom	30
Perca flavescens	L. Erie	13.4	17.6	0.45	F	J	B	Stom	30
Perca flavescens	L. Erie	13.4	12.6	0.59	F	J	B	Stom	30
Perca flavescens	L. Erie	13.4	21.6	0.96	F	J	B	Stom	30
Perca flavescens	L. Erie	49.4	19.6	1.49	F	J	B	Stom	30
Perca flavescens	L. Erie	49.4	17.6	0.89	F	J	B	Stom	30
Perca flavescens	L. Erie	49.4	16.3	2.74	F	J	B	Stom	30
Perca flavescens	L. Erie	49.4	16.7	1.71	F	J	B	Stom	30
Perca flavescens	L. Hertel	8.8	18.5	0.46	F	J	B	Stom	29
Perca flavescens	L. Hertel	9.3	18.0	1.22	F	J	B	Stom	29
Perca flavescens	L. Magog	9.3	23.0	0.92	F	J	B	Stom	29
Perca flavescens	L. Magog	18.4	20.0	1.53	F	J	B	Stom	29
Perca flavescens	L. Magog	86.7	23.0	8.07	F	J	B	Stom	29

Perca flavescens	L. Memphremagog	9.3	10.0	0.32	F	J	B	Stom	29
Perca flavescens	L. Memphremagog	14.6	18.7	0.79	F	J	B	Stom	29
Perca flavescens	L. Memphremagog	86.7	10.0	2.73	F	J	B	Stom	29
Perca flavescens	L. Roxton	16	20.3	0.77	F	J	B	Stom	29
Perca flavescens	L. Silver	11	18.5	0.75	F	J	B	Stom	29
Perca flavescens	L. Waterloo	9.3	18.0	0.50	F	J	B	Stom	29
Perca flavescens	L. Waterloo	16.4	19.7	0.35	F	J	B	Stom	29
Perca flavescens	L. Waterloo	86.7	18.0	1.15	F	J	B	Stom	29
Perca flavescens	Ottawa R.	5.6	12.0	0.13	F	J	F	^{137}Cs	3
Perca flavescens	Ottawa R.	9.1	12.0	0.26	F	J	F	^{137}Cs	3
Perca flavescens	Ottawa R.	20.2	12.0	0.47	F	J	F	^{137}Cs	3
Perca flavescens	Ottawa R.	29.1	12.0	0.66	F	J	F	^{137}Cs	3
Perca flavescens	Ottawa R.	51.4	12.0	1.18	F	A	F	^{137}Cs	3
Perca flavescens	Ottawa R.	74.4	12.0	1.39	F	A	F	^{137}Cs	3
Perca flavescens	Ottawa R.	103	12.0	2.49	F	A	F	^{137}Cs	3
Perca flavescens	Ottawa R.	154.3	12.0	4.35	F	A	F	^{137}Cs	3
Perca flavescens	Ottawa R.	201.3	12.0	4.81	F	A	F	^{137}Cs	3
Perca flavescens	Ottawa R.	257.1	12.0	8.61	F	A	F	^{137}Cs	3
Perca flavescens	Ottawa R.	278.7	12.0	4.88	F	A	F	^{137}Cs	3
Perca flavescens	Ottawa R.	348.9	12.0	9.00	F	A	F	^{137}Cs	3
Perca fluviatilis L.	L. Sövdeborgssjön	8.2	13.4	0.25	F	J	B	Stom	31
Perca fluviatilis	L. Sövdeborgssjön	11.9	13.4	0.38	F	J	B	Stom	31
Perca fluviatilis	L. Sövdeborgssjön	16.9	16.8	0.32	F	A	B	Stom	32
Percina caprodes (Rafinesque)	Ottawa R.	0.6	12.0	0.028	F	A	B	^{137}Cs	3
Percina caprodes	Ottawa R.	2.4	12.0	0.092	F	A	B	^{137}Cs	3
Stizostedion vitreum (Mitchill)	Ottawa R.	63.3	12.0	1.57	F	J	F	^{137}Cs	3
Stizostedion vitreum	Ottawa R.	147.7	12.0	1.96	F	J	F	^{137}Cs	3
Stizostedion vitreum	Ottawa R.	235.1	12.0	3.79	F	J	F	^{137}Cs	3
Stizostedion vitreum	Ottawa R.	323.4	12.0	4.98	F	J	F	^{137}Cs	3
Stizostedion vitreum	Ottawa R.	419.1	12.0	5.66	F	J	F	^{137}Cs	3
Stizostedion vitreum	Ottawa R.	501.1	12.0	10.32	F	A	F	^{137}Cs	3
Stizostedion vitreum	Ottawa R.	689.7	12.0	13.59	F	A	F	^{137}Cs	3
Scombridae									
Thunnus albacares[3] (Bonnaterre)	Pacific Ocean	5616	24.5	188.70	M	A	F	^{137}Cs	33
Thunnus albacares[3]	Pacific Ocean	15629	24.5	453.24	M	A	F	^{137}Cs	33
Thunnus albacares[3]	Pacific Ocean	38033	24.5	988.86	M	A	F	^{137}Cs	33

PLEURONECTIFORMES									
Pleuronectidae									
Hippoglossoides platessoides (Fabricius)	Atlantic Ocean	824.2	2.5	2.31	M	A	B	Stom	34
Lepidopsetta bilineata (Ayres)	Bering Sea	174.3	4.7	0.78	M	A	B	Stom	35
Limanda ferruginea (Storer)	Georges Bank	298.1	9.0	1.64	M	A	B	Stom	36
Limanda ferruginea	Georges Bank	330	10.0	1.32	M	A	B	Stom	36
Limanda ferruginea	Georges Bank	348.1	8.0	2.26	M	A	B	Stom	36
Limanda limanda L.	German Bight	45.3	7.0	0.86	M	A	B	Stom	37
Limanda limanda	German Bight	45.9	7.0	0.78	M	A	B	Stom	37
Limanda limanda	German Bight	78	7.0	1.17	M	A	B	Stom	37
Limanda limanda	German Bight	78.1	7.0	1.25	M	A	B	Stom	37
Pleuronectes platessa L.	North Sea	66	11.2	3.74	M	A	B	Stom	38
Pleuronectes platessa	North Sea	132.7	11.2	4.17	M	A	B	Stom	38
Pleuronectes platessa	North Sea	376.8	11.2	4.03	M	A	B	Stom	38
Pseudopleuronectes americanus (Walbaum)	Charlestown Pond	60.5	11.0	1.19	M	A	B	Stom	39
Pseudopleuronectes americanus	Charlestown Pond	60.5	20.0	1.75	M	A	B	Stom	39
Reinhardtius hippoglossoides[1] (Walbaum)	Atlantic Ocean	18.8	2.2	0.35	M	J	F	Stom	40
Reinhardtius hippoglossoides[1]	Atlantic Ocean	103.7	2.2	3.47	M	J	F	Stom	40
Reinhardtius hippoglossoides[1]	Atlantic Ocean	319.7	2.2	9.24	M	A	F	Stom	40
Reinhardtius hippoglossoides[1]	Atlantic Ocean	741.5	2.2	15.13	M	A	F	Stom	40
Reinhardtius hippoglossoides[1]	Atlantic Ocean	1450	2.2	23.49	M	A	F	Stom	40
Reinhardtius hippoglossoides[1]	Atlantic Ocean	2536	2.2	37.53	M	A	F	Stom	40
Reinhardtius hippoglossoides[1]	Atlantic Ocean	4093	2.2	79.40	M	A	F	Stom	40
Reinhardtius hippoglossoides[1]	Atlantic Ocean	6222	2.2	162.39	M	A	F	Stom	40
Reinhardtius hippoglossoides[1]	Bering Sea	538.9	2.6	5.55	M	A	F	Stom	41
Reinhardtius hippoglossoides[1]	Bering Sea	1885	2.9	18.85	M	A	F	Stom	41
Reinhardtius hippoglossoides[1]	Bering Sea	5528	3.0	182.42	M	A	F	Stom	41
Soleidae									
Solea vulgaris Quensel	Atlantic Ocean	9	19.8	0.28	M	J	B	Stom	42
Solea vulgaris	Atlantic Ocean	68.9	19.8	1.83	M	J	B	Stom	42
SALMONIFORMES									
Salmonidae									
Coregonus artedii Lesueur	Ottawa R.	9.8	17.6	0.18	F	J	Z	^{137}Cs	3
Coregonus artedii	Ottawa R.	19.2	12.0	0.87	F	A	Z	^{137}Cs	3

Coregonus artedii	Ottawa R.	37.5	12.0	1.38	F	A	Z	^{137}Cs	3
Coregonus artedii	Ottawa R.	74.3	12.0	1.93	F	A	Z	^{137}Cs	3
Coregonus artedii	Ottawa R.	105.5	12.0	2.93	F	A	Z	^{137}Cs	3
Coregonus clupeaformis (Mitchill)	Ottawa R.	406.5	12.0	9.67	F	A	B	^{137}Cs	3
Coregonus clupeaformis	Ottawa R.	938.6	12.0	25.72	F	A	B	^{137}Cs	3
Oncorhynchus gorbuscha (Walbaum)	Hecate Strait	17.25	11.3	1.14	M	J	Z	Stom	43
Oncorhynchus gorbuscha	Hecate Strait	20.5	12.1	1.63	M	J	Z	Stom	43
Oncorhynchus keta (Walbaum)	Hecate Strait	20.65	11.3	1.33	M	J	Z	Stom	43
Oncorhynchus keta	Hecate Strait	30.4	12.1	2.04	M	J	Z	Stom	43
Oncorhynchus kisutch (Walbaum)	Pacific Ocean	88.4	11.4	2.12	M	J	Z	Stom	44
Oncorhynchus kisutch	Pacific Ocean	88.4	13.7	3.27	M	J	Z	Stom	44
Oncorhynchus kisutch	L. Erie	1789	13.4	47.41	F	A	F	^{137}Cs	3
Oncorhynchus kisutch	L. Michigan	2279	8.6	34.41	F	A	F	^{137}Cs	3
Oncorhynchus kisutch	Chignik L.	8.4	5.8	0.36	F	J	F	Stom	45
Oncorhynchus kisutch	Chignik L.	10.3	7.2	0.35	F	J	F	Stom	45
Oncorhynchus kisutch	Chignik L.	10.9	7.2	0.50	F	J	F	Stom	45
Oncorhynchus kisutch	Chignik L.	11.1	7.5	0.21	F	J	F	Stom	45
Oncorhynchus mykiss (Richardson)	Henry's Fork	106	14.6	7.26	F	J	B	Stom	46
Oncorhynchus nerka (Walbaum)	Hecate Strait	24.9	12.1	0.85	M	J	Z	Stom	43
Oncorhynchus nerka	Hecate Strait	29.4	11.3	1.04	M	J	Z	Stom	43
Oncorhynchus nerka[4]	L. Washington	2.2	9.3	0.21	F	J	Z	Stom	47
Oncorhynchus nerka[4]	L. Washington	3.6	10.2	0.34	F	J	Z	Stom	47
Oncorhynchus nerka[4]	L. Washington	5.5	8.6	0.27	F	J	Z	Stom	47
Oncorhynchus nerka[4]	L. Washington	7.9	8.6	0.35	F	J	Z	Stom	47
Oncorhynchus nerka[4]	L. Washington	10.9	8.6	0.41	F	J	Z	Stom	47
Oncorhynchus nerka[4]	L. Washington	14.6	8.4	0.32	F	J	Z	Stom	47
Oncorhynchus nerka[4]	L. Washington	19	8.4	0.34	F	J	Z	Stom	47
Oncorhynchus nerka[4]	L. Washington	24.3	7.1	0.17	F	J	Z	Stom	47
Oncorhynchus tshawytscha (Walbaum)	Columbia R.	16.4	14.0	1.11	F	J	B	Stom	48
Oncorhynchus tshawytscha	Columbia R.	18.4	14.0	1.29	F	J	B	Stom	48
Oncorhynchus tshawytscha	L. Michigan	3448	8.2	45.17	F	A	F	^{137}Cs	3
Oncorhynchus tshawytscha	L. Michigan	4136	8.2	53.35	F	A	F	^{137}Cs	3
Oncorhynchus tshawytscha	Rakaia R.	4	15.5	0.33	F	J	B	Stom	49
Salmo trutta L.	L. Høysjøen	78	11.8	4.97	F	J	B	Stom	50
Salmo trutta	L. Høysjøen	87.8	10.8	3.71	F	J	B	Stom	50
Salvelinus alpinus (L.)	L. Takvatn	70	9.2	0.81	F	J	B	Stom	51
Salvelinus fontinalis (Mitchill)	L. Simpson	98.6	18.4	4.28	F	A	B	Stom	52

Salvelinus fontinalis	Stoney Brook	7.29	16.0	0.13	F	J	B	Stom	53
Salvelinus namaycush (Walbaum)	Great Slave L.	176.3	6.3	2.49	F	J	F	^{137}Cs	3
Salvelinus namaycush	Great Slave L.	392.8	6.5	2.91	F	J	F	^{137}Cs	3
Salvelinus namaycush	Great Slave L.	602.5	7.0	2.77	F	J	F	^{137}Cs	3
Salvelinus namaycush	Great Slave L.	906.3	6.6	5.71	F	J	F	^{137}Cs	3
Salvelinus namaycush	Great Slave L.	1037	6.8	2.90	F	J	F	^{137}Cs	3
Salvelinus namaycush	Great Slave L.	1288	6.1	5.15	F	J	F	^{137}Cs	3
Salvelinus namaycush	Great Slave L.	1494	6.3	4.33	F	J	F	^{137}Cs	3
Salvelinus namaycush	Great Slave L.	1747	7.4	9.78	F	J	F	^{137}Cs	3
Salvelinus namaycush	Great Slave L.	1956	6.6	12.13	F	A	F	^{137}Cs	3
Salvelinus namaycush	Great Slave L.	2109	6.7	15.82	F	A	F	^{137}Cs	3
Salvelinus namaycush	Great Slave L.	2571	6.9	12.60	F	A	F	^{137}Cs	3
Salvelinus namaycush	Great Slave L.	2747	7.0	19.23	F	A	F	^{137}Cs	3
Salvelinus namaycush	Great Slave L.	3250	6.2	21.45	F	A	F	^{137}Cs	3
Salvelinus namaycush	Great Slave L.	3478	6.2	21.22	F	A	F	^{137}Cs	3
Salvelinus namaycush	Great Slave L.	4494	6.6	40.00	F	A	F	^{137}Cs	3
Salvelinus namaycush	Great Slave L.	5360	6.8	37.52	F	A	F	^{137}Cs	3
Salvelinus namaycush	L. Michigan	6326	7.0	30.36	F	A	F	^{137}Cs	3
SILURIFORMES									
Ictaluridae									
Ictalurus punctatus (Rafinesque)	Vermillion R.	377	20.0	14.44	F	A	B	Stom	4
SQUALIFORMES									
Carcharhinidae									
Carcharhinus plumbeus (Nardo)	Chincotaegue Bay	1900	25.0	20.33	M	A	B	Stom	54
Negaprion brevirostris (Poey)	Florida Keys	2417	31.8	44.71	M	A	F	Stom	55

[1] Daily consumption rates were recalculated using the evacuation rate model of Durbin et al. (1983)
[2] Only estimates based on complete 24h feeding cycles were included
[3] Consumption rates were recalculated using the ^{137}Cs elimination model of Rowan and Rasmussen (1995)
[4] For each sampling date, fish daily consumption rates were recalculated using the maximum evacuation rate obtained on that date

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Appendix V. Fish size (W_t), and mercury concentration in dwarf and normal lake whitefish and cisco (C_t) and their prey (C_d). Fish size and mercury concentration was estimated by linear and non-linear regression analyses.

Phenotype	n	Age (years)	W_t (g)	C_t ($\mu g \cdot g^{-1}$)	C_d ($\mu g \cdot g^{-1}$)
		Caniapiscau Reservoir			
Normal					
	14	2 i	17.2	0.316	0.060
	11	3 i	39.6	0.316	0.060
	18	4 i	71.6	0.316	0.050
	19	5 i	113.4	0.316	0.040
	16	6 m	289.0	0.316	0.032
	33	7 m	476.5	0.316	0.032
	45	8 m	665.6	0.316	0.032
	40	9 m	893.8	0.316	0.032
	25	10 m	1163.5	0.316	0.032
	7	11 m	1477.0	0.316	0.032
Dwarf					
	2	2 i	14.4	0.384	0.060
	10	3 m	24.6	0.447	0.060
	24	4 m	36.0	0.520	0.060
	17	5 m	48.4	0.605	0.060
	22	6 m	61.5	0.704	0.060
	15	7 m	75.4	0.820	0.060
	6	8 m	90.0	0.955	0.060
		Lake Serigny			
Normal					
	9	2 i	38.8	0.164	0.03
	1	3 i	79.9	0.177	0.03
	2	4 i	133.3	0.186	0.03
	2	5 i	191.0	0.194	0.03
	3	6 m	251.5	0.200	0.03
	3	7 m	331.1	0.206	0.03
	2	8 m	435.9	0.211	0.03
	2	9 m	573.9	0.215	0.03
	1	10 m	755.5	0.219	0.03
	5	11 m	994.7	0.223	0.03
Dwarf					
	2	2 i	19.6	0.168	0.03
	6	3 m	35.1	0.195	0.03
	9	4 m	45.0	0.225	0.03
	10	5 m	50.6	0.260	0.03
	5	6 m	53.8	0.301	0.03
	5	7 m	55.7	0.348	0.03
		Lac Rond-de-Poêle			
Normal					
	3	1 i	48.5	0.063	0.015

6	2 i	89.4	0.069	0.015
7	3 i	148.7	0.076	0.015
8	4 i	227.0	0.083	0.015
8	5 i	322.8	0.091	0.015
2	6 m	432.7	0.100	0.021
7	7 m	552.1	0.110	0.021
7	8 m	676.2	0.121	0.021
5	9 m	800.5	0.133	0.021
3	10 m	921.1	0.146	0.021
2	11 m	1035.2	0.160	0.021
3	12 m	1140.8	0.176	0.021
3	13 m	1236.8	0.193	0.021
4	14 m	1322.8	0.213	0.021
3	15 m	1398.8	0.233	0.021
Cisco (*Coregonus artedii*)				
2	1 i	39.0	0.105	0.015
1	2 m	50.1	0.130	0.015
2	3 m	61.6	0.145	0.015
4	4 m	73.2	0.155	0.015

Note: i, immature; m, mature

Appendix VI. Fish size (W_t), and ^{137}Cs concentration in normal lake whitefish and cisco (C_t) and their prey (C_d). Fish size and ^{137}Cs concentration was estimated by linear and non-linear regression analyses.

Species	*n*	Age (years)	W_t (g)	C_t ($\mu g \cdot g^{-1}$)	C_d ($\mu g \cdot g^{-1}$)
Ottawa River					
Lake whitefish (*Coregonus clupeaformis*)					
	1	3 i	326.0	6.82	1.836
	1	4 m	487.0	7.70	1.836
	1	5 m	752.7	8.58	1.836
	1	6 m	1124.6	9.47	1.836
Cisco (*Coregonus artedii*)					
	1	1 i	12.2	1.55	0.589
	4	2 m	27.9	2.06	0.589
	2	3 m	52.6	2.56	0.589
	1	4 m	86.2	3.07	0.867
	1	5 m	122.5	3.83	0.867

Note: i, immature; m, mature