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**The Influence of Food Web Structure on the
Growth and Bioenergetics of Lake Trout
(*Salvelinus namaycush*)**

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A thesis submitted to the faculty of Graduate Studies and Research in partial fulfillment
of the requirements of the degree of Masters of Science

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Preface

The Faculty of Graduate Studies and Research of McGill University requires that the follow statements appear at the beginning of all manuscript-based theses:

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it is in the candidate's interest to make perfectly clear the responsibilities of all the authors of the co-authored papers."

This thesis is based on one chapter. This chapter represents a distinct manuscript that will be submitted for publication in the peer-reviewed scientific journal of Ecology. 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). I performed all the sampling, and data analyses. Fish aging however was carried out by Gary Ridout, senior lab technician at the Harkness Laboratory of Fisheries Research in Algonquin Provincial Park (Ontario Ministry of Natural Resources). This chapter was written by myself and was co-authored by my supervisor, Dr. Marc Trudel, and Dr. Mark Ridgway who in addition to providing technical advice and comments, contributed to the development of the ideas presented in this manuscript. In addition some data was provided by Dr. Marc Trudel.

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In loving memory of Orlando Pazzia who said,

"A me un giorno mi piacerebbe a studiare queste cose interessante che succedano nella natura."

"One day I would like to study these interesting things that take place in nature."

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Abstract

Most fish species tend to feed on larger prey as their size increases. The lack of suitable prey during critical periods of their life can prevent them from shifting their diet to larger prey and also from reaching larger body sizes. In this study, we compared the energy budget of lake trout (*Salvelinus namaycush*) populations with contrasting food webs. Non-piscivorous lake trout (NPLT) populations reached a much smaller size and grew at a much slower rate than piscivorous lake trout (PLT) populations. Food consumption rates were on average, 2-3 times higher in NPLT when they were expressed on a wet weight basis. However, only a slight difference in their energy intake was detected (less than 10%) once consumption rates were corrected for differences in prey caloric content. Growth efficiency was about two times lower in NPLT compared to PLT, while their metabolic costs were higher and assimilation efficiency was lower. It is most likely that the increased metabolic costs were associated with higher foraging costs, since more feeding attempts must be made to acquire a given quantity of food when fish are feeding on smaller prey. Furthermore, the portion of indigestible matter is likely to be higher in the diet of NPLT than in PLT (e.g. chitin versus bone). These results are consistent with theoretical models of fish growth that have showed that lake trout must have access to larger prey, even if they are rare, to reach larger body sizes. Our study also illustrates how the restructuring of a prey community by the arrival of an exotic species into a food web could alter the growth rate of a top predator. Furthermore, our study suggests that age at first maturity is influenced by growth efficiency in indigenous populations of fish. Therefore, the dynamic of a population and its vulnerability to exploitation are likely to be influenced by their energy allocation strategy.

Resumé

La plupart des espèces de poissons ont tendance à se nourrir de proies plus grosses lorsque leur taille augmente. En cas de manque de proies de tailles convenables lors des périodes critiques de leur vie, il est possible que les poissons ne puissent pas changer leur régime alimentaire pour des proies plus grosses, et par le fait même, d'atteindre de plus grandes tailles. Dans cette étude, nous avons comparé le bilan énergétique des populations de touladis (*Salvelinus namaycush*) aux divers réseaux trophiques. Les populations de touladis non-piscivores (TNP) ont atteint une taille beaucoup plus petite et ont grandi à un taux beaucoup plus lent que les populations de touladis piscivores (TP). Les taux de consommation de nourriture étaient, en moyenne, 2-3 fois plus élevé dans TNP lorsqu'exprimés sur une base de masse humide. Par contre, seulement une petite différence dans leur acquisition énergétique (moins que 10%) a été détectée une fois que les taux de consommation ont été corrigés pour des différences dans le contenu calorique des proies. L'efficacité de croissance dans TNP était deux fois plus basse par rapport à celle de TP, par contre leurs coûts métaboliques étaient plus élevés et l'efficacité d'assimilation était plus basse. Il est possible que leurs demandes métaboliques élevées étaient associées à de coûts de capture de proies plus élevés, puisque plus de tentatives doivent être faites pour acquérir une quantité donnée de nourriture quand le poisson se nourrit sur une plus petite proie. De plus, la portion de matière indigestible est probablement plus haute dans le régime de TNP que dans TP (e.g. l'os versus le chitine). Ces résultats se conforment aux modèles théoriques de croissance de poissons démontrant que les touladis doivent avoir accès à de grosses proies, même si elles sont rares, afin qu'ils puissent atteindre une grande taille. Nos travaux indiquent comment

une restructuration majeure de la communauté de proies induite par l'arrivée d'une espèce exotique dans un réseau trophique peut altérer radicalement la croissance des poissons. De plus, notre étude suggère que l'âge de maturité est influencée par l'efficacité de croissance dans les populations de poissons indigènes. Donc, le dynamique d'une population et sa vulnérabilité à l'exploitation est probablement influencé par leur stratégie d'allocation d'énergie.

Introduction

Most piscivores encounter a wide spectrum of prey size throughout their lifespan, as the size of prey they consume increases as they grow (Werner and Gilliam 1984; Vander Zanden and Rasmussen 1996). Most piscivorous species experience 3-4 diet shifts during their lifetime which are often associated with habitat shifts, behavioural changes, and possibly even extensive migrations between freshwater and marine environments (Werner and Gilliam 1984; Groot and Margolis 1991). At hatching, fry initially feed upon the nutrients deposited in their yolk sacs from their parents (Vander Zanden et al. 1998). Exogenous feeding usually commences with small crustaceans such as rotifers and nauplii, (Robichaud-LeBlanc et al. 1997) with a transition to larger zooplankton and benthic invertebrates, and ultimately other fish (Konkle and Sprules 1986; Hayes and Taylor 1990; Mittelbach and Persson 1998).

The prey communities encountered by most freshwater fish in both littoral and pelagic habitats, are characterized by very uneven size spectra, with abundant biomass in some size classes, and little or nothing in others (Kerr 1974; Sprules et al. 1983; Sprules et al. 1991; Rasmussen 1993). This is in sharp contrast to the "flat" or homogeneous size spectra seen in most marine pelagic communities (Sheldon et al. 1972). The irregularities in most freshwater communities reflect the general poverty of species, and their among-system variability reflects the variable species composition among systems. Thus, the ability of fish to perform these diet shifts to larger prey items mainly depends on prey composition and prey availability, and hence, on food web structure (Winemiller 1990). The prey community in a given lake depends on the post-glacial zoogeographic history (Dadswell 1974), or may be altered by anthropogenic activities such as the introduction

of exotic species (Vander Zanden et al. 1999) and pollution (Sherwood et al. 2000). Thus, in some systems, some fish species may be unable to complete certain diet shifts if appropriate prey are lacking from the food web.

A diet shift to larger sized prey, in lake trout (*Salvelinus namaycush*) and most other fish is usually followed by increased growth rates (Werner and Gilliam 1984). This may be the result of an increase in food consumption rates, a reduction of energy expenditures, or a combination of both processes. Theoretical models of fish growth suggest that foraging costs increase when the size of a predator increases relative to its prey, since it must find and consume more prey to satisfy its energy demands (e.g. decreased growth efficiency, Kerr 1971a, b). Thus fish that are foraging on larger prey are expected to have lower energy expenditures associated with foraging than fish feeding on smaller prey (Kerr and Martin 1970; Pyke et al. 1977). In addition, foraging costs are expected to increase faster with body size in fish consuming smaller prey (Kerr 1971a, b).

The effects of prey size on energy acquisition and energy allocation has rarely been examined in wild fish, possibly due to the difficulty of estimating energy intake of fish *in situ* using traditional approaches based on stomach contents. In a comparative study involving twelve populations of yellow perch (*Perca flavescens*), Boisclair and Leggett (1989a) showed that growth rate, growth efficiency, consumption rates, as well as activity costs of yellow perch were all negatively correlated to the percent contribution of small prey in their diet (Boisclair and Rasmussen 1996). More recently, Sherwood et al. (2000) compared the energy budget of yellow perch from metal-contaminated sites and reference sites. Yellow perch from the metal-contaminated sites consumed smaller

prey, had lower growth rates and growth efficiencies than fish from the reference sites. However, none of these studies attempted to examine how the relationships between consumption rate and fish size and between foraging cost and fish size were influenced by prey size and prey type.

The objectives of this study were to examine the effects of food web structure on the bioenergetics of a top predator in freshwater lakes, lake trout. More specifically, we compared growth and consumption rates, and growth efficiencies of non-piscivorous and piscivorous lake trout populations (NPLT and PLT, respectively). Lake trout populations that have suitable forage fish species available to them all year round demonstrate relatively rapid growth (Martin et al. 1970; Scott and Crossman 1973). In the absence of these prey fish, lake trout rely on littoral minnows during the winter months and in the summer feed primarily on zooplankton and benthic invertebrates due to thermal restraints during lake stratification (Martin 1966; Donald and Alger 1986; Konkle and Sprules 1986; Vander Zanden et al. 1999). NPLT tend to grow at a slower rate, mature at smaller sizes and earlier ages and are usually found in much higher fish densities than other piscivorous populations (Martin 1966; Paloheimo and Dickie 1966; Donald and Alger 1986; Konkle and Sprules 1986). Due to their small size, NPLT are usually considered to be stunted fish. Hence, in this study, we tested the hypotheses that the reduced growth observed in non-piscivorous compared to piscivorous lake trout populations is a result of: 1) a decrease in consumption rates and/or 2) a decrease in growth efficiency (increase in energetic costs).

In order to examine the differences in energy demands associated with foraging on different prey items, we estimated consumption rates of PLT populations (large prey)

with lake trout populations that forage mostly on invertebrates (small prey). To estimate consumption rates of NPLT and PLT, we used an approach based on the mass balance of persistent contaminants in the food web. Rowan and Rasmussen (1996) and Trudel et al. (2000a) have developed methods where the determination of the concentration of ^{137}Cs and Hg in fish and their prey as well as the chemical absorption efficiency from their food and the elimination rate of the chemical can be used to produce estimates of annual consumption rates of wild fish stocks. This approach has been corroborated with stomach content techniques (Forseth et al. 1992; 1994; Trudel et al. 2000a) and has recently been validated with laboratory data (Trudel et al. 2000a).

Methods

Study Sites

This study was conducted in Algonquin Provincial Park, Ontario at the Harkness Laboratory of Fisheries Research located on Lake Opeongo. Algonquin Park has an area of approximately 7800 square kilometers and is situated on the Precambrian shield with the parallels 45°45'N and 78°30'W. There are about 150 lakes containing self sustaining lake trout populations, all showing varying degrees of piscivory in their diets. Two NPLT (Happy Isle Lake and Source Lake) and one PLT (Lake Opeongo) populations were sampled in this area. Each of the three lakes sampled is easily accessible by road, except for Happy Isle, which requires a 14-km boat ride and a 2.2-km portage. Additional PLT population data were collected from the literature for Great Slave Lake (North Western Territories), Lake Ontario (Ontario-New York), and Lake Memphremagog (Quebec-Vermont) (Rowan and Rasmussen 1996; Trudel et al. 2000a). Lake Memphremagog and

Lake Ontario are stocked by governmental agencies with lake trout and other salmonids to sustain the high levels of fishing pressure from anglers. The PLT populations in this study had diets consisting almost entirely of forage fish (Table 1). Whereas the percent contribution of prey fish never made up more than 11% by weight of the non-piscivorous diet. The main prey item of the NPLT diet was over 89 % zooplankton and benthic invertebrates.

Fish Collection

Fish were collected from three lakes in Algonquin Park throughout the months of May until August during the sampling seasons of 1998 and 1999 by gillnet and rod and reel. Gillnets were set for approximately 4 hours and consisted of 6 panels of 50m nets varying from 1.3 to 6.4 cm mesh size. Lake trout heads were also obtained from anglers at the Creel Census Station on Lake Opeongo. These sites all support sport fisheries with angling pressure ranging from negligible to heavy depending on accessibility and quality of fishing. The total mass of each individual fish was measured to the nearest ± 0.1 -gram and fork length to the nearest millimeter.

Age Analysis

Lake trout were aged using the left sagitta otolith. Otoliths were removed and preserved in glycerol for three months. Otoliths were then cleaned in a 10% alcohol solution and embedded in an epoxy resin (araldite). Thin transverse sections were cut through the nucleus, at right angles to the long axis of the otolith. The section was mounted on a glass slide, buffed and polished with lapping film. Acetate replicates were

made of the polished surfaces of the section after being etched with a 2% HCl solution (Casselman and Gunn 1992). The acetate imprints were mounted and examined with a microscope at 40X and 100x magnification.

Lake trout were assigned ages based on the enumeration of annuli on their otoliths (Casselman 1983, 1987). The mounted otoliths were aged blindly, as they were only given a fish identification number in order to eliminate any prior bias that could have occurred while aging. An interpreter assessed the ages of each otolith (n=367) twice and the agreement of the two independent ages was within 93%. A subset of the sample of otoliths (n=125) was aged by a second interpreter and was in agreement with the first interpreter 87% of the time. When observations varied between the first and second interpreter they were within 1 to 3 years difference. When the two interpreters could not reach a consensus, a third interpreter was brought in and assessed the age until there was consensus.

Growth Rates

Growth curves were fitted on mean mass at age using various non-linear equations (Fig. 1, Appendix 1). Specific growth rates (G , $g \cdot g^{-1} \cdot d^{-1}$) were estimated as (Ricker 1979):

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

where W_t and $W_{t+\Delta t}$ are fish mass (g) at time t and $t+\Delta t$. All growth rates include both somatic and gonadal growth. In order to express growth on an energetic basis (kJ/d), the

energy density of lake trout was modeled as a function of lake trout size using the equation derived by Stewart et al. (1983) for Lake Michigan lake trout. The energy densities of the gonads were assumed to be 20% higher than the energy density of somatic tissue (Diana 1983). Males and females were pooled for this analysis, as the low sample size prevented us from adequately estimating the energy budget separately for each sex.

Consumption Rates

Annual consumption rates for lake trout from Lake Opeongo, Great Slave Lake, Lake Memphremagog, Happy Isle Lake, and Source Lake were estimated with the ^{137}Cs radiotracer approach. The ^{137}Cs approach requires the determination of lake trout age, body size, growth rate, ^{137}Cs concentration in fish tissue and their prey, the assimilation efficiency of ^{137}Cs from food, as well as the elimination rate of ^{137}Cs from fish (Rowan and Rasmussen 1996). Specific consumption rates ($s, \text{g} \cdot \text{g}^{-1} \cdot \text{d}^{-1}$) were estimated using a radiocesium mass balance model as (Rowan and Rasmussen 1996):

$$C = \frac{(Q_t - Q_o \cdot e^{-(E+D)t} + Q_g)}{\alpha [^{137}\text{Cs}_p] \cdot w_o \cdot (e^{-Gt} - e^{-(E+D)t})} \cdot (G + E + D) \quad (2)$$

where Q_t is the ^{137}Cs burden (Bq) at time t (days), Q_o is the initial ^{137}Cs burden (Bq), Q_g is the gonadal ^{137}Cs burden (Bq) released at spawning, G is the specific growth rate ($\text{g} \cdot \text{g}^{-1} \cdot \text{d}^{-1}$), E is the elimination rate of ^{137}Cs ($\text{Bq} \cdot \text{Bq}^{-1} \cdot \text{d}^{-1}$), D is the radioactive decay of ^{137}Cs ($\text{Bq} \cdot \text{Bq}^{-1} \cdot \text{d}^{-1}$), $[^{137}\text{Cs}_p]$ is the concentration of ^{137}Cs in the diet (Bq/kg), α is the assimilation efficiency of ^{137}Cs from the diet, and w_o is the initial body mass (kilogram).

^{137}Cs concentrations of lake trout and prey were determined by gamma spectroscopy with a coaxial or well germanium detector (model GCW 1521, Canberra Packard Canada, Mississauga, Ontario). In order to reduce the volume of the samples they were either dried at 60°C or ashed at 450°C according to size, and subsequently homogenized with a mortar and a pestle prior to performing the ^{137}Cs analyses. Ashing or drying does not in anyway alter the concentration of ^{137}Cs , as the boiling point of Cs is 670°C . ^{137}Cs concentrations were individually measured for each lake trout while prey items were pooled together according to lake and lake trout size class. ^{137}Cs concentrations for lake trout were modeled as a function of age using linear and non-linear regressions (Appendix 1). Annual average, age specific consumption rates were also converted to energy units (kJ/d) using published estimate of prey energy density (Cummins and Wuycheck 1971; Rottiers and Tucker 1982; Post 1990; Mason et al. 1998).

^{137}Cs concentrations of the prey items consumed by lake trout were measured on undigested gut contents. Lake trout stomach contents were removed and separated into one of two categories, as either fish or invertebrates. Each category was weighed to the nearest ± 0.01 g. The stomach contents were pooled according to site, size class, and prey type in order to increase the precision of ^{137}Cs concentrations. Each lake trout was assigned to one of six total length categories: 1) $<200\text{mm}$, 2) $200\text{-}299\text{mm}$, 3) $300\text{-}399\text{mm}$, 4) $400\text{-}499\text{mm}$, 5) $500\text{mm-}599\text{mm}$, 6) $>600\text{mm}$ for the purpose of this study. A weighted average of the ^{137}Cs concentrations by volume was utilized in order to calculate the overall concentration in the diets. The assimilation efficiency of ^{137}Cs of lake trout diet was estimated using published values that were mainly determined on salmonids. We

assumed that the assimilation efficiency of ^{137}Cs was 0.69 for fish prey (Rowan and Rasmussen 1996) and 0.234 for invertebrate prey (Forseth et al. 1992) (Table 3).

The elimination rate of ^{137}Cs from fish has been shown to be species independent and can be easily described as a function of body size (W , grams) and temperature (T , °C) as (Rowan and Rasmussen 1995):

$$E = e^{-6.583 - 0.111 \cdot \ln(W) - 0.0987T} \quad (3)$$

The temperature occupied by an individual lake trout appears to be a combination of changing water temperatures, preferred temperature, and recent temperatures experienced through vertical migration in the water column (Stewart et al. 1983). The annual water temperature cycle of Lake Opeongo, Happy Isle Lake, Source Lake, Great Slave Lake, Lake Ontario, and Lake Memphremagog were modeled with a Gaussian function (Table 1). However for the present study, a maximum preferred temperature for lake trout was assumed to be an isocline of 10°C (Stewart et al. 1983; but see Sellers et al. 1998 for small lakes).

The burden of ^{137}Cs lost through the gonads (Q_g) due to spawning was estimated as:

$$Q_g = [^{137}\text{Cs}_g] \cdot GSI \cdot W_{sp} \quad (4)$$

where $[^{137}\text{Cs}_g]$ is the concentration of ^{137}Cs in the gonads, GSI is the gonadosomatic index (%), and W_{sp} is fish weight (kg) at spawning. The GSI of lake trout was taken from

Creel Census Surveys carried out in Algonquin Provincial, maximum GSI values were taken for both male and female lake trout and were applied to other lake trout populations.

Annual consumption rates for Lake Ontario lake trout were estimated with a Hg mass balance model and were taken directly from Trudel et al. (2000a) (Appendix 2).

Allocation of Energy to Growth

The energy allocated to growth was estimated as:

$$GE = \frac{P}{DR} \quad (5)$$

where GE is the growth efficiency, P is the sum of somatic and gonad growth (kJ/d), and DR is the daily ration of the fish (kJ/d). DR was obtained by converting consumption rates from $\text{g} \cdot \text{g}^{-1} \cdot \text{d}^{-1}$ to kJ/d utilizing the energy content of the different prey items in the diet of these fish (Appendix 1 and 2)

Total Metabolic Rates and Activity Costs

The energy budget of a fish can be written as:

$$DR = P + R_T + F + U \quad (6)$$

where R_T is the total respiration or metabolic rate (kJ/d), F is egestion (kJ/d), and U is excretion (kJ/d). R_T can be estimated by difference, provided that C , G , F , and U are known as:

$$R_T = DR - (G + F + U) \quad (7)$$

R_T can be further divided into three components:

$$R_T = R_s + R_d + R_a \quad (8)$$

where R_s is the standard metabolic rate (kJ/d), R_d is the specific dynamic action or heat increment (kJ/d), and R_a is the cost of activity (kJ/d). R_s is a function of body size and water temperature, while R_d is assumed to be equal to 17 % of the assimilated energy (Stewart et al. 1983). Therefore, R_a can also be determined by difference if R_s and R_d are known:

$$R_a = R_T - (R_s + R_d) \quad (9)$$

The activity cost-production ratio was estimated as:

$$\frac{R_a}{P} \quad (10)$$

Trudel and Boisclair (1996) recently showed that activity costs determined using eq. (9) provided similar values (less than 8% difference) to those obtained by converting swimming speed into swimming costs. This suggests that this approach may be adequate for estimating activity costs of fish in the field. In this study, R_s , R_d , F , and U were determined using the parameters presented by Stewart et al. (1983) for lake trout. Fecal losses in Stewart's model (1983) are assumed to vary as a function of the proportion of indigestible matter (e.g. chitin and bone), such that lake trout feeding on invertebrates loses 22% of their energy budget in feces, while PLT lost only 16% of the consumed energy through feces.

Statistical Analyses

Consumption rates, growth rates, activity costs, and activity cost-production ratio of PLT and NPLT were compared with an analysis of covariance (ANCOVA; Sokal and Rohlf 1995) using body size as a covariant. The relationship between growth rates and consumption rates of PLT and NPLT were also compared with an ANCOVA. Growth efficiency and activity costs of PLT and NPLT were also compared with a two-way analysis of variance (2 way ANOVA; Sokal and Rohlf 1995) using diet and maturation status as main effects. Standard errors for C , and DR were derived by age class means from Monte Carlo simulations (Trudel and Boisclair 1993; Sherwood et al. 2000)

Results

Growth Rates

Growth rates ranged from 2.5 and 55.8 kJ/d and from 1.1 and 2.9 kJ/d for PLT and NPLT, respectively, and were positively correlated with body size (Fig. 2)($F_{1,38}=144.9$, $p<0.0001$, $F_{1,16}=146.4$, $p<0.0001$, respectively). PLT were able to reach much larger body sizes than NPLT for any given age. The non-indigenous PLT from Lake Memphremagog and Lake Ontario also had the largest body sizes compared to the indigenous PLT from Lake Opeongo and Great Slave Lake (Fig. 1). Growth rates tended to be higher for PLT than NPLT at any given body size (Fig. 2). PLT grew on the order of 2.2 to 3.6 times faster than NPLT. Growth rates were significantly higher in PLT than NPLT ($F_{1,55}=95.0$, $p<0.0001$).

Consumption Rates

Food consumption rates of PLT and NPLT ranged from 1.0 and 43.9 g/d, and from 1.7 and 19.9 g/d, respectively, and were positively correlated with body size (Fig 3) ($F_{1,38}=193.4$, $p<0.0001$, $F_{1,16}=302.7$, $p<0.0001$, respectively). The standard error of the consumption estimates of PLT and NPLT ranged from 12.8 to 16.7% and from 13.9 to 21.9%, respectively. Food consumption rates tended to be higher for NPLT than for PLT at any given size (Fig. 3). NPLT consumed in the order of 1.9 to 3.3-fold more food than PLT. There was no significant interaction between body size and diet type ($F_{1,54}=2.3$, $p>0.13$), indicating that the slopes of consumption rate-body size relationships did not vary significantly between diet. Only the intercepts of the relationship between consumption and body size differed ($F_{1,55}=57.7$, $p<0.0001$). However, when food

consumption rates were converted to energy units, differences between PLT and NPLT nearly disappeared, because water content is higher and energy densities are lower in invertebrates than in prey fish (Fig. 4)(Table 3, Appendix 3). The interaction between diet and lake trout body size was not significant ($F_{1,54}=3.4$, $p>0.06$), indicating that the relationship between consumption and body size did not differ between diet type. However the intercept of this relationship differed significantly between PLT and NPLT ($F_{1,55}=4.8$, $p<0.03$). On average PLT consume 0.69 kJ more than NPLT for any given body size. It is important to note though that this difference is smaller than the measurement error of these consumption rates, suggesting that the consumption rates of NPLT and PLT are not different. In addition it may be argued that this effect is the result of a single lake, as Lake Ontario fish tended to consume more food than NPLT and other PLT populations. Removing Lake Ontario from the analysis results in a non-significant effect on diet ($F_{1,48}=0.2$, $p>0.6$).

Energy Allocated to Growth

Growth rates were positively correlated to consumption rates for PLT and NPLT ($F_{1,38}=728.8$, $p<0.0001$, $F_{1,16}=62.3$, $p<0.0001$, respectively) (Fig. 5). PLT tended to have growth rates in the order of 1.7 to 3.5 times higher than NPLT at comparable consumption rates (Fig. 5). In addition, growth rates tended to increase faster with consumption rates in PLT than NPLT (Fig. 5). Growth rates between PLT and NPLT lake trout varied significantly ($F_{1,54}=6.9$, $p<0.05$). The interaction between growth rate and consumption rate was also significant ($F_{1,54}=42.9$, $p<0.0001$).

Growth efficiencies of PLT and NPLT ranged from 11.0 and 24.0%, and from 3.6 and 15.4%, respectively. The highest growth efficiency was observed in the PLT from Lake Memphremagog (24.0%) and the lowest growth efficiency was observed in NPLT from Source Lake (3.6%). Growth efficiency tended to be higher in PLT (15.8%) than NPLT (8.3%) even when maturation status was taken into consideration. Juvenile lake trout of either diet had higher growth efficiencies than adult lake trout, presumably because of the increased metabolic costs associated with maturity. However growth efficiency differences between juvenile and adult lake trout appear to be much greater in NPLT than PLT (Fig. 6). Growth efficiency varied significantly between diet type and life stages ($F_{1,54}=55.2$, $p<0.0001$, $F_{1,54}=13.4$, $p<0.001$, respectively) (Fig. 6). The interaction between diet type and life stage was also significant ($F_{1,54}=6.1$, $p<0.02$). Growth efficiency decreased significantly with body size in NPLT ($F_{1,16}=32.56$, $p<0.0001$) but not in PLT ($F_{1,38}=2.9$, $p>0.09$). In addition, growth efficiency tended to decrease much faster with body size in NPLT than PLT (Fig. 7) and the interaction between diet and body size was also significant ($F_{1,54}=42.7$, $p<0.0001$).

Activity Costs

Activity costs of PLT ranged from 2.4 and 148.1 kJ/d and from 0.9 and 24.2 kJ/d for NPLT. Adult fish invested a larger proportion of their budget to activity costs than juvenile fish. However, the difference in activity costs between juvenile and adult fish was higher in NPLT (18.4%) than in PLT (7.8%) (Fig. 8). Activity did not vary significantly between diet type however it did vary for lifestage ($F_{1,54}=3.3$, $p>0.1$, $F_{1,54}=3.8$, $p<0.0001$, respectively). The interaction between diet type and life stage was

also significant ($F_{1,54}=6.2$, $p<0.02$). The energy allocated to activity (active foraging) was positively correlated with body size in PLT and NPLT ($F_{1,38}=19.5$, $p<0.0001$, $F_{1,16}=29.9$, $p<0.0001$; respectively) (Fig. 9). In addition, activity costs tended to increase much faster with body size in NPLT than PLT. The interaction between diet and body size was also significant ($F_{1,54}=30.52$, $p<0.0001$) (Fig. 9).

The activity-production ratio of PLT ranged from 0.88 and 3.56 and from 0.79 and 11.06 for NPLT. The amount of activity required to generate one unit of growth was positively correlated with body size in PLT and NPLT ($F_{1,17}=111.9$, $p<0.0001$; $F_{1,38}=10.4$, $p<0.01$) (Fig. 10). In addition, this ratio tended to increase much faster with body size in NPLT than PLT. The interaction between diet and body size was also significant ($F_{1,54}=59.0$, $p<0.0001$), indicating the slopes of these two lines differed.

Discussion

Lake Trout Energetics

The analyses performed in this study showed that food consumption rates were two to three times higher in NPLT than PLT when they were expressed on a wet weight basis. However when differences in the energy content of the prey consumed by NPLT and PLT were accounted for, NPLT tended to consume slightly less food than PLT. However the mean difference in food consumption rates was within the measurement of error of these estimates and it is thus unlikely that differences in food consumption rates contributed much to explain the substantial difference between growth rates of PLT and NPLT. Our analysis showed that growth and growth efficiency were much lower in NPLT than PLT even when maturation status was taken into consideration, and that

growth efficiency decreased much faster with body size in NPLT. Thus, our analyses suggest that the lower growth and reduced growth efficiency of NPLT cannot be attributed to a lower rate of food consumption. Instead, these results imply that foraging on invertebrates incurs higher energetic costs in lake trout.

Energy losses could be higher in NPLT if they were feeding on prey that was less digestible, if they had higher metabolic rates, or a combination of both factors. Stewart et al. (1983) suggested that the proportion of indigestible matter was higher in invertebrates than in prey fish (e.g. chitin versus bone). Thus, the lower growth efficiency of NPLT observed in this study could possibly be explained by a lower assimilation efficiency of their prey. The magnitude of the difference in the assimilation efficiency assumed by Stewart et al. (1983) for NPLT and PLT (78% versus 84%) appears to be sufficient to explain the average difference in growth efficiency observed between NPLT and PLT in this study (8.3% versus 15.8%). However, it is important to note that the assimilation efficiency of lake trout feeding on invertebrates and on prey fish have yet to be determined. The values assumed by Stewart et al. (1983) in their bioenergetic model of lake trout were derived from experiments performed on walleye (*Stizostedion vitreum*) and brown trout (*Salmo trutta*), and are not necessarily valid for lake trout. Thus, the hypothesis that lake trout have lower assimilation efficiency when they are consuming invertebrates remains to be tested. In addition, the interpretation that the assimilation efficiency is lower in NPLT than PLT cannot explain the steeper reduction in growth efficiency of NPLT with body size observed in this study. Only the intercepts of the relationship between growth efficiency and body size are expected to differ if differences in growth efficiency were solely attributed to differences in assimilation efficiency for

invertebrates and prey fish. In this study, both the slope and intercept of the relationship between growth efficiency and body size differed, indicating that there are other bioenergetic losses beside prey digestibility that may be responsible for the lower growth and growth efficiency achieved by NPLT.

When comparing individuals of the same size foraging costs are also expected to be higher in NPLT than in PLT. First, NPLT consumed more food than PLT on a wet weight basis. Since activity costs are positively correlated with food consumption rates in actively foraging fish (Kerr 1982; Boisclair and Leggett 1989b, c; Boisclair 1992), foraging costs should also be higher in NPLT than in PLT. Secondly, fish that capture each prey individually, such as lake trout, must spend more time and more energy searching for food when they are foraging on smaller prey to obtain a given ration (Paloheimo and Dickie 1966; Kerr 1971a, b; Konkle and Sprules 1986). For instance, according to figure 3 a NPLT weighing 100 g (approximately 20cm) needs to consume approximately 225 dipteran pupae in a day (~10mg/pupae) to meet their energy requirement, while a PLT of that size would need to consume only one prey fish (~1g). Thus NPLT must perform more work to obtain their daily ration. Finally, theoretical models of fish growth also suggest that foraging costs are higher in fish feeding on smaller prey (Kerr 1971a, b). These models predict that foraging costs increase with predator-prey size ratio in gape-limited predators. As a consequence, growth efficiency is expected to (1) be negatively correlated with predator-prey size ratio, and (2) decrease faster with body size in predators feeding on smaller prey, since predator-size ratio increases faster with predator size when they are feeding on smaller prey. This interpretation is consistent with the results obtained in this study, as growth efficiency

decreased faster with body size in NPLT than in PLT. This is also consistent with the simulations performed by Kerr (1971a, b) which showed that growth efficiency decreased faster with body size in lake trout consuming smaller prey, even if smaller prey were more abundant. Thus, the results obtained in this study suggest that foraging on invertebrates is highly costly to lake trout, as invertebrates tend to be less digestible than prey fish, and more energy must be allocated to foraging by NPLT to achieve a given growth rate.

Genetic Controls of Growth

It may be argued that growth differed between NPLT and PLT simply because of genetic differences. However, this interpretation is not consistent with the results of the transplant experiment that has been performed on NPLT in the 1960s in Algonquin Provincial Park (Martin 1966). In 1961 and 1962, 303 lake trout consuming primarily invertebrates were captured from Lake Louisa (Ontario), marked, and transplanted into a lake containing pelagic prey fish (Lake Opeongo, Ontario). The stomach contents of 21 out of the 57 lake trout that were recaptured were examined. Fish was the dominant prey item in the stomachs of these fish. Growth rates of these fish increased tremendously after they were transplanted in their new environment (Martin 1966). Svärdsön (1970) similarly showed that the growth of dwarf whitefish (*Coregonus* sp.) increased after they were transplanted to whitefish-free lakes. Thus, growth rates of a given species appear to be primarily a function of the environment in which they live rather than fixed by their genetics (Werner and Gilliam 1984; Heath and Roff 1987, but see Billerbeck et al. 2000).

Energetics of Stunting in Fish

Stunting represents an extreme condition in the growth of fish, and has frequently been observed in several fish families including salmonidae, percidae, and centrarchidae (Roff 1992). Stunted fish are characterized by a much lower growth than normal fish, reach maturity earlier and at a smaller size, and also tend to have a shorter lifespan (Roff 1992). Stunted fish usually occur in lakes containing high densities of fish (Persson 1986; Amundsen 1989). It is commonly believed that the lower growth of stunted fish is the result of a lower rate of food consumption due to the high density of competitors. Field studies have shown that fish growth and food consumption rates increased following a large reduction in fish biomass (Persson 1986; Amundsen 1989), suggesting that stunting may be due to a strong exploitative competition. However, this may represent a response to a large perturbation of the system, and may not necessarily reflect the conditions experienced by fish when the system is in equilibrium (Boisclair and Leggett 1989b). Furthermore, the lack of a reference site in these studies does not rule out the possibility that the concomitant increase of growth and feeding rates resulted from changes in local environmental conditions, such as increased prey biomass, rather than from a reduction in fish density. The importance of using a reference site to assess the effects of fish removal on fish energetics can be illustrated by the work of Hayes et al. (1992). While food consumption rates of yellow perch from Douglas Lake (Michigan) increased following the massive removal of white sucker (*Catostomus commersoni*), it also increased in yellow perch from a nearby reference lake during the same period (Hayes et al. 1992). Thus, it is unclear if stunting occurs because food consumption rates decreases with fish density in these populations.

Stunting in fish may also occur when suitable prey are lacking or low in density (Martin 1966; Konkle and Sprules 1986). In many instances the organisms that make up the prey base for piscivorous fish such as lake trout do not always form a continuous prey-size spectrum and display gaps (e.g. significant reduction in biomass). If a gap in the prey size spectrum is large enough, the predator might be unable to achieve high growth rates and to reach a body size large enough to enable it to move onto the next size class of prey items. This is usually referred to as a trophic bottleneck (Heath and Roff 1996). Other instances when bottlenecks occur are when a predator reaches its maximum size and no other available prey in that system would otherwise increase predator growth. This trophic bottleneck implies that there is an upper limit in body size that is obtainable for a predator feeding on a particular prey or diet in that system. Heath and Roff (1996), using simulation analyses, showed that trophic bottlenecks occurred as a result of low per capita consumption. In contrast to these simulations, our empirical analyses indicate that NPLT reached a trophic bottleneck due to their high energetic costs associated with feeding on small (relative to their size) and less digestible prey.

Lake Trout Management

Piscivorous fish such as lake trout usually undergo 3 to 4 diet shifts throughout their lives all increasing in food particle size, e.g. zooplankton, invertebrates, minnows, and finally other pelagic fish (Werner and Gilliam 1984). It is these predator-prey interactions, and the specific life stages at which they occur, that are extremely important to community dynamics, and especially to lake trout growth (Mittelbach and Persson 1998). Lake trout going through several diet shifts can be viewed as moving through a

landscape of ecological niches as they increase in size, and move from littoral and benthic to the pelagic zones of the lake, where they will encounter a variety of different resources. Such discrete diet shifts in piscivores are usually associated with abrupt changes in growth and habitat that are reflective of both the abiotic and biotic characteristics of that food web. The introduction of an exotic species usually modifies these interactions, and alters the structure of the food web by redirecting energy flow, and hence, may cause a major restructuring of fish communities (Vander Zanden et al. 1999). Therefore the arrival of an exotic species into a food web can have severe implications at different life stages for native lake trout populations and can drastically alter their growth and life history patterns. The majority of species introductions that have occurred in lake trout lakes have been unintentional, mainly from bait bucket dumping, while others have clearly been deliberate acts in trying to enhance the growth of lake trout communities. Nevertheless, the consequences of altering the food web structure and the magnitude of the species interactions are still poorly understood and warrant strict regulations and guidelines which would prohibit the transferring of fish from one water body to another.

The introduction of rock bass (*Ambloplites rupestris*) and smallmouth bass (*Micropterus dolomieu*) in several lake trout lakes across North America are an example of an invasive species that has had profound effects in several aquatic ecosystems. One particular community interaction resulting from these non-native piscivorous predators has been in the littoral zone of lakes, where their introduction has been immediately followed by a drastic reduction in the composition and size of the minnow community. A similar scenario has occurred in some Haliburton Forest lakes, where a rock bass invasion has reduced the density of littoral prey fish to a point where presently the lake trout feed

almost entirely on zooplankton and benthic invertebrates (Casselman and Grant 1998; Vander Zanden et al. 1999). This example of an exotic species introduction coincides with an abrupt and drastic diet shift in lake trout, followed by both a reduction in the maximum observable size and in age and size at maturity of lake trout in these systems (J.M. Casselman, personal communication). In this instance, the introduction of bass influences and changes the food web structure of lake trout lakes to such a degree that there are severe repercussions for native lake trout populations in terms of diet and growth. The interaction between native lake trout populations and the prey species in their community are most often in a state of equilibrium that must be respected and conserved. The importance of food web structure and prey availability with regards to lake trout growth are demonstrated in this study. Our work also illustrate how the bioenergetics of a population can be utilized to make informative decisions in management policies of a fish species. Therefore, fisheries management would benefit greatly from taking a different point of view and should not consist of just a general management policy for individual species. It should also involve looking at individual food web structures in lakes, and hence utilizing a much broader ecosystem approach.

Energetics and Life History Strategies

The life history parameters of lake trout populations are important determinants of lake trout productivity. Understanding how life history parameters vary among populations is also important to predict potential fish yield and properly manage these exploited populations (Shuter et al. 1998). Most life history models that have been developed try to predict the age and size of maturity that will maximize lifetime

reproductive output (Roff 1984). In these models, the age at maturity is usually determined by optimizing trade-offs between growth, reproduction, and mortality (Roff 1992; Stearns 1992).

Growth and mortality are two factors that can greatly influence the age at first maturity (Roff 1984; Stearns and Koella 1986; Hutchings 1993), and will affect the renewal rates of populations, which has important implications for fisheries managers because it helps them to determine the potential for fish yield. Roff (1984) assumes that fast growing fish have high mortality rates, and as such his model predicts early maturation. However the Great Slave Lake and Lake Opeongo lake trout populations exhibit late maturation in combination with rapid growth, and this might suggest a relatively benign mortality curve. In contrast, stunted and dwarf fish usually mature earlier than fast or normally growing populations (Stearns and Koella 1986; Roff 1992; Fox 1994; Bertschy and Fox 1999; Trudel et al. 2000b). This seems reasonable, since stunted growth would imply a low potential fitness gain for delaying reproduction regardless of survivorship. Similarly, despite their lower growth rate, NPLT matured earlier than indigenous PLT populations in this study. Roff (1992) argued that stunted fish matured earlier because their mortality rates were also higher, although there is little evidence to support high mortality rates in stunted fish populations. However it seems likely that when stunting is severe, survivorship should have little effect on the onset of maturation.

Hutchings (1993) suggested that the age at maturity in fish was negatively correlated to the ratio of adult to juvenile growth. His model predicts that fish with high juvenile growth and low adult growth should mature earlier, while fish with fast adult

growth and low juvenile growth should mature later. Therefore, his model accurately predicts that stunted fish mature earlier (Fox 1994; Bertschy and Fox 1999). In accordance with Hutchings' model, Trudel et al. (2000b) recently argued that when growth levels off, fish should mature earlier, as the gain in fitness (e.g. more eggs) obtained by delaying maturation is likely to be smaller than the risk of dying before reproducing. They also showed that fish with low growth efficiency matured earlier than fish with high growth efficiency, probably because their growth rate leveled-off more rapidly. The results obtained in this study are consistent with this interpretation, as NPLT had lower growth efficiency than indigenous PLT populations, and they also matured at an earlier age. These results are also consistent with recent work performed on other salmonids that also showed that fish with low growth efficiency within a cohort matured earlier (Forseth et al. 1994; Tucker and Rasmussen 1999). Thus, life-history strategies might be linked to energy allocation patterns in fish.

The two stocked populations of PLT matured at an earlier age than the indigenous PLT populations. These stocked populations also had higher growth rate than the indigenous populations. These stocking programs are necessary in Lake Ontario and Lake Memphremagog to sustain the high demand of anglers in these lakes, and hence, to sustain the high mortality rates associated with exploitation. High levels of fishing exploitation in combination with high growth rates and a rapid growth early on in life, can possibly reduce the age of first maturation even more than just growth rate or mortality alone (Hutchings 1993). Alternatively, it is possible that these stocked populations are not in equilibrium and did not have sufficient time to evolve towards the optimum age at reproduction.

Thus, NPLT have a smaller size (low GE), mature earlier, have a shorter life-span and are recruited to a fishery at a much smaller size and age (Olver et al. 1991). In these NPLT populations, the age at vulnerability to fishing is similar to the age at first maturity. In contrast PLT have larger body size (high GE), mature later, and have longer life-spans (low mortality). In addition, the age at vulnerability from fishing precedes the age of first maturity by a number of years. Hence, NPLT are likely to be more resilient to increases in fishing pressures since most of the population has matured by the time they are exposed to fishing mortality (Olver et al. 1991). On the other hand PLT are more likely to be harvested prior to maturation and are less likely to escape fishing mortality and spawn. This might result in a population with a heightened sensitivity to overfishing (Matuszek et al. 1990). NPLT can therefore support a much higher level of fishing mortality before it causes population extinction than PLT (Payne et al. 1990). Therefore, there is a necessity for fisheries managers to enforce regulations that would ensure a balance between the age at vulnerability and the age at first maturity, such as slot limits for individual populations that would preserve natural fish populations and keep vulnerability and maturity schedules in check. In addition, the link between diet, growth efficiency, and age at first reproduction that was observed in this study suggest that fishery managers should take into consideration food web structure to properly assess the fishing pressure lake trout populations could sustain.

Conclusion

Our study analyses the bioenergetics of lake trout growth and growth efficiency, which permits a much better understanding of lake trout populations and characterization

of their life history patterns. The utilization of tracer mass balance methods for estimating consumption rates has allowed us to differentiate energy budgets within a salmonid species found in the wild. Our study associates a significant increase in energy allocated to active foraging and a decrease in prey digestibility when diet shifts leading to piscivory are not achieved in 2 of our 6 lake trout populations. Lack of suitable prey items when a predator such as the lake trout increases in size indeed leads to much greater energy demands as the individuals in that population mature. In neighboring lakes where the lake trout can easily go through ontogenetic diet shifts and switch up to a larger prey item, active foraging costs are kept relatively low and a greater portion of the energy budget can be allocated towards growth. Examining the bioenergetics of lake trout populations clearly allows us to see differences in ecosystem processes in terms of energy transfer, which are associated with different predator-prey interactions. The efficiency of the transfer of energy clearly is something that is quantifiable and can be readily measured in the wild. Many studies have done so with similar bioenergetic analyses and suggest that there may be links between age at maturity, population density and the transfer of trophic energy between predator and prey. This can have an enormous impact on the way we manage and view natural aquatic resources. Therefore the assessment of energy flow and its importance to ecosystem processes becomes a very informative tool as a measure of bioenergetic performance in the field.

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Table 1. Water temperature (T , °C) curves of 6 lake trout lakes in Canada.

Lake	Curve
Opeongo	$T = 3.7 + 17.7e^{-(J-204.7)^2/66.7^2}$
Ontario, Memphremagog ^a	$T = 3.8 + 14.7e^{-(J-219)^2/66.7^2}$
Great Slave ^b	$T = 3.8 + 12.0e^{-(J-220.6)^2/30.3^2}$
Happy Isle	$T = 2.6 + 21.0e^{-(J-200)^2/82.5^2}$
Source	$T = 2.6 + 21.0e^{-(J-199)^2/82.0^2}$

Note: J , day of the year

^aData from Trudel et al. (2000a)

^bData from Rowan and Ramussen (1996)

Table 2. Fish diet (% volume) arranged according to body size (mm).

Lake	<200mm	200-299mm	300-399mm	400-499mm	500-599mm	>600mm
Opeongo	80Inv,20Y	26Inv,74Y	100C	100C	100C	100C
Ontario ^a	50SS, 30RS, 20A	50SS, 30RS, 20A	40SS, 40RS, 20A	25SS, 50RS, 25A	10SS, 40RS, 50A	30RS,70A
Memphremagog ^b	----	100RS	100RS	100RS	100RS	100RS
Great Slave ^c	----	100C	100C	100C	100C	100C
Happy Isle	100Inv	100Inv	89Inv, 11Y	----	----	----
Source	100Inv	100Inv	97.8Inv, 2.2Y	----	----	----

Note: Cisco (C), Rainbow Smelt (RS), Slimy Sculpin (SS), Alewife (A), Young of the year perch (Y), Invertebrates (Inv)

^aData from Borgman and Whittle (1992)

^bData from Trudel et al. (2000a)

^cData from Rowan and Rasmussen (1996)

Table 3. Fish diet [$^{137}\text{Cs}_p$] of prey (SE in parenthesis), caloric content of prey, assimilation of ^{137}Cs from the prey (α).

Prey Item	Energy Density (J/g wet weight)	[$^{137}\text{Cs}_p$] (Bq/kg)	α
Opeongo			
Cisco	10 464 ^{a,b}	4.74(0.19)	0.69 ^c
Young of the year Perch	2511 ^d	4.13(0.36)	0.69 ^c
Benthic Invertebrates	3210 ^e	2.96(0.50)	0.234 ^f
Great Slave			
Cisco	10 464 ^{a,b}	3.14 ^c (0.21)	0.69 ^c
Memphremagog			
Rainbow Smelt	6655 ^a	0.70 ^g	0.69 ^c
Happy Isle			
Young of the year Perch	2511 ^d	4.72(0.43)	0.69 ^c
Benthic Invertebrates	3210 ^e	2.61(0.35)	0.234 ^f
Source			
Young of the year Perch	2511 ^d	6.68(1.04)	0.69 ^c
Benthic Invertebrates	3210 ^e	2.43(0.19)	0.234 ^f

Note: Opeongo (Op), Great Slave (GS), Memphremagog (Memp), Happy Isle (HI), Source (Sr)

^aData from Rottiers and Tucker (1982)

^bData from Mason et al. (1998)

^cData from Rowan and Rasmussen (1996)

^dData from Post et al. (1990)

^eData from Cuming and Wuycheck (1971)

^fData from Forseth et al. (1992)

^gData from Trudel et al. (2000a)

Table 4. Fish diet caloric content of prey, Hg concentration of prey according to prey size (length), Assimilation of Hg from the prey (α).

Prey Item	Energy Density (J/g wet weight)	[Hg _p] (µg/g)	α
Ontario			
Alewife	6822 ^a	$\text{Log}(C) = -5.22 + 3.22 \cdot \log(l_p)^b$	0.80 ^c
Rainbow Smelt	6655 ^a	$\text{Log}(C) = -3.42 + 1.72 \cdot \log(l_p)^b$	0.80 ^c
Slimy Sculpin	5743 ^a	$\text{Log}(C) = -2.28 + 0.93 \cdot \log(l_p)^b$	0.80 ^c

Note: length of prey (l_p)

^aData from Rottiers and Tucker (1982)

^bData from Borgman and Whittle (1992)

^cData from Trudel et al. (2000a)

Figure 1. Growth curves of six lake trout populations from across Canada. Solid lines represent piscivorous populations, while dashed lines represent non-piscivorous populations.

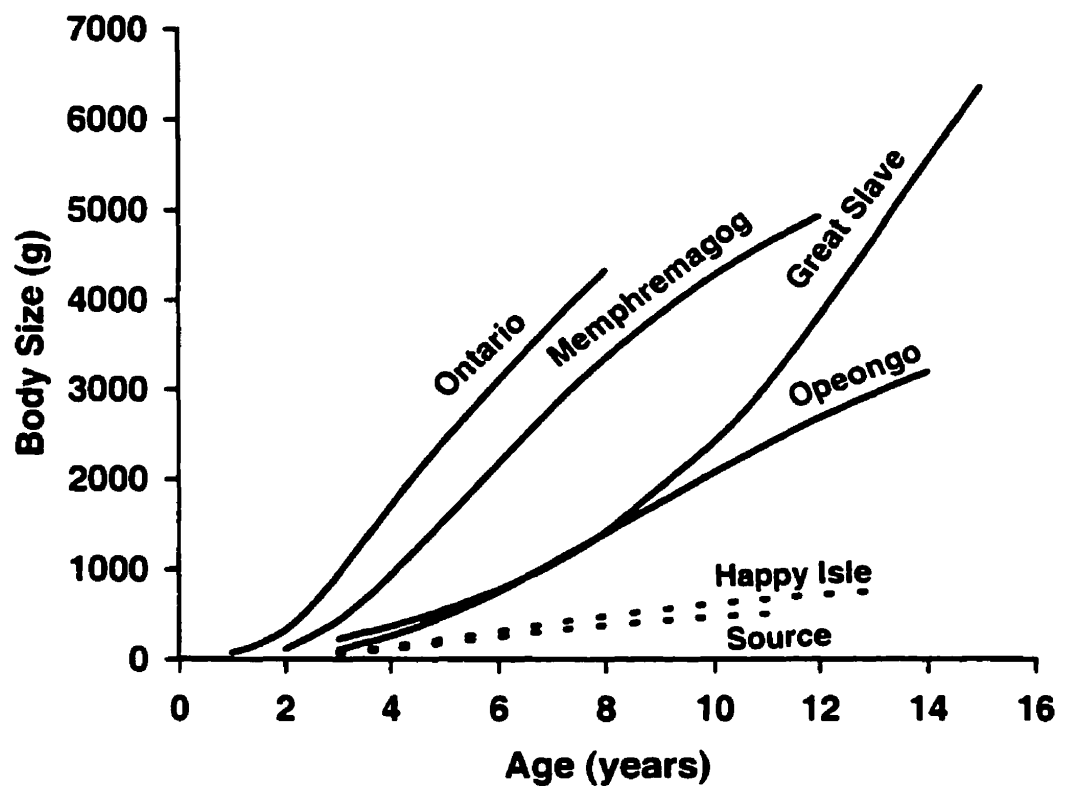


Figure 2. Absolute growth rate (kJ/d) as a function of body size (g).

NPLT; $\log_{10}P = 0.46(0.04) \cdot \log_{10}W - 0.86(0.10)$; $R^2=0.90$; $SE_{est}=0.05$; $n=18$; $p<0.0001$

PLT; $\log_{10}P = 0.66(0.06) \cdot \log_{10}W - 0.88(0.17)$; $R^2=0.79$; $SE_{est}=0.17$; $n=40$; $p<0.0001$

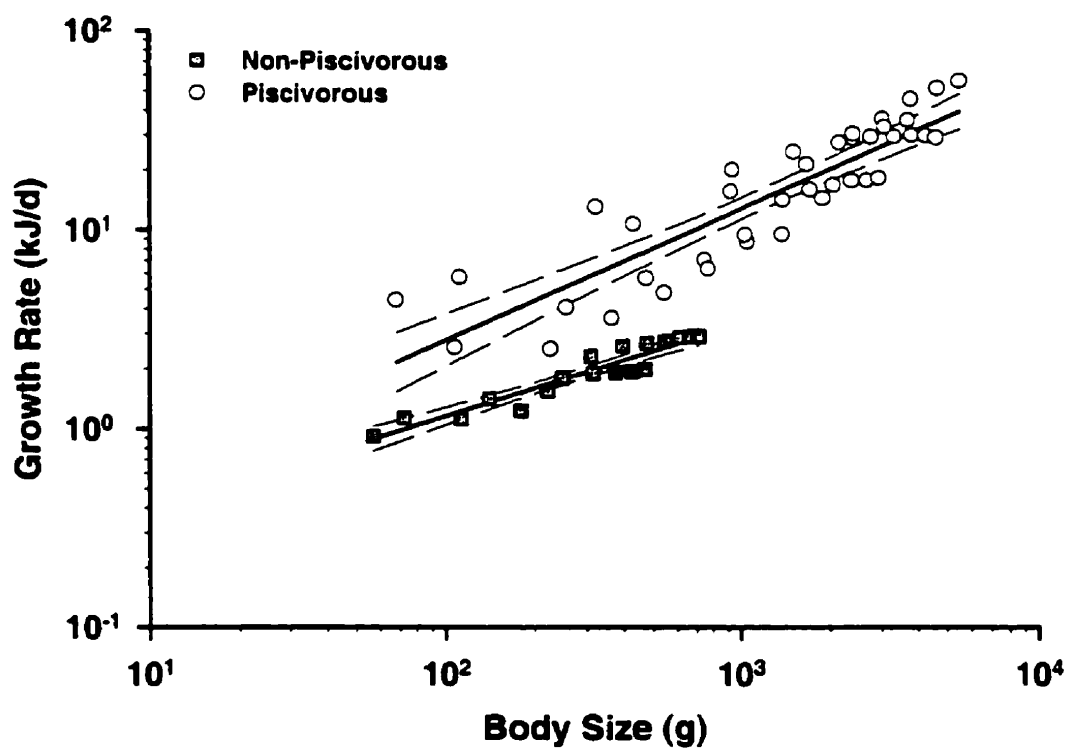


Figure 3. Absolute consumption rate (g/d) as a function of body size (g).

NPLT; $\log_{10}DR = 1.06(0.06) \cdot \log_{10}W - 1.77(0.15)$; $R^2=0.95$; $SE_{est}=0.08$; $n=18$; $p<0.0001$

PLT; $\log_{10}DR = 0.86(0.06) \cdot \log_{10}W - 1.69(0.19)$; $R^2=0.84$; $SE_{est}=0.19$; $n=40$; $p<0.0001$

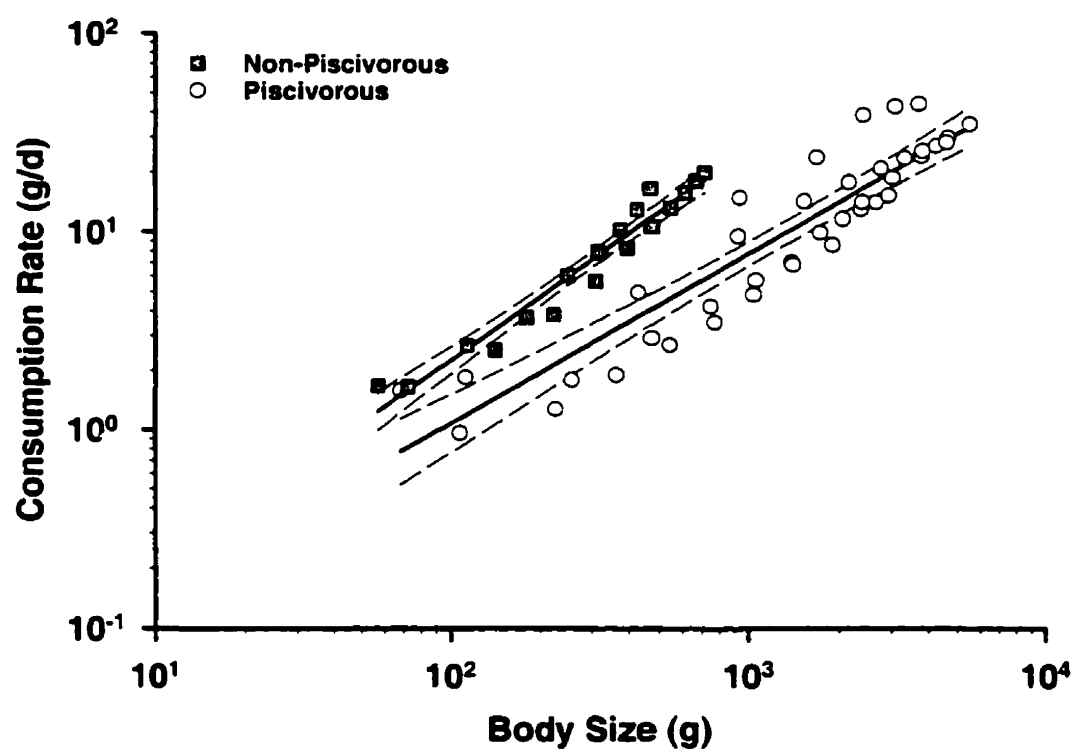


Figure 4. Absolute consumption rate (kJ/d) corrected for differences in energy density of the two diet types as a function of body size (g) (PLT black solid line, NPLT long dash, PLT (without Lake Ontario) grey short dash).

(—) $\log_{10}DR = 0.73(0.05) \cdot \log_{10}W - 0.29(0.14)$; $R^2=0.87$; $SE_{est}=0.14$; $n=40$; $p<0.0001$

(— —) $\log_{10}DR = 0.92(0.06) \cdot \log_{10}W - 0.88(0.15)$; $R^2=0.94$; $SE_{est}=0.08$; $n=18$; $p<0.0001$

(- - -) $\log_{10}DR = 0.79(0.04) \cdot \log_{10}W - 0.51(0.11)$; $R^2=0.94$; $SE_{est}=0.10$; $n=33$; $p<0.0001$

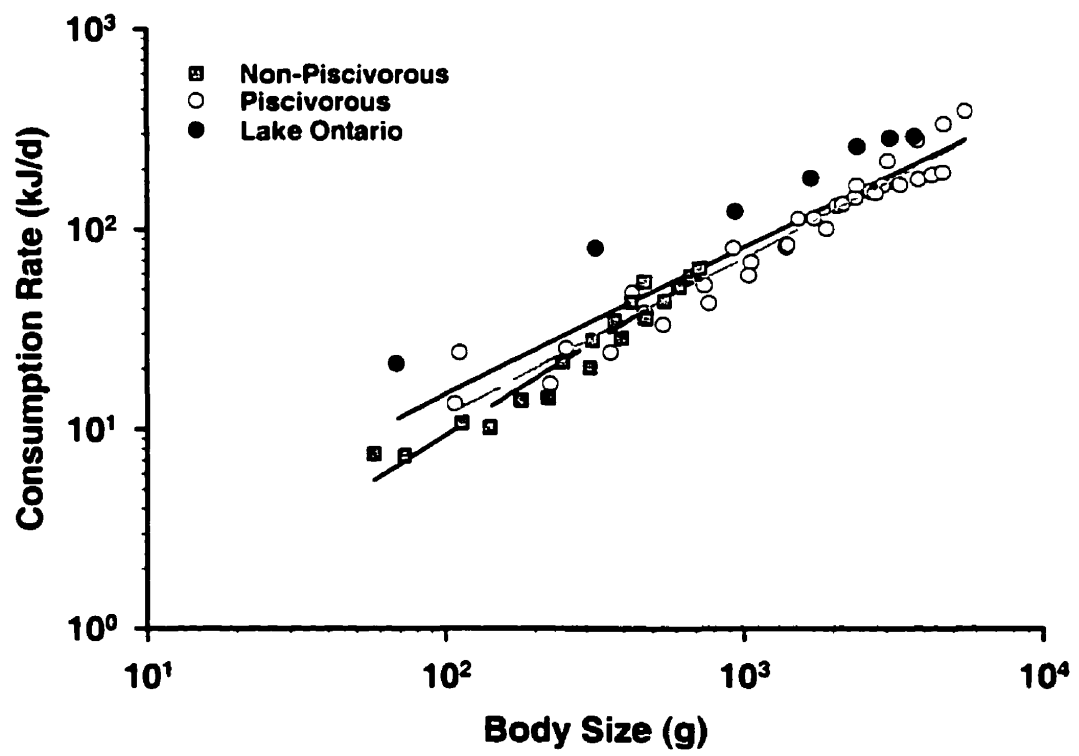


Figure 5. Relationship between growth rates (kJ/d) and absolute consumption rates (kJ/d).

NPLT; $\log_{10}P = 0.46(0.06) \cdot \log_{10}DR - 0.36(0.08)$; $R^2=0.80$; $SE_{est}=0.07$; $n=18$; $p<0.0001$

PLT; $\log_{10}P = 0.92(0.03) \cdot \log_{10}DR - 0.65(0.07)$; $R^2=0.95$; $SE_{est}=0.08$; $n=40$; $p<0.0001$

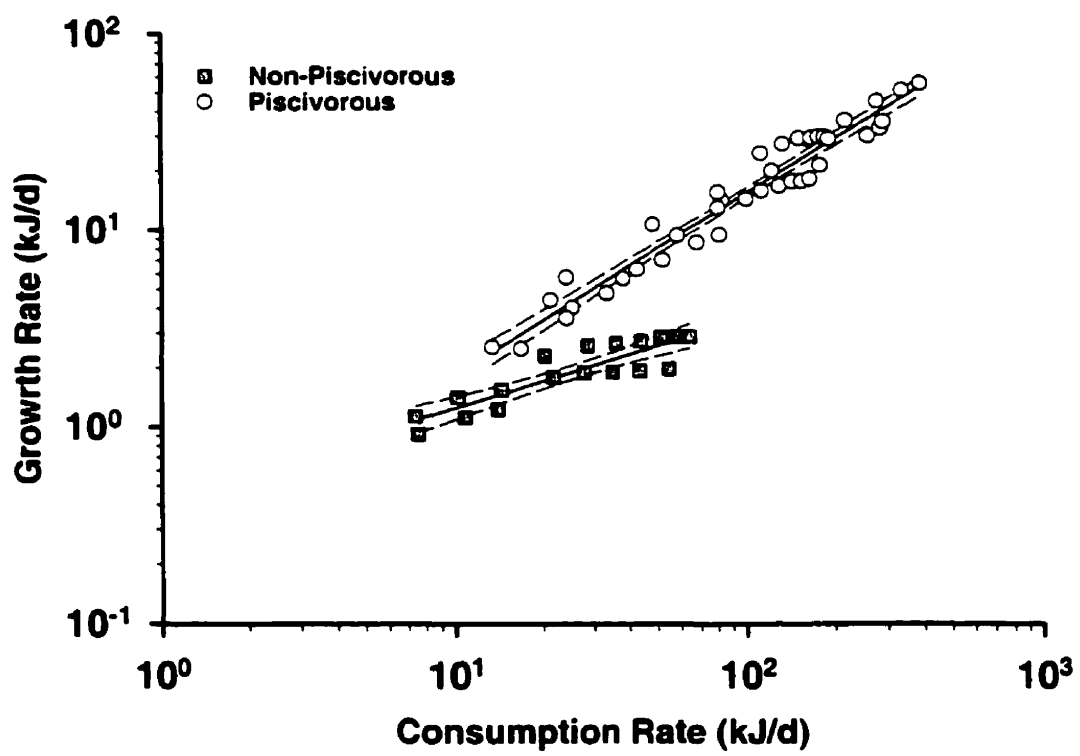


Figure 6. Proportion of the energy budget allocated to growth between juvenile and adult life stages of non-piscivorous and piscivorous lake trout (error bars represent 1 standard error).

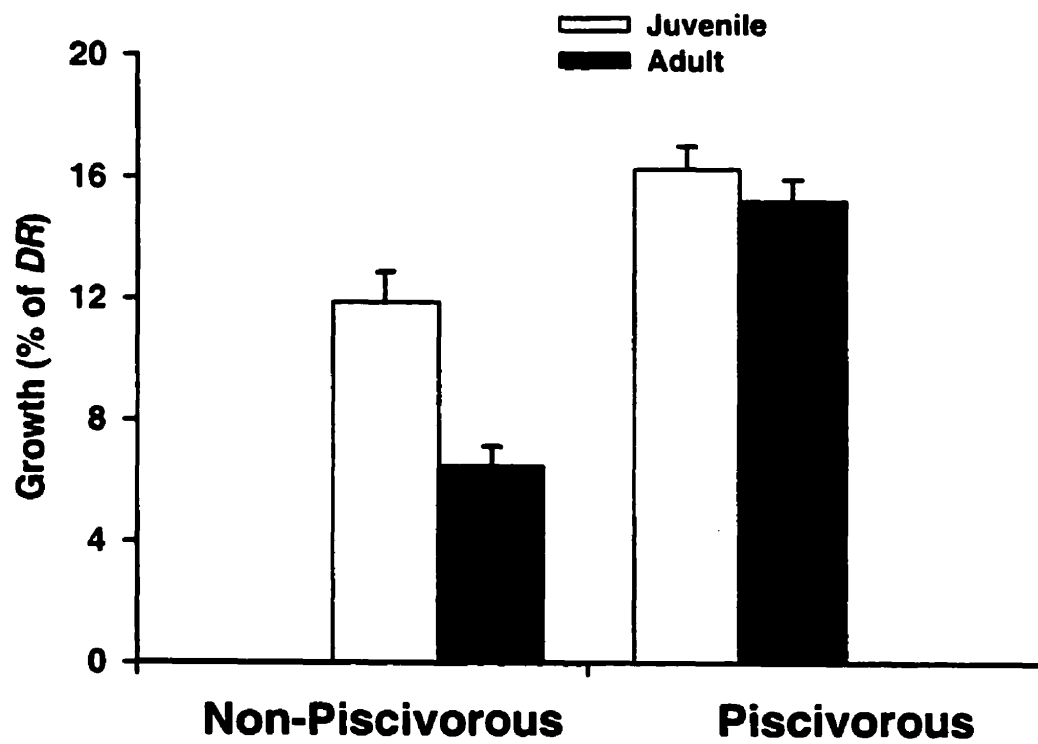


Figure 7. Relationship between growth efficiency (% *DR*) and body size (g) for juvenile and adult life stages in non-piscivorous and piscivorous lake trout.

NPLT; $\log_{10}GE = -7.4 \cdot 10^{-4}(0.00) \cdot W + 1.14(0.05)$; $R^2=0.67$; $SE_{\text{est}}=0.11$; $n=18$; $p<0.0001$

PLT; $\log_{10}GE = -1.6 \cdot 10^{-5}(0.00) \cdot W + 1.22(0.02)$; $R^2=0.07$; $SE_{\text{est}}=0.09$; $n=40$; $p<0.1$

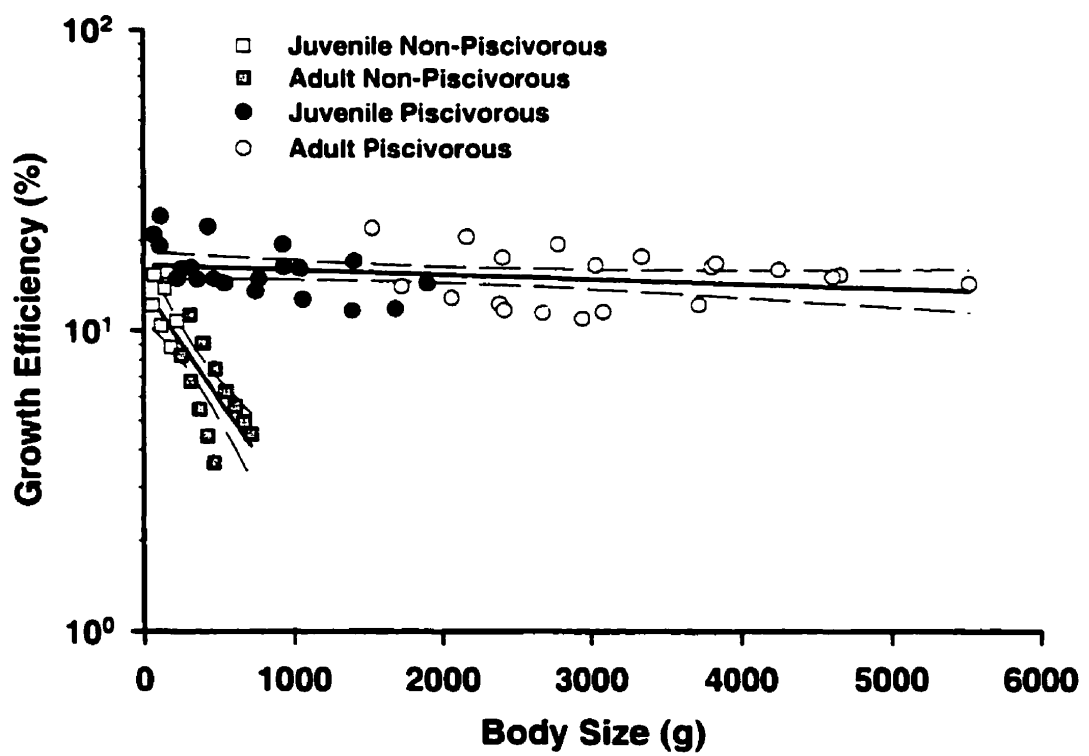


Figure 8. Proportion of the assimilated energy budget ($DR-F$) allocated to activity between juvenile and adult life stages of non-piscivorous and piscivorous lake trout (error bars represent 1 standard error).

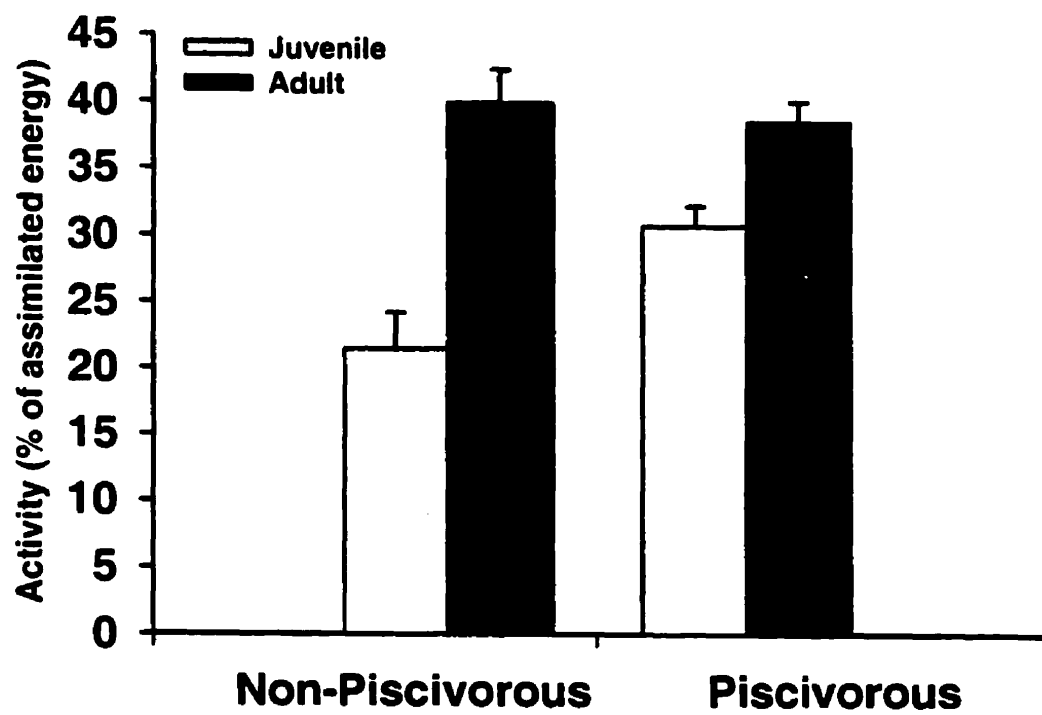


Figure 9. Relationship between activity and body size (g) for juvenile and adult life stages in non-piscivorous and piscivorous lake trout.

NPLT; $R_A = 4.71 \cdot 10^{-2} (0.01) \cdot W + 17.10 (3.49)$; $R^2 = 0.65$; $SE_{est} = 7.24$; $n = 18$; $p < 0.0001$

PLT; $R_A = 3.06 \cdot 10^{-3} (0.00) \cdot W + 28.58 (1.69)$; $R^2 = 0.33$; $SE_{est} = 6.42$; $n = 40$; $p < 0.0001$

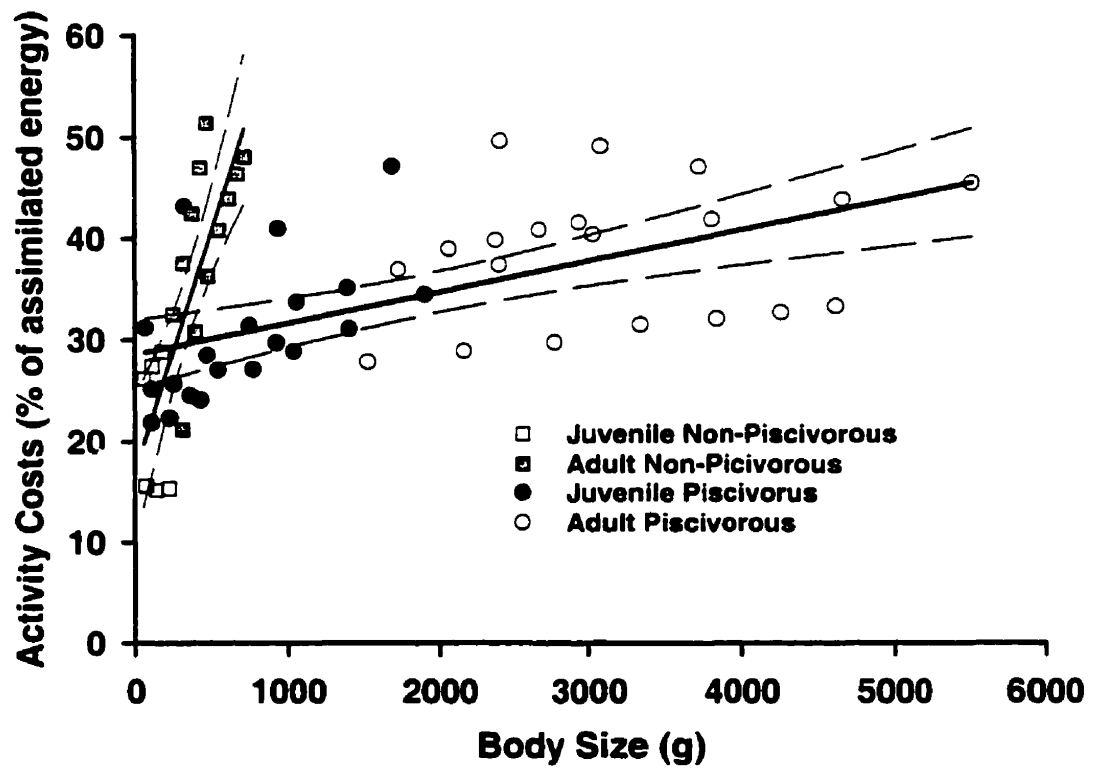
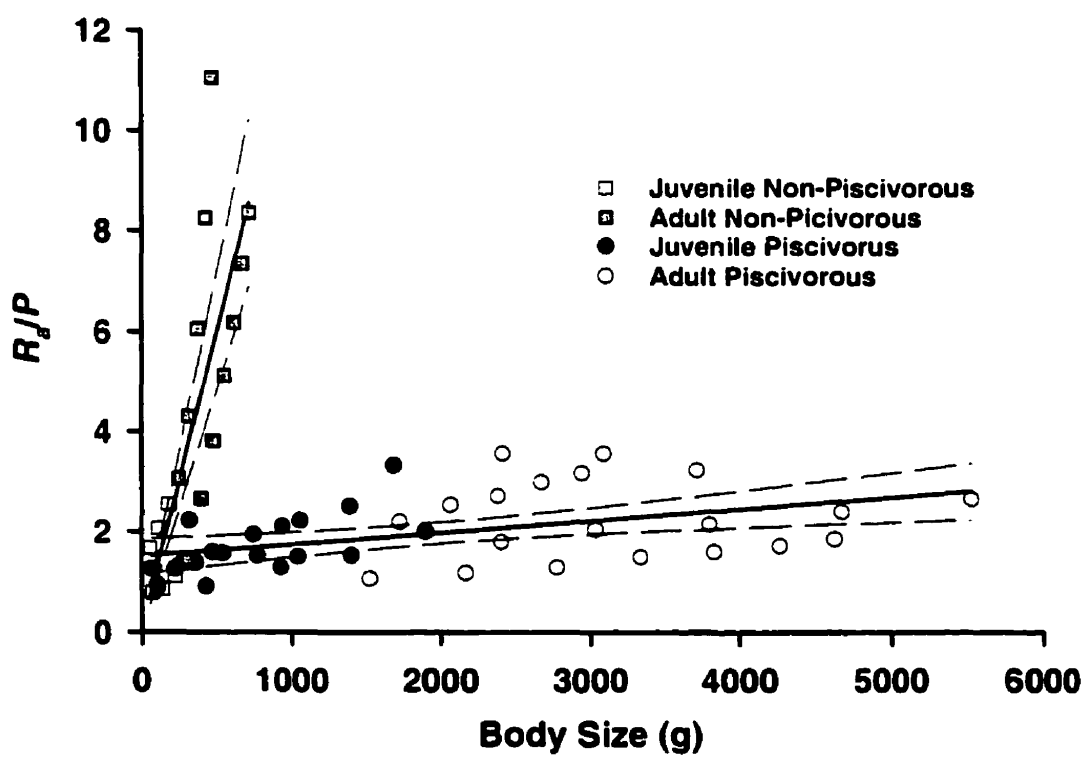


Figure 10. The relationship between the ratio R_A/P and body size (g).

NPLT; $R_A/P = 1.2 \cdot 10^{-2} (0.00) \cdot W$; $R^2=0.87$; $SE_{est}=1.94$; $n=18$; $p<0.0001$

PLT; $R_A/P = 2.3 \cdot 10^{-4} (0.00) \cdot W + 1.50(0.18)$; $R^2=0.21$; $SE_{est}=0.67$; $n=40$; $p<0.0001$



Appendix 1.

Sample size, Age, Body size, ^{137}Cs concentration in muscle tissue, ^{137}Cs concentration in the prey, pooled ^{137}Cs assimilation efficiency, energy density of diet for lake trout.

<i>n</i>	Age (years)	W_t (g)	$W_{t+\Delta t}$ (g)	$[^{137}\text{Cs}_t]$ (Bq/kg)	$[^{137}\text{Cs}_{t+\Delta t}]$ (Bq/kg)	$[^{137}\text{Cs}_p]$ (Bq/kg)	α	Energy Density of Diet (J/g)
Opeongo								
5	3i	108	257	4.49	5.69	3.19	0.33	3066
15	4i	257	474	5.69	6.54	4.28	0.57	8576
40	5i	474	748	6.54	7.17	4.74	0.69	10464
32	6i	748	1060	7.17	7.65	4.74	0.69	10464
29	7i	1060	1394	7.65	8.03	4.74	0.69	10464
21	8i	1394	1733	8.03	8.33	4.74	0.69	10464
20	9m	1733	2065	8.33	8.57	4.74	0.69	10464
11	10m	2065	2382	8.57	8.77	4.74	0.69	10464
8	11m	2382	2677	8.77	8.93	4.74	0.69	10464
3	12m	2677	2947	8.93	9.07	4.74	0.69	10464
3	13m	2947	3190	9.07	9.18	4.74	0.69	10464
Great Slave Lake^{a,b}								
1	3i	227	363	4.53	4.60	3.14	0.69	10464
1	4i	363	544*	4.60	4.69*	3.14	0.69	10464
0	5i	544*	771	4.69*	4.81	3.14	0.69	10464
3	6i	771	1043	4.81	4.94	3.14	0.69	10464
6	7i	1043	1406	4.94	5.12	3.14	0.69	10464
4	8i	1406	1905	5.12	5.37	3.14	0.69	10464
2	9i	1905	2404	5.37	5.62	3.14	0.69	10464
3	10m	2404	3039	5.62	5.94	3.14	0.69	10464
7	11m	3039	3810	5.94	6.33	3.14	0.69	10464
4	12m	3810	4672	6.33	6.76	3.14	0.69	10464

3	13m	4672	5534	6.76	7.19	3.14	0.69	10464
2	14m	5534	6350	7.19	7.60	3.14	0.69	10464

Lake Memphremagog^c

18	2i	112	430*	1.37	1.44*	0.7	0.69	6655
0	3i	430*	928	1.44*	1.50	0.7	0.69	6655
20	4i	928	1530	1.50	1.69	0.7	0.69	6655
4	5m	1530	2165	1.69	1.69	0.7	0.69	6655
13	6m	2165	2779	1.69	1.69	0.7	0.69	6655
11	7m	2779	3342	1.69	1.69	0.7	0.69	6655
7	8m	3342	3839	1.69	1.69	0.7	0.69	6655
7	9m	3839	4266	1.69	1.69	0.7	0.69	6655
8	10m	4266	4625	1.69	1.69	0.7	0.69	6655
4	11m	4625	4923	1.69	1.69	0.7	0.69	6655

Happy Isle Lake

9	3i	72	141	4.22	4.22	2.61	0.23	3204
19	4i	141	223	4.22	4.22	2.61	0.23	3204
6	5i	223	309	4.22	4.22	2.61	0.23	3204
7	6m	309	395	4.22	4.64	2.71	0.26	3170
8	7m	395	476	4.64	5.94	2.84	0.28	3128
12	8m	476	549	5.94	7.09	2.84	0.28	3128
9	9m	549	613	7.09	8.12	2.84	0.28	3128
5	10m	613	669	8.12	9.05	2.84	0.28	3128
3	11m	669	717	9.05	9.90	2.84	0.28	3128
3	12m	717	757	9.90	10.68	2.84	0.28	3128

Source Lake

6	3i	57	113	4.95	4.95	2.43	0.23	3204
15	4i	113	180	4.95	5.01	2.43	0.23	3204
35	5i	180	249	5.01	5.15	2.43	0.23	3204

13	6m	249	315	5.15	5.51	2.53	0.24	3189
11	7m	315	374	5.51	6.09	2.53	0.24	3189
8	8m	374	426	6.09	6.88	2.53	0.24	3189
1	9m	426	470	6.88	7.88	2.53	0.24	3189
2	10m	470	507	7.88	9.09	2.53	0.24	3189

Note: i, immature; m, mature.

^aData from Rowan and Rasmussen (1996)

^bData from Elliott et al. (1981)

^cData from Trudel et al. (2000a)

^{*}Data calculated from linear and non-linear regressions

Appendix 2.

Sample size, age, body size, Hg concentration lake trout at time $t + \Delta t$, Hg concentration in the prey, Hg assimilation efficiency, and energy density of diet consumed by lake trout.

Age (years)	W_t (g)	$W_{t+\Delta t}$ (g)	$[Hg_t]$ ($\mu\text{g/g}$)	$[Hg_{t+\Delta t}]$ ($\mu\text{g/g}$)	$[Hg_p]$ ($\mu\text{g/g}$)	α	Energy Density of Diet (J/g)
Lake Ontario^{a,b,c}							
1i	68	322	0.03	0.06	0.021	0.80	6228
2i	322	939	0.06	0.10	0.025	0.80	6320
3i	939	1690	0.10	0.12	0.029	0.80	6467
4i	1690	2414	0.12	0.15	0.032	0.80	6647
5i	2414	3090	0.15	0.18	0.035	0.80	6772
6m	3090	3723	0.18	0.20	0.038	0.80	6772
7m	3723	4320	0.20	0.21	0.041	0.80	6772

^aData from Borgmann and Whittle (1992)

^bData from Madenjian et al. (1995)

^cData From Trudel et al. (2000a)

Appendix 3.

Age, Consumption Rate, Growth Rate, Daily Ration, Production, Activity Rate, Activity Multiplier, Standard Metabolism and Growth Efficiency in lake trout (values in parenthesis are standard errors obtained from Monte Carlo Simulations).

Age (years)	<i>C</i> (g·g ⁻¹ ·d ⁻¹)	<i>G</i> (g·g ⁻¹ ·d ⁻¹)	<i>DR</i> (kJ/d)	<i>P</i> (kJ/d)	<i>R_a</i> (kJ/d)	Activity Multiplier	<i>R_s</i> (kJ/d)	<i>GE</i> (%)
Lake Opeongo								
3i	0.0089 (0.0010)	0.0024	13.33 (0.45)	2.55	2.41	1.73	3.28	19.1
4i	0.0070 (0.0007)	0.0017	25.18 (0.81)	4.06	5.41	1.86	6.32	16.1
5i	0.0061 (0.0006)	0.0013	37.94 (1.43)	5.68	9.03	2.00	9.07	15.0
6i	0.0056 (0.0007)	0.0009	52.06 (1.81)	7.05	13.69	2.15	11.88	13.5
7i	0.0054 (0.0006)	0.0008	67.89 (2.47)	8.65	19.15	2.30	14.75	12.7
8i	0.0050 (0.0005)	0.0006	80.88 (2.46)	9.47	23.79	2.37	17.42	11.7
9m	0.0057 (0.0007)	0.0008	112.97 (4.02)	15.88	34.90	2.74	20.02	14.1
10m	0.0056 (0.0006)	0.0007	130.19 (4.32)	16.76	42.48	2.90	22.35	12.9
11m	0.0054 (0.0005)	0.0006	143.71 (4.79)	17.68	47.91	2.96	24.48	12.3

12m	0.0053 (0.0005)	0.0005	154.55 (5.13)	17.72	52.84	3.01	26.30	11.5
13m	0.0052 (0.0005s)	0.0005	165.67 (5.48)	18.21	57.65	3.06	27.97	11.0

Great Slave Lake^{a,b}

3i	0.0056 (0.0007)	0.0013	16.75 (0.63)	2.50	3.13	1.64	4.87	14.9
4i	0.0052 (0.0007)	0.0011	24.04 (0.94)	3.57	4.93	1.75	6.57	14.9
5i	0.0049 (0.0005)	0.0010	33.17(1.09)	4.78	7.50	1.88	8.50	14.4
6i	0.0045 (0.0006)	0.0008	42.35 (1.74)	6.31	9.60	1.90	10.62	14.9
7i	0.0046 (0.0006)	0.0008	58.42 (2.18)	9.39	14.11	2.08	13.11	16.1
8i	0.0049 (0.0007)	0.0008	82.76 (0.64)	14.14	21.55	2.33	16.17	17.1
9i	0.0045 (0.0006)	0.0006	100.05(4.01)	14.42	28.85	2.49	19.43	14.4
10m	0.0058 (0.0006)	0.0009	165.28 (5.74)	28.89	51.68	3.25	23.00	17.5
11m	0.0061 (0.0008)	0.0009	218.26 (8.23)	36.08	73.74	3.73	26.97	16.5
12m	0.0063 (0.0008)	0.0008	278.10 (10.86)	45.34	97.50	4.10	31.44	16.3
13m	0.0063 (0.0008)	0.0008	335.36 (11.30)	51.37	122.99	4.44	35.80	15.3
14m	0.0063 (0.0008)	0.0007	388.93 (13.15)	55.85	148.07	4.72	39.82	14.4

Lake Memphremagog^c

2i	0.0164 (0.0023)	0.0037	23.98 (0.94)	5.75	5.04	2.19	4.24	24.0
3i	0.0115 (0.0016)	0.0021	48.08 (1.87)	10.68	9.69	1.99	9.76	22.2

4i	0.0102 (0.0015)	0.0014	80.24 (3.26)	15.56	19.93	2.35	14.79	19.4
5m	0.0093 (0.0011)	0.0012	112.35 (3.68)	24.63	26.14	2.33	19.63	21.9
6m	0.0082 (0.0012)	0.0010	133.48 (5.44)	27.36	32.24	2.34	24.05	20.5
7m	0.0075 (0.0011)	0.0008	151.32 (5.71)	29.30	37.61	2.35	27.91	19.4
8m	0.0070 (0.0010)	0.0007	166.72 (6.29)	29.46	43.89	2.41	31.13	17.7
9m	0.0066 (0.0010)	0.0006	177.79 (6.99)	29.88	47.68	2.41	33.86	16.8
10m	0.0063 (0.0008)	0.0005	186.37 (6.14)	29.75	50.94	2.41	36.10	16.0
11m	0.0061 (0.0009)	0.0005	192.28 (7.33)	29.05	53.56	2.41	37.89	15.1

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Lake Ontario^c

1i	0.0230(--)	0.0043	21.21(--)	4.42	5.53	2.68	3.29	20.8
2i	0.0240(--)	0.0029	80.05(--)	13.01	28.94	4.60	8.04	16.2
3i	0.0160(--)	0.0016	122.45(--)	20.02	42.01	3.91	14.44	16.3
4i	0.0140(--)	0.0010	179.82(--)	21.32	70.97	4.55	19.99	11.9
5m	0.0160(--)	0.0007	258.71(--)	30.24	107.56	5.53	23.74	11.7
6m	0.0140(--)	0.0005	284.69(--)	32.91	117.05	5.21	27.80	11.6
7m	0.0120(--)	0.0004	291.21(--)	35.57	114.81	4.65	31.45	12.2

Happy Isle Lake

3i	0.0228 (0.0043)	0.0018	7.38 (0.37)	1.13	0.90	1.40	2.27	15.4
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4i	0.0180 (0.0026)	0.0013	10.22 (0.36)	1.41	1.21	1.36	3.34	13.8
5i	0.0172 (0.0035)	0.0009	14.34 (0.80)	1.55	1.72	1.34	5.11	10.8
6m	0.0183 (0.0021)	0.0009	20.26 (0.69)	2.29	3.36	1.54	6.21	11.3
7m	0.0210 (0.0021)	0.0008	28.46 (0.78)	2.59	6.89	1.95	7.27	9.1
8m	0.0223 (0.0036)	0.0007	35.65 (1.42)	2.66	10.15	2.25	8.15	7.5
9m	0.0240 (0.0032)	0.0006	43.55 (1.54)	2.73	13.97	2.57	8.92	6.3
10m	0.0256 (0.0044)	0.0005	51.27 (2.38)	2.87	17.70	2.85	9.59	5.6
11m	0.0269 (0.0048)	0.0005	58.24 (2.52)	2.89	21.23	3.09	10.14	5.0
12m	0.0278 (0.0044)	0.0004	63.98 (2.72)	2.89	24.15	3.28	10.59	4.5

Source Lake

3i	0.0293 (0.0048)	0.0019	7.53 (0.36)	0.92	1.54	1.79	1.94	12.2
4i	0.0237 (0.0035)	0.0013	10.81 (0.44)	1.12	2.31	1.80	2.87	10.4
5i	0.0207 (0.0036)	0.0009	13.94 (0.73)	1.23	3.13	1.83	3.77	8.8
6m	0.0243 (0.0039)	0.0009	21.64 (1.00)	1.79	5.49	2.02	5.37	8.3
7m	0.0254 (0.0037)	0.0008	27.77 (1.13)	1.89	8.14	2.31	6.20	6.8
8m	0.0273 (0.0045)	0.0006	34.83 (1.56)	1.91	11.55	2.67	6.90	5.5
9m	0.0303 (0.0041)	0.0006	43.33 (1.72)	1.93	15.90	3.12	7.50	4.4
10m	0.0350 (0.0056)	0.0005	54.56 (2.59)	1.98	21.88	3.73	8.02	3.6

Note: i, immature; m, mature; (--), standard error for weight and [Hg] not available to run a Monte Carlo simulation

^aData from Rowan and Rasmussen (1996)

^bData from Elliott et al. (1981)

^cData from Trudel et al. (2000a)