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Trophic position in aquatic food webs

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A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements for the degree of Doctor of Philosophy

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ABSTRACT

This thesis examines broad-scale patterns in the food web structure of lake ecosystems. The unifying framework for this analysis is the concept of trophic position, which represents the energy-weighted trophic path length leading to a consumer or population. Trophic position was estimated for over 550 populations of fish (16 species) using quantitative dietary data. A method to estimate trophic position of aquatic consumers using stable isotope ratios was developed; this involved correcting for within- and among-lake variation in $\delta^{15}N$ of primary consumers (organisms used to represent the base of the food web). We report an overall correspondence between dietary and isotopic estimates of trophic position; for each species, trophic position generally ranged the equivalent of one trophic level unit among-populations. The concept of discrete trophic levels provided only a qualitative description of energy flow pathways in aquatic food webs. Among-population variation was much greater than within-population variation in trophic position of lake trout. Long-standing hypotheses about the determinants of food chain length were examined; food chain length was most closely correlated with species richness and lake area.

The trophic position approach was used to examine two separate environmental problems relevant to lakes: the bioaccumulation of persistent contaminants in food chains and the impacts of invasive species. Trophic position was the major determinant of PCB levels in lake trout; these relationships were used to characterize biomagnification factors (BMFs) for this and a number of other contaminants. Furthermore, the introduction of smelt into lakes was linked to increased levels of PCB and Hg contamination in lake trout. Stable isotopes were used to quantify the impacts of smallmouth bass and rock bass invasions on food webs leading to lake trout. Lake trout from invaded lakes exhibited reduced consumption on littoral prey fish; a food web shift that is likely to have detrimental impacts on native lake trout populations.

Résumé

Cette thèse examine les patrons de la structure des réseaux trophiques dans les écosystèmes aquatiques. La position trophique est le concept principal de cette étude réprésentant les chemins majeurs de flux d'énergie dans la chaîne alimentaire. La position trophique pour plus de 550 populations de poissons (16 espèces) a été estimée utilisant les données quantitatives alimentaires. Une méthode pour estimer la position trophique des consommateurs avec les isotopes stables (azote et carbone) est developée. Cette méthode implique une correction pour la variation (à l'interieur et entre les lacs) dans les signatures isotopiques des consommateurs primaires, qui représentent la base du réseau trophique. Les estimations des positions trophiques utilisant les méthodes alimentaires et isotopiques ont été similaires. Pour chaque espèces, des variations équivalentes à un niveau trophique ont été observées entre les populations. Ces analyses ont démontrées que l'utilisation des niveaux trophiques ne permet uniquement qu'une description qualitative des réseaux trophiques. La variation dans les positions trophiques des populations de touladi était plus important que la variation a l'intérieur des populations. Les hypothèses qui déterminent la longueur de la chaîne alimentaire ont été examinées. Le nombre d'espèces de poissons et la superficie des lacs se sont avérés être des facteurs déterminants afin de prédire la longueur de la chaîne alimentaire.

Deux problèmes écologiques différents ont été examinés dans les lacs: la bioaccumulation des contaminants dans les chaînes alimentaires et les impacts des espèces exotiques sur les écosystèmes aquatiques. Des correlations entre les concentrations de BPCs et la position trophique de touladi ont été démontrées. Les facteurs de biomagnification (BMFs) pour certains contaminants ont été quantifiés. De plus, une association a été observée entre l'introduction de l'éperlaine dans les lacs et l'augmentation des concentrations de BPCs et de mercure dans le touladi. Les impacts de l'invasion de l'achigan à petite bouche et le crapet de roche sur les chaînes alimentaires ont été quantifiées. Ces invasions ont modifié la structure des réseaux trophiques en

réduisant l'utilisation des ressources littorales du touladi. Ces invasions auraient des impacts sérieux et néfastes sur les populations des poissons indigènes.

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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 a 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 best interest to make perfectly clear the responsibilities of all authors of the co-authored papers. Under no circumstances can a co-author of such a thesis serve as an examiner for that thesis.

This thesis consists of six chapters, each of which has been prepared for publication in peer-review scientific journals. The first chapter has been published in *Ecological Monographs* (Vander Zanden and Rasmussen 1996, Ecol. Monogr. 66: 451-477), the second chapter in *Canadian Journal of Fisheries and Aquatic Sciences* (Vander Zanden et al. 1997, Can. J. Fish. Aquat. Sci. 54:1142-1158), the third chapter in *Ecology* (Vander Zanden and Rasmussen 1999, Ecology 80:1395-1404). The fourth chapter has been accepted in *Canadian Journal of Fisheries and Aquatic Sciences* (Vander Zanden et al. 2000 in press), the fifth chapter in *American Naturalist* (Vander Zanden et al. 1999, in press), and the sixth chapter in *Nature* (Vander Zanden et al. 1999, in press).

This thesis represents the results of my own independent research. All six chapters have been co-authored by my thesis supervisor, Dr. Joseph B. Rasmussen. Dr. Rasmussen contributed substantially to the design, execution, analysis, and presentation of the research presented herein. Dr. Gilbert Cabana, a former graduate student of Dr. Rasmussen, provided the stable isotope data and was actively involved in the research presented in Chapter 2, and is co-author of this chapter. Dr. Brian Shuter and Dr. Nigel Lester (Ontario Ministry of Natural Resources) participated in the development of the research presented in Chapter 4 and 5. They also provided editorial critique and are thus co-authors on these Chapters. Dr. John Casselman (Ontario Ministry of Natural Resources) provided samples, assistance, and editorial critique on Chapter 6, and appears as co-author of this chapter.

CONTRIBUTIONS TO ORIGINAL KNOWLEDGE

This thesis develops a conceptual framework for food web studies based on the concept of trophic position (Ch. 1).

This is the first study to use dietary data to characterize the pathways of energy flow through pelagic food webs of differing presumed trophic structure, and to test how well the use of discrete trophic levels represents actual trophic structure (Ch. 1 and 2).

This study provides the best known model predicting PCB concentrations in top predators: trophic position explained 83% of the among-lake variation in PCB concentrations in lake trout muscle tissues, unequivocally demonstrating the importance of food web properties in determining levels of persistent contaminants in the biota (Ch. 1).

This study used food web analyses to make and test hypotheses about the impacts of ongoing invasions of rainbow smelt on PCB and Hg levels in lake trout (Ch. 1).

Using dietary data and stable isotopes, this study quantified the average trophic position (across populations) for a seven species of littoral fish common in Eastern North America. This study also characterized the variance in trophic position for these species (Ch. 2).

This chapter compared dietary and stable isotope estimates of trophic position, providing field validation of the stable isotope-based approach (Ch. 1 and 2).

This thesis was the first to examine broad-scale patterns in the $\delta^{13}C$ and $\delta^{15}N$ of primary consumers (trophic level 2) across a range of lakes. A negative relationship between primary consumer $\delta^{13}C$ and $\delta^{15}N$ signatures was reported. A similar relationship was found among literature data (Ch. 3).

This study presents a simple method to estimate the trophic position of higher consumers that corrects for within-lake and among-lake variation in $\delta^{15}N$ at the base of the food web (Ch. 3).

This is the first study to use stable isotopes to quantify within-population variation in trophic position of aquatic consumers (Ch. 4).

This study demonstrates that among-population trophic variation was much greater than within population variation, and that lake trout failed to exhibit ontogenic shifts in trophic position (Ch. 4).

This is the first study to use stable isotopes to quantify among-lake differences in pelagic trophic structure and to examine long-standing hypotheses concerning the determinants of food chain length (Ch. 5).

This study uses stable isotopes to quantify the impacts of species invasions (smallmouth bass and rock bass) on food webs leading to lake trout. Stable isotopic descriptions of food web structure serve as a sensitive indicator of anthropogenic impacts (Ch. 6).

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So many individuals contributed in various ways to the development of the work presented in this thesis; it is here that I have the opportunity to thank them. First and foremost, I thank my thesis supervisor, Joe Rasmussen. Joe offered me the unique opportunity to conduct the research that is presented here, and has played the central role in my intellectual development. I have Joe to thank for my formation as a critical scientist. I also must thank Joe for assembling a group of fine students; their presence has created a fun and dynamic learning environment. The multitude of other graduate students, postdocs, and technicians from the Rasmussen lab and the limnology group have contributed in many ways. These include Adrian DeBruyn, Graham Sherwood, Marc Trudel, Jessica Meeuwig, Paul White, Stanley Hum, Strahan Tucker, Tony Ricciardi, Ivano Pazzia, Genvieve Morinville, Neil Rooney, Darla Saunders, Guillaume Chagnon, Pete St. Onge, Shapna Mazumder, Steve Baines, Bob France, and Helen Sarakinos. A special thanks is extended to Gilbert Cabana. Gilbert ushered me into the world of research and fieldwork, and I thank him for valuable guidance during the early stages of this project. Other friends have contributed in various ways, notably Yvonne Vadeboncouer, Dean Tweed, Harry Diner, and The Snitches.

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I thank my family, Mark, Meg and Jed for invaluable support, advice, and fun over the years. Finally, to Helen, my partner and my soulmate. You have been there for me every step of the way and in every way imaginable. This thesis is dedicated to you.

GENERAL INTRODUCTION

Ecologists are increasingly called upon to investigate the ecological aspects of contemporary environmental problems (Ehrlich and Daily 1991). Many aspects of the present environmental crisis are largely ecological in nature: the bioaccumulation of persistent environmental contaminants, the overharvesting and depletion of wildlife, the impacts of human activities on natural ecosystem through habitat loss, degradation and global warming, and the introduction of exotic species. One major consequence of these human impacts on nature is the massive loss of our planet's biological diversity. The consequence of these losses are, at present, unknown.

Holistic, ecosystem-level approaches in ecology have contributed substantially to our understanding of ecosystem processes and responses to anthropogenic activities (Schindler et al. 1985; Carpenter et al. 1995; Schindler 1998). Much of what is commonly referred to as the human impact on 'ecosystems' actually represents impacts on the interactions and relationships among the species inhabiting the impacted ecosystem. In the broadest sense, ecologists use the term 'food web' to represent the feeding interactions and interrelationships among the multitude of species inhabiting an ecosystem, spanning from primary producers up to the top predators (although rarely considering the important role of decomposers).

The concept of the food web dates back to Elton's classical text on Animal Ecology (Elton 1927). Elton's research revealed the complex interconnectedness of species in food web networks. An alternative view of the world was forwarded by Lindeman in his classic 1942 paper (Lindeman 1942). Lindeman arranged species into food chains that consisted of more or less discrete trophic levels. Plants were the primary producers (trophic level 1), herbivores were the primary consumers (trophic level 2), carnivores that feed on the herbivores were the secondary consumers (trophic level 3), and so on. The basic assumption of food chain studies is that these trophic levels can be treated as discrete populations (Hairston et al. 1960; Oksanen et al. 1981; Hairston Jr. and Hairston Sr. 1993; Hairston Jr. and Hairston Sr. 1997).

Since the early days of Elton and Lindeman, the fields of food chain and food web research (referred to generally here as food web studies) have blossomed into an active, sophisticated and exciting field of research; so much so that food chain dynamics has been termed the 'central theory of ecology' (Fretwell 1987). Thousands of food chain and food web studies have been published, having demonstrated that trophic structure plays a central role in regulating a broad range of ecological processes. These include patterns in species diversity (Paine 1980), energetic efficiencies and the biomass and productivity of trophic levels (Hairston et al. 1960; Power 1990; Hairston Jr. and Hairston Sr. 1993), the stability and persistence of ecological communities (May 1975; Pimm 1982), nutrient cycling (DeAngelis 1980), contaminant levels in the biota (Rasmussen et al. 1990; Vander Zanden and Rasmussen 1996), biogeochemical fluxes from ecosystems (Schindler et al. 1997), and fisheries production (Kerr and Martin 1970).

It is interesting to note that nearly all of the 'food web' studies of the 1980's and 90's can be easily categorized into one of two dominant food web paradigms, corresponding with Elton's food web and Lindeman's food chain. The shortcomings of both food chain and food web approaches have been addressed in a number of recent studies, reviews, and books (Martinez 1991; Polis 1991; Hall and Raffaelli 1993; Polis 1994; Polis and Winemiller 1996). Perhaps the most serious shortcoming of the food chain concept is the failure to incorporate the complexity and omnivory that are well known and inherent to many ecosystems (Polis 1991), as it is recognized by many field-oriented ecologists that species in nature rarely conform to distinct trophic levels.

Awareness of the shortcomings of the food chain paradigm has led many ecologists to examine food web patterns from the perspective of what is now called 'food web theory'. A food web is built using a species list and knowledge of the presence/absence of feeding links among those species. Close to 20 food web parameters (for example, mean food chain length, omnivory, linkage density, etc.) have been calculated from these simple food web matrices. Analysis of food web parameters across many food webs forms the basis for contemporary food web theory (Pimm 1982; Cohen et al. 1990; Pimm et al. 1991). Although in theory the food web paradigm possesses the distinct advantage of acknowledging the complexity of food webs, the harsh reality of food web theory is that defining links and trophic categories is a highly subjective process. Furthermore, food webs suffer by failing to consider the relative importance of trophic links. Finally, the food web approach has rarely proven useful in addressing applied ecological problems.

Both food chain and food web paradigms represent the *potential* food web structure of an ecosystem, i.e., they fail to represent the actual trophic relationships based on the pathways of energy flow through the ecosystem. In contrast to potential trophic structure, Kling et al. (1992) introduced the concept of *realized* trophic structure, referring to the measured or actual feeding relationships based on the energetic importance of feeding links.

This distinction between potential and realized food web structure sets the framework for the research to be presented in this thesis. Chapter 1 reviews the conceptual approaches to representing trophic structure. In addition to the two *potential* food web models (food chain and food web models), two realized models are introduced; an *energy flow model* directly quantifies the pathways of energy flow through the system, while a *trophic position model* uses energy flow information to estimate the trophic position of component populations. Trophic position is measured as a continuous rather than a discrete variable, and represents the energy-weighted number of (trophic) energy transfers that have occurred before passing to the population. This approach is less rigid than a food chain model because species are not forced to conform to discrete trophic levels, and site-specific information about diet, energy flow and omnivory are used to define the structure of the system. Relative to a food web, the trophic position model incorporates energetic information, yet it still offers a relatively simple depiction of trophic structure.

Chapter 1 advances a trophic position-based approach to representing trophic structure for the purpose of applied ecological studies. Although a trophic position approach may be conceptually attractive, its application hinges upon the practicality and reliability of measuring the trophic position of organisms in the field. One approach that can be used to estimate the trophic position of a consumer uses quantitative dietary data, estimates of the trophic position of prey items, and weighted average formulas (Levine 1980; Adams et al. 1983; Winemiller 1990). Stable nitrogen isotopes ratios ($^{15}N/^{14}N$; $\delta^{15}N$) provides an alternative approach to quantifying trophic position of consumers. Field and laboratory studies consistently demonstrate that heavy nitrogen atoms (^{15}N) become enriched in the tissues of predators relative to their prey (average increase = 3.4‰ ± 0.3 (DeNiro and Epstein 1981; Minagawa and Wada 1984; Peterson and Fry 1987; Hobson and Welch 1992; Kling et al. 1992; Cabana and Rasmussen 1994). The stable isotope approach provides a number of potential advantages over dietary methods of estimating trophic position. In particular, use of stable isotopes can provide time-integrated trophic information about the materials *assimilated* by the consumers, provided that stable isotope signatures of consumers are interpreted relative to an appropriate isotopic refence point (Cabana and Rasmussen 1996).

Stable carbon isotopes ($\delta^{13}C$) are also useful in food web studies and provide information that is complimentary to $\delta^{15}N$ results. Prey from different habitats of lakes (i.e., benthic vs. pelagic) typically have distinct $\delta^{13}C$ signatures (Hecky and Hesslein 1995). Because consumers acquire $\delta^{13}C$ signatures similar to that of their food, the $\delta^{13}C$ of consumers can be used to infer the feeding habitat of consumers in lake ecosystems.

The Study System: Pelagic Food Webs

Pelagic food webs with lake trout as top predator provide an ideal set of study systems for examining among-lake variation in food web structure. Trophic structure varies widely from lake-to-lake; Rasmussen et al. (1990) classified lakes according to the number of discrete trophic levels in the food chain based on the presence or absence of functional trophic levels in the lake (referred to as lake Class; Fig. 1). The number of trophic levels was closely related to the PCB and Hg levels in lake trout (Rasmussen et al. 1990; Cabana et al. 1994). In this thesis, Rasmussen et al.'s original 'lake Class' variable (Fig. 1) will continue to serve as the starting point for examining among-lake differences in pelagic trophic structure. Quantitative dietary data from over 550 fish populations, coupled with stable isotope data from over 60 lakes will serve as the basis for the present study of patterns of food web structure in aquatic ecoystems.

This thesis has been assembled in manuscript format, and consists of six separate chapters, each of which has been published or has been submitted for publication in peer-review journals. This thesis will attempt to provide advances in our understanding of food webs (as studied from the trophic position perspective) at conceptual, methodological, descriptive, and practical levels; the specific issues addressed in this thesis are listed and described here.

1) Conceptual

a) To develop a trophic position-based approach to the study of pelagic food web structure, culminating in the development of trophic position models of pelagic food webs (Ch. 1).

2) Methodology and Validation

a) To use dietary data to estimate trophic position of aquatic consumers to describe broad-scale patterns in consumer trophic position and food web structure (Ch. 1).

b) To advance the use of stable isotopes to estimate trophic position of aquatic consumers by developing a method that corrects for within- and among- lake variation in $\delta^{15}N$ characterizing the base of the food web (Ch. 3).

c) To compare dietary and stable isotope estimates of trophic position, in order to validate the stable isotope measure of trophic position (Ch. 1 and 2).

3) Examining Food Web Patterns

a) To quantify pelagic trophic structure, including the among-lake variability, and to test how well discrete trophic levels (lake Class; Rasmussen et al. 1990) correspond with pelagic trophic structure (Ch. 1 and 5).

b) To describe within-population patterns in trophic position of lake trout, including ontogenic trophic position shifts and the magnitude of individual-level trophic specialization (Ch. 4).

c) To test predictions of food web theory concerning the determinants of food chain length: in particular, the importance of species richness, lake area, productivity, and productive space (Ch. 5).

4) Applications to Environmental Problems

a) To test the importance of lake trout trophic position as a determinant of PCB and Hg concentrations in lake trout and to characterize biomagnification factors (BMFs) for these contaminants (Ch. 1).

b) To test predictions generated from the trophic position model that the introduction of smelt in lakes will be accompanied by elevated PCB and Hg levels in lake trout (Ch. 1).

c) To quantify the food web consequences of smallmouth bass and rock bass invasions on food webs leading to lake trout (Ch. 6).

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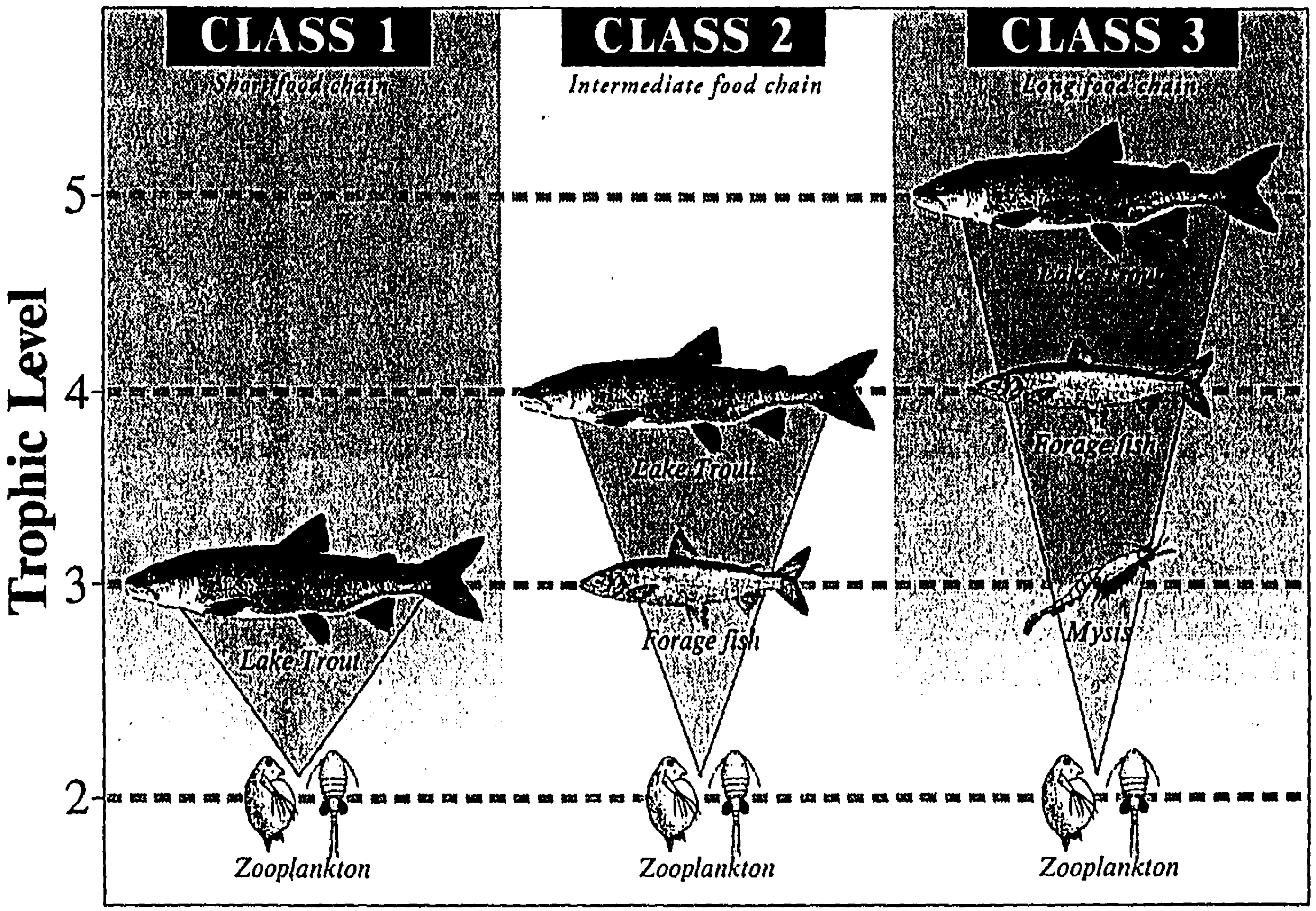
CHAPTER 1

A TROPHIC POSITION MODEL OF PELAGIC FOOD WEBS: IMPLICATIONS FOR CONTAMINANT BIOACCUMULATION IN LAKE TROUT (SALVELINUS NAMAYCUSH)

Figure 1. Presumed structure of pelagic food chains from Class 1, 2, and 3 lakes (based on Rasmussen et al. 1990).


CLASS 1
Short food chain
CLASS 2
Intermediate food chain
CLASS 3
Long food chain
Trophic Level
5
4
3
2
Lake Trout
Zooplankton
Lake Trout
Forage fish
Zooplankton
Lake Trout
Forage fish
Mysis
Zooplankton

ABSTRACT

To test how well use of discrete trophic levels represents pelagic trophic structure, we compiled dietary data from over 200 lake trout and pelagic forage fish populations, and calculated a continuous (fractional) measure of trophic position for each population. Although discrete trophic levels qualitatively represent broad-scale patterns in trophic structure, pelagic food webs are characterized by complexity and omnivory, thereby limiting the ability of discrete trophic levels to quantitatively represent trophic structure in terms of mass transfer and energy flow. Lake trout trophic position, which ranged from 3.0 to 4.6, explained 85% of the between-lake variability in mean PCB levels in lake trout muscle tissue, providing a significant improvement over the use of discrete trophic levels as a predictor of contaminant levels.

Having demonstrated the utility of trophic position, we develop a generalized "trophic position model" of lake trout food webs. This approach eliminates minor trophic linkages, calculates a fractional measure of each species' trophic position, and aggregates species of similar trophic position into trophic guilds. This "realized" model represents trophic structure in terms of mass transfer, and accounts for the complexity and omnivory that characterizes aquatic food webs. In our trophic position model, smelt (a species of pelagic forage fish) were designated a trophic guild separate from other pelagic forage fish due to their elevated trophic position. Separate consideration of smelt is supported by elevated lake trout trophic position, PCB, and Hg levels in lakes containing smelt. Consideration of omnivory causes biomagnification factors (BMFs) to be many times higher than BMFs that ignore omnivory. These omnivory-corrected BMF estimates appear to be more consistent with values calculated using stable nitrogen isotopes ($\delta^{15}N$), an alternative continuous measure of trophic position. $\delta^{15}N$ provided trophic position estimates that generally correspond with our diet-derived estimates.

INTRODUCTION

Modeling relationships between trophic levels is done with one of three major objectives; (1) “food web” studies search for consistent patterns of community structure among matrices of interconnected species (Briand 1985; Schoener 1989; Cohen et al. 1990; Polis 1991); (2) studies of "effects" attempt to determine factors structuring communities, often relying on experimental manipulations (Hairston et al. 1960; Paine 1966, 1980; Fretwell 1987; Spiller and Schoener 1990; Wooton and Power 1993); and (3) "flow" studies are concerned with the flow pathways of energy, nutrients, and contaminants through ecosystems (Burns 1989; Rasmussen et al. 1990; Kling et al. 1992). Both studies of flow and effects rely heavily on "trophic level", whereby species are lumped into integer trophic level groupings, which are treated as discrete populations for further modeling (Carpenter et al. 1985; Rasmussen et al. 1990; Perrson et al. 1992; Hairston and Hairston 1993).

The problem of bioaccumulation of persistent contaminants such as PCBs and mercury to dangerous levels in the biota has recently been approached by considering species' trophic level (Rasmussen et al. 1990; Cabana et al. 1994). Although direct trophic transfer is considered an important pathway for these contaminants (Woodwell et al. 1967; Oliver and Niimi 1988; Thomann 1989), controversy remains concerning the importance of biomagnification. Food chain effects are frequently neglected in attempts to explain contaminant levels in the biota, due to the difficulty in accurately quantifying an organism's trophic position. Rasmussen et al. (1990) and Cabana et al. (1994) used presence/absence of functional prey groups in pelagic lacustrine food webs to estimate the trophic level of lake trout, and used this to successfully explain much of the observed between-lake variability in PCB and Hg levels in lake trout. Although it provided evidence for the process of food chain biomagnification of these contaminants, their simple food chain classification did not directly quantify trophic interactions and ignored the omnivory and complexity of food webs by relying on discrete trophic levels.

Although multi-trophic level population models suggest that the destabilizing effect of omnivory should render it rare (Pimm and Lawton 1978; Pimm 1982), more recent observational studies show omnivory to be common in aquatic communities (Sprules and Bowerman 1988; Vadas Jr. 1990; Kling et. al 1992). Kling et. al. (1992) used nitrogen isotopic tracers to demonstrate that the prevalence of omnivory causes "realized" trophic position to deviate greatly from "potential" trophic level, casting doubt on the ability of discrete trophic level approaches to accurately represent trophic structure. Although dietary data can be used to quantify omnivory, Kling et al. (1992) and Cabana and Rasmussen (1994) present a simpler and potentially more accurate means of measuring omnivory and trophic position--the use of stable nitrogen isotopes ($^{15}N/^{14}N$ ratios, or $\delta^{15}N$ signature).

Building a Trophic Position Model

Food web and food chain models are extreme endpoints of a continuum of potential representations of trophic structure (Fig. 1). Connectance food web diagrams are not designed with the intention of representing energy flow, as they fail to weight trophic connections according to interaction strength (Paine 1988; Polis 1991). Food chain approaches too often clump species of different trophic position, and ignore the complexity and omnivory inherent to natural food webs (Murdoch 1966). Representing "realized" trophic structure (sensu Kling et al. 1992) requires a compromise between discrete food chain and food web approaches; one must quantify actual trophic relationships weighted according to their energetic importance (using biomass as a surrogate of energy), and must replace discrete trophic levels with a continuous trophic position measure.

A food web provides the starting block, whereby all potential trophic links are represented (Fig 1a). Direct dietary data are incorporated to establish the important trophic interactions, thereby permitting elimination of energetically unimportant trophic links (Fig. 1b). Going further, species of similar trophic position are clumped into trophic guilds (Burns 1989), and each trophic guild is assigned a continuous value of trophic position, based on the biomass weighted composition of its diet. The result is a trophic position model that incorporates the omnivory and complexity of the food web by considering the relative importance of various prey items to each predator (Fig. 1c). This trophic position model could be further simplified into a food chain model (using discrete trophic levels) by removing information about omnivory (Fig. 1d). If omnivory is important in structuring the pelagic food web, the trophic position model (Fig. 1c) should provide the most effective and accurate means of depicting realized trophic structure (Kling et al. 1992).

Conceptually, quantifying trophic position as a continuous variable is not new (Levine 1980; Adams et al. 1983; Winemiller 1990). However, this study formalizes a trophic position model by setting standards for its design (thus formally addressing the issue of "realized" trophic structure posed by Kling et al. 1992). The food chains leading to lake trout provide an ideal system for developing a trophic position model. Considerable dietary data are available from the literature, and the length of the food chain leading to lake trout varies greatly among lakes (Rasmussen et al. 1990). Using dietary data from lake trout and their common prey species, we apply the trophic position model to characterize the trophic relations of three types of food chains leading to lake trout. The trophic position variable is tested by comparing trophic position (a continuous variable) and trophic level (a discrete variable) as predictors of mean PCB concentrations in lake trout.

Our primary concern is the quantification of trophic structure in terms of material flow between trophic levels, with specific reference to contaminant bioaccumulation. Trophic structure exerts influence upon other aspects of food webs as well, not only the efficiency of energy transfer to higher trophic levels, but also the rates of primary production (reviewed by Hairston and Hairston 1993). Thus, improved measurement of trophic structure (in terms of mass transfer) has potential application to studies of ecological efficiencies, energetics, and production (Lindeman 1942; Kerr and Martin 1970; Adams et al. 1983; Matuszek et al. 1990; Strayer 1991; Hairston and Hairston 1993), as well as modeling of cascading trophic interactions (Carpenter et al. 1985; Fretwell 1987). The implications of omnivory have only recently been considered in studies of food chain dynamics, in a series of insightful studies by Diehl (1992, 1993, 1995).

Study Systems

Lake trout are a native, top pelagic predator in many larger lakes of the St. Lawrence drainage system (Scott and Crossman 1973). The food chains leading to lake trout are highly variable in length, due to the absence of important trophic links in some lakes (Rasmussen et al. 1990) caused by limited post-glacial dispersal of certain prey taxa (Dadswell 1974; Roff et al. 1981). All lake trout lakes contain zooplankton, but many lakes lack intermediate trophic links: Mysis relicta (a freshwater shrimp), and the common and available prey fish of lake trout, what we refer to as "pelagic forage fish" (smelt, cisco, whitefish, alewife, sculpins, ninespine stickleback, and troutperch). Although all these species, particularly whitefish and sculpins are not strictly pelagic, we retain the term "pelagic forage fish" for the sake of consistency with the previous literature. Numerous dietary studies indicate that adult lake trout feed on these pelagic forage fish when present (Martin 1970; Rasmussen et al. 1990; Trippel and Beamish 1993); in the absence of pelagic forage fish, lake trout exhibit planktivory (Martin 1952, 1966; Konkle and Sprules 1986). Pelagic forage fish feed on zooplankton and benthic invertebrates (Couey 1935; Godfrey 1955), but their diet shifts towards Mysis and its associate, Diporia hoyi when these large invertebrates are present (Dryer and Beil 1968; Evans and Loftus 1987; Trippel and Beamish 1993). Mysis exhibit a broad diet, but most commonly prey upon herbivorous cladoceran zooplankton (Cooper and Goldman 1980;

Grossnickle 1982). These observations prompted Rasmussen et al. (1990) to classify lake trout lakes according to food chain length; based on simple presence/ absence of intermediate prey items (Class 1, lakes lacking both Mysis and pelagic forage fish species; Class 2, lakes lacking Mysis but containing at least one species of pelagic forage fish; Class 3, lakes containing both Mysis and at least one species of pelagic forage fish, Fig. 1d).

METHODS

Data Collection and Analyses

Dietary data for lake trout (Salvelinus namaycush), and common prey fish species of lake trout ("pelagic forage fish"): Coregonids (Coregonus sp., Prosopium sp.), smelt (Osmerus mordax), alewife (Alosa pseudoharengus), sculpins (Cottus sp., Myoxocephalus quadricornis), ninespine stickleback (Pungitius pungitius), and trout-perch (Percopsis omiscomaycus) were collected from the literature, Ontario and Quebec Government files and documents, and our own data (lake trout; n = 92 lakes, 47,681 individual fish; forage fish species; n = 117 lakes, 47,734 individual fish).

The degree of taxonomic detail of prey categories reported was variable between studies. For pelagic forage fish, five common prey Classes (Fish, Zooplankton, Zoobenthos, Mysis, and Amphipods) were generally identified from published studies. For lake trout, the same five categories were used, except fish were further subdivided into 7 sub-categories when possible; cisco, whitefish, smelt, alewife, cottids, "other benthic-pelagic fish" (consisting of other salmonids, stickleback, trout-perch, and catastomids), and littoral species (percids, cyprinids, and centrarchids). "Unknown", "miscellaneous", or "other" were eliminated as a prey category. Remaining prey categories were scaled to sum to 100%.

Published sources commonly divided diet data into groupings based on fish size, year, season, depth, or time of day. Diet data from these different groupings were averaged for each lake. Averages were not weighted based on sample size to avoid bias in favor of better sampled components of the population. Results of multiple studies from the same lake were averaged for this analysis. Exceptions include when the lake was subject to a significant disturbance (such as an introduced prey species or eutrophication), or sample dates were separated by more than 20 years. Multiple studies of lake trout from the Great Lakes were treated separately due to the heterogeneity and large size of these lakes. Since lake trout from Class 1 lakes exhibit much greater reliance on fish prey during winter (Martin 1952, 1954), 10 lakes sampled only during winter months were considered separately. Data from other Class 1 lakes for which diet data comes from less than two seasons were eliminated from the data set. When possible, juvenile lake trout (total length < 25 cm.) were excluded from analysis, as these small lake trout generally prey on invertebrates, no matter what fish prey are present. Young-of-the-year (YOY) pelagic forage fish were also excluded from analysis, as they are not common prey of adult lake trout (Martin 1970; Trippel and Beamish 1993).

The classification of lake trout communities of Rasmussen et. al (1990) appears to break down at high latitudes and altitudes, as these coldwater lake trout populations generally exhibit lower levels of piscivory (Merrick et al. 1992; Donald and Alger 1993). A surrogate of mean annual air temperature (MAAT; average of mean January and mean July air temperatures) was calculated for each lake trout lake from The Hydrological Atlas of Canada (1978), and The Climatological Atlas of the United States (1968). -3° C corresponds with the lower mean annual air temperature for lakes included in Rasmussen et al. (1990) and Cabana et al. (1994). All lakes characterized by a MAAT less than -3° C were considered "coldwater" lakes. These lake were analyzed separately, and were excluded from the food web reconstructions presented herein.

Each lake for which lake trout diet data were available was classified as either Class 1,2, or 3 based on the presence of Mysis and pelagic forage fish (following Rasmussen et al. 1990), using the published diet data sources, Dadswell (1974), Rasmussen et al. (1990), Donald and Alger (1993), Cabana et al. (1994), and an Ontario Ministry of Natural Resources (OMNR) fish species distribution database. The mean percent volumetric contribution (± 1 SE) of each prey item to the diet of the predator was calculated for each fish species, further separated into Class 1, 2, and 3. All non-volumetric data were converted to percent volume using the conversion methodology presented in Appendix 1.

Calculation of Trophic Position

Conversion of average diet data into estimates of trophic position required assumptions concerning the trophic level of the common invertebrate prey organisms of lake trout and pelagic forage fish. Primary producers were assigned to trophic level 1, zooplankton and zoobenthos were assumed to represent trophic level 2. Mysis was assigned trophic level 3 due to their generally zooplanktivorous diet (Cooper and Goldman 1980; Grossnickle 1982), as were larval and littoral fish, who also prey upon zooplankton and zoobenthos (Keast 1977, 1980, 1985).

Amphipods were also assigned to trophic level 3. Although Class 1 and 2 lakes contain amphipods (Gammarus sp.), these species are restricted exclusively to benthic habitats of the littoral zone, thereby explaining the minor role of amphipods in the diet of Class 1 and 2 lake trout. However, Diporia hoyi is a deepwater, glacial relict amphipod with a biogeographic distribution very similar to that of Mysis (Dadswell 1974). D.hoyi is frequently present and abundant in Class 3 lakes, and migrates vertically within the water column at night, as does Mysis (Marzolf 1965; Evans et al. 1990). Stable nitrogen isotopes studies of D. hoyi and Mysis from Lake Memphremagog (Que.) and Lake Ontario suggests predatory feeding behavior for both species (D. Branstrator, personal communication; J. Vander Zanden, unpublished data), justifying their designation as trophic level 3. These assumptions concerning the trophic level of prey items may or may not represent the actual trophic interactions at lower levels of the food chain. Any bias accompanying this assignment of prey trophic level is expected to be consistent among lakes of the three lakes classes. Using diet data and estimates of trophic level of various prey items, the trophic position of each pelagic forage fish population was calculated using a previously employed equation (Adams et al. 1983; Winemiller 1990):

$$T_a = \sum(V_i * T_i)+1 \qquad (1)$$

where T_a = trophic position of the a^{th} predator, V_i = volumetric contribution of the i^{th} prey item, T_i = trophic position of the i^{th} food item. Although prey items were assigned to discrete trophic levels, omnivory among fish resulted in a continuous measure of trophic position for each pelagic forage fish population. The mean trophic position (± 1 SD and 1 SE) was calculated for each forage fish species from both Class 2 and Class 3 communities. This collection of mean pelagic forage fish trophic position values, the estimates of prey trophic position, and the lake trout feeding data (broken down to species of pelagic forage fish), were used to calculate the trophic position of each lake trout population using Eq. 1. The mean trophic position (± 1 SD and 1 SE) was calculated for lake trout from each trophic Class, further subdivided into coldwater and warmwater lakes. The standard deviation accompanying lake trout trophic position values was calculated by summing variances in trophic position of fish prey species (each weighted by their relative contribution to lake trout diet), and adding this value to the standard deviation in trophic position calculated for lake trout.

RESULTS

Forage Fish Diet

Our calculations of the average diet of pelagic forage fish generally corresponds with previous conceptions of their feeding habits (Table 1 and Appendix 2). Alewife feed primarily upon zooplankton in Class 2 and 3 lakes (76% and 59%), with little reliance on Mysis but some consumption of zoobenthos. Whitefish consume primarily zoobenthos in Class 2 lakes, while in Class 3 lakes whitefish increase their consumption of amphipods to 24%, due to the presence of D. hoyi. Class 2 cisco feed almost entirely upon zooplankton; cisco from Class 3 lakes consume some Mysis (28%) and amphipods (12%). Class 2 smelt fed on zooplankton (42%) and larval fish (36%), while Class 3 smelt consume Mysis (32%) and larval fish (30%). Sculpins of Class 2 lakes prey heavily on zoobenthos; while Class 3 sculpins consume amphipods (55%) and zoobenthos (24%).

All pelagic forage species consume Mysis to some degree in Class 3 lakes (mean = 15%). More interesting is the difference in mean amphipod consumption between Class 2 lakes (mean = 3%) and Class 3 lakes (mean = 21%). The increase in amphipod consumption in Class 3 lakes is due to the common occurrence of D. hoyi in Class 3 lakes. Thus, D. hoyi appear to be as important as Mysis in elevating the trophic position of Class 3 pelagic forage fish.

Lake Trout Diet

Mean diets of lake trout were calculated for each trophic Class (Table 2 and Appendix 3). Class 1, 2, and 3 lake trout from warmwater lakes exhibit 54.6%, 77.4%, and 94.7% piscivory respectively, differing significantly as a function of Class (ANOVA; N=70, F=15.75, $p<0.0001$, Table 2). Thus, addition of pelagic forage fish appears to be responsible for an initial increase in lake trout piscivory, and addition of Mysis is accompanied by a further increase in lake trout piscivory. Furthermore, fish prey still make up 55% of the diet of lake trout from lakes lacking pelagic forage fish (Class 1 lakes). Such use of littoral fish resources by lake trout indicates significant energy flow between littoral and pelagic zones of lake food webs. Consistent with this finding, Class 1 lake trout have been reported to make feeding excursions into littoral habitats (Martin 1952), and the pelagic habits of certain cyprinid species (spottail shiner) and young-of-the-year perch make them available to lake trout (Fry 1939; Martin 1954). Particularly during winter, lake trout are not thermally isolated from littoral fish by the hypolimnion, thereby making littoral fish available to lake trout (Martin 1952). We report mean winter Class 1 piscivory to be 87%, while year-round Class 1 lake trout piscivory averages 55%.

We present a diagrammatic summary of the average feeding interrelationships characterizing Class 1,2, and 3 food webs, as revealed from our review of the lake trout and pelagic forage fish diet data literature (Fig. 2).

General Patterns in Trophic Position and Omnivory

Trophic position was calculated for each fish population included in this study. This collection of trophic position values is summarized by calculating mean trophic position (± 1 SD and SE) values for each fish species, further subdivided by food chain Class (Table 3). All pelagic forage species exhibit a higher trophic position in Class 3 than in Class 2 lakes. The mean trophic position of Class 2 pelagic forage fish is 3.12 (± 0.19 trophic level), although Class 2 smelt exhibit an elevated trophic position of 3.36 (± 0.40 t.l.). Among Class 3 lakes, mean forage fish trophic position is 3.40 (± 0.40 t.l.), while smelt exhibit an elevated trophic position of 3.66 (± 0.29 t.l.). Class 3 pelagic forage fish, with the exception of smelt, exhibit a more variable trophic position than Class 2 pelagic forage fish (Fig. 3, Table 3), suggesting that presence of Mysis and D. hoyi increases the incidence of omnivory among pelagic forage fish.

Mean Class 1 lake trout trophic position was 3.55 (± 0.28 trophic levels). The trophic level estimates of Rasmussen et al. (1990) underestimated Class 1 lake trout trophic position (by 0.55 trophic levels) by neglecting piscivory on littoral fish. The mean Class 2 lake trout trophic position of 3.89 (± 0.48 trophic levels) generally corresponded with the Rasmussen trophic level estimate of 4.0. Class 3 lake trout exhibit a mean trophic position of 4.38 (± 0.38 trophic levels); more than 0.6 trophic level less than the Rasmussen trophic level estimate of 5.0 (Fig. 3, Table 3). The depressed trophic position of Class 3 lake trout is a result of omnivory by pelagic forage fish, since Class 3 adult lake trout exhibit virtually no omnivory (fish make up 95% of the adult diet). The increase in lake trout trophic position accompanying trophic Class is highly significant (ANOVA; n=70, F=69.73, p<0.0001). Furthermore, lake trout are more variable in trophic position than pelagic forage fish, as variation in trophic position is compounded up the food chain.

We report significant discrepancies between the mean trophic position of lake trout populations and traditional trophic level designations. These discrepancies are nearly exclusively generated from omnivory by Class 1 lake trout and Class 3 pelagic forage fish. As a result, the use of discrete trophic levels does not accurately represent trophic structure in these pelagic food webs.

Trophic Position Predicts PCBs Better Than Discrete Trophic Levels

We have shown that omnivory can average 50% at certain compartments of the pelagic food web. If variable food chain length were largely responsible for the between-lake differences in mean lake trout PCB levels (biomagnification), then trophic position, which can account for within-class variation in trophic structure, should be a better predictor of lake trout PCB levels than the use of discrete trophic levels--the approach taken in previous predictive models (Rasmussen et al. 1990; Rowan and Rasmussen 1992, 1994; Cabana et al. 1994). We supplemented PCB data from Rasmussen et al. (1990) with data from the Ontario Ministry of the Environment and Energy (Sport Fish Contaminant Monitoring Program), allowing us to match up mean PCB values and dietary trophic position estimates for a total of 21 lakes from Ontario.

A plot of lake trout PCB vs. trophic position (including lakes from all three Classes) shows a strong positive relationship (Fig. 4a).

$$\log PCB = -6.07\ (\pm 0.89) + 2.11\ (\pm 0.22)\ \text{trophic position}$$

$$n = 21 \qquad r2 = 0.83 \qquad SEest = 0.24 \qquad F = 95.10 \quad (2)$$

By comparison, use of the discrete trophic level variable of Rasmussen et al. (1990) provided a strong, though considerably less powerful model.

$$\log PCB = 1.25\ (\pm 0.20) + 0.60\ (\pm 0.09)\ \#\text{ of trophic levels } (1,2,\text{ or } 3)$$

$$n = 21 \qquad r2 = 0.72 \qquad SEest = 0.31 \qquad F = 47.83 \quad (3)$$

When these two predictor variables were tested together in a stepwise regression (SYSTAT), trophic position, the continuous measure based on diet displaced the discrete trophic level variable.

To statistically evaluate the improved prediction provided by the trophic position variable, we performed a pairwise comparison of the absolute values of the residuals from the two models (eq. 2 and 3) which share the same dependent variable, and are tested on the same set of lakes. The residual for the trophic position model averaged 0.07 lower than the corresponding residual for the trophic level model ($n = 21$, $t = 2.39$, $p = 0.027$). Thus, the use of the trophic position variable provides significant improvement in predictive power over use of discrete trophic levels.

Since Rasmussen et al. (1990) used a multiple regression model which included significant contributions from lipid content and latitude, these secondary variables must be considered as well. The best model for PCB levels in lake trout shows significant effects of trophic position and lipid content. Latitude was not significant, due to the limited geographic range of the lakes included in this data set.

$$\text{Log PCB} = -3.87\ (\pm 1.30) + 1.44\ (\pm 0.37)\text{ trophic position} + 0.72\ (\pm 0.34)\log \%\text{ lipid}$$

$$n = 21 \qquad r2 = 0.87 \qquad SEest = 0.22 \qquad F = 58.99 \quad (4)$$

Replacing trophic position with the discrete trophic level variable of Rasmussen et al. (1990) yields the following model:

$$\text{Log PCB} = 1.14\ (\pm 0.18) + 0.27\ (\pm 0.15)\ \#\text{ of trophic levels (1, 2, or 3)} + 1.14\ (\pm 0.44)\ \log \%\text{ lipid}$$

$n = 21 \quad r2 = 0.79 \quad SEest = 0.27 \quad F = 34.34$ (5)

The residuals of the model using trophic position average 0.06 lower than the model relying on discrete trophic levels. A paired t-test on the absolute value of the residuals of the two models shows a significant improvement in the residuals from the trophic position model (n=21; t= -2.51; p=.02).

Addition of a parameter for lipid to the multiple regression model results in a reduced coefficient for trophic position, since lake trout lipid content also increases with trophic position (Fig. 4b). Lake trout lipid levels are also highly correlated with PCB levels (Fig. 4c), suggesting important contributions of both trophic position and lipids in determining PCB levels. Yet despite a strong correlation between lipid content and PCB levels in lake trout, trophic position still explains 60% of the lipid corrected PCB levels in lake trout (Fig. 4d). This suggests an important role for trophic position in determining PCB levels in lake trout independent of lipid content.

Within-Class Relationships Between Trophic Position and PCBs

Further support for our trophic position variable as a predictor of PCB levels comes from significant within-trophic Class correlations between PCB levels and trophic position in Class 2 and 3 lakes:

Class 2:

$$\text{logPCB} = -2.98\ (\pm 2.83) - 0.005\ (\pm 0.002)\ \text{latitude} + 1.66\ (\pm 0.71)\ \text{trophic position}$$

$n=8 \quad r^2=0.65 \quad SEest=0.24 \quad F=4.58$ (6)

Class 3:

$$\text{logPCB} = -3.87\ (\pm 1.08) - 0.001\ (\pm 0.00)\ \text{latitude} + 1.65\ (\pm 0.25)\ \text{trophic position}$$

$n=9 \quad r^2=0.91 \quad SEest=0.11 \quad F=31.63 \quad (7)$

Trophic position is a significant predictor of PCB levels within both classes (Class 2: p=0.065; Class 3: p=0.001). No significant relationship between trophic position and PCBs was found among the 5 CLASS 1 lakes for which data were available.

Although we have both PCB and diet data from only 21 lakes, these results suggests that a continuous measure of trophic position is a better predictor of among-lake lake trout PCB levels than use of discrete trophic levels. In spite of the problems inherent in the use of dietary data to calculate trophic position, this continuous measure of trophic position provides significantly increased predictive power by accounting for more of the omnivory and complexity of food webs than possible using discrete trophic levels. This not only provides evidence for a close link between the flows of energy and certain contaminants, but suggests that more thorough consideration of omnivory has potential to further improve ecologist's understanding of contaminant flows through food webs.

A Trophic Position Model of Pelagic Food Webs

The improved relationship between trophic position and PCB levels in lake trout validates our hypothesis that trophic position represents realized trophic structure better than do trophic levels. To incorporate "trophic position" into a broader modeling framework, the dietary and trophic position data (Tables 1 - 3) were used to construct a trophic position model of lake trout food webs for Class 1, 2, and 3 lake trout communities. In this model, all pelagic forage fish species (with the exception of smelt) exhibit similar trophic position, allowing them to be lumped into the trophic guild "pelagic forage fish", whose mean trophic position is weighted by the dietary contribution of each species to lake trout; pelagic forage fish were assigned to trophic position 3.1 and 3.4 for Class 2 and 3 lakes, respectively. Smelt, a separate trophic guild, was assigned to trophic position 3.4 in Class 2, and 3.7 in Class 3 lakes. Lake trout were assigned trophic position values of 3.5, 3.9, and 4.4 in Class 1,2, and 3 lakes, respectively. This realized

(Kling et al. 1992) "trophic position model" depicts the average trophic structure of each of the three Classes of lake trout communities (Fig. 1c).

Comparison of the trophic position model (Fig. 1c) and the discrete trophic level model (Fig. 1d) reveals that the discrete trophic level model qualitatively captures the increase in lake trout trophic position accompanying the addition of functional prey groups to the food chain. But quantitatively, the trophic position model deviates from the discrete trophic level model. Particularly, Class 1 lake trout and Class 3 pelagic forage fish exhibit high levels of omnivory. As a result, the discrete trophic level model underestimates the length of the shortest food chain by roughly 1/2 trophic level, adequately represents the length of the intermediate food chain, and overestimates the length of the longest food chain by about 1/2 trophic level. Thus, our continuous measure of trophic position gives a "compressed" depiction of food chain length compared to the use of trophic levels.

The Trophic Position of Smelt

With the exception of smelt, which exhibit some degree of piscivory, pelagic forage fish generally exhibit similar trophic position estimates. Smelt were designated a separate trophic guild in the trophic position models of lake trout food webs (Fig. 1c). Here, we will statistically evaluate the validity of treating of smelt separately within the trophic position model. We also test the correspondence between the presence of the trophic guild, smelt, and PCB and Hg levels in lake trout, thereby reinforcing our test of food chain biomagnification.

Two-way ANOVA was used to compare the trophic position of smelt and cisco from Class 2 and 3 lakes. Smelt had a significantly higher trophic position than cisco (n=42, F=9.96, p<0.004). Smelt and cisco of Class 3 lakes also exhibited significantly higher trophic position than smelt and cisco of Class 2 lakes (n=42, F=13.1, p<0.001). More interestingly, two-way ANOVA reveals a significant increase in lake trout trophic position in lakes containing smelt over lakes of the same food chain Class, but lacking smelt ($n=45$, $F=9.25$, $p<0.004$; Fig. 5). Class effects on lake trout trophic position were also significant ($n=45$, $F=21.94$, $p<0.0001$).

If variable food chain length is responsible for the high levels of between-lake variation in mercury and PCB levels in lake trout, then the presence of smelt in the lake trout food web is expected to be accompanied by elevated lake trout contaminant levels. Mercury data from Cabana et al. (1994) were used to test if the presence of smelt was accompanied by elevated mercury levels in lake trout. In Class 2 lakes, presence of smelt was accompanied by an increase in mean mercury levels from 0.54 (± 0.37) ppm to 0.88 (± 0.55) ppm. In Class 3 lakes, smelt was accompanied by an increase in mean mercury levels from 0.64 (± 0.34) ppm to 1.19 (± 1.12) ppm. Two-way ANOVA on Class 2 and 3 lakes shows a significant effect of smelt on Hg levels in lake trout ($n=61$, $F=66.6$, $p=0.012$; Fig. 6a). Class was not a significant predictor of Hg in this analysis (2 vs. 3, $n=61$, $F=1.42$, $p=0.238$).

PCB data from Rasmussen et al. (1990) indicated that the presence of smelt in Class 2 lakes corresponded with an increase in mean lake trout PCB levels from 261.4 (± 293.6) ng/g (wet weight) to 426.7 (± 217.6) ng/g (ww). Among Class 3 lakes, mean PCB concentration increases from 426.0 (± 488.2) ng/g, to 1469.2 (± 1763.1) ng/g with the addition of smelt. Two-way ANOVA for Class 2 and 3 lakes shows a significant effect of smelt on log(PCB) concentration in lake trout ($n=74$, $F=15.07$, $p<0.0001$; Fig. 6b), as well as a significant effect of food chain Class on PCB concentrations ($n=74$, $F=7.86$, $p<0.008$).

Correspondence Between Dietary and $\delta^{15}N$ Estimates of Trophic Position

Stable nitrogen isotopes ($\delta^{15}N$) are increasingly used as a means of measuring trophic relationships, and potentially provide an alternative to use of dietary information as a continuous measure of trophic position. Laboratory and field studies for a range of taxa reveal $\delta^{15}N$ enrichment averaging 3.4 ‰ from prey to predator (Minagawa and Wada 1984; Estep and Vigg 1985; Owens 1987; Peterson and Fry 1987; Fry 1988, 1991).

Stable nitrogen isotopes have recently proven useful in studies characterizing the biomagnification of contaminants (Yoshinaga et al. 1992; Broman et al. 1992; Rolff et al. 1993; Cabana and Rasmussen 1994; Kidd et al. 1995a, 1995b; Schindler et al. 1995; Kiriluk et al. in press). Unfortunately, $\delta^{15}N$ and dietary information are currently not available from the same lakes, preventing lake-specific comparisons of dietary and $\delta^{15}N$ trophic position estimates. But dietary and $\delta^{15}N$ results can be compared using multi-lake averages for lake trout and pelagic forage fish from each of the three trophic Classes defined by Rasmussen et al. (1990). Mean lake trout and pelagic forage fish $\delta^{15}N$ data from Cabana and Rasmussen (1994) were used to calculate a continuous measure of lake trout and pelagic forage fish trophic position. The mean $\delta^{15}N$ signature of zooplankton (representing trophic level 2.0) of 4.5 ‰ in these lakes is used to represent the "baseline" $\delta^{15}N$ signature. A comparison of $\delta^{15}N$ and dietary mean trophic position values reveals a general correspondence between the two methods (Fig. 7). Discrepancies are observed for pelagic forage fish and lake trout of Class 3 lakes, with $\delta^{15}N$ evidence suggesting a longer food chain. This difference could be attributed to elevated primary producer $\delta^{15}N$ signature in Class 3 lakes (associated with elevated loading of human sewage; G. Cabana, personal communication). Conversely, the discrepancy could be attributed to errors associated with use of dietary data, particularly our prey trophic level assumptions.

DISCUSSION

Omnivory and the Trophic Position Model

This study demonstrates the prevalence of omnivory in pelagic systems, as there is considerable discrepancy between trophic position (realized) and discrete trophic level (potential) depictions of trophic structure (compare Fig. 1c and 1d). Omnivory as considered here refers to the proportion of energy (or biomass) coming from different trophic guilds. Clearly, this concept of omnivory differs greatly from that of classical food web ecologists (e.g. Sprules and Bowerman 1988; Havens 1993; Locke and Sprules 1994), who refer to the proportion of species that are hypothesized to feed on more than one trophic level. Thus, it is not suprising that our report of relatively short food chains contrasts with the classical food web analysis of Sprules and Bowerman (1988), who show zooplankton food webs to have a modal food chain length varying between 1 and 9 trophic levels (averaging 3 to 5 trophic levels).

Despite the potential problems with our prey trophic level assumptions (that most invertebrate prey organisms represent trophic level "2"), the general agreement between $\delta^{15}N$ and dietary estimates of trophic position for pelagic food web components (Fig. 7) suggests that our assumptions adequately represent invertebrate trophic structure. Thus, despite the complexity of food webs, the majority of ecosystem production channeled to pelagic fish appears to be transferred directly from primary consumers to planktivorous fish. This could be attributed to the greater ease of capture of herbivorous prey, and the higher abundance and productivity of herbivorous prey items.

Both extremes of the trophic modeling continuum, the food web approach (Fig. 1a), and the food chain approach (Fig. 1d), fail to adequately account for interaction strengths, omnivory, and the complexity of natural food webs. Classical connectance food webs represent trophic connections without regard to interaction strength and the relative importance of various energy flow pathways (but see Kitching 1987). Similarly, Lindeman's classic paper "The tropho-dynamic aspect of ecology" (1942) foreshadowed the difficulty in representing complex, natural trophic webs with simplified linear food chains and trophic levels. Meaningful use of discrete trophic levels implies two notions; the first being the existence of levels--natural groupings of species of similar trophic position; and the second being a linear trophic architecture--in other words, no omnivory (Ulanowicz and Kemp 1979). Clearly, use of discrete trophic level designations will yield only approximate descriptions of mass/energy flow since a "trophic level" contains species whose diets are only qualitatively similar, and ignores omnivory, which we show to be prominent in the pelagic food web. Despite the shortcomings of discrete trophic levels, they continue to be used (often successfully, in terms of generating qualitative predictions) in studies of cascading trophic interactions (Carpenter et al. 1985; Persson et al. 1992; Wooton and Power 1993), ecosystem energetics and production (Lindeman 1942; Kerr and Martin 1970), and contaminant biomagnification (Oliver and Niimi 1989; Rasmussen et al. 1990; Cabana et al. 1994; Rowan and Rasmussen 1992, 1994).

Accurate description of the trophic relationships in a food web requires a compromise between the two dominant means of representing communities; food web models--those that include all possible species links (Fig. 1a), and food chain models--those that simplify the system to include only discrete functional trophic compartments, thereby ignoring the complexity of food webs (Fig. 1d). We present such a compromise by using dietary information to eliminate minor trophic pathways, measure each species' trophic position, and clump species of similar trophic position into trophic guilds, to yield the model shown in Fig. 1c, a trophic position model. This representation preserves information about omnivory, and represents trophic position as a continuous variable, both essential when characterizing flows of energy and material through a food web.

The trophic position model clearly reflects our orientation towards modeling of mass transfer and the quantification of trophic relationships (Burns 1989), as opposed to food chain dynamics and effects (Paine 1980; Fretwell 1987), or patterns of food web connectance (Cohen et al. 1990; Polis 1991). Yet this approach may have application to studies of tropho-dynamics and cascading trophic interactions, as the degree of omnivory should determine the degree to which the trophic cascade propagates through the food web (Vadas Jr. 1990). In addition, use of omnivory-corrected estimates of food chain length will also have consequences for modeling of ecosystem energetics (Kercher and Shugart Jr. 1975; Adams et al. 1983). Assuming 10% trophic transfer efficiency, shortening a lake trout food chain from 4.0 to 3.4 trophic levels results in a 4x increase in estimated lake trout production.

Although our trophic position model represents trophic structure more accurately than the use of trophic levels by accounting for more of the natural complexity of food webs, it remains true that communities with similar species composition will exhibit a wide range of realized trophic structure (Kling et al. 1992; Trippel and Beamish 1993; this study Fig. 3). For this reason, site-specific measurement of food chain structure and trophic position is the only way to characterize the trophic structure of an individual system with confidence; this assertion is supported by the increased ability to predict PCB levels using site-specific trophic position estimates.

Implications of Omnivory for Contaminant Modeling

The difficulty in measuring trophic position has greatly impeded studies attempting to determine the importance of food chain effects in explaining the observed patterns of contaminant bioaccumulation. Rasmussen et al. (1990) and Cabana et al. (1994) overcame this problem by estimating the number of trophic levels between zooplankton and lake trout, based on the presence/absence of functional prey groups. This approach demonstrated the important role for trophic transfer of these contaminants, but failed to incorporate omnivory, which we show here to be prevalent in pelagic food webs. Our dietary estimate of trophic position accounts for omnivory, and provides improved prediction of between-lake lake trout PCB levels over the use of discrete trophic levels.

Our dietary calculation of trophic position attempts to mimic what use of $\delta^{15}N$ provides: quantification of the mean number of energy transfers between primary producers and the study organism. A series of recent studies have demonstrated the use of $\delta^{15}N$ as a general predictor of contaminant levels in the biota. Kidd et al. (1995) reported relationships between $\delta^{15}N$ of various components of the food web of an Arctic lake and hexachlorohexane levels ($r^2 = 0.67$), DDT ($r^2 = 0.81$), and hexachlorobenzene

($r^2 = 0.80$). Cabana and Rasmussen (1994) and Yoshinga et al. (1992) report strong relationships between mercury levels and $\delta^{15}N$ signatures. Other recent studies have used $\delta^{15}N$ to characterize contaminant flows in aquatic ecosystems (Bromann et al. 1992; Rolff et al. 1993; Kiriluk et al. in press).

Calculation of BMFs

Rasmussen et al. (1990) reported that addition of each "trophic level" (functional trophic group) contributed a 3.5-fold increase in PCB levels in lake trout. If we consider the results of this study, that addition of each functional trophic group actually elevates the "realized" trophic level of lake trout by 1/2 a trophic level, then our BMF estimate for PCBs becomes 12x for each realized trophic level increment. Likewise, Cabana et al. (1994) reported a mercury BMF of 2.0 for each additional trophic level; the omnivory corrected value is 4.0. BMF calculations generally ignore omnivory by measuring the increase in contaminant levels accompanying discrete trophic level increments (Oliver and Niimi 1988; Meili 1991; Evans et al. 1991; Rowan and Rasmussen 1992). Consideration of omnivory will generally result in higher estimates of BMFs accompanying each discrete trophic level.

Since each $\delta^{15}N$ increment of 3.4 ‰ represents 1 trophic level, the change in a contaminant accompanying each 3.4 $\delta^{15}N$ increment provides a BMF estimate that also incorporates omnivory. Kidd et al. (1995) relate increasing tissue concentrations of organochlorines to $\delta^{15}N$ levels in a Yukon lake food chain. Using the approach outlined above, we calculated BMFs of 3.5 for hexachlorohexane (ΣHCH), 12.3 for ΣDDT, and 9.8 for hexachlorobenzene (ΣHCB). Using contaminant and $\delta^{15}N$ data from Kiriluk et al. (in press), we calculate forage fish to lake trout BMFs of 10.7 for Mirex, 7.7 for DDE, and 7.9 for PCBs. BMFs for Mysis/Diporia to forage fish were 2.3 for Mirex, 2.62 for DDE, and 2.37 for PCBs. Similarly, using data from Cabana and Rasmussen (1994), a 6.5-fold increase in mercury accompanies each $\delta^{15}N$-defined trophic level increment.

Yoshinga et al. (1992) obtained a BMF estimate for mercury of 5.0 in a δ^{15}N-mercury study of a food-web from Papua New Guinea.

Although BMFs can be calculated to either include or exclude omnivory; it traditionally has been excluded in BMF calculations. But with omnivory averaging up to 50% in pelagic food webs, this greatly complicates comparison of BMF values from different systems. Stable nitrogen isotope BMF values appear to correspond more closely with the omnivory adjusted BMFs for lake trout food webs calculated in this study than with the empirical BMF estimates of Rasmussen et al. (1990) and Cabana et al. (1994). We suggest that future studies incorporate omnivory into BMF calculations by measuring the trophic position of organisms using δ^{15}N or dietary data. Consideration of omnivory should also result in more realistic mechanistic modeling of contaminant biomagnification. Cabana and Rasmussen (1994) use δ^{15}N to incorporate omnivory into the steady-state bioaccumulation model of Thomann (1981), which assumed a linear food chain structure.

The Elevated Trophic Position of Smelt, an Invasive Species

Smelt is an invasive species in many of the study lakes, and is the only species of pelagic forage fish to exhibit substantial levels of piscivory (frequently cannibalism). We show that smelt exhibit an elevated trophic position, and that lake trout from lakes containing smelt, on average, exhibit significantly elevated trophic position, mercury levels, and PCB levels (Fig. 3) over lake trout from lakes lacking smelt. This not only warrants the designation of smelt as a separate trophic guild (Fig. 1c), but further supports previous suggestions that smelt elevate contaminant levels in top predators by elongating the food chain (Akielaszek and Haines 1981, MacCrimmon et al. 1983; Mathers and Johansen 1985). Rasmussen et al. (1990) draw attention to the possibility of increasing contaminant levels in top piscivores, including humans and terrestrial wildlife, when food chains are lengthened by the addition of exotic prey species. Introductions of smelt appear to be a case in point, and underscores this concern. In addition to their impact on contaminant levels in piscivores, invasion by smelt has been accompanied by numerous other detrimental effects on native aquatic ecosystems (Loftus and Hulsman 1986; Evans and Loftus 1987).

The association between the presence of smelt and elevated contaminant levels in top piscivores gives support to the role of direct food chain biomagnification as an important mechanism responsible for the observed among-lake distributions of certain contaminants in the biota. Furthermore, it supports our contention that ecological descriptors that consider the natural complexity of ecosystems will provide more accurate predictions of contaminant levels. Finally, it underscores the potential for using contaminants as ecological tracers of food web processes. In this instance, we validate trophic guild designation of smelt by pointing out its role in augmenting contaminant levels in their predators. The use of biomagnifying contaminants as tracers of trophic relationships (and also bioenergetic processes, e.g. Borgmann and Whittle 1992) deserves further exploration.

Problems with Diet Data: Stable Isotopes as an Alternative

The use of dietary information to characterize energetic relationships in food webs is not without problems. For lack of specific trophic interaction data, our trophic position model assumes the trophic level of the invertebrates consumed by fish; zooplankton and zoobenthos were represented by trophic level "2", while Mysis and Diporia represent trophic level 3. In reality Mysis have a wide-ranging diet that includes phytoplankton, herbivorous zooplankton, detritus, and even other predatory zooplankton species (Lassenby and Langford 1973; Cooper and Goldman 1980; Grossnickle 1982). Our simplified representation of lower trophic levels ignores the potential complexity as well as important aspects of the detrital and microbial food webs (Wetzel 1995).

The analysis of trophic interactions at lower trophic levels is complicated by the observation that many invertebrates do not consume hard parts, making stomach contents potentially misleading in estimating trophic relationships. Even for fish, where this problem is not usually serious (Hyslop 1980), gut contents only provide a snapshot of the fish's diet. Reliable averages that integrate temporal and spatial variation require considerable investment of time and effort, not to mention the number of fish that must be sacrificed (see Winemiller 1990; Trippel and Beamish 1993). Other problems include the discrepancy between stomach contents and assimilated material (Boisclair and Leggett 1988), and error associated with the data conversions presented in this study.

Many of these problems may ultimately be circumvented through the application of stable isotopes to food-web studies. Use of $\delta^{15}N$ provides a continuous, time-integrated measure of relative trophic position which has been used to measure pelagic trophic structure and omnivory (Fry 1988; Cabana and Rasmussen 1994; Gu et al. 1994), and can be used to differentiate between realized and potential trophic structure (Kling et al. 1992). Furthermore, it does not require assumptions of prey trophic levels, thereby accounting for the complexity and omnivory at lower trophic levels, which is neglected in a dietary analysis. Thus, $\delta^{15}N$ serves as a more accurate alternative to diet data as measure of trophic position, as long as variation in primary producer (baseline) $\delta^{15}N$ (Toda and Wada 1990; Kline et al. 1993; Yoshioka et al. 1994) can be taken into consideration. The best depiction of trophic structure would be attained by using $\delta^{15}N$ to quantify trophic position and omnivory. Dietary information would then compliment isotopic evidence by verifying $\delta^{15}N$ interpretations of trophic structure and depicting specific trophic interactions with higher taxonomic resolution than possible using isotopic tracers (i.e., discerning among members of a trophic guild).

CONCLUSION

This study uses dietary information to calculate a continuous measure of trophic position for lake trout and pelagic forage fish populations, with the goal of investigating the importance and implications of omnivory in pelagic food webs. The major findings of this study are; (1) that although trophic levels qualitatively represent broad-scale patterns in trophic structure, they fail to quantitatively represent trophic structure, due to the prevalence of omnivory and other complexity of pelagic food webs; (2) that lake-specific estimates of lake trout trophic position provide improved prediction of PCB concentrations over previous trophic level approaches; (3) that high levels of complexity and omnivory in food webs necessitate a trophic position model of food webs. This model provides a continuous measure of trophic position for each species, and aggregates species with similar trophic positions into trophic guilds. This realized model represents the food web in terms of trophic linkages that are important in terms of their contributions to mass transfer. Separate trophic guild designation of smelt is validated by elevated lake trout mercury and PCB levels in the presence of smelt; (4) that mean dietary trophic position estimates generally correspond with average $\delta^{15}N$ estimates among components of the pelagic food web.

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Table 1. Summary of mean diet (bold type, +/-1 SE) for pelagic forage fish; cisco, whitefish, smelt, alewife, trout-perch, stickleback, and sculpin from Class 2 and Class 3 lakes. PLAN=zooplankton (Copepods, Cladocerans); BEN=benthic invertebrates (crayfish, aquatic insect larvae, oligochaetes, mollusks, isopods); AMP=amphipods (Gammarus sp., Hyalella sp., Diporia Hoyi); MYS=Mysis relicta; FIS=all fish species.

	Lake	N	N	% volumetric contribution									
Species	Class	Lakes	Fish	**PLA**	1 SE	**MYS**	1 SE	**BEN**	1 SE	**AMP**	1 SE	**FIS**	1 SE
Alewife	**2**	3	796	**76.1**	10.8	**0.0**	0.0	**14.4**	1.8	**0.0**	0.0	**9.5**	9.5
	3	3	4321	**65.4**	12.3	**4.3**	2.8	**23.5**	16.2	**6.7**	5.4	**0.0**	0.0
Cisco	**2**	9	2005	**91.7**	4.6	**0.0**	0.0	**8.3**	4.6	**0.0**	0.0	**0.0**	0.0
	3	16	11527	**49.9**	8.2	**27.6**	5.8	**9.4**	1.8	**12.4**	5.2	**0.6**	0.3
Sculpin	**2**	17	4335	**0.1**	0.1	**0.0**	0.0	**91.0**	3.2	**7.4**	3.1	**1.3**	0.5
	3	6	2086	**6.0**	4.3	**15.2**	6.5	**24.3**	9.5	**54.5**	12.8	**0.0**	0.0
Smelt	**2**	5	785	**42.1**	12.1	**0.0**	0.0	**21.7**	5.9	**0.4**	0.2	**35.8**	17.8
	3	12	14530	**16.6**	6.4	**32.0**	9.3	**17.5**	5.9	**3.6**	1.5	**30.3**	8.6
Stickleback	**3**	5	787	**13.2**	6.6	**8.6**	4.4	**61.5**	12.2	**16.7**	10.5	**0.0**	0.0
Trout-perch	**3**	2	353	**40.1**	18.8	**8.0**	8.0	**21.3**	19.8	**30.6**	30.6	**0.0**	0.0
Whitefish	**2**	18	1762	**16.0**	5.9	**0.0**	0.0	**77.1**	6.1	**4.7**	1.8	**2.3**	1.7
	3	21	4647	**4.4**	2.2	**2.6**	1.3	**66.5**	6.1	**23.4**	5.0	**3.1**	1.7
Total		**117**	**47934**										

Table 2. Summary of mean diet (bold type, +/- 1 SE) for lake trout from Class 1, 2, and 3 lakes. Lakes are further subdivided into cold water and warm water lakes. PLA=zooplankton; BEN=benthic invertebrates; AMP=amphipods; MYS=Mysis relicta; FIS=all fish species. The fish category is further divided into the following categories: CIS=cisco; WHI=lake whitefish and round whitefish; SME=smelt; SCU=sculpin; ALE=alewife; LIT=littoral species (centrarchids, percids, cyprinids); PEL=other "pelagic" fish species (sticklebacks, trout-perch, catastomids, other salmonids).

Lake		N	N	% volumetric contribution										Breakdown of fish (FIS) category						
Class	Temperature	Lakes	Fish	PLA	1 SE	MYS	1 SE	BEN	1 SE	AMP	1 SE	FIS	1 SE	ale	cis	cot	lit	pel	sme	whi
1	**warm water**	26	3587	**17.4**	2.9	-	-	**27.4**	5.3	**0.5**	0.5	**54.6**	5.5	-	-	-	54.6	-	-	-
1	**winter data**	10	192	**5.1**	2.6	-	-	**8.2**	4.3	**0.0**	-	**86.6**	4.5	-	-	-	86.6	-	-	-
2	**warm water**	22	19313	**1.9**	1.1	**0.1**	0.1	**15.3**	4.0	**5.3**	2.5	**77.4**	6.7	0.0	3.3	0.7	7.0	14.1	9.2	15.5
3	**warm water**	23	21369	**0.0**	-	**3.9**	1.3	**1.1**	0.4	**0.3**	0.2	**94.7**	1.6	21.0	31.9	14.8	4.2	3.3	19.0	0.4
2	**cold water**	4	523	**3.5**	2.9	**0.0**	-	**27.0**	17.0	**1.0**	1.0	**68.6**	20.5	0.0	4.6	2.2	0.0	13.6	0.0	29.4
3	**cold water**	7	2697	**0.0**	-	**2.8**	0.9	**11.0**	4.5	**2.0**	0.7	**84.2**	4.1	0.0	44.8	12.3	1.0	18.7	0.0	7.3
		92	47681																	

TABLE 3. Estimated trophic level (based on Rasmussen et al. 1990), and calculated mean trophic position (+/- 1 SD and 1 SE) for each pelagic fish species. Lake trout are further divided into cold water and warm water populations.

Species	N lakes	Estimated Trophic Level	Dietary Trophic Position	1 SD	1 SE
CLASS 1					
Lake Trout	26	**3.0**	**3.55**	0.28	0.06
CLASS 2					
Alewife	3	3.0	3.10	0.16	0.10
Cisco	10	3.0	3.00	0.00	0.00
Sculpin	10	3.0	3.08	0.14	0.03
Smelt	5	3.0	3.36	0.40	0.18
Whitefish	18	3.0	3.07	0.10	0.02
Lake Trout					
Warm-water	22	**4.0**	**3.89**	0.48*	0.06
Cold-water	4	**4.0**	**3.74**	0.44	0.22
CLASS 3					
Alewife	3	4.0	3.11	0.11	0.03
Cisco	16	4.0	3.41	0.38	0.08
Sculpin	6	4.0	3.70	0.28	0.11
Smelt	12	4.0	3.66	0.29	0.09
Stickleback	5	4.0	3.25	0.29	0.13
Trout-perch	2	4.0	3.39	0.55	0.39
Whitefish	21	4.0	3.29	0.25	0.05
Lake Trout					
Warm-water	23	**5.0**	**4.38**	0.38†	0.02
Cold-water	7	**5.0**	**4.24**	0.14	0.05

*Class 2 Lake trout - 40% of variation from pelagic forage fish, 60% from lake trout.

†Class 3 Lake Trout - 68% of variation from pelagic forage fish, 32% from lake trout.

Figure. 1. A continuum of models used to represent pelagic trophic structure leading to the top predator, lake trout (Salvelinus namaycush). Class 1 lakes lack preferred lake trout prey, pelagic forage fish, causing lake trout to feed on zooplankton and zoobenthos. Class 2 lakes contain at least one species of pelagic forage fish, resulting in piscivory. Class 3 lakes, in addition to pelagic forage fish, contain the glacio-marine relict invertebrate predator, Mysis relicta. Mysis is a common prey item of lake trout prey fish species, thereby elevating lake trout to the fifth trophic level. a) a classical, connectance lake trout food web, relying on trophic species; b) the major feeding relationships for Class 1, 2, and 3 communities based on dietary data. Numbers represent the average percent volume contribution of the prey to the predator; c) a realized trophic position model of Class 1, 2, and 3 lake trout communities. Omnivory is incorporated into this model, species of similar trophic path length are clumped into trophic guilds, and trophic guilds are assigned non-integer trophic position values; d) a food chain model of the three types of lake trout communities. LT=lake trout; FFISH=pelagic forage fish; FISH=other fish; SME=smelt; MEZO=megazooplankton (Mysis and Diporia); ZOOP=zooplankton; BENT=benthic invertebrates.

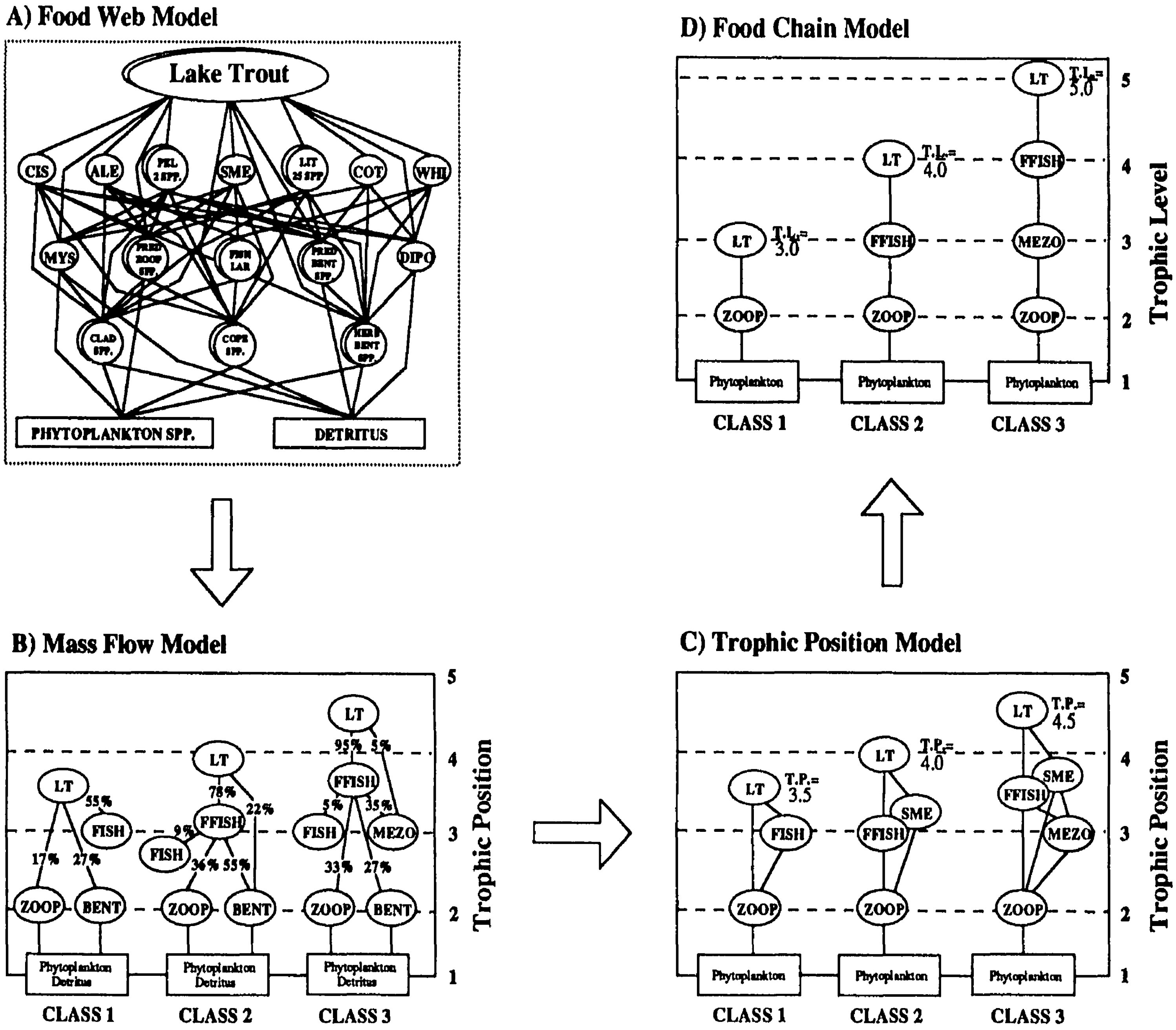

A) Food Web Model
Lake Trout
CIS
ALE
PEL 2 SPP.
SME
LIT 25 SPP
COT
WHI
MYS
PRED ZOOP SPP
FISH LAR
PRED BENT SPP
DIPO
CLAD SPP.
COPE SPP.
HERB BENT SPP.
PHYTOPLANKTON SPP.
DETRITUS
B) Mass Flow Model
LT
55%
FISH
17%
27%
ZOOP
BENT
Phytoplankton Detritus
LT
78%
22%
FFISH
9%
FISH
36%
55%
ZOOP
BENT
Phytoplankton Detritus
LT
95%
5%
FFISH
5%
35%
FISH
MEZO
33%
27%
ZOOP
BENT
Phytoplankton Detritus
CLASS 1
CLASS 2
CLASS 3
5
4
3
2
1
Trophic Position
C) Trophic Position Model
LT
T.P.= 3.5
FISH
ZOOP
Phytoplankton
LT
T.P.= 4.0
SME
FFISH
ZOOP
Phytoplankton
LT
T.P.= 4.5
SME
FFISH
MEZO
ZOOP
Phytoplankton
CLASS 1
CLASS 2
CLASS 3
5
4
3
2
1
Trophic Position
D) Food Chain Model
LT
T.L.= 3.0
ZOOP
Phytoplankton
LT
T.L.= 4.0
FFISH
ZOOP
Phytoplankton
LT
T.L.= 5.0
FFISH
MEZO
ZOOP
Phytoplankton
CLASS 1
CLASS 2
CLASS 3
5
4
3
2
1
Trophic Level

Figure 2. A diagram summarizing the diets of lake trout and pelagic forage fish, thereby representing the average trophic structure characterizing Class 1, 2, and 3 food webs.

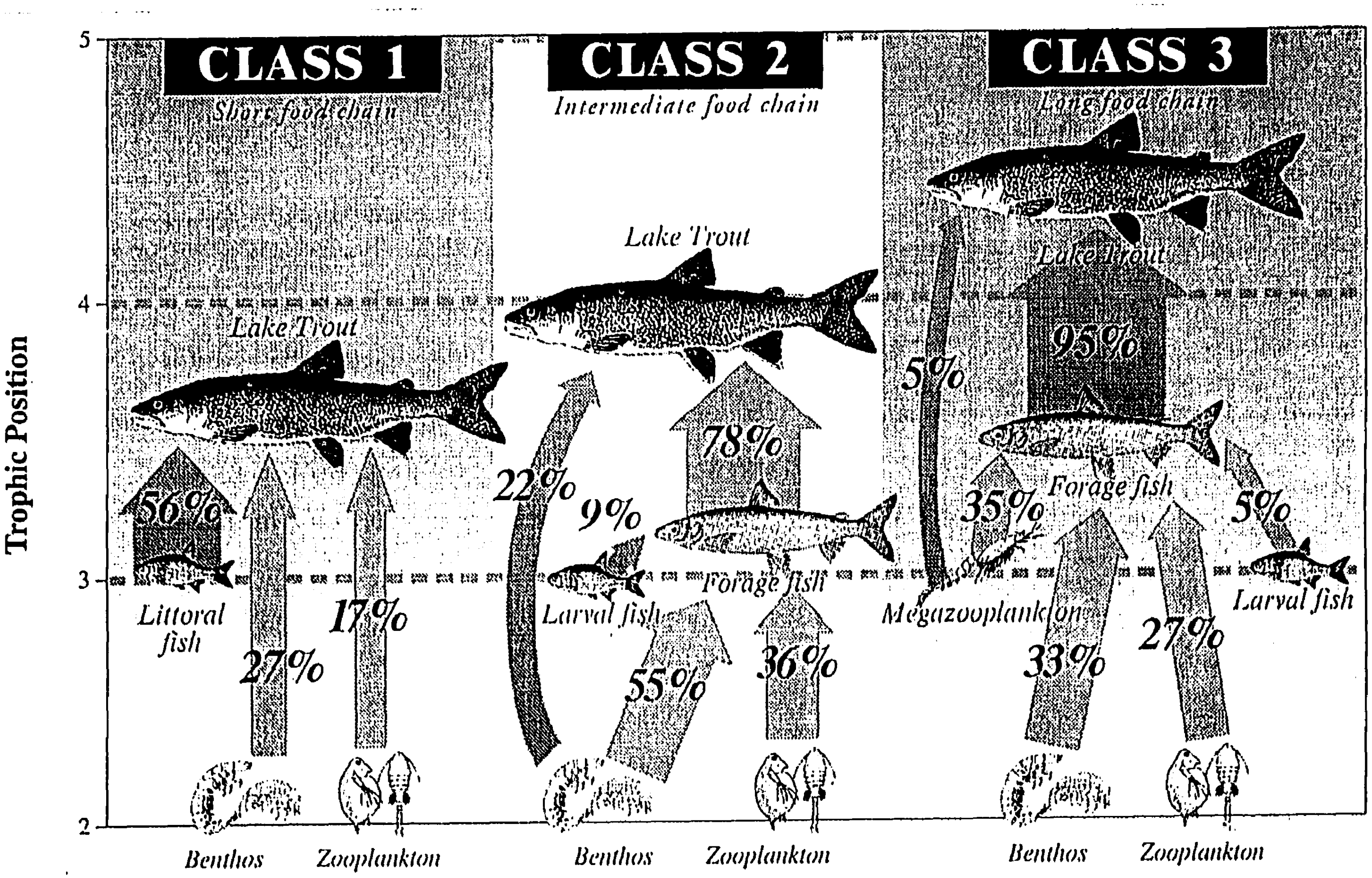

Trophic Position
5
4
3
2
CLASS 1
Short food chain
Lake Trout
56%
27%
17%
Littoral fish
Benthos
Zooplankton
CLASS 2
Intermediate food chain
Lake Trout
22%
9%
78%
Larval fish
Forage fish
55%
36%
Benthos
Zooplankton
CLASS 3
Long food chain
Lake Trout
95%
5%
35%
Forage fish
5%
Megazooplankton
Larval fish
33%
27%
Benthos
Zooplankton

Figure 3. Mean trophic position (+/- 1 SD) of lake trout and each pelagic forage fish species for Class 1, 2, and 3 food webs. a=alewife, c=cisco, w=whitefish, sm=smelt, sc=sculpin, p=trout-perch and stickleback, LT=lake trout.

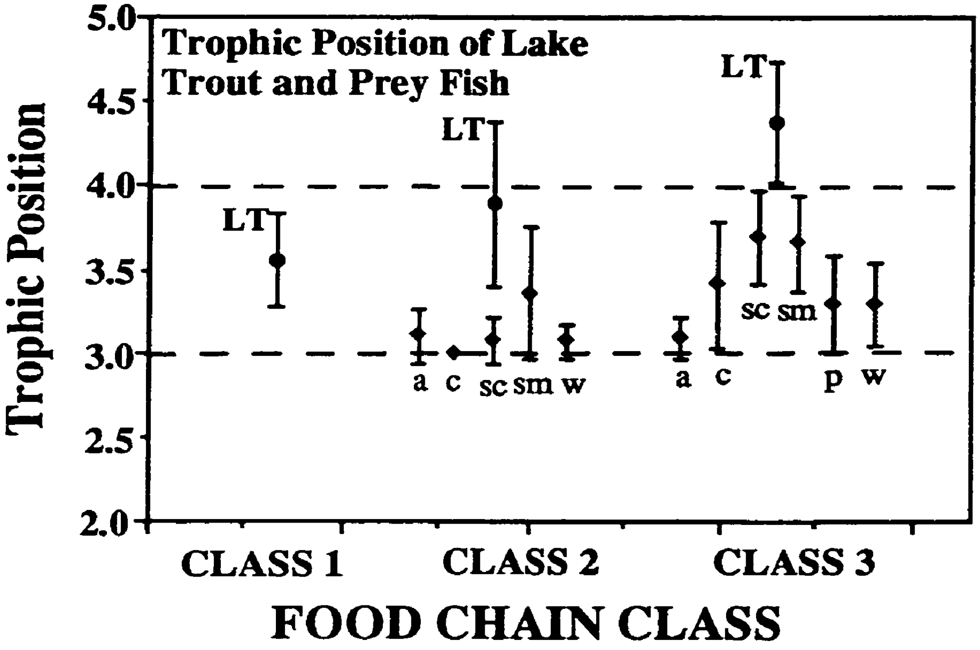

Trophic Position of Lake Trout and Prey Fish
Trophic Position
5.0
4.5
4.0
3.5
3.0
2.5
2.0
LT
LT
LT
a
c
sc
sm
w
a
c
sc
sm
p
w
CLASS 1
CLASS 2
CLASS 3
FOOD CHAIN CLASS

Figure 4. Relationships between PCB levels, lipid content, and dietary estimate of trophic position. a) trophic position vs. log PCB levels in lake trout; b) trophic position vs. log percent lipid in lake trout; c) log percent lipid vs. log PCB in lake trout; d) trophic position vs. log lipid corrected PCB levels [log (PCB/%lipid)]. Class 1 lake trout = (open square), Class 2 lake trout = (solid circle), Class 3 lake trout = (open triangle).

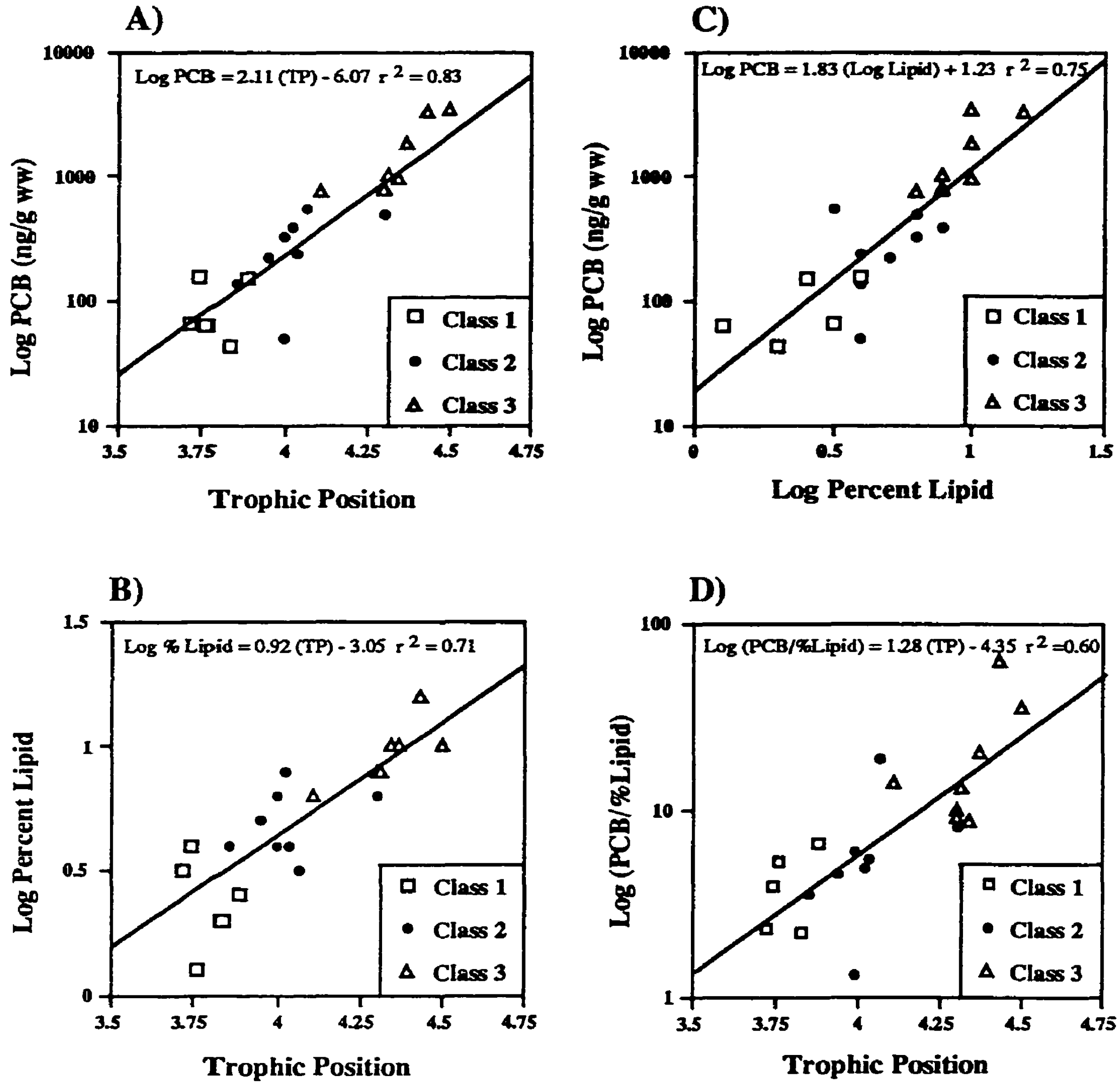

A)
Log PCB = 2.11 (TP) - 6.07 r 2 = 0.83
Log PCB (ng/g ww)
10000
1000
100
10
3.5
3.75
4
4.25
4.5
4.75
Trophic Position
Class 1
Class 2
Class 3
C)
Log PCB = 1.83 (Log Lipid) + 1.23 r 2 = 0.75
Log PCB (ng/g ww)
10000
1000
100
10
0
0.5
1
1.5
Log Percent Lipid
Class 1
Class 2
Class 3
B)
Log % Lipid = 0.92 (TP) - 3.05 r 2 = 0.71
Log Percent Lipid
1.5
1
0.5
0
3.5
3.75
4
4.25
4.5
4.75
Trophic Position
Class 1
Class 2
Class 3
D)
Log (PCB/%Lipid) = 1.28 (TP) - 4.35 r 2 =0.60
Log (PCB/%Lipid)
100
10
1
3.5
3.75
4
4.25
4.5
4.75
Trophic Position
Class 1
Class 2
Class 3

Figure 5. The influence of the presence of smelt on average lake trout trophic position (+/- 1 SE) from Class 2 and 3 food webs. The accompanying numbers represent sample size.

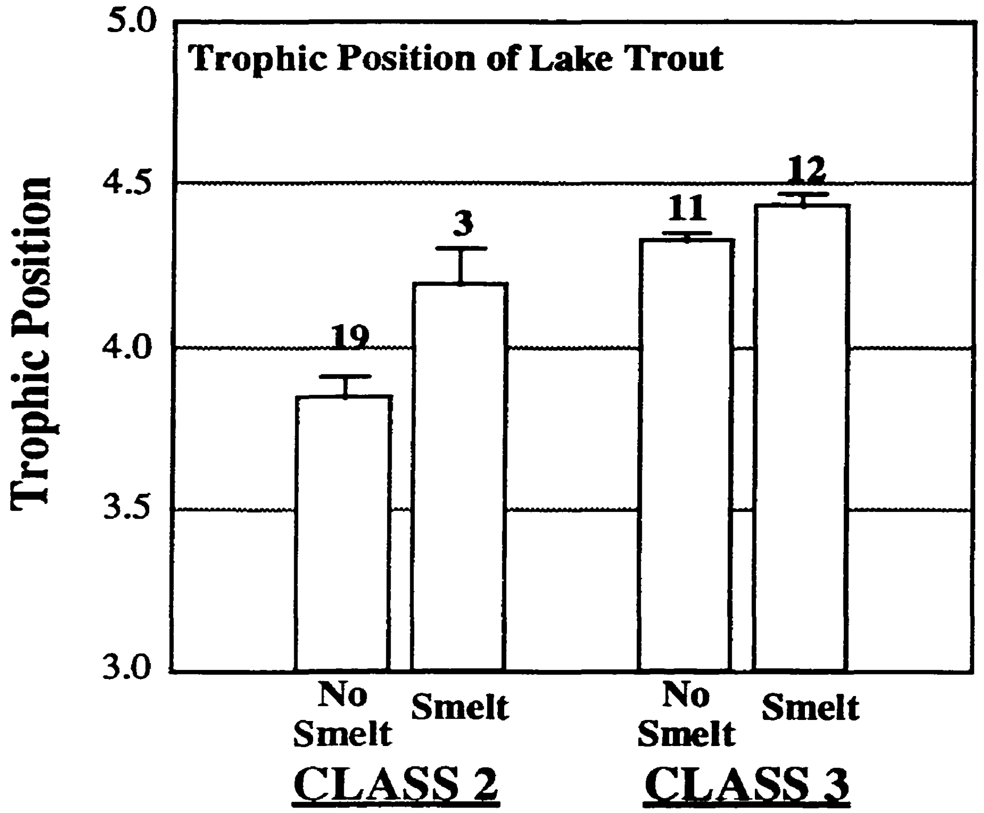

Trophic Position of Lake Trout
Trophic Position
5.0
4.5
4.0
3.5
3.0
19
3
11
12
No Smelt
Smelt
No Smelt
Smelt
CLASS 2
CLASS 3

Figure 6. The influence of the presence of smelt upon mean lake trout muscle tissue Hg (ug/g; +/- 1 SE) and PCB (ng/g wet weight; +/- 1 SE) levels from Class 2 and Class 3 food webs. The accompanying numbers represent sample size.

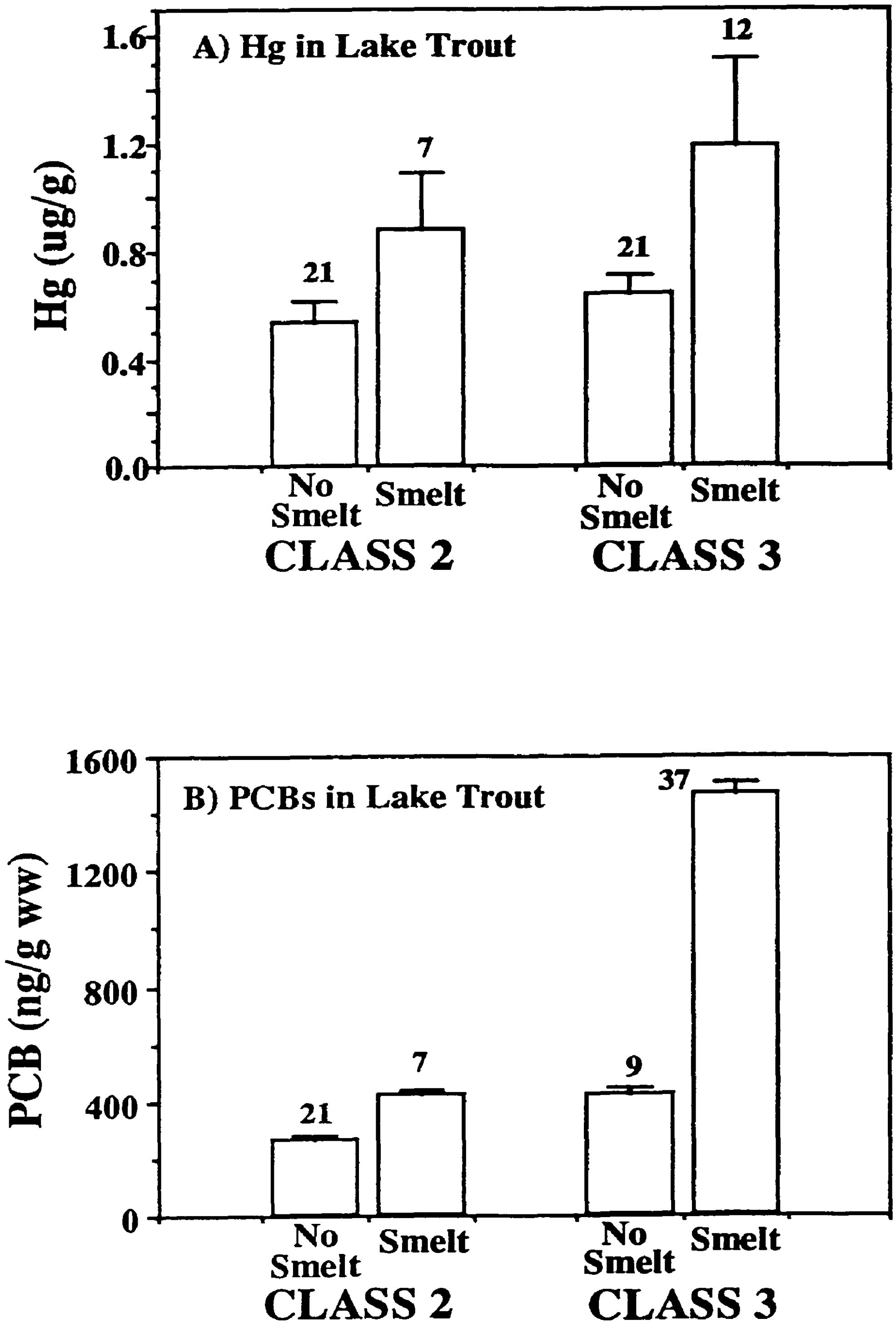
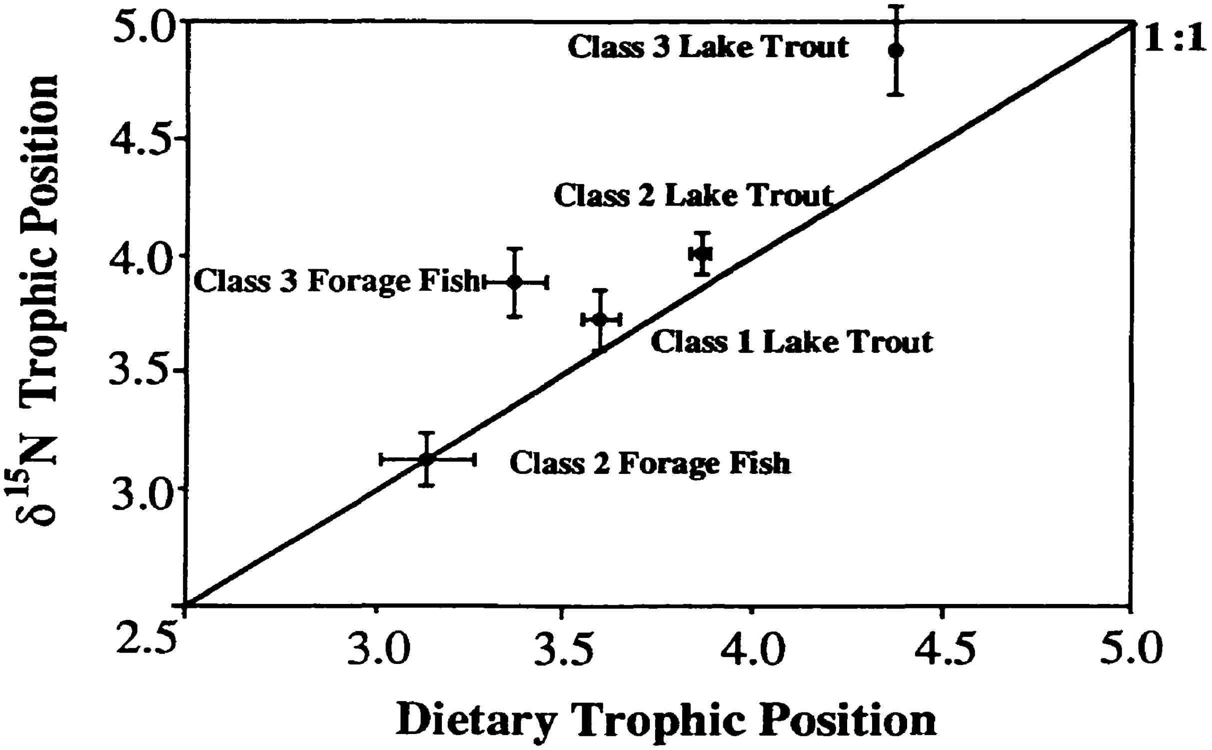

A) Hg in Lake Trout
Hg (ug/g)
1.6
1.2
0.8
0.4
0.0
21
7
21
12
No Smelt
Smelt
No Smelt
Smelt
CLASS 2
CLASS 3
B) PCBs in Lake Trout
PCB (ng/g ww)
1600
1200
800
400
0
21
7
9
37
No Smelt
Smelt
No Smelt
Smelt
CLASS 2
CLASS 3

Figure 7. A comparison of the mean stable nitrogen isotope ($d^{15}N$) and mean dietary estimates of trophic position (+/- 1 SE) for lake trout and pelagic forage fish from Class 1, 2, and 3 food webs.



Class 3 Lake Trout
Class 2 Lake Trout
Class 3 Forage Fish
Class 1 Lake Trout
Class 2 Forage Fish
1 :1
$\delta^{15}N$ Trophic Position
Dietary Trophic Position
5.0
4.5
4.0
3.5
3.0
2.5
3.0
3.5
4.0
4.5
5.0

CONNECTING STATEMENT

The preceding chapter presented the trophic position concept and examined broad-scale patterns in the trophic position of aquatic consumers, measured using quantitative dietary data and weighted average formulas. Although dietary data was found to be useful for examining trophic variation across lakes of a given lake Class, it was generally difficult to provide lake- or population-specific estimates of trophic position. Furthermore, use of dietary data provides only a snapshot in time of a consumers diet and requires estimating the trophic position of prey items. This next chapter presents stable isotope-based estimates of trophic position (Cabana and Rasmussen 1996) for seven littoral fish species from 36 lakes in Ontario and Quebec. These results are compared with dietary-based trophic position estimates from 342 populations of these same fish species. This study is a broad-scale analysis of patterns in the trophic position of littoral fish species, using both isotopic and dietary methods. This comparison of the two methods provides a validation of the stable isotope technique for estimating trophic position.

Cabana, G. and J. B. Rasmussen. 1996. Comparing aquatic food chains using nitrogen isotopes. Proceedings of the National Academy of Sciences (USA) **93**: 10844-10847.

CHAPTER 2

COMPARING TROPHIC POSITION OF FRESHWATER FISH CALCULATED USING STABLE NITROGEN ISOTOPE RATIOS ($\delta^{15}N$) AND LITERATURE DIETARY DATA

ABSTRACT

Stable nitrogen isotope ratios ($\delta^{15}N$) are commonly used to represent the trophic structure of aquatic systems, yet the ability of $\delta^{15}N$ to indicate the trophic position of aquatic consumers remains untested using traditional dietary methods. Interpreting the $\delta^{15}N$ signatures of aquatic consumers relative to large, long-lived primary consumers such as unionid mussels provides a continuous measure of an organism's trophic position that adjusts for among-system variation in baseline $\delta^{15}N$ signature. We used this method to estimates the trophic position of eight littoral fish species from 36 lakes in Ontario and Quebec. We validated these $\delta^{15}N$ measures of trophic position by compiling literature dietary data from 342 populations of these same fish species, and calculated a continuous measure of trophic position for each population. Mean dietary trophic position estimates corresponded closely with stable nitrogen isotope estimates, with mean trophic position ranging from 3.3 for pumpkinseed (*Lepomis gibbosus*) to 4.4 for walleye (*Stizostedion vitreum*). Both methods indicated approximately 1 trophic level of variation among populations of a species. This study confirms the ability of baseline-adjusted $\delta^{15}N$ to represent the trophic position of aquatic consumers.

INTRODUCTION

Accurate representation and description of trophic relationships are essential to a wide range of ecological studies. The concept of discrete trophic levels are commonly used in ecological studies, and has been used successfully in studies predicting contaminant bioaccumulation in top predators (Rasmussen et al. 1990; Cabana et al. 1994). Furthermore, trophic levels provide the framework for studies of cascading trophic interactions (Carpenter et al. 1985; Wooton and Power 1993) and ecological energetics and efficiencies (Lindeman 1942; Kerr and Martin 1970). The food chain approach contrasts with food web studies, which focus on the complexity of trophic relationships in nature (Sprules and Bowerman 1988). Although food web studies recognize and quantify important attributes such as omnivory, cannibalism, and reciprocal predation (Sprules and Bowerman 1988; Polis 1991), designation of "trophic linkages" is a subjective process that fails to consider the energetic importance of the represented trophic connections (Paine 1988).

Food chains and food webs represent extreme endpoints of models used to represent trophic relationships; both approaches have the potential to misrepresent the pathways of mass transfer and energy flow through ecosystems (Murdoch 1966; Kling et al. 1992; Vander Zanden and Rasmussen 1996). Use of a continuous measure of trophic position (analogous to the concept of "realized" trophic structure of Kling et al. (1992)), provides energetically-based representations of trophic relationships (Levine 1980). Trophic position calculations weigh trophic connections according to their relative energetic importance, thereby serving as a compromise between discrete food chain and food web models (Vander Zanden and Rasmussen 1996). This general approach has been successfully applied to modelling of mercury (Cabana and Rasmussen 1994) and PCB (Vander Zanden and Rasmussen 1996) bioaccumulation in aquatic food webs.

A continuous measure of an organism's trophic position can be obtained in two ways. The dietary approach uses estimates of the trophic position of prey organisms and volumetric stomach content data, preferably for large numbers of fish. Weighted averages are then used to calculate a continuous measure of the population's trophic position (Winemiller 1990; Vander Zanden and Rasmussen 1996). A second approach relies on the consistent enrichment of the stable nitrogen isotope, ^{15}N (3.4‰ ± 0.3‰) between prey and predator (Minagawa and Wada 1984; Owens 1987; Peterson and Fry 1987; Cabana and Rasmussen 1994), allowing its use as a measure of an organism's trophic position that accounts for omnivory (Cabana and Rasmussen 1994). Previous comparative food web studies using stable isotopes have been complicated by among-system variation in the stable nitrogen isotope signatures of organisms at the base of the food web. Cabana and Rasmussen (1996) overcame this problem by measuring an organism's $\delta^{15}N$ relative to the lake-specific $\delta^{15}N$ signature of commonly occurring primary consumers such as unionid mussels. This provides a continuous measure of an organism's trophic position amenable to comparative, multi-system studies of trophic structure.

The objective of this study is to verify $\delta^{15}N$ as a measure of trophic position for a series of littoral freshwater fish species. We calculate the trophic position of eight species of freshwater fish using dietary data and stable nitrogen isotopes, and compare the mean and variation in trophic position estimates attained using the two techniques. Previous studies have attempted to verify the $\delta^{15}N$ measure of trophic position using within-system comparisons between dietary data and $\delta^{15}N$ (Wainright et al. 1993), and attributed discrepancies to the inability of dietary data to represent temporal variation in feeding and errors in trophic position estimates of prey items. Our comparison differs in that it relies on dietary trophic position estimates for 342 fish populations and $\delta^{15}N$ estimates from 113 fish populations from 36 lakes. Although the actual fish populations for our two methods do not overlap, the large sample sizes provide a robust comparison of these two measures of trophic position and serve as a test of the $\delta^{15}N$ measure of trophic position recently proposed by Cabana and Rasmussen (1996).

MATERIALS AND METHODS

Dietary analysis and trophic position calculations

Dietary data for adults of eight common Eastern North American game fish species were collected from literature sources: northern pike *(Esox lucius)*, chain pickerel *(Esox niger)*, rock bass *(Ambloplites rupestris)*, pumpkinseed *(Lepomis gibbosus)*, smallmouth bass *(Micropterus dolomieui)*, largemouth bass *(Micropterus salmoides)*, yellow perch *(Perca flavescens)*, and walleye *(Stizostedion vitreum)*. Data for northern pike and chain pickerel were pooled due to the small number of lakes with chain pickerel, and the similar ecology, morphology, and feeding behavior of these species (Scott and Crossman 1973). These eight species were chosen because of the abundance of dietary data in the literature, and because we have stable isotope estimates of trophic position for these same species from a large number of lakes.

Although the degree of taxonomic detail of prey categories in the published studies were highly variable, it was usually possible to separate prey items into the following categories: fish, zooplankton, omnivorous zoobenthos, predatory zoobenthos, mollusks, crayfish, detritus/plants/debris, and others (includes mammals, birds, and amphibians, and unidentified materials). For the two highly piscivorous species, pike and walleye, the fish component was further subdivided to species where data permitted.

Diet data expressed as the percent contribution of a prey item to total gut volume were used for this study (also reported as percent of dry or wet weight). Data reported in the "percent of total number of prey organisms" format were converted to percent of total volume using prey weight values from the dietary study, or mean values from literature reports of invertebrate prey weight (Cummins and Wuycheck 1971; Driver et al. 1974; Smock 1980; Lawrence et al. 1987). Data expressed as "percent frequency of occurrence" were not utilized in this study due to the potential error accompanying conversion of dietary data into a volumetric format.

When data for adult and juvenile fish were reported separately, only adult fish were retained for analysis; division of data in the published sources according to fish size, age, month, season, depth, and time of day were averaged for each year and treated as a single observation. When possible, data for multiple years from a lake were treated as separate observations, as a year roughly corresponds with the period of time for which an adult fish's diet is integrated using stable nitrogen isotopes (Hesslein et al. 1993). The fish dietary data set contained 342 lake-year observations, for a total of 65, 987 individual fish. The average diet (percent volumetric contribution of each of the previously mentioned prey categories) was calculated for each fish species.

Calculation of "trophic position" of a fish population required estimating the trophic position of prey organisms. We define primary producers as trophic level "1", primary consumers as trophic level "2", and so on. Since specific trophic interactions among invertebrate organisms remain poorly understood, the simplest possible assumptions concerning the trophic position of prey were used in this study (Table 1). Prey items known to be predominantly predatory were assigned values of 3.0; strictly herbivorous prey were assigned values of 2.0. Prey items known to be omnivorous, such as zooplankton and most orders of aquatic insect larvae, were assigned an intermediate trophic position value of 2.5, for lack of information about their realized trophic position. For piscivorous fish, pike and walleye, trophic position was calculated in two ways. One used all the available dietary data and assigned all fish prey items to trophic level 3.5. The second approach used only data where the fish components of their diets was further broken down to species.

Clearly, a limitation of this dietary approach is that we must assume and simplify trophic interactions at lower levels of the food web. Although the trophic positions of prey items do vary within-systems and through time, our large sample sizes would cause any errors associated with these assumptions to remain constant among the fish species included in this study. Following Winemiller (1990) and Vander Zanden and Rasmussen

(1996), the fish dietary data from each lake and the trophic position estimates for prey items were used to calculate trophic position for each fish population using the formula:

$$(1) \qquad T_a = \sum (V_i * T_i) + 1$$

Where T_a = mean trophic position of the ath predator population, V_i = volumetric contribution of the ith prey item, T_i = trophic position of the ith food item. Although prey items may have been represented by discrete trophic level estimates, this weighted average calculation generates a continuous, fractional measure of trophic position for each fish population. The large number of populations included in this study permits a reliable estimate of the average trophic position for each species, as well as the degree of among-system variability in trophic position for each species.

Estimating trophic position using ^{15}N

Adult individuals of these eight fish species were collected from 36 lakes (113 fish populations) in Ontario and Quebec, and were analyzed for $\delta^{15}N$ ratios using a Europa Tracermass mass spectrometer (Cabana and Rasmussen 1996). These nitrogen isotopic values alone cannot be considered to represent trophic position, since the average $\delta^{15}N$ signatures of baseline organisms (baseline organisms being defined as organisms that convert inorganic N to organic N) are highly variable among systems (Kling et al. 1992; Kline et al. 1993; Cabana and Rasmussen 1996) and within systems through time (Toda and Wada 1990; Gu et al. 1994; Cabana and Rasmussen 1996). This necessitates that the isotopic signature of fish be measured relative to a lake-specific "baseline" $\delta^{15}N$ signature. Cabana and Rasmussen (1996) interpret fish $\delta^{15}N$ relative to unionid mussels. These relatively large and long-lived primary consumer organisms integrate temporal variability in the baseline $\delta^{15}N$ signature, thereby representing the average baseline $\delta^{15}N$ signature. Unionid mussel $\delta^{15}N$ signatures (n = 1 - 9 mussels per lake) were measured for each of the 36 study lakes. A continuous measure of trophic position (corresponding to the dietary estimates of trophic position) was calculated for each fish population using the formula:

$$\text{(2)} \quad \text{Trophic Position} = [(\text{fish } \delta^{15}\text{N} - \text{mussel } \delta^{15}\text{N}) / 3.4] + 2$$

where 3.4 represents a 1.0 trophic level increment in δ^{15}N.

RESULTS

Dietary estimates of trophic position

The raw dietary data compiled for this study are presented in Appendix 4. These data were summarized by calculating the average diet (percent of total stomach volume ± 1. SD) for each species (Table 2). The summary results of the average diets of these fish are generally consistent with previous reports of the diets characterizing these species. Nearly 40% of the average diet of pumpkinseed consisted of mollusks. 53% of perch prey consisted of zoobenthos, of which more than 10% were identified as amphipods. Rock bass consumed 42% benthic invertebrates and 32% crayfish. The diet of smallmouth bass consisted of 37% fish, 28% zoobenthos, and 28% crayfish. 50% of the prey of largemouth bass were fish prey. Both pike and walleye consumed about 85% fish. More detailed analysis of the fish components of the diets of pike and walleye (Appendix 5) indicated that walleye consumed 29% perch and only 8% cyprinids. Walleye diet also had major contributions from smelt, trout-perch, and centrarchids. Pike consumed a broader range of prey, consuming similar amounts of perch and cyprinids (13% each).

Species exhibited a mean dietary trophic position estimate ranging from 3.3 to 4.4 (Fig. 1). Pumpkinseed exhibited the lowest average dietary trophic position value of 3.3, while perch and rock bass averaged 3.7; these three species tend to be centered between what are considered (in the classical food chain sense) secondary and tertiary consumers. Smallmouth bass and largemouth bass exhibited intermediate trophic position values averaging approximately 4.0, making them tertiary consumers. The piscivores, pike and walleye, both exhibited trophic position estimates of 4.35 when all the available dietary data are considered, and all fish prey are assigned to trophic level 3.5. When the data are limited to include only piscivore populations for which fish prey are identified to species, the average trophic position estimate of walleye remained the same, while that of pike was 0.07 trophic level lower.

$\delta^{15}N$ Estimates of Trophic Position

Average unionid mussel $\delta^{15}N$ values (reported by lake) and estimates of mean trophic position for each fish population in this study are presented in Appendix 6. 78% of the variance in individual mussel $\delta^{15}N$ signatures is explained by the use of a categorical 'lake' variable. Furthermore, the species of mussel did not vary significantly with mussel $\delta^{15}N$ signature (ANOVA; $p < 0.05$). Trophic position estimates were generally similar to those determined using dietary methods, with average values ranging from 3.38 in pumpkinseed to 4.40 in walleye.

The mean $\delta^{15}N$ trophic position estimates (± 1 S. D.) are directly compared to the mean dietary estimates of trophic position for each species (Fig. 1; Table 3). The two measures of trophic position were in close correspondence ($\delta^{15}N$ trophic position = 0.78 * dietary trophic position + 0.81; $R^2 = 0.78$). Northern pike were the only outlier; pike gut content data indicated a mean trophic position value nearly 0.4 trophic level higher than the $\delta^{15}N$ trophic position estimate.

Among-Population Variability in Trophic Position

Both dietary and isotopic evidence indicated relatively high levels of among-population variability, as seen in frequency histograms of dietary and $\delta^{15}N$ trophic position values (Fig. 2). The total range of trophic position among all species spaned roughly 2 complete trophic levels. Trophic position also varied greatly among populations of a given species. The range in trophic position for a given species was about one trophic level for each of our study species; the degree of among-population variation was similar for dietary and isotopic estimates of trophic position. The observed among-population variation in trophic position resulted in a high degree of overlap in trophic position of littoral fish species.

The distribution and variation of trophic position values calculated using the two different methods corresponded quite closely. Using diet data, 1 standard deviation in trophic position averaged 0.23 trophic level (range 0.11 - 0.28 trophic level), while for $\delta^{15}N$ estimates, 1 standard deviation averaged 0.29 trophic level (range 0.18 - 0.34 trophic level).

DISCUSSION

The role of $\delta^{15}N$ in food web studies

The application of $\delta^{15}N$ as a tracer of an organism's trophic position eliminates many of the problems encountered when using diet data to estimate trophic position. Use of $\delta^{15}N$ represents the major energy flow pathways at lower trophic levels, offers a time integrated measure of the organism's trophic position, accounts for temporal and spatial variation in feeding at multiple levels of the food web, and detects trophic interactions that are otherwise "unobservable", as gut contents can differ from the material actually assimilated by an organism.

Although use of $\delta^{15}N$ ratios are increasingly common as a tracer of trophic relationships, the nitrogen isotopic signature of primary producers is highly variable among-systems (Kling et al. 1992; Kline et al. 1993; Cabana and Rasmussen 1996) and within-systems through time (Toda and Wada 1990; Gu et al. 1994; Cabana and Rasmussen 1996). As a result, $\delta^{15}N$ ratios should reflect organism's trophic position for single-system studies (see Hobson and Welsh 1992; Wainright et al. 1993), but the applicability of $\delta^{15}N$ as an absolute measure of trophic position (or food chain length) for comparative studies is limited because the isotopic signature of baseline organisms (phytoplankton and bacteria, which transform inorganic N into organic N) is highly variable, and can be mistakenly interpreted as variation in trophic structure (Kidd et al. 1995; Wainright et al. 1996). Cabana and Rasmussen (1996) use mussel $\delta^{15}N$ signatures to correct for variability in average baseline $\delta^{15}N$ signatures. These relatively large, long-lived primary consumer organisms filter-feed on phytoplankton and bacteria in the water column (Silverman et al. 1995), and thereby serve as integrators of temporal variation in the baseline nitrogen isotopic signature. Measurement of an organism's $\delta^{15}N$ relative to that of a unionid allows a continuous measure of the organism's trophic position suitable for among-system comparisons.

Using simple and uniform assumptions, we test the $\delta^{15}N$ method by comparing the average trophic position of eight common species of fish estimated from nitrogen isotope data to estimates obtained from a large fish dietary data base. The close correspondence between the estimates of trophic position based on $\delta^{15}N$ and those based on dietary data supports the validity of the isotope approach to the study of food chains proposed by Cabana and Rasmussen (1996). Although diet and $\delta^{15}N$ give corresponding estimates of average trophic position, the many advantages of $\delta^{15}N$ analysis (see above) make it a preferable measure of trophic position or food chain length for aquatic consumers. Understanding of trophic relationships is enhanced through complementary use of baseline corrected $\delta^{15}N$ and gut content evidence. $\delta^{15}N$ is used to quantify an organism's trophic position, while diet data, although subject to error when calculating trophic position for individual communities, reveals specifically which taxa are involved in feeding interactions.

The concept of trophic position

The prevalence of omnivory, and the complexity of natural food webs suggest than neither discrete food chain nor connectance food web approaches will adequately represent the pathways of energy flow and mass transfer in aquatic ecosystems (Vander Zanden and Rasmussen 1996). The use of a continuous measure of trophic position attempts to strike a balance between food web approaches, which fail to weigh trophic connections according to their energetic importance, and linear food chain approaches, which ignore the omnivory and complexity that characterizes ecosystems (Vander Zanden and Rasmussen 1996). Thus, trophic position quantifies, as a continuous variable, how many times the biomass consumed by an organism has been metabolically "processed" within the food chain since inorganic molecules have been first synthesized into organic compounds. Species with the same trophic position can be pooled into trophic guilds, which serve as functional groupings analogous to the trophic level, the difference being that they assume non-integer trophic position values (Vander Zanden and Rasmussen 1996). Note also that although a trophic guild includes organisms with similar trophic positions, members of a trophic guild may have different prey and different ecological niches within a food web (e.g., benthic vs. pelagic predators). Use of stable carbon isotope ratios augments nitrogen isotope trophic position evidence by serving as a means of discriminating between benthic and pelagic sources of food web production (Hecky and Hesslein 1995).

Patterns in trophic position

The range in trophic position values is approximately 1 trophic level among populations of each of the study species. This within-species variability in trophic position can be attributed to one of two factors; highly flexible and opportunistic feeding of these fish species (Dill 1983), or variation in trophic position of prey organisms. Although this variation is likely a combination of the two sources, determining the relative importance of these sources of variation would require measurement of the trophic position of organisms situated lower in the food chain. Furthermore, our estimate of the variation accompanying mean dietary trophic position values is conservative since it fails to account for the unknown variation in the trophic position of prey items.

Previous evidence (Rasmussen et al. 1990; Cabana and Rasmussen 1994; Vander Zanden and Rasmussen 1996) has shown that the presence/absence of pelagic forage fish and *Mysis relicta* are determinants of the trophic position of lake trout. However, the complexity of littoral food webs and the lack of presence/absence data for potential prey items make it impossible to follow a similar approach in the exploration of littoral aquatic food webs. The variability and unpredictability in trophic position among populations as shown by the $\delta^{15}N$ data presented here indicate that knowledge of the trophic position of a given population does not necessarily represent that of other populations of the same species. This is clearly shown by our trophic position data calculated from $\delta^{15}N$ where species can switch their trophic position from lake to lake (Appendix III). For example, smallmouth bass occupies a higher trophic position (4.43) than pike (3.69) by about 0.75 trophic level in Lake Mazinaw, but the respective trophic position of these two species are essentially reversed in Lake Doré (trophic positions of 3.91 and 4.41 for smallmouth bass and pike, respectively). The impact of the presence of a particular predator on a lake community will therefore vary from lake to lake. As a result, relying on simple assumptions stereotyping the feeding ecology of a predator species will undermine our ability to predict its impact on a particular food web.

Dietary versus isotopic approaches

Although we report a close correspondence between dietary and $\delta^{15}N$ estimates of trophic position, certain limitations of the dietary approach need be considered. One limitation is that dietary trophic position estimates require assumptions of the trophic position of prey items, thereby introducing a source of error in fish trophic position. Our estimate of 2.5 as the trophic position of zooplankton prey contrasts with Sprules and Bowerman (1988) who report that North American zooplankton food webs have a modal food chain length varying from 1 to 8 trophic levels (averaging between 3 and 5 trophic levels). Sprules and Bowerman (1988) tabulated food chain length without integrating omnivory into the food chain length estimate; inclusion of omnivory would result in shorter food chain length values, perhaps resembling values reported in this study.

Although our mean prey trophic position assumptions appear to be reasonable (since dietary and isotopic trophic position estimates correspond), trophic interactions among organisms at lower trophic levels remain unquantified, and may be characterized by high levels of variation. So although these assumptions appear adequate for broad-scale comparisons as presented herein, dietary estimates of trophic position may be inadequate where detailed information for individual communities is required.

Another problem with direct comparison of dietary and $\delta^{15}N$ estimates of trophic position involves the differences in which the two methods integrate variation in trophic position. $\delta^{15}N$ provides a relatively long-term and time-integrated measure of an organism's trophic position that also accounts for variation in feeding at lower trophic levels, in addition to the higher trophic levels. Use of dietary data provide a snapshot in time of an organism's diet, which certainly does not represent the average trophic position of a population over the year. Furthermore, when calculating trophic position using dietary data, the variability accompanying the trophic position of prey items, which would be compounded up the food chain, is not passed on to predators.

Comparison of gut content and stable nitrogen isotope estimates of trophic position on a lake-specific basis can only provide a robust test of $\delta^{15}N$ where a reliable dietary estimate of trophic position is available. But an accurate measure of trophic position for an individual population requires detailed gut content data for large numbers of fish, sampled throughout the year, a situation which is rare in dietary studies. We have overcome this problem by considering the mean trophic position of large numbers of populations, which serves to reduce the error that accompanies dietary trophic position estimates for any particular lake.

Explaining the difference between $\delta^{15}N$ and dietary data for northern pike

Although $\delta^{15}N$ and dietary estimates of trophic position are in general agreement, dietary estimates for pike overestimate trophic position relative to $\delta^{15}N$. Determining specifically which fish taxa serve as prey of pike and walleye reveals the importance of perch in the diet of walleye (29%) relative to pike (13%), while pike and walleye consume similar amounts of cyprinids. The high mean trophic position of perch (3.7) relative to cyprinids (M. J. Vander Zanden, unpubl. isotope data) may partially explain the discrepancy between $\delta^{15}N$ and dietary trophic position of pike.

But for studies that identify fish prey items to species, pike trophic position averages 4.24, compared to 4.31 when fish prey could not be further subdivided (Appendix 5). The value 4.24 is in closer agreement with the $\delta^{15}N$ estimate of trophic position (3.87), although there still remains a 0.37 trophic level discrepancy between these two pike trophic position estimates. Breakdown of the fish prey category did not affect walleye dietary trophic position estimates (4.33 versus 4.35); gut content and $\delta^{15}N$ measures of trophic position remain in close agreement ($\delta^{15}N = 4.40$; diet = 4.35).

Although pike are reported to be benthic invertebrate feeders in many lakes (Chapman et al. 1989; Craig and Babaluk 1989; Chapman and Mackay 1990), these lakes were not included in this analysis because published data were presented as percent occurrence, which may not be reliably converted into a volumetric format. An effect of lake size is another possible explanation for the pike discrepancy. For our pike diet data set, lake size was positively correlated with pike trophic position (pike trophic position = 0.026 (log lake area) + 4.21; $n = 36$; $p=.008$; $r^2=0.19$), and our pike diet study lakes tended to be larger lakes than our $\delta^{15}N$ study lakes. Although the difference in trophic position of pike remains unresolved, lake-specific diet data - $\delta^{15}N$ comparisons could serve to resolve the discrepancies between the two measures of trophic position.

The presence of the additional trophic level for piscivorous fish species greatly complicates gut content-based trophic position estimates and introduces an additional source of error, since the trophic position of prey fish species must also be estimated. Although this was not a major problem in the simple and relatively linear pelagic systems leading to lake trout (Vander Zanden and Rasmussen 1996), estimating prey fish trophic position in the highly complex and species-rich littoral food webs becomes problematic. Although our designated trophic position estimates of littoral prey fish appears to approximate the average values for these items, our dietary calculations neglect the variation in prey trophic position, thereby underestimating the true degree of variation in average predator trophic position.

In summary, the stable isotope approach to measuring trophic structure has become widely used in ecology, offering the possibility of obtaining objective and repeatable measures of trophic position, food chain length, and omnivory (Kling et al. 1992; Hobson and Welsh 1992; Cabana and Rasmussen 1994). However, our ability to compare systems has been hampered by the problem of spatial and temporal variation in the $\delta^{15}N$ signatures at the base of the food web. Cabana and Rasmussen (1996) proposed to use long-lived sedentary primary consumers such as unionid mussels to control for such baseline variation in $\delta^{15}N$ when calculating trophic position of consumers. The present study corroborates the use of $\delta^{15}N$-based trophic position estimates by demonstrating correspondence between $\delta^{15}N$- and dietary-based estimates of trophic position in eight species of fish are strongly correlated with their trophic position estimated from dietary data.

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Table 1. Assumed trophic position of prey items used in dietary calculations of trophic position.

Prey Category	Estimated Trophic Position	Includes
Fish	2.5	Cyprinids
	3.0	Alewife†
	3.2	Whitefish†, cisco†
	3.3	Centrarchids
	3.5	Suckers, trout, burbot, whitebass, Unidentified fish, others
	3.7	perch, trout-perch†, stickleback†, smelt†, sculpins†
Zooplankton	2.5	Cladocera, Copepoda, Ostracoda, Rotifera
Omnivorous Zoobenthos	2.5	Tricoptera, Ephemeroptera, Plecoptera, Hemiptera, Coleoptera, Diptera, Oligochaeta, Amphipoda*(Gammarus sp., Hyalella sp., Diporia, Mysis relicta)*, other unidentified insect larvae and benthic invertebrates
Predatory Zoobenthos	3.0	Odonata, Hirudinea, Megaloptera
Molluscs	2.0	Gastropoda, Pelecypoda
Crayfish	3.0	Decapoda
Detritus	1.0	Detritus, Plants, Mud
Other	2.5	Amphibians, Mammals, Waterfowl, Unidentified materials

† trophic position estimated using dietary data; from Vander Zanden and Rasmussen (1996)

Table 2. Mean dietary data for littoral fish species included in this study. Zoop = zooplankton, Ben = zoobenthos, Pred. Ben = predatory zoobenthos, Mol = molluscs, Cray = crayfish, Det = Detritus, Other = unidentified material, mammals, amphibians, birds.

Species	N Lakes	N Fish	Fish	Zoopl.	Benth.	Pred. Benth.	Mol.	Cray.	Det	Other
Pumpkinseed	27	2000	0.0	1.6	36.2	5.6	39.9	1.3	5.5	9.7
Perch	91	8075	17.2	13.6	53.9	4.3	2.3	4.4	0.8	3.1
Rock Bass	25	1962	10.0	3.0	42.2	2.8	1.7	31.2	2.1	6.4
Smallmouth Bass	79	3162	37.6	2.0	28.8	1.2	0.1	27.3	0.7	2.3
Largemouth Bass	21	5664	53.3	4.9	11.0	9.3	0.0	10.6	1.9	8.6
Northern Pike and Chain Pickerel	67	34738	84.1	0.1	3.5	2.5	0.0	7.8	0.2	1.9
Walleye	32	10386	83.3	2.0	10.7	0.5	0.0	2.5	0.2	0.8
total:	342	65987								

Table 3. The mean trophic position for each species of fish, 1 SD of the mean trophic position, and the range of trophic position values, and number of fish populations, calculated using dietary and stable nitrogen isotope methods.

	Dietary				Stable Nitrogen Isotope			
Species	Mean Trophic Position	S.D.	Range	N lakes	Mean Trophic Position	S.D.	Range	N lakes
Pumpkinseed	3.30	0.16	3.0 - 3.52	27	3.38	0.33	2.81 - 4.15	19
Yellow Perch	3.69	0.23	3.45 - 4.47	91	3.61	0.33	2.99 - 4.33	28
Rock Bass	3.74	0.20	3.45 - 4.08	25	3.87	0.27	3.45 - 4.43	14
Smallmouth Bass	4.02	0.29	3.46 -4.50	79	4.02	0.34	3.55 - 4.73	15
Largemouth Bass	4.12	0.26	3.55 - 4.49	21	4.08	0.18	3.87 - 4.41	7
Northern Pike	4.31 (4.24)*	0.22	4.15 - 4.51	67	3.87	0.32	3.38 - 4.51	20
Walleye	4.33 (4.35)*	0.25	3.91 - 4.50	32	4.40	0.24	4.09 - 4.86	10

* values in parentheses are mean trophic position estimates calculated only from populations where fish prey were identified to species.

Fig. 1. A comparison of mean trophic position estimates of the species included in this study, calculated using dietary and $\delta^{15}N$ methods. Error bars represent 1 standard deviation. The bold diagonal line represents the 1:1 line.

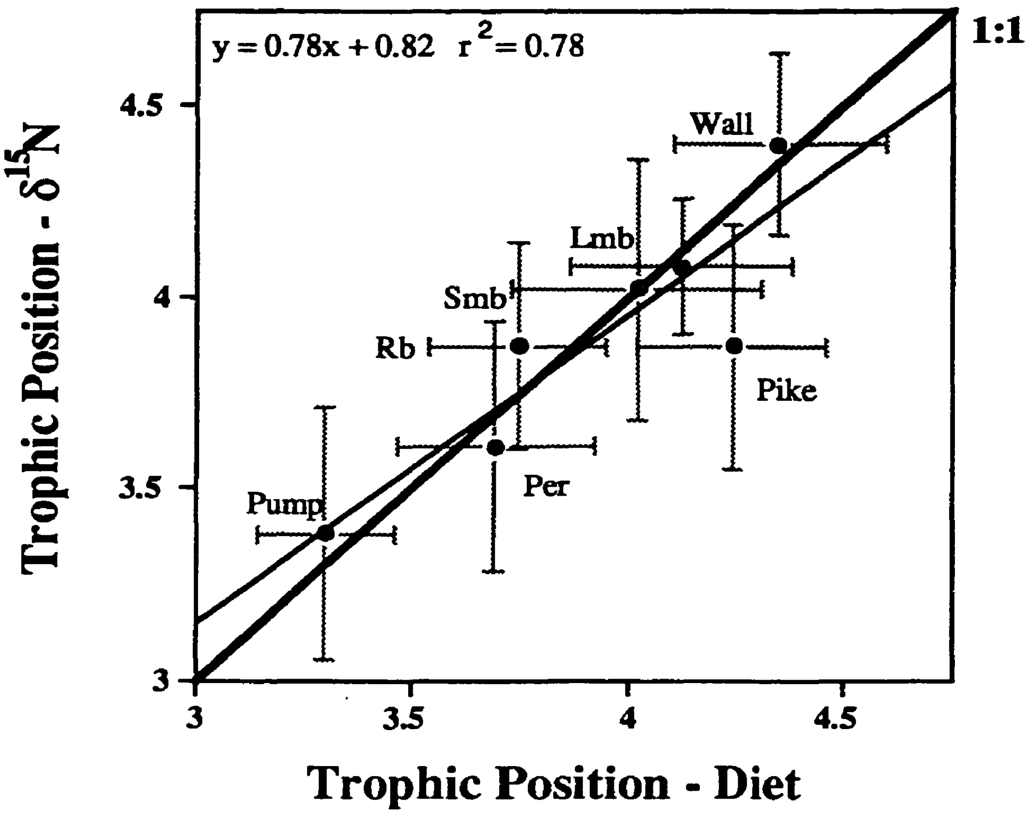
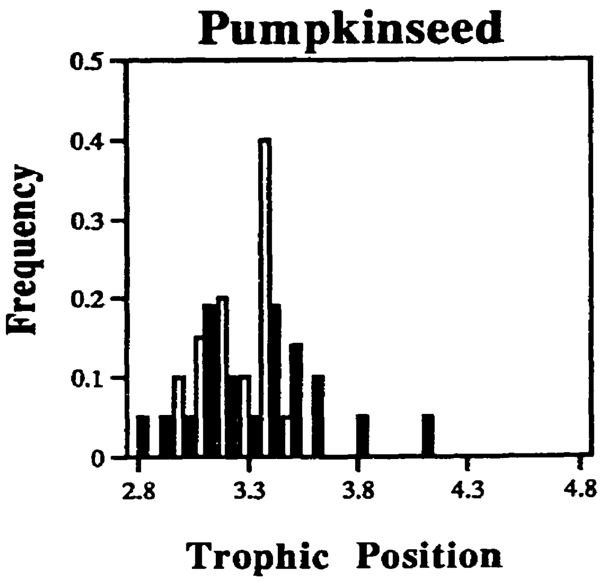
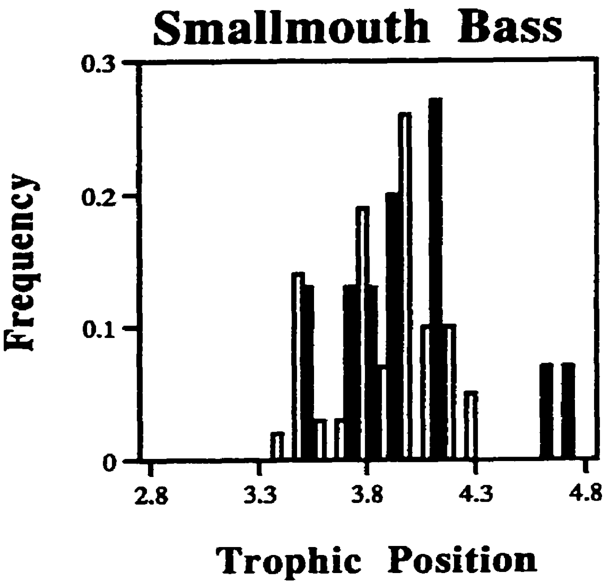
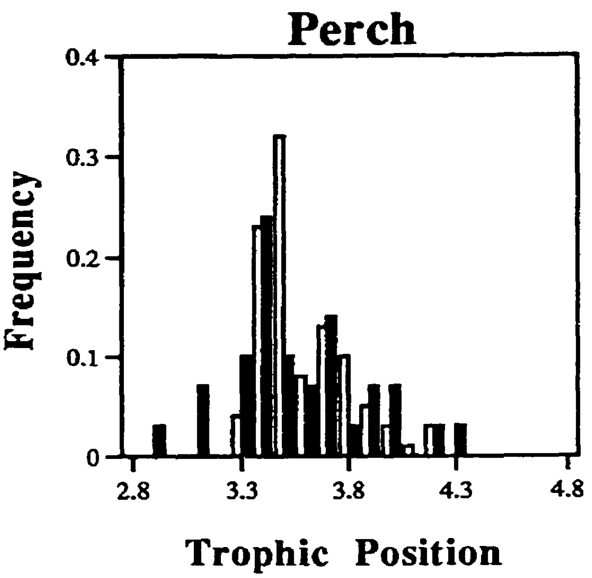
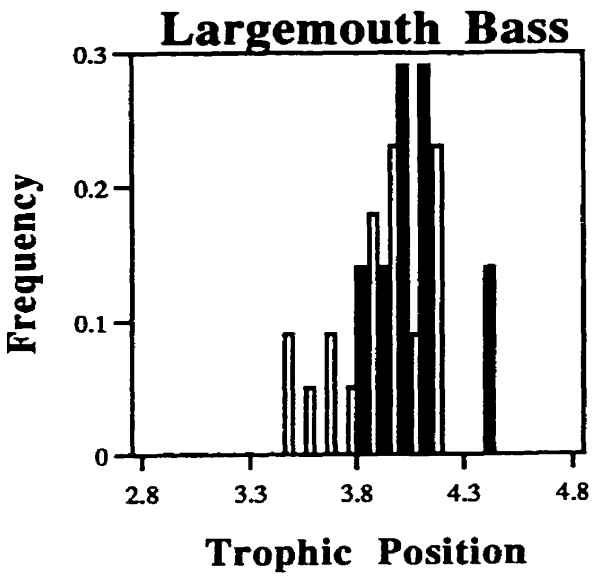

y = 0.78x + 0.82 r ^{2} = 0.78
1:1
Wall
Lmb
Smb
Rb
Pike
Pump
Per
Trophic Position - δ^{15}N
Trophic Position - Diet
4.5
4
3.5
3
3
3.5
4
4.5

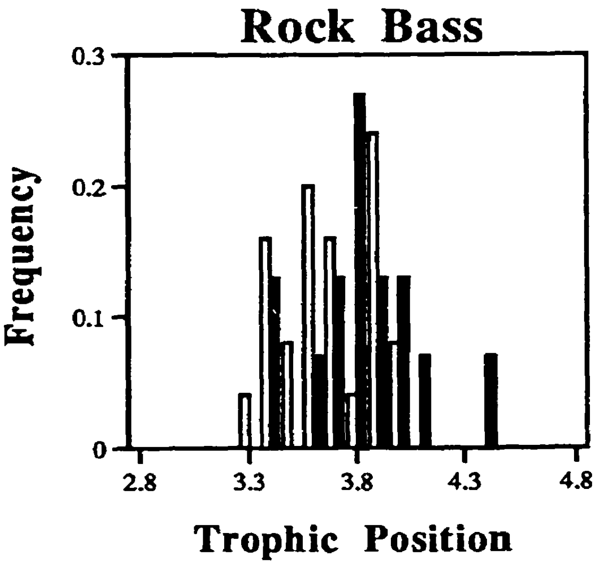
Fig. 2. Frequency distributions of lake-specific trophic position values for littoral fish, calculated using dietary data (light bars) and baseline corrected stable nitrogen isotope ratios (dark bars).

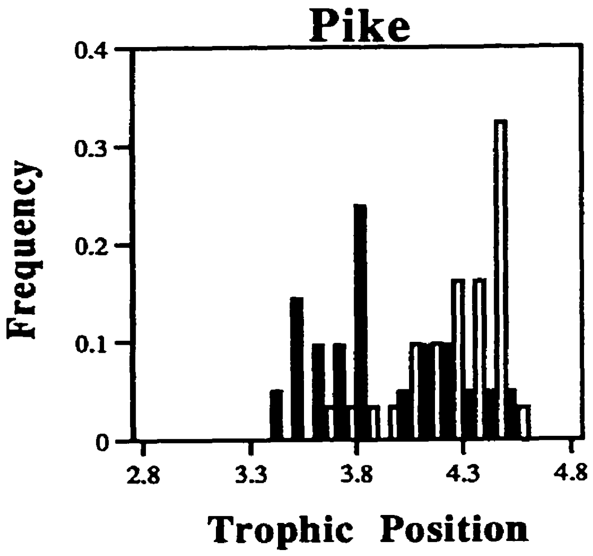

Pumpkinseed

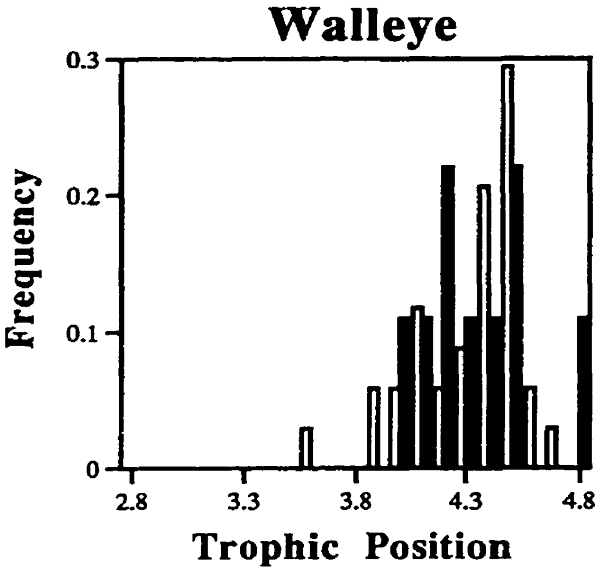

Smallmouth Bass


Perch


Largemouth Bass


Rock Bass


Pike


Walleye
Frequency
0.3
0.2
0.1
0
2.8
3.3
3.8
4.3
4.8
Trophic Position

CONNECTING STATEMENT

The previous chapter used stable isotopes to estimate trophic position; trophic position was estimated by considering the $\delta^{15}N$ of consumers in relation to that of an indicator primary consumer organism (unionid mussels) from that lake, an approach presented by Cabana and Rasmussen (1996). Although use of this approach detrends for the among-lake differences in $\delta^{15}N$ at the base of the food web, the potential for within-lake (habitat-specific) variation in $\delta^{15}N$ have not been considered. This chapter examines $\delta^{15}N$ and $\delta^{13}C$ signatures of primary consumers (i.e., presumed herbivores; trophic level 2) from all possible habitats in 14 lakes in Ontario and Quebec. This chapter reports substantial habitat-specific variation in $\delta^{15}N$ and $\delta^{13}C$ of primary consumers. Relationships between $\delta^{15}N$ and $\delta^{13}C$ are used to develop a simple method for estimating the trophic position of aquatic consumers that corrects for both within- and among-lake variation in $\delta^{15}N$ at the base of the food web.

Cabana, G. and J. B. Rasmussen. 1996. Comparing aquatic food chains using nitrogen isotopes. Proceedings of the National Academy of Sciences (USA) **93**: 10844-10847.

CHAPTER 3

PRIMARY CONSUMER $\delta^{15}N$ AND $\delta^{13}C$ AND THE TROPHIC POSITION OF AQUATIC CONSUMERS

ABSTRACT

Stable nitrogen isotope signatures ($\delta^{15}N$) are increasingly used to infer the trophic position of consumers in food web studies. Interpreting the $\delta^{15}N$ of consumers relative to the $\delta^{15}N$ characterizing the base of the food web provides a time-integrated measure of trophic position. We use primary consumers (trophic level 2) as baseline indicator organisms, and investigate the variation in baseline $\delta^{15}N$ values in 14 lakes in Ontario and Quebec. $\delta^{15}N$ values ranged from -2‰ to +9‰, and varied significantly as a function of lake habitat (mean littoral = 1.6‰, pelagic = 3.1‰, profundal = 5.2‰). Stable carbon isotopic signatures ($\delta^{13}C$) of primary consumers decreased along this same habitat gradient (mean littoral = -23.8‰, pelagic = -28.4‰, profundal = -30.5‰). Primary consumer $\delta^{13}C$ and a categorical lake variable explained 72% of the variability in primary consumer $\delta^{15}N$. This relationship was corroborated by primary consumer $\delta^{15}N$ and $\delta^{13}C$ data from the literature, indicating that habitat-specific variation in baseline $\delta^{15}N$ and $\delta^{13}C$ are a widespread phenomena in freshwater systems. We present a method that uses the presented baseline $\delta^{15}N$ - $\delta^{13}C$ relationship and the $\delta^{15}N$ and $\delta^{13}C$ values of the consumer to estimate trophic position; it is a method that corrects for the described variation in baseline $\delta^{15}N$. These results emphasize the general importance of accounting for patterns in isotopic signatures characterizing the base of the food web when inferring trophic structure using stable isotopes.

INTRODUCTION

The food chain and the food web are two dominant conceptual approaches used to represent trophic structure and feeding relationships at the whole-community level. Food chain studies assign species or populations to one of several discrete trophic levels; a shortcoming of the food chain approach is a failure to incorporate the complexity and omnivory that characterizes natural ecosystems (Polis and Strong 1996; Vander Zanden and Rasmussen 1996). Alternatively, classical food web studies rely on species lists and the presence or absence of feeding links, and search for across-system patterns in trophic structure (Cohen et al. 1990). Although food webs do recognize the complexity of natural systems, food webs do not weight feeding links according to their energetic or functional importance (Polis 1991; Vander Zanden and Rasmussen 1996).

An alternative to food webs or food chains is to use quantitative gut content data and weighted average formulas to assign organisms a continuous measure of trophic position, which represents the energetically-weighted average path length leading to a consumer. Although numerous authors recognize that a trophic position-based approach incorporates energy flow and omnivory (Levine 1980; Adams et al. 1983; Winemiller 1990; Kling et al. 1992; Gaedke et al. 1996; Vander Zanden and Rasmussen 1996), more general application of this approach hinges upon the ability of investigators to estimate the trophic position of organisms in the field. Indeed, greater consideration of trophic position has been limited by the difficulty in collecting the requisite quantitative dietary data for the many species interacting in a typical food web.

Stable carbon and nitrogen isotope ratios are increasingly used to provide time-integrated information about feeding relationships and energy flow through food webs (Peterson and Fry 1987; Kling et al. 1992; Cabana and Rasmussen 1994). Stable carbon isotope ratios ($\delta^{13}C$) of consumers are similar to that of their food (DeNiro and Epstein 1978; Fry and Sherr 1984; Wada et al. 1993; France 1995c; 1996). Yet phytoplankton and benthic algae in freshwater lakes often have distinct $\delta^{13}C$ signatures, as benthic algae generally exhibit less ^{13}C fractionation during carbon fixation than do phytoplankton (Hecky and Hesslein 1995; France 1995a, b). Additionally, organisms of the profundal zone of lakes tend to exhibit highly negative $\delta^{13}C$ values, presumably due to fixation of respired CO_2 (Rau 1980). Because $\delta^{13}C$ values are conserved "up the food chain", but vary at the base of the food chain, the $\delta^{13}C$ of aquatic consumers can provide information about the sources of energy to higher consumers.

Consumers become enriched in ^{15}N relative to their food by 3‰ - 4‰ (average = 3.4‰; DeNiro and Epstein 1981; Minagawa and Wada 1984; Owens 1987; Peterson and Fry 1987; Cabana and Rasmussen 1994). As a consequence of this stepwise trophic level enrichment in ^{15}N, stable nitrogen isotope ratios ($\delta^{15}N$) of consumer tissues serve as a time-integrated indicator of trophic position based on the pathways of energy flow (Fry 1988; Kling et al. 1992; Cabana and Rasmussen 1994). Use of $\delta^{15}N$ signatures of consumers as a measure of trophic position neglects intra-system variation in $\delta^{15}N$ values characterizing organisms at the base of the food web; this can be a significant problem as Cabana and Rasmussen (1996) found that the lake-specific average primary consumer $\delta^{15}N$ ranged from 1‰ - 13‰. Thus, an absolute measure of trophic position requires that the $\delta^{15}N$ of consumers be interpreted relative to an appropriate baseline $\delta^{15}N$ value. Primary consumers (rather than primary producers) were chosen as baseline indicators because their larger body size and greater longevity result in less seasonality in $\delta^{15}N$ signatures (Cabana and Rasmussen 1996).

Our previous studies used unionid mussels as a baseline $\delta^{15}N$ indicator for estimating trophic position, thereby correcting for among-system differences in baseline $\delta^{15}N$ (Cabana and Rasmussen 1996; Vander Zanden et al. 1997). Yet the $\delta^{15}N$ of primary consumers or primary producers from different habitats within a system can also vary substantially (Angradi 1994; Yoshii 1995; France 1997), such that the $\delta^{15}N$ of any one primary consumer may not reflect that of other primary consumers within the same system. With this in mind, the objective of this paper is to describe the spatial variability in stable isotopic values of primary consumers, and to develop a method that corrects for this variation for the purpose of estimating the trophic position of higher consumers.

METHODS

Invertebrate samples were collected from the 14 study lakes in central Ontario and southern Quebec, Canada (located between 47 00 N and 44 50 N latitude, and 80 00 W and 72 00 W longitude) between May and August 1995. Lakes ranged in area from 138 hectares to 20,972 hectares (Table 1). All study lakes are dimictic, oligotrophic, relatively deep lakes (maximum depth ranges from 24 to 117 meters) located on the Canadian shield.

Zooplankton was collected using a 250 μm zooplankton net. Horizontal zooplankton tows were conducted at the surface (0-3 m) to sample epilimnetic zooplankton, and at approximately 10 - 12 m to sample zooplankton from deeper water (metalimnetic-hypolimnetic). Zooplankton species known to be predatory were hand removed from net zooplankton samples. Net zooplankton consisted primarily of cladoceran and copepods, which are generally considered to be primary consumers, but were only included in analyses that consider mean (across-lake) $\delta^{15}N$ and $\delta^{13}C$ values. Zooplankton were excluded from analyses that use site-specific measurements because their relatively short life spans and small size produce temporally variable $\delta^{15}N$ and $\delta^{13}C$ values (Toda and Wada 1990; Gu et al. 1994; Yoshioka et al. 1994; Cabana and Rasmussen 1996).

Littoral (depth < 1m) benthic macroinvertebrates were collected using hand-held dip nets. Profundal benthic invertebrates (chironomids) were collected using a benthic sled and an Ekman grab sampler. Individual invertebrates were normally identified to the family level, and invertebrate samples were classified according to dietary preference based on published dietary descriptions, particularly Merritt and Cummins (1978) and Thorp and Covich (1991). A total of 133 invertebrate samples from the 14 study lakes were classified as non-predatory (primary consumers); partially or entirely predatory invertebrates were not considered in the present analysis. Primary consumers were pooled to order, producing nine general taxonomic/habitat classes: Unionidae, Amphipoda, Trichoptera, tadpoles, Ephemeroptera, shallow zooplankton (0 - 3m), deep zooplankton (10 - 12 m), Chironomidae (profundal), and miscellaneous littoral (littoral primary consumers collected from less than three lakes).

Whole samples were frozen, dried at 75° C for 48 hours in a drying oven, and ground into a fine powder using mortar and pestle. Dry sample material was packed into 4 x 6 mm tin capsules for subsequent isotopic analyses. Stable carbon and nitrogen isotope analyses were performed on the same sample using a continuous flow VG Micromass 903E isotope-ratio mass spectrometer at the Environmental Isotope Laboratory (Department of Earth Sciences, University of Waterloo, Waterloo, Ont.). Stable isotope ratios are expressed in delta (δ) notation, defined as the parts per thousand (‰ or "per mil") deviation from a standard material; $\delta^{13}C$ or $\delta^{15}N$ $= ([R_{sample} / R_{standard}] - 1) \times 1000$, where $R = {}^{13}C/{}^{12}C$ or ${}^{15}N/{}^{14}N$. A more positive (less negative for carbon) isotopic value is said to be isotopically enriched, meaning that the sample contains proportionally more of the heavy stable isotope (^{13}C or ^{15}N). The standard material is Pee Dee belemnite (PDB) limestone for $\delta^{13}C$ (Craig 1957), and atmospheric nitrogen for $\delta^{15}N$ (both standards have a ‰ value arbitrarily set at 0‰). 20% of the samples were analyzed in duplicate; the standard error of the mean for replicates was 0.13‰ for $\delta^{13}C$ and 0.15‰ for $\delta^{15}N$. When more than two $\delta^{15}N$ and $\delta^{13}C$ measurements for a taxon were available from a lake, we report the average isotopic value to avoid pseudo-replication and bias towards heavily sampled taxonomic groups. This pooling effectively reduced the sample size from 133 to 106 primary consumers.

We also collected the available freshwater literature data on the $\delta^{13}C$ and $\delta^{15}N$ of primary consumers in order to test the generality of our observations (Angradi 1994; Hecky and Hesslein 1995; Hobson and Welch 1995; Yoshii 1995; Keough et al. 1996).

Where multiple individuals of a particular taxon were collected from a habitat within a system, we considered their average isotopic value. Lakes were rejected from analysis if there was little range in average $\delta^{13}C$ values (less than 5‰), or if fewer than three different taxonomic groups were collected.

RESULTS

$\delta^{15}N$ and $\delta^{13}C$ of primary consumers

In our 14 study lakes, the $\delta^{15}N$ of primary consumers was highly variable, ranging from -2‰ to +9‰. There were highly significant differences in the $\delta^{15}N$ of primary consumers feeding in littoral (mean = 1.58‰), pelagic (mean = 3.05‰), and profundal (mean = 5.17‰) habitats (Fig. 1a; ANOVA; $p < 0.001$). There were also highly significant differences in $\delta^{13}C$ among littoral (mean = -23.8‰), pelagic (mean = -28.4‰), and profundal (mean = -30.5‰) primary consumers (Fig. 1b; ANOVA; $p < 0.001$), indicating that $\delta^{13}C$ values can be used to ordinate consumers along a littoral - pelagic - profundal trophic gradient. The $\delta^{15}N$ and $\delta^{13}C$ data used in the analysis are presented in Appendix 7.

Each of the 106 invertebrate samples was further classified into 9 general taxonomic-habitat categories. There was a negative relationship between mean, category-specific $\delta^{15}N$ and $\delta^{13}C$ (Fig. 2).

We plotted $\delta^{15}N$ versus $\delta^{13}C$ of individual primary consumers (zooplankton excluded), with values coded according to lake (Fig. 3a) and taxonomic category (Fig. 3b). A logistic curve fit provided unbiased trophic position estimates. Additionally, limits to the $\delta^{15}N$ of primary consumers are expected to be constrained by the fractionation associated with bacterial denitrification (upper limit) and N uptake by algae (lower limit). The overall $\delta^{15}N$ - $\delta^{13}C$ relationship was highly significant and described by the logistic equation:

$$\delta^{15}N_{pcon} = \frac{6.34}{1+e^{9.67 + (0.356*\delta 13Cpcon)}} \qquad (1)$$

where $n = 78$; $r^2 = 0.40$; $F = 71.73$; $df = 4, 74$; $P < 0.001$; $\delta^{15}N_{pcon}$ = the $\delta^{15}N$ of the primary consumer, and $\delta^{13}C_{pcon}$= the $\delta^{13}C$ of the primary consumer.

Lake effects in the $\delta^{15}N$ - $\delta^{13}C$ relationship

Analysis of covariance (ANCOVA) was used to test for lake-specific differences (a lake effect) in the general $\delta^{15}N$-$\delta^{13}C$ relationship (Fig. 3). In order to meet the assumptions of ANCOVA to test for the lake effect, we linearized the general primary consumer $\delta^{15}N$ - $\delta^{13}C$ relationship by using the *observed $\delta^{15}N$* values and the *predicted $\delta^{15}N$* from $\delta^{13}C$ using equation 1 (the predicted $\delta^{15}N$ values represent the $\delta^{13}C$ effect, and will be referred to as such). ANCOVA predicting primary consumer $\delta^{15}N$ values ($n = 78$; $r^2 = 0.72$; $df = 14, 63$) indicated highly significant effects of $\delta^{13}C$ (from equation 1; $F = 71.73$; $df = 1$; $P < 0.0001$) and lake ($n = 78$; $F = 4.44$; $df = 13$; $P < 0.0001$). Note that the lake variable explained an additional 32% of the observed variation in primary consumer $\delta^{15}N$. There was no significant interaction between the $\delta^{13}C$ and lake variables ($n = 78$; $F= 0.26$; $df = 13$; $P = 0.995$) indicating that the curvature of the relationship (the denominator of equation 1) could be used to describe each of the study lakes. Thus, the lake-effect influenced only the intercept of the $\delta^{15}N$-$\delta^{13}C$ relationship (6.34; the numerator in equation 1) and represented a shift of the primary consumer $\delta^{15}N$ - $\delta^{13}C$ curve up or down relative to the general $\delta^{15}N$ - $\delta^{13}C$ relationship (Fig. 3).

DISCUSSION

Application: estimating trophic position of aquatic consumers

The negative relationship between $\delta^{15}N$ and $\delta^{13}C$ of primary consumers has direct implications for stable isotope-food web studies since stable nitrogen isotope ratios are commonly used as an indicator of the trophic position of consumers. It is clear that $\delta^{15}N$ values of higher consumers alone cannot be used as indicators of trophic position, since the $\delta^{15}N$ of primary consumers (trophic level 2) are highly variable, ranging from -2‰ to +9‰ in the present study.

$\delta^{15}N$ values can be converted into trophic position estimates by interpreting the $\delta^{15}N$ of higher consumers relative to a representative baseline $\delta^{15}N$ value (Cabana and Rasmussen 1996). Here, we demonstrate how this primary consumer $\delta^{15}N$ - $\delta^{13}C$ relationship can be used as a baseline from which to estimate the trophic position of higher consumers. First, the lake-specific deviation from the general baseline curve (equation 1) is estimated using the following approach. For each primary consumer from a given lake (lake x) for which $\delta^{15}N$ and $\delta^{13}C$ information are available, the residual from equation 1 is calculated:

$$\text{resid} = \delta^{15}N_{pcon} - \frac{6.34}{1 + e^{9.67 + (0.356 * \delta_{13}C\ pcon)}} \qquad (2)$$

where resid is the residual value from equation 1. Next, the average residual value (U_{resid}) of all primary consumers from lake x is calculated (a U_{resid} value can be calculated for each lake). Having 1) established a general baseline curve (equation 1), and 2) estimated the U_{resid} for lake x (equation 2), the trophic position of a fish (or other any other consumer) from lake x can easily be estimated. The $\delta^{13}C$ of the fish is entered into equation 1, producing the "non lake-corrected" primary consumers $\delta^{15}N$. To correct for lake-specific differences, the U_{resid} value for lake x (from equation 2) is added to this $\delta^{15}N$ value:

$$\delta^{15}N_{corrected} = \frac{6.34}{1 + e^{9.67 + (0.356 * \delta_{13}C\ fish)}} + Uresid \quad (3)$$

where $\delta^{15}N_{corrected}$ is the lake-corrected baseline $\delta^{15}N$ value. Use of equation 3 produces an appropriate baseline $\delta^{15}N$ value for each individual fish based on the $\delta^{13}C$ signature of the fish, the general relationship between $\delta^{13}C$ and $\delta^{15}N$ and the lake-specific deviation (U_{resid}) from the general $\delta^{15}N$ - $\delta^{13}C$ relationship. Finally, the trophic position of the fish is estimated relative to the baseline $\delta^{15}N$ value from equation 3 using the equation:

$$TP_{fish} = ((\delta^{15}N_{fish} - \delta^{15}N_{corrected})/3.4) + 2 \quad (4)$$

where TP_{fish} = fish trophic position; $\delta^{15}N_{fish}$ = $\delta^{15}N$ of fish; 3.4 = 1 trophic level increment in $\delta^{15}N$.

The principle of the baseline correction is illustrated with a hypothetical example of lake trout and sculpins (Fig. 4). Sculpins live in the profundal zone of our study lakes (hence their more negative $\delta^{13}C$ value), and derive their energy from a food chain with high-$\delta^{15}N$ primary consumers. Conversely, lake trout are more pelagic (hence their more positive $\delta^{13}C$), and derive energy from a food chain with a lower $\delta^{15}N$ baseline. Consequently, the two populations exhibit similar $\delta^{15}N$ values, but differ by nearly 1 trophic level due to the disparate baseline $\delta^{15}N$ values.

The errors associated with the presented stable isotope baseline correction were quantified (Table 2). The error in the estimate of the baseline $\delta^{15}N$ value using no correction (the standard deviation of the global mean $\delta^{15}N$) was 2.55‰, which is equivalent to 0.75 trophic level. The general model that considered both within- and among- lake sources of error produced a greatly reduced error of 1.36‰ (where n = 1 primary consumer). Accounting for the mean lake-specific primary consumer sample size for our study ($/\sqrt{n}$, n = 6) produces an error of 0.55‰. This is equivalent to an error of 0.16 trophic level associated with the within- and among- lake baseline correction presented herein.

Generality and implications of $\delta^{15}N$ - $\delta^{13}C$ relationships

Our study lakes are deep, oligotrophic lakes located in a relatively restricted geographic area. To test whether primary consumer $\delta^{15}N$ - $\delta^{13}C$ relationships are a general phenomena, we surveyed the literature for $\delta^{15}N$ and $\delta^{13}C$ data for freshwater primary consumers. To compare the results from our study lakes and the literature data, we adjusted for system-specific differences in primary consumer $\delta^{15}N$ by subtracting the system-specific mean residual value (U_{resid} from equation 2) from each primary consumer $\delta^{15}N$ value, and plotted the "residual adjusted" primary consumer $\delta^{15}N$ versus $\delta^{13}C$. Data from the literature survey (triangles) and our 14 study lakes (circles) exhibited similar $\delta^{15}N$ - $\delta^{13}C$ relationships (Fig. 5).

We used equation 3 to estimate the "predicted $\delta^{15}N$" (based on $\delta^{13}C$ values) for the literature data set. Observed $\delta^{15}N$ explained 76% of the variability in predicted $\delta^{15}N$ (observed $\delta^{15}N = 0.98 *$ residual adjusted $\delta^{15}N + 0.14$; $p < 0.001$; $r^2 = 0.76$), indicating that the literature data is effectively described by the equation derived from our 14 study lakes. In addition, the $\delta^{15}N$ - $\delta^{13}C$ relationship from each of the 8 literature study systems (Charr Lake, Lake Superior, Grand Canyon, Lake Malawi, Lake 273, Skidoo Lake, South Lake, Lake Baikal) exhibited negative slopes (mean slope = -0.33; range -0.06 to -0.85), and the within-system correlations between $\delta^{15}N$ and $\delta^{13}C$ were generally quite strong (mean r = -0.80; range -0.32 to -0.99).

The systematic variation in $\delta^{15}N$ characterizing the base of the food chain has implications for the interpretation of previously published studies of the stable isotope signatures of fish. For example, Kiriluk et al. (1995) and Yoshii (1995) report negative relationships between the $\delta^{15}N$ and $\delta^{13}C$ of pelagic fish. The traditional interpretation of this would have been that the fish with higher $\delta^{15}N$ (and lower $\delta^{13}C$ due to their more profundal habitat) have a higher trophic position. In light of our findings, an alternative explanation arises, which is that fish with the higher $\delta^{15}N$ signatures are feeding from a food chain with a high $\delta^{15}N$ baseline. It may be that these fish with very different $\delta^{15}N$ values have similar trophic positions.

The correspondence of literature data suggests that habitat-specific variation in baseline $\delta^{15}N$ and $\delta^{13}C$ is a widespread phenomena in freshwater systems. Thus, isotopic food web studies should include $\delta^{15}N$ and $\delta^{13}C$ measurements of the widest possible range of baseline organisms. If in other freshwater systems, $\delta^{15}N$ and $\delta^{13}C$ covary in a manner similar to our data (low standard error in the U_{resid} value), then investigators can reasonably use our general $\delta^{15}N$ - $\delta^{13}C$ relationship (equation 3) as a baseline from which to estimate trophic position (although doing so still requires measurement of the $\delta^{15}N$ and $\delta^{13}C$ of a range of primary consumers to establish the lake-specific U_{resid} value). Conversely, if the standard error of the U_{resid} value is high, the investigator should certainly estimate trophic position relative to their lake-specific $\delta^{15}N$ - $\delta^{13}C$ relationship. Collection of primary consumer $\delta^{15}N$ and $\delta^{13}C$ data from additional freshwater systems will also permit further tests of the generality of the $\delta^{15}N$ - $\delta^{13}C$ relationship.

The habitat-specific variation in baseline $\delta^{15}N$ and $\delta^{13}C$ reported herein underscore the general importance of considering isotopic patterns at the base of the food web when using stable isotopes to infer trophic structure. Investigators studying other types of systems are likely to find spatial variation in baseline isotopic signatures, and it may be possible to similarly detrend for baseline variation when quantifying trophic structure.

Factors influencing variation in $\delta^{13}C$ and $\delta^{15}N$

Although this study does not specifically attempt to elucidate the factors *determining* the stable isotopic values of primary consumers, it appears that the process of lake stratification, and the ensuing isolation of water masses, in a general sense, is responsible for the unique stable carbon and nitrogen isotope values characterizing primary consumers of the profundal zone of our 14 lakes.

$\delta^{13}C$ can vary widely among primary producers within a system, and the factors influencing variation in $\delta^{13}C$ are fairly well understood. The biota inhabiting the depths of stratified lakes have been observed to be ^{13}C depleted due to algal uptake of respired CO_2, which is more abundant in deeper waters of stratified lakes (Rau, 1978; 1980). Benthic algae tend to be enriched in ^{13}C relative to phytoplankton due to a CO_2 boundary layer effect, which causes diffusion limitation to benthic algal cells in oligotrophic lakes (France 1995a, b; Hecky and Hesslein 1995). Additionally, algal use of bicarbonate as a carbon substrate results in enriched $\delta^{13}C$ values (Hecky and Hesslein 1995).

Compared to $\delta^{13}C$, much less is known about the factors influencing variation in $\delta^{15}N$ values at the lower levels of the food web. Cabana and Rasmussen (1996) report a wide range of unionid mussel $\delta^{15}N$ values and showed that 68% of the among-lake variation in primary consumer $\delta^{15}N$ is explained by human population density in the watershed. Although our study lakes tend to be relatively pristine, the study lakes that have substantial human population in the watershed, Lake Memphremagog, Que. and Lake Muskoka, Ont., contain primary consumers with the most elevated $\delta^{15}N$ values.

Nitrogen transformation processes such as denitrification and ammonification occur in the suboxic profundal zones of stratified lakes. These processes are accompanied by considerable N isotope fractionation, resulting in an ^{15}N enriched pool of inorganic N available for uptake by primary producers (Wada and Hattori 1978; Macko and Estep 1985; Owens 1987). Additionally, profundal primary consumers feed upon dead phytoplankton and detritus which could be enriched in $\delta^{15}N$. As a result, hypolimnetic and profundal biota such as Diporia and sculpins tend to be enriched in ^{15}N, an enrichment that does not reflect an elevated trophic position for these species.

Although reasons for the discrepancy between pelagic and benthic primary consumer $\delta^{15}N$ remain obscure, there are a few potential explanations for the low $\delta^{15}N$ of littoral primary consumers. Littoral consumers could be incorporating some terrestrial material with a lower $\delta^{15}N$ than benthic algae. This alternative is unlikely due to the relatively ^{13}C-enriched values of littoral primary consumers (c.a. -24‰) compared to the $\delta^{13}C$ of terrestrial materials (c.a. -28‰). Another explanation is that the benthic algae could be less influenced than phytoplankton by the infusion of high ^{15}N waters from the hypolimnion during lake mixing. Thirdly, potential inorganic nitrogen substrates (NO_3^- and NH_4^+) differ in $\delta^{15}N$, differences which can be passed on to consumers (Owens 1987; Paerl and Fogel 1994). Finally, Wada and Hattori (1978) and Pennock et al. (1996) show that algae can exhibit highly variable fractionation, depending on the N substrate (NO_3^-, NH_4^+, or N_2), algal growth rates, species composition, and ambient nutrient concentrations.

Trophic position in ecological studies

A trophic position-based approach to representing trophic structure incorporates omnivory and weights feeding links according to their relative energetic importance, thereby representing "realized", rather than "potential" trophic structure (Kling et al. 1992). Use of trophic position-based food web representations is likely to improve our ability to model and understand ecosystem processes. For example, trophic position provided a significant improvement over the use of trophic levels for predicting contaminant concentrations in pelagic consumers (Vander Zanden and Rasmussen 1996). A trophic position approach may also prove to be useful in studies of food web dynamics, as deviations from discrete trophic levels (i.e. complexity and omnivory) could dampen the predicted trophic cascades (Polis and Strong 1996; Hairston and Hairston 1997). Use of this approach may also be used to quantify the effects of ecosystem perturbations, and to model tropho-dynamics and ecosystem production (Kerr and Martin 1970).

Gut content data provides a snapshot of the diet of study populations, but will not provide estimates of food web structure and trophic position unless the diet of their prey (and the *prey* of their prey, etc.) are specifically studied as well (Vander Zanden and Rasmussen 1996; Vander Zanden et al. 1997). Interpreting $\delta^{15}N$ signatures of higher consumers relative to an appropriate baseline signature can provide time-integrated depictions of trophic structure. In light of this, a trophic position-based approach to representing trophic structure becomes an attractive alternative to connectance food webs and food chain -based models, which remain dominant paradigms in community and ecosystem ecology.

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Table 1. Summary data for the 14 study lakes. Lake number refers to Fig. 3. Sample size represents the number of primary consumers analysed for stable isotopes from that lake. Mean residual value is the lake-specific deviation from the general model based on all 14 lakes (equation 2; U resid).

Lake	Lake number	Lat.	Long.	Lake area (ha)	Maximum depth (m)	sample size	Mean residual	SE of mean residual
Memphremagog	1	45 08	72 16	15000	117	6	3.11	0.26
Muskoka	2	45 03	79 29	12215	67	7	2.38	0.76
Rosseau	3	45 10	79 35	5156	90	6	1.20	0.62
Twelve Mile	4	45 01	78 02	463	24	10	0.73	0.67
Dickey	5	44 47	77 45	214	54	6	0.67	0.98
Smoke	6	45 31	78 41	607	55	5	0.47	0.62
Victoria	7	45 37	78 01	892	45	9	0.39	0.66
Macdonald	8	45 14	78 34	138	40	9	-0.15	0.55
Opeongo	9	45 43	78 22	5860	50	11	-0.57	0.62
Source	10	45 33	78 39	271	-	8	-0.72	0.62
Happy Isle	11	45 45	78 30	536	-	5	-0.90	0.36
Clean	12	45 15	78 32	160	43	7	-1.26	0.58
Temagami	13	47 00	80 05	20972	61	6	-2.05	0.49
Louisa	14	45 28	78 29	490	61	11	-2.17	0.62

Table 2. Error associated with the presented isotopic baseline corrections.

Correction	**(SD)**[a]	**n**[b]	**Error SEest (SD/√n)**	**Error (T.L.)**[c]
No correction[d]	2.55‰	1[e]	2.55‰	0.75
Within-lake	2.00‰	6[f]	0.82‰	0.24
Within- and among-lake	1.36‰	6[f]	0.55‰	0.16

[a] standard deviation; equivalent to the standard error of the estimate with n = 1

[b] n represents sample sizes for this study

[c] units are trophic levels

[d] using the global mean $\delta^{15}N$ value of 2.97‰

[e] n is 1 due to use of global mean $\delta^{15}N$ value

[f] mean sample size (per lake) from this study (excluding zooplankton)

Figure 1. a) The mean $\delta^{15}N$ (± 1 SE) of primary consumers feeding in profundal, pelagic, and littoral habitats. b) The mean $\delta^{13}C$ (± 1 SE) of primary consumers from profundal, pelagic, and littoral habitats. Samples were collected from 14 lakes in Ontario and Quebec, Canada. Numbers above bars represent sample size.

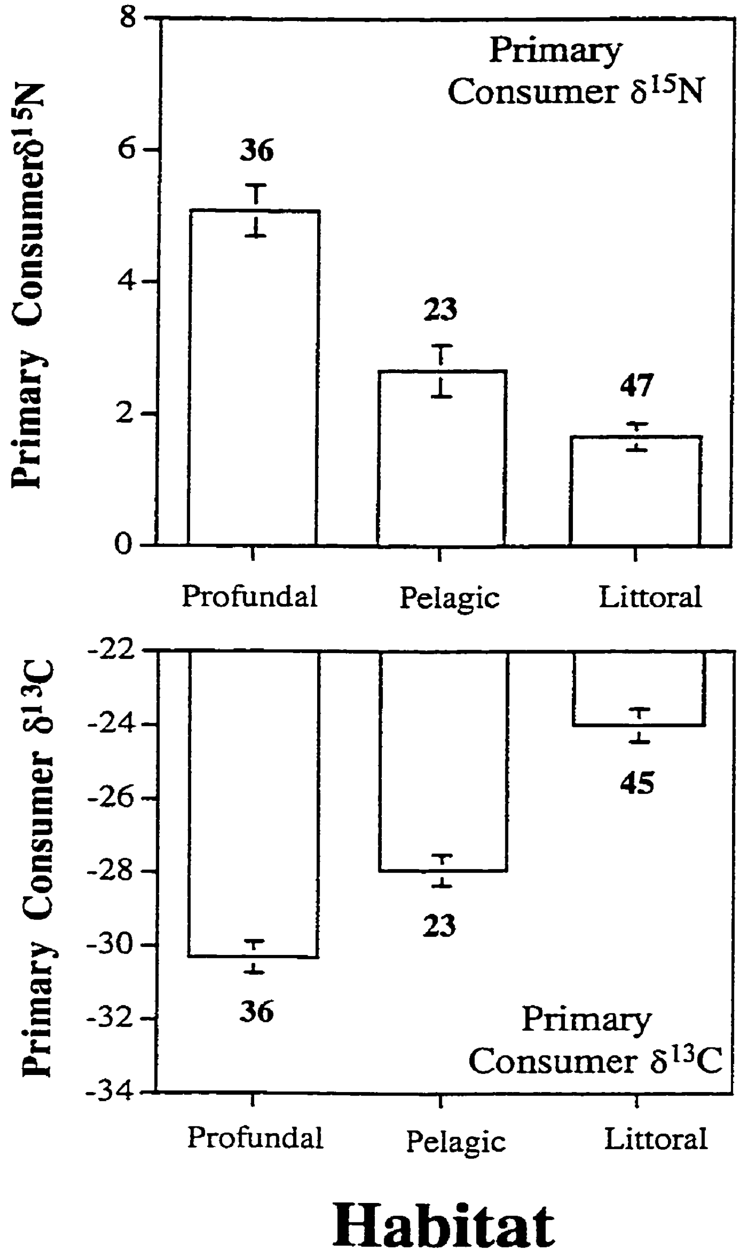

Primary Consumer δ15N
8
6
4
2
0
Primary Consumer δ15N
36
23
47
Profundal
Pelagic
Littoral
Primary Consumer δ13C
-22
-24
-26
-28
-30
-32
-34
45
23
36
Primary Consumer δ13C
Profundal
Pelagic
Littoral
Habitat

Figure 2. Mean $\delta^{15}N$ vs. mean $\delta^{13}C$ (± 1 SE) for the primary consumer taxonomic groups from 14 Ontario and Quebec lakes.

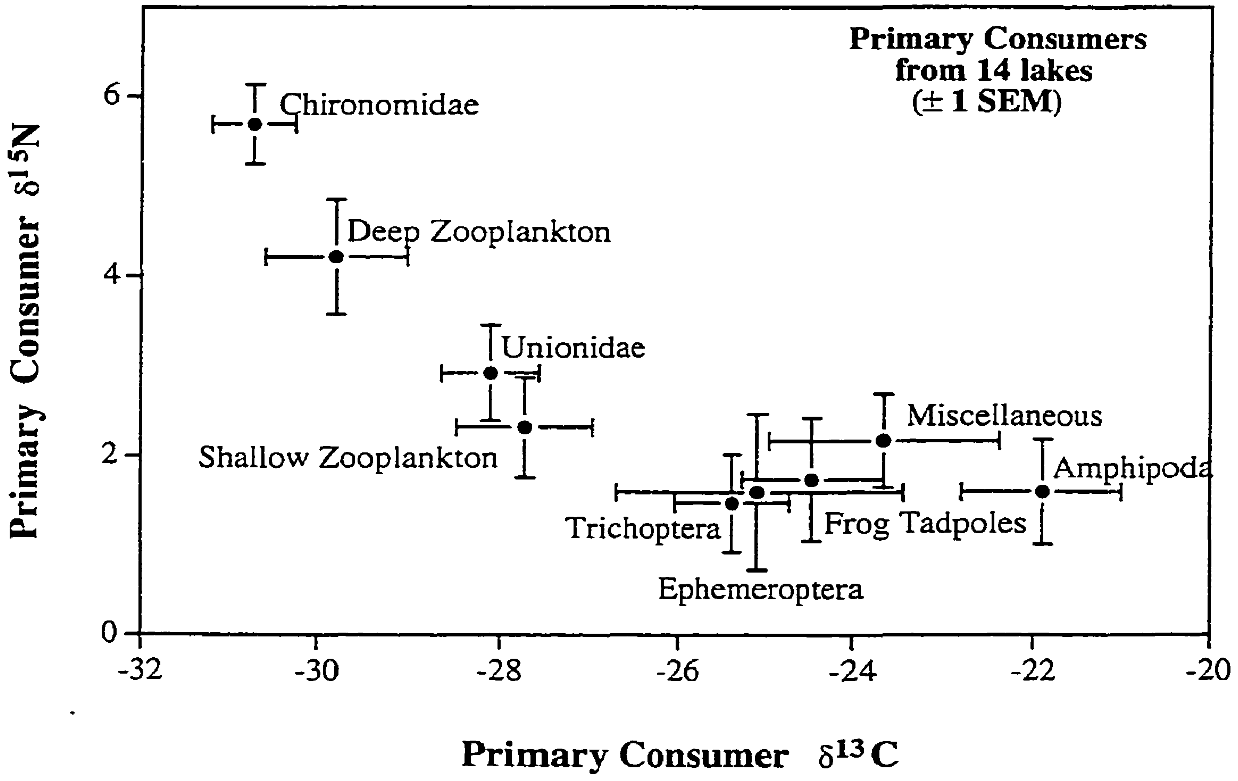
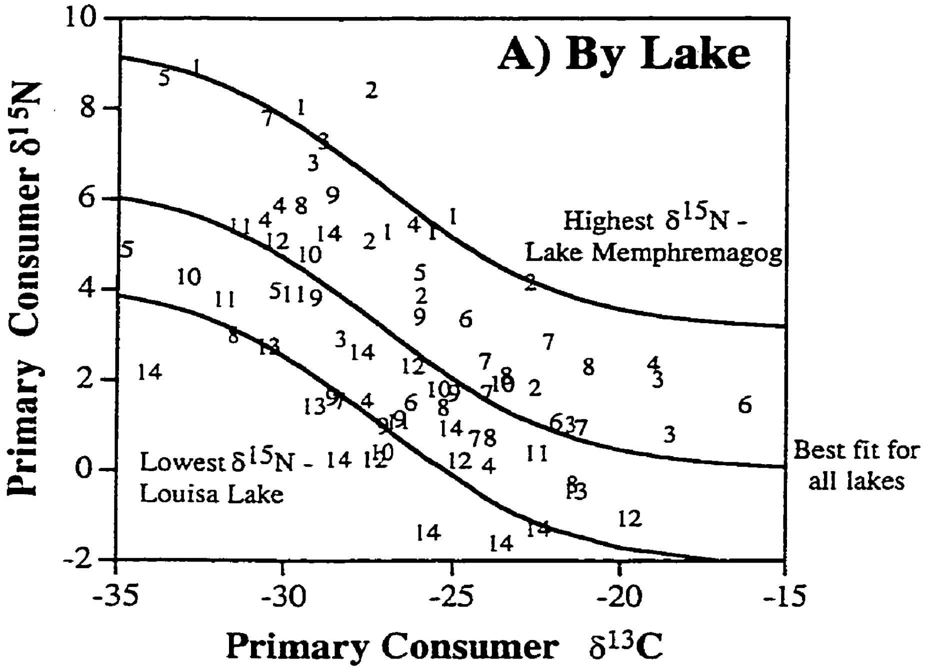

Primary Consumers
from 14 lakes
(± 1 SEM)
Chironomidae
Deep Zooplankton
Unionidae
Shallow Zooplankton
Miscellaneous
Amphipoda
Trichoptera
Frog Tadpoles
Ephemeroptera
Primary Consumer $\delta^{15}N$
0
2
4
6
-32
-30
-28
-26
-24
-22
-20
Primary Consumer $\delta^{13}C$

Figure 3. $\delta^{15}N$ vs. $\delta^{13}C$ for primary consumers (minus zooplankton) from 14 lakes in Ontario and Quebec. Each point represents the average value of a taxonomic group from a given lake. A) Coded according to lake, with lakes are arranged in order from most to the least elevated $\delta^{15}N$ lakes. 1, Memphremagog; 2, Muskoka; 3, Rosseau; 4, 12 Mile; 5, Dickie; 6, Smoke; 7, Victoria; 8, MacDonald; 9, Opeongo; 10, Source; 11, Happy Isle; 12, Clean; 13, Temagami; 14, Louisa. The curves for the highest and lowest $\delta^{15}N$ lakes (L. Memphremagog and Louisa Lake) are included. B) Points are coded according to major taxonomic categories. Ch, Chironomidae; Un, Unionidae; Tr, Trichoptera; Ep, Ephemeroptera; Ta, Tadpoles; Mi, Miscellaneous; Am, Amphipoda.


A) By Lake
Primary Consumer $\delta^{15}N$
Primary Consumer $\delta^{13}C$
10
8
6
4
2
0
-2
-35
-30
-25
-20
-15
Highest $\delta^{15}N$ - Lake Memphremagog
Lowest $\delta^{15}N$ - Louisa Lake
Best fit for all lakes

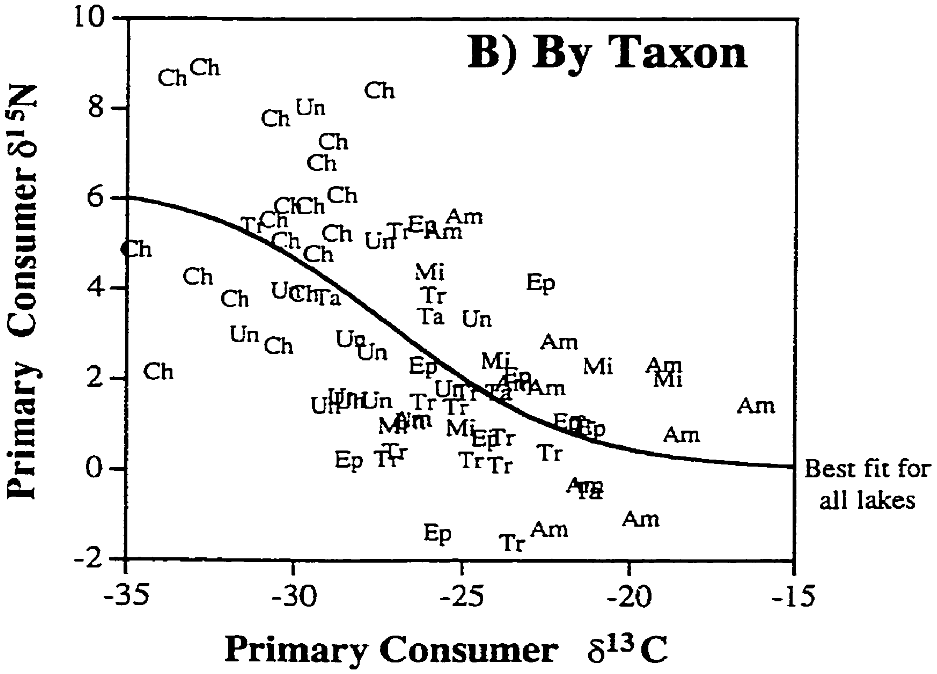

B) By Taxon
Primary Consumer $\delta^{15}N$
Primary Consumer $\delta^{13}C$
10
8
6
4
2
0
-2
-35
-30
-25
-20
-15
Best fit for all lakes
Ch
Un
Tr
Ep
Am
Mi
Ta

Figure 4. An illustration of the approach used to estimate trophic position. The baseline $\delta^{15}N$ - $\delta^{13}C$ primary consumer relationship is established, and the $\delta^{13}C$ of the higher consumer determines the appropriate $\delta^{15}N$ value from which to measure the trophic position of the consumer. Primary consumers have a trophic position of 2.0; organisms feeding exclusively on primary consumers would have a trophic position of 3.0. Note that the hypothetical sculpin and trout have similar $\delta^{15}N$ values, yet differ by nearly a trophic level.

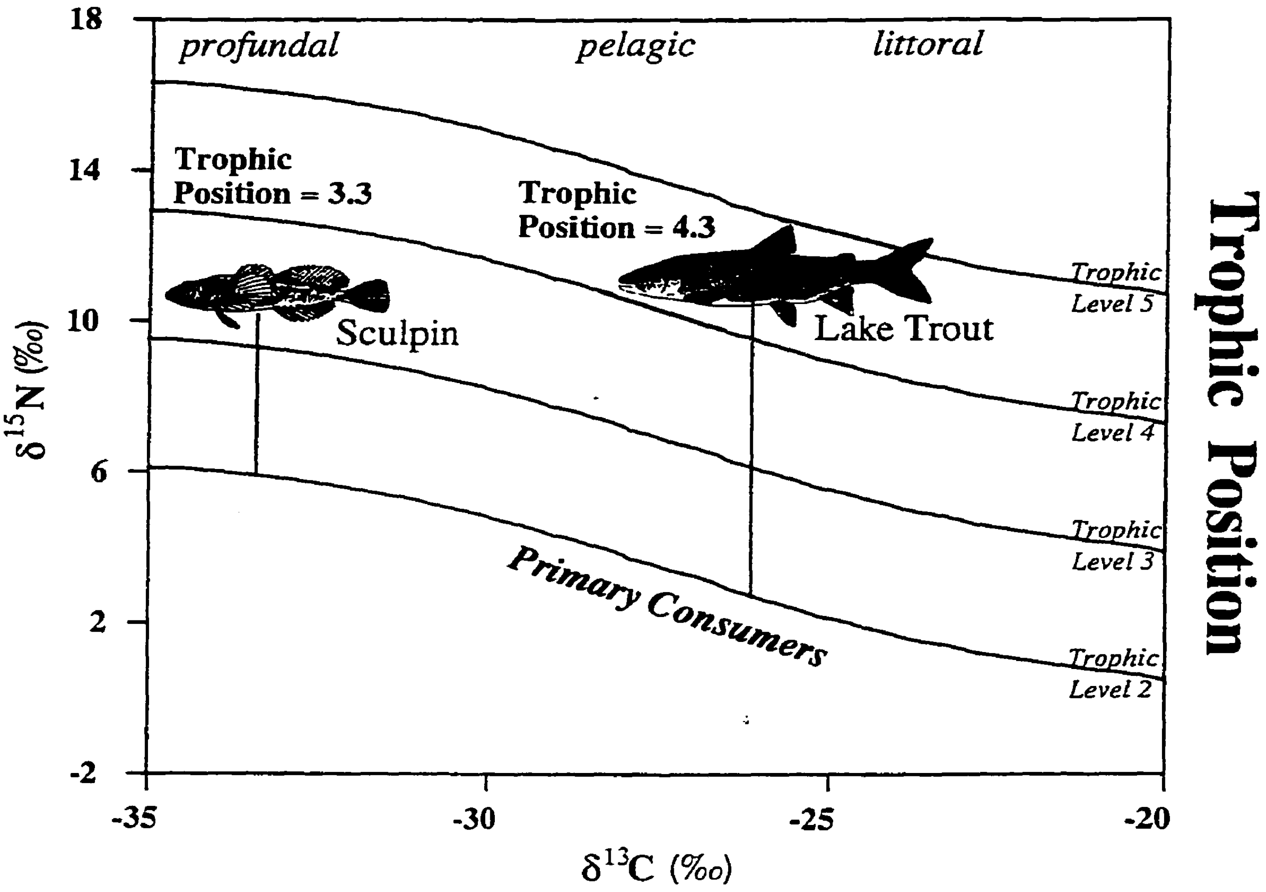
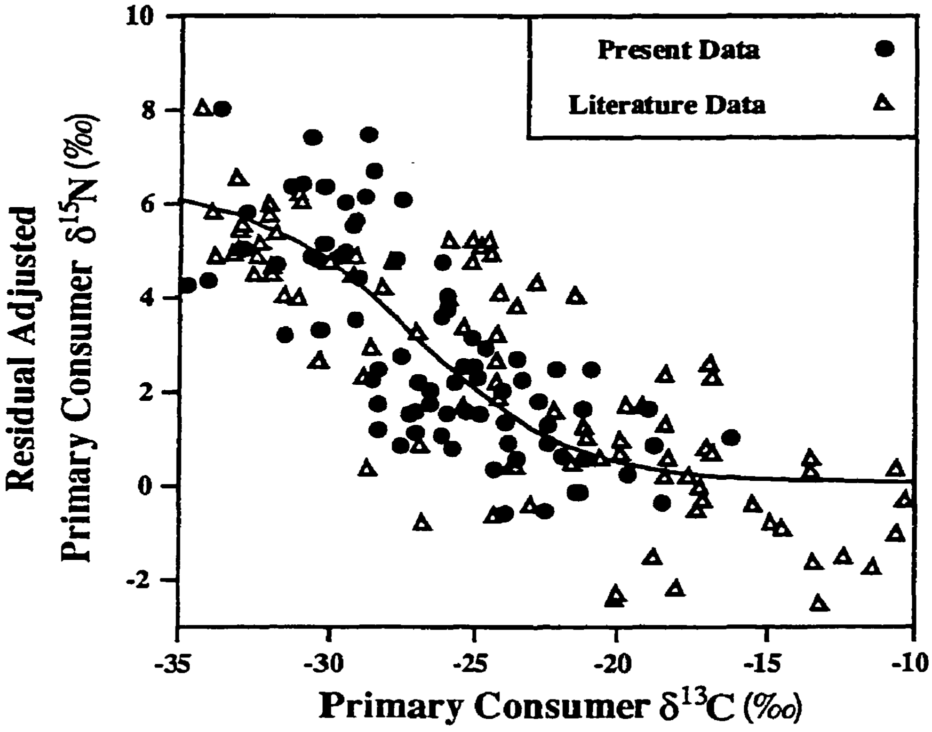

profundal
pelagic
littoral
Trophic Position = 3.3
Trophic Position = 4.3
Sculpin
Lake Trout
Primary Consumers
Trophic Level 5
Trophic Level 4
Trophic Level 3
Trophic Level 2
Trophic Position
18
14
10
6
2
-2
-35
-30
-25
-20
δ^{15}N (‰)
δ^{13}C (‰)

Figure 5. Primary consumer $\delta^{15}N$, adjusted for the lake-specific mean residual value (accounts for lake-specific differences in intercept in the $\delta^{15}N$ - $\delta^{13}C$ relationship) vs. $\delta^{13}C$ for our study lakes (solid circles) and literature data (open triangles). Literature data are from Angradi 1994, Hecky and Hesslein 1995, Hobson and Welch 1995, Yoshii 1995, and Keough et al. 1996.


Present Data ●
Literature Data △
Residual Adjusted
Primary Consumer $\delta^{15}N$ (‰)
10
8
6
4
2
0
-2
-35
-30
-25
-20
-15
-10
Primary Consumer $\delta^{13}C$ (‰)

CONNECTING STATEMENT

Having developed a method to estimate the trophic position of aquatic consumers in the previous chapter, the following two chapters will quantify both within- and among-lake variation in the trophic position of lake trout. The emphasis of Chapter 4 is within-population variation in trophic position of lake trout. In particular, this chapter will examine the magnitude of ontogenic shifts in trophic position. Furthermore, it will quantify the importance of individual-level differences in trophic position (the extent to which same-sized individuals differ in trophic position). Finally, this chapter will consider the magnitude of within-population variation in trophic position relative to that of variation at the among-population level.

CHAPTER 4

WITHIN- AND AMONG-POPULATION VARIATION IN THE TROPHIC POSITION OF LAKE TROUT

ABSTRACT

The diet and trophic position of a species varies both among-populations and within-populations of a species. The relative importance of these two sources of trophic variation were quantified for the pelagic top predator, lake trout (Salvelinus namaycush). Stable nitrogen and carbon isotope ratios were used to estimate trophic position of 13 - 21 individual lake trout from each of thirteen lakes in Ontario and Quebec. Lake-to-lake differences were responsible for 78% of the total variation in lake trout trophic position. Surprisingly, lake trout trophic position was generally independent of body size. This was attributed to weak predator size - prey size relationships, and to there being no relationship between prey fish trophic position and body size. The variance in trophic position of a population reflects the extent to which individuals forage as trophic specialists; yet we could not identify any one factor that was correlated with intra-population trophic variation. Our finding that much of the total variation in trophic position represents among-population differences indicates that considering the average trophic position of a population does not mask substantial within-population trophic variation.

INTRODUCTION

Many aquatic consumers have flexible feeding habits, and it is generally recognized that populations of a species can differ in their diet and trophic position (Dill 1983; Trippel and Beamish 1993; Vander Zanden and Rasmussen 1996; Vander Zanden et al. 1999). Although among-population trophic variation is well recognized, studies rarely consider that individuals within a population can differ in their feeding behaviour (Polis 1984; Lomnicki 1988). The few studies of within-population trophic differences have generally found evidence for variation and dietary specialization (Bryan and Larkin 1972; Zerba and Collins 1992; Gu et al. 1997b; Schindler et al. 1997). In addition, fish undergo dramatic ontogenetic trophic shifts, in which species commonly shift from invertebrates to fish prey items as they grow (Werner and Gilliam 1984; Werner 1986).

Lake trout are an ideal species for food web studies because a range of trophic structures lead to this top predator (Martin 1952; Martin 1966; Rasmussen et al. 1990; Trippel and Beamish 1993; Vander Zanden et al. 1999). In fact, Rasmussen et al. (1990) classified lakes according to food chain length leading to lake trout. Class 1 lakes (containing three trophic levels) lack pelagic forage fish species. In these lakes, lake trout consume primarily zooplankton and zoobenthos. Class 2 lakes (four trophic levels) contain at least one species of pelagic forage fish, which serve as the principle prey of adult lake trout. Finally, Class 3 lakes (five trophic levels) are lakes that contain both pelagic forage fish and the zooplankton predator, Mysis relicta. Mysis are an important prey of pelagic forage fish, which are consumed by lake trout. Recent dietary and stable isotope studies confirm that 'lake Class' qualitatively reflects among-lake differences in trophic structure, although much of the variation remains unexplained (Vander Zanden and Rasmussen 1996; Vander Zanden et al. 1999).

In light of the complexity and variability of food web relationships, integrative approaches are needed for broad-scale and comparative food web studies (Polis 1991; Polis and Winemiller 1996). Stable isotopes are increasingly used to provide integrative descriptions of feeding relationships. In particular, there is a consistent 3 - 4‰ enrichment in stable nitrogen isotope ratios ($^{15}N/^{14}N$; $\delta^{15}N$) from prey to predator (DeNiro and Epstein 1981; Minagawa and Wada 1984). Thus, $\delta^{15}N$ values (after correcting for differences at the base of the food web) can provide a time-integrated, continuous measure of consumer trophic position based on energy flow (Cabana and Rasmussen 1996; Vander Zanden and Rasmussen 1999). Recently, stable isotopes have been used to quantify within-population trophic variation (Gu et al. 1997b). This application of stable isotopes is particularly useful because detecting among-individual feeding differences (diet specialization) using gut content methods requires repeatedly examining the stomach contents of the same individual fish. Understandably, such studies are rarely performed as they are laborious and usually involve small sample sizes (Bryan and Larkin 1972; Zerba and Collins 1992; Schindler et al. 1997).

In the present study, stable isotopes are used to estimate the trophic position of individual lake trout and other pelagic consumers from 13 lakes in Ontario and Quebec (Vander Zanden and Rasmussen 1999). Three 'sources' of trophic variation will be quantified: among-population (that which is explained by a categorical 'lake' variable), ontogenetic (that which is explained by body size), and individual-level variation (the remaining, unexplained variation in trophic position). All three sources of variation are expected to occur for lake trout based on previously published studies (among-population: (Vander Zanden and Rasmussen 1996); ontogenetic: (Trippel and Beamish 1993; Madenjian et al. 1998); individual-level:(Schindler et al. 1997). The major objectives of this study are to: a) quantify ontogenetic shifts in trophic position, testing the hypothesis that lake trout will exhibit more dramatic ontogenetic trophic shifts with increasing food chain length and trophic complexity, b) quantitatively compare within- and among-population variation in lake trout trophic position, and c) characterize individual-level trophic variation for lake trout and examine the factors related to this variable.

METHODS

Thirteen lakes in central Ontario and southern Quebec (located between 46° 15' N and 44° 30' N latitude, and 80° 00' W and 72° 00' W longitude) containing lake trout as the top pelagic predator were sampled between May and September 1995. Lake trout (13-21 per lake; average = 17) and the available forage fish species: cisco (*Coregonus artedii*), lake whitefish (*Coregonus clupeaformis*), round whitefish (*Prosopium cylindraceum*), smelt (*Osmerus mordax*), and sculpins (*Cottus spp.*) from the littoral, pelagic, and profundal zones were collected using gill nets, seine nets, minnow traps, angling, and from local anglers. Littoral fish (Percidae, Centrarchidae, and Cyprinidae) less than 12 cm in length were considered potential lake trout prey since lake trout have access to these fish during the unstratified period (Martin 1954; Vander Zanden and Rasmussen 1996). Approximately one gram (wet weight) of whole white dorsal muscle tissue was removed from each sampled lake trout and forage fish. *Mysis* and *Diporia hoyi* were collected using a benthic sled. Zooplankton were collected during the day using horizontal tows with a 250 μm standard zooplankton net. All fish and invertebrate samples were frozen as quickly as possible after collection.

Fish and invertebrate specimens were dried at 75°C for 48 hours in a drying oven, ground into a fine powder using mortar and pestle, and packed into 4 x 6 mm tin capsules for isotopic analyses. Stable carbon and nitrogen isotope analysis was performed using a continuous flow VG Micromass 903E isotope-ratio mass spectrometer at the Environmental Isotope Laboratory (Department of Earth Sciences, University of Waterloo, Waterloo, Ont.). Stable isotope ratios are expressed in delta (δ) notation, defined as the parts per thousand (‰ or "per mil") deviation from a standard material; $\delta^{13}C$ or $\delta^{15}N = (\{R_{sample} / R_{standard}\} - 1) \times 1000$, where $R = {}^{13}C/{}^{12}C$ or ${}^{15}N/{}^{14}N$. The standard material is Pee Dee belemnite (PDB) limestone for $\delta^{13}C$ (Craig 1957), and atmospheric nitrogen for $\delta^{15}N$ (both standards have a ‰ value arbitrarily set at 0‰). One half of the samples were analyzed in duplicate; the standard error of the estimate was 0.12‰ for $\delta^{15}N$ and 0.10‰ for $\delta^{13}C$.

Despite the consistent enrichment in $\delta^{15}N$ from prey to predator, the $\delta^{15}N$ value of a consumer cannot be used as an *absolute* measure of an organism's trophic position because organisms at the base of the food web can differ greatly in $\delta^{15}N$ values (Cabana and Rasmussen 1996; Vander Zanden and Rasmussen 1999). Vander Zanden and Rasmussen (1999) present a dual isotope ($\delta^{15}N$ and $\delta^{13}C$) method for measuring trophic position of aquatic consumers that corrects for among-lake and within-lake variation in baseline $\delta^{15}N$ by: a) generating a primary consumer (baseline) $\delta^{15}N$ - $\delta^{13}C$ relationship specific to the study lakes, b) using the $\delta^{13}C$ value of the aquatic consumer to define the appropriate $\delta^{15}N$ value from which to estimate trophic position, and c) estimating the consumer's trophic position using the consumer $\delta^{15}N$ value and the $\delta^{13}C$-adjusted baseline $\delta^{15}N$ value using the formula:

$$\text{Trophic position} = ((\delta^{15}N_{\text{consumer}} - \delta^{15}N_{\text{baseline}})/3.4) + 2$$

where 3.4 = the assumed per trophic level ‰ increase in $\delta^{15}N$. The +2 term is added because trophic position is being estimated relative to primary consumers rather than primary producers. We used this method to estimate the trophic position of each fish and invertebrate specimen included in this study. Error associated with the baseline correction was approximately 0.17‰.

Analysis of Covariance (ANCOVA) was used to partition the total variance in lake trout trophic position into its component sources: among-population variation (that which is attributed to the lake trout's lake of origin; a categorical 'lake' variable), ontogenetic variation (that which is attributed to lake trout body size), and individual variation (the remaining within-population variation, independent of body size).

RESULTS

Seventy-eight percent of the total variation in lake trout trophic position represented among-lake differences (F = 64.62, $p < 0.001$, DF = 12, 215, $r^2 = 0.78$). Surprisingly, consideration of 'lake trout length' failed to explain any of the remaining variation in lake trout trophic position (F = 3.18; p = 0.076, DF = 1, 226). The interaction of 'lake' and 'lake trout length' (lake*lake trout length) was a significant predictor of lake trout trophic position (F = 2.52; p = 0.004, DF = 12, 215). This finding indicates that the slopes of the trophic position-body size relationships varied significantly among-lakes, although only an additional 3% of the total variation in lake trout trophic position was explained by this interaction term. Nearly 20% of the total variation in lake trout trophic position remained unexplained after considering the lake variable and body size; this remaining variation represented individual level (intra-population) trophic variation.

Plotting trophic position - total length relationships for lake trout from each lake confirms that trophic position generally fails to increase with body size (Fig. 1). In fact, none of the lake-specific trophic position - body size relationships were significant (using the Bonferroni corrected critical p-value of 0.004; 0.05/13). The power of our analysis was such that we were generally able to detect a significant body size effect if the slope was greater than 0.015 (mean standard error of slope * critical t-value with a p = 0.005).

Explaining the lack of trophic position - body size relationships

The general lack of trophic position - body size relationship for lake trout was unexpected, since lake trout are known to undergo ontogenetic trophic shifts (Trippel and Beamish 1993). The lack of relationship could be the result of: 1) weak or no relationships between lake trout size and prey size, or alternatively, 2) weak or no relationships between the trophic position and body size of lake trout prey items.

To examine the first hypothesis, dietary data from Trippel and Beamish (1993) were used to quantify predator size - prey size relationships for lake trout. Although there was an overall positive predator size - prey size relationship (mean prey length (cm) = 0.206*mean lake trout length (cm) + 0.46, $n = 27$, $r^2 = 0.44$, $F = 19.39$, $p < 0.001$), the mean prey size for a given size class of lake trout varied widely among lakes (Fig. 2).

We examined the second hypothesis; that the trophic position and body size of lake trout prey items were weakly correlated. A model that included zooplankton, Mysis, Diporia, and pelagic prey fish from the study lakes indicated that trophic position generally increased with prey body size (Fig. 3; prey trophic position = 0.67*prey length (cm) + 2.12, $n = 247$, $r^2 = 0.42$, $p < 0.001$). Considering only the pelagic prey fish items, no relationship between prey trophic position and body size was observed ($n = 206$, $r^2 = 0.005$, $p = 0.33$).

Variance in trophic position

We propose that a measure of the intra-population variation in trophic position reflects the degree of diet consistency and trophic specialization exhibited by the individuals from a population. Even though lake trout trophic position tended to be independent of body size (Fig. 1), lake trout populations with steeper trophic position-body size slopes tended to have a higher population-specific variance in trophic position ($r^2 = 0.54$, SEest = 0.025, $p = 0.004$). Thus, rather than considering a standard measure of the variance in lake trout trophic position, we consider the magnitude of the residuals from the trophic position-body size relationships for lake trout (calculated as the 'mean |residual|' from the lake trout trophic position-body size relationships; U_{resid}). This measure of variance was independent of the slope of the lake trout trophic position-body size relationship ($r^2 = 0.20$, SEest = 0.036, $p = 0.12$).

The new measure of trophic variation (U_{resid}) varied nearly three-fold among lakes (Table 1). We hypothesized that larger lakes with more food web complexity and longer food chains would have more prey items available to lake trout, resulting in more trophic variation for lake trout and a higher U_{resid} value. None of the tested variables (food chain length, lake Class, lake area, variance in the trophic position of lake trout prey items) were significantly correlated with U_{resid}, although U_{resid} was elevated for certain Class 1 populations (Table 1). We also hypothesized that the presence of other lake trout competitor species (i.e., piscivores) would result in less diet breadth and lower U_{resid} for lake trout, although no significant relationship was found with the number of species of potential competitors.

DISCUSSION

The present study compared among-population and within-population sources of variance in trophic position of lake trout; within-population variation was further partitioned into two types, ontogenetic variation (that which varies as a function of lake trout body size), and individual variation (independent of body size; indicating the degree to which same-sized individuals specialize). This comparison of within- and among-population trophic variation could only have been performed using isotopic techniques, as this approach provides a time-integrated measure of the trophic position of individual consumers (Vander Zanden and Rasmussen 1999). Trophic studies traditionally characterize feeding at the population level, thereby neglecting to consider that populations consist of individuals that can differ in their behaviour (Lomnicki 1988). Detecting within-population trophic variation using dietary data requires sampling the stomach contents of an individual fish numerous times. Understandably, such studies are rarely performed as they are laborious and usually involve small sample sizes (Bryan and Larkin 1972; Zerba and Collins 1992; Schindler et al. 1997).

We found that the trophic position of lake trout can vary substantially within certain populations, although surprisingly, lake trout trophic position was generally not correlated with body size (and presumably age as well). Other studies that have examined within-population trophic variation of aquatic consumers have found that individual consumers can differ considerably in their trophic habits (Bryan and Larkin 1972; Zerba and Collins 1992; Gu et al. 1997b; Schindler et al. 1997), although these studies did not consider the magnitude of within-population variation in relation to among-population variation. Although we found evidence of within-population variation, among-population variation was a much more important source, accounting for nearly 80% of the total variation in lake trout trophic position.

Trophic position - body size relationships

Although lake trout have been documented to undergo clear ontogenetic diet shifts (Trippel and Beamish 1993), lake trout trophic position and body size were generally not correlated in the present study, prompting an examination of why this expected pattern was not observed. A positive trophic position-body size relationship would be expected if lake trout consume increasingly large prey items with body size (Sheldon et al. 1977; Werner and Gilliam 1984; Warren 1989; Cohen et al. 1993). Although our data for lake trout indicate a general predator size - prey size relationship, lake trout of a given size class were found to consume a broad range of prey sizes. The range of prey sizes reflects opportunistic feeding, omnivory and trophic variability; factors that serve to obscure any clear trophic position - body size relationships.

Furthermore, it should be recognized that considering prey body size as an indicator of prey profitability fails to account for other aspects of prey profitability such as prey abundance. In fact, prey abundance should *decline* with increasing trophic position (as a consequence of the tropho-dynamic loss of energy at each trophic level). Thus, any potential advantages from feeding on high trophic position (presumably large) prey items may be countered by the decreased abundance of these high trophic position prey items (Vander Zanden et al. 1999). Consequently, the predator may not benefit from consuming larger prey items as it increases in body size. Such trade-offs may explain why positive trophic position - body size relationships were not observed within a given trophic level (i.e., lake trout or pelagic prey fish).

Positive trophic position - body size relationships are observed when all three trophic levels of potential prey items are included (zooplankton, Mysis, Diporia, and prey fish; Fig. 3). Yet among the fish prey items, trophic position was not correlated with body size, so that even if lake trout were to consume increasingly large fish prey items with increasing body size, their trophic position would not be expected to increase. One implication of the breakdown of trophic position - body size relationships is that food web models based on patterns of body size (Cousins 1980; Warren and Latwon 1987; Cohen et al. 1993) may fail to capture the structure of food webs.

A number of studies have reported body size - $\delta^{15}N$ relationships within a population (Sholto-Douglass et al. 1991; Hobson and Welch 1995; Wainright et al. 1996; Gu et al. 1997a; Gu et al. 1997b). Some of these ontogenetic $\delta^{15}N$ shifts may represent spatial or temporal variation in isotopic signatures of prey items (independent of trophic position), underscoring the importance of considering baseline isotopic variation when estimating the trophic position of consumers (Cabana and Rasmussen 1996; Vander Zanden and Rasmussen 1999). Hobson and Welch (1995) reported a dramatic increase in $\delta^{15}N$ with body size of arctic char in Char Lake, Northwest Territories. Being the only fish species in Char Lake, arctic char became cannibalistic in this system, constituting three entire trophic levels. Clearly cannibalism can generate ontogenetic trophic position shifts. Our data suggest that only 2 of the 228 lake trout included in this study are primarily cannibalistic; one from Louisa Lake and one from Lake Rosseau (Fig. 1).

Within-population trophic variation

Lake trout populations with variable trophic positions presumably exhibit individual-level trophic specialization. Our measure of within-population trophic variation, U_{resid}, varied widely among-lakes, leading to a number of hypotheses concerning the determinants of trophic variation. For example, co-existence with few competitor species may allow lake trout to consume a broad range of prey items, thereby allowing individual trophic specialization and diet separation. Similarly, large lakes should have a greater diversity of habitats and prey items upon which lake trout can specialize. Genetic/population differentiation within a population could also result in within-population trophic variation; such differentiation would be more likely in large lakes with multiple basins. Also, a number of the study lakes have been stocked with lake trout to various degrees, and trophic differences between native and stocked lake trout are unknown. It is likely that many factors can affect trophic variation of a population; our analyses failed to identify any variables that were significantly correlated with U_{resid}.

Although stable isotope techniques can provide estimates of trophic position of individual consumers, one limitation is that the resolution of trophic position is considerably lower than when considering actual dietary data, since different prey items may have similar trophic positions (see Schindler et al. 1997, which included 19 diet categories). Schindler et al. (1997) also distinguished between diet breadth (the overall range of prey items used), and diet consistency (the degree to which an individual repeatedly consumes the same prey item). In our analysis, a high U_{resid} is indicative of high diet breadth and high diet consistency. Conversely, a low U_{resid} can be the result of either: 1) high population diet breadth and low consistency (all individuals consume similar proportions of a wide range of prey types), or 2) low population diet breadth (all individuals specialize on one or a few prey types). This problem can be overcome by using dietary data to characterize the range of prey items consumed, and stable isotopes to estimate diet consistency. In the case of a low U_{resid}, it could be determined whether individuals consume similar proportions of a wide range of prey items, or conversely, if a narrow range of prey items are consumed.

Individual-level trophic variation and diet consistency is a poorly-understood and difficult to detect source of trophic variation. Yet if individual consumers differ in foraging, there can be major ecological implications. For example, trophic specialization is thought to reduce intra-specific competition (Bryan and Larkin 1972; Van Buskirk and

Smith 1989; Schindler et al. 1997) and can have profound consequences for population dynamics (Partridge and Green 1985; Lomnicki 1988). In addition, individual dietary differences may explain why individual fish from a population can differ widely in persistent contaminant concentrations (Madenjian et al. 1993). Similarly, these diet differences may explain why same-aged fish can vary widely in growth rates and body size; a potentially important factor for fish recruitment (DeAngelis and Coutant 1979; Cargnelli and Gross 1996; Cargnelli and Gross 1997; Vander Zanden et al. 1998).

Just as previous studies have found that among-system trophic differences largely determine patterns in the growth and life-history of lake trout (Martin 1966; Martin 1970), trophic differences among individuals of a population may be responsible for the within-population variation in growth rates and life-history of fish. Yet within- and among-population trophic variation are generally poorly understood due to the limitations of gut content methods. For lake trout, within-system trophic variation was relatively minor relative to the among-system variation. Although this may or may not be the case for other species, this study has demonstrated how stable isotopes can be used to characterize the importance of within- and among-population sources of trophic variation.

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Table 1. Lake-specific relationships between lake trout trophic position and total length (cm) for each of 13 Ontario and Quebec lakes. Lake, mean lake trout trophic position (TP), lake trout sample size (N), lake trout trophic position - total length (cm) equation (Equation), r^2, standard error of the estimate (SE), p-value (p), and the mean residual value, representing the intra-population variance in lake trout trophic position (U_{resid}).

Lake	TP	N	Equation	r^2	SE	p*	U_{resid}
Class 1							
Clear	3.87	14	TP= 0.010 * len + 3.54	0.10	0.16	0.14	.12
Dickie	3.38	16	TP= 0.019 * len + 2.84	0.08	0.38	0.16	.27
Happy Isle	3.17	17	TP= 0.015 * len + 2.75	0.22	0.29	0.03	.23
Louisa	4.90	19	TP= 0.003 * len + 4.78	0.00	0.26	0.60	.17
Source	3.72	18	TP= 0.001 * len + 3.69	0.00	0.27	0.90	.21
Class 2							
Opeongo	4.15	21	TP= 0.001 * len + 4.09	0.00	0.21	0.56	.15
Smoke	4.37	15	TP= 0.003 * len + 4.21	0.00	0.24	0.47	.19
Victoria	3.81	13	TP= 0.002 * len + 3.73	0.00	0.25	0.60	.18
Class 3							
Twelve Mile	4.31	14	TP= -0.020 * len + 4.94	0.31	0.29	0.02	.20
Memphremagog	4.55	19	TP= -0.006 * len + 4.89	0.19	0.20	0.03	.15
Muskoka	4.64	18	TP= 0.003 * len + 4.46	0.00	0.31	0.44	.21
Rosseau	4.46	21	TP= 0.008 * len + 4.09	0.25	0.25	0.01	.19
Temagami	4.60	21	TP= -0.002 * len + 4.68	0.00	0.25	0.54	.19

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*no relationships were significant at the Bonferroni corrected p = 0.004 (0.05/13).

Figure 1. Lake-specific relationships between lake trout trophic position and total length (cm) from 13 lakes in Ontario and Quebec, Canada. A) Class 1 lakes, symbols: (●) = Clear Lake, (◆) = Dickie Lake, (○) = Happy Isle Lake, (▲) = Louisa Lake, (◆) = Source Lake. B) Class 2 lakes, symbols: (●) = Opeongo Lake, (◇) = Smoke Lake, (○) = Victoria Lake. C) Class 3 lakes, symbols: (●) = Twelve Mile Lake, (◇) = Lake Memphremagog, (○) = Lake Muskoka, (▲) = Lake Rosseau, (■) = Lake Temagami.

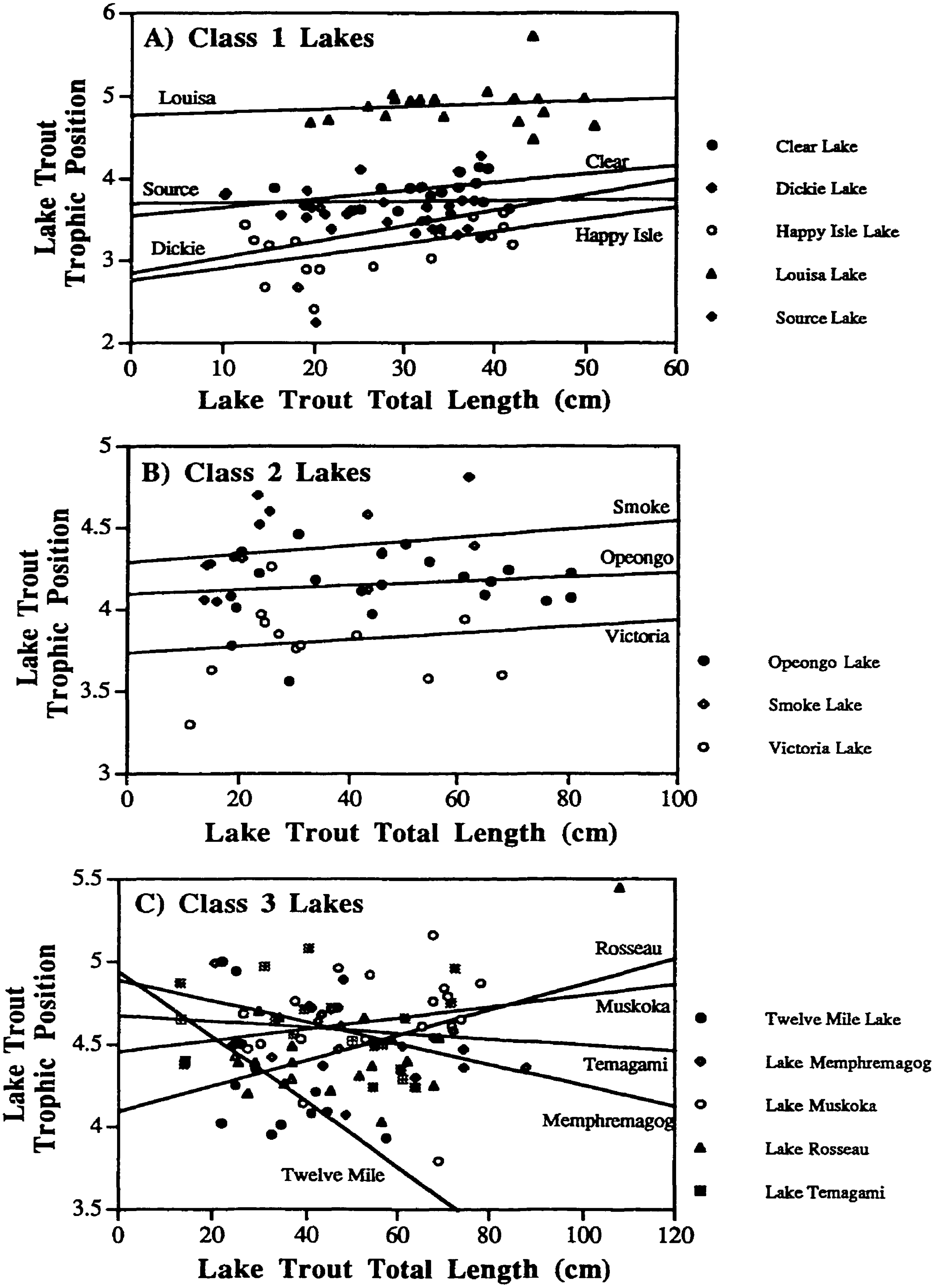

A) Class 1 Lakes
Lake Trout Trophic Position
6
5
4
3
2
Louisa
Source
Clear
Dickie
Happy Isle
0
10
20
30
40
50
60
Lake Trout Total Length (cm)
● Clear Lake
◆ Dickie Lake
○ Happy Isle Lake
▲ Louisa Lake
◆ Source Lake
B) Class 2 Lakes
Lake Trout Trophic Position
5
4.5
4
3.5
3
Smoke
Opeongo
Victoria
0
20
40
60
80
100
Lake Trout Total Length (cm)
● Opeongo Lake
◆ Smoke Lake
○ Victoria Lake
C) Class 3 Lakes
Lake Trout Trophic Position
5.5
5
4.5
4
3.5
Rosseau
Muskoka
Temagami
Memphremagog
Twelve Mile
0
20
40
60
80
100
120
Lake Trout Total Length (cm)
● Twelve Mile Lake
◆ Lake Memphremagog
○ Lake Muskoka
▲ Lake Rosseau
■ Lake Temagami

Figure 2. The relationship between average lake trout total length (cm) and average prey total length (cm) from 6 Northwestern Ontario lakes. Data are taken from Trippel and Beamish (1993).

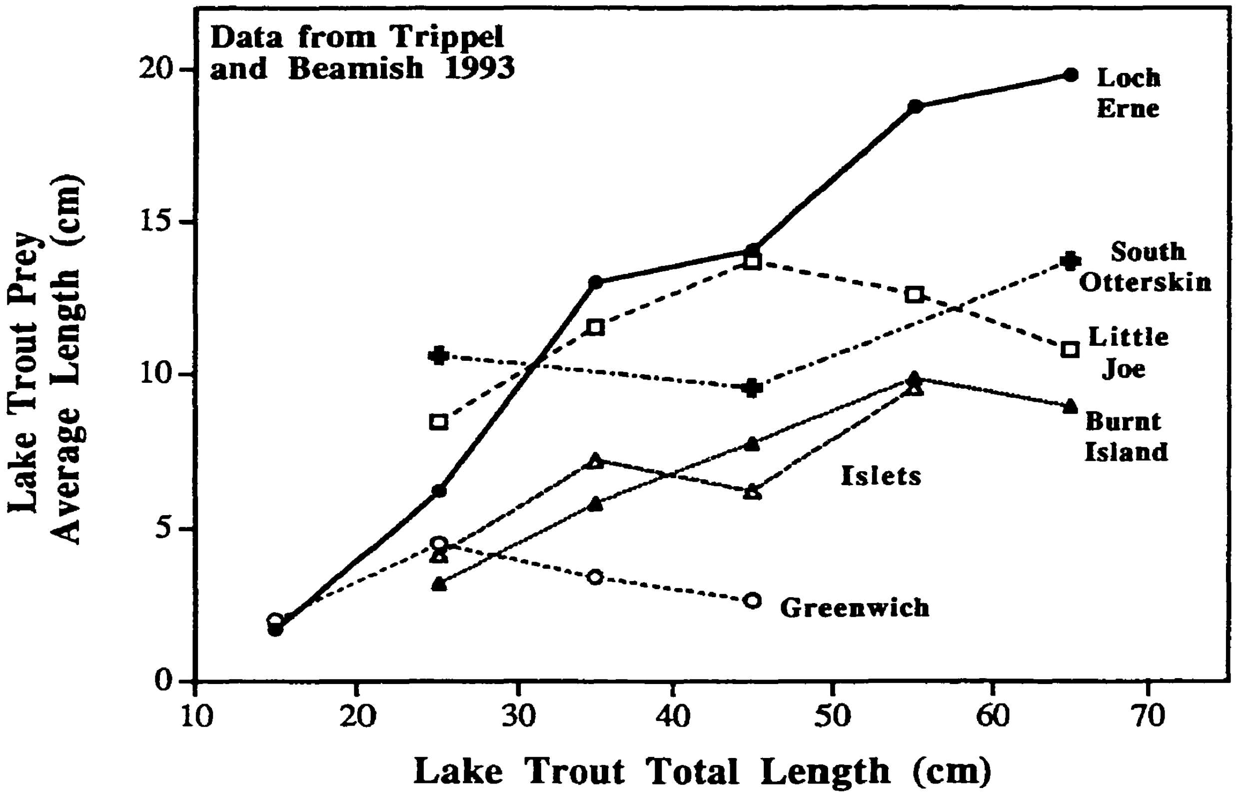
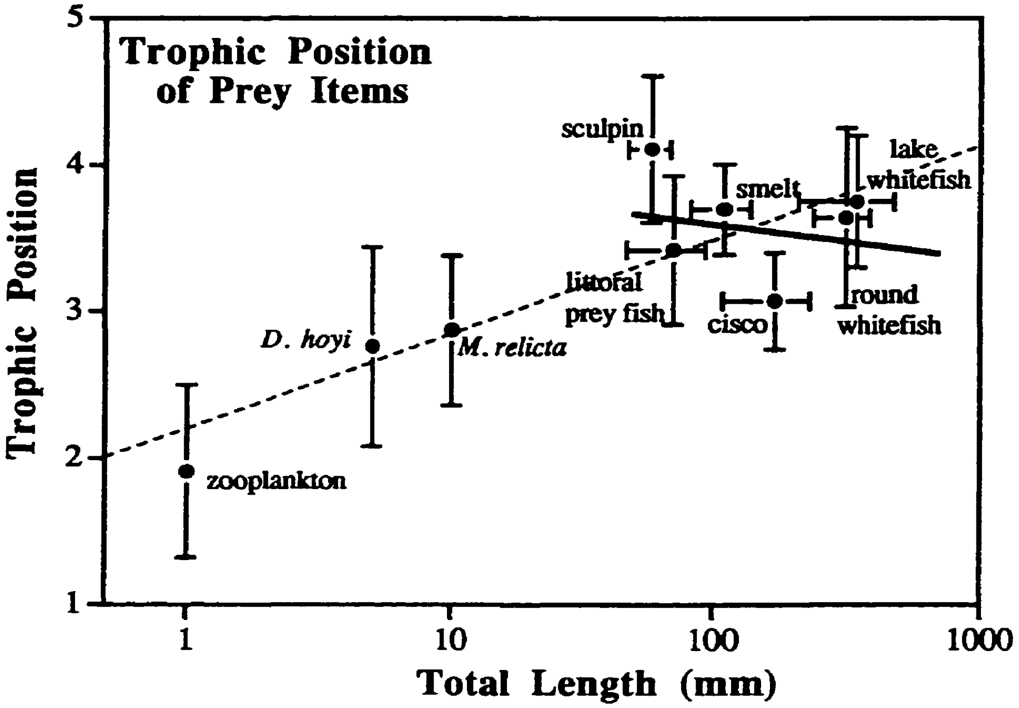

Data from Trippel and Beamish 1993
Lake Trout Prey Average Length (cm)
Lake Trout Total Length (cm)
0
5
10
15
20
10
20
30
40
50
60
70
Loch Erne
South Otterskin
Little Joe
Burnt Island
Islets
Greenwich

Figure 3. Relationship between trophic position and total length (mm) of potential lake trout prey items using taxon-specific mean trophic position estimates and mean sizes (error bars represent ±1 SD). The dashed curve is the relationship for all potential prey items; the solid curve is for the fish prey items only.


Trophic Position
of Prey Items
Trophic Position
Total Length (mm)
1
2
3
4
5
1
10
100
1000
sculpin
smelt
lake
whitefish
littoral
prey fish
cisco
round
whitefish
D. hoyi
M. relicta
zooplankton

CONNECTING STATEMENT

The previous chapter demonstrated that within-population variation in lake trout trophic position was not substantial. Instead, lake-to-lake differences was the major sources of variation in trophic position of lake trout. This finding indicates that considering the mean trophic position of a population is not likely to mask within-population variation in the trophic position of lake trout. Because lake trout are the top predator when present (Vander Zanden and Rasmussen 1996), chapter 5 uses the mean trophic position of lake trout as an energy-based measure of food chain length for 16 lakes. Using these data, this chapter empirically tests current hypotheses of food chain length by examining relationships with factors though the number of discrete trophic levels, lake productivity, lake area, fish species richness, and productive space.

Vander Zanden, M. J. and J. B. Rasmussen. 1996. A trophic position model of pelagic food webs: impact on contaminant bioaccumulation in lake trout. Ecological Monographs 66: 451-477.

CHAPTER 5

PATTERNS OF FOOD CHAIN LENGTH IN LAKES:
A STABLE ISOTOPE STUDY

ABSTRACT

Food web structure is paramount in regulating a variety of ecological patterns and processes, although food web studies are limited by poor empirical descriptions of inherently complex systems. In this study, stable isotope ratios ($\delta^{15}N$ and $\delta^{13}C$) were used to quantify trophic relationships and food chain length (measured as a continuous variable) in 14 Ontario and Quebec lakes. All lakes contained lake trout as the top predator, although lakes differed in the presumed number of trophic levels leading to this species. The presumed number of trophic levels was correlated with food chain length and explained 40% of the among-lake variation. Food chain length was most closely related to fish species richness ($r^2 = 0.69$) and lake area ($r^2 = 0.50$). However, the two largest study lakes had shorter food chains than lakes of intermediate size and species richness, producing hump-shaped relationships with food chain length. Lake productivity was not a powerful predictor of food chain length ($r^2 = 0.36$), and we argue that productive space (productivity*area) is a more accurate measure of available energy. This study addresses the need for improved food web descriptions that incorporate information about energy flow and the relative importance of trophic pathways.

INTRODUCTION

Since the publication of Hairston et al. (1960), there has been increasing recognition of the importance of food web structure in regulating a wide range of ecological patterns and processes (Paine 1980; Pimm 1982; Carpenter et al. 1985; Rasmussen et al. 1990; Persson et al. 1992; Hairston Jr. and Hairston Sr. 1993; Persson et al. 1996; Schindler et al. 1997). Trophic structure is commonly viewed as 'the number of trophic levels' or 'the length of the food chain' and the determinants of food chain length remains a long-standing question in ecology (Lindeman 1942; Hutchinson 1959). Pimm (1982) summarized four hypotheses of food chain length: *the energy constraints hypothesis* -diminishing energy at each successive trophic level limits food chain length, *the optimal foraging hypothesis* -food chains become shortened by consumers feeding on lower, more productive trophic levels, *the dynamic stability hypothesis* -long food chains are dynamically unstable, and *the design constraints hypothesis* - constraints such as predator - prey body size ratios place limits to the number of trophic levels. Alternatively, Schoener (1989) found that food chain length increases with ecosystem size, and proposed the productive space hypothesis; that area*primary productivity determines species richness and community composition, which in turn, determines food chain length. Persson et al. (1996) reviewed the implications of dynamic factors such as habitat heterogeneity, disturbance, size-structured interactions, and adaptive behavior for food chain length.

Studies of food webs have been plagued by the poor quality of the available data, a problem that seriously limits and biases the conclusions of these analyses (Hall and Raffaelli 1991; Polis 1991; Hall and Raffaelli 1993; Polis 1994). Studies attempting to describe food web structure are generally one of two types. Food chain studies assign species to one of several discrete trophic levels (Hairston et al. 1960; Oksanen et al. 1981; Persson et al. 1992; Abrams 1993). Although the food chain provides the basis for most studies of food web dynamics, this approach provides overly simplistic trophic depictions by assuming no omnivory and the existence of discrete levels (Polis 1994; Persson et al. 1996; Polis and Winemiller 1996). Alternatively, connectance food web studies catalog the presence/absence of feeding links, and food chain length represents the mean or maximum path length leading to the top predator. Recent critiques and studies of highly resolved webs indicate a variety of problems including poor taxonomic resolution, inconsistent sampling effort, general incompleteness of the food web data, and problems of scale. A common conclusion has been that many of the observed food web patterns are simply artifacts of methodologies and poor data (Winemiller 1990; Hall and Raffaelli 1991; Martinez 1991; Polis 1991; Hall and Raffaelli 1993; Polis 1994; Polis and Strong 1996; Polis and Winemiller 1996; Goldwasser and Roughgarden 1997). In response to these problems, numerous authors have called for food web approaches that quantify energy flow and the importance of feeding interactions (Cohen et al. 1990; Kenny and Loehle 1991; Martinez 1991; Pimm et al. 1991).

Stable isotopes are increasingly used in food web studies, particularly since they can provide energy flow-based measures of food web structure. Stable nitrogen isotope ratios ($^{15}N/^{14}N$; $\delta^{15}N$) exhibit a 3 - 4‰ enrichment in the heavy isotope (^{15}N) from prey to predator (DeNiro and Epstein 1981; Minagawa and Wada 1984; Hobson and Welch 1992; Cabana and Rasmussen 1994). Interpreting the $\delta^{15}N$ of a consumer relative to an appropriate baseline $\delta^{15}N$ value provides a reliable and quantitative measure of its *trophic position*; defined as a non-integer value reflecting the energy-weighted mean number of trophic energy transfers between the basal resources and the consumer (Vander Zanden and Rasmussen in press). Unlike previous isotopic food web studies, use of this baseline standardization method allows comparative food web studies (Cabana and Rasmussen 1996; Vander Zanden et al. 1997). Furthermore, the isotopic approach is sensitive to omnivory (Cabana and Rasmussen 1994) and provides time-integrated information based on the materials assimilated by consumers. In effect, many of the aforementioned problems with connectance food web and food chain approaches can be circumvented using the stable isotope method to quantify food web structure.

In the present study, we use stable isotopes to estimate the trophic position of a wide range of pelagic consumers from a series of 14 lakes from Ontario and Quebec, all of which contain lake trout (Salvelinus namaycush). Lake trout can reasonably be considered the top predator in our study systems. Lake trout generally have the highest trophic position of any pelagic fish species in our study lakes (Vander Zanden and Rasmussen 1996). Furthermore, it is unlikely that birds or mammals feed significantly on adult lake trout due to their large size and deepwater habitats. In addition to our 14 study lakes, we also include food chain length estimates (lake trout trophic position estimated using stable isotopes) from six other lakes (Hecky and Hesslein 1995; Kiriluk et al. 1995; Keough et al. 1996; Kidd et al. 1998), for a total of 20 study lakes.

Food chains leading to lake trout provide a valuable study system for examining hypotheses of food chain length. Previous studies report that trophic structure leading to lake trout differs substantially among-lakes (Martin 1952; Martin 1966; Rasmussen et al. 1990; Trippel and Beamish 1993; Vander Zanden and Rasmussen 1996). As a result of heterogeneous post-glacial dispersal of prey fishes and invertebrates (Dadswell 1974) and the introduction of non-native species by humans, only some lakes contain the pelagic species that serve as intermediate trophic levels leading to lake trout (the pelagic forage fish: cisco (Coregonus artedii), lake whitefish (Coregonus clupeaformis), round whitefish (Prosopium cylindraceum), smelt (Osmerus mordax), alewife (Alosa pseudoharengus), sculpins (Cottus spp), and the predatory relict zooplankton species, Mysis relicta). Rasmussen et al. (1990) used information on the presence/absence of these important intermediate prey groups to estimate the number of trophic levels in the pelagic food chain leading to lake trout: Class 1 lakes are those that are considered to be three trophic level systems, Class 2 lakes are 4 trophic level systems, and Class 3 lakes are 5 trophic level systems (the presumed trophic structures are presented in Fig. 1A).

The objectives of this study are to use stable isotope depictions of trophic structure to: 1) describe the among-lake variation in food chain length and trophic structure, 2) examine how well food chain length corresponds with the presumed number of trophic levels in the system (Rasmussen's lake Class variable), 3) examine relationships between food chain length and lake/ecosystem attributes in order to address hypotheses of food chain length.

METHODS

Study sites and field sampling

Fourteen lakes containing lake trout as the top pelagic predator were selected from central Ontario and southern Quebec. Lakes were selected to span a broad and representative range of presumed trophic structure and productivity. All lakes were located between 46° 15' N and 44° 30' N latitude, and 80° 00' W and 72° 00' W longitude. Sampling was conducted between May and September 1995. Mysis and Diporia were collected using a benthic sled. Lake trout (13-21 per lake; mean = 17) and potential prey fish species were collected from the littoral, pelagic, and profundal habitats using gill nets, seine nets, minnow traps, angling, and from local fishers. Littoral fishes (percids, centrarchids, and cyprinids) less than 12 cm in length were considered potential lake trout prey because lake trout have access to these fishes during the non-stratified periods (Martin 1954; Vander Zanden and Rasmussen 1996). We group these fishes together under the term "littoral forage fish". Approximately one gram (wet weight) of white dorsal muscle tissue was extracted from each fish specimen. All fish muscle tissue samples and whole invertebrate samples were frozen immediately after collection.

Stable isotope procedure

Fish and invertebrate tissues were dried at 75°C for 48 hours in a drying oven, ground into a fine powder using mortar and pestle, and packed into 4 x 6 mm tin capsules for isotopic analyses. Stable carbon and nitrogen isotope analyses were performed on the same sample using a continuous flow VG Micromass 903E isotope-ratio mass spectrometer at the Environmental Isotope Laboratory (Department of Earth Sciences, University of Waterloo, Waterloo, Ont.). Stable isotope ratios are expressed in delta (δ) notation, defined as the parts per thousand (‰ or "per mil") deviation from a standard material; $\delta^{13}C$ or $\delta^{15}N = (\{R_{sample} / R_{standard}\} - 1) \times 1000$, where $R = {}^{13}C/{}^{12}C$ or ${}^{15}N/{}^{14}N$. The standard material is Pee Dee belemnite (PDB) limestone for $\delta^{13}C$ (Craig 1957), and atmospheric nitrogen for $\delta^{15}N$ (both standards have a ‰ value arbitrarily set at 0‰). One half of the samples were analyzed in duplicate; the standard error of the estimate was 0.12‰ for $\delta^{15}N$ and 0.10‰ for $\delta^{13}C$.

In order for $\delta^{15}N$ values to provide a measure of the trophic position of a consumer, they must be interpreted relative to the $\delta^{15}N$ value representing the base of the food web (hereafter referred to as the 'baseline $\delta^{15}N$'). We use primary consumers (trophic level 2) as baseline indicators because their isotopic signatures are more temporally and spatially integrative relative to primary producers (Cabana and Rasmussen 1996). Vander Zanden and Rasmussen (in press) developed a method that uses $\delta^{15}N$ and $\delta^{13}C$ information to correct for within- and among-system variation in primary consumer (baseline) $\delta^{15}N$. Briefly, this method for estimating trophic position has three parts: a) it generates a primary consumer $\delta^{15}N$ - $\delta^{13}C$ relationship; b) it uses the $\delta^{13}C$ value of the consumer to define the appropriate baseline $\delta^{15}N$ value; and c) it estimates the consumer's trophic position using the formula:

$$\text{Trophic position}_{consumer} = ((\delta^{15}N_{consumer} - \delta^{15}N_{baseline})/3.4) + 2$$

where 3.4 represents the assumed per trophic level increase in $\delta^{15}N$. We used this method to estimate the trophic position of each fish and invertebrate specimen. Error associated with the baseline correction was approximately 0.17‰. For each study lake, the average trophic position of each pelagic species or trophic group (lake trout, smelt, lake whitefish, round whitefish, cisco, sculpin, littoral forage fish, Mysis, and Diporia) was calculated.

Fish species richness represents the number of fish species recorded as present in the lake at the time of study based on our field surveys and unpublished Ontario Ministry of Natural Resources data files. No direct measure of primary productivity was available for our lakes. The best available indicator of algal biomass and primary productivity was annual average secchi disk transparency (Carlson 1977). This is justified because all of our study lakes are low in color (< 10 Pt units) and dissolved organic carbon. Secchi disk transparency values (the depth in meters in which a secchi disk is no longer visible) for the study lakes were taken from unpublished Ontario Ministry of Natural Resources data files and represent the average transparency values recorded during the ice-free period. These values are expressed in the inverse (secchi^{-1}) so that increasing values reflect increasing algal biomass. Productive space (estimated primary productivity rate*lake area) was estimated for each lake. Primary productivity was estimated from Secchi disk transparency using published empirical relationships (Carlson 1977; Tolstoy 1988).

RESULTS

Empirical data

The method of Vander Zanden and Rasmussen (in press) was used to estimate the trophic position of each individual pelagic consumer from the 14 study lakes. For each lake, the mean trophic position of each species or trophic group was calculated and values were plotted along a vertical axis representing trophic position (Fig. 2). Lakes are arranged according to the presumed number of trophic levels (3, 4, or 5 levels; Rasmussen's lake Class variable).

Food web configurations of Class 1 lakes (three trophic level systems) varied widely among-lakes, with food chain length ranging from 3.0 to 4.8. Both among-lake variation in the trophic position of littoral forage fish and the difference in trophic position between lake trout and littoral forage fish (lake trout trophic position minus littoral forage fish trophic position) were responsible for the among-lake variation in Class 1 food chain length. Food chain length of Class 2 lakes (four trophic level systems) ranged from 3.8 to 4.4; much of this variation was attributed to variation in the trophic position of prey items. Food chain length of Class 3 systems (five trophic level systems) ranged from 4.3 to 4.6. Mean trophic positions of pelagic forage fish were highly variable among lakes, with sculpins and smelt exhibiting the highest average trophic position, followed by whitefish and cisco.

For each of the three lake Classes, the mean trophic position of each species and trophic group was calculated (Table 1). Our stable isotope trophic position estimates were used to characterize the typical trophic structure for each 'lake Class' in the form of a trophic position model (Fig. 1B), which is a means of representing trophic structure based on trophic position data, whereby species with similar trophic positions are grouped into trophic guilds (see Vander Zanden and Rasmussen 1996). Mean food chain length increased from 3.74 in Class 1 lakes, to 4.13 in Class 2 lakes, to 4.52 in Class 3 lakes; values that generally correspond with food chain length estimates calculated using dietary data (Vander Zanden and Rasmussen 1996).

Factors affecting food chain length

Food chain length as measured using stable isotopes ranged nearly two trophic levels across our 14 study lakes. This among-system variation in food chain length provides an opportunity to examine relationships between food chain length and lake/ food web characteristics that are pertinent to hypotheses of food chain length. Here, we examine relationships between food chain length and the presumed number of discrete trophic levels, fish species richness, lake area, a measure of lake productivity (secchi disk transparency^{-1}), and productive space.

One-way analysis of variance (ANOVA; SYSTAT) indicated that the number of discrete trophic levels (lake Class) explained 41% of the among-lake variation in mean lake trout trophic position (using lake averages; $n = 14$ lakes, $F = 3.74$, $P = 0.058$, $r^2 = 0.41$). Using individual lake trout, the number of discrete trophic levels (lake Class) explained 33% of the total variation in lake trout trophic position ($n = 243$ individual lake trout, $F = 58.52$, $P < 0.001$, $r^2 = 0.33$). This indicates that in a *qualitative* sense, discrete trophic levels represent the among-lake variation in trophic structure, even though trophic levels clearly failed to incorporate the complexity and omnivory that is prevalent in these food webs (compare Fig. 1A and 1B).

Food chain length increased with increasing fish species richness (Fig. 3A); species richness explained 66% (with Great Lakes) and 69% (without Great Lakes) of the among-lake variation in food chain length (Table 2). The two Great Lakes, Lake Ontario and Lake Superior (Kiriluk et al. 1995; Keough et al. 1996) had shorter food chains than lakes of intermediate species richness, producing a hump-shaped relationship. Food chain length also increased as a function of lake area (Fig. 3B); area explained between 45% (with Great Lakes) and 50% (without Great Lakes) of the among-lake variation in food chain length (Table 2). As was the case for species richness, Lake Ontario and Lake Superior had shorter food chains than intermediate-sized lakes.

If the available energy limits food chain length, then food chain length might be expected to increase with an indicator of primary productivity. Secchi^{-1} ranged approximately 4-fold across lakes, and explained 36% of the among-lake variation in food chain length (Fig. 4C; Table 2). Note that Lake Ontario and Superior did not differ from the other study lakes in the secchi^{-1} - food chain length relationship. We also examined Schoener's productive space hypothesis; that the total amount of primary production in an ecosystem (productive space = area*primary productivity; kgC*d^{-1}) should ultimately determine the length of the food chain. Our estimate of productive space was positively correlated with food chain length (Fig. 4D; Table 2), although lake area - food chain length and productive space - food chain length relationships were nearly identical.

DISCUSSION

In this study, stable isotopes were used to measure food chain length and trophic structure in a series of Ontario and Quebec lakes, all of which shared the common feature of having lake trout as the top predator. Food chains leading to lake trout varied by nearly two entire trophic levels among lakes, with the longest food chain consisting of just less than five trophic levels. These findings generally corresponds with our previous stable isotope studies indicating that the among-population range in trophic position of freshwater fish populations is typically one trophic level or more (Cabana and Rasmussen 1996; Vander Zanden et al. 1997). It is interesting to note that lakes containing the same presumed trophic levels (same lake Class) often differed substantially in trophic structure in terms of energy flow; the number of presumed trophic levels explained only 41% of the among-lake variation in food chain length. Clearly, lakes that are similar in terms of community composition can differ in trophic structure when energy flow is taken into account. Furthermore, the fact that populations do not conform to trophic levels provides direct evidence that omnivory is prevalent in these systems, supporting recent microcosm, observational, and modelling studies showing that omnivory is prevalent and can stabilize food webs (Polis 1991; Lawler and Morin 1993; Holyoak and Sachdev 1998; McCann et al. 1998). Still, the trophic level concept has proven useful in studies of trophic cascades (Power 1990; Mazumder 1994) and predicting contaminant bioaccumulation in fish (Rasmussen et al. 1990). Trophic levels continue to provide a framework for models and field studies of food web dynamics; indeed, the use of trophic levels often makes these studies possible by simplifying trophic structure to a manageable form.

Food chain length was most closely correlated with fish species richness; this variable explained 69% of the among-lake variation in food chain length. Food chain length also increased with increasing lake area, which is not surprising because lake area and fish species richness are closely correlated. The fact that lake area was a poorer predictor of food chain length than species richness indicates that food chain length was responding to changes in community composition and species richness rather than to the effects of increasing lake size per se. Our results suggest that although habitat size (lake area) may provide a reasonable and easy-to-measure indicator of web size for future food web studies (Cohen and Newman 1991), measures of species richness are a preferable (and biologically meaningful) indicator of food web size and complexity.

The largest lakes, Lake Superior and Lake Ontario, had shorter food chains than lakes of intermediate size and species richness (Figs 3A and 3B). In fact, this observation corresponds with predictions of Persson et al. (1996) that certain variables should exhibit a hump-shaped relationships with food chain length. We provide two possible explanations for why the Great Lakes might have shorter food chains. The first is that lake trout from the Great Lakes are isolated from the inshore and benthic food webs due to the low perimeter to area ratios in these systems. A potential consequence of interacting with a limited subset of the food web is that the food chain becomes shortened.

An alternative explanation is related to the fact that both Lake Ontario and Lake Superior contain populations of alewife, a species of pelagic forage fish found in none of our other study lakes. Lake trout often feed heavily on this species (Vander Zanden and Rasmussen 1996). Because alewife are generally not piscivorous and rarely feed on <u>Mysis</u> and <u>Diporia</u>, alewife have a low trophic position compared to other species of pelagic forage fish (Vander Zanden and Rasmussen 1996). Lake trout populations that feed on the low trophic position alewife will have lower trophic positions relative to those that feed on other prey fish species. This explanation is essentially an optimal foraging argument (Hutchinson 1959; Pimm 1982), in which food chain length reflects a balance between forces that tend to shorten food chains (that prey lower in the food web are more productive/abundant), and those that tend to lengthen food chains (that prey higher in the food web are likely to be larger, thereby making them more profitable). Because alewife are relatively large and are also often abundant, this species can be a highly profitable prey item for lake trout. Consequently, lake trout consume this low trophic position species, and the result is a shortened food chain.

The importance of species richness and lake area in determining food chain length in our study corresponds with findings of Schoener (1989), which found that island area (habitat size) explained the substantial variation in food chain length among Bahamian islands. Furthermore, his qualitative re-analysis of Briand and Cohen's (1987) data also suggested that food chain length increased with food web area (Schoener 1989). Schoener (1989) argued that larger systems have more total energy available as a result of their size. Such a system would support more individuals per species, and consequently, individual species would be more likely to persist. Increasing the primary productivity also increases the total production of a system. This reasoning led to the productive space hypothesis; that the total amount of primary production in an ecosystem (productive space = area*primary productivity rate; $kgC*d^{-1}$) determines species richness and community composition, which, in turn, determines the length of the food chain.

Productive space was positively correlated with food chain length, although lake area - food chain length and productive space - food chain length relationships were nearly identical. Productive space estimates were primarily a function of lake area because there was a relatively limited range in lake productivity compared to the range in lake area (nearly five orders of magnitude). Productive space was extremely closely correlated with lake area (ln productive space = 1.000 (ln area) - 1.893; $r^2 = 0.94$), indicating that lake area serves as a proxy for productive space in our study systems such that effects of lake area and productive space cannot be distinguished.

Although many dynamic food web models assume that increasing productivity allows addition of trophic levels (Oksanen et al. 1981; Abrams 1993), studies examining effects of productivity on food chain length have either found (Yodzis 1984; Jenkins et al. 1992; Persson et al. 1992; Kaunzinger and Morin 1998; Townsend et al. 1998) or not found (Pimm 1982; Briand 1983; Briand and Cohen 1987; Schoenly et al. 1991) positive relationships. Whether positive relationships were reported from microcosm studies depended on the range of productivity included; a two-fold range in productivity produced little effect (Spencer and Warren 1996; Spencer and Warren 1996), while those considering a broad range (i.e., orders of magnitude) of productivity found positive effects of productivity (Jenkins et al. 1992; Kaunzinger and Morin 1998).

Our indicator of lake productivity, secchi^{-1}, was positively correlated with food chain length, although this variable explained relatively little (36%) of the among-lake variation in food chain length. Additionally, secchi^{-1} failed to explain a significant portion of the residual variation from either species richness or lake area models, indicating no effect of productivity independent of these factors. Although this seems to suggest a relatively minor role of productivity, the available range in productivity may not have been enough to detect productivity effects (lake trout are not found in productive lakes). Additionally, if food chain length were truly limited by energetic constraints, food chain length in relatively well delineated systems such as lakes should be set by the total amount of primary production in the system (productive space) rather than primary productivity rates on a 'per unit area' basis. Because productive space was primarily a function of lake area in our study, lake area and productive space are the variables that are most indicative of ecosystem productivity, in fact, more so than our original indicator of productivity (secchi^{-1}). Future studies attempting to resolve the importance of habitat size (area), productive space, and productivity should include a broad range of both habitat size and productivity.

Trophic structure has crucial implications for both community and ecosystem patterns and processes, such as the regulation of species diversity (Paine 1980), energetic efficiencies and the biomass of trophic levels (Hairston et al. 1960; Oksanen et al. 1981;

Power 1990; Hairston Jr. and Hairston Sr. 1993), community stability (May 1975; Pimm 1982), contaminant levels in the biota (Rasmussen et al. 1990), and biogeochemical fluxes from ecosystems (Schindler et al. 1997). Although the importance of trophic structure is well recognized, food web studies have generally suffered from a lack of replicable and reliable measures of trophic structure, to the extent that conclusions of many food web studies are considered questionable, and the poor quality of the available food web data limits further progress (Paine 1988).

The recent trend away from analyzing catalogs of literature food webs (Cohen et al. 1990), in favor of observational food web studies of the same ecosystem type using standardized methodology (Sprules and Bowerman 1988; Schoener 1989; Townsend et al. 1998), as well as experimental microcosm studies (Jenkins et al. 1992; Holyoak and Sachdev 1998; Kaunzinger and Morin 1998) represents a movement in the right direction. But investigators have also repeatedly called for food web data that reflects energy flow and the importance of trophic links (Cohen et al. 1990; Kenny and Loehle 1991; Martinez 1991; Pimm et al. 1991). The stable isotope approach employed here provides a replicable, energy-weighted measure of trophic structure and food chain length for individual food webs. We show that this approach can be used not only to quantify trophic structure, but to examine the factors influencing the length of food chains in real ecosystems. Furthermore, this approach will likely be useful in applied studies examining how perturbations such as environmental pollution, extinctions, and species introductions affect food web structure and ecosystem function.

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Table 1. Mean trophic position (± 1 Standard Deviation) and mean total length (mm) of lake trout and other pelagic consumers for each of the three lake Classes. Data based on analysis of 14 Ontario and Quebec lake food webs.

Species or trophic group	N lakes	Mean Trophic Position (+- 1 SD)	Mean Total Length (mm)
Class 1 (Three trophic level systems)			
littoral forage fish	6	3.57 (0.54)	71
lake trout	6	3.74 (0.69)	296
Class 2 (Four trophic level systems)			
cisco	3	3.05 (0.33)	145
lake whitefish	2	3.68 (0.32)	359
round whitefish	3	3.82 (0.29)	274
sculpin	2	4.12 (0.55)	56
lake trout	3	4.13 (0.31)	400
Class 3 (Five trophic level systems)			
Diporia	4	2.76 (0.68)	-
Mysis	4	2.87 (0.51)	-
cisco	3	3.10 (0.34)	206
smelt	4	3.70 (0.31)	150
lake whitefish	2	3.80 (0.55)	309
sculpin	3	4.09 (0.46)	64
lake trout	5	4.52 (0.29)	468

Table 2. Equations relating food chain length to ln fish species richness (N), ln lake area (hectares; A), secchi disk transparancy^{-1} (meters; S), and ln productive space (kgC/d^{-1}; PS). Equations with Great Lakes (equations 2, 4 and 5) include stable isotope-based food chain length estimates for Lake Ontario (Kiriluk et al. 1995) and Lake Superior (Keough et al. 1996). Additional food chain length estimates in Equation 3 and 4 are for lakes 373, Laberge, Fox, and Kusawa (Hecky and Hesslein 1995; Kidd et al. 1998).

predictor variable	n lakes	Equation	r^2
1.ln Fish species richness (N) (without Great Lakes)	14	$FCL = 2.13*N^{0.65}$	$r^2 = 0.69$
2.ln Fish species richness (N) (with Great Lakes)	16	$FCL = -0.55N^2 + 3.83N - 2.16$	$r^2 = 0.67$
3.ln lake area (ha) (A) (without Great Lakes)	18	$FCL = 1.88A + 2.78$	$r^2 = 0.50$
4.ln lake area (ha) (A) (with Great Lakes)	20	$FCL = -0.021A^2 + 0.47A + 1.91$	$r^2 = 0.45$
5.Secchi^{-1} (S) (with Great Lakes)	16	$FCL = 6.18S^{0.22}$	$r^2 = 0.36$
6. ln Productive space (PS) (without Great Lakes)	14	$FCL = 2.94PS^{0.21}$	$r^2 = 0.48$
7. ln Productive space (PS) (with Great Lakes)	16	$FCL = -0.02PS^2 + 0.44PS + 2.63$	$r^2 = 0.48$

Figure 1. A) A food chain model of pelagic trophic structure (based on Rasmussen et al. 1990). B) The trophic position model of pelagic food webs based on our stable isotope-based estimates of trophic position. For each lake Class, the average trophic position of each species was estimated, and species with similar trophic positions were grouped into trophic guilds. Thick lines represent major links, thin lines represent minor links. The vertical extent of the trophic compartments represents 1 Standard Deviation.

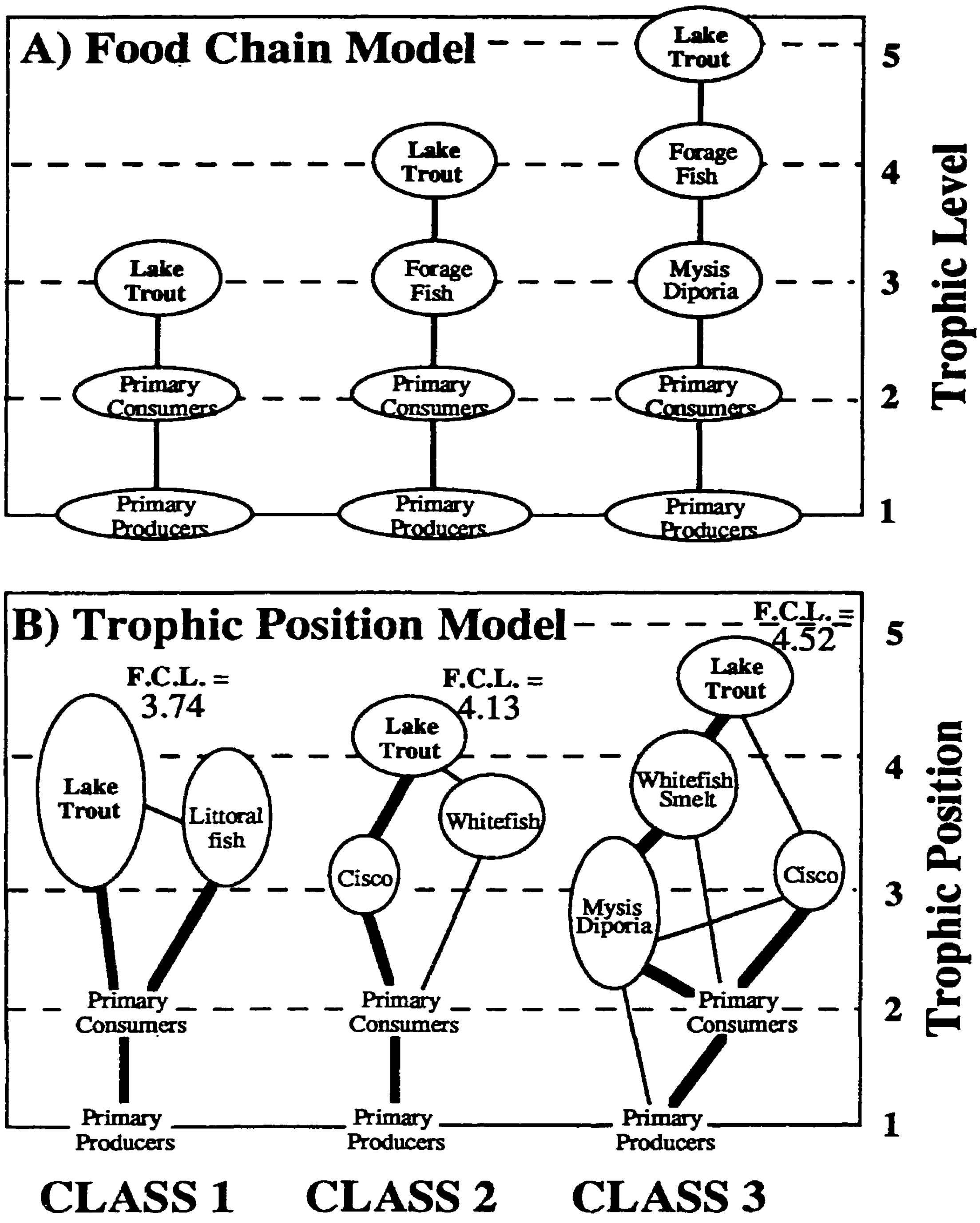
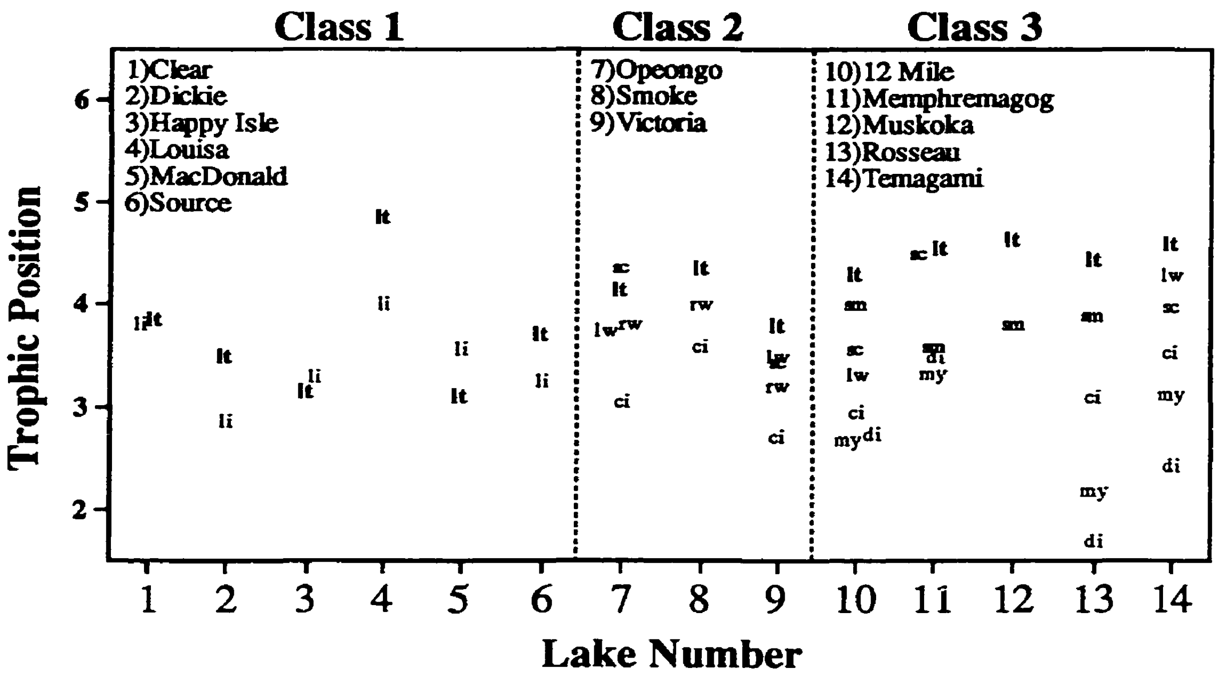

A) Food Chain Model
Lake Trout
Forage Fish
Mysis Diporia
Primary Consumers
Primary Producers
Trophic Level
5
4
3
2
1
B) Trophic Position Model
F.C.L. = 3.74
F.C.L. = 4.13
F.C.L. = 4.52
Lake Trout
Littoral fish
Cisco
Whitefish
Whitefish Smelt
Mysis Diporia
Primary Consumers
Primary Producers
Trophic Position
CLASS 1
CLASS 2
CLASS 3

Figure 2. Pelagic trophic structure for each of the 14 Ontario and Quebec study lakes. lt=lake trout, li=littoral fish, lw=lake whitefish, rw=round whitefish, sc=sculpin, ci=cisco, sm=smelt, di=*Diporia hoyi*, my=*Mysis relicta*.


Class 1
Class 2
Class 3
1)Clear
2)Dickie
3)Happy Isle
4)Louisa
5)MacDonald
6)Source
7)Opeongo
8)Smoke
9)Victoria
10)12 Mile
11)Memphremagog
12)Muskoka
13)Rosseau
14)Temagami
Trophic Position
2
3
4
5
6
Lake Number
1
2
3
4
5
6
7
8
9
10
11
12
13
14
li
lt
lt
li
li
lt
lt
li
li
lt
lt
li
sc
lt
lw
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ci
lt
rw
ci
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sc
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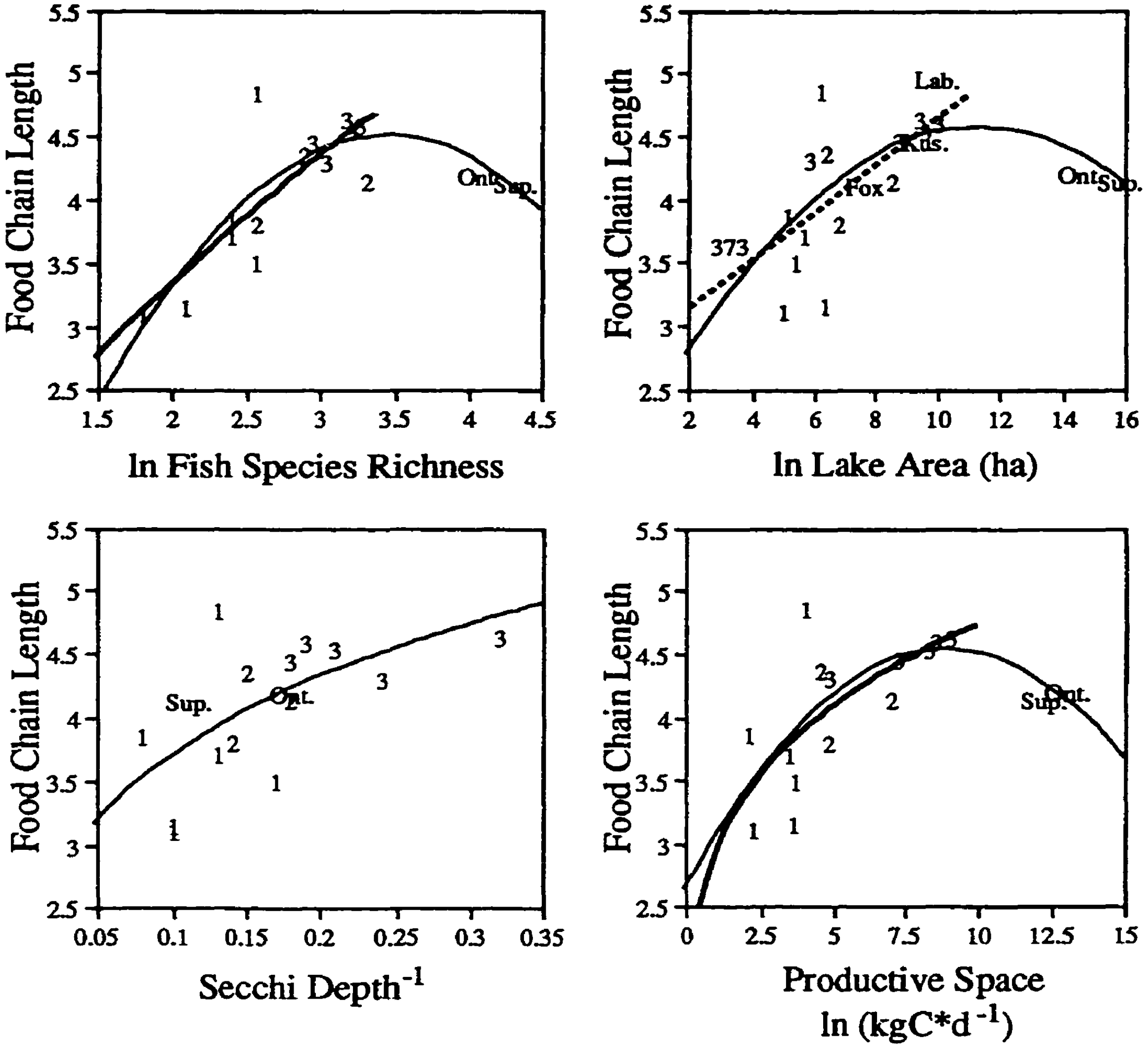
my
di

Figure 3. Relationships between food chain length and A) ln fish species richness, B) ln lake area (ha), and C) secchi^{-1} (a measure of lake productivity) and D) productive space (lake area*productivity). The dashed line represents the curve for the study lakes exclusive of the Great Lakes, the solid line includes Lake Ontario and Lake Superior. Codes: 1 = Class 1 lake, 2 = Class 2 lake, 3 = Class 3 lake, Ont. = Lake Ontario, Sup. = Lake Superior, Fox = Fox Lake, Kus. = Kusawa Lake, Lab. = Lake Laberge, 373 = Lake 373.


Food Chain Length
ln Fish Species Richness
1.5
2
2.5
3
3.5
4
4.5
2.5
3
3.5
4
4.5
5
5.5
Ont.
Sup.
ln Lake Area (ha)
2
4
6
8
10
12
14
16
Lab.
Kds.
Fox
373
Secchi Depth^{-1}
0.05
0.1
0.15
0.2
0.25
0.3
0.35
Productive Space
ln (kgC*d^{-1})
0
2.5
5
7.5
10
12.5
15

CONNECTING STATEMENT

Having described within- and among-lake patterns of trophic position and food chain length in Chapters 4 and 5, chapter 6 extends this descriptive analysis to examine the impacts of species invasions on food webs containing lake trout as the top predator. Species invasions pose a serious threat to aquatic ecosystems (Zaret and Paine 1973), although quantifying impacts of invasive species has been problematic for ecologists (Lodge 1993). Smallmouth bass and rock bass are presently invading a number of lakes across Ontario, presumably via the dumping of unused live bait by anglers. This chapter quantifies the impact of bass invasions on food web structure, with emphasis on the changes in lake trout trophic position and $\delta^{13}C$ signatures. This study includes a comparative study of 9 Ontario lakes, as well as a multi-year, 'before and after' comparison of food web structure of two recently-invaded lakes.

Lodge, D. M. Biological invasions: lessons for ecology. Trends in Ecology and Evolution **8**: 133-137.

Zaret, T. M. and R. T. Paine. Species introductions in a tropical lake. Science **182**: 449-455.

CHAPTER 6

STABLE ISOTOPE EVIDENCE FOR FOOD WEB SHIFTS FOLLOWING SPECIES INVASIONS OF LAKES

ABSTRACT

Species invasions pose a serious threat to biodiversity and native ecosystems although predicting and quantifying impacts of invasives has proven problematic. Here we use stable isotope ratios to document the food web consequences of the recent invasion of two non-native predators, smallmouth bass and rock bass in 9 Canadian lakes; our analysis included a comparison of food webs from invaded and reference lakes, as well as a comparison of pre- and post-invasion food webs of recently invaded lakes. Invasion was followed by substantial declines in littoral prey fish diversity and availability. $\delta^{13}C$ evidence revealed that lake trout underwent a habitat shift from littoral to pelagic prey in response to bass invasion, while $\delta^{15}N$ evidence showed that lake trout shifted from a diet of primarily fish to invertebrates. These results show that foraging of pelagic consumers in littoral habitats is an important way in which these two habitats can be closely coupled, and that the magnitude of this coupling is mediated by strong top-down effects of an introduced predator. In this instance, bass-induced food web shifts are likely to have severe consequences for native lake trout populations and fisheries.

INTRODUCTION

Human dominance over the earth's ecosystems has been accompanied by the widespread introduction of exotic species, which has led to the extinction of native species, the collapse of native fisheries, and the loss of ecological integrity and ecosystem functioning (Witte et al. 1992; Mills et al. 1994; Vitousek et al. 1996). Ecologists are far from being able to predict or even quantify the ecological impacts of species introductions (Taylor et al. 1984; Moyle 1986; Pimm 1991; Lodge 1993). This is not surprising because natural food webs are variable and complex (Polis 1991; Polis and Strong 1996), and using traditional methods to examine impacts of species introductions on aquatic food webs would be laborious, difficult, and costly.

Stable isotopes have recently emerged as a means of providing a time-integrated measure of food web relationships based on energy flows. Stable nitrogen isotope ratios ($^{15}N/^{14}N$; $\delta^{15}N$) become enriched by 3 - 4‰ from prey to predator tissues, thereby providing a measure of consumer trophic position (DeNiro and Epstein 1981; Cabana and Rasmussen 1994). Stable carbon isotope ratios ($\delta^{13}C$) of consumers generally match those of their prey, although pelagic and littoral prey items often differ substantially in $\delta^{13}C$; thus consumer $\delta^{13}C$ provides information about feeding habitat and the importance of littoral and pelagic sources of production in lakes (France 1995; Hecky and Hesslein 1995).

The utility of stable isotopes in food web studies has recently been demonstrated in studies characterizing contaminant biomagnification in aquatic food webs (Cabana and Rasmussen 1994; Kidd et al. 1995). In the present study we use stable isotope ratios to quantify the food web consequences of recent introductions of smallmouth bass (Micropterus dolomieu) and rock bass (Ambloplites rupestris) into lakes. Smallmouth bass has been widely introduced into lakes and rivers throughout the world, and both species have greatly expanded their geographical range over the last century (Scott and Crossman 1973; MacCrimmon and Robbins 1975). Both species are presently invading a number of relatively pristine lakes in North America's Northern Hardwood-Boreal Forest transition zone, many of which contain lake trout (Salvelinus namaycush) as the native top predator. Although lake trout are generally considered to be an open-water, pelagic piscivore (Scott and Crossman 1973; Vander Zanden and Rasmussen 1996), populations from lakes lacking pelagic prey fish can consume substantial amounts of fish from inshore habitats (Martin 1954; Vander Zanden and Rasmussen 1996). Considering the potential top-down impacts of predators such as bass on littoral prey fish communities (Mittelbach et al. 1995), we set out to examine impacts of bass invasion on food web structure; in particular, impacts on the pathways of energy flow leading to the native top predator, lake trout.

METHODS

Nine lakes in central Ontario (located between 46° 15' N and 44° 30' N latitude, and 80° 00' W and 77° 00' W longitude) containing lake trout as the top pelagic predator were sampled between May and September 1995 and 1996. The study lakes contain no species of pelagic forage fish, and lake trout are forced to become planktivorous in these lakes (these lakes are considered Class 1 in the lake classification of Rasmussen et al. 1990). Lake trout were collected using gill nets, by angling, and from local anglers. Prey fish from littoral habitats (primarily Percidae, Centrarchidae, and Cyprinidae) were collected using seine nets and minnow traps. Approximately one gram (wet weight) of whole white dorsal muscle tissue was removed from each individual lake trout and littoral prey fish. Zooplankton were collected during the day using horizontal tows with a 250 μm standard zooplankton net. All fish and zooplankton samples were frozen as quickly as possible after collection.

Fish and invertebrate specimens were dried at 75° C for 48 hours in a drying oven, ground into a fine powder using mortar and pestle, and packed into 4 x 6 mm tin capsules for isotopic analyses. Stable carbon and nitrogen isotope analysis was performed using a continuous flow VG Micromass 903E isotope-ratio mass spectrometer at the Environmental Isotope Laboratory (Department of Earth Sciences, University of Waterloo, Waterloo, Ont.). Stable isotope ratios are expressed in delta (δ) notation, defined as the parts per thousand (‰ or "per mil") deviation from a standard material; $\delta^{13}C$ or $\delta^{15}N = (\{R_{sample} / R_{standard}\} - 1) \times 1000$, where $R = {}^{13}C/{}^{12}C$ or ${}^{15}N/{}^{14}N$. The standard material is Pee Dee belemnite (PDB) limestone for $\delta^{13}C$ (Craig 1957), and atmospheric nitrogen for $\delta^{15}N$ (both standards have a ‰ value arbitrarily set at 0‰). One half of the samples were analyzed in duplicate; the standard error of the estimate was typically 0.12‰ for $\delta^{15}N$ and 0.10‰ for $\delta^{13}C$.

Despite the consistent enrichment in $\delta^{15}N$ from prey to predator, the $\delta^{15}N$ value of a consumer cannot be used as an *absolute* measure of trophic position because organisms at the base of the food web can differ greatly in $\delta^{15}N$ values (Cabana and Rasmussen 1996; Vander Zanden and Rasmussen 1999). Vander Zanden and Rasmussen (1999) present a dual isotope ($\delta^{15}N$ and $\delta^{13}C$) method for measuring trophic position of aquatic consumers that corrects for among-lake and within-lake variation in $\delta^{15}N$ signatures by: a) generating a baseline $\delta^{15}N$ - $\delta^{13}C$ relationship specific to the study lakes, b) using the $\delta^{13}C$ value of the aquatic consumer to define the appropriate $\delta^{15}N$ value from which to estimate trophic position, and c) estimating the consumer's trophic position using the consumer $\delta^{15}N$ value and the $\delta^{13}C$-adjusted baseline $\delta^{15}N$ value using the formula:

$$\text{Trophic position} = ((\delta^{15}N_{consumer} - \delta^{15}N_{baseline})/3.4) + 2$$

where 3.4 = the assumed per trophic level ‰ increase in $\delta^{15}N$. The +2 term is added because trophic position is being estimated relative to primary consumers rather than primary producers. We used this method to estimate the trophic position of each fish and zooplankton sample. The present analysis is based on $\delta^{15}N$ and $\delta^{13}C$ signatures of 433 individual lake trout and littoral prey fish from the 9 study lakes.

Fish species lists are based on our field sampling efforts (using minnow traps, gill nets, and seine nets), unpublished Ontario Ministry of Natural Resources documents, and annual quantitative electrofishing on MacDonald and Clean lakes. In these two lakes, only cyprinid species that made up more than 1% of the catch were considered to be present in significant numbers for inclusion in this analysis. We consider cyprinid species richness in this analysis, as this variable is indicative of the overall size of the prey fish community (Casselman and Grant 1998)

Two source mixing models (Peterson and Fry 1987) were used to estimate the % piscivory and % littoral contributions to lake trout diet. The model used lake-specific prey fish $\delta^{13}C$ and trophic position values. Average (cross-lake) zooplankton $\delta^{13}C$ and trophic position values were used because zooplankton exhibit high levels of temporal variability in $\delta^{15}N$ and $\delta^{13}C$ (Cabana and Rasmussen 1996).

RESULTS

Lakes invaded by bass had reduced cyprinid species richness relative to reference lakes in which bass have not become established (Table 1; Fig. 1A), providing evidence for impacts of bass invasion on the prey fish community. Lake trout populations responded to these shifts in the littoral prey fish community (Fig. 1B). The average lake trout trophic position was 3.9 in reference lakes (indicating a fish-based diet), compared to 3.3 in invaded lakes (indicating a plankton-based diet). $\delta^{13}C$ signatures of lake trout muscle tissue provide additional evidence for the food web changes following bass introductions (Fig. 1C). Lake trout $\delta^{13}C$ from reference lakes averaged -27.5‰, indicating primary reliance on littoral prey, while lake trout $\delta^{13}C$ from invaded lakes was -29.2‰, indicating closer trophic linkages with pelagic prey in these lakes.

For each lake trout population, a two-source mixing model was used to estimate the percent contribution of fish (% piscivory; based on trophic position) and littoral prey (% littoral; based on $\delta^{13}C$) to lake trout diet. Lake trout from reference lakes averaged 60% piscivory, while lake trout from invaded lakes had a mean piscivory of 16% (Table

1) . Similarly, lake trout from reference lakes averaged 62% littoral prey; this value was reduced to 26% for invaded lakes. Lake-specific estimates of % piscivory and % littoral prey for lake trout were closely correlated ($r^2 = 0.80$, $p < 0.001$). Because the bass-induced changes in piscivory and use of littoral prey were so closely coupled, these two lines of evidence were used simultaneously to summarize the food web shifts following the introduction of bass (Fig 2).

Our comparative analysis of the impacts of bass introduction on food webs is complemented by long-term studies on two lakes: MacDonald and Clean Lakes. These two lakes are in close proximity (less than 200 meters), and were nearly identical in lake area, morphometry, littoral habitat, and fish species composition prior to bass invasion. Both lakes have now been invaded by the two bass species, although the chronology of bass establishment differs for the two lakes (Fig. 3). Both bass species were fully established (defined as the first year in which all life-stages of both species were found in the appropriate habitats throughout the lake) in MacDonald Lake by 1987, which was followed by the extirpation of five dominant species of cyprinids and a dramatic decline in lake trout trophic position. In Clean Lake, smallmouth bass were found in small numbers during the 1980's, although it was not until 1993 that both bass species had become fully established. Recent electrofishing surveys indicate that Clean Lake is presently undergoing littoral fish community changes mirroring those observed in MacDonald Lake.

DISCUSSION

Lake ecologists commonly consider pelagic and littoral habitats to be relatively isolated components of lake ecosystems (Lodge et al. 1998). The results presented here show that the foraging of pelagic predators in the more productive littoral habitats provides an important way in which these two habitats can be coupled (Schindler et al. 1996). Furthermore, we find that the magnitude of this important habitat coupling is mediated by strong top-down effects of invasive predators. The impact of littoral predator introductions on pelagic consumers is likely to depend on the food web structure prior to invasion. For example, in lakes containing pelagic prey fish species (such as cisco, smelt or lake whitefish), introduction of a littoral predator may still reduce the flux of food resources from littoral habitats to a pelagic predator, while having virtually no impact on the trophic position of the pelagic predator. Alternatively, our study lakes lack pelagic prey fish species, so that bass invasion contributes to a reduction in lake trout trophic position as well as the magnitude of littoral-pelagic coupling. The present study shows that subsidies of resources from other systems or habitats can be both energetically significant and play an important role in food web dynamics, particularly in maintaining top-down food web regulation (Polis and Strong 1996). In the present study, the pelagic predator, lake trout, was sustained primarily by littoral-derived production. Ongoing research in these systems is showing that these documented bass-induced food web shifts are exerting dramatic and detrimental impacts on lake trout growth rates and fecundity (Brown and Casselman, *unpublished manuscript*).

Predicting the impact of perturbations on natural food webs presents a formidable challenge to ecology. It is increasingly recognized that broad-scale, ecosystem-level approaches (both experimental and comparative) are crucial, and even uniquely required to understand and predict ecosystem-level processes (Carpenter et al. 1995; Schindler 1998). This study demonstrates how the use of stable isotopes can provide time-integrated and energy-based depictions of food web structure. In fact, this isotopic approach provides a very sensitive indicator of environmental change that can be used to quantify the impacts of a broad range of anthropogenic activities on food web structure and the pathways of energy flow in natural ecosystems.

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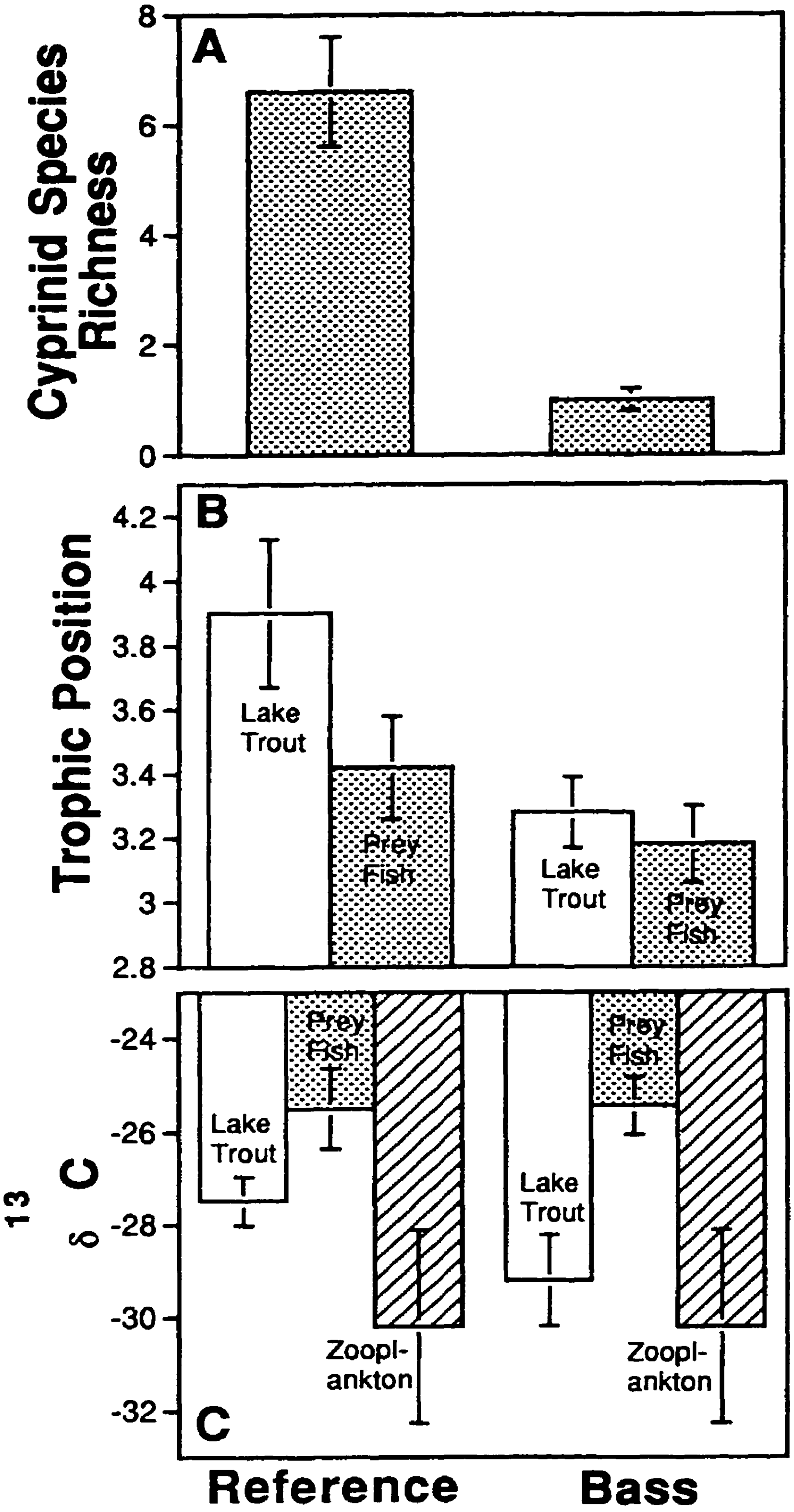
Table 1. Cyprinid community and stable isotope data from the nine Ontario lakes used in this analysis.

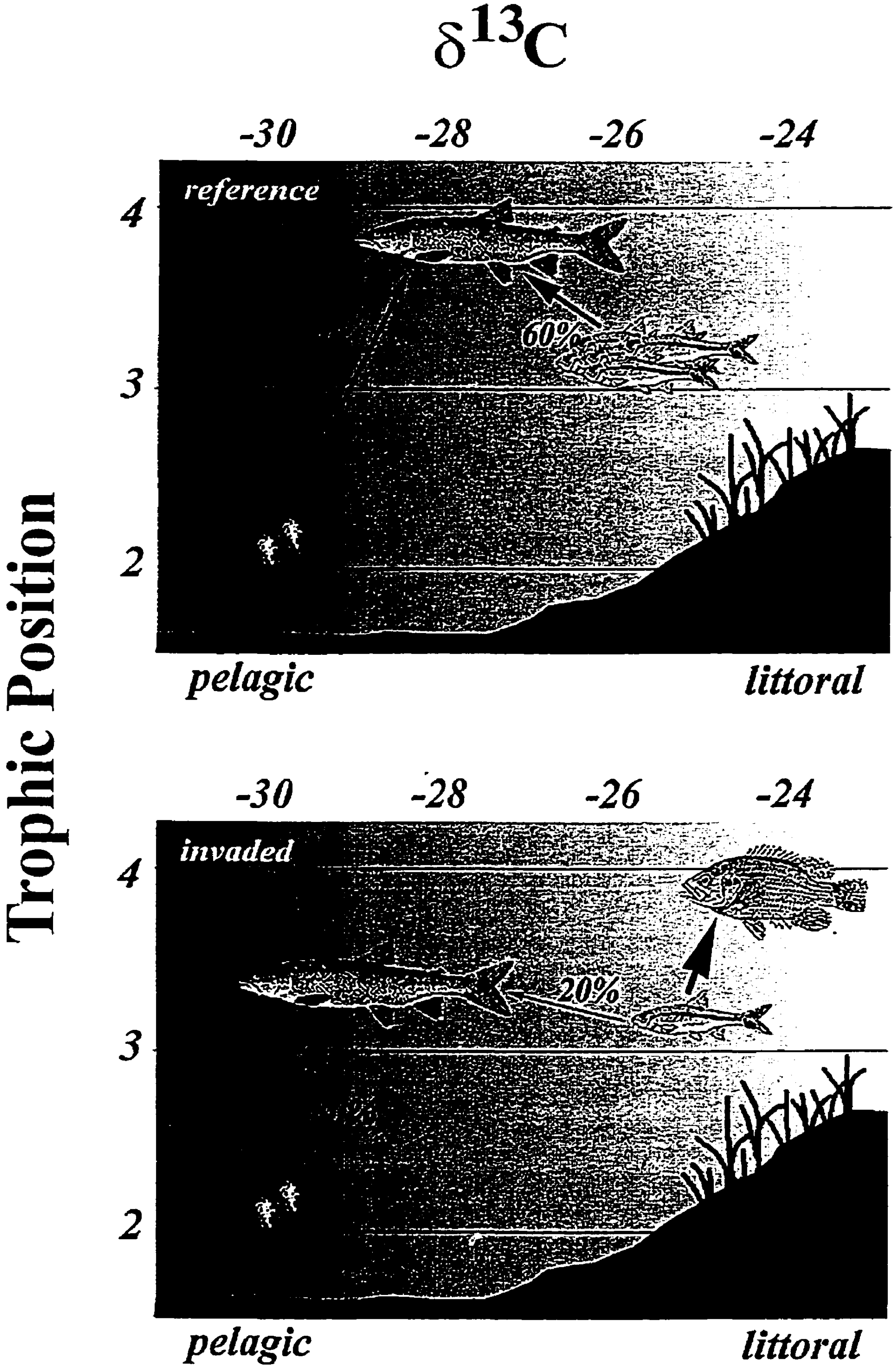
Lake	# of cyprinid species	Lake trout Trophic Position (± 1 SD)	Prey fish Trophic Position (± 1 SD)	Lake Trout diet % fish	Lake Trout diet % zoopl.	Lake trout $\delta^{13}C$ (‰) (± 1 SD)	Prey fish $\delta^{13}C$ (‰) (± 1 SD)	Lake Trout diet % littoral	Lake Trout diet % pelagic
Unimpacted									
Louisa	9	4.82 (0.25)	3.84 (0.52)	99	1	- 25.82 (0.35)	- 25.31 (2.15)	90	10
Havelock	5	3.73 (0.07)	3.01 (0.30)	70	30	- 27.77 (0.60)	- 27.63 (1.41)	93	7
Source	6	3.60 (0.26)	3.21 (0.22)	46	54	- 28.26 (1.12)	- 26.54 (0.87)	53	47
Clean	6	3.82 (0.18)	3.76 (0.26)	44	56	- 26.75 (0.98)	- 22.45 (1.33)	44	56
MacDonald (80's)	7	3.55 (0.14)	3.26 (0.22)	40	60	- 28.79 (1.25)	- 25.60 (4.24)	31	69
mean	**6.6**	**3.90**	**3.42**	**60**	**40**	**-27.48**	**-25.50**	**62**	**38**
Impacted									
MacDonald (90's)	2	3.11 (0.21)	3.26(0.22)	3	97	- 29.55 (1.02)	- 25.60 (4.24)	14	86
Dickie	1	3.18 (0.39)	2.92 (0.07)	12	88	- 32.59 (1.43)	- 27.49 (0.90)	0	100
Johnson	1	3.71 (0.29)	3.55 (-)	43	57	- 26.62 (1.26)	- 23.65 (-)	55	45
Kelly	1	3.29 (0.34)	3.23 (0.30)	18	82	- 28.83 (0.93)	- 25.40 (2.32)	28	72
Happy Isle	0	3.12 (0.33)	2.93 (.01)	5	95	- 28.39 (1.49)	- 25.02 (0.41)	35	65
mean	**1**	**3.28**	**3.18**	**16**	**84**	**-29.20**	**-25.43**	**26**	**74**

Figure 1. A) Invaded lakes had reduced cyprinid species richness relative to reference lakes (Student's t-test, $n = 10$, $t = 7.48$, DF = 8, $p < 0.001$). B) Lake trout from lakes invaded by bass had lower average trophic positions compared to reference lakes (t-test, $n = 10$, $t = 2.40$, DF = 8, $p = 0.043$). C) Lake trout from bass-invaded lakes also had more negative $\delta^{13}C$ values (t-test, $n = 10$, $t = 1.55$, DF = 8, $p = 0.16$). Error bars represent 1 standard error of the mean using lake-specific averages.



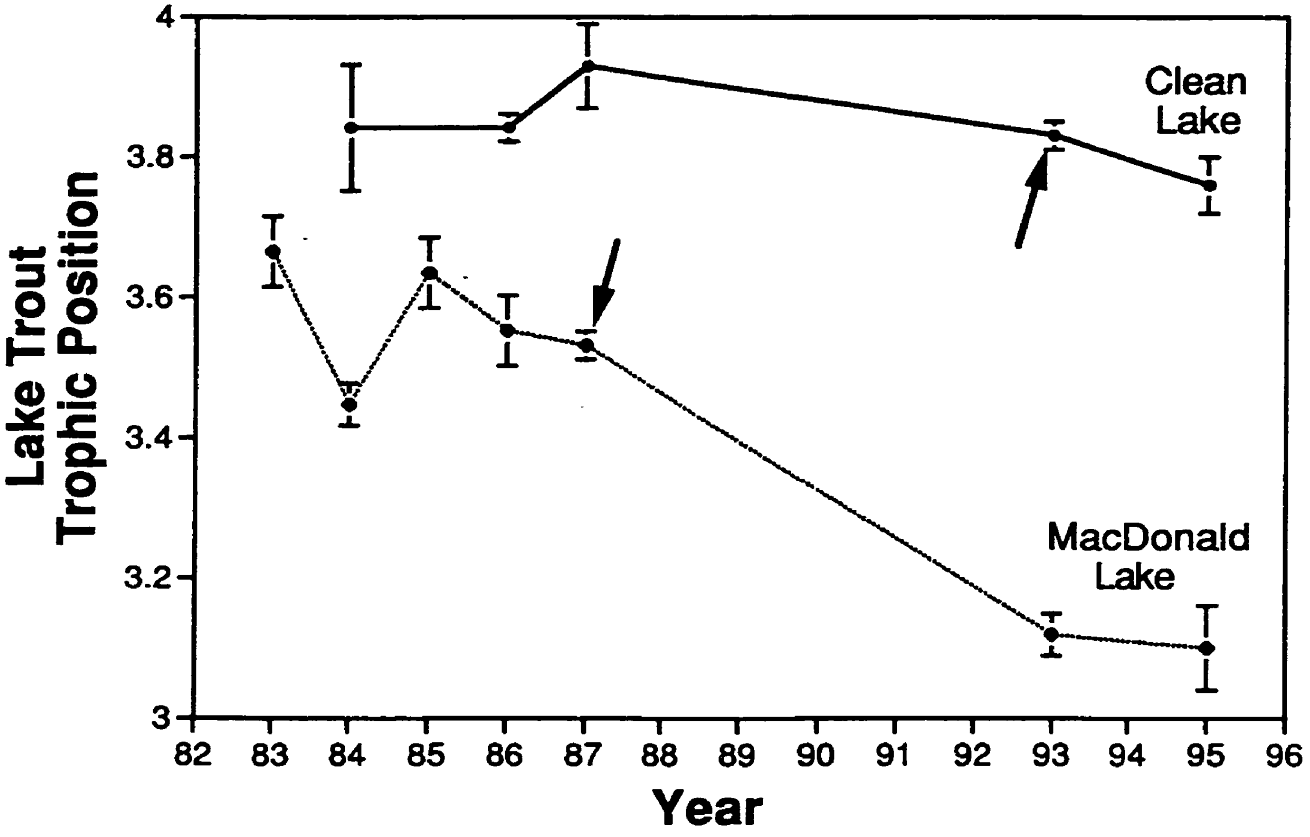
A
Cyprinid Species Richness
0
2
4
6
8
B
Trophic Position
2.8
3
3.2
3.4
3.6
3.8
4
4.2
Lake Trout
Prey Fish
Lake Trout
Prey Fish
C
δ 13 C
-24
-26
-28
-30
-32
Lake Trout
Prey Fish
Zoopl-ankton
Lake Trout
Prey Fish
Zoopl-ankton
Reference
Bass

Figure 2. The mean pathways of energy flow through the food web of reference lakes (lakes in which bass have not become established), and lakes invaded by bass, based on $\delta^{15}N$-based estimates of trophic position and $\delta^{13}C$ evidence.



$\delta^{13}C$
-30
-28
-26
-24
reference
4
3
2
60%
pelagic
littoral
-30
-28
-26
-24
invaded
4
3
2
20%
pelagic
littoral
Trophic Position

Figure 3. Temporal changes in the trophic position of lake trout from MacDonald Lake and Clean Lake for the period 1983-1995. Bold arrows indicate the year in which both smallmouth and rock bass became fully established.


Lake Trout Trophic Position
4
3.8
3.6
3.4
3.2
3
82
83
84
85
86
87
88
89
90
91
92
93
94
95
96
Year
Clean Lake
MacDonald Lake

GENERAL CONCLUSIONS

Attempts to understand both natural and agricultural ecosystems too often neglect to consider that each species is embedded in an intricate and variable food web context (Pimm 1991). Ultimately, studies of ecosystems that fail to consider these food web interactions will meet with limited success. Yet despite the potential importance of food webs, current food webs paradigms are problematic: food chain models (assuming species conform to discrete trophic levels) provide overly-simplistic depictions of food webs (Polis 1994), while classical food web approaches are highly subjective and fail to consider the importance of trophic linkages (Polis 1991).

This thesis adopts an integrative approach to quantify trophic structure by using the concept of trophic position as the basis for analysis of food web patterns (Adams et al. 1983; Cabana and Rasmussen 1996). Both dietary and stable isotope-based methods were successfully used to quantify food web structure for examining environmental problems. Chapter 1 used dietary data to estimate trophic position and to quantify the bioaccumulation of PCBs in pelagic food webs. The importance of food web structure in determining contaminant levels in top predators was evident in this study: over 80% of the among-system variation in PCB levels in lake trout was explained by a trophic position variable.

The stable isotope measure of trophic position was also useful for quantifying trophic structure. Chapter 3 developed a method to estimate trophic position that accounts for within- and among-system variation in $\delta^{15}N$ at the base of the food web. In Chapters 4 and 5, broad-scale patterns in trophic position of lake trout were examined, revealing that food chain length was closely correlated with lake variables such as species richness and lake area. Finally, in chapter 6, stable isotopes were used to quantify the impacts of bass invasions on pelagic food webs. In many lakes, lake trout relied on littoral-derived production, although the introduction of bass greatly reduced the magnitude of this littoral-pelagic coupling. Ongoing work is demonstrating that this food web shift is likely to have serious consequences for native lake trout populations. This component of the thesis demonstrates the potential uses of food web and stable isotope analyses for quantifying impacts of anthropogenic activities on aquatic ecosystems.

Not only does the approach used in this thesis provide an integrative and repeatable measure of food web structure, but it seems that application of food web approaches will lead to significant progress in our understanding and quantification of human impacts on the environment and natural ecosystems (Pimm 1991). These are issues that ecologists are increasingly called upon to address (Ehrlich and Daily 1991); the approaches to studying aquatic ecosystems presented here will provide a valuable contribution to this end.

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APPENDIX 1: Conversion equations used in Chapter 1 to convert dietary data into percent volume format.

Dietary studies generally present results in one of three data formats; percent of total volume, percent frequency of occurrence, or percent of total numbers. The percent volume (considered equivalent to percent weight) format was chosen over the other methods because volume was the most frequently reported format and best represents the contribution of a prey item to the diet of a population (Hyslop 1982). Studies that did not report results in a percent volumetric format were converted into percent volume using one of the three following methods.

When data were reported as percent of total numbers of organisms, they were converted to percent volume using the following formula:

$$Vp_i = (N_i * wt_i) / wt_a \qquad (1)$$

Where for prey item (i), Vp=% volume of prey item, N=% of total number, wt=estimate of prey weight, wt_a=weight of all prey items. Prey weight data were taken from the literature source, or were estimated from a literature compilation of invertebrate body sizes (J. Vander Zanden, unpubl. data).

Percent frequency of occurrence data was converted to percent volume using empirical conversion equations. Detailed lake trout stomach analysis data was obtained from Ontario Ministry of Natural Resources data files (included number, identity, and weight of prey items for each stomach) for 6 Class 1 lakes. This data set was used to compute the mean weight of each prey item when that prey item occurs in a fish stomach. The weight of fish was set to equal 1.0 gram; zooplankton = 0.14 gram; zoobenthos = 0.23 gram (3). Knowledge of the mean weight of prey (when present) allowed estimation of % total weight for each prey item.

$$Vp_i = (f_i * wt_i) / wt_a \qquad (2)$$

Where for prey item (i), Vp=% volume of prey item, f=frequency of occurrence of prey type, wt=mean weight when item present (1, 0.14, or 0.23), wt_a=total weight of all prey items. Application of this conversion ratio to Class 1 lakes gave less than 4% error on estimates of volumetric contribution of lake trout prey items.

Detailed lake trout diet data was not available from Class 2 and 3 lakes, requiring an alternate technique to convert percent frequency into percent volume. Data from ten papers that included percent frequency of occurrence and percent volume for piscivorous fish species (lake trout, burbot, smallmouth bass) were assembled (Tester 1932; VanOosten and Deason 1938; Doan 1940; Leonard and Leonard 1949; Kimsey 1960; Rawson 1961; Dryer et al. 1965; Bailey 1972; Swedburg and Peck 1984; Eck and Wells 1986). The % frequency and % volume observations of this data set were used to develop empirical relationships between percent frequency of occurrence and percent volume of a prey item. The following relationship was found between % volume and % frequency of occurrence.

$$\%\ \text{Volume} = -1.52\ (+/-0.98) + 0.80\ (+/-\ 0.02)\ \%\ \text{Frequency}$$

$$r^2 = 0.67 \qquad n = 578 \qquad SE_{est} = 16.43 \qquad (3)$$

Predictive power of the model was greatly increased when an interaction of % frequency and an estimate of log (predator/prey body weight ratio) was used as a second predictor variable. The final conversion equation is:

$$\%\ \text{Volume} = -\ 0.62\ (+/-\ 0.71) + 1.13\ (+/-\ 0.04)\ \%\ \text{Frequency} - 0.27\ (+/-\ 0.01)$$

$$\%\ \text{Frequency} * \log\ (\text{predator/prey body weight ratio})$$

$$r^2 = 0.83 \qquad n = 578 \qquad SE_{est} = 11.93 \qquad (4)$$

Percent frequency of occurrence data was converted to a percent volume format using Eq. 4. Volumes were scaled to sum to 100% and were included in the data set. Since each converted estimate is accompanied by 12% error, and converted data makes up 24% of the observations, the total error associated with use of this conversion is 2.9%.

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APPENDIX 2: Pelagic forage fish dietary data from from North American lakes. The following variables are listed: lake, data conversion, year, sample size, diet breakdown (percent of total volume), trophic position (T.P.), and references.

				% Volume contribution						
Lake	Data*	Year	N	Pla	Mys	Ben	Amp	Fis	T.P.	Ref†
ALEWIFE										
CLASS 2										
Black Pond	b	66	52	84.5	0.0	15.5	0.0	0.0	3.00	1
Clayton	a	78	533	54.7	0.0	16.8	0.0	28.5	3.29	2
Echo	a	67	211	89.1	0.0	10.9	0.0	0.0	3.00	3
N=3 LAKES				76.1	0.0	14.4	0.0	9.5	3.10	MEAN
N=796 FISH				18.7	0.0	3.1	0.0	16.5	0.16	SD
				10.8	0.0	1.8	0.0	9.5	0.10	SE
ALEWIFE										
CLASS 3										
Michigan	a	-	4205	71.2	1.5	4.9	22.5	0.0	3.24	4 thru 11
Ontario	a	72,88	-	83.1	12.4	0.0	4.5	0.0	3.17	98
Ontario	a	27	77	78.0	3.3	18.7	0.0	0.0	3.03	12
Upper Rideau	a	91	39	29.4	0.0	70.6	0.0	0.0	3.00	13
N=3 LAKES				65.4	4.3	23.5	6.7	0.0	3.11	MEAN
N=4321 FISH				24.5	5.6	32.4	10.7	0.0	0.11	SD
				12.3	2.8	16.2	5.4	0.0	0.1	SE
WHITEFISH										
CLASS 2										
Babine	a	46	39	8.9	0.0	90.2	0.0	0.9	3.01	14
Babine	a	46	121	3.6	0.0	96.2	0.2	0.0	3.00	14
Cree	a	55	50	0.0	0.0	66.7	2.1	31.3	3.33	15
Cree	a	55	50	5.6	0.0	72.2	22.2	0.0	3.22	15
Glacier	a	86	21	17.2	0.0	82.8	0.0	0.0	3.00	16
Hector	a	86	13	0.0	0.0	98.0	2.0	0.0	3.02	16
Heming	a	45	225	0.0	0.0	98.7	0.0	1.3	3.01	17
Morrison	a	46	95	94.8	0.0	5.2	0.0	0.0	3.00	14
Morrison	a	46	9	0.0	0.0	100	0.0	0.0	3.00	14
Pyramid	a	39-45	50	31.5	0.0	56.5	12.0	0.0	3.12	18
Pyramid	a	43	50	31.5	0.0	56.5	12.0	0.0	3.12	19
Shakespeare Island	a	27	76	39.5	0.0	42.4	17.5	0.5	3.18	20

				% Volume contribution						
Lake	Data*	Year	N	Pla	Mys	Ben	Amp	Fis	T.P.	Ref†
Sheep R.	b	73	190	0.0	0.0	100	0.0	0.0	3.00	21
Snake R.	b	70	250	0.0	0.0	93.9	0.0	6.1	3.06	22
Squanga	a	60	145	45.0	0.0	55.0	0.0	0.0	3.00	23
Trout	a	32	52	11.0	0.0	88.6	0.0	0.4	3.00	24
Waskesiu	a	27	50	0.0	0.0	100	0.0	0.0	3.00	25
Waterton	a	51	276	0.0	0.0	84.2	15.8	0.0	3.16	26
N=18 LAKES				16.0	0.0	77.1	4.7	2.3	3.07	MEAN
N=1762 FISH				24.8	0.0	25.8	7.5	7.4	0.10	SD
				5.9	0.0	6.1	1.8	1.7	0.02	SE
WHITEFISH										
CLASS 3										
Athabaska	a	45	30	0.0	0.0	56.6	43.4	0.0	3.43	30
Champlain	a	31	141	0.0	0.0	100	0.0	0.0	3.00	38
Great Bear	c	63-65	576	0.0	1.0	54.6	32.3	12.1	3.45	40
Great Bear Lake	a	45	86	11.0	0.0	75.0	14.0	0.0	3.14	28
Great Bear Lake	a	45	45	8.0	0.0	92.0	0.0	0.0	3.00	28
Great Slave	a	44-47	308	0.0	1.3	61.3	37.3	0.0	3.39	29,30
Keller	a	61-62	386	0.0	0.8	73.5	25.7	0.0	3.27	37
Lakelse	a	46	84	0.0	0.0	99.9	0.1	0.0	3.00	14
LaRonge	a	48-54	737	2.6	0.0	62.7	33.2	1.6	3.35	32
Michigan	a	72-74	640	0.0	0.0	97.7	1.6	0.6	3.02	31
Nipigon	a	21,27	382	0.0	3.1	73.3	20.4	3.2	3.27	25,33,34
Oneida	a	27	50	0.0	0.0	100	0.0	0.0	3.00	25
Ontario	a	27	45	0.0	3.3	17.8	78.9	0.0	3.82	20
Pagwashuan	a	27	8	0.0	0.0	86.5	13.5	0.0	3.14	20
Simcoe	a	27	174	0.9	1.8	58.8	3.1	35.4	3.40	20
Superior	a		60	6.3	15.0	18.7	60.0	0.0	3.75	27
Superior	a		72	26.9	24.2	39.1	3.0	6.7	3.34	27
Superior	a	52	116	37.4	0.3	12.0	50.3	0.0	3.51	35
Toolik	c	86	71	0.0	0.0	100	0.0	0.0	3.00	39
Winnipeg	a	27	536	0.0	0.0	69.7	30.3	0.0	3.30	36

				% Volume contribution						
Lake	Data*	Year	N	Pla	Mys	Ben	Amp	Fis	T.P.	Ref†
Wollaston	a	55	100	0.0	3.0	47.0	45.0	5.0	3.53	15
N=21 LAKES				4.4	2.6	66.5	23.4	3.1	3.29	MEAN
N=4647 FISH				9.9	6.0	28.1	23.1	8.0	0.25	SD
				2.2	1.3	6.1	5.0	1.7	0.05	SE
CISCO										
CLASS 2										
Black	a	32	71	89.1	0.0	10.9	0.0	0.0	3.00	41
Clear	a	32	225	98.0	0.0	2.0	0.0	0.0	3.00	41
Muskelunge	a	32	154	95.9	0.0	4.1	0.0	0.0	3.00	41
Pallette	a	31	23	96.2	0.0	3.8	0.0	0.0	3.00	41
Pallette	a	69	501	100	0.0	0.0	0.0	0.0	3.00	42
Silver	a	31	42	99.4	0.0	0.6	0.0	0.0	3.00	41
Swains	a	39	12	99.0	0.0	1.0	0.0	0.0	3.00	43
Trout	a	32	181	91.1	0.0	8.9	0.1	0.0	3.00	41
Waskesiu	a	27	100	56.4	0.0	43.6	0.0	0.0	3.00	25
N=9 LAKES				91.7	0.0	8.3	0.0	0.0	3.00	MEAN
N=1309 FISH				13.7	0.0	13.7	0.0	0.0	0.00	SD
				4.6	0.0	4.6	0.0	0.0	0.00	SE
CISCO										
CLASS 3										
Burnt Island	a	93	114	44.1	34.0	14.9	3.2	3.7	3.41	49
Great Bear Lake	a	45	135	74.5	15.0	10.0	0.0	0.5	3.16	28
Great Slave	a	44-47	378	60.6	28.3	10.1	1.0	0.0	3.29	29
Greenwich	a	93	27	100	0.0	0.0	0.0	0.0	3.00	49
Islet	a	93	118	20.3	54.9	17.6	3.8	3.3	3.62	49
Little Joe	a	93	102	2.7	80.7	3.0	13.7	0.0	3.94	49
Loch Erne	a	93	126	72.0	28.0	0.0	0.0	0.0	3.28	49
Michigan	a	54-80	6246	5.2	34.1	1.7	59.1	0.0	3.93	43,44,45
Nipigon	a	25	266	25.3	52.9	21.8	0.0	0.0	3.53	33,34,46
Nipissing	a	35	1446	73.4	10.4	16.2	0.0	0.0	3.10	50

				% Volume contribution						
Lake	Data*	Year	N	Pla	Mys	Ben	Amp	Fis	T.P.	Ref'
Ontario	a	25	258	4.2	49.9	13.0	33.0	0.0	3.83	46
S. Otterskin	a	93	175	24.5	2.7	7.8	62.8	2.1	3.68	49
Simcoe	a	27	31	81.0	0.0	19.0	0.0	0.0	3.00	25
Superior	a		836	73.5	17.6	3.0	5.9	0.0	3.24	27
Superior	a		333	91.4	3.3	2.4	3.0	0.0	3.06	27
Superior	a	50-65	936	45.7	30.0	10.8	13.4	0.1	3.44	47,48
N=16 LAKES				49.9	27.6	9.4	12.4	0.6	3.41	MEAN
N=11527 FISH				32.7	23.2	7.2	20.8	1.3	0.32	SD
				8.2	5.8	1.8	5.2	0.3	0.08	SE
SMELT										
CLASS 2										
Crystal	a	40	210	0.0	0.0	1.0	1.0	98.0	3.99	51
Devilfish	a	84	100	39.4	0.0	20.5	0.4	39.7	3.40	54
Echo	a	67	67	65.2	0.0	34.8	0.0	0.0	3.00	52
Gull	a	65	308	66.7	0.0	31.5	0.0	1.8	3.02	53
West Bearskin	a	84	100	39.4	0.0	20.5	0.4	39.7	3.40	54
N=5 LAKES				42.1	0.0	21.7	0.4	35.8	3.36	MEAN
N=785 FISH				27.0	0.0	13.2	0.4	39.8	0.40	SD
				12.1	0.0	5.9	0.2	17.8	0.18	SE
SMELT										
CLASS 3										
12 mile	c	84	100	17.7	5.5	49.0	0.9	26.9	3.33	55
Huron	a	47	300	0.0	82.0	9.0	0.0	9.0	3.91	57
Huron, Saginaw	a	56	3390	14.5	20.1	44.1	1.0	20.3	3.41	58
Memphremagog	a	94	50	11.0	0.0	0.0	0.0	89.0	3.89	59
Michigan	c	33	3015	0.8	77.1	2.0	11.1	9.0	3.97	56
Michigan	a	82	1497	8.0	37.3	9.9	3.6	41.1	3.82	60,61,62
N. Memphremagog	a	72	373	2.0	0.0	55.5	0.0	42.5	3.43	62
Ontario	a	84	2559	0.0	67.9	0.0	0.0	32.1	4.00	63
S. Memphremagog	a	72	135	0.0	0.0	16.1	0.0	83.9	3.84	62

				% Volume contribution						
Lake	Data*	Year	N	Pla	Mys	Ben	Amp	Fis	T.P.	Ref†
Simcoe	a	70	1416	68.5	0.0	21.1	2.6	7.7	3.10	64
Superior	a		490	50.6	40.6	1.3	7.6	0.0	3.48	27
Superior	a		1205	25.6	53.9	2.0	16.0	2.6	3.72	27
N=12 LAKES				16.6	32.0	17.5	3.6	30.3	3.66	MEAN
N=14530 FISH				22.0	32.1	20.5	5.3	29.8	0.29	SD
				6.4	9.3	5.9	1.5	8.6	0.09	SE
STICKLEBACK										
CLASS 3										
Nipigon	a	21	58	58.9	0.0	41.1	0.0	0.0	3.00	34
Superior	a		295	21.3	15.9	1.6	61.2	0.0	3.77	27
N=2 LAKES				40.1	8.0	21.3	30.6	0.0	3.39	MEAN
N=353 FISH				26.6	11.3	27.9	43.3	0.0	0.55	SD
				18.8	8.0	19.8	30.6	0.0	0.39	SE
TROUT-PERCH										
CLASS 3										
Erie	a	75	100	22.9	16.9	60.2	0.0	0.0	3.17	65
Erie	a	75	100	34.1	4.9	61.0	0.0	0.0	3.05	65
Nipigon	a	21	9	0.0	0.0	68.4	31.6	0.0	3.32	34
Nipigon	a	21	29	2.0	0.0	97.1	0.9	0.0	3.01	33
Superior	a		349	6.8	21.2	20.9	51.0	0.0	3.72	27
N=5 LAKES				13.2	8.6	61.5	16.7	0.0	3.25	MEAN
N=787 FISH				14.8	9.9	27.2	23.5	0.0	0.29	SD
				6.6	4.4	12.2	10.5	0.0	0.13	SE
SCULPIN										
CLASS 2										
New York	a	33	155	0.0	0.0	81.2	15.0	3.8	3.19	66
New York	a	33	730	0.0	0.0	97.2	2.2	0.6	3.03	66
New York	a	33	515	0.0	0.0	99.1	0.2	0.7	3.01	66
South Flor R.	a	66	300	0.0	0.0	99.7	0.2	0.2	3.00	67

				% Volume contribution						
Lake	Data*	Year	N	Pla	Mys	Ben	Amp	Fis	T.P.	Ref†
Toolik	a	80-82	51	2.4	0.0	95.7	0.0	0.0	2.96	70
Valley Cr.	a	70	116	0.0	0.0	69.8	30.2	0.0	3.30	68
Valley Cr.	a	70	326	0.0	0.0	50.6	49.4	0.0	3.49	68
W. Gallatin R.	a	50-51	783	0.0	0.0	100	0.0	0.0	3.00	69
N=17 LAKES				0.3	0.0	86.6	12.2	0.7	3.12	MEAN
N=4335 FISH				0.8	0.0	18.2	18.5	1.3	0.19	SD
				0.2	0.0	4.3	4.4	0.3	0.04	SE
SCULPIN										
CLASS 3										
Michigan	a	82	240	0.0	3.2	56.0	40.8	0.0	3.44	72
Nipigon	a	21	12	0.0	2.1	38.1	59.8	0.0	3.62	34
Superior	a		709	2.6	5.1	6.7	85.6	0.0	3.91	27
Superior	a		139	3.5	10.7	4.9	80.9	0.0	3.92	27
Superior	a		120	0.9	38.9	0.2	60.1	0.0	3.99	27
Washington	b	62	866	28.7	31.5	39.8	0.0	0.0	3.32	71
N=6 LAKES				6.0	15.2	24.3	54.5	0.0	3.70	MEAN
N=2086 FISH				11.2	15.9	23.3	31.2	0.0	0.28	SD
				4.6	6.5	9.5	12.8	0.0	0.11	SE

†1=Huchinson 1971; 2=Kohler 1980; 3=Lackey 1969; 4=Hewett and Stewart 1989; 5=Janssen and Brandt 1980; 6=Crowder 1980; 7=Wells 1970; 8=Morsell and Norden 1968; 9=Norden 1968; 10=Evans 1986; 11=Rhodes and McComish 1975; 12=Pritchard 1929; 13=Krishka 1991; 14=Godfrey 1955; 15=Rawson 1959; 16=Donald and Alger 1993; 17=Watson 1963; 18=Rawson and Elsey 1950; 19=Rawson 1948; 20=Hart 1931; 21=Thompson 1971; 22=Pontius 1976; 23=Lindsay 1963; 24=Couey 1931; 25=Rawson 1930; 26=Cuerrier and Schultz 1957; 27=Anderson and Smith Jr. 1971; 28=Kennedy 1949; 29=Rawson 1951; 30=Larkin 1948; 31=Armstrong et al. 1977; 32=Qadri 1961; 33=Clemens et. al. 1923; 34=Clemens et. al. 1924; 35=Eschmeyer 1954; 36=Bajkov 1930; 37=Johnson 1972; 38=Van Oosten and Deason 1937; 39=Merrick et al. 1992; 40=Johnson 1975; 41=Engel 1976; 42=Brown and Moffett 1942; 43= Wells and Beeton 1963; 44=Crowder and Crawford 1984; 45=Crowder 1986; 46=Pritchard 1931; 47=Dryer and Beil 1964; 48=Dryer and Beil 1968; 49=Trippel and Beamish 1993; 50=Langford 1938; 51=Beckman 1942; 52=Lackey 1969; 53=Burbidge 1969; 54=Hassinger and Close 1984; 55=Loftus and Hulsman 1986; 56=Schneberger 1936; 57=Baldwin 1948; 58=Gordon 1961; 59=Vander Zanden 1994; 60=Stedman and Arglye 1985; 61=Foltz and Norden 1977; 62=Nakashima and Leggett 1975; 63=Brandt and Madon 1986; 64=MacCrimmon and Pugsley 1979; 65=Muth and Busch 1989; 66=Koster 1936; 67=Novak and Estes 1974; 68=Petrosky and Waters 1975; 69=Bailey 1952; 70=Hershey and McDonald 1985; 71=Ikusemiju 1975; 72=Wojcik 1986; 98=Mills et al. 1992.

*a=percent volume format reported; b=percent of total number converted to percent volume using equation 6; c=percent frequency of occurence converted to percent volume using equation 7; d=percent frequency of occurence converted to percent volume using equation 9.

APPENDIX 3: Lake trout dietary data from North American lakes. The following variables are listed: lake, data type, latitude, longitude, lake area, mean annual air temperature, sample size, diet breakdown (percent of total volume), trophic position (T.P.), and references.

				area			% Volume contribution													
Lake	Data*	Lat	Long	(km^2)	Temp	N	Pla	Mys	Ben	Amp	Fis	ale	cis	cot	lit	pel	sme	whi	T.P.	References[1]
CLASS 1																				
(Warm water lakes; winter data)																				
Boot	d	4536	7811	0.9	2.5	15	1.1	0.0	3.7	0.0	95.2	0.0	0.0	0.0	95.2	0.0	0.0	0.0	3.95	73
Booth	d	4539	7812	4.9	2.5	5	0.0	0.0	0.0	0.0	100.0	0.0	0.0	0.0	100	0.0	0.0	0.0	4.00	73
Deer	d	4502	7806	1.9	4.5	58	15.5	0.0	0.7	0.0	83.8	0.0	0.0	0.0	83.8	0.0	0.0	0.0	3.84	74
Faraday	d	4504	7755	1.1	4.5	37	16.5	0.0	8.6	0.0	74.9	0.0	0.0	0.0	74.9	0.0	0.0	0.0	3.75	74
Fraser	d	4531	7819	0.5	2.5	8	0.0	0.0	12.1	0.0	87.9	0.0	0.0	0.0	87.9	0.0	0.0	0.0	3.88	73
Grace	d	4504	7814	2.3	4.5	50	18.4	0.0	3.8	0.0	77.9	0.0	0.0	0.0	77.9	0.0	0.0	0.0	3.78	74
Lobster	d	4532	7812	1.3	2.5	3	0.0	0.0	0.0	0.0	100.0	0.0	0.0	0.0	100	0.0	0.0	0.0	4.00	73
Shirley	d	4541	7808	4.8	2.5	5	0.0	0.0	9.1	0.0	90.9	0.0	0.0	0.0	90.9	0.0	0.0	0.0	3.91	73
Sylvia	d	4532	7820	0.4	2.5	5	0.0	0.0	44.4	0.0	55.6	0.0	0.0	0.0	55.6	0.0	0.0	0.0	3.56	73
Two rivers	d	4535	7829	2.9	2.5	6	0.0	0.0	0.0	0.0	100.0	0.0	0.0	0.0	100	0.0	0.0	0.0	4.00	73
N=10 lakes							5.1	0.0	8.2	0.0	86.6	0.0	0.0	0.0	86.6	0.0	0.0	0.0	3.87	MEAN
N=192 fish							2.6	0.0	4.3	0.0	4.5	0.0	0.0	0.0	4.5	0.0	0.0	0.0	0.04	SE
							8.1	0.0	13.5	0.0	14.2	0.0	0.0	0.0	14.2	0.0	0.0	0.0	0.14	SD

				area			% Volume contribution													
Lake	Data*	Lat	Long	(km²)	Temp	N	Pla	Mys	Ben	Amp	Fis	ale	cis	cot	lit	pel	sme	whi	T.P.	References¹
CLASS 1																				
(Warm water lakes)																				
Anstruther	a,d	4445	7812	6.3	4.5	729	2.7	0.0	8.9	0.0	88.4	0.0	0.0	0.0	88.4	0.0	0.0	0.0	3.88	74
Ashby	d	4505	7721	2.6	4.5	20	44.2	0.0	0.0	0.0	55.8	0.0	0.0	0.0	55.8	0.0	0.0	0.0	3.56	74
Aubin	d	4658	7300	1.4	2.5	22	8.9	0.0	14.6	0.0	76.4	0.0	0.0	0.0	76.4	0.0	0.0	0.0	3.76	77
Baude	d	4705	7318	3.2	2.5	81	31.1	0.0	51.1	0.0	17.8	0.0	0.0	0.0	17.8	0.0	0.0	0.0	3.18	77
Bay	d	4501	7752	0.8	4.5	35	8.6	0.0	16.2	0.0	75.2	0.0	0.0	0.0	75.2	0.0	0.0	0.0	3.75	74
Birch	a	4240	8310	1.3	9.7	25	0.0	0.0	11.7	0.0	88.3	0.0	0.0	0.0	88.3	0.0	0.0	0.0	3.88	78
Brewer	d	4535	7819	0.4	2.5	222	10.7	0.0	1.9	0.0	87.4	0.0	0.0	0.0	87.4	0.0	0.0	0.0	3.87	73
Canisbay	d	4534	7835	1.5	2.5	279	19.2	0.0	8.9	0.0	71.9	0.0	0.0	0.0	71.9	0.0	0.0	0.0	3.72	73
Carignan	d	4710	7245	5.2	2.5	72	11.2	0.0	28.6	0.0	60.2	0.0	0.0	0.0	60.2	0.0	0.0	0.0	3.60	77
Cinconsine	d	4720	7304	12.7	2.5	33	13.0	0.0	26.7	0.0	60.3	0.0	0.0	0.0	60.3	0.0	0.0	0.0	3.60	77
Costello	d	4535	7819	0.3	2.5	59	31.1	0.0	4.5	0.0	64.3	0.0	0.0	0.0	64.3	0.0	0.0	0.0	3.64	73
Dickie	a	4447	7744	2.1	4.5	300	30.6	0.0	12.7	12.9	43.9	0.0	0.0	0.0	41.1	2.9	0.0	0.0	3.57	74
Eels	a,d	4454	7808	9.5	4.5	176	1.4	0.0	15.3	0.0	83.3	0.0	0.0	0.0	83.3	0.0	0.0	0.0	3.83	74
Farquar	a,d	4505	7812	3.4	4.5	72	14.7	0.0	5.3	0.0	79.9	0.0	0.0	0.0	79.9	0.0	0.0	0.0	3.80	74
L'amable	d	4501	7749	1.8	4.5	26	5.8	0.0	52.7	0.0	41.5	0.0	0.0	0.0	41.5	0.0	0.0	0.0	3.41	74
Louisa	d	4528	7829	4.9	2.5	487	16.5	0.0	7.4	0.0	76.1	0.0	0.0	0.0	76.1	0.0	0.0	0.0	3.76	75

				area			% Volume contribution													
Lake	Data*	Lat	Long	(km^2)	Temp	N	Pla	Mys	Ben	Amp	Fis	ale	cis	cot	lit	pel	sme	whi	T.P.	References[1]
Louisa	a	4528	7829	4.9	2.5	205	43.0	0.0	8.0	0.0	49.0	0.0	0.0	0.0	49.0	0.0	0.0	0.0	3.49	76
Miette	a	5300	11837	0.1	-2.5	23	0.0	0.0	100.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.00	16
Norman	d	4705	7314	9.2	2.5	112	37.8	0.0	62.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.00	77
Sassenach	a	5314	11823	0.1	-2.0	49	15.6	0.0	84.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.00	16
Silent	d	4455	7804	1.2	4.5	87	3.0	0.0	22.7	0.0	74.3	0.0	0.0	0.0	74.3	0.0	0.0	0.0	3.74	74
Sincennes	d	4730	7352	13.5	2.5	7	16.2	0.0	37.4	0.0	46.4	0.0	0.0	0.0	46.4	0.0	0.0	0.0	3.46	77
Tallan	d	4451	7803	0.5	4.5	8	0.0	0.0	61.7	0.0	38.3	0.0	0.0	0.0	38.3	0.0	0.0	0.0	3.38	74
Weslemkoon	d	4502	7725	10.0	4.5	95	46.3	0.0	32.0	0.0	21.7	0.0	0.0	0.0	21.7	0.0	0.0	0.0	3.22	74
Wollaston	a,d	4452	7749	2.0	4.5	363	24.0	0.0	10.9	0.0	65.1	0.0	0.0	0.0	65.1	0.0	0.0	0.0	3.65	74
N=26 lakes							17.4	0.0	27.4	0.5	54.6	0.0	0.0	0.0	54.5	0.1	0.0	0.0	3.55	MEAN
N=3587 fish							2.9	0.0	5.3	0.5	5.5	0.0	0.0	0.0	5.6	0.1	0.0	0.0	0.06	SE
							14.7	0.0	26.8	2.6	28.3	0.0	0.0	0.0	28.3	0.6	0.0	0.0	0.28	SD
CLASS 2																				
(Cold water lakes)																				
Caniapiscau	a	5410	6950		-5.5	105	0.0	0.0	8.1	0.0	92.7	0.0	0.0	0.0	0.0	43.5	0.0	49.2	3.98	80
Grande Riviere	a	5300	7500		-5.0	145	0.0	0.0	2.2	0.0	97.8	0.0	18.4	0.0	0.0	10.9	0.0	68.5	4.03	80
Minnewanka	c	5115	11520	22.1	-3.0	169	0.0	0.0	20.8	4.1	75.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.87	79

				area			% Volume contribution													
Lake	Data*	Lat	Long	(km^2)	Temp	N	Pla	Mys	Ben	Amp	Fis	ale	cis	cot	lit	pel	sme	whi	T.P.	References[1]
Toolik	b	7000	14900	1.5	-10.0	104	14.1	0.0	76.7	0.0	8.9	0.0	0.0	8.9	0.0	0.0	0.0	0.0	3.09	39
N=4 lakes							3.5	0.0	27.0	1.0	68.6	0.0	4.6	2.2	0.0	13.6	0.0	29.4	3.74	MEAN
N=523 fish							3.5	0.0	17.0	1.0	20.5	0.0	4.6	2.2	0.0	10.3	0.0	17.4	0.22	SE
							7.1	0.0	34.1	2.1	41.0	0.0	9.2	4.5	0.0	20.6	0.0	34.9	0.44	SD
CLASS 2																				
(Warm water lakes)																				
Babine	a	5445	12600	446.7	-1.0	53	0.2	0.0	1.1	0.0	98.7	0.0	14.3	7.1	0.0	77.3	0.0	0.0	3.99	14
Chandos	c	4449	7800	13.9	4.5	128	1.3	0.0	2.3	0.0	96.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.06	74
Devilfish	a			1.6	3.0	200	0.0	0.0	2.5	0.0	97.5	0.0	0.0	0.0	0.0	0.0	97.5	0.0	4.37	54
Donner	a	3925	12005	3.0	4.4	44	0.0	0.0	0.3	0.0	99.7	0.0	0.0	1.2	2.4	96.0	0.0	0.0	4.00	82
Drag	a	4504	7823	10.0	4.5	121	0.0	0.0	20.0	10.0	70.0	0.0	20.0	0.0	50.0	0.0	0.0	0.0	3.80	74
Flathead	a	4755	11407	1170.0	5.6	201	0.1	0.0	0.2	0.1	100.0	0.0	0.0	0.0	0.0	26.5	0.0	73.5	4.06	16
Glacier	a	5155	11651	1.6	-1.0	35	21.7	0.0	52.5	0.0	25.8	0.0	0.0	0.0	0.0	0.0	0.0	25.8	3.28	16
Hector	a	5135	11621	5.9	-1.5	56	13.7	0.0	51.9	29.1	5.3	0.0	0.0	0.0	0.0	0.0	0.0	5.3	3.35	16
Koshlong	a	4458	7829	4.0	4.5	150	0.3	0.0	7.7	0.0	91.9	0.0	0.0	0.0	74.1	0.0	17.8	0.0	3.99	74
Limerick	a	4453	7737	8.3	4.5	21	1.0	0.0	14.0	0.0	85.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.94	74
Morrison	a	5514	12622	14.6	-1.0	23	0.0	0.0	0.1	0.0	99.9	0.0	0.0	2.7	3.5	93.8	0.0	0.0	4.00	14
Opeongo	a	4542	7823	51.5	2.5	17171	0.0	0.0	2.0	0.0	98.0	0.0	0.0	0.4	21.5	8.1	0.0	68.0	4.03	81

Lake	Data*	Lat	Long	area (km²)	Temp	N	% Volume contribution Pla	Mys	Ben	Amp	Fis	ale	cis	cot	lit	pel	sme	whi	T.P.	References¹
Opeongo	a	4542	7823	51.5	2.5		0.0	0.0	0.6	0.0	99.4	0.0	38.3	0.4	1.7	1.8	0.0	57.2	4.03	81
Papineau	c	4521	7749	8.3	4.5	21	0.0	0.0	2.4	0.0	97.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.07	74
Pyramid	a	5555	11806	1.3	0.0	50	2.1	0.0	47.9	42.6	7.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.28	18
Redrock	a	4546	7828	2.9	2.5	214	0.0	0.0	25.6	0.0	74.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.82	76
Shabomeka	c	4454	7708	2.7	4.5	46	0.0	0.0	7.6	0.0	92.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.02	74
Southesk	a	5238	11712	1.7	-0.5	22	1.1	0.0	40.4	28.1	30.3	0.0	0.0	0.0	0.0	0.0	0.0	30.3	3.61	16
Trout	a	4603	8935	20.8	5.8	22	0.0	0.0	0.0	0.0	100.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.10	24
West Bearskin	a			2.0	3.0	200	0.0	0.0	12.5	0.0	87.5	0.0	0.0	0.0	0.0	0.0	87.5	0.0	4.23	54
Waterton	c	4900	11330	9.4	2.5	337	0.0	0.0	37.5	7.1	55.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.68	79
Waterton	c	4900	11330	9.4	2.5	198	0.0	1.2	8.1	0.5	90.3	0.0	0.0	2.9	0.0	5.9	0.0	81.5	3.98	26
N=22 lakes							1.9	0.1	15.3	5.3	77.4	0.0	3.3	0.7	7.0	14.1	9.2	15.5	3.89	MEAN
N=19313 fish							1.1	0.1	4.0	2.5	6.7	0.0	2.0	0.4	4.0	6.7	5.8	5.9	0.06	SE
							5.3	0.3	18.6	11.9	31.5	0.0	9.3	1.7	18.8	31.2	27.3	27.8	0.29	SD
CLASS 3																				
(Cold water lakes)																				
Cree	a	5730	10630	1500 0	-4.5	100	0.0	0.0	5.0	0.0	95.0	0.0	71.3	0.0	0.0	0.0	0.0	23.8	4.31	15
Great Bear	c	6600	12200	30044.0	-9.5	1079	0.0	6.8	10.3	3.1	79.8	0.0	41.3	19.7	0.7	13.4	0.0	4.6	4.26	40
Great Bear	c	6600	12200	30044.0	-9.5	239	0.0	1.0	29.0	0.5	69.4	0.0	23.1	15.7	0.0	30.6	0.0	0.0	4.01	83

				area			% Volume contribution													
Lake	Data*	Lat	Long	(km^2)	Temp	N	Pla	Mys	Ben	Amp	Fis	ale	cis	cot	lit	pel	sme	whi	T.P.	References†
Great Slave	c	6200	11400	27195.0	-6.5	486	0.0	3.4	0.5	3.7	92.4	0.0	52.5	10.2	0.0	20.8	0.0	8.9	4.37	29
Keller	c	6350	12200	413.0	-7.8	224	0.0	0.8	26.7	0.6	71.9	0.0	23.4	21.4	0.0	26.0	0.0	1.0	4.06	37
La Ronge	c	5510	10500	900.0	-2.8	469	0.0	2.8	0.4	0.9	95.8	0.0	52.2	4.4	6.2	19.9	0.0	13.1	4.34	84
Wollaston	a	5815	10315	2000.0	-6.0	100	0.0	5.0	5.0	5.0	85.0	0.0	50.0	15.0	0.0	20.0	0.0	0.0	4.32	15
N=7 lakes							0.0	2.8	11.0	2.0	84.2	0.0	44.8	12.3	1.0	18.7	0.0	7.3	4.24	MEAN
N=2697 fish							0.0	0.9	4.5	0.7	4.1	0.0	6.5	3.0	0.9	3.7	0.0	3.3	0.05	SE
							0.0	2.5	12.0	1.9	10.9	0.0	17.2	7.9	2.3	9.8	0.0	8.8	0.14	SD
CLASS 3																				
(Warm water lakes)																				
12 Mile	a	4501	7843	3.4	4.5	150	0.0	3.6	0.4	0.0	96.4	0.0	6.8	0.0	7.7	0.0	81.9	0.0	4.58	74
Burnt Island	a	4847	9051	1.1	-1.5	90	0.0	6.4	1.7	0.0	91.9	0.0	38.4	27.3	26.2	0.0	0.0	0.0	4.33	49
Green	c	4349	8900	29.7	7.5	129	0.0	12.3	0.0	0.0	87.7	0.0	77.7	0.0	10.0	0.0	0.0	0.0	4.32	91
Greenwich	a	4848	8851	4.8	-0.3	203	0.0	18.4	2.6	0.0	79.0	0.0	52.0	6.2	2.2	18.6	0.0	0.0	4.29	49
Huron	c	4500	8230	59600.0	5.5	301	0.0	0.0	0.0	0.0	100.0	50.9	0.0	0.1	0.1	0.1	48.7	0.0	4.37	85
Islets	a	4913	9216	1.9	0.0	96	0.0	11.1	6.7	0.0	82.2	0.0	45.5	32.9	3.8	0.0	0.0	0.0	4.35	49
Keuka	a	4230	7705	65.0	8.3	29	0.0	0.0	1.0	0.0	99.0	95.0	0.0	4.0	0.0	0.0	0.0	0.0	4.10	86
Little Joe	a	5022	9327	2.2	-0.5	80	0.0	0.0	4.3	0.0	95.7	0.0	77.4	12.6	5.8	0.0	0.0	0.0	4.36	49
Loch Erne	a	4837	9021	1.7	-1.0	99	0.0	10.0	1.6	0.0	88.4	0.0	64.2	13.6	5.8	0.0	0.0	4.8	4.36	49

				area			% Volume contribution													
Lake	Data*	Lat	Long	(km^2)	Temp	N	Pla	Mys	Ben	Amp	Fis	ale	cis	cot	lit	pel	sme	whi	T.P.	References[1]
Memphremagog	a	4508	7216	150.0	4.5	250	0.0	0.0	0.0	0.0	100.0	0.0	0.0	3.0	1.0	0.0	96.0	0.0	4.65	96
Michigan	c	4400	8700	57800.0	5.5	479	0.0	0.0	0.0	0.0	100.0	69.8	0.0	3.5	2.4	2.0	22.1	0.0	4.24	90
Michigan	a	4400	8700	57800.0	5.5	254	0.0	0.0	0.0	0.0	100.0	53.2	0.8	34.8	1.9	0.0	9.3	0.0	4.36	87
Michigan	a	4400	8700	57800.0	5.5	2441	0.0	0.6	0.5	0.6	98.3	0.0	29.9	36.9	1.4	29.1	1.0	0.0	4.47	88
Nipigon	a	4902	8826	4850.0	-1.3	91	0.0	0.0	0.0	0.0	100.0	0.0	88.8	1.1	0.0	10.1	0.0	0.0	4.40	33,34
Ontario	c	4330	7800	18960.0	8.0	569	0.0	0.0	0.1	0.0	99.9	74.3	0.0	1.7	0.2	0.0	23.8	0.0	4.23	89
Ontario	c	4330	7800	18960.0	8.0	256	0.0	0.0	0.0	0.0	100.0	52.1	31.8	14.4	0.0	0.5	0.0	1.2	4.28	92
Ontario	a	4330	7800	18960.0	8.0	1863	0.0	0.0	0.0	0.0	100.0	36.2	0.0	22.0	0.4	0.0	41.4	0.0	4.46	93
Ontario	a	4330	7800	18960.0	8.0	1836	0.0	0.0	1.4	0.0	98.6	27.6	0.0	40.7	2.3	0.0	27.9	0.0	4.48	94
Ontario	a	4330	7800	18960.0	8.0	8233	0.0	0.0	3.6	0.0	96.4	24.3	0.0	40.7	2.6	0.0	28.8	0.0	4.46	95
South Otterskin	a	4913	9338	2.1	-0.3	85	0.0	0.0	0.6	0.0	99.4	0.0	73.0	8.8	17.6	0.0	0.0	0.0	4.35	49
Simcoe	a	4425	7920	728.0	5.3	50	0.0	0.0	0.0	0.0	100.0	0.0	90.9	0.0	2.0	4.0	0.0	3.0	4.39	25
Superior	a	4730	8700	82100.0	1.3	3642	0.0	9.5	0.5	1.1	88.9	0.0	56.9	5.7	0.1	1.2	25.1	0.0	4.44	97
Superior	a	4730	8700	82100.0	1.3	143	0.2	18.4	0.7	5.4	75.3	0.0	0.0	31.4	2.3	11.0	30.6	0.0	4.44	27
N=23 lakes							0.0	3.9	1.1	0.3	94.7	21.0	31.9	14.8	4.2	3.3	19.0	0.4	4.38	MEAN
N=21369							0.0	1.3	0.4	0.2	1.6	6.3	7.1	3.1	1.3	1.5	5.6	0.2	0.02	SE
							0.0	6.2	1.7	1.1	7.5	30.2	34.1	14.9	6.3	7.3	27.0	1.2	0.12	SD

†14=Godfrey 1955; 15=Rawson 1959; 16=Donald and Alger 1993; 18=Rawson and Eisey 1950; 24=Couey 1931; 25=Rawson 1930; 26=Cuerrier and Schultz 1957; 29=Rawson 1951; 33=Clemens et al. 1923; 34=Clemens et al. 1924; 37=Johnson 1972; 40=Johnson 1975; 39=Merrick et al. 1992; 49=Trippel and Beamish 1993; 54=Hassinger and Close 1984; 73=Martin 1954; 74=OMNR data files; 75=Konkle and Sprules 1986; 76=Martin 1952; 77=Lapointe 1987; 78=Leonard and Leonard 1948; 79=Cuerrier 1954; 80=Magnin 1978; 81=Martin 1970; 82=Kimsey 1960; 83=Miller 1948; 84=Rawson 1961; 85=Diana 1990; 86=Royce 1951; 87=Eck and Wells 1986; 88=Van Oosten and Deason 1938; 89=Brandt 1986; 90=Jude et al. 1987; 91=Hacker 1965; 92=Dymond 1928; 93=Christie et al. 1987; 94=Elrod 1983; 95=Elrod and O'Gorman 1991; 96=Vander Zanden 1994; 97=Dryer et al. 1965; 27=Anderson and Smith Jr. 1971.

*a=percent volume format reported; b=percent of total number converted to percent volume using equation 6; c=percent frequency of occurence converted to percent volume using equation 7; d=percent frequency of occurence converted to percent volume using equation 9.

App 3

APPENDIX 4: Dietary data used in Chapter 2. Variables listed are study lake, location (State or Province), year, sample size, dietary data, trophic position, and references. Dietary data are broken down into the prey categories described in Table 1. Summary presented at the end of each species represents the mean diet and trophic position for the species. References are presented after Appendix 5.

Appendix 4: Dietary data used in Chapter 2.

Lake	Location	Year	N	Prey Category Fish	Zoop	Ben	Pred. Ben	Mol	Cray	Det	Oth	Trophic Position	Reference
<u>Pumpkinseed (n = 2000 fish)</u>													
10 lakes	Maine	38	101	0.0	0.2	17.4	0.0	61.5	0.0	20.9	0.0	3.09	1
Bassett	Michigan	77	50	0.0	0.0	34.5	16.1	28.8	0.0	0.0	21.0	3.44	3
Deep	Michigan	77	50	0.0	0.0	29.9	0.0	17.4	0.0	0.0	53.0	3.42	3
Dowsley Pond	Ontario	87	280	0.0	0.0	62.8	15.3	16.7	0.0	0.0	5.0	3.49	4
Hamilton	Michigan	77	50	0.0	0.0	1.8	0.1	58.9	0.0	0.0	39.0	3.20	3
Little Cataraqui Cr.	Ontario	90	187	0.0	12.8	62.2	6.2	14.1	0.0	1.9	2.9	3.45	5
Long	Minnesota	62	8	0.0	0.0	17.8	4.4	77.7	0.0	0.0	0.0	3.13	6
Maple	Minnesota	57	367	0.0	0.0	39.0	0.0	49.0	0.0	3.5	9.5	3.25	7
Opinicon	Ontario	87	280	0.0	4.7	13.3	5.3	71.3	0.0	0.0	5.3	3.17	4
Opinicon	Ontario	66	103	0.0	3.7	57.7	21.3	12.3	2.3	0.0	0.0	3.52	8
Shaw	Michigan	77	50	0.0	0.0	0.2	0.0	99.7	0.0	0.0	0.0	3.00	3
Sieverson	Minnesota	62	66	0.0	0.0	16.9	3.9	79.2	0.0	0.0	0.0	3.12	6
Sister	Michigan	72	65	0.0	3.9	40.9	4.6	28.8	0.0	5.0	16.7	3.35	9
Squaw	Minnesota	62	25	0.0	0.0	42.6	3.0	33.5	20.3	0.0	0.6	3.45	6
Tuckahoe Creek	Virginia	58	35	0.0	0.2	79.1	0.0	0.0	0.0	20.7	0.0	3.40	10
U. Poole Pond	Ontario	87	280	0.0	2.0	46.3	14.3	29.3	0.0	0.0	8.0	3.43	4
Winona	Wisconsin	40	3	0.0	0.0	52.8	0.0	0.0	0.0	41.6	4.0	3.26	11
Mean				0.0	1.6	36.2	5.6	39.9	1.3	5.5	9.7	3.30	
<u>Perch (n = 8075 fish)</u>													
10 lakes	Maine	38	30	71.6	1.2	15.7	0.8	0.0	0.0	10.7	0.0	4.17	1
7 lakes	Maine	41	78	78.3	0.3	6.2	14.8	0.3	0.0	0.1	0.0	4.36	1
Alle	Wisconsin	31	3	0.0	0.0	100.0	0.0	0.0	0.0	0.0	0.0	3.50	12
Arbor	Wisconsin	31	8	0.0	0.0	89.5	0.0	0.0	0.0	0.0	9.0	3.48	12
Brome	Quebec	84	17	0.0	0.0	97.0	0.0	3.0	0.0	0.0	0.0	3.48	13
Bromont	Quebec	84	34	14.3	2.6	53.0	25.8	0.0	0.0	0.0	4.2	3.77	13
Brompton	Quebec	84	34	26.5	0.0	69.7	0.3	3.5	0.0	0.0	0.0	3.75	13
Cedar	Michigan	41	112	80.7	12.0	7.3	0.0	0.0	0.0	0.0	0.0	4.31	14
Clear	Wisconsin	31	13	11.0	0.0	86.5	0.0	0.0	0.0	1.5	0.0	3.59	12
Clear	Wisconsin	32	7	6.0	6.0	80.0	0.0	3.0	5.0	0.0	0.0	3.57	12
Crane	Wisconsin	32	11	10.5	0.0	85.5	0.0	0.0	0.0	0.0	4.0	3.61	12
Crystal	Wisconsin	31	9	56.5	2.0	33.0	0.0	0.0	0.0	0.0	8.0	4.06	12
Cub	Michigan	74	201	24.5	1.8	37.8	27.0	2.5	0.0	0.0	6.0	3.86	15
D'Argent	Quebec	84	34	0.0	11.2	86.2	0.0	1.6	0.0	0.9	0.0	3.49	13
Drolet	Quebec	84	17	0.0	19.1	76.9	3.3	0.7	0.0	0.0	0.0	3.51	13
Erie	Ohio	71	436	21.4	14.2	48.9	0.0	0.0	0.0	0.0	15.5	3.71	16
Erie	Ohio	83	-	4.0	37.0	59.0	0.0	0.0	0.0	0.0	0.0	3.54	17
Erie	Ohio	84	-	14.5	53.6	31.9	0.0	0.0	0.0	0.0	0.0	3.65	17
Erie	Ohio	85	-	7.8	34.9	57.3	0.0	0.0	0.0	0.0	0.0	3.58	17
Erie	Ohio	83	8	3.0	28.0	59.0	0.0	10.0	0.0	0.0	0.0	3.48	18

				Prey Category									
Lake	Location	Year	N	Fish	Zoop	Ben	Pred. Ben	Mol	Cray	Det	Oth	Trophic Position	Reference
Erie	Ohio	84	20	16.0	58.0	23.0	0.0	3.0	0.0	0.0	0.0	3.65	18
Erie	Ohio	85	13	5.0	43.0	48.0	0.0	4.0	0.0	0.0	0.0	3.53	18
Western Basin (Erie)	Ohio	81	82	19.6	53.9	23.4	0.0	3.2	0.0	0.0	0.0	3.68	19
Geneva	Wisconsin	21	19	5.3	40.0	40.0	0.0	0.0	0.0	0.0	15.0	3.56	20
Hertel	Quebec	84	17	0.0	13.5	80.8	0.0	5.7	0.0	0.0	0.0	3.47	13
Houghton	Michigan	39	78	24.6	6.0	69.4	0.0	0.0	0.0	0.0	0.0	3.75	21
Houghton	Michigan	40	267	69.1	1.8	27.8	1.3	0.0	0.0	0.0	0.7	4.21	21
Saginaw Bay (Huron)	Ontario	56	241	12.0	23.0	48.0	0.0	6.0	0.0	0.0	11.0	3.59	22
Little Minnow	Ontario	70-75	312	10.0	5.0	22.0	40.0	0.0	8.0	0.0	15.0	3.84	23
Long	Wisconsin	31	98	5.0	43.5	37.5	0.0	0.0	0.0	0.0	15.0	3.57	12
Magog	Quebec	84	17	0.0	0.6	83.8	0.0	8.2	7.4	0.0	0.0	3.50	13
Maple	Minnesota	57	97	49.0	0.0	40.0	0.0	1.5	0.0	0.0	10.0	3.99	7
Massawippi	Quebec	84	17	0.0	11.4	60.0	26.0	2.6	0.0	0.0	0.0	3.62	13
Memphramagog	Quebec	84	34	8.0	1.7	86.1	3.4	0.8	0.0	0.0	0.0	3.59	13
Muskellunge	Wisconsin	31	207	48.0	14.0	20.0	0.0	2.0	1.0	6.0	9.5	3.95	12
Muskellunge	Wisconsin	32	375	17.5	15.5	39.1	0.0	5.0	0.0	1.0	21.0	3.63	12
Nebish	Wisconsin	31	109	2.5	1.5	89.2	0.0	5.5	0.0	0.1	2.5	3.52	12
Nebish	Wisconsin	32	178	2.5	21.5	63.6	0.0	5.0	0.0	0.0	6.0	3.48	12
Nebish	Wisconsin	77	102	23.5	5.1	58.9	10.9	1.6	0.0	0.0	0.0	3.78	24
Nebish	Wisconsin	78	122	7.6	4.1	77.0	6.0	0.8	0.0	4.5	0.0	3.58	24
Nebish	Wisconsin	79	92	24.0	2.3	58.4	6.7	5.0	0.0	3.6	0.0	3.73	24
Nebish	Wisconsin	80	123	3.0	2.1	16.0	4.2	1.8	72.0	0.9	0.0	3.90	24
Nebish	Wisconsin	81	111	34.2	9.4	38.1	5.7	10.8	0.0	1.7	0.0	3.81	24
Nipigon	Ontario	21	14	7.1	36.8	56.1	0.0	0.0	0.0	0.0	0.0	3.57	25
Nipigon	Ontario	21	43	25.5	8.5	55.0	0.0	0.0	4.0	0.0	7.0	3.78	26
Nipigon	Ontario	27	-	0.0	0.0	100.0	0.0	0.0	0.0	0.0	0.0	3.50	27
Oneida	New York	75	254	0.0	91.8	8.2	0.0	0.0	0.0	0.0	0.0	3.50	28
Oneida	New York	76	212	0.0	88.5	11.5	0.0	0.0	0.0	0.0	0.0	3.50	28
Oneida	New York	77	232	0.0	73.7	26.3	0.0	0.0	0.0	0.0	0.0	3.50	28
Oneida	New York	27	-	0.0	0.0	100.0	0.0	0.0	0.0	0.0	0.0	3.50	27
Opinicon	Ontario	66	79	0.0	11.5	62.5	24.0	0.0	1.5	0.0	0.0	3.62	8
Opinicon	Ontario	1971	1033	18.4	11.5	13.6	30.9	2.8	19.6	0.0	0.0	3.87	29
Opinicon	Ontario	1972	49	7.5	17.0	5.0	48.0	2.0	15.0	0.0	0.0	3.80	29
Opinicon	Ontario	1973	49	9.5	19.5	8.0	33.0	1.0	14.0	0.0	0.0	3.60	29
Pallette	Wisconsin	31	8	55.0	0.0	33.0	0.0	13.5	0.0	0.0	0.0	4.01	12
Pepin	Wisconsin	21	15	11.3	18.8	59.6	0.0	5.8	0.0	0.0	4.0	3.58	20
Plum	Wisconsin	31	15	31.5	0.0	13.5	0.0	0.5	50.5	0.0	3.0	4.05	12
Rock	Wisconsin	31	23	33.5	0.1	51.5	0.0	0.5	0.0	12.0	3.5	3.79	12
Roxton	Quebec	84	34	0.0	0.0	96.9	0.0	3.1	0.0	0.0	0.0	3.48	13
Silver	Quebec	84	17	0.0	0.1	89.3	8.4	2.0	0.0	0.0	0.0	3.53	13
Silver	Wisconsin	31	176	6.5	9.5	57.1	0.0	3.5	11.0	2.0	8.0	3.56	12
Silver	Wisconsin	32	273	96.0	0.0	2.0	0.0	0.0	2.0	0.0	0.0	4.47	12
Simcoe	Ontario	27	13	11.0	0.0	77.0	0.0	4.0	8.0	0.0	0.0	3.63	27
Spider	Wisconsin	31	32	25.0	0.0	15.5	0.0	3.0	48.5	4.0	5.0	3.97	12

				Prey Category									
Lake	Location	Year	N	Fish	Zoop	Ben	Pred. Ben	Mol	Cray	Det	Oth	Trophic Position	Reference
Starr	Wisconsin	31	4	0.0	0.0	68.5	0.0	0.0	31.5	0.0	0.0	3.66	12
Susquehanna R.	Maryland	82	698	2.0	0.0	79.0	0.0	15.0	0.0	0.0	4.0	3.45	30
Trout	Wisconsin	31	160	36.0	4.0	35.7	0.0	1.0	16.0	2.0	4.5	3.91	12
Trout	Wisconsin	32	106	39.0	0.0	43.1	0.0	6.0	1.0	1.5	9.0	3.85	12
Vieux	Wisconsin	31	35	13.5	0.0	79.5	0.0	0.0	0.0	4.0	2.5	3.61	12
Vieux	Wisconsin	32	76	6.0	0.1	84.0	0.0	4.5	0.0	0.5	5.0	3.54	12
Waskesiu	Saskatchewan	27	-	0.0	0.0	100.0	0.0	0.0	0.0	0.0	0.0	3.50	27
Waterloo	Quebec	84	34	0.0	1.8	91.1	5.2	1.8	0.0	0.0	0.0	3.52	13
Weber	Wisconsin	31	178	6.5	2.5	85.6	0.0	0.1	0.0	0.5	5.0	3.57	12
Weber	Wisconsin	32	184	1.0	14.0	80.7	0.0	0.5	0.0	0.0	2.0	3.48	12
West Blue	Manitoba	71	240	5.5	21.8	45.5	0.0	0.0	3.8	0.0	23.0	3.57	31
Winona	Wisconsin	40	6	40.0	0.0	33.6	0.0	10.4	16.0	0.0	0.0	3.93	11
Mean				17.2	13.6	53.9	4.3	2.3	4.4	0.8	3.1	3.69	
<u>Rock Bass (n = 1962 fish)</u>													
Alle	Wisconsin	31	10	0.0	0.0	0.0	0.0	2.0	93.0	1.0	3.0	3.94	12
Bear	Wisconsin	31	12	0.0	0.0	40.5	0.0	3.5	47.0	0.0	9.0	3.72	12
Clear	Wisconsin	31	4	0.0	0.0	37.5	0.0	0.0	58.5	0.0	4.0	3.79	12
Clear	Wisconsin	32	3	0.0	0.0	97.0	0.0	3.0	0.0	0.0	0.0	3.49	12
Georgian Bay (Huron)	Ontario	28	40	28.5	0.0	10.2	0.0	0.0	60.4	0.9	0.0	4.08	32
Goose Creek	Virginia	86	40	0.0	14.0	86.0	0.0	0.0	0.0	0.0	0.0	3.50	33
Muskellunge	Wisconsin	31	338	22.5	0.0	41.0	0.0	3.0	13.5	11.0	6.0	3.68	12
Muskellunge	Wisconsin	32	371	12.0	0.1	58.8	0.0	0.5	5.5	2.0	20.5	3.63	12
Nebish	Wisconsin	31	184	3.5	7.5	81.1	0.0	5.0	0.0	0.1	2.0	3.50	12
Nebish	Wisconsin	32	209	7.5	3.5	79.7	0.0	0.5	0.0	0.1	6.0	3.53	12
Nebish	Wisconsin	32	27	3.5	50.5	31.5	0.0	12.0	0.0	0.0	2.0	3.47	12
Nipissing	Ontario	29-30	12	19.1	0.0	16.1	0.0	0.0	64.6	0.2	0.0	4.01	32
Opinicon	Ontario	66	96	10.0	0.0	6.7	52.7	0.0	30.0	0.0	0.0	4.00	8
Ozark streams	Arkansas	80	210	9.0	0.0	18.0	0.0	0.0	73.0	0.0	0.0	3.96	34
Pallette	Wisconsin	31	11	0.0	0.0	92.0	0.0	5.0	0.0	0.0	1.0	3.45	12
Plum	Wisconsin	31	1	0.0	0.0	0.0	0.0	0.0	100.0	0.0	0.0	4.00	12
Rock	Wisconsin	31	4	24.5	0.0	61.5	0.0	0.0	0.0	4.0	10.0	3.73	12
Silver	Wisconsin	31	124	5.0	0.0	52.0	0.0	0.1	35.5	1.0	4.5	3.69	12
Silver	Wisconsin	32	3	37.5	0.0	62.5	0.0	0.0	0.0	0.0	0.0	3.88	12
Simcoe	Ontario	27	9	4.0	0.0	22.0	0.0	0.0	74.0	0.0	0.0	3.91	27
Star	Wisconsin	31	1	20.0	0.0	20.0	0.0	0.0	30.0	30.0	0.0	3.70	12
Trout	Wisconsin	31	38	13.5	0.1	63.0	0.0	0.0	20.5	1.0	3.0	3.75	12
Trout	Wisconsin	32	103	4.0	0.5	45.1	0.0	0.0	36.5	0.0	14.0	3.72	12
Vieux	Wisconsin	32	2	0.0	0.0	24.0	0.0	0.0	0.0	0.0	76.0	3.50	12
Winona	Wisconsin	40	10	26.6	0.0	9.5	18.0	7.1	37.3	0.0	0.0	3.98	11
Mean				10.0	3.0	42.2	2.8	1.7	31.2	2.1	6.4	3.74	

Lake	Location	Year	N	Prey Category								Trophic Position	Reference
				Fish	Zoop	Ben	Pred. Ben	Mol	Cray	Det	Oth		
Smallmouth Bass (n = 3162 fish)													
11 lakes	Maine	36-38	31	14.9	0.3	6.0	12.5	0.0	66.3	0.0	0.0	4.04	1
7 lakes	Maine	40	66	80.3	0.0	3.6	0.0	0.0	14.4	1.7	0.0	4.37	44
8 lakes	Maine	41	259	83.9	5.8	8.0	1.6	0.0	0.0	0.7	0.0	4.34	1
-	Michigan	64	177	43.0	0.0	0.5	0.0	0.0	56.5	0.0	0.0	4.21	45
Bay de Noc (Michigan)	Michigan	66-68	57	75.0	0.0	0.1	0.0	0.0	25.0	0.0	0.0	4.38	46
Bay de Noc (Michigan)	Michigan	66-68	112	97.0	0.0	0.0	0.0	0.0	1.0	0.0	0.0	4.45	46
Bear	Wisconsin	31	1	100.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.50	12
Cacapon R.	Virginia	39	104	2.7	0.0	87.6	8.2	0.4	1.1	0.0	0.2	3.57	47
Cache	Ontario	35-36	52	28.7	16.0	19.7	0.0	0.0	35.7	0.0	0.0	3.97	48
Clear	Wisconsin	31	2	100.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.50	12
Crystal	Wisconsin	31	4	0.0	0.0	97.5	0.0	0.0	0.0	3.5	0.0	3.50	12
Douglas	Michigan	15	8	10.0	0.0	0.0	0.0	0.0	70.0	0.0	20.0	3.95	20
Erie	Ontario	38	157	82.5	0.0	0.2	0.0	0.0	17.5	0.0	0.0	4.41	48
Genesee R.	New York	27	13	18.4	0.0	24.2	0.0	0.0	56.0	0.0	0.0	3.94	20
Geneva	Wisconsin	21	21	33.0	4.0	43.0	0.0	0.0	20.6	0.0	0.0	3.94	20
Georgian Bay	Ontario	36	45	62.5	0.0	1.5	0.0	0.0	33.5	0.0	0.0	4.26	48
Georgian Bay	Ontario	28	98	27.7	0.0	0.4	0.2	0.0	71.7	0.2	0.0	4.14	32
Illinois R.	Illinois	1880	10	5.0	0.0	35.0	0.0	0.0	60.0	0.0	0.0	3.85	20
Juniata R.	Pennsylvania	90	102	0.0	0.0	93.9	0.0	0.0	6.2	0.0	0.0	3.53	49
Jute	Wisconsin	31	28	83.5	0.0	13.0	0.0	0.0	0.0	0.0	2.0	4.31	12
Katherine	Michigan	74	167	28.0	8.7	32.0	5.3	0.0	13.0	0.0	13.0	3.87	15
Larry	Wisconsin	31	14	0.0	2.0	94.5	0.0	0.0	0.0	1.5	0.0	3.46	12
Memphremagog	Quebec	73	24	50.1	0.0	3.2	0.0	0.0	50.0	0.0	0.0	4.30	50
Michigan	Wisconsin	21	2	98.5	0.0	0.0	0.0	0.0	0.0	1.5	0.0	4.48	20
Monona	Wisconsin	18	4	80.0	0.0	20.0	0.0	0.0	0.0	0.0	0.0	4.30	20
Muskellunge	Wisconsin	31	57	75.0	0.0	12.0	0.0	1.0	0.0	11.0	1.0	4.19	12
Muskellunge	Wisconsin	32	61	42.0	1.5	48.5	0.0	0.0	0.0	6.5	2.0	3.90	12
Nebish	Wisconsin	31	66	20.5	12.0	62.0	0.0	1.5	0.0	0.0	3.0	3.68	12
Nebish	Wisconsin	32	42	41.0	0.0	56.5	0.0	0.0	0.1	0.0	2.0	3.90	12
Nebish	Wisconsin	77	101	7.2	0.0	3.2	5.4	0.0	84.2	0.0	0.0	4.02	24
Nebish	Wisconsin	78	126	22.0	0.3	11.0	2.9	0.0	64.0	0.0	0.0	4.06	24
Nebish	Wisconsin	79	104	15.5	0.1	8.8	5.8	0.0	69.9	0.0	0.0	4.04	24
Nebish	Wisconsin	80	125	10.0	0.0	3.4	4.1	0.0	82.6	0.0	0.0	4.04	24
Nebish	Wisconsin	81	111	8.9	0.1	7.2	4.4	0.0	80.1	0.0	0.0	4.02	24
Nipigon	Ontario	21	9	48.0	35.3	16.6	0.0	0.0	0.0	0.0	0.0	3.98	25
Nipissing	Ontario	29	106	20.6	0.0	0.4	0.0	0.0	79.0	0.0	0.0	4.10	32
Opeongo	Ontario	36	91	9.7	0.0	2.3	0.0	0.0	87.0	0.0	0.0	4.02	48
Oxtongue R.	Ontario	30	6	20.0	0.0	80.0	0.0	0.0	0.0	0.0	0.0	3.70	32
Ozark streams	Arkansas	80	74	34.0	0.0	6.0	0.0	0.0	60.0	0.0	0.0	4.14	34
Pallette	Wisconsin	31	16	58.5	1.5	40.0	0.0	0.0	0.0	0.0	0.0	4.09	12
Pallette	Wisconsin	32	30	58.5	2.5	35.5	0.0	0.0	0.0	1.5	2.5	4.09	12
Pepin	Wisconsin	21	12	56.5	5.7	29.8	0.0	0.0	9.1	0.0	0.0	4.13	20

Lake	Location	Year	N	Prey Category Fish	Zoop	Ben	Pred. Ben	Mol	Cray	Det	Oth	Trophic Position	Reference
Perch	Ontario	30-31	123	49.7	1.7	5.3	0.1	0.0	39.2	0.2	3.9	4.19	32
Phantom	Ontario	30	18	4.0	0.0	22.6	0.0	0.0	71.7	1.7	0.0	3.89	32
Potomac	Virginia	39	96	4.1	0.0	94.6	0.5	0.1	0.6	0.0	0.1	3.55	47
Razor	Wisconsin	31	18	39.5	2.0	53.0	0.0	0.0	0.0	0.0	6.0	3.90	12
Rock	Wisconsin	31	6	5.0	0.0	88.5	0.0	0.0	0.0	5.5	1.0	3.52	12
Shenandoah R.	Virginia	39	108	37.3	0.0	49.8	8.1	0.0	4.3	0.0	0.5	3.93	47
Silver	Wisconsin	31	31	35.0	0.0	55.0	0.0	0.0	9.5	1.0	0.0	3.90	12
Silver	Wisconsin	32	5	100.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.50	12
Simcoe	Ontario	27	16	29.0	0.0	7.0	8.0	3.0	53.0	0.0	0.0	4.08	27
Spider	Wisconsin	31	3	0.0	0.0	27.0	0.0	0.0	15.5	0.0	58.0	3.59	12
Star	Wisconsin	31	1	0.0	0.0	50.0	0.0	0.0	50.0	0.0	0.0	3.75	12
Trout	Wisconsin	31	10	0.0	7.0	89.5	0.0	0.0	0.0	0.0	4.5	3.52	12
Trout	Wisconsin	32	1	0.0	0.0	0.0	0.0	0.0	100.0	0.0	0.0	4.00	12
Weber	Wisconsin	31	29	6.0	5.0	76.0	0.0	0.0	0.0	1.0	14.0	3.59	12
Weber	Wisconsin	32	2	83.0	0.0	17.0	0.0	0.0	0.0	0.0	0.0	4.33	12
Mean				37.6	2.0	28.8	1.2	0.1	27.3	0.7	2.3	4.02	
<u>Largemouth Bass (n = 5664 fish)</u>													
Bear	Wisconsin	31	5	80.0	0.0	20.0	0.0	0.0	0.0	0.0	0.0	4.30	12
Cub	Michigan	74	340	54.3	0.0	0.0	11.0	0.0	0.0	0.0	35.0	4.10	15
Deer Island	-	73	169	53.4	0.4	19.6	0.0	0.0	14.9	0.1	11.9	4.11	35
DeGray	Arkansas	76	748	59.0	0.0	0.3	0.0	0.0	37.6	0.5	3.0	4.28	36
Fork	-	41		48.0	0.0	18.2	11.0	0.0	11.3	0.0	11.0	4.08	37
Geneva	Wisconsin	18	78	8.7	18.1	48.1	0.0	0.0	0.0	0.0	25.0	3.59	20
L. Dixie	Missouri	64	900	50.1	0.0	1.5	0.7	0.0	39.4	0.6	6.3	4.18	38
Long	Wisconsin	31	3	50.0	0.0	4.0	0.0	0.0	0.0	0.0	46.0	4.00	12
Maple	Minnesota	57	83	96.0	3.0	0.0	0.0	0.0	0.0	1.0	0.0	4.46	7
Murphy flow	Wisconsin	61-64	1146	33.5	0.0	1.2	0.0	0.0	56.1	6.1	0.0	4.04	39
Muskellunge	Wisconsin	31	19	50.5	32.0	9.5	0.0	0.0	0.0	1.5	7.5	4.01	12
Muskellunge	Wisconsin	32	8	94.0	0.0	0.0	0.0	0.0	0.0	6.0	0.0	4.41	12
Opinicon	Ontario	91	10	85.7	1.8	0.0	0.0	0.0	11.4	0.0	0.0	4.40	2
Paul	Michigan	87	235	42.0	11.0	8.0	39.0	0.0	0.0	0.0	0.0	4.12	40
Paul	Michigan	88		55.0	10.0	14.0	21.0	0.0	0.0	0.0	0.0	4.16	40
Peter	Michigan	87	235	0.0	6.5	45.6	46.5	0.8	0.0	0.0	0.0	3.72	41
Peter	Michigan	88	235	54.0	6.0	8.0	32.0	0.0	0.0	0.0	0.0	4.20	40
Peter	Michigan	87		0.0	15.0	15.0	35.0	0.0	0.0	0.0	35.0	3.68	40
Shelbyville	Illinois	80	97	99.2	0.0	0.8	0.0	0.0	0.0	0.0	0.0	4.49	42
Shelbyville	Illinois	78-81	1347	88.8	0.0	0.6	0.0	0.0	11.4	0.0	0.0	4.46	43
Winona	Wisconsin	40	6	17.6	0.0	16.9	0.0	0.0	40.5	25.0	0.0	3.75	11
Mean				53.3	4.9	11.0	9.3	0.0	10.6	1.9	8.6	4.12	
<u>Northern Pike and Chain Pickerel (n = 34738 fish)</u>													
19 lakes	Maine	40	110	94.8	0.0	0.2	0.0	0.0	0.5	0.0	4.40	4.37	44

				Prey Category									
Lake	Location	Year	N	Fish	Zoop	Ben	Pred. Ben	Mol	Cray	Det	Oth	Trophic Position	Reference
20 lakes	Maine	37-41	95	95.1	0.0	0.0	0.1	0.0	0.0	0.0	4.84	4.24	1
Babcock Pond	Connecticut	41	71	91.4	0.0	0.0	3.7	0.0	0.0	0.0	4.80	4.04	51
Bay de Noc (Michigan)	Michigan	66-68	405	100.0	0.0	0.0	0.0	0.0	0.0	0.0	0.00	4.36	46
Bay of Quinte (Ontario)	Ontario	58-64	131	100.0	0.0	0.0	0.0	0.0	0.0	0.0	0.00	4.55	75
Brochet	Quebec	53	131	40.2	0.0	9.3	32.1	0.0	18.4	0.0	0.00	4.15	52
Cree	Saskatchewan	55	-	95.0	0.0	0.0	5.0	0.0	0.0	0.0	0.00	4.48	53
Georgian Bay (Huron)	Ontario	28	11	53.8	0.0	0.0	0.0	0.0	46.2	0.0	0.00	4.27	32
Grande Riviere	Quebec	77		97.9	0.0	0.3	0.0	0.0	0.0	0.0	1.80	4.48	52
Great Slave	NWT	44-47	73	95.0	0.0	5.0	0.0	0.0	0.0	0.0	0.00	4.45	54
Grove	Minnesota	57	133	90.0	0.0	0.0	0.0	0.0	0.0	0.0	10.00	4.40	7
Heming	Manitoba	50-62	29477	99.9	0.0	0.1	0.0	0.0	0.1	0.0	0.00	4.42	55
Keller	NWT	62	125	97.2	0.0	0.0	2.8	0.0	0.0	0.0	0.00	4.59	56
Lincoln Pond	New York	39	145	32.8	1.4	47.4	17.6	0.0	0.0	0.0	0.80	3.72	57
Maple	Minnesota	57	70	100.0	0.0	0.0	0.0	0.0	0.0	0.0	0.00	4.50	7
Mecan R.	Wisconsin	59	91	95.9	0.0	0.0	0.0	0.0	1.5	0.0	2.56	4.31	58
Memphremagog	Quebec	73	27	60.0	0.0	2.1	0.0	0.0	40.0	0.0	0.00	4.09	50
Mississippi	Mississippi	68	58	96.5	0.0	0.0	0.0	0.0	3.5	0.0	0.00	4.36	59
Monroe	Quebec	53	221	99.5	0.0	0.1	0.1	0.0	0.3	0.0	0.00	4.50	52
Murphy Flowage	Wisconsin	65	1412	99.1	0.0	0.0	0.0	0.0	0.2	0.0	0.00	4.29	60
Nipigon	Ontario	21	23	95.2	0.7	0.7	0.0	0.0	0.0	0.0	3.79	4.46	26
Nipissing	Ontario	29-30	10	36.3	0.0	0.0	0.0	0.0	59.4	0.0	4.00	4.15	32
Ontario	New York	72	87	100.0	0.0	0.0	0.0	0.0	0.0	0.0	0.00	4.02	61
Pocotopaug	Connecticut	-	30	63.0	0.0	11.0	11.0	0.0	8.0	4.0	4.00	4.19	77
Review paper	-	-	-	64.0	0.0	22.0	0.0	0.0	12.0	1.0	1.00	3.82	77
Seney Refuge	Michigan	41-42	378	69.5	0.0	1.8	0.9	0.1	23.1	0.0	4.60	4.31	2
Seney Refuge	Michigan	52	84	65.4	0.0	0.1	2.5	0.1	21.4	0.0	10.60	4.28	2
Simcoe	Ontario	82	50	100.0	0.0	0.0	0.0	0.0	0.0	0.0	0.00	4.49	62
Ste. Anne	Alberta	76-78	1290	99.5	0.0	0.5	0.0	0.0	0.0	0.0	0.00	4.50	63
Wollaston	Saskatchewan	56	-	95.0	0.0	5.0	0.0	0.0	0.0	0.0	0.00	4.45	53
Mean				84.1	0.1	3.5	2.5	0.0	7.8	0.2	1.9	4.31	
Walleye (n = 10386 lakes)													
Bay de Noc (Michigan)	Michigan	66-68	103	100.0	0.0	0.0	0.0	0.0	0.0	0.0	0.00	4.39	46
Bay of Quinte (Ontario)	Ontario	58-62	692	99.0	0.0	0.0	0.0	0.0	0.0	0.0	1.00	4.04	75
Clear	Wisconsin	31	15	60.0	12.0	19.5	0.0	0.0	0.0	4.5	5.00	4.06	12
Clear	Wisconsin	32	23	40.5	0.0	59.5	0.0	0.0	0.0	0.0	0.50	3.92	12
Erie	Ontario	79-81	906	100.0	0.0	0.0	0.0	0.0	0.0	0.0	0.00	4.50	64
Falcon	Manitoba	59	288	92.2	0.0	5.5	0.0	0.0	3.0	0.0	0.00	4.48	45
Great Slave	NWT	44-47	116	75.0	0.0	25.0	0.0	0.0	0.0	0.0	0.00	4.25	54
James Bay	Quebec	79	584	72.3	1.3	24.0	2.4	0.0	0.0	0.0	0.00	4.24	65
Lac La Ronge	Saskatchewan	48-55	276	97.0	0.0	2.8	0.0	0.0	0.3	0.0	0.00	4.35	66
Lake of the Woods	Ontario	68-70	1417	98.8	0.3	1.3	0.0	0.0	0.0	0.0	0.00	4.61	67

				Prey Category									
Lake	Location	Year	N	Fish	Zoop	Ben	Pred. Ben	Mol	Cray	Det	Oth	Trophic Position	Reference
Lake of the Woods	Ontario	68-70	1605	88.0	1.5	11.3	0.0	0.0	1.8	0.0	0.00	4.49	67
Lost	Wisconsin	32	18	99.0	0.0	0.0	0.0	0.0	1.0	0.0	0.00	4.50	12
Memphremagog	Quebec	73	8	100.0	0.0	0.0	0.0	0.0	0.0	0.0	0.00	4.70	50
Nipigon	Ontario	20-21	74	91.1	0.0	6.6	0.0	0.0	0.0	0.0	0.00	4.35	25
Nipigon	Ontario	21	4	50.0	47.4	2.5	0.0	0.0	0.0	0.0	0.00	4.00	26
Nipissing	Ontario	29-30	16	48.3	0.0	28.1	0.0	0.0	22.9	0.0	0.00	4.08	32
Oahe	South Dakota	93	478	99.6	0.0	0.4	0.0	0.0	0.0	0.0	0.00	4.50	68
Ontario	Michigan	66-68	103	100.0	0.0	0.0	0.0	0.0	0.0	0.0	0.00	4.50	46
Pike	Minnesota	62	470	43.2	0.0	26.5	9.3	0.0	18.0	3.0	0.00	4.11	73
Simcoe	Ontario	82	50	100.1	0.0	0.0	0.0	0.0	0.0	0.0	0.00	4.57	62
Sparkling	Wisconsin	82-83	113	97.8	0.0	2.2	0.0	0.0	0.0	0.0	0.00	4.42	69
Trout	Wisconsin	31	30	96.0	0.0	1.0	0.0	0.0	0.0	0.0	2.50	4.45	12
Trout	Wisconsin	32	22	100.0	0.0	0.0	0.0	0.0	0.0	0.0	0.00	4.50	12
West Blue	Manitoba	70	79	79.8	0.0	9.3	0.0	0.0	11.0	0.0	0.00	4.51	70
West Blue	Manitoba	66	-	78.0	0.0	4.2	0.6	0.0	15.6	0.0	1.50	4.53	76
West Blue	Manitoba	69-70	-	71.5	0.0	16.9	5.0	0.0	4.8	0.0	1.90	4.43	76
Wilson	Minnesota	64-65	390	70.7	0.0	27.6	0.0	0.0	0.0	0.0	1.70	4.19	74
Wilson	Minnesota	67-70	230	41.4	0.0	44.4	0.0	0.0	2.1	0.0	12.10	3.88	74
Winnebago	Wisconsin	60	1148	99.0	0.0	1.0	0.0	0.0	0.0	0.0	0.00	4.43	71
Winnebago	Wisconsin	60	629	99.7	0.0	0.3	0.0	0.0	0.0	0.0	0.00	4.26	71
Winnebago	Wisconsin	61	56	95.4	0.4	4.6	0.0	0.0	0.0	0.0	0.00	4.26	71
Winnebago	Wisconsin	61	231	81.6	0.0	18.4	0.0	0.0	0.0	0.0	0.00	4.10	71
Mean				83.3	2.0	10.7	0.5	0.0	2.5	0.2	0.8	4.33	

APPENDIX 5: Dietary data for the piscivores, northen pike and walleye, used in Chapter 2. These are the populations for which the fish prey items could be further separated to according to species. Variables listed are study lake, location (State or Province), year, sample size, dietary data, trophic position, and references. Summary presented at the end of each species represents the mean diet and trophic position for the species. Note: perch, yellow perch; cypr, cyprinids; cent, centrarchids; trpe, trout-perch; suck, suckers; other, non-specified species; scul, sculpins; alew, alewife; smel, smelt; core, coregonids; salm, salmonids; burb, burbot; stic, sticklebacks; whba, white bass.

Appendix 5: Diet data for northen pike and walleye used in Chapter 2.

					percent volume in diet															
Lake	Location	Year	N	% Fish	perch	cypr	cent	trpe	suck	other	scul	alew	smel	core	salm	burb	stic	whba	Trophic Position	Reference
Northern Pike and Chain Pickerel (n = 32284 fish)																				
19 lakes	Maine	40	110	94.8	7.9	14.6	0.0	0.0	0.0	11.2	0.0	0.0	3.2	0.0	0.0	0.0	0.0	58.0	4.37	44
20 lakes	Maine	37-41	95	95.1	19.4	22.5	1.0	0.0	0.0	1.0	0.0	0.0	1.0	0.0	24.5	0.0	0.0	25.6	4.24	1
Babcock Pond	Connecticut	41	71	91.4	0.0	42.4	5.2	0.0	0.0	43.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.04	51
Bay de Noc	Michigan	66-68	405	100.0	2.8	7.0	4.6	10.7	0.0	1.6	0.0	34.2	39.1	0.0	0.0	0.0	0.0	0.0	4.36	46
Bay of Quinte	Ontario	58-64	131	100.0	53.2	0.0	2.0	21.8	0.0	0.0	0.0	19.9	3.1	0.0	0.0	0.0	0.0	0.0	4.55	75
Heming	Manitoba	50-62	29477	99.9	22.5	19.8	0.0	34.4	12.9	10.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.42	55
Keller	NWT	62	125	97.2	0.0	0.0	0.0	0.0	5.7	2.9	28.6	0.0	0.0	0.0	0.0	37.2	22.9	0.0	4.59	56
Lincoln Pond	New York	39	145	32.8	0.0	17.4	15.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.72	57
Mecan River	Wisconsin	59	91	95.9	0.0	4.6	0.0	0.0	9.0	0.0	22.8	0.0	0.0	0.0	59.6	0.0	0.0	0.0	4.31	58
Memphremagog	Quebec	73	27	60.0	30.0	30.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.09	50
Mississippi	Mississippi	68	58	96.5	0.0	0.0	59.9	0.0	0.0	36.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.36	59
Murphy Flowage	Wisconsin	65	1412	99.1	13.8	6.0	77.7	0.0	0.0	1.4	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0	4.29	39
Ontario	New York	72	87	100.0	2.3	0.0	0.0	0.0	0.0	0.0	0.0	97.7	0.0	0.0	0.0	0.0	0.0	0.0	4.02	61
Review	-	-	-	64.0	12.6	41.0	2.3	0.0	0.6	7.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.82	77
Simcoe	Ontario	82	50	100.0	28.4	1.5	4.9	1.6	35.3	0.0	0.0	0.0	8.0	20.2	0.0	0.0	0.0	0.0	4.49	62
Mean				88.4	12.9	13.8	11.5	4.6	4.2	7.7	3.4	10.1	3.6	1.3	5.6	2.5	1.5	5.6	4.24	
Walleye (n = 8369 fish)																				
Bay de Noc	Michigan	66-68	103	100.0	0.0	0.0	0.0	0.0	8.8	13.8	0.0	37.3	40.1	0.0	0.0	0.0	0.0	0.0	4.39	46
Bay of Quinte	Ontario	58-62	692	99.0	0.4	0.0	0.0	0.0	0.0	0.0	0.0	94.6	4.0	0.0	0.0	0.0	0.0	0.0	4.04	75
Falcon	Manitoba	59	288	92.2	49.5	6.2	8.4	2.2	12.4	12.4	1.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.48	45
James Bay	Quebec	79	584	72.3	0.0	0.0	0.0	41.1	0.0	0.0	0.0	0.0	0.0	26.6	0.0	4.5	0.0	0.0	4.24	65
Lac La Ronge	Saskatchewan	48-55	276	97.0	1.0	2.0	0.0	31.0	7.0	0.0	0.0	0.0	0.0	56.0	0.0	0.0	0.0	0.0	4.35	66
Lake of the Woods	Ontario	68-70	1417	98.8	30.0	3.3	0.0	53.7	0.0	5.6	0.0	0.0	0.0	6.1	0.0	0.0	0.0	0.0	4.61	67
Lake of the Woods	Ontario	68-70	1605	88.0	72.8	9.5	0.0	5.1	0.0	0.0	0.0	0.0	0.0	0.6	0.0	0.0	0.0	0.0	4.49	67
Memphremagog	Quebec	73	8	100.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	100.0	0.0	0.0	0.0	0.0	0.0	4.70	50
Pike	Minnesota	62	470	43.2	27.4	0.1	0.0	0.5	13.3	0.0	1.3	0.0	0.0	0.0	0.0	0.6	0.0	0.0	4.11	73
Simcoe	Ontario	82	50	100.1	19.4	11.0	0.0	1.0	0.0	0.0	0.0	0.0	68.7	0.0	0.0	0.0	0.0	0.0	4.57	62
Sparkling	Wisconsin	82-83	113	97.8	69.2	19.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	9.5	0.0	0.0	4.42	69
West Blue	Manitoba	70	79	79.8	71.0	0.0	0.0	8.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.51	70
West Blue	Manitoba	66	-	78.0	77.2	0.0	0.0	0.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.53	76
West Blue	Manitoba	69-70	-	71.5	63.9	0.0	0.0	7.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.43	76
Wilson	Minnesota	64-65	390	70.7	55.8	14.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.19	74
Wilson	Minnesota	67-70	230	41.4	20.6	20.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.88	74
Winnebago	Wisconsin	60	1148	99.0	19.9	10.9	2.6	8.9	0.0	52.6	0.0	0.0	0.0	0.0	0.0	4.1	0.0	0.0	4.43	71
Winnebago	Wisconsin	60	629	99.7	0.0	34.3	7.1	58.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.26	71
Winnebago	Wisconsin	61	56	95.4	0.0	1.6	93.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.26	71
Winnebago	Wisconsin	61	231	81.6	0.0	16.1	47.0	18.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.10	71
Mean				85.3	28.9	7.5	7.9	11.9	2.1	4.2	0.1	6.6	10.6	4.5	0.0	0.9	0.0	0.0	4.35	

References for Appendices 4 and 5.

[a] (1) Cooper 1942; (2) Lagler 1956; (3) Laughlin and Werner 1980; (4) Fox and Keast 1990; (5) Snetsinger 1992; (6) Etnier 1971; (7) Seaburg and Moyle 1964; (8) Keast and Welsh 1968; (9) Sadzikowski and Wallace 1976; (10) Flemer and Woolcott 1966; (11) Parks 1949; (12) Couey 1935; (13) Boisclair 1988; (14) Moffett and Hunt 1943; (15) Clady 1974; (16) Griswold and Tubb 1977; (17) Parrish and Margraf 1990; (18) Parrish and Margraf 1994; (19) Schaeffer and Margraf 1986; (20) Adams and Hankinson 1928; (21) Hunt and Carbin 1950; (22) Tharratt 1959; (23) Fraser 1978; (24) Serns and Hoff 1984; (25) Clemens et al. 1923; (26) Clemens et al. 1924; (27) Rawson 1930; (28) Mills and Forney 1981; (29) Keast 1977; (30) Weisberg and Janicki 1990; (31) Ward and Robinson 1974; (32) Tester 1932; (33) Vadas Jr. 1990; (34) Probst et al. 1984; (35) Saiki and Tash 1978; (36) Bryant and Moen 1980; (37) Bennett 1948; (38) Herman et al. 1969; (39) Snow 1971; (40) Hodgson et al. 1991; (41) Hodgson et al. 1989; (42) Miller and Storck 1984; (43) Storck 1986;(44) Cooper 1941; (45) Fedoruk 1966;(46) Wagner 1972; (47) Surber 1941; (48) Doan 1940; (49) Johnson and Dropkin 1995; (50) Nakashima and Leggett 1975; (51) Foote and Blake 1945; (52) Vallieres and Fortin 1988; (53) Rawson 1959; (54) Rawson 1951; (55) Lawler 1965; (56) Johnson 1972; (57) Raney 1942; (58) Hunt 1965; (59) McIlwain 1970; (61) Wolfert and Miller 1978; (62) Mathers and Johansen 1985; (63) Diana 1979; (64) Knight et al. 1984; (65) Hazel and Fortin 1986; (66) Rawson 1965; (67) Swenson and Smith Jr. 1976; (68) Bryan et al. 1995 (69) Lyons and Magnuson 1987; (70) Kelso 1973; (71) Priegel 1963; (73) Johnson and Hale 1977; (74) Johnson 1977; (75) Hurley and Christie 1977; (76) Kelso and Ward 1977; (77) Hunter and Rankin Jr. 1939.

APPENDIX 6: Estimated trophic position of adult littoral fish species based on nitrogen isotope ratios from 36 lakes in Ontario and Quebec. Mus = unionid mussels, Pump = pumpkinseed, Perc = yellow perch, Rb = rock bass, Smb = smallmouth bass, Lmb = largemouth bass, Pike = northern pike and chain pickerel, Wall = Walleye.

Lake	$\delta^{15}N$ Mus	Trophic Position						
		Pump	Perc	Rb	Smb	Lmb	Pike	Wall
Ahmic	5.3	-	3.92	3.84	-	-	3.53	4.24
Balsam	4.1	3.45	3.73	3.65	-	-	-	-
Bernard	3.1	-	-	-	3.55	-	-	-
Big Rideau	4.7	3.23	2.99	-	-	-	3.82	-
Brandy	3.9	3.83	3.42	3.77	3.91	-	3.78	-
Buck	3.8	3.53	3.56	-	4.16	4.03	3.63	-
Carson	1.6	-	-	-	3.94	4.41	-	-
Christie	4.4	-	3.77	-	-	-	4.18	4.10
Clear	5.7	-	3.39	-	-	-	4.02	-
Cameron	4.5	2.81	3.50	3.45	-	-	-	-
Constan	3.3	-	-	-	-	-	3.38	-
Crotch	4.1	-	3.46	-	3.73	3.87	3.77	-
Dalrymple	6.0	3.14	-	-	3.89	-	4.02	-
Doe	4.7	3.36	3.73	3.96	3.87	-	3.59	-
Doré	5.1	3.45	3.34	3.92	3.91	-	4.41	-
Fox	4.2	3.68	-	-	-	4.13	3.73	-
Gloucester Pool	3.7	-	3.90	-	-	-	4.08	4.55
Golden	3.1	-	4.00	-	4.20	-	4.08	4.55
Hurds	3.2	3.45	4.25	4.04	-	4.18	4.31	-
Kashagawigamog	4.8	-	3.87	3.45	-	-	-	-
Kennisis	2.3	-	4.33	-	-	-	-	-
Mazinaw	1.3	4.15	3.76	4.43	4.73	-	3.69	4.86
Memphremagog	7.6	-	3.16	-	-	-	-	-
Memesagamesing	4.3	-	-	-	-	-	3.80	-
Mississippi	3.9	3.68	3.69	3.86	-	3.92	-	4.30
Oak	4.9	2.93	3.11	-	3.57	-	-	-
Obabika	3.9	-	3.52	-	-	-	3.49	-
Pickerel	4.2	3.05	3.42	-	-	4.02	3.57	4.53
Peninsula	3.3	-	-	-	4.63	-	-	-
Rice	7.3	-	3.34	3.76	-	-	-	4.09
Robertson	4.0	3.54	3.46	4.17	3.79	-	4.51	-
Round	5.4	3.18	3.40	-	4.17	-	-	4.48
Sand	3.9	-	4.07	-	-	-	-	-
Steenburg	3.9	3.21	3.43	3.81	4.18	-	-	-
Sturgeon	4.8	3.11	3.65	4.09	-	-	-	4.29
Wollaston	4.3	3.52	-	-	-	-	-	-

APPENDIX 7. Stable isotope data from 14 lakes used in this analysis. Numbers following lake names are lake number from Table 1. lit. = littoral, pel. = pelagic, pro. = profundal.

Taxon and lake	habitat	$\delta^{13}C$	$\delta^{15}N$
Twelve Mile Lake (4)			
Amphipoda	lit.	-19.01	2.35
Ephemeroptera	lit.	-26.23	5.45
Trichoptera	lit.	-23.91	0.10
Unionidae	pel.	-27.58	1.55
Shallow Zooplankton	pel.	-26.89	2.57
Shallow Zooplankton	pel.	-25.06	3.26
Chironomidae	pro.	-30.64	5.54
Chironomidae	pro.	-30.19	5.86
Ephemeroptera	pro.	-30.94	7.11
Deep Zooplankton	pro.	-26.36	2.59
Clean Lake (12)			
Amphipoda	lit.	-19.70	-1.06
Ephemeroptera	lit.	-26.20	2.32
Trichoptera	lit.	-27.31	0.25
Trichoptera	lit.	-24.80	0.22
Chironomidae	pro.	-30.25	5.08
Deep Zooplankton	pro.	-36.48	5.46
Deep Zooplankton	pro.	-25.42	2.84
Dickey Lake (5)			
Miscellaneous	lit.	-26.01	4.38
Unionidae	pel.	-30.28	3.98
Shallow Zooplankton	pel.	-30.40	5.17
Chironomidae	pro.	-34.74	4.88
Chironomidae	pro.	-33.70	8.68
Deep Zooplankton	pro.	-35.52	8.82
Happy Isle Lake (11)			
Trichoptera	lit.	-31.34	5.41
Trichoptera	lit.	-22.45	0.39
Unionidae	pel.	-26.59	1.08

Taxon and lake	habitat	$\delta^{13}C$	$\delta^{15}N$
Muskoka Lake (2)			
Amphipoda	lit.	-22.55	1.82
Ephemeroptera	lit.	-22.70	4.16
Trichoptera	lit.	-25.96	3.87
Unionidae	pel.	-27.53	5.08
Shallow Zooplankton	pel.	-26.32	4.38
Chironomidae	pro.	-27.52	8.43
Deep Zooplankton	pro.	-27.35	5.91
Lake Opeongo (9)			
Amphipoda	lit.	-26.55	1.14
Miscellaneous	lit.	-27.07	0.98
Frog tadpoles	lit.	-29.06	3.83
Frog tadpoles	lit.	-26.01	3.41
Trichoptera	lit.	-24.94	1.71
Unionidae	pel.	-28.57	1.63
Shallow Zooplankton	pel.	-31.77	2.32
Shallow Zooplankton	pel.	-29.32	2.07
Chironomidae	pro.	-28.60	6.11
Deep Zooplankton	pro.	-31.59	2.30
Deep Zooplankton	pro.	-28.04	3.48
Lake Rosseau (3)			
Amphipoda	lit.	-18.48	0.81
Miscellaneous	lit.	-18.85	2.02
Trichoptera	lit.	-21.45	1.01
Unionidae	pel.	-28.34	2.91
Chironomidae	pro.	-29.19	6.82
Chironomidae	pro.	-28.87	7.30
Smoke Lake (6)			
Amphipoda	lit.	-16.22	1.45
Ephemeroptera	lit.	-21.91	1.07

Chironomidae	pro.	-31.80	3.79
Chironomidae	pro.	-29.72	3.91
Louisa Lake (14)			
Amphipoda	lit.	-22.43	-1.29
Ephemeroptera	lit.	-28.39	0.25
Ephemeroptera	lit.	-25.75	-1.37
Miscellaneous	lit.	-25.06	0.93
Frog tadpoles	lit.	-	-0.52
Trichoptera	lit.	-23.54	-1.62
Unionidae	pel.	-27.73	2.62
Chironomidae	pro.	-34.08	2.16
Chironomidae	pro.	-30.74	5.32
Deep Zooplankton	pro.	-31.65	1.71
Deep Zooplankton	pro.	-31.58	3.35
MacDonald Lake (8)			
Amphipoda	lit.	-21.38	-0.32
Ephemeroptera	lit.	-23.38	2.09
Miscellaneous	lit.	-20.94	2.30
Trichoptera	lit.	-25.27	1.39
Trichoptera	lit.	-23.85	0.72
Unionidae	pel.	-31.54	3.00
Shallow Zooplankton	pel.	-24.40	3.01
Chironomidae	pro.	-29.53	5.86
Deep Zooplankton	pro.	-26.85	3.88
Lake Memphremagog (1)			
Amphipoda	lit.	-25.03	5.63
Amphipoda	lit.	-25.65	5.30
Trichoptera	lit.	-26.99	5.30
Unionidae	pel.	-29.58	8.05
Chironomidae	pro.	-32.74	8.91
Deep Zooplankton	pro.	-31.74	10.41
Trichoptera	lit.	-26.24	1.51
Unionidae	pel.	-24.61	3.35
Deep Zooplankton	pro.	-28.46	1.70
Source Lake (10)			
Amphipoda	lit.	-23.50	1.93
Trichoptera	lit.	-27.08	0.41
Unionidae	pel.	-25.42	1.80
Shallow Zooplankton	pel.	-27.32	0.41
Chironomidae	pro.	-32.92	4.27
Chironomidae	pro.	-29.29	4.79
Deep Zooplankton	pro.	-27.66	6.36
Deep Zooplankton	pro.	-29.35	2.55
Lake Temagami (13)			
Amphipoda	lit.	-	0.23
Frog tadpoles	lit.	-21.29	-0.45
Unionidae	pel.	-29.10	1.43
Shallow Zooplankton	pel.	-26.77	-0.41
Chironomidae	pro.	-30.46	2.75
Deep Zooplankton	pro.	-28.04	4.07
Victoria Lake (7)			
Amphipoda	lit.	-22.16	2.84
Ephemeroptera	lit.	-21.15	0.95
Ephemeroptera	lit.	-24.32	0.71
Miscellaneous	lit.	-24.02	2.41
Frog tadpoles	lit.	-23.95	1.72
Unionidae	pel.	-28.38	1.55
Shallow Zooplankton	pel.	-29.08	0.43
Chironomidae	pro.	-30.58	7.80
Deep Zooplankton	pro.	-30.33	2.16

APPENDIX 8: Data for Chapters 4 and 5. Trophic position estimates and total length (mm) for individual lake trout included in this study. Final bold value for each lake is the mean trophic position and variance.

lake trout trophic position Mean (Variance)	total length (mm)
Clean	
3.72	.
3.83	342
3.79	330
3.88	307
3.71	388
3.60	293
3.94	380
3.89	361
3.90	320
4.08	362
3.62	250
4.14	383
4.12	393
3.88	274
3.88	155
3.87 (0.03)	
Dickie	
3.38	218
3.64	206
3.27	385
3.33	313
3.38	341
3.38	332
3.56	235
3.49	326
3.66	188
3.57	352
3.52	190
3.65	326
3.66	351
3.73	378
3.51 (0.02)	
Happy Isle	
2.41	199
3.02	331
2.67	145
3.19	420
2.92	265
3.23	178
2.89	190
3.29	397
2.89	205
3.31	340
3.43	123
3.40	410
3.53	377
3.58	410
3.63	416
3.24	133
3.18	149
3.17 (0.11)	

lake trout trophic position Mean (Variance)	total length (mm)
Smoke	
4.12	435
4.05	161
4.46	306
4.35	460
4.06	139
4.28	149
4.52	235
4.27	142
4.31	205
4.58	432
4.60	253
4.09	650
4.39	630
4.70	232
4.81	620
4.37 (0.06)	
Victoria	
3.30	113
3.63	152
3.92	245
3.85	270
3.78	310
3.60	681
3.76	302
3.97	238
3.58	547
3.94	613
3.84	412
4.09	649
4.26	257
3.81 (0.06)	
Twelve Mile	
3.93	575
4.02	220
4.09	445
4.08	410
4.01	345
3.95	325
4.21	420
4.25	249
4.35	291
4.49	242
4.51	250
4.50	261
5.00	221
4.94	250
4.31 (0.12)	

lake trout trophic position Mean (Variance)	total length (mm)
Louisa	
4.48	442
4.65	508
4.70	426
4.69	194
4.72	214
4.77	278
4.76	344
4.81	453
4.88	259
4.98	497
4.95	307
4.97	289
4.98	421
4.97	334
5.06	392
4.95	.
4.97	318
4.97	447
5.03	287
5.72	441
4.90 (0.06)	
MacDonald	
3.07	250
3.12	250
3.31	94
3.23	.
3.33	.
2.67	.
2.76	.
2.84	.
2.93	.
3.49	.
3.53	.
3.09	.
3.16	.
3.14	.
3.10	.
3.12 (0.06)	

lake trout trophic position Mean (Variance)	total length (mm)
Memphremagog	
4.07	485
4.42	325
4.37	436
4.54	680
4.30	640
4.36	746
4.36	878
4.99	206
4.47	470
4.47	745
4.49	611
4.73	405
4.68	433
4.72	411
4.64	425
4.71	454
4.72	468
4.58	723
4.89	480
4.55 (0.05)	
Muskoka	
3.79	691
4.47	274
4.53	387
4.87	781
4.68	265
4.50	301
4.14	392
4.61	719
4.53	528
4.92	538
4.61	654
4.84	702
4.76	375
4.96	469
4.79	710
5.16	678
4.65	739
4.76	678
4.64 (0.10)	

lake trout trophic position Mean (Variance)	total length (mm)
Source	
3.31	360
3.38	371
3.89	318
3.71	277
3.61	243
3.48	320
3.73	365
3.47	281
3.61	239
3.64	196
3.56	211
3.55	162
3.85	191
4.09	361
3.82	103
4.28	385
3.80	102
4.11	250
3.72 (0.07)	
Opeongo	
3.56	290
3.78	187
4.08	185
4.01	194
4.18	337
4.46	305
4.32	190
4.05	758
4.35	204
3.97	441
4.29	549
4.22	235
4.22	803
4.11	421
4.34	459
4.24	691
4.07	803
4.40	504
4.20	611
4.15	459
4.17	660
4.15 (0.04)	

lake trout trophic position Mean (Variance)	total length (mm)
Rosseau	
4.22	452
4.25	681
4.29	368
4.31	515
4.39	255
4.20	274
4.39	369
4.43	248
4.26	352
4.53	589
4.61	474
4.54	691
4.49	369
4.40	622
4.66	525
4.03	565
4.39	290
4.70	297
4.66	341
4.37	543
5.45	1079
4.46 (0.08)	
Temagami	
4.38	142
4.65	135
4.40	144
4.24	546
4.87	133
4.35	608
4.52	499
4.24	640
4.29	613
4.56	372
4.49	549
4.71	395
4.64	331
4.72	454
4.97	310
4.50	568
4.66	617
4.51	549
4.96	726
4.75	717
5.08	404
4.60 (0.05)	