

Comparing trophic position of freshwater fish calculated using stable nitrogen isotope ratios ($\delta^{15}\text{N}$) and literature dietary data

M. Jake Vander Zanden, Gilbert Cabana, and Joseph B. Rasmussen

Abstract: Stable nitrogen isotope ratios ($\delta^{15}\text{N}$) are commonly used to represent the trophic structure of aquatic systems, yet the ability of $\delta^{15}\text{N}$ to indicate the trophic position of aquatic consumers remains untested using traditional dietary methods. Interpreting the $\delta^{15}\text{N}$ 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 $\delta^{15}\text{N}$. We used this method to estimate the trophic position of eight littoral fish species from 36 lakes in Ontario and Quebec. We validated these $\delta^{15}\text{N}$ 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 to ^{15}N estimates, with mean trophic position ranging from 3.3 for pumpkinseed (*Lepomis gibbosus*) to 4.4 for walleye (*Stizostedion vitreum*). Both methods indicated approximately one trophic level of variation among populations of a species. This study confirms the ability of baseline-adjusted $\delta^{15}\text{N}$ to represent the trophic position of aquatic consumers.

Résumé : Les rapports d'un isotope stable de l'azote ($\delta^{15}\text{N}$) sont couramment utilisés pour représenter la structure trophique des systèmes aquatiques; pourtant, la capacité du $\delta^{15}\text{N}$ d'indiquer la position trophique des consommateurs aquatiques n'a pas encore été testée employant des méthodes alimentaires traditionnels. L'interprétation de $\delta^{15}\text{N}$ des consommateurs aquatiques par rapport aux consommateurs primaires de grande taille et de longue durée de vie comme les moules de la famille des unionidés fournit une mesure continue de la position trophique d'un organisme qui s'ajuste pour tenir compte de la variation intersystèmes de $\delta^{15}\text{N}$ de base. Nous avons utilisé cette méthode pour estimer la position trophique de huit espèces de poissons littoraux dans 36 lacs du Québec et de l'Ontario. Nous avons validé ces mesures de position trophique par $\delta^{15}\text{N}$ en rassemblant, dans la documentation scientifique, les données sur le régime alimentaire de 342 populations de ces mêmes espèces de poisson et avons calculé une mesure continue de la position trophique de chacune de ces populations. Les valeurs estimées de la position trophique alimentaire moyenne correspondaient étroitement aux valeurs estimées de ^{15}N , la position trophique moyenne variant de 3,3 pour le crapet-soleil (*Lepomis gibbosus*) à 4,4 pour le doré jaune (*Stizostedion vitreum*). Les deux méthodes ont indiqué une variation d'environ un niveau trophique entre les populations d'une même espèce. Cette étude confirme la capacité du $\delta^{15}\text{N}$ ajusté en fonction de la ligne de base de représenter la position trophique des consommateurs aquatiques.

[Traduit par la Rédaction]

Introduction

Accurate representation and description of trophic relationships are essential to a wide range of ecological studies. The concept of discrete trophic levels is 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; Wootton 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

Received April 9, 1996. Accepted October 7, 1996.
J13395

M.J. Vander Zanden,¹ G. Cabana,² and J.B. Rasmussen.
Department of Biology, McGill University, 1205 Ave. Docteur
Penfield, Montreal, QC H3A 1B1, Canada.

¹ Author to whom all correspondence should be addressed.
e-mail: jzanden@bio1.lan.mcgill.ca

² Present address: Department of Integrative Biology,
University of California at Berkeley, Berkeley, CA 94720,
U.S.A.

1994) and polychlorinated biphenyls (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 ($3.4 \pm 0.3\text{‰}$) 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 stable isotope – food web studies have been complicated by among-system variation in the ^{15}N signatures characterizing primary producers at the base of the food web. Cabana and Rasmussen (1996) overcame this problem by measuring an organism's ^{15}N ratios ($\delta^{15}\text{N}$) relative to the lake-specific $\delta^{15}\text{N}$ signature of commonly occurring primary consumers such as unionid mussels. This provides a continuous measure of an organism's trophic position amenable to comparative, multisystem studies of trophic structure.

The objective of this study was to verify $\delta^{15}\text{N}$ as a measure of trophic position for a series of littoral freshwater fish species. We calculated the trophic position of eight species of freshwater fish using dietary data and ^{15}N and compared the mean and variation in trophic position estimates attained using the two techniques. Previous studies have attempted to verify the $\delta^{15}\text{N}$ measure of trophic position using within-system comparisons between dietary data and $\delta^{15}\text{N}$ (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 $\delta^{15}\text{N}$ 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 $\delta^{15}\text{N}$ 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 dolomieu*), 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 was 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, northern 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 percentage of dry or wet weight). Data reported in the "percentage of total number of prey organisms" format were converted to percentage 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 was 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 to the period of time for which an adult fish's diet is integrated using ^{15}N (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, northern 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 were 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

$$(1) \quad T_a = \sum(V_i T_i) + 1$$

where T_a = mean trophic position of the a th predator population, V_i = volumetric contribution of the i th prey item, and T_i = trophic position of the i th 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.

^{15}N calculation of trophic position

Adult individuals of these eight fish species were collected from 36 lakes (113 fish populations) in Ontario and Quebec and were analyzed for $\delta^{15}\text{N}$ using a Europa Tracer mass spectrometer (Cabana and

Table 1. Estimated trophic position values for prey items used in dietary calculations of trophic position.

Prey category	Estimated trophic position	Includes
Fish	2.5	Cyprinids
	3.0	Alewife ^a
	3.2	Whitefish, ^a cisco ^a
	3.3	Centrarchids
	3.5	Suckers, trout, burbot, white bass, unidentified fish, others
	3.7	Yellow perch, trout-perch, ^a stickleback, ^a smelt, ^a sculpins ^a
Zooplankton	2.5	Cladocera, Copepoda, Ostracoda, Rotifera
Omnivorous zoobenthos	2.5	Tricoptera, Ephemeroptera, Plecoptera, Hemiptera, Coleoptera, Diptera, Oligochaeta, Amphipoda (<i>Gammarus</i> sp., <i>Hyaella</i> sp., <i>Diporia hoyi</i> , <i>Mysis relicta</i>), 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

^aTrophic position estimated using dietary data (from Vander Zanden and Rasmussen 1996).

Rasmussen 1996). These N isotopic values alone cannot be considered to represent trophic position, since the $\delta^{15}\text{N}$ of primary producers (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" $\delta^{15}\text{N}$ signature. Cabana and Rasmussen (1996) interpreted fish $\delta^{15}\text{N}$ relative to unionid mussels. These relatively large and long-lived primary consumer organisms integrate temporal variability in primary producer $\delta^{15}\text{N}$, thereby representing the average baseline $\delta^{15}\text{N}$ signature. Unionid mussel $\delta^{15}\text{N}$ ($n = 1-9$ 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

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

where 3.4 represents a 1.0 trophic level increment in $\delta^{15}\text{N}$.

Results

Dietary estimates of trophic position

The raw dietary data compiled for this study are presented in Appendix I. These data were summarized by calculating the average diet (percentage 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. Fifty-

three percent of yellow 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. Fifty percent of the average diet of largemouth bass consisted of fish prey. Both northern pike and walleye consumed about 85% fish. More detailed analysis of the fish components of the diets of northern pike and walleye (Appendix II) shows that walleye consume 29% yellow perch and only 8% cyprinids. Walleye diet also shows major contributions from smelt, trout-perch, and centrarchids. Northern pike consumed a broader range of prey, consuming similar amounts of yellow perch and cyprinids (13% each).

Species exhibit a mean dietary trophic position estimate ranging from 3.3 to 4.4 (Fig. 1). Pumpkinseed exhibit the lowest average dietary trophic position value of 3.3, while yellow perch and rock bass average 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 exhibit intermediate trophic position values averaging approximately 4.0, making them tertiary consumers. The piscivores, northern pike and walleye, both exhibit 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 remains the same, while that of northern pike drops by 0.07 trophic level.

$\delta^{15}\text{N}$ estimates of trophic position

Average unionid mussel $\delta^{15}\text{N}$ values (reported by lake) and estimates of mean trophic position for each fish population in this study are presented in Appendix III. Seventy-eight percent of the variance in individual mussel $\delta^{15}\text{N}$ signatures is explained by the lake variable. Furthermore, the species of mussel did not vary significantly with mussel $\delta^{15}\text{N}$ (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 $\delta^{15}\text{N}$ trophic position estimates (± 1 SD) are directly compared with the mean dietary estimates of trophic position for each species (Fig. 1; Table 3). The two measures of trophic position are in close correspondence ($\delta^{15}\text{N}$ trophic position = $0.78 \times$ dietary trophic position + 0.81 ; $r^2 = 0.78$). Northern pike are the only outlier, as northern pike gut content data indicate a mean trophic position value nearly 0.4 trophic level higher than the $\delta^{15}\text{N}$ trophic position estimate.

Among-population variability in trophic position

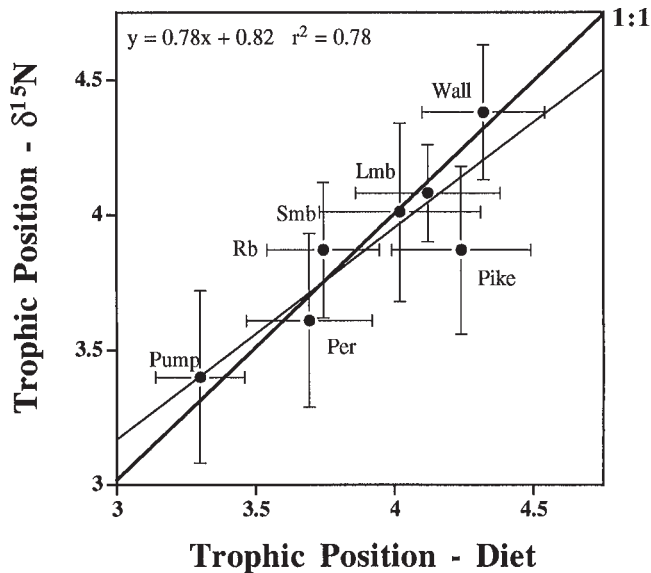
Both dietary and isotopic evidence indicates relatively high levels of among-population variability, as seen in frequency histograms of dietary and $\delta^{15}\text{N}$ trophic position values (Fig. 2). The total range of trophic position among all species spans roughly two complete trophic levels.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

Table 2. Mean dietary data for littoral fish species included in this study.

Species	<i>n</i> lakes	<i>n</i> fish	Fish	Zoop	Ben	Pred ben	Mol	Cray	Det	Other
Pumpkinseed	27	2 000	0.0	1.6	36.2	5.6	39.9	1.3	5.5	9.7
Yellow perch	91	8 075	17.2	13.6	53.9	4.3	2.3	4.4	0.8	3.1
Rock bass	25	1 962	10.0	3.0	42.2	2.8	1.7	31.2	2.1	6.4
Smallmouth bass	79	3 162	37.6	2.0	28.8	1.2	0.1	27.3	0.7	2.3
Largemouth bass	21	5 664	53.3	4.9	11.0	9.3	0.0	10.6	1.9	8.6
Northern pike and chain pickerel	67	34 738	84.1	0.0	3.5	2.5	0.0	7.8	0.2	1.9
Walleye	32	10 386	83.3	2.0	10.7	0.5	0.0	2.5	0.2	0.8
Total	342	65 987								

Note: Zoop, zooplankton; Ben, zoobenthos; Pred ben, predatory zoobenthos; Mol, molluscs; Cray, crayfish; Det, detritus; Other, unidentified material, mammals, amphibians, birds.

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



position causes 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 correspond quite closely. Using diet data, 1 SD in trophic position averages 0.23 trophic level (range 0.11–0.28 trophic level), while for $\delta^{15}\text{N}$ estimates, 1 SD averages 0.29 trophic level (range 0.18–0.34 trophic level).

Discussion

Role of ^{15}N in food web studies

The application of $\delta^{15}\text{N}$ 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 $\delta^{15}\text{N}$ 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 $\delta^{15}\text{N}$ is increasingly common as a tracer of trophic relationships, the N 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, $\delta^{15}\text{N}$ should reflect an organism’s trophic position for single-system studies (see Hobson and Welsh 1992; Wainright et al. 1993), but the applicability of $\delta^{15}\text{N}$ 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) used mussel $\delta^{15}\text{N}$ signatures to correct for variability in average baseline $\delta^{15}\text{N}$ 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 N isotopic signature. Measurement of an organism’s $\delta^{15}\text{N}$ 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 $\delta^{15}\text{N}$ method by comparing the average trophic position of eight common species of fish estimated from N isotope data with estimates obtained from a large fish dietary database. The close correspondence between the estimates of trophic position based on $\delta^{15}\text{N}$ 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 $\delta^{15}\text{N}$ give corresponding estimates of average trophic position, the many advantages of $\delta^{15}\text{N}$ 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 $\delta^{15}\text{N}$ and gut content evidence. $\delta^{15}\text{N}$ is used to quantify an organism’s trophic position, while diet data, although subject to error when calculating trophic position for individual communities, reveal specifically which taxa are involved in feeding interactions.

Concept of trophic position

The prevalence of omnivory and the complexity of natural food webs suggest that neither discrete food chain nor connectance food web approaches will adequately represent the pathways

Table 3. Mean trophic position for each species of fish, 1 SD of the mean trophic position, range of trophic position values, and number of fish populations, calculated using dietary and $\delta^{15}\text{N}$ methods.

Species	Dietary				$\delta^{15}\text{N}$			
	Mean trophic position	SD	Range	<i>n</i> lakes	Mean trophic position	SD	Range	<i>n</i> 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) ^a	0.22	4.15–4.51	67	3.87	0.32	3.38–4.51	20
Walleye	4.33 (4.35) ^a	0.25	3.91–4.50	32	4.40	0.24	4.09–4.86	10

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

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 characterize 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 noninteger 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 versus pelagic predators). Use of stable C isotope ratios augments N isotope trophic position evidence by serving as a means of discriminating between benthic and pelagic sources of production (Hecky and Hesslein 1995).

Patterns in trophic position

The range in trophic position values is approximately one 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 $\delta^{15}\text{N}$ 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 $\delta^{15}\text{N}$ 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 northern pike (3.69) by about 0.75 trophic level in Lake Mazinaw, but the respective trophic positions of these two species are essentially reversed in Lake Doré (trophic positions of 3.91 and 4.41 for smallmouth bass and northern 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.

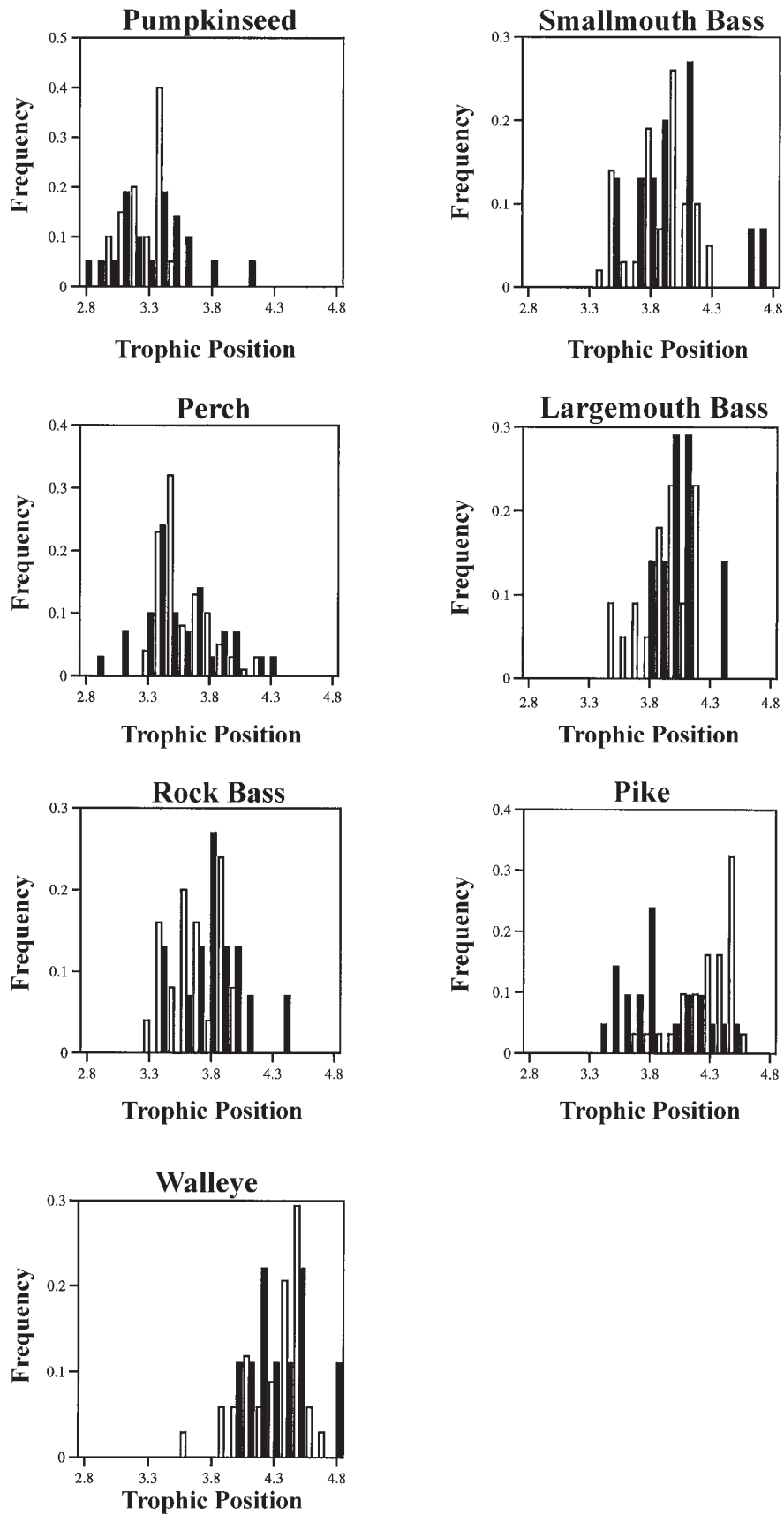
Dietary versus isotopic approaches

Although we report a close correspondence between dietary and $\delta^{15}\text{N}$ estimates of trophic position, certain limitations of the dietary approach need to 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 reported that North American zooplankton food webs have a modal food chain length varying from one to eight trophic levels (averaging between three and five 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 $\delta^{15}\text{N}$ estimates of trophic position involves the differences in the way the two methods integrate variation in trophic position.

Fig. 2. Proportional frequency distributions of lake-specific trophic position values for littoral fish, calculated using dietary data (open bars) and baseline-corrected $\delta^{15}\text{N}$ (solid bars).



$\delta^{15}\text{N}$ 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 provides 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 ^{15}N estimates of trophic position on a lake-specific basis can only provide a robust test of $\delta^{15}\text{N}$ 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 that 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 $\delta^{15}\text{N}$ and dietary data for northern pike

Although $\delta^{15}\text{N}$ and dietary estimates of trophic position are in general agreement, dietary estimates for northern pike overestimate trophic position relative to $\delta^{15}\text{N}$. Determining specifically which fish taxa serve as prey of northern pike and walleye reveals the importance of yellow perch in the diet of walleye (29%) relative to northern pike (13%), while northern pike and walleye consume similar amounts of cyprinids. The high mean trophic position of yellow perch (3.7) relative to cyprinids (M.J. Vander Zanden, unpublished isotope data; DeVries and Stein 1992) may partially explain the discrepancy between $\delta^{15}\text{N}$ and dietary trophic position of northern pike.

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

Although northern 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 northern pike discrepancy. For our northern pike diet data set, lake size was positively correlated with northern pike trophic position (northern pike trophic position = $0.026(\log \text{ lake area}) + 4.21$; $n = 36$, $p = 0.008$, $r^2 = 0.19$), and our northern pike diet study lakes tended to be larger than our $\delta^{15}\text{N}$ study lakes. Although the difference in trophic position of northern pike remains unresolved, lake-specific diet data – $\delta^{15}\text{N}$ 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 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 appear 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 $\delta^{15}\text{N}$ signatures at the base of the food web. Cabana and Rasmussen (1996) proposed the use of long-lived sedentary primary consumers such as unionid mussels to control for such baseline variation in $\delta^{15}\text{N}$ when calculating trophic position of consumers. The present study confirms the validity of this method by showing that $\delta^{15}\text{N}$ -based estimates of trophic position in eight species of fish are strongly correlated with their trophic position estimated from dietary data.

Acknowledgments

Thanks to Jennifer Viau for laboratory assistance and Shapna Mazumder for operation of the mass spectrometer. This study was supported by a NSERC strategic grant to J.B.R. G.C. was supported by a Vineberg Fellowship. M.J.V.Z. was supported by funding from the Ontario Ministry of Natural Resources.

References

- Adams, C.C., and Hankinson, T.L. 1928. The ecology and economics of Oneida lake fish. *Roosevelt Wildl. Ann.* **1**: 241–358.
- Bennett, G.W. 1948. The bass–bluegill combination in a small artificial lake. *Bull. Ill. Nat. Hist. Surv.* **24**: 377–412.
- Boisclair, D. 1988. Among population variability in fish growth rates: the influence of food consumption, prey type, and fish community. Ph.D. thesis, McGill University, Montreal, Que.
- Bryan, S.D., Hill, T.D., Lynott, S.T., and Duffy, W.G. 1995. The influence of changing water levels and temperatures on the food habits of walleye in Lake Oahe, South Dakota. *J. Freshwater Ecol.* **10**: 1–10.
- Bryant, H.E., and Moen, T.E. 1980. Food of largemouth bass (*Micropterus salmoides*) in Degray Reservoir, Arkansas, 1976. *Ark. Acad. Sci. Proc.* **34**: 34–37.
- Cabana, G., and Rasmussen, J.B. 1994. Modelling food chain structure and contaminant bioaccumulation using stable nitrogen isotopes. *Nature (Lond.)*, **372**: 255–257.
- Cabana, G., and Rasmussen, J.B. 1996. Comparing aquatic food chains using nitrogen isotopes. *Proc. Natl. Acad. Sci. U.S.A.* **93**: 10 844 – 10 847.
- Cabana, G., Tremblay, A., Kalff, J., and Rasmussen, J.B. 1994. Pelagic

- food chain structure in Ontario lakes: a determinant of mercury levels in lake trout. *Can. J. Fish. Aquat. Sci.* **51**: 381–389.
- Carpenter, S.R., Kitchell, J.F., and Hodgson, J.R. 1985. Cascading trophic interactions and lake productivity. *BioScience*, **35**: 381–389.
- Chapman, L.J., and Mackay, W.C. 1990. Ecological correlates of feeding flexibility in northern pike (*Esox lucius*). *J. Freshwater Ecol.* **5**: 313–322.
- Chapman, L.J., Mackay, W.C., and Wilkinson, C.W. 1989. Feeding flexibility in northern pike (*Esox lucius*): fish versus invertebrate prey. *Can. J. Fish. Aquat. Sci.* **46**: 666–669.
- Clady, M.D. 1974. Food habits of yellow perch, smallmouth bass and largemouth bass in two unproductive lakes in Northern Michigan. *Am. Midl. Nat.* **91**: 453–459.
- Clemens, W.A., Dymond, J.R., Bigelow, N.K., Adamstone, F.B., and Harkness, W.J.K. 1923. The food of Lake Nipigon fishes. *Univ. Toronto Stud. Biol.* **22**: 173–188.
- Clemens, W.A., Dymond, J.R., and Bigelow, N.K. 1924. Food studies of Lake Nipigon fishes. *Univ. Toronto Stud. Biol.* **25**: 103–165.
- Cooper, G.P. 1941. A biological survey of lakes and ponds of the Androscoggin and Kennebec River Drainage Systems in Maine. *Maine Dep. Inland Fish. Game Fish Surv. Rep. No. 4*.
- Cooper, G.P. 1942. A biological survey of lakes and ponds of the central coastal area of Maine. *Maine Dep. Inland Fish. Game Fish Surv. Rep. No. 5*.
- Couey, F.M. 1935. Fish food studies of a number of northeastern Wisconsin lakes. *Wis. Acad. Sci. Art. Lett.* **29**: 131–172.
- Craig, J.F., and Babaluk, J.A. 1989. Relationship of condition of walleye (*Stizostedion vitreum*) and northern pike (*Esox lucius*) to water clarity, with special reference to Dauphin Lake, Manitoba. *Can. J. Fish. Aquat. Sci.* **46**: 1581–1586.
- Cummins, K.W., and Wuycheck, J.C. 1971. Caloric equivalents for investigations in ecological energetics. *Int. Assoc. Theor. Appl. Limnol.* **18**: 1–158.
- DeVries, D.R., and Stein, P.A. 1992. Complex interactions between fish and zooplankton: quantifying the role of an open-water planktivore. *Can. J. Fish. Aquat. Sci.* **49**: 1216–1227.
- Diana, J.S. 1979. The feeding pattern and daily ration of a top carnivore, the northern pike (*Esox lucius*). *Can. J. Zool.* **57**: 2121–2127.
- Dill, L.M. 1983. Adaptive flexibility in the foraging behavior of fishes. *Can. J. Fish. Aquat. Sci.* **40**: 398–408.
- Doan, K.H. 1940. Studies of the smallmouth bass. *J. Wildl. Manage.* **4**: 241–267.
- Driver, E.A., Sugden, L.G., and Kovach, R.J. 1974. Calorific, chemical and physical values of potential duck foods. *Freshwater Biol.* **4**: 281–292.
- Etnier, D.A. 1971. Food of three species of sunfishes (*Lepomis, Centrarchidae*) and their hybrids in three Minnesota lakes. *Trans. Am. Fish. Soc.* **100**: 124–128.
- Fedoruk, A.N. 1966. Feeding relationships of walleye and smallmouth bass. *J. Fish. Res. Board Can.* **22**: 941–943.
- Flemer, D.A., and Woolcott, W.S. 1966. Food habits and distribution of the fishes of Tuckahoe Creek, Virginia, with special emphasis on the bluegill, *Lepomis m. macrochirus* Rafinesque. *Chesapeake Sci.* **7**: 75–89.
- Foote, L.E., and Blake, B.P. 1945. Life history of the eastern pickerel in Babcock Pond, Connecticut. *J. Wildl. Manage.* **9**: 89–96.
- Fox, M.G., and Keast, A. 1990. Effects of winterkill on population structure, body size, and prey consumption patterns of pumpkinseed in isolated beaver ponds. *Can. J. Zool.* **68**: 2489–2498.
- Fraser, J.M. 1978. The effect of competition with yellow perch on the survival and growth of planted brook trout, splake, and rainbow trout in a small Ontario lake. *Trans. Am. Fish. Soc.* **107**: 505–517.
- Griswold, B.L., and Tubb, R.A. 1977. Food of yellow perch, white bass, freshwater drum, and channel catfish in Sandusky Bay, Lake Erie. *Ohio J. Sci.* **77**: 43–47.
- Gu, B., Schell, D.M., and Alexander, V. 1994. Stable carbon and nitrogen isotopic analysis of the plankton food web in a subarctic lake. *Can. J. Fish. Aquat. Sci.* **51**: 1338–1344.
- Hazel, P.P., and Fortin, R. 1986. Le doré jaune (*Stizostedion vitreum* Mitchell) au Québec: biologie et gestion. Ministère du Loisir, de la Chasse et de la Pêche, Québec, Qué.
- Hecky, R.E., and Hesslein, R.H. 1995. Contributions of benthic algae to lake food webs as revealed by stable isotope analysis. *J. N. Am. Benthol. Soc.* **14**: 631–653.
- Herman, M.L., Campbell, R.S., and Redmond, L.C. 1969. Manipulation of fish populations through reservoir drawdown. *Trans. Am. Fish. Soc.* **98**: 293–304.
- Hesslein, R.H., Hallard, K.A., and Ramlal, P. 1993. Replacement of sulfur, carbon, and nitrogen in tissue of growing broad whitefish (*Coregonus nasus*) in response to a change in diet traced by ³⁴S, ¹³C, and ¹⁵N. *Can. J. Fish. Aquat. Sci.* **50**: 2071–2076.
- Hobson, K.A., and Welsh, H.E. 1992. Determination of trophic relationships within a high Arctic marine food web using $\delta^{13}\text{C}$ an $\delta^{15}\text{N}$ analysis. *Mar. Ecol. Prog. Ser.* **84**: 9–18.
- Hodgson, J.R., Carpenter, S.R., and Gripenrog, A.P. 1989. Effect of sampling frequency on intersample variance and food consumption estimates of nonpiscivorous largemouth bass. *Trans. Am. Fish. Soc.* **118**: 11–19.
- Hodgson, J.R., Hodgson, C.J., and Brooks, S.M. 1991. Trophic interaction and competition between largemouth bass (*Micropterus salmoides*) and rainbow trout (*Oncorhynchus mykiss*) in a manipulated lake. *Can. J. Fish. Aquat. Sci.* **48**: 1704–1712.
- Hunt, B.P., and Carbin, W.F. 1950. Food of young pike, *Esox lucius*, and associated fishes in Peterson's ditches, Houghton Lake, Michigan. *Trans. Am. Fish. Soc.* **79**: 67–83.
- Hunt, R.L. 1965. Food of northern pike in a Wisconsin trout stream. *Trans. Am. Fish. Soc.* **94**: 95–97.
- Hunter, G.W. III, and Rankin, J.S. Jr. 1939. The food of pickerel. *Copeia*, **4**: 194–199.
- Hurley, D.A., and Christie, W.J. 1977. Depreciation of the warmwater fish community in the Bay of Quinte, Lake Ontario. *J. Fish. Res. Board Can.* **34**: 1849–1860.
- Johnson, F.H. 1977. Response of walleye (*Stizostedion vitreum vitreum*) and yellow perch (*Perca flavescens*) populations to removal of white sucker (*Catostomus commersoni*) from a Minnesota lake, 1966. *J. Fish. Res. Board Can.* **34**: 1633–1642.
- Johnson, F.H., and Hale, J.G. 1977. Interrelations between walleye (*Stizostedion vitreum vitreum*) and smallmouth bass (*Micropterus dolomieu*) in four northeastern Minnesota lakes, 1948–69. *J. Fish. Res. Board Can.* **34**: 1626–1632.
- Johnson, J.H., and Dropkin, D.S. 1995. Diel feeding chronology of six fish species in the Juniata River, Pennsylvania. *J. Freshwater Ecol.* **10**: 11–18.
- Johnson, L. 1972. Keller Lake: characteristics of a culturally unstressed salmonid community. *J. Fish. Res. Board Can.* **29**: 731–740.
- Keast, A. 1977. Diet overlaps and feeding relationships between the year classes in the yellow perch (*Perca flavescens*). *Environ. Biol. Fishes*, **2**: 53–70.
- Keast, A., and Welsh, L. 1968. Daily feeding periodicities, food uptake rates, and dietary changes with h of day in some lake fishes. *J. Fish. Res. Board Can.* **25**: 1133–1144.
- Kelso, J.R. 1973. Seasonal energy changes in walleye and their diet in West Blue Lake, Manitoba. *Trans. Am. Fish. Soc.* **103**: 363–368.
- Kelso, J.R.M., and Ward, F.J. 1977. Unexploited percid populations of West Blue Lake, Manitoba, and their interactions. *J. Fish. Res. Board Can.* **34**: 1655–1669.
- Kerr, S.R., and Martin, N.V. 1970. Tropho-dynamics of lake trout production systems. *In* Marine food chains. Edited by J.H. Steele. Oliver and Boyd, Edinburgh, U.K. pp. 365–376.
- Kidd, K.A., Schindler, D.W., Hesslein, R.H., and Muir, D.C.G. 1995. Correlations between stable nitrogen isotope ratios and concentrations of organochlorines in biota from a freshwater food web. *Sci. Total Environ.* **161**: 381–390.

- Kline, T.C., Goering, J.J., Mathisen, O.A., Poe, P.H., Parker, P.L., and Scalan, R.S. 1993. Recycling of elements transported upstream by runs of Pacific salmon: II. $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ evidence in the Kvichak River watershed, Bristol Bay, Southwestern Alaska. *Can. J. Fish. Aquat. Sci.* **50**: 2350–2365.
- Kling, G.W., Fry, B., and O'Brien, W.J. 1992. Stable isotopes and planktonic trophic structure in arctic lakes. *Ecology*, **73**: 561–566.
- Knight, R.L., Margraf, F.J., and Carline, R.F. 1984. Piscivory by walleyes and yellow perch in western Lake Erie. *Trans. Am. Fish. Soc.* **113**: 677–693.
- Lagler, K.F. 1956. The pike, *Esox lucius* Linnaeus, in relation to waterfowl on the Seney National Wildlife Refuge, Michigan. *J. Wildl. Manage.* **20**: 114–124.
- Laughlin, D.R., and Werner, E.E. 1980. Resource partitioning in two coexisting sunfish: pumpkinseed (*Lepomis gibbosus*) and northern longear sunfish (*Lepomis megalotis peltastes*). *Can. J. Fish. Aquat. Sci.* **37**: 1411–1420.
- Lawler, G.H. 1965. The food of the pike, *Esox lucius*, in Heming lake, Manitoba. *J. Fish. Res. Board Can.* **22**: 1357–1377.
- Lawrence, S.G., Malley, D.F., Findlay, W.J., MacIver, M.A., and Delbaere, I.L. 1987. Method for estimating dry weight of freshwater planktonic crustaceans from measures of length and shape. *Can. J. Fish. Aquat. Sci.* **44**: 264–274.
- Levine, S. 1980. Several measures of trophic structure applicable to complex food webs. *J. Theor. Biol.* **83**: 195–207.
- Lindeman, R.L. 1942. The tropho-dynamic aspect of ecology. *Ecology*, **23**: 399–418.
- Lyons, J., and Magnuson, J.J. 1987. Effects of walleye predation on the population dynamics of small littoral zone fishes in a northern Wisconsin lake. *Trans. Am. Fish. Soc.* **116**: 29–39.
- Mathers, R.A., and Johansen, P.H. 1985. The effects of feeding ecology on mercury accumulation in walleye (*Stizostedion vitreum*) and pike (*Esox lucius*) in Lake Simcoe. *Can. J. Zool.* **63**: 2006–2012.
- McIlwain, T.D. 1970. Stomach contents and length–weight relationships of chain pickerel (*Esox niger*) in south Mississippi waters. *Trans. Am. Fish. Soc.* **99**: 439–440.
- Miller, S.J., and Storck, T. 1984. Temporal spawning distribution of largemouth bass and young-of-the-year, determined from daily otolith rings. *Trans. Am. Fish. Soc.* **113**: 571–578.
- Mills, E.L., and Forney, J.L. 1981. Energetics, food consumption, and growth of young yellow perch in Oneida Lake, New York. *Trans. Am. Fish. Soc.* **110**: 479–488.
- Minagawa, M., and Wada, E. 1984. Stepwise enrichment of ^{15}N along food chains: further evidence and the relation between $\delta^{15}\text{N}$ and animal age. *Geochim. Cosmochim. Acta*, **48**: 1135–1140.
- Moffett, J.W., and Hunt, B.P. 1943. Winter feeding habits of bluegill, *Lepomis macrochirus* (Rafinesque), and yellow perch, *Perca flavescens* (Mitchill), in Cedar Lake, Washtenaw County, Michigan. *Trans. Am. Fish. Soc.* **73**: 231–242.
- Murdoch, W.W. 1966. Community structure, population control, and competition — a critique. *Am. Nat.* **100**: 219–226.
- Nakashima, B.S., and Leggett, W.C. 1975. Yellow perch (*Perca flavescens*) biomass responses to different levels of phytoplankton and benthic biomass in Lake Memphremagog, Quebec–Vermont. *J. Fish. Res. Board Can.* **32**: 1785–1797.
- Owens, N.J.P. 1987. Natural variation in ^{15}N in the marine environment. *Adv. Mar. Biol.* **24**: 390–451.
- Paine, R.T. 1988. Food webs: road maps of interaction or grist for theoretical development? *Ecology*, **69**: 1648–1654.
- Parks, C.E. 1949. The summer food of some game fishes of Winona Lake. *Invest. Ind. Lakes Streams*, **3**: 235–245.
- Parrish, D.L., and Margraf, F.J. 1990. Interactions between white perch (*Morone americana*) and yellow perch (*Perca flavescens*) in Lake Erie as determined from feeding and growth. *Can. J. Fish. Aquat. Sci.* **47**: 1779–1787.
- Parrish, D.L., and Margraf, F.J. 1994. Spatial and temporal patterns of food use by white perch and yellow perch in Lake Erie. *J. Freshwater Ecol.* **9**: 29–35.
- Peterson, B.J., and Fry, B. 1987. Stable isotopes in ecosystem studies. *Annu. Rev. Ecol. Syst.* **18**: 293–320.
- Polis, G.A. 1991. Complex trophic interactions in deserts: an empirical critique of food web theory. *Am. Nat.* **138**: 123–155.
- Priegel, G.R. 1963. Food of walleye and sauger in Lake Winnebago, Wisconsin. *Trans. Am. Fish. Soc.* **92**: 312–313.
- Probst, W.E., Rabeni, C.F., Covington, W.G., and Marteney, R.E. 1984. Resource use by stream-dwelling rock bass and smallmouth bass. *Trans. Am. Fish. Soc.* **113**: 283–294.
- Raney, E.C. 1942. The summer food and habits of the chain pickerel (*Esox niger*) of a small New York pond. *J. Wildl. Manage.* **6**: 58–66.
- Rasmussen, J.B., Rowan, D.J., Lean, D.R.S., and Carey, J.H. 1990. Food chain structure in Ontario lakes determines PCB levels in lake trout (*Salvelinus namaycush*) and other pelagic fish. *Can. J. Fish. Aquat. Sci.* **47**: 2030–2038.
- Rawson, D.S. 1930. The bottom fauna of Lake Simcoe and its role in the ecology of the lake. *Univ. Toronto Stud. Biol.* **40**: 1–123.
- Rawson, D.S. 1951. Studies of the fish of Great Slave Lake. *J. Fish. Res. Board Can.* **8**: 207–240.
- Rawson, D.S. 1959. Limnology and fisheries of Cree and Wollaston lakes in northern Saskatchewan. *Fish. Branch Dep. Nat. Resour. Sask. Fish. Rep.* **4**: 5–73.
- Rawson, D.S. 1965. The life history and ecology of the yellow wall-eye, *Stizostedion vitreum*, in Lac La Ronge, Saskatchewan. *Trans. Am. Fish. Soc.* **86**: 15–37.
- Sadzikowski, M.R., and Wallace, D.C. 1976. A comparison of the food habits of size classes of three sunfishes (*Lepomis macrochirus* Rafinesque, *L. gibbosus* Linnaeus and *L. cyanellus* Rafinesque). *Am. Midl. Nat.* **95**: 220–225.
- Saiki, M.K., and Tash, J.C. 1978. Unusual population dynamics in largemouth bass, *Micropterus salmoides* (Lacepede), caused by a seasonally fluctuating food supply. *Am. Midl. Nat.* **100**: 116–125.
- Schaeffer, J.S., and Margraf, F.J. 1986. Food of white perch (*Morone americana*) and potential for competition with yellow perch (*Perca flavescens*) in Lake Erie. *Ohio J. Sci.* **86**: 26–29.
- Scott, W.B., and Crossman, E.J. 1973. Freshwater fishes of Canada. *Bull. Fish. Res. Board Can.* No. 184.
- Seaburg, K.G., and Moyle, J.B. 1964. Feeding habits, digestive rates, and growth of some Minnesota warmwater fishes. *Trans. Am. Fish. Soc.* **93**: 269–285.
- Serns, S.L., and Hoff, M.H. 1984. Food habits of adult yellow perch and smallmouth bass in Nebish lake, Wisconsin — with special reference to zooplankton density and composition. *Tech. Bull. No. 149*. Department of Natural Resources, Madison, Wis.
- Silverman, H., Achberger, E.C., Lynn, J.W., and Dietz, T.H. 1995. Filtration and utilization of laboratory-cultured bacteria by *Dreissena polymorpha*, *Corbicula fluminea*, and *Carunculina texasensis*. *Biol. Bull. Mar. Biol. Woods Hole*, **187**: 308–319.
- Smock, L.A. 1980. Relationship between body size and biomass of aquatic insects. *Freshwater Biol.* **10**: 375–383.
- Snetsinger, M.A. 1992. Resource division in a pond impoundment fish community with comparisons to other small water body systems. M.Sc. thesis, Queens University, Kingston, Ont.
- Snow, H.E. 1971. Harvest and feeding habits of largemouth bass in Murphy Flowage, Wisconsin. *Tech. Bull. No. 50*. Department of Natural Resources, Madison, Wis.
- Sprules, W.G., and Bowerman, J.E. 1988. Omnivory and food chain length in zooplankton food webs. *Ecology*, **69**: 418–425.
- Storck, T.W. 1986. Importance of gizzard shad in the diet of largemouth bass in Lake Shelbyville, Illinois. *Trans. Am. Fish. Soc.* **115**: 21–27.
- Surber, E.W. 1941. A quantitative study of the food of the smallmouth black bass, *Micropterus dolomieu*, in three eastern streams. *Trans. Am. Fish. Soc.* **70**: 311–324.

- Swenson, W.A., and Smith, L.L. Jr. 1976. Influence of food competition, predation, and cannibalism on walleye (*Stizostedion vitreum vitreum*) and sauger (*S. canadense*) populations in Lake of the Woods, Minnesota. *J. Fish. Res. Board Can.* **33**: 1946–1954.
- Tester, A.L. 1932. Food of the small-mouthed black bass (*Micropterus dolomieu*) in some Ontario waters. *Univ. Toronto Stud. Biol.* **22**: 171–203.
- Tharratt, R.C. 1959. Food of the yellow perch, *Perca flavescens* (Mitchill) in Saginaw Bay, Lake Huron. *Trans. Am. Fish. Soc.* **88**: 330–331.
- Toda, H., and Wada, E. 1990. Use of $^{15}\text{N}/^{14}\text{N}$ ratios to evaluate the food source of the mysid, *Neomysis intermedia* Czerniawsky, in a eutrophic lake in Japan. *Hydrobiologia*, **194**: 85–90.
- Vadas, R.L. Jr. 1990. The importance of omnivory and predator regulation of prey in freshwater fish assemblages of North America. *Environ. Biol. Fishes*, **27**: 285–302.
- Vallieres, L., and Fortin, R. 1988. Le grand brochet (*Esox lucius*) au Québec: biologie et gestation. Ministère du Loisir, de la chasse et de la Pêche, Québec, Qué.
- Vander Zanden, M.J., and Rasmussen, J.B. 1996. A trophic position model of pelagic food webs: impact on contaminant biomagnification in lake trout. *Ecol. Monogr.* **66**: 451–477.
- Wagner, W.C. 1972. Utilization of alewives by inshore piscivorous fishes in Lake Michigan. *Trans. Am. Fish. Soc.* **101**: 55–63.
- Wainright, S.C., Fogarty, M.J., Greenfield, R.C., and Fry, B. 1993. Long-term changes in the Georges Bank food web: trends in stable isotope compositions of fish scales. *Mar. Biol.* **115**: 481–493.
- Wainright, S.C., Fuller, C.M., Michener, R.H., and Richards, R.A. 1996. Spatial variation of trophic position and growth rate of juvenile striped bass (*Morone saxatilis*) in the Delaware River. *Can. J. Fish. Aquat. Sci.* **53**: 685–692.
- Ward, F.J., and Robinson, G.G.C. 1974. A review of research on the limnology of West Blue Lake, Manitoba. *J. Fish. Res. Board Can.* **31**: 977–1005.
- Weisberg, S.B., and Janicki, A.J. 1990. Summer feeding patterns of white perch, channel catfish, and yellow perch in the Susquehanna River, Maryland. *J. Freshwater Ecol.* **5**: 391–405.
- Winemiller, K.O. 1990. Spatial and temporal variation in tropical fish trophic networks. *Ecol. Monogr.* **60**: 331–367.
- Wolfert, D.R., and Miller, T.J. 1978. Age, growth, and food of northern pike in Eastern Lake Ontario. *Trans. Am. Fish. Soc.* **107**: 696–702.
- Wootton, J.T., and Power, M.E. 1993. Productivity, consumers, and the structure of a river food chain. *Proc. Natl. Acad. Sci. U.S.A.* **90**: 1384–1387.

Appendix I. Study lake, location (State or Province), year, sample size, dietary data, trophic position, and data source.

Lake	Location	Year	n fish	Prey category								Trophic position	Reference ^a
				Fish	Zoop	Ben	Pred ben	Mol	Cray	Det	Other		
Pumpkinseed (total n = 2000 fish)													
10 lakes	Maine	1938	101	0.0	0.2	17.4	0.0	61.5	0.0	20.9	0.0	3.09	1
Bassen	Michigan	1977	50	0.0	0.0	34.5	16.1	28.8	0.0	0.0	21.0	3.44	3
Deep	Michigan	1977	50	0.0	0.0	29.9	0.0	17.4	0.0	0.0	53.0	3.42	3
Dowsley Pond	Ontario	1987	280	0.0	0.0	62.8	15.3	16.7	0.0	0.0	5.0	3.49	4
Hamilton	Michigan	1977	50	0.0	0.0	1.8	0.1	58.9	0.0	0.0	39.0	3.20	3
Little Catarauqui Cr.	Ontario	1990	187	0.0	12.8	62.2	6.2	14.1	0.0	1.9	2.9	3.45	5
Long	Minnesota	1962	8	0.0	0.0	17.8	4.4	77.7	0.0	0.0	0.0	3.13	6
Maple	Minnesota	1957	367	0.0	0.0	39.0	0.0	49.0	0.0	3.5	9.5	3.25	7
Opinicon	Ontario	1987	280	0.0	4.7	13.3	5.3	71.3	0.0	0.0	5.3	3.17	4
Opinicon	Ontario	1966	103	0.0	3.7	57.7	21.3	12.3	2.3	0.0	0.0	3.52	8
Shaw	Michigan	1977	50	0.0	0.0	0.2	0.0	99.7	0.0	0.0	0.0	3.00	3
Sieverson	Minnesota	1962	66	0.0	0.0	16.9	3.9	79.2	0.0	0.0	0.0	3.12	6
Sister	Michigan	1972	65	0.0	3.9	40.9	4.6	28.8	0.0	5.0	16.7	3.35	9
Squaw	Minnesota	1962	25	0.0	0.0	42.6	3.0	33.5	20.3	0.0	0.6	3.45	6
Tuckahoe Creek	Virginia	1958	35	0.0	0.2	79.1	0.0	0.0	0.0	20.7	0.0	3.40	10
U. Poole Pond	Ontario	1987	280	0.0	2.0	46.3	14.3	29.3	0.0	0.0	8.0	3.43	4
Winona	Wisconsin	1940	3	0.0	0.0	52.3	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	
Yellow perch (total n = 8075 fish)													
10 lakes	Maine	1938	30	71.6	1.2	15.7	0.8	0.0	0.0	10.7	0.0	4.17	1
7 lakes	Maine	1941	78	78.3	0.3	6.2	14.8	0.3	0.0	0.1	0.0	4.36	1
Alle	Wisconsin	1931	3	0.0	0.0	100.0	0.0	0.0	0.0	0.0	0.0	3.50	12
Arbor	Wisconsin	1931	8	0.0	0.0	89.5	0.0	0.0	0.0	0.0	9.0	3.48	12
Brome	Quebec	1984	17	0.0	0.0	97.0	0.0	3.0	0.0	0.0	0.0	3.48	13
Bromont	Quebec	1984	34	14.3	2.6	53.0	25.8	0.0	0.0	0.0	4.2	3.77	13
Brompton	Quebec	1984	34	26.5	0.0	69.7	0.3	3.5	0.0	0.0	0.0	3.75	13
Cedar	Michigan	1941	112	80.7	12.0	7.3	0.0	0.0	0.0	0.0	0.0	4.31	14
Clear	Wisconsin	1931	13	11.0	0.0	86.5	0.0	0.0	0.0	1.5	0.0	3.59	12
Clear	Wisconsin	1932	7	6.0	6.0	80.0	0.0	3.0	5.0	0.0	0.0	3.57	12
Crane	Wisconsin	1932	11	10.5	0.0	85.5	0.0	0.0	0.0	0.0	4.0	3.61	12
Crystal	Wisconsin	1931	9	56.5	2.0	33.0	0.0	0.0	0.0	0.0	8.0	4.06	12

Appendix I (continued).

Lake	Location	Year	n fish	Prey category								Trophic position	Reference ^a
				Fish	Zoop	Ben	Pred ben	Mol	Cray	Det	Other		
Cub	Michigan	1974	201	24.5	1.8	37.8	27.0	2.5	0.0	0.0	6.0	3.86	15
D'Argent	Quebec	1984	34	0.0	11.2	86.2	0.0	1.6	0.0	0.9	0.0	3.49	13
Drolet	Quebec	1984	17	0.0	19.1	76.9	3.3	0.7	0.0	0.0	0.0	3.51	13
Erie	Ohio	1971	436	21.4	14.2	48.9	0.0	0.0	0.0	0.0	15.5	3.71	16
Erie	Ohio	1983	—	4.0	37.0	59.0	0.0	0.0	0.0	0.0	0.0	3.54	17
Erie	Ohio	1984	—	14.5	53.6	31.9	0.0	0.0	0.0	0.0	0.0	3.65	17
Erie	Ohio	1985	—	7.8	34.9	57.3	0.0	0.0	0.0	0.0	0.0	3.58	17
Erie	Ohio	1983	8	3.0	28.0	59.0	0.0	10.0	0.0	0.0	0.0	3.48	18
Erie	Ohio	1984	20	16.0	58.0	23.0	0.0	3.0	0.0	0.0	0.0	3.65	18
Erie	Ohio	1985	13	5.0	43.0	48.0	0.0	4.0	0.0	0.0	0.0	3.53	18
Western Basin (Erie)	Ohio	1981	82	19.6	53.9	23.4	0.0	3.2	0.0	0.0	0.0	3.68	19
Geneva	Wisconsin	1921	19	5.3	40.0	40.0	0.0	0.0	0.0	0.0	15.0	3.56	20
Hertel	Quebec	1984	17	0.0	13.5	80.8	0.0	5.7	0.0	0.0	0.0	3.47	13
Houghton	Michigan	1939	78	24.6	6.0	69.4	0.0	0.0	0.0	0.0	0.0	3.75	21
Houghton	Michigan	1940	267	69.1	1.8	27.8	1.3	0.0	0.0	0.0	0.7	4.21	21
Saginaw Bay (Huron)	Ontario	1956	241	12.0	23.0	48.0	0.0	6.0	0.0	0.0	11.0	3.59	22
Little Minnow	Ontario	1970–75	312	10.0	5.0	22.0	40.0	0.0	8.0	0.0	15.0	3.84	23
Long	Wisconsin	1931	98	5.0	43.5	37.5	0.0	0.0	0.0	0.0	15.0	3.57	12
Magog	Quebec	1984	17	0.0	0.6	83.8	0.0	8.2	7.4	0.0	0.0	3.50	13
Maple	Minnesota	1957	97	49.0	0.0	40.0	0.0	1.5	0.0	0.0	10.0	3.99	7
Massawippi	Quebec	1984	17	0.0	11.4	60.0	26.0	2.6	0.0	0.0	0.0	3.62	13
Memphramagog	Quebec	1984	34	8.0	1.7	86.1	3.4	0.8	0.0	0.0	0.0	3.59	13
Muskellunge	Wisconsin	1931	207	48.0	14.0	20.0	0.0	2.0	1.0	6.0	9.5	3.95	12
Muskellunge	Wisconsin	1932	375	17.5	15.5	39.1	0.0	5.0	0.0	1.0	21.0	3.63	12
Nebish	Wisconsin	1931	109	2.5	1.5	89.2	0.0	5.5	0.0	0.1	2.5	3.52	12
Nebish	Wisconsin	1932	178	2.5	21.5	63.6	0.0	5.0	0.0	0.0	6.0	3.48	12
Nebish	Wisconsin	1977	102	23.5	5.1	58.9	10.9	1.6	0.0	0.0	0.0	3.78	24
Nebish	Wisconsin	1978	122	7.6	4.1	77.0	6.0	0.8	0.0	4.5	0.0	3.58	24
Nebish	Wisconsin	1979	92	24.0	2.3	58.4	6.7	5.0	0.0	3.6	0.0	3.73	24
Nebish	Wisconsin	1980	123	3.0	2.1	16.0	4.2	1.8	72.0	0.9	0.0	3.90	24
Nebish	Wisconsin	1981	111	34.2	9.4	38.1	5.7	10.8	0.0	1.7	0.0	3.81	24
Nipigon	Ontario	1921	14	7.1	36.8	56.1	0.0	0.0	0.0	0.0	0.0	3.57	25
Nipigon	Ontario	1921	43	25.5	8.5	55.0	0.0	0.0	4.0	0.0	7.0	3.78	26
Nipigon	Ontario	1927	—	0.0	0.0	100.0	0.0	0.0	0.0	0.0	0.0	3.50	27
Oneida	New York	1975	254	0.0	91.8	8.2	0.0	0.0	0.0	0.0	0.0	3.50	28
Oneida	New York	1976	212	0.0	88.5	11.5	0.0	0.0	0.0	0.0	0.0	3.50	28
Oneida	New York	1977	232	0.0	73.7	26.3	0.0	0.0	0.0	0.0	0.0	3.50	28
Oneida	New York	1927	—	0.0	0.0	100.0	0.0	0.0	0.0	0.0	0.0	3.50	27
Opinicon	Ontario	1966	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	3.2	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
Palette	Wisconsin	31	8	55.0	0.0	33.0	0.0	13.5	0.0	0.0	0.0	4.01	12
Pepin	Wisconsin	1921	15	11.3	18.8	59.6	0.0	5.8	0.0	0.0	4.0	3.58	20
Plum	Wisconsin	1931	15	31.5	0.0	13.5	0.0	0.5	50.5	0.0	3.0	4.05	12
Rock	Wisconsin	1931	23	33.5	0.1	51.5	0.0	0.5	0.0	12.0	3.5	3.79	12
Roxton	Quebec	1984	34	0.0	0.0	96.9	0.0	3.1	0.0	0.0	0.0	3.48	13
Silver	Quebec	1984	17	0.0	0.1	89.3	8.4	2.0	0.0	0.0	0.0	3.53	13
Silver	Wisconsin	1931	176	6.5	9.5	57.1	0.0	3.5	11.0	2.0	8.0	3.56	12
Silver	Wisconsin	1932	273	96.0	0.0	2.0	0.0	0.0	2.0	0.0	0.0	4.47	12
Simcoe	Ontario	1927	13	11.0	0.0	77.0	0.0	4.0	8.0	0.0	0.0	3.63	27
Spider	Wisconsin	1931	32	25.0	0.0	15.5	0.0	3.0	48.5	4.0	5.0	3.97	12
Starr	Wisconsin	1931	4	0.0	0.0	68.5	0.0	0.0	31.5	0.0	0.0	3.66	12
Susquehanna R.	Maryland	1982	698	2.0	0.0	79.0	0.0	15.0	0.0	0.0	4.0	3.45	30
Trout	Wisconsin	1931	160	36.0	4.0	35.7	0.0	1.0	16.0	2.0	4.5	3.91	12
Trout	Wisconsin	1932	106	39.0	0.0	43.1	0.0	6.0	1.0	1.5	9.0	3.85	12

Appendix I (continued).

Lake	Location	Year	n fish	Prey category								Trophic position	Reference ^a
				Fish	Zoop	Ben	Pred ben	Mol	Cray	Det	Other		
Vieux	Wisconsin	1931	35	13.5	0.0	79.5	0.0	0.0	0.0	4.0	2.5	3.61	12
Vieux	Wisconsin	1932	76	6.0	0.1	84.0	0.0	4.5	0.0	0.5	5.0	3.54	12
Waskesiu	Saskatchewan	1927	—	0.0	0.0	100.0	0.0	0.0	0.0	0.0	0.0	3.50	27
Waterloo	Quebec	1984	34	0.0	1.8	91.1	5.2	1.8	0.0	0.0	0.0	3.52	13
Weber	Wisconsin	1931	178	6.5	2.5	85.6	0.0	0.1	0.0	0.5	5.0	3.57	12
Weber	Wisconsin	1932	184	1.0	14.0	80.7	0.0	0.5	0.0	0.0	2.0	3.48	12
West Blue	Manitoba	1971	240	5.5	21.8	45.5	0.0	0.0	3.8	0.0	23.0	3.57	31
Winona	Wisconsin	1940	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	
Rock bass (total n = 1962 fish)													
Alle	Wisconsin	1931	10	0.0	0.0	0.0	0.0	0.0	93.0	1.0	3.0	3.94	12
Bear	Wisconsin	1931	12	0.0	0.0	40.5	0.0	3.5	47.0	0.0	9.0	3.72	12
Clear	Wisconsin	1931	4	0.0	0.0	37.5	0.0	0.0	58.5	0.0	4.0	3.79	12
Clear	Wisconsin	1932	3	0.0	0.0	97.0	0.0	3.0	0.0	0.0	0.0	3.49	12
Georgian Bay (Huron)	Ontario	1928	40	28.5	0.0	10.2	0.0	0.0	60.4	0.9	0.0	4.08	32
Goose Creek	Virginia	1986	40	0.0	14.0	86.0	0.0	0.0	0.0	0.0	0.0	3.50	33
Muskellunge	Wisconsin	1931	338	12.5	0.0	41.0	0.0	3.0	13.5	11.0	6.0	3.68	12
Muskellunge	Wisconsin	1932	371	12.0	0.1	58.8	0.0	0.5	5.5	2.0	20.5	3.63	12
Nebish	Wisconsin	1931	184	3.5	7.5	81.1	0.0	5.0	0.0	0.1	2.0	3.50	12
Nebish	Wisconsin	1932	209	7.5	3.5	79.7	0.0	0.5	0.0	0.1	6.0	3.53	12
Nebish	Wisconsin	1932	27	3.5	50.5	31.5	0.0	12.0	0.0	0.0	2.0	3.47	12
Nipissing	Ontario	1929-30	12	19.1	0.0	16.1	0.0	0.0	64.6	0.2	0.0	4.01	32
Opinicon	Ontario	1966	96	10.0	0.0	6.7	52.7	0.0	30.0	0.0	0.0	4.00	8
Ozark streams	Arkansas	1980	210	9.0	0.0	18.0	0.0	0.0	73.0	0.0	0.0	3.96	34
Palette	Wisconsin	1931	11	0.0	0.0	92.0	0.0	5.0	0.0	0.0	1.0	3.45	12
Plum	Wisconsin	1931	1	0.0	0.0	0.0	0.0	0.0	100.0	0.0	0.0	4.00	12
Rock	Wisconsin	1931	4	24.5	0.0	61.5	0.0	0.0	0.0	4.0	10.0	3.73	12
Silver	Wisconsin	1931	124	5.0	0.0	52.0	0.0	0.1	35.5	1.0	4.5	3.69	12
Silver	Wisconsin	1932	3	37.5	0.0	62.5	0.0	0.0	0.0	0.0	0.0	3.88	12
Simcoe	Ontario	1927	9	4.0	0.0	22.0	0.0	0.0	74.0	0.0	0.0	3.91	27
Star	Wisconsin	1931	1	20.0	0.0	20.0	0.0	0.0	30.0	30.0	0.0	3.70	12
Trout	Wisconsin	1931	38	13.5	0.1	63.0	0.0	0.0	20.5	1.0	3.0	3.75	12
Trout	Wisconsin	1932	103	4.0	0.5	45.1	0.0	0.0	36.5	0.0	14.0	3.72	12
Vieux	Wisconsin	1932	2	0.0	0.0	24.0	0.0	0.0	0.0	0.0	76.0	3.50	12
Winona	Wisconsin	1940	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	
Smallmouth bass (total n = 3162 fish)													
11 lakes	Maine	1936-38	31	14.9	0.3	6.0	12.5	0.0	66.3	0.0	0.0	4.04	1
7 lakes	Maine	1940	66	80.3	0.0	3.6	0.0	0.0	14.4	1.7	0.0	4.37	44
8 lakes	Maine	1941	259	83.9	5.8	8.0	1.6	0.0	0.0	0.7	0.0	4.34	1
—	Michigan	1964	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	1966-68	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	1966-68	112	97.0	0.0	0.0	0.0	0.0	1.0	0.0	0.0	4.45	46
Bear	Wisconsin	1931	1	100.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.50	12
Cacapon R.	Virginia	1939	104	2.7	0.0	87.6	8.2	0.4	1.1	0.0	0.2	3.57	47
Cache	Ontario	1935-36	52	28.7	16.0	19.7	0.0	0.0	35.7	0.0	0.0	3.97	48
Clear	Wisconsin	1931	2	100.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.50	12
Crystal	Wisconsin	1931	4	0.0	0.0	97.5	0.0	0.0	0.0	3.5	0.0	3.50	12
Douglas	Michigan	1915	8	10.0	0.0	0.0	0.0	0.0	70.0	0.0	20.0	3.95	20
Erie	Ontario	1938	157	82.5	0.0	0.2	0.0	0.0	17.5	0.0	0.0	4.41	48
Genesee R.	New York	1927	13	18.4	0.0	24.2	0.0	0.0	56.0	0.0	0.0	3.94	20
Geneva	Wisconsin	1921	21	33.0	4.0	43.0	0.0	0.0	20.6	0.0	0.0	3.94	20
Georgian Bay	Ontario	1936	45	62.5	0.0	1.5	0.0	0.0	33.5	0.0	0.0	4.26	48
Georgian Bay	Ontario	1928	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

Appendix I (continued).

Lake	Location	Year	n fish	Prey category								Trophic position	Reference ^a
				Fish	Zoop	Ben	Pred ben	Mol	Cray	Det	Other		
Juniala R.	Pennsylvania	1990	102	0.0	0.0	93.9	0.0	0.0	6.2	0.0	0.0	3.53	49
Jute	Wisconsin	1931	28	83.5	0.0	13.0	0.0	0.0	0.0	0.0	2.0	4.31	12
Kathenne	Michigan	1974	167	28.0	8.7	32.0	5.3	0.0	13.0	0.0	13.0	3.87	15
Larry	Wisconsin	1931	14	0.0	2.0	94.5	0.0	0.0	0.0	1.5	0.0	3.46	12
Memphremagog	Quebec	1973	24	50.1	0.0	3.2	0.0	0.0	50.0	0.0	0.0	4.30	50
Michigan	Wisconsin	1921	2	98.5	0.0	0.0	0.0	0.0	0.0	1.5	0.0	4.48	20
Monona	Wisconsin	1918	4	80.0	0.0	20.0	0.0	0.0	0.0	0.0	0.0	4.30	20
Muskellunge	Wisconsin	1931	57	75.0	0.0	12.0	0.0	1.0	0.0	11.0	1.0	4.19	12
Muskellunge	Wisconsin	1932	61	42.0	1.5	48.5	0.0	0.0	0.0	6.5	2.0	3.90	12
Nebish	Wisconsin	1931	66	20.5	12.0	62.0	0.0	1.5	0.0	0.0	3.0	3.68	12
Nebish	Wisconsin	1932	42	41.0	0.0	56.5	0.0	0.0	0.1	0.0	2.0	3.90	12
Nebish	Wisconsin	1977	101	7.2	0.0	3.2	5.4	0.0	84.2	0.0	0.0	4.02	24
Nebish	Wisconsin	1978	126	22.0	0.3	11.0	2.9	0.0	64.0	0.0	0.0	4.06	24
Nebish	Wisconsin	1979	104	15.5	0.1	8.8	5.8	0.0	69.9	0.0	0.0	4.04	24
Nebish	Wisconsin	1980	125	10.0	0.0	3.4	4.1	0.0	82.6	0.0	0.0	4.04	24
Nebish	Wisconsin	1981	111	8.9	0.1	7.2	4.4	0.0	80.1	0.0	0.0	4.02	24
Nipigon	Ontario	1921	9	48.0	35.3	16.6	0.0	0.0	0.0	0.0	0.0	3.98	25
Nipissing	Ontario	1929	106	20.6	0.0	0.4	0.0	0.0	79.0	0.0	0.0	4.10	32
Opeongo	Ontario	1936	91	9.7	0.0	2.3	0.0	0.0	87.0	0.0	0.0	4.02	48
Oxtongue R.	Ontario	1930	6	20.0	0.0	80.0	0.0	0.0	0.0	0.0	0.0	3.70	32
Ozark streams	Arkansas	1980	74	34.0	0.0	6.0	0.0	0.0	60.0	0.0	0.0	4.14	34
Palette	Wisconsin	1931	16	58.5	1.5	40.0	0.0	0.0	0.0	0.0	0.0	4.09	12
Palette	Wisconsin	1932	30	58.5	2.5	35.5	0.0	0.0	0.0	1.5	9.5	4.09	12
Pepin	Wisconsin	1921	12	56.5	5.7	29.8	0.0	0.0	9.1	0.0	0.0	4.13	20
Perch	Ontario	1930–31	123	49.7	1.7	5.3	0.1	0.0	39.2	0.2	3.9	4.19	32
Phantom	Ontario	1930	18	4.0	0.0	22.6	0.0	0.0	71.7	1.7	0.0	3.89	32
Potomac	Virginia	1939	96	4.1	0.0	94.6	0.5	0.1	0.6	0.0	0.1	3.55	47
Razor	Wisconsin	1931	18	39.5	2.0	53.0	0.0	0.0	0.0	0.0	6.0	3.90	12
Rock	Wisconsin	1931	6	5.0	0.0	88.5	0.0	0.0	0.0	5.5	1.0	3.52	12
Shenandoah R.	Virginia	1939	108	37.3	0.0	49.8	8.1	0.0	4.3	0.0	0.5	3.93	47
Silver	Wisconsin	1931	31	35.0	0.0	55.0	0.0	0.0	9.5	1.0	0.0	3.90	12
Silver	Wisconsin	1932	5	100.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.50	12
Simcoe	Ontario	1927	16	29.0	0.0	7.0	8.0	3.0	53.0	0.0	0.0	4.08	27
Spider	Wisconsin	1931	3	0.0	0.0	27.0	0.0	0.0	15.5	0.0	58.0	3.59	12
Star	Wisconsin	1931	1	0.0	0.0	50.0	0.0	0.0	50.0	0.0	0.0	3.75	12
Trout	Wisconsin	1931	10	0.0	7.0	89.5	0.0	0.0	0.0	0.0	4.5	3.52	12
Trout	Wisconsin	1932	1	0.0	0.0	0.0	0.0	0.0	100.0	0.0	0.0	4.00	12
Weber	Wisconsin	1931	29	6.0	5.0	76.0	0.0	0.0	0.0	1.0	14.0	3.59	12
Weber	Wisconsin	1932	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	
Largemouth bass (total n = 5664 fish)													
Bear	Wisconsin	1931	5	80.0	0.0	20.0	0.0	0.0	0.0	0.0	0.0	4.30	12
Cub	Michigan	1974	340	54.3	0.0	0.0	11.0	0.0	0.0	0.0	35.0	4.10	15
Deer Island	—	1973	169	53.4	0.4	19.6	0.0	0.0	14.9	0.1	11.9	4.11	35
DeGray	Arkansas	1976	748	59.0	0.0	0.3	0.0	0.0	37.6	0.5	3.0	4.28	36
Fork	—	1941		48.0	0.0	18.2	11.0	0.0	113	0.0	11.0	4.08	37
Geneva	Wisconsin	1918	78	8.7	18.1	48.1	0.0	0.0	0.0	0.0	25.0	3.59	20
L. Dixie	Missouri	1964	900	50.1	0.0	1.5	0.7	0.0	39.	0.6	6.3	4.18	38
Long	Wisconsin	1931	3	50.0	0.0	4.0	0.0	0.0	0.0	0.0	46.0	4.00	12
Maple	Minnesota	1957	83	96.0	3.0	0.0	0.0	0.0	0.0	1.0	0.0	4.46	7
Murphy Flowage	Wisconsin	1961–64	1146	33.5	0.0	1.2	0.0	0.0	56.1	6.1	0.0	4.04	39
Muskellunge	Wisconsin	1931	19	50.5	32.0	9.5	0.0	0.0	0.0	1.5	7.5	4.01	12
Muskellunge	Wisconsin	1932	8	94.0	0.0	0.0	0.0	0.0	0.0	6.0	0.0	4.41	
Opinicon	Ontario	1991	10	85.7	1.8	0.0	0.0	0.0	11.4	0.0	0.0	4.40	2
Paul	Michigan	1987	235	42.0	11.0	8.0	39.0	0.0	0.0	0.0	0.0	4.12	40
Paul	Michigan	1988		55.0	10.0	14.0	21.0	0.0	0.0	0.0	0.0	4.16	40

Appendix I (continued).

Lake	Location	Year	n fish	Prey category								Trophic position	Reference ^a
				Fish	Zoop	Ben	Pred ben	Mol	Cray	Det	Other		
Peter	Michigan	1987	235	0.0	6.5	45.6	46.5	0.8	0.0	0.0	0.0	3.72	41
Peter	Michigan	1988	235	54.0	6.0	8.0	32.0	0.0	0.0	0.0	0.0	4.20	40
Peter	Michigan	1987		0.0	15.0	15.0	35.0	0.0	0.0	0.0	35.0	3.68	40
Shelbyville	Illinois	1980	97	99.2	0.0	0.8	0.0	0.0	0.0	0.0	0.0	4.49	42
Shelbyville	Illinois	1978–81	1347	88.8	0.0	0.6	0.0	0.0	11.4	0.0	0.0	4.46	43
Winona	Wisconsin	1940	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	
Northern pike and chain pickerel (total n = 34 738 fish)													
19 lakes	Maine	1940	110	94.8	0.0	0.2	0.0	0.0	0.5	0.0	4.4	4.37	44
20 lakes	Maine	1937–41	95	95.1	0.0	0.0	0.1	0.0	0.0	0.0	4.8	4.24	1
Babcock Pond	Connecticut	1941	71	91.4	0.0	0.0	3.7	0.0	0.0	0.0	4.8	4.04	
Bay de Noc (Michigan)	Michigan	1966–68	405	100.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.36	
Bay of Quinte (Ontario)	Ontario	1958–64	131	100.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.55	74
Brochet	Quebec	1953	131	40.2	0.0	9.3	32.1	0.0	18.4	0.0	0.0	4.15	52
Cree	Saskatchewan	1955	—	95.0	0.0	0.0	5.0	0.0	0.0	0.0	0.0	4.48	53
Georgian Bay (Huron)	Ontario	1928	11	53.8	0.0	0.0	0.0	0.0	46.2	0.0	0.0	4.27	32
Grande Rivière	Quebec	1977		97.9	0.0	0.3	0.0	0.0	0.0	0.0	1.8	4.48	52
Great Slave	N.W.T.	1944–47	73	95.0	0.0	5.0	0.0	0.0	0.0	0.0	0.0	4.45	54
Grove	Minnesota	1957	133	90.0	0.0	0.0	0.0	0.0	0.0	0.0	10.0	4.40	7
Heming	Manitoba	1950–62	29477	99.9	0.0	0.1	0.0	0.0	0.1	0.0	0.0	4.42	55
Keller	N.W.T.	1962	125	97.2	0.0	0.0	2.8	0.0	0.0	0.0	0.0	4.59	56
Lincoln Pond	New York	39	145	32.8	1.4	47.4	17.6	0.0	0.0	0.0	0.8	3.72	
Maple	Minnesota	1957	70	100.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.50	7
Mecan R.	Wisconsin	1959	91	95.9	0.0	0.0	0.0	0.0	1.5	0.0	2.6	4.31	58
Memphremagog	Quebec	1973	27	60.0	0.0	2.1	0.0	0.0	40.0	0.0	0.0	4.09	50
Mississippi	Mississippi	1968	58	96.5	0.0	0.0	0.0	0.0	3.5	0.0	0.0	4.36	59
Monroe	Quebec	1953	221	99.5	0.0	0.1	0.1	0.0	0.3	0.0	0.0	4.50	52
Murphy Flowage	Wisconsin	1965	1412	99.1	0.0	0.0	0.0	0.0	0.2	0.0	0.0	4.29	39
Nipigon	Ontario	1921	23	95.2	0.7	0.7	0.0	0.0	0.0	0.0	3.8	4.46	26
Nipissing	Ontario	1929–30	10	36.3	0.0	0.0	0.0	0.0	59.4	0.0	4.0	4.15	32
Ontario	New York	1972	87	100.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.02	61
Pocotopaug	Connecticut	—	30	63.0	0.0	11.0	11.0	0.0	8.0	4.0	4.0	4.19	76
Various	—	—	—	64.0	0.0	22.0	0.0	0.0	12.0	1.0	1.0	3.82	76
Seney Refuge	Michigan	1941–42	378	69.5	0.0	1.8	0.9	0.1	23.1	0.0	4.6	4.31	2
Seney Refuge	Michigan	1952	84	65.4	0.0	0.1	2.5	0.1	21.4	0.0	10.6	4.28	2
Simcoe	Ontario	1982	50	100.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.49	62
Ste. Anne	Alberta	1976–78	1290	99.5	0.0	0.5	0.0	0.0	0.0	0.0	0.0	4.50	63
Wollaston	Saskatchewan	1956	—	95.0	0.0	5.0	0.0	0.0	0.0	0.0	0.0	4.45	53
Mean				84.1	0.1	3.5	2.5	0.0	7.8	0.2	1.9	4.31	
Walleye (total n = 10 386 fish)													
Bay de Noc (Michigan)	Michigan	1966–68	103	100.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.39	46
Bay of Quinte (Ontario)	Ontario	1958–62	692	99.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	4.04	74
Clear	Wisconsin	1931	15	60.0	12.0	19.5	0.0	0.0	0.0	4.5	5.0	4.06	12
Clear	Wisconsin	1932	23	40.5	0.0	59.5	0.0	0.0	0.0	0.0	0.5	3.92	12
Erie	Ontario	1979–81	906	100.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.50	64
Falcon	Manitoba	1959	288	92.2	0.0	5.5	0.0	0.0	3.0	0.0	0.0	4.48	45
Great Slave	N.W.T.	1944–47	116	75.0	0.0	25.0	0.0	0.0	0.0	0.0	0.0	4.25	54
James Bay	Quebec	1979	584	72.3	1.3	24.0	2.4	0.0	0.0	0.0	0.0	4.24	65
Lac la Ronge	Saskatchewan	1948–55	276	97.0	0.0	2.8	0.0	0.0	0.3	0.0	0.0	4.35	66
Lake of the Woods	Ontario	1968–70	1417	98.8	0.3	1.3	0.0	0.0	0.0	0.0	0.0	4.61	67
Lake of the Woods	Ontario	1968–70	1605	88.0	1.5	11.3	0.0	0.0	1.8	0.0	0.0	4.49	67
Lost	Wisconsin	1932	18	99.0	0.0	0.0	0.0	0.0	1.0	0.0	0.0	4.50	12
Memphremagog	Quebec	1973	8	100.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.70	50
Nipigon	Ontario	1920–21	74	91.1	0.0	6.6	0.0	0.0	0.0	0.0	0.0	4.35	25
Nipigon	Ontario	1921	4	50.0	47.4	2.5	0.0	0.0	0.0	0.0	0.0	4.00	26

Appendix I (concluded).

Lake	Location	Year	n fish	Prey category								Trophic position	Reference ^a
				Fish	Zoop	Ben	Pred ben	Mol	Cray	Det	Other		
Nipissing	Ontario	1929–30	16	48.3	0.0	28.1	0.0	0.0	22.9	0.0	0.0	4.08	32
Oahe	South Dakota	1993	478	99.6	0.0	0.4	0.0	0.0	0.0	0.0	0.0	4.50	68
Ontario	Michigan	1966–68	103	100.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.50	46
Pike	Minnesota	1962	470	43.2	0.0	26.5	9.3	0.0	18.0	3.0	0.0	4.11	72
Simcoe	Ontario	1982	50	100.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.57	62
Sparkling	Wisconsin	1982–83	113	97.8	0.0	2.2	0.0	0.0	0.0	0.0	0.0	4.42	69
Trout	Wisconsin	1931	30	96.0	0.0	1.0	0.0	0.0	0.0	0.0	2.5	4.45	12
Trout	Wisconsin	1932	22	100.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.50	12
West Blue	Manitoba	1970	79	79.8	0.0	9.3	0.0	0.0	11.0	0.0	0.0	4.51	70
West Blue	Manitoba	1966	—	78.0	0.0	4.2	0.6	0.0	15.6	0.0	1.5	4.53	75
West Blue	Manitoba	1969–70	—	71.5	0.0	16.9	5.0	0.0	4.8	0.0	1.9	4.43	75
Wilson	Minnesota	1964–65	390	70.7	0.0	27.6	0.0	0.0	0.0	0.0	1.7	4.19	73
Wilson	Minnesota	67–70	230	41.4	0.0	44.4	0.0	0.0	2.1	0.0	12.1	3.88	73
Winnebago	Wisconsin	1960	1148	99.0	0.0	1.0	0.0	0.0	0.0	0.0	0.0	4.43	71
Winnebago	Wisconsin	1960	629	99.7	0.0	0.3	0.0	0.0	0.0	0.0	0.0	4.26	71
Winnebago	Wisconsin	1961	56	95.4	0.4	4.6	0.0	0.0	0.0	0.0	0.0	4.26	71
Winnebago	Wisconsin	1961	231	81.6	0.0	18.4	0.0	0.0	0.0	0.0	0.0	4.10	71
Mean				83.3	2.0	10.7	0.5	0.0	2.5	0.2	0.8	4.33	

Note: Dietary data are broken down into the prey categories described in Table 1. The summary presented at the end of each species represents the mean diet and trophic position for the species.

^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 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 1976; (68) Bryan et al. 1995; (69) Lyons and Magnuson 1987; (70) Kelso 1973; (71) Priegel 1963; (72) Johnson and Hale 1977; (73) Johnson 1977; (74) Hurley and Christie 1977; (75) Kelso and Ward 1977; (76) Hunter and Rankin 1939.

Appendix II. Diets of northern pike, chain pickerel, and walleye in lakes where fish prey items could be further separated into species.

Lake	Location	Year	<i>n</i> fish	% fish	% volume													Trophic position	Reference ^a	
					Perc.	Cypr.	Cent.	Trpe.	Cato.	Scul.	Alew.	Smel.	Core.	Salm.	Burb.	Stic.	Wb.			Other
Northern pike and chain pickerel (total <i>n</i> = 32 284 fish)																				
19 lakes	Maine	1940	110	94.8	7.9	14.6	0.0	0.0	0.0	0.0	0.0	3.2	0.0	0.0	0.0	0.0	58.0	11.2	4.37	44
20 lakes	Maine	1937–41	95	95.1	19.4	22.5	1.0	0.0	0.0	0.0	0.0	1.0	0.0	24.5	0.0	0.0	25.6	1.0	4.24	1
Babcock Pond	Connecticut	1941	71	91.4	0.0	42.4	5.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	43.7	4.04	51
Bay de Noc	Michigan	1966–68	405	100.0	2.8	7.0	4.6	10.7	0.0	0.0	34.2	39.1	0.0	0.0	0.0	0.0	0.0	1.6	4.36	46
Bay of Quinte	Ontario	1958–64	131	100.0	53.2	0.0	2.0	21.8	0.0	0.0	19.9	3.1	0.0	0.0	0.0	0.0	0.0	0.0	4.55	75
Heming	Manitoba	1950–62	29477	99.9	22.5	19.8	0.0	34.4	12.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	10.3	4.42	55
Keller	N.W.T.	1962	125	97.2	0.0	0.0	0.0	0.0	5.7	28.6	0.0	0.0	0.0	0.0	37.2	22.9	0.0	2.9	4.59	56
Lincoln Pond	New York	1939	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	1959	91	95.9	0.0	4.6	0.0	0.0	9.0	22.8	0.0	0.0	0.0	59.6	0.0	0.0	0.0	0.0	4.31	58
Memphremagog	Quebec	1973	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	1968	58	96.5	0.0	0.0	59.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	36.6	4.36	59
Murphy Flowage	Wisconsin	1965	1412	99.1	13.8	6.0	77.7	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0	1.4	4.29	39
Ontario	New York	1972	87	100.0	2.3	0.0	0.0	0.0	0.0	0.0	97.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.02	61
Various	—	—	—	64.0	12.6	41.0	2.3	0.0	0.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	7.5	3.82	77
Simcoe	Ontario	1982	50	100.0	28.4	1.5	4.9	1.6	35.3	0.0	0.0	8.0	20.2	0.0	0.0	0.0	0.0	0.0	4.49	62
Mean				88.4	12.9	13.8	11.5	4.6	4.2	3.4	10.1	3.6	1.3	5.6	2.5	1.5	5.6	7.7	4.24	
Walleye (total <i>n</i> = 8369 fish)																				
Bay de Noc	Michigan	1966–68	103	100.0	0.0	0.0	0.0	0.0	8.8	0.0	37.3	40.1	0.0	0.0	0.0	0.0	0.0	13.8	4.39	46
Bay of Quinte	Ontario	1958–62	692	99.0	0.4	0.0	0.0	0.0	0.0	0.0	94.6	4.0	0.0	0.0	0.0	0.0	0.0	0.0	4.04	75
Falcon	Manitoba	1959	288	92.2	49.5	6.2	8.4	2.2	12.4	1.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	12.4	4.48	45
James Bay	Quebec	1979	584	72.3	0.0	0.0	0.0	41.1	0.0	0.0	0.0	26.6	0.0	4.5	0.0	0.0	0.0	0.0	4.24	65
Lac la Ronge	Saskatchewan	1948–55	276	97.0	1.0	2.0	0.0	31.0	7.0	0.0	0.0	56.0	0.0	0.0	0.0	0.0	0.0	0.0	4.35	66
Lake of the Woods	Ontario	1968–70	1417	98.8	30.0	3.3	0.0	53.7	0.0	0.0	0.0	6.1	0.0	0.0	0.0	0.0	0.0	5.6	4.61	67
Lake of the Woods	Ontario	1968–70	1605	88.0	72.8	9.5	0.0	5.1	0.0	0.0	0.0	0.6	0.0	0.0	0.0	0.0	0.0	0.0	4.49	67
Memphremagog	Quebec	1973	8	100.0	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	0.0	4.70	50
Pike	Minnesota	1962	470	43.2	27.4	0.1	0.0	0.5	13.3	1.3	0.0	0.0	0.0	0.0	0.6	0.0	0.0	0.0	4.11	73
Simcoe	Ontario	1982	50	100.1	19.4	11.0	0.0	1.0	0.0	0.0	0.0	68.7	0.0	0.0	0.0	0.0	0.0	0.0	4.57	62
Sparkling	Wisconsin	1982–83	113	97.8	69.2	19.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	9.5	0.0	0.0	0.0	0.0	4.42	69
West Blue	Manitoba	1970	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	1966	—	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	1969–70	—	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	1964–65	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	1967–70	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	1960	1148	99.0	19.9	10.9	2.6	8.9	0.0	0.0	0.0	0.0	0.0	0.0	4.1	0.0	0.0	52.6	4.43	71
Winnebago	Wisconsin	1960	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	1961	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	1961	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	0.1	6.6	10.6	4.5	0.0	0.9	0.0	0.0	4.2	4.35	

Note: Perc., yellow perch; Cypr., cyprinids; Cent., centrarchids; Trpe., trout-perch; Cato., catostomids; Scul., sculpins; Alew., alewife; Smel., smelt; Core., coregonids; Salm., salmoninae; Burb., burbot; Stic., sticklebacks; Wb., white bass; Other, nonspecified species.

^aSee footnote *a* to Appendix I.

Appendix III. Estimated trophic position of adult littoral fish species based on $\delta^{15}\text{N}$ from 36 lakes in Ontario and Quebec.

Lake	$\delta^{15}\text{N}$ Unionid mussel	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	—
Pickereel	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	—	—	—	—	—
Stenburg	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	—	—	—	—	—	—

Note: Pump., pumpkinseed; Perc., yellow perch; Rb., rock bass; Smb., smallmouth bass; Lmb., largemouth bass; Pike, northern pike and chain pickerel; Wall., walleye.