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A TROPHIC POSITION MODEL OF PELAGIC FOOD WEBS: IMPACT ON CONTAMINANT BIOACCUMULATION IN LAKE TROUT¹

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Abstract. To test how well use of discrete trophic levels represents pelagic trophic structure, we compiled dietary data from >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 developed 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 characterize 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 was supported by elevated lake trout trophic position, PCB, and Hg levels in lakes containing smelt. Consideration of omnivory caused biomagnification factors (BMFs) to be many times higher than BMFs that ignored omnivory. These omnivory-corrected BMF estimates appeared to be more consistent with values calculated using stable nitrogen isotopes ($\delta^{15}\text{N}$), an alternative continuous measure of trophic position. $\delta^{15}\text{N}$ provided trophic position estimates that generally corresponded with our diet-derived estimates.

Key words: biomagnification; food chain; food web; lake trout; mercury; omnivory; PCBs; smelt; trophic level; trophic position; trophic structure.

INTRODUCTION

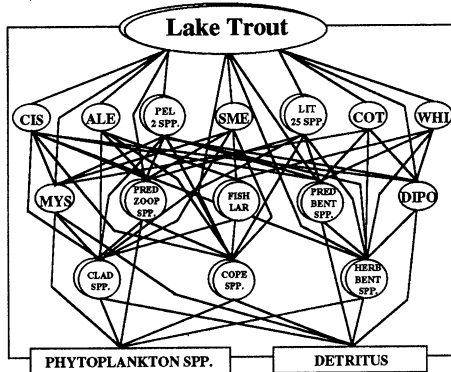
Modeling relationships between trophic levels is done with one of three major objectives: (1) “food web” studies search for consistent patterns of community structure among matrices of interconnected species (Briand 1985, Schoener 1989, Cohen et al. 1990, Polis 1991); (2) studies of “effects” attempt to determine factors structuring communities, often relying on experimental manipulations (Hairston et al. 1960, Paine 1966, 1980, Fretwell 1987, Spiller and Schoener 1990, Wootton 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, Persson 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 the pelagic food web to estimate the trophic level of lake trout, and used this successfully to 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.

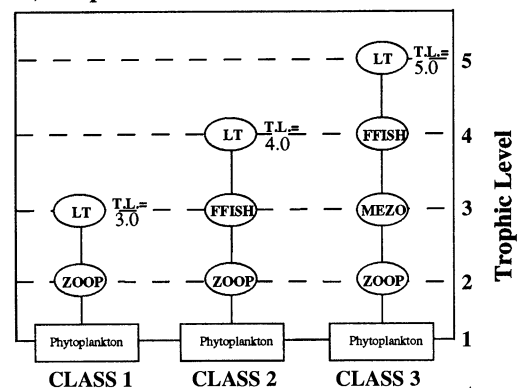
Although multitrophic-level population models sug-

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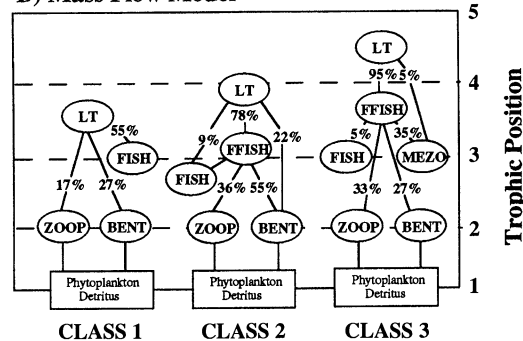
A) Food Web Model



D) Trophic Level Model



B) Mass Flow Model



C) Trophic Position Model

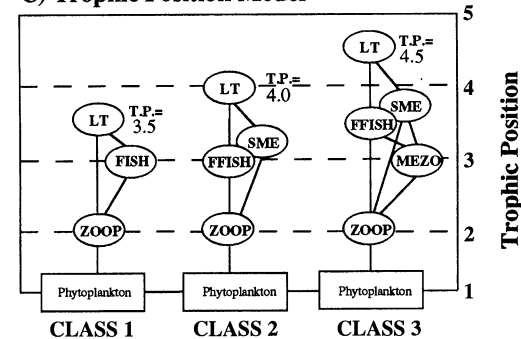


FIG. 1. A continuum of models used to represent pelagic trophic structure leading to the top predator, lake trout (*Salvelinus namaycush*). Class 1 lakes lack preferred lake trout prey, pelagic forage fish, causing lake trout to feed on zooplankton and zoobenthos. Class 2 lakes contain at least one species 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 mean 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 lumped into trophic guilds, and trophic guilds are assigned noninteger trophic position values; (D) a food chain model of the three types of lake trout communities. Abbreviations: LT, lake trout; FFISH, pelagic forage fish; FISH, other fish; SME, smelt; MEZO, megazooplankton (*Mysis* and *Diporia*); ZOOP, zooplankton; BENT, benthic invertebrates. T.P., trophic position; T.L., trophic level.

gest 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 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 ($^{15}\text{N}/^{14}\text{N}$ ratios, or $\delta^{15}\text{N}$ signature).

Building a trophic position model

Food web and food chain models are extreme end points of a continuum of potential representations of trophic structure (Fig. 1). Connectance food web diagrams are not designed to represent energy flow, because 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, measurement of a continuous measure of trophic position for a population 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 on 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 the average between-lake 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 in some lakes of important trophic links (Rasmussen et al. 1990) caused by limited postglacial 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 that we refer to as "pelagic forage fish" (smelt, cisco, whitefish, alewife, sculpins, nine-spine 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 they are 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

TABLE 1. Summary of diet (mean $\pm$ 1 SE) for pelagic forage fish, cisco, whitefish, smelt, alewife, trout-perch, stickleback, and sculpin from Class 2 and Class 3 lakes. Abbreviations: PLA, zooplankton (copepods, cladocerans); MYS, *Mysis relicta*; BEN, benthic invertebrates (crayfish, aquatic insect larvae, oligochaetes, mollusks, isopods); AMP, amphipods (*Gammarus* sp., *Hyalella* sp., *Diporia hoyi*); FIS, all fish species.

Species	Food chain class	N, lakes	n, fish	% volumetric contribution to diet				
				PLA	MYS	BEN	AMP	FIS
Alewife	2	3	796	76.1 $\pm$ 10.8	0.0	14.4 $\pm$ 1.8	0.0	9.5 $\pm$ 9.5
	3	3	4321	65.4 $\pm$ 12.3	4.3 $\pm$ 2.8	23.5 $\pm$ 16.2	6.7 $\pm$ 5.4	0.0
Cisco	2	9	2005	91.7 $\pm$ 4.6	0.0	8.3 $\pm$ 4.6	0.0	0.0
	3	16	11 527	49.9 $\pm$ 8.2	27.6 $\pm$ 5.8	9.4 $\pm$ 1.8	12.4 $\pm$ 5.2	0.6 $\pm$ 0.3
Sculpin	2	17	4335	0.1 $\pm$ 0.1	0.0	91.0 $\pm$ 3.2	7.4 $\pm$ 3.1	1.3 $\pm$ 0.5
	3	6	2086	6.0 $\pm$ 4.3	15.2 $\pm$ 6.5	24.3 $\pm$ 9.5	54.5 $\pm$ 12.8	0.0
Smelt	2	5	785	42.1 $\pm$ 12.1	0.0	21.7 $\pm$ 5.9	0.4 $\pm$ 0.2	35.8 $\pm$ 17.8
	3	12	14 530	16.6 $\pm$ 6.4	32.0 $\pm$ 9.3	17.5 $\pm$ 5.9	3.6 $\pm$ 1.5	30.3 $\pm$ 8.6
Stickleback	3	5	787	13.2 $\pm$ 6.6	8.6 $\pm$ 4.4	61.5 $\pm$ 12.2	16.7 $\pm$ 10.5	0.0
Trout-perch	3	2	353	40.1 $\pm$ 18.8	8.0 $\pm$ 8.0	21.3 $\pm$ 19.8	30.6 $\pm$ 30.6	0.0
Whitefish	2	18	1762	16.0 $\pm$ 5.9	0.0	77.1 $\pm$ 6.1	4.7 $\pm$ 1.8	2.3 $\pm$ 1.7
	3	21	4647	4.4 $\pm$ 2.2	2.6 $\pm$ 1.3	66.5 $\pm$ 6.1	23.4 $\pm$ 5.0	3.1 $\pm$ 1.7
Total		117	47 934					

reported varied 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 that fish were further subdivided into seven subcategories when possible: cisco, whitefish, smelt, alewife, cottids, "other benthic-pelagic fish" (consisting of other salmonids, stickleback, trout-perch, and catostomids), and littoral (percids, cyprinids, and centrarchids). "Unknown," "miscellaneous," or "other" were eliminated as prey categories. 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, except when the lake was subject to a significant disturbance (such as an introduced prey species or eutrophication), or sample dates were separated by >20 yr. 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. Other Class 1 lakes for which diet data came from fewer than two seasons were eliminated from the data set. When possible, juvenile lake trout (total length < 25 cm) were excluded from analysis, as they 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 by Rasmussen et al. (1990) appears to break down at high latitudes and altitudes, where these cold water 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 using the International Hydrological Decade (1978), and the U.S. Environmental Data Service (1968). For lakes included

TABLE 2. Summary of diet (mean $\pm$ 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, catostomids, other salmonids).

Food chain class	Temperature	N, lakes	n, fish	% volumetric contribution to diet		
				PLA	MYS	BEN
1	warm water	26	3587	17.4 $\pm$ 2.9		27.4 $\pm$ 5.3
1	winter data	10	192	5.1 $\pm$ 2.6		8.2 $\pm$ 4.3
2	warm water	22	19 313	1.9 $\pm$ 1.1	0.1 $\pm$ 0.1	15.3 $\pm$ 4.0
3	warm water	23	21 369	0.0	3.9 $\pm$ 1.3	1.1 $\pm$ 0.4
2	cold water	4	523	3.5 $\pm$ 2.9	0.0	27.0 $\pm$ 17.0
3	cold water	7	2697	0.0	2.8 $\pm$ 0.9	11.0 $\pm$ 4.5
Total		92	47 681			

in Rasmussen et al. (1990) and Cabana et al. (1994), -3°C corresponds with the lower mean annual air temperature. All lakes characterized by a MAAT $< -3^{\circ}\text{C}$ were considered "cold-water" 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 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 (± 1 SE) percent volumetric contribution 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 nonvolumetric data were converted to percent volume using the conversion methodology presented in Appendix A.

Calculation of trophic position

Conversion of mean 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 and zooplankton and zoobenthos were assumed to represent trophic level 2. *Mysis* was assigned to trophic level 3 due to its generally zooplanktivorous diet (Cooper and Goldman 1980, Grossnickle 1982), as were larval and littoral fish, which 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 their minor role 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 (Quebec) and Lake Ontario suggest 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 trophic classes. With diet data and estimates of trophic level of various prey items, we calculated the trophic position of each pelagic forage fish population using a previously employed equation (Adams et al. 1983, Winemiller 1990).

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

where T_a is the trophic position of the a th predator, V_i is the volumetric contribution of the i th prey item, and T_i is the 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. These mean pelagic forage fish trophic position values, estimates of prey trophic position, and 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 cold-water and warm-water 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 mean diet of pelagic forage fish generally correspond with previous conceptions of their feeding habits (Table 1 and Appendix B). Alewives 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, whereas

TABLE 2. Continued.

% volumetric contribution to diet		Breakdown of fish (FIS) category						
AMP	FIS	ale	cis	cot	lit	pel	sme	whi
0.5 $\pm$ 0.5	54.6 $\pm$ 5.5				54.6			
0.0	86.6 $\pm$ 4.5				86.6			
5.3 $\pm$ 2.5	77.4 $\pm$ 6.7	0.0	3.3	0.7	7.0	14.1	9.2	15.5
0.3 $\pm$ 0.2	94.7 $\pm$ 1.6	21.0	31.9	14.8	4.2	3.3	19.0	0.4
1.0 $\pm$ 1.0	68.6 $\pm$ 20.5	0.0	4.6	2.2	0.0	13.6	0.0	29.4
2.0 $\pm$ 0.7	84.2 $\pm$ 4.1	0.0	44.8	12.3	1.0	18.7	0.0	7.3

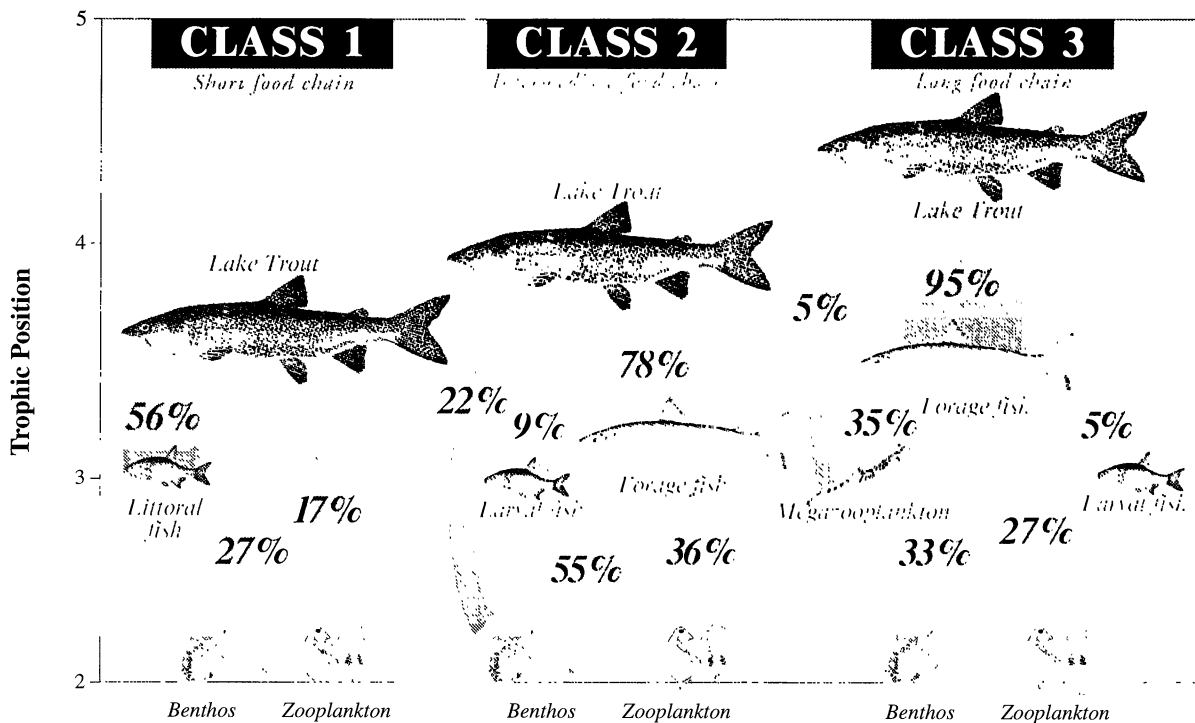


FIG. 2. A diagram summarizing the diets of lake trout and pelagic forage fish, representing the mean trophic structure that characterizes Class 1, 2, and 3 food webs. Percentages are volumetric contribution to the diet.

they increase their consumption of amphipods to 24% in Class 3 lakes, 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 feed on zooplankton (42%) and larval fish (36%), whereas Class 3 smelt consume *Mysis* (32%) and larval fish (30%). Sculpins of Class 2 lakes prey heavily on zoobenthos, whereas 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* (a relatively large, predatory, deepwater glacio-marine relict amphipod) in Class 3 lakes. Thus, *D. hoyi* appears 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 C). Class 1, 2, and 3 lake trout from warm-water lakes exhibit 54.6%, 77.4%, and 94.7% piscivory, respectively, differing significantly as a function of Class (ANOVA: $n = 70$; $F = 15.75$; $df = 2, 67$; $P < 0.0001$; Table 2). Thus, addition of pelagic forage fish appears to be responsible for an initial increase in lake trout piscivory, and ad-

dition 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 (Martin 1952). We report mean winter Class 1 piscivory to be 87%, whereas mean year-round Class 1 lake trout piscivory is 55%.

We present a diagrammatic summary of the mean feeding interrelationships characterizing Class 1, 2, and 3 food webs, as revealed from our literature review of lake trout and pelagic forage fish diet data (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) 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 (± 1 SD) position of Class 2 pelagic forage fish is 3.12 ($\pm$

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
A) Class 1					
Lake trout:					
Warm water	26	3.0	3.55	0.28	0.06
B) 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
C) 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.

0.19 trophic level, T.L.), 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.), whereas 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 T.L.). The trophic level estimates of Rasmussen et al. (1990) greatly underestimated Class 1 lake trout trophic position (by 0.55 trophic levels) by neglecting these high levels of piscivory. The mean Class 2 lake trout trophic position of 3.89 (± 0.48 T.L.) generally corresponds with the Rasmussen trophic level estimate of 4.0. Class 3 lake trout exhibit a mean trophic position of 4.38 (± 0.38 T.L.), 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: $n = 70$; $F = 69.73$; $df = 2, 67$; $P < 0.0001$). Furthermore, lake trout are more variable in trophic position than are 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 almost 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 PCBs vs. trophic position (linear regression, including lakes from all three classes; mean ± 1 SE) shows a strong positive relationship (Fig. 4A).

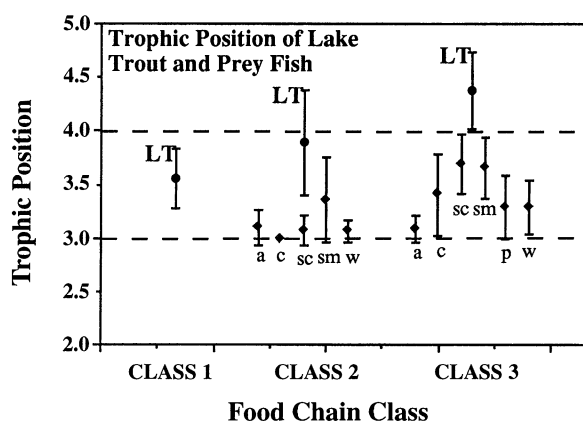


FIG. 3. Mean (± 1 SD) trophic position (T.P.), of lake trout and each pelagic forage fish species for Class 1, 2, and 3 food webs. Abbreviations: a, alewife; c, cisco; w, whitefish; sm, smelt; sc, sculpin; p, trout-perch and stickleback; LT, lake trout.

$$\log \text{PCB} = -6.07 (\pm 0.89) + 2.11 (\pm 0.22) \text{ trophic position}, \quad (2)$$

where $n = 21$ lakes, $r^2 = 0.83$, $\pm 1 \text{ SE}_{\text{est}} = 0.24$; $F = 95.10$; $\text{df} = 1, 19$; $P < 0.001$. By comparison, use of the discrete trophic level variable of Rasmussen et al. (1990) provided a strong, but considerably less powerful, model.

$$\log \text{PCB} = 1.25 (\pm 0.20) + 0.60 (\pm 0.09) \text{ no. of trophic levels (1, 2, or 3)}, \quad (3)$$

where $n = 21$ lakes, $r^2 = 0.72$, $\pm 1 \text{ SE}_{\text{est}} = 0.31$; $F = 47.83$; $\text{df} = 1, 19$; $P < 0.0001$. 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 (Eqs. 2 and 3) that 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 that included significant contributions from lipid content and latitude, these secondary variables must be considered as well. The best model (multiple linear regression) for PCB levels in lake trout shows significant effects of trophic position and lipid content. Latitude is not significant, due to the limited geographic range of lakes included in this data set.

$$\log \text{PCB} = -3.87 (\pm 1.30) + 1.44 (\pm 0.37) \text{ trophic position} + 0.72 (\pm 0.34) \log \% \text{ lipid}, \quad (4)$$

where $n = 21$ lakes, $r^2 = 0.87$, $\pm 1 \text{ SE}_{\text{est}} = 0.22$; $F = 58.99$; $\text{df} = 2, 18$; trophic position $P < 0.001$; $\log \% \text{ lipid } P = 0.045$.

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

$$\log \text{PCB} = 1.14 (\pm 0.18) + 0.27 (\pm 0.15) \text{ no. of trophic levels (1, 2, or 3)} + 1.14 (\pm 0.44) \log \% \text{ lipid}, \quad (5)$$

where $n = 21$ lakes, $r^2 = 0.79$, $\pm 1 \text{ SE}_{\text{est}} = 0.27$; $F = 34.34$; $\text{df} = 2, 18$; class variable $P = 0.084$; $\log \% \text{ lipid } P = 0.019$.

The residuals of the model using trophic position average 0.06 lower than those of 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 ($n = 21$; $t = -2.51$; $P = 0.02$).

Addition of 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 the strong lipid and PCB correlation, 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 lakes using multiple linear regression:

$$\log \text{PCB} = -2.98 (\pm 2.83) - 0.005 (\pm 0.002) \text{ latitude} + 1.66 (\pm 0.71) \text{ trophic position}, \quad (6)$$

where $n = 8$ lakes, $r^2 = 0.65$, $1 \text{ SE}_{\text{est}} = 0.24$; $F = 4.58$; $\text{df} = 2, 5$; and in Class 3 lakes:

$$\log \text{PCB} = -3.87 (\pm 1.08) - 0.001 (\pm 0.00) \text{ latitude} + 1.65 (\pm 0.25) \text{ trophic position}, \quad (7)$$

$n = 9$ lakes, $r^2 = 0.91$, $1 \text{ SE}_{\text{est}} = 0.11$; $F = 31.63$; $\text{df} = 3, 6$. Trophic position is a significant predictor of PCB levels within both classes (Class 2: $P = 0.065$; Class 3: $P = 0.001$), as is latitude (Class 2: $P = 0.082$; Class 3: $P = 0.023$). No significant relationship between trophic position and PCBs was found among the five Class 1 lakes for which data were available.

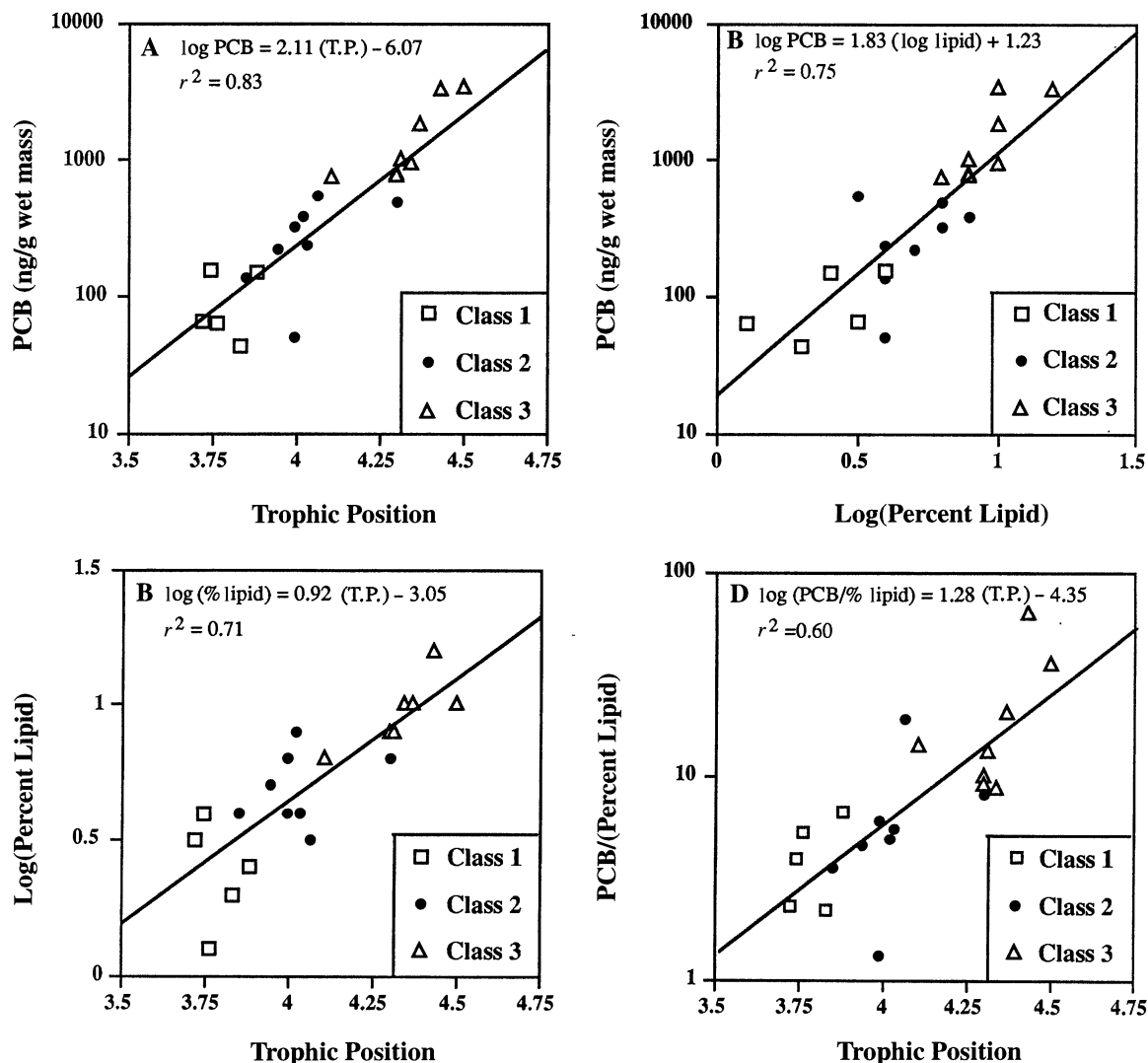


FIG. 4. Relationships between PCB levels, lipid content, and dietary estimate of trophic position. (A) trophic position vs. PCB levels (log scale) in lake trout; (B) trophic position vs. log(percent lipid) in lake trout; (C) log(percent lipid) vs. PCB (log scale) in lake trout; (D) trophic position vs. lipid-corrected PCB levels (PCB/percent lipid; log scale). Symbols: Class 1 lake trout (open square), Class 2 lake trout (solid circle), Class 3 lake trout (open triangle).

Although we have both PCB and diet data from only 21 lakes, these results suggest that a continuous measure of trophic position is a better predictor than discrete trophic levels of between-lake PCB levels in lake trout. In spite of the problems inherent in using 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 also suggests that more thorough consideration of omnivory has potential to further improve ecologists' 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 (continuous measure) represents realized trophic structure better than do trophic levels. To incorporate "trophic position" into a broader modeling framework, we used the dietary and trophic position data (Tables 1–3) 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, were 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 latter qualitatively captures the increase in lake trout trophic position accompanying the addition of functional prey groups to the food chain. Quantitatively, however, the trophic position model deviates from the discrete trophic level model. In particular, 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 ≈ 0.5 trophic level, adequately represents the length of the intermediate food chain, and overestimates the length of the longest food chain by about ≈ 0.5 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 unique 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 as a separate trophic guild in the trophic position models of lake trout food webs (Fig. 1C). Here, we statistically evaluate the validity of treating smelt separately within the trophic position model. We also test the correspondence between presence of the smelt trophic guild 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 positions of smelt and cisco from Class 2 and 3 lakes. Smelt had a significantly higher trophic position than cisco ($n = 42$; $F = 9.96$; $df = 1, 38$; $P < 0.004$). Smelt and cisco of Class 3 lakes also exhibited significantly higher trophic position than smelt and cisco of Class 2 lakes ($n = 42$; $F = 13.1$; $df = 1, 38$; $P < 0.001$). More interestingly, two-way ANOVA revealed a significant increase in lake trout trophic position in lakes containing smelt vs. lakes of the same food chain class, but lacking smelt ($n = 45$; $F = 9.25$; $df = 1, 41$; $P < 0.004$; Fig. 5). Class effects on lake trout trophic position were also significant ($n = 45$; $F = 21.94$; $df = 1, 41$; $P < 0.0001$).

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 levels of lake trout contaminants. Mercury data from Cabana et al. (1994) were used to test whether or not the presence of smelt was accompanied by

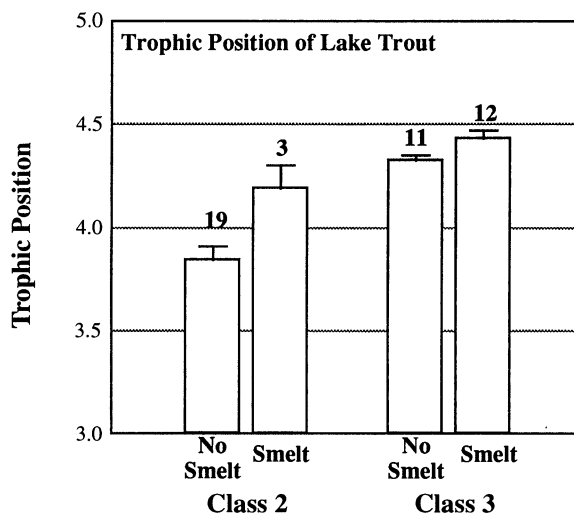


FIG. 5. The influence of the presence of smelt on mean lake trout trophic position (± 1 SE) from Class 2 and 3 food webs. The accompanying numbers represent sample size.

elevated mercury levels in lake trout. In Class 2 lakes, presence of smelt was accompanied by an increase in mean (± 1 SE) mercury levels from 0.54 ± 0.08 mg/kg to 0.88 ± 0.21 mg/kg. In Class 3 lakes, smelt presence was accompanied by an increase in mean mercury levels from 0.64 ± 0.07 mg/kg to 1.19 ± 0.32 mg/kg. Two-way ANOVA on Class 2 and 3 lakes shows a significant effect of smelt on Hg levels in lake trout ($n = 61$; $F = 66.6$; $df = 1, 57$; $P = 0.012$; Fig. 6A). Class was not a significant predictor of Hg in this analysis (Classes 2 vs. 3: $n = 61$; $F = 1.42$; $df = 1, 57$; $P = 0.238$).

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 (± 1 SE) from $261.4 (\pm 17.14)$ ng/g (wet mass) to $426.7 (\pm 14.75)$ ng/g (wet mass). Among Class 3 lakes, mean PCB concentration increased from $426.0 (\pm 22.10)$ ng/g, to $1469.2 (\pm 41.99)$ 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 ($n = 74$; $F = 15.07$; $df = 1, 70$; $P < 0.0001$; Fig. 6B), as well as a significant effect of food chain class on PCB concentrations ($n = 74$; $F = 7.86$; $df = 1, 70$; $P < 0.008$).

Correspondence between dietary and $\delta^{15}\text{N}$ estimates of trophic position

Stable nitrogen isotopes ($\delta^{15}\text{N}$ ratios) 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 $\delta^{15}\text{N}$ enrichment averaging 3.4 ‰ between predator and prey (Minagawa and Wada 1984, Estep and

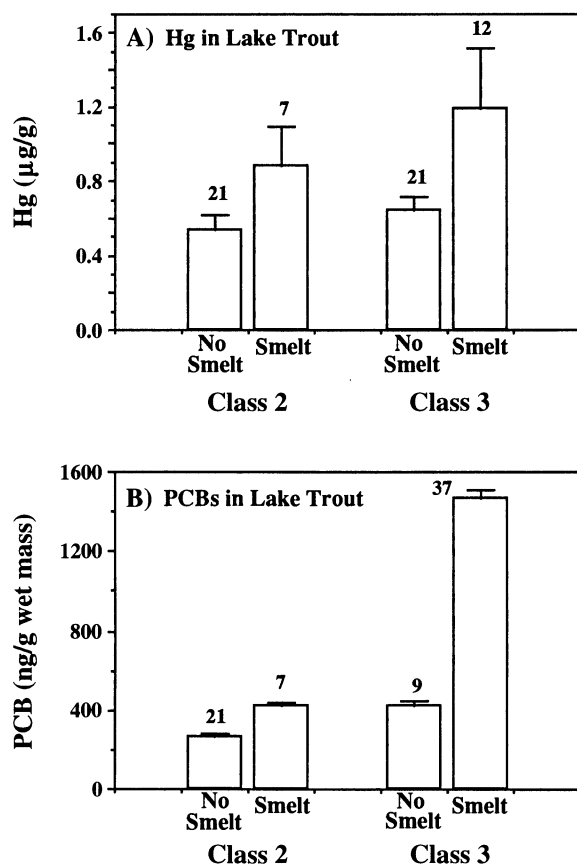


FIG. 6. The influence of the presence of smelt upon mean lake trout muscle tissue (A) mercury, Hg ($\mu\text{g/g}$; ± 1 SE), and (B) PCB (ng/g wet mass; ± 1 SE) levels from Class 2 and Class 3 food webs. The accompanying numbers represent sample size.

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 (Broman et al. 1992, Yoshinaga et al. 1992, Rolff et al. 1993, Cabana and Rasmussen 1994, Kidd et al. 1995a, b, Kiriluk et al. 1995, Schindler et al. 1995). Unfortunately, $\delta^{15}\text{N}$ and dietary information currently are not available from the same lakes, preventing lake-specific comparisons of dietary and $\delta^{15}\text{N}$ trophic position estimates. But dietary and $\delta^{15}\text{N}$ results can be compared using multilake means 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 $\delta^{15}\text{N}$ data from Cabana and Rasmussen (1994) were used to calculate a continuous measure of lake trout and pelagic forage fish trophic position. The mean $\delta^{15}\text{N}$ signature of zooplankton (representing trophic level 2.0) of 4.5‰ in these lakes was used to represent the "baseline" $\delta^{15}\text{N}$ signature. A comparison of $\delta^{15}\text{N}$ and dietary mean trophic position values reveals a general correspondence between the two methods (Fig. 7). Discrepancies are observed for

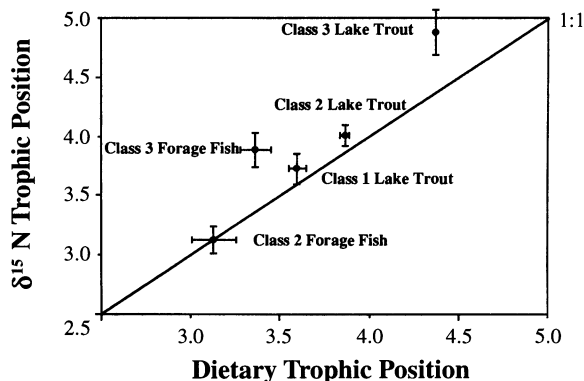


FIG. 7. A comparison of the mean stable nitrogen isotope ($\delta^{15}\text{N}$) and mean dietary estimates of trophic position (± 1 SE) for lake trout and pelagic forage fish from Class 1, 2, and 3 food webs.

pelagic forage fish and lake trout of Class 3 lakes, with $\delta^{15}\text{N}$ evidence suggesting a longer food chain. This difference could be attributed to elevated primary producer $\delta^{15}\text{N}$ signature in Class 3 lakes (associated with elevated loading of human sewage; Cabana and Rasmussen, *in press*). 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 approach to measuring omnivory differs greatly from that taken by 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 surprising 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 one and nine trophic levels (averaging three to five 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 $\delta^{15}\text{N}$ 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. We attribute this to the higher trophic efficiency as-

sociated with foraging at lower trophic levels, the greater ease of capture of herbivorous prey, and the higher abundance/production 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: first, the existence of levels, natural groupings of species of similar trophic position; and second, 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, Wootton and Power 1993), ecosystem energetics and production (Lindeman 1942, Kerr and Martin 1970), and contaminant biomagnification (Oliver and Niimi 1988, Rasmussen et al. 1990, Rowan and Rasmussen 1992, 1994, Cabana et al. 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, 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, yielding the trophic position model shown in Fig. 1C. 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 trophodynamics and cascading trophic interactions, because the

degree of omnivory should determine the degree to which the trophic cascade propagates through the food web (Vadas 1990). In addition, use of omnivory-corrected estimates of food chain length will also have consequences for modeling ecosystem energetics (Kercher and Shugart 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 fourfold increase in estimated lake trout production.

Although our trophic position model, by accounting for more of the natural complexity of food webs, represents trophic structure more accurately than the use of trophic levels 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 the use of $\delta^{15}\text{N}$ provides: quantification of the mean number of energy transfers between primary producers and the study organism. Recent studies have demonstrated the use of $\delta^{15}\text{N}$ as a general predictor of contaminant levels in the biota. Kidd et al. (1995a) reported relationships between $\delta^{15}\text{N}$ 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 Yoshinaga et al. (1992) report strong relationships between mercury levels and $\delta^{15}\text{N}$ signatures. Other recent studies have used $\delta^{15}\text{N}$ to characterize contaminant flows in aquatic ecosystems (Broman et al. 1992, Rolff et al. 1993, Kiriluk et al. 1995).

Calculation of biomagnification factors (BMFs)

Rasmussen et al. (1990) reported that addition of each "trophic level" (functional trophic group) con-

tributed 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 0.5 trophic level, then our biomagnification factor (BMF) estimate for PCBs increases by a factor of $3.5^2 = 12.25$ 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, Evans et al. 1991, Meili 1991, Rowan and Rasmussen 1992). Consideration of omnivory will generally result in higher estimates of BMFs accompanying each discrete trophic level.

Since each $\delta^{15}\text{N}$ increment of 3.4‰ represents one trophic level, the change in a contaminant accompanying each 3.4 $\delta^{15}\text{N}$ increment provides a BMF estimate that also incorporates omnivory. Kidd et al. (1995a) relate increasing tissue concentrations of organochlorines to $\delta^{15}\text{N}$ levels in a Yukon lake food chain. Using the approach outlined, we calculated BMFs of 3.5 for hexachlorohexane (ΣHCH), 12.3 for ΣDDT , and 9.8 for hexachlorobenzene (ΣHCB). Using contaminant and $\delta^{15}\text{N}$ data from Kiriluk et al. (1995), 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), we calculate a 6.5-fold increase in mercury accompanying each $\delta^{15}\text{N}$ -defined trophic level increment. Yoshinaga et al. (1992) obtained a BMF estimate for mercury of 5.0 in a $\delta^{15}\text{N}$ -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. However, 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 $\delta^{15}\text{N}$ or dietary data. Consideration of omnivory should also result in more realistic mechanistic modeling of contaminant biomagnification. Cabana and Rasmussen (1994) use $\delta^{15}\text{N}$ 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 exotic species

Smelt is an exotic species in most 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. Introduction of smelt appears to be a case in point, and underscores this concern. In addition to its 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 their 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, Rowan and Rasmussen, *in press*) 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 are represented by trophic level "2," whereas *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).

Analysis of trophic interactions at lower trophic lev-

els 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 investiture of time and effort, not to mention the number of fish that must be sacrificed (see Wine-miller 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 (DeNiro and Epstein 1981). Use of $\delta^{15}\text{N}$ provides a continuous, time-integrated measure of relative trophic position that 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, $\delta^{15}\text{N}$ serves as a more accurate alternative to diet data as measure of trophic position, as long as variation in primary producer (baseline) $\delta^{15}\text{N}$ (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 $\delta^{15}\text{N}$ to quantify trophic position and omnivory. Dietary information would then complement isotopic evidence by verifying $\delta^{15}\text{N}$ 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) Trophic levels qualitatively represent broad-scale patterns in trophic structure, but fail to quantitatively represent trophic structure, due to the prevalence of omnivory and other complexity of pelagic food webs. (2) Lake-specific estimates of lake trout trophic position provide improved prediction of PCB concentrations over previous trophic level approaches. (3) 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 by

trophic linkages that are important in terms of their contributions to mass transfer. Separate trophic guild designation of smelt is validated by elevated levels of mercury and PCB in lake trout in the presence of smelt. (4) Mean dietary trophic position estimates generally correspond with mean $\delta^{15}\text{N}$ estimates among components of the pelagic food web.

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APPENDIX A

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 mass) 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 1980). 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:

$$Vp_i = (N_i \cdot \text{mass}_i) / \text{mass}_a \quad (\text{A.1})$$

where for prey item i , Vp is the percent by volume of the prey item, N is the percent of the total number, mass_i is the estimate of prey mass, mass_a is the mass of all prey items. Prey mass data were taken from the literature source, or were estimated from a literature compilation of invertebrate body sizes (J. Vander Zanden, *unpublished data*).

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

$$Vp_i = (f_i \cdot \text{mass}_i) / \text{mass}_a \quad (\text{A.2})$$

where for prey item (i), Vp is the percent by volume of prey item, f is the frequency of occurrence of the prey type, mass_i is the mean mass when the item is present (1, 0.14, or 0.23), and mass_a is the total mass of all prey items. Application of this conversion ratio to Class 1 lakes gave <4% error on estimates of volumetric contribution of lake trout prey items.

Detailed lake trout diet data were not available from Class 2 and 3 lakes, requiring an alternate technique to convert percent frequency into percent volume. Data from 10 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 578 percent frequency and percent 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 percent volume and percent frequency of occurrence:

$$\% \text{ volume} = -1.52 (\pm 0.98) + 0.80 (\pm 0.02) \% \text{ frequency}, \quad (\text{A.3})$$

where $r^2 = 0.67$, $n = 578$, and $1 \text{ SE}_{\text{est}} = 16.43$.

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

$$\begin{aligned} \% \text{ volume} = & -0.62 (\pm 0.71) + 1.13 (\pm 0.04) \% \text{ frequency} \\ & - 0.27 (\pm 0.01) \% \text{ frequency} \cdot \log(\text{predator:prey body mass ratio}), \end{aligned} \quad (\text{A.4})$$

where $r^2 = 0.83$, $n = 578$, and $1 \text{ SE}_{\text{est}} = 11.93$. Percent frequency of occurrence data were converted to a percent volume format using conversion Eq. A.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 make up 24% of the observations, the total error associated with use of this conversion is 2.9%.

APPENDIX B

Pelagic forage fish dietary data from North American lakes. The following variables are listed: lake, data conversion, year, sample size (no. fish), diet composition (percent of total volume), trophic position (T.P.), and references.

Lake	Data†	Year	n	% volume contribution to diet‡					T.P.	Reference§	
				PLA	MYS	BEN	AMP	FIS			
A) Alewife											
Class 2 (N = 3 lakes; n = 796 fish)											
Black Pond	b	1966	52	84.5	0.0	15.5	0.0	0.0	3.00	1	
Clayton	a	1978	533	54.7	0.0	16.8	0.0	28.5	3.29	2	
Echo	a	1967	211	89.1	0.0	10.9	0.0	0.0	3.00	3	
Mean				76.1	0.0	14.4	0.0	9.5	3.10		
1 SD				18.7	0.0	3.1	0.0	16.5	0.16		
1 SE				10.8	0.0	1.8	0.0	9.5	0.10		
Class 3 (N = 3 lakes; n = 4321 fish)											
Michigan	a	...	4205	71.2	1.5	4.9	22.5	0.0	3.24	4–11	
Ontario	a	1972, 1988	...	83.1	12.4	0.0	4.5	0.0	3.17	98	
Ontario	a	1927	77	78.0	3.3	18.7	0.0	0.0	3.03	12	
Upper Rideau	a	1991	39	29.4	0.0	70.6	0.0	0.0	3.00	13	
Mean				65.4	4.3	23.5	6.7	0.0	3.11		
1 SD				24.5	5.6	32.4	10.7	0.0	0.11		
1 SE				12.3	2.8	16.2	5.4	0.0	0.1		
B) Whitefish											
Class 2 (N = 18 lakes; n = 1762 fish)											
Babine	a	1946	39	8.9	0.0	90.2	0.0	0.9	3.01	14	
Babine	a	1946	121	3.6	0.0	96.2	0.2	0.0	3.00	14	
Cree	a	1955	50	0.0	0.0	66.7	2.1	31.3	3.33	15	
Cree	a	1955	50	5.6	0.0	72.2	22.2	0.0	3.22	15	
Glacier	a	1986	21	17.2	0.0	82.8	0.0	0.0	3.00	16	
Hector	a	1986	13	0.0	0.0	98.0	2.0	0.0	3.02	16	
Heming	a	1945	225	0.0	0.0	98.7	0.0	1.3	3.01	17	
Morrison	a	1946	95	94.8	0.0	5.2	0.0	0.0	3.00	14	
Morrison	a	1946	9	0.0	0.0	100	0.0	0.0	3.00	14	
Pyramid	a	1939–1945	50	31.5	0.0	56.5	12.0	0.0	3.12	18	
Shakespeare Is.	a	1927	76	39.5	0.0	42.4	17.5	0.5	3.18	20	
Sheep R.	b	1973	190	0.0	0.0	100	0.0	0.0	3.00	21	
Snake R.	b	1970	250	0.0	0.0	93.9	0.0	6.1	3.06	22	
Squanga	a	1960	145	45.0	0.0	55.0	0.0	0.0	3.00	23	
Trout	a	1932	52	11.0	0.0	88.6	0.0	0.4	3.00	24	
Waskesiu	a	1927	50	0.0	0.0	100	0.0	0.0	3.00	25	
Waterton	a	1951	276	0.0	0.0	84.2	15.8	0.0	3.16	26	
Mean				16.0	0.0	77.1	4.7	2.3	3.07		
1 SD				24.8	0.0	25.8	7.5	7.4	0.10		
1 SE				5.9	0.0	6.1	1.8	1.7	0.02		
Class 3 (N = 21 lakes; n = 4647 fish)											
Athabaska	a	1945	30	0.0	0.0	56.6	43.3	0.0	3.43	30	
Champlain	a	1931	141	0.0	0.0	100	0.0	0.0	3.00	38	
Great Bear	c	1963–1965	576	0.0	1.0	54.6	32.3	12.1	3.45	40	
Great Bear Lake	a	1945	86	11.0	0.0	75.0	14.0	0.0	3.14	28	
Great Bear Lake	a	1945	45	8.0	0.0	92.0	0.0	0.0	3.00	28	
Great Slave	a	1944–1947	308	0.0	1.3	61.3	37.3	0.0	3.39	29, 30	
Keller	a	1961–1962	386	0.0	0.8	73.5	25.7	0.0	3.27	37	
Lakelse	a	1946	84	0.0	0.0	99.9	0.1	0.0	3.00	14	
LaRonge	a	1948–1954	737	2.6	0.0	62.7	33.2	1.6	3.35	32	
Michigan	a	1972–1974	640	0.0	0.0	97.7	1.6	0.6	3.02	31	
Nipigon	a	1921–1927	382	0.0	3.1	73.3	20.4	3.2	3.27	25, 33, 34	
Oneida	a	1927	50	0.0	0.0	100	0.0	0.0	3.00	25	
Ontario	a	1927	45	0.0	3.3	17.8	78.9	0.0	3.82	20	
Pagwashuan	a	1927	8	0.0	0.0	86.5	13.5	0.0	3.14	20	
Simcoe	a	1927	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	1952	116	37.4	0.3	12.0	50.3	0.0	3.51	35	
Toolik	c	1986	71	0.0	0.0	100	0.0	0.0	3.00	39	
Winnipeg	a	1927	536	0.0	0.0	69.7	30.3	0.0	3.30	36	
Wollaston	a	1955	100	0.0	3.0	47.0	45.0	5.0	3.53	15	
Mean				4.4	2.6	66.5	23.4	3.1	3.29		
1 SD				9.9	6.0	28.1	23.1	8.0	0.25		
1 SE				2.2	1.3	6.1	5.0	1.7	0.05		

APPENDIX B. Continued.

Lake	Data†	Year	n	% volume contribution to diet‡					T.P.	Reference§	
				PLA	MYS	BEN	AMP	FIS			
C) Cisco											
Class 2 (<i>N</i> = 9 lakes; <i>n</i> = 1309 fish)											
Black	a	1932	71	89.1	0.0	10.9	0.0	0.0	3.00	41	
Clear	a	1932	225	98.0	0.0	2.0	0.0	0.0	3.00	41	
Muskelunge	a	1932	154	95.9	0.0	4.1	0.0	0.0	3.00	41	
Pallette	a	1931	23	96.2	0.0	3.8	0.0	0.0	3.00	41	
Pallette	a	1969	501	100	0.0	0.0	0.0	0.0	3.00	42	
Silver	a	1931	42	99.4	0.0	0.6	0.0	0.0	3.00	41	
Swains	a	1939	12	99.0	0.0	1.0	0.0	0.0	3.00	43	
Trout	a	1932	181	91.1	0.0	8.9	0.1	0.0	3.00	41	
Waskesiu	a	1927	100	56.4	0.0	43.6	0.0	0.0	3.00	25	
Mean				91.7	0.0	8.3	0.0	0.0	3.00		
1 SD				13.7	0.0	13.7	0.0	0.0	0.00		
1 SE				4.6	0.0	4.6	0.0	0.0	0.00		
Class 3 (<i>N</i> = 16 lakes; <i>n</i> = 11 527 fish)											
Burnt Island	a	1993	114	44.1	34.0	14.9	3.2	3.7	3.41	49	
Great Bear Lake	a	1945	135	74.5	15.0	10.0	0.0	0.5	3.16	28	
Great Slave	a	1944–1947	378	60.6	28.3	10.1	1.0	0.0	3.29	29	
Greenwich	a	1993	27	100	0.0	0.0	0.0	0.0	3.00	49	
Islet	a	1993	118	20.3	54.9	17.6	3.8	3.3	3.62	49	
Little Joe	a	1993	102	2.7	80.7	3.0	13.7	0.0	3.94	49	
Loch Erne	a	1993	126	72.0	28.0	0.0	0.0	0.0	3.28	49	
Michigan	a	1954–1980	6246	5.2	34.1	1.7	59.1	0.0	3.93	43–45	
Nipigon	a	1925	266	25.3	52.9	21.8	0.0	0.0	3.53	33, 34, 46	
Nipissing	a	1935	1446	73.4	10.4	16.2	0.0	0.0	3.10	50	
Ontario	a	1925	258	4.2	49.9	13.0	33.0	0.0	3.83	46	
S. Otterskin	a	1993	175	24.5	2.7	7.8	62.8	2.1	3.68	49	
Simcoe	a	1927	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	1950–1965	936	45.7	30.0	10.8	13.4	0.1	3.44	47, 48	
Mean				49.9	27.6	9.4	12.4	0.6	3.41		
1 SD				32.7	23.2	7.2	20.8	1.3	0.32		
1 SE				8.2	5.8	1.8	5.2	0.3	0.08		
D) Smelt											
Class 2 (<i>N</i> = 5 lakes; <i>n</i> = 785 fish)											
Crystal	a	1940	210	0.0	0.0	1.0	1.0	98.0	3.99	51	
Devilfish	a	1984	100	39.4	0.0	20.5	0.4	39.7	3.40	54	
Echo	a	1967	67	65.2	0.0	34.8	0.0	0.0	3.00	3	
Gull	a	1965	308	66.7	0.0	31.5	0.0	1.8	3.02	53	
West Bearskin	a	1984	100	39.4	0.0	20.5	0.4	39.7	3.40	54	
Mean				42.1	0.0	21.7	0.4	35.8	3.36		
1 SD				27.0	0.0	13.2	0.4	39.8	0.40		
1 SE				12.1	0.0	5.9	0.2	17.8	0.18		
Class 3 (<i>N</i> = 12 lakes; <i>n</i> = 14 530 fish)											
12 Mile	c	1984	100	17.7	5.5	49.0	0.9	26.9	3.33	55	
Huron	a	1947	300	0.0	82.0	9.0	0.0	9.0	3.91	57	
Huron, Saginaw	a	1956	3390	14.5	20.1	44.1	1.0	20.3	3.41	58	
Memphremagog	a	1994	50	11.0	0.0	0.0	0.0	89.0	3.89	59	
Michigan	c	1933	3015	0.8	77.1	2.0	11.1	9.0	3.97	56	
Michigan	a	1982	1497	8.0	37.3	9.9	3.6	41.1	3.82	60–62	
M. Memphremagog	a	1972	373	2.0	0.0	55.5	0.0	42.5	3.43	62	
Ontario	a	1984	2559	0.0	67.9	0.0	0.0	32.1	4.00	63	
S. Memphremagog	a	1972	135	0.0	0.0	16.1	0.0	83.9	3.84	62	
Simcoe	a	1970	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	
Mean				16.6	32.0	17.5	3.6	30.3	3.66		
1 SD				22.0	32.1	20.5	5.3	29.8	0.29		
1 SE				6.4	9.3	5.9	1.5	8.6	0.09		
E) Stickleback											
Class 3 (<i>N</i> = 2 lakes; <i>n</i> = 353 fish)											
Nipigon	a	1921	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	

APPENDIX B. Continued.

Lake	Data†	Year	n	% volume contribution to diet‡					T.P.	Reference§
				PLA	MYS	BEN	AMP	FIS		
Mean				40.1	8.0	21.3	30.6	0.0	3.39	
1 SD				26.6	11.3	27.9	43.3	0.0	0.55	
1 SE				18.8	8.0	19.8	30.6	0.0	0.39	
F) Trout-perch										
Class 3 (N = 5 lakes; n = 787 fish)										
Erie	a	1975	100	22.9	16.9	60.2	0.0	0.0	3.17	65
Erie	a	1975	100	34.1	4.9	61.0	0.0	0.0	3.05	65
Nipigon	a	1921	9	0.0	0.0	68.4	31.6	0.0	3.32	34
Nipigon	a	1921	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
Mean				13.2	8.6	61.5	16.7	0.0	3.25	
1 SD				14.8	9.9	27.2	23.5	0.0	0.29	
1 SE				6.6	4.4	12.2	10.5	0.0	0.13	
G) Sculpin										
Class 2 (N = 17 lakes; n = 4335 fish)										
New York	a	1933	155	0.0	0.0	81.2	15.0	3.8	3.19	66
New York	a	1933	730	0.0	0.0	97.2	2.2	0.6	3.03	66
New York	a	1933	515	0.0	0.0	99.1	0.2	0.7	3.01	66
South Flor R.	a	1966	300	0.0	0.0	99.7	0.2	0.2	3.00	67
Toolik	a	1980–1982	51	2.4	0.0	95.7	0.0	0.0	2.96	70
Valley Creek	a	1970	116	0.0	0.0	69.8	30.2	0.0	3.30	68
Valley Creek	a	1970	326	0.0	0.0	50.6	49.4	0.0	3.49	68
W. Gallatin R.	a	1950–1951	783	0.0	0.0	100	0.0	0.0	3.00	69
Mean				0.3	0.0	86.6	12.2	0.7	3.12	
1 SD				0.8	0.0	18.2	18.5	1.3	0.19	
1 SE				0.2	0.0	4.3	4.4	0.3	0.04	
Class 3 (N = 6 lakes; n = 2086 fish)										
Michigan	a	1982	240	0.0	3.2	56.0	40.8	0.0	3.44	72
Nipigon	a	1921	12	0.0	2.1	38.1	59.8	0.0	3.62	34
Superior	a	...	708	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	1962	866	28.7	31.5	39.8	0.0	0.0	3.32	71
Mean				6.0	15.2	24.3	54.5	0.0	3.70	
1 SD				11.2	15.9	23.3	31.2	0.0	0.28	
1 SE				4.6	6.5	9.5	12.8	0.0	0.11	

† a, percent volume format reported; b, percent of total number converted to percent volume using Eq. A.1; c, percent frequency of occurrence converted to percent volume using Eq. A.2; d, percent frequency of occurrence converted to percent volume using Eq. A.4.

‡ PLA, zooplankton; MYS, *Mysis relicta*; BEN, zoobenthos; AMP, amphipods; FIS, all fish species.

§ 1, Hutchinson 1971; 2, Kohler and Ney 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 1948; 20, Hart 1931; 21, Thompson and Davies 1976; 22, Pontius 1973; 23, Lindsey 1963; 24, Couey 1935; 25, Rawson 1930; 26, Cuerrier and Schultz 1957; 27, Anderson and Smith 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; 53, Burbidge 1969; 54, Hassinger and Close 1984; 55, Loftus and Hulsman 1986; 56, Schneberger 1936; 57, Baldwin 1948; 58, Gordon 1961; 59, M.J. Vander Zanden, *unpublished data*; 60, Stedman and Argyle 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; 969, Bailey 1952; 70, Hershey and McDonald 1985; 71, Ikusemiju 1975; 72, Wojcik et al. 1986; 98, Mills et al. 1992.

APPENDIX C

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 (no. fish), diet (percent of total volume), trophic position (T.P.) and references.

Lake	Data†	Lat	Long	Area (km ²)	Temp	<i>n</i>
A) Class 1						
Warm-water; winter data (<i>N</i> = 10 lakes; <i>n</i> = 192 fish)						
Boot	d	45°36'	78°11'	0.9	2.5	15
Booth	d	45°39'	78°12'	4.9	2.5	5
Deer	d	45°02'	78°06'	1.9	4.5	58
Friday	d	45°04'	77°55'	1.1	4.5	37
Fraser	d	45°31'	78°19'	0.5	2.5	8
Grace	d	45°04'	78°14'	2.3	4.5	50
Lobster	d	45°32'	78°12'	1.3	2.5	3
Shirley	d	45°41'	78°08'	4.8	2.5	5
Sylvia	d	45°32'	78°20'	0.4	2.5	5
Two Rivers	d	45°35'	78°29'	2.9	2.5	6
Mean						
1 SE						
1 SD						
Warm-water lakes (<i>N</i> = 26 lakes; <i>n</i> = 3587 fish)						
Anstruther	a, d	44°45'	78°12'	6.3	4.5	729
Ashby	d	45°05'	77°21'	2.6	4.5	20
Aubin	d	46°58'	73°00'	1.4	2.5	22
Baude	d	47°05'	73°18'	3.2	2.5	81
Bay	d	45°01'	77°52'	0.8	4.5	35
Birch	a	42°40'	83°10'	1.3	9.7	25
Brewer	d	45°35'	78°19'	0.4	2.5	222
Canisbay	d	45°34'	78°35'	1.5	2.5	279
Carignan	d	47°10'	72°45'	5.2	2.5	72
Cinconsine	d	47°20'	73°04'	12.7	2.5	33
Costello	d	45°35'	78°19'	0.3	2.5	59
Dickie	a	44°47'	77°44'	2.1	4.5	300
Eels	a, d	44°54'	78°08'	9.5	4.5	176
Farquar	a, d	45°05'	78°12'	3.4	4.5	72
L'amable	d	45°01'	77°49'	1.8	4.5	26
Louisa	d	45°28'	78°29'	4.9	2.5	487
Louisa	a	45°28'	78°29'	4.9	2.5	205
Miette	a	53°00'	118°37'	0.1	-2.5	23
Norman	d	47°05'	73°14'	9.2	2.5	112
Sassenach	a	53°14'	118°23'	0.1	-2.0	49
Silent	d	44°55'	78°04'	1.2	4.5	87
Sincennes	d	47°30'	73°52'	13.5	2.5	7
Tallan	d	44°51'	78°03'	0.5	4.5	8
Weslemkoon	d	45°02'	77°25'	10.0	4.5	95
Wollaston	a, d	44°52'	77°49'	2.0	4.5	363
Mean						
1 SD						
1 SE						
B) Class 2						
Cold-water (<i>N</i> = 4 lakes; <i>n</i> = 523 fish)						
Caniapiscau	a	54°10'	69°50'	...	-5.5	105
Grande Riviere	a	53°00'	75°00'	...	-5.0	145
Minnewanka	c	51°15'	115°20'	22.1	-3.0	169
Toolik	b	70°00'	149°00'	1.5	-10.0	104
Mean						
1 SD						
1 SE						
Warm-water (<i>N</i> = 22 lakes; <i>n</i> = 19 313 fish)						
Babine	a	54°45'	126°00'	446.7	-1.0	53
Chandos	c	44°49'	78°00'	13.9	4.5	128
Devilfish	a	...	...	1.6	3.0	200
Donner	a	39°25'	120°05'	3.0	4.4	44
Drag	a	45°04'	78°23'	10.0	4.5	121
Flathead	a	47°55'	114°07'	1170.0	5.6	201
Glacier	a	51°55'	116°51'	1.6	-1.0	35
Hector	a	51°35'	116°21'	5.9	-1.5	56
Koshlong	a	44°58'	78°29'	4.0	4.5	150

APPENDIX C. Continued.

% volume contribution to diet‡					Breakdown of fish (FIS) category							T.P.	Refer- ences§
PLA	MYS	BEN	AMP	FIS	ale	cis	cot	lit	pel	sme	whi		
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
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
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
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
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
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
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
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
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
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
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	
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	
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	
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
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
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
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
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
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
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
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
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
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
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
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
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
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
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
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
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
0.0	0.0	100.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.00	16
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
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
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
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
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
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
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
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	
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	
14.7	0.0	26.9	2.6	28.3	0.0	0.0	0.0	28.3	0.6	0.0	0.0	0.28	
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
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
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
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
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	
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	
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	
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
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
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
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
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
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
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
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
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

APPENDIX C. Continued.

Lake	Data†	Lat	Long	Area (km ²)	Temp	n
Limerick	a	44°53'	77°37'	8.3	4.5	21
Morrison	a	55°14'	126°22'	14.6	-1.0	23
Opeongo	a	45°42'	78°23'	51.5	2.5	17 171
Opeongo	a	45°42'	78°23'	51.5	2.5	...
Papineau	c	45°21'	77°49'	8.3	4.5	21
Pyramid	a	55°55'	118°06'	1.3	0.0	50
Redrock	a	45°46'	78°28'	2.9	2.5	214
Shabomeka	c	44°54'	77°08'	2.7	4.5	46
Southesk	a	52°38'	117°12'	1.7	-0.5	22
Trout	a	46°03'	89°35'	20.8	5.8	22
West Bearskin	a	...	...	2.0	3.0	200
Waterton	c	49°00'	113°30'	9.4	2.5	337
Waterton	c	49°00'	113°30'	9.4	2.5	198
Mean						
1 SD						
1 SE						
C) Class 3						
Cold-water (N = 7 lakes; n = 2697 fish)						
Cree	a	57°30'	106°30'	1500.0	-4.5	100
Great Bear	c	66°00'	122°00'	30 044.0	-9.5	1079
Great Bear	c	66°00'	122°00'	30 044.0	-9.5	239
Great Slave	c	62°00'	114°00'	27 195.0	-6.5	486
Keller	c	63°50'	122°00'	413.0	-7.8	224
La Ronge	c	55°10'	105°00'	900.0	-2.8	469
Wollaston	a	58°15'	103°15'	2000.0	-6.0	100
Mean						
1 SD						
1 SE						
Warm-water (N = 23 lakes; n = 21 369 fish)						
12 Mile	a	45°01'	78°43'	3.4	4.5	150
Burnt Island	a	48°47'	90°51'	1.1	-1.5	90
Green	c	43°49'	89°00'	29.7	7.5	129
Greenwich	a	48°48'	88°51'	4.8	-0.3	203
Huron	c	45°00'	82°30'	59 600.0	5.5	301
Islets	a	49°13'	92°16'	1.9	0.0	96
Keuka	a	42°30'	77°05'	65.0	8.3	29
Little Joe	a	50°22'	93°27'	2.2	-0.5	80
Loch Erne	a	48°37'	90°21'	1.7	-1.0	99
Memphremagog	a	45°08'	72°16'	150.0	4.5	250
Michigan	c	44°00'	87°00'	57 800.0	5.5	479
Michigan	a	44°00'	87°00'	57 800.0	5.5	254
Michigan	a	44°00'	87°00'	57 800.0	5.5	2441
Nipigon	a	49°02'	88°26'	4850.0	-1.3	91
Ontario	c	43°30'	78°00'	18 960.0	8.0	569
Ontario	c	43°30'	78°00'	18 960.0	8.0	256
Ontario	a	43°30'	78°00'	18 960.0	8.0	1863
Ontario	a	43°30'	78°00'	18 960.0	8.0	1836
Ontario	a	43°30'	78°00'	18 960.0	8.0	8233
South Otterskin	a	49°13'	93°38'	2.1	-0.3	85
Simcoe	a	44°25'	79°20'	728.0	5.3	50
Superior	a	47°30'	87°00'	82 100.0	1.3	3642
Superior	a	47°30'	87°00'	82 100.0	1.3	143
Mean						
1 SD						
1 SE						

† a, percent volume format reported; b, percent of total number converted to percent volume using Eq. A.1; c, percent frequency of occurrence converted to percent volume using Eq. A.2; d, percent frequency of occurrence converted to percent volume using Eq. A.4.

‡ PLA, zooplankton; MYS, *Mysis relicta*; BEN, zoobenthos; AMP, amphipods; FIS, all fish species; ale, alewife; cis, cisco; cot, cottids; lit, littoral fish species; pel, trout-perch, sticklebacks, and salmonids; sme, smelt; whi, whitefish.

§ 14, Godfrey 1955; 15, Rawson 1959; 16, Donald and Alger 1993; 18, Rawson and Elsey 1950; 24, Couey 1931; 25, Rawson 1930; 26, Cuerrier and Schultz 1957; 27, Anderson and Smith 1971; 29, Rawson 1951; 33, Clemens et al. 1923; 34, Clemens et al. 1924; 37, Johnson 1972; 39, Merrick et al. 1992; 40, Johnson 1975; 49, Trippel and Beamish 1993; 54, Hassinger and Close 1984; 73, Martin 1954; 74, Ontario Ministry of Natural Resources, *unpublished data*; 75, Konkle and Sprules 1986; 76, Martin 1952; 77, LaPointe 1987; 78, Leonard and Leonard 1946; 79, Cuerrier 1954; 80, Magnin et al. 1978; 81, Martin 1970; 82, Kimsey 1960; 83, Miller and Kennedy 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 1956; 92, Dymond 1928; 93, Christie et al. 1987; 94, Elrod 1983; 95, Elrod and O'Gorman 1991; 59, M. J. Vander Zanden, *unpublished data*; 96, Dryer et al. 1965.

APPENDIX C. Continued.

% volume contribution to diet‡					Breakdown of fish (FIS) category							T.P.	Refer- ences§
PLA	MYS	BEN	AMP	FIS	ale	cis	cot	lit	pel	sme	whi		
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
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
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
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
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
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
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
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
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
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
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
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
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
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	.
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	
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	
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
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
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
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
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
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
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
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	
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	
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	
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
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
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
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
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
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
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
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
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
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	59
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
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
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
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
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
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
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
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
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
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
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
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	96
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
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	
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	
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	