Within- and among-population variation in the trophic position of a pelagic predator, lake trout (*Salvelinus namaycush*)

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Abstract: Many aquatic consumers have flexible feeding habits, and the diet and trophic position of a species can be expected to vary both within and among populations. In this study, we quantify the importance of both within- and among-population trophic variation for lake trout (*Salvelinus namaycush*) using stable isotope designations of trophic position from 13 Ontario and Quebec lakes. Lake-to-lake differences explained 78% of the total variation in lake trout trophic position. Analysis using both stable isotopes and published dietary data demonstrated that the trophic position of lake trout failed to increase appreciably as a function of animal body size. This finding was attributed to weak predator size – prey size relationships as well as to there being no relationship between prey fish trophic position and body size. The variance in trophic position of a population reflects the extent to which individuals forage as trophic specialists; however, we did not identify any one factor that was correlated with within-population trophic variation. Our finding that much of the total variation in trophic position represents among-population differences indicates that considering the average trophic position of a population does not mask substantial within-population trophic variation.

Résumé : Le régime alimentaire et la position trophique d'une espèce peuvent varier au sein d'un même niveau ou de niveaux différents de populations. Nous avons utilisé pour la présente étude les rapports d'isotopes stables pour estimer la position trophique de touladis (*Salvelinus namaycush*) provenant de 13 lacs de l'Ontario et du Québec, ce qui permettait de quantifier l'importance relative de la variation trophique au sein d'une même population ou entre des populations. Les écarts notés entre les lacs expliquaient 78% de la variation totale de la position trophique des touladis. Une analyse fondée sur les données des isotopes stables et du régime alimentaire a montré que la position trophique n'augmentait pas de façon appréciable avec la taille des poissons. Ce phénomène a été attribué au faible rapport taille des prédateurs – taille des proies ainsi qu'à l'absence de relations entre la position trophique des poissons proies et la taille. La variance de la position trophique d'une population reflète la mesure dans laquelle les individus cherchent leur nourriture en se spécialisant pour un niveau trophique particulier, mais nous n'avons pu trouver aucun facteur présentant une corrélation avec la variation trophique au sein d'une même population. Le fait que nous ayons trouvé qu'une grande partie de la variation totale de la position trophique reflétait des écarts entre populations montre que le fait d'utiliser la position trophique moyenne d'une population ne masque pas les variations trophiques appréciables au sein d'une même population.

[Traduit par la Rédaction]

Introduction

Trophic relationships can play a major structuring role in aquatic ecosystems (Carpenter et al. 1985; Vander Zanden et al. 1999*a*), and the trophic habits of fish have consequences for other aspects of their biology, including contaminant accumulation (Kidd et al. 1995; Vander Zanden and Rasmussen 1996) as well as patterns of life history and growth (Martin 1966; Shuter et al. 1998). Despite the importance of trophic relationships, attempts to understand and quantify feeding relationships are often confounded by high levels of food web complexity and spatial and temporal variation at a number of scales. First, it is well documented that different populations of a species can differ in their diet and trophic position (Trippel and Beamish 1993; Vander Zanden and Rasmussen 1996). A second type of trophic variation occurs

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among individuals of a population. Although this source of variation is difficult to detect using gut content data, studies have generally found evidence for within-population variation and individual-level dietary specialization (Bryan and Larkin 1972; Zerba and Collins 1992; Gu et al. 1997*b*; Schindler et al. 1997; Beaudoin et al. 1999). Finally, fish often undergo dramatic ontogenetic trophic shifts, typically shifting from invertebrates to fish prey items as they grow (Magnan and FitzGerald 1984; Werner and Gilliam 1984; Werner 1986). While each of these types of trophic variation have been singularly examined, no studies have simultaneously assessed these multiple sources of trophic variation.

Quantifying multiple levels of trophic variability is greatly facilitated by using integrative approaches to studying food web relationships. Stable isotopic tracers are increasingly used to provide time-integrated descriptions of feeding relationships. In particular, there is a consistent 3–4% enrichment in stable nitrogen isotope ratios ($^{15}N/^{14}N$, $\delta^{15}N$) from prey to predator (DeNiro and Epstein 1981; Minagawa and Wada 1984). Thus, $\delta^{15}N$ values (provided that isotopic differences at the base of the food web are accounted for) can provide a time-integrated, continuous measure of consumer trophic position that reflects the pathways of energy flow (Cabana and Rasmussen 1996; Vander Zanden and Rasmussen 1999). Recently, stable isotopes have been used to quantify individual specialization of aquatic consumers (Gu et al. 1997*b*; Beaudoin et al. 1999). This application of stable isotope techniques is particularly useful because detecting among-individual feeding differences (diet specialization) using the gut content method requires repeatedly examining the stomach contents of the same individual fish (Bryan and Larkin 1972; Zerba and Collins 1992; Schindler et al. 1997).

In the present study, we use stable isotope techniques to estimate the trophic position of individual lake trout (*Salvelinus namaycush*) and other pelagic consumers from 13 lakes in Ontario and Quebec (Vander Zanden and Rasmussen 1999). This study differs from previous trophic studies in that we quantify the relative importance of among-population (that which is explained by a categorical "lake" variable), ontogenetic (that which is explained by body size), and individual-level (differences among same-sized individuals) variation in the trophic position of lake trout. The objectives of this study are to (*i*) quantify ontogenetic shifts in lake trout trophic position as measured using stable isotope techniques and to validate these patterns by using dietary data, (*ii*) quantitatively compare the magnitude of within- and among-population variation in lake trout trophic position, and (*iii*) characterize individual-level (within-population) trophic variation for a series of lake trout populations and to examine the factors related to this variable.

Materials and methods

Study systems and field sampling

Previous studies have documented a wide range of food chain structures leading to lake trout (Martin 1952, 1966; Rasmussen et al. 1990; Trippel and Beamish 1993; Vander Zanden and Rasmussen 1996; Vander Zanden et al. 1999*b*). In fact, lakes can be classified according to the number of trophic levels leading to lake trout (either three, four, or five levels) based on the presence or absence of potential prey items that serve as functional trophic levels (Rasmussen et al. 1990). Class 1 lakes (containing three trophic levels) are lakes that lack pelagic forage fish species. In these lakes, lake trout consume large amounts zooplankton and zoobenthos. Class 2 lakes (four trophic levels) contain at least one species of pelagic forage fish that serve as the principle prey of adult lake trout. Finally, class 3 lakes (five trophic levels) are lakes that contain both pelagic forage fish and the zooplankton predator *Mysis relicta*. *Mysis* are an important prey of pelagic forage fish, which are consumed by lake trout. Analyses using stable isotopes and dietary data indicate that this food chain classification scheme qualitatively reflects the food web structure of these systems (Vander Zanden and Rasmussen 1996; Vander Zanden et al. 1999*b*).

Thirteen lakes in central Ontario and southern Quebec (located between 46°15′N and 44°30′N and 80°00′W and 72°00′W) containing lake trout as the top pelagic predator were sampled between May and September 1995. Lake trout (13–21 per lake, mean = 17) and the available forage fish species cisco (*Coregonus artedi*), lake whitefish (*Coregonus clupeaformis*), round whitefish (*Prosopium cylindraceum*), rainbow smelt (*Osmerus mordax*), and sculpins (*Cottus* spp.) from the littoral, pelagic, and profundal zones were collected using gill nets, seine nets, minnow traps, and angling and from local anglers. Littoral fish (primarily Percidae, Centrarchidae, and Cyprinidae) less than 12 cm in length were considered potential lake trout prey, since lake trout have access to these fish during the unstratified period (Martin 1954; Vander Zanden and Rasmussen 1996). Approximately 1 g (wet weight) of whole white dorsal muscle tissue was removed from each sampled lake trout and forage fish. *Mysis* and *Diporia* were collected using a benthic sled. Zooplankton were collected during the day using horizontal tows with a 250-μm-mesh standard zooplankton net. All fish and invertebrate samples were frozen after collection.

Laboratory procedures and estimating trophic position

Fish and invertebrate specimens were dried at 75°C for 48 h in a drying oven, ground into a fine powder using a mortar and pestle, and packed into 4 × 6 mm tin capsules for isotopic analyses. Stable carbon and nitrogen isotope analysis was performed using a continuous-flow VG Micromass 903E isotope ratio mass spectrometer at the Environmental Isotope Laboratory (Department of Earth Sciences, University of Waterloo, Waterloo, Ont.). Stable isotope ratios are expressed in delta (δ) notation, defined as the parts per thousand (‰ or "per mil") deviation from a standard material:

$$\delta^{13}C \text{ or } \delta^{15}N = (\{R_{sample}/R_{standard}\} - 1) \times 1000$$

where $R = {}^{13}C/{}^{12}C$ or $^{15}N/^{14}N$. The standard material is Pee Dee belemnite limestone for $\delta^{13}C$ (Craig 1957) and atmospheric nitrogen for $\delta^{15}N$ (both standards have a per mil value arbitrarily set at 0‰). One half of the samples were analyzed in duplicate; the standard error of the estimate was 0.12‰ for $\delta^{15}N$ and 0.10‰ for $\delta^{13}C$.

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

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

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

To complement our isotopic analysis, we also estimated trophic position using direct gut content data. Using this method, it is not possible to estimate the trophic position of an individual fish. Instead, dietary data can be used to estimate the trophic position of numerous fish from a size-class. Adequate dietary data were not available from our study lakes due to our relatively small sample sizes (less than 20 lake trout per lake). We used size-class-specific (separated by 10-cm size intervals) lake trout dietary data from Trippel and Beamish (1993) to estimate the trophic position of the sampled size-classes. Trophic position was calculated using quantitative gut content data (either percent weight or percent volume), weighted average formulas, and previously published estimates of the trophic position of lake trout prey items (Vander Zanden and Rasmussen 1996; Vander Zanden et al. 1997) using the formula

$$TP = \Sigma(V_i T_i) + 1$$

where TP is the trophic position of the population, V_i is the percent volumetric contribution of the ith prey item, and T_i is the trophic position of the ith prey item.

The within-population variation in trophic position reflects the magnitude of diet consistency and individual trophic specialization. We did not use the population variance because lake trout populations with steeper slopes in trophic position – body size relationships had a higher variance in trophic position ($r^2 = 0.54$, $SE_{est} = 0.025$, $p = 0.004$). Instead, we considered the magnitude of the residuals from the trophic position – body size relationships for lake trout (calculated as the "mean |residual|" from the lake trout trophic position – body size relationships); we call this variable VAR_{TP}. This measure of variance was independent of the slope of the lake trout trophic position – body size relationship ($r^2 = 0.20$, $SE_{est} = 0.036$, $p = 0.12$).

Analysis of covariance (ANCOVA, SYSTAT) was used to partition the total variance in lake trout trophic position (as determined using stable isotopes) into its component sources: among-population variation (that which is attributed to the lake trout's lake of origin; a categorical "lake" variable), ontogenetic variation (that which is attributed to lake trout body size), and individual variation (the remaining within-population variation, independent of body size). A portion of this remaining (individual) variation represents error in the stable isotope based trophic position estimates.

Results

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

Plotting trophic position – length relationships for each lake confirms that trophic position generally fails to increase with body size (Fig. 1). In fact, none of the lake-specific trophic position – body size relationships were significant (using the Bonferroni-corrected critical p value of 0.004 (0.05/13)). The power of our analysis was such that we were generally able to detect a significant body size effect if the slope was greater than 0.015 (mean SE of slope × critical t value with $p = 0.005$). We performed a similar analysis of ontogenetic shifts in trophic position using lake trout dietary data taken from Trippel and Beamish (1993). None of these six lake trout populations exhibited significant trophic position – body size relationships (using the Bonferroni-corrected critical p value of 0.008 (0.05/6)), although certain lakes suggested a pattern of increasing trophic position with body size (Fig. 2).

Variance in trophic position

Our measure of within-population variation in trophic position (VAR_{TP}) varied nearly threefold among lakes (Table 1). We hypothesized that there would be a relationship between VAR_{TP} and food chain length, since lake trout from longer food chains might be expected to have a broader range of available prey. Yet no relationship between VAR_{TP} and food chain length was observed ($VAR_{TP} = -0.032 \times TP + 0.32$; $r^2 = 0.20$, $p = 0.13$). In fact, none of the tested variables (food chain length, lake class, lake area, variance in the trophic position of lake trout prey items) were significantly correlated with VAR_{TP}, although VAR_{TP} was found to be elevated in certain class 1 populations (Table 1). We also hypothesized that the presence of species that compete with lake trout (i.e., piscivores) would result in narrower dietary habits and a lower VAR_{TP} for lake trout. However, there was no significant relationship between the number of species of potential competitors and VAR_{TP} ($VAR_{TP} = -0.001 \times$ number of competitor species + 0.19; $r^2 = 0.003$, $p = 0.87$).

Discussion

The present study examined variation in the trophic position of lake trout at multiple levels: among-population variation, ontogenetic variation, and individual variation. Our comparison of within- and among-population sources of trophic variation could only have been performed using isotopic techniques, as this method provides a time-integrated measure of the trophic position of individual consumers (Vander Zanden and Rasmussen 1999). Traditional dietary studies are typically useful for characterizing feeding at the population level only, thereby neglecting that populations consist of individuals that can differ in their behavior (Lomnicki 1988). Detecting within-population trophic variation using gut content data requires sampling the stomach contents of an individual fish numerous times. Understandably, such studies are rarely performed, as they are laborious and usually involve small sample sizes (Bryan and Larkin 1972; Zerba and Collins 1992; Schindler et al. 1997). The few studies of within-population trophic variation have been typically conducted on a single study system, thus precluding a comparison of within- and among-population variation.

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Fig. 1. Lake-specific relationships between lake trout trophic position and total length from 13 lakes in Ontario and Quebec. (A) Class 1 lakes: solid circles, Clear Lake; open diamonds, Dickie Lake; open circles, Happy Isle Lake; open triangles, Louisa Lake; solid diamonds, Source Lake. (B) Class 2 lakes: solid circles, Opeongo Lake; open diamonds, Smoke Lake; open circles, Victoria Lake. (C) Class 3 lakes: solid circles, Twelve Mile Lake; open diamonds, Lake Memphremagog; open circles, Lake Muskoka; open triangles, Lake Rosseau; open squares, Lake Temagami.

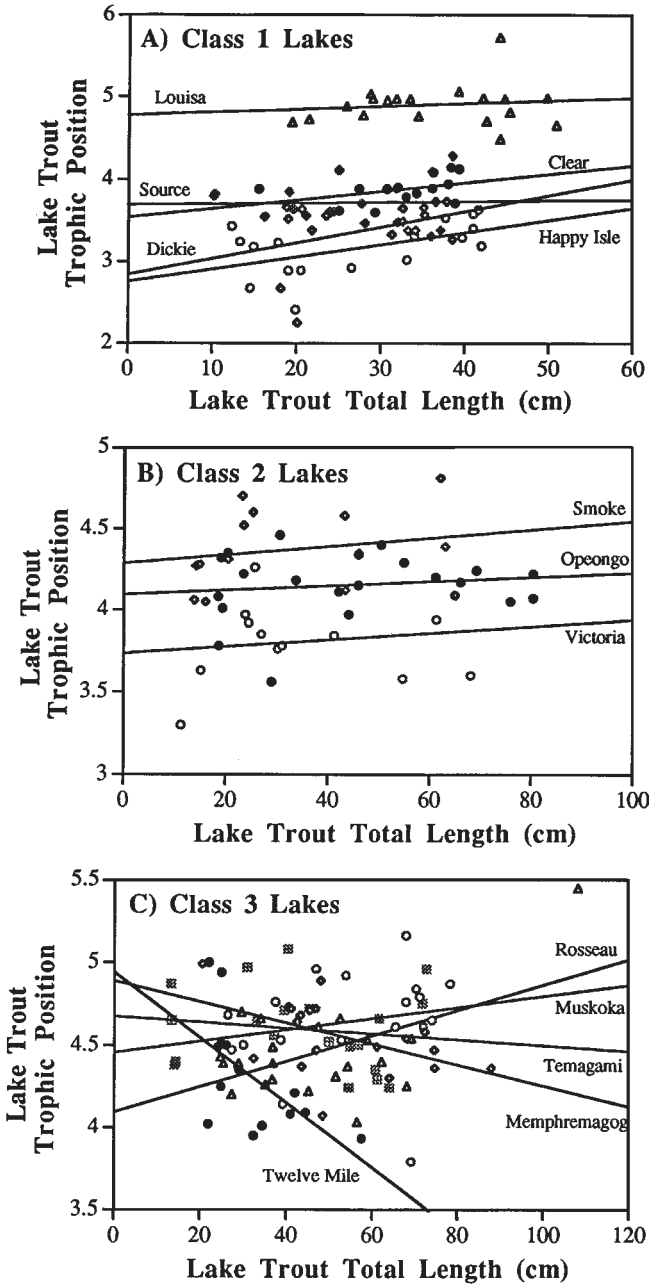
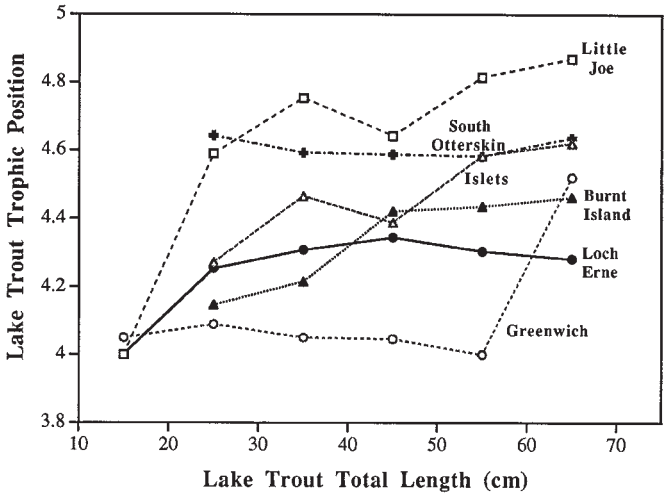


Fig. 2. Relationship between lake trout trophic position as estimated using dietary data and total length from six northwestern Ontario lakes. Data are from Trippel and Beamish (1993).



Trophic position – body size relationships

Our analysis using stable isotope data indicated that the trophic position of lake trout did not increase with increasing body size. This finding was further supported through our analysis of dietary data also showing that trophic position failed to increase with body size. The lack of relationship was unexpected, since lake trout have been found to undergo ontogenetic diet shifts (Trippel and Beamish 1993; Madenjian et al. 1998). Yet it should be recognized that ontogenetic diet shifts are not necessarily accompanied by an increase in trophic position. For example, lake trout may not consume increasingly large prey items with increasing size. Alternatively, larger prey may not necessarily have a higher trophic position than smaller prey, so that even if lake trout do shift from small to large prey items, this may not correspond to an ontogenetic increase in trophic position.

To further examine these two potential reasons for the weak relationships between trophic position and body size, we used dietary data from Trippel and Beamish (1993) to quantify the relationships between lake trout size and mean prey size for each of the six lakes included in that study (Fig. 3). Prey size did tend to increase with increasing lake trout size (average prey length (centimetres) = 0.206 × average lake trout length (centimetres) + 0.46; $n = 27$, $r^2 = 0.44$, $F = 19.39$, $p < 0.001$), although the mean prey size for a given size-class of lake trout varied widely among lakes. Clearly, a broad range of prey sizes is consumed by a given size-class of lake trout. This broad range of prey sizes is indicative of opportunistic feeding, omnivory, and trophic variability, factors that will obscure relationships between trophic position and body size.

Our prediction of ontogenetic shifts in trophic position was also contingent upon the assumption that larger prey items will tend to have a higher trophic position than smaller prey items. Across multiple trophic levels, this was found to be true (Fig. 4). Trophic position increased with prey size when zooplankton, *Mysis*, *Diporia*, and all pelagic prey fish were included (prey trophic position = 0.67 × prey length (centimetres) + 2.12; $n = 247$, $r^2 = 0.42$, $p < 0.001$). However when only the pelagic prey fish were considered, no relationship between trophic position and body size was observed ($n = 206$, $r^2 = 0.005$, $p = 0.33$). Thus, a lake trout population that switched diet from small fish to large fish

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Table 1. Lake-specific relationships between lake trout trophic position (TP) and total length (len, cm) for each of 13 Ontario and Quebec lakes.

Lake	TP	*n*	Equation	r^2	SE_{est}	*p*	VAR_{TP}
Class 1							
Clear	3.87	14	TP = 0.010 × len + 3.54	0.10	0.16	0.14	0.12
Dickie	3.38	16	TP = 0.019 × len + 2.84	0.08	0.38	0.16	0.27
Happy Isle	3.17	17	TP = 0.015 × len + 2.75	0.22	0.29	0.03	0.23
Louisa	4.90	19	TP = 0.003 × len + 4.78	0.00	0.26	0.60	0.17
Source	3.72	18	TP = 0.001 × len + 3.69	0.00	0.27	0.90	0.21
Class 2							
Opeongo	4.15	21	TP = 0.001 × len + 4.09	0.00	0.21	0.56	0.15
Smoke	4.37	15	TP = 0.003 × len + 4.21	0.00	0.24	0.47	0.19
Victoria	3.81	13	TP = 0.002 × len + 3.73	0.00	0.25	0.60	0.18
Class 3							
Twelve Mile	4.31	14	TP = –0.020 × len + 4.94	0.31	0.29	0.02	0.20
Memphremagog	4.55	19	TP = –0.006 × len + 4.89	0.19	0.20	0.03	0.15
Muskoka	4.64	18	TP = 0.003 × len + 4.46	0.00	0.31	0.44	0.21
Rosseau	4.46	21	TP = 0.008 × len + 4.09	0.25	0.25	0.01	0.19
Temagami	4.60	21	TP = –0.002 × len + 4.68	0.00	0.25	0.54	0.19

Note: *n*, lake trout sample size; SE_{est}, standard error of the estimate; VAR_{TP}, measure of the variance in lake trout trophic position. No relationships were significant at the Bonferroni-corrected $p = 0.004$ (0.05/13).

Fig. 3. Relationship between average prey total length and average lake trout total length from six northwestern Ontario lakes. Data are from Trippel and Beamish (1993).

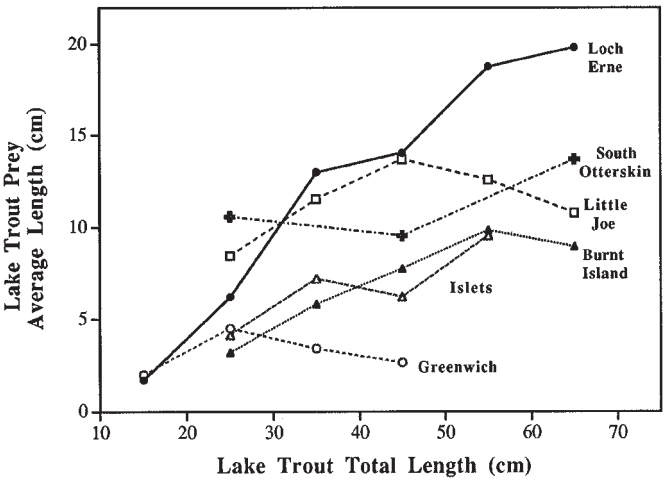
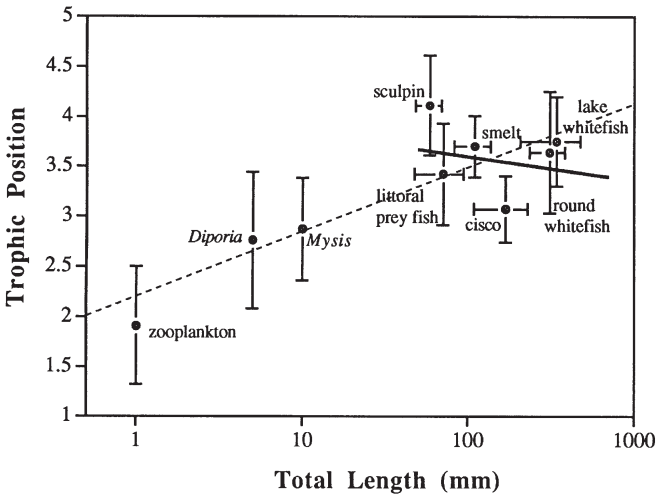


Fig. 4. Relationship between trophic position and total length of potential lake trout prey items using taxon-specific mean trophic position estimates and mean total length (error bars represent ±1 SD). The dashed curve is the relationship for all potential prey items; the solid curve is for fish prey items.



would not be expected to exhibit a corresponding increase in trophic position.

Overall, our results indicate that trophic position does not tend to increase with body size within what is traditionally considered a trophic level (Figs. 1, 2, and 4), although across multiple trophic levels, we find that trophic position does increase as a function of animal body size (Fig. 4). France et al. (1998) has presented the only broad-scale study of trophic position – body size relationships across a broad range of taxa and found close corelations between these two variables. Their results suggested that food webs are structured somewhat on the basis of body size, possibly as a result of size-dependent predation. The existence of trophic position – body size relationships has implications for the numerous studies of food web patterns and dynamics that are based on body size (Sheldon et al. 1977; Cousins 1980; Warren and Latwon 1987; Cohen et al. 1993). Although using body size as a proxy for trophic position may be reasonable across multiple trophic levels (spanning a broad range of body size), this relationship may not be applicable at finer scales.

In contrast with our findings, positive body size – $\delta^{15}N$ relationships have been reported for a number of species, including species of benthic invertebrates (Gu et al. 1997*a*), striped bass (*Morone saxatilis*) (Wainright et al. 1996), Dolly Varden (*Salvelinus malma*), least cisco (*Coregonus sardinella*), Arctic cisco (*Coregonus autumnalis*), and broad whitefish (*Coregonus nasus*) (Kline et al. 1998), and marine turtles (Godley et al. 1998). It is possible that some of these ontogenetic $\delta^{15}N$ shifts may represent spatial or temporal variation in isotopic signatures of prey items (independent of

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trophic position), underscoring the importance of accounting for baseline isotopic variation when estimating the trophic position of consumers (Cabana and Rasmussen 1996; Vander Zanden and Rasmussen 1999). Hobson and Welch (1995) reported a particularly dramatic increase in $\delta^{15}N$ with body size of Arctic char (*Salvelinus alpinus*) in Char Lake, Northwest Territories. Being the only fish species in Char Lake, Arctic char became cannibalistic in this system, constituting three entire trophic levels. Clearly, cannibalism can generate dramatic ontogenetic trophic position shifts. Our data suggest that only two of the 228 lake trout included in this study are primarily cannibalistic, one from Louisa Lake and one from Lake Rosseau (Fig. 1).

Within-population trophic variation

Our measure of within-population trophic variation, VAR_{TP}, varied widely among lakes; we tested a number of hypotheses to explain the among-lake trophic variation. For example, coexistence with few competitor species may allow lake trout to consume a broad range of prey items, thereby allowing increased individual trophic specialization and diet separation. Similarly, lakes with long food chains (typically large lakes) should have a greater diversity of habitats and prey items on which lake trout can specialize. Genetic/population differentiation within a population could also result in within-population trophic variation; such differentiation would be more likely in large lakes with multiple basins. Also, a number of the study lakes have been stocked with lake trout to various degrees, and trophic differences between native and stocked lake trout are unknown. Yet although we have tested several hypotheses for the factors affecting trophic variation, none of the tested variables were found to be significantly correlated with VAR_{TP}.

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

Individual-level trophic variation and diet consistency is a poorly understood and difficult to detect source of trophic variation. Yet whether individual consumers from a population differ in their foraging can have major ecological implications. For example, trophic specialization is thought to reduce intraspecific competition (Bryan and Larkin 1972; Van Buskirk and Smith 1989; Schindler et al. 1997) and can have profound consequences for population dynamics (Partridge and Green 1985; Lomnicki 1988). In addition, dietary differences may explain why individual fish from a population can differ widely in persistent contaminant concentrations (Madenjian et al. 1993). Furthermore, these dietary differences may explain why same-aged fish can vary widely in growth rate and body size. This is particularly relevant to studies of young-of-the-year fish because the largest individuals of a year-class typically have the highest first-winter survival rates (Cargnelli and Gross 1996, 1997).

Just as previous studies have found that among-population trophic differences largely determine patterns in the growth and life history of lake trout (Martin 1966, 1970), trophic differences among individuals of a population may be responsible for the within-population variation in growth and life history patterns of fish. Yet within- and among-population trophic variation is generally poorly understood due to the limited ability of gut content analysis to elucidate feeding patterns. For lake trout, within-system trophic variation was relatively minor relative to the among-system variation. Although this may or may not be the case for other species, this study has demonstrated the use of stable isotope techniques to quantify the relative importance of within- and among-population trophic variation.

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