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

M. JAKE VANDER ZANDEN[1] AND JOSEPH B. RASMUSSEN

Department of Biology, McGill University, 1205 Avenue Docteur Penfield, Montreal, PQ, H3A 1B1 Canada

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

Key words: *aquatic consumers; baseline; $\delta^{13}C$; $\delta^{15}N$; food chains; food webs; primary consumers; stable isotopes; trophic position; trophic structure.*

INTRODUCTION

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

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

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

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[1] E-mail: jzanden@bio1.LAN.mcgill.ca

TABLE 1. Summary data for the 14 study lakes in Ontario and Quebec.

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

† Lake number refers to Fig. 3.
‡ Sample size represents the number of primary consumers analyzed for stable isotopes from that lake.
§ Mean residual value is the lake-specific deviation from the general model based on all 14 lakes (Eq. 2: $U_{res(k)}$).

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

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

METHODS

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

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

Littoral (depth < 1 m) benthic macroinvertebrates were collected using hand-held dip nets. Profundal benthic invertebrates (chironomids) were collected using a benthic sled and an Ekman grab sampler. Individual invertebrates were normally identified to the family level, and invertebrate samples were classified according to dietary preference based on published dietary descriptions, particularly Merritt and Cummins (1978) and Thorp and Covich (1991). A total of 133 invertebrate samples from the 14 study lakes were classified as nonpredatory (primary consumers); partially or en-

tirely predatory invertebrates were not considered in the present analysis. Primary consumers were pooled to order, producing nine general taxonomic/habitat classes: Unionidae, Amphipoda, Trichoptera, tadpoles, Ephemeroptera, shallow zooplankton (0–3 m), deep zooplankton (10–12 m), Chironomidae (profundal), and miscellaneous littoral (littoral primary consumers collected from <3 lakes).

Whole samples were frozen, dried at 75°C for 48 h in a drying oven, and ground into a fine powder using mortar and pestle. Dry sample material was packed into 4 × 6 mm tin capsules for subsequent isotopic analyses. Stable carbon and nitrogen isotope analyses were performed on the same sample using a continuous flow VG Micromass 903E isotope ratio mass spectrometer at the Environmental Isotope Laboratory (Department of Earth Sciences, University of Waterloo, Waterloo, Ontario, Canada). Stable isotope ratios are expressed in delta (δ) notation, defined as the parts per thousand (‰ or "per mil") deviation from a standard material; $\delta^{13}C$ or $\delta^{15}N = ([R_{sample}/R_{standard}] - 1) \times 1000$, where $R = {}^{13}C/{}^{12}C$ or ${}^{15}N/{}^{14}N$. A more positive (less negative for carbon) isotopic value is said to be isotopically enriched, meaning that the sample contains proportionally more of the heavy stable isotope (^{13}C or ^{15}N). The standard material is Pee Dee belemnite (PDB) limestone for $\delta^{13}C$ (Craig 1957), and atmospheric nitrogen for $\delta^{15}N$ (both standards have a ‰ value arbitrarily set at 0‰). The working standard was DORM-1 powdered dogfish standard provided by the National Research Council of Canada, Institute for Environmental Chemistry, Ottawa, Canada. ($\delta^{15}N$ = 10.3‰; $\delta^{13}C$ = −19.5‰). Twenty percent of the samples were analyzed in duplicate; the standard error of the mean (1 SEM) for replicates was 0.13‰ for $\delta^{13}C$ and 0.15‰ for $\delta^{15}N$. When more than two $\delta^{15}N$ and $\delta^{13}C$ measurements for a taxon were available from a lake, we report the mean isotopic value to avoid pseudoreplication and bias towards heavily sampled taxonomic groups. This pooling effectively reduced the sample size from 133 to 106 primary consumers.

We also collected the available freshwater literature data on the $\delta^{13}C$ and $\delta^{15}N$ of primary consumers in order to test the generality of our observations (Angradi 1994, Hecky and Hesslein 1995, Hobson and Welch 1995, Yoshii 1995, Keough et al. 1996). Where multiple individuals of a particular taxon were collected from a habitat within a system, we considered their mean isotopic value. Lakes were rejected from analysis if there was little range in mean $\delta^{13}C$ values (<5‰), or if <3 different taxonomic groups were collected.

RESULTS

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

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

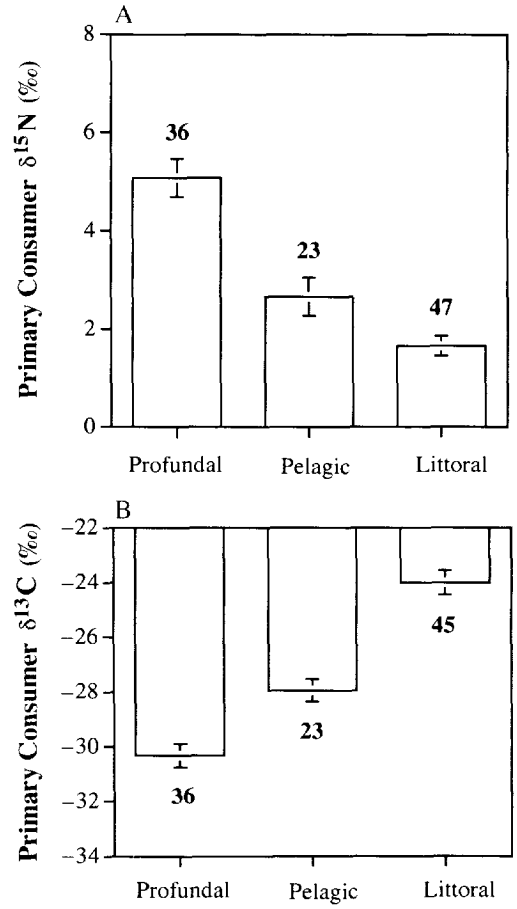

FIG. 1. (A) The mean $\delta^{15}N$ (±1 SE) of primary consumers feeding in profundal, pelagic, and littoral habitats. (B) The mean $\delta^{13}C$ (±1 SE) of primary consumers from profundal, pelagic, and littoral habitats. Samples were collected from 14 lakes in Ontario and Quebec, Canada. Numbers above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

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

We plotted $\delta^{15}N$ vs. $\delta^{13}C$ of individual primary consumers (zooplankton excluded) with values coded according to lake (Fig. 3a) and taxonomic category (Fig. 3b). A logistic curve fit provided unbiased trophic position estimates. Additionally, limits to the $\delta^{15}N$ of pri-

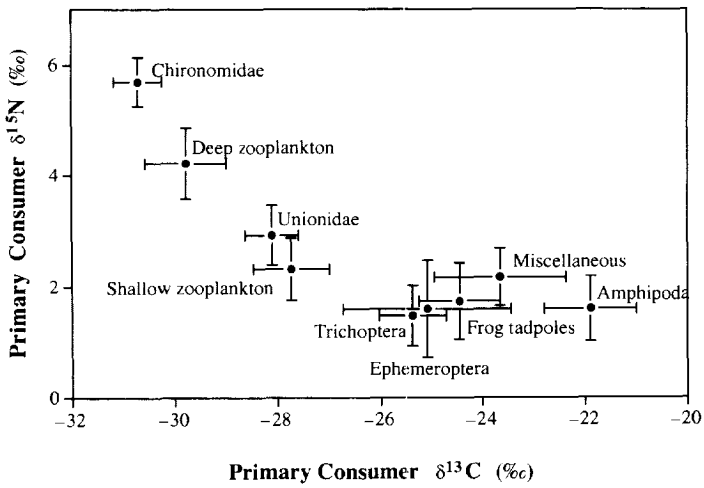

FIG. 2. Mean $\delta^{15}N$ vs. mean $\delta^{13}C$ (±1 SE) for the primary consumer taxonomic groups from 14 Ontario and Quebec lakes.

mary consumers are expected to be constrained by the fractionation associated with bacterial denitrification (upper limit) and N uptake by algae (lower limit). The overall $\delta^{15}N$–$\delta^{13}C$ relationship was highly significant and described by the following logistic equation:

$$\delta^{15}N_{pcon} = \frac{6.34}{1 + \exp[9.67 + (0.356 \times \delta^{13}C_{pcon})]} \quad (1)$$

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

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

Analysis of covariance (ANCOVA) was used to test for lake-specific differences (a lake effect) in the general $\delta^{15}N$–$\delta^{13}C$ relationship (Fig. 3). In order to meet the assumptions of ANCOVA to test for the lake effect, we linearized the general primary consumer $\delta^{15}N$–$\delta^{13}C$ relationship by using the *observed* $\delta^{15}N$ values and the *predicted* $\delta^{15}N$ from $\delta^{13}C$ using Eq. 1 (the predicted $\delta^{15}N$ values represent the $\delta^{13}C$ effect, and will be referred to as such). ANCOVA predicting primary consumer $\delta^{15}N$ values ($n = 78$; $r^2 = 0.72$; df = 14, 63) indicated highly significant effects of $\delta^{13}C$ from Eq. 1 ($F = 71.73$; df = 1; $P < 0.001$) and lake ($n = 78$; $F = 4.44$; df = 13; $P < 0.001$). Note that the lake variable explained an additional 32% of the observed variation in primary consumer $\delta^{15}N$. There was no significant interaction between the $\delta^{13}C$ and lake variables ($n = 78$; $F = 0.26$; df = 13; $P = 0.995$), indicating that the curvature of the relationship (the denominator of Eq. 1) could be used to describe each of the study lakes. Thus, the lake effect influenced only the intercept of the $\delta^{15}N$–$\delta^{13}C$ relationship (6.34; the numerator in Eq. 1) and represented a shift of the primary consumer $\delta^{15}N$–$\delta^{13}C$ curve up or down relative to the general $\delta^{15}N$–$\delta^{13}C$ relationship (Fig. 3).

DISCUSSION

Application: estimating trophic position of aquatic consumers

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

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

$$\text{resid} = \delta^{15}N_{pcon} - \frac{6.34}{1 + \exp[9.67 + (0.356 \times \delta^{13}C_{pcon})]} \quad (2)$$

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

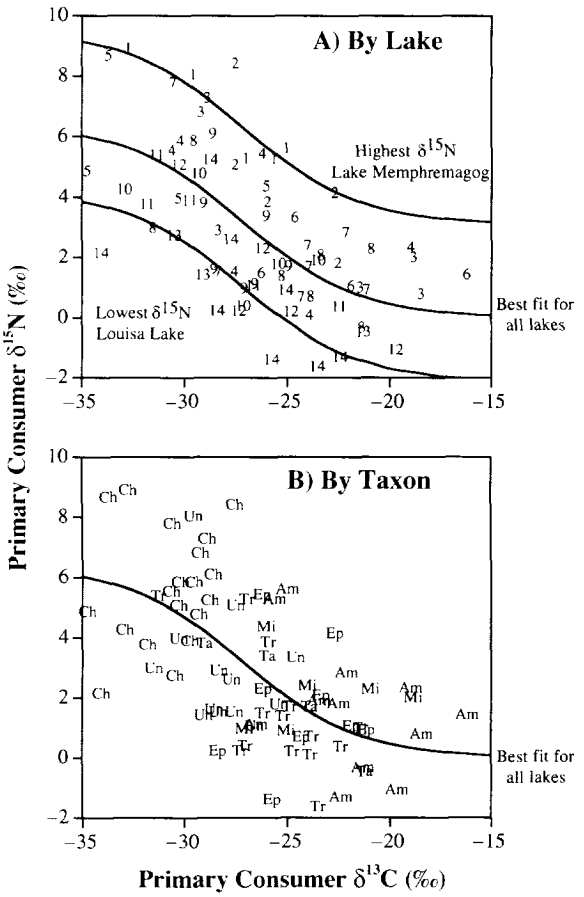

FIG. 3. $\delta^{15}N$ vs. $\delta^{13}C$ for primary consumers (minus zooplankton) from 14 lakes in Ontario and Quebec. Each point represents the mean value of a taxonomic group from a given lake. (A) Coded according to lake, lakes are arranged numerically in order from the most to the least elevated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

correct for lake-specific differences, the U_{resid} value for lake x (from Eq. 2) is added to this $\delta^{15}N$ value:

$$\delta^{15}N_{corrected} = \frac{6.34}{1 + \exp[9.67 + (0.356 \times \delta^{13}C_{fish})]} + U_{resid} \quad (3)$$

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

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

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

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

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

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

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

We used Eq. 3 to estimate the predicted $\delta^{15}N$ (based on $\delta^{13}C$ values) for the literature data set. Observed $\delta^{15}N$ explained 76% of the variability in predicted $\delta^{15}N$ (observed $\delta^{15}N$ = 0.98 × residual-adjusted $\delta^{15}N$ + 0.14; $P < 0.001$; $r^2 = 0.76$), indicating that the literature data is effectively described by the equation derived from our 14 study lakes. In addition, the $\delta^{15}N$–$\delta^{13}C$ relationship from each of the eight literature study systems (Charr Lake, Lake Superior, Grand Canyon, Lake Malawi, Lake 273, Skidoo Lake, South Lake,

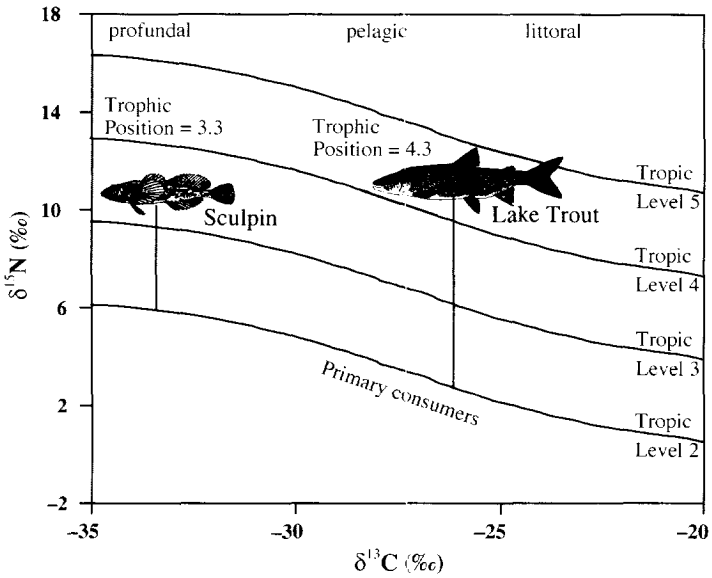

FIG. 4. An illustration of the approach used to estimate trophic position. The baseline $\delta^{15}N$–$\delta^{13}C$ primary consumer relationship is established, and the $\delta^{13}C$ of the higher consumer determines the appropriate $\delta^{15}N$ value from which to measure the trophic position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

Lake Baikal) exhibited negative slopes ($-0.85 <$ slope < -0.06; mean slope $= -0.33$), and the within-system correlations between $\delta^{15}N$ and $\delta^{13}C$ were generally quite strong ($-0.99 < r < -0.32$; mean $r = -0.80$).

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

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

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

Correction	Standard deviation (SD)†	n‡	Estimated SE (SD/$\sqrt{n}$)	Error§
No correction‖	2.55‰	1¶	2.55‰	0.75
Within-lake	2.00‰	6#	0.82‰	0.24
Within- and among-lake	1.36‰	6#	0.55‰	0.16

† Equivalent to the standard error of the estimate with $n = 1$.
‡ Sample sizes for this study.
§ Units are trophic levels.
‖ Using the global mean $\delta^{15}N$ value of 2.97‰.
¶ Here, $n = 1$ due to use of global mean $\delta^{15}N$ value.
# Mean sample size (per lake) from this study (excluding zooplankton).

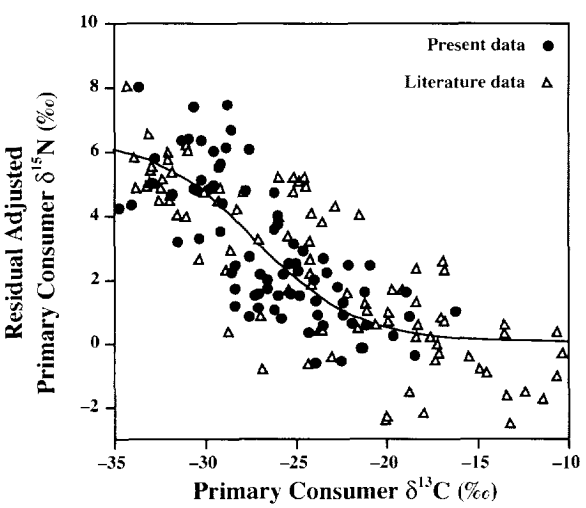

FIG. 5. Primary consumer $\delta^{15}N$, adjusted for the lake-specific mean residual value (accounts for lake-specific differences in intercept in the $\delta^{15}N$–$\delta^{13}C$ relationship) vs. $\delta^{13}C$ for our study lakes (solid circles) and literature data (open triangles). Literature data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

standard error of the U_{resid} value is high, the investigator should certainly estimate trophic position relative to their lake-specific $\delta^{15}N$–$\delta^{13}C$ relationship. Collection of primary consumer $\delta^{15}N$ and $\delta^{13}C$ data from additional freshwater systems will also permit further tests of the generality of the $\delta^{15}N$–$\delta^{13}C$ relationship.

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

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

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

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

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

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

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

Trophic position in ecological studies

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

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

food webs and food chain-based models, which remain dominant paradigms in community and ecosystem ecology.

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APPENDIX

Stable isotope data from 14 Ontario and Quebec lakes used in this analysis. Numbers following lake names are lake numbers from Table 1.

Taxon and lake	Habitat†	$\delta^{13}C$	$\delta^{15}N$
Twelve Mile Lake (4)			
Amphipoda	lit.	−19.01	2.35
Ephemeroptera	lit.	−26.23	5.45
Trichoptera	lit.	−23.91	0.10
Unionidae	pel.	−27.58	1.55
Shallow zooplankton	pel.	−26.89	2.57
Shallow zooplankton	pel.	−25.06	3.26
Chironomidae	pro.	−30.64	5.54
Chironomidae	pro.	−30.19	5.86
Ephemeroptera	pro.	−30.94	7.11
Deep zooplankton	pro.	−26.36	2.59
Clean Lake (12)			
Amphipoda	lit.	−19.70	−1.06
Ephemeroptera	lit.	−26.20	2.32
Trichoptera	lit.	−27.31	0.25
Trichoptera	lit.	−24.80	0.22
Chironomidae	pro.	−30.25	5.08
Deep zooplankton	pro.	−36.48	5.46
Deep zooplankton	pro.	−25.42	2.84
Dickey Lake (5)			
Miscellaneous	lit.	−26.01	4.38
Unionidae	pel.	−30.28	3.98
Shallow zooplankton	pel.	−30.40	5.17
Chironomidae	pro.	−34.74	4.88
Chironomidae	pro.	−33.70	8.68
Deep zooplankton	pro.	−35.52	8.82
Happy Isle Lake (11)			
Trichoptera	lit.	−31.34	5.41
Trichoptera	lit.	−22.45	0.39
Unionidae	pel.	−26.59	1.08
Chironomidae	pro.	−31.80	3.79
Chironomidae	pro.	−29.72	3.91
Louisa Lake (14)			
Amphipoda	lit.	−22.43	−1.29
Ephemeroptera	lit.	−28.39	0.25
Ephemeroptera	lit.	−25.75	−1.37
Miscellaneous	lit.	−25.06	0.93
Frog tadpoles	lit.	...	−0.52
Trichoptera	lit.	−23.54	−1.62
Unionidae	pel.	−27.73	2.62
Chironomidae	pro.	−34.08	2.16
Chironomidae	pro.	−30.74	5.32
Deep zooplankton	pro.	−31.65	1.71
Deep zooplankton	pro.	−31.58	3.35
MacDonald Lake (8)			
Amphipoda	lit.	−21.38	−0.32
Ephemeroptera	lit.	−23.38	2.09
Miscellaneous	lit.	−20.94	2.30
Trichoptera	lit.	−25.27	1.39
Trichoptera	lit.	−23.85	0.72
Unionidae	pel.	−31.54	3.00
Shallow zooplankton	pel.	−24.40	3.01
Chironomidae	pro.	−29.53	5.86
Deep zooplankton	pro.	−26.85	3.88
Lake Memphremagog (1)			
Amphipoda	lit.	−25.03	5.63
Amphipoda	lit.	−25.65	5.30
Trichoptera	lit.	−26.99	5.30
Unionidae	pel.	−29.58	8.05
Chironomidae	pro.	−32.74	8.91
Deep zooplankton	pro.	−31.74	10.41
Muskoka Lake (2)			
Amphipoda	lit.	−22.55	1.82
Ephemeroptera	lit.	−22.70	4.16
Trichoptera	lit.	−25.96	3.87
Unionidae	pel.	−27.53	5.08
Shallow zooplankton	pel.	−26.32	4.38
Chironomidae	pro.	−27.52	8.43
Deep zooplankton	pro.	−27.35	5.91
Lake Opeongo (9)			
Amphipoda	lit	−26.55	1.14
Miscellaneous	lit.	−27.07	0.98
Frog tadpoles	lit.	−29.06	3.83
Frog tadpoles	pel.	−26.01	3.41
Trichoptera	pel.	−24.94	1.71
Unionidae	pel.	−28.57	1.63
Shallow zooplankton	pro.	−31.77	2.32
Shallow zooplankton	pro.	−29.32	2.07
Chironomidae	lit.	−28.60	6.11
Chironomidae	pro.	−31.59	2.30
Deep zooplankton	pro.	−28.87	7.30
Lake Rosseau (3)			
Amphipoda	lit.	−18.48	0.81
Miscellaneous	lit.	−18.85	2.02
Trichoptera	lit.	−21.45	1.01
Unionidae	pel.	−28.34	2.91
Chironomidae	pro.	−29.19	6.82
Chironomidae	pro.	−28.87	7.30
Smoke Lake (6)			
Amphipoda	lit.	−16.22	1.45
Ephemeroptera	lit.	−21.91	1.07
Trichoptera	lit.	−26.24	1.51
Unionidae	pel.	−24.61	3.35
Deep zooplankton	pro.	−28.46	1.70
Source Lake (10)			
Amphipoda	lit.	−23.50	1.93
Trichoptera	lit.	−27.08	0.41
Unionidae	pel.	−25.42	1.80
Shallow zooplankton	pel.	−27.32	0.41
Chironomidae	pro.	−32.92	4.27
Chironomidae	pro.	−29.29	4.79
Deep zooplankton	pro.	−27.66	6.36
Deep zooplankton	pro.	−29.35	2.55
Lake Temagami (13)			
Amphipoda	lit.	...	0.23
Frog tadpoles	lit.	−21.29	−0.45
Unionidae	pel.	−29.10	1.43
Shallow zooplankton	pel.	−26.77	−0.41
Chironomidae	pro.	−30.46	2.75
Deep zooplankton	pro.	−28.04	4.07
Victoria Lake (7)			
Amphipoda	lit.	−22.16	2.84
Ephemeroptera	lit.	−21.15	0.95
Ephemeroptera	lit.	−24.32	0.71
Miscellaneous	lit.	−24.02	2.41
Frog tadpoles	lit.	−23.95	1.72
Unionidae	pel.	−28.38	1.55
Shallow zooplankton	pel.	−29.08	0.43
Chironomidae	pro.	−30.58	7.80
Deep zooplankton	pro.	−30.33	2.16

† Abbreviations: lit. = littoral; pel. = pelagic; pro. = profundal.