

Modelling food chain structure and contaminant bioaccumulation using stable nitrogen isotopes

Gilbert Cabana & Joseph B. Rasmussen

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

THE nitrogen pools of animals are enriched in ^{15}N relative to their food¹, with the top predators having the highest concentrations of this stable isotope². The use of $\delta^{15}\text{N}$ to indicate trophic position depends on the degree to which it reflects variation in the underlying food-web structure, rather than variable fractionation along the food chain. Here we compare adult lake trout, a top pelagic predator, from a series of lakes, and find that $\delta^{15}\text{N}$ values vary from 7.5 to 17.5‰, a surprisingly wide range for one species. The length of the food chain can explain this variation, supporting the idea that $\delta^{15}\text{N}$ is a food-web descriptor. Food-chain length was measured by the presence or absence of two intermediate trophic levels, pelagic forage fish and the macrozooplankton, *Mysis relicta*, each of which when present contributes about three $\delta^{15}\text{N}$ units to the trout signature. We find that $\delta^{15}\text{N}$ can be used as a continuous, integrative measure of trophic position, which is supported by its correlation to mercury levels in lake trout.

A general approach to the measurement of food-web processes has been suggested by studies of stable nitrogen isotope ratios ($^{15}\text{N}/^{14}\text{N}$) of organisms and their food sources^{2,3}. In laboratory experiments, the enrichment in $\delta^{15}\text{N}$ ($\delta^{15}\text{N} = ([^{15}\text{N}/^{14}\text{N}]_{\text{sample}} / [^{15}\text{N}/^{14}\text{N}]_{\text{standard}} - 1) \times 1,000$), where atmospheric nitrogen is the reference material, in animals relative to their diet is on average +3.4‰ for a wide variety of taxa¹. In field studies of aquatic food chains leading to different top predators, $\delta^{15}\text{N}$ increases from primary producer to top-level consumers⁴⁻⁷. Variation in the $\delta^{15}\text{N}$ signature of primary producers at the base of the food chain⁸⁻¹¹ and in the fractionation along the food chain can sometimes produce significant variation even within the same species of top predator^{10,11}, and thus the validity of $\delta^{15}\text{N}$ as a measure of trophic position has been questioned². Our ability to assess the utility of $\delta^{15}\text{N}$ as a food-web descriptor depends partly on the accumulation of a larger

database for comparative work, but also, and more importantly, on comparisons involving sites known to differ greatly in food-web structure.

We report here a wide variation in mean $\delta^{15}\text{N}$ (7.5–17.5‰) of adult lake trout from 24 Canadian shield lakes. Analysis of variance showed that over 90% of this variation was attributable to among-lake effects. Such a wide range in $\delta^{15}\text{N}$ across lakes could appear to invalidate $\delta^{15}\text{N}$ as a trophic indicator unless the trophic position of lake trout could be shown to vary by several trophic levels across these lakes, and to covary with $\delta^{15}\text{N}$.

Owing to limited postglacial dispersal¹² and anthropogenic introductions¹³⁻¹⁵, the length of the pelagic food chain leading to lake trout is highly variable, with some important functional groups such as pelagic forage fish and the crustacean *Mysis relicta* being absent in many lakes. In lakes with the shortest pelagic food chains (class 1 lakes), where *Mysis* and pelagic forage fish are absent, adult trout feed predominantly on zoo-

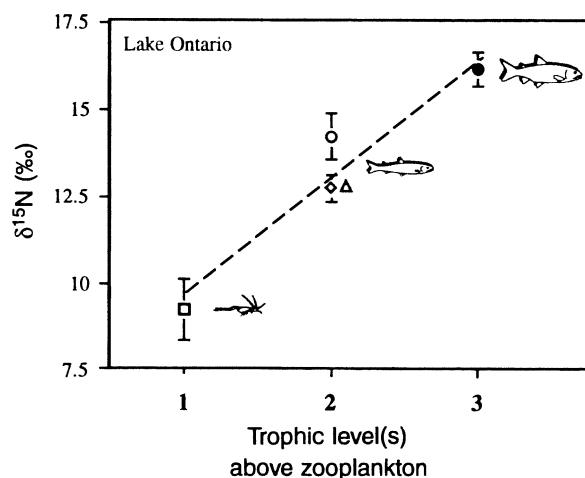


FIG. 1 Mean (\pm s.e.) $\delta^{15}\text{N}$ for components of the Lake Ontario pelagic food chain. *Mysis relicta*, pelagic forage fish (smelt, alewife, sculpin) and lake trout are represented by, respectively, square, circle, diamond, triangle and filled circle. The least-square regression equation $\delta^{15}\text{N} = 3.46L + 6.11$ (adj. $r^2 = 0.91$, $P < 0.01$, $n = 5$), where L_i represents the hypothesized number of trophic levels above zooplankton and is shown as a broken line. Samples were collected by M. Servos and R. Kiriluk (Department of Fisheries and Oceans (DFO), Canada).

plankton and benthic organisms¹⁶. Trout feed mainly on pelagic forage fish when these are present (classes 2 and 3)^{16,17}. These pelagic prey in turn feed predominantly either on zooplankton or on the larger *Mysis*, when this last species is present (class 3)^{15,17}. Finally, *Mysis* prey on zooplankton and some large phytoplankton^{13,14}. We have shown that this three-step biogeographic food-chain model predicts the levels of biomagnifying persistent contaminants such as polychlorinated biphenyls and mercury in lake trout^{18,19}.

In Lake Ontario, a class 3 lake, $\delta^{15}\text{N}$ increased by an average of +3.5‰ from *Mysis*, through pelagic forage fish, to lake trout (Fig. 1). This intra-lake study suggested that the absence of

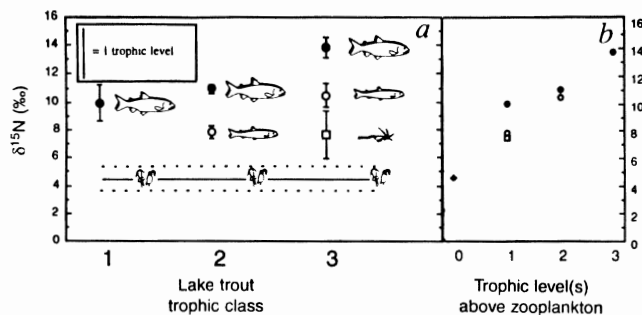


FIG. 2 a, Mean (\pm s.e.) $\delta^{15}\text{N}$ of lake trout dorsal muscle plotted against lake trout trophic class (filled circles). For class 2 and 3 food chains, mean $\delta^{15}\text{N}$ of pelagic forage fish (open circles: average of cisco, smelt, sculpin and/or alewife by lake) and *Mysis relicta* (square) are shown. For fish, sample size per lake was 1–13 (median, 6). Correlation between $\delta^{15}\text{N}$ and class: $r=0.58$, $n=24$, $P<0.01$; significant differences in lake trout $\delta^{15}\text{N}$ ($P<0.05$, Duncan's multiple range test) were found only between either class 1 or class 2 and class 3, but not between class 1 and class 2 lakes. Trout averaged +3.0‰ higher than forage fish in class 2 and class 3 lakes. Addition of *Mysis* to the pelagic food chain (class 3) resulted in the mean $\delta^{15}\text{N}$ of the two next trophic steps (trout and pelagic forage fish) being increased by, respectively, +2.7‰ and +2.6‰ $\delta^{15}\text{N}$ compared to class 2 lakes. In class 2 lakes, pelagic forage fish occupied a trophic position (+3.3 relative to zooplankton) similar to that of *Mysis* in class 3 lakes (+3.0‰ relative to zooplankton). Mean $\delta^{15}\text{N}$ in trout in class 1 lakes was found to be +5.4‰ higher than zooplankton. This last increment in $\delta^{15}\text{N}$ is higher than that expected if trout were fed exclusively on zooplankton (+3.4‰), indicating that trout in some of these lakes feed to a considerable degree on fish, probably from the littoral zone. Feeding studies on a class 1 lake, Lake Louise²⁸, support these large $\delta^{15}\text{N}$ increments, in that lake trout feed actively on littoral fish (cyprinids and catostomids) during winter when they are not thermally isolated from the littoral zone. Average s.e. of duplicate measurements made on a Europa Tracer mass spectrometer interfaced with a Roboprep-CN analyser was 0.3‰. Lake trout data for class 1 lakes: Anstruther, Happy Isle, Louise (mean $\delta^{15}\text{N}$, $9.9 \pm \text{s.e. } 1.28$); class 2 lakes: Bark, Du Cerf, Opeongo, Papineau, Poisson Blanc, Sherborne, lakes 468*, 442* and 377* (mean $\delta^{15}\text{N}$, 11.0 ± 0.33); class 3 lakes: Bernard, Big Rideau, Clear, Kashagawigamog, Mazinaw, Red Horse, Sand, Ontario, and lake 373* (mean $\delta^{15}\text{N}$, 13.7 ± 0.75). Pelagic forage fish data for class 2 lakes: Linge*, Trout and lakes 468* and 377* (mean $\delta^{15}\text{N}$ 7.83 ± 0.48); class 3 lakes: Kashagawigamog, Mazinaw, Musclow*, Ontario, Orange*, Red Horse and Sydney* (mean $\delta^{15}\text{N}$, 10.38 ± 0.87). *Mysis* data from lakes Ontario and Mazinaw (mean $\delta^{15}\text{N}$, 7.54 ± 1.71). Mean $\delta^{15}\text{N}$ (horizontal solid line) \pm s.e. (dashed lines) for zooplankton (<250 μm) from 31 Ontario and Quebec lakes (mean $\delta^{15}\text{N}$, 4.56 ± 0.50). An alternative indicator of $\delta^{15}\text{N}$ for a primary consumer other than zooplankton was also provided by unionid mussels, which, because of their greater size and longevity and more uniform trophic habits compared with zooplankton, were found to be only a third as variable as zooplankton among lakes (mussel $\delta^{15}\text{N}$ among 9 lakes, s.d. was 0.9; mean, 4.00; zooplankton s.d., 2.78). Asterisks indicate unpublished data from Ontario lakes kindly made available by R. Hesslein (DFO, Canada). b, Mean $\delta^{15}\text{N}$ plotted as a function of the number of trophic level(s) above that of zooplankton. Zooplankton shown as a solid diamond; symbols for the other groups as in a.

Mysis, or of both *Mysis* and pelagic forage fish in, respectively, class 2 and class 1 lakes should be reflected by a corresponding decrease in $\delta^{15}\text{N}$ of lake trout. Indeed, $\delta^{15}\text{N}$ of trout covaried with our three-step food-chain classification, and each of the two intermediate trophic levels, pelagic forage fish and *Mysis*, when present, accounted for increases of nearly 3‰ in $\delta^{15}\text{N}$ of trout (Fig. 2a). Mean trout $\delta^{15}\text{N}$ was positively related to the length of the pelagic food chain, increasing from 9.9‰ in class 1 lakes, through 11.0‰ (class 2 lakes) to 13.7‰ (class 3 lakes). The variable trophic positions of the same organisms in the three food-chain classes were better predicted from $\delta^{15}\text{N}$ values rather than from taxonomy (Fig. 2b).

The comparisons between $\delta^{15}\text{N}$ signature and trophic position made possible by this large dataset, and the ability of the food-chain descriptor to account for the broad variation in nitrogen isotope signature shown by the lake trout and their forage fish, provide a strong test of $\delta^{15}\text{N}$ as a food-web descriptor. By reflecting the effect of continuous among-population variation in food-chain properties such as trophic level and omnivory, $\delta^{15}\text{N}$ will be a more sensitive trophic descriptor and should therefore be a better predictor of contaminant biomagnification than a discrete food-chain classification such as our class variable⁷. Indeed, mercury levels in trout from seven lakes were significantly related to $\delta^{15}\text{N}$ (Fig. 3), but not to trophic class ($r=0.36$, $P>0.4$) (although mercury was significantly related to class in a much larger dataset¹⁹). This suggests that there was considerable variability in the degree of omnivory (feeding at more than one trophic level) within these lake food-chain classes, and that such omnivory influences both the level of contaminant biomagnification and the $\delta^{15}\text{N}$.

Omnivory is an important feature of food webs which has strong consequences, not only for contaminant biomagnification²⁰, but also for energetic efficiencies²¹, top-down feedback^{22–24}, and community stability^{25–27}. The patterns of $\delta^{15}\text{N}$ in our pelagic communities suggest an efficient, time-integrative method of estimating omnivory by comparing the $\delta^{15}\text{N}$ increment observed between two adjacent trophic levels to the increment of 3.4 expected from laboratory studies on pure diets¹.

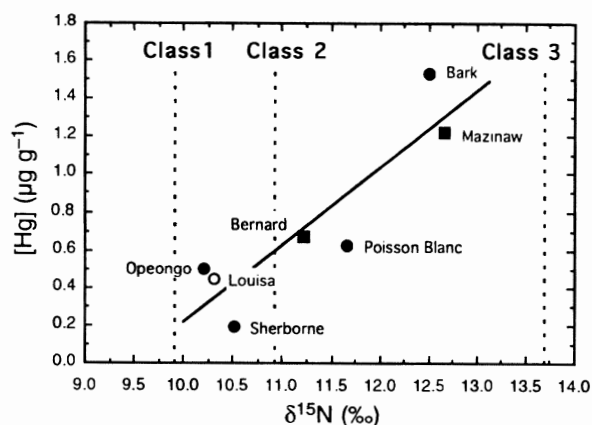


FIG. 3 Relationship between mean mercury concentration (wet weight) and mean $\delta^{15}\text{N}$ in lake trout in seven Ontario and Quebec lakes. Correlation between Hg and $\delta^{15}\text{N}$: $r=0.89$, $P<0.01$. The average $\delta^{15}\text{N}$ for each lake trout trophic class from Fig. 1 are shown as stippled lines. Class 1 lakes are shown as open circles, class 2 as solid circle, and class 3 as solid square. Lakes deviating from their respective class averages in $\delta^{15}\text{N}$ were not outliers on the Hg– $\delta^{15}\text{N}$ plot. For example, Bernard Lake, a class 3 lake which fell well below the class-3 $\delta^{15}\text{N}$ average, had moderate trout mercury levels that were more typical of class 2 lakes. Mercury data are from ref. 19 and were measured in 1976–82, with the exception of Poisson Blanc Lake, for which data were obtained for 1992 from the Quebec government. Samples used for $\delta^{15}\text{N}$ determination were collected in 1991–93.

Although we have not yet obtained sufficiently complete $\delta^{15}\text{N}$ profiles on all of our lakes to calculate the $\delta^{15}\text{N}$ trophic increments on an individual lake basis, the averages that we have calculated for each trophic pair in class 2 and 3 food chains, are all <3.4 , suggesting significant levels of omnivory in these pelagic food webs. To illustrate our approach to estimating omnivory, let us propose that the total ration of the i th trophic (C_i) level can be represented as a weighted sum of the contributions from lower levels

$$C_i = \sum_j \rho_{ij} C_j \quad \text{and} \quad \sum_j \rho_{ij} = 1$$

where the ρ_{ij} are the fractions of the i level's diet made up by each level (j), and for the whole web, $C = \rho C$, where ρ is a matrix of the type

$$\begin{bmatrix} 0 & 0 & 0 & 0 \\ \rho_{21} & 0 & 0 & 0 \\ \rho_{31} & \rho_{32} & 0 & 0 \\ 0 & \rho_{42} & \rho_{43} & 0 \end{bmatrix}$$

When the $\rho_{i,i-1} = 1$ and the rest of $\rho = 0$, then the food chain is linear and the $\delta^{15}\text{N}_i$ increments should equal 3.4‰, otherwise there will be omnivory and the $\delta^{15}\text{N}_i$ increments should be <3.4 ‰ because

$$\delta^{15}\text{N}_i = (\rho_{i,i-1} \delta^{15}\text{N}_{i-1} + \rho_{i,i-2} \delta^{15}\text{N}_{i-2} + \dots) + 3.4\text{‰}$$

and for the whole web, $\delta^{15}\text{N} - 3.4 = \rho \delta^{15}\text{N}$.

Although this equation relates the dietary weighting factors (ρ_{ij}) to the $\delta^{15}\text{N}$ profile ($\delta^{15}\text{N}_i$), it only provides explicit solutions for the ρ_{ij} when omnivory (defined as $1 - \rho_{i,i-1}$) is limited to one level, that is $\rho_{i,i-2} = 0$. Otherwise the approach will yield only an envelope, or range of values within which the ρ_{ij} must lie. As dietary studies on class 3 communities in a series of Ontario lakes¹⁷ show that omnivory does in fact only extend to one level (that is, adult lake trout eat *Mysis* in addition to forage fish, but no zooplankton, and pelagic forage fish eat *Mysis* and zooplankton), the ρ_{ij} calculated from our average class-3 $\delta^{15}\text{N}$ values (Fig. 2a), should then be valid. Our estimates based on these $\delta^{15}\text{N}$ values for lake trout indicate only 3% omnivory (97% of their diet is pelagic forage fish), but that omnivory at the next lower level of the food web is substantially higher (19%). Volumetric stomach-content studies on species from six class 3 lakes¹⁷ (different from ours) yield an estimate of 4% (0–15%) omnivory for adult lake trout, and again a much higher omnivory for their forage fish (ciscoes) of 66% (15–90%), paralleling our results based on $\delta^{15}\text{N}$.

Omnivory estimates such as these can be used to model the biomagnification of a persistent contaminant because they allow us to convert models developed under the assumption of linear food chains. Using Thomann's²⁰ steady-state model simplified by the exclusion of the direct uptake term, and written in vector and matrix form, we have $\mathbf{B} = \alpha \mathbf{C}[(\mathbf{K} + \mathbf{G})\mathbf{I}]^{-1}$, where \mathbf{B} is a vector of biomagnification ratios (ratio of tissue contaminant/concentration in prey), and α , \mathbf{C} , \mathbf{K} and \mathbf{G} represent vectors of assimilation efficiency, ration, contamination excretion rate and growth rate, respectively, for the i elements of the food web, and \mathbf{I} represents the identity matrix.

Such linear food-chain models will overpredict biomagnification in proportion to the degree of omnivory present. Using the omnivory matrix (ρ) we can rewrite this model much more realistically as

$$\mathbf{v}(\rho\mathbf{I})^{-1} = \alpha \mathbf{C}[(\mathbf{K} + \mathbf{G})\mathbf{I}]^{-1}$$

where \mathbf{v} represents a vector of tissue contaminant levels at the i trophic levels, and $\rho\mathbf{v}$ represents the weighted mean contaminant levels in the diet of each trophic level adjusted for omnivory.

Thus the ρ matrix can be estimated by stable isotope measurements, and these can potentially be used to model contaminant biomagnification much more realistically than is possible using conventional models that assume linear food chains. \square

Received 8 June; accepted 24 September 1994.

1. Minigawa, M. & Wada, E. *Geochim. cosmochim. Acta* **48**, 1135–1140 (1984).
2. Owens, N. J. P. *Adv. Mar. Biol.* **24**, 389–451 (1987).
3. Peterson, B. J. & Fry, B. A. *Rev. ecol. Syst.* **18**, 293–320 (1987).
4. Fry, B. *Limnol. Oceanogr.* **33**, 1182–1190 (1988).
5. Kidd, K. A., Schindler, D. W., Hesslein, R. H. & Muir, D. C. G. *Sci. Tot. Environ.* (in the press).
6. Hesslein, R. H., Capel, M. J., Fox, D. E. & Hallard, K. A. *Can. J. Fish. aquat. Sci.* **48**, 2258–2265 (1991).
7. Hobson, K. A. & Welch, H. E. *Mar. Ecol. Progr. Ser.* **84**, 9–10 (1992).
8. Kling, G. W., Fry, B. & O'Brien, W. J. *Ecology* **73**, 561–566 (1992).
9. Toda, H. & Wada, E. *Hydrobiologia* **194**, 85–90 (1990).
10. Estep, M. L. F. & Vigg, S. *Can. J. Fish. aquat. Sci.* **42**, 1712–1719 (1985).
11. Kline, T. C. Jr, Goering, J. J., Mathisen, O. A., Poe, P. H. & Parker, P. L. *Can. J. Fish. aquat. Sci.* **47**, 136–144 (1990).
12. Dadswell, M. J. *Distribution, Ecology, and Postglacial Dispersal in Certain Crustaceans and Fishes in Eastern North America* (National Museum of Canada, Ottawa, 1975).
13. Lasenby, D. C., Northcote, T. G. & Furst, M. *Can. J. Fish. aquat. Sci.* **43**, 1277–1284 (1986).
14. Martinez, P. J. & Bergersen, E. P. N. *Am. J. Fish. Manage* **9**, 1–11 (1989).
15. Evans, D. O. & Loftus, D. H. *Can. J. Fish. aquat. Sci.* **44** (suppl. 2), 249–266 (1987).
16. Martin, N. V. *J. Fish. Res. Board Can.* **11**, 5–10 (1954).
17. Trippel, E. A. & Beamish, W. H. *Can. J. Fish. aquat. Sci.* **50**, 1442–1455 (1993).
18. Rasmussen, J. B., Rowan, D. J., Lean, D. R. S. & Carey, J. H. *Can. J. Fish. aquat. Sci.* **47**, 2030–2038 (1990).
19. Cabana, G., Tremblay, A., Kalff, J. & Rasmussen, J. B. *Can. J. Fish. aquat. Sci.* **51**, 381–389 (1994).
20. Thomann, R. W. *Can. J. Fish. aquat. Sci.* **38**, 280–296 (1981).
21. Hairston, N. G. Jr & Hairston, N. G. *Am. Nat.* **142**, 379–411 (1993).
22. Spiller, D. A. & Schoener, T. W. *Nature* **347**, 469–471 (1990).
23. Power, M. E. *Ecology* **73**, 733–746 (1992).
24. Diehl, S. *Oikos* **68**, 151–157 (1993).
25. Pimm, S. L. *Food Webs* (Chapman and Hall, London, 1987).
26. Pimm, S. L. & Lawton, J. H. *Nature* **275**, 542–544 (1978).
27. Pimm, S. L. & Lawton, J. H. *Nature* **268**, 329–331 (1977).
28. Konkle, B. R. & Sprules, W. G. *Trans. Am. Fish. Soc.* **115**, 515–521 (1986).

ACKNOWLEDGEMENTS. We thank the NSERC, the Atomic energy of Canada Ltd, and the CANDU Owners Group for support. F. J. Hicks, W. Wilson, D. Ferguson, B. R. Stranix, A. Robichon and J. Vander Zanden helped in collecting fish samples. We also thank all cottagers and outfitters for preserving fish and S. Mazumder for operating the mass spectrometer. N. Price, R. Hesslein, D. W. Schindler, M. Power, J. Montoya, P. Yodzis, M. Trudel, G. Klein and J. Vander Zanden reviewed the manuscript.