

Patterns of Food Chain Length in Lakes: A Stable Isotope Study

M. Jake Vander Zanden,^{1,*} Brian J. Shuter,² Nigel Lester,³ and Joseph B. Rasmussen¹

1. Department of Biology, McGill University, Montreal, Quebec H3A 1B1, Canada;

2. Aquatic Ecology Group, Department of Zoology, University of Toronto, Toronto, Ontario M5S 3G5, Canada;

3. Aquatic Ecosystems Science Section, Ontario Ministry of Natural Resources, Peterborough, Ontario K9J 8M5, Canada

Submitted September 30, 1998; Accepted May 6, 1999

ABSTRACT: Food web structure is paramount in regulating a variety of ecologic patterns and processes, although food web studies are limited by poor empirical descriptions of inherently complex systems. In this study, stable isotope ratios ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) were used to quantify trophic relationships and food chain length (measured as a continuous variable) in 14 Ontario and Quebec lakes. All lakes contained lake trout as the top predator, although lakes differed in the presumed number of trophic levels leading to this species. The presumed number of trophic levels was correlated with food chain length and explained 40% of the among-lake variation. Food chain length was most closely related to fish species richness ($r^2 = 0.69$) and lake area ($r^2 = 0.50$). However, the two largest study lakes had shorter food chains than lakes of intermediate size and species richness, producing hump-shaped relationships with food chain length. Lake productivity was not a powerful predictor of food chain length ($r^2 = 0.36$), and we argue that productive space (productivity multiplied by area) is a more accurate measure of available energy. This study addresses the need for improved food web descriptions that incorporate information about energy flow and the relative importance of trophic pathways.

Keywords: trophic structure, productive space, food webs, food chains, trophic position, productivity.

Since the publication of Hairston et al. (1960), there has been increasing recognition of the importance of food web structure in regulating a wide range of ecologic patterns and processes (Paine 1980; Pimm 1982; Carpenter et al.

1985; Rasmussen et al. 1990; Persson et al. 1992; Hairston and Hairston 1993; Persson et al. 1996; Schindler et al. 1997). Trophic structure is commonly viewed as the number of trophic levels or the length of the food chain, and the determinants of food chain length remain a long-standing question in ecology (Lindeman 1942; Hutchinson 1959). Pimm (1982) summarized four hypotheses of food chain length: that diminishing energy at each successive trophic level limits food chain length (the energy constraints hypothesis); that food chains become shortened by consumers feeding on lower, more productive trophic levels (the optimal foraging hypothesis); that long food chains are dynamically unstable (the dynamic stability hypothesis); and that constraints such as predator-prey body size ratios place limits on the number of trophic levels (the design constraints hypothesis). Alternatively, Schoener (1989) found that food chain length increases with ecosystem size and proposed the "productive space hypothesis": that area multiplied by primary productivity determines species richness and community composition, which, in turn, determines food chain length. Persson et al. (1996) reviewed the implications of dynamic factors such as habitat heterogeneity, disturbance, size-structured interactions, and adaptive behavior for food chain length.

Studies of food webs have been plagued by the poor quality of the available data, a problem that seriously limits and biases the conclusions of these analyses (Hall and Raffaelli 1991; Polis 1991; Hall and Raffaelli 1993; Polis 1994). Studies attempting to describe food web structure are generally one of two types. Food chain studies assign species to one of several discrete trophic levels (Hairston et al. 1960; Oksanen et al. 1981; Persson et al. 1992; Abrams 1993). Although the food chain provides the basis for most studies of food web dynamics, this approach provides overly simplistic trophic depictions by assuming no omnivory and the existence of discrete levels (Polis 1994; Persson et al. 1996; Polis and Winemiller 1996). Alternatively, connectance food web studies catalog the presence/absence of feeding links, and food chain length represents the mean or maximum path length leading to the top predator. Recent critiques and studies of highly

* To whom correspondence should be addressed; present address: Department of Environmental Science and Policy, 2132 Wickson Hall, One Shields Avenue, University of California, Davis, California 95616.

resolved webs indicate a variety of problems, including poor taxonomic resolution, inconsistent sampling effort, general incompleteness of the food web data, and problems of scale. A common conclusion has been that many of the observed food web patterns are simply artifacts of methodologies and poor data (Winemiller 1990; Hall and Raffaelli 1991; Martinez 1991; Polis 1991; Hall and Raffaelli 1993; Polis 1994; Polis and Strong 1996; Polis and Winemiller 1996; Goldwasser and Roughgarden 1997). In response to these problems, numerous authors have called for food web approaches that quantify energy flow and the importance of feeding interactions (Cohen et al. 1990; Kenny and Loehle 1991; Martinez 1991; Pimm et al. 1991).

Stable isotopes are increasingly used in food web studies, particularly because they can provide energy flow-based measures of food web structure. Stable nitrogen isotope ratios ($^{15}\text{N}/^{14}\text{N}$; $\delta^{15}\text{N}$) exhibit a 3‰–4‰ enrichment in the heavy isotope (^{15}N) from prey to predator (DeNiro and Epstein 1981; Minagawa and Wada 1984; Hobson and Welch 1992; Cabana and Rasmussen 1994). Interpreting the $\delta^{15}\text{N}$ of a consumer relative to an appropriate baseline $\delta^{15}\text{N}$ value provides a reliable and quantitative measure of its trophic position, defined as a noninteger value reflecting the energy-weighted mean number of trophic transfers between the basal resources and the consumer (Vander Zanden and Rasmussen 1999). Unlike previous isotopic food web studies, use of this baseline standardization method allows comparative food web studies (Cabana and Rasmussen 1996; Vander Zanden et al. 1997). Furthermore, the isotopic approach is sensitive to omnivory (Cabana and Rasmussen 1994) and provides time-integrated information on the basis of the materials assimilated by consumers. In effect, many of the aforementioned problems with connectance food web and food chain approaches can be circumvented by using the stable isotope method to quantify food web structure.

In this study, we use stable isotopes to estimate the trophic position of a wide range of pelagic consumers from a series of 14 lakes from Ontario and Quebec, all of which contain lake trout (*Salvelinus namaycush*). Lake trout can reasonably be considered the top predator in our study systems. Lake trout generally have the highest trophic position of any pelagic fish species in our study lakes (Vander Zanden and Rasmussen 1996). Furthermore, it is unlikely that birds or mammals feed significantly on adult lake trout because of their large size and deepwater habitats. In addition to our 14 study lakes, we also include food chain length estimates (lake trout trophic position estimated by using stable isotopes) from six other lakes (Hecky and Hesslein 1995; Kiriluk et al. 1995; Keough et al. 1996; Kidd et al. 1998) for a total of 20 study lakes.

Food chains leading to lake trout provide a valuable study system for examining hypotheses of food chain

length. Previous studies report that trophic structure leading to lake trout differs substantially among lakes (Martin 1952; Martin 1966; Rasmussen et al. 1990; Trippel and Beamish 1993; Vander Zanden and Rasmussen 1996). As a result of heterogeneous postglacial dispersal of prey fish and invertebrates (Dadswell 1974) and the introduction of nonnative species by humans, only some lakes contain the pelagic species that serve as intermediate trophic levels leading to lake trout (the pelagic forage fish: cisco (*Coregonus artedii*), lake whitefish (*Coregonus clupeaformis*), round whitefish (*Prosopium cylindraceum*), smelt (*Osmerus mordax*), alewife (*Alosa pseudoharengus*), sculpins (*Cottus spp.*), and the predatory relict zooplankton species *Mysis relicta*. Rasmussen et al. (1990) used information on the presence/absence of these important intermediate prey groups to estimate the number of trophic levels in the pelagic food chain leading to lake trout: class 1 lakes are those that are considered to be three trophic level systems, class 2 lakes are four trophic level systems, and class 3 lakes are five trophic level systems (the presumed trophic structures are presented in fig. 1A).

The objectives of this study are to use stable isotope depictions of trophic structure to describe the among-lake variation in food chain length and trophic structure, test how well food chain length corresponds with the presumed number of trophic levels in the system (Rasmussen's lake class variable), and examine relationships between food chain length and lake/ecosystem attributes to address hypotheses of food chain length.

Material and Methods

Study Sites and Field Sampling

Fourteen lakes containing lake trout as the top pelagic predator were selected from central Ontario and southern Quebec. Lakes were selected to span a broad and representative range of presumed trophic structure and productivity. All lakes were located between 46°15'N and 44°30'N latitude and 80°00'W and 72°00'W longitude. Sampling was conducted between May and September, 1995. *Mysis* and *Diporia* were collected by using a benthic sled. Lake trout (13–21 per lake; $\bar{X} = 17$) and potential prey fish species were collected from the littoral, pelagic, and profundal habitats by using gill nets, seine nets, minnow traps, angling, and local fishers. Littoral fish (percids, centrarchids, and cyprinids) <12 cm in length were considered potential lake trout prey because lake trout have access to these fish during the nonstratified periods (Martin 1954; Vander Zanden and Rasmussen 1996). We group these fish together under the term "littoral forage fish." Approximately 1 g (wet weight) of white dorsal muscle tissue was extracted from each fish specimen. All fish mus-

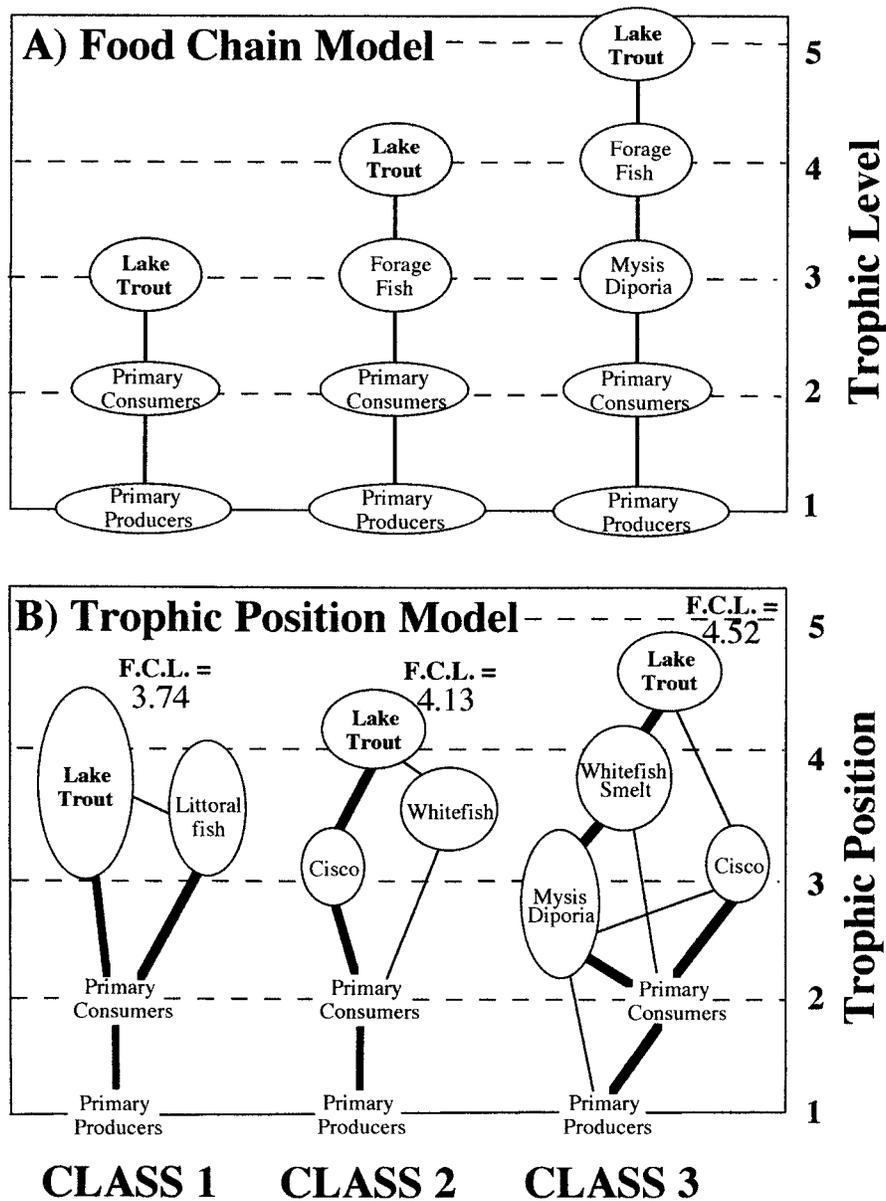


Figure 1: A, Food-chain model of pelagic trophic structure (on the basis of Rasmussen et al. 1990). B, Trophic position model of pelagic food webs based on our stable isotope-based estimates of trophic position. For each lake class, the average trophic position of each species was estimated, and species with similar trophic positions were grouped into trophic guilds. Thick lines represent major links, thin lines represent minor links. The vertical extent of the trophic compartments represents 1 SD. *F.C.L.* = food chain length.

cle tissue samples and whole-invertebrate samples were frozen immediately after collection.

Stable Isotope Procedure

Fish and invertebrate tissues were dried at 70°C for 48 h in a drying oven, ground into a fine powder by using mortar and pestle, and packed into 4 × 6-mm tin capsules

for isotopic analyses. Stable carbon and nitrogen isotope analyses were performed on the same sample by 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). Stable isotope ratios are expressed in delta (δ) notation, defined as the parts per thousand (‰) deviation from a standard material; δ¹³C or δ¹⁵N =

$[(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1,000$, where $R = {}^{13}\text{C}/{}^{12}\text{C}$ or ${}^{15}\text{N}/{}^{14}\text{N}$. The standard material is Pee Dee belemnite (PDB) limestone for $\delta^{13}\text{C}$ (Craig 1957) and atmospheric nitrogen for $\delta^{15}\text{N}$ (both standards have a ‰ value arbitrarily set at 0‰). One-half of the samples were analyzed in duplicate; the standard error of the estimate was 0.12‰ for $\delta^{15}\text{N}$ and 0.10‰ for $\delta^{13}\text{C}$.

For $\delta^{15}\text{N}$ values to provide a measure of the trophic position of a consumer, they must be interpreted relative to the $\delta^{15}\text{N}$ value representing the base of the food web (hereafter referred to as the baseline $\delta^{15}\text{N}$). We use primary consumers (trophic level 2) as baseline indicators because their isotopic signatures are more temporally and spatially integrative relative to primary producers (Cabana and Rasmussen 1996). Vander Zanden and Rasmussen (1999) developed a method that uses $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ information to correct for within- and among-system variation in primary consumer (baseline) $\delta^{15}\text{N}$. Briefly, this method for estimating trophic position has three parts: it generates a primary consumer $\delta^{15}\text{N} - \delta^{13}\text{C}$ relationship, it uses the $\delta^{13}\text{C}$ value of the consumer to define the appropriate baseline $\delta^{15}\text{N}$ value, and it estimates the consumer's trophic position by using the formula

$$\text{trophic position}_{\text{consumer}} = (\delta^{15}\text{N}_{\text{consumer}} - \delta^{15}\text{N}_{\text{baseline}})/3.4 + 2$$

where 3.4 represents the assumed per trophic level increase (‰) in $\delta^{15}\text{N}$. We used this method to estimate the trophic position of each fish and invertebrate specimen. Error associated with the baseline correction was ~0.17‰. To estimate the trophic position of lake trout from Lake Ontario, the mean mussel $\delta^{15}\text{N}$ value (8.5‰) was used as the $\delta^{15}\text{N}$ baseline in this equation. For each study lake, the average trophic position of each pelagic species or trophic group (lake trout, smelt, lake whitefish, round whitefish, cisco, sculpin, littoral forage fish, *Mysis*, and *Diporia*) was calculated.

Fish species richness represents the number of fish species recorded as present in the lake at the time of study, based on our field surveys and unpublished Ontario Ministry of Natural Resources data files. No direct measure of primary productivity was available for our lakes. The best available indicator of algal biomass and primary productivity was annual average Secchi disk transparency (Carlson 1977). This is justified because all of our study lakes are low in color (<10 platinum units) and dissolved organic carbon. Secchi disk transparency values (the depth in meters in which a Secchi disk is no longer visible) for the study lakes were taken from unpublished Ontario Ministry of Natural Resources data files and represent the average transparency values recorded during the ice-free pe-

riod. These values are expressed in the inverse (Secchi disk transparency⁻¹) so that increasing values reflect increasing algal biomass. Productive space (estimated primary productivity rate multiplied by lake area) was estimated for each lake. Primary productivity was estimated from Secchi disk transparency by using published empirical relationships (Carlson 1977; Tolstoy 1988).

Results

Empirical Data

The method of Vander Zanden and Rasmussen (1999) was used to estimate the trophic position of each individual pelagic consumer from the 14 study lakes. For each lake, the mean trophic position of each species or trophic group was calculated, and values were plotted along a vertical axis representing trophic position (fig. 2). Lakes are arranged according to the presumed number of trophic levels (three, four, or five levels; Rasmussen's lake class variable).

Food web configurations of class 1 lakes (three trophic level systems) varied widely among lakes, with food chain length ranging from 3.0 to 4.8. Both among-lake variation in the trophic position of littoral forage fish and the difference in trophic position between lake trout and littoral forage fish (lake trout trophic position less littoral forage fish trophic position) were responsible for the among-lake variation in class 1 food chains. Food chain length of class 2 lakes (four trophic level systems) ranged from 3.8 to 4.4; much of this variation was attributed to variation in the trophic position of prey items. Food chain length of class 3 systems (five trophic level systems) ranged from 4.3 to 4.6. Mean trophic positions of pelagic forage fish were highly variable among lakes, with sculpins and smelt exhibiting the highest average trophic position, followed by whitefish and cisco.

For each of the three lake classes, the mean trophic position of each species and trophic group was calculated (table 1). Our stable isotope trophic position estimates were used to characterize the typical trophic structure for each lake class in the form of a trophic position model (fig. 1B), which is a means of representing trophic structure on the basis of trophic position data whereby species with similar trophic positions are grouped into trophic guilds (see Vander Zanden and Rasmussen 1996). Mean food chain length increased from 3.74 in class 1 lakes to 4.13 in class 2 lakes, and to 4.52 in class 3 lakes: values that generally correspond with food chain length estimates calculated by using dietary data (Vander Zanden and Rasmussen 1996).

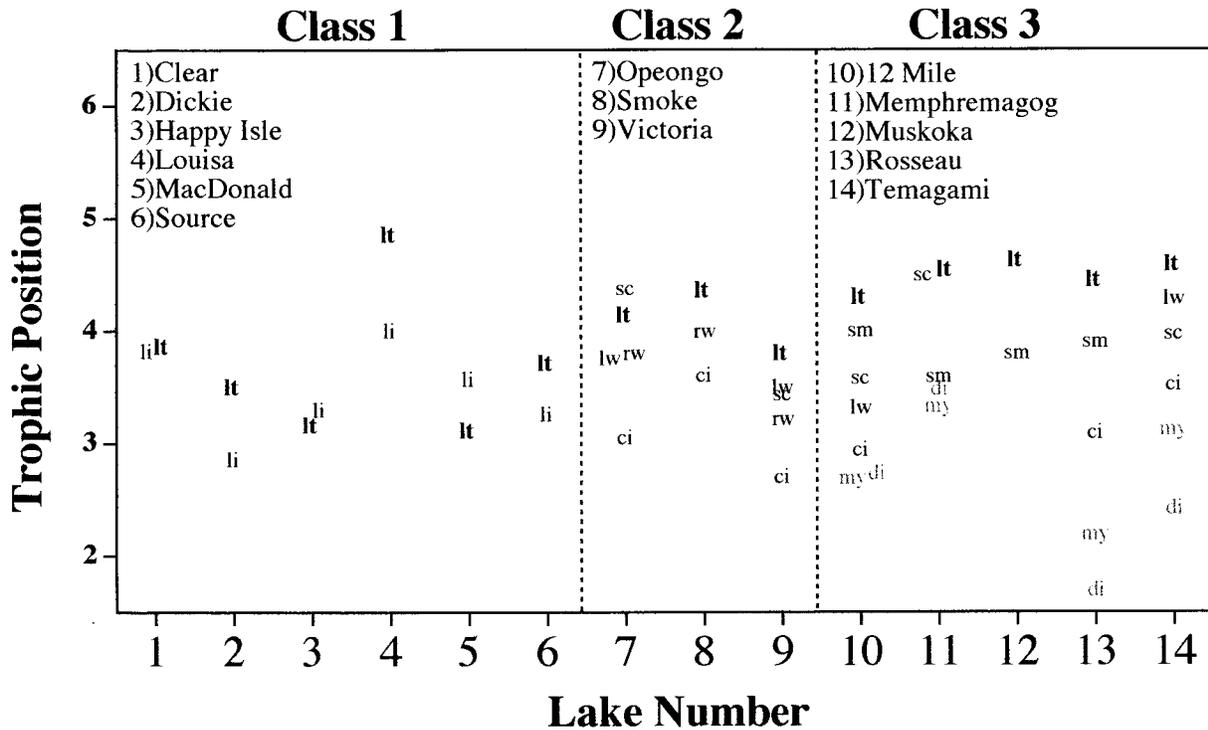


Figure 2: Pelagic trophic structure for each of the 14 Ontario and Quebec study lakes. *lt*, lake trout; *li*, littoral fish; *lw*, lake whitefish; *rw*, round whitefish; *sc*, sculpin; *ci*, cisco; *sm*, smelt; *di*, *Diporia hoyi*; *my*, *Mysis relicta*.

Factors Affecting Food Chain Length

Food chain length as measured by using stable isotopes ranged nearly two trophic levels across our 14 study lakes. This among-system variation in food chain length provides an opportunity to examine relationships between food chain length and lake/food web characteristics that are pertinent to hypotheses of food chain length. Here, we examine relationships between food chain length and the presumed number of discrete trophic levels, fish species richness, lake area, a measure of lake productivity (Secchi disk transparency⁻¹), and productive space.

One-way ANOVA (SYSTAT) indicated that the number of discrete trophic levels (lake class) explained 41% of the among-lake variation in mean lake trout trophic position (using lake averages; $n = 14$ lakes, $F = 3.74$, $P = .058$, $r^2 = 0.41$). Using individual lake trout, the number of discrete trophic levels (lake class) explained 33% of the total variation in lake trout trophic position ($n = 243$ individual lake trout, $F = 58.52$, $P < .001$, $r^2 = 0.33$). This indicates that, in a qualitative sense, discrete trophic levels represent the among-lake variation in trophic structure, even though use of trophic levels clearly failed to incorporate the complexity and omnivory that is prevalent in these food webs (cf. fig. 1A, 1B).

Food chain length increased with increasing fish species richness (fig. 3A); species richness explained 66% (with Great Lakes) and 69% (without Great Lakes) of the among-lake variation in food chain length (table 2). The two Great Lakes, Lake Ontario and Lake Superior (Kiriluk et al. 1995; Keough et al. 1996), had shorter food chains than lakes of intermediate species richness, producing a hump-shaped relationship. Food chain length also increased as a function of lake area (fig. 3B); area explained between 45% (with Great Lakes) and 50% (without Great Lakes) of the among-lake variation in food chain length (table 2). As was the case for species richness, Lake Ontario and Lake Superior had shorter food chains than intermediate-sized lakes.

If available energy limits food chain length, then food chain length might be expected to increase with an indicator of primary productivity. Secchi disk transparency⁻¹ ranged roughly fourfold across lakes and explained 36% of the among-lake variation in food chain length (fig. 3C; table 2). Note that Lake Ontario and Superior did not differ from the other study lakes in the relationship of Secchi disk transparency⁻¹ to food chain length. We also examined Schoener's productive-space hypothesis: that the total amount of primary production in an ecosystem (pro-

Table 1: Mean trophic position (± 1 SD) and mean total length (mm) of lake trout and other pelagic consumers for each of the three lake classes

Species or trophic group	Number of lakes	Mean trophic position (± 1 SD)	Mean total length (mm)
Class 1 (three trophic level systems):			
Littoral forage fish	6	3.57 (.54)	71
Lake trout	6	3.74 (.69)	296
Class 2 (four trophic level systems):			
Cisco	3	3.05 (.33)	145
Lake whitefish	2	3.68 (.32)	359
Round whitefish	3	3.82 (.29)	274
Sculpin	2	4.12 (.55)	56
Lake trout	3	4.13 (.31)	400
Class 3 (five trophic level systems):			
<i>Diporia</i>	4	2.76 (.68)	...
<i>Mysis</i>	4	2.87 (.51)	...
Cisco	3	3.10 (.34)	206
Smelt	4	3.70 (.31)	150
Lake whitefish	2	3.80 (.55)	309
Sculpin	3	4.09 (.46)	64
Lake trout	5	4.52 (.29)	468

Note: Data on the basis of analysis of 14 Ontario and Quebec lake food webs.

ductive space equals area multiplied by primary productivity; kgC d^{-1}) should ultimately determine the length of the food chain. Our estimate of productive space was positively correlated with food chain length (fig. 3D; table 2), although lake area to food chain length and productive space to food chain length relationships were nearly identical.

Discussion

In this study, stable isotopes were used to measure food chain length and trophic structure in a series of Ontario and Quebec lakes, all of which shared the common feature of having lake trout as the top predator. Food chains leading to lake trout varied by nearly two entire trophic levels among lakes, with the longest food chain consisting of just less than five trophic levels. These findings generally correspond with our previous stable isotope studies indicating that the among-population range in trophic position of freshwater fish populations is typically one trophic level or more (Cabana and Rasmussen 1996; Vander Zanden et al. 1997). It is interesting to note that lakes containing the same presumed trophic levels (same lake class) often differed substantially in trophic structure in terms of energy flow; the number of presumed trophic levels explained only 41% of the among-lake variation in food chain length. Clearly, lakes that are similar in terms of community composition can differ in trophic structure when energy flow is taken into account. Furthermore, the fact that populations do not conform to trophic levels provides direct

evidence that omnivory is prevalent in these systems, supporting recent microcosm, observational, and modelling studies showing that omnivory is prevalent and can stabilize food webs (Polis 1991; Lawler and Morin 1993; Holyoak and Sachdev 1998; McCann et al. 1998). Still, the trophic level concept has proven useful in studies of trophic cascades (Power 1990; Mazumder 1994) and predicting contaminant bioaccumulation in fish (Rasmussen et al. 1990). Trophic levels continue to provide a framework for models and field studies of food web dynamics; indeed, the use of trophic levels often makes these studies possible by simplifying trophic structure to a manageable form.

Food chain length was most closely correlated with fish species richness; this variable explained 69% of the among-lake variation in food chain length. Food chain length also increased with increasing lake area, which is not surprising as lake area and fish species richness are closely correlated. The fact that lake area was a poorer predictor of food chain length than species richness indicates that food chain length was responding to changes in community composition and species richness rather than to the effects of increasing lake size per se. Our results suggest that although habitat size (lake area) may provide a reasonable and easy-to-measure indicator of web size for future food web studies (Cohen and Newman 1991), measures of species richness are a preferable (and biologically meaningful) indicator of food web size and complexity.

The largest lakes, Lake Superior and Lake Ontario, had shorter food chains than lakes of intermediate size and

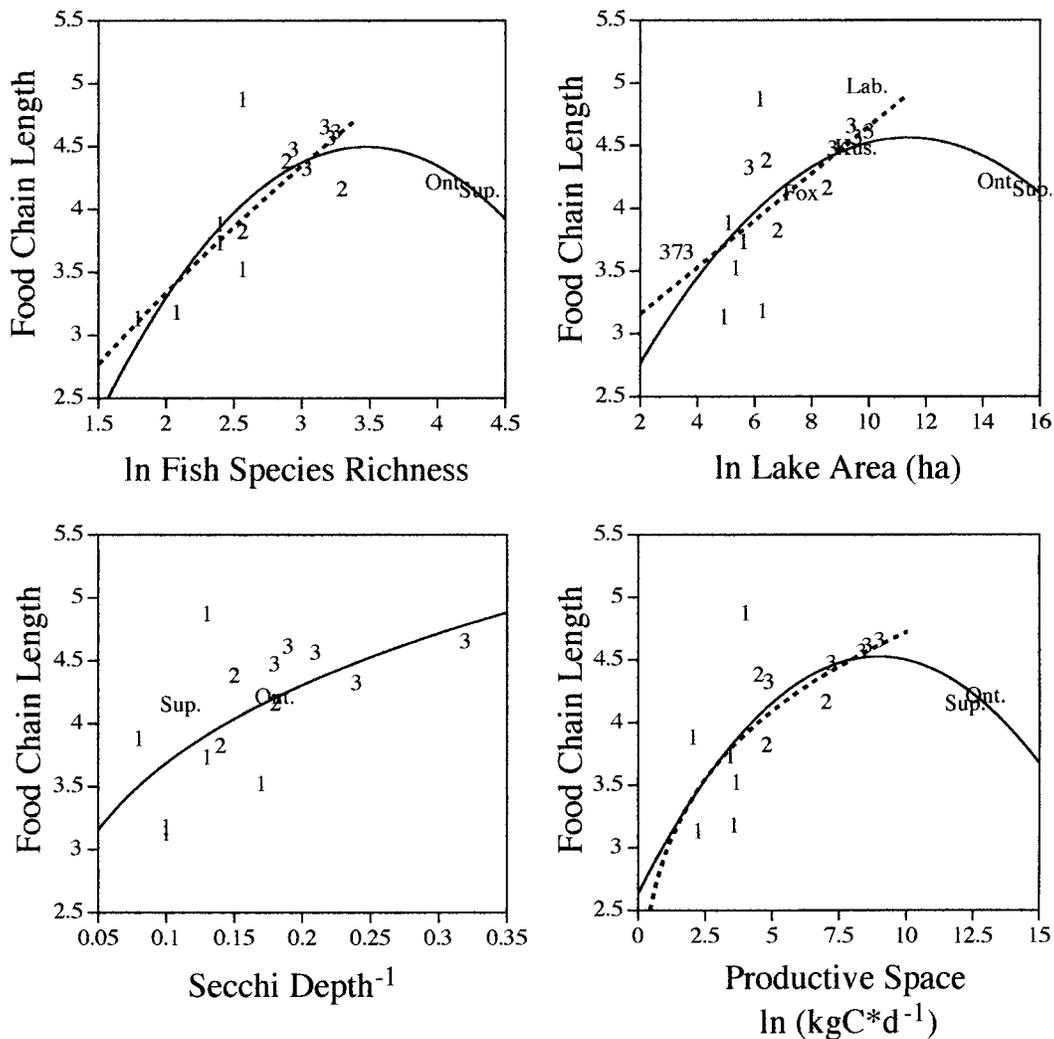


Figure 3: Relationships between food chain length and \ln fish species richness, \ln lake area (ha), Secchi disk transparency⁻¹ (a measure of lake productivity), and productive space (lake area multiplied by productivity). Dashed line represents the curve for the study lakes exclusive of the Great Lakes, solid line includes Lake Ontario and Lake Superior. 1, class 1 lake; 2, class 2 lake; 3, class 3 lake; *Ont.*, Lake Ontario; *Sup.*, Lake Superior; *Fox*, Fox Lake; *Kus.*, Kusawa Lake; *Lab.*, Lake Laberge; 373, Lake 373.

species richness (fig. 3A, 3B). In fact, this observation corresponds with predictions of Persson et al. (1996) that certain variables should exhibit a hump-shaped relationship with food chain length. We provide two possible explanations for why the Great Lakes might have shorter food chains. The first is that lake trout from the Great Lakes are isolated from the inshore and benthic food webs because of the low perimeter to area ratios in these systems. A potential consequence of interacting with a limited subset of the food web is that the food chain becomes shortened.

An alternative explanation is related to the fact that both Lake Ontario and Lake Superior contain populations of

alewife, a species of pelagic forage fish found in none of our other study lakes. Lake trout often feed heavily on this species (Vander Zanden and Rasmussen 1996). Because alewife are generally not piscivorous and rarely feed on *Mysis* and *Diporia*, alewife have a low trophic position compared to other species of pelagic forage fish (Vander Zanden and Rasmussen 1996). Lake trout populations that feed on the low-trophic-position alewife will have lower trophic positions relative to those that feed on other prey fish species. This explanation is essentially an optimal foraging argument (Hutchinson 1959; Pimm 1982), in which food chain length reflects a balance between forces that tend to shorten food chains (that prey lower in the food

Table 2: Equations relating food chain length to ln fish species richness (N), ln lake area (ha; A), Secchi disk transparency⁻¹ (m; S), and ln productive space (kgC/d⁻¹; PS)

Predictor variable	Number of lakes	Equation	r^2
(1) ln fish species richness (N) (without Great Lakes)	14	$FCL = 2.13 \times N^{.65}$.69
(2) ln fish species richness (N) (with Great Lakes)	16	$FCL = -.55N^2 + 3.83N - 2.16$.67
(3) ln lake area (ha) (A)(without Great Lakes)	18	$FCL = 1.88A + 2.78$.50
(4) ln lake area (ha) (A) (with Great Lakes)	20	$FCL = -.021A^2 + .47A + 1.91$.45
(5) Secchi ⁻¹ (S) (with Great Lakes)	16	$FCL = 6.18S^{.22}$.36
(6) ln productive space (PS) (without Great Lakes)	14	$FCL = 2.94PS^{.21}$.48
(7) ln productive space (PS) (with Great Lakes)	16	$FCL = -.02PS^2 + .44PS + 2.63$.48

Note: Equations with Great Lakes (equations [2], [4], [5]) include stable isotope-based food chain length estimates for Lake Ontario (Kiriluk et al. 1995) and Lake Superior (Keough et al. 1996). Additional food chain length estimates in equations (3) and (4) are for lakes 373, Laberge, Fox, and Kusawa (Hecky and Hesslein 1995; Kidd et al. 1998).

web are more productive/abundant) and those that tend to lengthen food chains (that prey higher in the food web are likely to be larger, thereby making them more profitable). Because alewife are relatively large and are also often abundant, this species can be a highly profitable prey item for lake trout. Consequently, lake trout consume this low-trophic position species, and the result is a shortened food chain.

The importance of species richness and lake area in determining food chain length in this study corresponds with findings of Schoener (1989) that found that island area (habitat size) explained the substantial variation in food chain length among Bahamian islands. Furthermore, Schoener's qualitative reanalysis of Briand and Cohen's (1987) data also suggested that food chain length increased with food web area (Schoener 1989). Schoener (1989) argued that larger systems have more total energy available as a result of their size. Such a system would support more individuals per species, and, consequently, individual species would be more likely to persist. Increasing the primary productivity also increases the total production of a system. This reasoning led to the productive-space hypothesis: that the total amount of primary production in an ecosystem (productive space equals area multiplied by primary productivity rate; kgC d⁻¹) determines species richness and community composition, which, in turn, determines the length of the food chain.

Productive space was positively correlated with food chain length, although the lake area to food chain length and productive space to food chain length relationships were nearly identical. Productive-space estimates were pri-

marily a function of lake area because there was a relatively limited range in lake productivity compared to the range in lake area (nearly five orders of magnitude). Productive space was extremely closely correlated with lake area (ln productive space = 1.000 [ln area] - 1.893; $r^2 = 0.94$), indicating that lake area serves as a proxy for productive space in our study systems such that effects of lake area and productive space cannot be distinguished.

Although many dynamic food web models assume that increasing productivity allows addition of trophic levels (Oksanen et al. 1981; Abrams 1993), studies examining effects of productivity on food chain length have either found (Yodzis 1984; Jenkins et al. 1992; Persson et al. 1992; Kaunzinger and Morin 1998; Townsend et al. 1998) or not found (Pimm 1982; Briand 1983; Briand and Cohen 1987; Schoenly et al. 1991) positive relationships. Whether positive relationships were reported from microcosm studies depended on the range of productivity included; a twofold range in productivity produced little effect (Spencer and Warren 1996a, 1996b), whereas those considering a broad range (i.e., orders of magnitude) of productivity found positive effects of productivity (Jenkins et al. 1992; Kaunzinger and Morin 1998).

Our indicator of lake productivity, Secchi disk transparency⁻¹, was positively correlated with food chain length, although this variable explained relatively little (36%) of the among-lake variation in food chain length. In addition, Secchi disk transparency⁻¹ failed to explain a significant portion of the residual variation from either species richness or lake area models, indicating no effect of productivity independent of these factors. Although this seems

to suggest a relatively minor role of productivity, the range in lake productivity may not have been enough to detect productivity effects. In addition, if food chain length were truly limited by the available energy in the system, food chain length should be set by the total amount of primary production in the system (productive space), rather than primary productivity rates on a per unit area basis. Because productive space was primarily a function of lake area in our study, lake area and productive space are the variables that are most indicative of ecosystem productivity, in fact, more so than our original indicator of productivity (Secchi disk transparency⁻¹). Future studies attempting to resolve the importance of habitat size (area), productive space, and productivity should include a broad range of both habitat size and productivity.

Trophic structure has crucial implications for both community and ecosystem patterns and processes, such as the regulation of species diversity (Paine 1980), energetic efficiencies and the biomass of trophic levels (Hairston et al. 1960; Oksanen et al. 1981; Power 1990; Hairston and Hairston 1993), community stability (May 1975; Pimm 1982), contaminant levels in the biota (Rasmussen et al. 1990), and biogeochemical fluxes from ecosystems (Schindler et al. 1997). Although the importance of trophic structure is well recognized, food web studies have generally suffered from a lack of replicable and reliable measures of trophic structure, to the extent that conclusions of many food web studies are considered questionable, and the poor quality of the available food web data limits further progress (Paine 1988).

The recent trend away from analyzing catalogs of literature food webs (Cohen et al. 1990) in favor of observational food web studies of the same ecosystem type by using standardized methodology (Sprules and Bowerman 1988; Schoener 1989; Townsend et al. 1998), as well as experimental microcosm studies (Jenkins et al. 1992; Holyoak and Sachdev 1998; Kaunzinger and Morin 1998), represents a move in the right direction. But investigators have also repeatedly called for food web data that reflects energy flow and the importance of trophic links (Cohen et al. 1990; Kenny and Loehle 1991; Martinez 1991; Pimm et al. 1991). The stable isotope approach employed here provides a replicable, energy-weighted measure of trophic structure and food chain length for individual food webs. We show that this approach can be used not only to quantify trophic structure but also to examine the factors influencing the length of food chains in real ecosystems. Furthermore, this approach will likely be useful in applied studies examining how perturbations such as environmental pollution, extinctions, and species introductions affect food web structure and ecosystem function (Vander Zanden et al. 1999).

Acknowledgments

Thanks are extended to H. Sarakinos and M. Trudel and two anonymous reviewers for comments on an early draft of this manuscript. Field assistance was provided by E. Ashley, S. Bonner, P. Hogan, and S. Milne. Sincere thanks to the staff at the Harkness Laboratory for Fisheries Research, in particular D. Brown, L. Carl, T. Middel, M. Ridgway, and G. Ridout. This research was supported by the Harkness Laboratory for Fisheries Research, the Ontario Ministry of Natural Resources, National Science and Engineering Research Council grants to J.B.R., and Friends of McGill, the Vineberg Family, and the Group de Recherche Limnologique graduate fellowships to M.J.V. This is contribution 99-04 of the Aquatic Ecosystem Science Section of the Ontario Ministry of Natural Resources.

Literature Cited

- Abrams, P. A. 1993. Effect of increased productivity on the abundance of trophic levels. *American Naturalist* 141: 351–371.
- Briand, F. 1983. Environmental control of food web structure. *Ecology* 64:253–263.
- Briand, F., and J. E. Cohen. 1987. Environmental correlates of food chain length. *Science (Washington, D.C.)* 238: 956–959.
- Cabana, G., and J. B. Rasmussen. 1994. Modelling food chain structure and contaminant bioaccumulation using stable nitrogen isotopes. *Nature (London)* 372:255–257.
- . 1996. Comparison of aquatic food chains using nitrogen isotopes. *Proceedings of the National Academy of Sciences of the USA* 93:10844–10847.
- Carlson, R. E. 1977. A trophic state index for lakes. *Limnology and Oceanography* 22:361–369.
- Carpenter, S. R., J. F. Kitchell, and J. R. Hodgson. 1985. Cascading trophic interactions and lake productivity. *BioScience* 35:634–639.
- Cohen, J. E., and C. M. Newman. 1991. Community area and food-chain length: theoretical predictions. *American Naturalist* 138:1542–1554.
- Cohen, J. E., F. Briand, and C. M. Newman. 1990. *Community food webs: data and theory*. Springer, New York.
- Craig, H. 1957. Isotopic standards for carbon and oxygen and correction factors for mass-spectrometric analysis of carbon dioxide. *Geochimica et Cosmochimica Acta* 12:133–149.
- Dadswell, M. J. 1974. Distribution, ecology, and postglacial dispersal in certain crustaceans and fishes in eastern North America. National Museum of Canada, Ottawa.
- DeNiro, M. J., and S. Epstein. 1981. Influence of diet on the distribution of nitrogen isotopes in animals. *Geochimica et Cosmochimica Acta* 45:341–353.
- Goldwasser, L., and J. Roughgarden. 1997. Sampling effects

- and the estimation of food-web properties. *Ecology* 78: 41–54.
- Hairston, N. G., Jr., and N. G. Hairston, Sr. 1993. Cause-effect relationships in energy flow, trophic structure, and interspecific interactions. *American Naturalist* 142: 379–411.
- Hairston, N. G., F. E. Smith, and L. B. Slobodkin. 1960. Community structure, population control, and competition. *American Naturalist* 94:421–425.
- Hall, S. J., and D. G. Raffaelli. 1991. Food-web patterns: lessons from a species-rich web. *Journal of Animal Ecology* 60:823–842.
- . 1993. Food webs: theory and reality. *Advances in Ecological Research* 24:187–239.
- Hecky, R. E., and R. H. Hesslein. 1995. Contributions of benthic algae to lake food webs as revealed by stable isotope analysis. *Journal of the North American Benthological Society* 14:631–653.
- Hobson, K. A., and H. E. Welch. 1992. Determination of trophic relationships within a high Arctic marine food web using $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ analysis. *Marine Ecology Progress Series* 84:9–18.
- Holyoak, M., and S. Sachdev. 1998. Omnivory and the stability of simple food webs. *Oecologia (Berlin)* 117: 413–419.
- Hutchinson, G. E. 1959. Homage to Santa Rosalie, or why are there so many kinds of animals? *American Naturalist* 93:145–159.
- Jenkins, B., R. L. Kitching, and S. L. Pimm. 1992. Productivity, disturbance and food web structure at a local spatial scale in experimental container habitats. *Oikos* 65:249–255.
- Kaunzinger, C. M. K., and P. J. Morin. 1998. Productivity controls food-chain properties in microbial communities. *Nature (London)* 395:495–497.
- Kenny, D., and C. Loehle. 1991. Are food webs randomly connected? *Ecology* 72:1794–1799.
- Keough, J. R., M. E. Sierszen, and C. A. Hagley. 1996. Analysis of a Lake Superior coastal food web with stable isotope techniques. *Limnology and Oceanography* 41: 136–146.
- Kidd, K. A., D. W. Schindler, R. H. Hesslein, and D. C. G. Muir. 1998. Effects of trophic position and lipid on organochlorine concentrations in fishes from subarctic lakes in Yukon Territory. *Canadian Journal of Fisheries and Aquatic Sciences* 55:869–881.
- Kiriluk, R. M., M. R. Servos, D. M. Whittle, G. Cabana, and J. B. Rasmussen. 1995. Using ratios of stable nitrogen and carbon isotopes to characterize the biomagnification of DDE, Mirex, and PCB in a Lake Ontario pelagic food web. *Canadian Journal of Fisheries and Aquatic Sciences* 52:2660–2674.
- Lawler, S. P., and P. J. Morin. 1993. Food web architecture and population dynamics in laboratory microcosms of protists. *American Naturalist* 141:675–686.
- Lindeman, R. L. 1942. The tropho-dynamic aspect of ecology. *Ecology* 23:399–418.
- Martin, N. V. 1952. A study of the lake trout, *Salvelinus namaycush*, in two Algonquin Park, Ontario, lakes. *Transactions of the American Fisheries Society* 81: 111–137.
- . 1954. Catch and winter food of lake trout in certain Algonquin Park lakes. *Journal of the Fisheries Research Board of Canada* 11:5–10.
- . 1966. The significance of food habits in the biology, exploitation, and management of Algonquin Park, Ontario, lake trout. *Transactions of the American Fisheries Society* 96:415–422.
- Martinez, N. D. 1991. Artifacts or attributes? effects of resolution on the Little Rock Lake food web. *Ecological Monographs* 61:367–392.
- May, R. M. 1975. *Stability and complexity in model ecosystems*. Princeton University Press, Princeton, N.J.
- Mazumder, A. 1994. Patterns of algal biomass in dominant odd- vs. even-link lake ecosystems. *Ecology* 75: 1141–1149.
- McCann, K., A. Hastings, and G. R. Huxel. 1998. Weak trophic interactions and the balance of nature. *Nature (London)* 395:794–798.
- Minagawa, M., and E. Wada. 1984. Stepwise enrichment of ^{15}N along food chains: further evidence for the relation between $\delta^{15}\text{N}$ and animal age. *Geochimica et Cosmochimica Acta* 48:1135–1140.
- Oksanen, L., S. D. Fretwell, J. Arruda, and P. Niemala. 1981. Exploitation ecosystems in gradients of primary productivity. *American Naturalist* 118:240–261.
- Paine, R. T. 1980. Food webs: linkage, interaction strength and community infrastructure. *Journal of Animal Ecology* 49:667–685.
- . 1988. Food webs: road maps of interaction or grist for theoretical development? *Ecology* 69: 1648–1654.
- Persson, L., S. Diehl, L. Johansson, G. Andersson, and S. F. Hamrin. 1992. Trophic interactions in temperate lake ecosystems: a test of food chain theory. *American Naturalist* 140:59–84.
- Persson, L., J. Bengtsson, B. A. Menge, and M. E. Power. 1996. Productivity and consumer regulation—concepts, patterns, and mechanisms. Pages 396–434 in G. A. Polis and K. O. Winemiller, eds. *Food webs: integration of patterns and dynamics*. Chapman & Hall, New York.
- Pimm, S. L. 1982. *Food webs*. Chapman & Hall, New York.
- Pimm, S. L., J. H. Lawton, and J. E. Cohen. 1991. Food web patterns and their consequences. *Nature (London)* 350:669–674.
- Polis, G. A. 1991. Complex trophic interactions in deserts:

- an empirical critique of food web theory. *American Naturalist* 138:123–155.
- . 1994. Food webs, trophic cascades and community structure. *Australian Journal of Ecology* 19: 121–136.
- Polis, G. A., and D. R. Strong. 1996. Food web complexity and community dynamics. *American Naturalist* 147: 813–846.
- Polis, G. A., and K. O. Winemiller. 1996. Food webs: integration of patterns and dynamics. Chapman & Hall, New York.
- Power, M. E. 1990. Effect of fish in river food webs. *Science* (Washington, D.C.) 250:411–415.
- Rasmussen, J. B., D. J. Rowan, D. R. S. Lean, and J. H. Carey. 1990. Food chain structure in Ontario lakes determines PCB levels in lake trout (*Salvelinus namaycush*) and other pelagic fish. *Canadian Journal of Fisheries and Aquatic Sciences* 47:2030–2038.
- Schindler, D. E., S. R. Carpenter, J. J. Cole, J. F. Kitchell, and M. L. Pace. 1997. Influence of food web structure on carbon exchange between lakes and the atmosphere. *Science* (Washington, D.C.) 277:248–251.
- Schoener, T. W. 1989. Food webs from the small to the large. *Ecology* 70:1559–1589.
- Schoenly, K., R. A. Beaver, and T. A. Heumier. 1991. On the trophic relations of insects: a food-web approach. *American Naturalist* 137:597–638.
- Spencer, M., and P. H. Warren. 1996a. The effect of habitat size and productivity on food web structure in small aquatic microcosms. *Oikos* 75:419–430.
- . 1996b. The effects of energy input, immigration and habitat size on food web structure: a microcosm experiment. *Oecologia* (Berlin) 108:764–770.
- Sprules, W. G., and J. E. Bowerman. 1988. Omnivory and food chain length in zooplankton food webs. *Ecology* 69:418–425.
- Tolstoy, A. 1988. Predicted and measured annual primary production of phytoplankton—examples from some Swedish lakes. *Archiv für Hydrobiologie* 113:381–404.
- Townsend, C. R., R. M. Thompson, A. R. McIntosh, C. Kilroy, E. Edwards, and M. R. Scarsbrook. 1998. Disturbance, resource supply, and food-web architecture in streams. *Ecology Letters* 1:200–209.
- Trippel, E. A., and F. W. H. Beamish. 1993. Multiple trophic level structuring in *Salvelinus-Coregonus* assemblages in boreal forest lakes. *Canadian Journal of Fisheries and Aquatic Sciences* 50:1442–1455.
- Vander Zanden, M. J., and J. B. Rasmussen. 1996. A trophic position model of pelagic food webs: impact on contaminant bioaccumulation in lake trout. *Ecological Monographs* 66:451–477.
- . 1999. Primary consumer $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ and the trophic position of aquatic consumers. *Ecology* 80: 1395–1404.
- Vander Zanden, M. J., G. Cabana, and J. B. Rasmussen. 1997. Comparing the trophic position of littoral fish estimated using stable nitrogen isotopes ($\delta^{15}\text{N}$) and dietary data. *Canadian Journal of Fisheries and Aquatic Sciences* 54:1142–1158.
- Vander Zanden, M. J., J. M. Casselman, and J. B. Rasmussen. 1999. Stable isotope evidence for the food web consequences of species invasions in lakes. *Nature* (London) 401:464–467.
- Winemiller, K. O. 1990. Spatial and temporal variation in tropical fish trophic networks. *Ecological Monographs* 60:331–367.
- Yodzis, P. 1984. Energy flow and the vertical structure of real ecosystems. *Oecologia* (Berlin) 65:86–88.