

NOTE

Mapping trophic continua of benthic foodwebs: body size - $\delta^{15}\text{N}$ relationships

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ABSTRACT: The stable nitrogen isotopic composition ($\delta^{15}\text{N}$) of benthic foodwebs was analyzed to determine trophic relationships among 23 taxa composited from 4 proximal oligotrophic lakes and 35 taxa composited from 2 proximal seagrass meadows. Because omnivory was prevalent, animals in both foodwebs existed along continua of trophic positions rather than in discrete trophic levels. These trophic continua were in turn related to organism body size in support of Elton's early suppositions about foodweb structuring. These foodweb delineations developed due to feeding hierarchies being determined by size-related predation, resulting in 'upper triangular' foodweb matrices as posited by Cohen's cascade model. Expressing aquatic foodweb structure in relation to the ataxonomic continuous variables of organismal trophic position ($\delta^{15}\text{N}$) and body size has the advantage of providing a convenient common currency for comparative purposes that dispenses with the artificiality and impossibility of constraining omnivorous animals into rigidly defined trophic levels.

KEY WORDS: Benthic foodwebs Body size $\delta^{15}\text{N}$ Trophic continua

'A little consideration will show that size is the main reason underlying the existence of food chains, and that it explains many of the phenomena connected with the food cycle.'
(Elton 1927)

Because omnivory is a prevalent attribute of aquatic foodwebs, many have questioned the designation of animals into rigidly delineated trophic 'levels' (Peters 1977, 1988a, Cousins 1987). Two approaches have been used to circumvent these problems of trophic level identification, both of which have important implications for the tracing of element pathways in aquatic foodwebs.

Body size is one of the most important of all biological attributes of aquatic foodwebs (Borgmann 1987, Dickie et al. 1987, Peters 1988b, Peters et al. 1996), and has been empirically linked to many ecological rate functions in both pelagic (Peters 1978, Platt & Denman 1978) and benthic (Gerlach et al. 1985, Schwinghamer et al. 1986, Morin & Nadon 1991) communities. By describing foodwebs in terms of biomass or size spectra (Platt 1985), the implicit assumption in explanatory models is that assemblages of animals are structured as a continuum wherein energy is transferred from the smallest to the largest through predation. Such models rely, therefore, on the belief that the size of an organism is a good measure of its trophic position.

The recent advent of the use of stable nitrogen isotope analysis in aquatic research has enabled the identification of trophic position and allowed for recognition of the existence of a continuum of such non-integer positions rather than a series of discrete trophic levels (e.g. Minagawa & Wada 1984, Wada et al. 1987, Hobson & Welch 1992, Kling et al. 1992, Cabana & Rasmussen 1994). Such models rely on the assumption that an organism's $\delta^{15}\text{N}$ value is a good measure of its trophic position, and, as such, its body size, given that foodwebs are considered to be size-structured.

Surprisingly few attempts have sought to conjoin these 2 approaches and test the ensuing implicit assumptions. Pahl-Wostl (1993) posited that the distribution of body mass and resulting trophic positions 'can be interpreted as a fingerprint for a food web's internal dynamic structure', and can therefore be conveniently used for cross-system comparisons. Gaedke et al. (1996) empirically determined that a correlation did exist between body size and trophic position within a pelagic foodweb, and that diagrams of such relationships provide a good summary of the trophic structure

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and function of these communities. However, Gaedke et al.'s (1996) estimates of *potential* trophic position, determined from the weighted average lengths of presumed feeding pathways, will not be as accurate as *realized* trophic positions measured through $\delta^{15}\text{N}$ analysis (Kling et al. 1992, Vander Zanden & Rasmussen 1996, France et al. 1997, Hansson et al. 1997). Attempts to interrelate realized trophic position (i.e. $\delta^{15}\text{N}$) to body size have been limited to tracking ontogenetic shifts in diet for individual species (e.g. Hobson & Welch 1995) or to differences among serial groupings of plankton (Fry & Quinones 1994). Our objective was to determine if a freshwater littoral foodweb and a coastal seagrass foodweb were structured with animals occurring within discrete trophic levels or instead whether continua of ranging trophic positions existed that defied such traditional trophodynamic compartmentalization. If trophic continua were observed, we were then interested in determining whether the $\delta^{15}\text{N}$ values could be related to organismal body size for the communities.

Methods. We sampled the littoral zone biota of 4 proximally located (0.1 to 1 km apart) oligotrophic lakes in northwestern Ontario for stable isotope analysis during the ice-free months of 1992 to 1994 (France 1995a, b, France & Steedman 1996) using funnel traps, a hand-held corer, a metal dip-screen, terrestrial litter colonization bags, minnow traps, and gill or trap nets. We also sampled autotrophs and consumers from 2 proximally located (0.5 km apart) seagrass beds in outer Boston Harbor for stable isotope analysis during June–July 1995 using gillnets, minnow traps and quadrats (Chandler et al. 1996).

Samples were acid-washed and hand-cleaned to remove inorganic and organic contaminants. Dissected muscles or whole organisms were ground and samples stored frozen until they could be analyzed for nitrogen isotopes on a Europa Tracermass mass spectrometer interfaced with a Roboprep-CN analyzer or on a VG Micromass 903E triple-collector mass spectrometer. Duplicate determinations on either machine did not differ. Analytical variability averaged ± 0.3 SD for standards following weight-related bias (beam value) correction. Two to three replicates were analyzed for each biological sample.

Because neither seasonal nor inter-lake isotopic differences occurred for the same taxon, these data were combined to examine for average trophic position variability in a composite (i.e. regional) foodweb (France 1995a, 1996a, b, c, 1999a, France & Steedman 1996). Similar nutrient levels among the 4 study lakes (del Giorgio & France 1996) precluded the possibility (France et al. 1997) that anthropogenic (Cabana & Rasmussen 1996) or microbial (France 1999b) source differences in $\delta^{15}\text{N}$ could have confounded our composite

foodweb analysis. The resulting sample sizes therefore ranged from 5 to 18 organisms per inter-lake taxonomic grouping.

Only samples from the extensive seagrass meadows at Nahant Peninsula in outer Boston Harbor are considered in this study. Because isotopic determinations for the same species did not differ between the 2 sites, these data were combined. Samples from the inner industrialized harbor of Boston were found to differ isotopically due to sewage pollution effects (France & Chandler unpubl.), and were not included in the present analysis. Sample sizes ranged from 2 to 19 organisms per inter-meadow species. Replicates were not obtained, however, for 10 species.

In addition to the autotrophic food source of epilithon (composed predominantly of diatoms but containing an indeterminate and variable amount of fine terrestrial detritus; France 1996c), lake consumers sampled for $\delta^{15}\text{N}$ analysis included microcrustaceans (Chydoridae, Cyclopodidae), gastropod snails (Viviparidae, Hydrobiidae, Planorbidae), ephemeropteran mayflies (Ephemerelellidae, Leptophebiidae), coleopteran beetles (Chrysomelidae, Elmidae), dipteran flies (Chironomini, Tanypodini, Tanytarsini, Orthoclaadiinae), collembolid springtails (Poduridae), oligochaete worms, turbellarian flatworms, tadpoles *Rana clamitans*, amphipod scuds *Hyaella azteca*, hydracarinid mites, crayfish *Orconectes virilis*, trichopteran caddisflies (Polycentropodidae, Leptocnidae, Glossomatidae), hemipteran true bugs (Belostomatidae, Corixidae), odonate dragonflies (Gomphidae, Libellulidae), white suckers *Catostomus commersoni*, leeches, northern redbelly and finescale dace (*Phoxinus* spp.), common shiners *Notropis cornutus*, brook sticklebacks *Culea inconstans*, slimy sculpins *Cotus cognatus* and lake trout *Salvelinus namaycush*. For lake trout and white suckers, only those individuals with $\delta^{13}\text{C}$ signatures indicative of littoral feeding (France 1995a, 1996c, France & Steedman 1996) were included in the present analysis, as in France (1996a), to circumvent ontogenetic trophic diet shifts. Several small macroinvertebrate species were grouped to improve analytical precision (e.g. dipterans) only if: (1) identified individuals were of the same functional guild as determined from gut content data, and (2) no significant differences (*t*-tests, $p = 0.05$) existed in their separate $\delta^{15}\text{N}$ values.

In addition to the autotrophic food source of epiphyton and fine seagrass detritus (France & Chandler unpubl.), the coastal consumers sampled for $\delta^{15}\text{N}$ analysis included blue mussels *Mytilus edulis*, hermit crabs *Parurus longicarpus*, amphipod scuds *Gammarus* sp., polychaete worms *Polynereis* sp., encrusting bryozoans, epiphytic sponges, slipper snails *Crepidula fornicata*, sand shrimps *Crangon septemspinus*, Jonah crabs *Cancer borealis*, rock crabs *Cancer irroratus*.

tus, periwinkle snails *Littorina littorea*, horse mussels *Modiolus modiolus*, ctenophores *Pleurobrachia pileus*, chink shells *Lacuna vincta*, isopods *Idotea baltica*, sea raven *Hemitripterus americanus*, Atlantic menhaden *Brevoortia tyrannus*, rainbow smelt *Osmerus mordax*, Atlantic cod *Gadus morhua*, pollock *Pollachius virens*, striped bass *Morone saxatilis*, cunner *Tautoglabrus adspersus*, Atlantic mackerel *Scomber scombrus*, windowpane flounder *Scophthalmus aquosus*, winter flounder *Pseudonectes americanus*, young lumpfish *Cyclopterus lumpus*, mummichog *Fundulus heteroclitus*, ocean pout *Macrozoarces americanus*, shorthorn sculpin *Myoxocephalus scorpius*, rock gunnel *Pholis gunnellus*, little skate *Raja erinacea*, winter skate *Raja ocellatus*, white hake *Urophycis tenuis* and spiny dogfish *Squalus acanthias*.

Fractionation between the isotopes ^{14}N and ^{15}N occurs during food assimilation (DeNiro & Epstein 1981). As these results are cumulative, $\delta^{15}\text{N}$ increases by about 3 to 4‰ per trophic category in foodwebs (Minagawa & Wada 1984). However, because of natural source variability in $\delta^{15}\text{N}$, animals of the same trophic position occupying ecotones may have different $\delta^{15}\text{N}$ values depending on the relative balance in their food provenance. For littoral freshwater ecotones, this can be an important source of nitrogen isotopic variability in organisms (France 1996c) as terrestrial plants are often depleted in ^{15}N by about 3‰ compared to aquatic autotrophs (France 1995b). Therefore the $\delta^{15}\text{N}$ values of all lake organisms considered to be exclusively assimilating attached algae based on their $\delta^{13}\text{C}$ signatures (i.e. enriched above -25‰ ; about 15% of the total number collected) were adjusted or normalized to values indicative of assimilation of terrestrial carbon (-29 to -26‰) intermixed in the epilithon samples based on empirical relationships developed between these isotopes for white suckers, tadpoles (France 1996c) and crayfish (France 1995b) in the study lakes. These resulting adjusted $\delta^{15}\text{N}$ values were generally within 1.5‰ of the actual measured values as most littoral organisms in the study lakes displayed $\delta^{13}\text{C}$ values close to those of terrestrial detritus to begin with (France 1995a, 1996a, b, e, 1999a), and therefore did not have to be substantially altered. The major effect of this differential food source adjustment was to reduce the taxon-specific variability in $\delta^{15}\text{N}$ by about 15%, which, if anything, would increase the likelihood of observing discrete trophic levels in the foodweb should they exist. For the coastal data, with the exception of chink shells and mackerel, whose $\delta^{13}\text{C}$ values were indicative of exclusive subsidence on seagrass and on plankton, respectively, all other animals were dependent on a mixture of benthic algae and seagrass detritus (France & Chandler unpubl.), both of which have the same $\delta^{15}\text{N}$ values (France et al. 1998). As a

result, coastal $\delta^{15}\text{N}$ data did not have to be adjusted for complicated feeding relationships as was the case for the freshwater data set.

Body size (as wet mass for the lake organisms and as length for the coastal organisms) was determined through dozens of measurements made from contemporaneous collections of macrofauna in the study systems. Variability in taxon size averaged 20% of the means. Size data for epilithon and epiphyton were obtained from literature values for similar species (Peters et al. 1996).

Results and discussion. Animals in the littoral benthic foodweb from oligotrophic lakes spanned a 15‰ range in $\delta^{15}\text{N}$, with taxon-specific means ranging from 1.4‰ for microcrustaceans to 9.6‰ for lake trout (Fig. 1). Because our $\delta^{15}\text{N}$ values for flies, crayfish, dace, white suckers, and lake trout were statistically indistinguishable from those estimated from the nearby Experimental Lakes Area (Hecky & Hesslein 1995), we added yellow perch, walleye, northern pike, and burbot from these lakes (i.e. species not sampled in our lakes) to construct a regional foodweb for oligotrophic littoral zones in northwestern Ontario. Animals in the benthic foodweb from seagrass meadows in outer Boston Harbor spanned a 13‰ range in

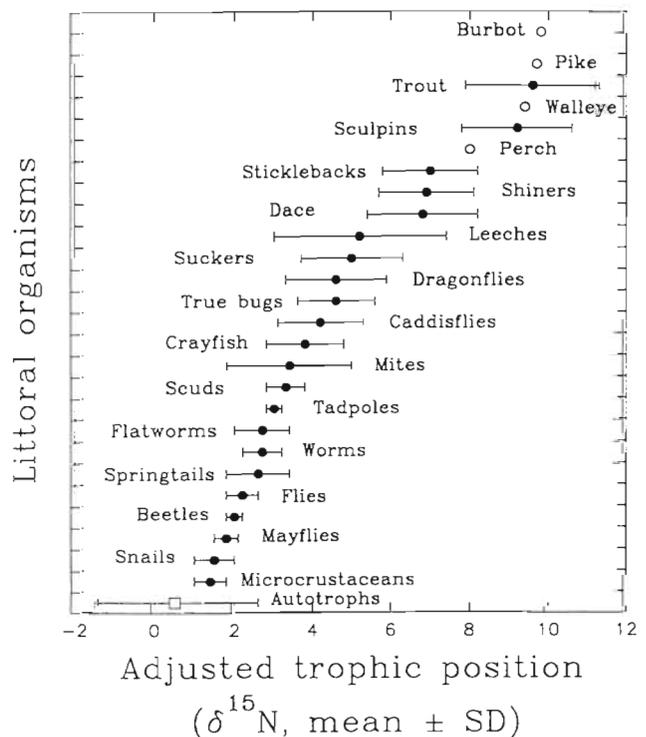


Fig. 1 Trophic continuum of the regional composite littoral benthic foodweb of Canadian Shield lakes in northwestern Ontario shown by stable nitrogen isotope analysis (means \pm SD). (O) Mean values of 4 fishes from Hecky & Hesslein (1995)

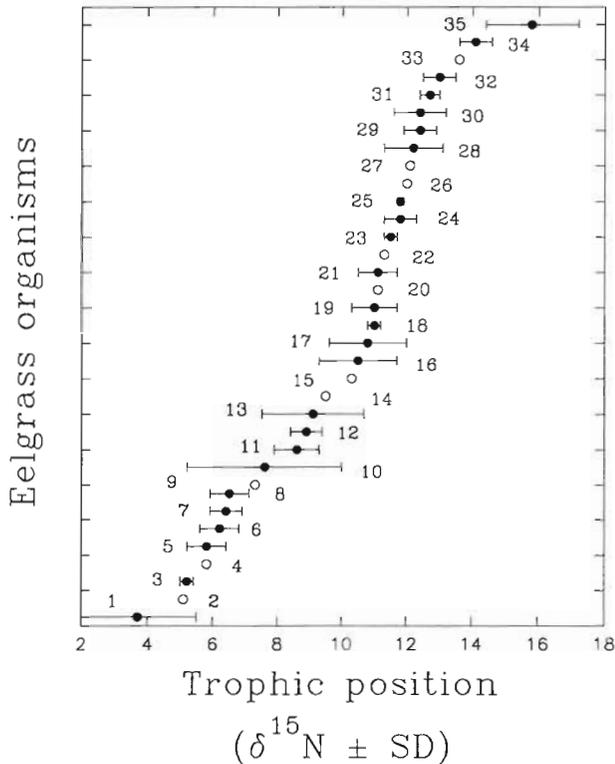


Fig. 2. Trophic continuum of the composite benthic foodweb of seagrass meadows in Boston Harbor shown by stable nitrogen isotope analysis (means \pm SD). (O) Species without replicate determinations. Species are:

- | | |
|-----------------------|-------------------------|
| 1, epiphytic algae | 19, sculpins |
| 2, amphipod scuds | 20, pout |
| 3, bryozoans | 21, winter flounder |
| 4, horse mussels | 22, dogfish |
| 5, hermit crabs | 23, smelt |
| 6, blue mussels | 24, pollock |
| 7, chink shells | 25, rock gunnel |
| 8, sponges | 26, white hake |
| 9, slipper snails | 27, windowpane flounder |
| 10, isopods | 28, menhaden |
| 11, periwinkle snails | 29, winter skate |
| 12, ctenophores | 30, cunner |
| 13, rock crabs | 31, mummichog |
| 14, baby lumpfish | 32, little skate |
| 15, polychaete worms | 33, cod |
| 16, sand shrimps | 34, sea raven |
| 17, Jonah crabs | 35, striped bass |
| 18, mackerel | |

$\delta^{15}\text{N}$, with taxon-specific means ranging from 5.2‰ for amphipods to 15.8‰ for striped bass (Fig. 2). For both foodwebs, bacteria, which might be expected to have $\delta^{15}\text{N}$ values not much higher than those of algae, were not sampled.

As Broman et al. (1992) stated: 'the δ values [of stable nitrogen isotopes] can be treated mathematically as continuous variables, which means that the numeric difference between δ of two organisms is a measure-

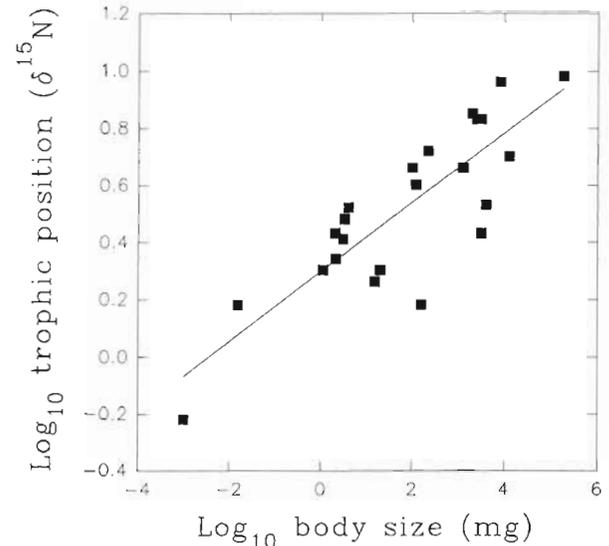


Fig. 3. Relationship of body size (as wet mass) to trophic position in the lake foodweb. Solid line indicates regression equation ($y = 0.30 + 0.12x$, $R^2 = 0.84$)

ment of the distance between their trophic levels [sic: positions]'. The general invalidity of the concept of discrete and absolute trophic levels is clearly demonstrated by the trophic cascades or ladders shown in Figs. 1 & 2. Discontinuity in the linear $\delta^{15}\text{N}$ trophic continua, indicative of broad trophic categories or guilds, occurred only towards the top of the freshwater foodweb, as for example between top predators (lake trout, slimy sculpins) and small minnows (brook sticklebacks, northern redbelly, finescale dace, common shiners), and between these small minnows and large invertebrates (dragonflies, true bugs, caddisflies). In both cases, however, the average $\delta^{15}\text{N}$ difference between these couplets of trophic categories, 2.5‰, is still less than that expected had omnivory been absent (about 3 to 4‰). Obviously, as has been found elsewhere, individual animals occupy the complete continuum or spectrum of every conceivable trophic position as reflected by their $\delta^{15}\text{N}$ values. Overall, our data therefore agree with other $\delta^{15}\text{N}$ analyses of aquatic foodwebs in supporting Darnell's (1961) early contention that 'evidently consumers exhibit a broad disregard for narrow trophic lines' as a result of 'rampant trophic opportunism' (cf. France 1998).

Strong relationships were observed between averaged trophic position and body size for organisms from the 2 taxonomically diverse foodwebs (Figs. 3 & 4). That these relationships existed, notwithstanding the many other sources of $\delta^{15}\text{N}$ variation (due to, for example, microbial influences, variable diet fractionation and nutritional conditions, intraspecific diet idiosyncrasies, subtle food source vagaries, etc.) and study

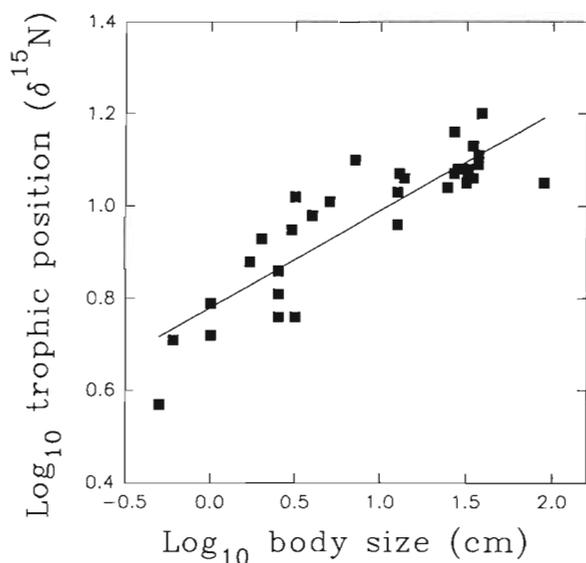


Fig. 4. Relationship of body size (as length) to trophic position in the coastal foodweb. Solid line indicates regression equation ($y = 0.77 + 0.21x$, $R^2 = 0.88$)

uncertainties (such as taxon size variabilities and measurement errors), highlights the overwhelming dominance of size-structured predation in these particular foodwebs.

An ordering of our taxa groupings into a sequential body size hierarchy as in Warren & Lawton (1987) produced foodweb matrices in which most interactions were situated above the size-equivalent diagonal in the upper triangle. The index of upper triangularity (number of non zero elements above the leading diagonal minus the number below, divided by the total number of off-diagonal non-zero elements) was 0.739 for the lake foodweb and 0.743 for the coastal foodweb, both similar to the value of 0.733 determined by Warren & Lawton (1987) for 14 invertebrate species from an acid pond community. Such size-structured feeding assemblages support Elton's (1927) early contentions about how foodwebs are structured, and, as Warren & Lawton (1987) advance, also represent the biological foundation of the stochastic 'cascade model' of Cohen & Newman (1985).

Two additional types of study are required before the generality and predictability of body size- $\delta^{15}\text{N}$ relationships can be widely accepted. First, an attempt should be made to relate the extant literature data on $\delta^{15}\text{N}$ in freshwater and marine foodwebs (France & Peters 1997, France 1998) to literature values of average body size (Peters 1983, 1988b, Peters et al. 1996). Second, a weakness of the present study is that the data groupings in Figs. 3 & 4 are still taxonomically based. A better approach would be to generate regression equations through measuring body size and $\delta^{15}\text{N}$

for each individual organism or group of pooled organisms for small animals, thereby obtaining true ataxonomic relationships. Once a corpus of such relationships is accumulated, their comparative analysis (slopes and intercepts) could provide insight into how different ecological efficiencies might influence the transfer of energy (and contaminants) along foodwebs between freshwater and marine environments, or across gradients of, for example, system productivity, latitude or terrestrial influences.

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LITERATURE CITED

- Borgmann U (1987) Models on the slope of, and biomass flow up, the biomass size spectrum. *Can J Fish Aquat Sci* 44 (Suppl 2):136-140
- Broman D, Naf C, Rolff C, Zebuhr Y, Fry B, Hobbie J (1992) Using ratios of stable nitrogen isotopes to estimate bioaccumulation and flux of polychlorinated dibenzo-p-dioxins (PCDDs) and dibenzofurans (PCDFs) in two food chains from the northern Baltic. *Environ Toxicol Chem* 11: 331-345
- Cabana G, Rasmussen JB (1994) Modelling food chain structure and contaminant bioaccumulation using stable nitrogen isotopes. *Nature* 372:255-257
- Cabana G, Rasmussen JB (1996) Comparison of aquatic food chains using nitrogen isotopes. *Proc Natl Acad Sci USA* 93:10844-10847
- Chandler M, Colarusso P, Buchsbaum R (1996) A study of eelgrass beds in Boston Harbor and northern Massachusetts bays. Office Res Develop US EPA, Narragansett, RI
- Cohen JE, Newman CM (1985) A stochastic theory of community food webs I. Models and aggregated data. *Proc R Soc Lond B* 224:421-448
- Cousins S (1987) Decline of the trophic level concept. *Trends Ecol Evol* 2:312-316
- Darnell RM (1961) Trophic spectrum of an estuarine community, based on studies of Lake Pontchartrain, Louisiana. *Ecology* 42:553-568
- del Giorgio PA, France RL (1996) Ecosystem-specific patterns in the relationship between zooplankton and POM or microplankton $\delta^{13}\text{C}$. *Limnol Oceanogr* 41:359-365
- DeNiro MJ, Epstein S (1981) Influence of diet on the distribution of nitrogen isotopes in animals. *Geochim Cosmochim Acta* 45:341-351
- Dickie LM, Kerr SR, Boudreau PR (1987) Size-dependent processes underlying regularities in ecosystem structure. *Ecol Monogr* 57:233-250
- Elton C (1927) *Animal ecology*. Sidgwick and Jackson Publ, London
- France RL (1995a) Differentiation between littoral and pelagic food webs in lakes using stable carbon isotopes. *Limnol*

- Oceanogr 40:1310–1313
- France RL (1995b) Source variability in $\delta^{15}\text{N}$ of autotrophs as a potential aid in measuring allochthony in freshwaters. *Ecography* 18:318–320
- France RL (1996a) Absence or masking of metabolic fractionations of ^{13}C in a freshwater benthic food web. *Freshwat Biol* 36:1–6
- France RL (1996b) Ontogenic shift in crayfish $\delta^{13}\text{C}$ as a measure of land-water ecotonal coupling. *Oecologia* 107: 239–242
- France RL (1996c) Stable carbon and nitrogen isotopic evidence for ecotonal coupling between boreal forests and fishes. *Ecol Freshwat Fish* 6:78–83
- France R (1998) $\delta^{15}\text{N}$ examination of the Lindeman-Hutchinson-Peters theory of increasing omnivory with trophic height in aquatic foodwebs. *Res Popul Ecol* 39:121–125
- France R (1999a) Density-weighted $\delta^{13}\text{C}$ analysis of detritivory and algivory in littoral macroinvertebrate communities of boreal headwater lakes. *Ann Zool Fenn* (in press)
- France R (1999b) Relationships between DOC concentration and epilithon stable isotopes in boreal lakes. *Freshwat Biol* (in press)
- France R, Peters R (1997) Ecosystem differences in the trophic enrichment of C-13 in aquatic foodwebs. *Can J Fish Aquat Sci* 54:1255–1258
- France RL, Steedman RJ (1996) Energy provenance for juvenile lake trout in small Canadian Shield lakes shown by stable isotopes. *Trans Am Fish Soc* 125:512–518
- France R, Westcott K, del Giorgio P, Klein G, Kalff J (1997) Vertical foodweb structure of freshwater zooplankton assemblages estimated by stable nitrogen isotopes. *Res Popul Ecol* 38:283–287
- France R, Holmquist J, Chandler M, Cattaneo A (1998) $\delta^{15}\text{N}$ evidence for nitrogen fixation associated with macroalgae from a seagrass-mangrove-coral reef system. *Mar Ecol Prog Ser* 167:297–299
- Fry B, Quinones RB (1994) Biomass spectra and stable isotope indicators of trophic level in zooplankton of the northwest Atlantic. *Mar Ecol Prog Ser* 112:201–204
- Gaedke U, Straile D, Pahl-Wostl C (1996) Trophic structure and carbon flow dynamics in the pelagic community of a large lake. In: Polis GA, Winemiller KO (eds) *Food webs, integration of patterns & dynamics*. Chapman and Hall Publ, New York, p 60–71
- Gerlach SA, Hahn AE, Schrage M (1985) Size spectra of benthic biomass and metabolism. *Mar Ecol Prog Ser* 26: 161–173
- Hansson S, Hobbie JE, Elmgren R, Larsson U, Fry B, Johansson S (1997) The stable nitrogen isotope ratio of food-web interactions and fish migration. *Ecology* 78:2249–2257
- Hecky RE, Hesslein RH (1995) Contributions of benthic algae to lake food webs as revealed by stable isotope analysis. *J N Am Benthol Soc* 14:631–653
- Hobson KA, Welch HE (1992) Determination of trophic relationships within a high Arctic marine food web using $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ analysis. *Mar Ecol Prog Ser* 84:9–18
- Hobson KA, Welch HE (1995) Cannibalism and trophic structure in a high Arctic lake: insights from stable-isotope analysis. *Can J Fish Aquat Sci* 52:1195–1201
- Kling GW, Fry B, O'Brien WJ (1992) Stable isotopes and planktonic trophic structure in arctic lakes. *Ecology* 73: 561–566
- Minagawa M, Wada E (1984) Stepwise enrichment of ^{15}N along food chains: further evidence and the relation between ^{15}N and animal age. *Geochim Cosmochim Acta* 48:1135–1140
- Morin A, Nadon D (1991) Size distribution of epilithic lotic invertebrates and implications for community metabolism. *J N Am Benthol Soc* 10:300–308
- Pahl-Wostl C (1993) Food webs and ecological networks across temporal and spatial scales. *Oikos* 66:415–432
- Peters RH (1977) The unpredictable problems of trophodynamics. *Environ Biol Fish* 2:97–101
- Peters RH (1978) Empirical physiological models of ecosystem processes. *Verh Int Verein Limnol* 20:110–118
- Peters RH (1983) *Ecological implications of body size*. Cambridge Univ Press, New York
- Peters RH (1988a) Some general problems for ecology illustrated by food web theory. *Ecology* 69:1673–1676
- Peters RH (1988b) Body size and limnology. *Atti Congr AIOL* 1-3:29–50
- Peters RH, Cabana G, Choulik O, Cohen T, Griesbach O, McCanny SJ (1996) General models for trophic fluxes in animals based on their body size. *Ecoscience* 3:365–377
- Platt T (1985) Structure of the marine ecosystem: its allometric basis. In: Ulanowicz RE, Platt T (eds) *Ecosystem theory for biological oceanography*. *Can Bull Fish Aquat Sci* 213: 55–64
- Platt T, Denman K (1978) The structure of pelagic marine ecosystems. *Rapp PV Reun Cons Int Explor Mer* 173: 60–65
- Schwinghamer P, Hargrave B, Peer D, Hawkins CM (1986) Partitioning of production and respiration among size groups of organisms in an intertidal benthic community. *Mar Ecol Prog Ser* 31:131–142
- Vander Zanden MJ, Rasmussen JB (1996) A trophic position model of pelagic food webs: impact on contaminant bioaccumulation in lake trout. *Ecol Monogr* 66:451–477
- Wada E, Terazaki M, Kabaya Y, Nemoto T (1987) ^{15}N and ^{13}C abundances in the Antarctic Ocean with emphasis on the biogeochemical structure of the food web. *Deep-Sea Res* 34:829–841
- Warren PH, Lawton JH (1987) Invertebrate predator-prey body size relationships: an explanation of upper triangularity in food webs and patterns in food web structure. *Oecologia* 74:231–235

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