FISHES AS INTEGRATORS OF BENTHIC AND PELAGIC FOOD WEBS IN LAKES

M. Jake Vander Zanden[1,3] and Yvonne Vadeboncoeur[2]

[1]*Department of Environmental Science and Policy, University of California, 1232 Wickson Hall,
One Shields Avenue, Davis, California 95616 USA*
[2]*Department of Biology, McGill University, 1205 Avenue Docteur Penfield, Montreal, Quebec H3A 1B1 Canada*

Abstract. Studies of lake ecosystems generally focus on pelagic food chains and processes. Recently, there has been an emerging recognition of the importance of benthic production and processes to whole-lake ecosystems. To examine the extent to which zoobenthos contribute to higher trophic level production in lakes, we synthesized diet data from 470 fish populations (15 species) and stable isotope data from 90 fish populations (11 species), all of which are common inhabitants of north-temperate lakes. Across all species considered, zoobenthos averaged 50% of total prey consumption. Indirect consumption of zoobenthos (i.e., feeding on zoobenthos-supported fishes) contributed another 15%, for a total of 65% reliance on benthic secondary production. Stable isotopes provided estimates of mean zoobenthivory ranging from 43% to 59%. For most fish species, consumption of zoobenthos was highly variable among populations. The overwhelming concern of ecologists with pelagic food chains and processes contrasts sharply with our finding that benthic secondary production plays a central role in supporting higher trophic level production. This extensive zoobenthivory can subsidize fish populations, leading to apparent competition and otherwise altering trophic dynamics and ecosystem processes in the pelagic zone. We argue for a more integrated view of lake ecosystems that recognizes the duality of benthic and pelagic production pathways. Food web models that explicitly consider energy flow from pelagic and benthic sources will provide a more realistic energy flow template for understanding the regulation of lake ecosystem functioning.

Key words: apparent competition; cross-chain omnivory; diet analysis; energy flow; food chain; food web; pelagic; stable isotope analysis; trophic dynamics; zoobenthos.

Introduction

Studies of ecosystems are often impeded by the fuzzy boundaries of many ecosystem types. Lakes provide useful model ecosystems because they are discrete, self-contained ecosystems with relatively well-defined boundaries, and not surprisingly, studies of lakes have played an important role in the development of ecological theory (Forbes 1925, Lindeman 1942, Carpenter et al. 1985). The dominant paradigm of limnologists and aquatic ecologists has been the study of pelagic, phytoplankton-based components of lake ecosystems, which are often modeled as simple three- or four-link food chains (McQueen et al. 1989, Hairston and Hairston 1993, Mittelbach et al. 1995). Interest in the trophic cascade hypothesis, and the potential applications to controlling lake eutrophication through food web biomanipulation, has been a primary motivation for burgeoning interest in pelagic processes (Carpenter et al. 1985, Carpenter and Kitchell 1993, Jeppesen et al. 1997).

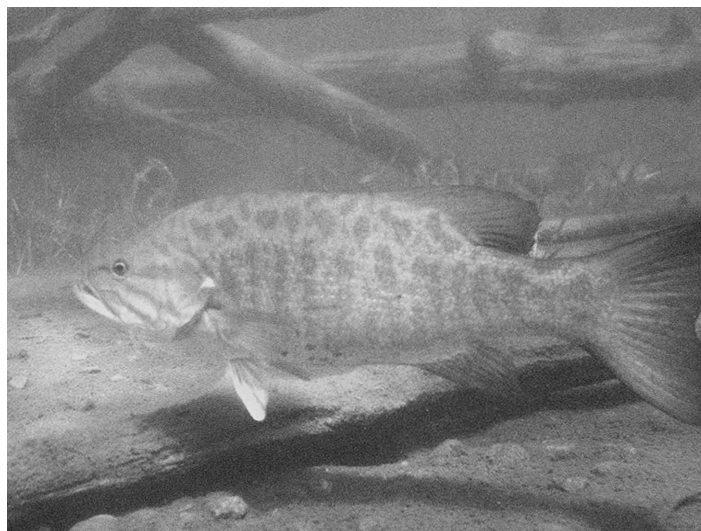It has long been recognized that benthic production can be a substantial contributor to whole-lake primary and secondary production (Forbes 1925, Lindeman 1942). Rather recently, a flurry of studies have drawn attention to the importance of benthic processes and energy flows when viewing lakes from the whole-lake perspective (Lodge et al. 1988, 1998, Hecky and Hesslein 1995, Schindler et al. 1996, Blumenshine et al. 1997, Jeppesen et al. 1997, Vadeboncoeur and Lodge 2000, Vadeboncoeur et al. 2001, 2002). Benthic and pelagic energy flows and processes can be coupled in a variety of ways (Blumenshine et al. 1997, Vadeboncoeur et al. 2002), including cross-habitat foraging by fishes. Many fishes exhibit flexible feeding habits and undergo diet shifts that deviate from their presumed food chain (Jeppesen et al. 1997). Furthermore, piscivores often forage broadly upon pelagic and benthic fishes, as well as benthic and terrestrial invertebrates, thereby linking pelagic and benthic food chains (Schindler et al. 1996, 1997). A number of food web configurations can be envisioned depending on the extent of trophic flows between littoral and pelagic food chains. At one extreme is the scenario of two unlinked food chains, indicating food chain specialization on the part of consumers. At the other extreme are closely linked food chains, in which fish consumers derive energy opportunistically from both habitats (Post et al. 2000).

How important are benthic food chains and processes to whole-lake ecosystem energetics? Can benthic and

PLATE 1. An adult smallmouth bass (*Micropterus dolomieui*) in Sparkling Lake, near Trout Lake Station, University of Wisconsin–Madison. Photograph courtesy of Brian Roth and Greg Sass.

pelagic habitats be considered separate food chains, or are these two food chains energetically linked? And if such linkages are energetically important, what are the broader implications for food web dynamics and lake ecosystem processes? This study presents a synthesis of the contributions of benthic and pelagic prey supporting fish consumers in north-temperate lakes, based on direct observation of gut contents and analysis of stable isotope ratios. The stable carbon isotope (δ^{13}C) of phytoplankton is generally isotopically depleted relative to benthic algae due to differences in isotopic discrimination for dissolved inorganic carbon (DIC) (Hecky and Hesslein 1995). δ^{13}C values tend to be conserved from prey to predator and can thus be used to infer energy sources (France 1995, Vander Zanden and Rasmussen 1999). If the δ^{13}C of benthic and pelagic prey are known, simple two-source mixing models can provide estimates of the contributions of the two prey items to consumers.

These two methods differ in that diet data reflect direct consumption, while stable isotopes reflect prey assimilation. Furthermore, a diet sample provides only a snapshot of fish feeding, and temporal variation in diet is often not adequately considered. We compensated for this limitation by relying on diet data from large numbers of fish populations. Stable isotope analysis provides a more time-integrated indication of energy provenance, but cannot detect the use of profundal (deepwater) zoobenthos because they have δ^{13}C signatures that reflect their diet of settling phytoplankton (Vander Zanden and Rasmussen 1999). While the two methods have different strengths and weaknesses, use of the two methods together provides a robust analysis. By using these two independent methods from a broad range of species and lake ecosystems, we can make generalizations about the importance of zoobenthic production from the whole-lake context of fish consumption. If benthic energy flows are substantial from

this perspective, this would indicate important consequences for our understanding of the variability of ecosystem processes and dynamics.

METHODS

Dietary analysis

Previous studies (Vander Zanden and Rasmussen 1996, Vander Zanden et al. 1997) summarized quantitative volumetric dietary data for adults of 16 fish species from 542 individual populations (lake–year combinations). The species considered are common and abundant native residents of north-temperate lakes of North America, although many of these species are found in other regions of North America. We eliminated data from river populations and also eliminated data for ninespine stickleback and trout-perch due to the small sample sizes (two and five populations, respectively). Our modified data set consisted of dietary data for 146 895 fish from 470 fish populations. Reliance on zoobenthos was examined as a function of consumer trophic position in the food web. Whereas trophic levels are discrete categories that assume that species have inflexible diet habits within and among populations, trophic position is a continuous variable that accounts for the tendency of fish to feed omnivorously (on prey with a variety of trophic positions). Mean (species-specific) trophic position values were taken directly from Vander Zanden and Rasmussen (1996) and Vander Zanden et al. (1997).

The original dietary data were simplified to represent the contributions of benthic and pelagic prey. Detritus made up <1.5% of the total diet of littoral species (pumpkinseed, perch, rock bass, smallmouth bass, largemouth bass, northern pike, and walleye) and was included in the zoobenthos category. In the few published studies in which terrestrial and aquatic insect prey were not differentiated, we assumed that the in-

TABLE 1. Summary diet data for 13 lacustrine fish species (expressed as mean percentage of gut volume or mass).

Species	Latin name	Species code	Habitat	No. populations	No. fish
Pumpkinseed	*Lepomis gibbosus*	pu	L	24	1778
Yellow perch	*Perca flavescens*	per	L	90	7377
Rock bass	*Ambloplites rupestris*	rb	L	24	1652
Smallmouth bass	*Micropterus dolomieui*	smb	L	74	2819
Largemouth bass	*Micropterus salmoides*	lmb	L	21	5664
Northern pike	*Esox lucius*	np	L	51	32 193
Walleye	*Stizostedion vitreum*	wal	L	20	8369
Alewife	*Alosa pseudoharengus*	ale	P	7	5117
Lake cisco	*Coregonus artedii*	cis	P	25	12 836
Sculpins	*Cottus* sp.	scu	P	10	3537
Rainbow smelt	*Omerus mordax*	sme	P	17	15 315
Whitefishes	*Coregonus clupeaformis*†	whi	P	37	5969
Lake trout	*Salvelinus namaycush*	lt	P	70	44 269
Total				470	146 895
Means					

Notes: Data were adapted from Vander Zanden and Rasmussen (1996) and Vander Zanden et al. (1997). Habitat indicates either littoral (L) or pelagic-profundal (P). ''Indirect zoobenthos'' represents the consumption of fishes that were themselves supported by zoobenthos.

† Includes *Prosopium* sp.

sects were primarily aquatic and classified them as ''zoobenthos'' (but see Hunt 1975). For the littoral species, the prey category ''others'' consisted of prey items that were either unidentified in the original study or those that did not fit into the broad prey categories used in Vander Zanden et al. (1997). The ''others'' prey category averaged <5% of total diet. We eliminated this prey category and scaled the remaining values to sum to 100%. Overall, prey items were easily assigned to prey categories, and the few assumptions we had to make had little effect on our conclusions.

In addition to direct consumption of zoobenthos, we also estimated indirect reliance on zoobenthos. Indirect zoobenthivory represents the consumption of prey fish that were, to some degree, supported by zoobenthos. The proportion of the ''fish'' component of the diet of piscivore j supported by zoobenthos (Z) was estimated as

$$Z_j = \sum (P_i \times B_i) \qquad (1)$$

where P_i is the proportional contribution of the ith prey fish species to the ''fish'' component of the diet of piscivore j and B_i is the proportional contribution of zoobenthos to the ith prey fish species. The value from Eq. 1 is multiplied by the contribution of fish to the total diet and added to the direct zoobenthivory value, which gives total zoobenthivory (direct and indirect). For three of the most piscivorous species (lake trout, walleye, and northern pike), we were able to resolve the ''fish'' component of their diet for a subset of the populations (Vander Zanden and Rasmussen 1996, Vander Zanden et al. 1997). Some of the fish species occurring in the diets of these piscivores were already included in the present study (rainbow smelt, cisco, whitefish, sculpin, trout-perch). We used additional di-

etary data from the literature to estimate zoobenthivory for prey fishes not included in our data set (see the Appendix). For lake trout, northern pike, and walleye, >50% of the consumed prey fish was supported by zoobenthos. Data were not available to resolve the ''fish'' component of the diets of other partially piscivorous fishes (smallmouth bass, rock bass, largemouth bass), thus we used a conservative estimate of 50% benthivory for their prey.

Stable isotopes

Stable carbon and nitrogen isotope ($\delta^{13}C$ and $\delta^{15}N$) information for fishes and invertebrates from 18 lakes in Ontario and Quebec form the basis for our $\delta^{13}C$ mixing models (Vander Zanden and Rasmussen 1999, Vander Zanden et al. 1999*a, b*). For each lake, we estimated $\delta^{13}C$ endpoints for pelagic (the mean zooplankton and unionid mussel isotopic values) and littoral (mean of all benthic-feeding littoral invertebrates) habitats for use as end members in two-source mixing models. The contributions of littoral secondary production to consumer populations was estimated using the formula

percentage contribution of littoral

$$= (\delta^{13}C_c - \delta^{13}C_p)/(\delta^{13}C_l - \delta^{13}C_p) \qquad (2)$$

where $\delta^{13}C_c$, $\delta^{13}C_l$, and $\delta^{13}C_p$ are the mean $\delta^{13}C$ of the consumer, littoral prey, and pelagic prey, respectively. Note that the model uses primary consumers (rather than primary producers) as isotopic endpoints and thus estimates the contributions of pelagic and benthic *secondary* production. Our mixing model assumed no trophic enrichment in $\delta^{13}C$ (trophic fractionation = 0‰).

TABLE 1.   Extended.

Zoo-plankton	Fish	Indirect zoobenthos	Direct zoobenthos	SD	CV	Direct and indirect zoobenthos	SD	CV
1	0	0	99	2	2	99	2	2
14	18	9	68	26	39	77	21	28
3	11	5	86	14	16	91	11	12
2	41	20	57	33	59	77	17	22
6	58	29	36	28	77	65	14	21
0	86	46	14	21	190	61	16	28
2	84	45	14	17	121	58	18	30
73	5	1	22	22	93	23	22	86
85	0	0	15	19	113	15	19	112
11	1	1	89	20	23	89	20	23
45	33	11	22	17	79	32	19	52
12	3	2	86	21	24	88	20	23
8	75	36	17	25	147	53	20	37
20%	32%	16%	48%			64%		

An alternative model assumed a $\delta^{13}C$ trophic enrichment of 1‰ over that of primary consumers. These two assumptions bracket the observed range of $\delta^{13}C$ trophic fractionation. The estimates used in this study assumed no fractionation, based on field fractionation estimates from three of the study lakes (Vander Zanden and Rasmussen 2001). If the $\delta^{13}C$ value of the consumer population fell beyond either end member in the mixing model (indicating >100% benthic reliance or <0% benthic reliance), values were set at either 100% or 0%. This occurred in 20% of the 90 fish populations included here. We calculated the mean $\delta^{13}C$ for each fish population and then calculated the species-specific $\delta^{13}C$ (the mean for all populations of a species). Final mixing models used the species-specific values so that the mean $\delta^{13}C$ values shown in Table 2 are the values used in the mixing model. Whether the mixing model was conducted at the level of the individual fish, population, or species did not alter the findings.

The stable isotope method provides an estimate of the contribution of littoral-derived secondary production, but does not include profundal zoobenthos. Thus, stable isotopes tend to underestimate the overall contribution of zoobenthos. Because our mixing model does not incorporate profundal zoobenthos, we did not include profundal-feeding fishes in our comparisons of estimates based on diets and stable isotopes.

RESULTS

Diet analysis

Across all fish species, zooplankton comprised 20% of the total diet, zoobenthos comprised 48%, and fish contributed 32% (percent of gut content, by mass or volume; Table 1). Consumption of zoobenthos was highly variable among species, with species-specific means ranging from 99% for pumpkinseed (a littoral benthivore) to 15% for cisco (a pelagic planktivore) and 14% for walleye (a piscivore).

In addition to feeding directly on zoobenthos, piscivores rely indirectly on zoobenthos because the prey fish consumed by piscivores are partially supported by zoobenthos. We estimated that the prey fish consumed by pike, walleye, and lake trout were supported by 54%, 53%, and 48% zoobenthos, respectively. Indirect reliance on zoobenthos was >35% of total prey consumption for piscivorous species (pike, walleye, and lake trout). Total benthivory, the sum of direct and indirect reliance on zoobenthos, averaged 64% of total consumption. The remaining 36% represents reliance on pelagic-based prey (20% direct and 16% indirect).

The positioning of fish along a benthic–pelagic gradient varied among populations of a given species (Fig. 1). Rock bass and pumpkinseed were the most consistently benthivorous species. Smallmouth bass, yellow perch, and largemouth bass exhibit broad distributions of benthivory, indicating high trophic flexibility for these species. Only a few populations of pike and walleye directly consumed large proportions of zoobenthos, although indirect reliance on zoobenthos was generally high for both species (46 ± 15.5% and 45 ± 11.5%, means ± 1 SD, respectively). Among pelagic fishes, benthivory was less variable than for littoral fishes. Most populations of alewife, smelt, and cisco exhibited minor reliance on zoobenthos (<20%), although there were exceptions for each species. Whitefish and sculpins were generally benthivores, although certain populations relied on non-benthic prey to varying degrees. Lake trout tend to be piscivores (Table 2), although select populations relied on zoobenthos. Lake area data were available only for lake trout populations (Vander Zanden and Rasmussen 1996). Lake trout from large lakes (>10 km²) did not consume zoobenthos, while lake trout from small lakes (<10 km²) exhibited variable and often substantial consumption of zoobenthos (Fig. 2).
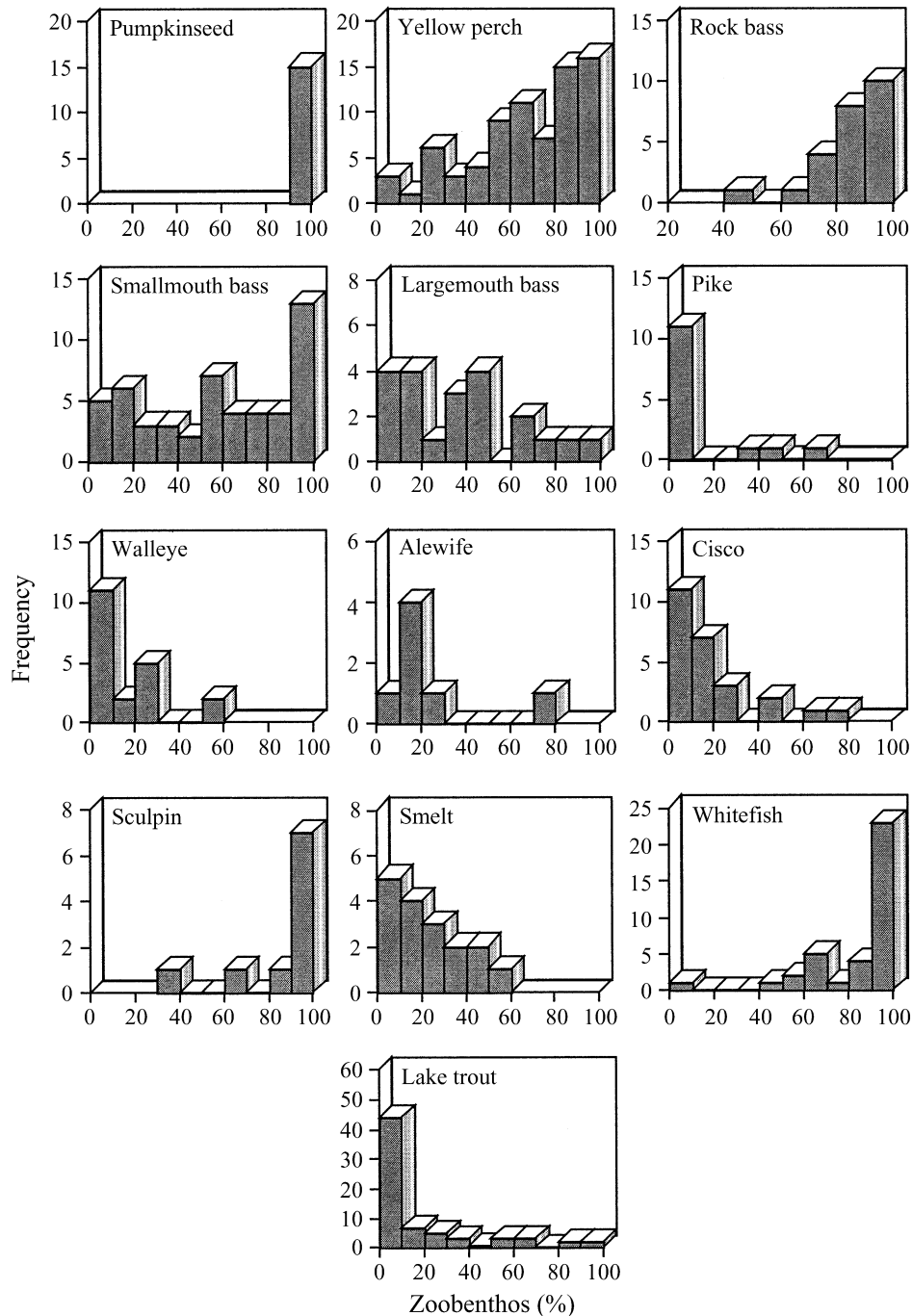
FIG. 1.   Frequency histograms showing the among-population variation in direct zoobenthivory (percentage of zoo-benthos in diet) for 13 fish species from north-temperate lakes of North America. The indirect use of zoobenthos is not included.

Stable isotopes

Our estimate of the mean contribution of littoral carbon, as estimated using $\delta^{13}C$ mixing models, ranged from 43% (assuming trophic enrichment of 1‰) to 59% (assuming no trophic fractionation; Table 2). Littoral reliance was lowest for open-water pelagic species such as smelt and cisco. Littoral zone fishes (yellow perch, northern pike, pumpkinseed, smallmouth bass, rock bass, and cyprinids) relied on at least 70% littoral-derived carbon. Estimates for whitefish and slimy sculpins indicated partial reliance on littoral carbon. These two benthivores are likely to forage in profundal and littoral habitats (Scott and Crossman 1973). As a result,

TABLE 2. Summary of mean stable carbon isotope data ($\delta^{13}C$) and mixing model results for 11 species of freshwater fish.

Species	Habitat	No. populations	No. fish	$\delta^{13}C$ littoral	$\delta^{13}C$ pelagic	$\delta^{13}C$ fish	Percentage of littoral reliance†	Percentage of littoral reliance‡
Pumpkinseed	L	9	14	−24.4	−29.4	−24.5	98	78
Yellow perch	L	12	36	−23.7	−28.8	−25.1	72	52
Rock bass	L	6	28	−24.1	−29.1	−23.4	100	92
Smallmouth bass	L	11	27	−23.5	−29.1	−23.4	100	84
Northern pike	L	1	2	−23.2	−29.0	−24.7	74	57
Minnows (cyprinids)	L	11	63	−24.6	−29.6	−25.5	82	62
Lake cisco	P	6	29	−22.1	−28.1	−27.8	6	0
Sculpins	P	5	18	−23.6	−28.8	−27.4	26	7
Rainbow smelt	P	4	16	−22.8	−28.2	−27.6	12	0
Whitefishes	P	8	34	−23.1	−28.9	−26.2	46	29
Lake trout	P	17	419	−23.9	−29.2	−27.7	29	10
Total		90	686					
Means							59%	43%

Notes: The habitat variable indicates either littoral (L) or pelagic-profundal (P). Values for $\delta^{13}C$ littoral, $\delta^{13}C$ pelagic and $\delta^{13}C$ fish are the mean of lake-specific means. Mixing models are described in *Methods: Stable isotopes*.
   † The mixing model assumes trophic fractionation of 0‰.
   ‡ The mixing model assumes trophic fractionation of 1‰.

estimation of zoobenthivory for these species using $\delta^{13}C$ mixing models is confounded because pelagic and benthic-profundal invertebrates have similar $\delta^{13}C$ values.

Comparison of two techniques

Species-specific estimates of zoobenthivory from diet data were closely correlated with isotope-based estimates of littoral carbon reliance (fractionation = 0‰; excluding sculpins and whitefish; percentage of littoral carbon = 0.98 × percentage of zoobenthos + 0.78; r^2 = 0.76). Frequency histograms of zoobenthivory based on diet data (Fig. 3A) and reliance on littoral carbon derived from stable isotopes (Fig. 3B) indicate that most fish populations were supported by a

mix of littoral and pelagic prey. For both techniques, χ^2 tests indicate significantly higher frequency of observations in the 0–10% and 90–100% zoobenthic categories ($\delta^{13}C$, χ^2 = 84.6, P = 4.9 × 10^{-30}; diet, χ^2 = 17.1, P = 3.5 × 10^{-5}), indicating a tendency for fish populations to specialize on either benthic or pelagic prey (Fig. 3).

Summary food web diagrams

Dietary and energy flow information is compiled into summary food web diagrams with the benthic–pelagic gradient on the horizontal axis and mean trophic position on the vertical axis (Fig. 4). Species with low trophic position (non-piscivores) spanned the entire range of benthivory, showing a tendency to cluster at the outer edges of the littoral–pelagic gradient. When direct consumption of zoobenthos is considered, piscivores are positioned at the upper left corner, indicating little direct reliance on zoobenthos (Fig. 4A). When both direct and indirect benthivory are considered, piscivores are positioned in the apex position (upper center) of the diagram, indicating that piscivores are supported by a mix of pelagic and benthic secondary production (Fig. 4B). The equivalent diagram based on stable isotope information suggests that littoral and pelagic food chains are less tightly coupled by the foraging of piscivorous fishes (Fig. 4C). While cross-chain omnivory is still evident, benthic and pelagic food chains do not converge at the apex of the food web, indicating that top predators do not fully integrate across littoral and pelagic food chains and habitats.
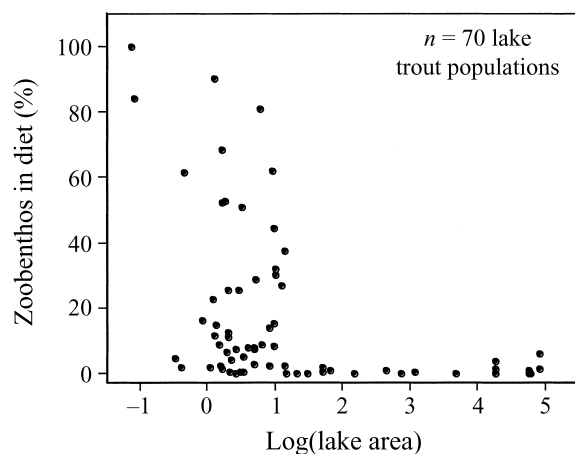

FIG. 2. Lake trout benthivory (percentage of zoobenthos in diet) vs. lake area (measured in square kilometers) in Canadian lakes. Data were taken from Vander Zanden and Rasmussen (1996).
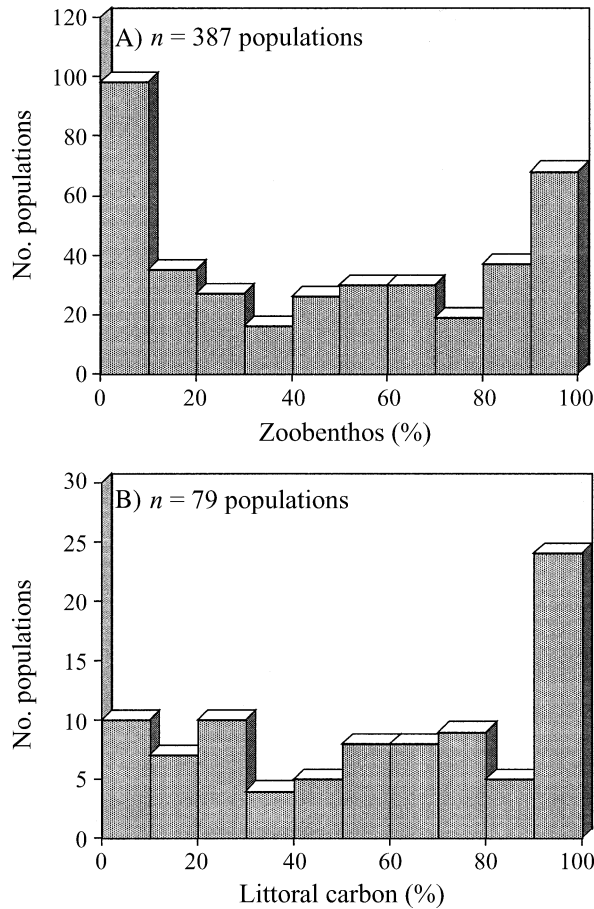
DISCUSSION

Both stable isotopes and diet-based evidence indicate that benthic energy pathways account for more than

FIG. 3. Frequency histograms of zoobenthivory across all populations: (A) direct use of zoobenthos based on gut content data; (B) the δ¹³C-based estimates of reliance on littoral carbon.

ferences in zoobenthivory result from a combination of both abiotic and biotic factors. Lake size and lake basin morphometry determine the relative importance of littoral habitat and the potential for zoobenthos to contribute to whole-lake secondary production (Fig. 2). Large lakes tend to have lower perimeter-to-area ratios (P/A), thereby diminishing the relative importance of
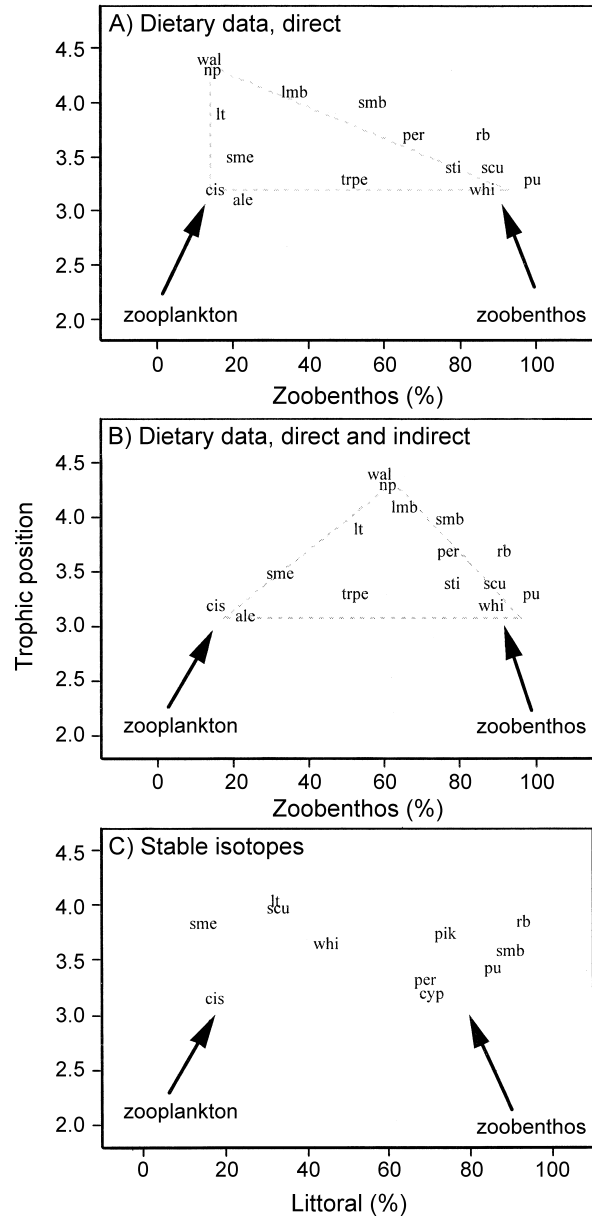

FIG. 4. Generalized food web diagrams based on dietary data representing mean trophic position and zoobenthivory (mean percentage of zoobenthos in diet): (A) direct consumption of zoobenthos by fish; (B) direct and indirect reliance on zoobenthos; (C) littoral reliance, as estimated using stable isotopes. Species abbreviations are shown in Table 1; cyp = cyprinids; sti = ninespine stickleback, trpe = trout-perch.

half of total fish consumption and that this pattern is a general feature among fishes common to north-temperate lakes of North America. Even species that are generally thought of as pelagic were partially supported by zoobenthos, indicating cross-chain omnivory (sensu Polis and Strong 1996) and trophic coupling between benthic and pelagic food chains. Furthermore, our analysis did not include detritivorous or phytobenthivorous fishes (i.e., gizzard shad) and other species typical of warm-water lakes and reservoirs of the southern United States and tropical areas, where reliance on benthic matter is expected to be even higher than for north-temperate fishes. For these reasons, our estimates based on north-temperate lakes probably provide a conservative assessment of the contributions of zoobenthos to higher trophic levels in lakes.

While zoobenthos are an important resource supporting a diversity of lacustrine fishes, reliance on zoobenthos varied widely among species (Table 1). Reliance of zoobenthos also varied among populations of a given species (Fig. 1). These population-level dif-

benthic and littoral habitats, compared to small lakes in which littoral habitats are often dominant (Gasith 1991, Fee and Hecky 1992). Large lakes also tend to be deeper than small lakes, further reducing the potential contribution of benthic and littoral habitats. Considering that the majority of lakes globally are small and shallow with high proportions of littoral habitat (Wetzel 1990), the central role of benthic and littoral production documented here is probably characteristic of a majority of lakes worldwide.

Both lines of evidence indicate that fish forage broadly across littoral and pelagic food chains (Figs. 1 and 3), but diet analysis indicates a more complete trophic coupling than stable isotope evidence (Fig. 4). There are a number of potential reasons for this difference. While diet study lakes spanned a broad geographic area and a range of size, productivity, and morphometry, stable isotope data are from 17 lakes in central Ontario, all of which were relatively similar in community composition, productivity, and morphometry. Furthermore, pike and walleye were poorly represented in the stable isotope study. Diet analysis indicates that these two species occupy the highest trophic positions and fully integrate benthic and pelagic food webs. Their absence in the isotope study may have served to artificially truncate the lake food webs. Alternatively, the inability of stable carbon isotopes to differentiate between pelagic and profundal prey may also explain why diet analysis indicates a more complete trophic coupling between pelagic and benthic food chains.

Ecosystem energetics and benthic–pelagic coupling

The heavy reliance of a variety of lacustrine fishes on benthic secondary production suggests a central role of benthic production in whole-lake ecosystem processes and a strong potential for dynamic coupling between benthic and pelagic food chains. A similar point was argued by Hecky and Hesslein (1995), who provided stable isotope evidence that benthic algae is a major contributor to fish production in lakes throughout the world. Omnivorous fishes are just one of many vectors that can link benthic and pelagic components of lake ecosystems, and a general view of lake ecosystems that incorporates both benthic and pelagic systems is coalescing (Lodge et al. 1988, 1998, Stein et al. 1995, Schindler et al. 1996, Vadeboncoeur et al. 2001, 2002). This newly emerging view of lake ecosystems stems from a growing realization that quantifying energy flow pathways serves as a necessary scaffold for studies of food web dynamics and interactions and the recognition that allocthonous energy inputs can greatly affect trophic dynamics and trophic cascades (Polis 1994, 1999, Polis and Strong 1996). This emerging picture of lake ecosystems contrasts sharply with the dominant view of lake ecosystems as comprised of a linear pelagic food chain consisting of either three or four discrete trophic levels (McQueen et al. 1986, 1989, Hairston and Hairston 1993, 1997).

Potential consequences of benthic–pelagic linkages

While models of trophic dynamics must rely on simplified renditions of food web structure, energy flows across traditionally defined habitat boundaries can have important consequences for food web dynamics (Winemiller 1990, Polis and Strong 1996, Polis et al. 1997). In some instances, the implications of benthic-pelagic linkages have been considered. For example, the excretion of nutrients by benthivorous fishes can represent a significant flux of new nutrients available to phytoplankton (Carpenter et al. 1992, Schindler et al. 1993, 1996, Vanni 1996). There has also been some suggestion that feeding on zoobenthos and detritus might subsidize food chain dynamics and trophic cascades in the pelagic zone (Stein et al. 1995, Schindler et al. 1996, Jeppesen et al. 1997). A few lake ecosystem models have incorporated energy flows from zoobenthos into the pelagic food chain (Carpenter 1988).

The importance of benthic energy flow in lakes may appear to contradict studies that have demonstrated top-down control in pelagic food chains (Brooks and Dodson 1965, Carpenter et al. 1985). On the contrary, the flow of energy from zoobenthos to the pelagic food chain may play an important role in mediating the pattern and magnitude of top-down food web regulation. Energy flow from sources external to the "focal" food chain can increase top-down control through phenomena such as apparent competition (Holt 1977, 1984, Polis and Strong 1996, Polis et al. 1997, Polis 1999). In fact, it has been argued that "consumers that exert strong cascading effects within a particular plant–herbivore food chain are almost always deeply subsidized by resources from many sources or channels outside this focal chain" (Polis 1999:10). Indeed, a consumer population that is subsidized by allocthonous energy sources may more effectively regulate prey populations in the focal food chain. An alternative scenario is that consumption of prey from outside of the focal food chain may weaken top-down regulation, because top-down impacts on the focal chain become more diffuse as the predator diet is diversified. Which scenario prevails depends on a number of factors, including the extent to which the predator is food limited, which trophic levels are subsidized, and the extent to which the predator selectively feeds on prey from the "focal" food chain. In either case, explicit consideration of energy flows from benthic trophic pathways will improve our understanding and prediction of pelagic trophic dynamics and stability in lake ecosystems (Schindler et al. 1996, Post et al. 2000). Such consideration may explain why lake biomanipulation sometimes produces unexpected results, such as the inability of piscivores to control planktivore populations where planktivores

are heavily subsidized by zoobenthos (Jeppesen et al. 1997).

SUMMARY

The predominant view of lake ecosystems has been that of pelagic food chains with simple, linear trophic architectures. There is an emerging realization of the importance of benthic processes and pathways within a broader, whole-lake context: the present analysis provides strong empirical support for this view of lake ecosystems. The study of trophic cascades has unified fisheries biology and limnology, providing a more holistic view of lake ecosystems. Recognition of the duality of pelagic and benthic production pathways, which are closely linked by mobile consumers such as fishes, will provide an enhanced energetic template for understanding lake trophic dynamics. This view reflects a shift towards a more integrated, whole-ecosystem perspective of lakes that considers the quantification of energetic flows as a precursor to an understanding of food web dynamics and lake ecosystem functioning.

ACKNOWLEDGMENTS

LITERATURE CITED

Blumenshine, S. C., Y. Vadeboncoeur, D. M. Lodge, K. L. Cottingham, and S. E. Knight. 1997. Benthic-pelagic links: responses of benthos to water-column nutrient enrichment. Journal of the North American Benthological Society **16**: 466–479.

Brooks, J. L., and S. I. Dodson. 1965. Predation, body size, and composition of plankton. Science **150**:28–35.

Carpenter, S. R. 1988. Transmission of variance through lake food webs. Pages 119–135 in S. R. Carpenter, editor. Complex interactions in lake communities. Springer-Verlag, New York, New York, USA.

Carpenter, S. R., and J. F. Kitchell. 1993. The trophic cascade in lakes. Cambridge University Press, Cambridge, UK.

Carpenter, S. R., J. F. Kitchell, and J. R. Hodgson. 1985. Cascading trophic interactions and lake productivity. BioScience **35**:634–639.

Carpenter, S. R., C. E. Kraft, R. Wright, X. He, P. A. Soranno, and J. R. Hodgson. 1992. Resilience and resistance of a lake phosphorus cycle before and after food web manipulation. American Naturalist **140**:781–798.

Fee, E. J., and R. E. Hecky. 1992. Introduction to the Northwest Ontario lake size series (NOLSS). Canadian Journal of Fisheries and Aquatic Sciences **49**:2434–2444.

Forbes, S. A. 1925. The lake as a microcosm. Bulletin of the Illinois Natural History Survey **15**:537–550.

France, R. L. 1995. Differentiation between littoral and pelagic foodwebs in lakes using stable carbon isotopes. Limnology and Oceanography **40**:1310–1313.

Gasith, A. 1991. Can littoral resources influence ecosystem processes in large, deep lakes? Internationale Vereinigung für Theoretische und Angewandte Limnologie **24**:1073–1076.

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., Jr., and N. G. Hairston, Sr. 1997. Does food web complexity eliminate trophic-level dynamics? American Naturalist **149**:1001–1007.

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.

Holt, R. D. 1977. Predation, apparent competition, and the structure of prey communities. Theoretical Population Biology **12**:197–229.

Holt, R. D. 1984. Spatial heterogeneity, indirect interactions, and the coexistence of prey species. American Naturalist **124**:377–406.

Hunt, R. L. 1975. Use of terrestrial invertebrates as food by salmonids. Pages 137–151 in A. D. Hasler, editor. Coupling of land and water systems. Springer-Verlag, New York, New York, USA.

Jeppesen, E., J. P. Jensen, M. Sondergaard, T. Lauridsen, L. J. Pedersen, and L. Jensen. 1997. Top-down control in freshwater lakes: the role of nutrient state, submerged macrophytes and water depth. Hydrobiologia **342/343**:151–164.

Lindeman, R. L. 1942. The trophic-dynamic aspect of ecology. Ecology **23**:399–418.

Lodge, D. M., J. W. Barko, D. Strayer, J. M. Melack, G. G. Mittelbach, R. W. Howarth, B. Menge, and J. E. Titus. 1988. Spatial heterogeneity and habitat interactions in lake communities. Pages 181–208 in S. R. Carpenter, editor. Complex interactions in lake communities. Springer-Verlag, New York, New York, USA.

Lodge, D. M., S. C. Blumenshine, and Y. Vadeboncoeur. 1998. Insights and application of large scale, long-term ecological observations and experiments. Pages 181–208 in W. J. Resetarits and J. Bernardo, editors. Experimental ecology: issues and perspectives. Oxford University Press, Oxford, UK.

McQueen, D. J., M. R. S. Johannes, J. R. Post, T. J. Stewart, and D. R. S. Lean. 1989. Bottom-up and top-down impacts on freshwater pelagic community structure. Ecological Monographs **59**:289–309.

McQueen, D. J., J. R. Post, and E. L. Mills. 1986. Trophic relationships in freshwater pelagic ecosystems. Canadian Journal of Fisheries and Aquatic Sciences **43**:1571–1581.

Mittelbach, G. G., A. M. Turner, D. J. Hall, J. E. Rettig, and C. W. Osenberg. 1995. Perturbation and resilience: a long-term, whole-lake study of predator extinction and reintroduction. Ecology **76**:2347–2360.

Polis, G. A. 1994. Food webs, trophic cascades and community structure. Australian Journal of Ecology **19**:121–136.

Polis, G. A. 1999. Why are parts of the world green? Multiple factors control productivity and the distribution of biomass. Oikos **86**:3–15.

Polis, G. A., W. B. Anderson, and R. D. Holt. 1997. Toward an integration of landscape and food web ecology: the dynamics of spatially subsidized food web. Annual Review of Ecology and Systematics **28**:289–316.

Polis, G. A., and D. R. Strong. 1996. Food web complexity and community dynamics. American Naturalist **147**:813–846.

Post, D. M., M. E. Conners, and D. S. Goldberg. 2000. Prey preference by a top predator and the stability of linked food chains. Ecology **81**:8–14.

Schindler, D. E., S. R. Carpenter, K. L. Cottingham, X. He, J. R. Hodgson, J. F. Kitchell, and P. A. Soranno. 1996. Food web structure and littoral zone coupling to pelagic trophic cascades. Pages 95–105 in G. A. Polis and K. O.

Winemiller, editors. Food webs: integration of patterns and dynamics. Chapman and Hall, New York, New York, USA.

Schindler, D. E., J. R. Hodgson, and J. F. Kitchell. 1997. Density-dependent changes in individual foraging specialization of largemouth bass. Oecologia **110**:592–600.

Schindler, D. E., J. F. Kitchell, X. He, S. R. Carpenter, J. R. Hodgson, and K. L. Cottingham. 1993. Food web structure and phosphorus cycling in lakes. Transactions of the American Fisheries Society **122**:756–772.

Scott, W. B., and E. J. Crossman. 1973. Freshwater fishes of Canada. Bulletin of the Fisheries Research Board of Canada number 184.

Stein, R. A., D. R. DeVries, and J. M. Dettmers. 1995. Food-web regulation by a planktivore: exploring the generality of the trophic cascade hypothesis. Canadian Journal of Fisheries and Aquatic Sciences **52**:2518–2526.

Vadeboncoeur, Y., and D. M. Lodge. 2000. Periphyton production on wood and sediment: substratum-specific response to laboratory and whole-lake nutrient manipulations. Journal of the North American Benthological Society **19**:68–81.

Vadeboncoeur, Y., D. M. Lodge, and S. R. Carpenter. 2001. Whole-lake fertilization effects on distribution of primary production between benthic and pelagic habitats. Ecology **82**:1065–1077.

Vadeboncoeur, Y., M. J. Vander Zanden, and D. M. Lodge. 2002. Putting the lake back together: reintegrating benthic pathways into lake food webs. BioScience **52**:44–54.

Vander Zanden, M. J., G. Cabana, and J. B. Rasmussen. 1997. Comparing the trophic position of littoral fish estimated using stable nitrogen isotopes (δ^{15}N) and dietary data. Ca-

nadian Journal of Fisheries and Aquatic Sciences **54**:1142–1158.

Vander Zanden, M. J., J. M. Casselman, and J. B. Rasmussen. 1999a. Stable isotope evidence for the food web consequences of species invasions in lakes. Nature **401**: 464–467.

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.

Vander Zanden, M. J., and J. B. Rasmussen. 1999. Primary consumer δ^{15}N and δ^{13}C and the trophic position of aquatic consumers. Ecology **80**:1395–1404.

Vander Zanden, M. J., and J. B. Rasmussen. 2001. Variation in δ^{15}N and δ^{13}C trophic fractionation: implications for aquatic food web studies. Limnology and Oceanography **46**:2061–2066.

Vander Zanden, M. J., B. J. Shuter, N. P. Lester, and J. B. Rasmussen. 1999b. Patterns of food chain length in lakes: a stable isotope study. American Naturalist **154**: 406–416.

Vanni, M. J. 1996. Nutrient transport and recycling by consumers in lake food webs: implications for algal communities. Pages 81–95 *in* G. A. Polis and K. O. Winemiller, editors. Food webs: integration of patterns and dynamics. Chapman and Hall, New York, New York, USA.

Wetzel, R. G. 1990. Land-water interfaces: metabolic and limnological regulators. Internationale Vereinigung für Theoretische und Angewandte Limnologie **24**:6–24.

Winemiller, K. O. 1990. Spatial and temporal variation in tropical fish trophic networks. Ecological Monographs **60**: 331–367.

APPENDIX

A table presenting mean zoobenthivory (as a percentage of gut content volume) of prey fish species consumed by piscivores is available in ESA's Electronic Data Archive: *Ecological Archives* E083-039-A1.