

Primary Research Paper

## Trophic ecology of the Lake Superior wave zone: a stable isotope approach

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### Abstract

Stable carbon and nitrogen isotope ratio analyses were used to characterize the primary energy sources and trophic positions of 16 common Lake Superior wave zone invertebrate species. Isotope data from six tributary species that were taxonomically and ecologically matched with common wave zone species revealed broad energetic separation between these similarly structured benthic food webs. Previously published stable isotope data for Lake Superior wetland and pelagic food webs were used to assess the relative importance of inter-habitat energy flow within the Lake Superior ecosystem. The results of these comparisons indicate that the Lake Superior wave zone is energetically distinct from its tributaries, wetlands, and to a lesser extent from its vast pelagic realm. This information and approach should prove useful in future studies on the bioenergetics of inter-zonal migrants and other species that forage in multiple habitats within the lake and also in revealing energetic connections among terrestrial, riverine, littoral, and pelagic food webs in the coastal ecosystems of Lake Superior.

### Introduction

The benthic habitat along the wave-swept shoreline of Lake Superior has a distinct riverine quality imparted by strong currents and nearly constant exposure to wave action. The lotic nature of this 'wave zone' presumably explains why benthic invertebrate communities in Lake Superior and other large lake littoral zones characteristically include wave zone specialists diverged from predominantly lotic lineages and populations of species that more commonly occur in streams (Barton & Hynes, 1978; Barton & Smith, 1984). Although very little is known about wave zone trophic ecology, the presence of species with lotic tendencies indicates that foraging strategies similar to those in streams can also be employed in wave zones, e.g., scraping epilithic algae from rock surfaces. Wave zone invertebrate communities also include many lentic species (Barton & Hynes, 1978) including some with apparent energetic ties

to pelagic habitat, e.g., through consumption of settled phytoplankton cells. Thus, it appears that invertebrates with lotic attributes interact with lentic specialists in wave zone food webs to couple carbon flows from benthic and pelagic producers.

Due to benthic boundary layer influences on carbon acquisition conditions, benthic primary producers in littoral zones typically utilize more heavy isotopic carbon ( $^{13}\text{C}$ ) than their pelagic counterparts (France, 1995). This phenomenon makes it possible to use stable carbon isotope ratio analysis ( $^{13}\text{C}/^{12}\text{C}$  or  $\delta^{13}\text{C}$ ) to distinguish between littoral and pelagic carbon flows in lentic food webs (France, 1995; Yoshii, 1999; James et al., 2000). By combining  $\delta^{13}\text{C}$  analysis with stable nitrogen isotope ratio analysis ( $^{15}\text{N}/^{14}\text{N}$  or  $\delta^{15}\text{N}$ ), which can be used to reveal trophic structuring in food webs (Kling et al., 1992; Cabana & Rasmussen, 1994), it is possible to simultaneously compare the trophic structures of aquatic communities and detect energetic exchange among

interconnected aquatic habitats (Keough et al., 1996; Yoshii, 1999; France & Schlaepfer, 2000).

The objective of this study was to use  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  analyses to characterize the primary energy sources and trophic positions of representatives of 16 benthic invertebrate species collected from wave zone sites along the south-central shoreline of Lake Superior. Six species from Lake Superior tributaries, taxonomically and ecologically matched with wave zone species, were included to compare the trophic roles of morphologically and behaviorally similar animals in wave zone and tributary food webs and to determine if these physically connected habitats were linked by carbon flow. Previously published stable isotope ratio data for Lake Superior wetland and pelagic food webs (Keough et al., 1996) were used to assess the relative importance of inter-habitat energy flow within the Lake Superior ecosystem.

## Methods

This study was conducted in six wave zone sites along the south-central shoreline of Lake Superior, one offshore island site (10 km from land), and in the most downstream erosional zones of two tributaries. For the purposes of this study, the wave zone is defined as coastal habitat 1–3 m in depth that is constantly exposed to wave action. The benthic substrates in the nearshore sites were granitic boulders lying on sandstone. The substrates in the island site were granitic bedrock and boulders. The tributary sites were typical of riffle habitat in low-order, south-shore tributaries of Lake Superior. One stream site (Carp River) was approximately 10 m from Lake Superior. Its mouth was constrained by rail and highway infrastructure producing tributary mouth habitat that graded directly from lotic erosional to wave zone. One species (*Ceratopsyche sparna*) was collected from this site. The remaining five tributary species were collected from the last riffle of Harlow Creek, approximately 350 m from Lake Superior. As is typical of tributaries of this part of Lake Superior, the last riffle was separated from the wave zone by a sandy bottomed, 'drowned mouth' wetland complex.

Epilithion was collected by hand from rocks roughly 50–100 cm in diameter, in 2 m deep water, during the middle of the ice-free season (9 July,

2003). All macroscopic animals (mostly chironomid midges) and large mineral particles were removed from the sample under 10–60 $\times$  magnification. The most abundant epilithic midges (*Dicrotendipes* sp.) were retained for isotope analyses. Half of the epilithion sample was dried at 55 °C, pulverized, and analyzed. A small amount was wet mounted on glass slides for inspection under a compound microscope. The rest was passed through a 53  $\mu\text{m}$  Nytex mesh using a vacuum pump while rinsing with deionized water. The small particle component was filtered onto 0.43  $\mu\text{m}$  precombusted glass fiber filters which were acidified and ground prior to analysis.

Benthic invertebrates were collected during the ice-free months of 2002 and 2003. Collections were made by hand, net, or multi-plate samplers, which mimic the conditions of many natural substrates, i.e., exposed surfaces and crevices. Specimens were transported to the lab in lake water, allowed 6–12 h for gut clearance, dispatched by freezing, cleaned of organic and inorganic material by cavitation with deionized water in an ultrasonic cleaner for 15 s, dried at 55 °C, and pulverized prior to stable isotope analysis. Two duplicate subsamples were analyzed for each sample. Multiple samples for nine species (*Physa* sp., *Orconectes propinquus*, *Leptophlebia nebulosa*, *Stenonema tripunctatum*, *Stenonema fuscum*, *Ceratopsyche alternans*, *Cheumatopsyche* spp., and *C. sparna*) were analyzed to assess intra-specific variation and to allow for inter-habitat (wave zone vs. tributaries), intra-generic (*C. alternans* and *C. sparna*, *Cheumatopsyche* spp., *S. tripunctatum* and *S. fuscum*)  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  comparisons. Stable isotope analyses were performed by the staff of the Alaska Stable Isotope Facility at the University of Alaska Fairbanks.

Invertebrate identifications followed keys in Ross (1944), Burks (1953), Flowers & Hilsenhoff (1975), Pescador & Berner (1981), Scheffer & Wiggins (1986), Merritt & Cummins (1996), Wiggins (2000), Smith (2001), and Thorp & Covich (2001). Diet records used to generate a priori predictions of trophic status were published by Merritt & Cummins (1996), Benke & Wallace (1997), Wiggins (2000), Smith (2001), and Thorp & Covich (2001).

Inter-habitat (wave zone vs. tributary) comparisons of isotopic signatures for species pairs

were made using two sample *t*-tests. One-way ANOVA models were used to assess the influence of species (nine species) and habitat (wave zone vs. tributaries) on isotopic ratios.

## Results

Results of the isotope analyses are presented in Table 1 and Figure 1. Wave zone organisms were generally enriched in  $\delta^{13}\text{C}$  and depleted in  $\delta^{15}\text{N}$  relative to those from tributaries. Previously published  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values for Lake Superior wetland and pelagic organisms (Keough et al., 1996) also appeared to be distinctly depleted in  $\delta^{13}\text{C}$  and enriched in  $\delta^{15}\text{N}$  relative to the wave zone species analyzed here.

Two sample *t*-tests indicated that the wave zone species used in inter-habitat species pair comparisons were significantly enriched in  $\delta^{13}\text{C}$  and depleted in  $\delta^{15}\text{N}$  relative to tributary species (*Stenonema* spp.  $t = 9.80$ ,  $p = 0.005$  for  $\delta^{13}\text{C}$  and  $t = -3.53$ ,  $p = 0.036$  for  $\delta^{15}\text{N}$ ; *Ceratopsyche* spp.  $t = 5.54$ ,  $p = 0.001$  for  $\delta^{13}\text{C}$  and  $t = -13.24$ ,  $p = 0.000$  for  $\delta^{15}\text{N}$ ; *Cheumatopsyche* spp.  $t = 5.38$ ,  $p = 0.016$  for  $\delta^{13}\text{C}$  and  $t = -9.17$ ,  $p = 0.006$  for  $\delta^{15}\text{N}$ ).

An ANOVA model that included data from all populations sampled more than once (*Physa* sp., *O. propinquis*, *L. nebulosa*, *S. tripunctatum*, *C. alternans*, and *Cheumatopsyche* sp. from wave zone sites; *S. fuscum*, *C. sparna*, and *Cheumatopsyche* sp. from tributary sites) revealed a pattern similar to that for inter-habitat species pairs. Significant effects of habitat were detected for both  $\delta^{13}\text{C}$  (wave zone and tributary means =  $-19.41$  and  $-31.62$ , respectively,  $F = 63.40$ ,  $p = 0.000$ ) and  $\delta^{15}\text{N}$  (wave zone and tributary means =  $0.635$  and  $6.243$ , respectively,  $F = 29.31$ ,  $p = 0.000$ ) analyses. A model that excluded the highly  $\delta^{15}\text{N}$  enriched *C. sparna* also produced similar results for  $\delta^{15}\text{N}$  analyses (wave zone and tributary means =  $0.635$  and  $3.004$ , respectively,  $F = 13.96$ ,  $p = 0.0013$ ).

Within-habitat comparisons used to identify isotopic signature differences among species revealed significant differences in  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  ratios for both wave zone and tributary food webs (wave zone  $\delta^{13}\text{C}$   $F = 13.21$ ,  $p = 0.000$ ,  $\delta^{15}\text{N}$   $F = 4.42$ ,  $p = 0.019$ ; tributaries  $\delta^{13}\text{C}$   $F = 1619.28$ ,  $p = 0.000$ ,  $\delta^{15}\text{N}$   $F = 149.02$ ,  $p = 0.000$ ). Pairwise

comparisons using Tukey's procedure on  $\delta^{13}\text{C}$  data showed that within the wave zone, a group containing *Cheumatopsyche* sp. and *C. alternans* were significantly depleted relative to *Physa* sp. and *O. propinquis*. A group containing *L. nebulosa* and *S. tripunctatum* were also significantly depleted in  $\delta^{13}\text{C}$  relative to *Physa* sp. Pairwise comparisons using Tukey's procedure on  $\delta^{15}\text{N}$  data for wave zone species showed *O. propinquis* to be significantly enriched relative to *S. tripunctatum*. *Physa* sp., *L. nebulosa*, *C. alternans*, and *Cheumatopsyche* sp.  $\delta^{15}\text{N}$  signatures were intermediate to, and not significantly different than *O. propinquis* and *S. tripunctatum*. Tukey's pairwise comparisons for tributary taxa showed that all three populations had distinct  $\delta^{15}\text{N}$  signatures and that *Cheumatopsyche* sp. was significantly depleted in  $\delta^{13}\text{C}$  relative to *S. fuscum* and *C. sparna*.

## Discussion

Existing stable isotope data indicate that the wave zone food web in Lake Superior is energetically distinct from its tributaries, wetlands, and to a lesser extent from offshore pelagic food webs. Future stable isotope studies encompassing all of these habitats would be necessary to confirm this result, but intra-generic species pair comparisons strongly indicate carbon source separation between wave zone and tributary consumers in this region. These results were consistent with inter-habitat variation in crayfish (*O. propinquis*) and carnivorous stoneflies (*Isogenoides* sp. vs. *Acroneuria* and *Paragnetina*), and with the general pattern for all species analyzed (Table 1, Fig. 1). Keough et al. (1996) concluded that a wetland food web in the western arm of Lake Superior was energetically isolated from a nearby pelagic habitat. Data from this offshore site were intermediate to those from the wave zone and tributary species from this study (Fig. 1) suggesting that an inter-habitat gradient in  $\delta^{13}\text{C}$  ratios exists (streams + wetlands < offshore < wave zone) which could be used to predict the relative importance of these food webs in the bioenergetics of trans-zonal migrants such as the coaster brook trout (*Salvelinus fontinalis*) and numerous other fish and bird species that utilize multiple Lake Superior and tributary habitats.

Table 1. Stable isotope data and trophic status for wave zone and tributary taxa

Sample	No. samples	No. inds.	Collection technique	Mean $\delta^{13}\text{C}$	Range $\delta^{13}\text{C}$	Mean $\delta^{15}\text{N}$	Range $\delta^{15}\text{N}$	Trophic status
Wave zone								
Epilithion	1	–	H	–14.8	–14.8 to –14.7	–2.8	–2.9 to –2.7	
Epilithion <53 $\mu\text{m}$	1	–	H	–16.8	–17.3 to –16.3	–2.5	–3.3 to –1.6	
Hydrozoa								
<i>Hydra</i> sp.	1	>1000	MP	–25.4	–25.6 to –25.1	2.9	2.9 to 2.9	Carnivore
Gastropoda								
<i>Physa</i> sp.	4	4	MP	–14.9	–19.1 to –12.0	0.1	–0.8 to 0.7	Herbivore–detritivore
Crustacea								
Amphipoda								
<i>Gammarus</i> sp.	1	9	MP	–18.3	–18.4 to –18.2	–1.8	–2.1 to –1.6	Herbivore–detritivore
Decapoda								
<i>Orconectes propinquus</i>	2	2	H	–16.4	–16.7 to –16.2	1.9	1.6 to 2.3	Omnivore
Isopoda								
<i>Lirceus lineatus</i>	1	95	MP	–14.6	–14.9 to –14.2	1.5	1.3 to 1.6	Herbivore–detritivore
Insecta								
Ephemeroptera								
<i>Baetisca laurentina</i>	1	7	H	–19.8	–21.2 to –18.5	–0.8	–1.4 to –0.2	Herbivore–detritivore
<i>Leptophlebia nebulosa</i>	2	8	H	–21.3	–22.1 to –20.3	–0.4	–0.7 to 0.2	Herbivore–detritivore
<i>Heptagenia pulla</i>	1	1	H	–25.0	–25.1 to –25.0	–0.3	–0.5 to –0.1	Herbivore–detritivore
<i>Stenonema tripunctatum</i>	2	16	MP	–19.4	–20.6 to –18.1	–0.8	–2.0 to 0.1	Herbivore–detritivore
Plecoptera								
<i>Isogenoides</i> sp.	1	3	H	–23.7	–23.7 to –23.7	3.2	2.9 to 3.5	Carnivore
Trichoptera								
<i>Ceratopsyche alternans</i>	5	68	H, MP	–22.7	–25.8 to –19.7	1.4	–0.2 to 3.1	Omnivore
<i>Cheumatopsyche</i> sp.	2	4	MP	–22.8	–25.2 to –20.7	0.3	–0.4 to 0.8	Omnivore
<i>Lepidostoma</i> sp.	1	19	MP	–12.6	–12.6 to –12.5	–0.2	–0.3 to 0.0	Detritivore
<i>Polycentropus</i> sp.	1	9	MP	–20.0	–20.7 to –19.3	2.6	2.4 to 2.8	Carnivore

Diptera										
<i>Dicrotenidipes</i> sp.	1	>100	H	-13.2	-13.8 to -12.6	-0.1	-0.3 to 0.1	Detritivore		
<i>Antocha</i> sp.	1	3	MP	-15.9	-16.0 to -15.8	-3.6	-3.6 to -3.5	Herbivore-detritivore		
Tributaries										
Decapoda										
<i>Orconectes propinquus</i>	1	1	H	-29.0	-29.0 to -29.0	5.4	5.2 to 5.5	Omnivore		
Insecta										
Ephemeroptera										
<i>Stenonema fuscum</i>	2	40	H	-36.8	-31.0 to -30.6	2.3	1.8 to 2.7	Herbivore-detritivore		
Plecoptera										
<i>Acroneuria</i> sp.	1	9	H	-31.2	-31.2 to -31.2	4.3	4.1 to 4.5	carnivore		
<i>Paragnetina</i> sp.	1	9	H	-31.2	-31.2 to -31.2	4.2	3.9 to 4.5	Carnivore		
Trichoptera										
<i>Ceratopsyche sparna</i>	3	54	H	-30.3	-30.5 to -30.3	10.6	10.3 to 11.0	Omnivore		
<i>Cheumatopsyche</i> sp.	2	32	H	-34.4	-35.0 to -33.8	3.7	3.5 to 3.9	Omnivore		

Taxa identified as omnivores reportedly feed on a mixture of animals, live primary producers, detritus and associated microbes. Collection techniques included by hand "H" and by multi-plate samplers (MP).

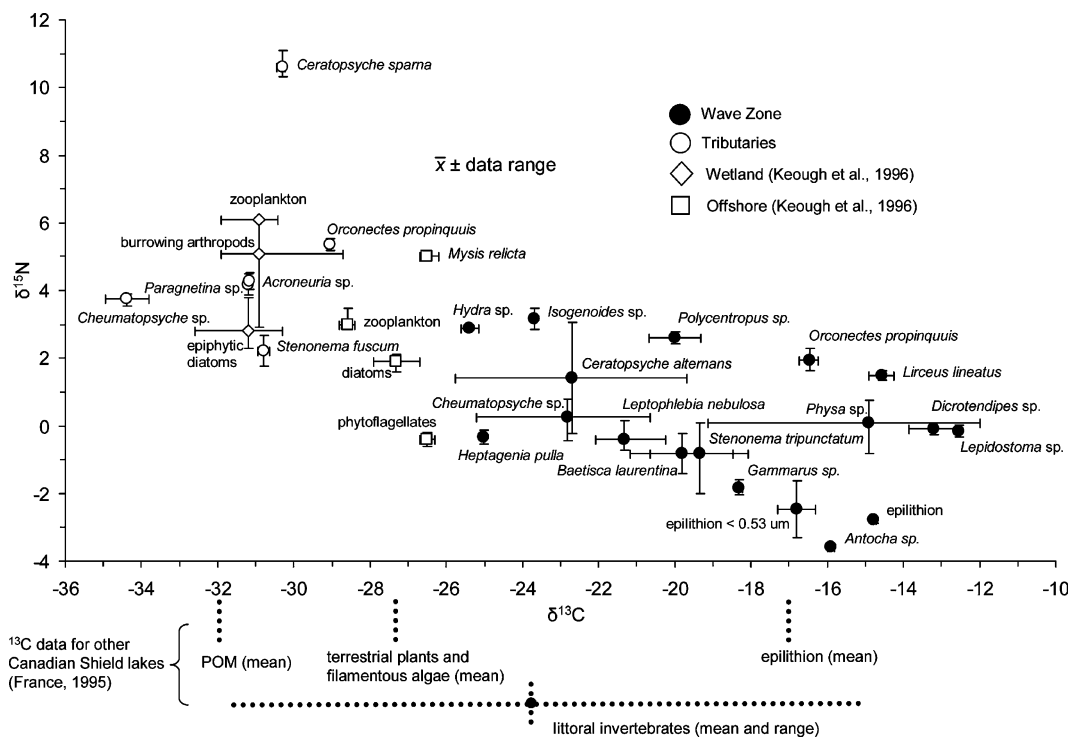


Figure 1.  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  ratio data for producers and consumers from Lake Superior and tributary communities. Increasing  $\delta^{15}\text{N}$  values indicate increasing trophic level. Increasing  $\delta^{13}\text{C}$  (less negative) values within the wave zone (closed circles) indicate increasing benthic carbon contribution.

Most of the wave zone consumer  $\delta^{13}\text{C}$  ratios fell within the broad range of previously published values for the epilithion and littoral fauna of Canadian Shield lakes (France, 1995) and were consistent with the prediction that epilithic biofilm is an important source of energy for wave zone benthos in this part of Lake Superior (Fig. 1). The epilithion analyzed in this study was composed of green algae, diatoms, and amorphous organic matter in a mucilaginous matter interpreted to be microbial glycocalyx. Similar material was found in the guts of species that encompass the entire range of  $\delta^{13}\text{C}$  reported here for wave zone benthos (*Lepidostoma* sp., *Antocha* sp., and *C. alternans*) and thus is obviously a common food source for wave zone benthos. However, the wide range of  $\delta^{13}\text{C}$  found in these and other wave zone species indicates multiple carbon sources, broad variation in epilithion quality, and/or selective feeding by epilithion grazers. For example, the grazers collected at the same time as the epilithion samples (*Dicrotendipes* sp., *Antocha* sp., and one of the two *L. nebulosa* samples) had  $\delta^{13}\text{C}$  signatures ranging

from  $-21.13$  to  $-12.58$ . The epilithion subsample that included only particles and cells less than  $53\ \mu\text{m}$  in size varied considerably among replicates, but was generally depleted in  $\delta^{13}\text{C}$  relative to the unfiltered subsample. Selective feeding on very small particles could therefore produce  $\delta^{13}\text{C}$  signatures similar to those of the amphipod *Gammarus* sp. and the mayflies *Baetisca laurentina* and *S. tripunctatum*.

Some of the wave zone species in this study showed  $\delta^{13}\text{C}$  depletion near the range of values for the offshore Lake Superior food web studied by Keough et al. (1996) suggesting that they could have derived much or all of their energy from pelagic production. As predicted by hundreds of years of observation, *Hydra* sp. clearly fit into this category. Their orange color derived from a tri-trophic transfer of phytoplankton pigments indicate that like their profundal counterparts in Lake Superior, they preferentially fed on wax ester-rich calanoid copepods (Nalepa et al., 1987; Link & Keen, 1995). Wind-driven currents and upwelling events presumably ensure a constant supply of

small pelagic organisms for wave zone suspension feeders like *Hydra*. Some of the larval net-spinning caddisfly (*C. alternans* and *Cheumatopsyche* sp.) samples also had  $\delta^{13}\text{C}$  signatures suggestive of littoral-pelagic energetic linkage via planktivory, which is consistent with observations of carnivory by other Hydropsychidae species (Benke & Wallace, 1997). However, the broad range of  $\delta^{13}\text{C}$  ratios from both net-spinner species indicates that the strength of this linkage varies considerably among sites and perhaps seasonally. It is also possible that depleted  $\delta^{13}\text{C}$  signatures resulted from consumption of terrestrially derived carbon sources. The relatively depleted  $\delta^{13}\text{C}$  signatures of the mayfly *Heptagenia pulla*, some of the net-spinning caddisflies mentioned above, and the carnivorous stonefly *Isogenoides* sp. together suggest that wave zone-pelagic energetic coupling and/or wave zone - terrestrial coupling can occur at multiple trophic levels and through a wide range of food acquisition strategies.

The trophic structure of the benthic invertebrate community in Lake Superior's wave zone food web, revealed for the first time here using  $\delta^{15}\text{N}$  data, was generally consistent with predictions based on literature records (Table 1, Fig. 1). Two levels of consumers can be identified. A primary consumer group represented in statistical tests by the lentic specialist *S. tripunctatum*, members of a genus known to scrape algae from substrate surfaces (Merritt & Cummins, 1996), was distinctly depleted in  $\delta^{15}\text{N}$  from a group of predators represented by the omnivorous crayfish *O. propinquus*, which in both wave zone and tributary populations appeared to have functioned as carnivores. Other predators included the caddisfly *Polycentropus* sp. and an assemblage of stoneflies represented here by *Isogenoides* sp. The relatively enriched condition of the detritivorous isopod *Lirceus lineatus* was surprising and warrants further investigation. Perhaps it, and the chironomid midges collected from the epilithion sample (*Dicrotendipes* sp.), preferentially consumed enriched biofilm constituents such as decomposing animal remains. The close concurrence of *S. tripunctatum*  $\delta^{15}\text{N}$  ratios with those from a group of species including other the other mayfly species (*B. laurentina*, *H. pulla*, *L. nebulosa*), a case-making caddisfly (*Lepidostoma* sp.), two flies (*Dicrotendipes* sp. and *Antocha* sp.),

and the amphipod *Gammarus* sp. indicate a mixed producer base and multiple herbivore–detritivore niches in the expansive cobble and boulder fields along Lake Superior's south-central shoreline.

From a whole-lake perspective where Lake Superior's relatively small littoral zone pales in spatial comparison to its vast pelagic realm, benthic photosynthesis probably plays a minor role in system-wide energetics (Jackson et al., 1990; Keough et al., 1996). However, because several ecologically and commercially important pelagic fish species, like the lake trout (*Salvelinus namaycush*) and lake whitefish (*Coregonus chupeaformis*) periodically forage in wave zone habitat (Becker, 1983), and because many other Lake Superior invertebrate, fish, and bird species appear to derive much or all of their energy from shallow water food webs, the influence of the wave zone to lake-wide energy flow has probably been underestimated in the past. Future studies using the species-level stable isotope analysis approach demonstrated here could be very useful in assessing the relative importance of wave zone, tributary, pelagic, and wetland habitats to lake energetics and also in revealing energetic connections among terrestrial, riverine, littoral, and lentic food webs in Lake Superior's coastal ecosystems.

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