

# Isotopic variability in lake littoral organisms presents a challenge for food web studies

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## Introduction

Most studies of lake ecosystems, including those that use stable isotope analysis (SIA), have traditionally concentrated on the pelagic system (BEAUDOIN et al. 2001, VANDER ZANDEN & VADEBONCOEUR 2002). Hence, temporal, spatial, and interspecies variability in isotopic signatures of pelagic food web components (especially zooplankton) have been the focus of recent studies (e.g., MATTHEWS & MAZUMDER 2003, 2007). Recent SIA studies have also clearly indicated, however, that benthic production and the littoral areas of lakes may contribute more than previously thought to the whole lake ecosystem energy budget (HECKY & HESSLEIN 1995, VANDER ZANDEN & VADEBONCOEUR 2002, VANDER ZANDEN et al. 2006).

Studies of lake food webs based on SIA often assume single isotope values to represent baseline values for pelagic and littoral food webs. These values may then be used as “end members” in isotope mixing models, such as to assess trophic positions or relative contributions from different energy sources. But such single values ignore temporal, spatial or especially inter-specific variation in stable isotope values for these primary consumers, as shown for pelagic consumers by MATTHEWS & MAZUMDER (2003). Such variability may have considerable impacts on the outputs from mixing models and hence on the inferences drawn about food web structure. Lake littoral habitats have received much less attention in this respect, despite being important feeding areas for many fish species and therefore contributing significantly to the observed stable isotope signatures at higher trophic levels. Littoral habitats are also inherently more heterogeneous than pelagic habitats, and primary production from phytoplankton, periphyton, and macrophytes, combined with allochthonous sources of energy, potentially result in complex and variable isotopic signatures in littoral primary consumers (SYVÄRANTA et al. 2006). We present stable isotope data for littoral invertebrate consumer populations (benthic invertebrates and zooplankton) from Lake Jyväsjärvi in central Finland and show how variation in isotope signatures between different littoral invertebrate consumers can be reflected at higher trophic levels.

**Key words:** food web, littoral, macroinvertebrates, perch, stable isotopes, zooplankton

## Methods

Jyväsjärvi (62°14'N; 25°46'E) is an urban lake in central Finland, in the immediate vicinity of the city of Jyväskylä. The lake has an area of 3.37 km<sup>2</sup>, a maximum depth of 27 m, and a mean depth of 7.2 m and is thermally stratified in summer. Jyväsjärvi was heavily polluted in the 1960s and 1970s by industrial and municipal waste waters, and today is recovering from severe eutrophication (MERILÄINEN et al. 2003, SALONEN et al. 2005).

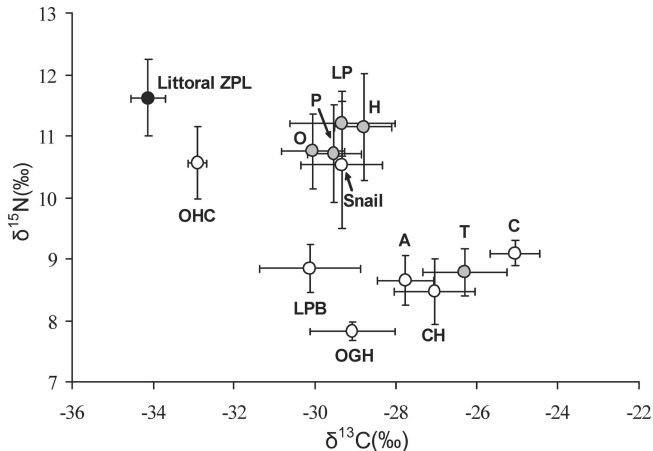
Zooplankton samples were collected in summer 2006 by hauling a zooplankton net (100-µm mesh size) horizontally behind a boat in the littoral area. Samples were then carefully sieved through 500, 200 and 100 µm sieves with clean water to remove all extra material. Zooplankton samples were then left in clean water to allow gut evacuation. Samples were later picked onto glass fibre filters and dried in an oven at 60 °C. About 0.6 mg of zooplankton sample was then carefully weighed into tin cups for SIA. Macroinvertebrate samples were collected in summer 2005 and 2006 by kick-netting (mesh size 500 µm) at depths < 1 m. Collected samples were transferred into clean water in the laboratory to allow the guts to void. The following day individuals were identified (usually to family level) and sorted onto glass fibre filters. After drying at 60 °C, samples were picked from filters and weighed into small tin cups (0.5–0.6 mg). All snails were removed from their shells and only the soft tissue was dried and analysed. For smaller species, each sample was a mixture of several individuals to obtain sufficient sample for analysis.

Larval and juvenile perch (*Perca fluviatilis* L.) were collected on 6 occasions between June and August 2006 from offshore pelagic habitats (larval perch) and, as the perch grew >15 mm in length, from vegetated areas in the littoral habitat. Larval perch were collected by hauling a large zooplankton net (500 µm) behind a boat, and juvenile perch by sweeping the vegetated area with a hand net (mesh size 500 µm). After measuring the total length from each fish, heads and stom-

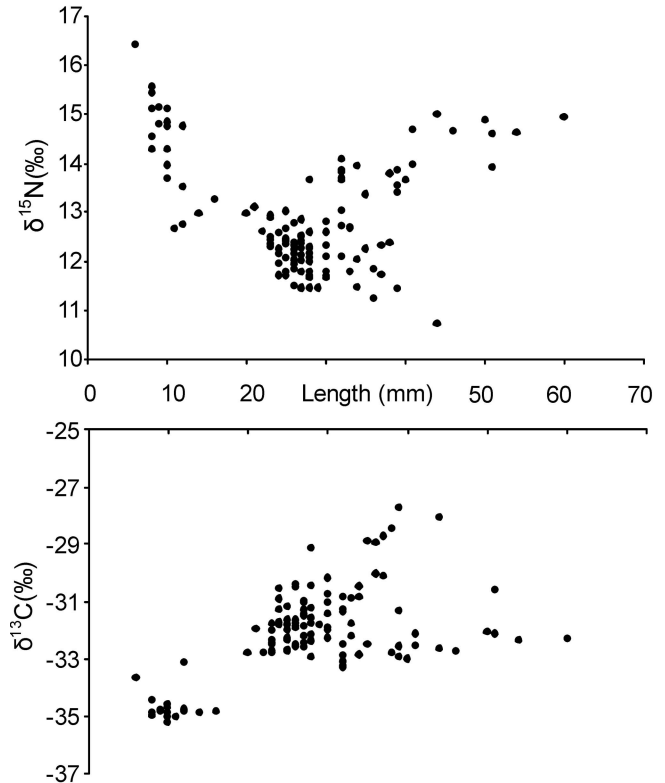
achs were removed and the fish were dried at 60 °C. After drying, the fish samples were ground into a fine powder and stored in small (2 ml) glass vials for later SIA. Stomach contents were visually inspected for comparison with SIA data. All stable isotope analyses were done at the Institute for Environmental Research, University of Jyväskylä, following standard procedures (described in more detail in SYVÄRANTA et al. 2006).

## Results

Invertebrates collected from littoral areas of Jyväsjärvi spanned a range over 10‰ in their mean  $\delta^{13}\text{C}$  values and over 4‰ in their mean  $\delta^{15}\text{N}$  values (Fig. 1). The  $\delta^{15}\text{N}$  values of typical littoral primary consumers (such as Ephemeroptera, *Asellus aquaticus*, Oligochaeta) were similar, but considerably lower than those for snails or Orthocla-diinae larvae (also considered as mainly primary consumers). Surprisingly the isotope values for Orthocla-diinae larvae were closer to the values for littoral zooplankton than for any other benthic invertebrates. Most predators and scavengers (like Trichoptera larvae) were also clearly separated by their  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values from all other benthic invertebrates, except from snails (Fig. 1). Also, Tanypodinae larvae had isotope values matching those of



**Fig. 1.** Isotope biplot showing mean ( $\pm$  SE) stable carbon and nitrogen isotope values for the most abundant littoral invertebrates in Jyväsjärvi. Filled black circle indicates mean for all analysed littoral zooplankton (cladocera and cyclopoida). Filled grey symbols indicate species that are presumed predators or scavengers and open symbols indicate primary consumers. Abbreviations: O = Odonata, H = Hirudinea, P = Phryganeidae (Trichoptera), LP = Limnephilidae (Trichoptera), OHC = Orthocla-diinae (Diptera: Chironomidae), C = Chironominae (Chironomidae), T = Tanypodinae (Chironomidae), LPB = Leptophlebiidae (Ephemeroptera), CH = *Caenis horaria* (Ephemeroptera), A = *Asellus aquaticus* (Isopoda), OGH = Oligochaeta (Annelida).



**Fig. 2.** Stable carbon and nitrogen isotope values for individual larval and juvenile perch sampled between June and August 2006 in Jyväsjärvi.

most benthic primary consumers, although they are usually considered carnivorous.

The 124 larval and juvenile perch analysed ranged in total length from 6 to 60 mm. The smallest individuals analysed still reflected isotope signatures 'inherited' from their parents (VANDER ZANDEN et al. 1998, MURCHIE & POWER 2004). After this the  $\delta^{13}\text{C}$  values increased and  $\delta^{15}\text{N}$  values decreased rapidly to indicate external feeding and a subsequent change in diet. Fish length and  $\delta^{13}\text{C}$  values correlated significantly (Pearson  $r = 0.598$ ,  $p < 0.001$ ), but length and  $\delta^{15}\text{N}$  values did not ( $r = -0.172$ ,  $p = 0.056$ ), because of the greater variability in  $\delta^{15}\text{N}$  values of larger individuals (Fig. 2).

## Discussion

Littoral invertebrates from Jyväsjärvi exhibited a considerable range in both mean  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values. Snails have been proposed as isotopic baseline indicators for littoral habitat in lakes (POST 2002), but snails in Jyväsjärvi had elevated (by  $\sim 2\text{‰}$ )  $\delta^{15}\text{N}$  values compared to most other primary consumers, suggesting they would not be

appropriate baseline indicators. Stomach contents showed that fish were preying primarily on chironomids (Orthocladinae and Chironominae), *A. aquaticus*, and littoral zooplankton, which all had mean isotope signatures very different from snails. Isotope values of littoral zooplankton (Fig. 1) differed from those of pelagic zooplankton in Jyväsjärvi (SYVÄRANTA et al. 2006), having higher  $\delta^{13}\text{C}$  and lower  $\delta^{15}\text{N}$  values, which further complicates the assessment of trophic positions and especially contributions from pelagic–benthic production.

Because isotope signatures in fish muscle tissue change with the synthesis of new tissue material (i.e., as fish grow), isotope signatures in rapidly growing juvenile fish can change within a week or 2, as seen in our samples, and can therefore be used to track ontogenetic diet shifts in these small fish. We expected the diets of developing perch to shift from pelagic zooplankton to primarily littoral zoobenthic prey (PERSSON & GREENBERG 1990), which at first seemed to be a valid assumption (Fig. 2). However, as perch grew larger, they started to show more variable dietary preferences as some individuals selectively consumed littoral benthic invertebrates and others littoral zooplankton. This specialisation resulted in highly variable isotope values (both  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ) observed in larger juvenile perch (>30 mm; Fig. 2). Although stomach contents confirmed that these perch had a diet dominated by primary consumers in both cases, there was ~3‰ difference in their  $\delta^{15}\text{N}$  values, which is typically considered almost one trophic level increase in  $\delta^{15}\text{N}$ . The data presented here for juvenile perch illustrate how isotopic variability in prey items, even within the same habitat, can result in considerable inter-individual variation in  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values analysed from consumer muscle tissue.

The range observed, especially in the  $\delta^{13}\text{C}$  values of littoral consumers, has serious implications for selecting a single value as an end member in more complicated isotope mixing models. The variation in pelagic primary consumer  $\delta^{13}\text{C}$  values is usually less than presented here for littoral consumers, and seasonal averages for different zooplankton taxa can provide a reasonably good end member to represent the pelagic habitat (MATTHEWS & MAZUMDER 2003). In contrast, littoral areas clearly present more problems for calculating such end member values. Taking the mean  $\delta^{13}\text{C}$  value for all primary consumers may be one possibility but, at least in the case of Jyväsjärvi, would result in considerable underestimation of littoral contribution in mixing models. Another possibility is to use stomach contents of fish to emphasise the importance of certain prey types when calculating end members. Isotope mixing models are typically highly vulnerable to uncertainties in their end member values,

and even a few ‰ difference in  $\delta^{13}\text{C}$  values may result in significant differences in the interpretation of results. We conclude that studies relying on single isotope values as end members in isotope mixing models may be seriously compromised by overlooked variability in isotope signatures of the organisms used to calculate these end member values. More attention should be paid especially to assessing values to represent littoral–benthic end members.

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