Master's thesis

Food web structure of an Arctic lake (Pulmankijärvi, northern Finland) studied by stable isotope analyses

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ABSTRACT

The food web structure in Pulmankijärvi was studied using stable isotope analyses to evaluate the relative importance of littoral and pelagic food sources to a relatively diverse Arctic fish community. European whitefish is the most abundant species in the lake, and three groups were separated based on size and gill raker number. Results from a two-source mixing model indicated that littoral food sources dominated the energy flow to most of the fish populations, but pelagic food sources were essential to the diets of two groups of European whitefish as well as Arctic char. Densely-rakered whitefish are primarily supported by zooplankton, and mysids are probably an important component in the partially pelagic diets of both sparsely-rakered whitefish >100 g and Arctic char. Because sparsely-rakered whitefish aged 5+ to 9+ years are likely the most abundant fish in Pulmankijärvi, pelagic production may be extremely important to the overall fish biomass in this Arctic lake. Comparisons with other Arctic lakes having contrasting fish communities indicate that larger lake size and increased inter-specific competition probably explain the reduced reliance on littoral food sources for Arctic char and brown trout in Pulmankijärvi.

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TIIVISTELMÄ

Pulmankijärven ravintoverkon rakennetta selvitettiin vakaiden isotooppien avulla tutkittaessa litoraalin ja pelagiaalin ravintokohteiden merkitystä järven kalayhteisölle. Siika (*Coregonus lavaretus*) on Pulmankijärven runsain kalalaji, josta erotettiin kolme eri muotoa koon ja kidusten siivilähampaiden lukumäärän perusteella. Isotooppiaineiston perusteella järven litoraalin ravintokohteet muodostivat suurimman osan useimpien kalalajien ravinnosta, mutta pelagiaalin ravintokohteet olivat erityisen tärkeitä kahdelle eri siikamuodolle sekä nieriälle (*Salvelinus alpinus*). Tiheäsiivilähampaiset siiat käyttivät ravintonaan pääasiassa pientä eläinplanktonia ja muut siikamuodot sekä nieriä söivät enemmän halkoisjalkaäyriäisiä (*Mysis*). Koska 5-9 vuoden ikäiset harvasiivilähampaiset siiat ovat järven yleisimpiä kaloja, pelaginen tuotanto ja ravintokohteet ovat todennäköisesti hyvin tärkeitä ajatellen koko järven kalabiomassaa. Verratessa aineistoa muihin kalastolta erilaisiin arktisiin järviin voidaan havaita, että järven koko ja lisääntyvä lajienvälinen kilpalu todennäköisesti selittävät litoraalin ravintokohteiden pienemmän merkityksen Pulmankijärven nieriöiden ja taimenten (*Salmo trutta*) ravinnossa.

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1. INTRODUCTION

1.1. Ecology of Arctic lakes and their fish communities

While temperate lakes typically have food webs dominated by pelagic production, Arctic lakes are commonly thought to be unproductive and have food webs dominated by benthic energy flows. Arctic lakes generally have simple food webs with low species diversity, which can be sensitive indicators to environmental disturbances such as global warming (McDonald *et al.* 1996). A study of planktonic trophic structure in Arctic lakes indicated that only two or three trophic levels existed in the macrozooplankton, compared to five or six trophic levels reported in temperate lakes (Kling *et al.* 1992). Benthic algae tend to form biofilm or mats while phytoplankton are diluted in the water column, leading to larger-bodied (in the magnitude of one order) zoobenthos feeding on benthic algae while smaller-bodied zooplankton feed on phytoplankton (Karlsson & Byström 2005). These characteristics of food web size structure and distribution in Arctic lakes could provide an energy efficiency explanation for fish foraging more in benthic habitats.

Arctic lakes typically support small fish populations with slow growth rates (Sierszen *et al*. 2003). Therefore, food source availability may be extremely important in dictating dietary habits for fish communities in Arctic lakes. A study of Arctic char in five Norwegian lakes showed that juveniles foraged mainly in epibenthic habitats and began exploiting the pelagic zone in summer when they grew to 13-18 cm, demonstrating both an ontogenetic and phenological habitat shift (L'Abee-Lund *et al*. 1993). Other studies also confirm that young-of-the-year and small Arctic char feed primarily on benthic near-shore prey (Byström *et al*. 2004, Karlsson & Byström 2005). However, field data also demonstrated that one-year-old Arctic char increasingly used offshore habitats at high fish densities, revealing an early trade-off in habitat use due to density dependence (Byström *et al*. 2004). Furthermore, juvenile Arctic char were observed to have larger age-specific lengths in pelagic areas than in benthic habitats, and few moved to pelagic waters in the presence of the piscivorous brown trout (L'Abee-Lund *et al*. 1993). Adult Arctic char and brown trout are reported to have similar dietary preferences in allopatry, but a comparative study of sympatric habitat use showed that brown trout dominate the littoral areas during summer, forcing Arctic char to forage offshore (Langeland *et al*. 1991).

Omnivory is common among many fish species, and piscivores often provide a link between food chains by feeding upon both pelagic fishes and benthic fishes and invertebrates (Vander Zanden & Vadeboncoeur 2002). Littoral piscivore dietary data has shown widespread omnivory with a large dependence on zoobenthos, thereby regulating top-down control on prey fish (Vander Zanden *et al*. 2005). Dietary data of common fish species of north-temperate lakes averaged 65% zoobenthic prey consumption, including 15% indirectly derived from consumption of fish prey supported by zoobenthos (Vander Zanden & Vadeboncoeur 2002). Zoobenthivory can provide a subsidy to pelagic food resources and create competition among fish populations (Vander Zanden &Vadeboncoeur 2002). Perhaps in Arctic lakes, pelagic food sources could be a subsidy to zoobenthivory.

1.2. Stable isotope analysis and its application to Arctic food webs

Stable isotope analyses have been increasingly used in ecological research, particularly with food web studies evaluating energy sources in lakes. Stable isotope data can provide food source information because certain elements have naturally occurring isotopic compositions that change (fractionate) through the food web in a rather predictable manner (Peterson & Fry 1987). ^{13}C and ^{15}N are naturally occurring stable isotopes that are measured as ratios ($^{13}C/^{12}C$, $^{15}N/^{14}N$) and expressed in standardized delta

values (δ) of permil (‰). Carbon isotope ratios ($\delta^{13}C$) can be used as a tracer to identify dietary components of consumers because the $\delta^{13}C$ values of food items remain relatively unchanged through the food web (Vander Zanden & Rasmussen 2001). Nitrogen isotope ratios ($\delta^{15}N$) can be used to estimate trophic position because ^{15}N becomes enriched in consumers by about 3.4‰ at each step through the food chain (Vander Zanden *et al.* 1997). These general characteristics of isotopic signatures can be applied to evaluations of food web structure by using dual-isotope plots (Figure 1) and mixing models for estimating the relative contribution of food sources to consumers.

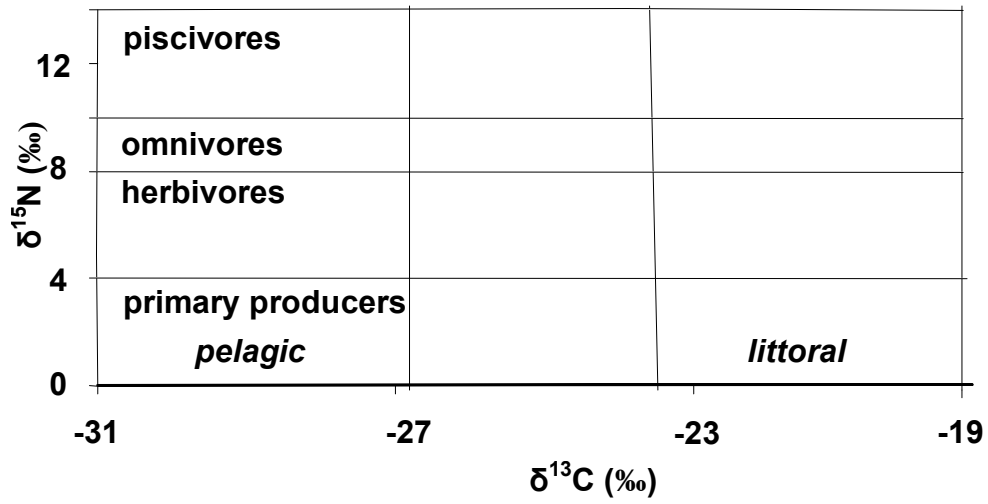


Figure 1. General dual-isotope plot in freshwater ecosystems (modified from Jardine *et al.* 2003).

Stable isotope analysis reveals dietary components of consumers over a time-integrated scale but cannot be used for instantaneous conclusions as stomach content analysis can. This is because stable isotope analysis measures assimilation instead of digestion in consumers, and different consumer tissues can have different assimilation efficiencies. Tissue turnover rates can be used in conjunction with stable isotope analysis to infer dietary habits over different time periods. For example, relative turnover rates of tissues in Japanese quail (*Coturnix japonica*) were ranked as liver > blood and muscle >> bone collagen, with carbon half-lives calculated for liver (2.6 days), blood (11.4 days), muscle (12.4 days), and bone collagen (173.3 days) (Jardine *et al.* 2003). Lipid formation can also affect $\delta^{13}C$ values, which can be "lipid-normalized" using a model, and it is therefore recommended that a variety of tissues be analyzed to accurately reflect overall consumption patterns and fractionation effects in food webs (Jardine *et al.* 2003).

Stable isotope analyses of pelagic food webs have been used extensively in the past, when the focus has been on pelagic production as being the dominant energy pathway in lakes (Sierszen *et al*. 2003, Vander Zanden & Vadeboncoeur 2002). More recently, stable isotope analyses of whole-lake food webs have shown a greater importance of benthic energy pathways to top consumers and coupling of pelagic and benthic food webs (Karlsson & Byström 2005, Vander Zanden & Vadeboncoeur 2002). While much knowledge has been gained from studying plankton-based Arctic communities (Sierszen *et al.* 2003), there have been few studies on the relative importance of littoral versus pelagic resource contributions to energy flow in unproductive Arctic lakes (Karlsson and Byström 2005). Sierszen *et al*. (2003) used stable isotope analyses to examine the food webs of two Arctic lakes in Alaska and found that benthos was the primary carbon source for adults of

all species of benthic and pelagic fish present. This study on the Arctic lake, Pulmankijärvi, is part of ongoing research at the University of Jyväskylä using stable isotope analyses to investigate food web structures in Arctic/sub-Arctic lakes with contrasting fish communities.

1.3. Characteristics of Pulmankijärvi and its fish community

Pulmankijärvi is an oligotrophic lake located in a sparsely populated area in Arctic Finland. The lake is long and narrow with a straight shoreline, and its limnological characteristics are listed in Table 1. Catch statistics from Ilmast & Sterligova (2002) indicated European whitefish (*Coregonus lavaretus* L.) as the most abundant fish species in Pulmankijärvi (83% of their catch), followed by Arctic char (*Salvelinus alpinus* L.), burbot (*Lota lota* L.), Eurasian grayling (*Thymallus thymallus* L.), flounder (*Platichtys flesus* L.), brown trout (*Salmo trutta* L.), northern pike (*Esox lucius* L.), Eurasian perch (*Perca fluviatilis* L.), and Atlantic salmon (*Salmo salar* L.).

Ilmast & Sterligova (2002) also differentiated the European whitefish in Pulmankijärvi into two forms based on the number of gill rakers, with 93% of individuals comprising a sparsely-rakered form (range 20-30 gill rakers; 90% aged 5+ to 9+ years) and 7% comprising a medium-rakered form (range 35-46 gill rakers; all aged 2+ to 6+ years). Stomach content analyses showed imago stages of insects and chironomid pupae for sparsely-rakered whitefish, while analyses for medium-rakered whitefish showed chironomid pupae and larvae as well as zooplankton.

Table 1. Limnological characteristics of Lake Pulmankijärvi (Ilmast & Sterligova 2002).

Characteristics	Value of the parameters
Altitude (m)	17
Drainage area (km^2)	800
Surface area (km^2)	11.2
Maximum depth (m)	34
Mean depth (m)	11
Water transparency (m)	3.3
pH	7.19
Total phosphorus ($\mu g\ P\ l^{-1}$)	7
Total nitrogen ($\mu g\ N\ l^{-1}$)	210
Phytoplankton biomass (g fresh weight m^{-3})	0.18
Zooplankton biomass (g dry weight m^{-3})	22.6
Macrozoobenthos biomass (g dry weight m^{-2})	0.4

1.4. Objectives of this study

The main aim of this research was to use stable isotope analyses coupled with a two-source mixing model to evaluate the relative importance of littoral and pelagic energy sources to the fish community of Pulmankijärvi. As this study is part of a larger research project, comparison is made with findings of Eloranta (2007) for another Arctic lake, Saanajärvi, which has a much less diverse fish community. Reference is also made to Kilpisjärvi, which has a similar fish community to Pulmankijärvi. I hypothesized 1) that littoral production will dominate over pelagic production in the energy flow of the Pulmankijärvi food web, but 2) that the relative contributions of littoral food sources to

fish will vary between species and between Arctic lakes due to differences in competition for limited resources.

2. MATERIAL AND METHODS

2.1. Study site

Pulmankijärvi (70º00'N, 28º00'E) is located within the Teno River system on the north-eastern border of Finland and Norway (Figure 2). Four sampling areas (Figure 3) were chosen for data collection from 20-24 June, 2007. Additional fish samples from 20 October, 2006, were provided by the Finnish Game and Fisheries Research Institute (RKTL). All sampling gear was sterilized before use by drying or disinfecting for the parasite *Gyrodactylus salaris.*

Figure 2. Location of Pulmankijärvi (Ilmast & Sterligova 2002).

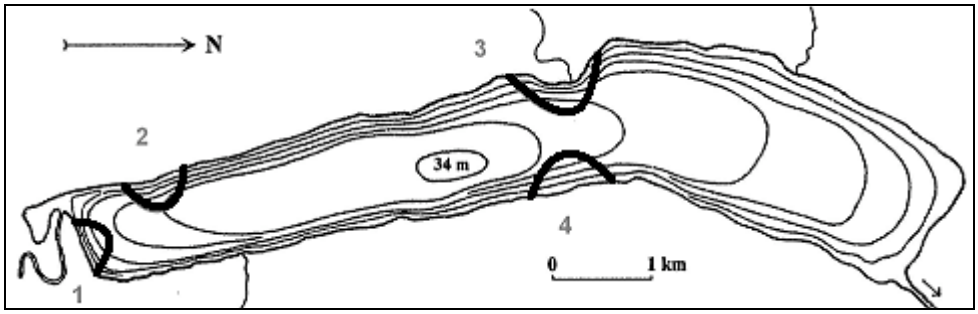


Figure 3. Bathymetric map of Pulmankijärvi with sampling areas numbered 1 through 4 (modified from Ilmast & Sterligova 2002).

2.2. Sample collection

2.2.1. Biofilm, zooplankton, and macroinvertebrates

Biofilm was collected by scraping rocks from <1 m depth at various sites in the four sampling areas. Two replicate biofilm samples were filtered with 100 μm nets and concentrated on glass-fiber filter papers.

Zooplankton was collected using a 100 μm zooplankton net hauled vertically from about 30 m depth to the water surface at three sites (one site between sample areas #1 and #2; two sites between sample areas #3 and #4). Samples were then placed in filtered water for a few hours to void guts. One larger mysid and several smaller mysids were separated from the three replicate zooplankton samples, which contained mostly small copepods.

Benthic macroinvertebrates were collected along transects in the four sampling areas using a kick-net in <1 m depth (littoral) and an Eckman grab in 5 m depth and 10 m depth. Samples were sieved through a 500 μm mesh and then placed in filtered water overnight to void guts. Littoral samples consisted of oligochaetes (4 replicates), trichopterans (4 replicates), plecopterans (2 replicates), ephemeropterans (5 replicates), and tabanids (4 replicates). 5 m depth and 10 m depth samples consisted of oligochaetes (2 replicates). Samples from 10 m depth consisted of oligochaetes (4 replicates), chironomids (2 replicates), and one trichopteran.

All biofilm, zooplankton, and benthic macroinvertebrates were collected from 20-24 June, 2007. Samples were placed on glass-fiber filter papers in Petri dishes and oven-dried at 60º C for 48 hours.

2.2.2. Fish

Frozen whole fish provided by RKTL (Oulu, Finland) were caught with gill nets on 20 October, 2006. Samples used for stable isotope analyses consisted of 31 European whitefish (*Coregonus lavaretus*), 12 grayling (*Thymallus thymallus*), 6 Arctic char (*Salvelinus alpinus*), and 3 brown trout (*Salmo trutta*).

All other fish were collected from 20-24 June, 2007. Five gill nets (1.5 m X 30 m) with 9 mesh sizes (10 to 55 mm from knot to knot) were set overnight along transects in the four sampling areas from littoral (~2 m depth) to profundal (~30 m depth) zones. Angling was also conducted along the shoreline near the brook in sampling area #3, in which only grayling were caught. Samples used for stable isotope analyses consisted of 28 (all frozen whole) European whitefish, 14 (5 frozen whole) grayling, 3 (all frozen whole) Arctic char, 6 (3 frozen whole) brown trout, 12 (8 frozen whole) flounder (*Platichtys flesus*), and 2 Atlantic salmon (*Salmo salar*). Also, one bullhead (*Cottus gobio*) and one three-spine stickleback (*Gasterosteus aculeatus*) were collected while kick-netting for benthic macroinvertebrates, and these were then oven-dried whole (excluding head and stomach) in Petri dishes at 60º C for 48 hours.

Unfrozen fish were prepared at Pulmankijärvi for measuring total length (mm) and weight (g), dissecting and freezing samples of liver and posterior muscle, removing and preserving stomachs in alcohol, and removing and freezing European whitefish gills. All samples were then taken to the University of Jyväskylä, where all frozen fish were thawed in tap water before measuring total length (mm) and weight (g), dissecting samples of liver and posterior muscle, and removing stomachs and European whitefish gills. Fish muscle and liver samples were oven-dried at 60º C for 48 hours. For background diet information, fish stomach contents were emptied into Petri dishes filled with tap water to identify recent

prey items to family level. Fullness of stomach was estimated according to Kahilainen *et al*. (2004) by scoring on a scale from 0 (empty) to 10 (full) and then allocating a portion of this fullness value to the relative contribution of each prey item. Also, two gammarid shrimps were removed from two unpreserved grayling stomachs and oven-dried at 60º C for 48 hours. European whitefish gills were examined for the number of gill rakers to identify sparsely-rakered (18-30 rakers) and densely-rakered (28-42 rakers) morphs according to Amundsen *et al.* (2004).

2.3. Stable isotope analyses

All samples for biofilm, zooplankton, macroinvertebrates, and fish were prepared for stable isotope analyses at the University of Jyväskylä. Biofilm samples were scraped from the filter papers with a scalpel and approximately 7.0 mg was precisely weighed into tin cups. Zooplankton samples were crushed in small glass vials with a spatula and approximately 0.6 mg was precisely weighed into tin cups. Macroinvertebrate samples were cut into small pieces with a scalpel and approximately 0.6 mg was precisely weighed into tin cups. Fish muscle and liver samples, the bullhead sample, and the three-spine stickleback sample were ground to a fine powder with mortar and pestle and approximately 0.6 mg was precisely weighed into tin cups. For comparison, 10 random liver sub-samples from whitefish and 2 random liver sub-samples from each of the other fish species (except bullhead and three-spine stickleback) were lipid-extracted by adding 4 ml of chloroform:methanol:water (1:2:0.8) (Bligh & Dyer 1959). Excess liquid was removed with a pipette after one day, and the sub-samples were then oven-dried at 60º C for 24 hours before weighing into tin cups. All tin cups were crushed into balls after weighing.

Stable isotope analyses of carbon and nitrogen in the samples were conducted from September through October 2007 at the Institute for Environmental Research, University of Jyväskylä, using a FlashEA 1112 elemental analyser coupled to a Thermo Finnigan DELTA^{plus} Advantage mass spectrometer. Pike white muscle tissue was used as an internal working standard, and replicates for standards and samples were run repeatedly in every sequence. Stable isotope ratios are expressed as parts per thousand (‰) delta values ($\delta^{13}C$ or $\delta^{15}N$), referring to the international standards for carbon (PeeDee Belemnite) and nitrogen (atmospheric nitrogen) (Peterson & Fry 1987). Internal precision for standards was always less than 0.7‰ for C and 0.3‰ for N in each run (usually both <0.1‰).

2.4. Data analyses

2.4.1. Dual-isotope plots

The $\delta^{13}C$ and $\delta^{15}N$ values for biofilm, zooplankton, macroinvertebrates, and fish muscle and liver were plotted on graphs using Microsoft Excel software to show differences in stable isotope signatures between groups of organisms, between seasons, and between fish tissues. Based on observations of these graphs along with gill raker and weight data, European whitefish were separated into three groups: densely-rakered whitefish (DRW), sparsely-rakered whitefish >100 g (SRW>100g), and sparsely-rakered whitefish <100 g (SRW<100g).

2.4.2. Lipid-normalization of $\delta^{13}C$ values for fish muscle

A lipid-normalization model from McConnaughey & McRoy (1979) and modified by Kiljunen *et al*. (2006) was used to account for the varying content of $\delta^{13}C$-depleted lipids associated with C:N ratios in fish muscle samples. This lipid-normalization procedure is based on two equations:

$$L = 93 / [1 + (0.246 \text{ x } (C : N) - 0.775)^{-1}]$$

$$\delta^{13}C' = \delta^{13}C + D \text{ x } [I + 3.90 / (1 + 287 / \text{L})]$$

where L is the proportional lipid content of the sample and δ^{13}C' is the lipid-normalized value of the sample; C and N are the proportions of carbon and nitrogen in the sample; δ^{13}C is the measured value of the sample; D is the isotopic difference between protein and lipid (assigned a value of 7.018); and I is a constant (assigned a value of 0.048).

2.4.3. Two-source mixing model for food source partitioning

A two-source mixing model described by Karlsson & Byström (2005) was used to estimate the contribution of littoral food sources relative to pelagic food sources in the observed δ^{13}C values of individual fish muscle and liver tissues. The estimates of littoral contribution to fish tissue δ^{13}C are given as percentage values using the equation:

$$LF_{\text{fish tissue}} = [\delta^{13}C_{\text{fish}} - \delta^{13}C_{\text{pel}} - (\delta^{15}N_{\text{fish}} - \delta^{15}N_{\text{pel}}) \text{ x TS}] / (1 - \text{TS x BS}) / (\delta^{13}C_{\text{lit}} - \delta^{13}C_{\text{pel}})$$

where TS is the slope of the trophic fractionation of carbon and nitrogen in the food web (Δ_C/Δ_N), and BS is the slope of the linear relationship between the pelagic and littoral baselines (-0.74). The TS value for fish muscle was calculated with the commonly used isotopic fractionation of carbon (Δ_C = 0.47 ‰) and nitrogen (Δ_N = 3.46 ‰) between fish muscle tissue and whole fish prey (Vander Zanden & Rasmussen 2001). The TS value for fish liver was estimated by adding the Δ_C and Δ_N values used for fish muscle trophic fractionation to the corresponding differences between fish liver and muscle mean δ^{13}C values (–0.93 ‰) and between fish liver and muscle mean δ^{15}N values (–0.16 ‰). The pelagic baseline $\delta^{13}C_{\text{pel}}$ and $\delta^{15}N_{\text{pel}}$ values were estimated by calculating the mean of δ^{13}C and δ^{15}N values for zooplankton (mean of 3 samples), the small mysids sample, and the large mysid sample. Based on observations of dual-isotope plots along with stomach content data, the littoral baseline $\delta^{13}C_{\text{lit}}$ and $\delta^{15}N_{\text{lit}}$ values were estimated to account for important littoral food sources that were not sampled (such as littoral chironomids, mollusks, and dytiscids). The littoral baseline stable isotope signature was therefore estimated by first calculating the mean of the stable isotope signatures for littoral macroinvertebrates consisting of oligochaetes (mean of 4 samples), trichopterans (mean of 4 samples), ephemeropterans (mean of 5 samples), tabanids (mean of 4 samples), and gammarids (mean of 2 samples). These δ^{13}C and δ^{15}N mean values were then averaged with the δ^{13}C and δ^{15}N values for littoral plecopterans (average of 2 samples) to approach a more representative littoral baseline stable isotope signature associated with the dual-isotope plots. All estimated $LF_{\text{fish tissue}}$ values <0% were assigned 0% littoral contributions, and all estimated $LF_{\text{fish tissue}}$ values >100% were assigned 100% littoral contributions.

2.4.4. Statistical methods

SPSS software was used to test significant differences between data sets with one-way analysis of variance (ANOVA) and Tukey pair-wise comparisons. When the ANOVA assumption of homogeneity of variances was not met (Levene's test, $p<0.05$), Kruskal-Wallis and Mann-Whitney non-parametric tests were used. These statistical analyses were used to compare δ^{13}C and δ^{15}N values between whitefish groups, δ^{13}C and δ^{15}N values between fish tissues, and littoral contributions between fish tissues. Linear regression analyses were also used for comparing δ^{13}C and δ^{15}N values between fish tissues. Seasonal data were not analyzed with statistical methods because of unequal sample numbers between groups.

3. RESULTS

3.1. Stable isotope analyses for biofilm, zooplankton, and macroinvertebrates

Biofilm, zooplankton, and mysids had $\delta^{13}C$ and $\delta^{15}N$ values clearly separated from those of benthic macroinvertebrates (Figure 4). Littoral macroinvertebrates had a large variation in stable isotope signatures between groups, while macroinvertebrates from 5 m and 10 m depths had a large variation in stable isotope signatures within and between groups.

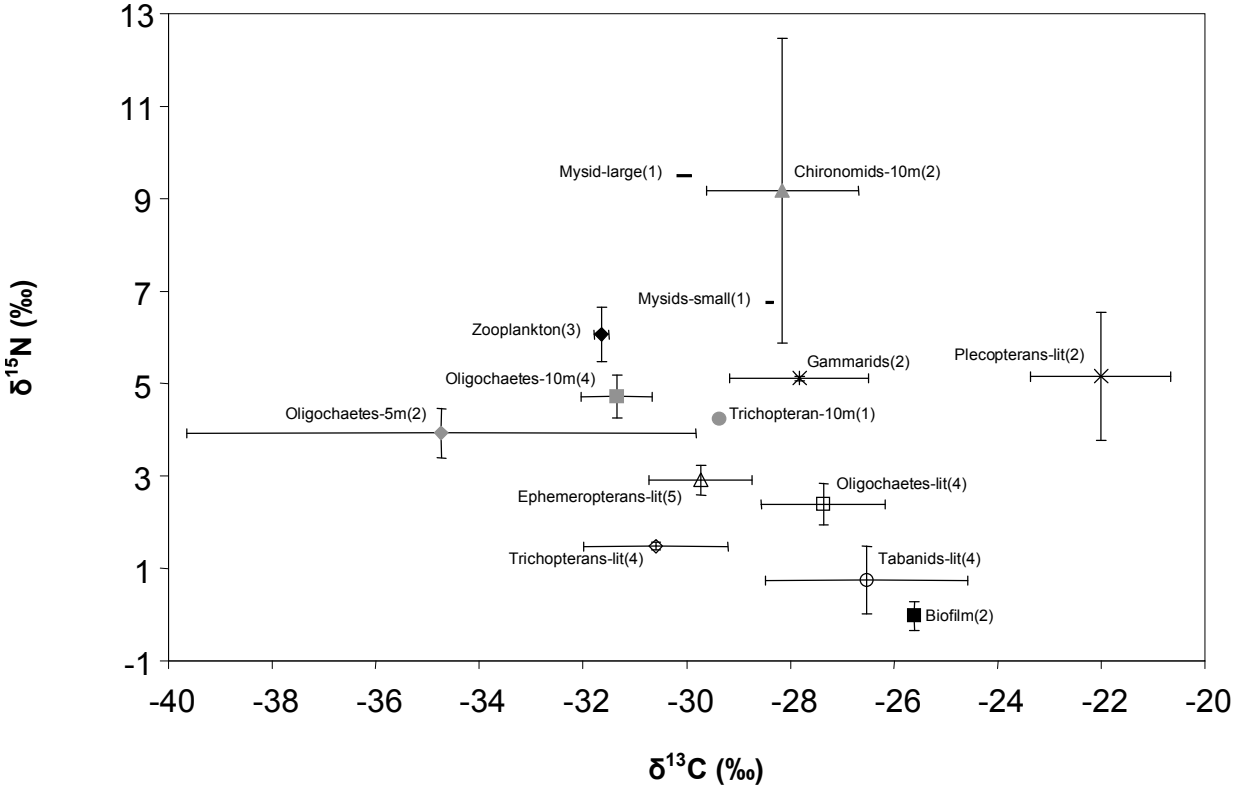


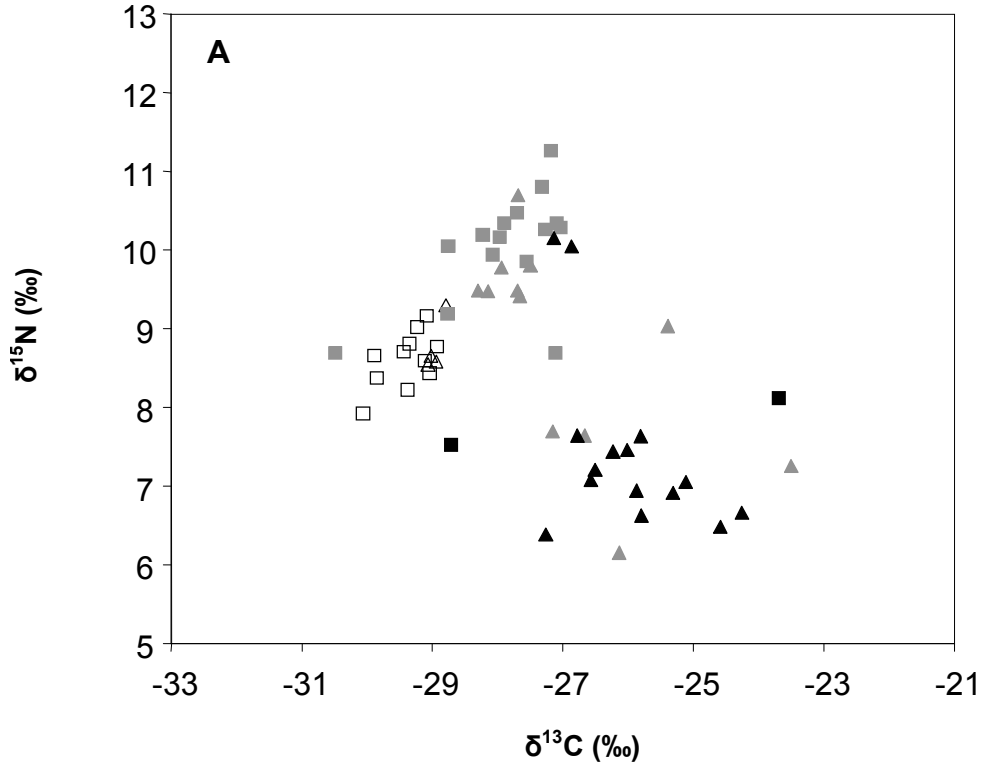
Figure 4. Mean stable isotope values for biofilm, zooplankton, and macroinvertebrates in Pulmankijärvi. Error bars show standard deviations. Sample numbers (*n*) are indicated in brackets within the labels. Sampling depths for benthic macroinvertebrates are indicated in the labels as 5 m, 10 m or lit (littoral <1 m).

3.2. Stable isotope analyses for fish

3.2.1. Comparisons of seasonal data and European whitefish groups

Stable isotope signatures for European whitefish, Arctic char, brown trout, and grayling showed some differences between seasons (Figures 5 and 6). There were significant differences between European whitefish groups (Figure 5) in their muscle $\delta^{13}C$ values ($F_{2,58} = 36.5$, $p<0.001$), muscle $\delta^{15}N$ values ($\chi^2 = 25.9$, df = 2, $p<0.001$), liver $\delta^{13}C$ values ($\chi^2 = 21.0$, df = 2, $p<0.001$), and liver $\delta^{15}N$ values ($F_{2,57} = 30.7$, $p<0.001$). All three whitefish groups differed significantly from each other in their muscle $\delta^{13}C$ values (Tukey's test, all $p<0.001$) and liver $\delta^{13}C$ values (Mann-Whitney tests, all $p<0.004$) (mean values: DRW < SRW>100g < SRW<100g), as well as in their muscle $\delta^{15}N$ values (Mann-

Whitney tests, all $p<0.002$) (mean values: SRW<100g < DRW < SRW>100g). However, only SRW<100g had significantly lower liver $\delta^{15}N$ values (Tukey's test; both $p<0.001$).



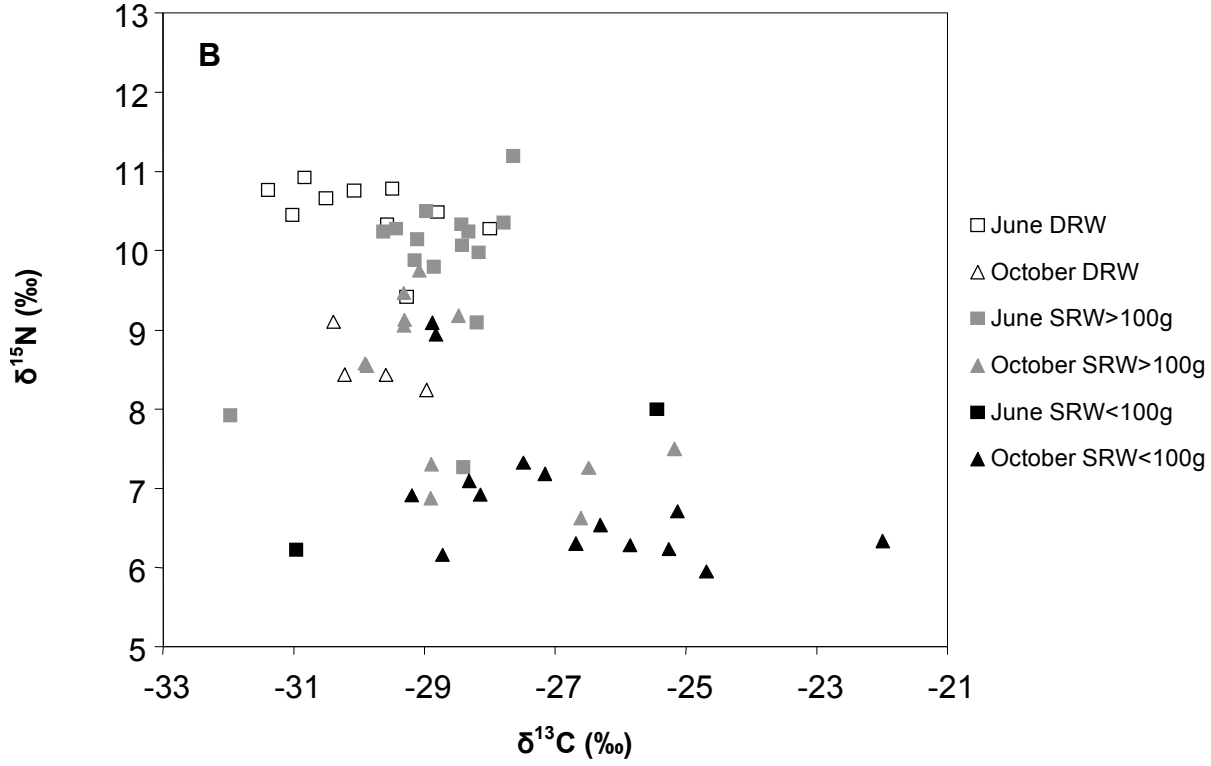
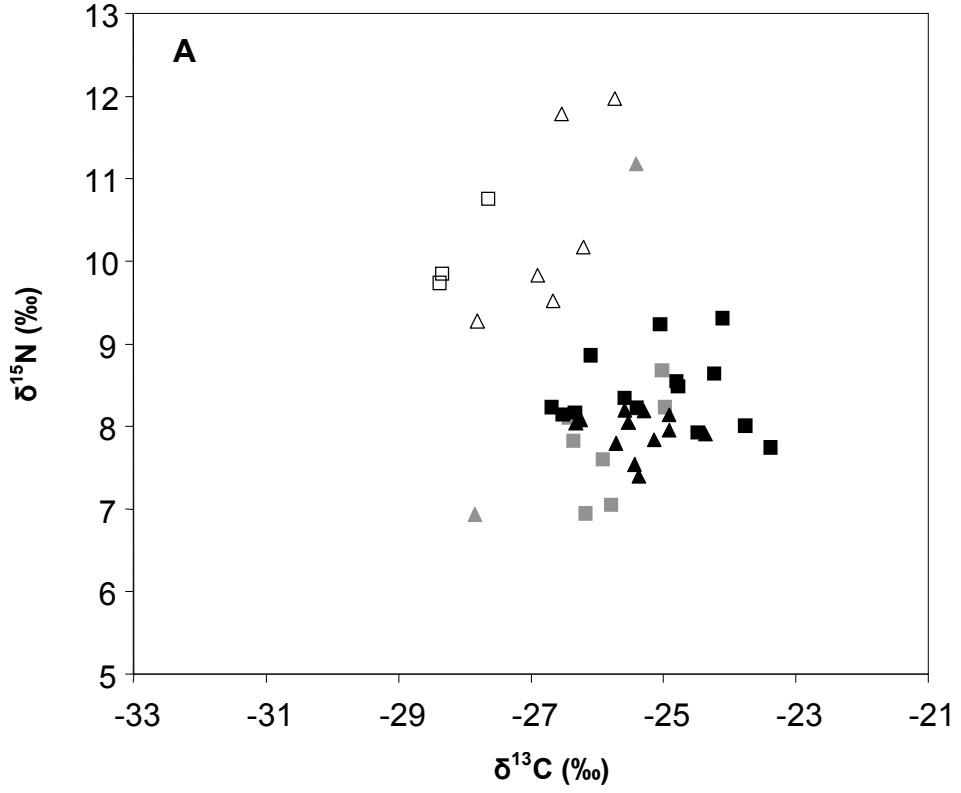


Figure 5. Seasonal variation in A) muscle (M) and B) liver (L) stable isotope values for European whitefish groups in Lake Pulmankijärvi. DRW = densely-rakered whitefish (n_M = 15, n_L = 14); SRW>100g = sparsely-rakered whitefish >100 g (n_M = 27, n_L = 27); SRW<100g = sparsely-rakered whitefish <100 g (n_M = 17, n_L = 17).



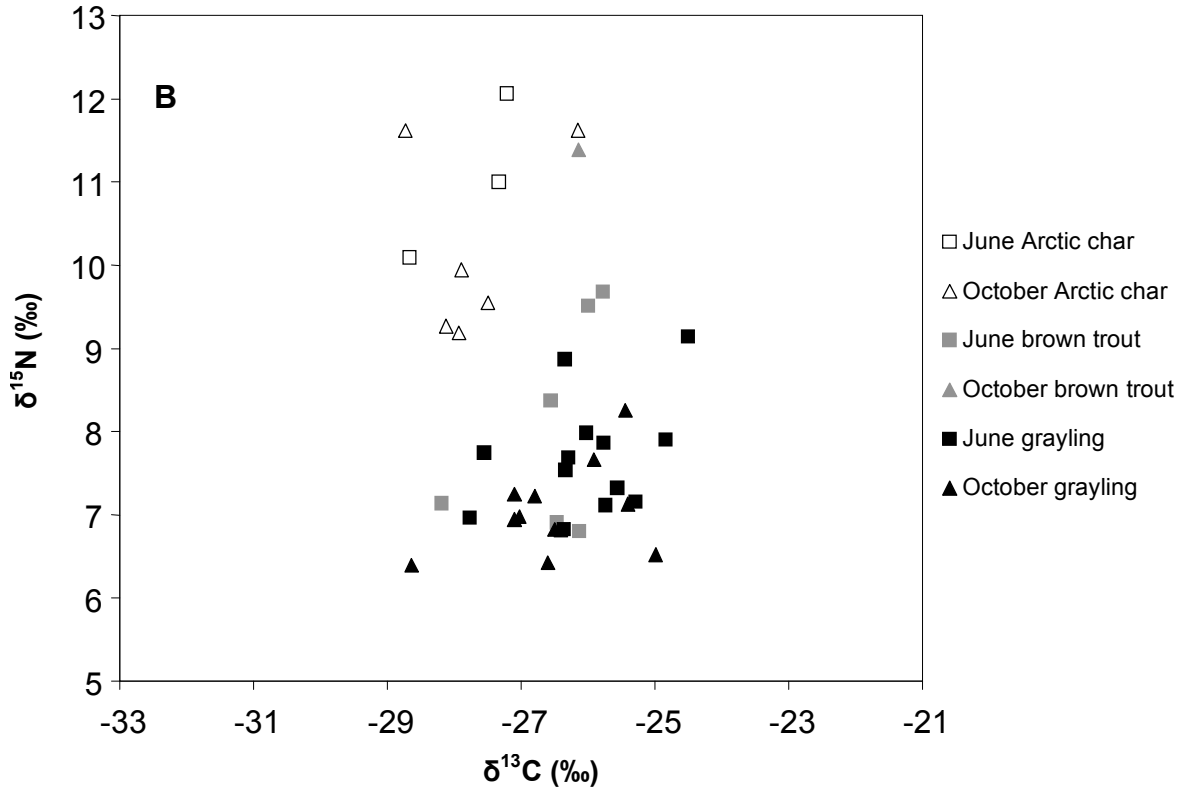


Figure 6. Seasonal variation in A) muscle (M) and B) liver (L) stable isotope values for Arctic char ($n_M = 9$, $n_L = 9$), brown trout ($n_M = 9$, $n_L = 7$), and grayling ($n_M = 26$, $n_L = 25$) in Pulmankijärvi.

3.2.2. Comparisons of fish muscle and liver tissues

Muscle $\delta^{13}C$ and lipid-normalized muscle $\delta^{13}C$ for all fish had a linear relationship (Figure 7) with a slope close to one (1.09 ± 0.05, 95% CI) and an intercept above zero (3.19 ± 1.27, 95% CI). Liver $\delta^{13}C$ and lipid-extracted liver $\delta^{13}C$ for random sub-samples of European whitefish, Arctic char, grayling, flounder, and Atlantic salmon had a linear relationship (Figure 8A) with a slope below one (0.73 ± 0.09, 95% CI) and an intercept below zero (-5.69 ± 2.35, 95% CI). However, liver $\delta^{15}N$ and lipid-extracted liver $\delta^{15}N$ for the same random sub-samples of fish had a linear relationship (Figure 8B) with a slope close to one (0.99 ± 0.09, 95% CI) and an intercept close to zero (0.29 ± 0.81, 95% CI). Muscle $\delta^{13}C$ and liver $\delta^{13}C$ for all fish had a linear relationship (Figure 9A) with a slope close to one (0.96 ± 0.09, 95% CI) and an intercept below zero (-2.10 ± 2.32, 95% CI). Muscle $\delta^{15}N$ and liver $\delta^{15}N$ for all fish had a linear relationship (Figure 9B) with a slope close to one (0.99 ± 0.13, 95% CI) and an intercept close to zero (-0.08 ± 1.12, 95% CI).

There were significant differences between muscle (n = 117), lipid-normalized muscle (n = 112), and liver (n = 107) in their $\delta^{13}C$ values for all fish ($F_{2,335} = 17.2$, $p<0.001$), and all three tissues were significantly different from each other (Tukey's test, all $p<0.023$) (mean values: liver < muscle < lipid-normalized muscle). However, there were no significant differences between muscle and liver in their $\delta^{15}N$ values for all fish ($\chi^2 = 0.345$, df = 1, $p = 0.557$). Dual-isotope plots revealed some variations between muscle and liver $\delta^{15}N$ values for each fish group (Figures 10 and 11); most notably, densely-rakered whitefish had considerably higher $\delta^{15}N$ values for liver than for muscle.

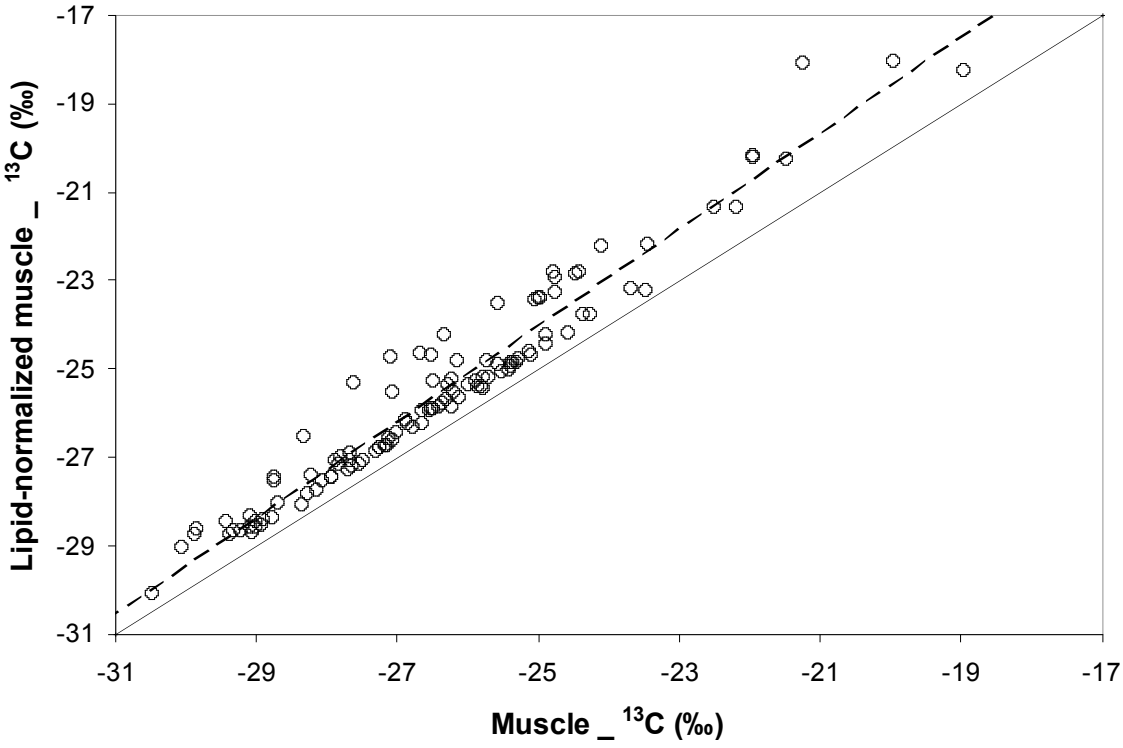
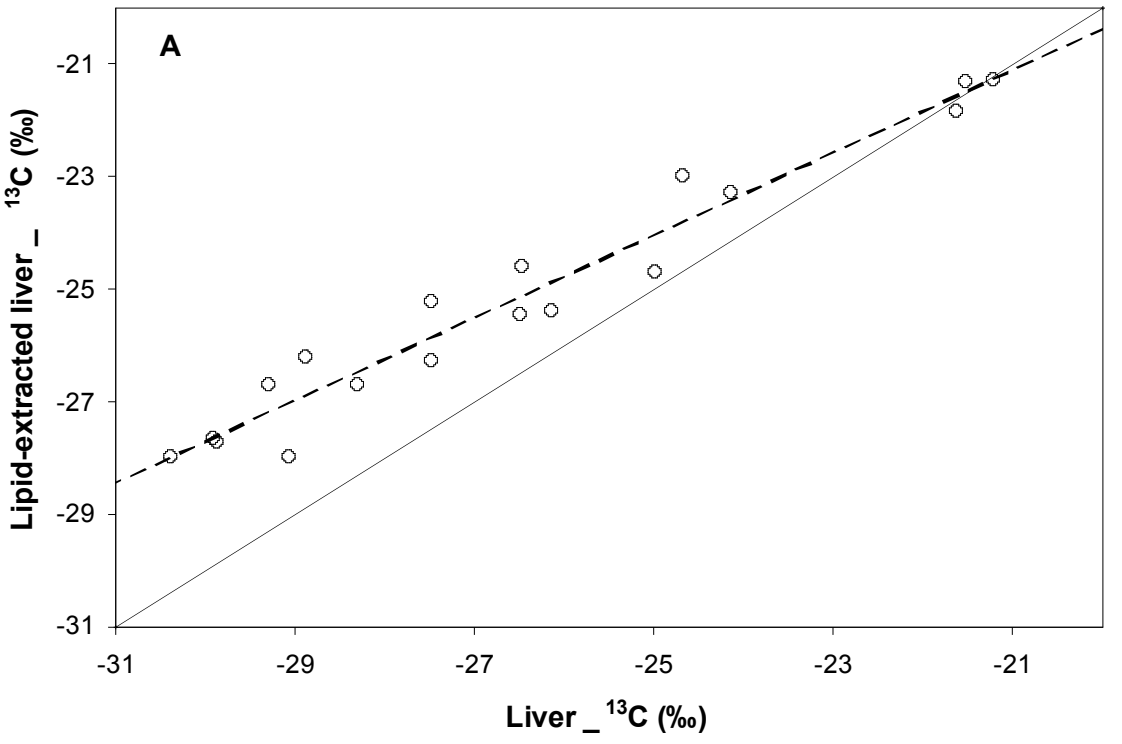


Figure 7. Relationship between muscle $\delta^{13}C$ and lipid-normalized muscle $\delta^{13}C$ values for European whitefish (n = 59), Arctic char (n = 9), brown trout (n = 9), grayling (n = 21), flounder (n = 12), and Atlantic salmon (n = 2) in Pulmankijärvi. Dashed line is the fitted linear regression (y = 1.09x + 3.19, R^2 = 0.95). Solid line shows 1:1 ratio.



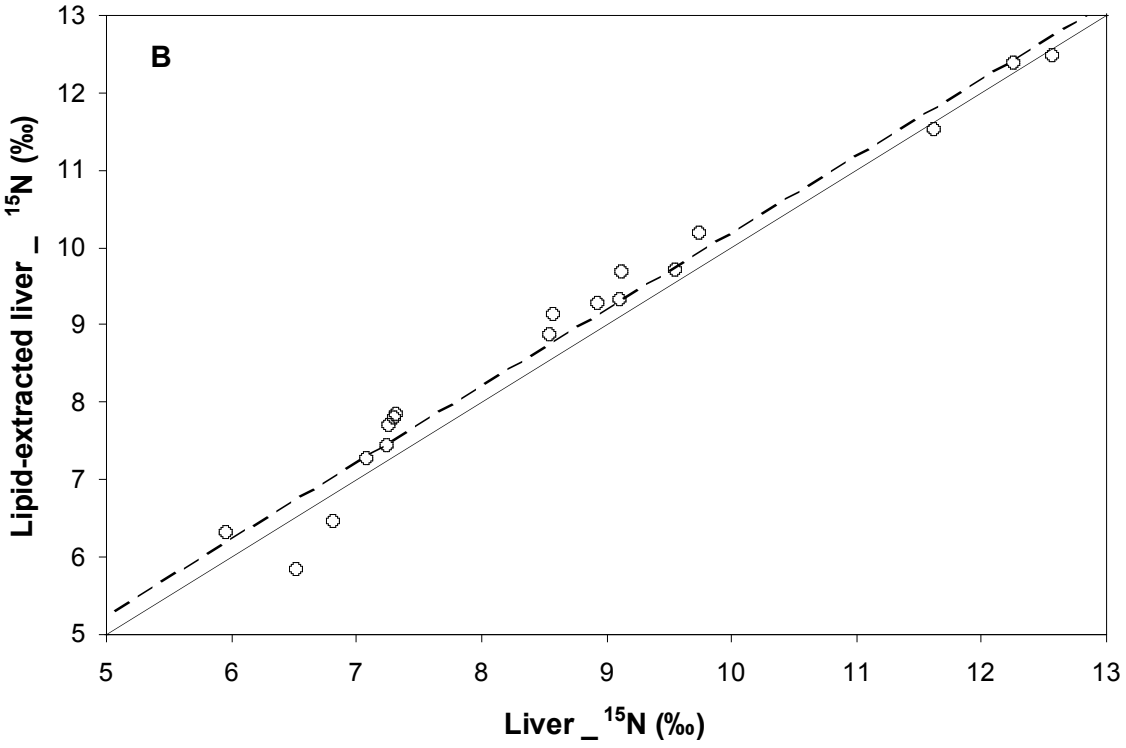
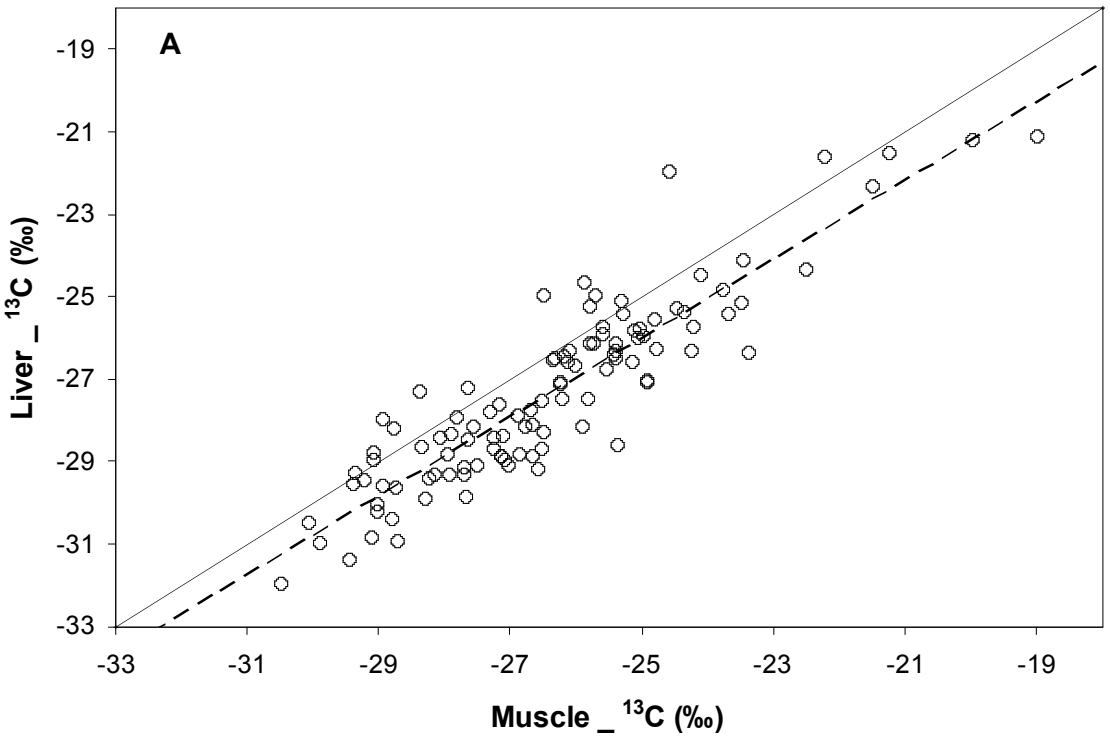


Figure 8. Relationship between A) liver $\delta^{13}C$ and lipid-extracted liver $\delta^{13}C$ values and B) liver $\delta^{15}N$ and lipid-extracted liver $\delta^{15}N$ values for random sub-samples of European whitefish (n = 10), Arctic char (n= 2), grayling (n = 2), flounder (n = 2), and Atlantic salmon (n = 2) in Pulmankijärvi. Dashed line is the fitted linear regression (A: y = 0.73x - 5.69, R^2 = 0.95; B: y = 0.99x + 0.29, R^2 = 0.97). Solid line shows 1:1 ratio.



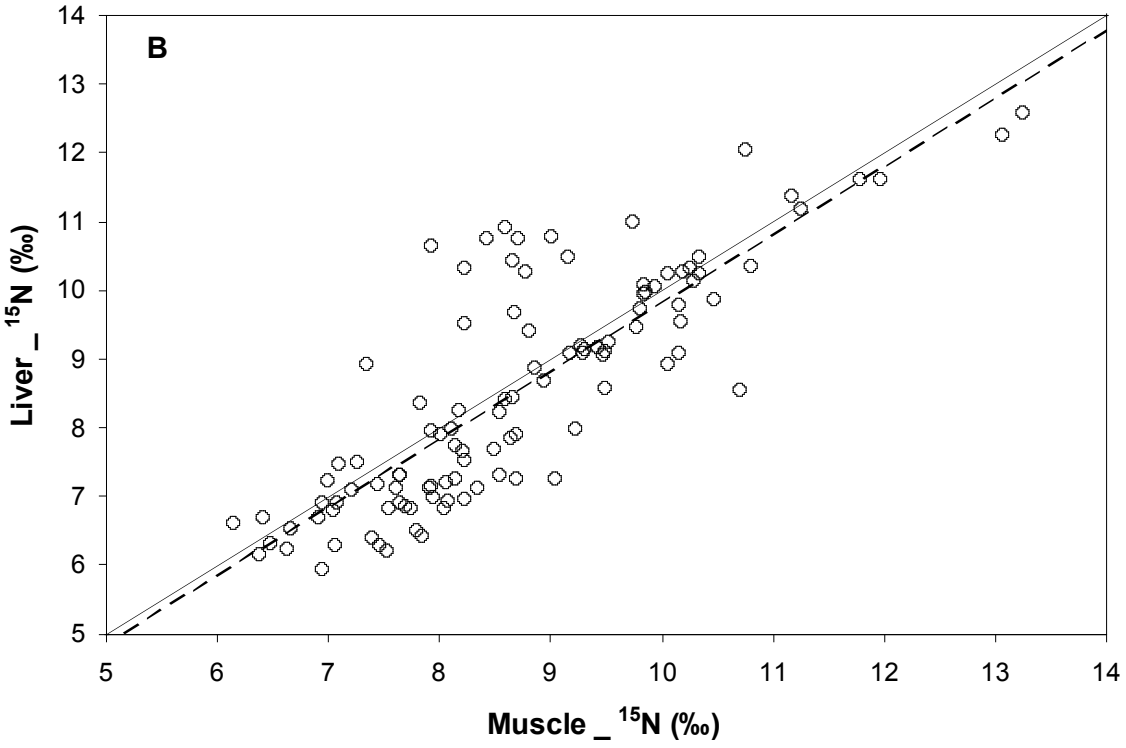


Figure 9. Relationship between A) liver $\delta^{13}C$ and muscle $\delta^{13}C$ values and B) liver $\delta^{15}N$ and muscle $\delta^{15}N$ values for European whitefish (n = 58), Arctic char (n = 9), brown trout (n = 7), grayling (n = 25), flounder (n = 6), and Atlantic salmon (n = 2) in Pulmankijärvi. Dashed line is the fitted linear regression (A: y = 0.96x - 2.10, R^2 = 0.82; B: y = 0.99x - 0.08, R^2 = 0.70). Solid line shows 1:1 ratio.

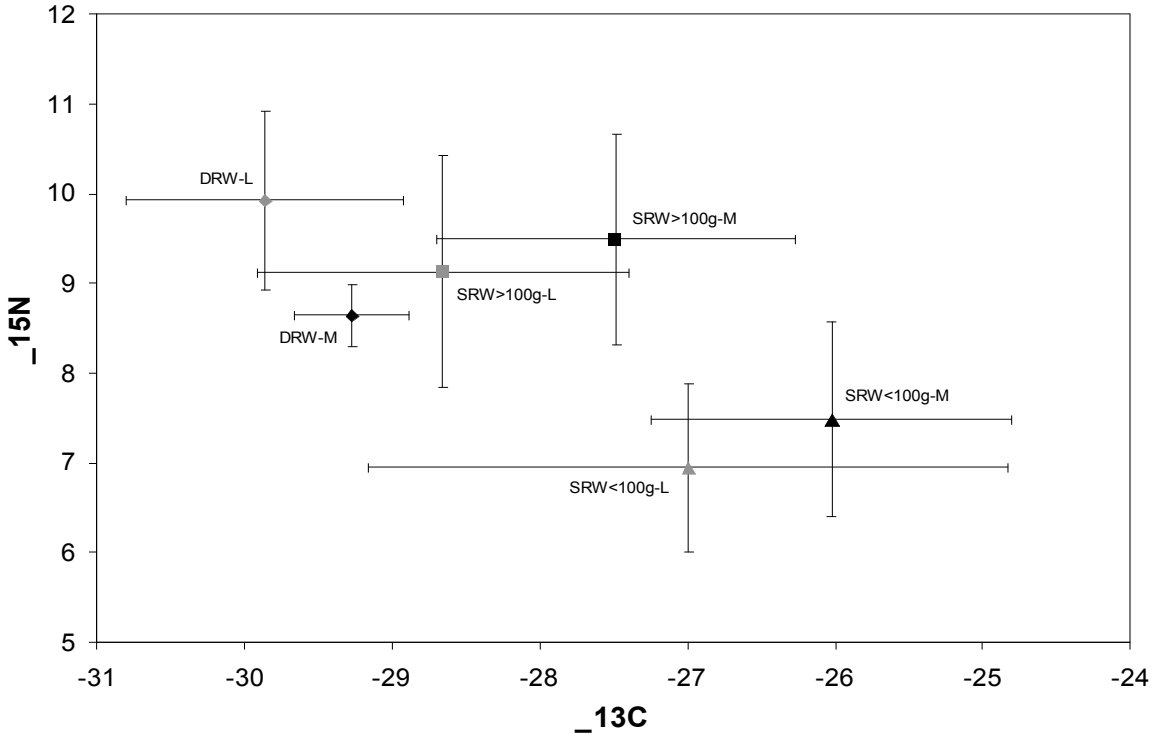


Figure 10. Muscle (M) and liver (L) mean stable isotope signatures for European whitefish groups in Pulmankijärvi. DRW = densely-rakered whitefish (n_M = 15, n_L = 14); SRW>100g = sparsely-rakered whitefish >100 g (n_M = 27, n_L = 27); SRW<100g = sparsely-rakered whitefish <100 g (n_M = 17, n_L = 17). Error bars show standard deviations.

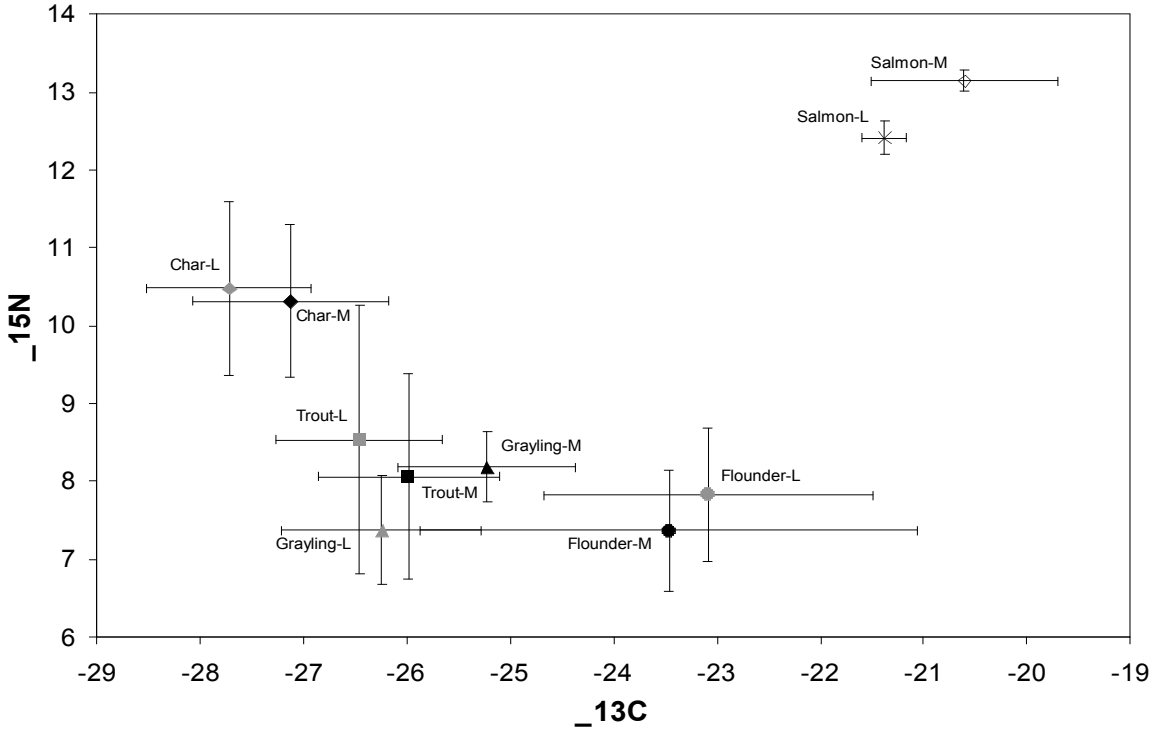


Figure 11. Muscle (M) and liver (L) mean stable isotope signatures for Arctic char (n_M = 9, n_L = 9) brown trout (n_M = 9, n_L = 7), grayling (n_M = 26, n_L = 25), flounder (n_M = 12, n_L = 6), and Atlantic salmon (n_M = 2, n_L = 2) in Pulmankijärvi. Error bars show standard deviations.

3.3. Littoral contributions to fish muscle and liver $\delta^{13}C$

The estimated stable isotope signatures for the pelagic and littoral baselines in Pulmankijärvi were clearly separated from each other (Figure 12). Muscle mean $\delta^{13}C$ values for DRW, SRW>100g, SRW<100g, Arctic char, brown trout, and grayling were between the pelagic and littoral baseline $\delta^{13}C$ values (Figure 13). However, mean $\delta^{13}C$ values for flounder muscle, Atlantic salmon muscle, three-spine stickleback (n = 1), and bullhead (n = 1) were outside the pelagic and littoral baseline $\delta^{13}C$ values. This same pattern was also shown with liver mean $\delta^{13}C$ values (Figure 14).

The mean of $LF_{fish\ tissue}$ values (Figure 15) was lowest for DRW (17%) but considerably higher for all other fish groups, increasing in the order of SRW>100g (45%), Arctic char (59%), SRW<100g (73%), brown trout (82%), grayling (89%), and flounder (96%). There were significant differences between muscle (n = 115), lipid-normalized muscle (n = 113), and liver (n = 105) in their $LF_{fish\ tissue}$ values for European whitefish, Arctic char, brown trout, grayling, and flounder ($F_{2,332}$ = 5.2, p = 0.006). Lipid-normalized muscle had significantly higher LF values than muscle (Tukey test, p = 0.029) and liver (Tukey test, p = 0.009). However, muscle and liver did not differ significantly from each other (Tukey's test, p = 0.886).

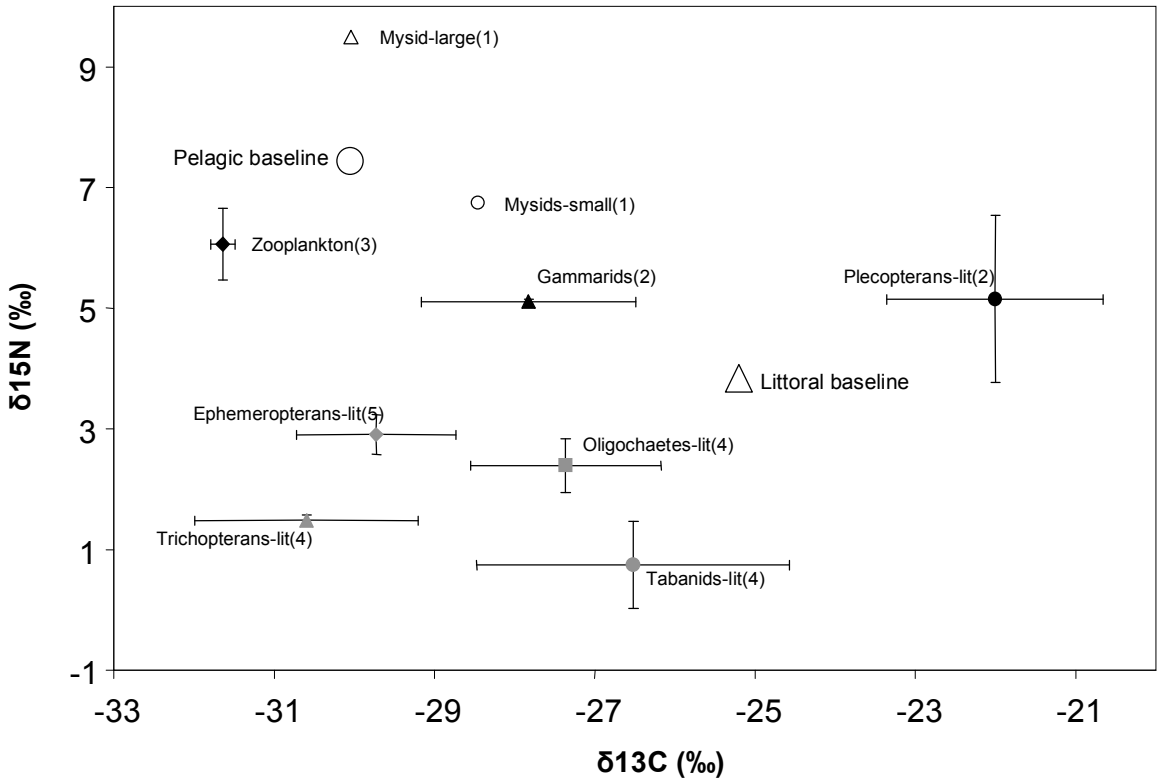


Figure 12. Stable isotope values for pelagic (zooplankton and mysids) and littoral (gammarids and littoral (lit) macroinvertebrates) baselines in Pulmankijärvi. Error bars show standard deviations. Sample numbers are indicated in brackets within the labels.

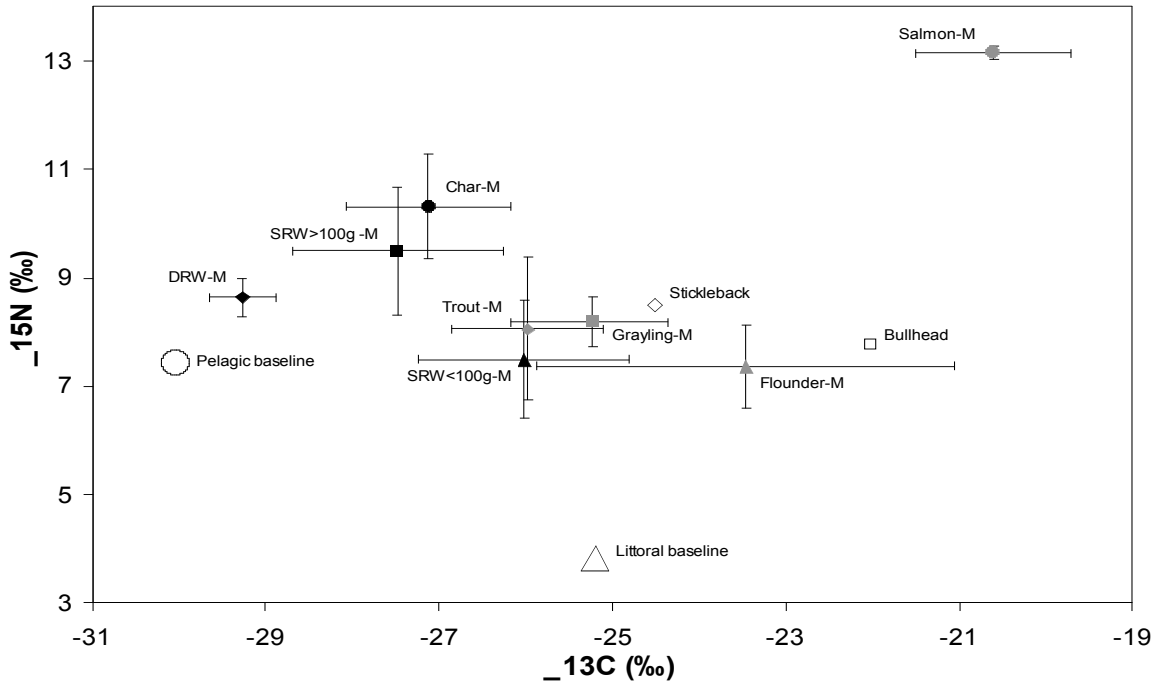


Figure 13. Mean stable isotope signatures for Pulmankijärvi food web components with muscle (M) $\delta^{13}C$ and $\delta^{15}N$ values for DRW (n = 15), SRW>100g (n = 27), SRW<100g (n = 17), Arctic char (n = 9), brown trout (n = 9), grayling (n = 26), flounder (n = 12), and Atlantic salmon (n = 2). Error bars show standard deviations. DRW = densely-rakered whitefish; SRW = sparsely-rakered whitefish.

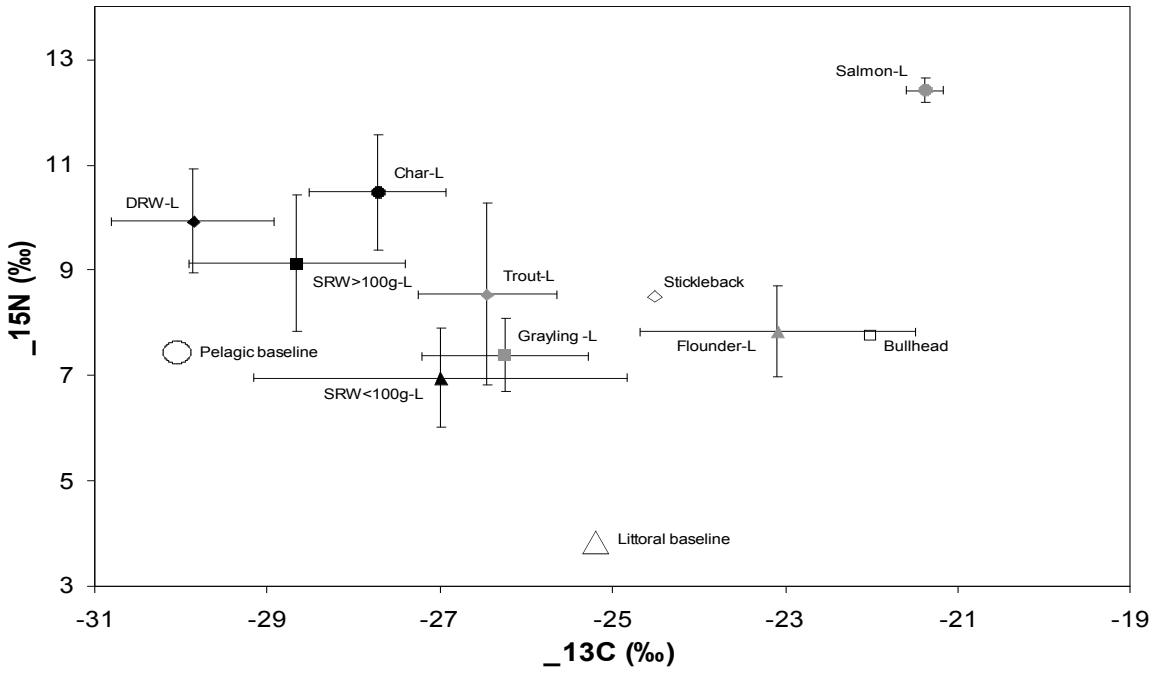


Figure 14. Mean stable isotope signatures for Pulmankijärvi food web components with liver (L) $\delta^{13}C$ and $\delta^{15}N$ values for DRW (n = 14), SRW>100g (n = 27), SRW<100g (n = 17), Arctic char (n = 9), brown trout (n = 7), grayling (n = 25), flounder (n = 6), and Atlantic salmon (n = 2). Error bars show standard deviations. DRW = densely-rakered whitefish; SRW = sparsely-rakered whitefish.

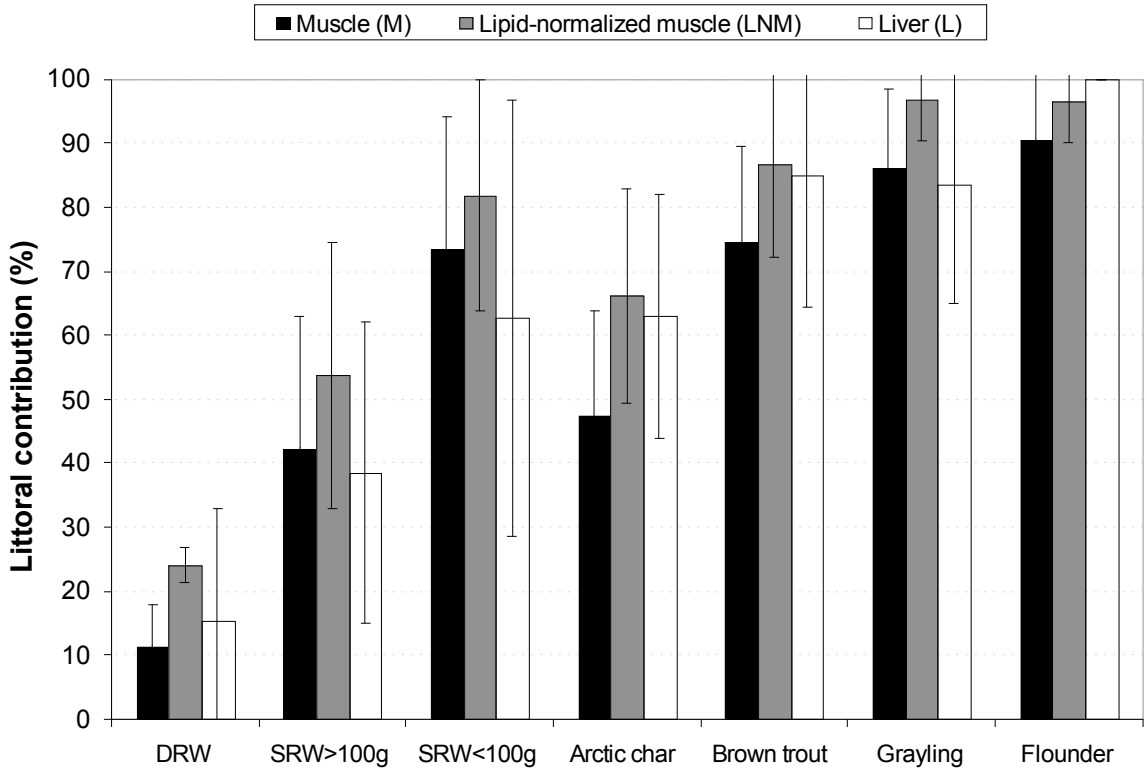


Figure 15. Mean littoral contributions to fish tissue $\delta^{13}C$ ($LF_{fish\ tissue}$) for DRW (n_M = 15, n_{LNM} = 15, n_L = 14), SRW>100g (n_M = 27, n_{LNM} = 27, n_L = 27), SRW<100g (n_M = 17, n_{LNM} = 17, n_L = 17), Arctic char (n_M = 9, n_{LNM} = 9, n_L = 9), brown trout (n_M = 9, n_{LNM} = 9, n_L = 7), grayling (n_M = 26, n_{LNM} = 24, n_L = 25), and flounder (n_M = 12, n_{LNM} = 12, n_L = 6) in Pulmankijärvi. Error bars show standard deviations. DRW = densely-rakered whitefish; SRW = sparsely-rakered whitefish.

4. DISCUSSION

4.1. Pelagic and littoral baselines in Pulmankijärvi

Stable isotope signatures at the primary consumer level of food webs in lakes can be highly variable (Hecky & Hesslein 1995, Jardine *et al.* 2003). Nevertheless, if $\delta^{13}C$ values for primary consumer endpoints are sufficiently distinct, the errors in dietary mixing model outputs are generally minor (Vander Zanden & Rasmussen 2001). The zooplankton and mysid samples in Pulmankijärvi had $\delta^{13}C$ values that indicated a clear endpoint for the pelagic baseline stable isotope signature. Profundal macroinvertebrates are not used in baseline calculations for the two-source mixing model described by Karlsson & Byström (2005), but they could be indirectly represented in the pelagic baseline because of their reliance on pelagic energy sources.

In contrast to the pelagic food sources, $\delta^{13}C$ values for the littoral macroinvertebrates were highly variable and not sufficiently distinct from the pelagic baseline $\delta^{13}C$ value to give reliable outputs from the two-source mixing model. Furthermore, other littoral macroinvertebrates pertinent to the base of the food web and fish diets were absent from the dual-isotope plot in Figure 4. Periphyton is important in Arctic lakes and a known food source for invertebrates such as snails, which have been indicated from diet studies as a major food source for trout (Sierszen *et al.* 2003). Stomach content analyses of brown trout and other fish in Pulmankijärvi revealed a substantial contribution of snails, as well as dytiscids and small chironomid larvae. Saanajärvi, in Arctic northwestern Finland, also

contained these littoral macroinvertebrates, which had considerably more enriched $\delta^{13}C$ values than trichopterans and ephemeropterans from the same lake (Eloranta 2007). Therefore, the estimated stable isotope signature for the littoral baseline in Pulmankijärvi was biased towards the more enriched $\delta^{13}C$ values for plecopterans in order to be more representative of all littoral food sources for fish.

During sampling for littoral macronivertebrates, the water in Pulmankijärvi was noted to be turbid from recent bank erosion. Terrestrial materials generally have a $\delta^{13}C$ value around -28‰ (Vander Zanden & Rasmussen 1999), and terrestrial DOC in the sediments supports much benthic invertebrate production in oligotrophic lakes (Hershey *et al.* 2006). The increase of allochthonous DOC in Pulmankijärvi probably contributed to the relatively depleted $\delta^{13}C$ values observed for most of the littoral macroinvertebrates sampled at the time. Additional sample collections of littoral macroinvertebrates in Pulmankijärvi would give a more reliable estimate of the littoral baseline stable isotope signature.

4.2. Feeding patterns of European whitefish groups

Dual-isotope plots for European whitefish in Pulmankijärvi showed three distinct groups of whitefish based on the number of gill rakers and size class. Densely-rakered whitefish were all approximately <100 g and had the most depleted $\delta^{13}C$ values, indicating a relatively more pelagic diet that coincided with the zooplankton found in stomach content analyses. Stable isotope signatures for sparsely-rakered whitefish indicated a shift to a more pelagic diet for individuals approximately >100 g, with relatively few exceptions. These findings correspond with catch statistics from Ilmast & Sterligova (2002) which revealed that sparsely-rakered whitefish aged 4+ to 7+ years were mostly caught in the pelagic zone, while young age-groups 2+ to 3+ years were observed as feeding in the littoral zone.

Although gill raker number was used to identify two different morphs of European whitefish in Pulmankijärvi, Kahilainen *et al.* (2004) has separated sympatric whitefish forms into three distinct taxonomic groups, referred to as densely-rakered, smaller sparsely-rakered, and larger sparsely-rakered. Harrod & Kahilainen (unpublished data) showed that larger sparsely-rakered whitefish from Finnish Arctic lakes actually had more enriched $\delta^{13}C$ values than smaller sparsely-rakered whitefish, indicating a more littoral diet for the larger form. This may explain why several of the sparsely-rakered whitefish sampled from Lake Pulmankijärvi did not have stable isotope signatures corresponding with the other individuals in the same size class. However, stomach content analyses revealed a substantial contribution of mysids to the diets of sparsely-rakered whitefish >100 g, while gammarids appeared to be an important component of the diets of sparsely-rakered whitefish <100 g. Historical information has shown that the diets of whitefish in the North American Great Lakes traditionally consisted of mysids (Ihssen *et al.* 1981). Perhaps of more general importance, Byström *et al.* (2004) suggested that habitat use by larger individuals should depend mainly on foraging gains, while smaller individuals have a trade-off with predation risk. Ilmast & Sterligova (2002) concluded from their analyses of European whitefish in Pulmankijärvi that the differences in observed feeding patterns depended on food resource availability rather than gill raker morphology. Further research is needed on sympatric whitefish forms in Arctic lakes and the importance of mysids and gammarids in their diets to more conclusively explain the results from stable isotope analyses of Pulmankijärvi whitefish groups.

4.3. Inferences from fish muscle and liver data

Different tissues tend to reflect the ratios of new diets at different rates (Jardine *et al.* 2003). Because the slope was near one for the linear regression analysis between fish muscle and liver $\delta^{13}C$ values, most fish probably maintained relatively consistent diets over time. The same conclusion can be applied for the linear regression analysis between fish muscle and liver $\delta^{15}N$ values, although there was considerably more variability between fish groups. The $\delta^{15}N$ values of primary consumers can be highly variable (Vander Zanden & Rasmussen 1999), and temporal changes in the $\delta^{15}N$ values of certain primary consumers will probably be reflected in the liver samples of fish groups that primarily feed on them. This could be the cause particularly for the considerable difference between muscle and liver mean $\delta^{15}N$ values for densely-rakered whitefish, which had $\delta^{13}C$ values indicating a diet of mostly zooplankton. Harrod & Kahilainen (unpublished data) remarked that the reduced scatter in their relationships between muscle and liver stable isotope values for European whitefish from Finnish Arctic lakes may indicate that individual whitefish maintain relatively similar diets over time. More seasonal data would need to be collected for further analyses.

Lipid-extraction or lipid-normalization is sometimes performed for fish tissues with C:N ratios >4.0 (Jardine *et al.* 2003). Fish muscle and liver samples from Pulmankijärvi generally had C:N ratios <4.0, with the exception of Atlantic salmon, but both of these lipid-correcting procedures were used to test their effects on the data. Although lipid-extraction was only done for a small sub-set of random liver samples from different fish groups, there seemed to be a trend of decreasing change in $\delta^{13}C$ values as liver $\delta^{13}C$ values increased. However, there was no apparent change in $\delta^{15}N$ values, and more lipid-extracted data would be required for further use of their stable isotope signatures in analyses. Lipid-normalized muscle $\delta^{13}C$ values were ultimately used to compare the effect the mathematical procedure had on littoral contributions to fish tissue. Kiljunen *et al.* (2006) warned how mixing model output was greatly influenced by whether prey or consumer values alone or together were lipid-normalized, and they advised against using the model for invertebrate $\delta^{13}C$ values. Therefore, lipid-normalization was not performed for any food source data.

4.4. Importance of littoral food sources to the fish populations

Littoral contributions to fish tissue $\delta^{13}C$ ($LF_{fish\ tissue}$) indicated that populations of sparsely-rakered whitefish <100 g, brown trout, grayling, and flounder rely mostly on littoral food sources in Pulmankijärvi. Grayling are known to be insectivorous (Sierszen *et al.* 2003), and flounder diets in freshwater have been shown to be comprised largely of aquatic insects, molluscs, and crustaceans (Beaumont & Mann 1984). Piscivores, such as brown trout, often forage broadly upon benthic and terrestrial invertebrates as well (Vander Zanden & Vadeboncoeur 2002). Densely-rakered whitefish are clearly more dependent on pelagic food sources in Pulmankijärvi, while populations of sparsely-rakered whitefish >100 g and Arctic char have near equal dependence on littoral and pelagic food sources. Stomach content analyses of Arctic char from Pulmankijärvi indicated that mysids were likely an important source of food in their diets. All fish populations in Pulmankijärvi tend to exhibit a wide range of $LF_{fish\ tissue}$ values among individuals, but mean LF values for muscle and liver are relatively similar within each population. However, lipid-normalization of fish muscle $\delta^{13}C$ values generally gives higher LF values and probably should not be used alone for making specific conclusions.

$LF_{fish\ tissue}$ values were not estimated for Atlantic salmon in Pulmankijärvi because their tissue $\delta^{13}C$ values reflected those of marine signatures, which have been found to be

between -20 and -21.8‰ (Jardine *et al.* 2003). Individuals of flounder also had $\delta^{13}C$ values that resembled a marine influence, but tissue mean $\delta^{13}C$ values probably indicated an isotopic dilution reflecting local food sources after a short but rapid period of growth <2 months (Jardine *et al.* 2003). LF values were not shown for three-spined stickleback and bullhead because there was only one sample for each, but their stable isotope signatures indicated that they both feed primarily on littoral food sources.

Pulmankijärvi has a similar fish community (including European whitefish, Arctic char, brown trout, and grayling) to Kilpisjärvi, an Arctic lake in northwestern Finland with a greater surface area (37 km^2) and maximum depth (57 m). The mean of the $LF_{fish\ tissue}$ values for Arctic char in Pulmankijärvi (59%) corresponds closely with the mean littoral contribution to Arctic char in Kilpisjärvi (64%) (Eloranta 2007). In contrast, Saanajärvi, also in northwestern Finland, has a less diverse Arctic fish community (only Arctic char and brown trout) with a smaller surface area (0.7 km^2) and maximum depth (24 m). Mean littoral contributions to Saanajärvi Arctic char (84%) and brown trout (90%) (Eloranta 2007) were both higher than the mean of the $LF_{fish\ tissue}$ values for Pulmankijärvi Arctic char (59%) and brown trout (82%). A study on nine sub-Arctic lakes in northern Sweden revealed that the contribution of littoral energy sources to char body carbon ranged between 62% and 94% among the lakes (Karlsson & Byström 2005).

These lake comparisons probably reflect the greater competition for limited littoral food resources in more complex Arctic fish communities, thereby encouraging an increase in pelagic feeding for fish that would typically rely on a more littoral diet. A study on the food web consequences of two invasive fish species in Canadian lakes indicated a shift in the diet of native lake trout towards zooplankton and a reduced dependence on littoral fish (Vander Zanden *et al.* 1999). Vander Zanden & Vadeboncoeur (2002) remarked that many types of fish exhibit flexible feeding patterns and undergo diet shifts that deviate from their presumed position in the food web. Furthermore, lake surface area and maximum depth influence the proportion of littoral area, which likely affects the relative availability of littoral food resources to fish. Littoral habitat and lake size may also influence coupling between benthic and pelagic energy pathways (Vander Zanden *et al.* 2005).

There is evidence that benthic production makes important contributions to the support of food webs in Arctic lakes (Sierszen *et al.* 2003). Karlsson & Byström (2005) concluded that top consumers in sub-Arctic lakes rely heavily on littoral energy sources possibly because primary consumers in littoral habitats are larger and more efficient at energy mobilization. Sierszen *et al.* (2003) suggested that the importance of benthos in the Arctic lake food webs they studied is due to the extreme oligotrophy, resulting in planktonic resources that are insufficient to support planktivorous consumers. Stable isotope analyses of the food web structure in Pulmankijärvi indicated that littoral production dominates the energy flow to most of the fish populations. However, densely-rakered whitefish are primarily supported by zooplankton, and mysids are probably an important component in the partially pelagic diets of sparsely-rakered whitefish >100 g and Arctic char. Because catch statistics by Ilmast & Sterligova (2002) showed that sparsely-rakered whitefish aged 5+ to 9+ years were the most abundant fish in Pulmankijärvi, pelagic production may be extremely important to the overall fish biomass in this Arctic lake. Further research in Arctic lakes could be directed towards the importance of mysids and other pelagic prey to sympatric whitefish forms and Arctic char.

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