Variations in feeding habitats and mercury levels in fish from Lake Norsjø, Southern Norway

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Sammendrag

Variasjoner i næringshabitat og kvikksølvnivåer i fisk fra Norsjø, Sør-Norge

Variasjoner i fødehabitat og total kvikksølv (THg) i fisk ble undersøkt i 9 ulike arter i innsjøen Norsjø, Telemark. En stabil isotop datamodell ($\delta^{13}C$ og $\delta^{15}N$) med zooplankton (pelagisk habitat) og zoobentos (littoralt habitat) som ytterpunkter i en fødevalgmodell, viste at fisk på lave trofisk nivåer furasjerer over hele den littorale-pelagiale fødeaksen. Mens krøkle (*Osmerus eperlanus*) primært inntar pelagisk føde, furasjerer trepigget stingsild (*Gasterosteus aculeatus*) primært littoralt. Sik (*Coregonus lavaretus*) viser mye større plastisitet, fra rene zooplankton-spisere til rene zoobentos-spisere. Variasjonene i $\delta^{15}N$ i fiskematerialet tilsvarer en variasjon i trofisk nivå (Λ) på 2,4, hvor de høyeste trofiske nivåene ($\Lambda > 4$) ble funnet hos fiskespisende gjedde (*Esox lucius*), brunørret (*Salmo trutta*) og røye (*Salvelinus alpinus*). Disse hadde også de høyeste Hg-konsentrasjonene. At disse også hadde de mest intermediære $\delta^{13}C$-verdiene, indikerer at fiskespisende fisk i stor grad spiser fisk fra både littorale og pelagiale habitater.

Abstract

Variation in feeding habitat and total mercury (THg) levels in muscle tissue from 9 fish species have been investigated in Lake Norsjø, Southern Norway. By use of stable isotope data ($\delta^{13}C$ and $\delta^{15}N$) in a two-source mixing model with zooplankton (pelagic habitats) and zoobenthos (littoral habitats) as end-members, fish with low trophic position together spanned the entire range of benthivory. Smelt (*Osmerus eperlanus*) and stickleback (*Gasterosteus aculeatus*) showed a tendency to cluster at the outer edges of the pelagic-littoral gradient, while the whitefish (*Coregonus lavaretus*) population covered individuals from an almost obligate benthos diet to an almost obligate zooplankton diet. By use of $\delta^{15}N$ data for estimation of trophic levels (Λ), the investigated fish covered about 2.4 trophic levels, and the highest values ($\Lambda > 4$) were found in piscivore individuals of pike (*Esox lucius)*, brown trout (*Salmo trutta*) and Arctic charr (*Salvelinus alpinus*). Besides having the highest Λ and the subsequent highest Hg concentrations in muscle tissue, the piscivore species exhibited the most intermediate $\delta^{13}C$ signatures of the investigated species, indicating that piscivore fish significantly integrate across littoral and pelagic food chains and habitats.

Introduction

Even though mercury (Hg) occurs naturally in the environment, anthropogenic sources contribute significantly to Hg deposition and distribution in nature (Streets et al., 2005; Pacyna et al., 2006; Pacyna et al., 2010; Pirrone et al., 2010). High Hg concentrations in freshwater fishes remain a major problem of concern in the Nordic countries, with long-range transport of atmospheric Hg as the main source to aquatic ecosystems (Rognerud and Fjeld, 1993; Munthe et al., 2004). Human and wildlife exposure to Hg occurs mostly through the consumption of contaminated freshwater and marine fish (Alexander et al., 2007). Studies have shown that the main Hg form accumulated in fish is monomethylmercury, CH_3Hg^+ (MeHg), a persistent bioaccumulating toxic form of Hg, mainly obtained from the diet (Huckabee et al., 1979; Mathers and Johansen, 1985; Lindqvist et al., 1991; Bloom, 1992). Accordingly, Hg concentrations in fish typically increase towards higher trophic levels, i.e. piscivorous fish have higher MeHg concentrations than planktivorous fish (Wren et al., 1983; Watras and Bloom, 1992; Dietz et al., 1996). The majority of MeHg is stored in muscle tissue (proteins), but other tissues such as liver, kidney and spleen are also shown to accumulate MeHg (Giblin and Massaro, 1973). The greatest increase in MeHg concentration as it moves up the food chain, is the first step between abiotic matrices, such as water and sediments, and organisms at the base of the food chain (Fitzerald et al., 2007; Pickhardt and Fisher, 2007). Organisms at higher trophic levels biomagnify MeHg primarily from ingestion of prey items (Hall et al., 1997; Hrenchuck et al., 2012) due to the high affinity of MeHg for thiol groups in proteins and its lipophilic nature when bound to ligands such as Cl^- (Harris et al., 2003). Accordingly, the proportion of total Hg (THg) as MeHg increases in the food web, from 15% in phytoplankton to > 95% in fish (Watras and Bloom, 1992).

Stable carbon and nitrogen isotope ratios ($\delta^{13}C = {}^{13}C/{}^{12}C$ and $\delta^{15}N = {}^{15}N/{}^{14}N$) are widely used to provide time-integrated information about feeding relationships and energy flow through food webs (Peterson and Fry, 1987; Cabana and Rasmussen, 1994; Post, 2002). The relatively high isotope fractionation of $\delta^{15}N$ up the food web, averaging about 3.4 ± 1 ‰ per trophic level (Post, 2002), provides a good approach to the measurement of food web processes in the field (Owens, 1987, Peterson and Fry, 1987) and further extended to modelling of biomagnification of persistent contaminants such as Hg (Cabana and Rasmussen, 1994; Yoshioka et al., 1994). Because of strong fractionation of inorganic carbon among different primary producers and low fractionation up the food web (0.4 ± 1.3 ‰; Post 2002), the $\delta^{13}C$ signature of aquatic consumers can provide information about energy sources, deriving from pelagic, littoral and terrestrial habitats (DeNiro and Epstein, 1978; France, 1996, 1997; Vander Zanden and Rasmussen, 1999; Post 2002; Karlsson and Byström, 2005; Carpenter et al., 2005). However, due to large variations in isotope signatures of inorganic N and C compounds in aquatic systems (Paerl and Fogel, 1994; Yoshioka et al., 1994; Cabana and Rasmussen, 1996), as well as variations in fractionation during the fixation of these compounds by different primary producers in various lake habitats (Hecky and Hesslein, 1995; France, 1996; Rau, 1980; Cabana and Rasmussen, 1996; Vander Zanden and Rasmussen, 1999), large variations in $\delta^{15}N$ and $\delta^{13}C$ of primary producers may occur within and between lakes both in time and space (Gray et al., 2001; Vander Zanden and Rasmussen, 1999). This carbon (C) might be consumed directly by grazing or recycled via the microbial loop (Wetzel, 2001). Zooplankton thus utilizes autochthonous C by grazing on phytoplankton or on bacteria and other organisms depending on phytoplankton production. However, bacteria can also utilize allochthonous organic C as energy source (De Haan, 1977; Tranvik, 1988). Furthermore, allochthonous matter can enter the food web directly by detritivorous zooplankton (Hessen et al., 1990) and, especially in oligotrophic lakes, allochthonous material may constitute a substantial C source for zooplankton (Salonen and Hammar, 1986; Meili et al., 1996, 2000; Grey et

al., 2001). Zoobenthos also use allochthonous organic C as an important energy source (Karlsson et al., 2012) in addition to the primary produced autochthonous C (mainly by periphyton) in the littoral zone (Björk-Ramberg, 1983; Vadebonceour et al., 2002). Thus, as with primary producers, spatio-temporal variations are also seen in stable isotope signatures of zoobenthos and zooplankton (Gray et al., 2001; Berggren al., 2010).

Classical food web theory has been challenged by the recognition of the complexity and multi-chain omnivory that characterizes natural aquatic ecosystems (Polis and Strong 1996; Vander Zanden and Rasmussen, 1996; Vander Zanden and Vadeboncoeur, 2002; Jansson et al., 2007). This combined with the diurnal vertical migration behaviour of many pelagic invertebrates, the diurnal horizontal migration of many littoral invertebrates (Thorp and Covich, 2001), and the passive transport of plankton by strong winds and internal currents and seiches (Wetzel, 2001), especially in large lakes, implies that primary production from a given location in a lake can move around as it is transferred up the food web.

Regarding fishes, a fundamental characteristic is their large change in body size over their lifetimes (Werner and Gilliam, 1984; Cohen et al., 2003), which means that an individual may change its food resources during development (Keast, 1977; Werner and Gilliam, 1984; Persson, 1988; Gerking, 1994; Osenberg et al., 1994; Olsson et al., 1995). In addition, trophic polymorphism occurs within various fish species (Clabaut et al., 2007; Harrod et al., 2010; Eloranta et al., 2011), as well as individual specialized foraging tactics (Ringler, 1983). This means that there are a lot of ecological variations among fishes, both intraspecific and interspecific (Cohen et al., 2003), and this is potentially reflected in their stable isotope signatures.

Depending on the extent of interactions between various lake habitats and the variation in use of C energy sources within these habitats, many food web configurations can be envisioned both in time and space. Knowledge about the importance of such linkages and the implication for food web dynamics and lake-ecosystem processes is still limited. Despite this, as $\delta^{15}N$ and $\delta^{13}C$ signatures in consumers vary between lakes and among habitats within lakes, $\delta^{15}N$ and $\delta^{13}C$ data from primary consumers in each lake and within various habitats (littoral, pelagic, profundal) are still very useful for baseline correction in order to obtain better estimates of relative trophic positions of organisms present at higher trophic levels (Cabana and Rasmussen, 1996; Vander Zanden and Rasmussen, 1999; Post, 2002). This is further useful for the interpretation of biomagnification of persistent contaminants in food, such as Hg.

In our study, total Hg (THg), $\delta^{15}N$ and $\delta^{13}C$ signatures have been investigated in pelagic and littoral invertebrates and in 9 fish species from the northern parts of Lake Norsjø, a large, deep clear-water lake in southern Norway. The data primarily include fish caught during autumn (August/September) and early winter (December). The main object was to study intraspecific and interspecific variations in food selection and habitat use among fishes and subsequent consequences for THg-content in muscle tissue.

Material and methods

Site description

Lake Norsjø is situated in the county of Telemark, Southern Norway, a few kilometres from the ocean, 15.3 m a.s.l. With its lake and catchment area of 55.5 km^2 and 10 377.6 km^2, respectively, it is among the 20 largest lakes in Norway. The total lake volume is 5.10 km^3, theoretical residence time 0.5 years, and mean and maximum depths 87 m and 176 m, respectively (Tjomsland et al., 1983). Three main rivers enter the lake, all draining large high mountain areas north of the lake. The lake is surrounded by agricultural areas, west and north, and by forest and mountainous areas in the east. In 2009, annual average volume-weighted conductivity and pH at the lake outlet were 2.05 mS m^{-1} and 6.74, while the concentrations of total organic C, total nitrogen (N) and total phosphorous (P) were 2.6 mg C L^{-1}, 309 mg N L^{-1} and 11 mg P L^{-1}, respectively (Skarbøvik

et al., 2010). They also reported average concentration of total Hg (THg) in water at the lake outlet in 2009 to be 1.46 ng L^{-1}.

Historically, at least two main local Hg emitters have been located in the nearby area of the lake: Tinfoss paper mill, located about 30 km north of Lake Norsjø, and the historical use of Hg as fungicide by farmers primarily located in the lowland areas around the three incoming rivers and around the lake. The paper mill was closed in 1972, while Hg has been forbidden as fungicide in Norwegian agriculture since 1990.

Sampling

All invertebrate and fish sampling was conducted in the northern part of the lake. Fish were caught by gillnets with eight different mesh sizes (from 10 mm – 52 mm), by trolling, by landing nets and fish pots. Invertebrates were collected in July, while the majority of fish (≈ 67 %) were sampled in August/September. In addition another 20 % of the fish (only European whitefish, *Coregonus lavaretus* and northern pike, *Esox lucius*) were caught in December. All European smelt, *Osmerus eperlanus* (n = 10) were caught during their spawning season in May. Except one individual captured by gill net, all brown trout (*Salmo trutta*), were caught by trolling in May or August/September. All fish species were caught during one year, except for Arctic charr (*Salvelinus alpinus*) which were collected in September, the following year, after we have succeeded in localizing an important spawning site at a depth of 20-30 m.

Benthic macroinvertebrates were collected (depth < 1 m) using hand-held dip nets, while zooplankton were collected using a 150 µm zooplankton net. Horizontal zooplankton tows were conducted at about 1 m and 8 m depth. Individual benthic invertebrates and zooplankton were identified at least to orders (Benthic: Ephemeroptera, Trichoptera, Hemiptera, Gastropda; Zooplankton: Calanoida, Cyclopoida, Cladocera) and classified according to dietary preference, based on published dietary description by Thorp and Covich (2001).

All biological samples were stored in a freezer (< -18°C) before analysed for Hg and stable isotopes.

Preparation and analysis

Morphometric analysis of fish

Total length and weight of all fishes were measured, and otoliths taken for age determination. In addition, scales (all species), metapterygoid bones (northern pike) and operculum bones (perch, *Perca fluviatilis*) were collected as useful support for age determination by otoliths. All fish were individually labelled and stored in a freezer in separate plastic bags. Muscle tissue for analyses of THg and stable N and C isotopes was taken from the mid dorsal muscle, posterior to the dorsal fin above the lateral line. The otolith structure was heated up with a butane lighter until it became light brown and, thereafter, transversally sectioned through the nucleus into two pieces prior to stereomicroscope investigation.

Mercury analysis

Total Hg (THg) in fish was measured at The University College of Southeast Norway by the standard operating procedure (No. HC520B.SOP). About 1 g (± 0.02 g) of skinless, dorsal muscle tissue was dissolved in concentrated nitric acid under high pressure and temperature using a microwave digestion system. The Hg in solution was analysed using a non-dispersive atomic fluorescence spectrometer, PSA 10.025 Millenium Merlin system (PS Analytical). The sample digestion procedure is described by Feng and Barrat (1994), while the procedure for instrumental measurement of Hg is described by Bloom and Fitzerald (1988). The calibration curve is prepared by reducing standard solution from a Perkin Elmer Hg standard stock solution. All the labvare (glass and teflon) were decontaminated according to the procedure described by Nriagu et al. (1993). The detection limit of the instrument is 0.01 ng L^{-1}. All THg data in fish is expressed in ppm wet weight (ww).

Stable isotope analysis

Five to ten individuals of various benthic invertebrate groups (Gastropoda, ΣEphemeroptera/Trichoptera and Hemiptera), were pooled together into one sample before freeze dried. As the abundance of zooplankton species known to be pred-

atory was low (< 1 %), they were not removed from the zooplankton samples before freeze dried. Skinless, dorsal muscle tissue was taken from each individual fish, except for sticklebacks, where whole skinless fillets from 5 individuals were pooled together, due to limited tissue material. The samples were dried overnight in an oven, at 60-80° C, before ground into fine powder using mortar and pestle and dried again at the same temperature for another six hours. About 1 mg of dried material was then transferred into 9x15 mm tin capsules for subsequent isotopic analysis (C and N) at the Norwegian Institute for Energy Technology (IFE). The accuracy and precision of $\delta^{13}C$ and $\delta^{15}N$ analyses were analysed by replicate analysis of internal standard (IFE trout) and international standards IAEA-N-2 ($\delta^{15}N$) and USGS-24 ($\delta^{13}C$). The house standard was prepared by Soxhlet extraction with CH_2Cl_2 : 7 % CH_3OH for approximately 2 hours, cleaned with HCl and rinsed with distilled water to neutral pH. Typical results with one standard deviation for analyses of the IFE trout standard analysed together with the samples are: $\delta^{15}N_{AIR}$: 11.40‰ ± 0.12, $\delta^{13}C_{VPDB}$: -20.20‰ ± 0.12. All isotope values are referring to primary standards. For C the reference standard, VPDB, is marine carbonate, Vienna Pee Dee Belemnite (Craig, 1953). For N the reference standard is atmospheric N (Mariotti, 1983). The relationships between stable isotopes of C and N ($\delta^{13}C = {}^{13}C/{}^{12}C$ and $\delta^{15}N = {}^{15}N/{}^{14}N$) are reported in ‰ and expressed by the following equation:

$$\delta^{15}N \text{ or } \delta^{13}C = \left(\frac{R_{sample}}{R_{s\,\tan\,dard}} - 1 \right) * 1000 \quad (1)$$

where R represents the ratio between the heavy and light isotope, i.e. $^{13}C/^{12}C$ or $^{15}N/^{14}N$.

A more positive (less negative for C) isotopic value is said to be isotopically enriched, meaning that the sample contains proportionally more of the heavy stable isotope compared with the standard. In the opposite case, a more negative isotope value (more negative for C) is said to be isotopically depleted.

Since Hg biomagnifies through the food web, a measure of a relative trophic position is needed. This might be defined by the stable C and N isotope ratios. Since lipids are depleted in $\delta^{13}C$ compared to proteins and carbohydrates (more negative), and as lipid content varies among organisms or among tissue types, there exists a potential to induce bias into stable isotope analyses. Thus, we have fat-adjusted ($\delta^{13}C^*$) all samples according to Post et al. (2007) by the following empirical relationship:

$$\delta^{13}C^* = \delta^{13}C_{untreated} - 3.32 + 0.99 * C{:}N \quad (2)$$

where C:N is the weight ratio (in %) between C and N.

In the literature C:N-ratio is reported either by weight or by atoms (mol ratio). The conversion is straight forward, as C:N "by weight" is equal to C:N "by atoms" multiplied by 1.1667 (14/12).

According to Post et al. (2007), a C:N-ratio < 3.5 means an average fat content in aquatic organisms < 5 %. Thus, for most of our data the fat-adjusted $\delta^{13}C$ signatures, i.e. $\delta^{13}C^*$ according to Eq. 2, have relatively little influence of the $\delta^{13}C$ values. The Kruskal Wallis test (KW-test) showed no significant difference between measured and fat-adjusted $\delta^{13}C$ (median $\delta^{13}C$:-26.41 ‰, median $\delta^{13}C^*$: -26.95 ‰). Despite relatively small effects, all calculations related with stable C isotopes rely on fat-adjusted $\delta^{13}C$, denoted $\delta^{13}C^*$.

In order to compare stable isotopes in food webs between lakes or within lakes with distinct differences in stable isotopes signatures in the littoral, pelagic and profundal food webs, baseline corrections need to be done. Normally, primary consumers are used for such baseline corrections because their larger body size and greater longevity result in less seasonality in the $\delta^{15}N$ signatures and, thus, level out much of the large temporal variations typically present in short living primary producers such as algae (Cabana and Rasmussen, 1996). Common primary consumers used for baseline correction of pelagic food webs are shallow zooplankton and mussels, while gastropods, amphipods and trichopterans are often used for baseline corrections in littoral food webs, while chironomids

and deep zooplankton often are used in profundal food webs (Vander Zanden and Rasmussen, 1999). According to Post (2002), there is an average mean trophic fractionation of $\delta^{15}N$ by 3.4 ‰ and of $\delta^{13}C$ by 0.4 ‰.

As various individuals of one fish species may prefer different lake habitats (littoral, pelagic and profundal) and/or diet, due to fundamental factors as ontogeny, diurnal and/or seasonal migration strategies, or simply individual foraging behaviour, large individual variations in $\delta^{15}N$ and $\delta^{13}C$ may occur within each fish species. Thus, all baseline corrections are performed at individual level. As we do not have stable isotope data from profundal primary consumers in our study, we have used a two-source mixing model to quantify the relative contribution of food derived from littoral (zoobentos) or pelagic habitats (zooplankton) for each individual fish, similar to Vander Zanden and Rasmussen (1999):

$$Prey_{zoobenthos} = (\delta^{13}C^{*}_{fish} - \delta^{13}C^{*}_{zooplankton})/ (\delta^{13}C^{*}_{zoobenthos} - \delta^{13}C^{*}_{zooplankton}) \quad (3)$$

and

$$Prey_{zooplankton} = 1 - Prey_{zoobenthos} \quad (4)$$

The baseline corrections ($\delta^{15}N - k_{fish}$, $\delta^{13}C^{*} - k_{fish}$) are then calculated by the following equations:

$$[\delta^{15}N–k]_{fish} = \delta^{15}N_{fish} - [Prey_{zoobenthos} * \delta^{15}N_{zoobenthos} + Prey_{zooplankton} * \delta^{15}N_{zooplankton}] \quad (5)$$

And

$$[\delta^{13}C^{*}–k]_{fish} = \delta^{13}C^{*}_{fish} - (\delta^{15}N–k_{fish}/3.4) * 0.4 \quad (6)$$

where k is the baseline isotope value. As the habitat variation in baseline $\delta^{15}N$ and $\delta^{13}C$ is a widespread phenomenon in freshwater systems, isotope food web studies should include $\delta^{15}N$ and $\delta^{13}C$ measurements of the widest possible range of baseline organisms (Vander Zanden and Rasmussen, 1999). Thus, we have used the most extreme $\delta^{15}N$ and fat-adjusted $\delta^{13}C$ values ($\delta^{13}C^{*}$) found in our investigated zoobenthos and zooplankton as baseline correction values for $\delta^{15}N$ and $\delta^{13}C^{*}$ (Table 1). Accordingly, the $\delta^{15}N$ signature of the gastropod *Lymnaea peregra* ($\delta^{15}N$ = 4.5 ‰) was used for baseline correction of $\delta^{15}N$ for littoral zoobenthos as this species only graze on periphytic algae (Post, 2002, Rognerud et al. 2003) and therefore, the best estimate of the $\delta^{15}N$ level of primary consumers (trophic level 2) in the littoral habitat of the investigated lake area. However, as < 40 % of the investigated fish individuals had less depleted $\delta^{13}C^{*}$ signatures than that of *L. peregra*, this species was likely not a significant littoral prey organism for fish. As only 8% of the investigated fish individuals had less depleted $\delta^{13}C^{*}$ signatures than ΣEphemeroptera/Trichoptera, compared with 24% with less depleted $\delta^{13}C$ signatures than ΣEphemeroptera/Trichoptera, we decided to use the fat-adjusted $\delta^{13}C^{*}$ signature of ΣEphemeroptera/Trichoptera (-23.2 ‰) as the C baseline correction value from littoral zoobenthos.

Depth m	Taxon	$\delta^{15}N$ ‰	$\delta^{13}C$ ‰	C:N w%	$\delta^{13}C^{*}$ ‰
1	Zooplankton	8.8	-33.4	4.0	-32.8
8	Zooplankton	6.5	-33.3	3.9	-32.8
1	Gastropoda	4.5	-28.1	5.0	-26.5
1	Ephemeroptera/Trichoptera	6.1	-24.4	4.6	-23.2
1	Hemiptera	8.3	-31.2	3.5	-31.1

Table 1. Measured $\delta^{15}N$, $\delta^{13}C$, C:N-ratio and fat-adjusted $\delta^{13}C$ ($\delta^{13}C^{*}$) in pooled samples from various invertebrate taxa in Lake Norsjø. Fat-adjustments implemented according to Eq. 2. The bold values in primary consumers from pelagic ($\delta^{15}N$ = 6.5 ‰ and $\delta^{13}C^{*}$ = -32.8 ‰) and littoral ($\delta^{15}N$ = 4.5 ‰ and $\delta^{13}C^{*}$ = -23.2 ‰) habitats are used for baseline correction of fish from Lake Norsjø.

Finally, the relative trophic position (Λ) of each individual fish was calculated by the following equation:

$$\Lambda = (\delta^{15}N - k)/3.4 + 2 \quad (7)$$

where 3.4 is the $\delta^{15}N$ increment (‰) per unit of trophic level, and the constant 2 corresponds to the trophic level of primary consumers used for baseline corrections.

Statistics

As the statistical analyses only included fish species for which we had a sample size ≥ 10, 7 species were incorporated in the statistical tests.

As most of the data were not normally distributed, nonparametric Kruskal-Wallis (KW) tests were run for statistical comparisons tests between groups (fish species). However, when the KW-test is significant, it only indicates that at least one of the groups is different from at least one of the others. It does not tell which ones are different, nor how many of the groups are different from each other. Thus, in order to determine which pair of groups being significantly different from each other, we have used the procedure proposed by Siegel and Castellan (2000). All analyses were performed by Minitab 16 statistical software (Minitab Ltd).

Results

Size and age distribution

The age of the captured fish (n = 131) ranged from 1 to 19 years, table 2. As all Arctic charr were caught by gillnet at a spawning site, and all brown trout were relatively large individuals caught by trolling, all individuals within these species were relatively old; brown trout within the age interval of 7-11 years and Arctic charr 7-14 years old. The ten individuals of pike covered eight year classes within the age interval of 3-13 years. The catch of whitefish covered 11 year classes within the age interval of 3-13 years. The perch were dominated by 4 year old individuals (64 %), with only one individual < 3 years and 3 individuals > 5 years, while the captured

Species	Statistics	Length cm	Weight g	Age years	$\delta^{15}N$ ‰	$\delta^{13}C$ ‰	CN w%	Hg ppm ww
Stickleback (10)	mean ± SD min-max	3.4 ± 0.5 2.9 - 4.2	0.24 ± 0.10 0.16 - 0.41	n.a. n.a.	6.0 ± 1.3 4.8 - 7.3	-26.0 ± 0.8 -26.9 - -25.2	4.6 ± 0.2 4.3 - 4.7	0.07 ± 0.02 0.05 - 0.10
W.fish (36)	mean ± SD min-max	31 ± 4 22 - 37	262 ± 99 90 - 470	7 ± 3 3 - 13	9.7± 1.0 7.6 - 10.9	-25.1 ± 2.5 -28.9 - -20.2	2.6 ± 0.5 2-2 - 3.3	0.11 ± 0.03 0.04 - 0.16
Smelt (11)	mean ± SD min-max	10 ± 1 9 - 12	5.1 ± 1.6 3.0 - 8.1	5 ± 2 2 - 7	10.9 ± 0.5 9.9 - 11.5	-29.2 ± 0.7 -30.3 - -27.8	3-3 ± 0.1 3.2 - 3.6	0.22 ± 0.08 0.08 - 0.35
Perch (25)	mean ± SD min-max	23 ± 6 6 - 34	163 ± 113 2.1 - 516	4 ± 1 1 - 7	10.3 ± 0.8 7.8 - 11.3	-24.1 ± 1.3 -26.9 - -21.3	3.1 ± 0.1 2.7 - 3.5	0.13 ± 0.07 0.07 - 0.40
Tench (4)	mean ± SD min-max	45 ± 4 42 - 50	1550 ± 470 1275 - 2250	7 ± 2 6 - 10	10.0 ± 0.7 9.0 - 10.7	-25.2 ± 1.4 -26.3 - -24.0	2.7 ± 0.3 2.3 - 3.1	0.17 ± 0.10 0.11 - 0.33
C.carp (2)	mean ± SD min-max	 19 - 41	 132 - 1474	 5 - 19	 8.0 - 10.3	 -30.4 - -27.1	 3.1 - 3.2	 0.03 - 0.19
B.trout (10)	mean ± SD min-max	58 ± 12 37 - 71	2465 ± 1174 520 - 4000	9 ± 2 7 - 11	11.8 ± 0.4 11.3 - 12.4	-27.6 ± 0.9 -29.7 - -26.5	3.1 ± 0.2 2.5 - 3.4	0.75 ± 0.53 0.29 - 1.95
A.charr (23)	mean ± SD min-max	28 ± 4 21 - 34	268 ± 103 101 - 470	11 ± 2 7 - 14	12.4 ± 0.5 11.7 - 13.4	-27.6 ± 0.5 -29.2 - -27.1	3.3 ± 0.2 3.1 - 3.9	0.46 ± 0.15 0.25 - 0.92
Pike (10)	mean ± SD min-max	64 ± 19 41 - 97	2565 ± 2725 428 - 9250	7 ± 3 3 - 13	11.1 ± 0.9 10.0 - 12.5	-26.2 ± 0.4 -26.9 - -25.3	3.0 ± 0.3 2.4 - 3.3	0.62 ± 0.48 0.09 - 1.39

Table 2. Mean (± SD), minimum and maximum values of length, weight, age and measured $\delta^{15}N$, $\delta^{13}C$, C:N-ratio and Hg in various fish species from Lake Norsjø. While skinless, dorsal muscle tissue was taken from each individual fish for Hg and stable isotope analyses, whole skinless fillets from 5 individuals were pooled together for analysis of stable isotopes in stickleback.

smelts varied from 2 to 7 years old. The oldest fish captured was a 19 years old crucian carp.

Three-spined stickleback was the smallest investigated fish species, with an average length and weight of 3.4 ± 0.5 cm and 0.24 ± 0.10 g, respectively, table 2, while the average length and weight of smelt was 10 ± 1 cm and 5.1 ± 1.6 g. Perch varied in length from 6 to 34 cm (weight-interval: 2 - 516 g), with an average length of 23 ± 6 cm and an average weight of 163 ± 113 g. 84 % of the captured perch were within the length-interval 20-30 cm. The whitefish varied in length from 22 to 37 cm (weight-interval: 90 - 470 g), with an average length of 31 ± 4 cm and an average weight of 262 ± 99 g. The smallest pike (3 - 4 years old) were in the length-class 40-45 cm, while the largest was a 13 year old individual, 97 cm long, weighing 9 250 g. Average length of pike was 64 ± 19 cm. Fish were found in the stomachs of almost all captured individuals of Arctic charr and brown trout. Despite a significantly lower average age of brown trout (8.5 ± 1.5 years, 2-sample T-test, $p < 0.05$) compared with Arctic charr (10.9 ± 2.2 years), the brown trout was much larger, both regarding average weight (brown trout: 2465 ±1174 g; Arctic charr: 268 ±103 g) and by weight comparison of age classes.

Stable isotopes in invertebrates and fish

In the zooplankton samples from July (at 1 and 8 m), about 65-75 % of the biomass consisted of cyclopoid and calanoid copepods, while the cladocerans constituted about 25-35 %, with large individuals of *Holopedium gibberum* as the predominant cladoceran. Both the herbivorous cladoceran *Bosmina longispina* (Porter et al., 1983) and the predaceous cladoceran *Leptodora kindti*

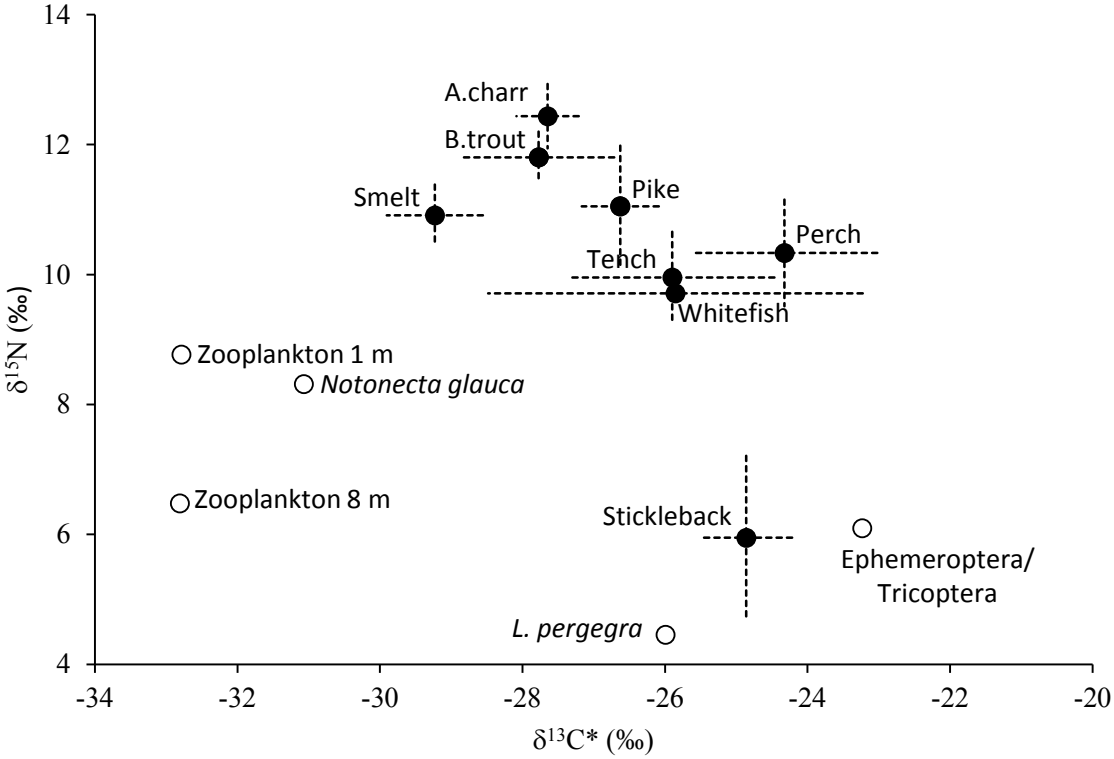

Figure 1. Average values (± SD) of fat-adjusted $\delta^{13}C$ ($\delta^{13}C^*$) and measured $\delta^{15}N$ in fish, in pelagic invertebrates (zooplankton from 1 and 8 m, and the carnivore backswimmer, Notonecta glauca), and in littoral invertebrates (Gastropoda: L. peregra and ΣEphemeroptera/Trichoptera) in Lake Norsjø.

(Browman et al., 1989) were also present in the samples, but constituted < 1 % of the biomass. The $\delta^{13}C^*$ signatures in zooplankton from 1 and 8 m were identical, i.e. -32.8 ‰, table 1. The predominately pelagic feeding backswimmer, *Notonecta glauca* (Svensson et al., 2000) had somewhat less depleted $\delta^{13}C^*$ signature (-31.1 ‰) compared with zooplankton, figure 1. In littoral zoobenthos, the $\delta^{13}C^*$ signatures in the gastropod *L. peregra* and in the ΣEphemeroptera/Trichoptera were -26.5 ‰ and - 23.2 ‰, respectively, table 1. Thus, the maximum difference in $\delta^{13}C^*$ between littoral and pelagic invertebrate species ($\Delta\delta^{13}C^*$) was 9.6 ‰, i.e. from -23.2‰ in littoral zoobenthos to the far more depleted $\delta^{13}C^*$signature (-32.8 ‰) in zooplankton.

The individual $\delta^{13}C^*$ values in fish primarily varied within the average $\delta^{13}C^*$ signatures of the two end-members, the average $\delta^{13}C^*$ signature in zooplankton, -32.8 ‰, and the $\delta^{13}C^*$ signature of zoobenthos, -23.2 ‰, figure 1. Only six whitefish and four perch showed less depleted $\delta^{13}C^*$ signatures than in zoobenthos (ΣEphemeroptera/Trichoptera). No fish individuals had more depleted $\delta^{13}C^*$ signatures than present in zooplankton.

Whitefish showed the largest individual $\delta^{13}C^*$ variation, i.e. from -30.0 ‰ to -20.6 ‰ (Table 3), which implies a $\Delta\delta^{13}C^*$ of 9.4 ‰. Also, the investigated perch showed a relatively high $\Delta\delta^{13}C^*$ (6.1 ‰), i.e. from a $\delta^{13}C^*$ value of -27.6 ‰ up to -21.5 ‰. The $\Delta\delta^{13}C^*$ in the remaining fish species varied from 3.4 ‰ in brown trout (-30.0 to -26.6 ‰) down to only 1.3 ‰ in stickleback (-25.5 ‰ to -24.2 ‰).

Among the fish species investigated, smelt exhibited the most depleted $\delta^{13}C^*$ signatures (Figure 1), while perch exhibited the least

Species	Statistics	$\delta^{13}C^*$ ‰	Littoral reliance (%)	Baseline adjusted		
				$\delta^{15}N$-k ‰	$\delta^{13}C^*$-k ‰	Λ
Sticleback (10)	mean ± SD min-max	-24.9 ± 0.6 -25.5 - -24.2	83 ± 7 76 - 89	1.1 ± 1.3 0.0 - 2.6	-25.0 ± 0.6 -25.6 - -24.5	2.3 ± 0.4 2.0 - 2.8
W.fish (36)	mean ± SD min-max	-25.9 ± 2.6 -30.0 - -20.6	73 ± 27 29 - 128	4.7 ± 1.5 1.8 - 8.0	-26.4 ± 2.5 -30.4 - -21.5	3.4 ± 0.4 2.5 - 4.1
Smelt (11)	mean ± SD min-max	-29.2 ± 0.7 -30.0 - -27.8	37 ± 7 29 - 52	5.2 ± 0.4 4.2 - 5.7	-29.8 ± 0.7 -30.7 - -28.5	3.5 ± 0.1 3.3 - 3.7
Perch (25)	mean ± SD min-max	-24.3 ± 1.3 -27.6 - -21.5	89 ± 14 55 - 118	5.6 ± 1.0 2.4 - 6.6	-25.0 ± 1.2 -27.8 - -22.2	3.7 ± 0.3 2.7 - 3.9
Tench (4)	mean ± SD min-max	-25.9 ± 1.4 -27.3 - -24.3	72 ± 15 58 - 89	4.9 ± 0.9 3.8 - 5.9	-26.5 ± 1.4 -27.8 - -24.9	3.5 ± 0.3 3.1 - 3.7
C.carp (2)	mean ± SD min-max	 -30.6 - -27.3	 23 - 58	 2.0 - 5.0	 -30.8 - -27.9	 2.6 - 3.5
B.trout (10)	mean ± SD min-max	-27.8 ± 1.1 -30.0 - -26.6	53 ± 11 29 - 65	6.4 ± 0.4 5.9 - 7.1	-28.5 ± 1.0 -30.7 - -27.4	3.9 ± 0.1 3.7 - 4.1
A.charr (23)	mean ± SD min-max	-27.7 ± 0.4 -28.7 - -27.2	54 ± 5 43 - 59	7.0 ± 0.5 6.3 - 8.0	-28.5 ± 0.4 -29.5 - -28.0	4.1 ± 0.2 3.9 - 4.3
Pike (10)	mean ± SD min-max	-26.6 ± 0.5 -27.2 - -25.5	65 ± 6 59 - 76	5.9 ± 1.0 4.7 - 7.4	-27.3 ± 0.5 -27.8 - -26.1	3.7 ± 0.3 3.4 - 4.2

Table 3. Mean (± SD), minimum and maximum values of fat-adjusted $\delta^{13}C$ ($\delta^{13}C^*$), baseline adjusted $\delta^{15}N$ ($\delta^{15}N$-k), $\delta^{13}C$ ($\delta^{13}C^*$-k), and calculated relative trophic position (Λ) of various fish species from Lake Norsjø based on analysis of fish muscle tissue. The calculations rely on Eqs. 2-7.

depleted $\delta^{13}C^*$ signature. The Kruskal Wallis test with multi-comparisons procedure between pair of groups according to Siegel and Castellan (2000), showed that $\delta^{13}C^*$ in smelt (median $\delta^{13}C^*_{smelt}$: -29.2 ‰) was significantly more depleted ($p < 0.05$) than perch (median $\delta^{13}C^*_{perch}$: -24.2 ‰), stickleback (median$^{13}C^*_{stickleback}$: -24.8 ‰) and pike (median$^{13}C^*_{pike}$: -26.8 ‰), while Arctic charr and brown trout had significantly more depleted $\delta^{13}C^*$ signatures (both medians: -27.5 ‰) than perch.

By the baseline adjustments of fish, table 3, using the $\delta^{13}C^*$ signatures in zooplankton and zoobenthos as end-members, table 1, we might indirectly quantify the percentage contribution of food derived from littoral and pelagic habitats for each individual fish. By this calculation, perch and stickleback exhibited the highest average indirect zoobenthos reliance (IZB), i.e. 89 ± 14 % and 83 ± 7 % (Figure 2), respectively; while smelt showed the lowest IZB reliance (37 ± 7 %). The Kruskal Wallis test with multi-comparisons procedure between pair of groups according to Siegel and Castellan (2000), showed that smelt had a significantly lower median IZB (38 %) than perch (90 %), stickleback (84 %), whitefish (79 %) and pike (63 %). Perch individuals besides having a significantly higher IZB reliance than smelt, also had a significantly higher IZB reliance than brown trout (56 %) and Arctic charr (55 %).

The lowest $\delta^{15}N$ value (4.5 ‰) was measured in the littoral, algae-feeding gastropod *L. peregra*, while the other measured zoobenthos, ΣEphemeroptera/Trichoptera, had a somewhat more enriched $\delta^{15}N$ signature, i.e. 6.1 ‰ ,table 1. The backswimmer *N. glauca*, with a relatively $\delta^{13}C$ depleted signature, had an even more enriched $\delta^{15}N$ signature, 8.3 ‰, figure 1.

Pelagic zooplankton showed more enriched $\delta^{15}N$ signatures (6.5 – 8.8 ‰) than zoobenthos (4.5 – 6.1 ‰). Despite a relatively small differ-

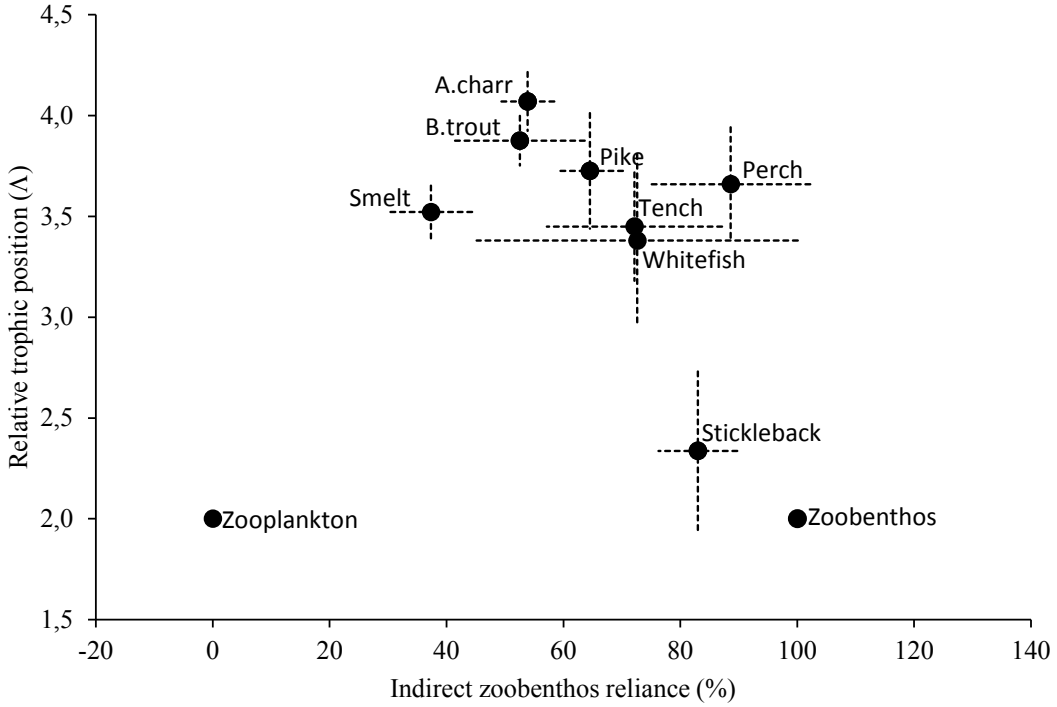

Figure 2. Generalized food web diagram for fish species in Lake Norsjø. The indirect zoobenthos reliance (%) is calculated according to equations 3 and 4, based on the $\delta^{13}C^*$ signatures in individual fishes in relation to the average $\delta^{13}C^*$ signatures of the two end-members (littoral and pelagic prey in Table 1), in a simple two-source mixing model.

ence in the biomass distribution of zooplankton species in the samples from 1 and 8 m, a more enriched $\delta^{15}N$ value was found in zooplankton at 1 m depth (8.8 ‰) compared with at 8 m depth (6.5 ‰). The measured $\delta^{15}N$ signatures in fish varied from 4.8 ‰ (a stickleback) to 13.4 ‰ (an Arctic charr), i.e. a variation interval in $\delta^{15}N$ ($\Delta\delta^{15}N$) of 8.6 ‰. Assuming a $\delta^{15}N$ enrichment of 3.4 ‰ per trophic level (Λ), the individual fish captured covered about 2.5 Λ. The baseline adjusted $\delta^{15}N$ values ($\delta^{15}N$ - k), showed that the lowest individually estimated Λ, was found in a stickleback (Λ = 2.0), equal to the predefined Λ of investigated pelagic and littoral invertebrates, figure 2. Highest calculated Λ was found in an Arctic charr individual (Λ = 4.3).

The baseline adjustments showed that Arctic charr had the highest estimated average Λ among the investigated fish species, i.e. Λ = 4.1 ± 0.2, followed by brown trout (Λ = 3.9 ± 0.1) and pike (Λ =3.7 ± 0.3). The baseline adjusted $\delta^{15}N$ values ($\delta^{15}N$ – k) showed that the investigated fish covered 2.3 trophic positions (from Λ from 2.0 to 4.3).

Total mercury (THg) in fish

The measured concentration of THg in fish, figure 3, varied from 0.03 ppm, in a relatively small crucian carp (19 cm, 5 years) to 1.95 ppm in a brown trout (67 cm, 11 years). The Kruskal Wallis test with multi-comparisons procedure between pair of groups according to Siegel and Castellan (2000), showed that stickleback exhibited the lowest THg concentration (median Hg = 0.07 ppm), significantly lower than brown trout (0.56 ppm), Arctic charr (0.43 ppm), pike (0.45 ppm) and smelt (0.24 ppm), but not significantly different from perch (0.11 ppm) and whitefish (0.11 ppm). The concentration of THg in brown trout was not found to be significantly different from the other piscivore species (pike and Arctic charr).

In order to obtain good or reliable trophic magnification factors of various biomagnifying compounds, organisms from at least 3 trophic levels should be included in the food web (Borgå et al., 2012). In our study the measured $\delta^{15}N$ varies from 4.8 ‰ to 13.8 ‰. Assuming a $\delta^{15}N$ enrichment of 3.4 ‰ per Λ, the nominal Λ of captured fish in our investigation covered 2.3 Λ.

The slope of the relationship between measured $\delta^{15}N$ and $\log_{10}$ transformed THg concentration, often called the trophic magnification slope (TMS), was used for calculating the bioconcentration of THg up the food web. In our data the following regression equation was found when all investigated fish individuals were included:

$\log_{10}[THg]$ (ppm ww) = 0.163 x $\delta^{15}N$ – 2.45
($r^2 = 0.45$; $p < 0.05$)

where the TMS is 0.163, with a SE of 0.017.

When doing similar correlation for separate fish species, only whitefish and smelt exhibited significant positive correlation between $\log_{10}[THg]$ and measured $\delta^{15}N$, table 4. In whitefish (n = 36) we found a significant positive correlation between individual adjusted $\delta^{13}C^*$-k and $\delta^{15}N$-k ($\delta^{15}N\text{-k} = 0.53_{*}\delta^{13}C^*\text{-k} + 18.6$, $r^2 = 0.80$, $p < 0.001$). In addition $\delta^{13}C^*$-k in whitefish was significantly correlated by both length (Length (cm) = $1.31_{*}\delta^{13}C^*\text{-k} + 65.1$, $r^2 = 0.66$, $p < 0.001$) and age (Age (year) = $0.66_{*}\delta^{13}C^*\text{-k} + 24.1$, $r^2 = 0.38$, $p < 0.001$). Despite so, no significant positive correlations were found between $\log_{10}[THg]$ and age, length, or weight, only a weak, but significant ($p < 0.05$) relationship was found between $\log_{10}[THg]$ and $\delta^{15}N$ in whitefish, table 4.

While no significant regressions were found between $\log_{10}[THg]$ and age, length or weight in whitefish or Arctic charr (Table 3), brown trout, pike, perch, and smelt exhibited significant positive regressions between $\log_{10}[THg]$ and age. Except for smelt, the same species also exhibited significant relationships between $\log_{10}[THg]$ and length. Only brown trout and perch exhibited significant positive regressions between $\log_{10}[THg]$ and weight, while the similar regressions in pike and smelt were nearly significant, table 4.

Besides having the highest Hg concentrations, the predominately piscivore species (brown trout, pike and Arctic charr) also exhibit the most intermediate $\delta^{13}C^*$ or baseline adjusted

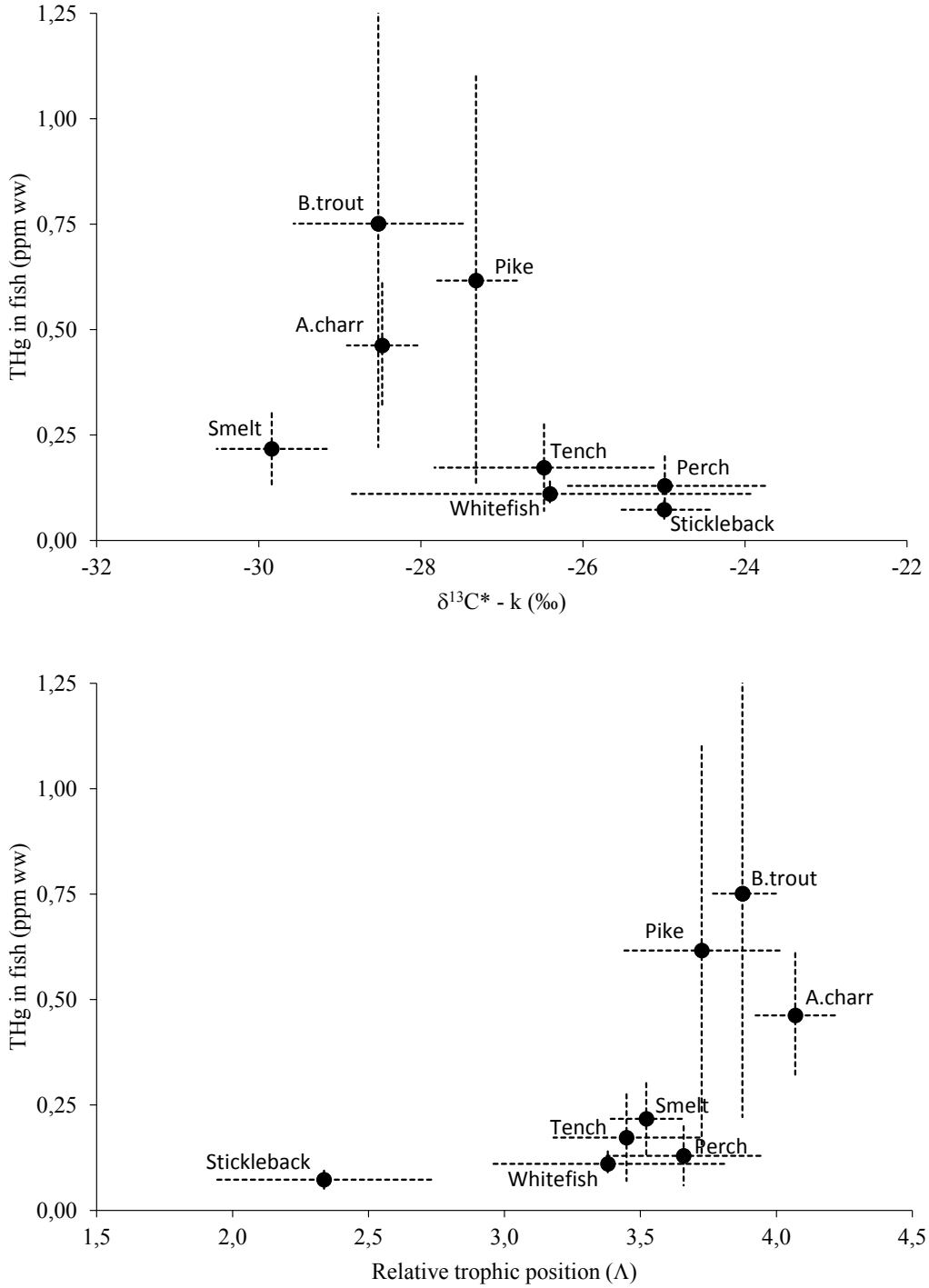

Figure 3. Relationships between average (± SD) individual baseline adjusted $\delta^{13}C$ ($\delta^{13}C^{*}$-k) and THg) in piscivore fish species (upper panel), and between trophic position and THg in various fish species (lower panel) from Lake Norsjø. The individual baseline adjustments were performed according to Eqs. 3-6.

$\delta^{13}C^{*}$-signatures of all investigated species, figure 1 and 3.

Discussion

Feeding habitats and trophic levels of fish

The measured $\delta^{13}C$ signature (-24.4 ‰) in the most enriched zoobenthic end-member in Lake Norsjø, ΣEphemeroptera/Trichoptera of, table 1, was very similar to the mean value reported by Vander Zanden and Rasmussen (1999) from 14 dimictic, oligotrophic and relatively deep Canadian lakes (-23.8 ‰). Data from high non-regulated mountain lakes on the Hardangervidda plateau, southern Norway (Rognerud et al., 2003), basically belonging to the upper catchment areas of the Lake Norsjø, exhibited less

	Regression	n	min x	max x	min y	max y	intercept	slope	r^2	p
Brown trout	log Hg vs $\delta^{15}N$ (‰)	10	11.3	12.4	0.29	1.95	2.95	-0.267	0.16	0.246
	log Hg vs Age (yr)		7	11			**-1.21**	**0.119**	**0.47**	**0.028**
	log Hg vs Lt (cm)		37	71			**-1.21**	**0.017**	**0.62**	**0.007**
	log Hg vs Weight (g)		520	4000			**-0.66**	**0.0002**	**0.71**	**0.002**
Pike	log Hg vs $\delta^{15}N$ (‰)	10	10	12.5	0.09	1.39	-1.98	0.146	0.11	0.362
	log Hg vs Age (yr)		3	13			**-1.12**	**0.107**	**0.51**	**0.020**
	log Hg vs Lt (cm)		41	97			**-1.44**	**0.017**	**0.56**	**0.012**
	log Hg vs Weight (g)		428	9250			-0.61	9.5x10-5	0.38	0.058
Artic charr	log Hg vs $\delta^{15}N$ (‰)	23	11.7	13.4	0.25	0.92	-1.32	0.077	0.09	0.173
	log Hg vs Age (yr)		7	14			-0.48	0.011	0.03	0.396
	log Hg vs Lt (cm)		21	34			-0.38	0.001	0.00	0.905
	log Hg vs Weight (g)		101	470			-0.36	2.7x10-5	0.00	0.920
Perch	log Hg vs $\delta^{15}N$ (‰)	25	7.8	11.3	0.07	0.40	-0.58	-0.034	0.03	0.446
	log Hg vs Age (yr)		1	7			**-1.37**	**0.101**	**0.38**	**0.001**
	log Hg vs Lt (cm)		6	34			**-1.44**	**0.022**	**0.49**	**0.000**
	log Hg vs Weight (g)		2.1	516			**-1.12**	**0.001**	**0.55**	**0.000**
Smelt	log Hg vs $\delta^{15}N$ (‰)	11	9.9	11.5	0.08	0.35	**-4.44**	**0.342**	**0.60**	**0.005**
	log Hg vs Age (yr)		2	7			**-1.25**	**0.111**	**0.94**	**0.000**
	log Hg vs Lt (cm)		9	12			-2.15	0.145	0.29	0.089
	log Hg vs Weight (g)		3.0	8.1			-1.10	0.078	0.34	0.058
Whitefish	log Hg vs $\delta^{15}N$ (‰)	36	7.6	11.9	0.04	0.16	**-1.42**	**0.046**	**0.12**	**0.043**
	log Hg vs Age (yr)		3	13			-1.08	0.015	0.09	0.074
	log Hg vs Lt (cm)		22	37			-1.11	0.005	0.02	0.418
	log Hg vs Weight (g)		90	470			-1.02	0.0002	0.02	0.470

Table 4. Regression of log-transformed Hg (log_{10}THg) in fish against measured $\delta^{15}N$, age, total length and weight of various fish species in Lake Norsjø. The intercept, slope, r^2 and p values of the regressions, as well as total numbers of individuals (n) and maximum and minimum values of the various parameters, x ($\delta^{15}N$, age, length, weight) and y (Hg) are presented. Results with $p < 0.05$ are written in bold.

depleted signatures in zoobenthos, i.e. $\delta^{13}C$: -20.9 ± 1.0 ‰, while several regulated lakes in the same area exhibited more depleted $\delta^{13}C$ signatures (-25.0 ± 2.3 ‰) compared with Lake Norsjø. As the water table variation in Lake Norsjø is small (< 2 m), and the lake is deep and very wind-exposed, the best explanatory factors for the relatively depleted $\delta^{13}C$ signatures in zoobenthos from The Årnes Bay, in northern part of Lake Norsjø may be:

- The CO_2 boundary layer effect, which causes diffusion limitation to benthic algal cells in oligotrophic lakes (France, 1995[a,b]; Heckey and Hesslein, 1995) is reduced in large wind-exposed lakes. Accordingly, the conditions for stable isotope fractionation of C are improved with subsequent more depleted $\delta^{13}C$ signatures in benthic algae. This can also explain the much depleted $\delta^{13}C$ signature found in the littoral gastropod *L. peregra* (-28.1 ‰, table 1, collected on emerged macrophytes along the shore, about 0.5 m below the surface in the very wind-exposed Årnes Bay.
- The very wind-exposed Årnes Bay is impacted by pelagic algae and zooplankton that enter the littoral areas by strong onshore winds at daytime during the growth seasons. Thus, pelagic organic C might be included in the diet of many zoobenthos, which accordingly will lead to a more depleted $\delta^{13}C$ signature in littoral zoobenthos.
- As the inorganic $\delta^{13}C$ signature in hypolimnion water normally is more depleted than both pelagic and littoral $\delta^{13}C$ signatures from large, deep lakes, upwelling of $\delta^{13}C$ depleted hypolimnion water after long-lasting wind exposures, may temporarily incorporate more depleted $\delta^{13}C$ signatures into littoral and pelagic food webs. In addition, diurnal migration of zooplankton across the thermocline may contribute to transport of $\delta^{13}C$ depleted organic carbon from profundal habitats into pelagic habitat which again might be distributed (by wind driven surface currents) into littoral habitats.
- The $\delta^{13}C$ signatures in allochthonous matter in lakes from comparable latitudes normally range from -29 to -27 ‰ (Meili et al., 1996; Grey et al., 2001; Karlsson et al., 2003, 2012). Thus, as omnivory is common among aquatic invertebrates, this may also contribute to more depleted $\delta^{13}C$ signatures in littoral invertebrates compared with invertebrates mainly feeding on sediment-surface-derived periphyton. As the River Bøelva enters into the Årnes Bay, this bay is significantly affected by allochthonous matter.

The $\delta^{13}C^*$ values of individual fish varied primarily within the average $\delta^{13}C^*$signatures of the two end-members, the average $\delta^{13}C^*$ signature of zooplankton (-32.8 ‰) and the littoral $\delta^{13}C^*$ signature of zoobenthos (ΣEphemeroptera/Trichoptera), i.e. -23.2 ‰, figure 1. Thus, as the difference in the two $\delta^{13}C^*$ end-members was large ($\Delta\delta^{13}C$ = 9.6 ‰), the error variance (1 SD) in the mixing model outputs should be relatively small (Vander Zanden and Rasmussen, 2001). Data from the two-source mixing model indicate that fish with low trophic position as stickleback, smelt and whitefish, together spanned the entire range of benthivory. Smelt and stickleback show a tendency to cluster at the outer edges of the pelagic-littoral gradient, while the whitefish population covers individuals from an almost obligate benthos diet to an almost obligate zooplankton diet, confirmed by the large span in their $\delta^{13}C^*$ signatures, table 3 and figure 1. The piscivore species (brown trout, pike and Arctic charr) are located in the apex position (upper center) of the diagrams, figure 1 and 2, indicating that piscivore fish species are supported by a mix of pelagic and benthic diet, through their choice of fish diet. Accordingly, they significantly integrate across littoral and pelagic food chains and habitats. This, combined with impacts of allochthonous matter, and the increasing documentation of omnivory among invertebrates and fishes, significantly links the various food webs and habitats in lakes (Polis and Strong, 1996; Vander Zanden and Rasmussen, 1996; Vander Zanden and Vadeboncoeur, 2002; Vadeboncoeur et al., 2002; Jansson et al., 2007).

The generally high IZB reliance in fish species in the large and deep Lake Norsjø (55.48 km^2, mean depth: 87 m) might be somewhat unexpected as the degree of zoobenthivory decreases significantly by lake area (Vander Zanden and Vadeboncoeur, 2002). However, despite the significantly higher total amounts of pelagic-derived C compared with littoral-derived C in large, deep lakes, locally, as in shallow areas outside river outlets, substantial amounts of littoral C might likely be produced and assimilated into local food webs in areas of large lakes, as in the 0-20 m deep Årnes Bay. Among the piscivore fish species, pike had the highest IZB reliance, i.e. 65 ± 6% (Table 3), compared with Arctic charr (54 ± 5%) and brown trout (53 ± 11%).

Perch behave somewhat differently from the other fish species when relating δ^{15}N or trophic position with Hg in fish muscle tissue, figure 1, 3. Their high zoobenthos reliance (89 ± 14%) was expected as perch was only caught in shallow littoral areas. However, their high δ^{15}N – k, table 3, compared with the low Hg levels in muscle tissue, table 2, indicates that they might occupy a habitat and/or feed on organisms with different stable isotope signatures compared with the other investigated fish species. One possible explanation is local contamination by sewage and manure in limited areas of the Årnes Bay, as where the perch were caught. Manure and sewage are known to have relatively high δ^{13}C and enriched δ^{15}N signatures compared with uncontaminated littoral-derived C (Wada and Hattori, 1978; Van Dover et al., 1992; Pearl and Fogel, 1994; Cabana and Rasmussen, 1996; Vander Zanden and Rasmussen, 1996, 1999). For N, this enrichment is due to transformation processes such as denitrification and ammonification, resulting in a ^{15}N-enriched pool of inorganic N available for primary consumers (Wada and Hattori, 1978; Macko and Estep, 1985; Owens, 1987; Vander Zanden and Rasmussen, 1999). Thus, this δ^{15}N enrichment does not reflect an elevated trophic position for perch. Neither our study, nor the studies by Jensen (1954) or Borgstrøm (1974), have implemented stomach investigation of perch, but all studies conclude that the perch population basically consists of young and relatively small individuals, an investigation of invertebrates in the local perch habitats should be conducted to elucidate the high δ^{15}N signature in these perch populations compared with their relatively low Hg concentrations.

As whitefish is the predominant fish species, harvesting of this species has been locally important, but today only minor harvesting occur. Jensen (1954) claimed that there were likely 3 subpopulations or phenotypes of whitefish in Lake Norsjø:

- A littoral whitefish (0.3 - 1.0 kg) which spawns in shallow water along the shoreline of the lake, predominantly in November.
- A stream spawning whitefish with weight generally lower weight than the littoral phenotype, reproducing in inlet rivers during October – November
- A smaller winter spawning whitefish (≈ 0.25 kg) reproducing in very deep water areas (15-70 m) of the lake in January – February.

The large variations in δ^{13}C observed in whitefish from Lake Norsjø, i.e. from -28.9 to -20.2 ‰, table 2, should indicate the presence of more than one phenotype (morph) due to different lake habitat use. Similar observations are made in many other whitefish populations (e.g. Schluter, 1996; Robinson and Parsons, 2002; Clabaut et al., 2007; Harrod et al., 2010; Eloranta et al., 2011).

Stomach investigations by Jensen (1954) showed that the smallest whitefish (< 300 g) primarily feed on planktonic crustaceans, while larger individuals, primarily the shallow whitefish population, preferred benthic food such as snails, chironomids and chydorids, which are large-bodied cladocerans (up to 2-4 mm) grazing on periphyton and thus closely associated with macrophytes (Beklioglu and Jeppesen, 1999). This size-dependent feeding strategy was well revealed in the isotope signatures of whitefish, with significant positive correlation between δ^{13}C*-k and δ^{15}N-k, length and age. As larger or

older whitefish had significantly higher zoobenthos reliance (higher $\delta^{13}C^{*}$-k) than smaller individuals, it indicates that ontogeny is an important factor for food selection of whitefish.

It has also been documented that whitefish partly or completely displaces Arctic charr populations in northern Europe, basically due to its better ability to utilize pelagic food resources (Nilsson and Pejler, 1973; Svärdson, 1976). However, it is also documented that they may naturally coexist in deep Fennoscandic lakes with a large profundal zone (Svärdson, 1976; Sandlund et al., 2010), as documented in Lake Norsjø.

As the gastropod *L.peregra* feeds on periphytic algae, the $\delta^{15}N$ signature of 4.5 ‰ in this species should reflect the $\delta^{15}N$ signatures of primary consumers in the northern, littoral habitats of the lake, and thereby the $\delta^{15}N$ level of the 2nd trophic level (Λ) in the littoral zone in northern areas of Lake Norsjø. Accordingly, the somewhat higher $\delta^{15}N$ value (6.1‰) found in omnivorous zoobenthos as ΣEphemeroptera/Trichoptera indicates a Λ of ≈ 2.5. This is very similar to the estimates reported by Vander Zanden et al. (1997) for these organism groups. They also estimated zooplankton (Cladocera, Copepoda, Ostracoda, Rotifera) to represent Λ = 2.5. The somewhat more enriched $\delta^{15}N$ signatures found in zooplankton (6.5 – 8.1‰) compared with zoobenthos in Lake Norsjø, corresponds well with the observations made in 14 oligotrophic lakes in Canada (Vander Zanden and Rasmussen, 1999). They interpreted this somewhat more enriched $\delta^{15}N$ in pelagic primary consumers as an effect of higher infusion of high ^{15}N waters from the hypolimnion during lake mixing and/or due to the fact that the potential inorganic substrates (NO_3^- and NH_4^+) differ in $\delta^{15}N$ signatures, differences which can be passed on to consumers (Owens, 1987; Paerl and Fogel, 1994).

The $\delta^{13}C^{*}$ signature (-31.1 ‰) in the backswimmer, table 1, indicates a predominant pelagic diet, which should be expected as it mainly hunts zooplankton in the upper water layer, from its "hunting base" at the lake surface, normally in shore-near areas. Thus, by calculating the average $d^{15}N$ in zoobenthos and zooplankton, table 1, and assuming zooplankton and zoobenthos representing Λ = 2.5 and *L. peregra* representing Λ = 2, $\delta^{15}N$ in this "average prey" was 6.6 ‰. Compared with the $\delta^{15}N$ in the backswimmer (8.3‰), this species have a calculated Λ of ≈ 3.

The variations in individual baseline adjusted $\delta^{15}N$-k in fish ranged between 0 - 8 ‰, corresponding to a range in trophic position (Λ) from 2.0 – 4.4. The estimated Λ of stickleback (2.3 ± 0.4) was far lower than reported by Vander Zanden and Rasmussen, (1996), i.e. 3.3 ‰. A fish community study in an oligotrophic lake in Canada (Power et al., 2002) with similar $\delta^{15}N$ levels in several fish species, as those found in Lake Norsjø, also showed a Λ in three-spined stickleback about 0.8 Λ higher than in Lake Norsjø. According to Allen and Wootton (1984), the omnivore three-spined stickleback predominately preferred copepods in spring and autumn, and ephemeropteran nymphs in summer. Chironomid pupae and stickleback eggs were also elements of the diet in summer, whereas algae, plant material and debris were more important in autumn and winter. Accordingly, the low trophic position of three-spined stickleback in Lake Norsjø may indicate that plant material and debris might be an important part of their diet at the time they were caught (August). In addition, such diet might be more important for younger individuals, as the average size of our investigated stickleback individuals were significantly smaller (3.4 ± 0.5 cm), compared with 5.0 ± 0.5 cm in the study by Power et al. (2002). Accordingly age differences might be a reason for this differences, but age was not determined in none of the studies. The estimated trophic positions of whitefish, pike, perch and smelt were very similar to earlier investigations in other lakes in Canada and Norway (Cabana and Rasmussen, 1996; Vander Zanden and Rasmussen, 1996; Vander Zanden et al., 1997; Sharma et al., 2008; Sandlund et al., 2013).

The high $\delta^{15}N$ signatures and trophic position documented in brown trout from Lake Norsjø rely on the fact that only large individuals were

included in the catch, i.e. average weight of about 2.5 kg. Accordingly, they only represent obligate piscivore brown trout individuals. In some lakes at the Hardangervidda plateau (Lake Skaupsjøen and Lake Skjerja), where minnow (*Phoxinus phoxinus*) has been introduced and is known to be an important prey for brown trout, the estimated Λ in brown trout ranged from 3.7 to 4.5 (Rognerud et al., 2003), very similar values to the individually estimated Λ levels in Lake Norsjø (3.7- 4.1), where smelt and whitefish are the predominant prey fishes (Jensen, 1954; Borgstrøm, 1974).

The Arctic charr in our catch were relatively large (100-470 g), and almost all stomachs contained fish at the time when they were caught, late August, on their spawning sites, at a depth of 20-40 m. The relatively small variation in stable isotope signatures within the investigated individuals may indicate that they occupy a relatively narrow trophic niche in deeper areas of the lake. Similar observations exist from other lakes with relatively complex fish communities (Svärdson, 1976; Pethon, 2005; Museth et al., 2007; Sandlund et al., 2010). In the southern part of the lake, at depths > 40 m (unpublished data), we have also caught a small morphotype, varying in weight from 26 – 164 g, with age 5 - 20 years. This morphotype is earlier referred to as the dwarf form of Arctic charr (Guiguer et al., 2002). When distinctive forms exist, Arctic charr most commonly exhibit two morphotypes (Skùlason and Smith, 1995; Guiguer et al., 2002). An interesting observation is that while Guiguer et al. (2002) observed that the large morphotype had a more enriched δ15N and more depleted δ13C compared with the small, dwarf population in the very large (542 km^2) and deep (280 m) Lake Hazen in northern Canada, the opposite seems to be the case in Lake Norsjø.

Total Hg (THg) concentrations in fish

The average THg concentrations in fish ranged from < 0.1 ppm (ww) in individuals at low trophic level (as stickleback) to > 0.5 ppm (ww) in large and old piscivore individuals of brown trout and pike at high trophic levels. These Hg levels are comparable with other studies in Norwegian freshwaters (Rognerud et al., 2003; Sharma et al., 2008; Fjeld and Rognerud, 2009; Fjeld et al., 2010). By omitting the youngest pikes (4 individuals), the captured individuals of pike and brown trout were all > 7 years old. In our study, Arctic charr had a significantly lower average THg concentration (0.43 ppm) than pike (1.03 ppm; Mann-Whitney, $p < 0.05$), and almost significantly lower THg concentration than brown trout (0.56 ppm, Mann-Whitney, $p = 0.057$), despite the fact that the investigated individuals of Arctic charr were significantly older (11 years) compared with brown trout (8.5 years; Mann-Whitney, $p < 0.05$) and pike (8.0 years; Mann-Whitney, $p < 0.05$). Accordingly, the most thermophilic and obligate piscivore species (pike) had significantly higher Hg concentrations compared with the far more cold water adapted Arctic charr, with brown trout in an intermediate position. Furthermore, in contrast to the other piscivore species, Arctic charr showed no significant relationships neither between $\log_{10}$[THg] and age, nor between $\log_{10}$[THg] and length. This may rely on the fact that Arctic charr primarily occupy profundal habitats in the lake (> 20 m), where the water temperature seldom exceeds 10°C. Accordingly, the metabolism and activity costs are lower than in pike and brown trout which occupy higher water temperature habitats (littoral and pelagic) during the growth season and, thus, need more energy for the basal metabolism and higher growth rates. In other words, the lower Hg concentration in Arctic charr compared with the other two piscivore species, figure 4, is basically a consequence of lower growth rate and lower basal metabolism, a phenomenon earlier described by Trudel and Rasmussen (2006).

Based on risk assessments and other societal considerations, the Food and Agriculture Organization/World Health Organisation (Codex Alimentarius, 1995) and the European Community (2006) use advisory levels of 0.5-1.0 ppm MeHg (ww) in fish that are considered safe for human consumption. These guideline levels are also intended for MeHg in fresh or processed

fish and fish products moving in international trade. In accordance with these advisory levels, highest advisory level for pike is 1.0 ppm MeHg (ww), while 0.50 ppm MeHg (ww) is the highest advisory level for the remaining investigated species in Lake Norsjø. Thus, theoretically, brown trout in Lake Norsjø reach the Hg advisory limit of 0.5 ppm at an age of ≈ 8 years, or at a weight ≈ 1.9 kg, table 4, while pike theoretically reach the advisory level of 1.0 ppm MeHg (ww) at an age of about 11 years old or at a weight of about 6.5 kg. In the lake brown trout, pike and perch theoretically double their Hg concentration within ≈ 3 years. In 2014, US-EPA published an updated advisory level for Hg in fish of 0.2 ppm as a general recommendation, and not eating freshwater fish at all for pregnant women (US-EPA, 2014).

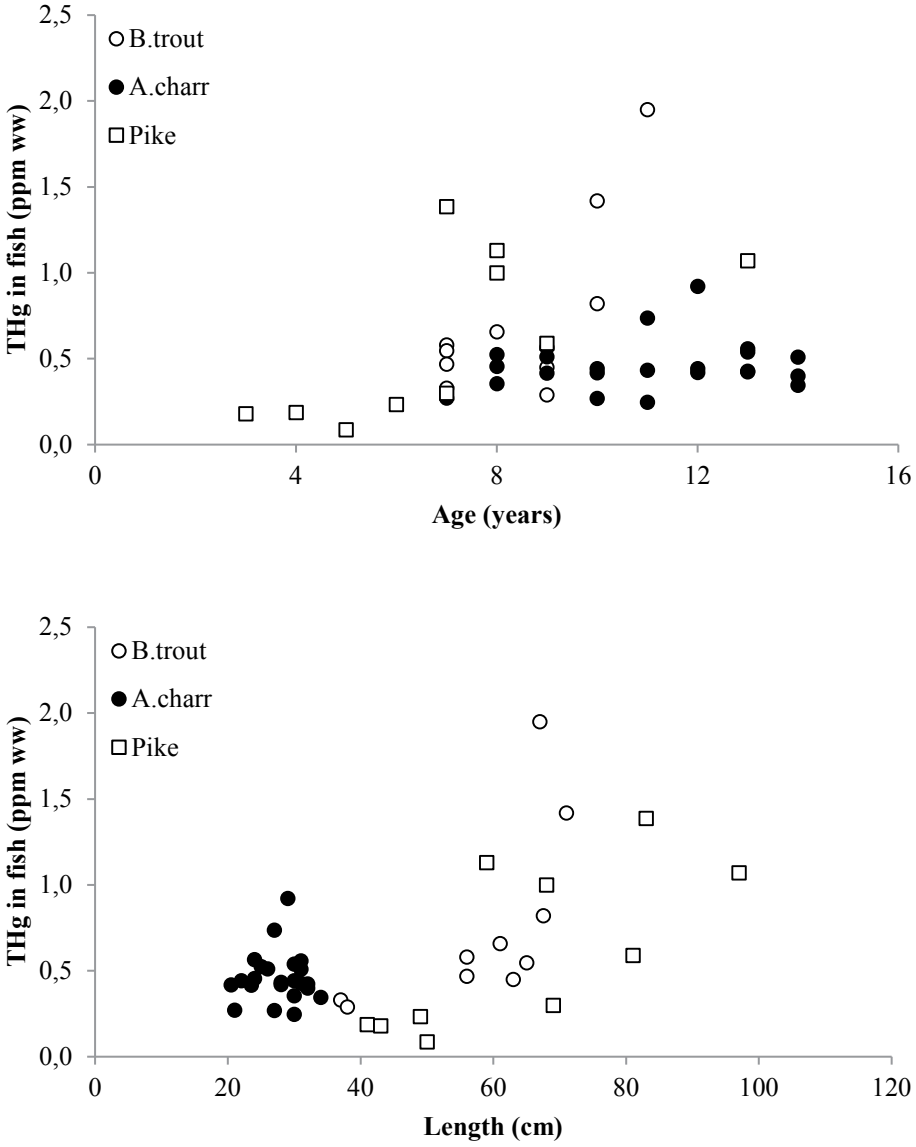

Figure 4. Relationships between age (years) or length (cm) and THg concentrations in piscivore fish species from Lake Norsjø.

Besides having the highest Hg concentrations, the predominately piscivore species (brown trout, pike and Arctic charr) exhibit the most intermediate $\delta^{13}C$ signatures of the investigated species, figure 3. Thus, piscivore fish in Lake Norsjø significantly integrate across littoral and pelagic food chains and habitats, as also shown by Vander Zanden and Vadeboncoeur (2002).

The trophic magnification slope (TMS), i.e. the slope of the simple linear regression between $\log_{10}$ [THg] and measured $\delta^{15}N$, was found to be $0.163\delta^{15}N - 2.45$ ($p < 0.001$), in the fish caught in Lake Norsjø in 2008-2010. This was almost identical to the TMS of 0.16 ± 0.11 reported from a worldwide meta-analysis study, including 69 sites (Lavoie et al., 2013) and the TMS value of 0.163 reported from a fish-species rich, eutrophic Norwegian lake, Lake Årungen (Sharma et al., 2008). A TMS of about 0.16 in all 3 studies indicates an average trophic magnification factor ($TMF = 10^{(0.163*3.4)}$) of about 3.5 per trophic level.

Conclusions

Implementation of a multi-fish species investigation to obtain knowledge about feeding habitats and Hg levels in fish from a large lake as Lake Norsjø, is a large challenge. Variations in factors such as inter- and intra-population abundance, habitat use, daily and seasonal migration patterns, fish catchability, fishing method, fishing sites, etc., imply a significant challenge both in time and space in order to obtain sufficient individuals to reach a reliable interpretation basis. In addition, seasonal variations in stable isotope signatures and Hg levels occur in lakes and within different lake habitats (pelagic, littoral and profundal), causing seasonal variations in inorganic and algal stable isotope signatures and, subsequently, further up in the food webs. Despite all these variations or limitations, however, we believe it is still possible to draw many relatively reliable conclusions and interpretations related to diet, habitat use, trophic position and Hg levels in fish from the northern parts of the fish species rich Lake Norsjø.

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