

Pro gradu –tutkielma

**Dependence of Arctic char (*Salvelinus alpinus* L.) on
littoral and pelagic energy sources in a subarctic lake,
Saanajärvi**

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TIIVISTELMÄ

Pohjalevien ja litoraalin ravintoverkon tuotannon on havaittu olevan erityisen tärkeitä niukkatuottoisten ja kirkasvetisten tunturijärvien ekosysteemin toiminnalle. Viimeaikaiset tutkimukset osoittavat, että litoraalin tuotanto dominoi myös näiden järvien yleisen huippukuluttajan, nieriän (*Salvelinus alpinus* L.), energiansaantia. Huippukuluttajien riippuvuus litoraalin ja pelagiaalin energialähteistä voi kuitenkin suuresti riippua mm. kalan koosta (eli kasvuvaiheesta) sekä vuodenajasta. Tämän tutkimuksen päätavoitteet olivat (1) arvioida Saanajärven nieriäpopulaation suhteellinen riippuvuus litoraalin ja pelagiaalin energialähteistä, sekä tarkastella kuinka litoraaliriippuvuus muuttuu (2) nieriän kasvun aikana (kalat jaettu kokoryhmiin <100 g, 100–500 g ja >500 g) ja (3) kasvukauden aikana (kalanäytteet pyydetty huhtikuussa, heinäkuussa, elokuussa ja syyskuussa vuonna 2006). Tutkimusjärvi eli Saanajärvi sijaitsee Luoteis-Lapissa ja sen nieriäpopulaatio on lähes allopatrinen, kääpiöitynyt sekä ylitieheä. Vakaiden isotooppien analyysi ja syönnösanalyysi osoittivat, että nieriäpopulaatio riippui suuresti litoraalin energialähteistä. Litoraaliriippuvuus ei juuri riippunut kalan koosta todennäköisesti siksi, koska alle 3-vuotiaita kaloja ei saatu lainkaan. Yleisesti ottaen <500 g nieriöillä oli hyvin laaja trofialokero ja kalojen ravinto koostui kaikista niistä ravintokohteista, mitä kyseisenä vuodenaikana tai kyseisessä elinympäristössä oli tarjolla. Surviaissääsken toukat ja pupat olivat <500 g nieriöiden pääravintoa, kun taas kaikki >500 g nieriät olivat kannibaaleja, mutta saattoivat käyttää ajoittain myös alempia trofiatasoja ravintonaan. Kaikista runsaimmat, <100 g nieriät eivät muuttaneet energialähdettään kasvukauden aikana ja olivat todennäköisesti saalistuspaineen vuoksi rajoittuneet ruokailemaan lähinnä litoraalivyöhykkeellä. Sen sijaan 100–500 g nieriät siirtyivät syksyllä osittain litoraalin ravintokohteista pelagiaalin energialähteisiin, mikä on todennäköisesti seurausta pelagiaalin ravintoresurssien kasvusta sekä lajinsisäisen ja lajienvälisen kilpailun lisääntymisestä litoraalilla. Nieriäpopulaation suuri riippuvuus litoraalin energialähteistä on todennäköisimmin seurausta Saanajärven kirkkaasta ja ultra-oligotrofisesta vedestä, joka tukee suurta litoraalin tuotantoa suhteessa pelagiaalin tuotantoon. Nieriä kykenee myös käyttämään suurempikokoisia pohjaeläimiä tehokkaammin ravintonaan kuin pientä pelagiaalin eläinplanktonia. Nieriäpopulaation havaittu laaja trofialokero sekä suuri yksilöllinen vaihtelu kasvunopeuksissa ja kuntokertoimissa ovat oletettavasti seurausta voimakkaasta lajinsisäisestä, mutta alhaisesta lajienvälisestä kilpailusta, mikä on pakottanut yksilöt käyttämään mitä erilaisimpia ravintokohteita.

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Hydrobiology and limnology

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ABSTRACT

Production of benthic algae and of the associated littoral food web has been shown to be of particular importance in the function of unproductive, clearwater arctic lake ecosystems. Recent evidence suggests that littoral production also dominates the energy supply for the common top consumer, Arctic char (*Salvelinus alpinus* L.). However, the relative reliance of top consumers on littoral and pelagic energy sources may depend strongly on the fish size (i.e. stage of ontogeny) and on season. The main aims of this study were (1) to estimate the relative reliance of the char population of Saanajärvi on littoral and pelagic energy sources, and to study how this reliance changes (2) during the char ontogeny (fish divided into size groups <100 g, 100–500 g and >500 g) and also (3) through the year (fish samples caught in April, July, August and September in 2006). The study lake, Saanajärvi, is situated in north-western Finnish Lapland and has a stunted, overcrowded and nearly allopatric char population. Stable isotope analysis and stomach contents analysis revealed that the char population relied heavily on littoral energy sources. The observed strong littoral reliance was largely independent of char size, perhaps because no char of age under 3 years were caught within this study. Generally, the population of <500 g char showed a wide trophic niche and diet consisted of all those prey items available in a particular season or habitat. Chironomid larvae and pupae generally dominated the diets of <500 g char, whereas all >500 g char were cannibals, but did show occasional foraging on lower trophic levels. The most abundant <100 g char did not show any clear seasonal switch in the energy source basis and were generally restricted to littoral habitat and food sources, most likely due to their high vulnerability to cannibalistic predation. In contrast, 100–500 g char showed a partial shift from littoral to pelagic energy sources in autumn, which is most probably a consequence of the increased pelagic resources, but may also result from increased intra- and interspecific competition in the littoral zone. The strong littoral reliance of the char population is suggested to result from the clear, ultra-oligotrophic water of Saanajärvi, which supports high littoral production in relation to pelagic production. Char can also utilize large-sized benthic macroinvertebrates with higher efficiency than small pelagic zooplankton. The observed wide trophic niche of the char population and the great individual variation in growth rates and condition factors are suggested to result from the strong intraspecific, but low interspecific, competition forcing individuals to utilize all kinds of different prey items.

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1. INTRODUCTION

1.1. Littoral and pelagic food webs and the energy source basis of char

Lakes have been widely used as model systems in ecological studies because, unlike most terrestrial ecosystems, they typically have clear boundaries and connections to nearby ecosystems (Kalff 2002). Due to their relatively closed character, lakes are also ideal targets for investigating the energy and nutrient transfer from primary producers to consumers at higher trophic levels, i.e. food web structures (Vadeboncoeur *et al.* 2002). Lake food webs are generally divided into pelagic (the open water area of the lake) and littoral (the lake shore with illuminated bottom area) food webs. In pelagic food webs, the energy is produced in the photosynthesis of phytoplankton and by bacterioplankton and further mobilized via grazing zooplankton to higher consumers such as planktivorous and piscivorous fish (Jones 1992, Kalff 2002). Benthic macroinvertebrates and decomposing bacteria living in the deep, aphotic profundal zone can be regarded as part of this pelagic food web, because they mainly recycle the energy produced in the upper pelagic zone by utilizing settling pelagic organisms (Karlsson & Byström 2005). In contrast, in littoral or benthic food webs the production is based on photosynthetic benthic algae growing on the surface of rocks and sediment of shallow, photic littoral zone (Kalff 2002, Libourissen & Jeppesen 2003, Vadeboncoeur *et al.* 2003). From benthic algae, energy is further mobilized to higher consumers such as benthivorous and piscivorous fish via grazing littoral benthic macroinvertebrates.

Littoral and pelagic food webs have commonly been regarded as relatively separate systems (Vadeboncoeur *et al.* 2002). However, interactions between littoral and pelagic energy-flow pathways have recently received more attention, because coupling between these habitats can have important consequences in nutrient cycling and in predator-prey dynamics (Polis & Strong 1996, Polis *et al.* 1997, Schindler & Scheuerell 2002). Because of their high mobility and flexible feeding on both littoral and pelagic resources, fishes often play a particularly important role as integrators of littoral and pelagic food webs (Vander Zanden & Vadeboncoeur 2002) and also as top-down controllers of organisms at lower trophic levels (e.g. McCann *et al.* 2005, Schindler & Scheuerell 2002). McCann *et al.* (2005) suggested that fishes, as large mobile consumers, not only link food webs in space but can also strongly affect the dynamics and stability of food webs with their rapid behavioural responses. Moreover, production at lower trophic levels sets the limit for production at higher trophic levels, because only 5–15 % of the energy produced in one trophic level transfers to the next (Wetzel 2001). Consequently, in a particular lake ecosystem, the energy source basis of top consumers typically reflects the dominant primary production pathway and the associated food web (e.g. McCann *et al.* 2005, Schindler & Scheuerell 2002). Fishes are thus prominent targets in studying trophic interactions and energy-flow from primary producers to top consumers. In fact, these factors are generally regarded to have fundamental importance for the function of lake ecosystems (e.g. Karlsson & Byström 2005). To clarify the interactions between littoral and pelagic food webs and to estimate their relative contribution in the lake total production, Vadeboncoeur *et al.* (2002) and Vander Zanden & Vadeboncoeur (2002) called for more comprehensive limnological studies, which are not restricted to a particular habitat or food web but instead pay attention to the whole lake ecosystem functioning.

Arctic lakes are promising targets for such whole-ecosystem studies because of their generally small size, low production and thus simple food web structures. Although they are rather abundant worldwide and also sensitive to several environmental stressors such as climate change (Smol *et al.* 2005), acidification, (Hesthagen & Sandlund 1995) and

eutrophication (Vadeboncoeur *et al.* 2003), lakes situated in high-latitude regions have been rather little studied (Kalff 2002). Production of phytoplankton is very low in typical (i.e. small, shallow and clearwater) high-latitude lake, because the long, dark winters of north and the absence of abundant vegetation, soft bedrock and major human activities in the catchment areas reduce the annual amount of solar radiation, dissolved nutrients (especially phosphorus and nitrogen) and dissolved organic carbon entering the lake (Kalff 2002). The general conception, that phytoplankton and the associated pelagic food webs account for most production in lake ecosystems, derives from the abundant studies of temperate and tropical lakes (Libourissen & Jeppesen 2003). These lakes have typically nutrient-rich and turbid water, which supports high phytoplankton production, but diminishes the amount of solar radiation and nutrients needed for the abundant growth of benthic algae (Hecky & Hesslein 1995, Vadeboncoeur *et al.* 2003). However, the situation is reversed in arctic lakes, where the nutrient-poor, clear water prevents high phytoplankton production, but enables the photosynthesis of benthic algae at much greater depths than in turbid lakes (Libourissen & Jeppesen 2003). Benthic algae also have access to sedimented nutrients and they can regulate the release of these nutrients to water column (Libourissen & Jeppesen 2003) and thus strongly compete with phytoplankton in oligotrophic, clearwater lakes (Vadeboncoeur *et al.* 2003). In fact, studies of arctic lakes have revealed that the production of benthic algae may make up as much as 80 % of the whole-lake primary production (Welch & Kalff 1974, Vadeboncoeur *et al.* 2003). Recent stable isotope studies have shown that in typical high-latitude lakes, production of benthic algae and of the associated littoral food web are particularly important also for the energy supply to top consumers, such as lake trout (*Salvelinus namaycush* L.) (Sierszen *et al.* 2003) and Arctic char (*Salvelinus alpinus* L.) (Karlsson & Byström 2005). This common observation is suggested to result from the extreme oligotrophy and clear water of arctic lakes resulting in pelagic resources that are insufficient for the support of planktivorous consumers (Sierszen *et al.* 2003), but also results from the relatively higher littoral primary production and larger sizes of prey organisms in littoral than in pelagic food webs (Karlsson & Byström 2005).

In high-latitude lakes, Arctic char (hereafter char) is the most common top consumer that can inhabit even lakes ice-covered year-round, where other fish species cannot survive (Klemetsen *et al.* 2003). In northern regions, char is a valuable household fish for natives, but also attracts sport fishermen (Klemetsen *et al.* 2003). Moreover, it has characteristics of a good indicator species due to its sensitivity to many anthropogenic disturbances such as climate change, reduced water quality and introduction of new species (Adams *et al.* 2007). Because of its wide northern distribution, flexible habitat demands and generalistic feeding behaviour (Amundsen 1995, Klemetsen *et al.* 2003), char has exceptional importance also in northern lake ecosystems (Adams *et al.* 2007). Char seems to have all the adaptations needed to take different kinds of lacustrine prey such as zooplankton, benthic macroinvertebrates and fish (Klemetsen *et al.* 2003) and thus it can strongly regulate the abundance and composition of organisms at lower trophic levels (e.g. Nilsson & Peljer 1973, Byström 2006). Hence, char may both link the benthic and pelagic food webs in typical high-latitude lakes, but also have strong impacts on the trophic dynamics and energy-flow pathways within these unproductive and sensitive ecosystems.

Although char populations in typical high-latitude lakes generally rely more on littoral than on pelagic production and food webs, individuals within populations and even whole populations may greatly differ from this general pattern. For instance, (1) the intensity of inter- and intraspecific competition within fish communities (e.g. predation, competition for habitat and food resources), (2) char ontogenetic stage (i.e. size or age), (3)

morphometric characteristics of the lake (i.e. size and depth) and also (4) seasons may all strongly affect the main energy source basis and trophic niche width of char. Even though char has a wide potential feeding niche (e.g. Klemetsen *et al.* 2003), in sympatric fish communities, where char coexists with other competitive fish species, strong interspecific resource and habitat competition may considerably restrict the feeding niche of char having further effects on the growth and recruitment of char populations (e.g. Nilsson 1955, Jansen *et al.* 2002). Svårdson (1949) and Werner (1977) stated that when interspecific competition is intense, species tend to be restricted to narrow feeding niches, whereas during periods of or within populations continuously subjected to strong intraspecific competition, species spread out over their optimum niches to less favourable food sources and foraging areas. For example, brown trout (*Salmo trutta* L.) has frequently been shown to restrict the feeding niche of char by its more aggressive and less flexible behaviour (e.g. Nilsson 1955, Jansen *et al.* 2002, Forseth *et al.* 2003). According to previous Scandinavian studies, allopatric populations (i.e. no other fish species coexist in the lake) of brown trout and char often have very similar diets mostly consisting of benthic macroinvertebrates, but in sympatry, char shifts to feed mainly on zooplankton, whereas brown trout continues to feed on benthic prey (Nilsson 1965) and may exclude char from the littoral zone (Langeland *et al.* 1991). In contrast, the frequently observed wide feeding niches of allopatric char populations are generally assumed to be related to the strong intraspecific competition for limited food resources, which forces individuals to specialize on different prey types (e.g. Nilsson 1955, Amundsen 1995). Hence, although char populations may show generalistic foraging and wide trophic niches, individuals within populations may be strictly specialized to different prey targets (Amundsen 1995). To cope with the limited food resources and to minimize intraspecific competition, even distinct morphs of char have evolved within some char populations. These char morphs may differ in their feeding habits, growth rates, morphology, colouration and even spawning seasons (e.g. Jonsson & Jonsson 2001). The specialized char morphs have been observed to be more effective foragers than their intermediate counterparts, but the genetic basis behind these morphs is still rather controversial (see e.g. Jonsson & Jonsson 2001, Klemetsen *et al.* 2003 and references therein for more details of char morphs).

Most fish species, including char, may undergo ontogenetic dietary shift during their lifespan, because resource utilization ability and predation risk are generally related to fish size (e.g. Werner & Gilliam 1984, Godin 1997). Prey selection (i.e. how large prey items fish can ingest) and reliance on littoral and pelagic energy sources may thus strongly depend on char size and age. In most char populations, juveniles feed mostly on zooplankton, but as they grow they generally switch to benthic macroinvertebrates due to the larger size and thus higher foraging efficiency of macroinvertebrates (e.g. Forseth *et al.* 1994, Klemetsen *et al.* 2003). In other lakes, where pelagic energy sources are relatively abundant, juvenile char may instead switch diet from small-sized benthic macroinvertebrates to pelagic zooplankton as they have outgrown the size most vulnerable to predation (e.g. Jonsson & Jonsson 2001, Byström *et al.* 2004). Those char individuals who have grown large enough for fish ingestion typically switch to piscivory (Amundsen 1994). Cannibalism is rather frequent within allopatric char populations, where no other prey fish species than conspecifics are available (L'Abée-Lund *et al.* 1992, Amundsen 1994). The existence of only a few fast-growing cannibals may further have importance in controlling the habitat use, growth and abundance of smaller char and thereby they may prevent the char population from becoming stunted and overcrowded (e.g. Svenning & Borgstrøm 1995).

The effect of lake morphometry and seasons on the energy source basis of char has received little attention. The few studies of high-latitude lakes which have estimated the contributions of littoral versus pelagic energy sources in top consumer body carbon (e.g. Hecky & Hesslein 1995, Sierszen *et al.* 2003, Karlsson & Byström 2005) have focused on relatively small and shallow lakes. This is likely one of the main reasons, why fish populations in high-latitude lakes have proved to rely strongly on littoral energy sources. However, in large and deep lakes often situated at low altitudes, the relative contribution of the pelagic zone in the lake total area is much larger and the annual ice-cover period is also shorter, which may support relatively higher pelagic production and thus higher reliance of top consumers on pelagic energy sources. In the aforementioned studies (Sierszen *et al.* 2003, Karlsson & Byström 2005), fish have been sampled only once in a year and the impact of seasons on the energy source basis of top consumers has thus been largely ignored. However, during the short northern summer, pelagic production may increase considerably due to the continuous solar radiation, whereas the abundance of benthic macroinvertebrates simultaneously decreases due to the emergence of most species during the early summer (Amundsen 1995). In consequence, increased intraspecific competition for limited littoral resources may drive char populations to shift their diet from littoral to pelagic energy sources in late open-water seasons, as shown by a few previous studies (Amundsen 1995, Bjøru & Sandlund 1995).

Despite their fundamental importance for the function of lake ecosystems, there exist very few estimates of the relative importance of littoral versus pelagic energy sources for the ecosystem energy-flow in high-latitude lakes (Karlsson & Byström 2005). The fact that arctic lakes and their integrated littoral and pelagic food webs have received so little attention is most probably a consequence of their remoteness, but also results from the methodological constraints and from the general scarcity of whole-ecosystem studies (Vadeboncoeur *et al.* 2002). However, modern stable isotope analysis, often used in tandem with traditional fish stomach contents analysis, can offer a powerful tool for studies of lake food webs and energy-flow from primary producers up to top consumers.

1.2. Stomach contents and stable isotope analyses in studies of fish diets and lake food webs

Stomach contents analysis is the traditional method used in studies of fish diets and food web structures of lake ecosystems (e.g. Vander Zanden & Vadeboncoeur 2002, Jardine *et al.* 2003). Because the ingested prey items may preserve in the fish stomach for a few days and often be precisely identified, this analysis can give valuable information of the recent diet of individual fish with high taxonomic resolution (Jardine *et al.* 2003). However, due to the differences in digestion rates, the contribution of hard-bodied prey organisms, such as snails and clams, may be overestimated, while the contribution of quickly assimilated prey items are often underestimated in the fish diets (Vander Zanden & Vadeboncoeur 2002). Some fishes may also have empty stomachs, which can be problematic in traditional diet analyses. Moreover, stomach contents analysis provides a measure of fish diet only for a short time period and probably from a small part of the fish total foraging area and thus may not reflect the assimilated food sources in a longer temporal and larger spatial scale (Vander Zanden & Rasmussen 1999). To get a more complete picture of fish diets, samples for stomach contents analysis should be taken many times during the growing season and from all habitats, which may lead to large financial and time costs.

Modern stable isotope analysis offers an effective technique to study the energy-flow in aquatic food webs and fish diets over a longer time-scale (Peterson & Fry 1987). In

ecological studies, the two natural stable isotopes of carbon (^{13}C and ^{12}C) and nitrogen (^{15}N and ^{14}N) are the most frequently used elements. Every organism within a lake food web has a unique composition or ratio of the lighter (^{12}C and ^{14}N) and heavier (^{13}C and ^{15}N) carbon and nitrogen stable isotopes depending mainly on the isotopic compositions of their food sources. The isotopic ratios of sample organism are referred to the isotope ratios of international standards to give delta values $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ (see e.g. Jardine *et al.* 2003 for more details of the equation used in defining delta values). The carbon isotope ratio changes (i.e. fractionates) very little between an animal and its diet (only around 0.4 ‰), whereas the $\delta^{15}\text{N}$ value rises approximately 3.4 ‰ per trophic transition (Vander Zanden & Rasmussen 2001). Hence, the $\delta^{13}\text{C}$ value offers a tool to trace the main energy sources of different consumers, while the $\delta^{15}\text{N}$ value can be used as a measure of an animal's trophic position within a particular food web (e.g. Vander Zanden & Rasmussen 2001).

In lake ecosystems, carbon isotope signatures generally differ extensively between pelagic and benthic primary producers due to differences in their isotopic discrimination for dissolved inorganic carbon (Vander Zanden & Vadeboncoeur 2002). Benthic algae are CO_2 limited and therefore cannot preferentially take up the lighter carbon dioxide isotope ($^{12}\text{CO}_2$), whereas phytoplankton is surrounded by an abundance of available CO_2 and therefore can discriminate against the heavier isotope ($^{13}\text{CO}_2$) (Jardine *et al.* 2003). In consequence, benthic algae are enriched (i.e. have higher $\delta^{13}\text{C}$ value), while phytoplankton is depleted in ^{13}C . The differences in $\delta^{13}\text{C}$ values are further passed on to consumers, which enables the separation between consumers that are depending on littoral (e.g. littoral benthic macroinvertebrates, benthivorous fish) or pelagic (e.g. pelagic zooplankton, planktivorous fish) energy sources. Based on the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of different littoral and pelagic organisms, it is possible to construct a schematic food web model of the particular lake ecosystem (Figure 1). In addition, if the $\delta^{13}\text{C}$ values of littoral and pelagic prey organisms, such as pelagic zooplankton and littoral benthic macroinvertebrates, are sufficient distinct, simple two-source mixing models can be used to estimate the relative contributions of these two energy sources in the diets of individual fish (Karlsson & Byström 2005). In a simplified manner, the similarity between $\delta^{13}\text{C}$ values of fish and its possible prey items with distinct $\delta^{13}\text{C}$ values gives an idea of the relative importance of these food sources to the fish energy supply (Philips 2001). Unlike stomach contents, the stable isotope signatures of fish reflect the assimilated and not only digested food sources over a longer time-scale depending on the turnover rate of the tissue used (Vander Zanden & Rasmussen 2001). For instance, the isotopic composition of muscle tissue reflects the main food or carbon sources of fish during the last month, while liver tissue reflects the diet of the last one or two weeks (Perga & Gerdeaux 2005). Hence, use of different tissues with distinct turnover rates in stable isotope analysis and stomach contents analysis in tandem is the best way to estimate the relative importance of littoral and pelagic energy sources for fish energy supply and also the timing of possible dietary shifts of individual fish or of the whole fish population (Philips & Eldridge 2006). Moreover, variance (or standard deviation) of stable isotope signatures can be used as a simple but powerful method in determining the trophic niche width of the fish population studied (Bearhop *et al.* 2004).

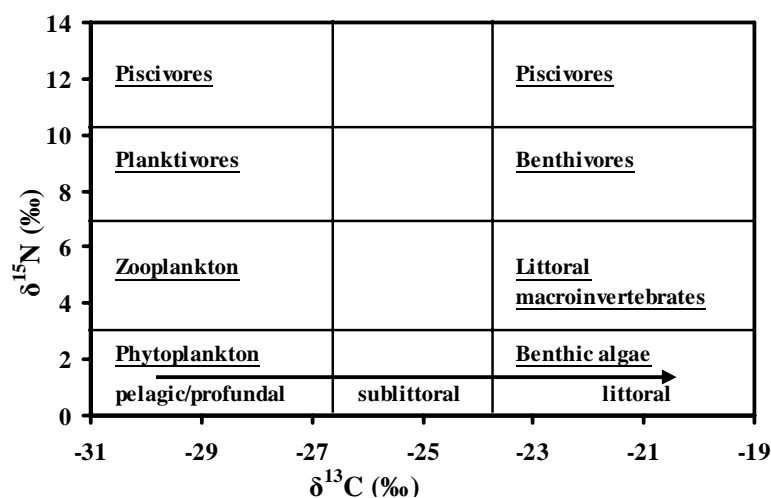


Figure 1. Generalized dual isotope plot ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) for biota in lake ecosystems showing the distinction between organisms relying on littoral and pelagic/profundal energy sources ($\delta^{13}\text{C}$) and occupying different trophic positions ($\delta^{15}\text{N}$). Values presented here to delimit pelagic and littoral food webs and trophic positions of different organisms are only suggestive and differ between ecosystems. Figure modified from the one presented by Jardine *et al.* (2003).

1.3. Objectives of this study

The main aim of this Master's thesis was to study the food web structures of subarctic Saanajärvi and particularly to estimate the relative dependence of the char population on littoral and pelagic energy sources. Stomach contents analysis and stable isotope analysis with a simple two-source mixing model were used in tandem to reveal the energy source basis and trophic positions of individual fish within different size groups (<100 g, 100–500 g and >500 g) and in different times of growing season from early April to the end of September in 2006. The specific objectives of this study were: (1) to estimate the relative dependence of char population on littoral energy sources, (2) to study whether there are any temporal or seasonal changes in this littoral reliance, (3) to see whether char size groups differ by their energy source basis or diet (i.e. do char undergo ontogenetic dietary shift), (4) to estimate trophic positions of char within different size groups and (5) to evaluate individual differences in the char feeding behaviour. The main hypotheses were that the char population (1) mostly depends on littoral energy sources, but (2) shift to feed more on pelagic energy sources (i.e. pelagic zooplankton) in the late open-water seasons due to the increase in pelagic resources and simultaneous decrease of benthic macroinvertebrate density causing strong resource competition in the littoral zone. Other hypotheses were that any individual char (3) undergoes an ontogenetic dietary shift from pelagic to littoral energy sources or vice versa, (4) becomes cannibalistic as it reaches the size large enough for fish ingestion and (5) shows specialized feeding strategy due to the strong intraspecific resource competition within the overcrowded char population of Saanajärvi.

2. MATERIAL AND METHODS

2.1. Study area

Saanajärvi (N 69°, E 21°) is situated in the extreme northwest part of Finnish Lapland in the vicinity of Kilpisjärvi village (Figure 2). Kilpisjärvi belongs to Enontekiö county and the village has approximately 100 inhabitants. The region can be considered as natural and relatively undisturbed both in terms of land use and airborne pollution (Rautio 2001). Like other subarctic and arctic regions, Kilpisjärvi is subjected to great annual fluctuations of temperature, light and precipitation. The mean annual temperature in this region is -2.6°C , whereas the temperatures may range from -35°C to $+25^{\circ}\text{C}$ within a year (Järvinen 1987). Winter lasts up to nine months and is characterized by limited light. In contrast, there appears continuous light for over two months during the short summer of north. In Kilpisjärvi region, most annual precipitation accumulates during winter as snow, whereas summers are often relatively dry (Sorvari 2001).

Saanajärvi is a relatively small, dimictic and ultra-oligotrophic clearwater lake (Table 1). It is situated above the tree-line at 679 m a.s.l. between two fells, Saana (1029 m a.s.l.) and Iso-Jeahkas (960 m a.s.l.) (Figure 2), and is usually ice-free between late June and mid-October (Sorvari 2001). The northern slope of Saana fell consists mainly of bare rocks and boulder fields, whereas other parts of the catchment area are covered by meadow-type, subalpine vegetation (Sorvari 2001). The shorelines are rocky all over the lake and macrophytes are nearly absent from the littoral zone. Lake margins are steep in many places, and there is a relatively large, even-bottomed deeper central area in the lake (Figure 2). However, the south-eastern parts of the lake are much shallower and also have gentler slopes. In contrast to most recently studied subarctic and arctic lakes, Saanajärvi is overall a relatively deep lake in relation to its small surface area and thus consists of both relatively large profundal (or pelagic) and littoral areas (Figure 2, Table 1). Hence, these areas can serve as distinct primary production pathways, but also as different foraging habitats for the fish community.

Saanajärvi has a very simple fish community, which consist almost solely of char, while brown trout exists in very small numbers. Saanajärvi was earlier almost fishless, but was stocked with char in 1993 and 1997 for recreational purposes. According to the personal knowledge of the staff of Finnish Forest Research Institute, char grew very fast before the stocking from Pahtajärvi in 1993 and their diet consisted solely of amphipods at that time (Ranta pers. comm.). In 1997, stunted char from Tsuugijärvi were introduced to Saanajärvi. These char were soon found to reproduce in great numbers and, in consequence, the overcrowded char population largely consumed the previously abundant amphipods and became stunted. Despite its beauty and rather good accessibility, Saanajärvi attracts only very few sport fishermen nowadays, because char of satisfactory size are so hard to catch (Ranta pers. comm.). No comprehensive study of char food sources has previously been done in Saanajärvi.

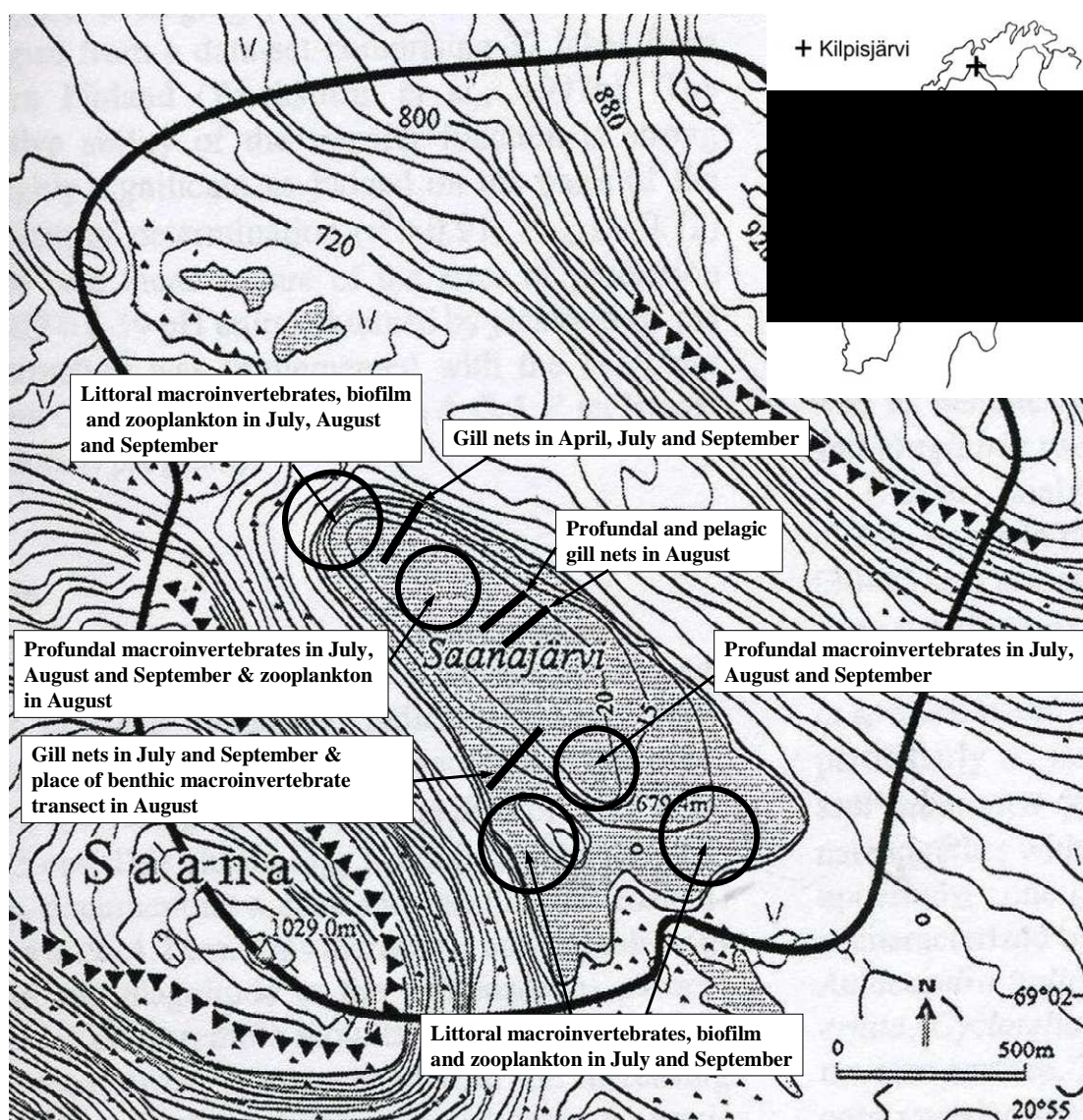


Figure 2. Location and catchment area (line surrounding the lake) of Saanajärvi. Sampling sites (see 2.2. Data collection) for benthic macroinvertebrates, biofilm and zooplankton are marked with circles, whereas gill net locations are marked with lines. Sampling times at each site are also given in text boxes. Map modified from the one presented by Sorvari (2001).

Table 1. Some morphometric and hydrographic parameters of Saanajärvi. Information obtained from (1) Sorvari (2001), (2) Battarbee *et al.* (2002) and (3) Arctic limnology -field course report (2006). Proportions of littoral and profundal area were estimated by measuring the contributions of area within (profundal zone) and outside (littoral zone) the 15 meter depth contour in Figure 2.

Parameter	Value
Latitude (°N) ⁽¹⁾	69° 05'
Longitude(°E) ⁽¹⁾	20° 55'
Altitude (m a.l.s.) ⁽¹⁾	679
Surface area (ha) ⁽¹⁾	70
Proportion of littoral area (%)	53
Proportion of profundal area (%)	47
Catchment area (ha) ⁽¹⁾	461
Catchment / surface area (ratio) ⁽¹⁾	6.6
Maximum depth (m) ⁽²⁾	24.0
Mean depth (m) ⁽²⁾	5.1
1 % PAR light depth (m) ⁽³⁾	16.0
Volume (10 ⁶ m ³) ⁽²⁾	3.6
Retention time (years) ⁽²⁾	1.0
pH (units) ⁽¹⁾	6.8
Conductivity (µS cm ⁻¹) ⁽¹⁾	27.7
DOC (mg l ⁻¹) ⁽¹⁾	1.6
Colour (PT mg l ⁻¹) ⁽¹⁾	5.0
TP (µg l ⁻¹) ⁽¹⁾	3.0
TN (µg l ⁻¹) ⁽¹⁾	97.0

2.2. Data collection

2.2.1. Sampling times

All samples (fish, benthic macroinvertebrates, zooplankton and biofilm) were collected on three occasions in 2006: (1) in early July by the author, (2) in early August by the participants on the Arctic limnology course arranged by University of Helsinki and University of Jyväskylä, and finally (3) in late September by the author. In addition, some fish samples were collected in early April under ice by the staff of the Finnish Forest Research Institute. Samples of benthic macroinvertebrates, zooplankton and biofilm were collected only once on every sampling occasion, whereas fish were collected as long as sufficient samples were obtained. Except stable isotope analyses, all laboratory work was done at the Kilpisjärvi Biological Station, University of Helsinki.

2.2.2. Fish

Fishing was conducted using 30 m long gill nets (N = 5–12) of varying knot-to-knot size from 12 mm to 60 mm and height of 1.5–2.0 m. Each gill net series (4–6 gill nets in a line) was usually set down on the bottom from the shoreline to the deep (Figure 2). Exceptionally, in August, one gill net series was set on the bottom of the lakes deepest area (profundal gill nets), while the other was set near the lake surface to the pelagic zone. None of the gill nets were set on the lake littoral area at that time. Gill nets were checked every day or every other day and after enough samples of a given fish size group were caught (after a few days in open-water seasons and after two weeks in April), the fishing was stopped and gill nets were removed. After capture, fish were immediately killed and

transported in cool bags before storing in a freezer in the laboratory. In the laboratory, total length (mm) and total wet weight (g) were measured from each fish and they were grouped into three size groups according to their weight: <100 g, 100–500 g and >500 g. In addition, otoliths were removed for later age definition (Raitaniemi *et al.* 2000). In the beginning, the age definition was done by sanding down otoliths with water sandpaper from the wider end to the midpoint and dyeing them for 15 minutes in a mixture of neutral red and 0.5 % acetum acid before examining under a stereo microscope. However, it soon became evident that the easiest and most reliable method was to define fish ages from the whole, clear otoliths, which were first put under water for at least one minute before the magnification. For stable isotope analysis, a sample of white muscle tissue was dissected from each fish posterior to the dorsal fin. In addition, the whole or a piece of liver was dissected and washed out under cool tap water. Both muscle and liver samples were either first wrapped in aluminium foil and stored frozen or immediately oven-dried at 60°C for two days. Later, the dried tissue samples were ground to a fine powder using a mortar and pestle and stored frozen in 2 ml glass vials for later analysis.

The fish stomach contents were examined by emptying the stomach into a Petri dish filled with tap water. The contribution of each prey type was estimated by using the points method described by Hynes (1950). The stomach fullness was first visually estimated using a relative scale from 0 to 10 (0 = empty stomach, 10 = extended full stomach). The contribution of each prey item was then given as a part of this fullness value, giving an estimate of the volume of each prey type in the fish stomach. The prey items were identified to order, family or species level. Later they were categorized into (1) zooplankton (cladocerans, calanoid copepods and *Bythotrephes* sp. predatory cladocerans), (2) molluscs (*Lymnaea* sp. snails and *Pisidium* sp. clams), (3) other littoral macroinvertebrates (*Gammarus lacustris* amphipods, trichopteran larvae, plecopteran nymphs and *Corixidae* sp. European water crickets), (4) chironomids (larvae and pupae), (5) aerial or surface insects (adults of coleopterans, hymenopterans, dipterans, tipulids and plecopterans) and (6) fish (char). The division into these prey categories is more or less specious, because *Lymnaea* sp. snails, *Pisidium* sp. clams and chironomids could all be defined as littoral macroinvertebrates. On the other hand, some *Pisidium* sp. clams and chironomids may be of profundal origin and thus represent different energy-flow pathway for fish than littoral organisms. In addition to considering the energy source basis, these aforementioned categories were further divided into (1) benthic (littoral macroinvertebrates, molluscs, chironomid larvae), (2) pelagic (zooplankton, chironomid pupae, aerial insects) and (3) fish prey types to better illustrate the foraging strategies and habitats of different fish size groups and species. To clarify, for instance pelagic prey type does not refer to pelagic energy sources like zooplankton alone does, but describes those prey organisms found in the pelagic habitat.

Some common prey items, such as *Daphnia* sp. cladocerans, *Lymnaea* sp. snails and chironomid pupae, were hard to obtain by general sampling methods. In these cases, the examined undigested prey organisms were picked from the Petri dish into a 0.5 L plastic container filled with tap water, filtered through a 200 µm sieve to remove excess water and picked from the sieve into 2 ml glass vials. After drying at 60°C for two days, samples were ground and stored frozen until later isotope analysis. This procedure has been shown to be a useful and reliable method in studying fish diets and food web structures by stable isotopes, when it is otherwise hard to obtain samples of fish prey items (Grey *et al.* 2002).

2.2.3. Zooplankton, biofilm and benthic macroinvertebrates

Zooplankton, biofilm (i.e. benthic algae) and benthic macroinvertebrates were sampled in July, in August and in September, and only once on every sampling occasions. In July and September, zooplankton, biofilm and littoral macroinvertebrates were sampled from three distant sampling areas: (1) from the northern end of the lake, (2) from the south-western part near the island and (3) from the shallow south-eastern end of the lake (Figure 2). In addition, profundal benthic macroinvertebrates were collected from two sites at the same time: one situated in the northern end and the other in the southern end of the lake deep. In August, littoral macroinvertebrates, littoral and sublittoral biofilm and pelagic and littoral zooplankton sampled from the northern end of the lake. At that time, benthic macroinvertebrates were sampled in a transect from the shallow littoral to the deep profundal zone near the island (Figure 2).

Zooplankton was collected by several 20–40 m long horizontal hauls using a plankton net of 200 μm mesh. Sampling depth varied between 2–7 m depending on the depth of the sampling site (3–20 m). A total of 10 to 15 replicate hauls were needed to obtain sufficient samples. Zooplankton samples were stored in 0.5 L plastic bottles, brought to the laboratory, sieved through a 200 μm mesh and put into a 1 L plastic container filled with cool tap water. After the samples were stored in a fridge overnight and the zooplankters had voided their guts, samples were sorted into cladocerans and calanoid copepods. This sorting was done only for the samples collected in July and September, whereas zooplankton samples collected in August were mixed samples of all zooplankton groups. Most of the cladocerans were separated from the copepods by gently scraping the floating cladoceran individuals with a scalpel and needle from the water surface into a Petri dish filled with tap water. After removing the excess cladocerans on the water surface with a pipette, the swimming calanoid copepods were separated by gently pouring most of the sample water through a 200 μm mesh, picking the copepods from the mesh into a Petri dish filled with tap water and leaving dead zooplankton on the bottom of container. Both cladoceran and calanoid copepod samples were checked under a stereo microscope and all unwanted material, including predatory cladocerans (*Bythotrephes* sp.), was removed from the samples. After filtration through a 200 μm mesh to remove the excess water, zooplankton samples were scraped from the mesh onto glass fibre filter papers and oven-dried at 60°C for two days. Dried zooplankton samples were then picked from the filter papers into small glass vials and stored frozen until later analysis.

Samples of littoral benthic algae (hereafter biofilm) were collected by picking up small stones from the shallow shoreline into a 1 L plastic container half-filled with water and by scraping off the epilithic algae using a potato brush. After enough biofilm material was scraped, samples were stored in 0.5 L plastic bottles. In the laboratory, biofilm samples were first filtered through a 200 μm mesh and after all visible non-periphyton particles were removed manually, the samples were scraped from the mesh onto aluminium dishes and oven-dried at 60°C for two days. Dried biofilm samples were ground to a fine powder by hand using a mortar and pestle and stored frozen in glass vials for later isotope analysis.

Littoral macroinvertebrates were collected both by using a kick net with a mesh size 500 μm in the shallow littoral area (depth <1 m) and an Ekman grab (15.7 cm x 15.7 cm) in the deeper littoral areas (depth 2–6 m). All profundal macroinvertebrates were collected with an Ekman grab from depths of 17–24 m. Several replicates were needed to obtain sufficient samples with the Ekman grab: 5–8 replicates at deeper littoral areas and 10–15 replicates at profundal areas. All macroinvertebrate samples were first sieved through a

500 µm mesh and then taken to the laboratory in 1 L plastic bottles. Finally the macroinvertebrate individuals were transferred into clean water to allow them to void their guts. The following day macroinvertebrates were identified and sorted into 2 ml glass vials. Usually each sample was a mixture of several individuals of the same taxon, but sometimes even samples of the same taxon from different sampling sites were combined to obtain sufficient samples for isotope analysis. For molluscs, only the soft body tissue was dissected for final sample. After drying at 60°C for two days, the samples were ground to a fine powder either by using a mortar and pestle (large and abundant macroinvertebrates) or by grinding the samples in glass vials with spatula. All ground samples were stored frozen in glass vials for later isotope analysis.

2.2.4. Stable isotope analyses

All stable isotope analyses of carbon and nitrogen were done between December 2006 and February 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 (*Esox lucius* L.) white muscle tissue was used as an internal working standard for animal tissues, whereas potato leaves were used for biofilm samples. Two replicates were run from each sample and in each run replicate standards were inserted after every five samples. In each run, standard deviation of both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of pike muscle standard was less than 0.2 ‰ and for potato standard less than 0.6 ‰.

Fish individuals may have varying contents of ^{13}C -depleted lipids in tissues resulting from the different lipid-contents of their food sources. This difference in lipid composition can give rise to variation in $\delta^{13}\text{C}$ values between individuals that is higher than the commonly assumed 0–1 ‰ difference between trophic levels. Here, a lipid-normalization procedure described by Kiljunen *et al.* (2006) was used to remove this probable bias in carbon isotope values. This procedure was used for both fish muscle and liver $\delta^{13}\text{C}$ values, even though it was developed for fish muscle tissue and has not been tested for liver. The lipid-normalization procedure is based on two equations:

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

$$\delta^{13}\text{C}' = \delta^{13}\text{C} + D \times \left(I + \frac{3.90}{1 + 287/L} \right)$$

where L = the proportional lipid content of the sample and $\delta^{13}\text{C}'$ = the lipid-normalized value of the sample; C and N = the proportions of carbon and nitrogen in the sample; $\delta^{13}\text{C}$ = the measured value of the sample; D = the isotopic difference between protein and lipid (assigned a value of 7.018); and I = a constant (assigned a value of 0.048) (see Kiljunen *et al.* 2006 for more details of the constants shown in the equations).

2.3. Fish calculations

2.3.1. Length-weight relationship, condition factor and growth

The relationship between total length and weight of char and brown trout was defined by the equation:

$$\text{weight}(g) = a \times \text{length}(mm)^b$$

where a = a constant; and b = the slope of the linear regression between log-transformed weight and length variables. The one >500 g starved char was excluded from the regression model as an outlier.

Condition factors are generally used to compare the condition, performance or shape of fish (Bagenal 1978). Because char growth is not isometric (i.e. large fish are on average fleshier than small ones) and the range of char length is large, a modified version of the Fulton's condition factor (Bagenal 1978) was used:

$$CF = \frac{\text{weight}(g)}{\text{length}(mm)^b} \times 100000$$

where the exponent b is defined as above-mentioned (see length-weight relationship). This procedure makes the association between weight and length linear and thus enables the comparison of conditions between small and large-sized fish.

To measure the char growth, the von Bertalanffy's non-linear growth model (Bagenal 1978) was used. The expression for length (l_t) at age t as a function of t (i.e. the prediction for the fish length at a particular age) is written as:

$$l_t = L_\infty \times \left| 1 - e^{-K \times (t - t_0)} \right|$$

where L_∞ = infinity length, K = the rate at which the growth curve approaches the asymptote, and t_0 = a time scaler equivalent to the starting time when the fish would have been zero-sized if they had always grown according to the equation.

2.3.2. Diet analyses

Diet similarity or overlap between char size groups and also between char and brown trout was estimated by using the Schoener (1970) index:

$$\alpha = 1 - 0.5 \times \left(\sum_{i=1}^n |p_{xi} - p_{yi}| \right)$$

where p_{xi} = proportion of food item i used by the size group or species x , p_{yi} = proportion of food item i used by the size group or species y , and n = the number of prey categories. A value of zero indicates no overlap or similarity between size groups or species, whereas a value of 1 suggests complete overlap. A diet similarity value of 0.6 or higher was considered biologically significant (Wallace 1981).

2.3.3. Mixing model of littoral contribution

To estimate the contribution of littoral energy sources in the diet of individual fish, a two-source mixing model described by Karlsson & Byström (2005) was used. This mixing model compares the observed $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of fish to the means of littoral and pelagic baselines, and uses generally accepted values for trophic isotopic fractionation of carbon ($\Delta_C = 0.47$ ‰) and nitrogen ($\Delta_N = 3.46$ ‰) (Vander Zanden and Rasmussen 2001). The model estimates the relative contribution of littoral carbon or energy sources in the fish diet (LF, %) as:

$$LF = \left(\frac{[\delta^{13}\text{C}_{fish} - \delta^{13}\text{C}_{pel} - (\delta^{15}\text{N}_{fish} - \delta^{15}\text{N}_{pel}) \times TS]}{[(1 - TS \times BS) / (\delta^{13}\text{C}_{lit} - \delta^{13}\text{C}_{pel})]} \right) \times 100$$

where TS = the slope of the trophic fractionation of carbon and nitrogen in the food web (Δ_C/Δ_N , 0.47/3.46 ‰), and BS = the slope of the linear relationship between the pelagic and littoral baselines (here assigned a value of 0.0214). In this study, the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for pelagic baseline ($\delta^{13}\text{C}_{\text{pel}}$ and $\delta^{15}\text{N}_{\text{pel}}$) were assigned as the mean of isotopic signatures of cladocerans and calanoid copepods sampled in July and September, whereas the values for littoral baseline ($\delta^{13}\text{C}_{\text{lit}}$ and $\delta^{15}\text{N}_{\text{lit}}$) were assigned as the mean of isotopic signatures of littoral chironomid larvae, *Lymnaea* sp. snails and *Gammarus lacustris* amphipods also sampled in July and September. Because littoral baseline is a mean value of several groups of organisms collected in two sampling occasions, it is possible that the estimated value for an individual fish exceeds 100 % if, for example, the fish has been solely feeding on a particular littoral prey item with exceptionally high $\delta^{13}\text{C}$ signature.

This two-source mixing model ignores the contribution of profundal benthic macroinvertebrates in the fish diet. To estimate the contributions of all these three prey types (pelagic zooplankton, profundal macroinvertebrates and littoral macroinvertebrates) in the fish diet, a three-source mixing model should be performed. However, these models are far too complicated for this kind of study and moreover, as aforementioned, the profundal macroinvertebrates can be seen to largely correspond to the energy-flow pathway and also to the isotopic signatures of pelagic organisms.

2.4. Statistical analyses

Analysis of variance (ANOVA) was used in testing the differences in means of condition factor, $\delta^{13}\text{C}$ value and LF estimate between all char size groups and also between sampling seasons within the populations of <100 g and 100–500 g char. ANOVA was also used to test the differences in mean $\delta^{15}\text{N}$ values of different char size groups. In few cases, when the ANOVA assumption of homogeneity of variances was not met, non-parametric Kruskal-Wallis χ^2 -test was used in testing differences. When the result of ANOVA test was statistically significant ($p < 0.05$), Tukey's pairwise comparisons were performed to test the differences between each size group and sampling season. In addition, linear regression was used to evaluate the change in char and brown trout $\delta^{15}\text{N}$ values (i.e. trophic positions) and also in LF estimates as a function of increasing fish total length. Student's t-test was used in testing the differences in mean of $\delta^{13}\text{C}$ values, LF estimates and $\delta^{15}\text{N}$ values between 100–500 g brown trout and 100–500 g char both sampled in September. Except in the case of regression analyses, all the details of statistical tests and test significances are only given in Appendixes 1–3. All statistical analyses were performed by using SPSS for Windows v. 14.0 (SPSS Inc. 2005).

3. RESULTS

3.1. Numbers, length, weight and age distributions and condition factors of char and brown trout

The total number of fish in the study was 148 char and 18 brown trout. Most char were small (<100 g) and only 23 belonged to the size group 100–500 g, while six were of weight >500 g (Figure 3). Because <100 g char were caught in huge numbers in July and in September, only randomly chosen subsamples were chosen at those times. In August, all fish samples were caught by the profundal gill nets. In contrast, fish were caught from various depth zones on other sampling occasions, but especially <100 g char were mostly caught from the lake littoral and sublittoral areas. Only one 100–500 g brown trout was caught in July; all the others were caught in September.

Char weight ranged from 18 g to 2155 g and length varied between 136 mm and 555 mm (Table 2). The weight of brown trout ranged from 105 g to 627 g and length from 222 mm to 403 mm (Figure 3). None of the fish were of weight between 400 g and 1300 g or of length between 350 mm and 500 mm (Figure 4), except the largest individual brown trout (627 g, 403 mm) and one >500 g char (668 g, 528 mm), which had a blockage (i.e. hank of fishing line) in its intestine and therefore was severely starved. The size distributions clearly indicate a stunted and overcrowded char population with a bimodal size structure (Figure 3).

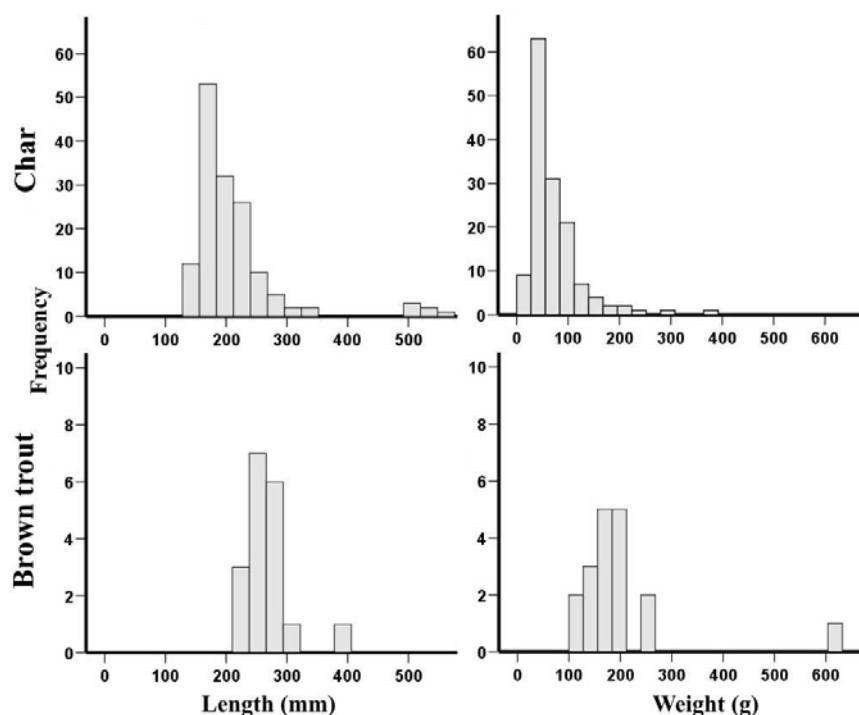


Figure 3. Length (left) and weight (right) distributions of char (upper) and brown trout (lower). In the weight distribution figure of char, only <500 g fish are shown to better illustrate the size distribution of small-sized char.

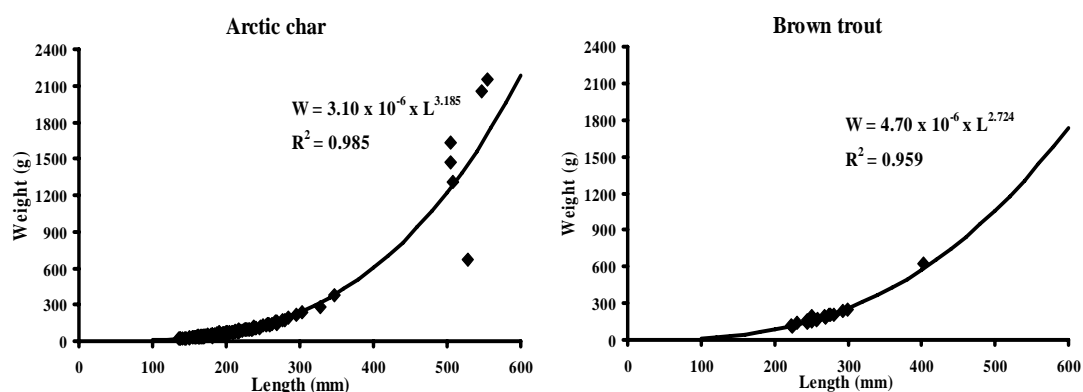


Figure 4. Length-weight relationships of char (left) and brown trout (right). In both figures, the equation of the regression model and coefficient of determination (R^2) are shown. The one starved >500 g char was excluded from the regression, even though shows in the figure.

Table 2. Numbers (N) and mean lengths and weights of char and brown trout within each size group and in different sampling seasons. Range indicates the minimum and maximum observed values and SD stands for standard deviation from the mean value.

Species/ Size group	Season	N	Length (mm)		Weight (g)	
			Mean \pm SD	Range	Mean \pm SD	Range
Arctic char						
<100 g	April	10	190 \pm 29	161–234	61 \pm 26	40–97
<100 g	July	55	182 \pm 23	136–235	51 \pm 20	19–98
<100 g	August	20	190 \pm 28	137–236	56 \pm 25	18–98
<100 g	September	34	183 \pm 24	138–217	54 \pm 21	20–96
100–500 g	April	3	256 \pm 27	230–284	144 \pm 50	101–199
100–500 g	July	5	262 \pm 25	238–303	152 \pm 50	117–240
100–500 g	August	5	275 \pm 33	241–328	167 \pm 69	111–284
100–500 g	September	10	267 \pm 34	228–347	168 \pm 83	101–382
>500 g	July	2	518 \pm 14	508–528	986 \pm 449	668–1303
>500 g	August	1	505 \pm 0		1634 \pm 0	
>500 g	September	3	536 \pm 27	505–555	1890 \pm 371	1466–2155
Total		148	211 \pm 76	136–555	131 \pm 313	18–2155
Brown trout						
100–500 g	July	1	293 \pm 0		241 \pm 0	
100–500 g	September	16	257 \pm 21	222–299	173 \pm 35	105–245
>500 g	September	1	403 \pm 0		627 \pm 0	
Total		18	267 \pm 40	222–403	202 \pm 112	105–627

On average, >500 g char had significantly higher condition factors than <100 g and 100–500 g char, whereas <100 g and 100–500 g char did not significantly differ by their condition factors (Appendix 1). However, <100 g char and >500 g char showed higher individual variation in condition factors than 100–500 g char (Figure 5).

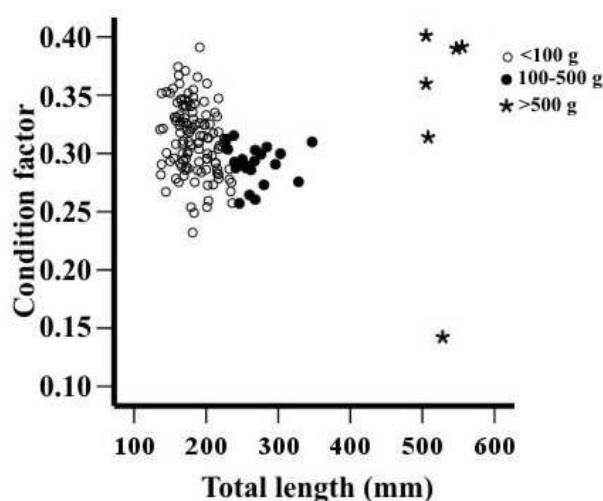


Figure 5. Condition factors of char as a function of total length. Individuals belonging to different size groups are separated by symbols. Note the exceptionally low condition factor of one starved >500 g char (excluded from statistical tests). Number of samples: $N_{<100\text{ g}} = 119$, $N_{100-500\text{ g}} = 23$, $N_{>500\text{ g}} = 6$.

The mean condition factors of <100 g char differed significantly between seasons (Appendix 1). In August, when char samples were solely caught from the lake profundal zone, <100 g char had significantly lower mean condition factor than those caught in other seasons, while there were no significant differences between other seasons (Appendix 3). At the same time, 100–500 g char did not show any significant seasonal differences in mean condition factors (Appendix 1). The higher individual variation in condition factors of <100 g char in relation to 100–500 g char was independent of sampling season (Figure 6), but may partly result from differences in sample sizes.

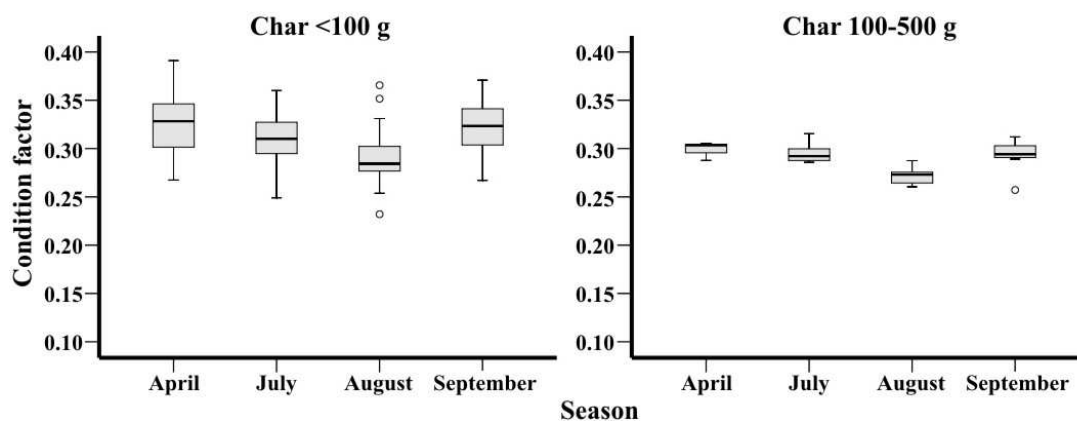


Figure 6. Boxplot figures of condition factors of <100 g (left) and 100–500 g char (right) in different sampling seasons. The line indicates the median, the boxes indicate the upper (75 %) and lower (25 %) quartiles and the whiskers indicate the observed minimum and maximum values. Number of samples: $N_{<100\text{ g}} = 119$, $N_{100-500\text{ g}} = 23$.

Age was determined from a total of 75 char and 12 brown trout. For the sake of simplicity, all ages are given here as full numbers rather than divided into full (April) and + (other seasons) years. Char age ranged from 3 to 15 years, but most individuals were of age 6–8 years (Figure 7). No juvenile char of age under 3 years were caught within this study. All the aged 100–500 g brown trout were either 6 or 7 years old, while the otoliths of the largest individual brown trout were lost.

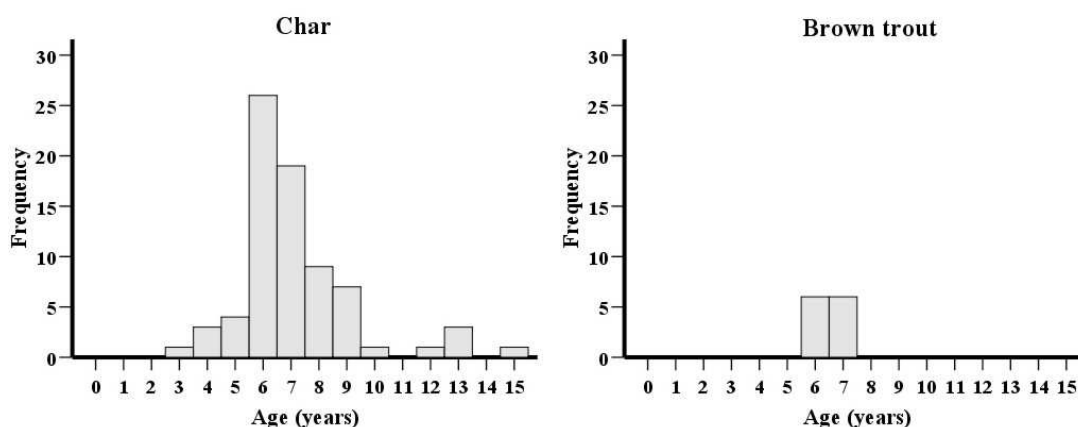


Figure 7. Age frequency distributions of char (left) and brown trout (right). Number of samples: $N_{\text{Char}} = 75$, $N_{\text{Brown trout}} = 12$.

The age of <100 g char ranged from 3 to 9 years, while all the 100–500 g char were of age 6–9 years. Except the starved, 15 years old individual, all the other >500 g char were of age 10–13 year. Especially among <500 g char, the total length at a particular age

varied greatly, which indicates large individual differences in growth rates (Figure 8). Some of the <100 g char were clearly dwarf and overall the growth rate of <100 g char was very low. In contrast, most 100–500 g char were clearly larger at a given age and thus had generally higher growth rates than <100 g char. In fact, the von Bertalanffy non-linear growth curves of <100 g char and >100 g char had very distinct slopes (Figure 8) and, according to the model, >100 g char can reach much larger infinity length than <100 g char (Table 3).

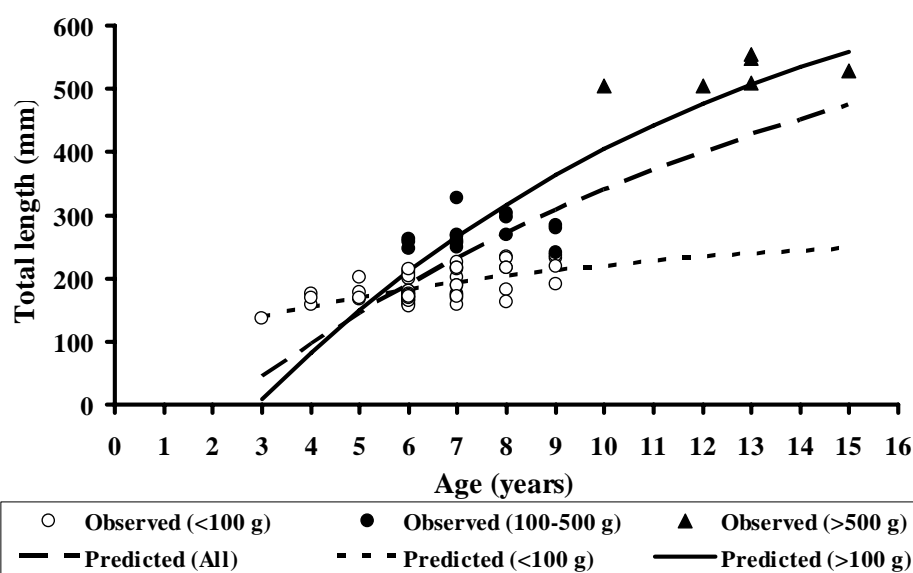


Figure 8. Observed total length of individual char at a particular age. Individuals belonging to different size groups are separated by symbols. The von Bertalanffy non-linear growth models for all char (bold dash), <100 g char (thin dash) and >100 g char (solid) are shown as lines. Number of samples: $N_{<100\text{ g}} = 53$, $N_{100-500\text{ g}} = 16$, $N_{>500\text{ g}} = 6$.

Table 3. The growth coefficient (K), infinity length (L_{∞}) and age at 0 cm length (t_0) for <100 g, >100 g and for all char according to the von Bertalanffy non-linear growth model.

Size group	Growth coefficient	Infinity length (mm)	Age at 0 cm length
<100 g	0.12	281	-2.6
>100 g	0.10	807	2.9
All	0.07	773	2.2

3.2. Stomach contents of char and brown trout

Stomach contents were analyzed from every char and brown trout chosen for the study. All in all, 132 of the 148 char (89 %) and 17 of the 18 brown trout (94 %) had some remains of recent prey organisms in their stomach. The stomach contents indicated a wide trophic niche of the char population. In total, 17 different prey types were identified including zooplankton, aerial insects and chironomid pupae (pelagic prey), chironomid larvae, molluscs and different kinds of other littoral benthic macroinvertebrates (benthic prey) and fish (Table 5) (see 2.1.2. for the categorisation of benthic and pelagic prey types).

The diets of <100 g and 100–500 g char were rather similar (Figure 9) and showed significant overlap (Table 4). In contrast, the diets of >500 g char and 100–500 g brown

trout did not significantly overlap with any other size groups or species, respectively (Table 4). The largest individual (383 g, 347 mm) of 100–500 g char had an exceptional diet consisting of a smaller char of length around 150 mm. Otherwise, 100–500 g char had generally fed slightly more on pelagic prey items (54 %) than <100 g char (38 %), and <100 g char had respectively fed more on benthic prey (62 %) than 100–500 g char (38 %). Overall, the most dominant food sources of these char size groups were chironomid larvae and pupae, whereas zooplankton basically represented only a small contribution of the diet (Figure 9). Generally, <100 g char had eaten more littoral macroinvertebrates than 100–500 g char, whereas aerial insects and molluscs contributed relatively little to the char diet. Nearly all >500 g char had recently fed on smaller char of length around 170–190 mm. Only the one starved >500 g char had a completely empty stomach, whereas the other large individual caught at the same time in July had exceptionally fed on *Gammarus lacustris*, adult tipulids and plecopteran nymphs (Table 5).

The largest brown trout had an empty stomach and therefore only the stomach contents of 100–500 g brown trout are considered here. The population of 100–500 g brown trout seemed to have generally diverging diet compared to char of the same size group (Table 5). The one 100–500 g brown trout caught in July had mostly fed on aerial insects such as hymenopterans and adult dipterans, but also on large amounts of chironomid pupae (Table 5). In September, the other 16 brown trout had nearly exclusively been feeding on littoral macroinvertebrates, of which trichopteran larvae were the most abundant prey, whereas *Corixidae* sp., *Gammarus lacustris* and plecopteran nymphs were found in smaller amounts (Table 5). Compared to the relatively homogeneous diet of brown trout, the 100–500 g char had eaten a wide range of different prey types in September (Figure 9). Unlike any brown trout, many char had eaten large amounts of zooplankton and chironomid larvae, whereas none of the brown trout had eaten fish (Table 5, Figure 9).

Table 4. Schoener diet similarity indices between all char size groups and between 100–500 g brown trout (B. trout) and char size groups. Values in bold indicate biologically significant overlaps (>0.6).

	Char 100-500 g	Char >500 g	B. trout 100-500 g
Char <100 g	0.61	0.14	0.27
Char 100-500 g		0.21	0.17
Char >500 g			0.11

The char population showed clear seasonal differences in the dominant food sources and also in the trophic niche width depending on the seasonal, but also spatial availability of different prey types. Because only few >500 g char were caught within this study, they are not considered in the following examination of seasonal dietary changes.

Under ice in April, the population of <100 g char had exclusively fed on benthic prey, of which chironomid larvae were the most abundant prey, while *Gammarus lacustris* and *Lymnaea* sp. were found less frequently (Figure 9, Table 5). Also the 100–500 g char had mostly fed on chironomid larvae, but a few individual also had remains of calanoid copepods in their stomachs (Figure 9, Table 5).

In contrast to April, pelagic prey dominated the diets of <100 g char and 100–500 g char in July. At that time, the diet of the <500 g char contained nearly all kinds of different prey organisms indicating a wide trophic niche of the char population (Table 5). The dominant food source of <100 g char was chironomid pupae, while chironomid larvae were less abundant (Figure 9). The contribution of zooplankton in the diet of <100 g char

increased considerably from April. Aerial insects, such as adult dipterans, coleopterans, hymenopterans and tipulids, were also important prey for <100 g char, as were the other littoral macroinvertebrates like *Gammarus lacustris*, trichopteran larvae, *Lymnaea* sp. and plecopteran nymphs (Table 5). Unlike <100 g char, none of the 100–500 g char had eaten chironomid larvae or zooplankton in July, but the diet consisted nearly solely of chironomid pupae (Figure 9). Other food sources of 100–500 g char included aerial insects, such as adult tipulids, dipterans, hymenopterans and coleopterans, but only a few had eaten *Gammarus lacustris* (Table 5).

In August, when all char samples were caught from the profundal zone only, the diets of <100 g and 100–500 g char consisted nearly solely of chironomids (Figure 9, Table 5). At this time, the feeding habitats of <100 g and 100–500 g char clearly differed, because <100 g char had fed substantially more on chironomid larvae (i.e. benthic prey) than pupae (i.e. pelagic prey), while the situation was reversed among 100–500 g char. However, none of the 100–500 g char had eaten calanoid copepods or cladocerans, while a few <100 g char had. Notably some individuals had remains of littoral prey items in their stomachs, such as *Gammarus lacustris* and *Pisidium* sp., suggesting some degree of continuous habitat shift by some char individuals between littoral, profundal and pelagic habitats.

Unlike in April and in July, the diets of <100 g and 100–500 g char differed markedly in September. All kinds of prey, except chironomid pupae and aerial insects, were found from char stomachs at that time (Table 5). The dominant food sources of <100 g char were benthic prey including chironomid larvae, *Gammarus lacustris* and trichopteran larvae, while *Pisidium* sp., *Lymnaea* sp., *Corixidae* sp. European water boatmen and plecopteran nymphs were found less frequently. The contribution of zooplankton in the diets of <100 g char did not much differ between July (9 %) and September (12 %) (Figure 9). Even though chironomid larvae also dominated the diets of 100–500 g char, the contribution of zooplankton was higher in September (24 %) than in July (0 %) (Figure 9). Most zooplankton was cladocerans and only two char had eaten *Bythotrephes* sp (Table 5). Other food sources of 100–500 g char consisted of *Gammarus lacustris*, *Pisidium* sp., *Lymnaea* sp. and trichopteran larvae. The largest 100–500 g char had eaten one smaller char of length around 150 mm.

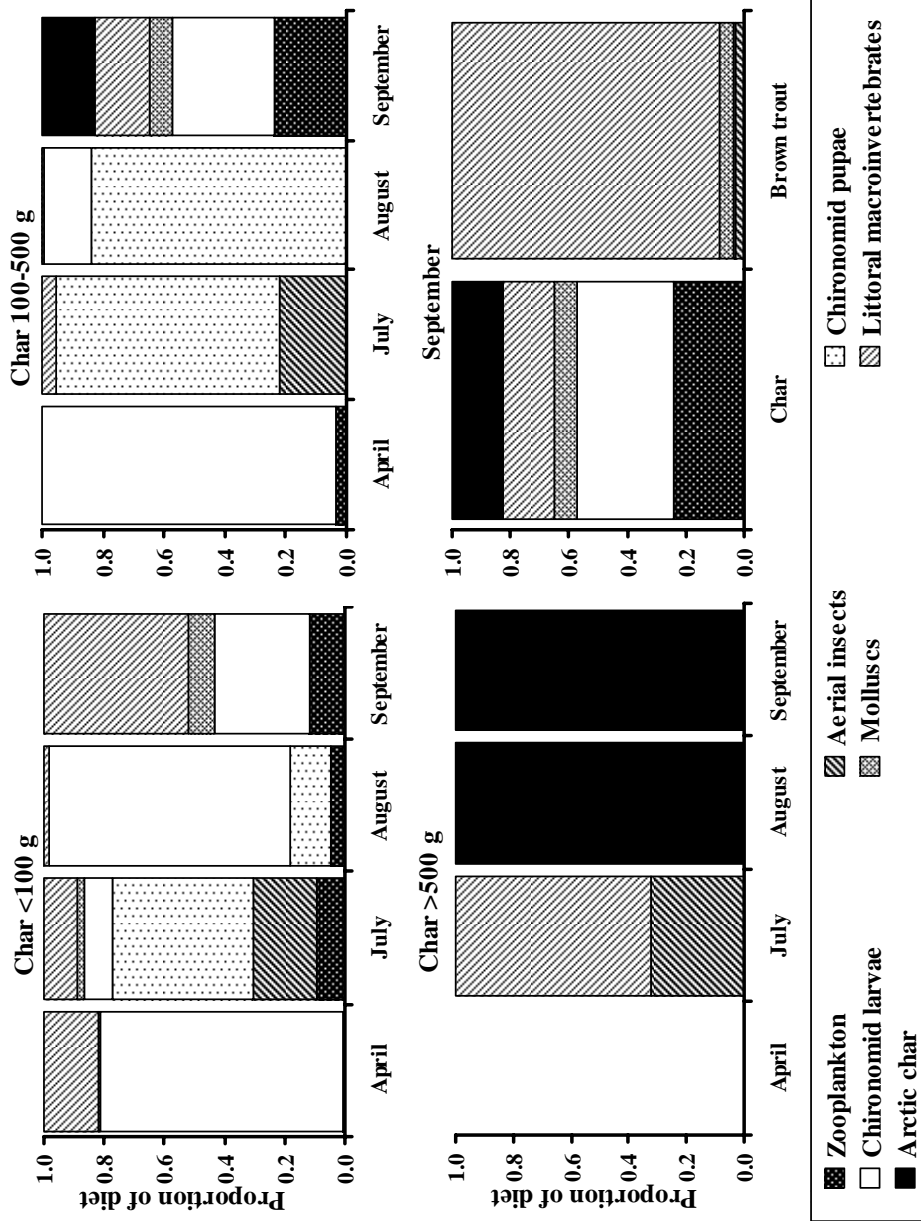


Figure 9. Proportions of different prey types in the stomach contents of <100 g, 100–500 g and >500 g char caught in different sampling seasons, and also of 100–500 g char and 100–500 g brown trout caught in September. Numbers of samples are given in Table 5.

Many char individuals showed rather generalistic feeding behaviour with diet consisting of several different prey types (Appendix 4). However, the largest char were mostly specialized in cannibalistic foraging, although the one individual caught in July had at least recently fed on lower trophic levels, too. Opportunistic foraging by <500 g char was especially common in July, when all possible prey types (e.g. benthic macroinvertebrates, zooplankton, aerial insects) were available. However, especially in September, some individuals had strictly specialized in foraging for a particular prey organism. Some of these individuals had clearly an exceptional diet consisting solely of zooplankton or molluscs such as *Pisidium* sp., while others had fed more on chironomid and trichopteran larvae (Appendix 4). In contrast in April and in August, when char were caught under ice or only from the lake profundal, respectively, nearly every <500 g char had fed on nothing but chironomids, which were probably the only, or at least the most abundant, prey target available in that particular season or habitat.

The great individual variation in condition factors (Figure 5) and growth rates (Figure 8) also suggests that individuals may truly differ by their dominant diet and foraging strategy. However, differences in growth and condition may also partly result from the differences in sexes and stages of sexual maturity, which were not recorded within this study.

3.3. Stable isotopes

3.3.1. The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of biofilm, zooplankton, littoral macroinvertebrates and profundal macroinvertebrates, and the general food web models of Saanajärvi

Regardless of sampling occasion, most littoral, pelagic and profundal primary consumers differed markedly in their $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures (Table 6). Zooplankton had much lower $\delta^{13}\text{C}$ values (range of mean from -30.8 to -33.9 ‰) compared to most littoral macroinvertebrates (range of mean from -20.5 to -27.9 ‰) and to biofilm (mean -21.6 ‰), but rather similar values to profundal chironomid larvae (mean -30.5 ‰) (Table 6, Figure 10). The fairly similar $\delta^{13}\text{C}$ values but much higher $\delta^{15}\text{N}$ signatures of profundal chironomids compared to zooplankton proved that the profundal chironomids relied strongly on pelagic energy sources, i.e. on settling pelagic zooplankton. The relatively low $\delta^{13}\text{C}$ signature of *Pisidium* sp. also reflects a predominant reliance on pelagic energy sources. The $\delta^{13}\text{C}$ values of most littoral macroinvertebrates corresponded to those of biofilm, with the exception of trichopteran larvae and ephemeropteran nymphs having unexpectedly low $\delta^{13}\text{C}$ values. Most consumers showed relatively high spatial and temporal variation in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures (Table 6, Figure 10). Especially biofilm showed high temporal and also spatial shifts in $\delta^{13}\text{C}$ value, whereas copepods and cladocerans showed more variation in their $\delta^{15}\text{N}$ than in $\delta^{13}\text{C}$ values. In the end, the clear distinction between littoral and pelagic $\delta^{13}\text{C}$ baselines made it possible to later estimate the relative contributions of these two energy sources in the fish diets.

The simplified food web models indicate that there exists approximately four trophic levels in Saanajärvi, where biofilm and phytoplankton (samples not obtained within this study) are primary producers, littoral benthic macroinvertebrates and zooplankton are primary consumers, <500 char (as well as all brown trout) and to some extent also profundal macroinvertebrates are secondary consumers and >500 char are top predators (Figure 11). The biplots clearly show the observed large individual variation particularly in the isotopic signatures of biofilm, littoral macroinvertebrates and fish.

Table 6. Mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of biofilm and different groups of zooplankton, littoral macroinvertebrates and profundal macroinvertebrates. SD stands for standard deviation from the mean value and range indicates the minimum and maximum observed values.

Organism	N	$\delta^{13}\text{C}$		$\delta^{15}\text{N}$	
		Mean \pm SD	Range	Mean \pm SD	Range
Biofilm	10	-21.6 \pm 4.3	-27.3--14.9	1.1 \pm 0.6	0.2–2.3
Zooplankton					
Cladocera	6	-32.8 \pm 1.9	-34.3--29.8	4.8 \pm 1.9	2.1–6.4
Calanoida	6	-33.9 \pm 0.6	-34.8--33.1	4.3 \pm 1.5	2.5–6.1
<i>Bythotrephes sp.</i>	1	-33.4 \pm 0		4.2 \pm 0	
Mixed sample	5	-30.8 \pm 1.5	-32.3--28.5	4.1 \pm 1.5	2.7–6.3
Littoral macroinvertebrates					
<i>Lymnaea sp.</i>	6	-24.1 \pm 2.5	-28.1--21.8	3.0 \pm 0.8	1.6–3.8
<i>Pisidium sp.</i>	5	-27.4 \pm 1.5	-28.5--25.4	4.1 \pm 0.1	3.9–4.3
Oligochaeta	5	-23.4 \pm 1.6	-25.8--21.9	3.5 \pm 0.3	3.1–3.9
Chironomids	18	-20.5 \pm 2.2	-23.6--17.1	5.6 \pm 1.2	2.8–7.5
Tipulidae	4	-22.4 \pm 0.5	-22.8--21.6	2.3 \pm 0.0	2.3–2.3
<i>Gammarus lacustris</i>	10	-21.8 \pm 1.6	-23.8--18.2	4.1 \pm 0.6	3.3–5.2
Ephemeroptera	5	-27.9 \pm 1.4	-29.1--25.8	3.5 \pm 0.6	2.8–4.2
Trichoptera	6	-26.7 \pm 1.6	-29.7--25.0	4.9 \pm 1.1	3.5–6.0
Plecoptera	3	-24.3 \pm 2.5	-26.2--21.4	4.0 \pm 0.8	3.2–4.8
Dytiscidae	3	-25.2 \pm 3.6	-28.5--21.4	4.4 \pm 0.5	3.8–4.8
Hydrachnidae	2	-22.5 \pm 2.2	-24.1--20.1	3.9 \pm 0.1	3.8–3.9
Profundal macroinvertebrates					
Chironomids	12	-30.5 \pm 1.1	-31.9--28.5	7.0 \pm 0.8	6.0–8.6
Oligochaeta	3	-25.8 \pm 0.8	-26.6--25.3	9.4 \pm 1.3	7.9–10.0

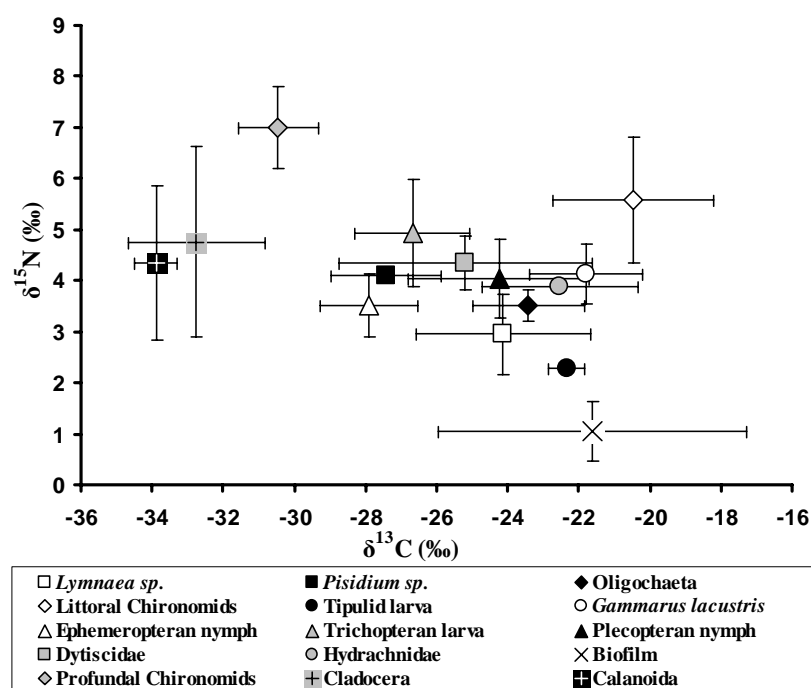


Figure 10. A general biplot of the mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of biofilm and different primary consumers collected from several sampling sites and in different seasons. The error bars indicate the standard deviation from the mean. Numbers of samples are given in Table 6.

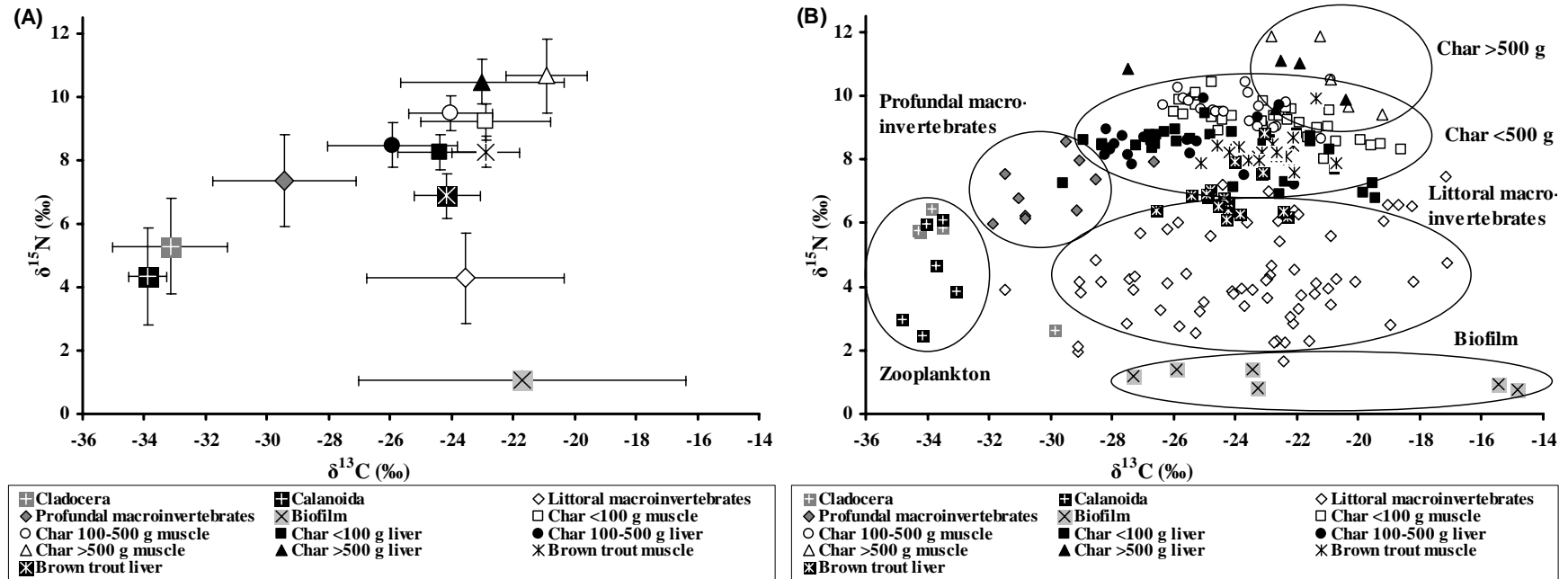


Figure 11. The schematic food web models of Saanajärvi showing (A) the mean values with error bars (standard deviation) and (B) the observed individual $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of biofilm, zooplankton, profundal macroinvertebrates, littoral macroinvertebrates and of muscle and liver of different char size groups and of all brown trout. These biplot figures are only based on those samples collected by the author in July and in September, because fish samples were only obtained in April and the sampling procedure differed little in August compared to July and September.

3.3.2. The $\delta^{13}\text{C}$ values, LF estimates and $\delta^{15}\text{N}$ values of char and brown trout

A total of 81 char and 18 brown trout were used for the stable isotope analyses of fish muscle and liver tissues. Of the 55 <100 g char caught in July and of the 34 caught in September, only sub-samples of 10 and 12 individuals were randomly chosen, respectively.

Char and brown trout had generally corresponding $\delta^{13}\text{C}$ signatures. The mean $\delta^{13}\text{C}$ value of char was -22.9‰ with individual range from -26.8‰ to -17.3‰ , whereas the respective estimates for brown trout were -22.1‰ and from -24.6‰ to -19.9‰ (Table 7). Based on both muscle and liver isotope compositions, the mixing model estimated for the whole char population a mean of 82 % reliance on littoral energy sources with individual range from 49 % to 129 % (Table 7; explanation for the estimate values over 100 %, see 3.1.1.). For brown trout, the mixing model estimated a mean of 90 % dependence on littoral energy sources with individual range from 69 % to 109 % (Table 7).

The mean muscle and liver $\delta^{13}\text{C}$ values and LF estimates differed significantly between the char size groups (Appendix 1). The >500 g char had significantly higher means of $\delta^{13}\text{C}$ value and LF estimates than <100 g and 100–500 g char, whereas there were no significant differences between <100 g and 100–500 g char (Appendix 3). For >500 g char, the mixing model estimated a mean of 102 % reliance on littoral energy sources, whereas the respective estimates were 82 % for <100 g char and 75 % for 100–500 g char.

Although >500 g char had significantly higher mean LF estimate, the linear regression models did not indicate any significant increase in char LF values with increasing total length:

$$LF_{\text{muscle}} = 73.87 + 0.033 \times \text{Length} \quad LF_{\text{liver}} = 73.68 + 0.034 \times \text{Length}$$

in which $r^2 = 0.03$, $F = 2.61$, $p = 0.110$ for muscle and $r^2 = 0.02$, $F = 1.79$, $p = 0.184$ for liver. As demonstrated by the r^2 -values, the total length of char explained very little of the variation in both muscle (3 %) and liver (2%) LF estimates. The individual variation in LF estimates was largest among <100 g char and decreased slightly with increasing total length (Figure 12), but this may largely be caused by the differences in sample sizes. Still, even the >500 g char showed quite large individual variation in the LF estimates.

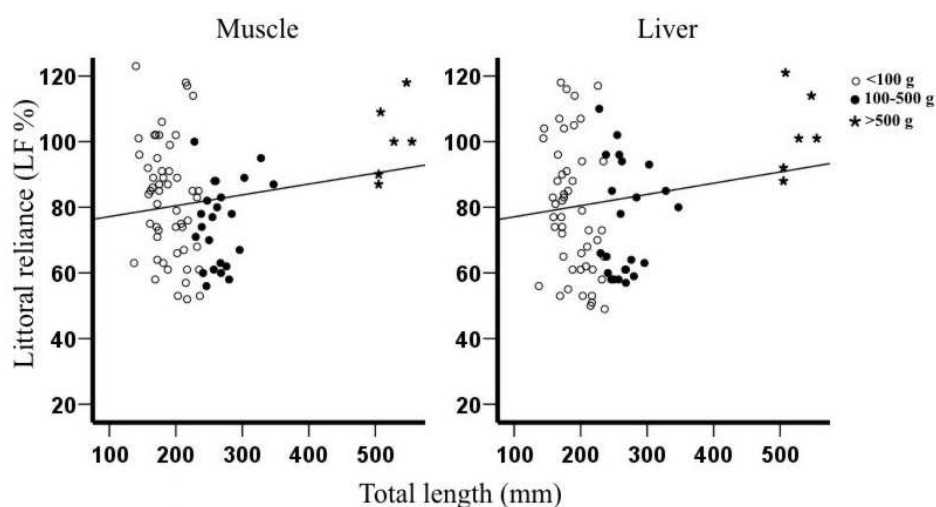


Figure 12. The LF estimates (i.e. % littoral reliance) based on muscle (left) and liver (right) isotope signatures of char as a function of total length. Individuals belonging to different size groups are separated with symbols. Numbers of samples are given in Table 7.

Unlike char, the linear regression model based on muscle LF estimates of brown trout showed that the largest individuals were generally more dependent on littoral energy sources than the smaller ones (Figure 13). However, the linear regression between the liver LF estimates and total length of brown trout was not statistically significant:

$$LF_{muscle} = 49.16 + 0.143 \times Length \quad LF_{liver} = 69.33 + 0.086 \times Length$$

in which $r^2 = 0.44$, $F = 12.56$, $p = 0.003$ for muscle and $r^2 = 0.17$, $F = 3.33$, $p = 0.087$ for liver. As demonstrated by the r^2 -values, the total length of brown trout explained relatively much (44 %) of the variation in muscle LF estimates, but little (17 %) of the variation in liver LF estimates.

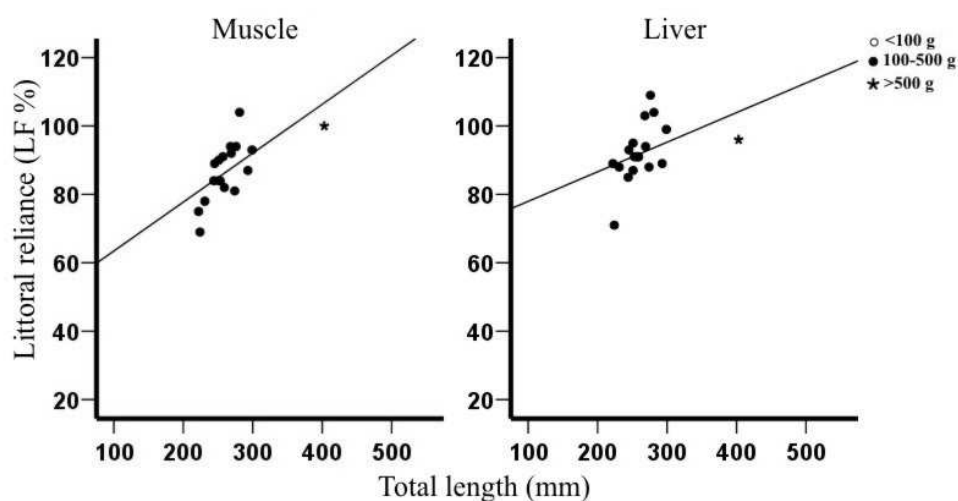


Figure 13. The LF estimates (i.e. % littoral reliance) based on muscle (left) and liver (right) isotope signatures of brown trout as a function of total length. Individuals belonging to different size groups are separated with symbols. Numbers of samples are given in Table 7.

Table 7. Means of muscle and liver $\delta^{13}\text{C}$ values, LF estimates and $\delta^{15}\text{N}$ values of <100 g char and 100–500 g char in different seasons and of all >500 g char and 100–500 g and >500 g brown trout. SD stands for standard deviation from the mean and range indicates the minimum and maximum observed values.

Species/ Size group	Season	N	$\delta^{13}\text{C}$ (‰)				LF (%)				$\delta^{15}\text{N}$ (‰)			
			Muscle		Liver		Muscle		Liver		Muscle		Liver	
			Mean \pm SD	Range	Mean \pm SD	Range	Mean \pm SD	Range	Mean \pm SD	Range	Mean \pm SD	Range	Mean \pm SD	Range
Char														
<100 g	April	10	-22.1 \pm 1.7	-23.9--18.9	-21.6 \pm 2.2	-23.9--18.5	87.7 \pm 13.7	71.5–114.2	92.0 \pm 17.7	73.3–117.5	9.2 \pm 0.6	8.4–10.4	8.7 \pm 0.3	8.3–9.4
<100 g	July	10	-22.7 \pm 2.0	-25.4--20.0	-22.4 \pm 2.3	-25.0--18.9	82.7 \pm 16.0	61.0–105.8	86.0 \pm 19.1	65.3–115.5	9.5 \pm 0.4	8.6–9.9	8.4 \pm 0.6	7.1–8.9
<100 g	August	20	-23.6 \pm 1.8	-26.3--20.4	-24.3 \pm 2.0	-26.8--20.1	74.9 \pm 15.4	52.1–101.9	69.7 \pm 16.2	49.0–104.4	9.6 \pm 0.8	8.2–11.2	9.0 \pm 0.6	7.5–10.2
<100 g	September	12	-21.8 \pm 2.8	-25.4--17.9	-21.8 \pm 3.5	-26.7--17.3	90.4 \pm 22.5	60.6–122.5	91.5 \pm 28.9	51.2–129.3	9.0 \pm 0.6	8.0–10.1	7.7 \pm 0.7	6.8–8.6
100-500 g	April	3	-23.5 \pm 0.6	-24.2--23.2	-22.6 \pm 2.3	-24.9--20.3	75.3 \pm 4.0	70.7–78.1	83.5 \pm 17.9	65.9–101.7	10.0 \pm 0.5	9.5–10.4	9.5 \pm 0.6	8.7–9.9
100-500 g	July	5	-22.7 \pm 0.6	-23.4--21.9	-22.6 \pm 0.6	-24.8--21.2	83.5 \pm 4.7	78.1–88.9	92.5 \pm 4.6	84.5–95.9	9.1 \pm 0.6	8.2–9.8	8.4 \pm 0.7	7.5–9.3
100-500 g	August	5	-23.9 \pm 2.2	-25.6--21.2	-24.5 \pm 1.6	-25.9--22.4	72.0 \pm 17.9	57.8–94.9	67.6 \pm 12.8	56.6–84.7	10.0 \pm 0.5	9.4–10.6	9.5 \pm 0.4	8.9–9.9
100-500 g	September	10	-24.0 \pm 1.6	-25.9--20.7	-24.7 \pm 2.0	-25.9--19.6	72.3 \pm 13.6	56.2–99.7	67.8 \pm 16.2	57.7–110.2	9.6 \pm 0.5	8.6–10.2	8.2 \pm 0.5	7.2–8.9
>500 g	July	2	-19.9 \pm 0.7	-20.4--19.4	-19.1 \pm 1.6	-20.2--17.9	104.8 \pm 6.6	100.2–109.4	110.9 \pm 14.1	100.9–120.8	10.1 \pm 0.6	9.7–10.5	10.4 \pm 0.8	9.9–11.0
>500 g	August	1	-21.5 \pm 0	0	-21.2 \pm 0	0	89.8 \pm 0	0	92.3 \pm 0	0	11.7 \pm 0	0	11.8 \pm 0	0
>500 g	September	3	-20.1 \pm 1.8	-21.8--18.3	-20.3 \pm 1.5	-21.8--18.8	101.9 \pm 15.7	87.2–118.5	101.2 \pm 13.1	88.2–114.3	11.0 \pm 1.4	9.4–11.9	10.5 \pm 0.8	9.6–11.1
Total		81	-22.8 \pm 2.1	-26.3--17.9	-22.9 \pm 2.6	-26.8--17.3	81.7 \pm 17.2	52.1–122.5	81.7 \pm 21.3	49.0–129.3	9.5 \pm 0.8	8.0–11.9	8.8 \pm 0.9	6.8–11.8
Brown trout														
100-500 g	July	1	-22.3 \pm 0	0	-22.1 \pm 0	0	86.8 \pm 0	0	89.1 \pm 0	0	8.5 \pm 0	0	7.9 \pm 0	0
100-500 g	September	16	-22.4 \pm 1.0	-24.6--20.3	-21.9 \pm 1.1	-24.5--19.9	86.5 \pm 8.5	68.9–103.7	92.4 \pm 8.8	71.4–108.6	8.1 \pm 0.3	7.6–8.7	6.7 \pm 0.4	6.1–7.6
>500 g	September	1	-20.6 \pm 0	0	-21.1 \pm 0	0	99.5 \pm 0	0	96.3 \pm 0	0	9.9 \pm 0	0	8.8 \pm 0	0
Total		18	-22.3 \pm 1.1	-24.6--20.3	-21.8 \pm 1.0	-24.5--19.9	87.2 \pm 8.5	68.9–103.7	92.5 \pm 8.4	71.4–108.6	8.3 \pm 0.5	7.6–9.9	6.9 \pm 0.7	6.1–8.8

Because only six >500 g char were caught in total and nearly all brown trout were caught in September, all the statistical comparisons of $\delta^{13}\text{C}$ values and LF estimates between sampling seasons were performed for the <100 g and 100–500 g char only. The means of muscle $\delta^{13}\text{C}$ value and LF estimates of <100 g char did not differ significantly between sampling seasons, whereas the means of liver $\delta^{13}\text{C}$ value and LF estimate did (Appendix 1). The <100 g char had significantly lower mean liver $\delta^{13}\text{C}$ value and LF estimate in August than in April and in September (Appendix 3, Figure 14). These results indicate that the population of <100 g char did not show any clear seasonal shifts in their energy source basis. Instead, those char caught in August from the lake profundal zone had recently been less dependent on littoral energy sources than those caught on other occasions from littoral, profundal and pelagic habitats.

In the same way, the means of muscle $\delta^{13}\text{C}$ values and LF estimates for 100–500 g char did not significantly differ between sampling seasons, but the means of liver $\delta^{13}\text{C}$ value and LF estimates did (Appendix 1). In September, 100–500 g char had significantly lower means of liver $\delta^{13}\text{C}$ values and LF estimates than in July, while there were no significant differences between other seasons (Appendix 3, Figure 14). These results suggest that in September, the population of 100–500 g char had recently partially shifted from littoral to pelagic energy sources.

Overall, the individual variation in LF estimates of <100 g char was fairly high on each sampling occasion, but highest in September (Table 7, Figure 14). This indicates that the population of <100 g char had a wide trophic niche regardless of season, but may also result from the relatively large sample sizes of <100 g char. Among 100–500 g char, the individual variation in muscle $\delta^{13}\text{C}$ values and LF estimates was particularly high in September and lowest in April and in July.

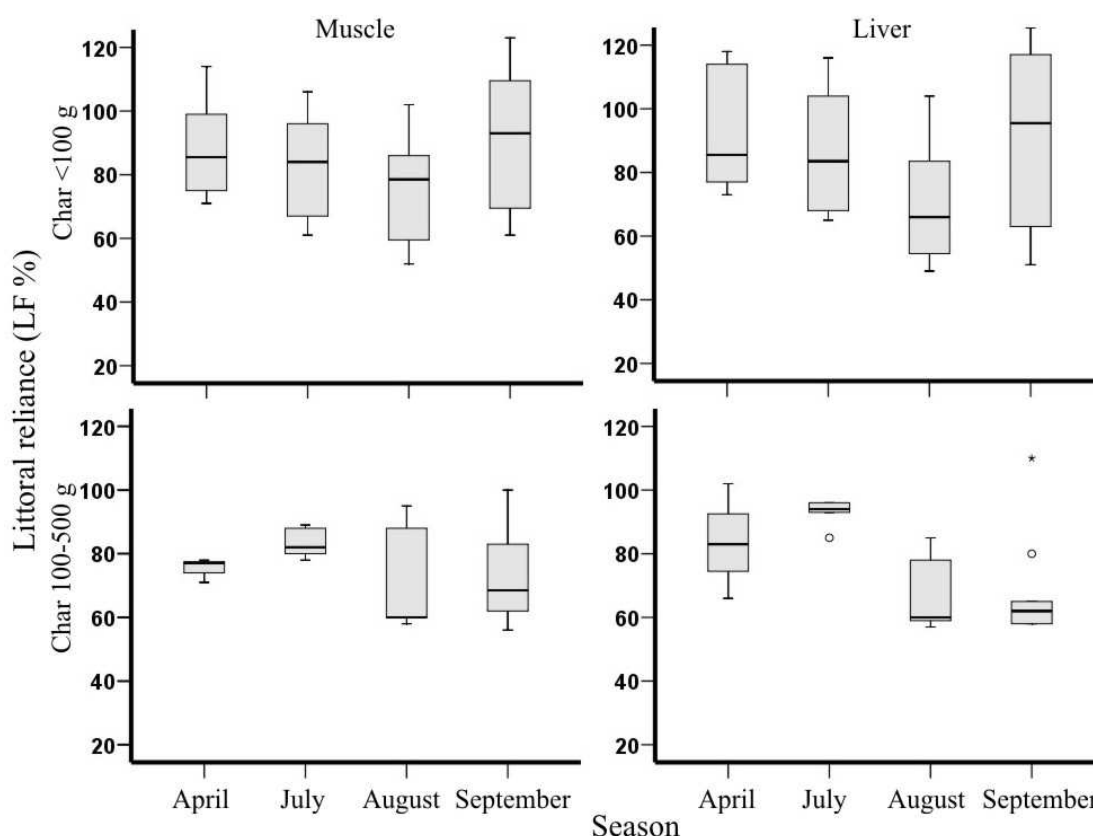


Figure 14. Boxplot figures of LF estimates (i.e. % littoral reliance) of muscle (left) and liver (right) of <100 g char (upper) and 100–500 g char (lower) in different sampling seasons. The line indicates the median, the boxes indicate the upper (75 %) and lower (25 %) quartiles and the whiskers indicate the observed minimum and maximum values. Numbers of samples are given in Table 7.

The mean $\delta^{15}\text{N}$ value of char was 9.1 ‰ with individual range from 6.8 ‰ to 11.9 ‰ (Table 7). The mean $\delta^{15}\text{N}$ value differed significantly between char size groups (Appendix 1). On average, >500 g char had significantly higher $\delta^{15}\text{N}$ values than <100 g and 100–500 g char, whereas <100 g and 100–500 g char did not significantly differ by their mean $\delta^{15}\text{N}$ values (Appendix 2). This suggests that >500 g char generally occupied higher trophic positions than <500 g char.

In the same way, the regression models suggest that char became generally more enriched in $\delta^{15}\text{N}$ with increasing total length (Figure 17):

$$\delta^{15}N_{\text{muscle}} = 8.51 + 0.004 \times \text{Length} \quad \delta^{15}N_{\text{liver}} = 7.39 + 0.006 \times \text{Length}$$

in which $r^2 = 0.27$, $F = 28.42$, $p < 0.001$ for muscle and $r^2 = 0.33$, $F = 38.35$, $p < 0.001$ for liver. However, the r^2 -values indicate that the char total length generally explains rather little of the variation in muscle (27 %) and liver (33 %) $\delta^{15}\text{N}$ values. Overall, the $\delta^{15}\text{N}$ signatures showed extensive individual variation regardless of char size group (Table 7, Figure 15). Some of the <100 g char showed even as high $\delta^{15}\text{N}$ values as a few >500 g individual, while the others occupied lower trophic positions.

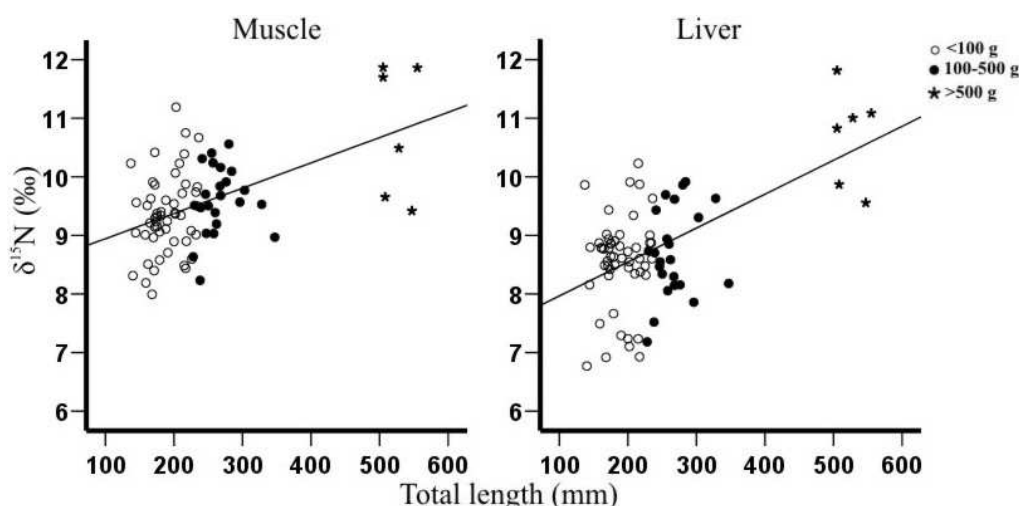


Figure 15. The $\delta^{15}\text{N}$ values of muscle (left) and liver (right) of individual char as a function of total length. Individuals belonging to different size groups are separated with symbols. Numbers of samples are given in Table 7.

The mean $\delta^{15}\text{N}$ value of brown trout was 7.6 ‰ with individual range from 6.1 ‰ to 9.9 ‰ (Table 7). Although the sample size was small and was clearly influenced by a single large individual, the linear regression model showed that brown trout also became more enriched in $\delta^{15}\text{N}$ with increasing total length (Figure 16):

$$\delta^{15}\text{N}_{\text{muscle}} = 5.83 + 0.009 \times \text{Length} \quad \delta^{15}\text{N}_{\text{liver}} = 3.50 + 0.013 \times \text{Length}$$

in which $r^2 = 0.55$, $F = 19.84$, $p < 0.001$ for muscle and $r^2 = 0.53$, $F = 18.05$, $p = 0.001$ for liver. According to the r^2 -values, the total length of brown trout explains relatively much of the variation in muscle (55 %) and liver (53 %) $\delta^{15}\text{N}$ signatures. Thus, at least the largest brown trout seemed to occupy slightly higher trophic position than most of the smaller individuals. However, as indicated by the constants of regression models and also by the mean values (Figures 15 and 16, Table 7), most brown trout individuals seemed to occupy generally lower trophic positions than most char individuals.

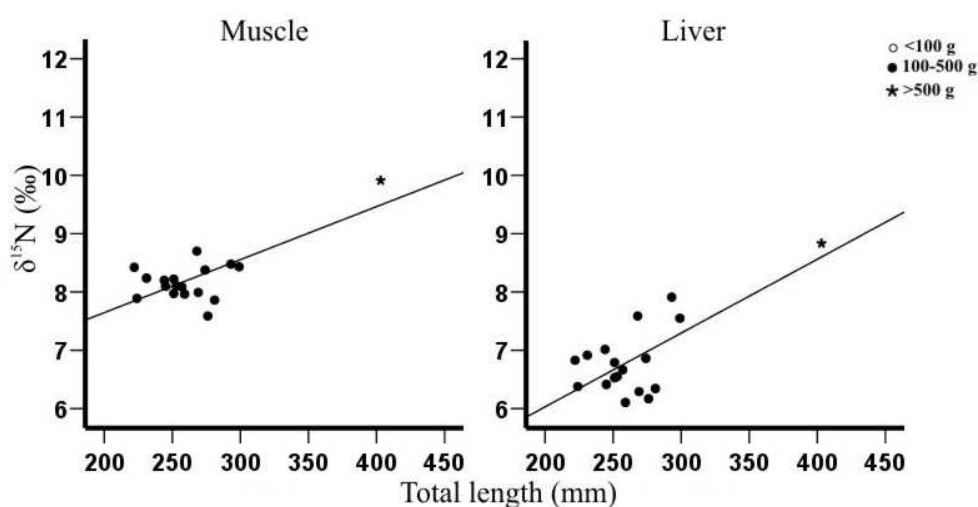


Figure 16. The $\delta^{15}\text{N}$ values of muscle (left) and liver (right) of individual brown trout as a function of total length. Individuals belonging to different size groups are separated with symbols. Numbers of samples are given in Table 7.

Because sufficient samples of both 100–500 g char and 100–500 g brown trout were obtained in September, it was possible to compare the littoral reliance and trophic positions of these two fish species at that time. Char and brown trout differed significantly by their means of $\delta^{13}\text{C}$ values, LF estimates and $\delta^{15}\text{N}$ values (Appendix 1). Brown trout had significantly higher means of $\delta^{13}\text{C}$ values and LF estimates than char of the same size (Table 7, Figure 17). According to the muscle LF estimates, brown trout was on average 86 % reliant on littoral energy sources, while the mean LF estimate was 72 % for char. However, the difference in average littoral dependence was much higher in liver LF estimates, brown trout being 92 % reliant on littoral energy sources, while char was on average 68 % reliant (Table 7). In addition, char had significantly higher means of $\delta^{15}\text{N}$ values than brown trout (Table 7, Figure 17). All these results suggest that, at least in September, the populations of 100–500 g char and 100–500 g brown trout had to some degree segregated trophic niches.

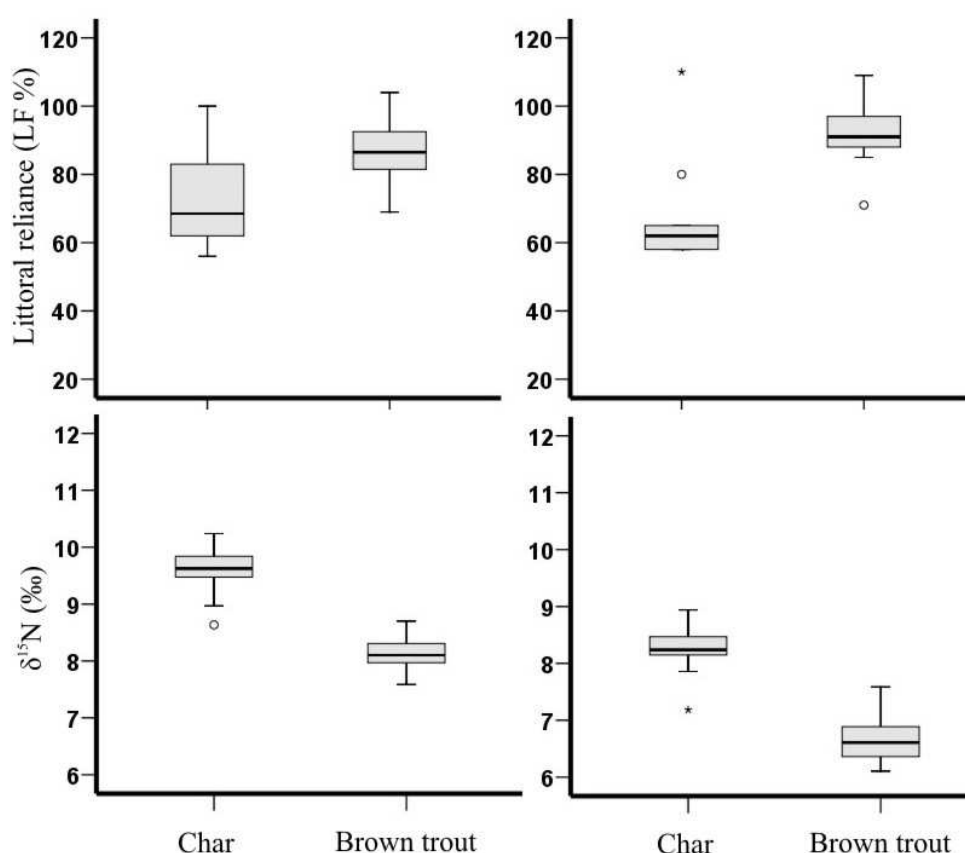


Figure 17. Boxplot figures of LF estimates (upper) and $\delta^{15}\text{N}$ values (lower) of muscle (left) and liver (right) of 100–500 g char and 100–500 g brown trout caught in September. The line indicates the median, the boxes indicate the upper (75 %) and lower (25 %) quartiles and the whiskers indicate the observed minimum and maximum values. Numbers of samples are given in Table 7.

4. DISCUSSION

4.1. Size distribution, growth and littoral reliance of the char population

The fish catch and size distribution of sample char in Saanajärvi indicated a stunted, overcrowded and nearly allopatric char population with a bimodal size structure. Small

char were extremely abundant, whereas larger char of weight >100 g existed only in very small numbers. Such a bimodal size structure is rather common within stunted char populations, where the strong resource competition and thus generally slow growth rates enable only few individuals to reach the size large enough for fish ingestion and to become fast-growing cannibals (e.g. Hammar 2000, Byström 2006). In Saanajärvi, the <100 g char had generally much slower growth rates than the >100 g char. Hence, those char of age under 8 years, which have already grown over the weight of 100 g, are most likely going to reach the cannibalistic size, while smaller conspecifics of the same age or older will probably stay dwarf for their whole life. The observed large individual variation in growth rates and also in condition factors suggest that individuals within the char population of Saanajärvi are under strong intraspecific competition for limited food resources and thus differ in their performance and shape.

This study supported the previous evidence that littoral production dominates the energy supply for top consumers in typical, small high-latitude lakes. In Saanajärvi, the estimated mean littoral dependence within the char population was 82 % with individual range from 49 % to 129 %, while the corresponding estimates for brown trout were 90 % and from 69 % to 109 %, respectively. Compared to the generally small and shallow study lakes of Karlsson & Byström (2005) and also of Sierszen *et al.* (2003), where the littoral energy sources has previously been demonstrated to support the top consumers, Saanajärvi is a relatively deep lake consisting 47 % of profundal zone. Hence, pelagic production could be expected to be of greater importance to the energy supply for top consumers than was observed. The suggested reasons for the observed strong littoral reliance of char population are the clear, ultra-oligotrophic water of Saanajärvi supporting higher benthic than pelagic primary production (Libourissen & Jeppesen 2003, Vadeboncoeur *et al.* 2003), and the more effective foraging of adult char on larger littoral benthic macroinvertebrates than on small, diluted pelagic zooplankton (Sierszen *et al.* 2003, Jansen *et al.* 2003, Karlsson & Byström 2005). Moreover, because the char population of Saanajärvi consists mostly of very small-sized fish, which are most vulnerable to cannibalistic predation, the existence of few large cannibals may restrict the foraging habitat of smaller char to the littoral zone (Svenning & Borgström 1995, Keyse *et al.* 2007), even though the pelagic habitat could offer relatively abundant food resources at least for a short period during the northern summer.

Karlsson & Byström (2005) estimated the mean littoral dependences of char populations to be between 62 % and 94 % with individual range from 51 % to over 100 % in nine subarctic lakes situated in the northern Sweden. Although the study lakes of Karlsson & Byström (2005) varied greatly by the size structures of char populations and by the lake morphometries, the individual variation in LF estimates was much higher in Saanajärvi than was observed within their study in total. One of their study lakes, G, corresponded best to Saanajärvi by its limnological characteristics, but in this lake, char coexisted with generally planktivorous nine-spined sticklebacks (*Pungitius pungitius* L.). In G, the estimated mean littoral reliance of the char population was the lowest observed: 62 % with individual range from 51 % to 68 % (Karlsson & Byström 2005). The lower mean littoral reliance and individual variation are most probably a consequence of the existence of profitable, small-sized prey fish, which can effectively utilize pelagic resources and thus also link this energy source to top consumers. However, Karlsson & Byström (2005) observed that char in G fed mostly on small-sized sticklebacks, which were found to be benthivorous unlike their larger planktivorous conspecifics. This explains why char were not fully relying on pelagic energy sources but slightly more on littoral production in G. These observed differences in the mean values and in the individual

variation of littoral reliance between Saanajärvi and G most likely result from the smaller range in char total length (294–575 mm) and from the smaller sample size ($N = 25$) of char in G than in Saanajärvi, but also from the single sampling of Karlsson & Byström (2005) in late summer or in mid-winter. In fact, if char would have been sampled in spring or in summer, when all kinds of prey items were available for fish, the char population of G could have shown stronger reliance on littoral energy sources with larger individual variation.

Although this study and previous stable isotope studies (Sierszen *et al.* 2003, Karlsson & Byström 2005) have shown that the littoral production dominates the energy supply for top consumers in typical, small high-latitude lakes, the situation may be different in a lake, which has (1) a longer ice-free period, (2) more turbid or humic water, (3) greater depth and larger surface area or (4) a profitable pelagic prey item for char population. Because Saanajärvi, and also the study lakes of Karlsson & Byström (2005), are located at relatively high altitudes (445–993 m a.s.l.) and the annual ice-free period in these lakes is therefore very short, crustacean zooplankton, which has a short lifespan and relies heavily on phytoplankton production (e.g. Kalff 2002), is probably available for char only for a very short annual period. This may be one of the main reasons for the strong reliance of char on littoral food sources. However, in Takvatn and in Fjellfrøsvatn in north Norway (Amundsen 1995, Klemetsen *et al.* 2003 a), which are located at lower altitudes (214 m a.s.l. and 125 m a.s.l., respectively) than Saanajärvi (679 m a.s.l.) and thus have longer ice-free period further supporting higher annual pelagic production, char populations have been shown to utilize substantial amounts of pelagic zooplankton. Also the char population in Store Renne, central Norway, consumes large amounts of crustacean zooplankton (Bjørn & Sandlund 1995). Store Renne is not only located at lower altitude (312 m a.s.l.) and latitude ($63^{\circ}22'N$) than Saanajärvi, but also has highly humic water, which likely suppresses benthic primary production, but supports pelagic production. These cases indicate that the energy source basis of a char population may, at least partially, shift from littoral to pelagic dominance, if the lake has a longer ice-free period or more turbid water supporting relatively higher pelagic production.

Although this Master's thesis focused on studying the char population of Saanajärvi, some preliminary studies were also done in Kilpisjärvi located near Saanajärvi but at lower altitude (473 m a.s.l.) and having a much more complex fish community (with nine fish species in total), greater surface area (3700 hectares) and maximum depth (57 m), and thus smaller proportion of littoral area (30 %) (Harrod *et al.* unpublished). According to the preliminary results, the char population in Kilpisjärvi is more reliant on pelagic energy sources (36 %) than char in Saanajärvi (16 %) (Eloranta unpublished). In Kilpisjärvi, char feed mostly on small omnivorous whitefish, which consume substantial amounts of pelagic zooplankton, but also benthic macroinvertebrates. The char population of Kilpisjärvi is thus strongly, although not directly, relying on pelagic energy sources. The observed relatively strong pelagic reliance of char in Kilpisjärvi is suggested to result from the high contribution of pelagic area, but also from the high availability of sympatric, omnivorous (i.e. partially pelagic) prey fish species. This was also the case in the study lake G of Karlsson & Byström (2005), where char fed on large-sized, planktivorous sticklebacks together with small-sized, benthivorous sticklebacks. A char population may also undergo a shift from littoral to pelagic energy sources, if man introduces a profitable pelagic prey organism into the lake. This was the case in the large, strongly regulated reservoir of Limingen, central Norway, where the introduction of pelagic mysid, *Mysis relicta* Lovén, radically changed the energy source basis of char from littoral to pelagic, whereas brown trout stayed feeding on littoral benthic macroinvertebrates. As a conclusion, the lake

morphometry and the availability of profitable pelagic prey items may strongly affect the energy source basis of char population, as may the lake water colour and the duration of ice-free period due to their strong effect on the production of benthic and pelagic primary producers.

4.2. Seasonal changes in the energy source basis and diets of char

Contrary to the second hypothesis, the char population of Saanajärvi did not undergo any clear seasonal shifts in the energy source basis. Instead, only a small proportion of the most abundant <100 g char had fed on zooplankton and in most cases zooplankton was only a supplementary food source, while other prey items made larger contributions to the whole stomach contents. In September, the population of <100 g char had not consumed more pelagic zooplankton than in July, and the estimated mean littoral dependence did not significantly differ between April, July and September. Most <100 g char were also caught from the lake littoral areas and they generally seemed to avoid the pelagic habitat. In addition, because the efficiency of feeding on small-sized prey, such as zooplankton, decreases dramatically with increasing size of char compared to the foraging efficiency on relatively large benthic macroinvertebrates (Jansen *et al.* 2003), it is not surprising that most <100 g char caught in this study had preferred littoral macroinvertebrates over small pelagic zooplankton. However, in contrast to <100 g char, the population of 100–500 g char had a markedly higher contribution of zooplankton in their stomach contents and also had significantly lower mean LF estimate in September than in April or in July. These observations suggest that, unlike <100 g char, this char size group had partially shifted from littoral to pelagic energy sources in the late growing season. Why did <100 g char not change their energy source basis, but the 100–500 g char did? Although pelagic food resources may have been relatively abundant at the end of the growing season and thus probably offered an alternative food source for <100 g char during the period of strong resource competition for the limited resources of the littoral habitat, these small-sized char were most probably restricted to the littoral habitat and food sources due to their higher vulnerability to cannibalistic predation in open-water areas (Svenning & Borgstrøm 1995, Keyse *et al.* 2007). In contrast, those char which had already reached a size over 100 g have largely outgrown the size most vulnerable to predation and thus can more freely switch between littoral and pelagic foraging habitats and food sources. Svenning & Borgstrøm (1995) studied the seasonal and ontogenetic habitat and dietary shifts within the stunted char population of Store Rennen, central Norway. They found that only part of the adult char age groups (i.e. char of age over 4 years and length over 150 mm) migrated from benthic to pelagic areas in the late summer and autumn, while the younger and smaller char stayed in the littoral areas, where they were less vulnerable to predation by brown trout. Svenning & Borgstrøm (1995) suggested that the most probable proximate reason for the partial seasonal habitat shift was the increase in pelagic food resources (i.e. crustacean zooplankton) in late summer, which is also most likely the main reason for the dietary shift of 100–500 g char in Saanajärvi. Svenning & Borgstrøm (1995) also argued that there might be one or a mixture of several alternative mechanisms that have caused the partial habitat shift of adult char, such as ideal free distribution, diverging habitat and prey preferences among age, size or sex groups within population or a difference between competitively dominant and subdominant individuals.

The fish catch in September revealed that brown trout is more abundant in Saanajärvi than was previously thought. Due to its more aggressive behaviour and more rigid habitat demands (e.g. Nilsson 1955, Jansen *et al.* 2002, Forseth *et al.* 2003), the population of brown trout may thus have partially forced the 100–500 g char out from the littoral

foraging areas in late autumn, when they were actively swimming in the shallow spawning grounds and were also easily caught by the bottom gill nets. Several previous studies in Sweden (Nilsson 1955, Nilsson 1965, Langeland *et al.* 1991) and in Norway (Jansen *et al.* 2002, Forseth *et al.* 2003) have shown that in sympatry, char and brown trout have typically segregated habitats and food sources, and that char is the more flexible species in terms of diet and habitat choice. For instance, Nilsson (1965) studied the diets of char and brown trout in 21 allopatric and 14 sympatric fish populations. He found that in allopatry, char and brown trout seemed to have very similar diets consisting mainly of benthic macroinvertebrates such as amphipods, gastropods, mayflies and terrestrial insects, but when they were sympatric, char shifted to feed mainly on zooplankton, whereas brown trout continued to feed on more profitable benthic prey. In addition, other studies have shown that char is a more effective zooplankton forager than brown trout (e.g. Nilsson 1955, Jansen *et al.* 2002), and this may be one of the reasons why 100–500 g char, but not brown trout, changed their energy source basis in the late growing season, when zooplankton most probably became more abundant. In Saanajärvi, the observed differences in the diets, growth rates and isotopic compositions of 100–500 g char and brown trout indicate that, at least in autumn, these two fish species have to some extent segregated trophic niches. This kind of frequently observed niche segregation between char and brown trout has commonly been suggested to be an adaptation to the sympatric coexistence of these species in the unproductive, high-latitude lakes with limited food resources (Klemetsen *et al.* 2003). By restricting the feeding niche and habitat use of char, brown trout can strongly affect the growth and recruitment of char populations (e.g. Nilsson 1955, Jansen *et al.* 2002). However, because brown trout are so few in Saanajärvi, they probably cannot have a major impact on the growth and recruitment of the whole overcrowded char population.

Although the energy source basis of the whole char population did not undergo any clear seasonal changes, char diet varied greatly depending on the availability of different prey items. The observed dominance of chironomids in the diets of <500 g char can partially be explained by the high contribution of chironomids (90 %) in the total benthic macroinvertebrate composition of Saanajärvi (Arctic limnology -field course report 2006). However, for the examination of density and composition of benthic macroinvertebrates in Saanajärvi, samples were collected only from three depth zones (2, 10 and 20 m) by using an Ekman grab and thus the estimates ignore the contribution of macroinvertebrates inhabiting the shallowest part of the littoral zone (<2 m) and those organisms more likely caught by a kick-net, like amphipods. In any case, when char samples were obtained under ice in April and only from the lake profundal zone in August, chironomid larvae and pupae nearly exclusively dominated the diets of <500 g char. In addition to amphipods and to some other benthic macroinvertebrates, chironomid larvae were probably the only highly available prey item for small char during the ice-cover seasons. Likewise, in the profundal habitat, littoral macroinvertebrates are absent and thus chironomid larvae and pupae dominated the diets of <500 g char caught in August. However, these char individuals must also have utilized littoral food resources, because their LF estimates indicated stronger reliance on littoral than on pelagic energy sources, and some had even remains of littoral amphipods in their stomach contents. Thus, instead of being solely restricted to a particular habitat, there seems to be some degree of habitat exchange of char individuals between the littoral, pelagic and profundal habitats. This observation is also supported, for instance, by the omnivorous diets of some individuals consisting of both benthic and pelagic prey items. Within the stunted char population of Store Renne, central Norway, Bjørn & Sandlund (1995) observed a similar pattern with char individuals continuously shifting between different feeding habitats and depth zones during the open-water seasons. In fact,

because of the small surface area and steep slopes of Saanajärvi, it is not surprising that char individuals can rapidly switch between littoral, pelagic and profundal foraging habitats.

4.3. Ontogenetic dietary shift and cannibalistic predation of char

Contrary to the third hypothesis, the strong littoral reliance was largely independent of char size. However, on average, the 100–500 g char relied slightly less on littoral energy sources than <100 g and >500 g char and were the only size group that underwent a partial seasonal shift in the energy source basis. In addition, the population of 100–500 g char fed substantially more on chironomid pupae (pelagic prey) than on larvae (benthic prey) in July and in August, while <100 g char foraged mostly on chironomid larvae in August. This indicates that these two char size groups showed slight segregation in their feeding habitats and strategies during the open-water seasons. However, because no char of age under 3 years were caught within this study, it is hard to conclude, whether the char individuals in Saanajärvi undergo any radical ontogenetic shift in the energy source basis or main prey items during their whole lifespan. Several studies (e.g. Forseth *et al.* 1994, Byström *et al.* 2004) have shown that the age of 1 to 3 years can be critical for the survival of char juveniles and thus char often undergoes ontogenetic dietary and/or habitat switch around that age. Small juvenile char may be superior zooplankton foragers, but as char grows, increasing foraging costs (i.e. higher energetic costs, but still high predation risk) may force char from pelagic prey and habitat to shift to larger littoral prey items (i.e. benthic macroinvertebrates) and to the more sheltered littoral foraging areas (Forseth *et al.* 1994). It is possible that within the char population of Saanajärvi, some individuals undergo ontogenetic dietary shift from pelagic (i.e. zooplankton) to littoral energy sources (i.e. benthic macroinvertebrates), while the others already feed on small-sized benthic prey in their early stages of ontogeny. This could be one of the reasons for the observed differences in the individual growth rates and condition factors. Previous studies have shown that juvenile char prefer feeding either on zooplankton or on small-sized benthic macroinvertebrates among stones and gravel in the very shallow littoral areas, or in some lakes may also inhabit the deepest profundal areas (Klemetsen *et al.* 2003). To get samples of juveniles from these habitats, special traps or electro fishing equipment would certainly be needed. It seems unlikely that juvenile char would actually be missing in Saanajärvi, although it is surprising that none of the large char had recently fed on very small-sized char. On the other hand, most juveniles may be eaten very quickly after the hatching and after ingestion they are probably quickly digested and thus may not be detected from the stomach contents (Amundsen pers. comm.). Moreover, remarkable fluctuations in recruitment are rather common among char populations (e.g. Byström 2006), and thus the overcrowded char population of Saanajärvi may in fact have largely failed to recruit during the last two years. Annual fluctuations in recruitment may also be the reason for the large number of individuals of age around 6 and 7 years in the char population.

Although char of age under 3 years were not caught, the largest char had clearly undergone an ontogenetic dietary shift from lower trophic levels to cannibalistic predation, as was the prediction of the fourth hypothesis. All the six >500 g char had grown relatively fast and most had recently eaten nothing but smaller conspecifics of length 150–190 mm. In fact, char of this size was the most abundant and therefore also the general size of prey fish for cannibals. Although there seems to exist only very few cannibalistic giants within the char population of Saanajärvi, they may still have a crucial role in the dynamics of the char population as regulators of the growth (i.e. restricting the feeding habitat to littoral zone) and abundance (direct predation) of small, <100 g char (Svenning & Borgström

1995). In Saanajärvi, the shift to cannibalism seems to occur around a total length of 300–350 mm or weight of 350–400 g, as indicated by the stomach contents of the largest (383 g, 347 mm) 100–500 g char. According to previous studies, this is a rather typical size threshold for char to become cannibalistic in allopatric char lakes, where no other small-sized prey fish species are present. In Ruozuajure, northern Sweden, Byström (2006) found that cannibalism was not evident until char had reached a total length of circa 350 mm. In the same way, within five allopatric char populations in Svalbard, Hammar (2000) observed ontogenetic dietary switch of char from slow-growing planktivorous or benthivorous individuals to large, fast-growing cannibals at the age of 10 to 15 years and in the total length of around 200–300 mm. Respectively, the average fork length of char at the start of piscivory was 200 mm in Guolasjavri, Takvatn and Stuorajavri situated in northern Norway (Amundsen 1994), and 220 mm in Thingvallavatn, Iceland (Malmquist *et al.* 1992). However, if char lives in sympatry with some other small-sized prey fish species, it may shift to piscivory already at much smaller size or younger age. For example, in Loch Ericht, Scotland, char coexists with minnows (*Phoxinus phoxinus* L.) and switches to piscivory already at an average fork length of 165 mm (Fraser *et al.* 1998, McCarthy *et al.* 2004). L'Abée-Lund *et al.* (1992) found that the mean total length of char at the shift to piscivory was 160 mm in 13 Norwegian study lakes, where char and brown trout were able to consume three-spined sticklebacks (*Gasterosteus aculeatus* L.), minnows and small-sized whitefish. According to my preliminary studies in Kilpisjärvi, the shift of char to piscivory seems to occur around a total length of 200–250 mm, and even some individual char of length only 170 mm had already eaten small Alpine bullheads (*Cottus poecilopus* L.) (Eloranta unpublished). Based on these observations, in sympatry, char may shift to piscivory and accelerate growth at much smaller size than in allopatry, because of the higher availability of small-sized prey fish, unless other competitively dominant fish species, such as brown trout or pike (*Esox lucius* L.), prevent it. However, in allopatric lakes, char may show cannibalistic foraging at much smaller size, but the young-of-the-year char may be highly available only for a very short period after hatching and also so quickly digested that they can hardly ever be detected from the fish stomach contents (Amundsen pers. comm.).

On average, the largest char in Saanajärvi had also relatively high $\delta^{15}\text{N}$ signatures, suggesting that they generally occupied slightly higher trophic positions than most <500 g char. Although both stomach contents and $\delta^{15}\text{N}$ signatures indicated that >500 g char were generally cannibals, some individuals may also occasionally forage on lower trophic levels. This was indicated by the relatively low $\delta^{15}\text{N}$ signatures of few individuals and by the exceptional diet of the single other large char caught in July. Because this individual had a comparable growth rate to the other giants, it must also have previously been feeding on small-sized char and not just on *Gammarus lacustris* amphipods and adult tipulids. On the other hand, amphipods have high energy content (Kahilainen pers. comm.) and thus may be a profitable, supplementary prey item even for the largest individuals. Moreover, foraging on smaller prey is more frequent than feeding on prey above the optimal size (Godin 1997). The observed individual variation in the $\delta^{15}\text{N}$ signatures of >500 g char may either be a result of individual differences in isotopic fractionation or it may reflect differences in the feeding strategies with some individuals consuming purely piscivorous diet, while others may exhibit prey switching between fish and prey of lower trophic levels (McCarthy *et al.* 2004). Although the $\delta^{15}\text{N}$ signatures generally rose along with the increase in char size, even some of the <100 g char had as high trophic positions as the cannibalistic giants. This is most probably a consequence of the wide range in $\delta^{15}\text{N}$ signatures of prey organisms. For instance, those <500 g char feeding predominantly on profundal chironomids may have much higher $\delta^{15}\text{N}$ signatures (i.e. trophic positions) than

those feeding mostly on littoral macroinvertebrates with low $\delta^{15}\text{N}$ signatures. Hence, the great variation in $\delta^{15}\text{N}$ signatures of prey organisms has most likely caused the great individual differences in the trophic positions of <500 g char. The existence of small-sized char with contrasting trophic positions may have further caused the observed individual differences in the $\delta^{15}\text{N}$ signatures of large char, because those cannibals consuming solely littoral prey fish likely have lower trophic positions than those foraging substantially more on profundal prey fish.

But what are the factors inducing cannibalism in allopatric char lakes? Hammar (2000) suggested that seasonal prey shortage and slow juvenile growth in association with fitness components favouring large body size were the main mechanisms inducing cannibalism. Byström (2006) found that in Ruozutjaure, northern Sweden, a recruitment pulse resulted in the emergence of cannibalism and acceleration in growth of a few individual char. The observed recruitment pulse had negative effects on macroinvertebrate abundance and led to a strong intercohort competition, decrease in body condition and increase in mortality of adult char (Byström 2006). In Saanajärvi, the extensive fish stockings conducted in the 1990s could also be regarded as recruitment pulses, which thus may not only have caused the char population to become stunted, but also probably induced some individuals to shift to cannibalism. Mass-removal of stunted char has frequently been shown to increase the growth of remaining char (e.g. Klemetsen *et al.* 2002, Amundsen *et al.* 2007), so it would be reasonable to contemplate such fishery management in Saanajärvi rather than stocking any more char.

4.4. Impacts of intraspecific competition on the char feeding behaviour

As predicted by the fifth hypothesis, some char individuals showed specialized feeding strategies with diets consisting solely of a particular, and often exceptional, prey item such as crustacean zooplankton or molluscs. Because the diets of <100 g and 100–500 g char showed significant overlap, these char size groups must strongly compete for the limited food resources of Saanajärvi. Also the observed large individual variation in growth rates and in condition factors suggest that the stunted and overcrowded char population of Saanajärvi is under a strong intraspecific competition, which gives rise to competitively dominant and subdominant individuals differing in their performance and shape, and forces some individuals to specialize on a particular prey type. In the same way, Amundsen (1995) observed a wide trophic niche within the stunted char population of Takvatn, northern Norway, and concluded that this was a consequence of the specialized, rather than opportunistic, feeding strategy of individual char caused by the strong intraspecific resource competition. During the open-water seasons (July and September), when char were caught from various depth zones and foraging habitats, the char population of Saanajärvi had a wide trophic niche with individuals foraging on all kinds of prey items available at that time. The large individual variation in LF estimate also supports the existence of wide trophic niche, where some individuals rely solely on littoral energy sources, while some others are utilizing both littoral and pelagic energy sources equally. However, during periods of scarce food resources like in winter and in spring, char has to feed on whatever is available at that time. In Saanajärvi, the only food sources for small char under ice seemed to be chironomid larvae, amphipods, molluscs and copepods. Hence, an individual char has to feed, for instance, on chironomid larvae like the others, because it cannot specialize on some different prey item, such as cladocerans or aerial insects, due to their scarcity or total absence. This is probably also the case in the profundal zone of Saanajärvi, where nothing but chironomid larvae and pupae are highly available

for char during the open-water seasons, and thus char inhabiting profundal areas cannot specialize on a particular, exceptional prey.

In Saanajärvi, only a few char had specialized in feeding on crustacean zooplankton and overall, zooplankton represented only a small contribution to the diet of whole char population. As previously observed in some other lakes, (e.g. Dahl-Hansen *et al.* 1994), char seemed to prefer cladocerans over copepods as the major zooplankton prey. Amundsen (1995) found that planktivorous char in Takvatn, northern Norway, were very selective and usually excluded other prey types from their diets, but in Saanajärvi, most individuals had fed on others prey types besides zooplankton. Although showing strict planktivory at the time of capture, the few specialized zooplankton foragers in Saanajärvi had previously also utilized littoral prey, according to their relatively high $\delta^{13}\text{C}$ signatures and LF estimates. However, the isotopic signatures of recently specialized zooplankton foragers may not indicate a strong pelagic reliance due to the time delay of isotopic turnover of fish muscle and liver tissues. As aforementioned, due to the long ice-cover period of Saanajärvi, pelagic crustacean zooplankton is probably available for char only for a very short annual period. Thus, it is unlikely that an individual char would survive through the long winter if it were strictly specialized on foraging on pelagic zooplankton. Although distinct char morphs appear to have developed within populations with intense intraspecific competition and in lakes with separate littoral, pelagic and profundal zones offering specific opportunities for different morphological feeding adaptations (Jonsson & Jonsson 2001), and these criteria seem to become fulfilled in Saanajärvi, it is unlikely that separate pelagic and benthic char morphs would exist in Saanajärvi. This is because the char population is very young (introduced in the 1990s) and therefore have not had time to adapt to the particular ecosystem. Moreover, although individual variation in condition factors have frequently been evinced to be linked to the morphological differences of char morphs (i.e. the pelagic morph typically has lower condition factors due to their longer snouts and more streamlined body shape) (e.g. Jonsson & Jonsson 2001), the large individual variation of condition factors observed within the char population of Saanajärvi most probably results from differences between sexes and sexual maturities, which were not recorded within this study, or from differences between dominant and subdominant individuals. It is possible, for instance, that those char caught in August from the lake profundal zone were mostly subdominant individuals, which had been chased out from the more resource-rich littoral areas. In consequence, some of these individuals had become starved and showed lower condition factors than those mostly caught from the lake littoral zone in other seasons. Jonsson & Jonsson (2001) argued that in some lakes the emergence of different char morphs may be a result of introduction of two allopatric, divergent char morphs into one lake by man. Hence, if distinct char morphs would exist in Saanajärvi, they most probably have evolved either in Pahtajärvi or in Tsuugijärvi, and nowadays have also segregated into distinct trophic niches in Saanajärvi. Char originating from Pahtajärvi in 1993 may well grow faster and show different feeding strategies and ontogenetic dietary shifts than those originating from the stunted char population of Tsuugijärvi stocked in 1997. Char of Tsuugijärvi may for instance reproduce more effectively (Ranta pers. comm.), but grow extremely slowly, have low performance and thus be unable to switch to cannibalism, further causing the char population to stay stunted and overcrowded.

4.5. Stomach contents and stable isotope analyses and limitations of the study

Simultaneous use of stable isotopes and stomach contents analysis proved to be the most reliable and effective method in studying the food web structures of Saanajärvi and the prevailing energy-flow pathways from primary producers to top consumers. For

example, stomach contents analysis revealed that chironomids were the most abundant prey of <500 g char, but stable isotope analysis showed that these chironomids were mostly of littoral and not profundal origin, thus representing a littoral rather than a pelagic energy source for the char population. Moreover, one could argue that all those char, which had recently fed on nothing but zooplankton, were strict planktivores. However, their isotopic signatures showed that they were in fact, either briefly or predominantly, more reliant on littoral than on pelagic energy sources. On the other hand, stable isotopes did not reveal the seasonal, taxonomic changes in the prey variety of <500 g char as the stomach contents did. Variation in the isotopic signatures proved to be a powerful and reliable tool for evaluating the trophic niche width of char population (Bearhop *et al.* 2004), and overall the results corresponded well to those of stomach contents analysis. However, the lipid-normalization procedure described by Kiljunen *et al.* (2006) seemed to change the $\delta^{13}\text{C}$ signatures of fish liver tissue more than it likely should. In a few cases, the original liver $\delta^{13}\text{C}$ value of individual char actually reflected a recent, strong reliance on pelagic energy sources, and so did the stomach contents, but the lipid-normalization raised the $\delta^{13}\text{C}$ signature to correspond more to a littoral-based diet. Hence, the isotopic signatures would have indicated even wider trophic niche of char population (total individual range of LF estimates from 30 % to 129 %), if liver $\delta^{13}\text{C}$ value had not been lipid-normalized. Further testing would be needed in developing a lipid-normalization procedure suitable for the isotope samples of fish liver tissue.

This study was mainly conducted by one man and inevitably some aspects of sampling and sample preparation could not be done as comprehensively as if there had been at least one assistant during the whole study. In future studies, fish samples should always be collected from distinct littoral, pelagic and profundal habitats with separate gill net series, so that the habitat use and density (i.e. catch per unit effort, CPUE) of char in these habitats could be estimated. In addition, sex, stage of sexual maturity, colouration and morphology should be recorded from every individual fish to get a better idea of the impacts of these variables to the char growth and performance, and also to detect different morphs of char. To study early phase of char ontogenetic dietary shift, char juveniles could be sampled using Ella traps or electro fishing equipment. Moreover, seasonal changes in the density and community of benthic and pelagic organisms could be studied together with other samplings to see how those changes could probably explain the observed seasonal changes in the char diets. Overall, the whole sampling procedure should be consistent during every sampling occasion to avoid bias in the final results.

5. CONCLUSIONS

The results clearly indicate that top consumers, such as char and brown trout, may rely strongly on littoral energy sources even in a relatively deep subarctic lake, where pelagic production and food webs might be assumed to be of greater importance. This is likely a consequence of the extremely clear and oligotrophic water of Saanajärvi, which enables light to penetrate to great depths creating a large and relatively productive littoral zone, but also of the long ice-cover season, which greatly inhibits pelagic production. Because of their larger size, benthic macroinvertebrates are also more profitable prey for adult char, which are not as effective zooplankton foragers as juveniles. Moreover, the results indicate that an allopatric char population has a wide potential feeding niche due to the absence of other competitively dominant fish species and also due to the specialized feeding behaviour of individuals within the overcrowded char population competing for the limited food resources. In allopatry, individual char also seem to shift to piscivory and

accelerate growth at much larger size than in sympatry with other small-sized prey fish species.

Overall, the results highlight the importance of taking the seasonality and fish size in consideration, when studying the lake food webs and the energy source basis of top consumers, but also emphasize the effectiveness of complementary use of stable isotope and stomach contents analyses. However, more information about the impacts of seasons, lake size and fish community structure is required for more thorough evaluation of the factors that control the energy source basis and trophic niche widths of top consumers and to understand the trophic dynamics in high-latitude lake ecosystems.

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6. APPENDIXES

Appendix 1. Statistical comparisons of different variables between char size groups, sampling seasons and between char and brown trout (Source). Fish size groups (Size group) included into the comparison, statistical test used (Test), test measure (F / χ^2 / t, symbol depend on the statistical method used), degrees of freedom (df) and the p-values (p) and test significances (* = p < 0.05, ** = p < 0.01, *** = p < 0.001) are given in the table.

Source	Variable	Size group	Test	F / χ^2 / t	df	p
Size groups	Condition factor	All	Kruskal-Wallis	7.603	2	0.022*
Size groups	Condition factor	<100 g & 100-500 g	Kruskal-Wallis	0.034	1	0.853
Size groups	$\delta^{13}\text{C}$ muscle	All	Anova	7.207	80	0.001***
Size groups	$\delta^{13}\text{C}$ liver	All	Anova	5.330	80	0.007**
Size groups	LF muscle	All	Anova	6.054	80	0.004**
Size groups	LF liver	All	Anova	4.301	80	0.017*
Size groups	$\delta^{15}\text{N}$ muscle	All	Anova	12.587	80	< 0.001***
Size groups	$\delta^{15}\text{N}$ liver	All	Anova	20.671	80	< 0.001***
Seasons	Condition factor	<100 g	Anova	6.419	118	< 0.001***
Seasons	$\delta^{13}\text{C}$ muscle	<100 g	Anova	2.433	51	0.076
Seasons	$\delta^{13}\text{C}$ liver	<100 g	Anova	3.981	51	0.013*
Seasons	LF muscle	<100 g	Anova	2.454	51	0.075
Seasons	LF liver	<100 g	Anova	4.137	51	0.011*
Seasons	Condition factor	100-500 g	Anova	2.592	22	0.083
Seasons	$\delta^{13}\text{C}$ muscle	100-500 g	Kruskal-Wallis	3.149	3	0.369
Seasons	$\delta^{13}\text{C}$ liver	100-500 g	Anova	4.406	22	0.016*
Seasons	LF muscle	100-500 g	Kruskal-Wallis	3.606	3	0.307
Seasons	LF liver	100-500 g	Anova	4.375	22	0.017*
Species	$\delta^{13}\text{C}$ muscle	100-500 g	t-test	-2.982	24	0.006**
Species	$\delta^{13}\text{C}$ liver	100-500 g	t-test	-4.754	24	< 0.001***
Species	LF muscle	100-500 g	t-test	-3.244	24	0.003**
Species	LF liver	100-500 g	t-test	-5.027	24	< 0.001***
Species	$\delta^{15}\text{N}$ muscle	100-500 g	t-test	9.948	24	< 0.001***
Species	$\delta^{15}\text{N}$ liver	100-500 g	t-test	8.440	24	< 0.001***

Appendix 2. Tukey's pairwise comparisons of different variables between char size groups. The p-values and test significances (* = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$) are given in the table.

Variable	Size group	<100 g	100-500 g	>500 g
$\delta^{13}\text{C}$ muscle	<100 g	1	0.173	0.011*
	100-500 g		1	0.001***
	>500 g			1
$\delta^{13}\text{C}$ liver	<100 g	1	0.368	0.024*
	100-500 g		1	0.005**
	>500 g			1
LF muscle	<100 g	1	0.178	0.029*
	100-500 g		1	0.003**
	>500 g			1
LF liver	<100 g	1	0.382	0.057
	100-500 g		1	0.012*
	>500 g			1
$\delta^{15}\text{N}$ muscle	<100 g	1	0.332	< 0.001***
	100-500 g		1	0.001***
	>500 g			1
$\delta^{15}\text{N}$ liver	<100 g	1	0.748	< 0.001***
	100-500 g		1	< 0.001***
	>500 g			1

Appendix 3. Tukey's pairwise comparisons of different variables of <100 g and 100–500 g char between sampling seasons. The p-values and test significances (* = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$) are given in the table.

Variable	Size group	Season	April	July	August	September
Condition factor	<100 g	April	1	0.290	0.004**	0.934
		July		1	0.033*	0.269
		August			1	0.001***
		September				1
$\delta^{13}\text{C}$ liver	<100 g	April	1	0.895	0.035	0.998
		July		1	0.202	0.944
		August			1	0.038*
		September				1
LF liver	<100 g	April	1	0.919	0.036*	1.000
		July		1	0.183	0.928
		August			1	0.028*
		September				1
$\delta^{13}\text{C}$ liver	100-500 g	April	1	0.862	0.423	0.278
		July		1	0.062	0.019*
		August			1	0.999
		September				1
LF liver	100-500 g	April	1	0.809	0.430	0.347
		July		1	0.062	0.020*
		August			1	1.000
		September				1

Appendix 4. On CD: Stomach contents and stable isotope signatures of individual char and brown trout.

Species	Code	Season (1=April, 2=July, 3=August, 4=September)			Total length (mm)	Total weight (g)	Condition factor	Stomach fullness (0-10)	Cladocera	Calanoida	Boedetströmi	Chironomid pupa	Chironomid larva	Lymnae	Pisidium	Gammarus l.	Tipulidae larva	Trichoptera larva	Plecoptera, nymph	Cottidae	Coleoptera, adult	Hymenopt., adult	Diptera adult	Tipulidae, adult	Plecoptera, adult	Char
		1	2	3																						
Char	S1 r 28	1	1	165	40	0,35	3						3													
Char	S1 r 32	1	1	161	40	0,37	2						2													
Char	S1 r 30	1	1	170	42	0,33	3						3													
Char	S1 r 31	1	1	175	42	0,30	6						6													
Char	S1 r 27	1	1	172	43	0,33	4						4													
Char	S1 r 29	1	1	171	44	0,34	3						3													
Char	S1 r 24	1	1	191	72	0,39	7						5													
Char	S1 r 23	1	1	234	94	0,27	4,2		0,2				1			2										
Char	S1 r 25	1	1	232	95	0,28	2						2			3										
Char	S1 r 26	1	1	226	97	0,31	4,2						2	0,2		2										
Char	S1 r 22	1	2	230	101	0,30	5,2		0,2				5													
Char	S1 r 15	1	2	255	133	0,29	1						1													
Char	S1 r 16	1	2	284	199	0,31																				
Char	S1 r 4	2	1	138	19	0,29	5					2				3										
Char	S1 r 1	2	1	136	20	0,32	3					2					0,5	0,5								
Char	S1 r 3	2	1	145	23	0,30																				
Char	S1 r 5	2	1	155	28	0,30	1																			
Char	S1 r 2	2	1	163	36	0,32	5,2					4				0,2										
Char	S1 r 6	2	1	176	44	0,31	5,2									0,2										
Char	S2 r 8	2	1	158	33	0,33	2					1											1			
Char	S2 r 21	2	1	166	34	0,29	6					6														
Char	S2 r 20	2	1	167	36	0,30	5,2					3	0,2													
Char	S2 r 9	2	1	163	40	0,36	8					8														
Char	S2 r 22	2	1	184	45	0,28	7	3				3											0,5	0,5		
Char	S2 r 11	2	1	179	48	0,32	1					0,5											0,5			
Char	S2 r 12	2	1	190	53	0,29	0,2																			
Char	S2 r 15	2	1	185	54	0,32	1,2					1	0,2													
Char	S2 r 18	2	1	189	55	0,31	1,2					0,5											0,2	0,5		
Char	S2 r 10	2	1	190	56	0,31																				
Char	S2 r 14	2	1	192	59	0,32																				
Char	S2 r 16	2	1	191	60	0,33	1,2	0,2				1														
Char	S2 r 19	2	1	202	60	0,27	5,2	4				1											0,2			
Char	S2 r 13	2	1	200	61	0,29	2,2	0,2				0,5											0,5		1	
Char	S2 r 17	2	1	196	63	0,32	0,2																			
Char	S2 r 7	2	1	205	75	0,33																				
Char	S2 r 5	2	1	226	97	0,31																				
Char	S2 r 6	2	1	227	97	0,30	6					6														
Char	S1 r 8	2	1	145	27	0,35	1																			
Char	S1 r 10	2	1	168	36	0,29																				
Char	S1 r 9	2	1	164	37	0,33	8					3											2	1	2	
Char	S1 r 15	2	1	170	44	0,35	5					2											1	2		
Char	S1 r 12	2	1	177	46	0,32																				
Char	S1 r 14	2	1	179	46	0,31	2,4					0,2	0,2	1												
Char	S1 r 11	2	1	235	98	0,28	1,4					0,2	0,2			1										
Char	S2 r 32	2	1	150	30	0,35	4																1		2	
Char	S2 r 39	2	1	154	33	0,36	4					1	1										2			
Char	S2 r 36	2	1	160	36	0,34	4,2					0,2		4												
Char	S2 r 27	2	1	171	37	0,29	1					1														
Char	S2 r 28	2	1	167	37	0,31	1																1			
Char	S2 r 33	2	1	163	37	0,33	1						1													
Char	S2 r 23	2	1	183	40	0,25	6					4														
Char	S2 r 35	2	1	165	40	0,35																				
Char	S2 r 37	2	1	167	41	0,34	1																	1		
Char	S2 r 24	2	1	181	52	0,34	3					2	1													
Char	S2 r 29	2	1	193	54	0,28	7					3											1	3		
Char	S2 r 26	2	1	201	64	0,30	8					8														
Char	S2 r 31	2	1	201	64	0,30	7					3	1										2	1		
Char	S2 r 38	2	1	210	68	0,27	5,2						3										1	0,2	1	
Char	S2 r 30	2	1	202	69	0,31	7	2				2	1										2			

Char	S2 r 42	2	1	217	77	0,28	6		5	1						
Char	S2 r 40	2	1	201	78	0,36	3		1						1	1
Char	S2 r 25	2	1	212	86	0,34	7		2					1	2	2
Char	S2 r 41	2	1	222	91	0,31	1		1							
Char	S1 r 19	2	1	172	39	0,30	4	1	1							2
Char	S1 r 20	2	1	173	43	0,32	8			4						4
Char	S1 r 21	2	1	175	48	0,34	3	1	1	1						
Char	S1 r 18	2	1	201	55	0,25	3	0,5	0,5	1						1
Char	S1 r 17	2	1	210	79	0,32	3,4	2	0,2	1	0,2					
Char	S1 r 7	2	2	303	240	0,30	6			5				1		
Char	S2 r 3	2	2	247	122	0,29	6			4				0,5	0,5	1
Char	S2 r 4	2	2	258	138	0,29	5			5						
Char	S2 r 2	2	2	262	144	0,29	5,2			5			0,2			
Char	S2 r 34	2	2	238	117	0,32	5			1					1	3
Char	S2 r 1	2	3	508	1303	0,31	6,2							4	0,2	
Char	S1 r 13	2	3	528	668	0,14										2
Char	sn1	3	1	137	18	0,28	2			2						
Char	sn2	3	1	169	35	0,28	8		3							
Char	sn3	3	1	175	40	0,29	8									
Char	sn4	3	1	188	50	0,29	10			3						
Char	sn7	3	1	232	98	0,29	4,1				3,9		0,2			
Char	sn8	3	1	236	93	0,26	5			4						
Char	sn9	3	1	225	97	0,31	4	2		0,5	1,5					
Char	sn10	3	1	217	78	0,28	3			0,5	2,5					
Char	sn11	3	1	215	76	0,28	5			2,5	2,5					
Char	sn13	3	1	188	64	0,37	3									
Char	sn14	3	1	208	72	0,30	7			1	6					
Char	sn15	3	1	203	58	0,26	7	0,5	1	0,5	5					
Char	sn16	3	1	181	36	0,23	7			0,2	6,8					
Char	sn17	3	1	179	38	0,25	4			0,5	3,5					
Char	sn18	3	1	159	34	0,33	1			0,3	0,7					
Char	sn19	3	1	175	49	0,35										
Char	sn20	3	1	158	28	0,28	6				5,2		0,8			
Char	sn21	3	1	218	86	0,31	9,1			0,4	8,5		0,2			
Char	sn22	3	1	172	38	0,29	9			0,1	8,9					
Char	sn23	3	1	162	30	0,28	3				2			1		
Char	sn5	3	2	280	170	0,27	4			3,5	0,5					
Char	sn6	3	2	241	111	0,29	9			9						
Char	sn12	3	2	260	130	0,26	2				2					
Char	sn24	3	2	268	141	0,26	3,1			2	0,9		0,2			
Char	sn25	3	2	328	284	0,28	5			4,9	0,1					
Char	sn26	3	3	505	1634	0,40	7									7
Char	S2 r 66	4	1	213	76	0,29	1,2			0,2					1	
Char	S1 r 36	4	1	144	20	0,27	2,2	0,5	0,5					1	0,2	
Char	S1 r 38	4	1	140	22	0,32	4							2	2	
Char	S1 r 37	4	1	138	23	0,35	8								8	
Char	S1 r 41	4	1	156	32	0,33	1								1	
Char	S1 r 39	4	1	164	33	0,29	9							2		
Char	S1 r 40	4	1	168	38	0,31	3	2							1	
Char	S1 r 43	4	1	168	40	0,33	1								1	
Char	S1 r 42	4	1	184	56	0,34	7							5	2	
Char	S1 r 44	4	1	217	84	0,30	6				5		1			
Char	S1 r 46	4	1	217	88	0,32	6				6					
Char	S1 r 45	4	1	217	96	0,35	4				3					
Char	S2 r 50	4	1	150	25	0,29	5							1		
Char	S2 r 51	4	1	158	31	0,31	3,4	1	0,2		0,2			2		
Char	S2 r 45	4	1	164	36	0,32	3				2			1		
Char	S2 r 47	4	1	162	40	0,37										
Char	S2 r 65	4	1	174	41	0,30	3	1			2					
Char	S2 r 44	4	1	172	45	0,34	2								2	
Char	S2 r 55	4	1	171	48	0,37										
Char	S2 r 46	4	1	181	50	0,32	9	9								
Char	S2 r 60	4	1	179	51	0,34	5	1			2				2	
Char	S2 r 49	4	1	182	52	0,33	9				4				5	
Char	S2 r 43	4	1	182	55	0,35	8				3				5	
Char	S2 r 52	4	1	190	55	0,30	7				2	3			2	
Char	S2 r 64	4	1	182	56	0,35										
Char	S2 r 57	4	1	202	66	0,30	1	1								
Char	S2 r 63	4	1	197	66	0,32										
Char	S2 r 61	4	1	198	67	0,32	7,2	0,2			2	1			4	
Char	S2 r 53	4	1	203	70	0,31										
Char	S2 r 54	4	1	197	70	0,34	7				2				5	
Char	S2 r 58	4	1	200	71	0,33	8				1		7			
Char	S2 r 59	4	1	215	77	0,29	8,2				2		0,2		6	
Char	S2 r 48	4	1	215	89	0,33										
Char	S2 r 66	4	1	213	76	0,29	1,2			0,2					1	

