Pro gradu –tutkielma

Trophic niche of Arctic charr (*Salvelinus alpinus*) coexisting with lake trout (*Salvelinus namaycush*) and European whitefish (*Coregonus lavaretus*) in two divergent subarctic lakes

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TIIVISTELMÄ

Uusien kalalajien istutukset sekä lajien luontainen leviäminen saattavat tulevaisuudessa uhata nieriäkantoja (*Salvelinus alpinus*) lajienvälisen kilpailun kautta, joka voi johtaa lajin populaatiokokojen pienenemiseen ja jopa paikallisiin sukupuuttoihin. Tämän pro gradu – tutkielman tavoitteena oli tutkia nieriän ja istutetun vieraslajin, harmaanieriän (*Salvelinus namaycush*), ravinnonkäyttöä ja kasvua laajassa ja syvässä Inarijärvessä, sekä nieriän ja istutetun siian (*Coregonus lavaretus*) ravinnonkäyttöä ja kasvua pienessä ja matalassa Skaidijärvessä. Syönnösanalyysi ja vakaiden isotooppien analyysi osoittivat nieriän ja harmaanieriän ravinnonkäytön olevan samankaltaista Inarijärvessä, kuvastaen näin ollen kilpailutilannetta lajien välillä. Molempien lajien ravinto koostui pääosin kalasta: suuret nieriä- ja harmaanieriäyksilöt (> 280 mm) saalistivat lähes yksinomaan pieniä siikoja ja muikkuja (*Coregonus albula*), mutta pienemmät nieriäyksilöt (< 280 mm) söivät pääosin selkärangattomia ja kymmenpiikkejä (*Pungitius pungitius*). Vaikka nieriä ja harmaanieriä kilpailevat samasta ravinnosta, on mahdollista, että suurikokoiset saaliskalapopulaatiot pystyvät tukemaan niiden rinnakkaiseloa Inarijärvessä. Skaidijärvessä nieriän ja siian ravinnonkäyttö oli hyvin eriytynyttä ja molemmilla lajeilla oli selkeästi oma trofialokeronsa. Siellä nieriä käytti ravintonaan kolmipiikkejä (*Gasterosteus aculeatus*), vesiperhosen toukkia ja *Gammarus*-suvun katkoja, kun taas siika oli syönyt eläinplanktonia ja surviaissääsken toukkia. Eriytyneet trofialokerot ovat todennäköisesti seurausta lajienvälisestä kilpailusta. Kalojen energialähteissä (litoraalin ja pelagiaalin ravintoverkot) oli eroja tutkimusjärvien välillä, mikä todennäköisesti johtui järvien suuresta kokoerosta. Inarijärvessä harmaanieriät (> 280 mm) sekä pienet nieriät (< 280 mm) saivat suurimman osan energiastaan litoraalin ravintoverkon kautta, kun taas suuret nieriät (> 280 mm) käyttivät enemmän pelagiaalisia resursseja. Skaidijärvessä molemmat kalalajit olivat riippuvaisia litoraalin energialähteistä. Istutettu vieraslaji kasvoi nopeammin kuin alkuperäinen nieriä molemmissa tutkimusjärvissä. Tämä voi tarkoittaa, että ne ovat tehokkaampia käyttämään rajallisia resursseja. Harmaanieriän nopea kasvu voi tosin johtua osittain lajin laitosalkuperästä. Vieraslajien istuttamista järviin, joissa nieriä esiintyy, tulisi harkita tarkkaan, koska vieraslajit saattavat lisätä lajienvälistä kilpailua ja täten olla vaaraksi rautupopulaatioille.

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ABSTRACT

Introductions and invasions of new fish species can pose a threat to Arctic charr (*Salvelinus alpinus*) causing population declines and even local extinctions through interspecific competition. In this thesis, the diet, main energy flow pathway and growth of Arctic charr and introduced alien species, lake trout (*Salvelinus namaycush*), were studied in large and deep Lake Inarijärvi. Similarly, the diet, main energy flow pathway and growth of Arctic charr and introduced European whitefish (*Coregonus lavaretus*) were studied in small and shallow Lake Skaidijärvi. Stomach contents and stable isotope analyses revealed a dietary and isotopic niche overlap between Arctic charr and lake trout in Lake Inarijärvi, indicating that the species are competing for the same food resources. Both species exhibited piscivory and large individuals (> 280 mm) had almost exlusively been feeding on small European whitefish and vendace (*Coregonus albula*). Small individuals (< 280 mm) of Arctic charr consumed mainly zoobenthos and nine-spined sticklebacks. Despite the apparent resource competition, abundant prey fish populations may be able to support the coexistence of Arctic charr and lake trout in Lake Inarijärvi. In Lake Skaidijärvi, the results of stomach contents and stable isotope analysis showed a distinct resource partitioning, as Arctic charr foraged on three-spined sticklebacks (*Gasterosteus aculeatus*), *Gammarus* sp. and trichopterans, while European whitefish consumed zooplankton and chironomids. This niche segregation is likely to be a result of interspecific competition between the species. The energy mobilization through littoral and pelagic food webs up to fish seemed to differ between the study lakes. A probable reason for this was the size difference between the lakes. In Lake Inarijärvi, lake trout (> 280 mm) and small Arctic charr (< 280 mm) gained most of their energy via the littoral food web, whereas large Arctic charr (> 280 mm) relied slightly more on pelagic production. In Lake Skaidijärvi, both Arctic charr and European whitefish relied clearly on the littoral production. Introduced fish species grew faster than the native Arctic charr in both study lakes, indicating that they might be competing more effectively on the limited resources. However, the faster growth rate of lake trout in Lake Inarijärvi may be partly due to the aquacultural origin of the species. Introductions of non-native species to Arctic charr lakes should be always considered with caution as they may increase the competitive interactions and thereby be a risk to Arctic charr populations.

Contents

1. INTRODUCTION

Introductions of organisms to areas outside their natural distribution have taken place for centuries, causing many species to spread and establish populations outside their native range (Williamson 1996). In freshwater systems, intentional (e.g. fish stocking) and unintentional (e.g. releases of ballast water and live bait) introductions of non-native fish species can affect native fauna through many different interactions, such as hybridization (Kitano *et al*. 2009), predation (Goudswaard *et al*. 2008) and resource competition (Winfield & Durie 2004, Korsu *et al*. 2007). Through these interactions, non-native fish species can cause significant ecological changes at different levels of biological organization, ranging from genes to communities and even whole ecosystems (Cucherousset & Olden 2011). As it is usually impossible to eradicate established populations of non-native species without excessive damage to native species (Myers *et al*. 2000), these changes are most likely to become permanent. Anthropogenic disturbances increase the invasion success of species as native assemblages of organisms may have already been temporarily disrupted or depleted (Byers 2002). Thus, competition from non-native species often acts synergistically with habitat loss and fragmentation (Vitousek 1997, Byers 2002). Particularly strong community effects of invasions are often observed where the number of species is low (Moyle & Light 1996), which is often the case in high-latitude lakes. Therefore, introductions and invasions of different fish species can pose a threat to Arctic charr (*Salvelinus alpinus* L., hereafter charr), having already caused population declines and local extinctions (Winfield & Durie 2004, Byström *et al*. 2007). Within the British Isles, several extinctions and widespread declines in charr populations have been observed at its southernmost distribution limit due to synergistic effects of competition by non-native species (such as roach, *Rutilus rutilus* L.), habitat degradation and climate change (Igoe *et al*. 2001, Maitland *et al*. 2007, Winfield *et al*. 2010, Corrigan *et al*. 2011). Also in alpine Lake Geneva, charr stocks have declined due to indirect or direct causes of climate change (Gerdeaux 2011). In the future, climate change may facilitate invasions of southern species to higher latitudes (Wrona *et al*. 2006), increasing competitive interactions in Scandinavia, where most of the world's charr populations exist (Klemetsen *et al*. 2003).

Charr is the northernmost freshwater fish in the world having a circumpolar distribution and being the only fish species present in the most northern lakes (Klemetsen *et al.* 2003). It is a stenothermal fish being capable of tolerating temperatures as low as -0.99 °C (Elliott & Elliott 2011), whereas warmer temperatures of 16–20 °C can already limit the habitat choice of the species (Langeland & L'abée Lund 1998). The typical environment of charr is an oligotrophic or ultraoligotrophic lake in which it can utilize all major habitats (Klemetsen *et al.* 2003). Charr is usually described as a generalist feeder which can consume a wide range of prey, including zooplankton, zoobenthos, terrestrial insects and fish (Johnson 1980). Charr shows extreme variety in its ecology (e.g. in feeding behaviour and morphology) and in some lakes exists as several distinct morphs such as a large piscivore as well as a small planktivore (Johnson 1980, Jonsson & Jonsson 2001, Klemetsen 2010). However, the potentially wide trophic niche (i.e. diet and habitat use) of charr is typically restricted in practice due to interspecific competition with sympatric fish species (e.g. Nilsson 1965, Svärdson 1976, Langeland *et al*. 1991, Knudsen *et al*. 2010). Interspecific competition can be defined as a negative interaction between different species which results from a shared need for a resource that is in limited supply (Vanni *et al*. 2009). Competition may lead to 1) extinction of one species, 2) coexistence with reduced population size, or 3) trophic niche shifts (Vanni *et al*. 2009). Sympatric fish species with completely overlapping trophic niches are not able to coexist over time as eventually

interspecific competition will lead to disappearance of the weaker species (Hardin 1960). However, sympatric species with a similar niche preference may avoid competition by segregating with respect to food, habitat or time (Ross 1986). For example, when living in sympatry with brown trout (*Salmo trutta* L.), charr is commonly confined to deep profundal and pelagic areas and forages mainly on profundal zoobenthos and/or zooplankton, whereas allopatric charr exploits littoral areas and feeds more on littoral zoobenthos (Nilsson 1965, Langeland *et al.* 1991). However, this segregation is largely season dependent, as during winter charr usually inhabits the littoral zone together with brown trout (Amundsen & Knudsen 2009). During the ice-cover season, charr may be superior to brown trout due to higher activity at low temperature and poor light conditions (Elliott 2011, Helland *et al.* 2011). These seasonal dynamics may partly enable coexistence of brown trout and charr in the same lake (Helland *et al.* 2011). Habitat choice of charr is therefore associated with both competitive interactions and season, and these factors also largely determine which prey items are available for charr. Furthermore, prey selection by charr is dependent on the size of the individual fish, as both the mouth gape size and alimentary tract morphology can restrict the size of prey that a fish is able to ingest (Wootton 1990). Consequently, the trophic niche of charr varies with age and size due to ontogenetic dietary shifts (L'Abée-Lund *et al.* 1993, Eloranta *et al.* 2010). The timing of ontogenetic shift may be affected by predation risk. L'Abée-Lund *et al.* (1993) observed a trade-off between food demand/habitat selection and predator presence (brown trout). The pelagic zone can offer substantial planktonic food resources for small charr during the Arctic summer, but also a high risk of predation because of the lack of refuges. To avoid predation, small charr commonly feed on zoobenthos in the profundal zone until they have reached a certain size threshold which lowers the predation risk (130–180 mm), and only then move to pelagic areas to feed on zooplankton (L'Abée-Lund *et al.* 1993).

In northern America, one of the resource competitors against charr is lake trout (*Salvelinus namaycush* Walbaum). It is an omnivorous feeder which usually consumes the most abundant and available prey items, and like charr, may exhibit different morphs within a lake (Martin & Olver 1980, Eshenroder *et al.* 2008). The natural distribution of lake trout is confined to North America, particularly to the northernmost parts, but it has been introduced to other parts of the world (Martin & Olver 1980), including Finland (Salonen & Mutenia 2007). In North America, lake trout and charr have partly overlapping native distributions and a rather similar trophic behaviour (Johnson 1980, Martin & Olver 1980). However, they seem to rarely exist in the same lakes (Hershey *et al.* 1999, Hershey *et al.* 2006). Hershey *et al.* (1999) and Hershey *et al.* (2006) suggested that competitive exclusion is occurring naturally in their study region (Northern Alaska, vicinity of Tooley lake), as lake trout replaces charr in accessible lakes. Nevertheless, also lake trout can be displaced from the top predator role. Introductions of certain non-native species to native lake trout lakes may be accompanied by a shift in prey communities and food web structure (Vander Zanden *et al.* 1999). In the presence of introduced competitors, such as smallmouth bass (*Micropterus dolomieu* Lacépède) and rock bass (*Ambloplites rupestris* Rafinesque), lake trout may feed primarily on zooplankton and zoobenthos (Vander Zanden *et al.* 1999).

In Europe, one strong competitor with charr is European whitefish (*Coregonus lavaretus* L., hereafter whitefish) (Amundsen *et al.* 2010, Eloranta *et al.* 2011). Whitefish is also a widespread species in the northern hemisphere (Tammi *et al.* 2003) and has a generalist feeding behaviour (Amundsen *et al.* 2010). In some northern Scandinavian lakes, the whitefish population has divided into several sympatric morphs which can vary distinctly in their diet and habitat use (Kahilainen *et al.* 2004, Harrod *et al.* 2010).

Whitefish is an efficient zooplankton predator in the pelagic zone (Svärdson 1976, Amundsen *et al.* 2004) but can also use littoral and profundal zones as feeding habitats (Kahilainen *et al.* 2004). Previous studies have shown that in small subarctic and Arctic lakes, charr and other fish top consumers rely heavily on production of littoral benthic algae and zoobenthos (Sierzen *et al.* 2003, Karlsson & Byström 2005, Eloranta *et al.* 2010). In these clear oligotrophic lakes planktonic resources are usually scarce, and most energy flows through the littoral rather than pelagic zone (Sierzen *et al.* 2003). Here, charr may be dominated by competing sympatric fish species and is forced to shift its trophic niche from the preferred littoral zone to the pelagic or profundal areas (Svärdson 1976, Langeland *et al.* 1991, Klemetsen *et al.* 2003). Introductions of whitefish into charr-lakes or *vice versa* have rarely resulted in established coexistence of the two species (Svärdson 1976). In fact, in lakes with no free niche or habitat refuge for charr, whitefish may become the dominant species and even eliminate charr (Svärdson 1976). However, the relative importance of littoral habitat and the contribution of zoobenthos to whole-lake secondary production are determined by lake size and lake basin morphometry (Vander Zanden & Vadeboncoeur 2002). If a lake is large and deep with vast pelagic areas, charr can take its place in the deep profundal or as a large piscivore (Svärdson 1976). Thus, the stable coexistence of charr and whitefish is most probable in large and deep lakes with an extensive profundal zone, which can serve as a refugium for charr. If the littoral zone is unprofitable for whitefish due to dominance of a predator or other competitor, charr can even be the dominant of the two species (Sandlund *et al.* 2010). Amundsen *et al.* (2010) concluded that a third competing fish species, such as grayling (*Thymallus thymallus* L.), may facilitate the coexistence of charr and whitefish. Thus, the trophic niche of charr depends largely on the quality and quantity of competitors, ontogenetic stage of individual charr, season and lake morphology.

Recently, competitive interactions between fish species have been increasingly studied by using stable isotope analysis (Cucherousset *et al.* 2012). This method has become a valuable tool for studying food web interactions and energy flow in lake ecosystems (Vander Zanden & Vadeboncoeur 2002, Jardine *et al.* 2003, Fry 2006) and is often coupled with the more traditional method of stomach content analysis (Hyslop 1980, Jardine *et al.* 2003). Whereas stomach content analysis reveals only the most recently ingested prey items, the stable isotope analysis reflects the longer-term assimilated food sources, giving a broader perspective on the dietary sources of the fish (Peterson & Fry 1987, Vander Zanden & Vadeboncouer 2002, Fry 2006). The carbon isotope ratio (^{13}C:^{12}C, denoted by δ^{13}C) can particularly reveal which prey items (e.g., littoral zoobenthos, zooplankton) are important food sources for consumers, while the nitrogen isotope ratio (^{15}N:^{14}N, denoted by δ^{15}N) indicates the trophic level of an organism (Peterson & Fry 1987, France 1995, Vander Zanden & Rasmussen 1999).

This MSc thesis was related to the Ph.D. work of MSc Antti Eloranta and to the fish (particularly coregonid species) research projects of prof. Kimmo Kahilainen. The aim of the study was to evaluate the trophic niche differences between native charr and an introduced alien species, lake trout, in large and deep Lake Inarijärvi (hereafter Inarijärvi) and between charr and introduced whitefish in small and shallow Lake Skaidijärvi (hereafter Skaidijärvi). This was done by conducting stomach contents and stable isotope analyses from fish caught from the lakes in autumn 2009 and 2010. The main hypothesis for both study lakes was that the tropic niche of charr and the introduced species differ from each other because they appear to coexist in the study lakes. It was also hypothesized that in Inarijärvi, charr and lake trout gain most energy via the pelagic food web (i.e. phytoplankton –> zooplankton –> planktivorous fish –> piscivorous fish) as Inarijärvi is a

large, deep lake with extensive pelagic zone and both species are known to be capable of becoming large piscivores feeding on pelagic prey fish (Salonen & Mutenia 2007). In contrast, Skaidijärvi is a small and shallow lake with no profundal or pelagic zone, and consequently the littoral food web (i.e. benthic algae –> littoral zoobenthos –> benthivorous fish –> piscivorous fish) was hypothesized to act as the main energy source for both charr and whitefish in Skaidijärvi.

2. MATERIAL & METHODS

2.1. Study lakes

2.1.1. Inarijärvi

Inarijärvi is a large subarctic lake in northern Finland (69°N, 28°E). It covers an area of 1102 km^2 and is therefore the third largest lake in Finland after Lake Saimaa and Lake Päijänne. Inarijärvi flows to the Arctic Ocean via the Paatsjoki river system and its water level has been regulated since the 1940s with a maximum amplitude of 2.4 m. The lake is oligotrophic and has a maximum depth of 95 m and a mean depth of 14.4 m (Salonen 1998). The fish community consists mostly of salmonids and has 13 species in total of which 10 are native and 3 are introduced (Salonen & Mutenia 2007). Native fish species include charr, brown trout, whitefish, grayling, pike (*Esox lucius* L.), burbot (*Lota lota* L.), perch (*Perca fluviatilis* L.), nine-spined stickleback (*Pungitius pungitius* L.), three-spined stickleback (*Gasterosteous aculeatus* L.) and common minnow (*Phoxinus phoxinus* L.). Introduced fish species include vendace (*Coregonus albula* L.), land-locked salmon (*Salmo salar* m. *sebago* L.), and lake trout, which is a non-native species for Finland. Introduction of vendace has had a particularly large impact on the lake ecosystem and Salonen (1998) considered it as a profitable addition to the fish composition of Inarijärvi, both in terms of catch and as a prey species for predatory salmonids. However, vendace can also have profound impacts on the genetics of the native coregonid, whitefish, through hybridization and introgression (Kahilainen *et al*. 2011).

Lake trout was translocated to Finland in 1955 from Lake Superior in North America and has been stocked in Inarijärvi since 1972 (Salonen & Mutenia 2007). Lake trout was considered as a complementary species to native charr and the goal of introducing it to the lake was to increase the catch of salmonid species and to diversify the species-poor ecosystem (Salonen & Mutenia 2007). According to the Finnish Game and Fisheries Research Institute, the lake trout population is maintained by stocking of 1 to 3 year old individuals which are marked with alizarin. No natural spawning has been observed in the lake (Salonen & Mutenia 2007) even though in 2009, some fish of year-class 2004 without alizarin marking were caught (Salonen *et al*. 2010), indicating that the species might spawn in the lake. The native charr population is also supported with extensive stockings: in 2009, the proportion of charr individuals of stocked origin in the total catch varied from 48 to 79 % among different year-classes (Salonen *et al*. 2010). In 2009, the total catch of charr was 8.5 tonnes, and the catch of lake trout was 6.7 tonnes (Salonen *et al*. 2010).

2.1.2. Skaidijärvi

Skaidijärvi is a small, shallow lake with a surface area of 0.44 km^2 and a maximum depth of around 6 m. It is located in the northernmost part of Finland (70°N, 28°E). Whitefish was stocked into the lake a few decades ago (Jarmo Huhtamella from Metsähallitus, pers. comm.), after which the charr stock declined substantially. Subsequent

intensive fishing for whitefish and supplementary stocking of charr from nearby lakes have partly restored the charr stock. A third fish species in the lake is three-spined stickleback.

2.2. Data collection

2.2.1. Fish

Fish from Inarijärvi were caught with gillnets during the autumns of 2009 and 2010 and fish from Skaidijärvi were caught with gillnets during the autumn 2009.

The 2009 fishing took place at two different locations in Inarijärvi and was conducted by two different groups. A research group from the universities of Helsinki and Jyväskylä conducted fishing using two kinds of gillnet series in Nanguvuono (Figure 1) between the 1 and 9 September 2009. One of the series ("small gillnet series") consisted of nine 1.5–1.8 m high and 30 m long gillnets with different mesh sizes attached to each other in random order; the total length of these gillnet series was 270 m. The mesh sizes (knot-to-knot) of the first eight nets were 10, 12, 15, 20, 25, 35, 45 and 60 mm. The ninth piece was a NORDIC-net which has 12 different mesh sizes in 2.5 m long panels (Specziár *et al*. 2009). The other type of gillnet series ("large gillnet series") consisted of five nets which were 5 m high and 60 m long being in total 300 m long. These had mesh sizes of 35, 40, 45, 50 and 55 mm in random order. The net sets were set into three different depth zones in Nanguvuono: pelagic surface nets were in a depth of 0–5 m, littoral benthic nets in 0–15 m and profundal benthic nets in 15–25 m. The gillnet series with smaller nets were fishing for approximately 12 hours at a time, whereas the bigger gillnet series were sometimes fishing for even longer but were checked at least once a day. A second fishing location in Inarijärvi in 2009 was Kasariselkä (Figure 1), where a local fisherman, Tapio Aarnipuro, fished between the 4 and 6 September. He used nets which were 6 m high and had a mesh size of 50–55 mm, with a few exceptions which had a mesh size of 60 mm. The nets were put in lines of several hundred meters and were used between the depths of 15 and 25 m. The fish caught from Inarijärvi in 2009 were kept frozen at -20 °C until the laboratory analysis which was conducted in autumn 2010.

In 2010, the fishing location in Inarijärvi was Sammakkoselkä (Figure 1) where the same fisherman, Tapio Aarnipuro, fished between 1 and 8 September with the same methods as in 2009. All caught fish were kept frozen at -20 °C until the laboratory analysis which was done in spring 2011. For the data analysis, the caught fish from both fishing years were pooled together.

Fish from Skaidijärvi (Figure 1) were caught between the 28 September and 1 October 2009 by Antti Eloranta (University of Jyväskylä) and Kimmo Kahilainen (University of Helsinki). They fished with a similar "small gillnet series" that was used in Inarijärvi. In Skaidijärvi, fishing was conducted only in the littoral zone (1–5 m) as the maximum depth of the lake is 6 m. Caught fish were frozen at -20 °C immediately after capture and were analysed in the laboratory during the spring 2011.
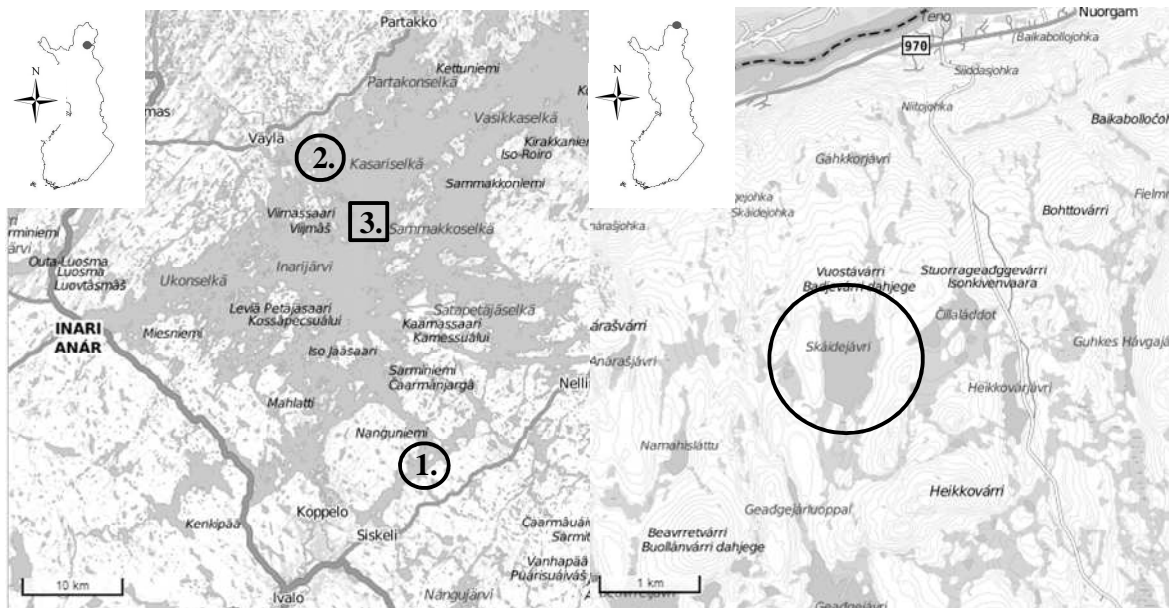
Figure 1. Location of the two study lakes in northern Finland (marked with • in the map of Finland). Left map: Inarijärvi. Fishing sites in 2009 are circled, 1. Nanguvuono, 2. Kasariselkä; fishing site of 2010 is marked with a square, 3. Sammakkoselkä. Right map: Skaidijärvi (circled).

2.2.2. Littoral zoobenthos and zooplankton

Sampling for littoral zoobenthos and zooplankton was conducted similarly in both lakes. Zoobenthos samples were collected with an Ekman grab from depths of 1, 2 and 3 m. Three replicate samples were taken from each depth. In addition, zoobenthos samples were collected from the littoral zone of 0–1 m with a kick net of mesh 500 μm and by taking animals directly from stone surfaces with pincers. Ekman grab and kick net samples were sieved through a 500 μm mesh sieve and put into small plastic containers for later laboratory analysis. In the laboratory, animals were usually identified to family level but sometimes to species or genus level. They were then separated to their own Eppendorf tubes for the subsequent processes preceding the stable isotope analysis. Here, collected *Eurycercus* sp. crustaceans were considered as "littoral zoobenthos" due to their littoral origin, instead of considered as zooplankton.

Qualitative samples of zooplankton were taken with a 50 μm mesh plankton net towed slowly behind a boat. This was done several times until there was enough material. Samples were preserved in water in 0.5 L bottles and later sieved through a 200 μm mesh. From the sieve they were washed to 0.5 L plastic containers and left to settle for a few hours. Finally, cladocerans and copepods were separated from the sample to Eppendorf tubes for the subsequent processes preceding the stable isotope analysis.

2.2.3. Laboratory analyses

In the laboratory, total length (mm) and weight (g) were measured from each fish. Whitefish were identified to a morph according to gill raker morphology (Harrod *et al*. 2010). Moreover, otoliths were removed from all the fish for age determination which was done from whole, clear otoliths under a stereo microscope (Raitaniemi *et al.* 2000). Some otoliths were also burned and cracked to verify the result (Christensen 1964). To increase the visibility of the opaque zones, otoliths were placed in a Petri dish filled with tap water for some minutes before the microscopy. Stomach content and stable isotope analysis were used to evaluate the dietary and niche width differences between the caught fish species.

The stomach fullness of the fish was assessed with a scale from 0 (empty) to 10 (extended full stomach). The fullness value was then divided according to the relative contribution (or volume) of each prey item in the fish stomach contents. The stomach contents were mostly identified to family or genus level. The fish muscle tissue reflects the main energy source during the previous months (Tieszen *et al.* 1983) and was used in the stable isotope analysis to reveal possible long-term dietary differences between the fish species. Muscle samples were taken from the fish below the dorsal fin and stored frozen in Eppendorf tubes until dried in a freeze-drier for 48 hours. Samples of zoobenthos and zooplankton were likewise all dried for 48 hours but at 60 °C in an oven, as no freeze-drier was available. After drying, all samples were ground in their own Eppendorf tubes using a stainless steel bar or with a mortar and pestle if the sample was large and/or hard. From each dried and homogenized sample of fish muscle, zoobenthos and zooplankton, 0.5–0.6 mg of powder was accurately weighed into a tin cup for the stable isotope analysis.

The stable isotopes from all samples were analysed in Jyväskylä during spring 2011 with a FlashEA 1112 elemental analyser coupled to a Thermo Finnigan DELTAplus Advantage mass spectrometer. Muscle tissue of pike was used as an internal working standard. Standard deviation of the internal standard was less than 0.24 ‰ for $\delta^{13}C$ and 0.20 ‰ for $\delta^{15}N$ in each run.

2.3. Data analysis

2.3.1. Growth

The von Bertalanffy non-linear growth model (Busacker *et al.* 1990) was used to measure the growth of the fish. It estimates the length of the fish at a certain age (L_t):

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

where L_t = length at certain age, L_∞ = size at infinity, K = growth coefficient, t = age (years) and t_0 = estimated age at length of 0 mm.

2.3.2. Dietary analyses

Stomach contents of fish were used to evaluate the dietary overlap between different species by using Schoener's index (Schoener 1970). A value of zero indicates no dietary overlap between species whereas a value of 1 indicates a complete overlap. A value of 60 % or higher was considered biologically significant (Wallace 1981).

$$\alpha = 100 \left(1 - 0.5 \left(\sum_{}^{n} \left| p_{xi} - p_{yi} \right| \right) \right)$$

where p = proportion of prey item i in the stomachs of species x and y and n = number of different prey items in the species' diets.

The niche breadth of the different fish species was estimated by using Levin's index of niche breadth (B) and standardized measure (B_A) as given by Marshall and Elliot (1997):

Levin's index B:

$$B = \frac{1}{\sum p^2_j}$$

standardized measure B_A:

$$B_A = \frac{(B-1)}{(n-1)}$$

where p = proportion of prey item j in the diet of a species and n = total number of different prey items found in the stomachs of a species.

2.3.3. Stable isotopes and statistical analyses

To avoid any possible bias caused by varying content of δ^{13}C-depleted lipids in the fish muscle samples, lipid adjustment of their δ^{13}C values was done as described by Kiljunen *et al.* (2006). This mathematical normalization uses the C:N ratio and an estimate of D to produce a lipid-normalized value of δ^{13}C for each sample. It is based on two equations:

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

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

where L = the proportional lipid content of the sample, δ^{13}C' = the lipid-normalized value of the sample, C:N = the ratio of carbon and nitrogen in the sample, δ^{13}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).

Because δ^{13}C and δ^{15}N values can have considerable variation at the base of the food web between ecosystems, δ^{13}C and δ^{15}N values of an organism provide little information about its ultimate source of carbon or absolute trophic position (Post 2002). Thus, for cross-ecosystem comparisons, δ^{13}C and δ^{15}N values need to be transformed to account for differences in the baseline isotopic signatures of pelagic and littoral food webs (Newsome *et al.* 2007). Here, the average isotopic signatures of littoral zoobenthos and zooplankton were used as baselines for littoral and pelagic food webs, respectively. To compare the trophic positions between charr populations of Inarijärvi and Skaidijärvi, the δ^{15}N values were transformed to an index of trophic position with a two-end-member mixing model, which allows for the differentiation between two sources, such as the littoral and pelagic food webs (Post 2002):

$$\text{Trophic position} = \lambda + \frac{\left[\delta^{15}N_{sc} - \left(\delta^{15}N_{base1} \times \alpha + \delta^{15}N_{base2} \times (1-\alpha) \right) \right]}{\Delta_n}$$

where λ = the trophic position of the organism used to estimate the baseline (two for primary consumers), $\delta^{15}N_{sc}$ = δ^{15}N value of fish, $\delta^{15}N_{base1}$ = pelagic baseline signature, $\delta^{15}N_{base2}$ = littoral baseline signature, Δ_n = enrichment in δ^{15}N per trophic level (here commonly used 3.4 ‰; Post 2002) and α = the proportion of nitrogen in the consumer ultimately derived from the base of food web one (pelagic food web). When the movement of nitrogen and carbon through the food web is similar, α can be estimated using δ^{13}C values:

$$\alpha = \frac{\left(\delta^{13}C_{sc} - \delta^{13}C_{base2} \right)}{\left(\delta^{13}C_{base1} - \delta^{13}C_{base2} \right)}$$

Assumptions in this model are that there is little or no trophic fractionation of carbon and that mixing is linear.

The differences in $\delta^{13}C$ and $\delta^{15}N$ values between the fish species within the study lakes were compared with non-parametric Mann-Whitney U-test as assumptions for parametric tests were not met. The same test was also used to compare the total length of the fish species within the study lakes. Possible ontogenetic diet shifts were studied using a linear regression between the total length of the fish and the $\delta^{13}C$ and $\delta^{15}N$ values.

The stable isotope mixing model SIAR (Stable Isotope Analysis in R; Parnell *et al.* 2010) was used to estimate the contribution of two different energy sources (littoral and pelagic food web) in the fish diets. The model uses a Bayesian approach and the diet contribution estimates are therefore reported in the results as 95 % Bayesian credibility intervals (Parnell *et al.* 2010). Widely applied trophic fractionation factors (mean ± SD) of 0.4 ± 1.3 ‰ for $\delta^{13}C$ and 3.4 ± 1.0 ‰ for $\delta^{15}N$ (Post 2002) were used in the model.

Minimum Convex Polygon Estimator (in the package "adehabitat" in R; Calenge 2006) was used to calculate the convex hull areas for different fish species. The convex hull area encompasses the individuals of each species in the $\delta^{13}C$–$\delta^{15}N$ bi-plot space and can be used to examine the trophic niche width and dietary plasticity of different fish species (Layman *et al.* 2007). In this study, instead of calculating the total convex hull area (TA) which encompasses all individual data points in $\delta^{13}C$–$\delta^{15}N$ space (Layman *et al.* 2007), the isotopic niche area was restricted to include 95 % of the individuals of each species to exclude possible outliers which could overextend the niche area. All statistical analyses were done with IBM SPSS Statistics 19 and R 2.14.0.

3. RESULTS

3.1. Inarijärvi

3.1.1. Size, age and growth

In 2009, 70 charr were caught from Nanguvuono and 19 charr and 21 lake trout were caught from Kasariselkä. In 2010, 28 charr and 58 lake trout were caught from Sammakkoselkä. Thus, a total of 117 charr and 79 lake trout were caught and analysed from Inarijärvi. All the fish were caught from the profundal zone.

Table 1. Sampling year, number of caught fish (N), total lengths and weights (mean ± SD) and minimum and maximum observed values (range) of Inarijärvi charr and lake trout.

Lake	Species	Sampling year	N	Length (mm)		Weight (g)	
				Mean ± SD	Range	Mean ± SD	Range
Inarijärvi	Charr	2009	89	242 ± 144	112–703	341 ± 669	10–4540
		2010	28	461 ± 100	256–700	1217 ± 850	132–4234
		Total	117	294 ± 164	112–703	550 ± 805	10–4540
	Lake trout	2009	21	458 ± 60	354–578	871 ± 344	366–1631
		2010	58	434 ± 84	281–590	760 ± 427	155–1634
		Total	79	441 ± 78	281–590	788 ± 407	155–1634

Length and age distributions of charr differed greatly between Nanguvuono and the two other fishing sites in Inarijärvi. Almost all of the charr caught from Nanguvuono were less than 200 mm in total length (1 to 2 years old), whereas most of the charr from the two other fishing sites had a total length of over 450 mm. Small charr from Nanguvuono lowered the total length (mean ± SD) of all caught charr to 294 ± 164 mm, whereas it was 441 ± 78 mm for lake trout (Table 1). Hence, there was a statistically significant difference

between the total lengths of charr and lake trout (Mann-Whitney U: Z = 6.001, N = 196, p < 0.001) (Figure 2). To establish more comparable size categories of charr and lake trout for the dietary and stable isotope analyses, it was decided that charr < 280 mm in total length formed their own size group (hereafter called small charr) because they were smaller than the smallest lake trout (Table 2). The charr > 280 mm in total length (hereafter called large charr) and lake trout groups had the same minimum length (281 mm) and more similar size distribution after the rearrangement (Mann-Whitney U: Z = -0.871, N = 132, p = 0.384) (Table 2).

Table 2. Number of caught fish (N), total lengths and weights (mean ± SD) and minimum and maximum observed values (range) of Inarijärvi fish after the formation of two different size groups of charr.

Lake	Species	N	Length (mm)		Weight (g)	
			Mean ± SD	Range	Mean ± SD	Range
Inarijärvi	Small charr	64	159 ± 39	112–277	35 ± 36	10–170
	Large charr	53	458 ± 91	281–703	1173 ± 851	199–4234
	Lake trout	79	441 ± 78	281–590	788 ± 407	155–1634

The age of charr ranged from 1 to 9 years and the age of lake trout ranged from 2 to 8 years. Most charr were 1 to 2 years old (caught from Nanguvuono) and most of the lake trout were 3 to 5 years old (Figure 2). The length at age of charr varied notably reflecting individual differences in growth rates (from 5 to 9 years) (Figure 3). Lake trout had a higher length at age, less individual variation in length at age and faster growth rate than the charr (Figure 3, Table 3). However, according to the von Bertalanffy growth model, charr can reach larger infinity length than lake trout (Table 3).
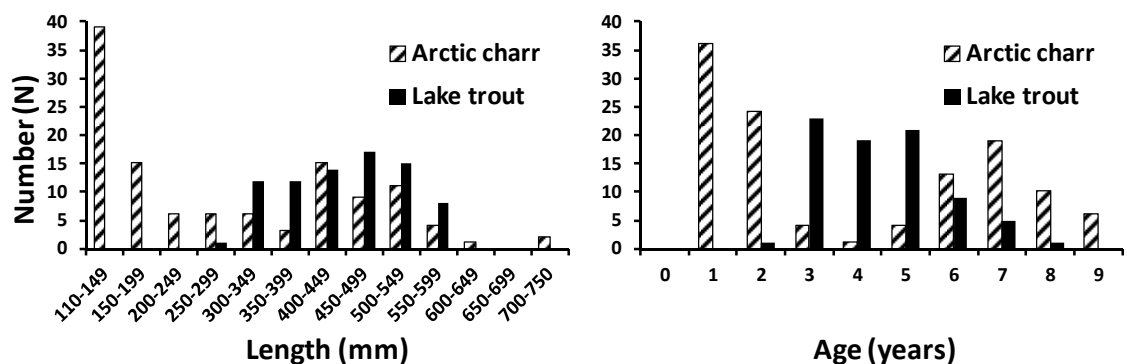

Figure 2. Length and age distribution of charr (N = 117) and lake trout (N = 79) caught from Inarijärvi.

● Observed mean length at age
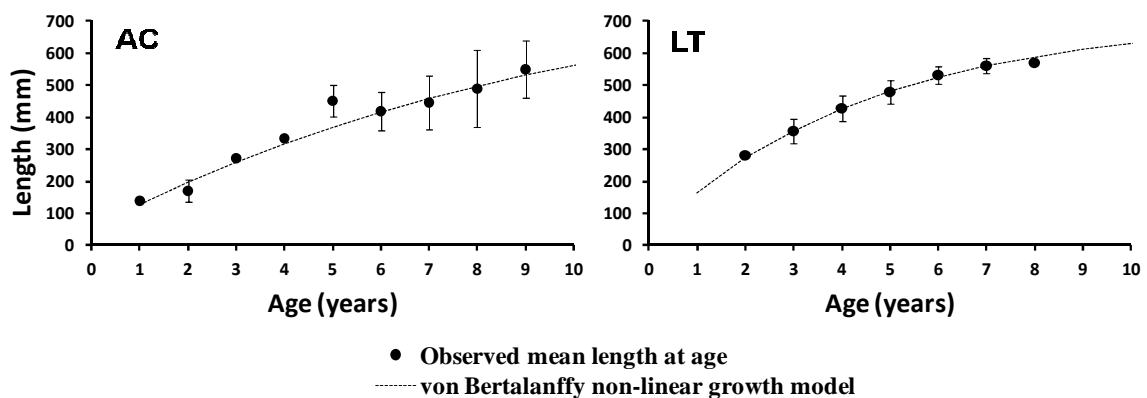
------ von Bertalanffy non-linear growth model

Figure 3. Observed mean (± SD) length at age and predicted growth (von Bertalanffy non-linear growth model) for Inarijärvi charr (AC) and lake trout (LT).

Table 3. Growth coefficient (K), infinity length (mm) and age at length of 0 mm for Inarijärvi charr and lake trout according to the von Bertalanffy non-linear growth model.

Lake	Species	Growth coefficient (K)	Infinity length (mm)	Age at length of 0 mm
Inarijärvi	Charr	0.10	865	-0.6
	Lake trout	0.23	699	-0.2

3.1.2. Dietary analyses

According to Schoener's index, large charr and lake trout showed a biologically significant overlap ($\alpha = 73$ %), but their diet clearly differed from that of small charr ($\alpha = 8$ % and 27 %, respectively). Large charr and lake trout had almost exclusively been feeding on fish and the main prey item found in the stomachs of both species was *Coregonus* sp. (small whitefish and vendace) (Figure 4). Lake trout had also fed on nine-spined sticklebacks to some extent. Increasing size did not change diet composition of large charr and lake trout except that all charr over 550 mm had empty stomachs, including the two largest individuals (700 mm & 703 mm) (Figure 5). Lake trout of 280–399 mm in length seemed to have the most variable diet (Figure 5). According to Levin's index, the niche breadth of lake trout ($B = 2.0$; $B_A = 0.12$) was wider than that of large charr ($B = 1.1$; $B_A = 0.03$).

Small charr used a much broader spectrum of prey items than large charr or lake trout (Figure 6) and consequently had a much wider niche breadth ($B = 8.4$; $B_A = 0.28$). Charr less than 200 mm in length had been feeding mainly on zoobenthos (mostly chironomids, trichopteran larvae, *Pisidium* sp. and *Eurycercus* sp. but also *Asellus aquaticus*, *Gammarus* sp., *Sialis* sp., Ephemeroptera nymphs, Diptera pupae, Zygoptera nymphs, Hirudinea, arachnids and aerial insects), different kind of zooplankton (Calanoida, Cladocera, *Bythotrepes* sp. and *Polyphemus* sp.) and nine-spined sticklebacks. The smallest charr with a prey fish in stomach was 130 mm in length. After reaching the length of 200 mm, small charr had been feeding mostly on fish, including *Coregonus* sp.
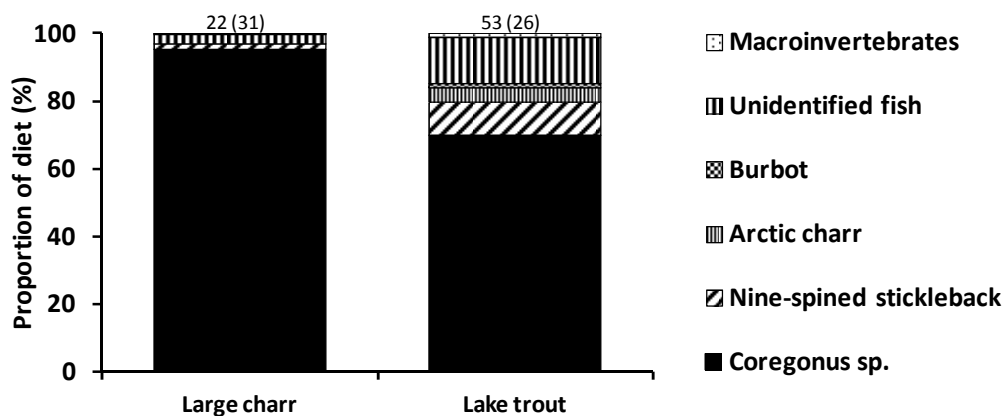

Figure 4. Proportions of different prey items found from the stomachs of large charr and lake trout in Inarijärvi. The number of stomachs which contained prey items is given above the bars (number of empty stomachs in brackets).
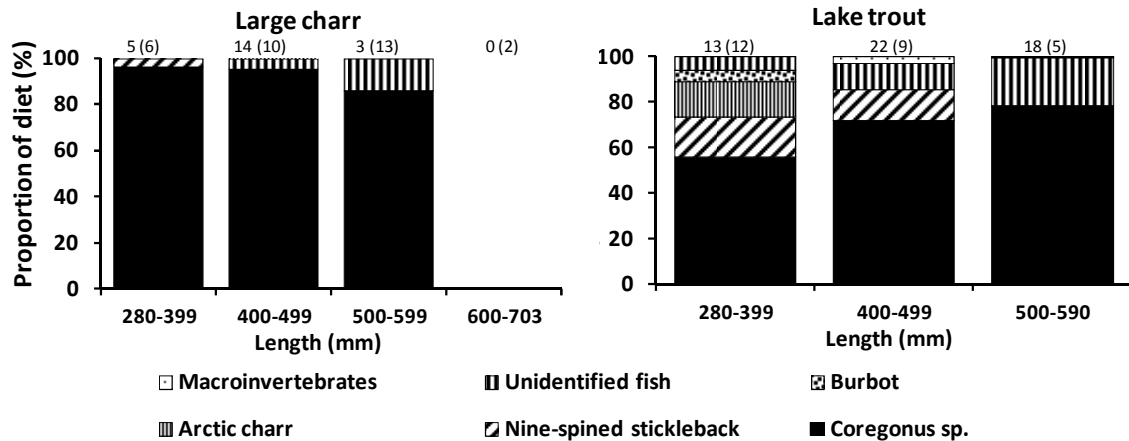
Figure 5. Proportions of different prey items found from the stomachs of different size categories of large charr and lake trout in Inarijärvi. The number of stomachs which contained prey items is given above the bars (number of empty stomachs in brackets).
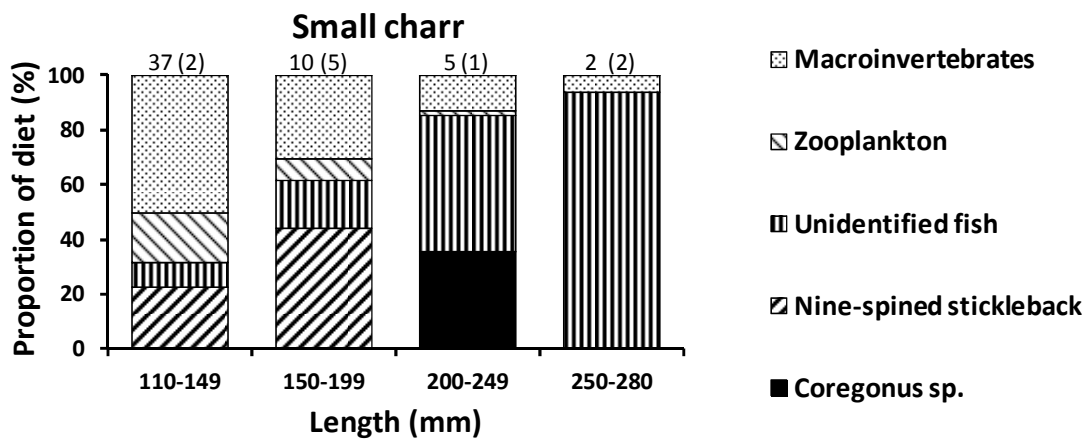

Figure 6. Proportions of different prey items found from the stomachs of different size categories of small charr in Inarijärvi. The number of stomachs which contained prey items is given above the bars (number of empty stomachs in brackets).

3.1.3. Stable isotopes

The δ^{13}C values of littoral baseline (littoral zoobenthos) and pelagic baseline (zooplankton) differed markedly from each other in Inarijärvi (Figure 7). Organisms which were used to calculate the mean baselines are described in Appendix 1.

Large charr had significantly lower δ^{13}C and higher δ^{15}N values compared to lake trout (Mann-Whitney U: Z = 7.030, N = 132, p < 0.001; Mann-Whitney U: Z = -3.920, N = 132, p < 0.001). In turn, small charr had significantly higher δ^{13}C and δ^{15}N values compared to lake trout (Mann-Whitney U: Z = -3,796, N = 143, p < 0.001; Mann-Whitney U: Z = -4.421, N = 143, p < 0.001). Large charr had significantly lower δ^{13}C values compared to small charr (Mann-Whitney U: Z = 8.295, N = 117, p < 0.001), but the two groups had no difference in δ^{15}N values (Mann-Whitney U: Z = 1.446, N = 117, p = 0.148). According to these results, all three groups seemed to have significant differences in their dietary source (δ^{13}C values) (Table 4, Figure 7). However, when Mann-Whitney test was done between the δ^{13}C and δ^{15}N values of all charr (size groups < 280 mm and > 280 mm put together) and lake trout, charr still had significantly higher δ^{15}N values compared to lake trout (Mann-Whitney U: Z = -4.964, N = 196, p < 0.001) but there was

no statistically significant difference between the $\delta^{13}C$ values (Mann-Whitney U: Z = 1.488, N = 196, p = 0.137), which, conversely, indicated generally the same dietary source for charr and lake trout. Even though there was a statistically significant difference in $\delta^{15}N$ values between charr and lake trout, ecologically, the 0.3–0.4 ‰ difference between the species was small. Thus, despite the results of the statistical analysis, both species occupied a rather similar trophic position in Inarijärvi (Figure 7). Mean trophic position value for small charr was 4.4 (individual range 3.9–4.8), for large charr 4.4 (individual range 3.4–4.7) and for lake trout 4.3 (individual range 4.1–4.7). According to the SIAR isotope mixing model, lake trout and small charr gained most of their energy via the littoral food web (69–83 % and 83–99 %, respectively; Figure 8). In contrast, large charr got slightly more of its energy via the pelagic food web (51–63 %; Figure 8).

Table 4. Mean (± SD) and range (minimum and maximum observed values) of $\delta^{13}C$ and $\delta^{15}N$ values of Inarijärvi charr and lake trout.

Species / size group	N	$\delta^{13}C$ (‰)		$\delta^{15}N$ (‰)	
		Mean ± SD	Range	Mean ± SD	Range
Small charr	64	-22.3 ± 2.1	-27.6– -20.0	11.7 ± 0.7	10.1–12.8
Large charr	53	-26.7 ± 1.5	-28.2– -23.0	11.6 ± 0.8	8.1–12.6
Small + large charr	117	-24.3 ± 2.8	-28.2– -20.0	11.7 ± 0.7	8.1–12.6
Lake trout	79	-24.0 ± 2.4	-27.4– -20.2	11.3 ± 0.5	10.5–12.6

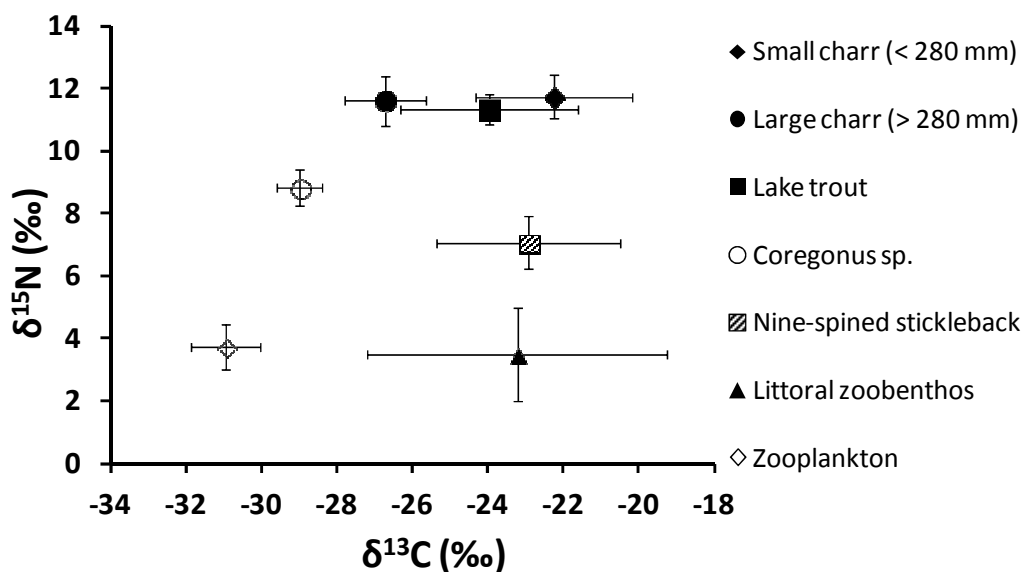

Figure 7. Biplot of mean (± SD) $\delta^{13}C$ and $\delta^{15}N$ values of small charr, large charr, lake trout, prey fish (*Coregonus* sp., N = 100; nine-spined stickleback, N = 30), littoral zoobenthos and zooplankton sampled from Inarijärvi.
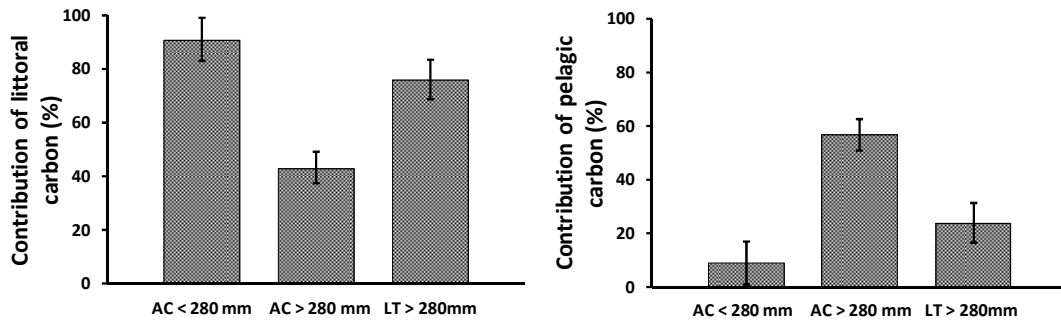
Figure 8. Estimated mean (± 95 % Bayesian credibility intervals) contribution of littoral (left) and pelagic (right) carbon sources in the diets of small charr (AC < 280 mm), large charr (AC > 280 mm) and lake trout (LT > 280 mm) in Inarijärvi as given by the SIAR two-source isotopic mixing model.

Lake trout showed an increase in $\delta^{15}N$ values with increasing total length, whereas no similar trend can be seen in charr (Table 5, Figure 9). Thus, it seemed that the larger lake trout occupied higher trophic levels than the smaller ones. According to the coefficient of determination (R^2), the length of lake trout explains 62 % of the variation in the $\delta^{15}N$ values of muscle tissue.

The $\delta^{13}C$ values of both charr and lake trout became lower with increasing total length (Table 5, Figure 9). This result suggested that both species tend to shift their dietary source from littoral towards pelagic with increasing total length. Coefficient of determination indicated that the total length of charr and lake trout explained 70 % and 72 %, respectively, of the variation in the $\delta^{13}C$ values of muscle tissue (Table 5).

Table 5. Linear regression model between the total length and $\delta^{15}N$ and $\delta^{13}C$ values of all charr and lake trout from Inarijärvi.

Lake	Species	Linear regression	R^2	F	p
Inarijärvi	Charr (all)	$\delta^{15}N = 11.69 - 0.00004 \times length$	7E-05	0.01	0.930
	Lake trout	$\delta^{15}N = 9.15 + 0.005 \times length$	0.62	128.90	< 0.001
	Charr (all)	$\delta^{13}C = -20.08 - 0.014 \times length$	0.7	269.43	< 0.001
	Lake trout	$\delta^{13}C = -12.69 - 0.026 \times length$	0.72	199.1	< 0.001
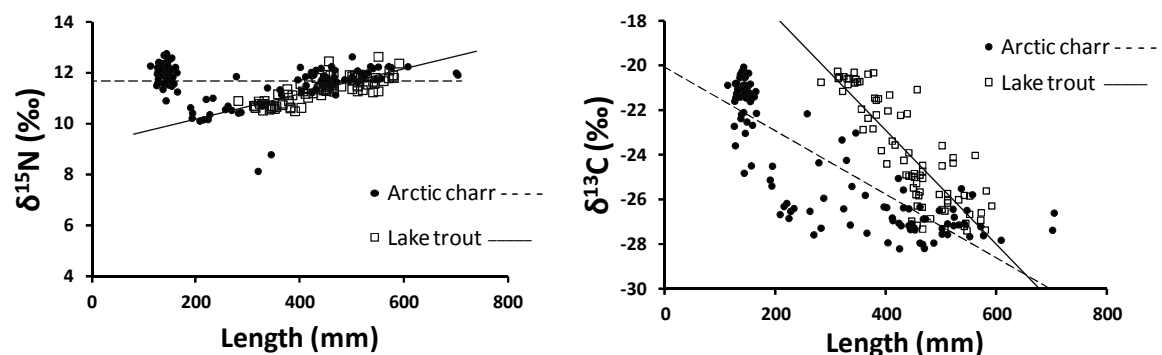
Figure 9. The $\delta^{15}N$ (left) and $\delta^{13}C$ values (right) of all Inarijärvi charr (N = 117) and lake trout (N = 79) as a function of total length (mm).

In Inarijärvi, the calculated convex hull areas indicated that lake trout had the widest isotopic niche with an area of 11.9 ‰^{2} (Figure 10). Large charr had an isotopic niche are of 5.0 ‰^{2} and the value for small charr was 8.7 ‰^{2}. Hence, 95 % of the individual isotope

values of lake trout encompassed an area over twice that for similar sized large charr. Due to its large area, the isotopic niche of lake trout overlaps quite significantly with both large charr and small charr whose isotopic niches are relatively distinct from each other. According to $\delta^{13}C$ values, large charr are clustered in a more pelagic niche whereas small charr and lake trout showed a higher variation, consisting of individuals with both littoral and pelagic $\delta^{13}C$ values (Figure 10). Even though the Mann-Whitney U-test gave a result that generally charr occupies a higher trophic position in the lake, the highest $\delta^{15}N$ values of charr and lake trout were rather similar. Thus, at least some lake trout individuals have a capability to reach similar trophic position in the lake as charr (Figure 10).
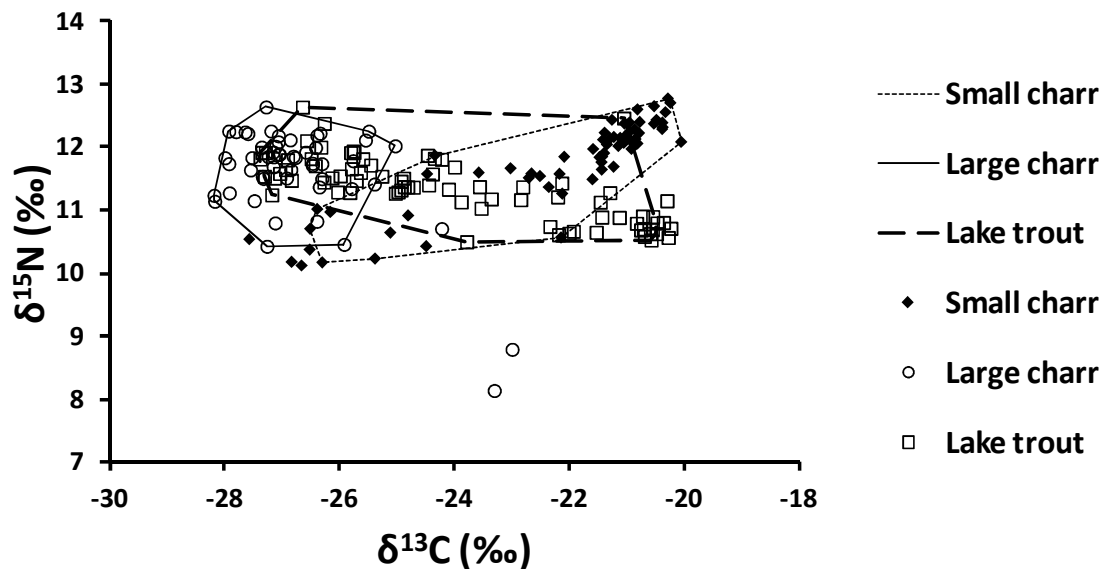

Figure 10. Calculated convex hull areas (lines) in $\delta^{13}C$ – $\delta^{15}N$ bi-plot space delineating 95% of individual small charr, large charr and lake trout from Inarijärvi.

3.2. Skaidijärvi

3.2.1. Size, age and growth

The total catch from Skaidijärvi and the number of analysed fish was 73 charr and 36 whitefish (Table 6). All the whitefish individuals were the LSR-morph (large sparsely rakered).

Table 6. Sampling year, number of caught fish (N), total lengths and weights (mean ± SD) and minimum and maximum observed values (range) of Skaidijärvi charr and whitefish.

Lake	Species	Sampling year	N	Length (mm)		Weight (g)	
				Mean ± SD	Range	Mean ± SD	Range
Skaidijärvi	Charr	2009	73	224 ± 69	131–388	131 ± 126	19–590
	Whitefish	2009	36	285 ± 75	152–448	261 ± 255	25–889

Charr had smaller mean length than whitefish (Mann-Whitney U: Z = 3.666, N = 109, p < 0.001) (Table 6). The most abundant size group of charr was 150–199 mm, whereas the most abundant size group of whitefish was 200–249 mm (Figure 11). The age of charr ranged from 2 to 9 years and the age of whitefish ranged from 2 to 14 years. Most individuals of both species were 3 to 6 years old (Figure 11). The length at age varied greatly for both charr and whitefish reflecting individual differences in growth rates (Figure 12).

Whitefish had a higher length at age and a faster growth rate than the charr (Table 7, Figure 12). However, according to the von Bertalanffy growth model, charr can reach a slightly larger infinity length than whitefish (Table 7).
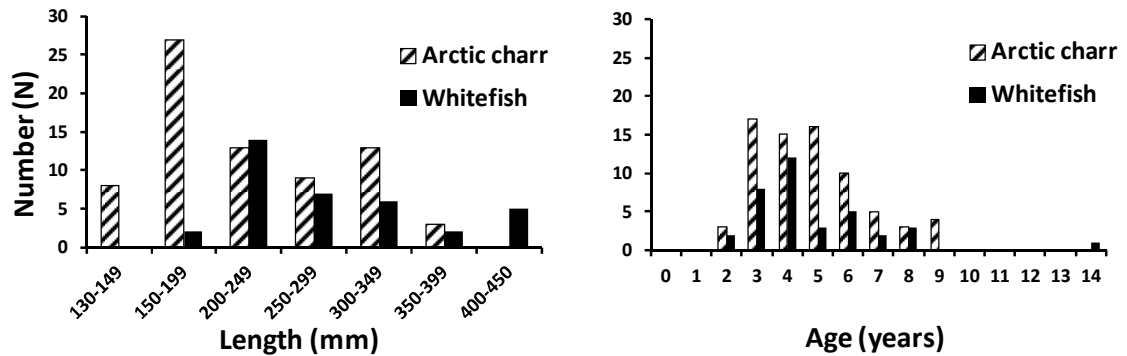

Figure 11. Length and age distribution of charr (N = 73) and whitefish (N = 36) caught from Skaidijärvi.

● Observed mean length at age
-------- von Bertalanffy non-linear growth model
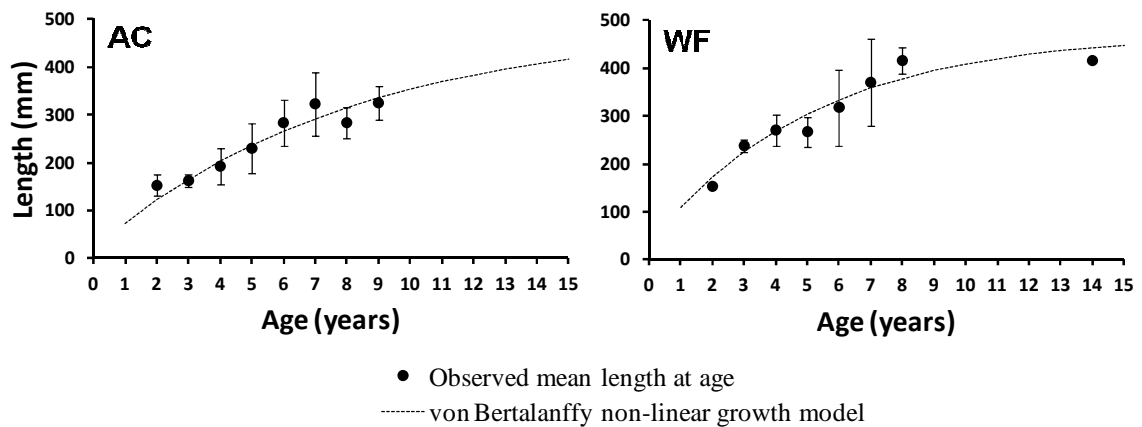
Figure 12. Observed mean (± SD) length at age and predicted growth (von Bertalanffy non-linear growth model) for Skaidijärvi charr (AC) and whitefish (WF).

Table 7. Growth coefficient (K), infinity length (mm) and age at length of 0 mm for Skaidijärvi charr and whitefish according to the von Bertalanffy non-linear growth model.

Lake	Species	Growth coefficient (K)	Infinity length (mm)	Age at length of 0 mm
Skaidijärvi	Charr	0.12	488	-0.3
	Whitefish	0.20	471	-0.3

3.2.2. Dietary analyses

According to Schoener's index, charr and whitefish showed no biologically significant dietary overlap (α = 18 %). Zoobenthos made approx. 50 % of the stomach contents of both species but the composition of these prey items differed (Figure 13). Charr ate *Gammarus* sp. amphipods and trichopteran larvae whereas whitefish consumed mainly chironomid larvae and small *Eurycercus* sp. crustaceans. Zooplankton (Calanoida, *Daphnia* sp., *Bosmina* sp.) constituted approx. 40 % of the whitefish diet whereas 33 % of the charr diet was based on three-spined stickleback. According to Levin's index, the niche breadth of whitefish (B = 3.8; B_A = 0.35) was wider than of charr (B = 3.4; B_A = 0.18).

Figure 13. Proportions of different prey items found from the stomachs of charr and whitefish in Skaidijärvi. The number of stomachs which contained prey items is given above the bars (number of empty stomachs in brackets).
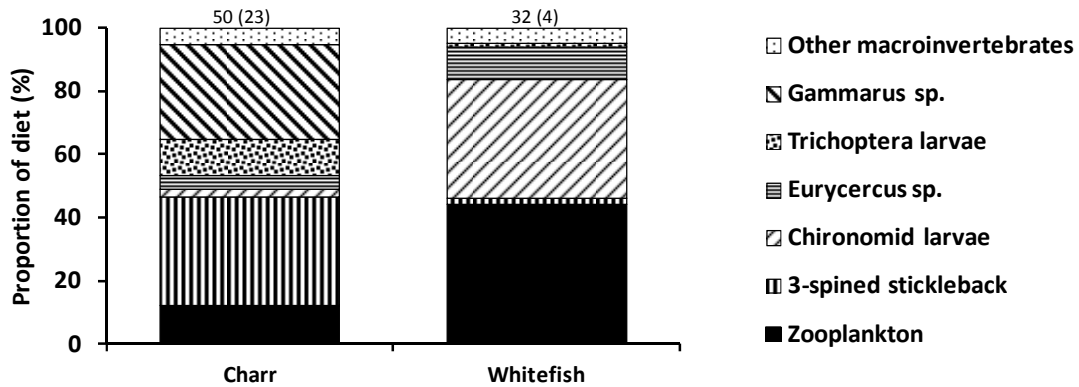
There were differences in the diet composition between size categories within species (Figure 14). Charr less than 250 mm in length fed mainly on *Gammarus* sp. and trichopteran larvae. The abundance of three-spined stickleback as a prey item started to increase after charr had reached the length of 250 mm. In the diet of whitefish, the importance of zooplankton decreased with increasing size, being most important for the small (< 200 mm) and mid-sized (250–299 mm) fish. Also *Eurycercus* sp. crustaceans were somewhat utilized by small whitefish. Chironomids were consumed in all size categories being the most important prey item, together with zooplankton. Largest whitefish individuals fed also on some trichopterans and three-spined sticklebacks.
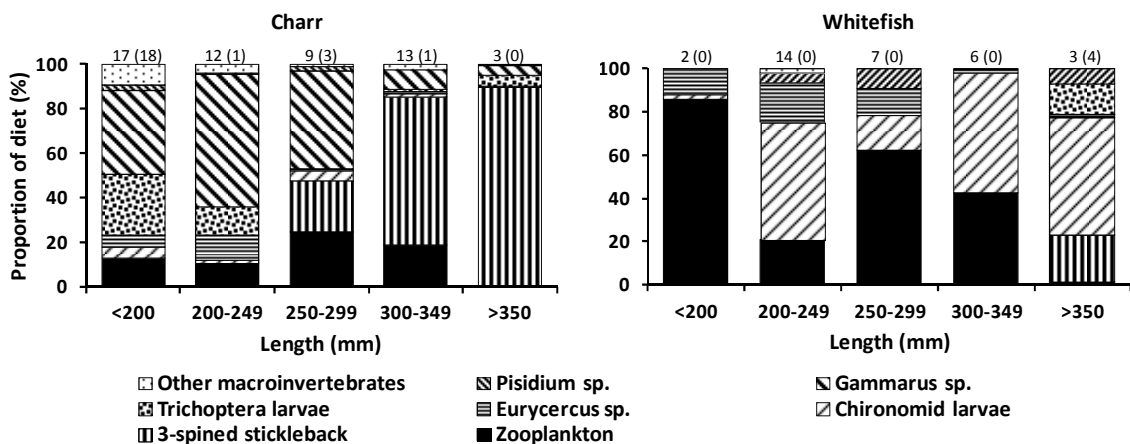
Figure 14. Proportions of different prey items found from the stomachs of different size categories of charr and whitefish in Skaidijärvi. The number of stomachs which contained prey items is given above the bars (number of empty stomachs in brackets).

3.2.3. Stable isotopes

In Skaidijärvi, the $\delta^{13}C$ values of littoral baseline (littoral zoobenthos) and pelagic baseline (zooplankton) differed markedly from each other (Figure 15). Organisms which were used to calculate the mean baselines are described in Appendix 2.

Charr had significantly higher $\delta^{13}C$ values compared to whitefish (Mann-Whitney U: Z = -7.750, N = 109, p < 0.001), but the two species had no significant difference in the $\delta^{15}N$ values (Mann-Whitney U: Z = -1.115, N = 109, p = 0.265) (Table 8, Figure 15). These results from the statistical analyses reveal that charr and whitefish have a similar

trophic position in the lake (δ^{15}N values) but have statistically significant differences in their dietary source (δ^{13}C values) (Figure 15). Mean trophic position value for charr was 3.1 (individual range 2.5–3.7) and for whitefish 2.9 (individual range 2.6–3.4). According to the SIAR isotope mixing model, both charr and whitefish got most of their energy via the littoral food web (93–100 % and 60–78 %, respectively; Figure 16).

Table 8. Mean (± SD) and range (minimum and maximum observed values) of δ^{13}C and δ^{15}N values of Skaidijärvi charr and whitefish.

Species	N	δ^{13}C (‰)		δ^{15}N (‰)	
		Mean ± SD	Range	Mean ± SD	Range
Charr	73	-25.2 ± 1.2	-27.9– -20.4	8.0 ± 0.9	6.1–10.0
Whitefish	36	-27.4 ± 0.7	-29.1– -25.2	7.8 ± 0.6	6.6–9.1
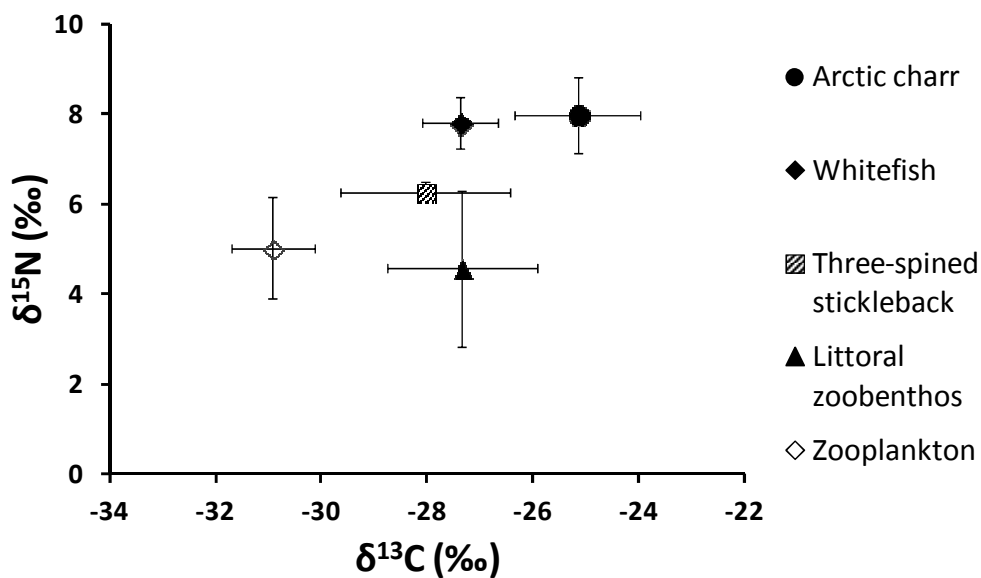
Figure 15. Biplot of mean (± SD) δ^{13}C and δ^{15}N values of charr, whitefish, prey fish (three-spined stickleback, N = 3), littoral zoobenthos and zooplankton sampled from Skaidijärvi.
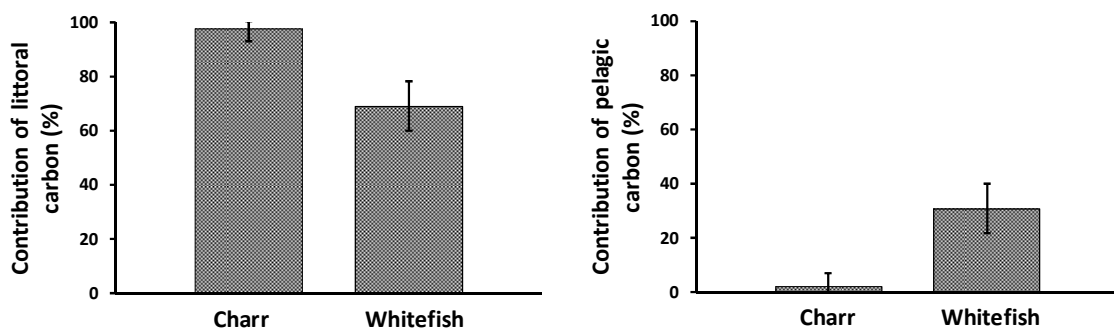
Figure 16. Estimated mean (± 95 % Bayesian credibility intervals) contribution of littoral (left) and pelagic (right) carbon sources in the diets of charr and whitefish in Skaidijärvi as given by the SIAR two-source isotopic mixing model.

Whitefish showed increased δ^{15}N values with increasing total length, but no similar trend was seen in charr (Table 9, Figure 17). According to the coefficient of determination, the length of whitefish explained 87 % of the variation in the δ^{15}N values of muscle tissue.

Total length of a fish had no impact on the $\delta^{13}C$ values of charr or whitefish (Table 9, Figure 17).

Table 9. Linear regression model between the total length and $\delta^{15}N$ and $\delta^{13}C$ values of charr and whitefish from Skaidijärvi.

Lake	Species	Linear regression	R^2	F	p
Skaidijärvi	Charr	$\delta^{15}N = 6.89 - 0.005 \times length$	0.15	12.49	0.001
	Whitefish	$\delta^{15}N = 5.76 + 0.007 \times length$	0.87	232.5	< 0.001
	Charr	$\delta^{13}C = -25.84 + 0.003 \times length$	0.03	2.28	0.136
	Whitefish	$\delta^{13}C = -27.70 + 0.001 \times length$	0.01	0.46	0.502
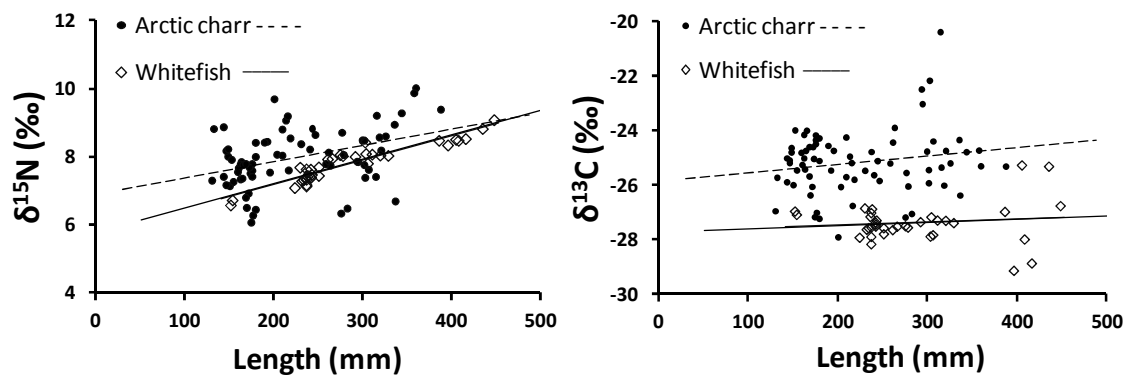
Figure 17. The $\delta^{15}N$ (left) and $\delta^{13}C$ values (right) of Skaidijärvi charr (N = 73) and whitefish (N = 36) as a function of total length (mm).

In Skaidijärvi, the calculated convex hull areas indicated that 95 % of the individual charr isotope values covered an area over twice that for whitefish (Figure 18). Charr had an isotopic niche area of 8.4 ‰^{2} and whitefish an area of 3.3 ‰^{2}. Distinct isotopic niche segregation between the species was evident as there was only a slight overlap in the delineated convex hull areas. Charr were clustered to more littoral niche (higher $\delta^{13}C$ values) and were also able to occupy higher trophic positions (higher individual $\delta^{15}N$ values) in the lake than whitefish (Figure 18).
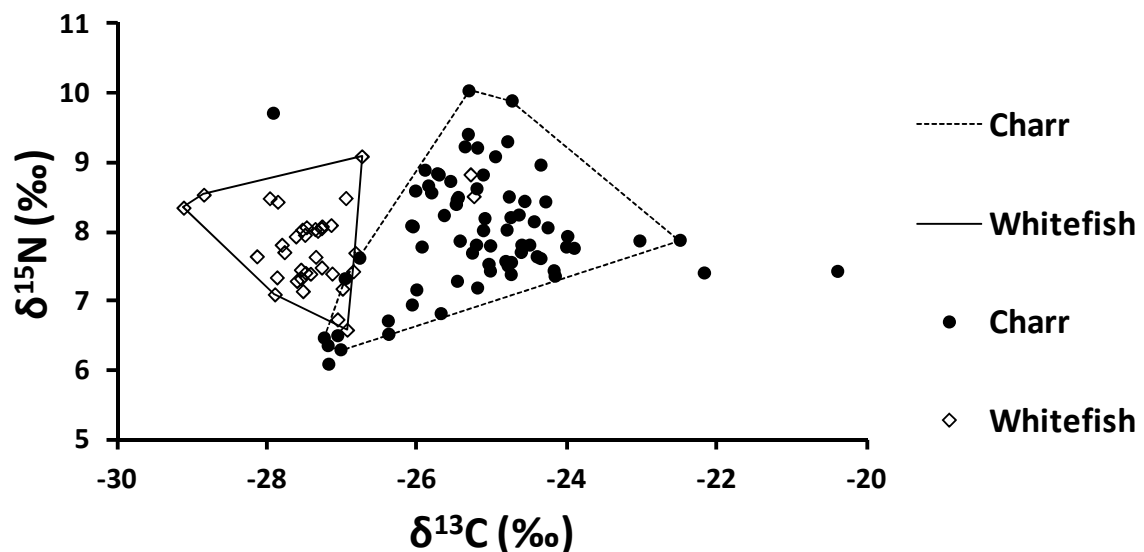
Figure 18. Calculated convex hull areas (lines) in $\delta^{13}C – \delta^{15}N$ bi-plot space delineating 95% of individual charr and whitefish from Skaidijärvi.

4. DISCUSSION

4.1 Diets of charr, lake trout and whitefish

The results of stomach contents analysis showed that the similar sized large charr and lake trout had rather similar diets in Inarijärvi, as the 73% dietary overlap between them can be considered biologically significant (Wallace 1981). However, lake trout had used a more diverse set of prey items and relied more on littoral prey than large charr, which gained most of its energy from pelagic resources. In turn, small charr seemed to rely on littoral resources even more than lake trout and had the most versatile diet of the three groups, indicated by the high Levin's index and by the rather wide isotopic niche. The results of stable isotope analysis revealed that overall, there is a dietary overlap between Inarijärvi charr and lake trout. Having the widest isotopic niche, lake trout seems to compete with both small and large charr. However, it is also possible that no real competition occurs in Inarijärvi as small populations of two different species may be able to use the same food resource to some extent, if the resource is very abundant. Vendace can be abundant in Inarijärvi, even though yearly fluctuations in the population size can be large (Salonen 1998). According to the Finnish Game and Fisheries Research Institute, the total catch of charr has decreased by over two-fold after water regulation started in the 1940s. Thus, nowadays the charr population is much smaller than it used to be and the abundant prey populations can therefore possibly also support a small population of overlapping species, such as lake trout.

In Skaidijärvi, the results of stomach contents and stable isotope analysis showed that charr and whitefish clearly had different trophic niches. Distinct resource partitioning can be seen as charr had specialized in foraging on three-spined sticklebacks, *Gammarus* sp. and trichopterans, whereas whitefish consumed zooplankton and chironomids. This niche segregation between charr and whitefish could be a sign of low competition as the species are feeding on different prey items, but may equally be a sign of severe competition which has led to the niche segregation; according to this study, the latter is the more probable option. Despite the zooplanktivory of whitefish, both species seemed to rely heavily on the littoral production. Calculated convex hull areas showed that charr had much wider isotopic niche than whitefish but according to Levin's index, whitefish had a larger dietary niche. This apparent contradiction could arise because stomach content analysis tends to be only a snapshot of the dietary behaviour of an organism, whereas the isotope values reflect a longer period of time. Thus, charr seemed to generally have a wider dietary niche than whitefish in Skaidijärvi.

The traditional view has been that under competition charr is dominated by whitefish and is forced to shift its trophic niche from the littoral to the pelagic or profundal niche (Svärdson 1976). As Skaidijärvi is such a shallow lake that there is virtually no profundal or true pelagic habitat available, it is impossible for charr to find a habitat refuge there. Therefore it is not surprising that after the introduction of whitefish, the charr stock almost vanished from Skaidijärvi (Jarmo Huhtamella from Metsähallitus, pers. comm.), indicating that the two fish species had generally used the same trophic niche. The energy source of charr in Skaidijärvi did not seem to differ from certain lakes where it is the only species present, or co-occurs only with a small prey-fish. In the nine study lakes of Karlsson & Byström (2005), charr occurred as the only species present or in sympatry with nine-spined stickleback, so the species composition in these lakes was rather similar to that in Skaidijärvi before the introduction of whitefish. Karlsson & Bysröm (2005) observed that littoral zoobenthos and small sticklebacks, when available, were the main energy source for charr in their study lakes. Also in Lake Saanajärvi (hereafter Saanajärvi), zoobenthos

dominated the charr diet, even though some dietary shifts occured depending on the seasonal availability of different prey items (Eloranta *et al.* 2010). There, charr was almost the only species present, co-occurring with only a few brown trout. However, the composition of zoobenthos which charr utilize in Saanajärvi differs from Skaidijärvi. In Saanajärvi, chironomids were common in the charr diet (Eloranta *et al.* 2010), whereas in Skaidijärvi they were hardly used by charr, instead being one of the main prey items of whitefish. Thus, charr has apparently survived in Skaidijärvi by switching its diet to prey items which are not used by whitefish (eg. *Gammarus* sp.). Possibly the availability of small fish prey, three-spined stickleback, is also an important factor in supporting the charr stock, as observed by Eloranta *et al.* (2011). All in all, coexistence of charr and whitefish seems to be possible in Skaidijärvi. It is supported partly by dietary segregation, but also with supplementary stocking of charr from nearby lakes and intensive fishing to reduce the whitefish population of the lake (Jarmo Huhtamella, Metsähallitus, pers. comm.).

In general, there is great variation in the feeding behaviour between different charr populations (Klemetsen *et al.* 2003). Charr is able to utilize all major lake habitats and feed on a wide range of prey types, including zooplankton, zoobenthos, surface insects and fish (Johnson 1980, Klemetsen *et al.* 2003). When in sympatry with other fish species, this potentially wide trophic niche of charr is typically restricted due to interspecific competition. For example, dense populations of burbot can restrict charr from using the profundal zone and in the presence of this profundal predator and competitor for zoobenthos, charr feeds mainly on pelagic zooplankton (Knudsen *et al.* 2010). Eutrophication and negative interactions with roach have had an impact on charr population of Lake Windermere, England, where charr has switched its diet from zooplanktivory towards benthivory since the 1950s (Corrigan *et al.* 2011). Generally, in the presence of strong benthivorous competitors (e.g. brown trout) charr often becomes a pelagic zooplantivore (e.g. Langeland *et al.* 1991, Hesthagen *et al.* 2011), but in co-occurrence with planktivorous competitors (e.g. whitefish), charr commonly avoids the pelagic habitat and becomes benthivorous or piscivorous (e.g. Svärdson 1976, Amundsen *et al.* 2010, Eloranta *et al.* 2011). Invasion of pike to small subarctic lakes can lead to total extirpation of charr populations through predation and competition (Byström *et al.* 2007). These trophic niche restrictions of charr due to competing species can also be seen in the present study. In both study lakes, charr feeds mainly on zoobenthos and fish, as the more efficient zooplanktivore, whitefish is abundant. Furthermore, also brown trout exists in Inarijärvi and is more abundant than charr and lake trout (Salonen *et al.* 2010). The presence of brown trout may limit the use of littoral habitat of charr (Langeland *et al.* 1991) and large brown trout may exhibit a predatory impact on juvenile charr (L'Abée-Lund *et al.* 1993). It is also likely that piscivorous brown trout competes from the same pelagic prey with charr and lake trout to some extent (Kahilainen & Lehtonen 2003).

Juvenile charr are usually epibenthic zoobenthivores which may also utilize pelagic zooplankton at a certain size (L'Abée-Lund *et al.* 1993, Jonsson & Jonsson 2001, Klemetsen *et al.* 2003). Charr commonly start to become piscivorous at a length of 200 mm and the proportion of piscivorous fish increases with increasing body size (L'Abée-Lund *et al.* 1992, Amundsen 1994). These observations seem to apply to both lakes of this study where charr are mainly benthivorous and become piscivorous when they have reached a certain size threshold. In Inarijärvi, charr showed a clear ontogenetic shift from macroinvertebrate based diet towards piscivory after reaching 150 mm in the length. The smallest charr that had included fish (nine-spined sticklebacks) in its diet was as small as 130 mm in length. $\delta^{13}C$ values of Inarijärvi charr started changing towards the pelagic values between the lengths of 200–300 mm indicating a change from littoral to more

pelagic prey items, such as *Coregonus* sp., which is the main prey for charr also in subarctic Lake Muddusjärvi, Finland (Kahilainen & Lehtonen 2003). In Skaidijärvi, the smallest piscivorous charr was 259 mm in length and a clear ontogenetic shift from macroinvertebrate dominated diet to piscivory (three-spined sticklebacks) occurred when the fish reached a length of 250–300 mm. For comparison, in Loch Ericht, Scotland, charr switches to piscivory at an average fork length of 165 mm (Fraser *et al*. 1998, McCarthy *et al*. 2004) and in Lake Muddusjärvi, Finland, charr shift to piscivory at a length of 257 mm (Kahilainen & Lehtonen 2003).

The diet of lake trout in Inarijärvi is quite typical for the species. In large lakes with pelagic prey fish species, it is often piscivorous (Vander Zanden & Rasmussen 1996, Madenjian *et al*. 1998), but the small individuals (< 200 mm) may also utilize zoobenthos, e.g. *Mysis* sp. (Madenjian *et al*. 1998). In lakes which lack pelagic prey, lake trout can also consume substantial amounts of fish from littoral habitats (Vander Zanden & Rasmussen 1996). In Inarijärvi, lake trout seems to consume mainly these littoral resources, but according to δ^{13}C values and stomach content analysis, the diet changes towards pelagic *Coregonus* sp. prey with increasing length.

Earlier studies have shown that the diet of whitefish partly depends on whether it is in allopatry or in sympatry with other whitefish forms (Kahilainen *et al*. 2004, Harrod *et al*. 2010). When in sympatry with a more efficient zooplanktivorous (i.e. the densely-rakered morph, DR) morph the niche of the common large sparsely rakered (LSR) morph is restricted to the littoral habitat and to foraging mainly on zoobenthos such as chironomid larvae, Trichoptera, Ephemeroptera, *Sialis* sp., *Valvata* sp., *Lymnaea* sp. and also epibenthic *Eurycercus* sp. (Amundsen *et al*. 2004, Kahilainen *et al*. 2004, Harrod *et al*. 2010). In monomorphic (LSR) whitefish populations, whitefish commonly uses all available habitats and feeds mainly on pelagic zooplankton, although zoobenthos can also be important in the diet (Amundsen *et al*. 2004, Kahilainen *et al*. 2004, Harrod *et al*. 2010). In two subarctic lakes in Finland, Lake Kilpisjärvi (max. depth 57 m), and Lake Vuontisjärvi (max. depth 31 m), the contributions of pelagic prey in the diet of monomorphic whitefish, given by the SIAR model, were 60 % and 56 %, respectively (Harrod *et al*. 2010). In contrast to these findings, the monomorphic whitefish population in Skaidijärvi relied mainly on littoral production, but this is probably due to the small water volume available for pelagic production compared to the two rather deep lakes.

4.2 Coupling between littoral and pelagic food webs

In Inarijärvi, charr seemed to rely on both pelagic and littoral energy sources, whereas the littoral food web clearly dominated the energy mobilization to charr in Skaidijärvi. This is not surprising because large lakes tend to have low perimeter-to-area ratios (P/A) and therefore the relative importance of benthic and littoral habitats is not as high as in small lakes (Vander Zanden & Vadeboncouer 2002). The strong reliance of top consumers on littoral production in small Arctic and subarctic lakes, such as Skaidijärvi, has been also shown in previous studies (Sierzen *et al*. 2003, Karlsson and Byström 2005, Eloranta *et al*. 2010). Due to their high mobility, fish can feed on prey items from both littoral and pelagic food webs, thereby linking these systems (Vander Zanden & Vadeboncouer 2002). It seems that charr and lake trout may play an important role as a habitat and food web couplers in Inarijärvi, which can have profound effects on the stability of food webs through important outcomes in nutrient cycling and in predator-prey dynamics (Schindler & Scheuerell 2002). All the lake trout and small charr were caught from the profundal zone, but had mainly relied on littoral energy sources, which indicates that the fish have moved between these two habitats. Small and shallow lakes tend to have

the strongest coupling between littoral and pelagic habitats (Schindler & Scheuerell 2002). However, the strong reliance of Skaidijärvi charr on littoral resources indicates a low degree of habitat coupling and that the charr individuals have specialized to feed particularly on the littoral prey items. Specialized fish individuals tend not to change their prey types and habitat, resulting in a low degree of habitat coupling (Quevedo *et al*. 2009). Moreover, one reason for low degree of habitat coupling in Skaidijärvi may be the fact that it consists of only one principal habitat type. Despite of that, food web coupling seems evident for the whitefish of Skaidijärvi, which gets its energy from both pelagic and littoral food webs.

McCann *et al*. (2005) compared lake trout lakes with sizes ranging from few hectares to over 50 000 km^2. They found that the trophic position of lake trout increased with increasing lake size from 3.5 to 4.5 and argued that the increase in trophic position resulted from decreased omnivory. Lake trout in small lakes can impose a stronger top-down pressure, which may lead to scarcity of favorable prey items and increasing omnivory as a result. For example, benthic habitats can provide alternative resources which can maintain pelagic planktivore or piscivore populations once they have eaten their preferred prey items to low densities or even to local extinction (Schindler & Scheuerell 2002). McCann *et al*. (2005) suggested that top consumer movement between food webs may begin to increase below the lake size of 129 km^2 by driving greater top-down pressure and thus increasing the tendency for omnivory. In small lakes, lake trout consumes more benthos and zooplankton, and fish make up a smaller proportion of their diet than in large lakes (Vander Zanden & Rasmussen 1996; Vander Zanden *et al*. 1999). These findings seem to correspond to charr in this study, as the mean trophic position of charr in large Inarijärvi was approximately one level higher than in small Skaidijärvi (i.e. 4.4 and 3.1, respectively). Also the size of charr in Inarijärvi and Skaidijärvi differed from each other quite significantly. It seems that in Inarijärvi, charr reaches larger sizes compared to charr in Skaidijärvi. A probable reason for this is a high availability of proper small-sized prey fish species which can support the piscivory of charr. In Skaidijärvi, charr clearly rely more on littoral resources than in Inarijärvi, which is probably due to size differences between the lakes. In Inarijärvi, which has a greater depth, larger surface area and a profitable pelagic prey item for charr, littoral production is generally not as important an energy source to top consumers as it is in small and shallow Skaidijärvi.

4.3 Growth differences

In both study lakes, the introduced competitor had faster growth rate than the native charr, which could mean that in general they are competing more effectively on the limited resources. Earlier studies have shown that introduced species can have negative effect on the growth of native species by causing trophic niche shifts and being more effective on the utilization of available food resources (Marchetti 1999, Baxter *et al*. 2007). Thus, it is possible that the growth of Skaidijärvi charr has decelerated after the introduction of whitefish. The faster growth rate of whitefish may indicate that it is dominating over the preferred food resources, but according to the gillnet catch, charr seems to dominate in quantity. However, the latter may be a result of the supplement stocking and intensive fishing for whitefish. In a more complex fish community of Inarijärvi with many interacting species, the rather slow growth of charr may be caused due to a high rate of interspecific competition in the first two years of life. The growth clearly improves after the age of 2, when charr reaches the length of 150 mm. After reaching this size threshold, charr may shift from macroinvertebrate based diet towards piscivory. There seems to be a high pressure to switch to piscivory because as small charr as 130 mm had already

consumed fish. Lake trout of Inarijärvi are of stocked origin and have spent their first couple years in aquacultural conditions with constant food supply, thereby growing fast. Their faster growth rate is therefore not necessarily caused by a competitive advantage. Another problem arising from the stocked origin of lake trout is that if they were caught quickly after the stocking, their isotope values could have been biased, as they might still reflect the food that they had utilized in the fish farm. The significant difference in the isotopic values of small and large charr could also be due to this reason, as small charr may have been stocked to the lake recently before being caught. In any case, it should be kept in mind that similarity of isotopic values does not necessarily mean ecological similarity. Two individuals may have the same isotopic niche but different ecological niches as different source pools can be characterized by similar stable isotope values even though the trophic pathways that support the two individuals are different (Layman *et al.* 2011).

4.4 Future prospects for fish introductions in northern Finland

Stocking programs have been a common and widespread practice of fishery management in Finland. In Inarijärvi, as in most other cases, introduction of lake trout has been intentional as a part of stocking program intended to enhance and diversify aquatic communities for fishing (Salonen & Mutenia 2007). However, these introductions of non-native species to Finnish waters may have strong ecological and genetic effects on the native fish populations and should be always considered with caution. For example, introduced brook trout (*Salvelinus fontinalis* Mitchill) has established populations in the headwaters of the Kemijoki river system, partly displacing the native brown trout population in this area (Korsu *et al*. 2007). Krueger & May (1991) noted that introductions may alter the community structure and cause native species to be eliminated, show changes in their survival and growth, or be genetically changed. An actual outcome of an introduction may also be a combination of the above-mentioned factors or not show any detectable changes (Krueger & May 1991). In the long term, success of an invader depends on its physiological and life history requirements, and the characteristics of the system being invaded (Moyle & Light 1996). In aquatic systems with intermediate levels of human disturbance, any species with the right physiological and morphological characteristics can become established (Moyle & Light 1996). As characteristics of charr and lake trout are rather similar (e.g. Johnson 1980, Martin & Olver 1980), the stockings in Inarijärvi might eventually lead to establishment of a spawning lake trout population. In certain Arctic lakes in Alaska, where charr and lake trout naturally co-occur, displacement of charr by lake trout seems to occur, but over a much longer time scale than with management introductions (Hershey *et al*. 1999). Therefore, Hershey *et al*. (1999) suggested that lake trout introductions to charr lakes should not be initiated at all in the Alaskan Arctic. In Inarijärvi, which is already a heavily modified system with three introduced fish species, water level regulation and extensive stocking of different predatory salmonids, it is hard to distinguish possible negative interactions on charr caused only by lake trout. However, it is clear that they have largely overlapping diets, and theoretically, when two species have the same niche, one species will likely exclude the other (Hardin 1960). This can happen over time, but in Inarijärvi it seems unlikely, so long as both species continue to be supported by extensive stocking. A high proportion of the total catch of all predatory salmonids from the lake is stocked origin (Salonen *et al*. 2010). Moreover, no natural spawning of lake trout has been observed and none of the lake trouts examined for this study were sexually mature, but this does not exclude the possibility that some natural spawning may occur. Nevertheless, according to present knowledge, charr would most likely become the only species left of the two over time if the stocking of lake trout would be discontinued.

However, if spawning of lake trout does occur in Inarijärvi, interspecific mating would be a possible threat to the native charr. Natural hybridization between these species occurs in the Canadian Arctic and also limited transfer of lake trout mtDNA into charr populations through introgression have been observed (Wilson & Hebert 1993). Hybrids are ordinarily a result of matings between charr males and lake trout females, which is likely due to the earlier maturation of charr males (Wilson & Hebert 1993). Charr males mature earlier than charr females (Johnson 1980), so it is possible that charr males mistakenly spawn with lake trout females if they happen to be in the same spawning grounds with charr females not yet present. Introgression means gene flow from the gene pool of one species into the gene pool of another species (Krueger & May 1991). Native species have evolved and adapted to their own particular niche and a large amount of gene flow from another species may disrupt their adaptive gene complexes (Krueger & May 1991).

Distinct resource partitioning between charr and whitefish has been also observed in earlier studies. Charr and whitefish coexist together with grayling in Lake Biggijavri, Norway (max. depth 49 m; Amundsen *et al*. 2010). There, whitefish was the most numerous in all lake habitats and fed on small planktonic (*Bosmina* sp., *Daphnia* sp.) and benthic (*Eurycercus lamellatus*) crustaceans. In contrast, most charr were found to feed on insects and snails (especially *Lymnea* sp.) in the littoral zone. Despite the resource partitioning, Amundsen *et al*. (2010) concluded that the restricted trophic niche of charr implies a strong competition from whitefish, and that the presence of grayling might facilitate their coexistence through a competitive impact on the whitefish. Segregation in diet and habitat use between charr and whitefish was also observed in a study of five different Norwegian lakes (Sandlund *et al*. 2010). These study lakes were very deep compared to Skaidijärvi with maximum depths ranging from 58 m to 309 m. In all lakes, whitefish were more common in the littoral and near-surface pelagic zones, whereas charr occupied deeper waters. Both species were mainly zooplanktivores but their diets differed in terms of the zooplankton species eaten. For example, charr fed on *Daphnia* sp. and *Bythotrephes longimanus*, while whitefish utilized *Bosmina* sp., *Holopedium gibberum*, *E. lamellatus* and zoobenthos. The results from Sandlund *et al*. (2010) support Svärdson's (1976) proposition that the availability of deep profundal habitat is important for the coexistence of charr and whitefish. In two of their study lakes, charr were actually dominant over whitefish. In these lakes, the littoral zone had been rendered inaccessible to whitefish by competing and predating species (i.e. perch) and water level regulations. Thus they concluded that, whereas availability of profundal habitat zone is important for charr, availability of proper littoral habitat zone is important for whitefish (Sandlund *et al*. 2010). In Skaidijärvi, which has no profundal habitat for charr but instead an extensive littoral habitat, a probable reason for their coexistence is the intensive fishing for whitefish, which is acting as a disturbance factor by restricting the population growth of the species. Without intensive fishing for whitefish and supplementary stocking of charr, it would probably be difficult for the charr population to persist in Skaidijärvi.

In the future, increased understanding of fish interactions can have implications for fishery management in areas where non-native species have been deliberately introduced into aquatic ecosystems. Contrary to the belief that introductions represent a form of fishery enhancement, attention should be drawn to the possible adverse competitive impacts of introduced fish to native fish populations. Even though charr seems to survive with whitefish in Skaidijärvi, further introductions of whitefish to charr lakes should not be made. Continued stocking of non-native salmonids, such as lake trout in Inarijärvi, should not be implemented if the fish have direct access and contact with native salmonid

populations. These introductions always pose high and unpredictable ecological and genetic risks. If there is a need for fishery management to implement supplementation programs to enhance the fish populations, then local stocks of native species should be used.

4.5 Limitations of the study

Sample material for this study was not collected by the author and therefore it was not possible to influence the sampling. In an optimal scenario, data would have been sampled before and after the introduction of a new species. This way it would have been easier to distinguish the impacts (e.g. a trophic niche shift) that fish introductions have possibly caused to native charr populations in Inarijärvi and Skaidijärvi. As a before-after situation was not available as a research framework, the interpretation of the results is challenging.

The sample material from Inarijärvi was collected with different sampling strategies as all lake trouts and most of the large charr were obtained from the fisherman, Tapio Aarnipuro, and the charr of Nanguvuono were caught by a research group. The size distributions of species also differed quite a lot as no small lake trouts were caught, due to the stocked origin of the species. The size distribution of charr and whitefish differed in Skaidijärvi, too. In the best case, more similar size distributions of the different species would have been sampled from both lakes.

It is known that charr can exhibit distinct seasonal variations in its feeding ecology (Amundsen *et al*. 2008, Amundsen & Knudsen 2009, Amundsen *et al*. 2010, Eloranta *et al*. 2010, Sandlund *et al*. 2010). It was not possible to take these seasonal variations into account in this study, as the samples were collected only in the autumn.

5. CONCLUSIONS

The results of this study show dietary and isotopic niche overlap between charr and lake trout in Inarijärvi, indicating that the species are competing for the same resources. Both species were piscivorous and large individuals (> 280 mm) had been feeding almost exlusively on pelagic *Coregonus* sp. Small individuals (< 280 mm) of charr consumed mainly zoobenthos and nine-spined sticklebacks. Continuous stocking of both charr and lake trout is maintaining their populations in Inarijärvi and therefore the impacts of the apparent interspecific competition are difficult to interpret. Nevertheless, it is possible that the abundant prey fish populations are able to support the coexistence of lake trout and the reduced population of charr. In Skaidijärvi, both stable isotope and stomach contents analysis revealed a distinct resource partitioning. There, charr foraged on three-spined sticklebacks, *Gammarus* sp. and trichopterans, whereas whitefish consumed zooplankton and chironomids. A probable reason for this niche segregation is interspecific competition between the species. Charr seems to have survived in the lake by switching its diet to prey items which are not used by whitefish. Thus, coexistence of charr and whitefish in Skaidijärvi may be partly facilitated by the dietary segregation and the availability of profitable small prey fish, but intensive fishing for whitefish and supplementary stocking of charr are likely to be important factors as well.

In Inarijärvi, the main energy flow pathway for small charr (< 280 mm) and lake trout was the littoral food web, whereas large charr (> 280 mm) relied slightly more on pelagic production. In Skaidijärvi, both charr and whitefish relied on the littoral production. The introduced competitor had a faster growth rate than the native charr in

both study lakes, indicating a more effective utilization of the limited resources. However, the faster growth rate of lake trout in Inarijärvi may be partly a result of the aquacultural origin of the species.

Ecological and genetic risks should always be taken into account with fish introductions and native stocks should be favoured in the stocking programmes. Introductions of non-native species may increase the competitive interactions in charr lakes and thereby be a risk to charr populations in the future. More information and research is needed on the spawning behaviour of lake trout in Inarijärvi. Is it really true that the species does not reproduce in the lake after 40 years of stocking?

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Appendix 1. δ^{13}C and δ^{15}N values of the organisms used to calculate littoral (Littoral zoobenthos) and pelagic (Zooplankton) baselines of Inarijärvi.

Sampling method	Depth	Organism	δ^{13}C	δ^{15}N	Sampling method	Depth	Organism	δ^{13}C	δ^{15}N
Ekman	1 m	**Littoral zoobenthos**			Kick net	0–1 m	**Littoral zoobenthos**		
		Plecotera	-19.0	1.8			Dytiscidae adult	-25.3	4.5
		Asellus aquaticus	-21.4	2.4			Dytiscidae larva	-26.0	4.9
		Pisidium sp.	-14.0	2.0			*Eurycercus* sp.	-25.0	2.0
		Megacyclops	-22.0	5.3			*Lymnaea* sp.	-23.9	2.2
		Hirudinea	-21.0	1.6			Plecoptera	-30.2	1.8
		Hydracarina	-20.8	4.2			Tabanidae	-30.3	3.9
		Ostracoda	-12.0	5.7			*Asellus aquaticus*	-27.0	2.9
		Eurycercus sp.	-17.9	1.5			*Gammarus lacustris*	-23.4	3.0
		Chironomidae	-20.7	3.6			*Aranea* sp.	-26.7	7.4
		Oligochaeta	-22.5	2.8			*Gordius* sp.	-25.0	6.0
		Trichoptera	-20.6	3.0			Corixidae	-30.7	3.4
		Gammarus lacustris	-19.6	2.8			Trichoptera	-28.2	3.0
	2 m	Hydrachinidia	-21.3	3.9			Chironomidae	-27.3	4.2
		Chironomidae	-19.8	3.7			Megacyclops	-25.6	5.5
		Megacyclops*	-23.9	5.7			Ephemeroptera	-29.3	2.5
		Eurycercus sp.	-20.1	0.8			Hydracarina	-26.6	4.5
		Trichoptera	-23.9	4.7			Oligochaeta	-27.6	2.8
		Ephemeroptera	-20.7	1.7			**MEAN value**	**-23.2**	**3.5**
		Oligochaeta	-20.5	4.1					
		Gammarus lacustris	-19.8	2.4	Plankton net	20–0 m	**Zooplankton**		
		Asellus aquaticus	-20.4	2.3			Copepoda	-31.9	4.5
	3 m	*Gammarus lacustris*	-24.4	3.5			Cladocera	-30.1	3.0
		Oligochaeta	-23.4	3.8			Mixture	-30.9	3.7
		Chironomidae	-23.5	3.1			**MEAN value**	**-30.1**	**3.7**
		Eurycercus sp.	-23.6	2.1					
		Hydrachinidia	-23.2	6.5					
		Trichoptera	-23.6	3.8					

* Combined from 2 m and 3 m to obtain sufficient sample size.

Appendix 2. δ^{13}C and δ^{15}N values of the organisms used to calculate littoral (Littoral zoobenthos) and pelagic (Zooplankton) baselines of Skaidijärvi.

Sampling method	Depth	Organism	δ^{13}C	δ^{15}N
Ekman	1 m	**Littoral zoobenthos**		
		Gammarus sp.	-26.9	1.8
		Chironomidae	-23.6	3.6
	2 m	*Gammarus* sp.	-28.8	3.4
		Trichoptera	-28.1	5.1
		Eurycercus sp.	-27.5	3.5
		Megacyclops	-26.9	6.0
		Chironomidae	-27.8	4.0
		Hirudinea	-26.9	7.1
	3 m	Chironomidae	-28.4	4.6
		Eurycercus sp.	-28.1	3.6
		Hirudinea	-27.7	7.6
		MEAN	**-27.3**	**4.6**
Plankton net	5–0 m	**Zooplankton**		
		Mixture	-31.2	5.3
		Large Copepods	-30.0	6.1
		Cyclopoida	-31.9	5.3
		Cladocera	-30.6	3.4
		MEAN	**-30.9**	**5.0**