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Feeding strategies and resource partitioning of whitefish (*Coregonus lavaretus*) and perch (*Perca fluviatilis*) in the Pasvik watercourse

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Abstract

Interspecific competition for resources is, alongside abiotic factors like climate and geography, a very important factor in shaping communities. Since competition is difficult to prove directly, resource partitioning is frequently used as an indication of the presence of interspecific competition. Over the last 20 years perch abundance in the Pasvik watercourse has increased immensely, presumably because of a rise in water temperature. In this study resource partitioning and feeding strategies of sympatric large sparsely rakered (LSR) whitefish (*Coregonus lavaretus*) and perch (*Perca fluviatilis*) in the littoral zone of two lakes in the Pasvik watercourse were studied. Stomach content and stable isotope ($\delta^{13}C$ and $\delta^{15}N$) analyses were done to determine short- and long-term diets, respectively, of all four populations. In both lakes, Perch had a generalist population diet with some specialization on the individual level, and showed clear ontogenetic niche shifts. Small perch were specialized on relatively small invertebrates (crustaceans), intermediate sized perch had a more generalist diet consistent of larger invertebrates and fish, while the largest perch were specialized piscivores. LSR whitefish displayed a population specialization in molluscs. Therefore, the diet overlap between LSR whitefish and perch in Lake Tjærebukta was only 12%. Isotopic niche overlap was low as well (20.6%). In contrast, in Lake Skrukkebukta the diet overlap between the two species was relative high (53%). Overlap in isotopic niches was similar (48.5%). Here LSR whitefish had a more generalist feeding strategy at both population and individual level. In addition they had an ontogenetic shift in diet as LSR whitefish <250 mm had a mixed diet of small *Eurycercus lamellatus*, molluscs and insect larvae, while larger LSR whitefish had a diet dominated by different species of larger insect larvae. The low overlaps in diet and isotopic niches were a good indication of clear resource partitioning on both short- and long-term, between LSR whitefish and perch in the two study lakes. A difference in feeding strategies and ontogenetic dietary niche shifts of perch likely strengthened the resource partitioning in both lakes. The resource partitioning was more intense in Lake Tjærebukta, where perch has been present in high abundance for over a longer period than in Lake Skrukkebukta. Longstanding interspecific competition between perch and LSR whitefish in Lake Tjærebukta could have caused the distinct resource partitioning, while in Lake Skrukkebukta this process is likely still on-going, and has not fully established yet. If perch spreads to more areas/increases in density because of climate change, this might have a distinct effect on other whitefish populations as well.

Introduction

Interspecific competition for resources is, alongside abiotic factors like climate and geography, a very important factor in shaping communities (Connell 1980, Tilman 1982, Roughgarden and Diamond 1986, Amarasekare 2009). When two or more coexisting species utilize the same limited set of resources, exploitative interspecific competition can occur, negatively affecting both species. When conspecifics utilize the same limited resources, intraspecific competition can occur (Wootton 1999, Molles 2002). Every population and each individual in a population has a set of resources that they could potentially exploit. This is the broadest possible dietary niche of a population or an individual, their fundamental niche (Hutchinson 1957). In most cases a population or individual will utilize a subset of this possible diet, this is the realized dietary niche (Hutchinson 1957, Stephens and Krebs 1986, Stephens et al. 2007). Inter- and intraspecific competition for resources are important factors in determining which resources are a part of the realized dietary niche (Stephens and Krebs 1986, Stephens et al. 2007, Araújo et al. 2011).

Interspecific competition for resources, as a result of a high dietary niche overlap between two or more species can eventually lead to the competitive exclusion of one of the species (Hardin 1960). A separation of species along complementary resource dimensions can reduce this competition. For example, if two species live in the same habitat, there is likely to be a separation in food type use (dietary niche) between them. In such a case the realized niche of one or both species will be narrowed or shifted (Schoener 1974, Pianka 1994), thereby avoiding competitive exclusion between two or more species (Schoener 1974, 1986). Shifts in resource utilization behavior can include changes in the choice of prey type, feeding strategies and habitat. This separation in dietary niche is called resource partitioning (Schoener 1968, 1974). Resource partitioning between two or more coexisting species can be commonly seen in marine and freshwater fish communities (Ross 1986). Since competition is very difficult to prove directly, the presence of resource partitioning is frequently used as an indication of the presence of interspecific competition (Schoener 1974, Nilsson 1978, Ross 1991).

However, resource partitioning need not be a consequence of competition. Other reasons for this phenomenon could be physiological restraints to certain physical-chemical variables, tolerance to environmental change, predation risks and prey availability (Schoener 1974, Ross

1986). Unfortunately, it is difficult to distinguish between these causes in field studies, and even in experimental studies (Schoener 1974).

Populations and individuals can exhibit multiple feeding strategies. Generalist feeders have no specific preference for a certain food source and therefore have a broad dietary niche (Schoener 1971, 2009, Gerking 1994a, Pianka 1994). Specialist feeders concentrate all their efforts on utilizing a specific prey type or types, and therefore have a narrow dietary niche (Gerking 1994a, Schoener 2009). A generalist population can be made up of individuals that are generalists (broad individual niche), and/or individuals that utilize a subset of the population diet (narrow individual niche), and therefore are individual specialists (Giller 1984, Amundsen 1995, Schoener 2009). As well as being either generalist or specialist feeders, most fish species are also opportunistic feeders (Gerking 1994a). Intra- and interspecific competition can influence the type of feeding strategy a population or individual exhibits. According to general niche theory, high intraspecific competition can lead to a higher individual specialization, and an increase in the population dietary niche width (Bolnick et al. 2003, Svanbäck and Persson 2004, Araújo et al. 2011, Eloranta et al. 2013). High interspecific competition can lead to a specialization in diet of the population, and a decrease in the population dietary niche width (Pianka 1994, Putman 1994). Individual specialization may however remain unchanged. This specialization may lead to a decrease in interspecific diet overlap, illustrating how resource partitioning can be a consequence of competition.

Feeding strategies, the use of prey type and/or habitat often change with fish size. While fish larvae are very limited in which prey types they can utilize, bigger fish are often able to utilize larger, more energy rich and more diverse prey species (Gerking 1994b). These shifts between prey types, feeding strategies and/or habitat can be discrete or continuous over a fish's lifetime, and are known as ontogenetic niche shifts. These shifts increase energy intake and therefore maximize the growth rate of an individual, reducing the individual's risk of predation, and increasing its chances of survival (Werner and Gilliam 1984, Werner 1986). There are many examples of ontogenetic shifts in diet, feeding strategy and habitat in fish species (Werner and Gilliam 1984, Mittelbach and Persson 1998). Ontogenetic niche shifts can decrease dietary overlap, leading to an increased resource partitioning with other fish species (Werner and Gilliam 1984).

European whitefish (*Coregonus lavaretus* L., hereafter referred to as whitefish) and Eurasian perch (*Perca fluviatilis* L., hereafter referred to as perch) are common fish species in lake systems in northern Scandinavia (Tammi et al. 2003, Hayden et al. 2013, 2014). Whitefish is a highly plastic species occurring in various morphs (Svärdson 1979, Amundsen 1988, Siwertsson et al. 2010). The morphs differ in the number, length and width of their gillrakers, influencing which resources they are able to utilize and therefore the habitats that they can occupy (Amundsen 1988, Amundsen et al. 2004a). The most common morph is the large sparsely rakered (LSR) whitefish. This morph is known as a generalist that utilizes zoobenthos, such as molluscs, benthic crustaceans and insect larvae mainly in the littoral zone of lakes (Amundsen 1988, Amundsen et al. 2004b). Perch may occur in all lake habitats, but often prefers the littoral habitat (Amundsen et al. 2003, Hayden et al. 2014). Perch is typically considered a generalist and opportunistic consumer (Craig 1987, Hayden et al. 2014), being able to consume littoral, pelagic and profundal resources. Furthermore, perch is known to show clear ontogenetic niche shifts. Young fish utilize pelagic zooplankton, typically shifting to first zoobenthos and then fish, as they increase in size (Persson 1986, Craig 1987, Mittelbach and Persson 1998, Hjelm et al. 2000, Amundsen et al. 2003).

Historically, whitefish has been the most abundant fish species in all major lake habitats (i.e. littoral, pelagic and profundal) in subarctic lakes in the Pasvik watercourse (Amundsen et al. 1999, 2004a). However, recent findings in many watercourses in northern Scandinavia, including the Pasvik watercourse, demonstrate an increase in the density of percids in the littoral zone (Hayden et al. 2013, 2014, Ylikörkkö et al. 2015). This is suggested to be as a result of increased water temperature due to on-going climate change (Reist et al. 2006, Hayden et al. 2013, 2014). Since LSR whitefish and perch prefer the same lake habitat and may have similar dietary niches, there is a potential for interspecific dietary resource competition when these species live in sympatry. Subsequently, resource partitioning may be taking place in order to decrease this interspecific competition (Schoener 1974, 2009). Potential resource competition and resource partitioning between percids and whitefish have not often been studied. However, Hayden et al. (2013, 2014) recently studied the degree of dietary niche overlap between perch and LSR whitefish in other lakes in northern Scandinavia. Their results indicated some resource partitioning between LSR whitefish and perch in the littoral zone, by the utilization of different benthic prey species.

Both stomach content and muscle tissue stable isotopes (carbon and nitrogen) of LSR whitefish and perch from the littoral zone of two lakes in the Pasvik watercourse were analyzed to get an overview of the short- and long-term diet of both fish species. The aim of this study was to explore the feeding strategies and resource partitioning of sympatric LSR whitefish and perch. Therefore, I hypothesized that (1) there will be resource partitioning between LSR whitefish and perch, explaining their ability to coexist in the same habitat. (2) There will be differences in the feeding strategies of LSR whitefish and perch in the littoral zone, facilitating the potential resource partitioning between the two species. LSR whitefish will be generalists both at the population and individual level, while perch will be generalists at the population level and specialists at an individual level. Perch will in addition show clear ontogenetic dietary niche shifts. (3) The feeding strategies and resource partitioning of the two species will be similar in the two study lakes with relatively similar abiotic factors.

Material and methods

Study area description

The Pasvik watercourse (69 'N 30 'E) originates from the Finnish Lake Inari (1102 km^2) and separates Norway and Russia over approximately 120 km. The total catchment area is 18404 km^2, the total area of the Norwegian-Russian part of the watercourse is 142 km^2, and the mean water flow reaches about 175 m^3/s. The watercourse contains 7 hydropower dams, and therefore most of its rapids and waterfalls have disappeared. Present day, reservoirs and lakes dominate the river system. Even though there are many dams, the water level fluctuations remain small, usually less than 0.8 m. The ice-free season in the lakes and reservoirs lasts from May/June until October/November. In the last 15 years the water temperature has had a maximum of around 20°C in summer, but during most of the ice-free period it does not rise above 12°C. The lakes and reservoirs of the system are oligotrophic with some humic impacts, and the Secchi-depths range from 2 to 5 m. The geology in the region is dominated by gneiss bedrock. The catchment area is covered by birch- and pinewoods, intermingled with stretches of bogs. The annual mean air temperature is low with -0.3°C, and minimum and maximum monthly air temperatures are -13.5°C (February) and +14°C (July), respectively. There is low precipitation in the area, with an annual mean of 358 mm (Amundsen et al. 1999, 2003).

In this study, two lakes in the Pasvik watercourse were sampled. Lake Tjærebukta (69°13 'N 29°11 'E) in the upper part (hereafter referred to as Tjærebukta) and Lake Skrukkebukta (69°33 'N 30°7 'E) in the lower part of the watercourse (hereafter referred to as Skrukkebukta) (Figure 1). Tjærebukta has an area of 5.6 km^2, a mean depth of 4 m and a maximum depth of 30 m. It has an altitude of 52 m a.s.l. Skrukkebukta has an area of 6.6 km km^2, a mean depth of 14 m, and a maximum depth of 38 m. It has an altitude of 21 m a.s.l. (Amundsen et al. 1999, Kahilainen et al. 2011).

Figure 1 Part of the Pasvik watercourse (69 ‘N, 30 ‘E), with the sampled lakes Lake Tjærebukta and Lake Skrukkebukta.

Fish community

More than 15 fish species have been recorded in the Pasvik water system. The most common ones are (polymorphic) European whitefish (*Coregonus lavaretus*), vendace (*Coregonus albula*), Eurasian perch (*Perca fluviatilis*), northern pike (*Esox lucius*), burbot (*Lota lota*), brown trout (*Salmo trutta*), ninespine sticklebacks (*Pungitius pungitius*) and grayling (*Thymallus thymallus*) (Amundsen et al. 1999). Whitefish is a highly plastic species and can occur as various morphs within the same lake (Siwertsson et al. 2010). In the Pasvik watercourse there are three different whitefish morphs present (Siwertsson et al. 2010, Kahilainen et al. 2011). These include a large-sized sparsely-rakered morph (LSR), a densely-rakered morph (DR) (Amundsen et al. 2004a), and a smaller-sized sparsely-rakered morph (SSR) (Siwertsson et al. 2010, Kahilainen et al. 2011). The number and form of gillrakers reflect the diet of the different morphs and therefore their habitat. The long and dense gillrakers of the DR whitefish are especially functional for feeding on zooplankton and DR whitefish are therefore mostly found in the pelagic zone (Amundsen 1988, Amundsen et al. 2004a, Kahilainen et al. 2011), but they may also use the littoral zone (Amundsen et al. 1999). The LSR morph feeds mostly on zoobenthos (molluscs, benthic crustaceans and insect larvae), and is therefore mostly found in the littoral zone (Amundsen 1988, Amundsen et al. 2004a). The SSR morph feeds on soft zoobenthos like chironomids in the profundal zone of the lakes (Kahilainen and Østbye 2006). Vendace was introduced to Lake Inari in Finland around 1950/1960 and started spreading through the Pasvik watercourse around 1989 (Amundsen et al. 1999). Nowadays vendace has largely replaced DR whitefish as the dominant fish species in the pelagic habitat in most of the lakes in the watercourse (Amundsen et al. 1999, Gjelland et al. 2007, Bøhn et al. 2008, Sandlund et al. 2013).

Fish sampling

Fish sampling was carried out in September 2014. Gillnets were put out in Tjærebukta on the 10th, 11th and 14th of September and in Skrukkebukta on the 15th and 16th of September. The nets were set out in the littoral habitat of the lake (the area where the water column is less deep then the compensation depth) during the evening and taken out in the morning, approximately 12 hours later.

Benthic gillnets (1.5 m deep) of two types were used in the littoral zones; multi-mesh gillnets (bar mesh size 10, 12.5, 15, 18.5, 22, 26, 35 and 45 mm, 40 meter long) and standard size single mesh gillnets (30 m long). In Tjærebukta 11 multi-mesh gillnets and 10 standard sized single mesh gillnets were used (bar mesh size 28, 32, 34, 40, 42, 52 and 54 mm). In Skrukkebukta 7 multi-mesh gillnets and 15 standard sized gillnets were used (bar mesh size 24, 26, 32, 34, 40, 42, 52 and 54 mm). It is well known there is a catch size bias with the use of gillnets (Carol and García-Berthou 2007), but it was attempted to get a representative overview of the size distribution of the populations present in the lake.

Catches in the littoral zone included mostly perch and LSR whitefish, and some DR whitefish, SSR whitefish, pike, grayling, brown trout and burbot. Whitefish morphs were differentiated between by examining gill raker morphology (Amundsen et al. 2004a, Kahilainen and Østbye 2006). All fish species were examined, but for this study only the data from the LSR whitefish and perch, the two dominant species in the littoral habitat, were included. Fork length (mm) and weight (g) were measured and sex and stage (immature/mature) were determined. Thereafter the body cavities of both perch and LSR whitefish were opened and stomachs were taken out and stored in 96% ethanol until analyzed. Muscle samples for stable isotope analyses were taken and stored at -20 °C. The fish were divided into different length groups per lake and per species, dependent on the range of fork lengths found (Table 1, 2). These different groups were chosen to have enough fish in most of the groups for significant testing. The size groups were therefore different for stomach content analyses and stable isotope analyses (Table 2).

Table 1 Mean ±SD fork length (mm) of all LSR whitefish and perch used for this study (including fish with empty stomachs), caught in Lake Tjærebukta and Lake Skrukkebukta in September 2014. LSR whitefish in Tjærebukta had a larger fork length than in Skrukkebukta (Mann-Whitney U: U: 1342, N: 197, P = 0.000), while perch mean fork length did not differ between lakes.

	Mean	**Size range**
Tjærebukta		
LSR whitefish	311.4 ±67.4	176-480
Perch	201.0 ±71.2	79-315
Skrukkebukta		
LSR whitefish	236.3 ±45.9	146-442
Perch	190.9 ±63.9	80-325

Table 2 Fork length distribution and number (N) of **a.** LSR whitefish and **b.** perch caught in Lake Tjærebukta and Lake Skrukkebukta in September 2014, and the number of LSR whitefish and perch used for stomach content (SC) and stable isotope analyses (SI) (including fish with empty stomachs). Stippled lines are the separations for stable isotope data analyses groups.

a.

	Tjærebukta			**Skrukkebukta**		
Fork length (mm)	**N**	**N (SC)**	**N (SI)**	**N**	**N (SC)**	**N (SI)**
<150				1	1	1
150-199	4	4	3	19	19	7
200-249	13	13	13	48	48	18
250-299	31	19	13	21	20	10
300-349/≥300	28	22	18	7	7	4
350-399	17	15	13			
≥400	8	8	8			
Total	**101**	**81**	**68**	**96**	**95**	**40**

b.

	Tjærebukta			Skrukkebukta		
Fork length (mm)	**N**	**N (SC)**	**N (SI)**	**N**	**N (SC)**	**N (SI)**
<100	33	20	4	100	13	6
100-149	15	10	5	61	24	10
150-199	42	23	11	29	26	13
200-249	41	22	12	40	40	17
250-299	62	37	28	20	19	9
≥300	6	3	2	8	7	4
Total	**199**	**115**	**62**	**258**	**129**	**59**

Catch per unit effort

The catch per unit effort (CPUE) in number of fish per 100 m^2 multi-mesh gillnet per night for LSR whitefish and perch consisted of 6.4 LSR whitefish and 19.7 perch in Tjærebukta. In Skrukkebukta the CPUE for LSR whitefish was 10.7 and the CPUE for perch was 49.8. The percentages of perch in the littoral catches (all nets) were 64.4 % in Vaggatem (Tjærebukta and Ruskebukta) and 65.8% in Skrukkebukta. Both are in line with the increasing trend seen over the past years (Figure 2).

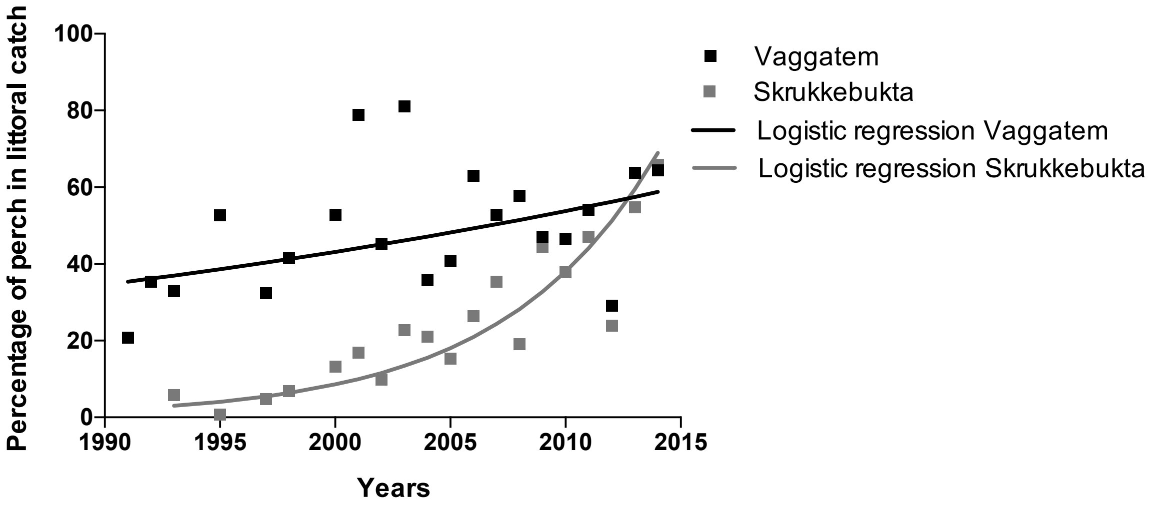

Figure 2 Percentage of perch in the total catch of the littoral zones of Lake Vaggatem (Lake Tjærebukta and Ruskebukta) and Lake Skrukkebukta from 1991 to 2014. Logistic regression: Vaggatem R^2=0.213, P=0.035, Skrukkebukta R^2=0.737, P=0.000.

Stomach content analyses

Laboratory analysis

In the laboratory at the university the stomachs were opened and the percentage of fullness of each stomach was estimated (0-100%). The prey items in the stomach content were determined mostly to species, genus or family level and subsequently the contribution of each prey type to the total stomach fullness was estimated (0-100%). The different prey types were divided over nine main prey groups; zooplankton, small benthic crustaceans, *Assellus aquaticus*, molluscs, surface insects, insect larvae, bugs and mites, ninespine sticklebacks and other fish (Appendix a, b, c, d). In Tjærebukta there were 3 LSR whitefish (3.7%) and 35 perch (30.4%) with empty stomachs, whereas in Skrukkebukta 19 (20.0%) LSR whitefish and 48 (38.6%) perch had empty stomachs (Appendix a, b, c and d). Fish with empty stomachs are not included in the stomach content analyses, unless pointed out otherwise.

Data analyses

Diet composition

From the fullness percentages of the prey types in the stomachs, the percent abundance (A_i), the frequency of occurrence (F_i) and the prey specific abundance (P_i) of each prey type were calculated (Amundsen et al. 1996):

$$A_i = (\Sigma\, S_i / \Sigma\, S_t) \times 100 \qquad (1)$$

where S_i is the total percentage of prey type i in the stomachs and S_t is the total stomach fullness of all the fish in a size group or population.

$$F_i = N_i / N \times 100 \qquad (2)$$

where N_i is the number of fish that had prey type i in their stomach and N is the total number of fish with stomach content in a size group or population.

$$P_i = (\Sigma\, S_i / \Sigma\, S_{ti}) \times 100 \qquad (3)$$

where S_i is the total percentage of prey type i in the stomachs and S_{ti} is the total stomach fullness in those fish with prey i in their stomachs in a size group or population. For the prey specific abundance all the stomachs with a fullness of less than 10% were excluded, and each individuals' stomach content was scaled up to 100%.

Diet overlap

The Schoener's index (Schoener 1970) was used to calculate the diet overlap (O_{jk}) between the LSR whitefish and perch populations and between the different size groups of each species within each lake. In addition it was used for the diet overlap between size groups within LSR whitefish and perch. The amount of diet overlap is a measurement of resource partitioning:

$$O_{jk}= 100 * (1- 0.5 \Sigma |p_{ij}-p_{ik}|) \quad (4)$$

where O_{jk} is the prey item overlap in percentage between size group/population j and size group/population k. p_{ij} is the fraction of prey item i eaten by species j, and p_{ik} is the percent abundance of prey item i eaten by species k. An overlap >60% is generally considered a significant overlap in diet (Wallace 1981).

Diet width

The diet niche width of size groups and populations was determined using the Levins' index (L) (Levins 1968):

$$L = 1/\sum p_i^2 \quad (5)$$

where p_i is the fraction of each prey type i in the stomachs of a size group or population, L can have values between 1 and n, where 1 is the narrowest (when only one prey item is found) and n the broadest diet niche width (n is equal to the total number of prey items when each prey item is present with an equal percent abundance in the diet of the individuals). The diet niche width is a measure of the level of population specialization (at a specific location) (Krebs 1989).

Individual dietary specialization

Individuals within a population can have a diet varying from completely different to similar to the overall populations diet. To calculate the overlap in diet of individual i and the diet of the population, a proportional similarity index (PS_i) (Formula 6) was used (Bolnick et al. 2002). Fish with stomach contents <10% were not used in these calculations, because they could have an influence that is out of proportion compared to their importance.

$PS_i = 1 - 0.5 \mathbf{\Sigma} |p_{ij}-q_j|$ (6)

Where p_{ij} is the proportion of prey item j in individual i's diet and q_j is the proportion of prey item j in the populations diet.

The average similarity index (IS) is calculated by the average of the individual PS_i values in a population (or size group). The prevalence of individual specialization (1-IS) is the inverse of the average similarity index (Quevedo et al. 2009, Eloranta et al. 2013). It ranges from 0-1, where values close to 0 indicate generalization, while values close to 1 indicate a high individual specialization.

Feeding strategies

The prey specific abundance (Y-axis) and the frequency of occurrence (X-axis) were used to determine the feeding strategy at the individual and population level. This was done for size groups and populations (Amundsen et al. 1996) (Figure 3). The distribution of the prey types along the diagonals and axes explains the prey importance, feeding strategy and niche width contribution. The diagonal axis from the lower left to the upper right explains prey importance. Prey types that are rarely eaten are found in the lower left, while dominant prey types are found in the upper right corner. Since prey importance is a function of prey specific abundance and frequency of occurrence, it is not a linear increase. The distribution of prey types along the Y-axis explains predator feeding strategy. Prey types found in the upper half of the diagram have been specialized on by the predator, while prey types found in the lower part of the graph are part of a more generalized diet and preyed upon on more occasionally. When there are a few prey types located in the upper right corner of the diagram, this could indicate a population specialization on one or a few prey types (Figure 3b). When prey types are found either in the upper left or lower right corner the population will have a generalist feeding strategy with a broad diet width. The diagonal axis from the lower right to the upper left corner explains niche width contribution. The prey types found in either of these corner make up the same overall contribution to the population diet, but are however evidence of two opposite feeding strategies of individuals in the population. Individuals in the population can be generalists, in which case the points on the feeding strategy diagram are concentrated towards the lower right corner reflecting a high within-phenotype contribution to the niche width (Figure 3c). The broad diet width could also be caused by specialized individuals, in which case the points on the diagram are concentrated towards the upper left corner reflecting a high between-phenotype contribution to the niche width (Figure 3a)(Amundsen et al. 1996).

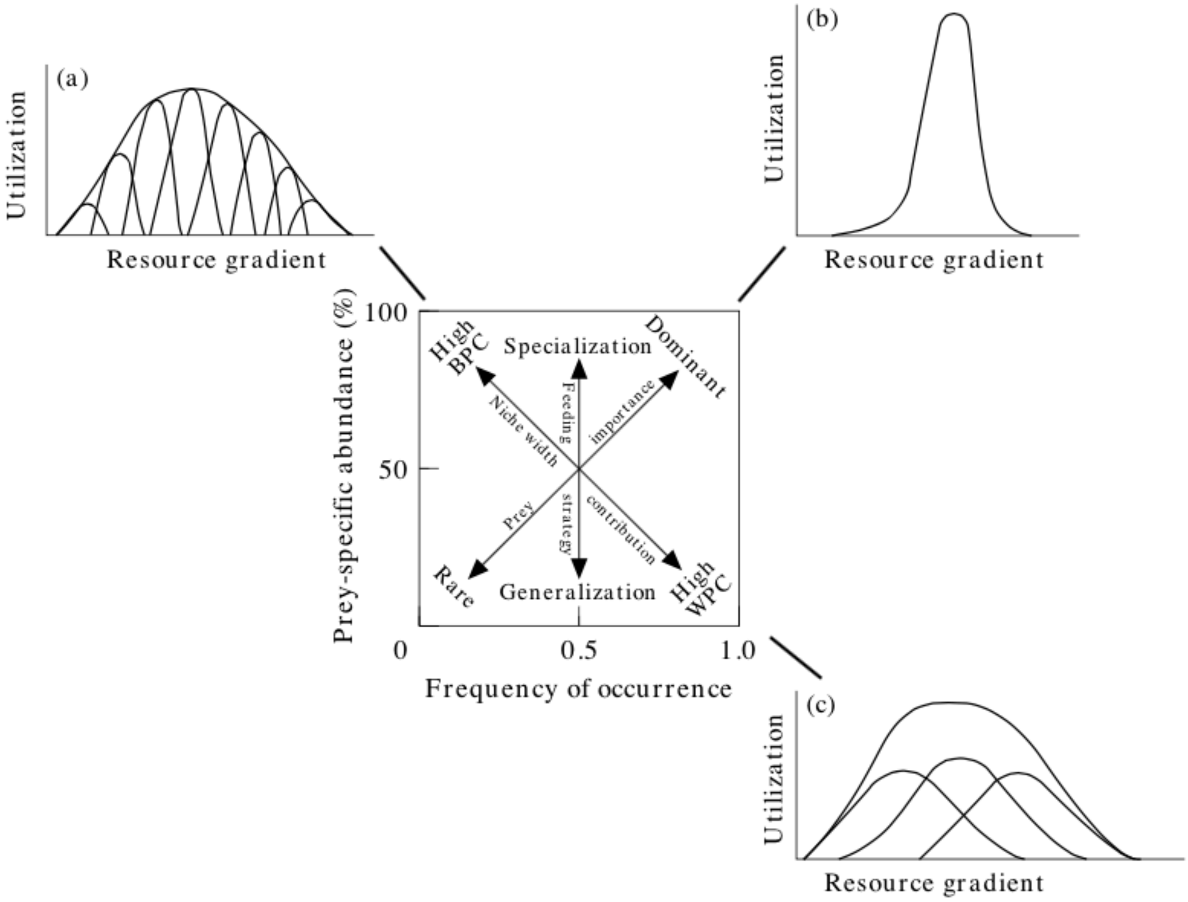

Figure 3 Explanatory diagram for the interpretation of feeding strategy, niche width contribution and prey importance for populations and size groups of perch and LSR whitefish and their niche interpretation curves; (a) a generalist population with specialized individuals; a high between-phenotype component (BPC) to the niche width, (b) a population specialization with a narrow niche width and (c) a generalist population with generalist individuals; high within-phenotype component (WPC) (Amundsen et al. 1996).

Statistical analyses

Statistical analyses were done with SPSS (IBM Corp. 2013. IBM SPSS Statistics for Macintosh, Version 22.0. Armonk, NY: IBM Corp.) and R 3.0.2 GUI 1.62 Snow Leopard build (R Core Team 2013).

Piscivory in perch

A logistic regression model (Formula 7) in SPSS was used to determine if there was a relationship between fish fork length and a piscivorous diet in perch. The formula was also used to determine the 50% chance at which length perch switched to a piscivorous diet.

Whether a fish had a piscivorous diet or not was a binary value. When the fish had a diet that consisted of at least 1% fish, 1 was used. When the fish had absolutely no fish in its stomach 0 was used. Piscivorous diet or non-piscivorous diet was used as the dependent valuable in the logistic regression. Fish fork length was used as the predictor value.

$$Y = e^{(a + bL)} [1 + e^{(a + bL)}]^{-1} \qquad (7)$$

Where Y is the probability a fish has a piscivorous diet (between 0-1) and L is the fish fork length (mm). Constant a is the slope and b is the starting point of the regression.

Spearman's rank correlations were used to determine if there was a correlation between fork length and the percentage of fish in the diet. Spearman's rank correlation was used since the data were not normally distributed and there was a monotonic, however not linear, relationship.

Individual dietary specialization

To compare the prevalence of individual specialization values between two size groups or populations Mann-Whitney U comparison were done in SPSS. For comparison between multiple size groups Kruskall Wallace tests were done. The Mann-Whitney U and Kruskall Wallis tests are non-parametric test, which do not require a normal distribution. They calculate the mean rank for each group and compare these. For a comparison of the mean ranks a similar distribution of the shape of the data is also not necessary.

Non-parametric multidimensional scaling (NMDS)

To assess the dissimilarity in prey type composition of the LSR whitefish and perch populations, a non-parametric multidimensional scaling ordination technique was used (NMDS) (Kruskal and Wish 1978). This was done with the vegan package in R (Oksanen 2013, R Core Team 2013, Oksanen et al. 2015). Individuals with a stomach fullness <10% were excluded from the analyses. The prey type percentage abundance data for each prey type in each individual fish were ranked. With this data, dissimilarities in prey composition between fish individuals were calculated using the Bray-Curtis index of dissimilarity. The stress criterion was used to assess how well the NMDS model fit the data (stress 0-0.3 meant an ok fit) (Kruskal and Wish 1978). In R convex hulls were made that include all sampled individuals of the LSR whitefish or perch populations. After that, ellipses of standard deviation were drawn for each population.

Stable isotope analyses

Laboratory and data analyses

From each lake muscle tissue samples from LSR whitefish and perch were chosen for stable isotope analysis (Table 2). The samples were dried at 60 °C for 48 hours, and should ideally constitute 5-10 mg dry weight of white muscle tissue (excluding skin, scales and bones). In addition to the muscle samples from LSR whitefish and perch, 6 samples of sticklebacks found in stomachs of perch were analyzed. Prey items used for stable isotope analyses were collected from both lakes in September 2013 by Brianne Kelly (Department of Biology, University of Waterloo, Canada). Next to this, extensive prey sampling was done in Tjærebukta by Kimmo Kahilainen in September 2014 (Department of Environmental Sciences, University of Helsinki, Finland). Prey $\delta^{13}C$ and $\delta^{15}N$ values were given to me by them.

The tissue samples were analyzed for carbon and nitrogen stable isotopes with a Delta Plus continuous flow isotope-ratio mass spectrometer (CF-IRMS) (Thermo- Finnigan; Bremen, Germany), interfaced to the EA via the Conflo II, at the Canadian Rivers Institute, Stable Isotope in Nature Laboratory (SINLAB). The results from the stable isotope analyses were given as $\delta^{13}C$ and $\delta^{15}N$ values, which were calculated by the equation:

$$\delta X = [(R_{sample}/R_{standard}) - 1] * 10^3 \qquad (8)$$

where X is either ^{13}C or ^{15}N, R_{sample} is the corresponding $^{13}C/^{12}C$ or $^{15}N/^{14}N$ ratio in parts per thousand (‰) of the tissue sample and $R_{standard}$ is the standard ratio for carbon (Vienna PeeDee Belemnite) or for nitrogen (atmospheric nitrogen) (Peterson and Fry 1987). Isotope values are normalized using secondary standards: NICOTINAMIDE, BLS and SMB- M.

$\delta^{15}N$ values are be an indication of trophic position, since $\delta^{15}N$ values increase with an increase in trophic level (Vander Zanden and Rasmussen 1999, Post 2002). $\delta^{13}C$ values can indicate the origin of the carbon source; e.g. littoral, pelagic and profundal carbon sources have a different $\delta^{13}C$ value (high to low respectively) (Vander Zanden and Rasmussen 1999). It is however difficult to compare $\delta^{15}N$ and $\delta^{13}C$ values between lakes, since there is a lot of variation between localities (Post 2002).

Statistical analyses

Mean stable isotope values between size groups and populations

To test for differences in mean $\delta^{13}C$ and $\delta^{15}N$ values between the LSR whitefish and perch populations in each lake student's t-tests or Mann-Whitney U tests (rank) were used (dependent on distribution of the data). To test for differences in mean $\delta^{13}C$ and $\delta^{15}N$ values between two different length groups of LSR whitefish (<250, ≥250 mm) and three length groups of perch (<150, 150-249 and ≥250 mm), Tukey HSD tests were used, since the data in each size group was normally distributed.

Stable isotopes with fork length

Pearson's or Spearman's (when data was not normally distributed) correlations were used to determine if there was a correlation between $\delta^{13}C$ or $\delta^{15}N$ and fork length of the fish.

Isotopic niche width and overlap

To study isotopic niche widths the SIBER (Stable Isotope Bayesian Ellipses in R) (Jackson et al. 2011) method was used in the SIAR package (version 4.2). Convex hull area (Total area; TA) is a measurement of the total niche area, and includes all individuals of a group/population in a $\delta^{13}C$-$\delta^{15}N$ bi-plot space (Layman et al. 2007). This method is however sensitive to differences in sample sizes between groups/populations, and is especially inaccurate with small sample size (N <30) (Syväranta et al. 2013). The core isotopic niche is measured by the standard ellipse area, either with a small sample size correction (SEA_C) or a Bayesian estimation (SEA_B) (Jackson et al. 2011). Both of these are less biased with respect to sample size than the convex hull area method (Syväranta et al. 2013). SEA_C and SEA_B are robust methods to measure isotopic niche width (Jackson et al. 2011). The amount of isotopic niche overlap is a measurement of resource partitioning. To measure isotopic overlap between two or more groups/populations/species the core isotopic niche overlap of SEA_C (CIO) was calculated (adapted from: Cucherousset and Villéger 2015, Hinke et al. 2015). The overlap in area (‰^{2}) was calculated with the SIBER method and the overlap in percentage was calculated with the following formula:

$\mathrm{CIO} = \text{overlapping area} / (\mathrm{SEA_C}(1) + \mathrm{SEA_C}(2) - \text{overlapping area}) *100$ (9)

With $\mathrm{SEA_C}$ of two different size groups or populations. A CIO >60% was considered as a significant (high) overlap in isotopic niche area (Wallace 1981, Vaslet et al. 2015).

To measure what the influence of the least impacted species (smallest overlapping area compared to its $\mathrm{SEA_C}$) on the most impacted species is (biggest overlapping area compared to its $\mathrm{SEA_C}$) a complementary index is used. This shows what percentage of the overlapping area covers the group with the smallest area (OSA) (Cucherousset and Villéger 2015).

$\mathrm{OSA} = \text{overlapping area} / \min(\mathrm{SEA_C}(1), \mathrm{SEA_C}(2)) *100$ (10)

Where the overlapping area is divided by the smallest $\mathrm{SEA_C}$ of the two size groups or populations.

Results

Variation in diet between fish populations

In Tjærebukta there was a high consumption of molluscs (percent abundance: 76.3%) by LSR whitefish, while fish (46.1%) and the isopod *Assellus aquaticus* (39.7%) dominated the perch diet (Figure 4a, Appendix a and b). There was a low diet overlap of 12% between the two species in Tjærebukta. In Skrukkebukta both species consumed a high abundance of small benthic crustaceans (mostly *Eurycercus lamellatus*) and insect larvae (Figure 4b, Appendix c and d). Therefore the diets of perch and LSR whitefish caught in Skrukkebukta had a higher similarity, with a diet overlap of 53%. However, there were some differences as well. While fish prey contributed over 25% of the stomach contents of perch, LSR whitefish did not consume any. Furthermore, zooplankton constituted 11.4% of the stomach contents of perch, while LSR whitefish hardly had eaten any zooplankton (1.6%). On the other hand, molluscs were part of the diet of LSR whitefish (19.8 %), but were not present in the diet of perch. Diet similarity between LSR whitefish from the two lakes was as low as 26.7%, while the similarity in diet between perch from the two lakes was 24.9%. The total number of prey types (prey richness) found in the stomachs of fish in the two lakes differed as well; 17 prey types in Tjærebukta and 23 prey types in Skrukkebukta.

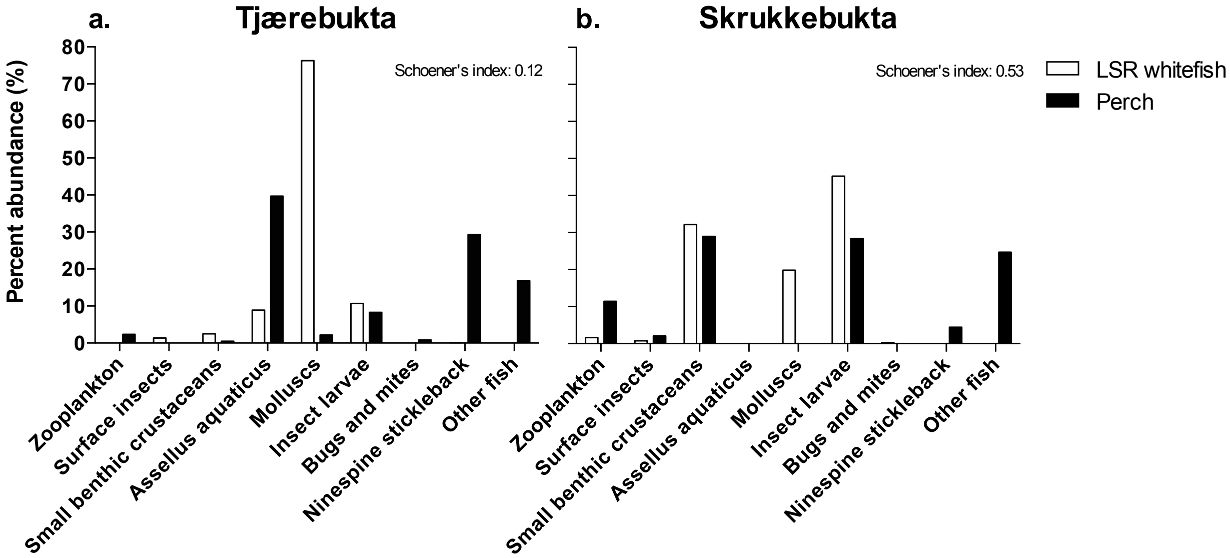

Figure 4 Percent abundances of prey groups found in stomach contents of LSR whitefish (white) and perch (black) caught in **a.** Lake Tjærebukta and **b.** Lake Skrukkebukta in September 2014. And the Schoener's index comparing LSR whitefish and perch in each lake.

Variation in diet between size groups

In Tjærebukta, molluscs were the most important prey group for all length groups of LSR whitefish (Figure 5a). In fish ≥200 mm *Lymnea* sp. was the dominant mollusc species (Appendix a). Accordingly, there was little variation in diet between the length groups ≥200 mm, which was reflected by an intermediate to high dietary overlap exceeding 50% (Appendix e). However, for the length groups <200 mm there was low intraspecific dietary overlap, which was related to a utilization of different mollusc species. *Valvata* sp. was the dominant prey item in the group 150-199 mm (n = 4)(Appendix a).

Perch in Tjærebukta <250 mm had a high abundance of *A. aquaticus* in their diets (Figure 5b, Appendix b). All length groups utilized ninespine sticklebacks, with the smallest piscivorous perch being 97 mm. The percentage abundance of fish in the perch diet increased with increasing fish length, up to 51% in the 250-299 mm length group. There were three main dietary groups, including fish <150 mm feeding predominantly on *A. aquaticus*, 150-249 mm with a more mixed diet of *A. aquaticus* and fish, and perch ≥250 mm feeding predominantly on fish. Diet overlap was high between successive length groups, but low between distant length groups (Appendix f).

In Skrukkebukta small benthic crustaceans (*E. lamellatus*) and molluscs were prevalent in the diet of LSR whitefish in the smallest size group (150-199 mm), but their abundance decreased with increasing fish length (Figure 5c, Appendix c). Small benthic crustaceans were no longer present in the stomach contents of the biggest length group (≥300 mm). Insect larvae (mostly Chironomidae, Ephemeroptera and Trichoptera larvae with house) abundance in the diet increased with increasing fish length, and made up 99% of the diet in the biggest length group. There were two main dietary groups; fish <250 feeding on *E. lamellatus,* insect larvae and molluscs, and fish ≥250 mm feeding mainly on insect larvae. Diet overlap was high between successive length groups and low between distant length groups (Appendix g).

For perch in the length groups <150 mm small benthic crustaceans (*E. lamellatus*) was the most important prey group, but it (almost) disappeared from the diets of larger length groups (Figure 5d, Appendix d). The contribution of insect larvae to the diet increased with length to a maximum of 43% in length groups 150-249 mm (mostly Trichoptera larvae). Fish became a part of the diet in fish ≥150 mm, and the mean percentage abundance of fish increased up to

100% in the biggest fish (≥300 mm). Other fish (coregonids and perch) were far more abundant than ninespine sticklebacks in the diet. There were three main dietary groups; fish <150 mm fed predominantly on *E. lamellatus*, 150-249 mm perch had a more mixed diet of insect larvae and fish, and perch ≥250 mm fed predominantly on fish. Diet overlap was intermediate to high between successive length groups, but low between distant size groups (Appendix h).

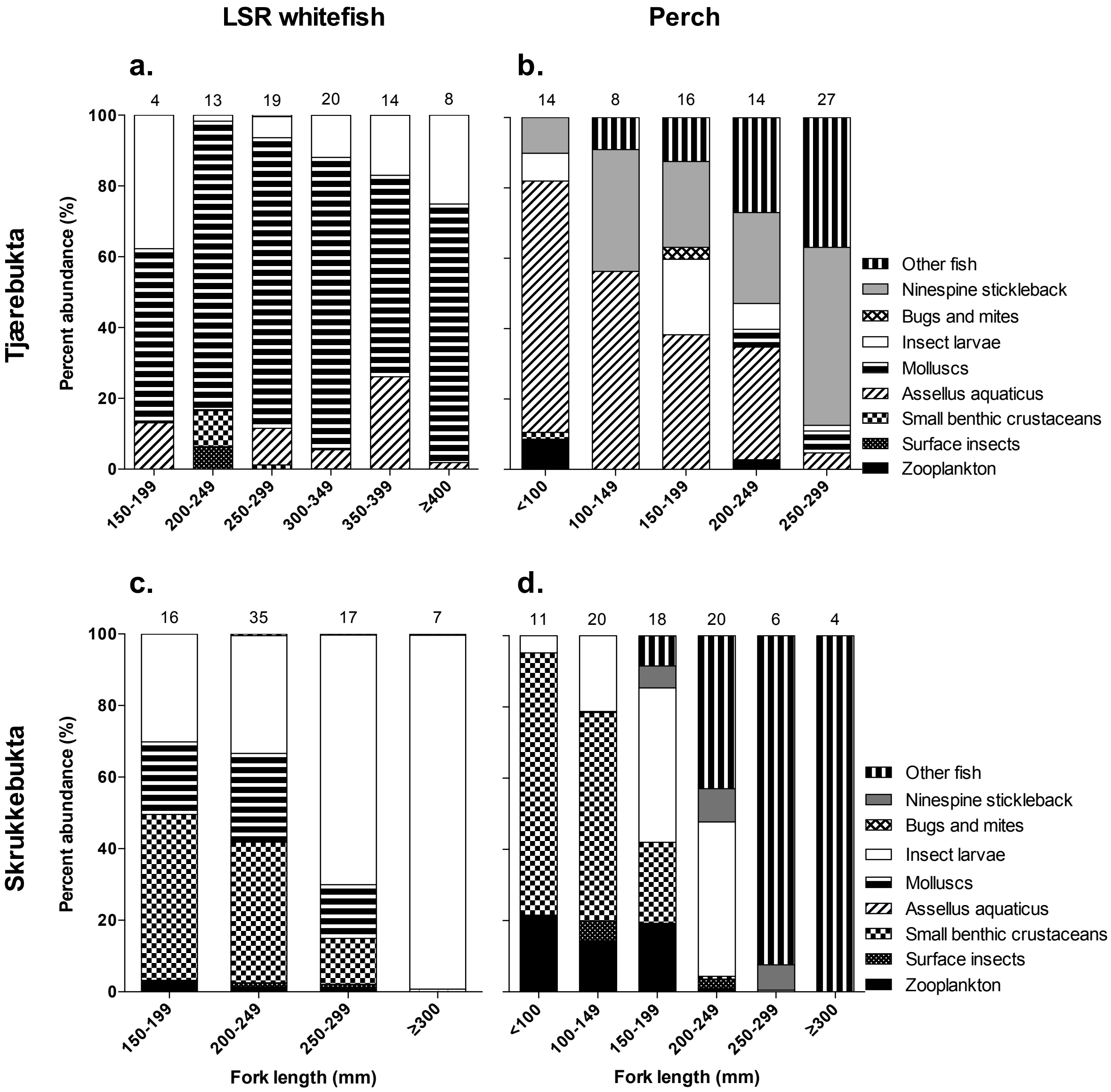

Figure 5 Mean percent abundance of the main prey groups found in the stomach contents of different size groups of **a.** LSR whitefish caught in Lake Tjærebukta, **b.** perch caught in Lake Tjærebukta, **c.** LSR whitefish caught in Lake Skrukkebukta and **d.** perch caught in Lake Skrukkebukta in September 2014. Numbers of fish with stomach content for each size group are indicated above the columns. Stomach contents were scaled up to 100%.

In Tjærebukta the interspecific dietary overlap between all length groups was very low (Table 3a). The highest overlap was observed between 200-249 mm perch and 350-399 mm LSR whitefish (31.2%). The interspecific dietary overlap in Skrukkebukta was higher than in Tjærebukta (Table 3b). Generally there was an intermediate to high diet overlap between perch <200 mm and LSR whitefish <250mm (43.3-61.5%). Perch ≥250 mm had little or no overlap with any of the size groups of LSR whitefish due to their fish dominated diet.

Table 3 Schoener's index comparing diet overlap between perch and LSR whitefish of all size groups caught in **a.** Lake Tjærebukta and **b.** Lake Skrukkebukta in September 2014.

a.

LSR Whitefish **Perch**	**150-199**	**200-249**	**250-299**	**300-349**	**350-399**	**≥400**
<100	13.1	2.3	12.0	5.5	26.1	1.8
100-149	13.1	0.3	10.7	5.4	26.1	1.8
150-199	14.0	1.5	11.8	6.3	27.0	2.7
200-249	18.1	5.7	15.9	10.5	31.2	6.9
250-299	10.9	6.8	11.4	10.9	10.9	8.1

b.

LSR Whitefish **Perch**	**150-199**	**200-249**	**250-299**	**≥300**
<100	46.6	44.4	18.8	4.8
100-149	**61.5**	53.9	30.1	13.3
150-199	43.3	50.1	48.5	31.8
200-249	23.0	27.9	39.6	34.7
250-299	0.5	0.5	0.5	0.5
≥300	0	0	0	0

Piscivory in perch

There was a positive relationship between the presence of a piscivorous diet and the fork length of perch (Figure 6). In both lakes the logistic regression model showed a significant relationship (P <0.05). The fork length at which 50% of the perch had switched to a fish diet was 187 mm (95% CI 140, 225 mm) in Tjærebukta and 215 mm (95% CI 195, 244 mm) in Skrukkebukta (Figure 6, Appendix i).

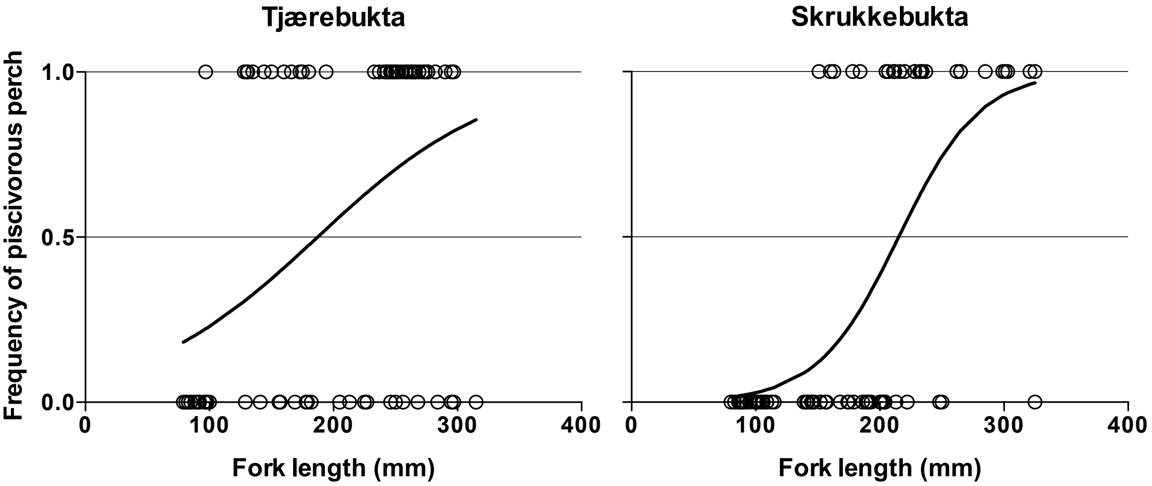

Figure 6 Frequency of piscivorous perch caught in **a.** Lake Tjærebukta and **b.** Lake Skrukkebukta in September 2014, with the found data (○) and the regression curve estimated with a logistic regression model (Appendix i).

The proportion of fish found in the stomach was also positively correlated with the fork length in Tjærebukta (Spearman's test: $r_s = 0.418$, $n = 80$, $P = 0.000$) and in Skrukkebukta ($r_s = 0.668$, $n = 81$, $P = 0.000$).

Diet width

The population diet widths (Appendix j and k) for both species were broader in Skrukkebukta (LSR whitefish: 5.02, perch: 5.90) than in Tjærebukta (LSR whitefish: 3.12, perch; 3.80). Overall perch had a broader diet width than LSR whitefish. In both lakes, perch had a large variation in diet widths between length groups, with small and large perch having a more narrow diet niche than intermediate length perch (Figure 7). The diet width was less varied among length groups in LSR whitefish.

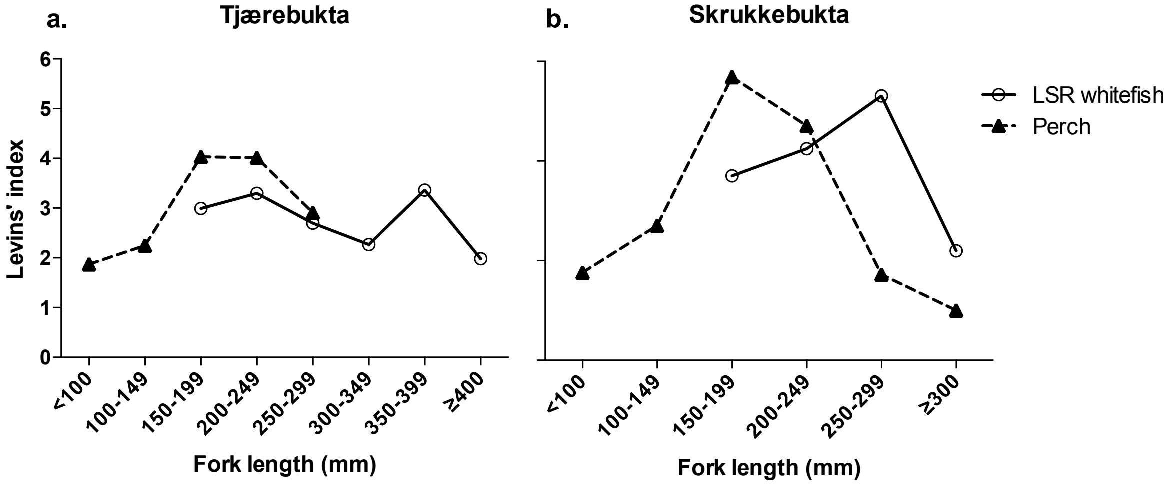

Figure 7 Levins' index for different size groups of LSR whitefish (○) and perch (▲) caught in **a.** Lake Tjærebukta and **b.** Lake Skrukkebukta in September 2014.

Individual specialization

The prevalence of individual dietary specialization (1-IS) was significantly higher in perch than in LSR whitefish in both lakes (Mann Whitney U tests: p <0.01) (Appendix j, k and l). The mean 1-IS in Tjærebukta was 0.60 for LSR whitefish and 0.68 for perch. The mean 1-IS in Skrukkebukta was 0.63 for LSR whitefish and 0.73 for perch. The individual specialization was for both species significantly higher in Skrukkebukta than in Tjærebukta (Mann Whitney U tests: p <0.05) (Appendix m). The LSR whitefish population in Tjærebukta seemed to have a bimodal distribution for individual specialization (Figure 8a). About half of the fish seemed to have a low individual specialization, while the other half had a high individual specialization. Almost half of the LSR whitefish in Skrukkebukta had an individual specialization between 0.5 and 0.6 (Figure 8c). Perch showed a similar pattern of individual specialization in both Tjærebukta and Skrukkebukta, as most fish had an individual specialization above 0.65 (Figure 8d). Between 10-15% of the fish even had an extremely high individual specialization (0.9-1) in both lakes.

Generally the prevalence for individual specialization increased with increasing fork length, expect for LSR whitefish in Tjærebukta, which showed a decrease (Figure 9). There was no difference in mean ranks of 1-IS between the size groups of LSR whitefish in Tjærebukta (Kruskall Wallis: p=0.684). In Tjærebukta the two largest perch groups from 200-299 mm had a higher 1-IS than perch of 100-149 mm (Mann Whitney U tests: p <0.05). In

Skrukkebukta LSR whitefish 250-299 mm had the highest mean 1-IS (0.77), and was different from the two smaller length groups (Mann Whitney U tests: p <0.01). Perch ≥200 mm in Skrukkebukta had a higher prevalence for individual specialization than smaller individuals (Mann Whitney U test: p=0.000).

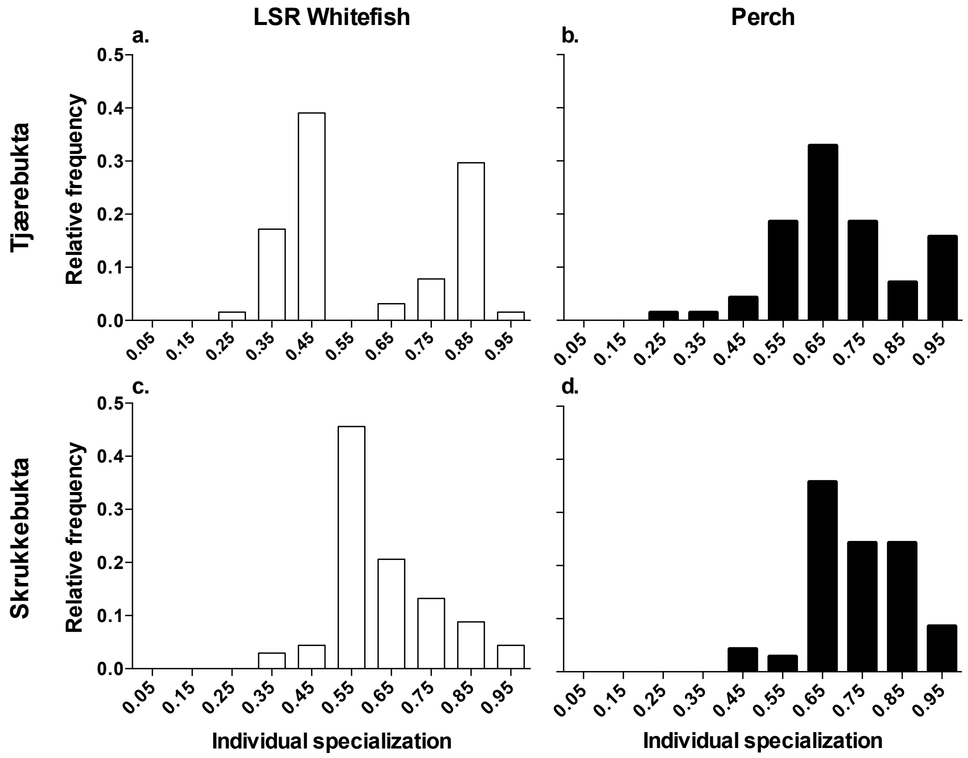

Figure 8 Relative frequency of the degree of individual specialization (0-1) for **a.** LSR whitefish in Lake Tjærebukta, **b.** perch in Lake Tjærebukta, **c.** LSR whitefish in Lake Skrukkebukta and **d.** perch in Lake Skrukkebukta, caught in September 2014.

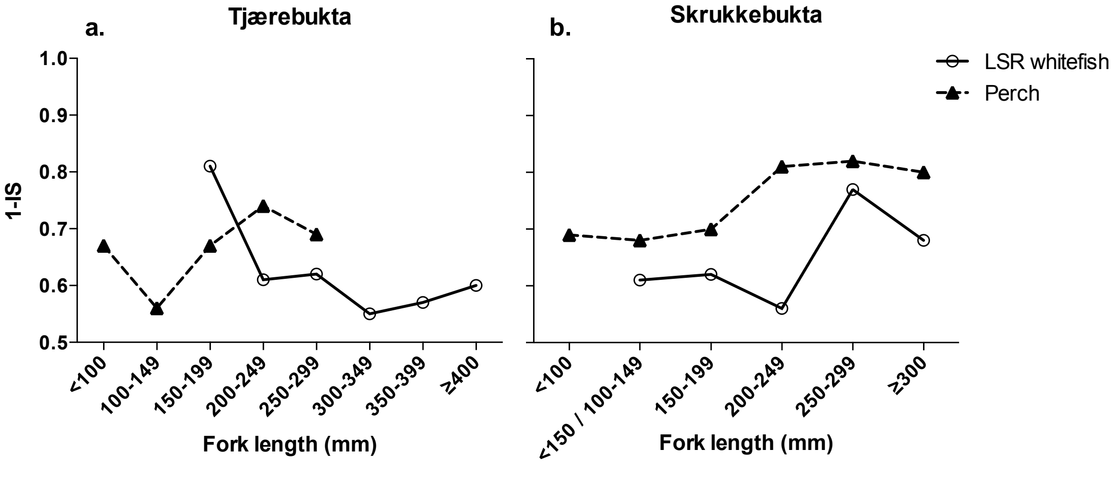

Figure 9 Prevalence for individual specialization (1-IS) for LSR whitefish (○) and perch (▲) caught in **a.** Lake Tjærebukta and **b.** Lake Skrukkebukta in September 2014.

Feeding strategies

In Tjærebukta *Lymnea* sp. had a high prey specific abundance and frequency of occurrence in the LSR whitefish diet (Figure 10a), suggesting a population specialization on this prey type. The rest of the prey types had prey specific abundance around 50% and a low frequency of occurrence (<0.3) (Figure 10a). The diet of the LSR whitefish in Skrukkebukta consisted of prey items that have a high frequency of occurrence, but a low prey-specific abundance (Figure 10a and b). All the prey specific abundances were below 50% (Figure 10c). *Eurycercus lamellatus* and Trichoptera larvae (w.h.) seemed to indicate that the individuals in the population have a generalized diet, but have these as common prey types (high within phenotype component). There were no big differences in distribution of prey items between the size groups of LSR whitefish in the two lakes (<250mm/≥250 mm) (Appendix n).

In the diet of perch most prey types had a low frequency of occurrence (Figure 10b and d). This indicates a generalist population in both lakes. Ninespine stickleback, perch and coregonids had a high prey specific abundance (>60%) and a low (<0.35) frequency of occurrence in both lakes, indicating an individual specialization on these prey items (high between phenotype component). In Tjærebukta *A. aquaticus* had a high frequency of occurrence and prey specific abundance (>50%) (Figure 10b). In Skrukkebukta this was similar for *E. lamellatus* (>50%) (Figure 10d). This indicates that these are commonly utilized prey items in their respective lakes. For perch there were some differences in distribution of prey items between the size groups in both lakes. Small fish had *A. aquaticus* and *E. lamellatus* in the upper right corner of the graph in Tjærebukta and Skrukkebukta respectively (Appendix o). Intermediate sized fish had most prey items on the left side of the feeding strategy graph in both lakes. Large fish had ninespine sticklebacks and coregonids in the upper right corner of the graph in Tjærebukta and Skrukkebukta respectively.

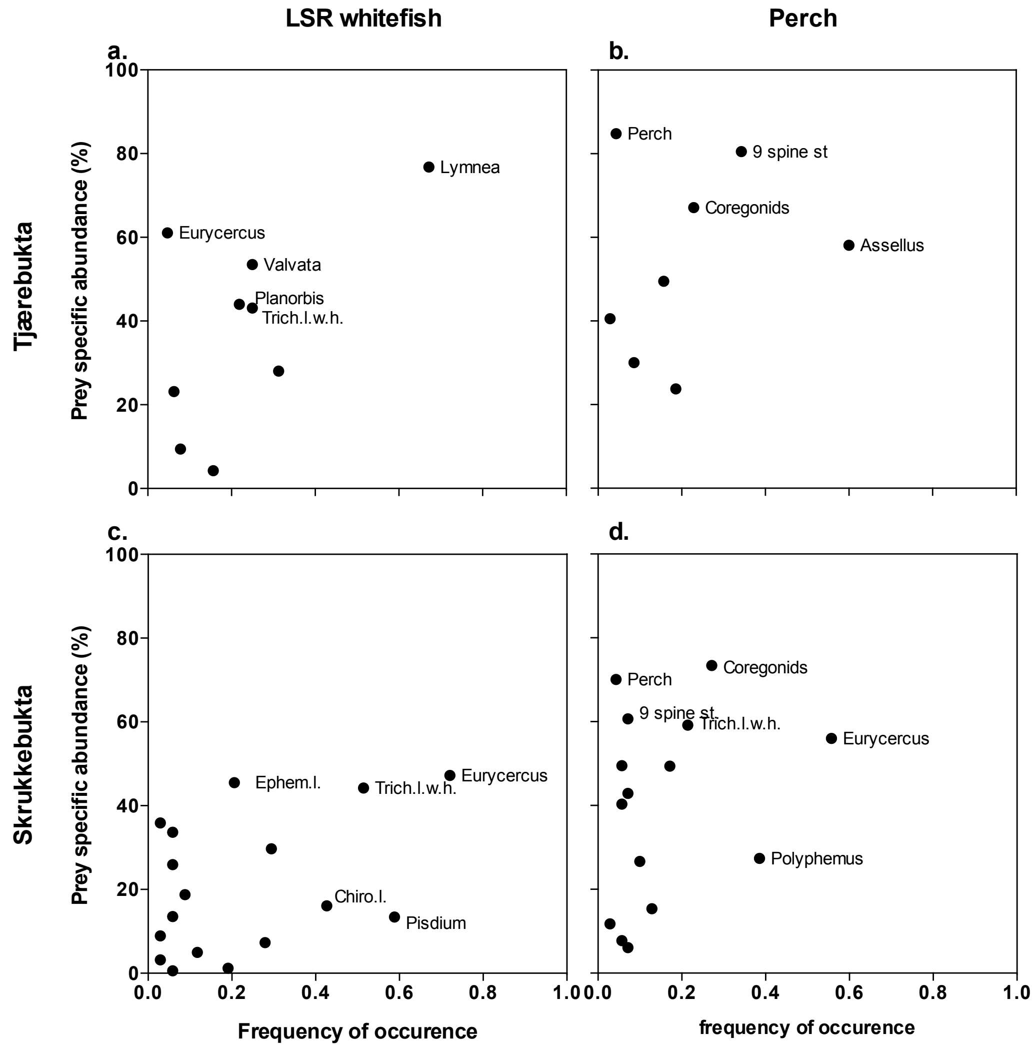

Figure 10 Feeding strategies of LSR whitefish (**a.**) and perch (**b.**) caught in Lake Tjærebukta, and LSR whitefish (**c.**) and perch (**d.**) caught in Lake Skrukkebukta in September 2014.

Non-metrical multidimensional scaling (NMDS)

In Tjærebukta molluscs seemed mostly important for LSR whitefish, while ninespine sticklebacks, other fish and zooplankton were only utilized by perch (Figure 11a). *Assellus aquaticus* was utilized by both, but seemed most important for perch. As the two species had very little overlap in their diets, there was no overlap between the ellipse area (SD) of the two species, and a small overlap between the convex hull areas. In both lakes LSR whitefish had a smaller ellipse area and convex hull than perch (Figure 11). In Skrukkebukta there was somewhat more overlap between the diets of the two species, reflected both in the ellipse areas and the convex hull areas. LSR whitefish had a bigger convex hull area and ellipse area in Skrukkebukta than in Tjærebukta. In Skrukkebukta ninespine stickleback and other fish were only important for perch, while all other prey types were utilized by both LSR whitefish and perch (Figure 11b).

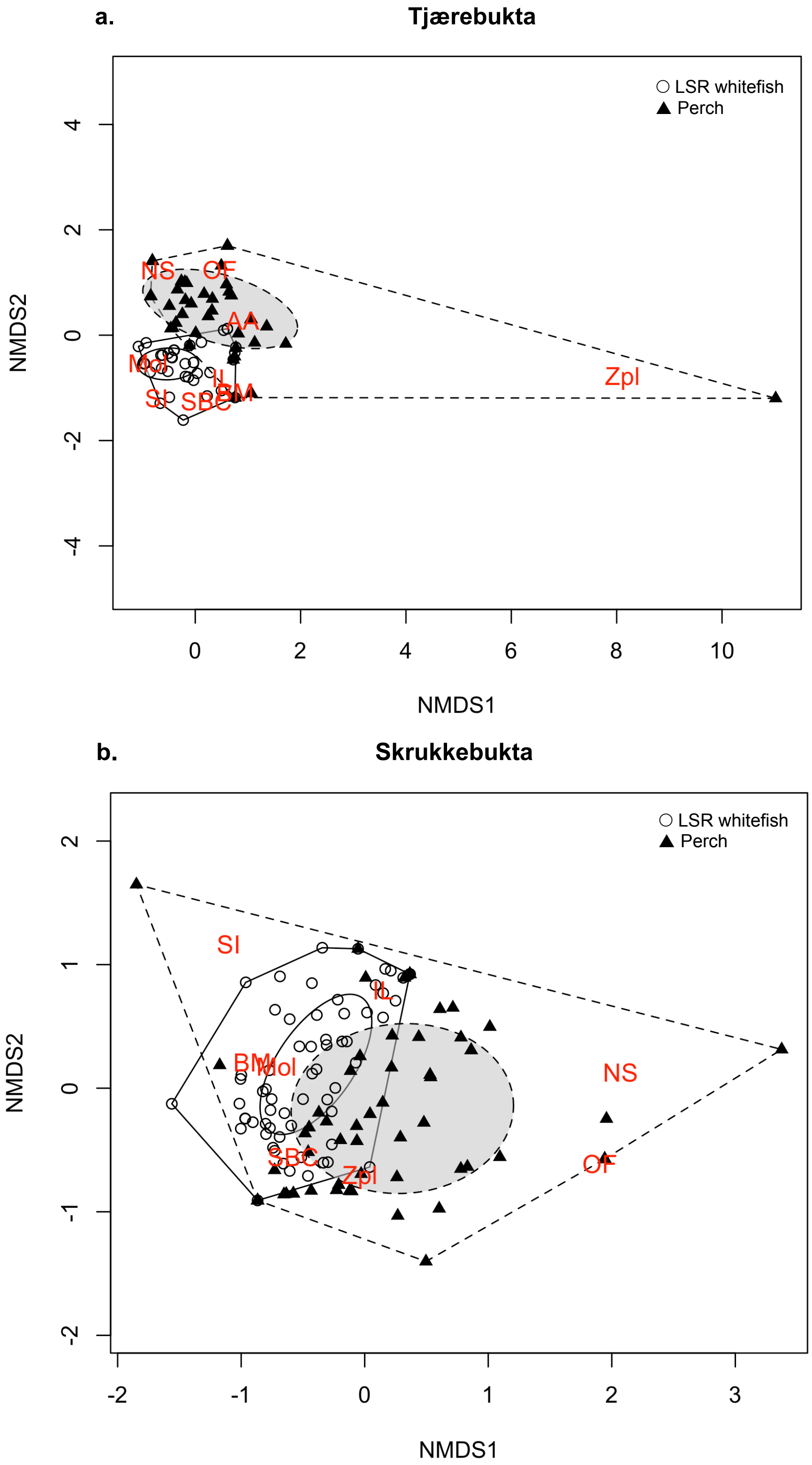

Figure 11 Non-metrical multidimensional scaling (NMDS), with convex hull area and ellipse are of standard deviation, of the diets of individual LSR whitefish (○, unbroken line) and perch (▲, dashed line) caught in (**a**) Tjærebukta (stress: 0.107) and (**b**) Skrukkebukta (stress: 0.114) (2 dimensions) in September 2014. Zpl = zooplankton, SBC = small benthic crustaceans, AA = *Asellus aquaticus*, Mol = molluscs, SI = surface insects, IL = insect larvae, BM = bugs and mites, NS= ninespine sticklebacks, OF = other fish.

Mean stable isotope values

There were small but significant differences for mean $\delta^{13}C$ and $\delta^{15}N$ values between the species in both lakes (Appendix t). In Tjærebukta LSR whitefish had higher $\delta^{13}C$ values than perch (Mann-Whitney U: mean rank LSR whitefish: 76.25, perch: 53.71, U=1377, n=130, p=0.001). Perch had a slightly higher mean $\delta^{15}N$ value than LSR whitefish in this lake (perch: 8.25‰, LSR whitefish: 7.71‰; Student's t-test: t(96.014)= 2.148, p=0.000). In Skrukkebukta LSR whitefish had a mean $\delta^{13}C$ value of -23.79‰, while perch had a higher mean value of -23.15‰ (t(96)= -2.107, p=0.038). For $\delta^{15}N$ it was the other way around, and LSR whitefish surprisingly had a slightly higher mean value (LSR whitefish: 9.47‰, perch: 9.09‰; t(77.410)=2.148, p=0.035).

Stable isotopes and fork length

LSR whitefish showed no significant correlation between $\delta^{13}C$ values and fork length in either of the lakes (Figure 12a and b). There was however a significant positive correlation between $\delta^{15}N$ values and length of LSR whitefish in Skrukkebukta (Spearman correlation: r_s= 0.512, n= 40, p=0.001) (Figure 12d), but not in Tjærebukta (Figure 12c). Perch however, showed a significant positive correlation between $\delta^{13}C$ values and length in Tjærebukta (r_s =0.413, n= 62, p=0.001) (Figure 12a), but not in Skrukkebukta. The positive correlation between $\delta^{15}N$ values and fork length of perch was significant for both lakes (Tjærebukta: r_s= 0.600 n= 62, p=0.000, Skrukkebukta: Pearson correlation: r_p= 0.716, n= 59, P= 0.000) (Figure 12c and d).

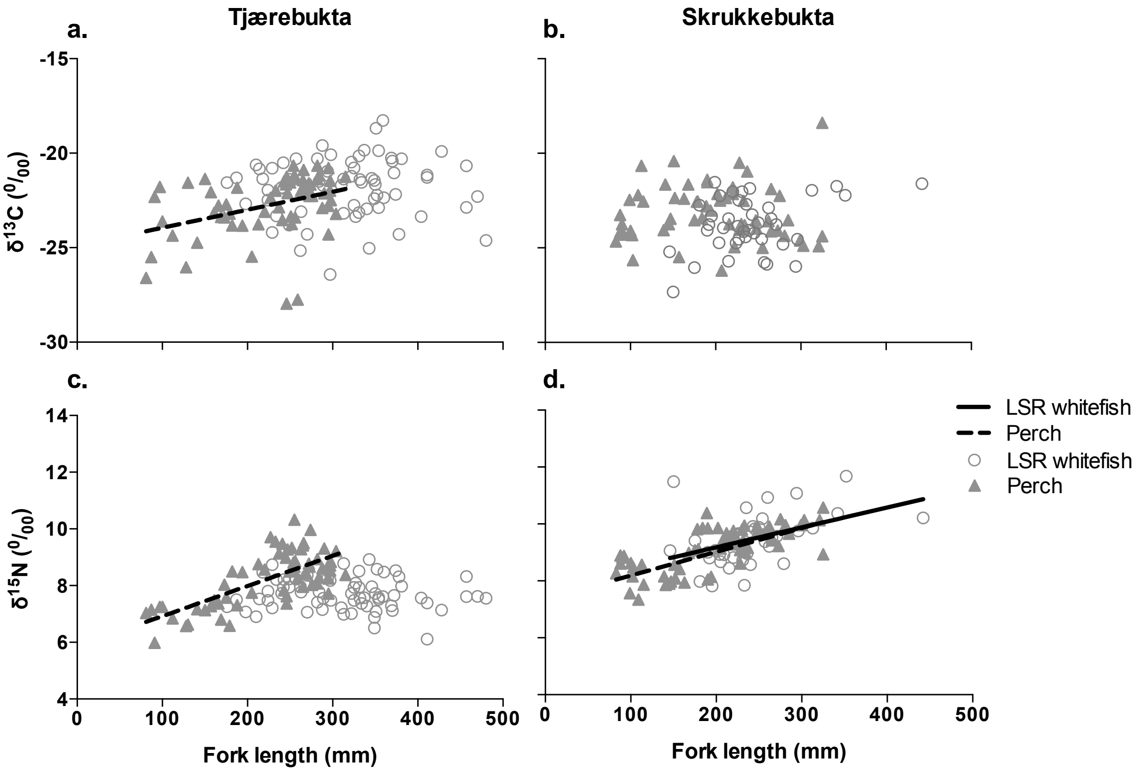

Figure 12 Stable isotope plots showing $\delta^{13}C$ (**a and b**) and $\delta^{15}N$ with increasing fork length (**c and d**) for LSR whitefish (○) and perch (▲) caught in Tjærebukta and Skrukkebukta in September 2014, and their significant linear regression lines.

The only difference between the two size groups of LSR whitefish was that fish ≥250 mm had a higher mean $\delta^{15}N$ value (Tukey HSD test: p =0.003) (Figure 13, Appendix s). Perch mean $\delta^{15}N$ values increased with perch length group in both lakes, and $\delta^{13}C$ values increased with length group in Tjærebukta (Figure 13). Small perch (<150 mm) had significantly lower mean $\delta^{15}N$ values than both larger perch groups in both lakes and a lower mean $\delta^{13}C$ value than perch ≥250 mm in Tjærebukta (Tukey HSD tests: p <0.05)(Appendix: p, q and s). In Tjærebukta all three perch groups were significantly different from each other in $\delta^{15}N$ values (Tukey HSD tests: p <0.01). Perch <150 mm also had significantly lower mean $\delta^{13}C$ and $\delta^{15}N$ values than both LSR whitefish groups in Tjærebukta and a lower mean $\delta^{15}N$ value in Lake Skrukkebukta (Tukey HSD tests: p <0.05). Perch ≥250 mm was only significantly different for mean $\delta^{15}N$ values from both LSR whitefish groups in Tjærebukta (Tukey HSD tests: p <0.01).

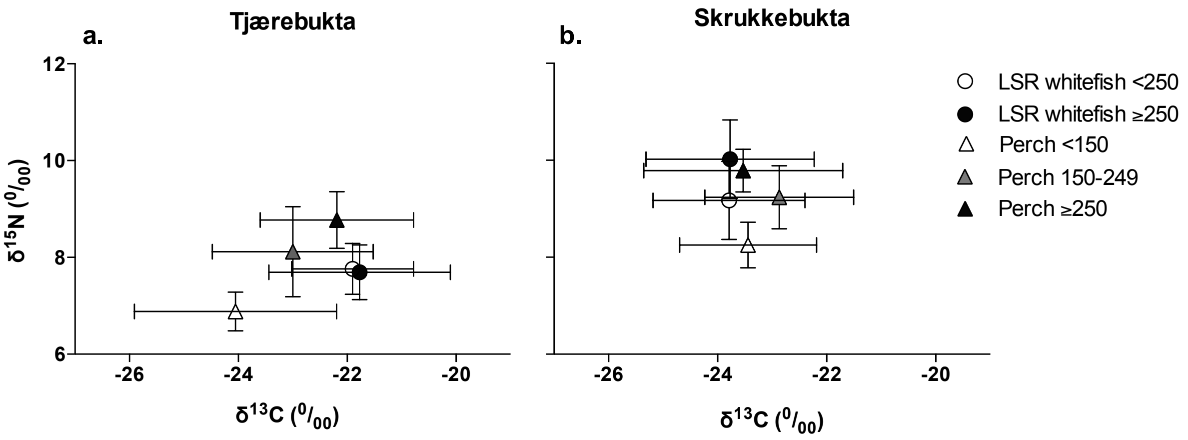

Figure 13 Stable isotope biplots showing the mean (±SD) $\delta^{13}C$ and $\delta^{15}N$ values of fish muscle tissue from LSR whitefish (○) and perch (▲) of different size groups (mm) from (**a.**) Lake Tjærebukta and (**b.**) Lake Skrukkebukta in September 2014.

The $\delta^{13}C$ values of the fish were in compliance with a mixed littoral and pelagic diet in both lakes (Appendix t). The fish from Tjærebukta have a $\delta^{13}C$ value similar to the littoral prey (insect larvae, *A. aquaticus*, small benthic crustaceans) (Appendix v). The $\delta^{13}C$ values of perch ≥150 mm correspond well with the mean $\delta^{13}C$ value for ninespine sticklebacks. The $\delta^{15}N$ values of the fish are higher than all of their prey items (including ninespine sticklebacks).

Isotopic niche width and overlap

In Tjærebukta LSR whitefish individuals had little variation in $\delta^{13}C$ and $\delta^{15}N$ values and therefore had the smallest convex hull area (TA; 12.71‰^{2}). They had the narrowest isotopic niche width, with a Bayesian standard ellipse area (SEA$_B$) of 2.59‰^{2} (Figure 14, Table 4). The niche width of perch was broader with a SEA$_B$ of 4.69‰^{2} and a TA of 19.73‰^{2}. The core isotopic niche overlap between LSR whitefish and perch was small with 20.6%. The impact of the overlap was bigger on LSR whitefish than perch. In Lake Skrukkebukta the niche widths of LSR whitefish and perch were quite similar (SEA$_B$ 3.98 and 3.66‰^{2} respectively). The core isotopic niche overlap between the two species in Skrukkebukta was bigger than in Tjærebukta (48.5%). In this lake the impact of the overlap was similar for both species (Figure 14, Table 4).

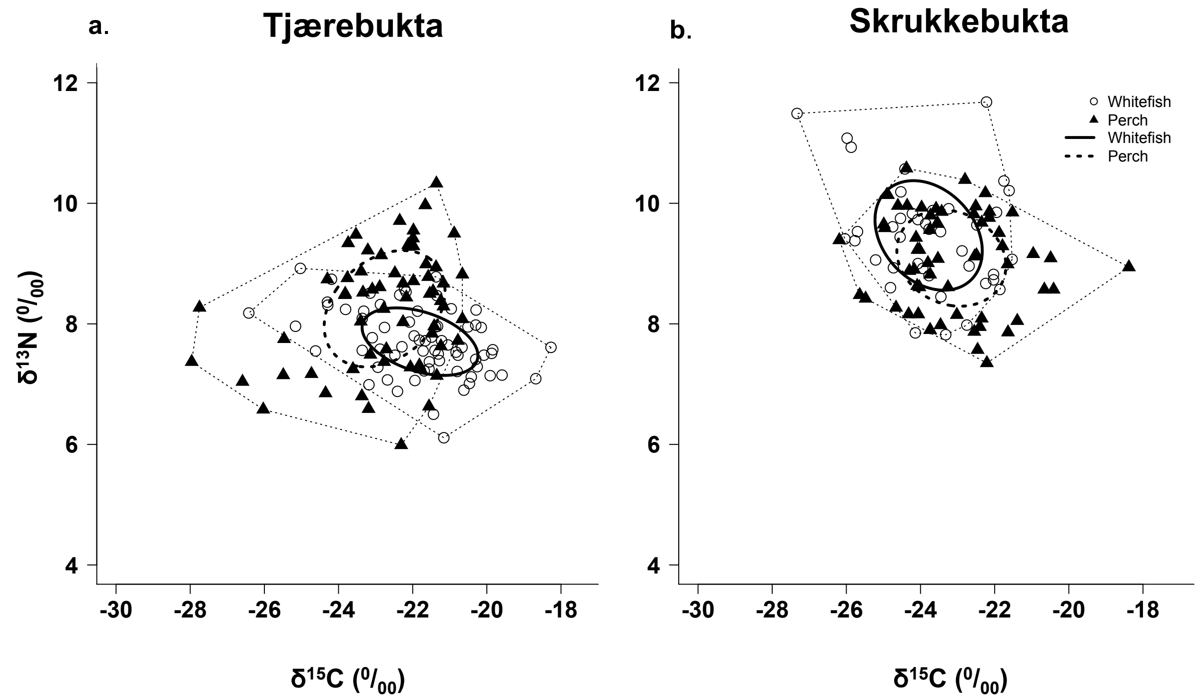

Figure 14 Standard ellipse area (SEA$_c$) and convex hulls for LSR whitefish (○) and perch (▲) caught in Lake Tjærebukta and Lake Skrukkebukta in September 2014.

Table 4 Estimated isotopic niches (SEA$_C$, SEA$_B$; mean and upper and lower 95% Bayesian credibility intervals for standard ellipse area) and convex hull total area (TA), core isotopic overlap and overlap of the smallest area of LSR whitefish and perch from both lakes.

Lake	Fish species	N	SEA$_C$ ($^0/_{00}{}^2$)	SEA$_B$ ($^0/_{00}{}^2$)	TA ($^0/_{00}{}^2$)	CIO(%)	OSA(%)
Tjærebukta						20.6	49.1
	LSR whitefish	68	2.50	2.59 (1.99-3.22)	12.72		
	Perch	62	4.71	4.69 (3.57-5.89)	19.73		
Skrukkebukta						48.5	68.2
	LSR whitefish	40	3.96	3.98 (2.83-5.25)	15.57		
	Perch	59	3.64	3.66 (2.75-4.60)	14.11		

In Tjærebukta perch of 150-249 mm had the biggest SEA$_B$ (4.45‰^{2}) (Figure 15, Appendix w) and had some SEA$_C$ overlap with all of them (CIO = 0.8-25.5%) (Table 5a). Contrarily there was (almost) no overlap in isotopic niche between perch <150 mm and all other groups. Perch ≥250 mm had the most overlap with perch 150-249 mm, but had very low overlap with LSR whitefish. The isotopic niche of LSR whitefish <250 mm is almost completely encompassed by the isotopic niche of LSR whitefish ≥250 mm (OSA = 97.9%, CIO = 58.5) (Figure 15, Table 5a).

In Skrukkebukta there was in general more overlap between the 5 groups than in Tjærebukta (Figure 15, Table 5b). LSR whitefish ≥250 mm had the broadest isotopic niche (SEA_B = 4.24‰^{2}) and had some overlap with all the groups except for perch <150 mm. Perch <150 mm had, similar to Tjærebukta, very little overlap with any of the groups (CIO = 0-8.5%).

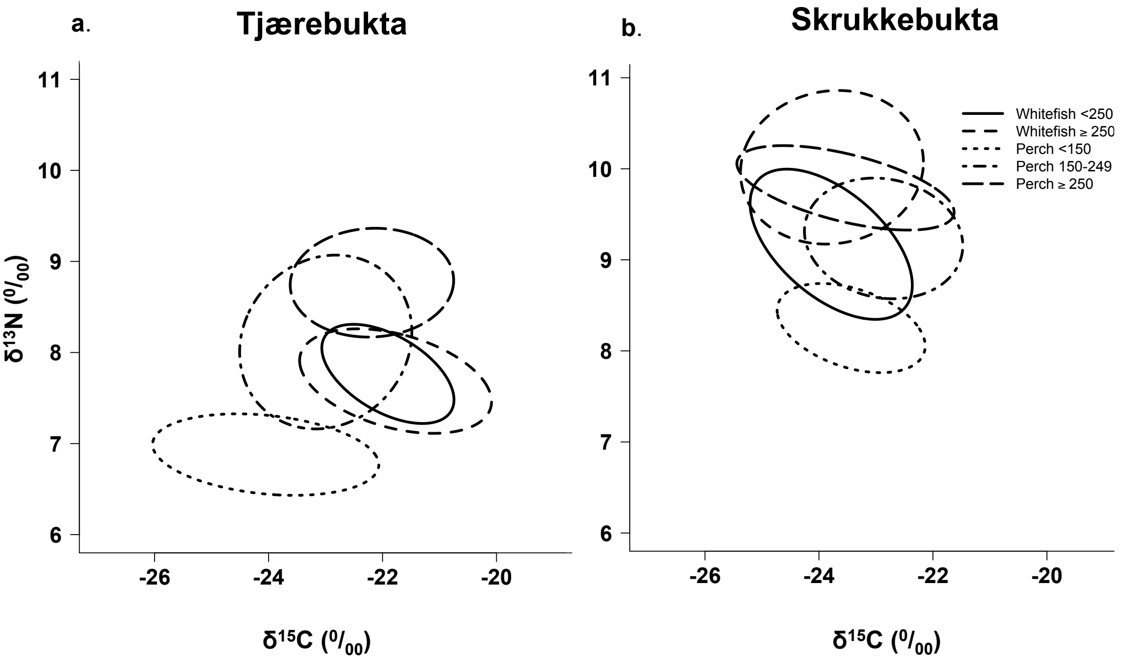

Figure 15 Standard ellipse area (SEA_c) for LSR whitefish and perch caught in Lake Tjærebukta and Lake Skrukkebukta in September 2014. See appendix v for a more detailed graph with the individual fish.

Table 5 Core isotopic overlap (CIO) and overlap of the smallest area (OSA) in % of LSR whitefish and perch of different size groups for (**a.**) Lake Tjærebukta and (**b.**) Lake Skrukkebukta in September 2014.

a.

	CIO				**OSA**			
	W≥250	**P<150**	**P150-249**	**P≥250**	**W≥250**	**P<150**	**P150-249**	**P≥250**
LSR whitefish <250	58.5	0	18.9	2.4	97.9	0	58.3	6.0
LSR whitefish ≥250		0	22.8	1.3		0	48.5	2.6
Perch <150			0.8	0			2.0	0
Perch 150-249				25.5				54.2

b.

	CIO				OSA			
	W≥250	**P<150**	**P150-249**	**P≥250**	**W≥250**	**P<150**	**P150-249**	**P≥250**
LSR whitefish <250	22.1	8.5	8.5	15.7	43.0	21.0	53.6	32.0
LSR whitefish ≥250		0	0	41.4		0	34.7	83.6
Perch <150			8.5	0			1.0	0
Perch 150-249				24.6				44.7

Discussion

This study revealed distinct resource partitioning between LSR whitefish and perch in the two study lakes as hypothesized. LSR whitefish in Tjærebukta had a population specialization on molluscs, with no obvious ontogenetic changes. In Skrukkebukta, LSR whitefish had a different feeding strategy with a generalization both at the population and individual level. They showed a clear ontogenetic dietary niche shift, as small individuals utilized the small benthic crustaceans *Eurycercus lamellatus*, molluscs and insect larvae and large individuals only utilized a variety of insect larvae. In contrast, perch had similar feeding strategies in both lakes, constituting a generalist population with some specialization at the individual level, as expected. Both perch populations showed strong ontogenetic shifts in diet and feeding strategy as smaller individuals ate crustaceans and/or insect larvae while larger individuals specialized on fish. Differences in feeding strategies between the species and in their ontogenetic dietary niche shifts increased the resource partitioning between the two species. Unexpectedly, there were substantial differences in the diet, feeding strategy and resource partitioning of both species between the two localities.

Diet and feeding strategies of LSR whitefish and perch

The diet and feeding strategy of LSR whitefish in Tjærebukta revealed a population specialization towards the snail *Lymnea* sp. Earlier studies in the connected lake Ruskebukta have similarly shown a LSR whitefish diet dominated by molluscs (Amundsen et al. 2004a, Østbye et al. 2006). This population specialization was associated with a narrow diet width and narrow isotopic niche width. Furthermore, LSR whitefish in Tjærebukta had the lowest prevalence for individual specialization out of the four studied fish populations, indicating that the individuals had a diet that was similar to their population’s diet. Strangely, approximately half of the individuals had quite a low individual specialization, while the other half had a very high specialization, towards only one or two prey types. In contrast, the LSR whitefish population in Skrukkebukta showed a population and individual generalization as hypothesized. This was the result of inclusion of *E. lamellatus,* molluscs and insect larvae in the diet of most individuals (i.e. a high within phenotype component). The difference in feeding strategies between the two LSR whitefish populations was reflected by a much lower diet width, isotopic niche width and prevalence of individual specialization in Tjærebukta than in Skrukkebukta. So there was a distinct difference in diet and feeding strategies of LSR whitefish between lakes, whereas LSR whitefish in Tjærebukta had a population specialization in molluscs, the population in Skrukkebukta had a generalist diet both at the population and individual level. Since LSR whitefish is normally regarded as a generalist species (Amundsen 1988), the population specialization in Tjærebukta is a specialization of the realized, not the fundamental niche (Bolnick et al. 2003).

In Tjærebukta, there were no big differences in diet between the different length groups of LSR whitefish. This was reflected by an intermediate to high diet and isotopic niche overlap between the length groups. Unfortunately, it was difficult to conclude from the stable isotope results whether the mollusc diet was a long term diet choice or whether it resulted from a seasonally high consumption of these prey items under e.g. the absence or low availability of other suitable prey. In contrast, LSR whitefish in Skrukkebukta unexpectedly had a quite distinct ontogenetic dietary niche shift from mainly small benthic crustaceans, insect larvae and molluscs to larger insect larvae with increasing length. The low intraspecific diet and isotopic niche overlap between small and large LSR whitefish similarly indicate an ontogenetic diet shift in this population. A similar ontogenetic diet shift in LSR whitefish has been seen before in a lake in northern Finland where it shifted from the small benthic crustacean *E. lamellatus*, to molluscs and eventually to insect larvae (Kahilainen and Østbye 2006). Feeding strategies of LSR whitefish in Skrukkebukta were similar at the population and individual level for fish <250 mm and ≥250 mm. The feeding strategy graph showed that both length groups were generalists with a high within phenotype component. Similar diet widths and isotopic niche widths supported this. Individual specialization was a bit higher for large perch because of the slightly more specialized insect larvae diet. Although the LSR whitefish population in Tjærebukta showed no ontogenetic changes, the population in Skrukkebukta had an ontogenetic shift in diet according to stomach content data.

As hypothesized, the perch populations in both Tjærebukta and Skrukkebukta appeared to be generalist populations, with individual fish specializing on different prey items, in particular among the piscivorous fish. In Tjærebukta the isopod *Assellus aquaticus* was an important prey item for a big part of the population. A large importance of *A. aquaticus* in the diet of perch has also been shown in other studies (e.g. Mccormack 1970, Bye 2005). In Skrukkebukta *E. lamellatus* seemed to take over the role as an important benthic crustacean prey for a large part of the population. In both lakes, perch had a broader diet width than LSR whitefish, supporting that these are generalists at the population level. A similar pattern of diet and isotopic niche width has been seen for perch and LSR whitefish in a lake in north-western Fennoscandia (Hayden et al. 2013). In Tjærebukta perch also had a much broader isotopic niche width than the specialist LSR whitefish, while isotopic niche widths of the two species in Skrukkebukta were very similar. The prevalence of individual dietary specialization in both lakes was higher in perch than in LSR whitefish. This indicates that the individuals within the generalist perch populations are more specialized at the individual level than individuals in both LSR whitefish populations. Although individual specialization might have some trade-offs, it might decrease intraspecific competition greatly (Amundsen 1995, Bolnick et al. 2003). The high prevalence of individual specialization found in perch was similar to the specialization "patterns" observed for littoral perch in a Swedish lake (Quevedo et al. 2009). So both of the perch populations had a generalist feeding strategy at the population level, with specialized individuals.

Perch in Tjærebukta and Skrukkebukta showed clear ontogenetic niche shifts as expected. These shifts in diet and feeding strategy have been shown to maximize the growth rate of an individual, which reduces the individual's risk of being predated upon, increases survival and also reduces intraspecific competition (Werner and Gilliam 1984, Werner 1986). In Tjærebukta and Skrukkebukta the diet shifted with increasing perch length from a specialization in benthic crustaceans, *A. aquaticus* or *E. lamellatus*, respectively, to a specialization in piscivory by large individuals. The shift from a benthic crustacean to a piscivorous diet in perch has been seen before in Pasvik (Amundsen et al. 2003, Bye 2005). As expected there was a clear positive relationship between fish length and the presence of a piscivorous diet (Hjelm et al. 2000, Amundsen et al. 2003). Ninespine sticklebacks were the most important fish prey in Tjærebukta, while coregonids, like whitefish, were the most important fish prey in Skrukkebukta. Coregonids are known to be an important prey for piscivorous perch in other lakes in the area as well (Amundsen et al. 2003, Hayden et al. 2013, 2014). This could mean LSR whitefish and perch are competitors and predator-prey both at the same time (Werner and Gilliam 1984, Werner 1986). Consequently, this could lead to a lower recruitment of LSR whitefish, and to a decrease in competition in favour of perch (Hayden et al. 2013, 2014). Perch also exhibits some cannibalism in both of the lakes. This may cause a decrease in the perch abundance and therefore lead to a decrease in both intra- and interspecific competition (Polis 1988, Persson et al. 2000). In these lakes it is hard to say which one has a larger influence since coregonids are including DR whitefish and vendace as well.

The low to intermediate intraspecific stomach content overlap and isotopic niche overlap between the three different size groups of perch in both Tjærebukta and Skrukkebukta were an indication for ontogenetic diet shifts of perch as well. Besides prey type, feeding strategies changed with perch size as well, as in both lakes the smallest fish had a specialized diet, intermediate fish shifted to a generalist diet with some specialized individuals and the largest fish switched to a specialized diet again. The prevalence of individual specialization also increased with length, supporting the notion that large perch are specialized piscivores. The ontogenetic change in feeding strategy could also be observed from the narrow diet and isotopic niche widths of the smallest and largest size groups, and the broader diet and isotopic niche width of the intermediate sized perch. In Tjærebukta small perch had low $\delta^{13}C$ values, which is in line with the depleted $\delta^{13}C$ value of zooplankton (France 1995) and *A. aquaticus* in Tjærebukta (see Appendix u). Intermediate and big perch had $\delta^{13}C$ values similar to the mean $\delta^{13}C$ value of ninespine sticklebacks and coregonids. In both lakes $\delta^{15}N$ values increased with increasing perch length, suggests an increase in trophic level (Peterson and Fry 1987, Vander Zanden and Rasmussen 1999). Thus $\delta^{13}C$ and $\delta^{15}N$ values complied with the switch from a benthic crustacean to a piscivorous dominated diet (Power et al. 2002). Therefore both stable isotope data and stomach content data support the hypothesis of ontogenetic dietary niche shifts in the perch populations in both lakes.

Normally you would expect a generalist species like LSR whitefish to shift to a more zooplankton/pelagic diet in the presence of a strong benthic competitor like perch (Eloranta et al. 2013). Likewise it is common for perch to utilize zooplankton in early life stages (Hjelm et al. 2000, Amundsen et al. 2003). However in the study lakes the presence of strong pelagic competitors like DR whitefish and vendace might limit LSR whitefish and perch to the littoral zone where they are unable to utilize high amounts of zooplankton (Horppila et al. 2000, Bøhn and Amundsen 2001, Bøhn et al. 2008, Hayden et al. 2014). Thus, the two superior pelagic species could restrict the dietary niches of both LSR whitefish and perch.

Resource partitioning between LSR whitefish and perch

As hypothesized the present study revealed a distinct resource partitioning between LSR whitefish and perch in Tjærebukta, with a low diet overlap (12%) (Wallace 1981). The main differences in diet were that molluscs dominated the LSR whitefish diet, while benthic crustaceans *A. aquaticus* and fish dominated the diet of perch. These differences between the two species were reflected by a lack of overlap in ellipse area in the NMDS graph, and by the low overlap in the isotopic niches suggesting consistent resource partitioning over a longer time period. The more specialist feeding strategy of the LSR whitefish population compared with the generalist perch population was crucial to the low overlap between the two species. Additionally, perch showed clear ontogenetic diet shifts compared to LSR whitefish, therefore there was low diet overlap between all size groups of LSR whitefish and perch. Combined the specialist diet of LSR whitefish and the ontogenetic dietary shifts of perch led to a distinct resource partitioning on the short- and long-term between LSR whitefish and perch.

The study indicates there was less resource partitioning (diet overlap = 53%) between LSR whitefish and perch in Skrukkebukta, with several common prey species such as *E. lamellatus* and insect larvae. The intermediate diet overlap was reflected by some overlap in the ellipse area of the NMDS graph, as well as intermediate overlap in the isotopic niche suggesting a more limited resource partitioning between these two species in Skrukkebukta. Both of the species were generalists with a broad diet width, including mainly the same prey species in their diets. However, both species showed an ontogenetic diet shift, which increased the resource partitioning between both species, especially due to the specialized piscivorous diet of large perch. The ontogenetic shift of perch to a piscivorous diet has been shown to greatly reduce diet overlap with LSR whitefish (Hayden et al. 2013). The highest isotopic niche overlap (41.4%) occurred between large LSR whitefish and large sized perch. This could either mean that the diets of these large fish were more overlapping in the past few months, or it was a consequence of perch feeding on smaller LSR whitefish, with similar $\delta^{13}C$ values, but a lower $\delta^{15}N$ value (trophic level). Taking the stomach content and stable isotope overlap between size groups and populations into account, the study shows there was distinct resource partitioning between LSR whitefish and perch in both lakes, as hypothesized.

Between lake differences

There were considerable between lake differences in LSR whitefish en perch diet, feeding strategies and resource partitioning. Diet similarity between LSR whitefish from both lakes and between perch from both lakes was very low (26.7 and 24.9%, respectively). In addition, feeding strategies of both LSR whitefish populations differed between lakes and resource partitioning between the LSR whitefish and perch populations was much more extensive in Tjærebukta than in Skrukkebukta. One reason for these relatively large between lake differences might be that the abiotic factors in the two lakes are not as similar as expected. The difference in abiotic factors like lake productivity and lake morphology could have influenced the prey availability and number of fish in each population.

Differences in prey type availability and abundance between the two lakes might be a cause for the differences in diet, feeding strategy (diet width) and resource partitioning seen in the two lakes. In Tjærebukta molluscs and *A. aquaticus* were by far the most abundant invertebrate prey type in the stomach contents of all fish, while in Skrukkebukta different insect larvae species and *E. lamellatus* had this role. This was probably a consequence of prey type availability, not a difference in prey type preference between lakes. Since the prey richness in the stomach content of both LSR whitefish and perch was higher in Skrukkebukta than Tjærebukta, this might indicate that the (momentary) prey type availability in Skrukkebukta was higher than in Tjærebukta. It is known there can be distinct differences in zoobenthos richness and density between lakes in the watercourse (Ylikörkkö et al. 2015). The difference in prey richness might explain why diet widths of both species were much broader in Skrukkebukta than Tjærebukta.

Another difference in prey acquisition between lakes was the different ratios of fish species utilized by piscivorous perch in Tjærebukta and in Skrukkebukta. ninespine sticklebacks were dominant in stomach contents of perch in Tjærebukta, while piscivores in Skrukkebukta mainly utilized perch and coregonids. If present in sufficient amounts, ninespine stickleback would most likely be the preferred prey fish species for small and intermediate perch, since it is smaller and therefore can be preyed upon by smaller individuals (Amundsen et al. 2003). Although no data are available on the abundance of ninespine sticklebacks in the two lakes, a plausible reason for this difference may be that ninespine sticklebacks are far less abundant in Skrukkebukta. The fact that perch switched to a piscivorous diet at a bigger length in

Skrukkebukta than in Tjærebukta supports this suggestion. This low abundance of ninespine sticklebacks might have led to a smaller part of the population growing larger than 250 mm (Mittelbach and Persson 1998), which was reflected by the lower number of large perch individuals caught in Skrukkebukta. Because of the later switch to piscivory and the low fraction of large perch, a bigger part of the population consumed similar benthic resources as LSR whitefish. This potentially added to the higher diet overlap with LSR whitefish in Skrukkebukta. So these potential differences in prey type availability between the lakes might have added to the between lake differences in diet, feeding strategies and resource partitioning.

The number of fish in each lake and in each population can also be strongly affected by abiotic factors like lake nutrient availability and lake morphology (Quiros 1990, Jeppesen et al. 1997). CPUE of both LSR whitefish and perch were higher in Skrukkebukta than in Tjærebukta, this might indicate the presence of larger LSR whitefish and perch populations in Skrukkebukta. CPUE has to be used with caution as a measurement of population size though (Peltonen et al. 1999, Linløkken and Haugen 2006). The abundance of LSR whitefish and perch in each lake could influence the intra- and interspecific competition, and therefore feeding strategies and resource partitioning in both lakes. However, more data about fish biomass and prey abundance would be needed to make any conclusions.

As mentioned before, another noticeable between lakes difference was the broader diet width of both species in Skrukkebukta compared to Tjærebukta. Except for a higher prey richness in Skrukkebukta, this could also indicate that the strength of intra- and interspecific competition in the two lakes might differ. According to general niche width theory, a broad population dietary niche and a high prevalence of individual specialization might be an indication of high intraspecific competition (Amundsen 1995, Bolnick et al. 2003, Svanbäck and Persson 2004, Araújo et al. 2011). Thus there might be higher intraspecific competition in both species in Skrukkebukta than in Tjærebukta. In both lakes perch have increased in abundance in the littoral zone probably because of the increasing water temperatures due to climate change (Ylikörkkö et al. 2015). However, there has been a high abundance of perch much longer in Tjærebukta than in Skrukkebukta (Ylikörkkö et al. 2015). The narrow diet width of the specialized LSR whitefish in Tjærebukta might be explained by a longstanding interspecific competition between perch and LSR whitefish (see also e.g. Schoener 1974, Pianka 1994, Mooney and Cleland 2001, Eloranta et al. 2013). This could have eventually led to a distinct resource partitioning between LSR whitefish and perch. Because perch has not been as abundant as long in Skrukkebukta, the interspecific competition probably has been strongly increasing over the years. Therefore the resource partitioning has not fully established yet in Skrukkebukta. This might explain why there was a more distinct resource partitioning in Tjærebukta than in Skrukkebukta.

Climate change can have a large influence on fish species distribution. Every fish species has its own optimal living temperature, which strongly influences species distribution on a local and global scale (Carpenter et al. 1992). Since climate change is leading to an increase in water temperature in subarctic regions, the distribution of fish species have been changing over the last years (Parmesan 2006, Reist et al. 2006, Heino et al. 2009), this is what is observed for the northern distribution of percids (Reist et al. 2006, Ylikörkkö et al. 2015). These distributional changes may lead to new species compositions and cause substantial changes in ecological interactions between sympatric species (Hellmann et al. 2008, Rahel and Olden 2008). It could also lead to an increase in abundance of certain species that are better adapted to the warmer temperature, and therefore have a competitive advantage (Persson 1986, Woodward et al. 2010). This is probably the cause for the increase of perch in the Pasvik watercourse and the rest of northern Scandinavia, as perch has a higher optimal temperature than whitefish (Fiogbé and Kestemont 2003, Siikavuopio et al. 2013, Hayden et al. 2014). Due to these differences in temperature adaptations, the projected temperature changes following the on-going global warming may change the competitive interactions between the LSR whitefish and perch in favor of perch (Hayden et al. 2014). Because of this increase in interspecific competition, these two species with a similar dietary niche should partition their resources, in order to avoid competitive exclusion (of probably LSR whitefish). This is potentially the situation in Tjærebukta, Skrukkebukta and other lakes in northern Scandinavia.

Concluding remarks

The competitive exclusion theory states that two species with very similar dietary niches cannot coexist (Hardin 1960). Therefore, a shift in realized niche and consequently a division in resources between species, resource partitioning, can be a way to escape or decrease this competition (Schoener 1974, Ross 1986). From the present results and other studies, there are examples of resource partitioning between sympatric fish species from freshwater lakes all over the world (Mittelbach 1984, Ross 1986, Langeland et al. 1991, Specziár and Rezsu 2009, Amundsen et al. 2010). Resource partitioning seems an important factor in community structuring. This study showed a distinct resource partitioning on both short- and long-term between LSR whitefish and perch, which was reinforced by differences in feeding strategies and ontogenetic niche shifts between the populations of both species. The conclusion that this was an adaptation in order to escape competition needs to be handled with caution, since there is a number of other requirements that have to be met (Schoener 1974). It is however, a strong indication that on-going interspecific competition has eventually led to resource partitioning between the two coexisting species, with LSR whitefish and perch in Tjærebukta having a more extensive division of their resources. Even though resource partitioning is not the perfect way to study competition in a field situation, it is one of the best methods there is (Schoener 1974, Ross 1986). Since ongoing climate change might lead to new interspecific interactions and changes in community compositions (Parmesan 2006, Reist et al. 2006, Hayden et al. 2014), it is highly important to learn more about competition and the influence this may have on different communities, and the study of resource partitioning is a big part of this.

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Appendix

a. Stomach content in percentage abundance per prey type and other stomach content information of all fork length groups of LSR whitefish caught in Lake Tjærebukta in September 2014.

	150-199	**200-249**	**250-299**	**300-349**	**350-399**	**≥400**	**Pop.**
Zooplankton	**-**	**-**	**-**	**0.1**	**-**	**-**	0.0
Bosmina sp.	-	-	-	-	-	-	-
Daphnia sp.	-	-	-	-	-	-	-
Holopedium sp.	-	-	-	-	-	-	-
Polyphemus sp.	-	-	-	0.1	-	-	0.0
Cyclopoid copepod	-	-	-	-	-	-	-
Calanoid copepod	-	-	-	-	-	-	-
Small benthic crustaceans	**-**	**10.1**	**1.2**	**-**	**-**	**-**	**2.5**
Eurycercus lamellatus	-	10.1	1.2	-	-	-	2.5
Ostracoda	-	-	-	-	-	-	-
Asellus aquaticus	**13.1**	**0.3**	**10.3**	**5.4**	**26.1**	**1.8**	**8.9**
Molluscs	**49.2**	**81.5**	**82.1**	**82.6**	**56.9**	**73.1**	**76.3**
Lymnea sp.	8.2	40.8	56.0	63.7	43.3	66.3	52.3
Planorbis sp.	-	34.6	5.4	4.1	1.4	3.4	10.4
Valvata sp.	41.0	4.8	20.1	14.2	11.8	3.3	12.9
Pisidium sp.	-	1.2	0.6	0.6	0.4	0.0	0.6
Surface insects	**-**	**6.4**	**-**	**-**	**-**	**-**	**1.4**
Insect larvae	**37.7**	**1.7**	**5.9**	**11.9**	**16.9**	**25.1**	**10.7**
Chironomidae larvae	-	0.2	0.8	1.6	0.2	0.0	0.7
Trichoptera with house larvae	37.7	1.2	5.0	10.3	16.7	25.1	9.9
Trichoptera no house larvae	-	0.3	-	-	-	-	0.0
Ephemeroptera larvae	-	-	-	-	-	-	-
Plecoptera larvae	-	-	-	-	-	-	-
Sialidae larvae	-	-	-	-	-	-	-
Unidentified larvae	-	-	0.1	-	-	-	0.0
Bugs and mites	**-**	**-**	**0.1**	**0.0**	**0.0**	**-**	**0.0**
Waterbugs	-	-	0.1	-	-	-	0.0
Watermites	-	-	-	0.0	0.0	-	0.0
Ninespine stickleback (*Pungitius pungitius)*	**-**	**-**	**0.4**	**-**	**-**	**-**	**0.1**
Other fish	**-**	**-**	**-**	**-**	**-**	**-**	**-**
Coregonus sp.	-	-	-	-	-	-	-
Perch (*Perca fluviatilis)*	-	-	-	-	-	-	-
Number of fish	4	13	19	22	15	8	81
Number of stomachs with content	4	13	19	20	14	8	78
Empty stomachs (%)	0.0	0.0	0.0	9.1	6.7	0.0	3.7
Mean stomach fullness (%)	15.3	49.4	44.3	29.2	32.7	37.4	36.7
Mean stomach fullness (excl. empty stomachs) (%)	15.3	49.4	44.3	32.1	35.0	37.4	38.1

b. Stomach content in percentage abundance per prey type and other stomach content information of all fork length groups of perch caught in Lake Tjærebukta in September 2014. *Size groups with only one individual with stomach content were taken out of further length group data analyses.

	<100	**100-149**	**150-199**	**200-249**	**250-299**	**≥300**	**Pop.**
Zooplankton	**8.6**	**-**	**-**	**2.7**	**-**	**-**	**2.4**
Bosmina sp.	-	-	-	-	-	-	-
Daphnia sp.	-	-	-	-	-	-	-
Holopedium sp.	-	-	-	-	-	-	-
Polyphemus sp.	0.7	-	-	2.7	-	-	0.5
Cyclopoid copepod	-	-	-	-	-	-	-
Calanoid copepod	7.9	-	-	-	-	-	1.9
Small benthic crustaceans	**2.0**	**-**	**-**	**-**	**-**	**-**	**0.5**
Eurycercus lamellatus	2.0	-	-	-	-	-	0.5
Ostracoda	-	-	-	-	-	-	-
Asellus aquaticus	**71.4**	**56.3**	**38.3**	**32.0**	**4.7**	**100.0**	**39.7**
Molluscs	**-**	**-**	**-**	**5.0**	**6.2**	**-**	**2.2**
Lymnea sp.	-	-	-	5.0	6.2	-	2.2
Planorbis sp.	-	-	-	-	-	-	-
Valvata sp.	-	-	-	-	-	-	-
Pisidium sp.	-	-	-	-	-	-	-
Surface insects	**-**	**-**	**-**	**-**	**-**	**-**	-
Insect larvae	**7.9**	**-**	**21.5**	**7.3**	**1.6**	**-**	**8.3**
Chironomidae larvae	-	-	-	-	-	-	-
Trichoptera with house larvae	-	-	0.9	-	-	-	0.2
Trichoptera no house larvae	-	-	5.8	1.6	1.1	-	1.8
Ephemeroptera larvae	-	-	-	-	-	-	-
Plecoptera larvae	-	-	-	-	-	-	-
Sialidae larvae	-	-	-	-	-	-	-
Unidentified larvae	7.9	-	14.8	5.7	0.5	-	6.2
Bugs and mites	**-**	**-**	**3.4**	**-**	**-**	**-**	**0.8**
Waterbugs	-	-	3.4	-	-	-	0.8
Watermites	-	-	-	-	-	-	-
Ninespine stickleback (*Pungitius pungitius*)	**10.1**	**34.6**	**24.4**	**25.9**	**50.6**	**-**	**29.3**
Other fish	**-**	**9.1**	**12.5**	**27.0**	**36.9**	**-**	**16.8**
Coregonus sp.	-	9.1	12.5	27.0	10.1	-	10.1
Perch (*Perca fluviatilis*)	-	-	-	-	26.8	-	6.8
Number of fish	20	10	23	22	37	3	115
Number of stomachs with content	14	8	16	14	27	1*	80
Empty stomachs (%)	0.30	0.2	30.4	36.4	27.0	66.7	30.4
Mean stomach fullness (%)	44.4	54.9	38.3	19.9	25.2	0.3	32.1
Mean stomach fullness (excl. empty stomachs) (%)	63.4	68.6	55.1	31.2	34.6	1.0	46.1

c. Stomach content in percentage abundance per prey type and other stomach content information of all fork length groups of LSR whitefish caught in Lake Skrukkebukta in September 2014. * Size groups with only one individual with stomach content were taken out of further length group data analyses.

	<150	**150-199**	**200-249**	**250-299**	**≥300**	**Pop.**
Zooplankton	**10.0**	**3.2**	**1.3**	**1.2**	**-**	**1.6**
Bosmina sp.	-	-	-	-	-	-
Daphnia sp.	-	-	-	-	-	-
Holopedium sp.	-	-	-	-	-	-
Polyphemus sp.	-	-	0.4	1.1	-	0.4
Cyclopoid copepod	10.0	3.2	0.9	0.1	-	1.2
Calanoid copepod	-	-	-	-	-	-
Small benthic crustaceans	**80.0**	**46.4**	**39.3**	**12.8**	**-**	**32.2**
Eurycercus lamellatus	80.0	46.2	39.2	12.8	-	32.1
Ostracoda	-	0.1	0.1	-	-	0.1
Asellus aquaticus	**-**	**-**	**-**	**-**	**-**	**-**
Molluscs	**-**	**20.3**	**24.8**	**15.0**	**0.8**	**19.8**
Lymnea sp.	-	-	0.9	10.1	-	2.6
Planorbis sp.	-	-	-	-	-	-
Valvata sp.	-	9.5	14.6	0.2	-	9.3
Pisidium sp.	-	10.8	9.3	4.7	0.7	8.0
Surface insects	**-**	**-**	**1.2**	**0.9**	**-**	**0.8**
Insect larvae	**10.0**	**30.1**	**32.9**	**69.8**	**98.8**	**45.2**
Chironomidae larvae	10.0	0.4	5.1	10.2	19.0	6.3
Trichoptera with house larvae	-	15.3	21.8	33.7	63.1	26.1
Trichoptera no house larvae	-	3.2	-	2.5	-	1.2
Ephemeroptera larvae	-	10.1	3.6	18.2	14.7	9.0
Plecoptera larvae	-	-	0.3	-	0.7	0.2
Sialidae larvae	-	-	1.0	3.7	0.7	1.3
Unidentified larvae	-	1.3	1.1	1.5	0.7	1.2
Bugs and mites	**-**	**-**	**0.5**	**0.3**	**0.4**	**0.3**
Waterbugs	-	-	-	-	0.4	0.0
Watermites	-	-	0.5	0.3	-	0.3
Ninespine stickleback (*Pungitius pungitius)*	**-**	**-**	**-**	**-**	**-**	**-**
Other fish	**-**	**-**	**-**	**-**	**-**	**-**
Coregonus sp.	-	-	-	-	-	-
Perch (*Perca fluviatilis)*	-	-	-	-	-	-
Number of fish	1	19	48	20	7	95
Number of stomachs with content	1*	16	35	17	7	76
Empty stomachs (%)	0.0	15.8	27.1	0.2	0.0	20.0
Mean stomach fullness (%)	10.0	41.8	38.7	40.6	40.7	39.6
Mean stomach fullness (excl. empty stomachs) (%)	10.0	49.6	53.1	47.8	40.7	49.5

d. Stomach content in percentage abundance per prey type and other stomach content information of all fork length groups of perch caught in Lake Skrukkebukta in September 2014.

	<100	**100-149**	**150-199**	**200-249**	**250-299**	**≥300**	**Pop.**
Zooplankton	**21.5**	**14.4**	**19.2**	**0.9**	**-**	**-**	**11.4**
Bosmina sp.	-	-	0.1	-	-	-	0.0
Daphnia sp.	-	0.9	0.7	0.1	-	-	0.4
Holopedium sp.	-	-	0.3	-	-	-	0.1
Polyphemus sp.	11.6	8.6	18.1	0.8	-	-	8.6
Cyclopoid copepod	-	0.1	-	-	-	-	0
Calanoid copepod	10.0	4.7	0.1	-	-	-	2.2
Small benthic crustaceans	**73.6**	**58.5**	**22.7**	**0.8**	**-**	**-**	**28.9**
Eurycercus lamellatus	73.6	58.5	22.7	0.8	-	-	28.9
Ostracoda	-	-	-	-	-	-	-
Asellus aquaticus	**-**	**-**	**-**	**-**	**-**	**-**	**-**
Molluscs	**-**	**0.2**	**-**	**-**	**-**	**-**	**0.1**
Lymnea sp.	-	-	-	-	-	-	-
Planorbis sp.	-	-	-	-	-	-	-
Valvata sp.	-	0.2	-	-	-	-	0.1
Pisidium sp.	-	-	-	-	-	-	-
Surface insects	**-**	**5.6**	**-**	**2.7**	**-**	**-**	**2.1**
Insect larvae	**4.8**	**21.3**	**43.3**	**43.3**	**0.5**	**-**	**28.4**
Chironomidae larvae	4.8	1.2	2.4	-	-	-	1.5
Trichoptera with house larvae	-	10.3	26.9	30.9	-	-	17.5
Trichoptera no house larvae	-	4.9	7.9	8.7	-	-	5.5
Ephemeroptera larvae	-	0.6	0.5	3.7	-	-	1.2
Plecoptera larvae	-	3.9	3.4	-	-	-	2.0
Sialidae larvae	-	-	1.1	-	-	-	0.3
Unidentified larvae	-	0.4	1.2	-	0.5	-	0.5
Bugs and mites	**-**	**-**	**-**	**-**	**-**	**-**	**-**
Waterbugs	-	-	-	-	-	-	-
Watermites	-	-	-	-	-	-	-
Ninespine stickleback (*Pungitius pungitius*)	**-**	**-**	**6.2**	**9.3**	**7.1**	**-**	**4.4**
Other fish	**-**	**-**	**8.5**	**42.9**	**92.4**	**100.0**	**24.7**
Coregonus sp.	-	-	8.5	26.9	73.5	100.0	19.6
Perch (*Perca fluviatilis*)	-	-	-	16.0	19.0	-	5.0
Number of fish	13	24	26	40	19	7	127
Number of stomachs with content	11	20	18	20	6	4	78
Empty stomachs (%)	15.4	16.7	30.8	50.0	68.4	42.9	38.6
Mean stomach fullness (%)	23.9	34.3	34.1	18.8	11.7	31.8	25.0
Mean stomach fullness (excl. empty stomachs) (%)	28.3	41.1	49.2	37.5	35.2	47.8	40.7

e. Schoener's index comparing the stomach contents of each length group within LSR whitefish caught in Lake Tjærebukta in September 2014.

	200-249	**250-299**	**300-349**	**350-399**	**≥400**
150-199	14.6	43.6	38.1	49.9	38.5
200-249		54.5	52.0	49.2	49.2
250-299			**86.1**	**72.5**	**69.6**
300-349				**72.8**	**82.6**
350-399					**66.7**

f. Schoener's index comparing the stomach contents of each length group within perch caught in Lake Tjærebukta in September 2014.

	100-149	**150-199**	**200-249**	**250-299**
<100	**66.4**	56.3	48.6	15.4
100-149		**71.8**	**67.0**	48.4
150-199			**76.2**	40.8
200-249				47.3

g. Schoener's index comparing the stomach contents of each length group within LSR whitefish caught in Lake Skrukkebukta in September 2014.

	200-249	**250-299**	**≥300**
150-199	**79.4**	47.3	27.2
200-249		52.9	33.0
250-299			**60.8**

h. Schoener's index comparing the stomach contents of each length group within perch caught in Lake Skrukkebukta in September 2014.

	100-149	**150-199**	**200-249**	**250-299**	**≥300**
<100	**73.1**	36.8	1.6	0.0	0.0
100-149		52.8	20.2	0.4	0.0
150-199			51.6	15.1	8.5
200-249				50.0	26.9
250-299					**73.5**

i. Statistical outcome of the logistic regression model for fork length and the presence (1) or absence (0) of a piscivorous diet in Perch caught in Lake Tjærebukta and Lake Skrukkebukta in September 2014, with the estimated length at which 50% of the fish have switched to a piscivorous diet (and its 95% confidence interval).

Lake	Parameter	Value	P-value	Probability 0.5	95% CI
Tjærebukta	a constant	-2.598	0.001	187 mm	140-225
	b regression slope	0.014	0.000		
Skrukkebukta	a constant	-6.577	0.000	215 mm	195-244
	b regression slope	0.031	0.000		

j. Levins' index (bold is population diet width) and mean 1-IS ± SD for all fork length groups of fish caught in Lake Tjærebukta in September 2014.

Length	Levins' index	1-IS
LSR whitefish	**3.12**	**0.60 ± 0.21**
150-199	2.99	0.81 ± 0.11
200-249	3.30	0.61 ± 0.24
250-299	2.70	0.62 ± 0.22
300-349	2.27	0.55 ± 0.19
350-399	3.36	0.57 ± 0.21
≥400	1.98	0.60 ± 0.22
Perch	**3.80**	**0.68 ± 0.16**
<100	1.87	0.67 ± 0.14
100-149	2.25	0.56 ± 0.09
150-199	4.03	0.67 ± 0.22
200-249	4.01	0.74 ± 0.14
250-299	2.91	0.69 ± 0.13

k. Levins' index (bold is population diet width) and mean 1-IS ± SD for all fork length groups of fish caught in Lake Skrukkebukta in September 2014. (* only one individual)

Length	Levins' index	1-IS
LSR whitefish	**5.02**	**0.63 ± 0.13**
< 150	*	0.61
150-199	3.70	0.62 ± 0.12
200-249	4.25	0.56 ± 0.08
250-299	5.31	0.77 ± 0.12
≥300	2.20	0.68 ± 0.11
Perch	**5.90**	**0.73 ± 0.12**
<100	1.76	0.69 ± 0.09
100-149	2.70	0.68 ± 0.10
150-199	5.69	0.70 ± 0.13
200-249	4.71	0.81 ± 0.11
250-299	1.72	0.82 ± 0.08
≥300	1.00	0.80 ± 0.00

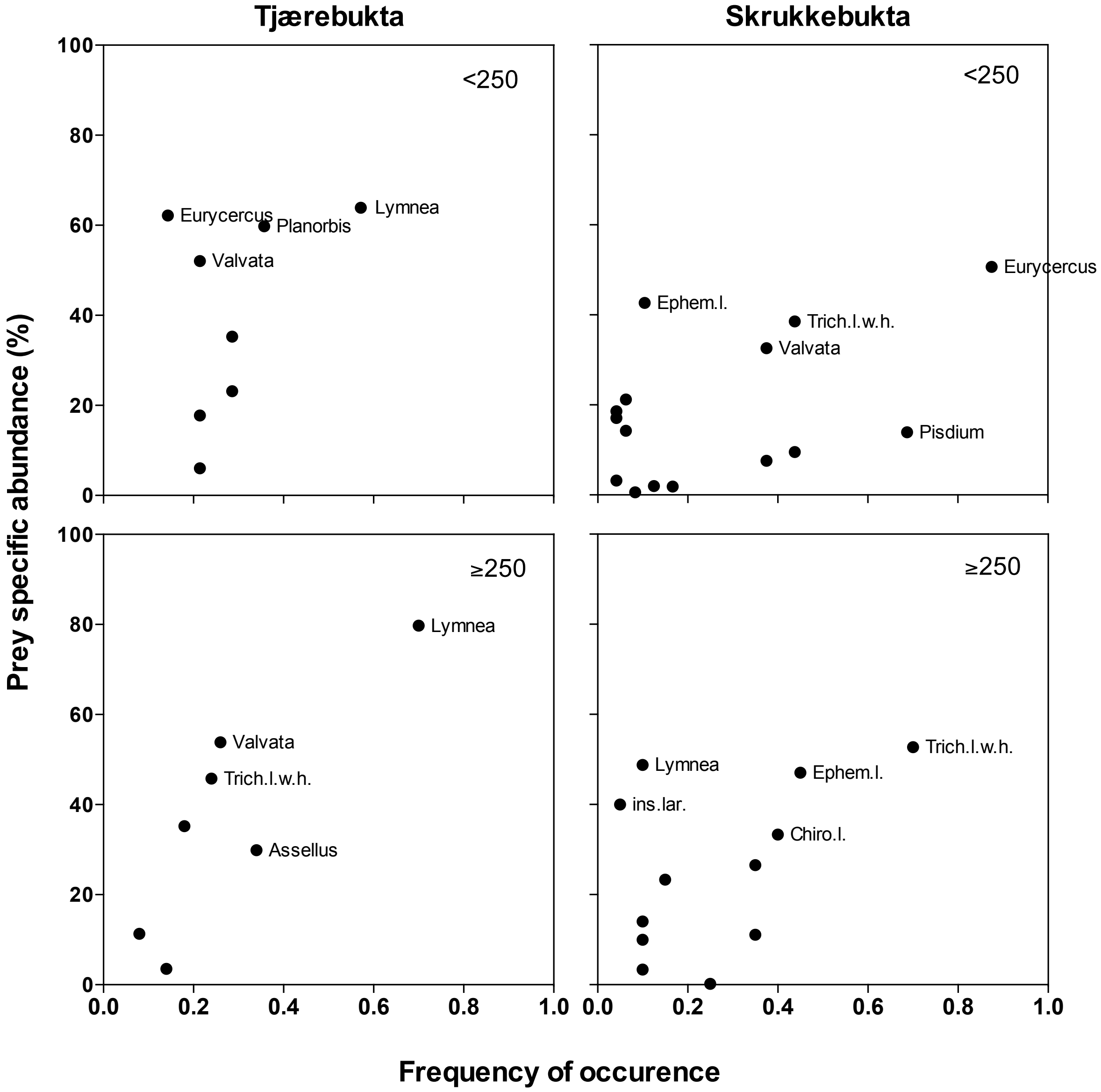
l. Outcome of Mann-Whitney U test on mean ranks of 1-SD, comparing whitefish and perch caught in September 2014 in Tjærebukta and Skrukkebukta.

Lake	Species	Mean rank	U	N	P
Tjærebukta					
	LSR whitefish	57.33	1589	134	0.004*
	Perch	76.80			
Skrukkebukta					
	LSR whitefish	51.78	1175	138	0.000*
	Perch	86.71			

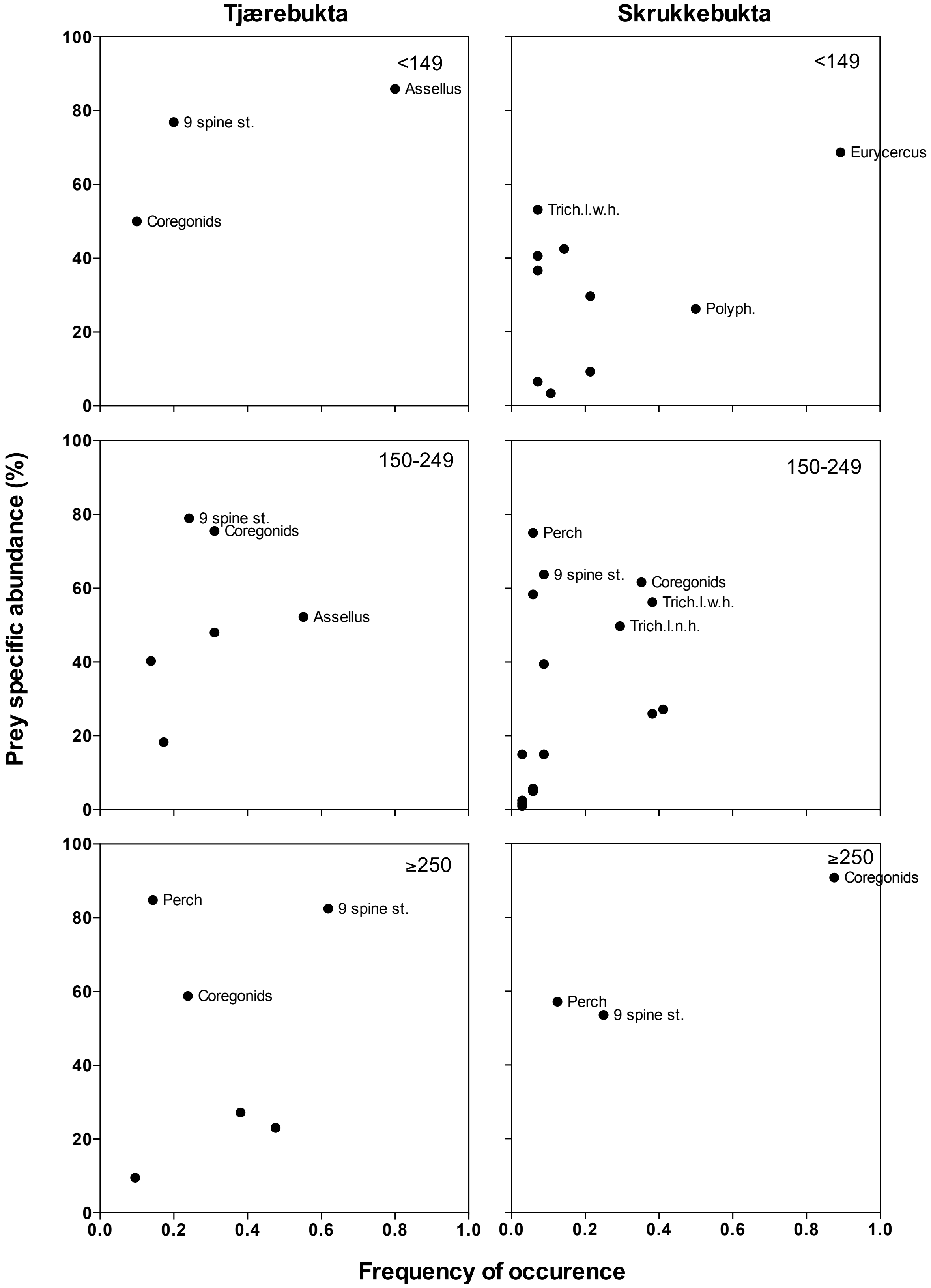
m. Outcome of Mann-Whitney U test on mean ranks of 1-SD, comparing whitefish and perch caught in September 2014 between Lake Tjærebukta and Lake Skrukkebukta.

Species	Lake	Mean rank	U	N	P
LSR whitefish					
	Tjærebukta	59.73	1743	132	0.048*
	Skrukkebukta	72.87			
Perch					
	Tjærebukta	60.33	1738	140	0.003*
	Skrukkebukta	80.67			

n. Feeding strategy for two fork length groups (<250, ≥250) of LSR whitefish caught in Lake Tjærebukta and Lake Skrukkebukta in September 2014.



o. Feeding strategy for three fork length groups (<150, 150-249, ≥250) of perch caught in Lake Tjærebukta and Lake Skrukkebukta in September 2014.



p. Harmonic mean δ^{13}C per size group (mm) of LSR whitefish and perch caught in Lake Tjærebukta in September 2014, and outcome of a multiple comparison Tukey HSD test.

Fish group (I)	Mean δ^{13}C ($^{0}/_{00}$)	Fish group (J)	Mean difference (I-J)	SE	P-value
LSR whitefish <250	-21.90				
		LSR whitefish ≥250	-0.154	0.441	0.997
		Perch <150	2.144	0.639	**0.009***
		Perch 150-249	1.032	0.491	0.226
		Perch ≥250	0.280	0.475	0.976
LSR whitefish ≥250	-21.75				
		Perch <150	2.299	0.556	**0.001***
		Perch 150-249	1.186	0.376	**0.017***
		Perch ≥250	0.435	0.354	0.736
Perch <150	-24.05				
		Perch 150-249	-1.112	0.596	0.342
		Perch ≥250	-1.864	0.583	**0.015***
Perch 150-249	-22.94				
		Perch ≥250	-0.752	0.415	0.373
Perch ≥250	-22.19				

q. Harmonic mean δ^{15}N per size group (mm) of whitefish and perch caught in Lake Tjærebukta in September 2014, and outcome of a multiple comparison Tukey HSD test.

Fish group (I)	Mean δ^{15}N ($^{0}/_{00}$)	Fish group (J)	Mean difference (I-J)	SE	P-value
LSR whitefish <250	7.77				
		LSR whitefish ≥250	0.045	0.186	0.999
		Perch <150	0.886	0.270	**0.012***
		Perch 150-249	-0.248	0.208	0.756
		Perch ≥250	-1.002	0.201	**0.000***
LSR whitefish ≥250	7.72				
		Perch <150	0.841	0.235	**0.004***
		Perch 150-249	-0.293	0.159	0.355
		Perch ≥250	-1.047	0.150	**0.000***
Perch <150	6.88				
		Perch 150-249	-1.134	0.252	**0.000***
		Perch ≥250	-1.888	0.247	**0.000***
Perch 150-249	8.01				
		Perch ≥250	-0.754	0.176	**0.000***
Perch ≥250	8.77				

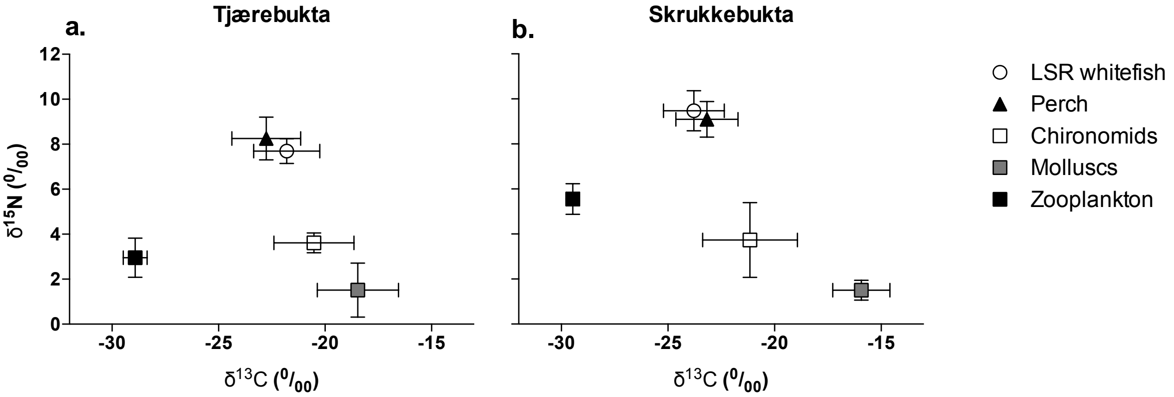
r. Harmonic mean δ^{13}C per size group (mm) of whitefish and perch caught in Lake Skrukkebukta in September 2014, and outcome of a multiple comparison Tukey HSD test.

Fish group (I)	**Mean δ^{13}C ($^{0}/_{00}$)**	**Fish group (J)**	**Mean difference (I-J)**	**SE**	**P-value**
LSR whitefish <250	-23.79				
		LSR whitefish ≥250	-0.013	0.480	1.000
		Perch <150	-0.350	0.460	0.941
		Perch 150-249	-0.920	0.388	0.133
		Perch ≥250	-0.251	0.492	0.986
LSR whitefish ≥250	-23.77				
		Perch <150	-0.337	0.530	0.969
		Perch 150-249	-0.906	0.469	0.307
		Perch ≥250	-0.238	0.558	0.993
Perch <150	-23.44				
		Perch 150-249	-0.569	0.448	0.710
		Perch ≥250	0.100	0.541	1.000
Perch 150-249	-22.87				
		Perch ≥250	0.669	0.481	0.635
Perch ≥250	-23.53				

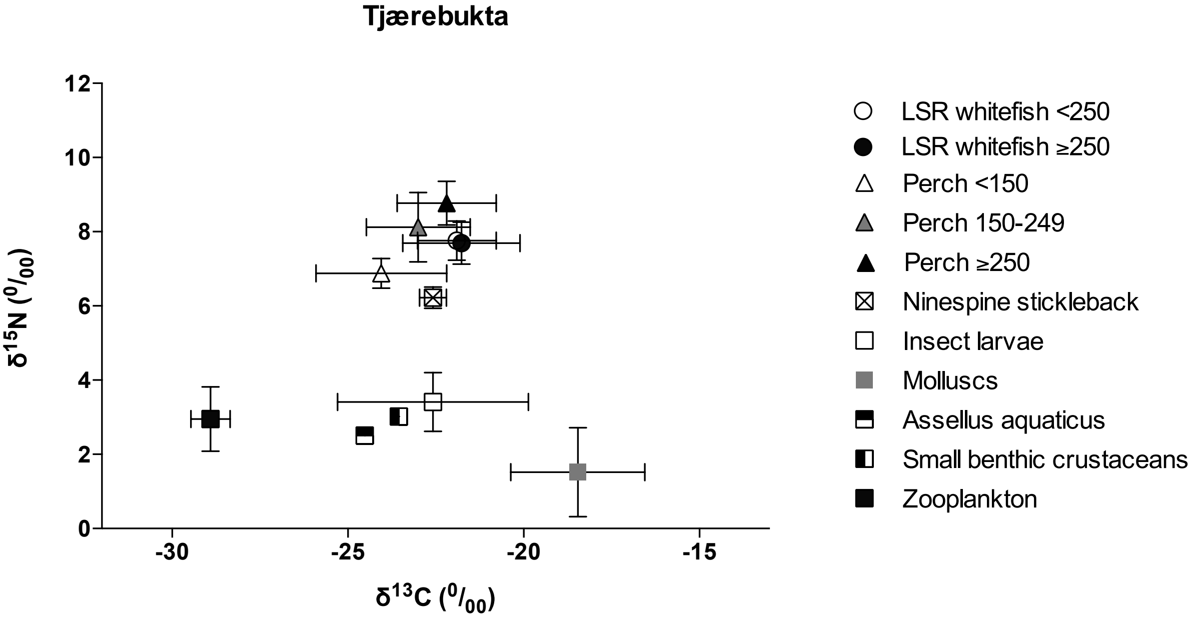
s. Harmonic mean δ^{15}N per size group (mm) of whitefish and perch caught in Lake Skrukkebukta in September 2014, and outcome of a multiple comparison Tukey HSD test.

Fish group (I)	Mean δ^{15}N **($^{0}/_{00}$)**	**Fish group (J)**	**Mean difference (I-J)**	**SE**	**P-value**
LSR whitefish <250	9.17				
		LSR whitefish ≥250	-0.845	0.224	**0.003***
		Perch <150	0.921	0.215	**0.000***
		Perch 150-249	-0.064	0.181	0.997
		Perch ≥250	-0.620	0.229	0.061
LSR whitefish ≥250	10.02				
		Perch <150	1.766	0.247	**0.000***
		Perch 150-249	0.781	0.219	**0.005***
		Perch ≥250	0.226	0.260	0.908
Perch <150	8.25				
		Perch 150-249	-0.985	0.209	**0.000***
		Perch ≥250	-1.540	0.252	**0.000***
Perch 150-249	9.24				
		Perch ≥250	-0.555	0.224	0.105
Perch ≥250	9.79				

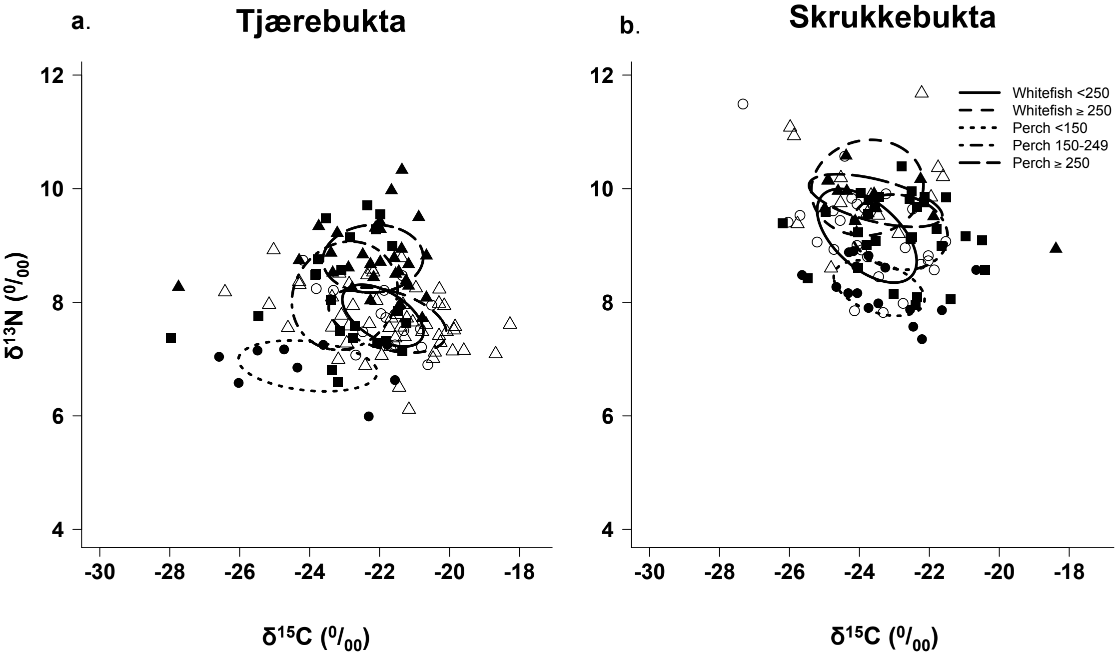
t. Stable isotope biplots showing the mean (±SD) δ^{13}C and δ^{15}N values of fish muscle tissue from LSR whitefish (○) and perch (▲) and of three prey groups from **a.** Lake Tjærebukta (collected by Kahilainen and Kelly) and **b.** Lake Skrukkebukta (collected by Kelly).



u. Stable isotope biplots showing the mean (±SD) δ^{13}C and δ^{15}N values of fish muscle tissue from LSR whitefish (○) and perch (▲) of different size groups (mm) and different prey items from Lake Tjærebukta (collected by Kahilainen and Kelly).



v. SEA$_c$ and convex hulls for LSR whitefish (<250○, >250△) and perch (<150●, 150-250■, >250▲) caught in Lake Tjærebukta and Lake Skrukkebukta in September 2014.



w. Estimated isotopic niches (SEA$_C$, SEA$_B$ = mean and upper and lower 95% Bayesian credibility intervals for standard elipse are) and convex hull total area (TA) of different size groups of whitefish and perch caught in Tjærebukta and Skrukkebukta in September 2014.

Lake	**Fish species**	**N**	**SEA$_C$ ($^0/_{00}{}^2$)**	**SEA$_B$ ($^0/_{00}{}^2$)**	**TA ($^0/_{00}{}^2$)**
Tjærebukta					
	Whitefish <250	16	1.69	2.05 (1.15-3.09)	4.25
	Whitefish ≥250	52	2.79	2.91 (2.15-3.71)	12.72
	Perch <150	9	2.70	3.5 (1.57-5.93)	4.21
	Perch 150-249	23	4.50	4.45 (2.78-6.33)	11.94
	Perch ≥250	30	2.69	2.83 (1.90-3.89)	9.53
Skrukkebukta					
	Whitefish <250	26	3.09	3.19 (2.05-4.45)	9.51
	Whitefish ≥250	14	4.24	4.24 (2.25-6.63)	9.23
	Perch <150	16	1.83	2.22 (1.24-3.36)	3.96
	Perch 150-249	30	2.87	2.96 (1.97-4.08)	9.19
	Perch ≥250	13	2.27	3.03 (1.59-4.73)	4.98