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**The effect of climate change on the fish community in Lille Rostavatn,
northern Norway**

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Abstract

Over the last 20 years there has been a large change in the fish community structure in Lille Rostavatn, northern Norway. The relative contribution of the cold-water adapted fish species, Arctic charr (*Salvelinus alpinus*) and burbot (*Lota lota*), has distinctly decreased whereas the more temperate-adapted fish species, grayling (*Thymallus thymallus*) and brown trout (*Salmo trutta*), have increased, presumably because of a rise in water temperature which is shown to be a significant increase in the Målselv watercourse from 1991 to 2018. In this study the spatial and temporal variation in relative contribution, habitat use, and diet of these four fish species were studied from four years of gill net sampling in August and October between 1997 and 2018, exploring general patterns in resource partitioning and possible climate-related changes in habitat and dietary utilization.

Arctic charr dominated the total catches, followed by grayling. A distinct resource segregation was observed between the cold-water and the temperate-adapted fish species according to habitat use and the selection of specific prey types, especially in the littoral habitat. The habitat partitioning was particularly clear in August, when the cold-water adapted fish species decreased in densities in the littoral habitat over time. In October, at lower water temperatures, Arctic charr and burbot, showed a minor increase in the littoral catches. The dietary overlap between the species were in general low and the intraspecific dietary similarity showed high overlap between the four years, indicating small changes in resource utilization over time. Analysis of stomach content revealed a narrow trophic niche of Arctic charr as they fed mainly on zooplankton in all habitats of the lake. Previous field studies from Lille Rostavatn have demonstrated that Arctic charr are adapted to a planktivore diet due to strong interspecific resource competition for the benthic resources by burbot and in the more recent years this may have been amplified due to increasing grayling and brown trout population. The diet of burbot was dominated mainly by benthic invertebrates in all habitats whereas grayling and brown trout consumed surface insects and benthic invertebrates. These findings suggest that interspecific competition leading to changes in resource partitioning under a changing climate is not the key factor influencing the shift in fish community structure in Lille Rostavatn. The observed resource segregation might be a result of biotic interactions mediated by abiotic conditions.

1 Introduction

Climate change is considered to be one of the most severe threats to ecosystems around the globe (ACIA 2004, IPCC 2014). Ecosystems at high latitudes are experiencing some of the most rapid and severe climate change on earth with an temperature increase twice as large as the rest of the global average (Taylor et al. 2017). For instance, in northern Norway air temperature has increased 0.1°C per decade during the latest 100 years (Førland et al. 2009). There have been major biological changes in the structure and functioning of aquatic ecosystems due to climate change both in the past (eg., Magnuson et al. 2000, ACIA 2004, Jeppesen et al. 2012) and in future model-based projections (eg., IPCC 2014, Bryndum-Buchholz et al. 2019, Smalås et al. 2020). Studies have shown that the chemical and physical features of a lake are affected by climate change and thereby affect the whole ecosystem composition and function (Poff et al. 2002, Prowse et al. 2006, Wrona et al. 2006, Jeppesen et al. 2010, Woodward et al. 2010). This will influence the seasonal and annual ecosystem productivity in the lake and the habitat suitability for e.g., fish species, and thus the species composition and abundance. It is predicted that at high latitudes, more warm-water adapted fish species will benefit from warming and displace more cold-water adapted fish species (Jeppesen et al. 2010). Here, I study how the species composition of freshwater fish, and their resource use, change through time in high latitude ecosystem related to the ongoing climate warming.

Freshwater ecosystems at high latitudes are complex and highly diverse with respect to size, connectivity, structure and function (Reist et al. 2006). These ecosystems are also pristine systems with relatively low effects of direct human activity, such as fishing and agriculture (Reist et al. 2016). Oligotrophic high-latitude lakes often consist of a small number of species at various trophic levels and most of the primary and secondary production typically occurs in the littoral habitat (Eloranta et al. 2015). As climate warms, and the ice cover period decrease, the water temperature increase will likely lead to a general increase in freshwater productivity and longer growth seasons. Temperature is the driver of many biological processes in freshwater ecosystems (Wetzel 2001), including physiological variables in fish such as the amount of resources that is required for growth and reproduction (Myrick and Cech 2000). This is particularly important for ectothermic fish species that rely on environmental temperatures to control their internal temperatures (Jeppesen et al. 2010). Even small increases in ambient water temperature may preclude some fish species from specific aquatic

habitats as conditions above their thermal optima are likely to stress populations to such an extent that they avoid certain habitats (Wrona et al. 2006).

In freshwater ecosystems at high latitudes, cold-water adapted salmonids are the dominant fish species and they play a central ecological role in the ecosystem (Smalås et al. 2020). Resource competition and predatory interactions might be amongst the main factors influencing the resource use by top predators and thus, important factors in shaping communities (Werner 1986). The use of resources by organisms has a major influence on population and community interactions and species rarely get to utilize their fundamental niche due to the presence of other species (Werner 1986). However, the effects of a narrower niche due to interspecific competition might contribute to facilitate the coexistence of species with similar ecology (Jensen et al. 2017). Resource partitioning is often used as an indication of the presence of interspecific competition (Schoener 1974, 1986). Shifts in resource utilization can include changes in the choice of prey and habitat and generalist species can adapt their diet in response to prey availability and interspecific interactions (Eloranta et al. 2013). On the other hand, resource partitioning does not need to be a consequence of competition. Physiological restraints, tolerance to environmental change, predation risk and prey availability might also be reasons for species to segregate (Schoener 1974, Ross 1986). Temperature has a strong effect on the foraging behavior of individuals (Woodward et al. 2010) and the strength of interactions between the organisms and ecosystem components such as food webs and interspecific components may be altered with temperature changes. Complex changes in fish community structure may be expected with climate change due to both direct and indirect effects on fish metabolism and biotic interactions (Jeppesen et al. 2010).

Arctic charr (*Salvelinus alpinus*), brown trout (*Salmo trutta*), burbot (*Lota lota*) and European grayling (*Thymallus thymallus*, hereafter referred to as grayling) are all common fish species in lake systems in northern Fennoscandia. In the present thesis, the fish species have been grouped into two thermal guilds defined by their thermal niches: temperate-adapted fish species (preferred summer temperatures centered upon 13-18 °C; Northcote 1995, Larsson 2005, Ingram et al. 2013) and cold-water adapted fish species (10-12 °C; Hofmann and Fischer 2002, Siikavuopio et al. 2014). Cold-water adapted fish species such as Arctic charr and burbot have lower thermal optima than temperate-adapted fish species like grayling and

brown trout. Thus, it is expected a shift in dominance of the fish community structure, not only on as a direct effect of temperature, but also as a result of superior competition with more warm-water adapted fish species. Arctic charr is the most cold-water adapted salmonid and hence also the salmonid with the lowest tolerance to increased water temperature (Siikavuopio et al. 2014). Arctic charr is considered to have an opportunistic behavior and wide trophic niche, both in habitat and dietary use (Klemetsen et al. 2003, Eloranta et al. 2013, Reist et al. 2013). However, their wide trophic niche is often restricted because of interspecific interactions with sympatric fish species such as burbot (Knudsen et al. 2010), grayling (Amundsen et al. 2010, Eloranta et al. 2011) and brown trout (Langeland et al. 1991, Forseth et al. 2003, Amundsen and Knudsen 2009). These fish species prefer to use the littoral habitat as this is the most productive, diverse and best foraging habitat in the lake (Karlsson and Byström 2005). Arctic charr tend to shift towards a more pelagic zooplanktivore diet in the presence of strong benthivorous competitors (Klemetsen et al. 2003). Burbot is a cold-water, benthic and omnivorous species (Hofmann and Fischer 2001, Knudsen et al. 2010). Burbot is a strong predator on young Arctic charr and Arctic charr tend to utilize more zooplankton in lakes with high burbot densities (Knudsen et al. 2010). There is also a clear resource partitioning between Arctic charr and brown trout in sympatry (Nilsson 1967, Langeland et al. 1991, Klemetsen et al. 2003). Brown trout are often found to dominate the littoral habitat whereas Arctic charr are often relegated to the pelagic or profundal habitat to avoid both competition and predation. Grayling tend to occupy the littoral habitat feeding on benthos and aquatic insects. Both grayling and brown trout are considered to be more territorial and aggressive feeders with a higher temperature tolerance than Arctic charr and burbot (Northcote 1995, McPhail and Paragamian 2000, Larsson 2005, Elliott and Elliott 2010). This difference in thermal tolerance may be more beneficial for grayling and brown trout under a warming climate providing a competitive edge that might lead to the decline of Arctic charr and burbot populations.

The study site, Lille Rostavatn, is a subarctic, oligotrophic lake in northern Norway. In 1997, cold-water adapted fish species like Arctic charr and burbot dominated the lake (Knudsen et al. 2010), whereas grayling and brown trout have become more prevalent in more recent years (Eloranta et al. 2013). Fish metabolism and the biotic interactions among fish species are expected to change with climate warming (Jeppesen et al. 2010). The aim of this study was to explore the long-term changes in the fish community at Lille Rostavatn within a period with strong change in climate including also dietary studies of the dominant fish species, which

could reveal any changes in their resource partitioning patterns. Therefore, I hypothesized that (1) there would be distinct changes in the fish community structure of the lake during the study period related to the ongoing climate warming. I expect that the temperate-adapted fish species, grayling and brown trout, will have an increase in their population densities and be the dominant species in the littoral zone in the most recent years. Furthermore, the cold-water adapted fish species, Arctic charr and burbot, will expectedly have an overall decline in population densities and/or a shift in habitat utilization to deeper and colder waters during warm water summer periods. (2) The change in fish species composition will influence the habitat and diet utilization of the cold-water adapted fish species due to increased interspecific interactions.

2 Material and methods

2.1 Study site

Lille Rostavatn ($61^{\circ}00'N$, $69^{\circ}35'E$, vatn = lake) is located in Målselv municipality in Troms og Finnmark county. Lille Rostavatn is an oligotrophic and dimictic lake with a surface area of 12.9 km^2 (Knudsen et al. 2010). Mean and maximum depth of the lake is 30m and 92m, respectively (NVEAtlas, web). The lake has well-developed littoral, pelagic and profundal habitats, and the littoral zone constitutes $<25\%$ of the surface area (Knudsen et al. 2010). At this latitude, there are approximately two months of midnight sun during summer (May-July) and two months of polar night in winter (November-January). The lake is usually ice-covered from November to May. Birch forests dominate the surroundings on the east side of the lake with some farming areas, whereas pine forests dominate the westside. The shore regions are mostly sandy and stony with scarce emergent vegetation. The biggest inlet river, Rostaelva, comes in from the south and the biggest outlet river drains in the west as a part of Målselv watercourse.

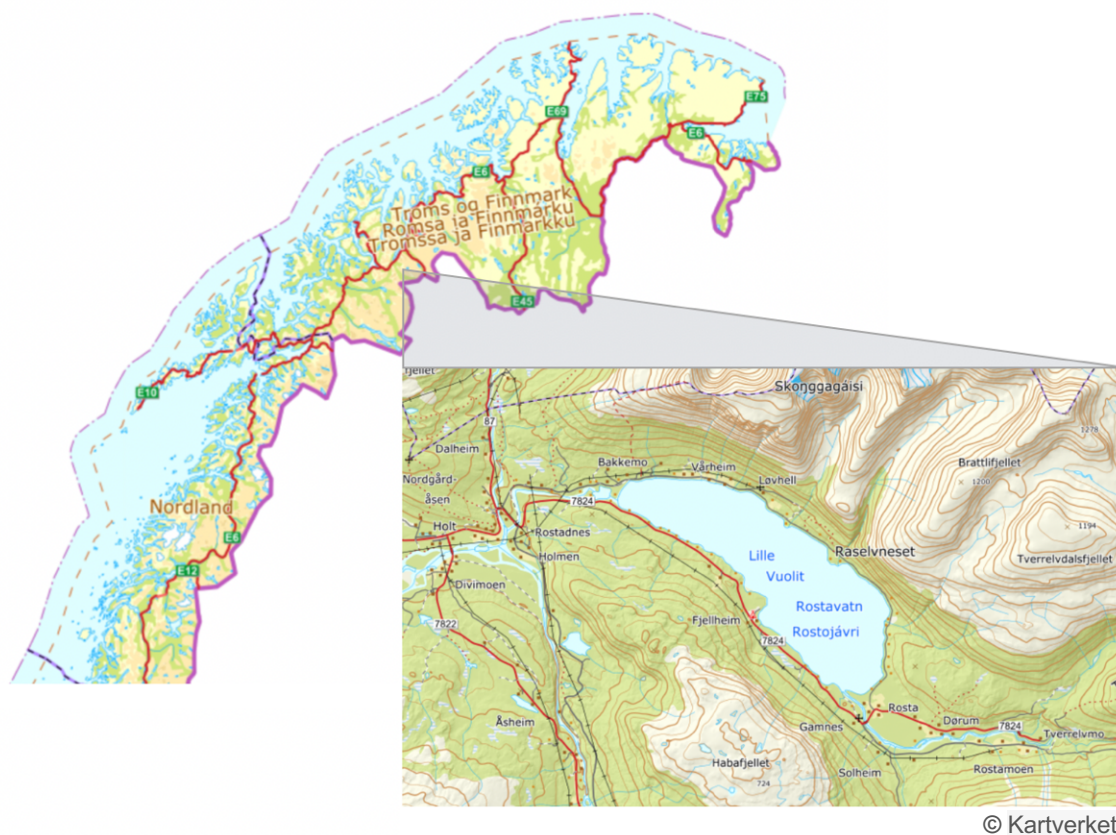


Figure 1: Map of Lille Rostavatn ($61^{\circ}00'N$, $69^{\circ}35'E$; 102 m.o.h) and its location in Troms og Finnmark county (NVEAtlas 2020).

2.2 Trophic niches of target fish species

The fish community in Lille Rostavatn consist of Arctic charr (*Salvelinus alpinus*), brown trout (*Salmo trutta*), burbot (*Lota lota*), grayling (*Thymallus thymallus*), minnow (*Phoxinus phoxinus*) and Atlantic salmon parr (*Salmo salar*).

Arctic charr is the most cold-water adapted salmonid and hence also the salmonid with the lowest tolerance to increased water temperatures (Siikavuopio et al. 2014). Arctic charr is a habitat generalist and is found in all habitats of oligotrophic lakes (Klemetsen et al. 2003, Reist et al. 2013). Arctic charr prefer the littoral zone in allopatry but under competition in sympatry with other fish species like brown trout they often shift to the pelagic or the profundal zone (Klemetsen et al. 2003). Arctic charr, like many other fish species, undergo ontogenetic dietary shifts from small pelagic zooplankton to larger benthic macroinvertebrates and finally to piscivory (Eloranta et al. 2015). The thermal preferences for Arctic charr is between 10-12 °C, but they can survive and feed very close to 0 °C (Larsson 2005, Siikavuopio et al. 2014). Arctic charr spawn in the shallow areas of lakes over a 2-3-week period in the autumn (Klemetsen et al. 2003).

Burbot is the only freshwater member of the cod family Gadidae (McPhail and Paragamian 2000). Burbot is a cold water, benthic and omnivorous freshwater fish (Hofmann and Fischer 2001). Burbot inhabits several habitats during its ontogeny. In lakes, burbot larvae are typically pelagic and they migrate to the surface, whereas adult burbot move to deeper and cooler water in the benthic zone (Knudsen et al. 2010). In lakes, burbot spawns over near-shore shallows in winter or early spring (McPhail and Paragamian 2000). Spawning often occur at low temperatures (1- 4 °C) under the ice. The preferred summer temperature is 10-14 °C (Hofmann and Fischer 2002, Stapanian et al. 2010). The main food items for burbot are other fish species and invertebrates (Ryder and Pesendorfer 1992, McPhail and Paragamian 2000, Hofmann and Fischer 2001). The proportion of fish in the diet increases in adult burbot, but even large fish eat insects and invertebrates. Burbot are adapted to the absence of light and they hunt from ambush (Knudsen et al. 2010).

Grayling is a member of the salmon family Salmonidae (Northcote 1995). They are adapted to life in rivers but can also live in lakes. Grayling also inhabits several habitats during their ontogeny (Ingram et al. 2013). The grayling larvae forage pelagically. As juveniles, they catch drifting invertebrates, mainly chironomid larvae and copepods. As they get larger and

older, they begin bottom feeding in the littoral zone. Chironomid pupae, Ephemeroptera, Simuliidae and Trichoptera are the preferred prey types (Sempeski et al. 1995). Grayling are spring spawners, unlike other salmonids that spawn during fall (Northcote 1995). They spawn in rivers and often move into their spawning areas after the ice breaks up at temperatures between 4 to 7 °C. They spawn from around April to June. Both sexes of grayling show aggressive behavior throughout the year, but during spawning they get even more aggressive and they attack anyone coming into their territory (Ingram et al. 2013). The preferred temperature is 18 °C, but their upper thermal tolerance is 25 °C whereas the lower critical is between 0-4 °C (Northcote 1995, Ingram et al. 2013).

Brown trout is also a member of the salmonid family. Brown trout is an opportunistic feeder with a diverse foraging behavior (Hyvärinen and Huusko 2006). The diet varies with habitat, season, fish size and age (Klemetsen et al. 2003). Brown trout exploit the surface areas of the lake and when they live in allopatry they have a wider habitat than in sympatry. As young, the main food items are insect larvae and chironomids (Klemetsen et al. 2003). They can also take surface arthropods. As the fish increases in size, they start to feed on larger food items such as insect larvae of the groups Ephemeroptera, Plecoptera, Simuliidae and Trichoptera. Brown trout can also be piscivorous and they will gradually start feeding on fish as they increase in size (Steingrímsson and Gíslason 2002, Klemetsen et al. 2003, Hyvärinen and Huusko 2006). Brown trout is a visual feeder and the transparency of the water is an important determinant for its vertical distribution (Klemetsen et al. 2003). Brown trout spawn in rivers during autumn and winter and the optimal temperature for growth is around 13-18°C (Klemetsen et al. 2003, Larsson 2005), whereas the upper critical temperature is 25-26 °C. The lower critical temperature for growth is 3-6 °C.

Atlantic salmon is also a member of the salmonid family. Salmon is an anadromous species, and their life cycle is typically divided between freshwater and marine environments (Power 1958). In Norway, most salmon enter the rivers from May to October (Klemetsen et al. 2003). Atlantic salmon parr is an opportunistic feeder on all types of invertebrates (Jørgensen et al. 2000). Atlantic salmon parr have an indicated optimal temperature around 18-19 °C (Forseth et al. 2001, Larsson et al. 2001).

Minnow is a member of the carp family Cyprinidae. Minnow prefers cold, well-oxygenated water and it feed mainly on benthic invertebrates (Frost 1943). Spawning usually takes place in May or June, but in some parts of Norway it can be delayed to July (Holmen 2013).

Minnow tolerates ice-covered waters and temperatures up to 23 °C (Frost 1943).

2.3 Field sampling

The field sampling was performed in August and October 2018 with the aim to look at the fish community structure and fish populations in Lille Rostavatn. In August, the fish were sampled over three nights, 12th -15th of August 2018. In October, the fish were sampled over two nights, 08th – 10th of October 2018. All nets were put out in the evening and were retrieved the following morning, approximately 12 hours later. Previous fish sampling has been done in August and October 1997, August 2010 and August 2016 (see appendix 1 for an overview of the total fish samples in all years).

We used multi-mesh gillnets placed in the littoral (benthic nets, 0-12 m depth), pelagic (offshore gillnets set from the surface; 0-6 m depth) and profundal (benthic nets; at 20-36 m depth) zones. In order to get a representative overview of the habitat distribution and size composition of the fish populations present in the lake, three different types of multi-mesh gillnets were used; one type called BGO (40 m long and 1.5 m deep), used in the benthic areas both in the littoral and profundal zone. The second gillnet is called FGO (40 m long and 6 m deep) and they are used in the pelagic zone. These two gillnet types have a range of mesh size in 5-meter intervals from 10, 12.5, 15, 18.5, 22, 26, 35, 45 mm, knot to knot. The third type of multi-mesh gillnet is called NORDIC net (30 m long and 1.5 m deep) and is used in the benthic areas. These gillnets have a range of mesh sizes in 2.5 m intervals from 5 to 55 mm, knot to knot. We only used NORDIC net during the sampling in August 2016 and 2018.

Catches in the littoral zone included all six fish species: Arctic charr, brown trout, grayling, burbot, Atlantic salmon parr and minnow for all four years. All captured fish were sampled and recorded. In the field laboratory the individual fish was given a number. The fish was weighed (g), the fork-length of each fish was measured (mm) and the otoliths were taken for age determination. Thereafter the body cavity of the fish was opened, and the stomach were sampled and stored in 96% ethanol until analyzed. The sex and stage of sexual maturity of each fish was determined by examining the gonads, and the stage of sexual maturity was classified in three groups; 1) juvenile or immature, 2) sexually mature and spawning this

following breeding season and 3) sexually mature, but not spawning the following breeding season or already spent.

2.3.1 *Catch per unit effort*

The catch per unit effort (CPUE) was calculated as the number of fish caught per 100 m² gillnet per night. CPUE is used as an indicator of relative fish density in different habitats of the lake (Bøhn et al. 2008). The habitat use of Arctic charr, burbot, grayling and brown trout were compared by estimating the percent habitat distribution of each species at each sampling from the littoral, pelagic and profundal habitats (Amundsen and Knudsen 2009). CPUE calculations are only based on the catches from multi mesh gillnets. Nordic nets with mesh size below 10 mm were only used in 2016 and 2018, therefore all fish individuals from all years with a length below 90 mm is excluded from these calculations to get a representative overview of the fish samples.

Pearson correlation coefficient (r) was used to measure the strength of the relationship between the CPUE, years and habitat of the August data.

2.4 Laboratory analysis

The diet of the fish were based on the presence-absence method and relative-fullness method as described by Amundsen and Sánchez (2019). The stomachs were opened, and the total fullness of all stomach content was estimated by using a percentage scale from 0% (empty) to 100% (full). The prey ingested by the fish, or an identifiable part of the prey, were identified on a species, genus or family level and their contribution to the stomach fullness was evaluated. The different prey types were first divided into four main groups to get a general overview: zooplankton, benthic invertebrates, surface insects and fish. The zooplankton group include cladocerans and copepods. The surface insect group include surface insects, insect pupae, water bugs and water mites. Insects larvae are included in the benthic invertebrate group together with mollusks, *Gammarus lacustris*, *Eurycercus lamellatus* and *Sida crystallina*.

The different prey types were further divided into 11 categories for a more detailed overview: cladocera, copepods, small benthic crustaceans, Gammarus, molluscs, surface insects, chironomidae pupae, chironomidae larvae, trichoptera larvae, other insects and fish (see appendix 20 to 35 for a more detailed overview). Fish with empty stomach content is not included in the stomach content analysis. If there were less than five fish individuals of one

species caught in one habitat of the lake in one year, they were excluded from the stomach content analysis (see appendix 2 for an overview of the number of stomach samples for each fish species in each habitat each year).

2.5 Data and statistical analysis

Statistical analysis was done with RStudio (version 1.2.5033, RStudio Inc.) based on R, version 3.6.2 (2019 The R Foundation for Statistical computing).

2.5.1 Simpson's diversity index (*D*)

Simpson's reciprocal diversity index (*D*) was used as a measure of the fish diversity in the lake (based on the four target species of the present study) and the index takes the number of species present and the relative abundance of each species into account (Harper and Hawksworth 1995). The Simpson's diversity index is defined as:

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

where p_i is the proportion of species i in the fish community. Simpson's diversity index varies from 1 to s , where s is the total number of species in the sample. A low number indicates that one of the species is dominating the fish community, while a high number indicates an even distribution of the species, thus also higher diversity, throughout the fish community.

Evenness is a measure of the relative abundance of the different species making up the species richness in the lake (Krebs 1999). Evenness is measured as:

$$E = D / D_{\max} \quad (2)$$

where D is the observed index of species diversity and D_{\max} is the maximum possible index of diversity. Evenness is constrained between 0 and 1. A community where all species are equally common is considered even and has a high degree of evenness.

2.5.2 Diet composition

The diet characterizations on stomach contents analysis is based on two variables; frequency of occurrence and relative prey abundance (Amundsen and Sánchez-Hernández 2019). The frequency of occurrence of a given prey type is defined as the number of stomachs in which that prey occurs relative to the total number of stomachs, and the relative abundance of a prey is defined as the percentage of total stomach contents in all predators comprised by each given prey type.

The relative prey abundance (A_i) and the frequency of occurrence (F_i) of each prey type were calculated from their presence and fullness in the stomachs:

$$A_i = (\sum S_i / \sum S_t) \times 100 \quad (3)$$

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

$$F_i = N_i / N \times 100 \quad (4)$$

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

2.5.3 Diet overlap

The Schoener's similarity index (Schoener 1970) was used to study the diet overlap (O_{jk}) between the fish species and the different years they were sampled (appendix 36, 37, 38, 39). The diet overlap is a measurement of resource partitioning:

$$O_{jk} = 100 * (1 - 0.5 \sum |p_{ij} - p_{ik}|) \quad (5)$$

where O_{jk} is the prey item overlap in percentage between population j and 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, 40-60% show small differences and 20-30% or less show large differences in diet (Wallace 1981).

2.5.4 Diet width

The diet niche width of fish in different habitats and size groups was determined using the Levins's index (\hat{B}) (Krebs 1999, see appendix 40):

$$\hat{B} = \frac{1}{\sum \hat{p}_j^2} \quad (6)$$

where \hat{p}_j is the proportion of each prey type j in the stomachs of a size group or population. N is the number of individuals found in or using resource state j and Y is the total number of individuals sampled. \hat{B} can have values between 1 and n , where 1 is the narrowest (when only one prey item is found) and n is the broadest diet niche width (n is equal to the total number of prey items). If $\hat{B}=n$, then all diet items are equally represented in the diet of the individuals.

2.5.5 *Temperature data*

Water temperature data from Lille Rostavatn is not available, however, water temperature data has been collected by the Norwegian Water Resources and Energy Directorate (NVE) in the Målselv watercourse (NVEAtlas, web), the outlet river in Lille Rostavatn. For this thesis, water temperature data has been collected from two different stations located not far from each other (approximately 133 meters); Måselva ovf. Barduelva and Måselvsfossen. These stations are located approximately 40 km from Lille Rostavatn. Daily water temperature from 1991 to 2018 is used, except for 1997-2000 where data is missing. Temperature data from June in 1993 and 1995 were missing, therefore mean from June in all of the other years were calculated and used for those dates. Water temperature data from fall (October to November) in 2016 and 2017 were used from Måselvfossen, as well as in 2018 (September to November). The water temperatures were summarized as the mean of three categories: growth season (June to November), summer (June to September) and fall (September to November). The temperature data showed a significant increase in water temperature from 1997 to 2018 (Welch Two Sample T-test: p-value= 0.00075, figure 2). The mean water temperature in 1997 was 6 °C, whereas in 2018 7,2 °C. As the water temperature in Målselv watercourse have been increasing over the last decades, it is reasonable to assume that the water temperatures in Lille Rostavatn have increased.

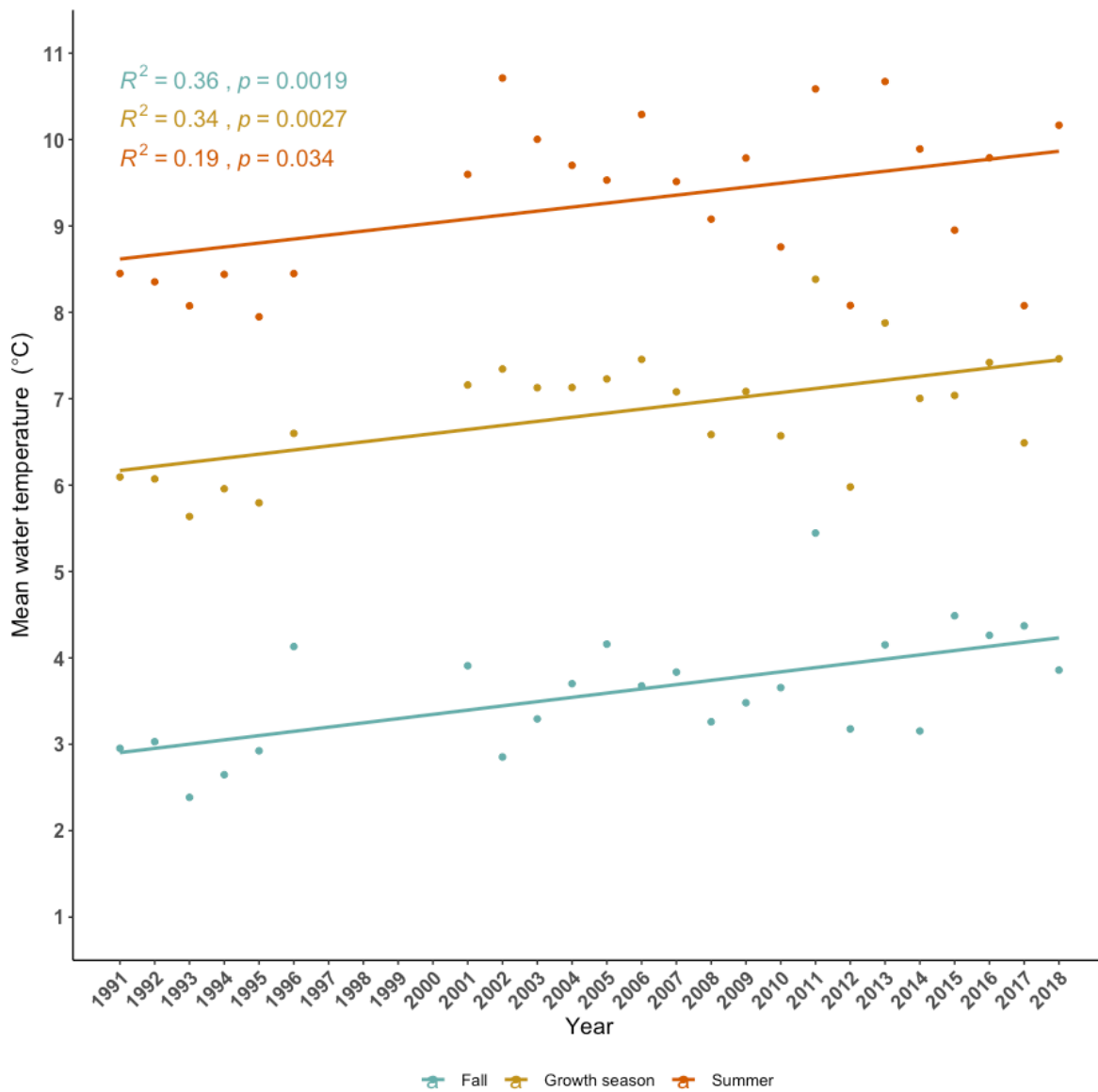


Figure 2: Time series of mean water temperature (°C) in Målselv river system from 1991 to 2018. Note that there are no data from 1997 to 2000. There is a significant increase in the water temperature both in fall (blue line, $R^2 = 0.36, p = 0.0019$) and summer (red line, $R^2 = 0.19, p = 0.034$), as well as during growth season (yellow line, $R^2 = 0.34, p = 0.0027$).

3 Results

3.1 Variation in fish density between habitats

The CPUE (catch per unit effort) values in the three different habitats (e.g., littoral, pelagic and profundal) showed a relatively large variation over time with an extensive use of the pelagic habitat in 2010 (appendix 3). The combined CPUE for all four fish species in all habitats increased, but non-significantly, from 1997 to 2018 in August (Pearson correlation, $R: 0.9, p = 0.1$) whereas in October there is a slight decrease (figure 3).

The CPUE values of the fish species were relatively stable through the study period with some minor fluctuations (figure 3). The CPUE values for the cold-water adapted fish species (Arctic charr and burbot) were relatively stable with a slight decrease in fish density in August (Pearson correlation, $R: -0.79, p = 0.21$) and October throughout the study period (figure 3). Both Arctic charr and burbot showed a minor decrease in the littoral habitat over time in August and October (appendix 4). Arctic charr were the main species caught in the profundal habitat and the density increased distinctly over time in August (appendix 5). The density of burbot was consistently low in the profundal habitat in August but increased slightly over time in October (appendix 5). The density of Arctic charr were relatively stable in the pelagic habitat in August (except for a peak in 2010), while the CPUE values in October increased markedly from 1.9 in 1997 to 14.2 in 2018 (appendix 6).

The temperate-adapted species showed a significant increase in August CPUE values over the study period (Pearson correlation, $R: 0.96, p = 0.036$) with increasing density of both grayling and brown trout (figure 3). The density of these two species increased in the littoral habitat in both August and October, but the density was overall higher in August than October (appendix 4).

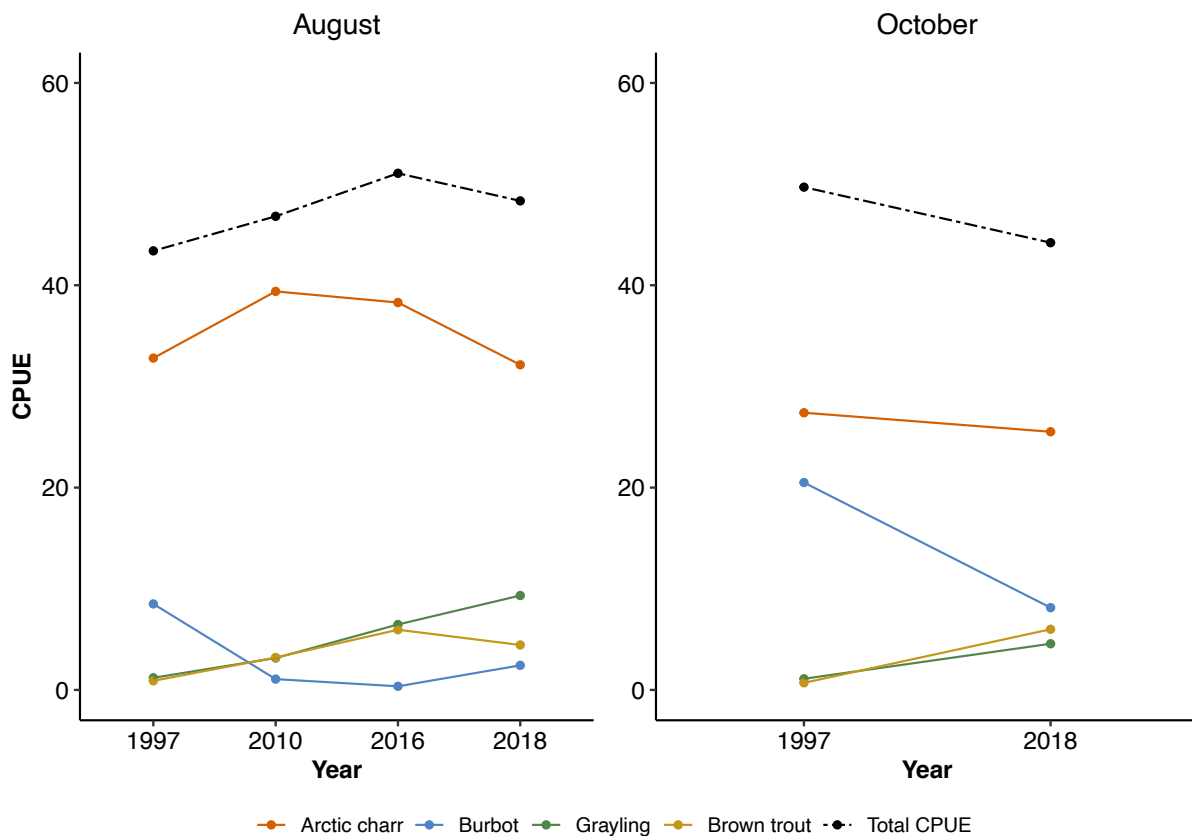


Figure 3: Catch per unit effort (CPUE) values of Arctic charr (red), burbot (blue), grayling (green) and brown trout (yellow) in all three habitats combined in August and October. Black stippled line (Total CPUE) shows the combined CPUE values for all fish species together. See appendix 7 for a total overview of the CPUE values in each habitat for each species.

3.2 Changes in fish community structure

From 1997 to 2018, there has been a major shift in the fish community structure at Lille Rostavatn where cold-water adapted species (Arctic charr and burbot) have gradually declined, and more temperate-adapted species (grayling and brown trout) have increased their relative contribution substantially (figure 4). The cold-water adapted species were the dominating species representing 95% of the total catch in 1997 (appendix 8). Arctic charr was the dominant species in both August and October 1997 representing around 65% of the catch (figure 4). Burbot constituted 26% of the catch in August and 31% in October 1997. In 2018, the relative contribution of the cold-water adapted species had decreased to 57% with the relative contribution of Arctic charr and burbot being 44% and 13%, respectively (figure 4, appendix 8).

The temperate-adapted species had in contrast increased substantially from 5% in 1997 to 43% in 2018 (appendix 8). Grayling represented 2% and 25% of the August catch in 1997 and 2018, respectively, and brown trout similarly 4% and 18% (figure 4). The temperate-adapted species showed in general a small decrease in their relative contribution to the fish catches from August to October (1997: 7% to 3%, 2018: 46% to 39%, appendix 8). In addition, some minnows and Atlantic salmon parr were also caught in Lille Rostavatn (appendix 10).

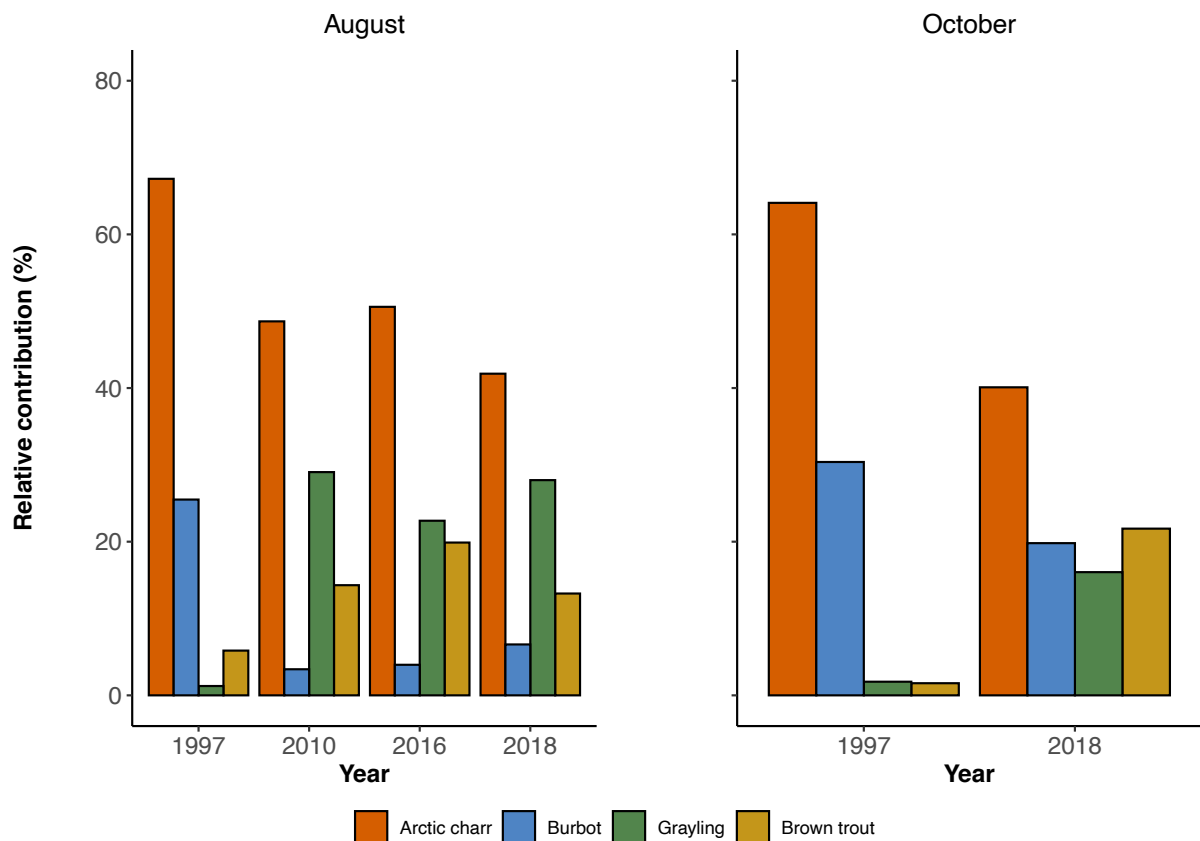


Figure 4: The relative contribution (%) of Arctic charr (red), burbot (blue), grayling (green) and brown trout (yellow) in all habitats combined in Lille Rostavatn in August 1997, 2010, 2016 and 2018 and October 1997 and 2018.

Littoral zone

The cold-water adapted species dominated the fish community in the littoral habitat with 90% in 1997 whereas by 2018 they only represented 33% (appendix 9). The cold-water adapted species showed a marked increase in relative contribution from August to October in 2018, increasing from 33% to 49% whereas in 1997 the relative contribution to the fish catch was the same in both months. The dominance of Arctic charr in the littoral zone decreased over time and the fish community showed higher evenness and diversity in the more recent years (appendix 41). In 1997, Arctic charr dominated the littoral zone with 52% in August and 57% in October (figure 5). In 2010, 2016 and 2018 the relative contribution of Arctic charr strongly decreased being only 22% (average value of the three years) in August and 32% in October 2018. In August 1997, burbot represented 38% of the littoral catch, whereas in 2010, 2016 and 2018 its contribution was down at 6% (average value of the three years). There was a marked increase in the relative contribution of burbot from August to October in 2018, increasing from 8% to 17%.

The temperate-adapted species were mainly caught in the littoral zone. In August 1997, they represented only 10% of the littoral catch, whereas in August 2018 they dominated the littoral catch with 67% (appendix 9). The temperate-adapted species showed a markedly increase in their relative catch contribution from October 1997 to October 2018, increasing from 4% to 51%. Grayling represented 2% of the catch in August 1997, whereas by August 2018 they had increased to 46% (figure 5). Brown trout similarly constituted 8% and 21% of the fish catches these two years.

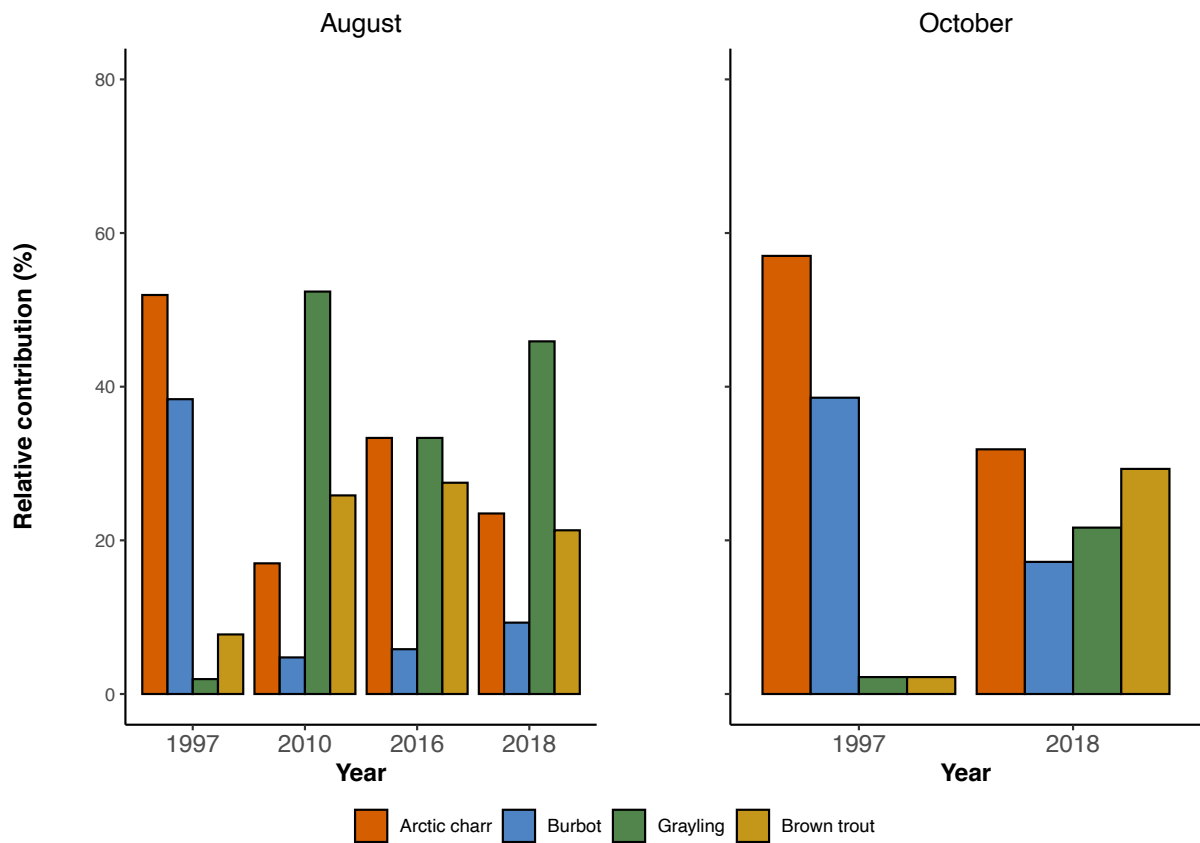


Figure 5: The relative contribution (%) of Arctic charr (red), burbot (blue), grayling (green) and brown trout (yellow) in the littoral habitat in Lille Rostavatn in August 1997, 2010, 2016 and 2018 and October 1997 and 2018.

Profundal zone

The cold-water adapted species dominated the profundal habitat in all years, with Arctic charr being the most abundant species in both August and October (figure 6, appendix 9). In 2018, there was a small decline in the relative contribution of Arctic charr from the previous years (> 90% to 80%). The contribution of burbot was low in all years in August, with a maximum of 5%. However, from August to October, burbot had a marked increase in contribution to around 40% in both years when October samples were available.

The temperate-adapted species showed low abundance in the profundal zone in all years, both in August and October (appendix 9). However, for the August samples from 1997 to 2018 there was a small increase in their abundance from 3% in 1997 to 11% in 2018. Grayling were only occasionally caught in the profundal zone (figure 6). The contribution of brown trout in

the profundal catches was low (<3%) in all years, and no brown trout were caught in the profundal in the October samples.

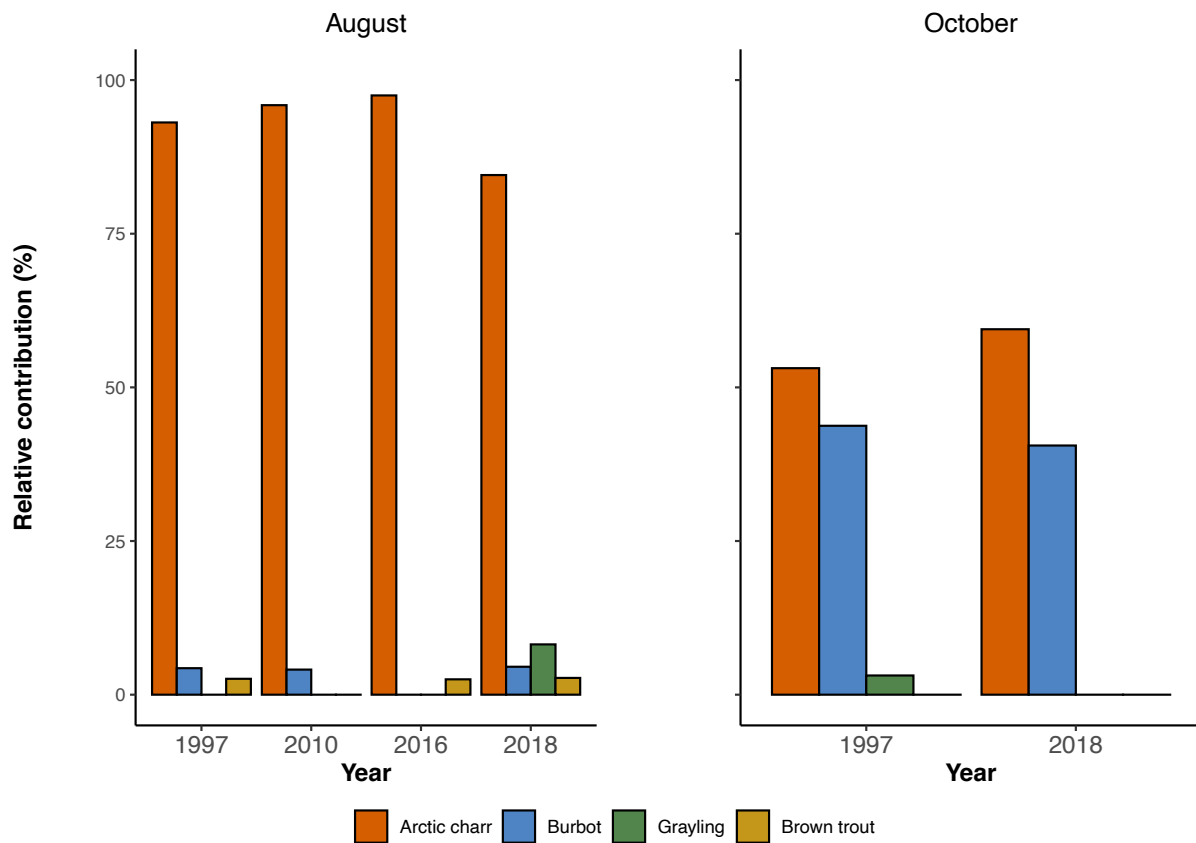


Figure 6: The relative contribution (%) of Arctic charr (red), burbot (blue), grayling (green) and brown trout (yellow) in the profundal habitat in Lille Rostavatn in August 1997, 2010, 2016 and 2018 and October 1997 and 2018.

Pelagic zone

Arctic charr were the only fish species caught in the pelagic zone, except in 2016 when one brown trout was caught (see appendix 11 for the fish species composition in the pelagic zone).

3.3 Variation in diet between fish species

Arctic charr differ from the other fish species in Lille Rostavatn by having a high consumption of zooplankton (figure 7). Zooplankton was the most important prey of Arctic charr in all habitats, except in the littoral zone in August 2016 where surface insects dominated the diet (figure 7, appendix 12, 13, 14, 15, 16). The diet of burbot was dominated mainly by benthic invertebrates and fish in the benthic habitats, except in the profundal zone in October 1997 where zooplankton constituted 34% (figure 7). Grayling and brown trout consumed mainly surface insects and benthic invertebrates (figure 7, appendix 13). Littoral brown trout included fish in their diet in October. In addition, minnow and Atlantic salmon parr mainly consumed benthic invertebrates and surface insects (appendix 17).

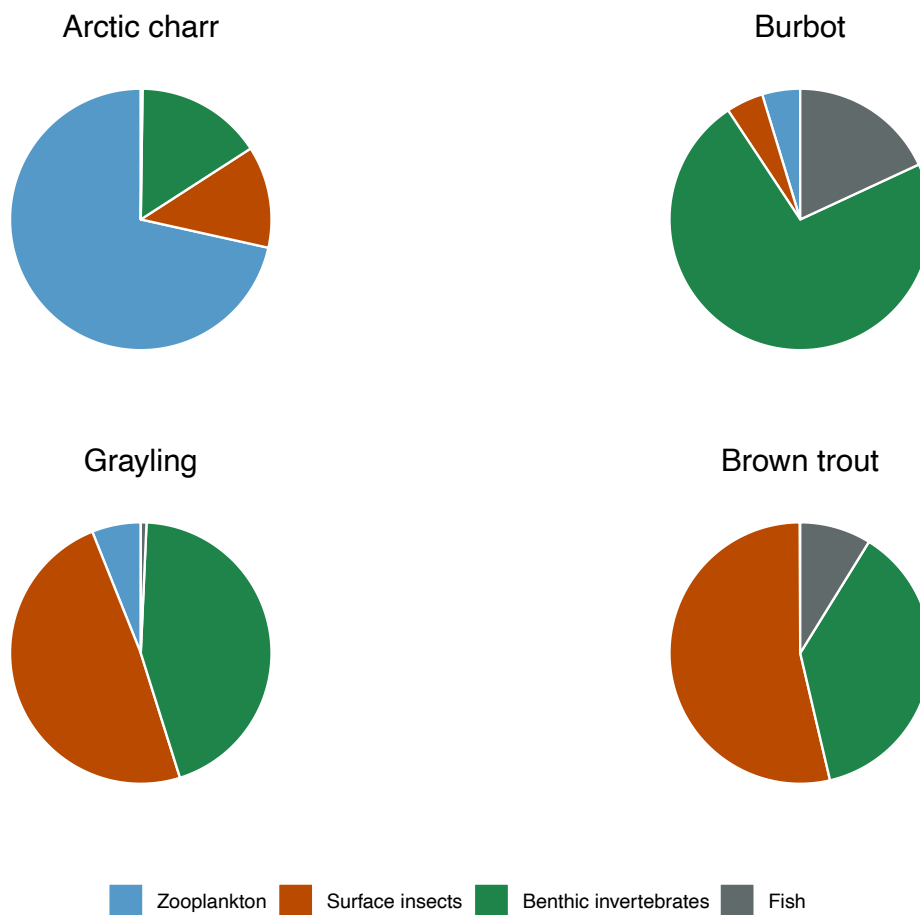


Figure 7: The main prey categories (zooplankton, surface insects, benthic invertebrates and fish) found in the stomach samples of Arctic charr, burbot, grayling and brown trout in Lille Rostavatn during the sampling period. The entire data set for all habitats and years are combined for each fish species.

3.3.1 Variation in diet in the different habitats

Cladoceran zooplankton were the most dominant prey for Arctic charr in all habitats each year with regular and often high frequencies of occurrence and abundance (figure 8, appendix 18, 19, 20, 21, 22, 23). Small benthic crustaceans, *Gammarus lacustris*, molluscs and fish were the most important prey categories for burbot in the benthic habitats each year (figure 8, appendix 24, 25, 26, 27). Surface insects and insect larvae were the most important prey categories for both grayling and brown trout (figure 8, appendix 28, 29, 30, 31, 32, 33, 34, 35). The interspecific dietary overlap between the four species was higher in August than in October (appendix 36, 37). Arctic charr had a low to intermediate dietary overlap with all three co-existing species. Arctic charr and burbot had an intermediate dietary overlap in 1997 (Schoeners O_{jk} = 52%), whereas from 2010 and onwards it was low (Schoeners O_{jk} = < 25%). The highest overlap observed was between grayling and brown trout in 2010 (Schoeners O_{jk} = 65%), representing a significant diet overlap between the two species. However, for the remaining years the dietary overlap was intermediate (Schoeners O_{jk} = < 58%). The lowest observed dietary overlap was between burbot and brown trout (Schoeners O_{jk} = 4%), as well as between burbot and grayling (Schoeners O_{jk} = 5%).

Littoral zone

Arctic charr had taken cladoceran zooplankton (mainly *Bosmina* sp. and *Daphnia* sp.), small benthic crustaceans (*Eurycerus lamellatus*), molluscs and insects (mostly surface insects and Chironomidae pupae) as a part of their diet in all of the years (figure 8). However, cladoceran zooplankton were the most important prey category for Arctic charr, except in 2016 where chironomid pupae dominated their diet with 31%. Accordingly, there was little variation in their zooplanktivore diet in October 1997 and 2018 which was reflected by a high intraspecific dietary similarity between the years exceeding 80% (appendix 39). The intraspecific dietary similarity between all years was relatively high in both August and October (appendix 38, 39). The lowest similarity was observed between 2010 and 2016 (Schoeners O_{jk} = 37%) as the diet consisted of more cladoceran zooplankton in 2010 and chironomid pupae in 2016.

Burbot fed on a large variety of prey types, but small benthic crustaceans (*Eurycerus lamellatus*), fish, molluscs (mostly *Lymnea* sp.), *Gammarus lacustris* and insects (surface insects and Ephemeropter larvae) were mainly the preferred dietary choice in the littoral zone in both August and October (figure 8). There was relatively low variation in their diet in the

littoral habitat between all years in August and in October, reflected by a generally intermediate dietary similarity (appendix 39).

Grayling had mainly taken insects (surface insects, Ephemeroptera larvae, Chironomid larvae, Trichoptera larvae with house and Trichoptera pupae), small benthic crustaceans (*Eurycercus lamellatus*) and molluscs (*Lymnea* sp. and *Planorbis* sp.) in the littoral zone (figure 8). There was an intermediate to high dietary similarity between all four years in August (appendix 38) and the lowest similarity was observed between 1997-2010 (Schoeners O_{jk} = 35%). In October, there was an intermediate similarity between 1997 and 2018 (Schoeners O_{jk} = 46%, appendix 39) mainly because grayling also included *Daphnia* sp. in their diet, as well as *Gammarus lacustris*.

Brown trout had eaten the same prey groups as grayling in the littoral zone (figure 8). Surface insects was the most important dietary choice in August and Trichoptera larvae in October. The intraspecific dietary similarity in August had some variation between the years (appendix 38). The lowest dietary similarity was observed between 1997 and 2016 and between 2016 and 2018 (Schoeners O_{jk} = 20%), regard to whether surface insect or insect larvae/pupae dominated their diet. In October, the dietary similarity was high (Schoeners O_{jk} = 77%, appendix 39).

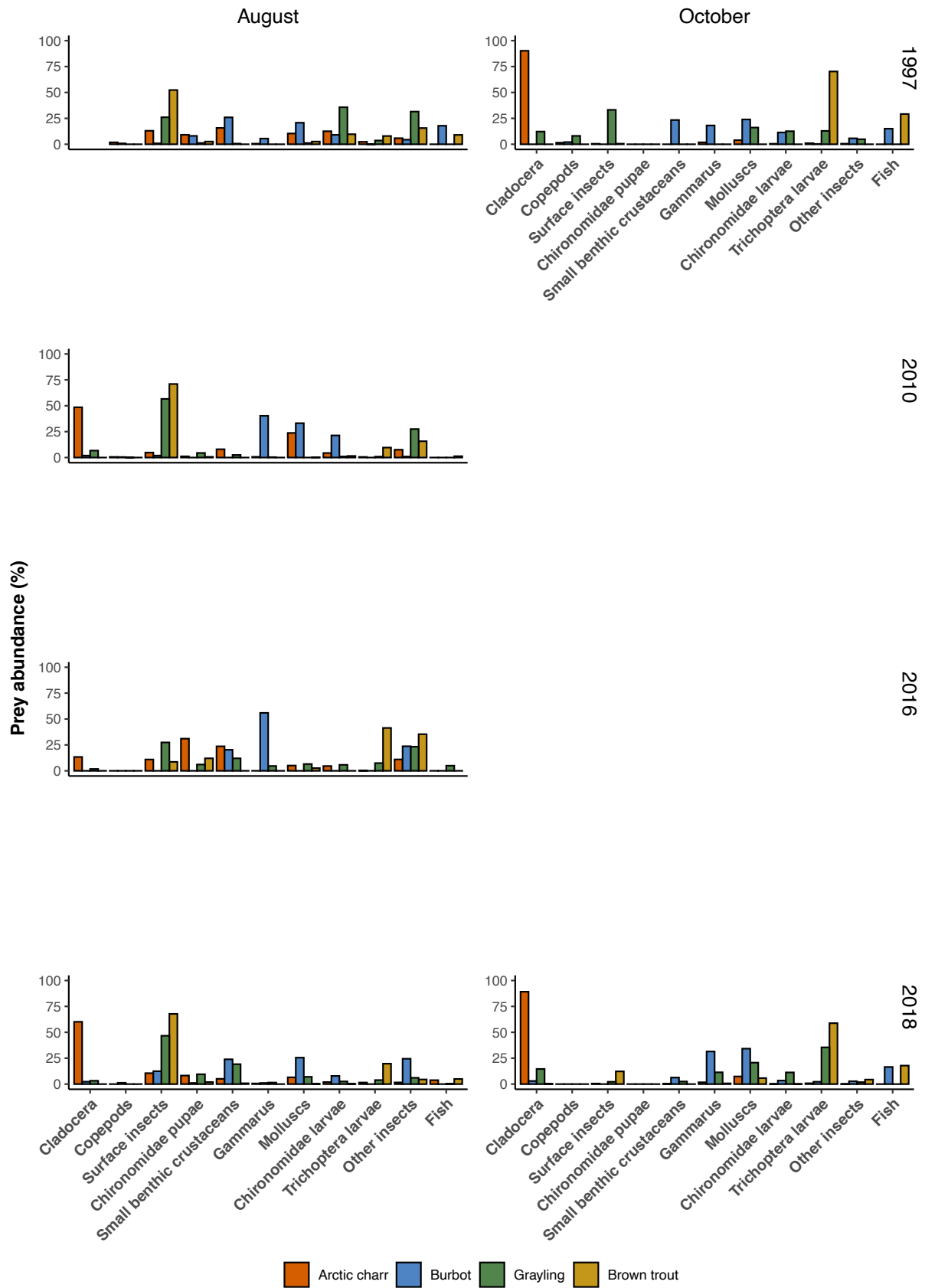


Figure 8: Percent abundance (%) of prey groups found in the stomach content of littoral caught Arctic charr (red), burbot (blue), grayling (green) and brown trout (yellow) in August 1997, 2010, 2016 and 2018 and in October 1997 and 2018.

Profundal zone

The diet of the profundal Arctic charr consisted mainly of cladoceran zooplankton (mostly *Bosmina* sp. and *Daphnia* sp), both in August and October (appendix 18). The intraspecific dietary similarity between all years was relatively high (appendix 38, 39; Schoeners $O_{jk} = >58\%$).

Burbot had taken fish, small benthic crustaceans (*Eurycerus lamellatus*) and insects as the preferred dietary choice (appendix 18). Fish were an important prey type both in August and October in all years. In August, the intraspecific dietary similarity was intermediate between all the years (appendix 38). In October, the dietary similarity was low (Schoeners $O_{jk} = 14\%$, appendix 39) because the contribution of fish in the diet decreased from 64% (1997) to 12% (2018).

Pelagic zone

Arctic charr had a high abundance of cladoceran zooplankton (*Bosmina* sp., *Daphnia* sp., and *Bythotrephes* sp.) in their diet and this was the most important prey groups both in August and October in all years (appendix 19). The intraspecific dietary similarity between all years was relatively high, except between 1997 and 2018 (Schoener's $O_{jk} = 29\%$, appendix 38, 39), mainly because the use of cladoceran zooplankton almost doubled from 45% to 85%.

3.3.2 *Diet width*

The population diet widths for all fish species were highest in the littoral zone, and it was broader in August than in October (figure 9, appendix 40). Both the cold-water adapted and the temperate-adapted fish species showed an overall decrease in diet width in August over the study period whereas in October the diet width stayed at the same level. Arctic charr showed a distinct reduction in diet width from August to October in all habitats, whereas burbot, grayling and brown trout showed a minor reduction.

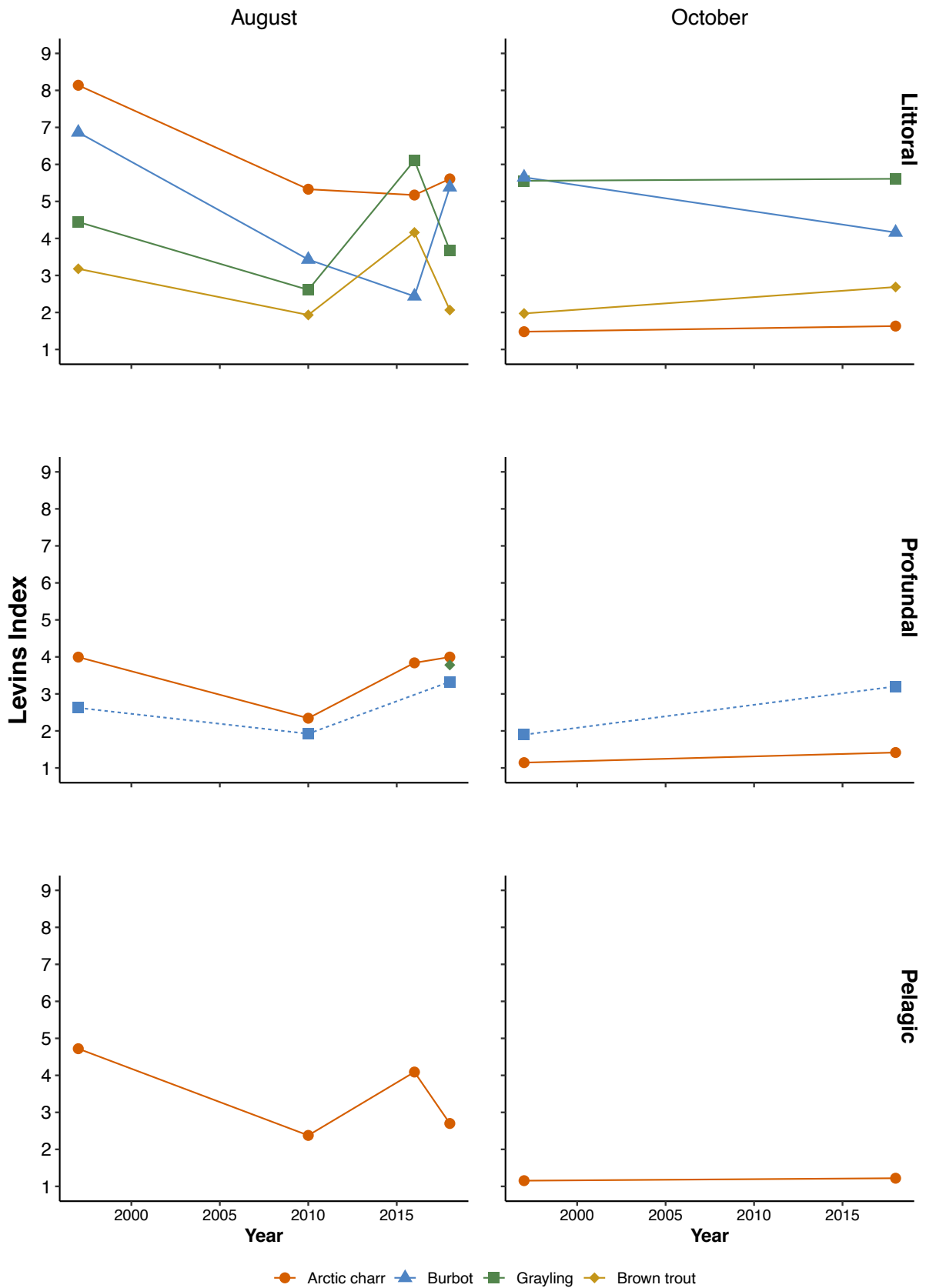


Figure 9: Levin's index for Arctic charr (red), burbot (blue), grayling (green) and brown trout (yellow) caught in the littoral, profundal and pelagic zone in Lille Rostavatn in both August (left) and October (right).

4 Discussion

The fish community in Lille Rostavatn showed a clear change in the community structure over the 22-year period as expected. In general, the cold-water adapted species, Arctic charr and burbot, have had a drastic decline in their relative contribution, whereas the temperate-adapted species, grayling and brown trout, have increased their density and relative contribution in the littoral zone. Despite this community shift, the total fish density and the overall diet of all four fish species were relatively stable throughout the observation period. The low to intermediate diet overlap between the four species in Lille Rostavatn indicated a clear segregation in habitat use and prey-resource utilization. These changes could occur as a result of predator-prey or competitive interactions as they may have a significant role in regulating freshwater fish community structure (Brabrand and Faafeng 1993, Forseth et al. 2003, Sandlund et al. 2013, Eloranta et al. 2015). Thus, evidently there has been an increase in water temperature in the Målselv watercourse during this time period and climate warming could explain the observed shift in community structure of the fish species (Jeppesen et al. 2012). The habitat choice of fish species is often a result of biotic interactions mediated by abiotic conditions and several similar studies have reported changes in fish community structure due to climate change caused by increasing water temperatures (Daufresne et al. 2003, 2009, Ficke et al. 2007, Jeppesen et al. 2010, Hayden et al. 2017).

Changes in fish community structure

As expected, the present study demonstrated a distinct segregation of cold-water and temperate-adapted fish species according to habitat use. The habitat partitioning between the cold-water and temperate-adapted fish species were clear in August, as they shifted from the littoral zone towards the deep profundal through time. Similar community shifts through time are also observed in other lakes (Aass et al. 2004, Saksgård and Hesthagen 2004, Amundsen et al. 2015, 2019). Saksgård and Hesthagen (2004) observed variation in the abundance of brown trout and Arctic charr in the deep and oligotrophic Lake Atnsjøen in southern Norway over a period of 14 years. They concluded that the abundance of Arctic charr was dependent on the density of brown trout in the littoral zone and zooplankton density in the pelagic habitat but could not relate these results to any climatic variability. Similar in Lille Rostavatn, the effects of an increasing water temperature might influence the ecological interactions with grayling and brown trout resulting in superior competitive interactions. As expected, the temperate-adapted species became more common over time in the warmer littoral zone,

especially in August. This could probably be related to increasing water temperatures and to restricted niches in the littoral habitat as both Arctic charr and burbot have their temperature preferences lower than 12 degrees (Hofmann and Fischer 2002, Larsson 2005, Siikavuopio et al. 2014). Such segregation into distinct sub-communities of sympatric living fish species in different habitats (i.e., littoral, pelagic and profundal) are shown in other studies in deep subarctic lakes (Haugen and Rygg 1996, Sandlund et al. 2013, Eloranta et al. 2015, Hayden et al. 2017).

In 1997 in the Målselv watercourse, Arctic charr and brown trout showed the same pattern in habitat distribution in Lille Rostavatn as in Takvatn and Fjellfrøsvatn (Eloranta et al. 2013). However, in the more recent years, both Arctic charr and burbot is evidently less abundant in the littoral habitat in Lille Rostavatn. Both Takvatn and Fjellfrøsvatn, have less complex fish communities and they might not be subjected to the same competitive and/or predation pressure as in Lille Rostavatn. In a multispecies fish community, the competition and predation pressure are stronger and may likely induce niche shifts (Eloranta et al. 2015). The strong competition for littoral resources by grayling and brown trout may promote the use of the pelagic and profundal habitat by Arctic charr and burbot. Such a shift was observed through time in Lille Rostavatn as there was an abrupt shift from a dominance of Arctic charr and burbot in the fish community to a total supremacy of grayling and brown trout in the littoral habitat. The clear habitat segregation observed may be the outcome of competitive interactions for food. Arctic charr have a wide dietary resource niche (Amundsen 1995, Klemetsen et al. 2003, Eloranta et al. 2011, Reist et al. 2013), but living in sympatry with other fish species their wide niche is often restricted as they generally are considered a less superior competitor (Jansen et al. 2002).

Arctic charr differed from the other fish species by having a high consumption of zooplankton in all habitats of the lake. Large lakes, such as Lille Rostavatn, typically have longer open-water seasons and more extensive pelagic areas which promotes phyto- and zooplankton production (Eloranta et al. 2015). The dominating cladoceran species in Lille Rostavatn, *Daphnia* sp. and *Bosmina* sp., (Skoglund et al. 2013) were eaten throughout the whole period. Knudsen and Amundsen (2010) suggested that the Arctic charr population was forced towards a predominant pelagic habitat use and diet use to avoid the predation pressures and competitive interactions from burbot already in 1997. Now, a large population of grayling and brown trout could have the same effect. Zooplankton are smaller and less energetic prey than

benthic invertebrates, however, the diet data might indicate that zooplankton is a sufficient resource providing ample energy for the Arctic charr population to persist in Lille Rostavatn. This is also supported by the relatively stable fish densities in the pelagic habitat.

Nevertheless, Arctic charr is known to utilize similar resources as the other co-occurring fish species in allopatry (Jansen et al. 2002, Forseth et al. 2003), so the observed niche segregation might be due to strong competitive interactions and lack of shelter in the littoral habitat.

Today, grayling and brown trout are the dominant benthivore competitors (Langeland et al. 1991, Forseth et al. 2003, Amundsen et al. 2010, Eloranta et al. 2013). A model developed by Abrams & Rueffler (2009), argued that the coexistence of three competing species may occur if the intermediate species (i.e. Arctic charr) is more similar in niche use to one of the other co-occurring species (i.e. grayling). This is also supported by other salmonid studies (Aass et al. 2004, Amundsen et al. 2010, Eloranta et al. 2011, Jensen et al. 2017). Arctic charr is the only species that utilized both benthic invertebrates and pelagic prey and thus, by far, had the widest resource niche amongst the three species.

Grayling and brown trout had overlapping ecological niches both in habitat and diet use, as found in other sympatric systems (Elliott 1976, Sempeski et al. 1995, Haugen and Rygg 1996, Hyvärinen and Huusko 2006, Ingram et al. 2013). The relative contribution and densities of grayling have exceeded the brown trout population in the most recent years in Lille Rostavatn, probably as they partition in different microhabitats (i.e. different depths) in the littoral habitat (Greenberg et al. 1996, Haugen and Rygg 1996, Watz et al. 2014). According to a study conducted by Riley et al (2006), grayling showed the least range in habitat preference in Brandy stream in southern England, indicating a more definite habitat requirements than brown trout. Langeland et al (1991) demonstrated, however, that the resource utilization of brown trout is restricted to the upper strata of the lake, and that they also might exploit pelagic areas. Brown trout did, however, not exploit the pelagic areas in Lille Rostavatn, most likely as this is occupied by Arctic charr, a superior zooplankton competitor (Jansen et al. 2002). Grayling are also known to spawn in rivers after the ice breaks up (Northcote 1995, Ingram et al. 2013) and they might avoid some predation pressure from the other fish species on their eggs (and fry). It might also be likely that the interspecific competition between the two species is connected to difference in prey preferences. Grayling and brown trout did show a high dietary overlap but segregated in their utilization of some key prey types. Brown trout have a larger mouth than grayling (Northcote 1995) and are known to shift towards a more piscivorous diet as they become larger (Amundsen et al. 2003).

Both grayling and brown trout are known to be rather aggressive and territorial (Haugen and Rygg 1996, Ingram et al. 2013). Thus, the two superior benthivorous species could restrict the trophic niche of the cold-water adapted species and force them towards the open limnetic water and the profundal habitat.

The profundal habitat is obviously a refuge for Arctic charr from brown trout and grayling competitors, but burbot is a direct competitor for large charr, as well as a predator, as they prey upon juvenile charr (Knudsen et al. 2010). Arctic charr and burbot exhibited a clear resource partitioning as almost the entire Arctic charr population fed on limnetic prey while burbot fed mainly on benthos. Comparable to other studies (Jensen et al. 2017), these findings suggest that Arctic charr rely upon the profundal habitat as a refuge area and less as a feeding habitat. There may however be a predation pressure from larger piscivorous burbot residing in the profundal as the potential habitat space for burbot in the littoral habitat has likely been limited in recent years due to the increased abundance of grayling and brown trout. The profundal habitat provides low food resources for fish growth in subarctic lakes (Knudsen et al. 2006) and the low growth (<35 cm) observed in burbot in Lille Rostavatn as well as the relatively small proportion of fish prey found in their stomachs in the most recent years indicate that they mostly do not get large enough to be piscivore. Kahilainen and Lehtonen (2003) stated that the gillnet catchability of burbot is low and that burbot might be more abundant in the lake than presumed. But evidently the catch has decreased over time in Lille Rostavatn, indicating a decrease in total population.

The recruitment in the burbot population may be subjected to several bottlenecks. Burbot is known to spawn in shallow areas in the autumn (McPhail and Paragamian 2000). Brown trout and grayling may feed on their eggs (and fry) on their spawning grounds and, thus, suppress their recruitment (L'Abée-Lund et al. 1992, Jensen et al. 2008). High grayling and brown trout densities may also induce an earlier migration of small juvenile burbot towards the profundal habitat to avoid predation risk. Fischer et al (2004) showed that increasing competition for shelter in the littoral habitat is an important trigger for juvenile burbot to undergo the littoral-profundal habitat shift. However, in the profundal habitat the juvenile burbot may also likely be subjected to increased predation, for example by larger and cannibalistic adult burbot or Arctic charr. Thus, increased interspecific competition for food and shelter, increased predation pressure, and negative environmental factors such as

increased water temperature can thus contribute to a bottleneck for the burbot population, and thereby to the overall decreased densities observed.

An unknown factor that can be influencing the fish community structure in Lille Rostavatn is the presence of minnow and Atlantic salmon. Minnow fed mainly on benthic invertebrates. There was no focus on catching minnow in 1997 and it is unclear how the densities have evolved over time. The possible impact of minnow on Arctic charr populations is not known. However, a large minnow population is able to displace small brown trout into deeper water (Borgstrøm et al. 1996) which might be an indication that they may be able to impact the fish community in Lille Rostavatn. Atlantic salmon parr is also known to feed on benthos and surface insects in lakes in northern Norway (Jørgensen et al. 2000). The Atlantic salmon population have stayed at a stable low level and should not have a considerable effect on the overall fish community.

Possible climate change effects on the fish community structure

There were clear indications of an abrupt shift in the fish community structure throughout the study period. Temperature is one of the most important environmental cues for fish (Jeppesen et al. 2012) as they are exotherms and therefore their biological performance is directly influenced and dependent on the ambient water temperature in lakes (Jeppesen et al. 2010). As water temperatures of Lille Rostavatn likely have increased over the recent decades as indicated by the available temperature data from the Målselv watercourse, and also supported by future model-based projections in Lake Takvatn (1.5 °C in the climate scenario from 2000-2100; Smalås et al. 2020), it may be expected that the interactions between the cold-water and temperate-adapted fish species have increased as the intensity and outcome of species interactions are highly temperature dependent (Taniguchi et al. 1998). Abiotic factors such as temperature could enable species co-existence through habitat partitioning, or possibly lead to competitive exclusion (Beier 2016). The cold-water adapted fish species are adapted to life in cold water and therefore they may be displaced from habitats with increasing water temperatures through ecological interactions with species more adapted to warmer waters (Byström et al. 2007).

The temperate-adapted fish species increased in the littoral habitat over time. An increase in water temperature could be beneficial for the temperate-adapted fish species as the water temperatures will remain within the preferred range for longer periods, thus producing a longer growing season. The optimal temperatures at which grayling and brown trout grow is

higher than the optimal growth temperature for Arctic charr and burbot (Northcote 1995, Hofmann and Fischer 2002, Larsson 2005, Ingram et al. 2013, Siikavuopio et al. 2014), thus, grayling and brown trout are favored by increasing temperatures with higher reproduction and survival rate. Burbot for instance, showed an overall decline in the lake over the study period and may not be able to recover. In Norway, the status of burbot is unknown (Stapanian et al. 2010). In Finland, burbot populations have declined or been extirpated in 16% of the lakes due to climate change (Tammi et al. 1999). In contrast, the densities of Arctic charr increased over time in the profundal habitat. Arctic charr and burbot may be restricted to the profundal habitat when the summer temperatures are exceeding their optimal temperatures. Studies have shown that burbot and Arctic charr seem to avoid habitats with temperatures above 13 and 16°C, respectively, and prefer to reside in cooler, deeper waters (Hackney 1973, Langeland and L'Abée-Lund 1998, Sandlund et al. 2013). The growth in the cold-water adapted species might be slower during summer as they are confined in the cooler and less profitable feeding areas of the lake due to the increased interactions with the temperate-adapted fish species in the littoral habitat and increased water temperatures.

Even small increases in water temperature may have large consequences for fish species interactions (Taniguchi et al. 1998). Interspecific competition related to both habitat occupancy and feeding may be influenced by changes in water temperature (Svenning et al. 2016). The cold-water adapted fish species showed an overall decrease over time in their relative contribution to the littoral fish community. The cold-water adapted fish species is likely more favored in colder conditions and with increasing water temperatures these interactions may change and shift to an advantage for the temperate-adapted species. Such changes have also been shown in other field studies, for instance brown trout is suggested to replace white-spotted char (*Salvelinus leucomaenis*) at localities with higher water temperatures (Takami et al. 2002). Climate change will produce a threat to Arctic charr and burbot in the littoral habitat through thermally stressful temperatures and thus also by boosting the competitive abilities of grayling and brown trout as they are considered more aggressive and active at higher temperatures (Vehanen et al. 2000, Amundsen and Knudsen 2009). Studies have demonstrated that the water temperature drop in late autumn and during winter, might allow Arctic charr to temporarily resume their littoral diet and niche use (Langeland et al. 1991, Hammar 1998, Huusko et al. 2007). Hammar (1998) suggested that mechanisms responsible for dietary segregation in summer in Swedish lakes broke down during winter when the reduced water temperatures restricted brown trout activity. Climate

warming will, however, likely change the aquatic temperatures, which to some extent will have positive effects on the temperate-adapted fish species as they become more active and efficient foragers for longer periods. Thus, Arctic charr might be forced on a zooplanktivore diet during most seasons as grayling and brown trout will become more active in late autumn. Further south Arctic charr is an obligate zooplanktivore often relegated to the pelagic and profundal habitats during summer due to preference of water temperatures below 12°C (Saksgård and Hesthagen 2004, Jensen et al. 2017, Paterson et al. 2019).

Concluding remarks

Over the last 20 years there has been a large change in the fish community structure in Lille Rostavatn. The relative contribution of the cold-water adapted fish species, Arctic charr and burbot, has distinctly decreased whereas the more temperate-adapted fish species, grayling and brown trout, have increased, presumably because of a rise in water temperature. The present study does not provide clear evidence of the underlying mechanisms of the changes in fish community structure in Lille Rostavatn. However, it might be that the shift in fish species composition is an effect of increased interspecific interactions in the littoral habitat mediated by increased water temperatures. The observed niche segregation between the four fish species is probably decreasing the effects of competitive interactions and thereby facilitating the coexistence of the four species in Lille Rostavatn. It may be difficult to predict how species respond to climate change without knowledge of how species interactions change with climate. These findings suggest that climate warming may intensify the strength of interspecific interactions and that future climate warming may induce strong changes in fish community structure. Thus, further studies are needed to see how climate change may affect biotic interactions in ecosystems.

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Appendix

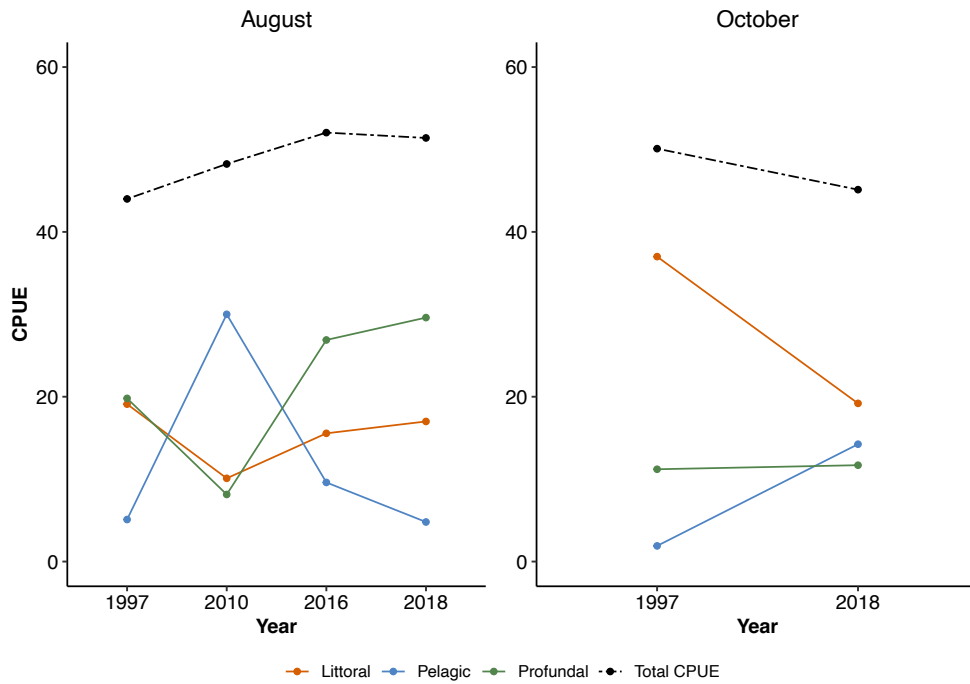
Appendix 1. The number of individuals sampled of each fish species (Arctic charr, brown trout, grayling, burbot, Atlantic salmon and minnow) in each habitat over the four sampling years in August and October.

Year	Species	AUGUST			OCTOBER		
		Littoral	Profundal	Pelagic	Littoral	Profundal	Pelagic
1997	Arctic charr	134	108	35	207	17	101
	Burbot	99	5	0	140	14	0
	Grayling	5	0	0	8	1	0
	Brown trout	20	3	0	8	0	0
	Atlantic salmon	1	0	0	0	0	0
	Minnow	5	0	0	11	0	0
	Total number of fish	264	116	35	374	32	101
2010	Arctic charr	25	47	57			
	Burbot	7	2	0			
	Grayling	77	0	0			
	Brown trout	38	0	0			
	Atlantic salmon	12	0	0			
	Minnow	11	0	0			
	Total number of fish	170	49	57			
2016	Arctic charr	40	39	10			
	Burbot	7	0	0			
	Grayling	40	0	0			
	Brown trout	33	1	1			
	Atlantic salmon	5	0	0			
	Minnow	44	0	0			
	Total number of fish	169	40	11			
2018	Arctic charr	43	93	3	50	22	13
	Burbot	17	5	0	27	15	0
	Grayling	84	9	0	34	0	0
	Brown trout	39	3	0	46	0	0
	Atlantic salmon	34	5	0	5	0	0
	Minnow	96	15	0	0	0	0
	Total number of fish	313	130	3	162	37	13

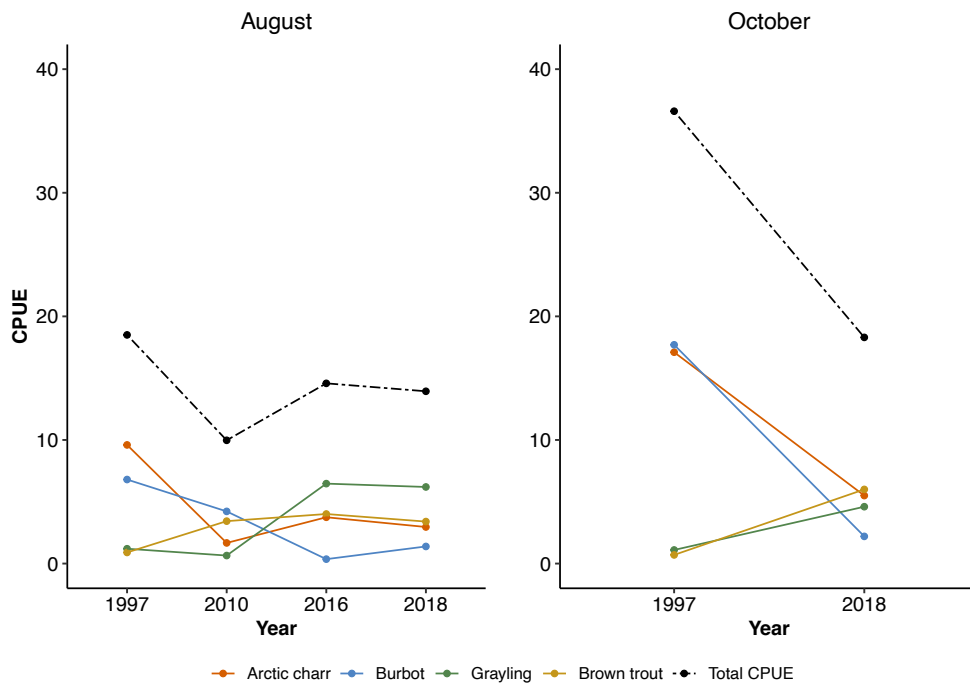
Appendix 2. The number of fish stomachs sampled from Arctic charr, brown trout, grayling, burbot, Atlantic salmon and minnow in each habitat over the four sampling years in August and October.

Year	Fish species	AUGUST			OCTOBER		
		Littoral	Profundal	Pelagic	Littoral	Profundal	Pelagic
1997	Arctic charr	134	108	35	207	17	101
	Burbot	99	5	0	140	14	
	Grayling	5	0	0	8	0	0
	Brown trout	20	0	0	8	0	0
	Atlantic salmon	5	0	0	0	0	0
	Minnow	1	0	0	11	0	0
	Total number of fish	264	113	35	374	31	101
2010	Arctic charr	25	47	57			
	Burbot	7	2	0			
	Grayling	55	0	0			
	Brown trout	35	0	0			
	Atlantic salmon	12	0	0			
	Minnow	9	0	0			
	Total number of fish	143	49	57			
2016	Arctic charr	40	39	10			
	Burbot	7	0	0			
	Grayling	40	0	0			
	Brown trout	33	0	0			
	Atlantic salmon	5	0	0			
	Minnow	42	0	0			
	Total number of fish	167	39	11			
2018	Arctic charr	42	89	3	47	22	12
	Burbot	16	3	0	27	15	0
	Grayling	82	9	0	34	0	0
	Brown trout	40	0	0	43	0	0
	Atlantic salmon	34	0	0	5	0	0
	Minnow	53	15	0	0	0	0
	Total number of fish	267	116	3	156	37	12

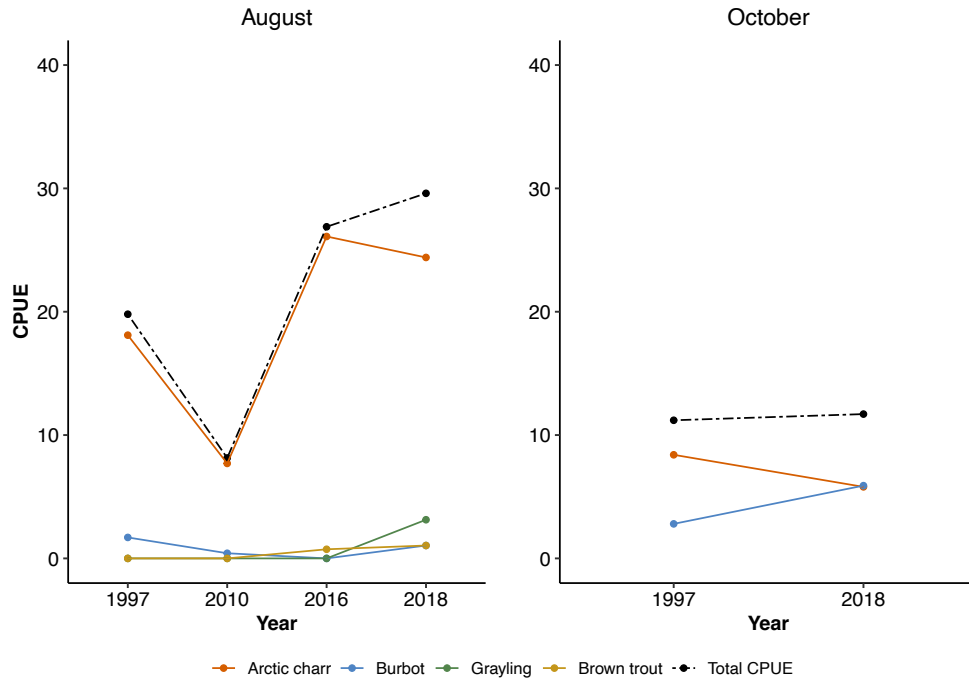
Appendix 3. Catch per unit effort (CPUE, fish 100 m⁻² net night⁻¹) in the littoral (red), profundal (green) and pelagic zone (blue) in August 1997, 2010, 2016 and 2018 and October 1997 and 2018. Black stippled line shows the total CPUE values for all three habitats combined.



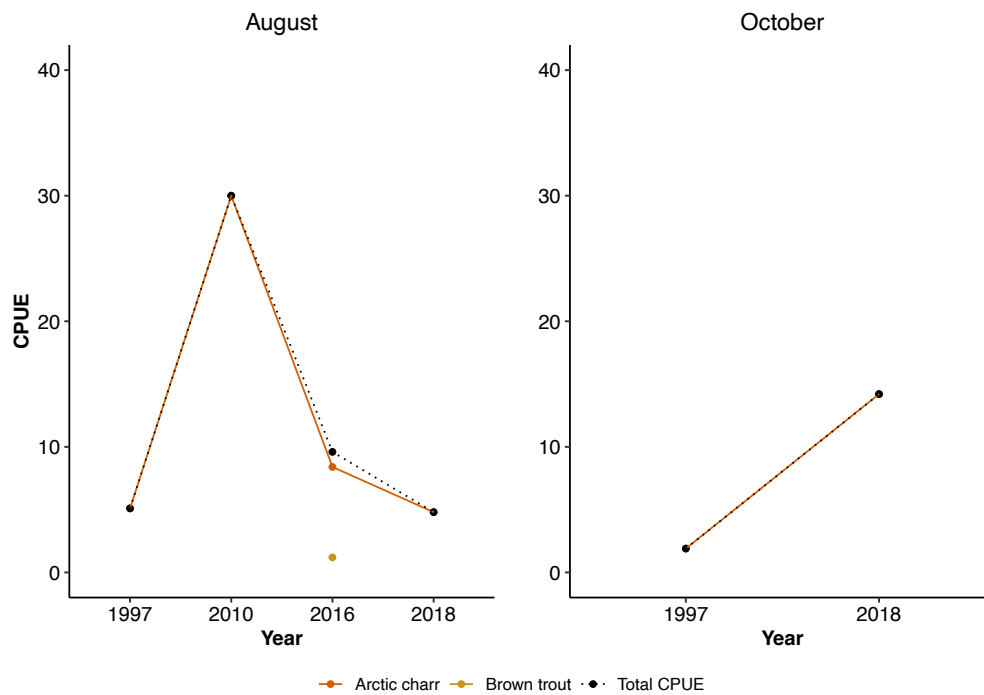
Appendix 4. Catch per unit effort (CPUE, fish 100 m⁻² net night⁻¹) of Arctic charr (red), burbot (blue), grayling (green) and brown trout (yellow) in the littoral zone in August 1997, 2010, 2016 and 2018 and October 1997 and 2018. Black stippled line shows the total CPUE values for all fish species together.



Appendix 5. Catch per unit effort (CPUE, fish 100 m⁻² net night⁻¹) of Arctic charr (red), burbot (blue), grayling (green) and brown trout (yellow) in the profundal zone in August 1997, 2010, 2016 and 2018 and October 1997 and 2018. Black stippled line shows the total CPUE values for all fish species together.



Appendix 6. Catch per unit effort (CPUE, fish 100 m⁻² net night⁻¹) of Arctic charr (red), burbot (blue), grayling (green) and brown trout (yellow) in the pelagic zone in August 1997, 2010, 2016 and 2018 and October 1997 and 2018. Black stippled line shows the total CPUE values for all fish species together.



Appendix 7. Catch per unit effort (CPUE, fish 100 m⁻² net night⁻¹) values of Arctic charr, burbot, grayling, brown trout, Atlantic salmon and minnow from 1997, 2010, 2016 and 2018. n is the number of all fish individuals in total for all three habitats.

Catch per unit effort (CPUE)						
Fish species	1997		2010	2016	2018	
	August (n = 309)	October (n = 283)	August (n = 197)	August (n = 171)	August (n = 284)	October (n = 200)
<i>Littoral zone</i>						
Arctic charr	9.6	17.1	1.7	3.7	3.0	5.5
Burbot	6.8	17.7	4.2	0.4	1.4	2.2
Grayling	1.2	1.1	0.6	6.5	6.2	4.6
Brown trout	0.9	0.7	3.4	4.0	3.4	6.0
Atlantic salmon	0.6	0.4	0.1	1.0	3.1	0.9
Total	19.1	37.0	10.1	15.6	17.0	19.2
<i>Pelagic zone</i>						
Arctic charr	5.1	1.9	30.0	8.4	4.8	14.2
Burbot	0	0	0	0	0	0
Grayling	0	0	0	0	0	0
Brown trout	0	0	0	1.2	0	0
Atlantic salmon	0	0	0	0	0	0
Total	5.1	1.9	30.0	9.6	4.8	14.2
<i>Profundal zone</i>						
Arctic charr	18.1	8.4	7.7	26.1	24.4	5.8
Burbot	1.7	2.8	0.4	0	1.0	5.9
Grayling	0	0	0	0	3.1	0
Brown trout	0	0	0	0.7	1.0	0
Atlantic salmon	0	0	0	0	0	0
Total	19.8	11.2	8.1	26.9	29.6	11.7

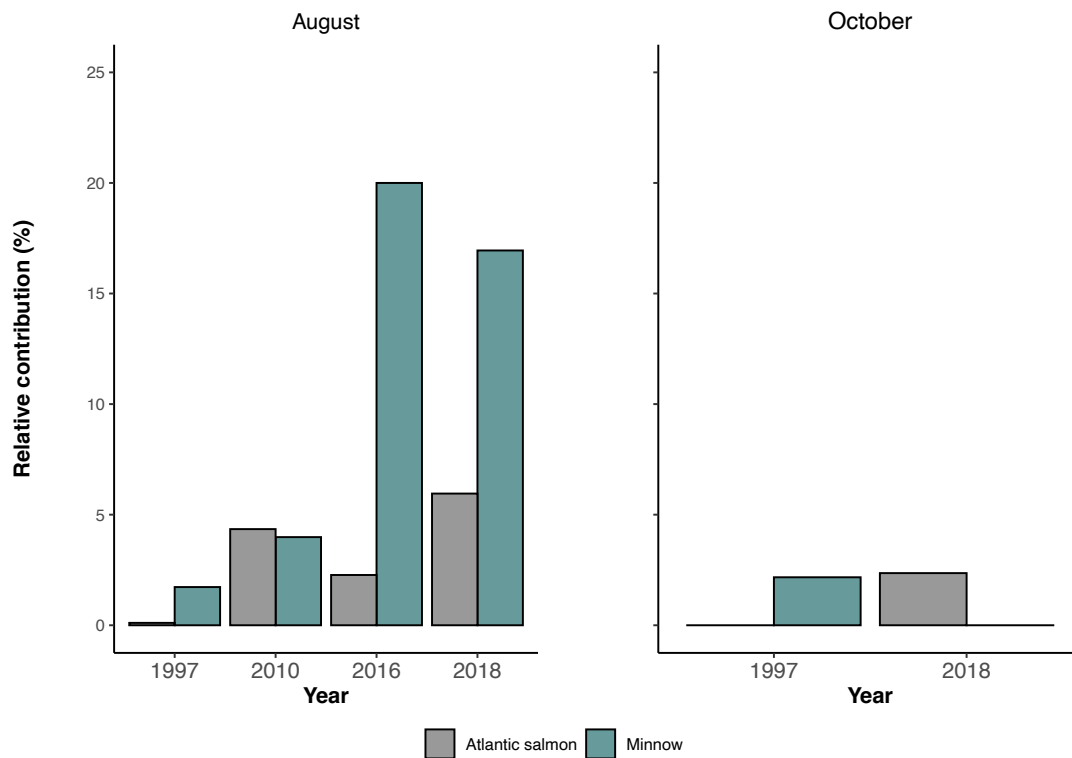
Appendix 8. The relative contribution (%) of the cold-water adapted and temperate-adapted fish species over the four sampling years. Total (%) is both August and October combined. Note that there is no sampling in October 2010 and 2016.

Relative contribution of the cold-water and temperate-adapted fish species				
	Species	Total (%)	August (%)	October (%)
1997	Cold-water adapted species	95	93	97
	Temperate-adapted species	5	7	3
2010	Cold-water adapted species	55	55	
	Temperate-adapted species	45	45	
2016	Cold-water adapted species	56	56	
	Temperate-adapted species	44	44	
2018	Cold-water adapted species	57	54	61
	Temperate-adapted species	43	46	39

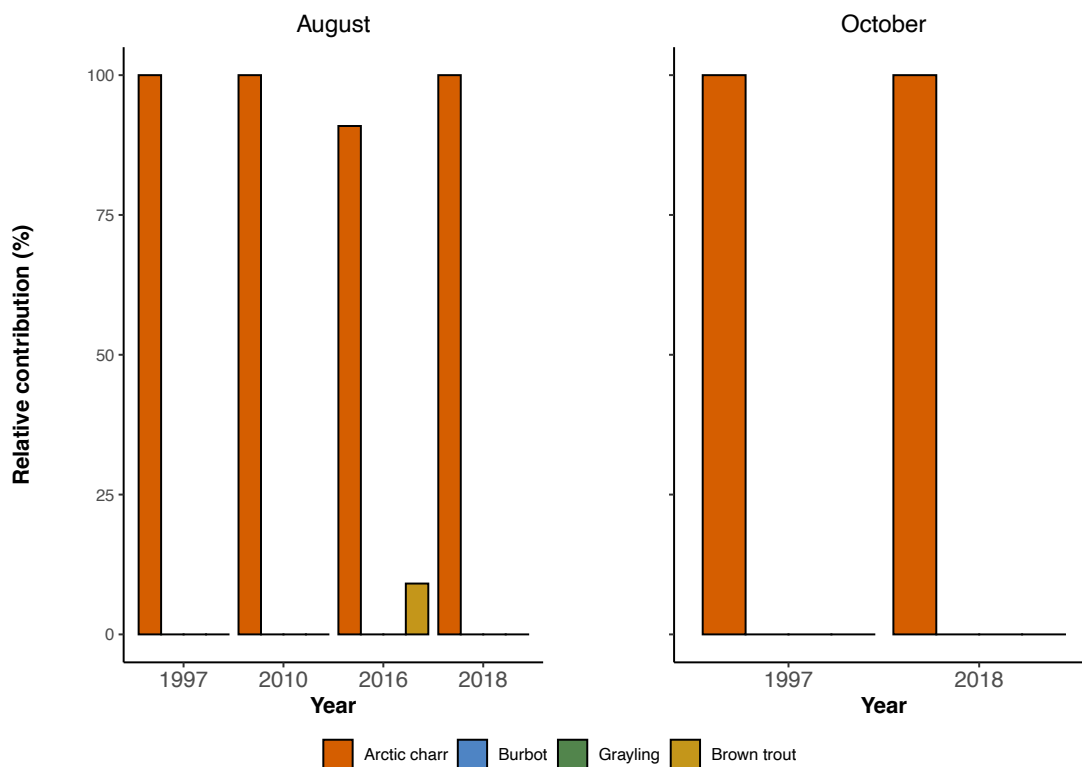
Appendix 9. The relative contribution (%) of the cold-water and temperate-adapted fish species in each habitat over the four sampling years. Note that there is no sampling in October 2010 and 2016.

	Species	AUGUST (%)			OCTOBER (%)		
		Littoral	Pelagic	Profundal	Littoral	Pelagic	Profundal
1997	Cold-water adapted species	90	100	97	96	100	97
	Temperate-adapted species	10	0	3	4	0	3
2010	Cold-water adapted species	22	100	100			
	Temperate-adapted species	78	0	0			
2016	Cold-water adapted species	39	98	91			
	Temperate-adapted species	61	3	9			
2018	Cold-water adapted species	33	100	89	49	100	100
	Temperate-adapted species	67	0	11	51	0	0

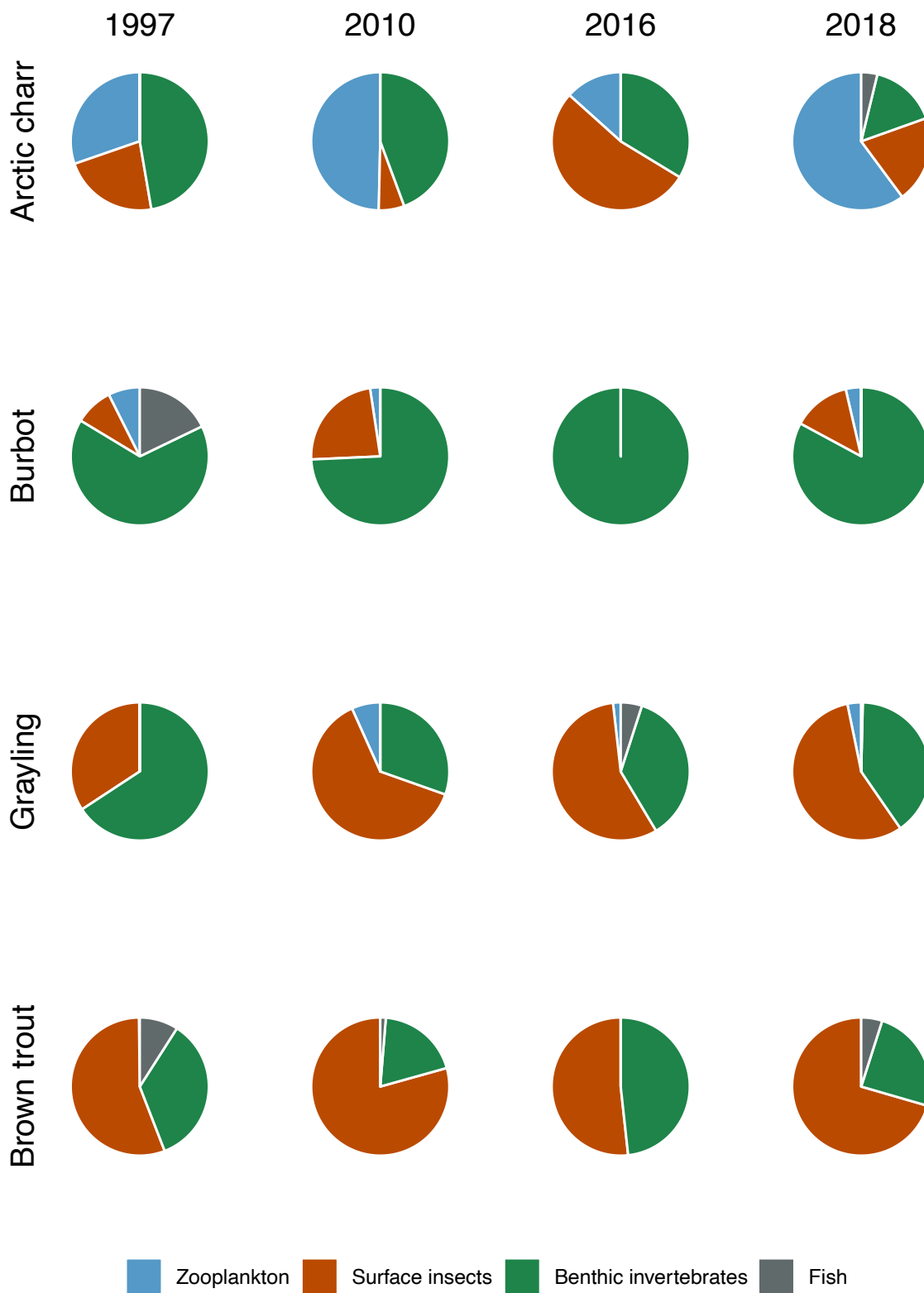
Appendix 10. The relative contribution (%) of minnow and Atlantic salmon in the gill net catches in August 1997, 2010, 2016 and 2018 and October 1997 and 2018.



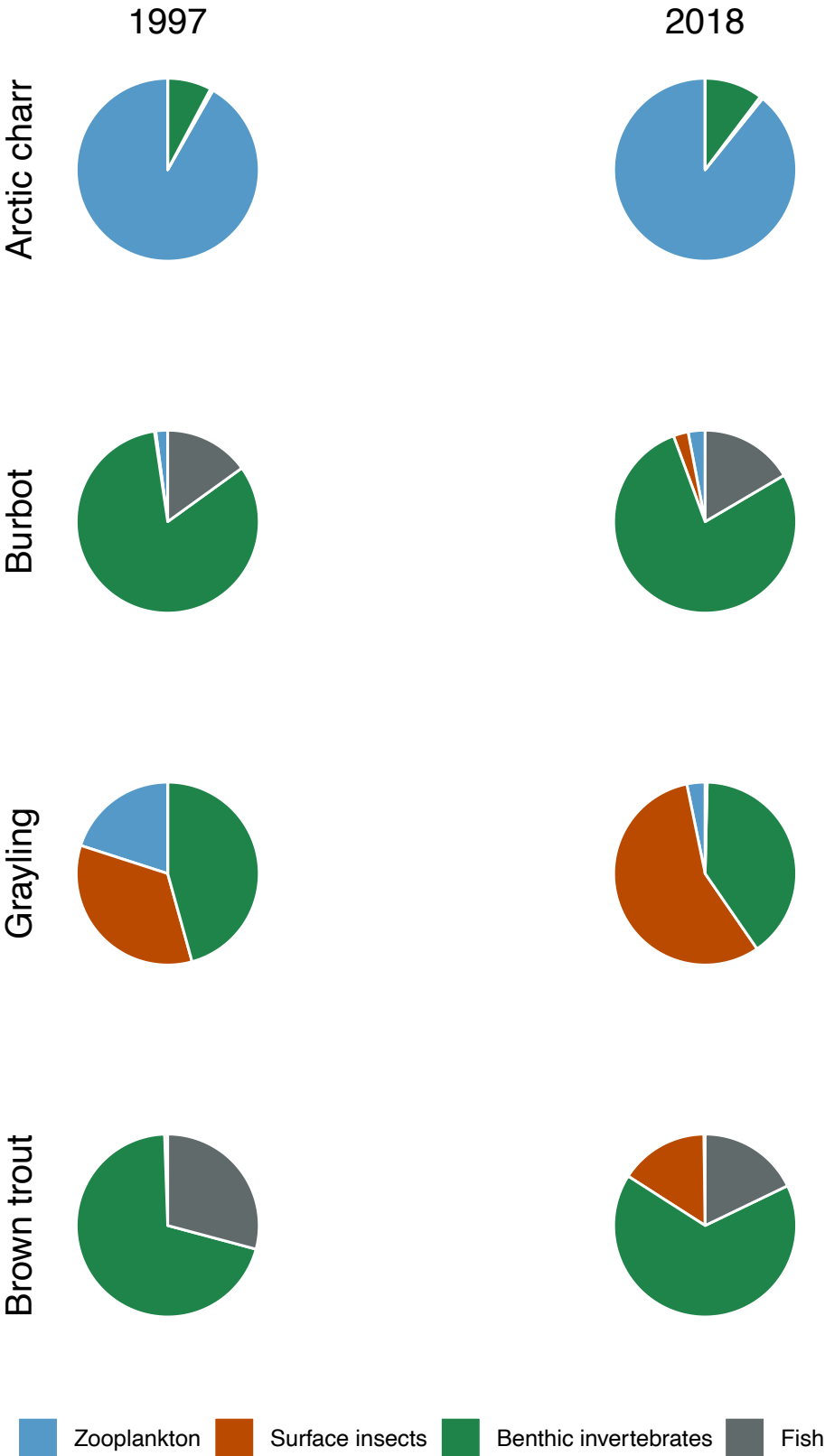
Appendix 11. The relative contribution (%) of Arctic charr (red), burbot (blue), grayling (green) and brown trout (yellow) in the pelagic habitat in Lille Rostavatn in August 1997, 2010, 2016 and 2018 and October 1997 and 2018.



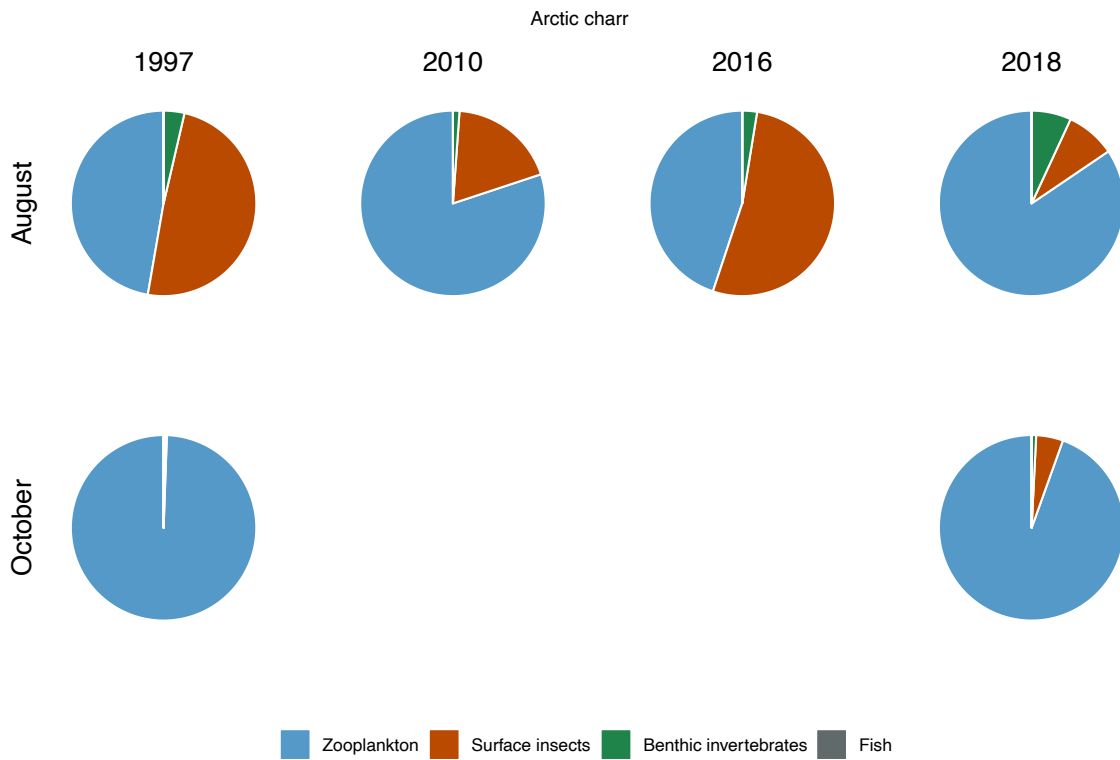
Appendix 12. The main prey categories of littoral caught Arctic charr, burbot, grayling and brown trout in August 1997, 2010, 2016 and 2018.



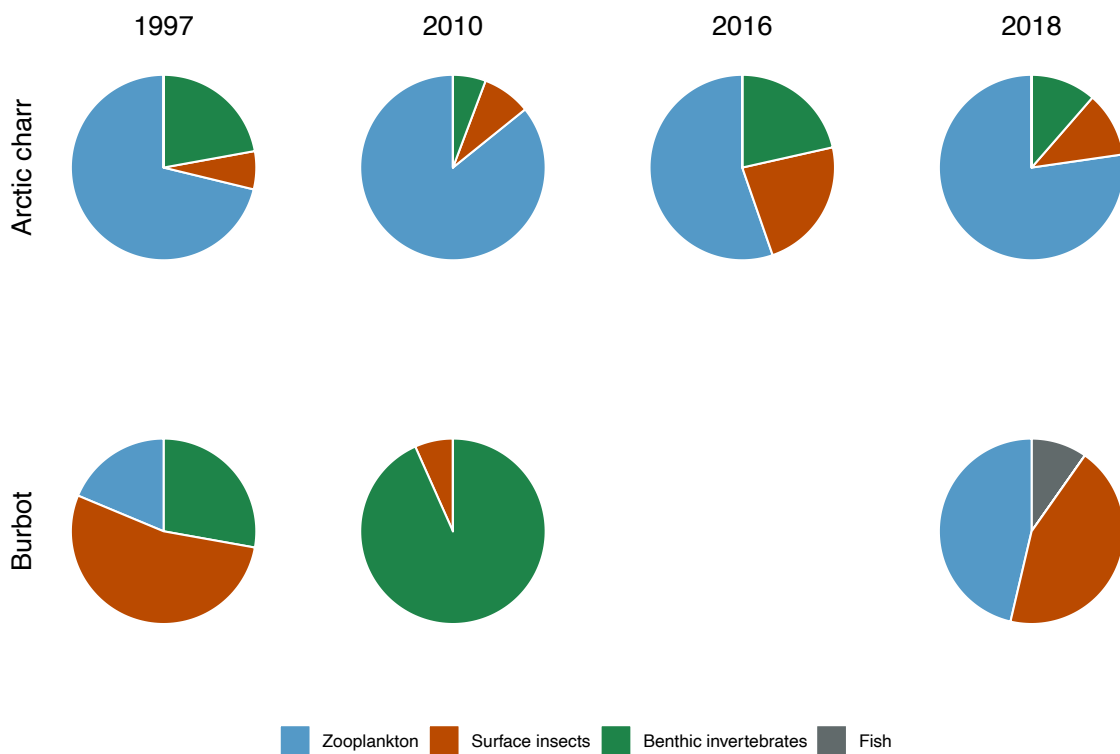
Appendix 13. The main prey categories of littoral caught Arctic charr, burbot, grayling and brown trout in October 1997 and 2018.



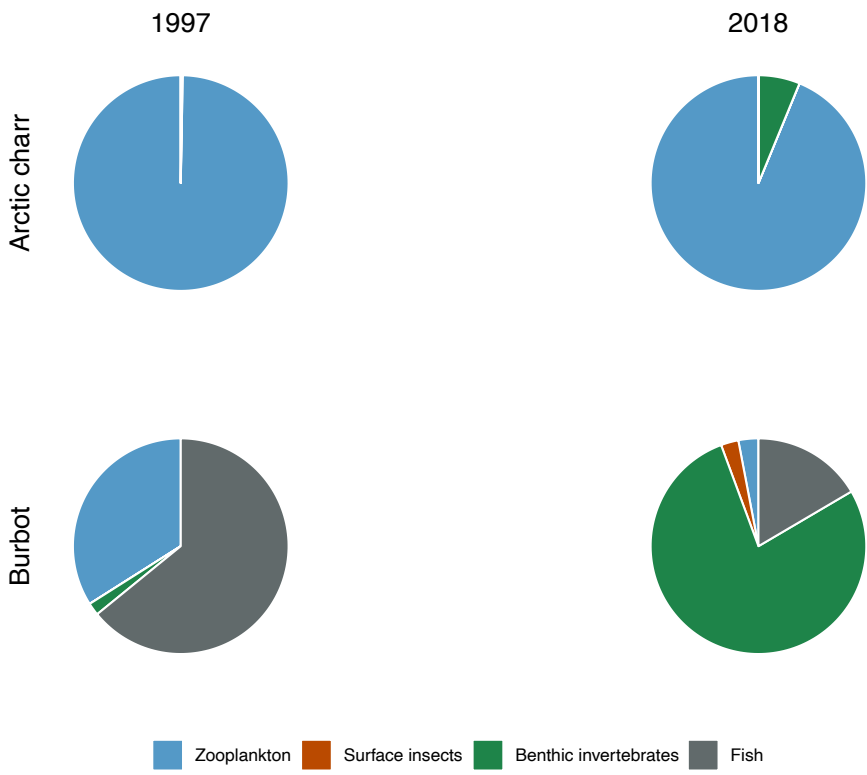
Appendix 14. The main prey categories of pelagic caught Arctic charr in August 1997, 2010, 2016 and 2018 and October 1997 and 2018.



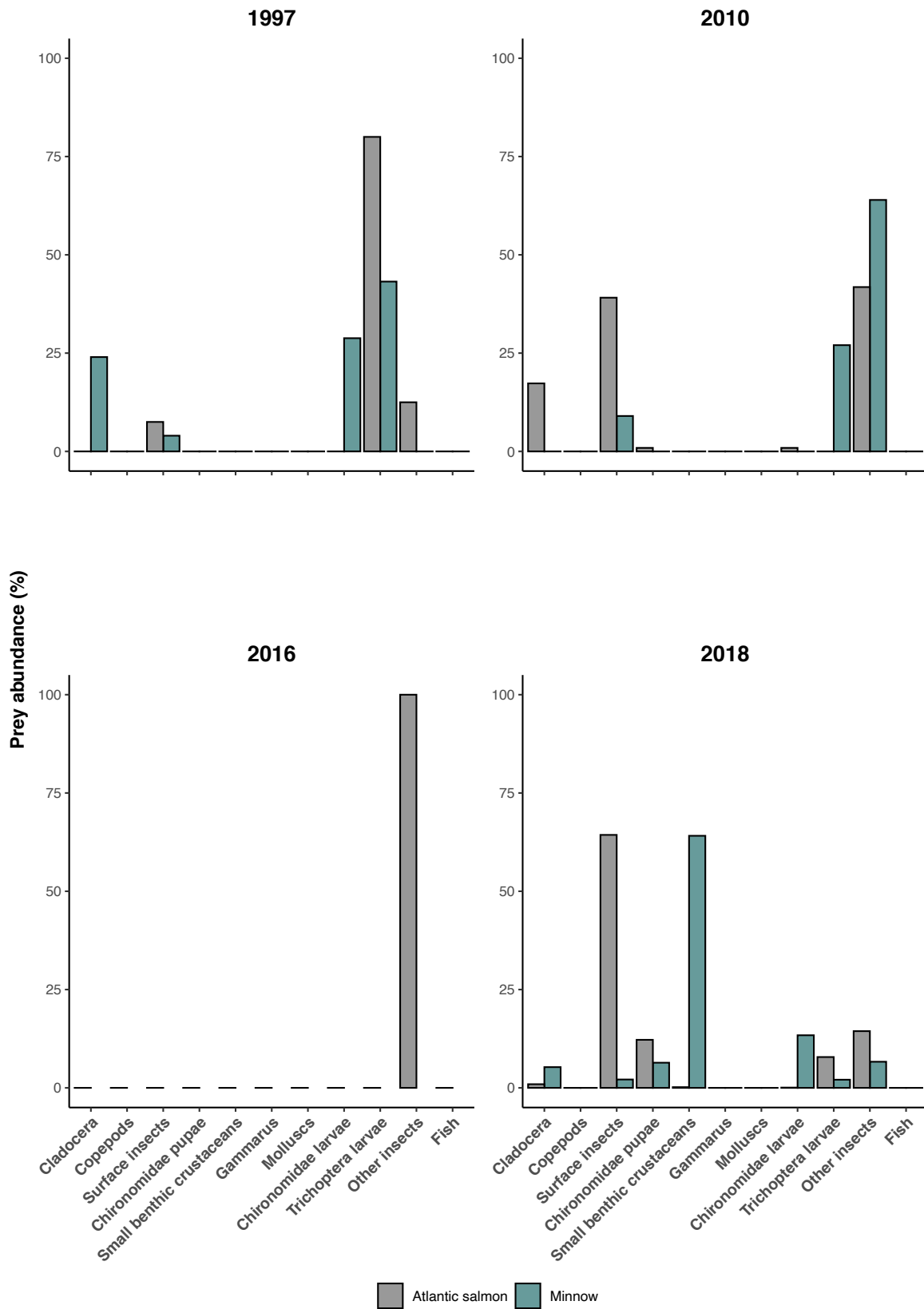
Appendix 15. The main prey categories of profundal caught Arctic charr and burbot in August 1997, 2010, 2016 and 2018.



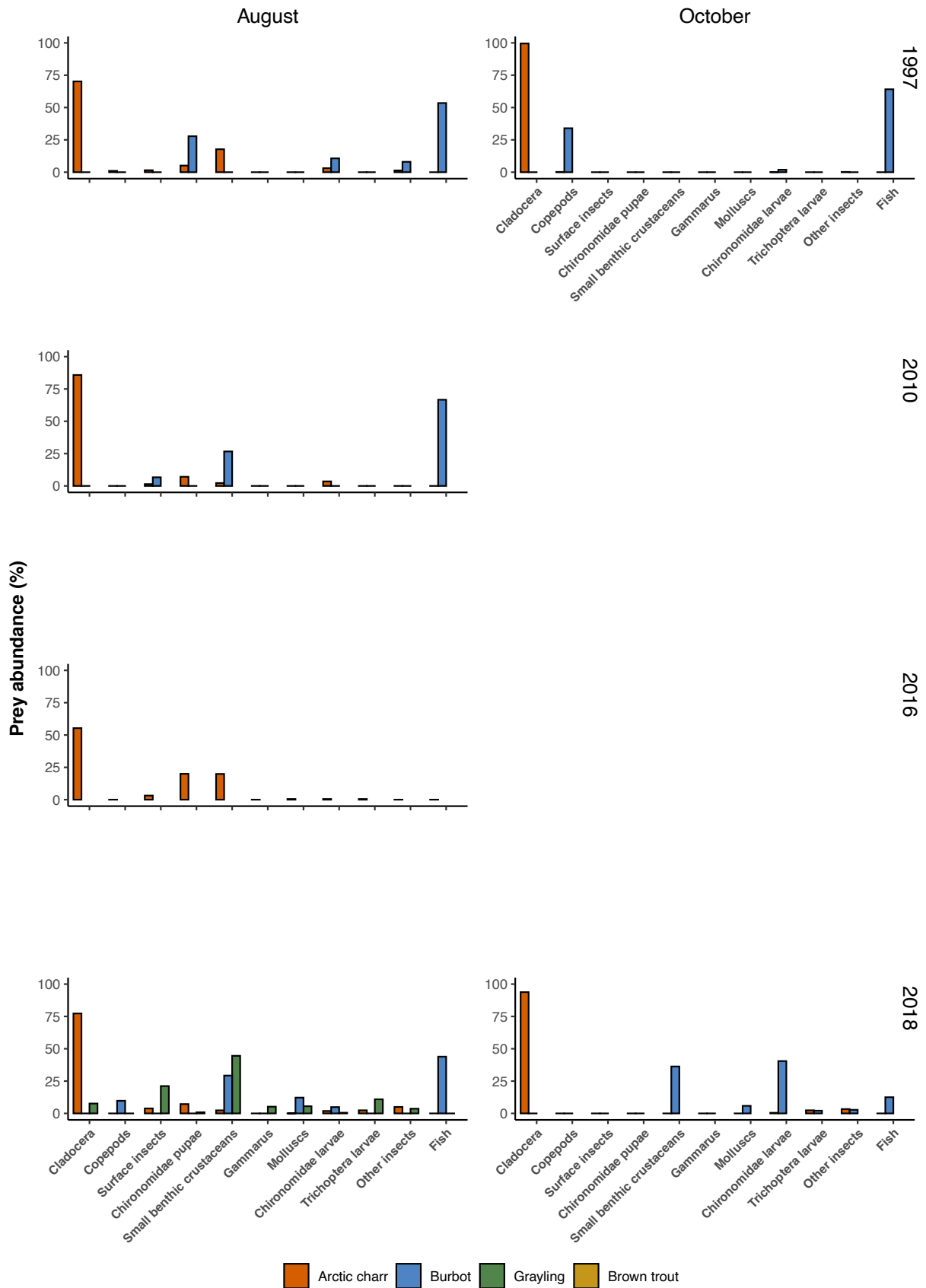
Appendix 16. The main prey categories of profundal caught Arctic charr and burbot in October 1997 and 2018.



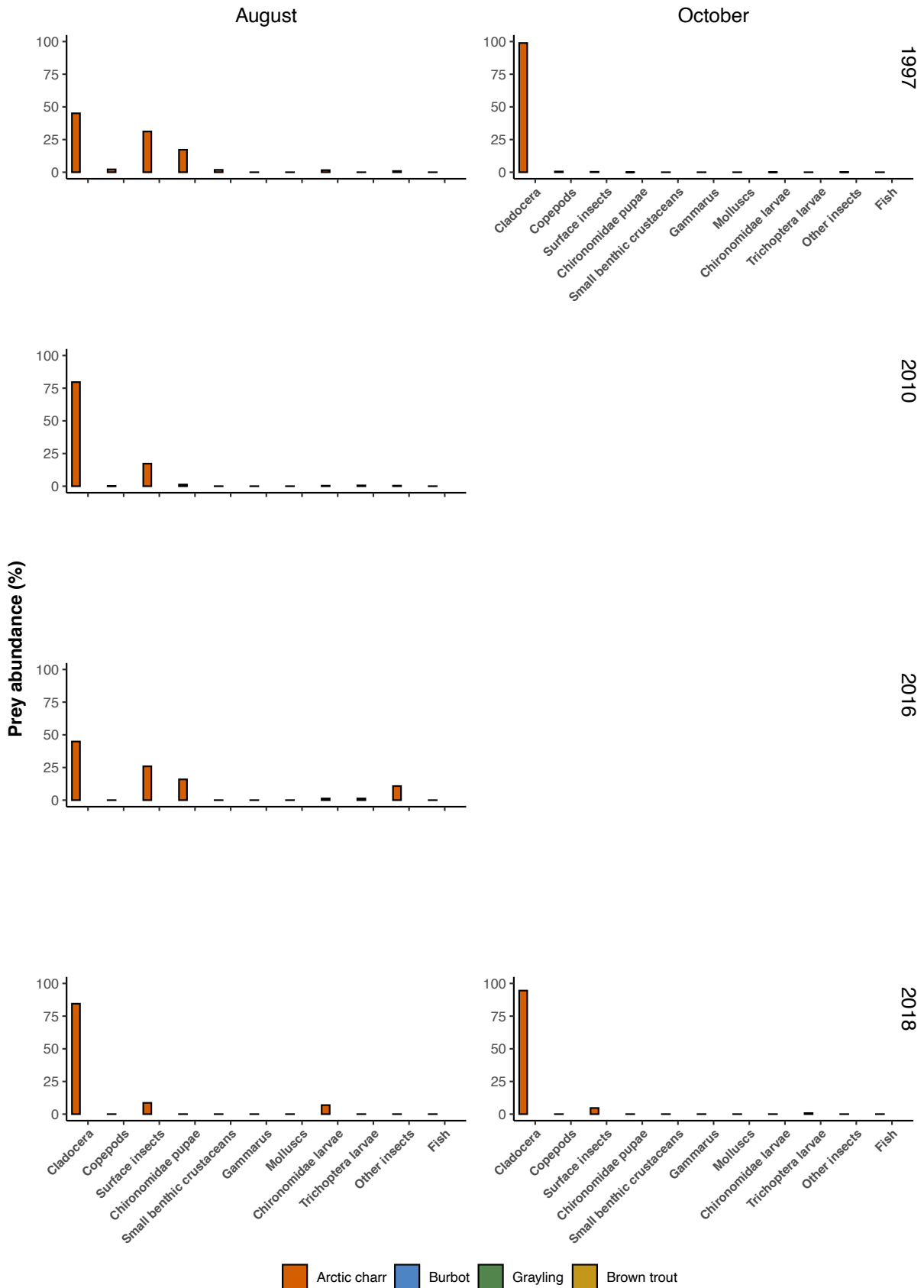
Appendix 17. The relative prey abundance (%) of prey groups found in the stomach content of littoral caught minnow and Atlantic salmon parr in August 1997, 2010, 2016 and 2018.



Appendix 18. The relative prey abundance (%) of prey groups found in the stomach content of profundal caught Arctic charr, burbot, grayling and brown trout in August 1997, 2010, 2016 and 2018 and in October 1997 and 2018.



Appendix 19. The relative prey abundance (%) of prey groups found in the stomach content of pelagic caught Arctic charr in August 1997, 2010, 2016 and 2018 and in October 1997 and 2018.



Appendix 20. The relative prey abundance (PA) and frequency of occurrence (FO) of stomach content in Arctic charr sampled in all habitats in August and October 1997

	AUGUST						OCTOBER					
	Littoral		Pelagic		Profundal		Littoral		Pelagic		Profundal	
N - total	112		34		78		120		69		16	
n - empty stomachs (%)	4 (4%)		4 (13%)		5 (6%)		8 (7%)		0		0	
Mean stomach fullness	42.1		16.1		38.5		45.2		55.1		67.2	
	PA	FO	PA	FO	PA	FO	PA	FO	PA	FO	PA	FO
Cladocera	28.5	65.7	45.1	200.0	70.2	200.0	90.2	214.3	98.9	260.9	99.5	250.0
<i>Bosmina</i> sp.	23.6	41.7	21.5	90.0	30.9	94.5	1.9	37.5	1.5	56.5	2.9	50.0
<i>Daphnia</i> sp.	2.7	14.8	19.0	70.0	34.7	64.4	81.9	96.4	93.0	98.6	93.5	100.0
<i>Holopedium</i> sp.	0.0	0.9	0.4	3.3	0.6	2.7	0.1	1.8	0.5	4.3	0.1	6.3
<i>Bythotrephes</i> sp.	0.0	1.9	0.2	3.3	0.3	8.2	1.1	43.8	1.8	62.3	1.1	56.3
<i>Polyphemus</i> sp.	1.0	0.9	0.0	3.3	1.0	8.2	0.0	0.0	0.0	0.0	0.0	0.0
Uidentified plankton	1.1	5.6	4.0	30.0	2.7	21.9	5.1	34.8	2.0	39.1	2.0	37.5
Copepods	1.8	13.0	2.2	40.0	1.0	17.8	1.5	2.7	0.6	5.8	0.2	12.5
Cyclopoid copepod	1.7	8.3	2.0	33.3	0.7	12.3	1.5	2.7	0.0	2.9	0.1	6.3
Calanoid copepod	0.1	4.6	0.2	6.7	0.3	5.5	0.0	0.0	0.5	2.9	0.1	6.3
Small benthic invertebrates	16.3	43.5	1.8	6.7	17.7	19.2	1.8	5.4	0.0	0.0	0.0	0.0
<i>Eurycercus lamellatus</i>	13.4	33.3	0.0	0.0	0.6	4.1	0.0	0.0	0.0	0.0	0.0	0.0
<i>Sida crystallina</i>	2.4	5.6	1.8	6.7	17.1	15.1	0.0	0.0	0.0	0.0	0.0	0.0
Ostracoda	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
<i>Gammarus lacustris</i>	0.6	4.6	0.0	0.0	0.0	0.0	1.8	5.4	0.0	0.0	0.0	0.0
Molluscs	10.4	31.5	0.0	0.0	0.0	0.0	3.9	12.5	0.0	0.0	0.0	0.0
<i>Lymnea</i> sp.	6.3	12.0	0.0	0.0	0.0	0.0	1.3	4.5	0.0	0.0	0.0	0.0
<i>Planorbis</i> sp.	2.4	11.1	0.0	0.0	0.0	0.0	1.0	4.5	0.0	0.0	0.0	0.0

<i>Valvata</i> sp.	1.5	4.6	0.0	0.0	0.0	0.0	1.7	3.6	0.0	0.0	0.0	0.0
<i>Pisidium</i> sp.	0.2	3.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Surface insects	13.0	27.8	31.2	56.7	1.5	6.8	0.5	4.5	0.3	7.2	0.0	0.0
Chironomidae pupae	9.1	31.5	17.2	46.7	5.1	11.0	0.0	0.0	0.0	1.4	0.0	0.0
Chironomidae larvae	12.6	32.4	1.6	13.3	3.1	8.2	0.5	9.8	0.1	4.3	0.1	12.5
Trichoptera larvae	2.4	4.6	0.0	0.0	0.0	0.0	1.0	2.7	0.0	0.0	0.0	0.0
Trichoptera w.h.l	2.2	2.8	0.0	0.0	0.0	0.0	1.0	2.7	0.0	0.0	0.0	0.0
Trichoptera n.h.l	0.1	1.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Other insects	5.8	25.0	0.9	10.0	1.3	2.7	0.5	9.8	0.1	7.2	0.2	12.5
Trichoptera pupae	0.1	2.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Ephemeroptera larvae	1.2	3.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Plecoptera larvae	2.2	5.6	0.0	0.0	1.3	2.7	0.5	8.0	0.1	7.2	0.1	6.3
Sialidae larvae	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.9	0.0	0.0	0.0	0.0
Tipulidae larvae	1.9	2.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Waterbugs	0.0	2.8	0.0	0.0	0.0	0.0	0.0	0.9	0.0	0.0	0.1	6.3
Coleoptera larvae	0.2	4.6	0.2	3.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Watermites	0.1	2.8	0.7	6.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Other insects	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Unidentified insect larvae	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Fish	1.1	5.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0

Appendix 21. The relative prey abundance (PA) and frequency of occurrence (FO) of stomach content in Arctic charr sampled in all habitats in August 2010.

	AUGUST					
	Littoral		Pelagic		Profundal	
N - total	25		57		47	
n - empty stomachs (%)	1 (4%)		0		2 (4%)	
Mean stomach fullness	35.0		45.0		52.7	
	PA	FO	PA	FO	PA	FO
Cladocera	48.5	54.2	79.6	233.3	85.8	191.1
<i>Bosmina</i> sp.	7.4	12.5	10.5	54.4	19.0	64.4
<i>Daphnia</i> sp.	38.8	33.3	61.3	96.5	61.8	91.1
<i>Holopedium</i> sp.	0.0	0.0	0.9	7.0	0.0	0.0
<i>Bythotrephes</i> sp.	1.1	4.2	6.4	64.9	0.8	6.7
<i>Polyphemus</i> sp.	0.0	0.0	0.6	10.5	4.2	28.9
Unidentified plankton	1.1	4.2	0.0	0.0	0.0	0.0
Copepods	0.6	4.2	0.2	1.8	0.0	0.0
Cyclopoid copepod	0.0	0.0	0.0	0.0	0.0	0.0
Calanoid copepod	0.6	4.2	0.2	1.8	0.0	0.0
Small benthic invertebrates	8.7	12.5	0.0	0.0	2.2	4.4
<i>Eurycerus lamellatus</i>	8.0	8.3	0.0	0.0	2.2	4.4
<i>Sida crystallina</i>	0.0	0.0	0.0	0.0	0.0	0.0
Ostracoda	0.0	0.0	0.0	0.0	0.0	0.0
<i>Gammarus lacustris</i>	0.7	4.2	0.0	0.0	0.0	0.0
Molluscs	23.7	91.7	0.0	0.0	0.0	0.0
<i>Lymnea</i> sp.	6.1	29.2	0.0	0.0	0.0	0.0
<i>Planorbis</i> sp.	5.8	25.0	0.0	0.0	0.0	0.0
<i>Valvata</i> sp.	10.2	25.0	0.0	0.0	0.0	0.0

<i>Pisidium</i> sp.	1.7	12.5	0.0	0.0	0.0	0.0
Surface insects	4.8	20.8	17.2	63.2	1.4	4.4
Chironomidae pupae	1.1	4.2	1.3	14.0	7.1	20.0
Chironomidae larvae	4.3	25.0	0.4	5.3	3.5	13.3
Trichoptera larvae	0.7	8.3	0.6	1.8	0.0	0.0
Trichoptera w.h.l	0.6	4.2	0.6	1.8	0.0	0.0
Trichoptera n.h.l	0.1	4.2	0.0	0.0	0.0	0.0
Other insects	7.5	20.8	0.4	3.5	0.0	0.0
Trichoptera pupae	0.0	0.0	0.0	0.0	0.0	0.0
Ephemeroptera larvae	4.9	8.3	0.0	0.0	0.0	0.0
Plecoptera larvae	0.0	0.0	0.0	0.0	0.0	0.0
Sialidae larvae	0.0	0.0	0.2	1.8	0.0	0.0
Tipulidae larvae	0.0	0.0	0.0	0.0	0.0	0.0
Waterbugs	0.0	0.0	0.0	0.0	0.0	0.0
Coleoptera larvae	0.0	0.0	0.0	0.0	0.0	0.0
Watermites	0.0	0.0	0.2	1.8	0.0	0.0
Other insects	1.1	4.2	0.0	0.0	0.0	0.0
Unidentified insect larvae	1.5	8.3	0.0	0.0	0.0	0.0
Fish	0.0	0.0	0.0	0.0	0.0	0.0

Appendix 22. The relative prey abundance (PA) and frequency of occurrence (FO) of stomach content in Arctic charr sampled in all habitats in August 2016.

	AUGUST					
	Littoral		Pelagic		Profundal	
N - total	40		10		39	
n - empty stomachs (%)	8 (20%)		4 (40%)		20 (51%)	
Mean stomach fullness	46.6		39.0		24.1	
	PA	FO	PA	FO	PA	FO
Cladocera	13.4	46.9	44.9	100.0	55.3	121.1
<i>Bosmina</i> sp.	1.5	12.5	0.0	0.0	15.2	47.4
<i>Daphnia</i> sp.	11.7	28.1	36.7	50.0	39.6	68.4
<i>Holopedium</i> sp.	0.0	0.0	0.0	0.0	0.0	0.0
<i>Bythotrephes</i> sp.	0.1	3.1	0.3	16.7	0.5	5.3
<i>Polyphemus</i> sp.	0.1	3.1	7.9	33.3	0.0	0.0
Unidentified plankton	0.0	0.0	0.0	0.0	0.0	0.0
Copepods	0.0	0.0	0.0	0.0	0.0	0.0
Cyclopoid copepod	0.0	0.0	0.0	0.0	0.0	0.0
Calanoid copepod	0.0	0.0	0.0	0.0	0.0	0.0
Small benthic invertebrates	23.6	46.9	0.0	0.0	19.9	36.8
<i>Eurycerus lamellatus</i>	23.6	46.9	0.0	0.0	19.9	36.8
<i>Sida crystallina</i>	0.0	0.0	0.0	0.0	0.0	0.0
Ostracoda	0.0	0.0	0.0	0.0	0.0	0.0
<i>Gammarus lacustris</i>	0.0	0.0	0.0	0.0	0.0	0.0
Molluscs	5.1	31.3	0.0	0.0	0.5	5.3
<i>Lymnea</i> sp.	2.3	15.6	0.0	0.0	0.0	0.0
<i>Planorbis</i> sp.	2.0	6.3	0.0	0.0	0.0	0.0
<i>Valvata</i> sp.	0.8	6.3	0.0	0.0	0.0	0.0

<i>Pisidium</i> sp.	0.1	3.1	0.0	0.0	0.5	5.3
Surface insects	10.9	28.1	25.9	83.3	3.2	5.3
Chironomidae pupae	31.0	62.5	15.9	50.0	20.0	42.1
Chironomidae larvae	4.6	21.9	1.3	16.7	0.5	5.3
Trichoptera larvae	0.3	9.4	1.3	16.7	0.5	5.3
Trichoptera w.h.l	0.2	6.3	1.3	16.7	0.5	5.3
Trichoptera n.h.l	0.1	3.1	0.0	0.0	0.0	0.0
Other insects	11.0	43.8	10.8	66.7	0.0	0.0
Trichoptera pupae	11.0	43.8	10.5	50.0	0.0	0.0
Ephemeroptera larvae	0.0	0.0	0.0	0.0	0.0	0.0
Plecoptera larvae	0.0	0.0	0.0	0.0	0.0	0.0
Sialidae larvae	0.0	0.0	0.0	0.0	0.0	0.0
Tipulidae larvae	0.0	0.0	0.0	0.0	0.0	0.0
Waterbugs	0.0	0.0	0.3	16.7	0.0	0.0
Coleoptera larvae	0.0	0.0	0.0	0.0	0.0	0.0
Watermites	0.0	0.0	0.0	0.0	0.0	0.0
Other insects	0.0	0.0	0.0	0.0	0.0	0.0
Unidentified insect larvae	0.0	0.0	0.0	0.0	0.0	0.0
Fish	0.0	0.0	0.0	0.0	0.0	0.0

Appendix 23. The relative prey abundance (PA) and frequency of occurrence (FO) of stomach content in Arctic charr sampled in all habitats in August and October 2018.

	AUGUST						OCTOBER					
	Littoral		Pelagic		Profundal		Littoral		Pelagic		Profundal	
N - total	42		3		89		47		12		22	
n - empty stomachs (%)	2 (5%)		1 (33%)		4 (4%)		4 (9%)		0		5 (23%)	
Mean stomach fullness	50.3		19.3		44.3		40.3		53.2		28.5	
	PA	FO	PA	FO	PA	FO	PA	FO	PA	FO	PA	FO
Cladocera	60.1	122.5	84.5	200.0	77.3	175.3	89.2	139.5	94.5	175.0	93.8	158.8
<i>Bosmina</i> sp.	32.3	45.0	0.0	0.0	29.9	65.9	4.9	9.3	0.0	0.0	7.5	35.3
<i>Daphnia</i> sp.	21.4	40.0	39.7	100.0	37.6	65.9	77.7	86.0	90.3	100.0	83.6	82.4
<i>Holopedium</i> sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
<i>Bythotrephes</i> sp.	5.6	30.0	44.8	100.0	9.5	42.4	3.9	41.9	4.2	75.0	2.7	41.2
<i>Polyphemus</i> sp.	0.1	5.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Uidentified plankton	0.7	2.5	0.0	0.0	0.3	1.2	2.6	2.3	0.0	0.0	0.0	0.0
Copepods	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Cyclopoid copepod	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Calanoid copepod	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Small benthic invertebrates	5.7	20.0	0.0	0.0	2.4	17.6	2.0	14.0	0.0	0.0	0.0	0.0
<i>Eurycerus lamellatus</i>	5.1	15.0	0.0	0.0	2.4	17.6	0.2	4.7	0.0	0.0	0.0	0.0
<i>Sida crystallina</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Ostracoda	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
<i>Gammarus lacustris</i>	0.6	5.0	0.0	0.0	0.0	0.0	1.7	9.3	0.0	0.0	0.0	0.0
Molluscs	6.5	42.5	0.0	0.0	0.1	2.4	7.4	9.3	0.0	0.0	0.0	0.0
<i>Lymnea</i> sp.	2.4	20.0	0.0	0.0	0.0	0.0	5.7	4.7	0.0	0.0	0.0	0.0
<i>Planorbis</i> sp.	3.5	15.0	0.0	0.0	0.0	0.0	1.6	2.3	0.0	0.0	0.0	0.0
<i>Valvata</i> sp.	0.6	5.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0

<i>Pisidium</i> sp.	0.0	2.5	0.0	0.0	0.1	2.4	0.1	2.3	0.0	0.0	0.0	0.0
Surface insects	10.5	20.0	8.6	50.0	3.9	8.2	0.5	2.3	4.7	41.7	0.0	0.0
Chironomidae pupae	8.3	42.5	0.0	0.0	7.2	36.5	0.0	0.0	0.0	0.0	0.0	0.0
Chironomidae larvae	1.9	27.5	6.9	50.0	1.9	23.5	0.1	4.7	0.0	0.0	0.5	5.9
Trichoptera larvae	1.5	10.0	0.0	0.0	2.4	5.9	0.8	4.7	0.8	8.3	2.4	11.8
Trichoptera w.h.l	1.5	7.5	0.0	0.0	2.4	4.7	0.8	4.7	0.0	0.0	0.0	0.0
Trichoptera n.h.l	0.0	2.5	0.0	0.0	0.0	1.2	0.0	0.0	0.8	8.3	2.4	11.8
Other insects	1.6	12.5	0.0	0.0	5.0	9.4	0.1	2.3	0.0	0.0	3.3	29.4
Trichoptera pupae	1.5	7.5	0.0	0.0	0.3	1.2	0.0	0.0	0.0	0.0	0.0	0.0
Ephemeroptera larvae	0.0	0.0	0.0	0.0	0.0	0.0	0.1	2.3	0.0	0.0	1.8	11.8
Plecoptera larvae	0.0	0.0	0.0	0.0	0.1	1.2	0.0	0.0	0.0	0.0	0.6	5.9
Sialidae larvae	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Tipulidae larvae	0.0	0.0	0.0	0.0	4.4	4.7	0.0	0.0	0.0	0.0	0.0	0.0
Waterbugs	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Coleoptera larvae	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Watermites	0.0	0.0	0.0	0.0	0.0	1.2	0.0	0.0	0.0	0.0	0.0	0.0
Other insects	0.0	2.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Unidentified insect larvae	0.1	2.5	0.0	0.0	0.3	1.2	0.0	0.0	0.0	0.0	1.0	11.8
Fish	3.8	2.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0

Appendix 24. The relative prey abundance (PA) and frequency of occurrence (FO) of stomach content in burbot sampled in all habitats in August and October 1997.

A.	AUGUST				OCTOBER			
	Littoral		Profundal		Littoral		Profundal	
N - total	65		4		55		7	
n - empty stomachs (%)	10 (15%)		0		6 (11%)		2 (29%)	
Mean stomach fullness	39.2		46.8		38.8		37.9	
	PA	FO	PA	FO	PA	FO	PA	FO
Cladocera	6.6	21.8	0.0	0.0	0.0	2.0	0.0	0.0
<i>Bosmina</i> sp.	5.8	12.7	0.0	0	0.0	2.0	0.0	0.0
<i>Daphnia</i> sp.	0.4	3.6	0.0	0	0.0	0.0	0.0	0.0
<i>Holopedium</i> sp.	0.2	1.8	0.0	0	0.0	0.0	0.0	0.0
<i>Bythotrephes</i> sp.	0.0	1.8	0.0	0	0.0	0.0	0.0	0.0
<i>Polyphemus</i> sp.	0.0	0.0	0.0	0	0.0	0.0	0.0	0.0
Unidentified plankton	0.2	1.8	0.0	0	0.0	0.0	0.0	0.0
Copepods	0.8	7.3	0.0	0.0	2.1	28.6	34.0	60.0
Cyclopoid copepod	0.8	7.3	0.0	0	2.1	28.6	34.0	60.0
Calanoid copepod	0.0	0.0	0.0	0	0.0	0.0	0.0	0.0
Small benthic invertebrates	31.4	65.5	0.0	0.0	41.5	85.7	0.0	0.0
<i>Eurycercus lamellatus</i>	25.9	54.5	0.0	0	23.4	59.2	0.0	0.0
<i>Sida crystallina</i>	0.1	1.8	0.0	0	0.0	0.0	0.0	0.0
Ostracoda	0.0	0.0	0.0	0	0.0	0.0	0.0	0.0
<i>Gammarus lacustris</i>	5.5	9.1	0.0	0	18.1	26.5	0.0	0.0
Molluscs	20.8	43.6	0.0	0.0	24.0	69.4	0.0	0.0
<i>Lymnea</i> sp.	15.2	30.9	0.0	0	22.8	34.7	0.0	0.0
<i>Planorbis</i> sp.	2.5	5.5	0.0	0	0.7	10.2	0.0	0.0
<i>Valvata</i> sp.	2.5	1.8	0.0	0	0.3	10.2	0.0	0.0

<i>Pisidium</i> sp.	0.5	5.5	0.0	0	0.2	14.3	0.0	0.0
Surface insects	0.9	7.3	0.0	0	0.0	0.0	0.0	0.0
Chironomidae pupae	8.1	34.5	27.8	50	0.0	0.0	0.0	0.0
Chironomidae larvae	9.1	34.5	10.7	25	11.4	77.6	1.9	20.0
Trichoptera larvae	0.0	1.8	0.0	0.0	0.3	4.1	0.0	0.0
Trichoptera w.h.l	0.0	1.8	0.0	0	0.3	4.1	0.0	0.0
Trichoptera n.h.l	0.0	0.0	0.0	0	0.0	0.0	0.0	0.0
Other insects	4.4	12.7	8.0	25.0	5.7	24.5	0.0	0.0
Trichoptera pupae	0.0	0.0	0.0	0	0.2	2.0	0.0	0.0
Ephemeroptera larvae	2.9	3.6	0.0	0	0.0	0.0	0.0	0.0
Plecoptera larvae	0.8	3.6	0.0	0	0.5	4.1	0.0	0.0
Sialidae larvae	0.0	0.0	0.0	0	1.4	6.1	0.0	0.0
Tipulidae larvae	0.0	0.0	0.0	0	3.5	10.2	0.0	0.0
Waterbugs	0.0	0.0	0.0	0	0.0	0.0	0.0	0.0
Coleoptera larvae	0.0	1.8	0.0	0	0.0	0.0	0.0	0.0
Watermites	0.0	0.0	0.0	0	0.0	0.0	0.0	0.0
Other insects	0.0	0.0	0.0	0	0.0	0.0	0.0	0.0
Unidentified insect larvae	0.7	3.6	8.0	25	0.2	2.0	0.0	0.0
Fish	17.8	12.7	53.5	25	15.0	12.2	64.1	40.0

Appendix 25. The relative prey abundance (PA) and frequency of occurrence (FO) of stomach content in burbot sampled in all habitats in August 2010.

	AUGUST			
	Littoral		Profundal	
N - total	7		2	
n - empty stomachs (%)	1 (14%)		0	
Mean stomach fullness	30.1		75.0	
	PA	FO	PA	FO
Cladocera	1.9	33.3	0.0	0.0
<i>Bosmina</i> sp.	0.9	16.7	0.0	0.0
<i>Daphnia</i> sp.	0.9	16.7	0.0	0.0
<i>Holopedium</i> sp.	0.0	0.0	0.0	0.0
<i>Bythotrephes</i> sp.	0.0	0.0	0.0	0.0
<i>Polyphemus</i> sp.	0.0	0.0	0.0	0.0
Uidentified plankton	0.0	0.0	0.0	0.0
Copepods	0.5	16.7	0.0	0.0
Cyclopoid copepod	0.5	16.7	0.0	0.0
Calanoid copepod	0.0	0.0	0.0	0.0
Small benthic invertebrates	40.3	16.7	26.7	50.0
<i>Eurycercus lamellatus</i>	0.0	0.0	26.7	50.0
<i>Sida crystallina</i>	0.0	0.0	0.0	0.0
Ostracoda	0.0	0.0	0.0	0.0
<i>Gammarus lacustris</i>	40.3	16.7	0.0	0.0
Molluscs	33.2	33.3	0.0	0.0
<i>Lymnea</i> sp.	28.4	16.7	0.0	0.0
<i>Planorbis</i> sp.	0.0	0.0	0.0	0.0
<i>Valvata</i> sp.	4.7	16.7	0.0	0.0

<i>Pisidium</i> sp.	0.0	0.0	0.0	0.0
Surface insects	1.9	16.7	6.7	50.0
Chironomidae pupae	0.0	0.0	0.0	0.0
Chironomidae larvae	21.3	33.3	0.0	0.0
Trichoptera larvae	0.0	0.0	0.0	0.0
Trichoptera w.h.l	0.0	0.0	0.0	0.0
Trichoptera n.h.l	0.0	0.0	0.0	0.0
Other insects	0.9	16.7	0.0	0.0
Trichoptera pupae	0.0	0.0	0.0	0.0
Ephemeroptera larvae	0.0	0.0	0.0	0.0
Plecoptera larvae	0.0	0.0	0.0	0.0
Sialidae larvae	0.0	0.0	0.0	0.0
Tipulidae larvae	0.0	0.0	0.0	0.0
Waterbugs	0.0	0.0	0.0	0.0
Coleoptera larvae	0.0	0.0	0.0	0.0
Watermites	0.0	0.0	0.0	0.0
Other insects	0.0	0.0	0.0	0.0
Unidentified insect larvae	0.9	16.7	0.0	0.0
Fish	0.0	0.0	66.7	50.0

Appendix 26. The relative prey abundance (PA) and frequency of occurrence (FO) of stomach content in burbot sampled in all habitats in August 2016.

	AUGUST	
	Littoral	
	7	
	2 (29%)	
	42.1	
	PA	FO
N - total		
n - empty stomachs (%)		
Mean stomach fullness		
Cladocera	0.0	0.0
<i>Bosmina</i> sp.	0.0	0.0
<i>Daphnia</i> sp.	0.0	0.0
<i>Holopedium</i> sp.	0.0	0.0
<i>Bythotrephes</i> sp.	0.0	0.0
<i>Polyphemus</i> sp.	0.0	0.0
Uidentified plankton	0.0	0.0
Copepods	0.0	0.0
Cyclopoid copepod	0.0	0.0
Calanoid copepod	0.0	0.0
Small benthic invertebrates	76.3	120.0
<i>Eurycercus lamellatus</i>	20.3	80.0
<i>Sida crystallina</i>	0.0	0.0
Ostracoda	0.0	0.0
<i>Gammarus lacustris</i>	55.9	40.0
Molluscs	0.0	0.0
<i>Lymnea</i> sp.	0.0	0.0
<i>Planorbis</i> sp.	0.0	0.0
<i>Valvata</i> sp.	0.0	0.0

<i>Pisidium</i> sp.	0.0	0.0
Surface insects	0.0	0.0
Chironomidae pupae	0.0	0.0
Chironomidae larvae	0.0	0.0
Trichoptera larvae	0.0	0.0
Trichoptera w.h.l	0.0	0.0
Trichoptera n.h.l	0.0	0.0
Other insects	23.7	20.0
Trichoptera pupae	0.0	0.0
Ephemeroptera larvae	23.7	20.0
Plecoptera larvae	0.0	0.0
Sialidae larvae	0.0	0.0
Tipulidae larvae	0.0	0.0
Waterbugs	0.0	0.0
Coleoptera larvae	0.0	0.0
Watermites	0.0	0.0
Other insects	0.0	0.0
Unidentified insect larvae	0.0	0.0
Fish	0.0	0.0

Appendix 27. The relative prey abundance (PA) and frequency of occurrence (FO) of stomach content in burbot sampled in all habitats in August and October 2018.

	AUGUST				OCTOBER			
	Littoral		Profundal		Littoral		Profundal	
N - total	16		3		27		15	
n - empty stomachs (%)	3 (19%)		0		3 (11%)		0	
Mean stomach fullness	29.4		68.3		60.5		47.9	
	PA	FO	PA	FO	PA	FO	PA	FO
Cladocera	2.3	15.4	0.0	0.0	3.0	4.2	0.0	0.0
<i>Bosmina</i> sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
<i>Daphnia</i> sp.	0.2	7.7	0.0	0.0	3.0	4.2	0.0	0.0
<i>Holopedium</i> sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
<i>Bythotrephes</i> sp.	2.1	7.7	0.0	0.0	0.0	0.0	0.0	0.0
<i>Polyphemus</i> sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Uidentified plankton	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Copepods	1.3	23.1	9.8	33.3	0.0	0.0	0.0	0.0
Cyclopoid copepod	1.3	23.1	9.8	33.3	0.0	0.0	0.0	0.0
Calanoid copepod	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Small benthic invertebrates	25.0	69.2	29.3	33.3	37.8	87.5	36.3	53.3
<i>Eurycercus lamellatus</i>	23.9	61.5	29.3	33.3	6.3	29.2	35.9	46.7
<i>Sida crystallina</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Ostracoda	0.0	0.0	0.0	0.0	0.0	0.0	0.4	6.7
<i>Gammarus lacustris</i>	1.1	7.7	0.0	0.0	31.5	58.3	0.0	0.0
Molluscs	25.5	15.4	12.2	66.7	34.2	75.0	5.8	26.7
<i>Lymnea</i> sp.	21.3	7.7	9.8	33.3	32.6	54.2	5.7	20.0
<i>Planorbis</i> sp.	0.0	0.0	0.0	0.0	0.9	12.5	0.0	0.0
<i>Valvata</i> sp.	4.3	7.7	0.0	0.0	0.6	4.2	0.0	0.0

<i>Pisidium</i> sp.	0.0	0.0	2.4	33.3	0.1	4.2	0.1	6.7
Surface insects	12.4	23.1	0.0	0.0	0.0	0.0	0.0	0.0
Chironomidae pupae	1.1	7.7	0.0	0.0	0.0	0.0	0.0	0.0
Chironomidae larvae	7.9	30.8	4.9	33.3	3.4	50.0	40.5	53.3
Trichoptera larvae	0.0	0.0	0.0	0.0	2.3	12.5	2.1	13.3
Trichoptera w.h.l	0.0	0.0	0.0	0.0	2.3	12.5	2.1	13.3
Trichoptera n.h.l	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Other insects	24.5	23.1	0.0	0.0	2.8	8.3	2.8	26.7
Trichoptera pupae	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Ephemeroptera larvae	24.3	15.4	0.0	0.0	0.0	0.0	0.0	0.0
Plecoptera larvae	0.0	0.0	0.0	0.0	0.1	4.2	0.7	6.7
Sialidae larvae	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Tipulidae larvae	0.0	0.0	0.0	0.0	0.0	0.0	1.4	13.3
Waterbugs	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Coleoptera larvae	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Watermites	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Other insects	0.0	0.0	0.0	0.0	2.6	4.2	0.0	0.0
Unidentified insect larvae	0.2	7.7	0.0	0.0	0.0	0.0	0.7	6.7
Fish	0.0	0.0	43.9	33.3	16.5	12.5	12.5	13.3

Appendix 28. The relative prey abundance (PA) and frequency of occurrence (FO) of stomach content in grayling sampled in all habitats in August and October 1997

	AUGUST		OCTOBER	
	Littoral		Littoral	
N - total	5		8	
n - empty stomachs (%)	0		0	
Mean stomach fullness	66.0		38.8	
	PA	FO	PA	FO
Cladocera	0.0	0.0	12.3	25.0
<i>Bosmina</i> sp.	0.0	0	0.0	0
<i>Daphnia</i> sp.	0.0	0	11.9	12.5
<i>Holopedium</i> sp.	0.0	0	0.0	0
<i>Bythotrephes</i> sp.	0.0	0	0.3	12.5
<i>Polyphemus</i> sp.	0.0	0	0.0	0
Uidentified plankton	0.0	0	0.0	0
Copepods	0.0	0.0	8.1	37.5
Cyclopoid copepod	0.0	0	8.1	37.5
Calanoid copepod	0.0	0	0.0	0
Small benthic invertebrates	0.6	20.0	0.0	0.0
<i>Eurycercus lamellatus</i>	0.6	20	0.0	0
<i>Sida crystallina</i>	0.0	0	0.0	0
Ostracoda	0.0	0	0.0	0
<i>Gammarus lacustris</i>	0.0	0	0.0	0
Molluscs	1.2	40.0	16.1	25.0
<i>Lymnea</i> sp.	0.6	20	4.8	12.5
<i>Planorbis</i> sp.	0.6	20	11.3	12.5
<i>Valvata</i> sp.	0.0	0	0.0	0

<i>Pisidium</i> sp.	0.0	0	0.0	0
Surface insects	26.1	80	33.2	50
Chironomidae pupae	1.2	20	0.0	0
Chironomidae larvae	35.8	60	12.6	25
Trichoptera larvae	3.6	40.0	12.9	75.0
Trichoptera w.h.l	3.6	40	12.9	75
Trichoptera n.h.l	0.0	0	0.0	0
Other insects	31.5	120.0	4.8	75.0
Trichoptera pupae	3.0	20	0.0	0
Ephemeroptera larvae	4.5	20	0.0	0
Plecoptera larvae	6.1	20	3.2	50
Sialidae larvae	0.0	0	0.0	0
Tipulidae larvae	0.0	0	0.0	0
Waterbugs	3.9	20	0.0	0
Coleoptera larvae	13.9	40	0.0	0
Watermites	0.0	0	1.6	25
Other insects	0.0	0	0.0	0
Unidentified insect larvae	0.0	0	0.0	0
Fish	0.0	0	0.0	0

Appendix 29. The relative prey abundance (PA) and frequency of occurrence (FO) of stomach content in grayling sampled in all habitats in August 2010.

	AUGUST	
	Littoral	
N - total	55	
n - empty stomachs (%)	0	
Mean stomach fullness	74.1	
	PA	FO
Cladocera	6.7	23.6
<i>Bosmina</i> sp.	2.8	10.9
<i>Daphnia</i> sp.	3.9	12.7
<i>Holopedium</i> sp.	0.0	0.0
<i>Bythotrephes</i> sp.	0.0	0.0
<i>Polyphemus</i> sp.	0.0	0.0
Uidentified plankton	0.0	0.0
Copepods	0.0	1.8
Cyclopoid copepod	0.0	0.0
Calanoid copepod	0.0	1.8
Small benthic invertebrates	2.8	12.7
<i>Eurycercus lamellatus</i>	2.3	3.6
<i>Sida crystallina</i>	0.0	0.0
Ostracoda	0.1	5.5
<i>Gammarus lacustris</i>	0.4	3.6
Molluscs	0.0	0.0
<i>Lymnea</i> sp.	0.0	0.0
<i>Planorbis</i> sp.	0.0	0.0

<i>Valvata</i> sp.	0.0	0.0
<i>Pisidium</i> sp.	0.0	0.0
Surface insects	56.6	85.5
Chironomidae pupae	4.4	20.0
Chironomidae larvae	1.0	9.1
Trichoptera larvae	0.9	5.5
Trichoptera w.h.l	0.0	0.0
Trichoptera n.h.l	0.9	5.5
Other insects	27.5	43.6
Trichoptera pupae	0.7	1.8
Ephemeroptera larvae	23.9	30.9
Plecoptera larvae	0.0	0.0
Sialidae larvae	1.8	5.5
Tipulidae larvae	0.0	0.0
Waterbugs	1.1	5.5
Coleoptera larvae	0.0	0.0
Watermites	0.0	0.0
Other insects	0.0	0.0
Unidentified insect larvae	0.0	0.0
Fish	0.0	0.0

Appendix 30. The relative prey abundance (PA) and frequency of occurrence (FO) of stomach content in grayling sampled in all habitats in August 2016.

	AUGUST	
	Littoral	
N - total	40	
n - empty stomachs (%)	19 (48%)	
Mean stomach fullness	40.2	
	PA	FO
Cladocera	1.8	4.8
<i>Bosmina</i> sp.	0.0	0.0
<i>Daphnia</i> sp.	0.0	0.0
<i>Holopedium</i> sp.	0.0	0.0
<i>Bythotrephes</i> sp.	0.0	0.0
<i>Polyphemus</i> sp.	0.0	0.0
Uidentified plankton	1.8	4.8
Copepods	0.0	0.0
Cyclopoid copepod	0.0	0.0
Calanoid copepod	0.0	0.0
Small benthic invertebrates	16.7	47.6
<i>Eurycercus lamellatus</i>	12.0	38.1
<i>Sida crystallina</i>	0.0	0.0
Ostracoda	0.0	0.0
<i>Gammarus lacustris</i>	4.7	9.5
Molluscs	6.5	23.8
<i>Lymnea</i> sp.	2.2	9.5
<i>Planorbis</i> sp.	4.3	14.3
<i>Valvata</i> sp.	0.0	0.0

<i>Pisidium</i> sp.	0.0	0.0
Surface insects	27.4	61.9
Chironomidae pupae	6.1	28.6
Chironomidae larvae	5.8	33.3
Trichoptera larvae	7.5	14.3
Trichoptera w.h.l	7.5	14.3
Trichoptera n.h.l	0.0	0.0
Other insects	23.3	42.9
Trichoptera pupae	23.3	42.9
Ephemeroptera larvae	0.0	0.0
Plecoptera larvae	0.0	0.0
Sialidae larvae	0.0	0.0
Tipulidae larvae	0.0	0.0
Waterbugs	0.0	0.0
Coleoptera larvae	0.0	0.0
Watermites	0.0	0.0
Other insects	0.0	0.0
Unidentified insect larvae	0.0	0.0
Fish	1.8	4.8

Appendix 31. The relative prey abundance (PA) and frequency of occurrence (FO) of stomach content in grayling sampled in all habitats in August and October 2018.

	AUGUST				OCTOBER	
	Littoral		Profundal		Littoral	
N - total	82				34	
n - empty stomachs (%)	0				0	
Mean stomach fullness	66.1				55.4	
	PA	FO	PA	FO	PA	FO
Cladocera	3.2	17.1	7.6	22.2	14.6	32.4
<i>Bosmina</i> sp.	0.4	2.4	6.9	11.1	0.0	0.0
<i>Daphnia</i> sp.	2.1	7.3	0.7	11.1	14.1	23.5
<i>Holopedium</i> sp.	0.0	0.0	0.0	0.0	0.0	0.0
<i>Bythotrephes</i> sp.	0.0	1.2	0.0	0.0	0.1	5.9
<i>Polyphemus</i> sp.	0.0	0.0	0.0	0.0	0.0	0.0
Uidentified plankton	0.7	6.1	0.0	0.0	0.4	2.9
Copepods	0.0	0.0	0.0	0.0	0.0	0.0
Cyclopoid copepod	0.0	0.0	0.0	0.0	0.0	0.0
Calanoid copepod	0.0	0.0	0.0	0.0	0.0	0.0
Small benthic invertebrates	20.7	48.8	49.7	77.8	13.9	55.9
<i>Eurycerus lamellatus</i>	19.2	41.5	44.5	66.7	2.5	26.5
<i>Sida crystallina</i>	0.0	0.0	0.0	0.0	0.0	0.0
Ostracoda	0.0	0.0	0.0	0.0	0.0	0.0
<i>Gammarus lacustris</i>	1.5	7.3	5.2	11.1	11.4	29.4
Molluscs	7.0	30.5	5.5	33.3	20.7	73.5
<i>Lymnea</i> sp.	6.6	20.7	5.5	33.3	16.3	41.2
<i>Planorbis</i> sp.	0.3	6.1	0.0	0.0	2.8	20.6
<i>Valvata</i> sp.	0.0	0.0	0.0	0.0	0.3	2.9

<i>Pisidium</i> sp.	0.1	3.7	0.0	0.0	1.4	8.8
Surface insects	46.7	74.4	21.1	77.8	2.2	23.5
Chironomidae pupae	9.5	32.9	0.9	11.1	0.0	0.0
Chironomidae larvae	2.6	14.6	0.5	11.1	11.3	52.9
Trichoptera larvae	3.9	17.1	10.9	55.6	35.5	67.6
Trichoptera w.h.l	3.3	15.9	10.1	44.4	32.0	61.8
Trichoptera n.h.l	0.6	1.2	0.9	11.1	3.5	5.9
Other insects	6.1	35.4	3.6	66.7	1.9	8.8
Trichoptera pupae	0.1	1.2	0.0	0.0	0.0	0.0
Ephemeroptera larvae	3.4	15.9	1.7	11.1	0.0	0.0
Plecoptera larvae	0.4	3.7	0.3	11.1	0.3	5.9
Sialidae larvae	0.3	1.2	0.0	0.0	0.0	0.0
Tipulidae larvae	1.4	6.1	0.0	0.0	1.6	2.9
Waterbugs	0.0	0.0	0.4	11.1	0.0	0.0
Coleoptera larvae	0.0	0.0	0.0	0.0	0.0	0.0
Watermites	0.1	4.9	1.1	33.3	0.0	0.0
Other insects	0.0	1.2	0.0	0.0	0.0	0.0
Unidentified insect larvae	0.4	1.2	0.0	0.0	0.0	0.0
Fish	0.4	1.2	0.0	0.0	0.0	0.0

Appendix 32. The relative prey abundance (PA) and frequency of occurrence (FO) of stomach content in brown trout sampled in all habitats in August and October 1997.

	AUGUST				OCTOBER	
	Littoral		Profundal		Littoral	
N - total	19		3		8	
n - empty stomachs (%)	3 (16%)		0		1 (13%)	
Mean stomach fullness	40.7		50		45	
	PA	FO	PA	FO	PA	FO
Cladocera	0.2	12.5	0.0	0.0	0.0	0.0
<i>Bosmina</i> sp.	0.1	6.3	0.0	0.0	0.0	0.0
<i>Daphnia</i> sp.	0.1	6.3	0.0	0.0	0.0	0.0
<i>Holopedium</i> sp.	0.0	0.0	0.0	0.0	0.0	0.0
<i>Bythotrephes</i> sp.	0.0	0.0	0.0	0.0	0.0	0.0
<i>Polyphemus</i> sp.	0.0	0.0	0.0	0.0	0.0	0.0
Uidentified plankton	0.0	0.0	0.0	0.0	0.0	0.0
Copepods	0.0	0.0	0.0	0.0	0.0	0.0
Cyclopoid copepod	0.0	0.0	0.0	0.0	0.0	0.0
Calanoid copepod	0.0	0.0	0.0	0.0	0.0	0.0
Small benthic invertebrates	0.0	0.0	0.0	0.0	0.0	0.0
<i>Eurycerus lamellatus</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Sida crystallina</i>	0.0	0.0	0.0	0.0	0.0	0.0
Ostracoda	0.0	0.0	0.0	0.0	0.0	0.0
<i>Gammarus lacustris</i>	0.0	0.0	0.0	0.0	0.0	0.0
Molluscs	2.6	6.3	0.0	0.0	0.0	0.0
<i>Lymnea</i> sp.	0.0	0.0	0.0	0.0	0.0	0.0
<i>Planorbis</i> sp.	0.0	0.0	0.0	0.0	0.0	0.0
<i>Valvata</i> sp.	0.0	0.0	0.0	0.0	0.0	0.0

<i>Pisidium</i> sp.	2.6	6.3	0.0	0.0	0.0	0.0
Surface insects	52.3	62.5	40.0	66.7	0.6	14.3
Chironomidae pupae	2.6	12.5	20.0	33.3	0.0	0.0
Chironomidae larvae	9.7	25.0	33.3	66.7	0.0	0.0
Trichoptera larvae	7.9	37.5	0.0	0.0	70.3	100.0
Trichoptera w.h.l	7.8	31.3	0.0	0.0	64.7	85.7
Trichoptera n.h.l	0.1	6.3	0.0	0.0	5.6	14.3
Other insects	15.6	37.5	6.7	33.3	0.0	0.0
Trichoptera pupae	0.0	0.0	0.0	0.0	0.0	0.0
Ephemeroptera larvae	0.0	0.0	0.0	0.0	0.0	0.0
Plecoptera larvae	12.3	18.8	6.7	33.3	0.0	0.0
Sialidae larvae	0.0	0.0	0.0	0.0	0.0	0.0
Tipulidae larvae	2.6	6.3	0.0	0.0	0.0	0.0
Waterbugs	0.8	12.5	0.0	0.0	0.0	0.0
Coleoptera larvae	0.0	0.0	0.0	0.0	0.0	0.0
Watermites	0.0	0.0	0.0	0.0	0.0	0.0
Other insects	0.0	0.0	0.0	0.0	0.0	0.0
Unidentified insect larvae	0.0	0.0	0.0	0.0	0.0	0.0
Fish	9.0	6.3	0.0	0.0	29.2	28.6

Appendix 33. The relative prey abundance (PA) and frequency of occurrence (FO) of stomach content in brown trout sampled in all habitats in August 2010.

	AUGUST	
	Littoral	
N - total	35	
n - empty stomachs (%)	1 (3%)	
Mean stomach fullness	66.8	
	PA	FO
Cladocera	0.0	0.0
<i>Bosmina</i> sp.	0.0	0.0
<i>Daphnia</i> sp.	0.0	0.0
<i>Holopedium</i> sp.	0.0	0.0
<i>Bythotrephes</i> sp.	0.0	0.0
<i>Polyphemus</i> sp.	0.0	0.0
Uidentified plankton	0.0	0.0
Copepods	0.0	0.0
Cyclopoid copepod	0.0	0.0
Calanoid copepod	0.0	0.0
Small benthic invertebrates	0.0	0.0
<i>Eurycercus lamellatus</i>	0.0	0.0
<i>Sida crystallina</i>	0.0	0.0
Ostracoda	0.0	0.0
<i>Gammarus lacustris</i>	0.0	0.0
Molluscs	0.2	2.9
<i>Lymnea</i> sp.	0.0	0.0
<i>Planorbis</i> sp.	0.2	2.9
<i>Valvata</i> sp.	0.0	0.0

<i>Pisidium</i> sp.	0.0	0.0
Surface insects	71.0	91.2
Chironomidae pupae	0.6	5.9
Chironomidae larvae	1.5	11.8
Trichoptera larvae	9.6	23.5
Trichoptera w.h.l	7.9	17.6
Trichoptera n.h.l	1.7	5.9
Other insects	15.7	52.9
Trichoptera pupae	0.0	0.0
Ephemeroptera larvae	3.6	5.9
Plecoptera larvae	1.7	2.9
Sialidae larvae	1.5	8.8
Tipulidae larvae	0.4	2.9
Waterbugs	6.6	14.7
Coleoptera larvae	0.0	0.0
Watermites	0.0	0.0
Other insects	1.3	11.8
Unidentified insect larvae	0.6	5.9
Fish	1.3	2.9

Appendix 34. The relative prey abundance (PA) and frequency of occurrence (FO) of stomach content in brown trout sampled in all habitats in August 2016.

	AUGUST			
	Littoral		Profundal	
N - total	33		1	
n - empty stomachs (%)	24 (73%)		0	
Mean stomach fullness	17.6		40.0	
	PA	FO	PA	FO
Cladocera	0.0	0.0	0.0	0.0
<i>Bosmina</i> sp.	0.0	0.0	0.0	0.0
<i>Daphnia</i> sp.	0.0	0.0	0.0	0.0
<i>Holopedium</i> sp.	0.0	0.0	0.0	0.0
<i>Bythotrephes</i> sp.	0.0	0.0	0.0	0.0
<i>Polyphemus</i> sp.	0.0	0.0	0.0	0.0
Uidentified plankton	0.0	0.0	0.0	0.0
Copepods	0.0	0.0	0.0	0.0
Cyclopoid copepod	0.0	0.0	0.0	0.0
Calanoid copepod	0.0	0.0	0.0	0.0
Small benthic invertebrates	0.0	0.0	0.0	0.0
<i>Eurycercus lamellatus</i>	0.0	0.0	0.0	0.0
<i>Sida crystallina</i>	0.0	0.0	0.0	0.0
Ostracoda	0.0	0.0	0.0	0.0
<i>Gammarus lacustris</i>	0.0	0.0	0.0	0.0
Molluscs	2.6	11.1	0.0	0.0
<i>Lymnea</i> sp.	2.6	11.1	0.0	0.0
<i>Planorbis</i> sp.	0.0	0.0	0.0	0.0
<i>Valvata</i> sp.	0.0	0.0	0.0	0.0

<i>Pisidium</i> sp.	0.0	0.0	0.0	0.0
Surface insects	8.6	22.2	100.0	100.0
Chironomidae pupae	12.1	11.1	0.0	0.0
Chironomidae larvae	0.0	0.0	0.0	0.0
Trichoptera larvae	41.4	44.4	0.0	0.0
Trichoptera w.h.l	41.4	44.4	0.0	0.0
Trichoptera n.h.l	0.0	0.0	0.0	0.0
Other insects	35.3	55.6	0.0	0.0
Trichoptera pupae	12.1	11.1	0.0	0.0
Ephemeroptera larvae	4.3	22.2	0.0	0.0
Plecoptera larvae	0.0	0.0	0.0	0.0
Sialidae larvae	0.0	0.0	0.0	0.0
Tipulidae larvae	0.0	0.0	0.0	0.0
Waterbugs	1.7	11.1	0.0	0.0
Coleoptera larvae	0.0	0.0	0.0	0.0
Watermites	17.2	11.1	0.0	0.0
Other insects	0.0	0.0	0.0	0.0
Unidentified insect larvae	0.0	0.0	0.0	0.0
Fish	0.0	0.0	0.0	0.0

Appendix 35. The relative prey abundance (PA) and frequency of occurrence (FO) of stomach content in brown trout sampled in all habitats in August and October 2018.

	AUGUST				OCTOBER	
	Littoral		Profundal		Littoral	
N - total	40		3		43	
n - empty stomachs (%)	3 (8%)		0		4 (9%)	
Mean stomach fullness	63.4		38.7		50.8	
	PA	FO	PA	FO	PA	FO
Cladocera	0.0	0.0	0.0	0.0	0.2	2.6
<i>Bosmina</i> sp.	0.0	0.0	0.0	0.0	0.0	0.0
<i>Daphnia</i> sp.	0.0	0.0	0.0	0.0	0.0	0.0
<i>Holopedium</i> sp.	0.0	0.0	0.0	0.0	0.0	0.0
<i>Bythotrephes</i> sp.	0.0	0.0	0.0	0.0	0.2	2.6
<i>Polyphemus</i> sp.	0.0	0.0	0.0	0.0	0.0	0.0
Uidentified plankton	0.0	0.0	0.0	0.0	0.0	0.0
Copepods	0.0	0.0	0.0	0.0	0.0	0.0
Cyclopoid copepod	0.0	0.0	0.0	0.0	0.0	0.0
Calanoid copepod	0.0	0.0	0.0	0.0	0.0	0.0
Small benthic invertebrates	0.8	2.7	0.0	0.0	0.7	5.1
<i>Eurycerus lamellatus</i>	0.8	2.7	0.0	0.0	0.0	0.0
<i>Sida crystallina</i>	0.0	0.0	0.0	0.0	0.0	0.0
Ostracoda	0.0	0.0	0.0	0.0	0.0	0.0
<i>Gammarus lacustris</i>	0.0	0.0	0.0	0.0	0.7	5.1
Molluscs	0.2	2.7	0.0	0.0	5.8	17.9
<i>Lymnea</i> sp.	0.0	0.0	0.0	0.0	1.4	2.6
<i>Planorbis</i> sp.	0.0	0.0	0.0	0.0	4.3	12.8
<i>Valvata</i> sp.	0.2	2.7	0.0	0.0	0.0	2.6

<i>Pisidium</i> sp.	0.0	0.0	0.0	0.0	0.0	0.0
Surface insects	67.8	75.7	8.6	33.3	12.3	17.9
Chironomidae pupae	1.9	2.7	0.0	0.0	0.0	0.0
Chironomidae larvae	0.2	2.7	0.9	33.3	0.0	2.6
Trichoptera larvae	19.7	45.9	0.0	0.0	58.8	71.8
Trichoptera w.h.l	7.1	24.3	0.0	0.0	56.7	66.7
Trichoptera n.h.l	12.6	21.6	0.0	0.0	2.1	5.1
Other insects	4.5	16.2	21.6	66.7	4.3	7.7
Trichoptera pupae	0.0	0.0	0.0	0.0	3.2	2.6
Ephemeroptera larvae	2.7	8.1	17.2	33.3	0.0	0.0
Plecoptera larvae	0.2	2.7	0.0	0.0	0.0	0.0
Sialidae larvae	0.0	0.0	4.3	33.3	0.0	0.0
Tipulidae larvae	0.8	2.7	0.0	0.0	0.0	0.0
Waterbugs	0.0	0.0	0.0	0.0	0.2	2.6
Coleoptera larvae	0.0	0.0	0.0	0.0	0.0	0.0
Watermites	0.0	0.0	0.0	0.0	0.0	0.0
Other insects	0.8	2.7	0.0	0.0	0.0	0.0
Unidentified insect larvae	0.0	0.0	0.0	0.0	0.9	2.6
Fish	4.9	8.1	69.0	33.3	17.8	15.4

Appendix 36. Schoeners' index comparing diet overlap between Arctic charr, brown trout, grayling and burbot in August for all four years in A) Littoral zone B) Profundal zone. Arctic charr was the only species caught in pelagic zone and is therefore not included. Significant values shown in bold.

A.		LITTORAL				
	Arctic charr – Brown trout	Arctic charr - Grayling	Arctic charr - Burbot	Brown trout - Grayling	Brown trout - Burbot	Grayling - Burbot
1997	32	35	52	47	23	17
2010	13	21	21	65	4	5
2016	34	49	20	36	4	17
2018	19	35	25	58	17	47

B.		PROFUNDAL				
	Arctic charr – Brown trout	Arctic charr - Grayling	Arctic charr - Burbot	Brown trout - Grayling	Brown trout - Burbot	Grayling - Burbot
1997	11	-	8	-	31	-
2010	-	-	4	-	-	-
2016	3	-	-	-	-	-
2018	5	18	4	11	45	35

Appendix 37. Schoeners' index comparing diet overlap between Arctic charr, brown trout, grayling and burbot in October 1997 and 2018 in A) Littoral zone B) Profundal zone. Arctic charr was the only species caught in pelagic zone and is therefore not included.

A.

LITTORAL

	Arctic charr – Brown trout	Arctic charr - Grayling	Arctic charr - Burbot	Brown trout - Grayling	Brown trout - Burbot	Grayling - Burbot
1997	1	18	7	13	15	20
2018	5	25	13	41	22	40

B.

PROFUNDAL

	Arctic charr – Brown trout	Arctic charr - Grayling	Arctic charr - Burbot	Brown trout - Grayling	Brown trout - Burbot	Grayling - Burbot
1997	-	-	0	-	-	-
2018	-	-	2	-	-	-

Appendix 38. Schoeners' index comparing diet overlap between august 1997, 2010, 2016 and 2018. A. Littoral zone, B. Pelagic zone, C. Profundal zone. Significant values shown in bold.

SCHOENERS' INDEX

A.	LITTORAL					
	1997-2010	1997-2016	1997-2018	2010-2016	2010-2018	2016-2018
Arctic charr	42	48	61	37	52	46
Brown trout	67	20	68	23	83	20
Grayling	35	42	39	36	62	57
Burbot	36	29	57	40	37	45

B.	PELAGIC					
	1997-2010	1997-2016	1997-2018	2010-2016	2010-2018	2016-2018
Arctic charr	49	62	29	57	55	47
Brown trout	-	-	-	-	-	-
Grayling	-	-	-	-	-	-
Burbot	-	-	-	-	-	-

C.	PROFUNDAL					
	1997-2010	1997-2016	1997-2018	2010-2016	2010-2018	2016-2018
Arctic charr	65	58	74	67	70	67
Brown trout	-	40	9	-	-	9
Grayling	-	-	-	-	-	-
Burbot	53	-	49	-	71	-

Appendix 39. Schoeners' index comparing diet overlap between October 1997 and October 2018. 2010 and 2016 is not included as there were no October sampling these years.

SCHOENERS' INDEX

	LITTORAL	PELAGIC	PROFUNDAL
	1997-2018	1997-2018	1997-2018
Arctic charr	89	92	88
Brown trout	77	-	-
Grayling	46	-	-
Burbot	67	-	14

Appendix 40. Levin's index for all fish species caught in the littoral, profundal and pelagic zone in **(A)** August and **(B)** October.

AUGUST				
A.	Year	Littoral	Profundal	Pelagic
Arctic charr	1997	8,1	4,0	4,7
	2010	5,3	2,3	2,4
	2016	5,2	3,8	4,1
	2018	5,6	4,0	2,7
Burbot	1997	6,9	2,6	-
	2010	3,4	1,9	-
	2016	2,4	-	-
	2018	5,4	3,3	-
Grayling	1997	4,4	-	-
	2010	2,6	-	-
	2016	6,1	-	-
	2018	3,7	3,8	-
Brown trout	1997	3,2	-	-
	2010	1,9	-	-
	2016	4,2	-	-
	2018	2,1	-	-
OCTOBER				
B.	Year	Littoral	Profundal	Pelagic
Arctic charr	1997	1,5	1,1	1,2
	2018	1,6	1,4	1,2
Burbot	1997	5,7	1,9	
	2018	4,2	3,2	
Grayling	1997	2,0		
	2018	5,6		
Brown trout	1997	2,0		
	2018	2,7		

Appendix 41. Simpsons reciprocal diversity index (D) and evenness (E) for all four sampling years in the littoral habitat in August and October from the four target species.

	August				October	
	1997	2010	2016	2018	1997	2018
Simpson's diversity index	2.36	2.69	3.32	3.13	0.51	2.73
Evenness	0.59	0.67	0.83	0.78	0.13	0.68

