Interactions between European minnow (*PHOXINUS PHOXINUS*) and brown trout (*SALMO TRUTTA*) in a subalpine lake 40 years after the minnow establishment.

Interaksjoner mellom ørekyt (*PHOXINUS PHOXINUS*) og brun ørret (*SALMO TRUTTA*) i en subalpin innsjø 40 år etter etablering av ørekyt.

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Preface

This Master thesis completes my study in Natural Resource Management at the Norwegian University of Life Sciences (UMB). The motivation for the thesis work comes from my interest in fish and freshwater systems, and working on the thesis has given me insight into what affects an alien species may have on an entire ecosystem over time. In addition, the subject is of current interest, as we may experience alien invasive species at a larger extent in the future.

First of all, I would like to thank my supervisor Reidar Borgstrøm for helpful comments and guidance regarding this thesis. I would also like to thank John E. Brittain, and the University of Oslo for use of the field station and necessary equipment. In addition, I would like to thank Jon Gunnar Dokk and Jon Museth for help in the field.

Special thanks are given to my student collaborator Thor Endre Nytrø, especially for his help in the field, but also for help with data processing and useful comments. I would also like to thank Håkon B. Sundet for help and good advices. Thanks to Ragnhild Wendelbo and Maarten Slangen for useful comments on earlier drafts of the thesis. My dearest Lars Ø. Hemsing deserves a huge thank for all his help and patience during the whole process. In the end, I would like to thank my parents for being there for me, both financially and supportively.

Ås, 12 May 2011

Elisabeth Iversen

Summary

The aim of this study is to clarify the interaction between European minnow (*Phoxinus phoxinus*) and brown trout (*Salmo trutta*), in the subalpine lake, Øvre Heimdalsvatn, with special emphasis on habitat use and diet between the two species about 40 years after the establishment of minnows in the lake. The fieldwork was carried out in three periods: June-July, July-August and August-September 2009. Nordic gillnets were used for collecting fish and to study the habitat use at four different depths (0.5 m, 1.5 m, 3 m and 6 m) in the littoral zone.

The results indicate a clear segregation in habitat use between the European minnow and brown trout. Most of the European minnows were captured at the shallowest depth, i.e. 0.5 m depth, whereas the majority of European minnow, regardless of depth, were captured at the lowermost section, 0-25 cm from the bottom. Few brown trout were captured compared to European minnow, but most brown trout was captured at 1.5 m depth and within the whole gillnet height. However, there was a clear trend towards higher catches in the two deepest sections, 0-25 and 25-50 cm.

Catches by electrofishing revealed that small European minnows, not captured by the gillnets, were frequent in the shallowest part of the littoral. Brown trout caught at deeper depths (3 and 6 m) had a larger body length (> 20 cm), than brown trout caught at 0.5 m and 1.5 m depths (< 20 cm).

The European minnow and juvenile brown trout (< 20 cm) forage mostly on the same prey organisms i.e. Cladocera, terrestrial insects, Ephemeroptera-, Plecoptera- and Trichoptera -species, *Gammarus* and chironomids. Additionally, juvenile brown trout foraged on European minnow, especially in the last period, where 28.9 volume % of the juvenile brown trout’s diet was minnow. In June-July there was a significant diet overlap (D = 63.6 %), whereas there was no significant diet overlap in the two other periods (D = 52.2 % and 42.5 %).

These results indicate a considerable interaction between brown trout and European minnow in Øvre Heimdalsvatn regarding both habitat use and diet. The large density of European minnow on shallow water may be a result of predation risk from brown trout. At the same time, the high European minnow density may strongly reduce available invertebrate prey for juvenile brown trout, which may seek to deeper water, where predation risk for small individuals may be higher. These interactions may lead to a reduced growth rate in brown trout due to reduced food availability, but also result in reduced recruitment to the harvestable stock because of predation on juvenile brown trout by larger brown trout. European minnow in high altitude lakes like Øvre Heimdalsvatn may thus reduce the catch potential of brown trout.

Sammendrag

Målet til denne studien er klarlegge interaksjoner mellom ørekyt (*Phoxinus phoxinus*) og ørret (*Salmo trutta*) i den subalpine innsjøen Øvre Heimdalsvatn, med spesiell vekt på habitatbruk og diett hos de to artene ca 40 år etter introduksjonen av ørekyt. Feltabeidet til dette studiet ble gjennomført i tre perioder sommeren 2009: juni-juli, juli-august og august-september. For innsamling av fisk og studier av habitatbruken ble det benyttet nordiske settegarn satt på fire ulike dybder i litoralsonen (0,5 m, 1,5 m, 3 m og 6 m).

Resultatene indikerer et klart skille i habitatbruk for både ørekyt og ørret. Det ble fanget flest ørekyt i den grunneste lokaliteten, på 0,5 m dyp, men dessuten ble de aller fleste ørekytene uavhengig av settedybde faget i den nederste garnseksjonen, 0-25 cm over bunn. Sammenliknet med ørekyt, ble det samlet tatt få ørret, men flest ørret ble fanget på 1,5 m dyp fordelt over hele garnhøyden. Det var likevel en klar tendens til at flest ørret ble fanget i de to nederste seksjonene av garna, 0-25 of 25-50 cm over bunn.

Ørekyt som ble fanget med elektrofiskeapparat avslørte at mindre ørekyt, som ikke ble fanget med garnene, var vanlig i de grunneste områdene av litoralen. Ørret som ble fanget på større dyp (3 m og 6 m) hadde en større kroppslengde (> 20 cm) enn ørret fanget på 0,5 m og 1,5 m dyp (< 20 cm).

Ørekyt og ørretunger (< 20 cm) predaterte på de samme byttedyrene som for eksempel vannlopper, landlevende insekter, døgnflue- (Ephemeroptera) steinflue- (Plecoptera) og vårflue- (Trichoptera) arter, marflo (*Gammarus lacustris*) og fjærmygg (*Chironomids spp.*). I tillegg predaterte yngre ørret på ørekyten, spesielt i den siste perioden (august-september), hvor 28,9 volume % av ørretens diett bestod av ørekyt. I perioden juni-juli var det en signifikant diettoverlapp (*D* = 63,6 %), men det var ingen signifikant diettoverlapp i de to andre periodene (*D* = 52,2 % og 42,5 %).

Disse resultatene antyder at det er en betydelig interaksjon mellom ørret og ørekyt i Øvre Heimdalsvatn med henhold til både habitatbruk og diett. Den store tettheten av ørekyt på helt grunt vann kan være et resultat av predasjonsrisiko fra ørret, men samtidig kan den store tettheten føre til sterk nedbeiting av næringsdyr som også kunne vært utnyttet av ørret. Ørretungene får dermed mindre mattilgang, og søker kanskje mot dypere vann der predasjonsrisikoen er høyere. Sluttresultatet kan bli at ørret både får redusert vekst på grunn av mindre tilgang på mat, og økt dødelighet på grunn av predasjon fra større ørret på mindre individer. Ørekyt i høgfjellsvann med ørret kan dermed redusere fangstpotensialet for ørret.

Contents

1 Introduction

Introduction of alien species is of great global concern (IUCN 2000; Mooney & Hobbs 2000; Kolar & Lodge 2001). Increased abundance of alien species may lead to irretrievable loss and alternation of species and ecosystem composition (IUCN 2000). The large negative effects on ecosystems are one of the most significant impacts of invasive species (Kolar & Lodge 2000; Canonico et al. 2005; Ellis et al. 2011). Increased abundance of an alien species at the expense of native species may be considered as an invasive species (Tømmerås et al. 2003; Valéry et al. 2008). Freshwater communities are especially vulnerable as they usually have a high proportion of endemic species that may be exterminated (Mills et al. 1994; Sala et al. 2000; Hesthagen & Sandlund 2007). For example, the introduction of opossum shrimp (*Mysis relicta*) in Flathead Lake USA, made a collapse in the native kokanee salmon (*Oncorhynchus nerka*) population (Spencer et al. 1991).

The spread of freshwater species is usually related to human activities such as aquaculture, river regulations, water transfers between catchments, angling and transportations as well as for ornamental reasons (Welcomme 1988; Mills et al. 1994; Kolar & Lodge 2000, 2001; Hesthagen & Sandlund 2007). According to García-Berthou et al. (2005), the ten most frequently introduced aquatic species in the world are all freshwater fish. The majority of alien freshwater fishes in Europe have been introduced from North-America, Africa, former Soviet Union and Eastern Asia over the last 60 years (Welcomme 1988; Grabowska et al. 2010; Koščo et al. 2010). However, there have also been several translocations among European countries and within the countries (García-Berthou et al. 2005).

Alien fish species may alter the abundance of prey organisms and disturb the food web dynamics (Nyström et al. 2003), and alter habitat use and diet of the native fish species (Brabrand & Faafeng 1993; Baxter et al. 2004, 2007; Museth et al. 2007). Alien fish may also become potential competitors, predators or prey for the native species (Museth et al. 2003; Borgstrøm et al. 2010; Tsunoda et al. 2010; Winfield et al. 2011).

The small bodied European minnow (*Phoxinus phoxinus*) is reported to have a negative impact on brown trout populations (*Salmo trutta*) after establishments in high altitude lakes (Borgstrøm & Brabrand 1996; Muset et al. 2007; Borgstrøm et al. 2010), partly because they may utilize the same prey organisms (Museth et al. 2010). European minnow occurs naturally in the southeastern and northern parts of Norway (Huitfeldt-Kaas 1918). However, at present it has been recorded in all Norwegian counties (Hesthagen & Sandlund 2007). As a consequence, the European minnow is listed on the Norwegian black list for ecological risk analyses of alien species (Gederaas et al. 2007), and categorized as a "high risk" species which is defined as "*species that have negative impacts on indigenous biological diversity*" (Gederaas et al. 2007).

The European minnow has also been spread to high altitude lakes; often due to its use by anglers as live bait (Hesthagen et al. 1992; Hesthagen & Sandlund 2007). Brown trout was the only fish species in the lake, Øvre Heimdalsvatn, until the European minnow was established in the last part of the 1960ies. This was probably a result of either the use of European minnow as live bait or from European minnow stocked by a mistake together with brown trout in the lake, Brurskardstjørni, which lies within the catchment area of Øvre Heimdalsvatn (Lien 1981). The aim of the present Master project is to study interactions between brown trout and European minnow in the lake, Øvre Heimdalsvatn, with special emphasis on the habitat use and diet of the two species, about 40 years after the establishment of European minnows in this lake. As the European minnow may be both a food competitor and a prey for brown trout, little overlap both in habitat use and diet between the two species is expected.

2 Study site

The subalpine lake, Øvre Heimdalsvatn, is situated 1088 m a.s.l. on the eastern slope of the Jotunheimen mountain massif in southern Norway (Figure 2.1). It has a catchment area of 23.6 km^2 (Brittain & Borgstrøm 2010). The lake surface area is 0.78 km^2, with a length of 3 km and 396 m at its widest part. Brurskardsbekken in the western end is the main inlet. The 3 km long outlet stream, Hinøgla, flows down to the lake Nedre Heimdalsvatn (1052 m a.s.l.).

During summer, Øvre Heimdalsvatn has a short renewal time. The lake is wind exposed, and this gives a poorly developed stratification during the ice free period (Vik 1978). Approximately two thirds of the energy available for secondary production is produced within the lake, from autochthonous sources like macrophytes and phytoplankton. The remaining plant material for secondary production consists of external inputs, from terrestrial sources and from the inlet (Larsson et al. 1978). The pH is usually in the range 6-7, even though values down to 5.1 and as high as 7.4 have been registered (Larsson et al. 1978). The conductivity of the lake water varies between 6.9 and 31.8 µS/cm, with high concentrations in the late winter as a result of trickle of groundwater (Grøterud & Kloster 1978).

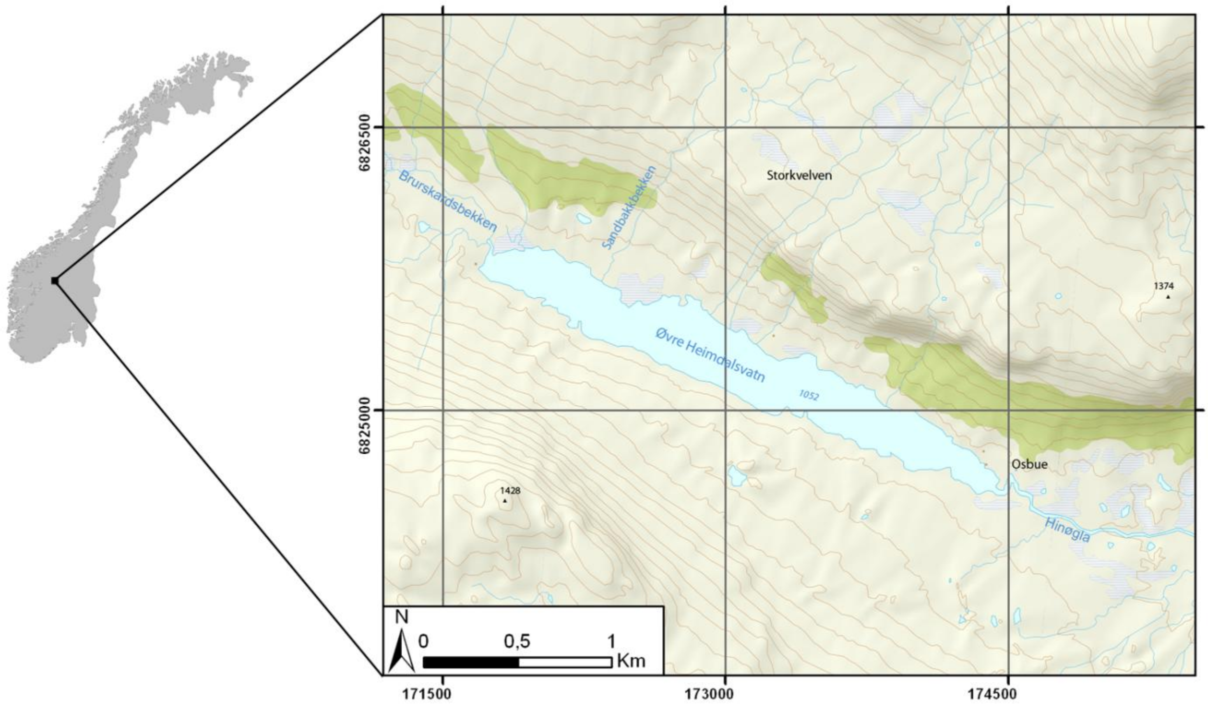

Figure 2.1 Location of Øvre Heimdalsvatn in southern Norway (Map projection WGS84/UTM33N). Source: FKB-Norway.

Heimdalen is situated in the zone between a subarctic and continental climate. The cold mountain climate results in an ice covered lake from the end of October to the beginning of June. After the ice breaks, the water temperature rises to 10-14 °C, and sometimes to above 17 °C and temperature may even exceed 20 °C in sheltered bays (Kloster 1978). During summer 2009, the water- and air temperatures were at the warmest in late June, early July, and decreased thereafter (Figure 2.2). According to Kvambekk & Melvold (2010) the water temperature has increased 2-3 °C in each of the months, August, September and October for the period1985 to 2008. At the same time, the air temperature has had a descending trend in June.

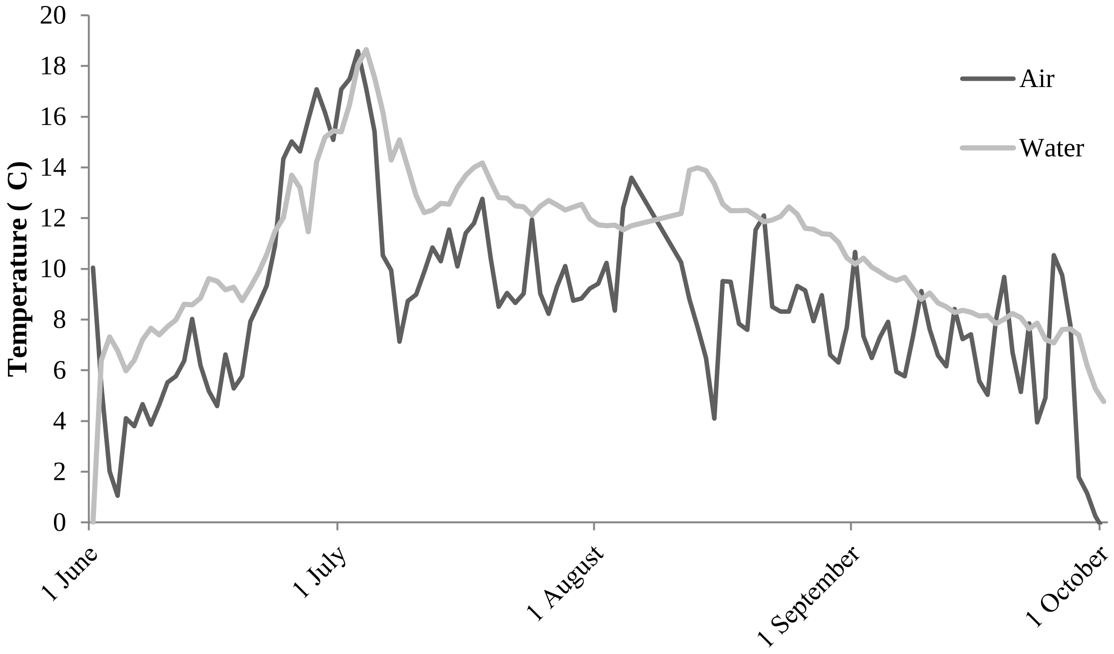

Figure 2.2 Daily mean water- and air temperatures from 1 June 2009 – 1 October 2009. The water temperature is measured in the outlet of Øvre Heimdalsvatn, Hinøgla. The air temperature is measured at Øvre Heimdalsvatn weather station in the eastern end of the lake. (Data kindly given by John E. Brittain, University of Oslo).

The lake, Øvre Heimdalsvatn has an average depth of 4.7 m, with a maximum depth of 13 m (Vik 1978; Figure 2.3), and there are three distinguishable depth zones in the lake (Aarefjord et al. 1978). The uppermost littoral zone, termed the exposed zone, where the substrate is affected by waves and ice erosion, varying from boulders to sand. The lower limit of this zone is mostly situated in depths less than 2 m, however the depth can vary from sheltered bays (0.75 m) to more exposed areas (4 m). The macrophyte zone is the second zone, and evidently characterized by growth of macrophytes of which the most common species are *Carex rostrata*, *Scorpidium scorpoides* and *Isöetes lacustris*. It ranges down to 5 -5.5 m for the whole lake. The macrophytes do not occur lower than 5-5.5 m depth, and this forms the natural boundary towards the third zone, termed the non-macrophytic zone. Soft sediment is dominating this zone, although some areas are covered with rocks- and stones (Aarefjord et al. 1978).

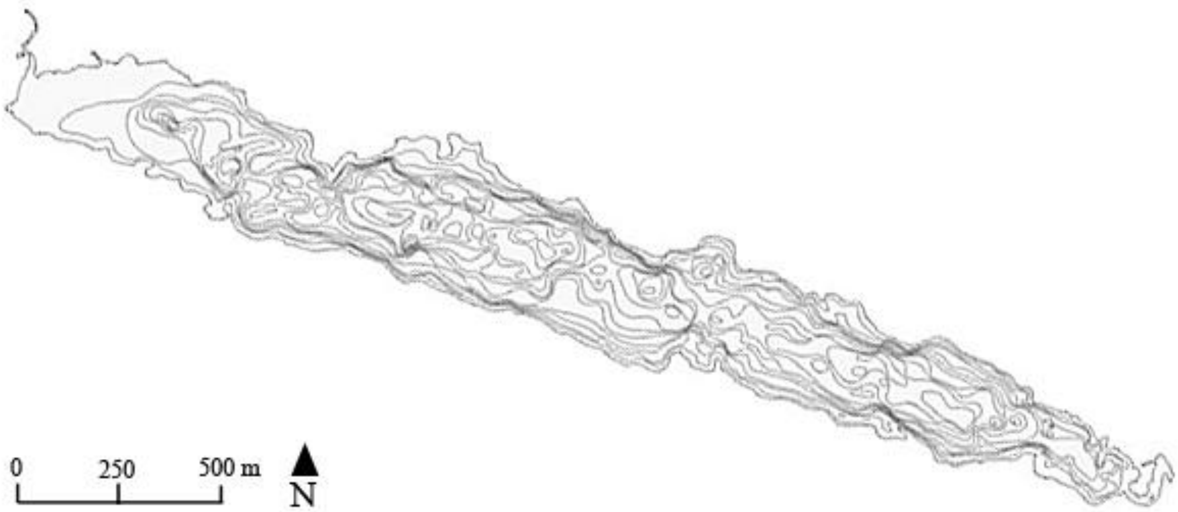

Figure 2.3 Contour map of Øvre Heimdalsvatn. Contours are at 1 meter intervals. Modified after Brittain & Borgstrøm (2010).

The lake, Øvre Heimdalsvatn contains only two fish species; brown trout and European minnow (Figure 2.4). In the 1960s the brown trout population decreased by about 50 % in comparison to the population size in the 1950s, due to extensive fishing (Jensen 1977). Findings from Nytrø (2010) indicate that the brown trout population in 2009 shows characteristics of an over-population. The European minnow population in the lake is characterized by slow growth and by a high density (Museth et al. 2002).The benthic community in the lake is dominated by chironomids, however, other benthos such as Ephemeroptera-, Trichoptera- and Plecoptera-species, *Gammarus lacustris* and oligochaeta are also well represented. The richness of the benthic fauna is in the macrophytic zone (Næstad & Brittain 2010). The zooplankton community consists chiefly of the cladocerans *Holopedium gibberum* and *Bosmina longispina*, with *Cyclops scutifer* and *Heterocope saliens* as the most common copepods, whereas *Conochilus unicornis*, *Polyarthra vulgaris* and *Kellicottia longispina* are common rotifers (Larsson 1978; Larsson et al. 2010). Allocthonous organic matter is one of the most important foods for zooplankton and benthos (Aarefjord et al. 1978).

Figure 2.4 European minnow. Photo: Thor Østbye.

Research in the lake, Øvre Heimdalsvatn (Figure 2.5) started with a study of the brown trout population by Kjell W. Jensen, aiming to find the relationship between maximum yields and fishing effort for a brown trout population with good recruitment conditions (Jensen 1977). From 1968 to 1974 the lake ecosystem studies in Øvre Heimdalsvatn were part of the International Biological Program (IBP), leading to international publishing; including the special issue of the journal Holarctic Ecology devoted to the lake in 1978 (Vik 1978). Further studies of the lake have discovered long-term changes and trends in ecological conditions of the lake and its catchment (Brittain & Borgstrøm 2010).

Figure 2.5 View over Øvre Heimdalsvatn taken from SE in the direction to NW. Photo: T.E. Nytrø.

3 Material and methods

3.1 Definitions

Different terms have been used in studies concerning alien and invasive species (Colautti & MacIsaac 2004); therefore, terms used in the present thesis are defined and presented in Table 3.1.

Table 3.1 The definitions of terms used in the present thesis.

Term	Definition	Reference
Alien (non-native and introduced) species	A species outside of its natural range (past or present).	IUCN 2000 Mooney & Hobbs 2000
Invasive species	An alien species that increase in abundance at the expense of the native species.	Tømmerås et al. 2003 Valéry et al. 2008
Native (indegenous) species	A species occurring within the range it occupies naturally or could occupy.	IUCN 2000 Kolar & Lodge 2001

3.2 Habitat use

To study the habitat use of European minnow and brown trout in the littoral zone, Nordic survey gillnets were set parallel to the shore at depths 0.5 m, 1.5 m, 3 m and 6 m. The gillnets were set in randomly chosen areas within zone 1, 2 and 3, either on the north or south side of the lake (Figure 3.1; Appendix 1) between 1900-2100 hours and lifted between 0700-0900 hours the following morning. The gillnets was 1.5 m height and 30 m long, consisting of twelve 2.5 m sections with the following mesh-sizes (knot to knot): 5, 6.25, 8, 10, 12.5, 15.5, 19.5, 24, 29, 35, 43 and 55 mm. The vertical position of each European minnow and brown trout captured by the gillnets was recorded in each 25 cm horizontal sections of the gillnets from the bottom line to the top of the gillnet. In total, the gillnets were set in seven, five and three nights, in three periods: 24 June - 3 July, 28 July - 2 August and 31 August - 3 September, 2009, respectively. All captured European minnow and brown trout was measured to the nearest mm with the caudal fin spread in a “natural” position.

Catch per unit effort (CPUE) was calculated for total capture of brown trout and European minnow, to compare the relative fishing effort between the species. CPUE is defined as the numbers of fish captured per 100 m^2 gillnet area per night. In June, electrofishing (made by Paulsen, Trondheim) was performed on 100 m shore line on the north side of the lake in zone 1 to capture European minnow in the littoral zone. See Borgstrøm & Skaala (1993) for a detailed description of the apparatus used.

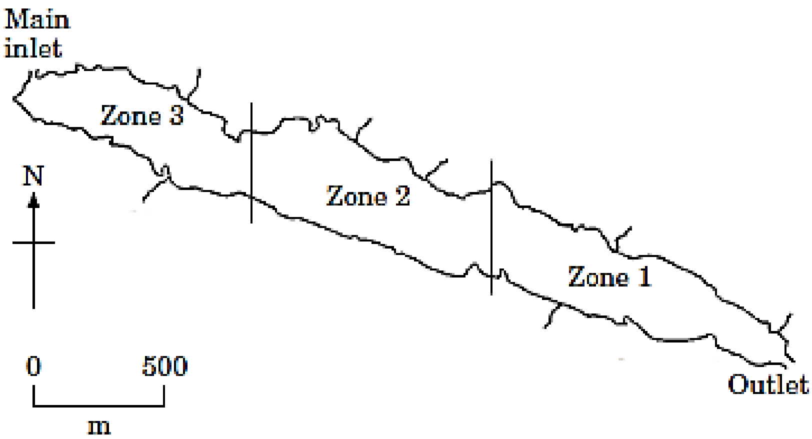

Figure 3.1 The Nordic survey gillnets were set at 0.5, 1.5, 3 and 6 m depths, in random stations within three zones of Øvre Heimdalsvatn during the three periods June-July, July-August and August-September, 2009 (Modified after Museth et al. 2002).

3.3 Diet-analyses

In total, 71 stomachs of brown trout in the length class from 9 – 19.9 cm (juvenile brown trout) were examined. The numbers of stomach samplings were 34 in June-July, 23 in July-August, and 14 in August-September. In total 149, stomachs of European minnow were examined, with 79 in June-July, 38 in July-August and 32 in August-September. The examined European minnows were in the length class 50 - 100 mm.

Samples were conserved in small vials with ethanol, and later examined under a binocular microscope. The stomach contents were first sorted into 16 categories. Some of the prey organisms were identified to species, others to higher taxonomic levels. The categories where later merged to eleven categories (Table 3.2). The volumetric method was applied to get the volume percentage of the different categories (Windell 1971).

Table 3.2 Stomach content categories and description of prey organisms of European minnow and juvenile brown trout from Øvre Heimdalsvatn, during the three periods June-July, July-August and August-September, 2009.

Category	Description
Gammarus	*Gammarus lacustris*
EPT –species	Ephemeroptera, Plecoptera and Trichoptera imagoes, nymphs/larvae
Terrestrial insects	Diptera and Formicidae
Chironomids	Larvae and pupae
Cladocera	Mainly *Eurysercus lamellatus*
Minnow	European minnow, *Phoxinus phoxinus*
Tadpole shrimps	*Lepidurus arcticus*
Other aquatic insects	Beetles, Megaloptera larvae, Tipulidae larvae
Mollusca	Gastropoda and Bivalvia
Others	Nematoda and Hirudinea
Unidentified	Digested material and fragments of insects.

3.4 Diet- and habitat overlap

The degree of diet- and habitat overlap between European minnow and brown trout was calculated using Shoener's (1970) similarity index:

$$D = 100 - \left[(0.5) * \sum |p_i - q_i|\right]$$

The dietary overlap p_i and q_i is the volume percent of different stomach content categories found in juvenile brown trout and European minnow. For calculating habitat overlap, European minnow and brown trout symbolize p_i and q_i, respectively. Percentages of total brown trout and European minnow catch at each 25 cm depth interval, of each gillnets set, at the four depths was compared. Schoener's *D* is presented in percent and overlap is considered significant when *D* exceeds 60 % (Wallace 1981).

The accuracy of the Schoener's (1970) similarity index has been measured and compared with other similarity indexes by Linton et al. (1981). Schoener's similarity index proved to be most accurate with *D*-values between 7 and 85 % (Linton et al. 1981)

3.5 Data treatments and statistics

Microsoft Excel 2010 was used for data processing and creation of some figures. However, most of the figures was created in SigmaPlot version 11.0 for making of the majority of figures. SPSS (Statistical Package for Social Science) Version 17 was used to perform the statistical test. Difference between mean length of captured brown trout at four different depths (0.5, 1.5, 3 and 6 m) were tested with the Kruskal-Wallis one-way analyzes with subsequent Mann-Whitney U-tests. Non-parametric tests were used as the data set had a non-normal distribution (Mackenzie 2005). P-values were considered significant < 0.05. MapSource was used for map-management of GPS-points (Global Position System) from the fieldwork during summer 2009 (Appendix 1).

4 Results

4.1 Habitat use of European minnow and brown trout

The European minnow was most frequently captured in the lowermost 0-25 cm section of the Nordic gillnets at all four depths (0.5, 1.5, 3 and 6 m), throughout the three periods (Figure 4.1; N = 1138). In contrast, brown trout was captured in the whole gillnet height. Especially in gillnets set at 0.5, 1.5 and 3 m depth. However, there was a clear trend towards higher catches in the two deepest sections, 0-25 and 25-50 cm, with 0-25 cm section predominating with highest catch (N = 64).

The catch of European minnows in gillnets set at 0.5 m depth (N = 723) was considerably higher compared to the catch in gillnets set at 1.5 m (N = 385), 3 m (N = 46) and 6 m (N = 37). Highest catch of brown trout was obtained in gillnets set at 1.5 m depth (N = 72). Moreover, the total catches at 0.5 m (N = 20), 3 m (N = 37) and 6 m depth (N = 26) was more evenly distributed regarded to depth.

European minnow and brown trout had a significant habitat overlap at depths of 0.5, 3 and 6 m (*D*- value > 60 %; Table 4.1) in August September. The habitat overlap was at the lowest in June-July, especially at 3 m depth (*D*- value 22.2 %), whereas there was medium habitat overlap in July-August (*D*- value 42.8-50 %).

Table 4.1 Habitat overlap between European minnow and brown trout in the littoral habitat of the lake Øvre Heimdalsvatn during the three periods June-July, July-August and August-September, 2009. The presented numbers are *D*- values in percent after using Schoener's similarity index.

	June-July	**July-August**	**August-September**
0.5 m	36.9	42.9	66.7
1.5 m	44.6	40.9	40.8
3 m	22.2	50	72
6 m	33.3	42.8	60

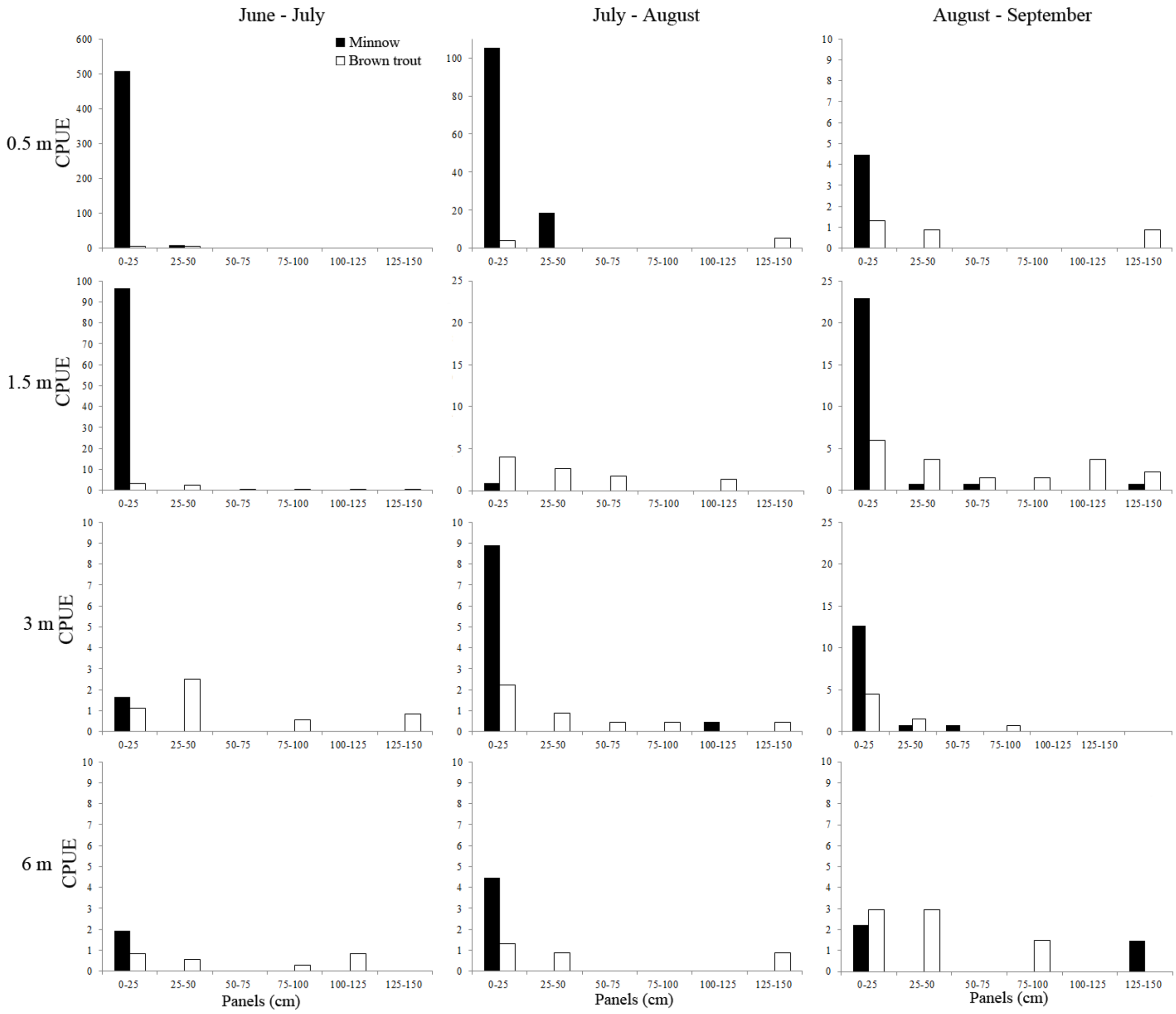

Figure 4.1 Vertical distribution of brown trout (white columns) and European minnow (black columns) captured in 25 cm sections, from bottom-up of Nordic survey gillnets in Øvre Heimdalsvatn, during the three periods June-July, July-August and August-September, 2009. NB! Note different scales on the y-axis.

4.2 Length distribution of European minnow and brown trout

Body length of European minnow captured in gillnets ranged from 40-109 mm (Figure 4.2). Length-class 70- 74 mm was the most numerous for all three periods (*N* = 298), whereas only few exceeded 95 mm (*N* = 5). In June-July, most of the European minnows caught at depths 0.5 m and 1.5 m were in the 65-74 mm length-class (*N* = 488). The majority of the few individuals captured at 3 m and 6 m had a body length within the length-classes 65-74 mm (*N* = 6) and 70-89 mm (*N* = 5), respectively. In July-August, the majority of European minnows captured at 0.5 m depth, had a body length of 50-54 mm (*N* = 27). Only two individuals were captured with a body length of 65-69 mm at 1.5 m depth in the same period. Most individuals captured at 3 m depth had a body length of 50-54 mm (*N* = 3), whereas the majority of captured European minnow at 6 m depth were 70-74 mm (*N* = 7). The majority captured in August-September had a body length of 50-54 mm (*N* = 11) and 80-84 mm (*N* = 12). Body length of European minnow at 0.5 m, 1.5 m and 3 m depths were evenly distributed from length-class 50-54 mm to 85-89 mm. Only three length-classes were represented at 6 m depth: 60-64 mm (*N* = 2), 75-79 mm (*N* = 1) and 80-84 mm (*N* = 2).

The majority of the captured brown trout in gillnets for all three periods had a body length of 15-19 cm (*N* = 72).This was also represented by the June-July catch, where most individuals were captured in length-class 15-19 cm (*N* = 38), particular at 0.5 m depth (*N* = 14). However, larger fish was captured at deeper depths (1.5 m, 3 m and 6 m). In addition, brown trout > 30 cm were more numerous in June-July (*N* = 7) compared to July-August (*N* = 4) and August-September (*N* = 6). In July-August, all brown trout at 3 and 6 m depths were larger than those captured in shallower gillnets, at 0.5 m and 1.5 m depths. Except for one individual captured at 1.5 m depth in July-August, no brown trout had body length < 9 cm. The majority of brown trout captured in August-September had a body length ranging from 10-19 cm, although several had a body length > 25 cm (*N* = 13).

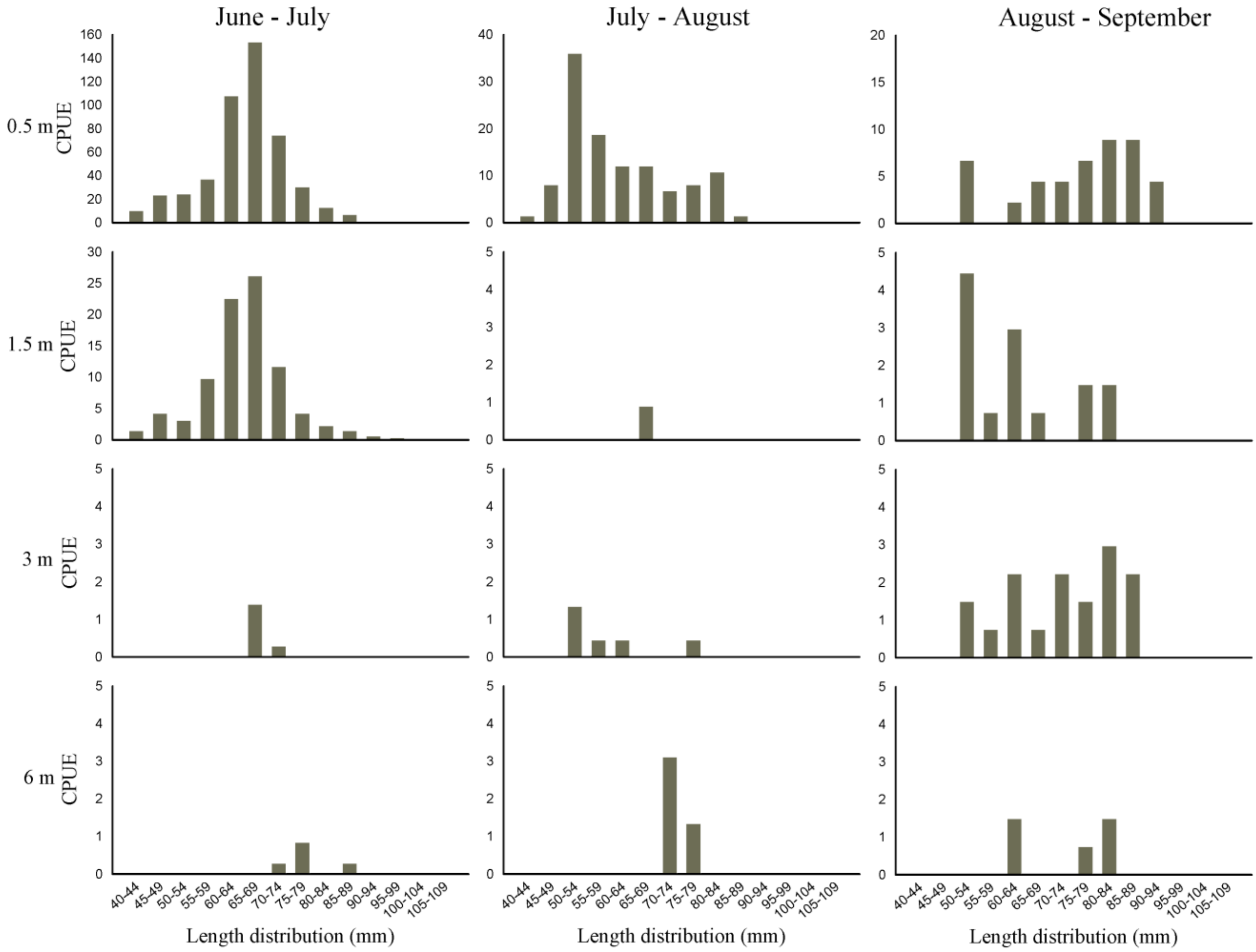

Figure 4.2 The length distribution of European minnow caught in Nordic survey gillnets in four depths in the lake in the littoral area of the lake, Øvre Heimdalsvatn, during the three periods June-July, July-August and August-September, 2009. NB! Note different scales on the y-axis.

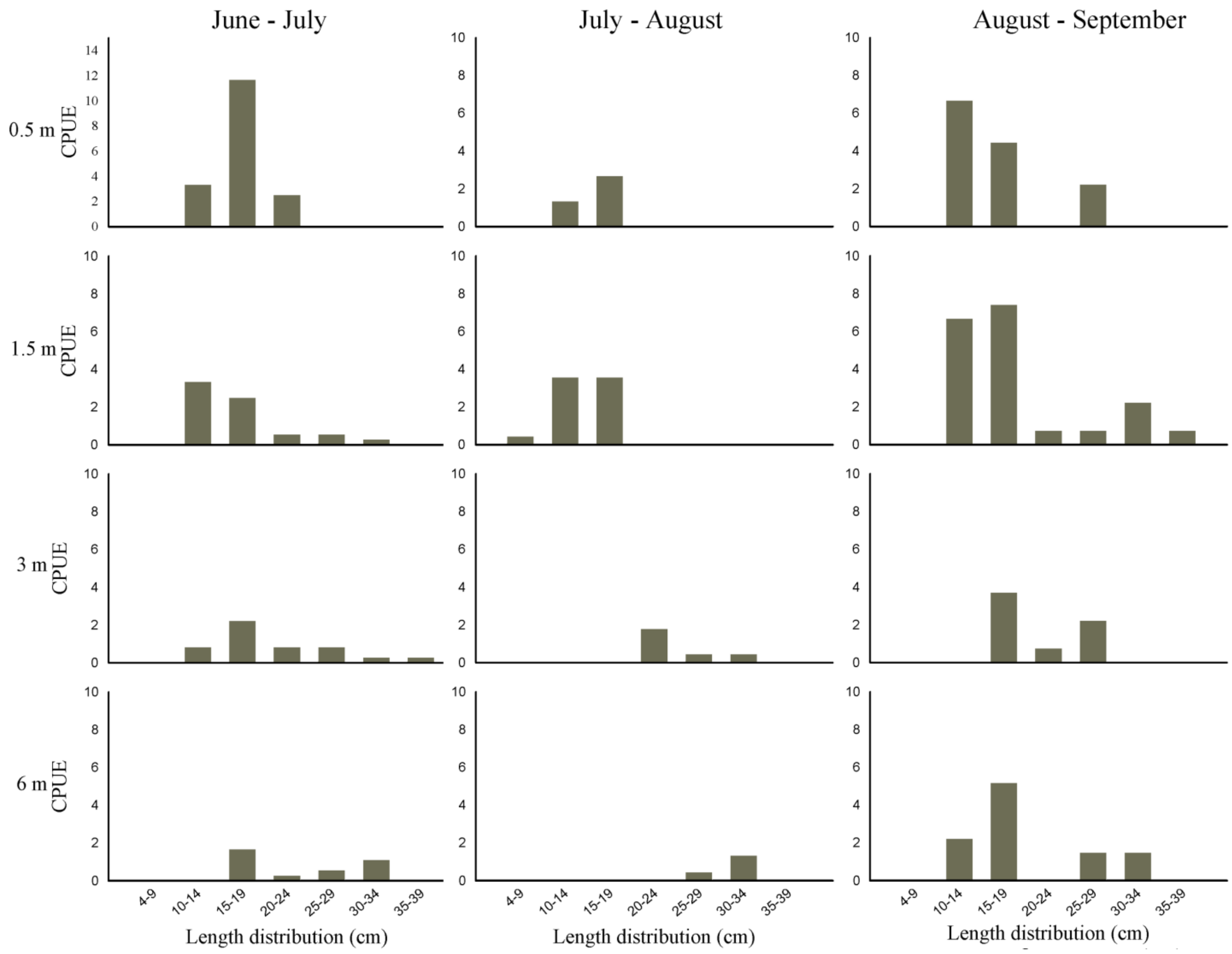

Figure 4.3 The length distribution (cm) of brown trout caught in Nordic survey gillnets at four depths in the littoral area of Øvre Heimdalsvatn, during the three periods June-July, July-August and August-September, 2009. NB! Note different scales on the y-axis.

Catches by electrofishing revealed that small European minnows, which not captured by gillnets, were frequently in the shallowest part of the littoral (< 0.2 m) of Øvre Heimdalsvatn (Figure 4.4). The majority of the European minnows had a body length of 35-49 mm (N = 329).

There was a trend that small brown trout (< 20 cm) being captured in the shallow areas whereas larger brown trout (> 20 cm) were captured in deeper areas during the summer (Figure 4.6). Pairwise comparison of length at different depths showed that mean length at 0.5 m and 3 m (z = -2.99, N = 62, p = 0.003), 0.5 m and 6 m (z = -2.96, N = 64, p = 0.003), 1.5 m and 3 m (z = -3.83, N = 99, p = <0.001), 1.5 m and 6 m (z = -3.81), N = 100, p = <0.001) differed significantly.

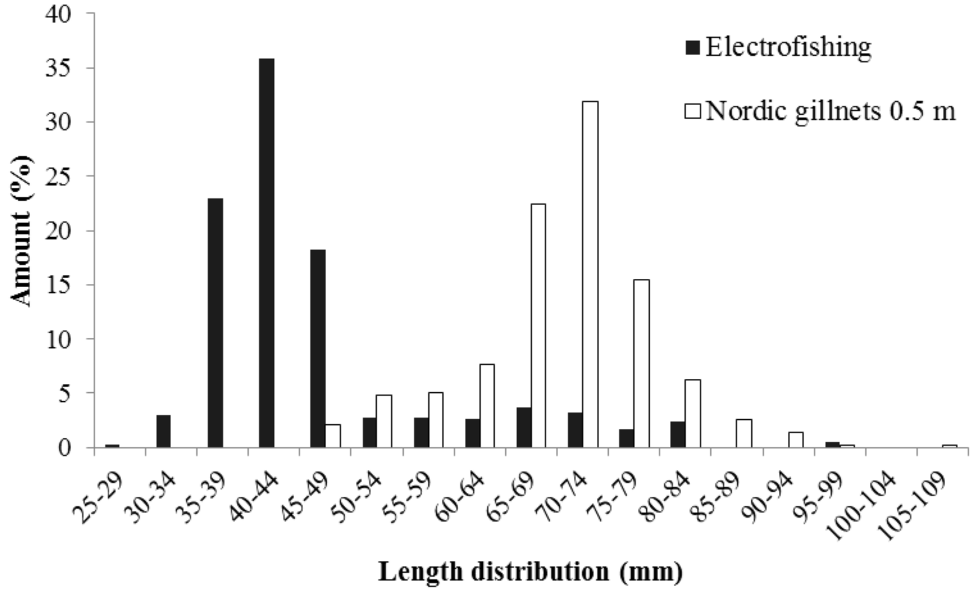

Figure 4.4 Length distribution (mm) of European minnow captured in Nordic survey gillnet at 0.5 m depth (white columns) in June-July 2009 and by electrofishing (black columns) in the shallowest part of the littoral 24 June 2009, in the lake, Øvre Heimdalsvatn.

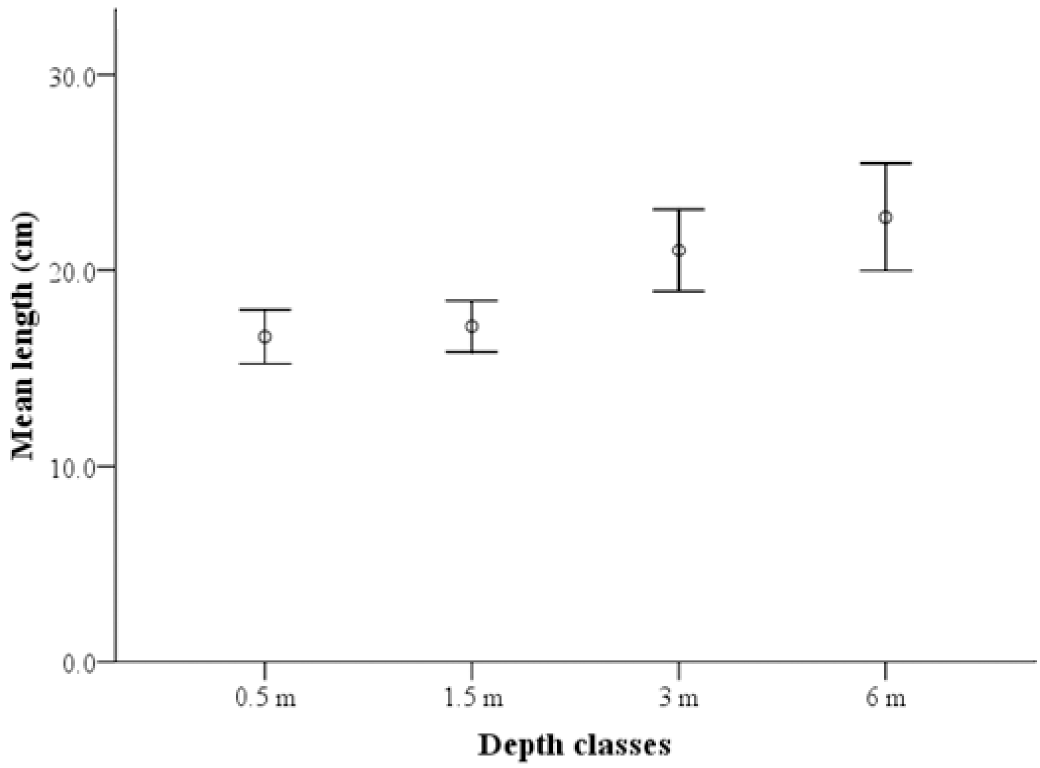

Figure 4.5 Mean lengths (cm) of brown trout captured in Nordic gillnets set at four depths in the littoral area of lake, Øvre Heimdalsvatn, during the three periods June-July, July-August and August-September, 2009 (Error bars: 95 % confidence intervals).

4.3 Diet of European minnow and juvenile brown trout

Several prey organisms were of importance for the European minnow's diet, such as Cladocera (21.2 %), Ephemeroptera-, Trichoptera- and Plecoptera-species (18.5 %), chironomids (17.8 %), *Gammarus* (15.8 %) and other aquatic insects (14.7 %; Figure 4.6). In July-August, Ephemeroptera, Trichoptera and Plecoptera-species were the major prey organisms in the European minnow's diet. Additionally, Cladocera and Mollusca were important with 20.5 and 15.3 % by volume, respectively. *Gammarus* was the dominating prey organism for European minnow in August-September (41.4 %), however Cladocera (25 %) as well as Ephemeroptera-, Trichoptera- and Plecoptera-species (17.8 %) were also important prey organisms in this period.

Terrestrial insects (39 %) and Cladocera (22.8 %) were the dominating prey organisms for juvenile brown trout in June-July (Figure 4.6). However, no *Gammarus* was consumed in the same period. In July-August, however, several prey organisms occurred about equally in the brown trout's diet. The prey organisms of importance were *Gammarus* (18.6 %), Chironomids (15.9 %), terrestrial insects (15.9 %) and Ephemeroptera, Trichoptera and Plecoptera-species (13.3 %). European minnow dominated the brown trout's diet in August-September (28.9 %). However, only two of the studied brown trout (2.8 %) with length 16.2 and 19.6 cm, had European minnow in their stomach contents. Additionally to European minnow, terrestrial insects were important in the diet during this latter period (20 %).

The dietary analyses revealed European minnow and juvenile brown trout to a large extent utilizing the same prey organisms (Figure 4.6). Ephemeroptera-, Trichoptera- and Plecoptera-species, Cladocerans, Chironomids and terrestrial insects were important elements in the summer diet for both species. According to Schoener's similarity index, European minnow and juvenile brown trout had a significant diet overlap in the period June-July (D = 63.6 %). However, there was no significant overlap in July-August (D = 52.2 %) and August-September (D = 42.5 %). There was a medium similarity in diet (D = 55. 6 %) for all three periods together.

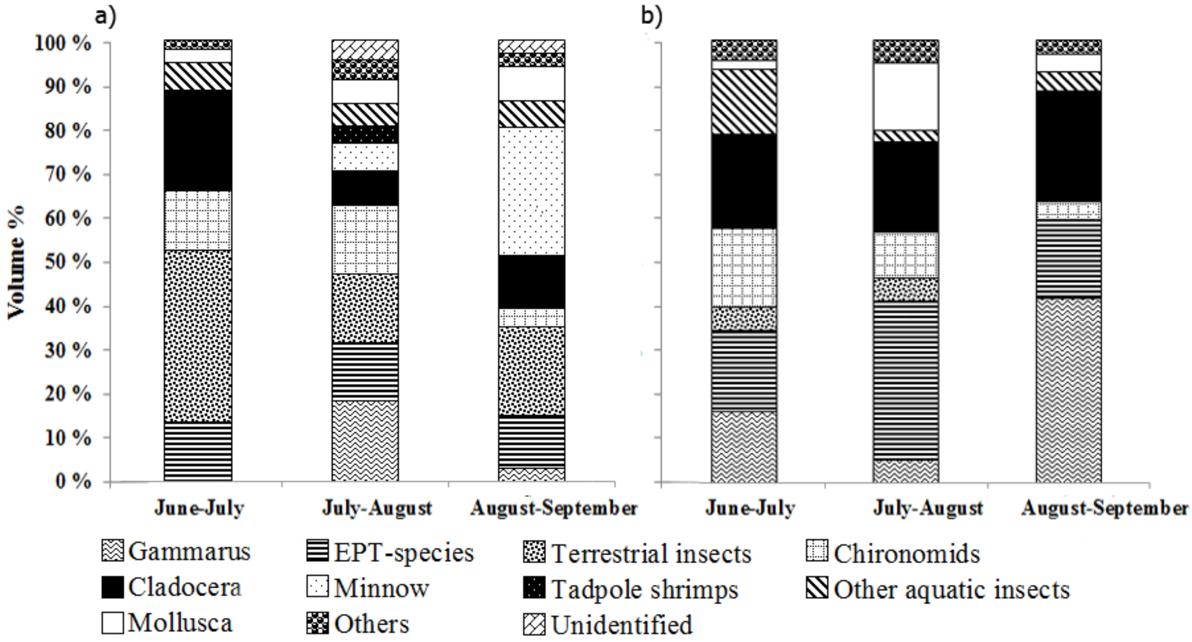

Figure 4.6 Diet of a) juvenile brown trout and b) European minnow from the littoral area of in Øvre Heimdalsvatn expressed as volume percent during the three periods June-July, July-August and August-September, 2009.

5 Discussion

According to the catches of European minnow and brown trout by Nordic gillnets set in the littoral area in the lake, Øvre Heimdalsvatn, there was a clear segregation in habitat use between the two species. European minnow was mainly captured near the bottom at all capture depths between 0.5 and 6 m; whereas brown trout was captured in the whole gillnet height. European minnow completely outnumbered brown trout, especially in gillnets set at 0.5, 1.5 and 3 m depth. The high numbers of European minnow captured in the shallowest part of the littoral zone in June-July may be explained by high activity during the spawning period, occurring in June-July in the lake, Øvre Heimdalsvatn (Museth et al. 2002). Since catches by electrofishing revealed that small European minnows, not captured by gillnets, were frequent in the shallowest part of the littoral. European minnow may be even more dominant in this habitat than indicated by the gillnet catches only. The concentration of European minnows in the shallowest parts of the littoral zone (0.5 and 1.5 m gillnet sets), with most captures in the lowermost section of the gillnets, may indicate an anti-predator behavior as suggested by Museth et al. (2002). When staying near the bottom, European minnow can easily hide in this habitat dominated by a substrate of stones. However, Frost (1943) reported that European minnow prefers a substrate of stones and gravels, which characterizes the shallow part of the littoral zone in Øvre Heimdalsvatn (Aarefjord et al. 1978).

Habitat use of brown trout may be affected by the high density of European minnows (Hesthagen et al. 1992). The increased density of European minnow in Øvre Heimdalsvatn, from 14, 500 individuals in 1977 to 108, 000 individuals in 1999 (Lien 1981; Museth et al. 2002), may therefore have affected the brown trout. In accordance with this, Borgstrøm & Brabrand (1996) suggested that high concentration of European minnows in the shallowest and safest areas regarding predation, may force juvenile brown trout into deeper water, where hiding places are scarcer. The occurrence of brown trout juveniles in diet of larger brown trout in the lake (Borgstrøm et al. 2010), may also be a result of habitat shift of the juvenile brown trout, as suggested by Borgstrøm & Brabrand (1996). In addition, Borgstrøm et al. (2010) suggests that increased cannibalism might explain the reduced recruitment found in Øvre Heimdalsvatn. However, cannibalism were not reported in Øvre Heimdalsvatn during summer 2009 (Nytrø 2010), although it has been observed at low frequencies in previous studies (Borgstrøm et al. 2010).

Body length may influence habitat use, especially for species with ontogenetic niche shifts (Werner et al. 1983), like the brown trout. Smaller brown trout (< 20 cm) were caught in gillnets at shallower depths, and longer brown trout (> 20 cm) at deeper depths, i.e. the same trend as reported by other studies (Hegge et al. 1993; Haugen & Rygg 1996). Additionally, it has been shown that small brown trout may have a strong association to the bottom, whereas larger brown trout occur more frequently higher up in the water column (Hesthagen et al. 1992; Hegge et al. 1993). This is similar to the vertical distribution as found in the lake, Øvre Heimdalsvatn. No brown trout (< 10 cm) or European minnows were caught in the open water in Øvre Heimdalsvatn (Nytrø pers. comm), this indicate that small fish do not utilize the pelagic zone, due to the possible effect of high predation risk in open water. Similar size dependent habitat use, explained by predator avoidance, is described for several fish species (Mittelbach 1981; Brabrand & Faafeng 1993).

The change in distribution of European minnow with a more diverse habitat use at all four depths from June-July to August-September, may be explained by a change in abundance of prey organism during the summer. A shift in habitat use may be expected due to changes in food profitability. It is commonly observed that habitats vary temporally and spatially in both foraging profitability and predation risk (Mittelbach 1981). This suggests that many animals need to balance gains and risks in their decisions on where and when to forage (Werner et al. 1983).

The small overlap regarding diet is in contrast to the results found by Museth et al. (2010), where the dietary overlap from 1975 to 1996 in Øvre Heimdalsvatn was summarized. Museth et al. (2010) reported that juvenile brown trout and European minnow had a significant dietary overlap (D= > 60 %), whereas in this present study, a significant diet overlap was found only in June-July (D= 63.6 %), with a declining trend towards August-September (42.5 %). According to Werner & Hall (1977) the diet overlap among fish is minimal when food resources become scarce, probably because a greater variety of prey organisms will be taken when the resource levels are low. On the other hand, Pyke et al. (1977) suggested that when resource levels are low, the diet of the two species tend to converge. Hence, it can be assumed that the majority of prey organisms were more abundant in June-July with little competition between the two species when the dietary overlap was significant.

Unlike results from previous studies in the lake Øvre Heimdalsvatn, where the brown trout predation on European minnow was greatest in June (Lien 1981; Markhus & Meland 1997; Museth et al. 2002, 2003; Bilstad & Bilstad 2006), the predation was greatest in August-September 2009. The high predation reported on European minnow in June is evidently due to higher activity level during spawning (Museth et al. 2003). Also, there was an upward trend for brown trout predation on European minnow in Øvre Heimdalsvatn from 1988 to 2005 (Lien 1978, 1981; Museth et al. 2002, 2003; Bilstad & Bilstad 2006). This might be explained by an increased density of European minnow, as suggested by Museth et al. 2003. On the other hand, Museth et al. 2002 found a reduced European minnow population from the peak in 1999 to only 57, 000 individuals in 2000. The predation on European minnow is additionally related to the size of brown trout. According to L'Abée-Lund et al. (2002) the brown trout may start feeding on European minnows at a body length of 17 cm. Nytrø (2010) found the same trend for brown trout in Øvre Heimdalsvatn, where the larger length-classes, 20-29.9 cm and 30-39.9 cm, preyed on European minnows. Hence, it may be assumed that a large proportion of the brown trout population is potential minnow predators in the lake (Museth et al. 2003). Thus, the increased brown trout predation on European minnow might be explained by an increased numbers of larger brown trout in the lake, which will result in decreased density of European minnow.

European minnow is well documented as an omnivorous and opportunistic forager (Frost 1943), foraging on the most available prey organisms. This forage behavior may affect both the benthic and zooplankton community (Larsson et al. 2010; Næstad & Brittain 2010). For instance, after the introduction of European minnow in Øvre Heimdalsvatn, a strong decline in tadpole shrimp population was observed and the species were nearly extinction from the lake (Brittain et al. 1988). A study by Næstad & Brittain (2010) carried out in the lake, Øvre Heimdalsvatn, indicates a change in benthic community due to the introduction of minnow. For instance, Ephemeroptera, Trichoptera, Plecoptera and *Gammarus* were the dominant benthos in the shallow littoral zone in 1972, whereas chironomids dominated this habitat in 2000 (Næstad & Brittain 2010).

Compared to brown trout, European minnow are a more effective predator of *Gammarus* (Brittain et al. 1988). The amount of *Gammarus* consumed by brown trout has declined from the late 1960ies until 2009, where *Gammarus* was a minor part of the diet (Nytrø 2010). The minor amount of *Gammarus,* as well as the lack of the tadpole shrimp may have affected the food quality of the brown trout diet, and therefore resulted in reduced growth rates in the lake, Øvre Heimdalsvatn (Borgstrøm et al. 2010). In August-September 2009, *Gammarus* was the most important food item for European minnow in the lake, Øvre Heimdalsvatn. Næstad & Brittain (2010) found a reduction of juvenile *Gammarus* in the lake in August and September 2000, probably due to European minnow mainly foraging on juvenile *Gammarus* since the mouth gap of the European minnow may limit consumption of larger individuals. Moreover, a migration of *Gammarus* abundance from deeper water to more shallow water was detected during summer in 1970-71 and 1985 (Brittain & Lillehammer 1978; Brittain et al. 1988). The migration did not occur to a great extent in 2000 (F. Næstad pers.comm), probably due to a less numerous *Gammarus* population. The high amount of consumed *Gammarus* in August-September 2009 may therefor indicate that the migration has started again, as a response of increased *Gammarus* population. This may also indicate a reduced abundance of European minnow.

The zooplankton community in Øvre Heimdalsvatn is not directly affected by the introduction of European minnow (Larsson et al. 2010), even though the European minnow may be consuming large amount of zooplankton (Hartley 1948). However, Larsson et al. (2010) reports that the European minnow may have indirect effect on the zooplankton community due to its contribution in reducing potential invertebrate predators, like the tadpole shrimp and *Megacyclops gigas*. The reason why Cladocera was an important part of the European minnow's diet during summer 2009 may be a result of the high June temperature which results in a more rapid development of the zooplankton and higher biomass (Larsson 1978).

Evidently, habitat use is connected to diet of the brown trout and minnow. For instance the cladoceran *Eurysercus lamellatus* most often live close to the bottom (Hesthagen et al. 1992; Haugen & Rygg 1996; Einarsson & Örnólfsdottir 2004). It may therefore be assumed that especially European minnow has occupied the benthic areas, since a large share of Cladocera, mainly *E. lamellatus*, was found as prey. According to Pyke et al (1977) there is a variety of habitats with different prey organisms, where brown trout and European minnow, may converge or diverge depending on the similarity of their responses to declining food resources. The sum of habitat and food choices determines the coexistence of the species. However, more thorough examinations of the diet at different depths may be necessary in order to better understand the competition and forage behavior of both European minnow and brown trout. It is, however, important to stress that no method of stomach analysis gives a complete picture of the diet as some of the prey organisms may be underrepresented in the stomachs because they are digested faster than others (Hyslop 1980).

The ability to predict habitat use and diet in natural systems may be both complex and difficult to clarify (Mittelbach 1981; Brabrand & Faafeng 1993), but it is highly probable that the introduction of European minnow has caused severe effects on the ecosystem of Øvre

Heimdalsvatn (Borgstrøm et al. 2010). Based on the present study it may be concluded that brown trout and European minnow strongly interact in the lake, Øvre Heimdalsvatn, especially with regard to habitat use and diet. The large density of European minnows in the shallowest habitat may be a result of high predation risk from brown trout. At the same time, the high European minnow density may strongly reduce available invertebrate prey for juvenile brown trout, which may seek to deeper water where predation risk for small individuals is higher than in the stony shallow habitat. These interactions may lead to reduced growth rate for brown trout due to reduced food availability, but may also result in reduced recruitment to the harvestable stock because of predation on juvenile brown trout by larger brown trout. European minnow in high altitude lakes like Øvre Heimdalsvatn may thus reduce the catch potential of brown trout.

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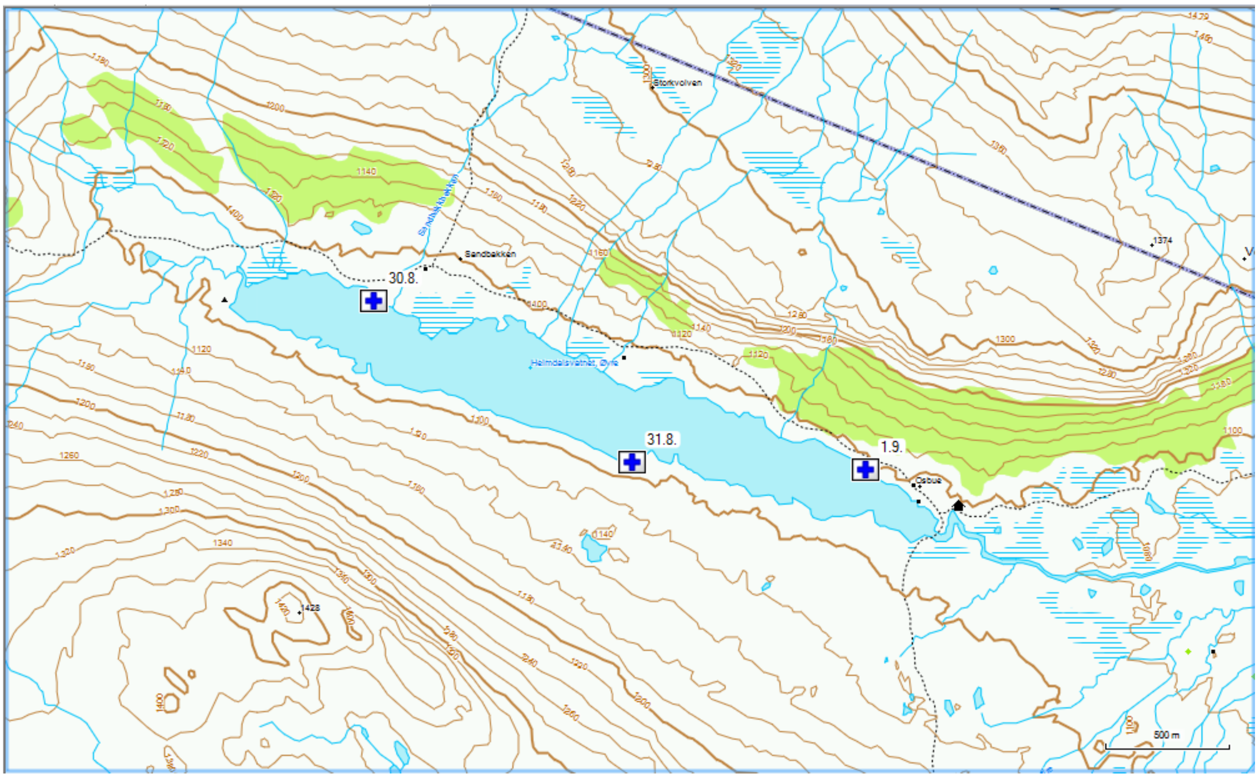
Appendices

Appendix 1

The gillnets were set on every other day on either the north and south side in the different zones (zone 1, 2 and 3). This example shows were the four Nordic survey gillnets were set during three nights in August-September. Location was recorded using GPS.



Appendix 2

The diet composition of juvenile brown trout (Table 1) and European minnow (Table 2) in Øvre Heimdalsvatn expressed as volume percent during the three periods June-July, July-August and August-September, 2009.

Table 1 Juvenile brown trout

	June-July	July-August	August-September
Gammarus	0	18,6	3
EPT-species	13,5	13,3	12
Terrestrial insects	39	15,9	20
Chironomids	13,5	15,9	4
Cladocera	22,8	8	12
Minnow	0	6,4	28,9
Tadpole shrimps	0	4	0
Other aquatic insects	6,2	5,3	6
Mollusca	3,1	5,3	8
Others	2,1	4,7	3
Unidentified	0	4,7	3

Table 2 European minnow

	June-July	July-August	August-September
Gammarus	15,8	5,1	41,4
EPT-species	18,5	35,9	17,8
Terrestrial insects	5,3	5,1	0
Chironomids	17,8	10,3	4,2
Cladocera	21,1	20,6	25
Other aquatic insects	14,8	2,5	4,2
Gastropoda	2	15,3	4,2
Others	5	5,2	3,2