

**Ecology of sympatric whitefish (*Coregonus lavaretus* (L.)) forms  
in a subarctic lake**

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Academic dissertation in Fisheries Science

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## Abstract

This thesis concerns the ecology of sympatric whitefish (*Coregonus lavaretus* (L.)) forms in a subarctic lake, northern Finland. Despite of rather common occurrence of sympatric whitefish forms in the northern hemisphere, limited amount of information exist about their ecology and morphological divergence. Furthermore, whitefish form data is usually gathered in various different lakes and collective studies of the various ecological aspects in a single lake has been scarce. Thus, this thesis focuses on the ecology of sympatric whitefish forms in Lake Muddusjärvi. The main objectives were to examine the level of morphological divergence, morphometry-feeding environment relationship and niche segregation of sympatric whitefish forms. In addition, the impacts of predation on sympatric whitefish forms were evaluated.

Morphometric and meristic analyses indicated divergence of whitefish population into three distinct forms. The most pronounced differences between sympatric whitefish forms were found in gillrakers, head and pectoral fin traits, which were correlated with their feeding environment. Deep water (>10 m) dwelling benthivore, small sparsely rakered whitefish (SSR) had the lowest number of short and extremely widely spaced gillrakers. Shallow water (<10 m) dwelling benthivore, large sparsely rakered whitefish (LSR) had intermediate number of short and widely spaced gillrakers. Planktivorous densely rakered whitefish (DR) used partly pelagic habitats having the largest number of densely spaced and the longest gillrakers. Distinct specialization to benthic and pelagic niches was supported also by low food and habitat overlap between sympatric whitefish forms.

The food resources available for different whitefish forms influenced to their growth. LSR, which used littoral bottoms providing the greatest benthic food resources, had the fastest growth. SSR utilized scanty benthic food resources in profundal bottoms had the slowest growth. The growth of DR consuming mainly pelagic zooplankton was also slow. Whitefish was the main prey for piscivores in Lake Muddusjärvi. However, the importance of whitefish forms in predator's diet differed distinctly. DR was the main prey for all piscivores. Especially, salmonids brown trout (*Salmo trutta* L.) and Arctic charr (*Salvelinus alpinus* (L.)) used almost exclusively DR, whereas burbot (*Lota lota* (L.)) and pike (*Esox lucius* L.) used also other species and benthic whitefish forms. LSR was able to reach size refuge from predation earliest due to the fastest growth. SSR used profundal habitat, where feeding efficiency of visually chasing predators is low, and was the least preyed whitefish form. Risk of predation was high for pelagic DR, which avoided predation by habitat selection. DR dwelled in vicinity of bottom during continuous daylight in mid summer. Towards autumn DR performed diel vertical migrations ascending to midwater and surface during dusk and descending to bottom at dawn. Vertical migrations of DR were related to risk of predation induced by brown trout, which dwelled in pelagic habitat. Benthic habitat offered refuge for LSR and SSR, which did not perform diel vertical migrations.

## List of papers

This thesis is based on the following articles:

- I. Kahilainen, K. & Østbye, K. Resource polymorphism of sympatric whitefish forms *Coregonus lavaretus* (L.) (Pisces: Salmonidae) in a subarctic lake: morphologic and diet differentiation. Submitted manuscript.
- II. Kahilainen, K., Lehtonen, H. & Könönen, K. 2003: Consequence of habitat segregation to growth rate of two sparsely rakered whitefish (*Coregonus lavaretus* (L.)) forms in a subarctic lake. *Ecology of Freshwater Fish* 12: 275-285.
- III. Kahilainen, K., Malinen, T., Tuomaala, A. & Lehtonen, H. 2004: Diel and seasonal habitat and food segregation of three sympatric *Coregonus lavaretus* forms in a subarctic lake. *Journal of Fish Biology* 64: 418-434.
- IV. Kahilainen, K. & Lehtonen, H. 2002: Brown trout (*Salmo trutta* L.) and Arctic charr (*Salvelinus alpinus* (L.)) as predators on three sympatric whitefish (*Coregonus lavaretus* (L.)) forms in the subarctic Lake Muddusjärvi. *Ecology of Freshwater Fish* 11: 158-167.
- V. Kahilainen, K. & Lehtonen, H. 2003: Piscivory and prey selection of four predator species in a whitefish dominated subarctic lake. *Journal of Fish Biology* 63: 659-672.

These articles are referred to by their Roman numerals in the text.

## Author's contribution in articles

- I. KKK and KØ planned the study. KKK gathered and analysed part of the data. The first version of manuscript was written by KKK.
- II. KKK planned the study and performed sampling. KKK handled the fish data and KK the benthic macroinvertebrates. KKK wrote the first version of the manuscript.
- III. Original idea and planning was conducted jointly. TM and AT were responsible of sampling and analysing of hydroacoustic data. KKK handled the fish data and wrote the first version of the manuscript.
- IV. KKK and HL planned the study jointly. KKK performed sampling, analysed data and wrote the first version of the manuscript.
- V. KKK designed the study and sampled the data. KKK analysed the data and the manuscript was written jointly.

Abbreviations of authors:

AT=Antti Tuomaala

HL=Hannu Lehtonen

KK=Katriina Könönen

KKK=Kimmo Kahilainen

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TM=Tommi Malinen

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# 1. Introduction

## 1.1 Resource polymorphism

Resource polymorphism is the occurrence of distinct intraspecific morphs or forms differing in niche use including for example differences in habitat and food resource use (Smith & Skúlason 1996). In addition, these intraspecific morphs may have evolved and continuously coexist in sympatry (Skúlason & Smith 1995). Resource polymorphism is considered to emerge in novel environments, such as remote islands and newly formed lakes, where interspecific competition is low and number of available niches is high (Schluter 1996a, Smith & Skúlason 1996). In these environments, high ecological opportunity promotes polymorphism in birds, reptiles, amphibians and fishes (Schluter & McPhail 1993, Skúlason & Smith 1995, Smith & Skúlason 1996, Losos *et al.* 1998, Schluter 1998). Continuous use of distinct niche throughout time may induce morphological divergence related to resource use (Skúlason & Smith 1995). Morphology and feeding are usually correlated: for example Darwin's ground finches, *Geospiza* spp., are specialized to different seeds having divergent beak size, *Anolis* lizards hindlimb length correlates with utilized perch diameter, and in postglacial lakes gillraker number of sympatric fish morphs correlates with feeding in benthic or pelagic habitats (Schluter *et al.* 1985, Robinson & Wilson 1994, Losos *et al.* 1997). Maintenance and increased degree of morphological divergence requires assortative mating of morphs suggesting also possibility for sympatric speciation (Rice & Hostert 1993, Schlieuwen *et al.* 1994, Orr & Smith 1998, Dieckmann & Doebeli 1999, Via 2001). Resource polymorphism has been recognized as an important component in speciation (Smith & Skúlason 1996, Schluter 1998).

In postglacial lakes, high availability of open niches and low number of species are considered as reasons for resource polymorphism of fish (Schluter 1996a). Resource polymorphism in postglacial lakes is documented among many fish species, such as Arctic charr (*Salvelinus alpinus* (L.)), lake whitefish (*Coregonus clupeaformis* Mitchell), whitefish (*Coregonus lavaretus* (L.)) and three-spined stickleback (*Gasterosteus aculeatus* L.) (Svärdson 1952, Fenderson 1964, Bodaly 1979, Svärdson 1979, Bergstrand 1982, McPhail 1984, Amundsen 1988, Malmquist *et al.* 1992, McPhail 1993, Skúlason *et al.* 1999). These taxonomically distant fish species show parallelism in their divergence as most of the systems have a limnetic (or pelagic) and a benthic morph. This is typical for lakes in the northern hemisphere suggesting availability of these two particular niches (Schluter & McPhail 1993, Robinson & Wilson 1994). In more complex lakes, such as tropical lakes in Africa, number of available niches is high inducing rapid adaptive radiation of fishes, such as in the cichlids (e.g. Meyer 1993, Galis & Metz 1998, Turner 1999). Increasing evidence suggests that divergence of sympatric morphs has been rapid (Johnson *et al.* 1996, Schluter 2000a). Different morphs/species may have evolved sympatrically via sexual selection and/or ecological speciation (Meyer *et al.* 1990, Meyer 1993, Schlieuwen *et al.* 1994, Seehausen *et al.* 1997, Orr & Smith 1998, Galis & Metz 1998, Schluter 1998, 2001). In contrast, sympatric morphs may occur as a result of phenotypic plasticity *i.e.* being single genotype, which produce more than one alternative form in response of environmental conditions (Stearns 1989, West-Eberhard 1989, Scheiner 1993). Sympatric forms could also evolve via adaptive radiation, which is the diversification of a single lineage into divergent forms utilizing two or more niches through morphological, life history and physiological specialization (Schluter 2000b). The ecological theory of adaptive radiation suggests that phenotypic divergence of forms is driven by divergent natural selection between environments (Schluter 2000b). Phenotypic divergence could be induced by resource competition driving forms to exploit different environments with contrasting selection pressures and as a by-product of same processes with time these forms may accumulate higher levels of reproductive isolation

(Schluter 1996b, 2000b, 2001, Saint-Laurent *et al.* 2003). Recently, adaptive radiation has been considered to have importance also in evolution of coregonid fishes (Bernatchez *et al.* 1999, Bernatchez 2004).

In the northern hemisphere, postglacial lakes with sympatric fish morphs are usually ice-covered during winter, growing season is concordantly short and the overall number of fish species is low. In most of the cases, only two morphs, limnetic and benthic, have been observed (Schluter & McPhail 1993, Robinson & Wilson 1994). Sympatric morphs have often similar resource use in various fish species: limnetic morph uses pelagic zooplankton and benthic morph consumes larger food items, such as benthic macroinvertebrates (Schluter & McPhail 1993, Robinson & Wilson 1994). Specialization of sympatric morphs in their resource use has induced variable level of morphological differentiation (McPhail 1984, 1993, Chouinard *et al.* 1996, Bernatchez *et al.* 1999, Dynes *et al.* 1999, Gislason *et al.* 1999, Saint-Laurent *et al.* 2003). In the most evident cases, limnetic form is better adapted to zooplankton consumption having a slender body, long, numerous, and densely spaced gillrakers, whereas the more robust benthic form is specialized to larger food items having less numerous, shorter and widely spaced gillrakers (McPhail 1984, 1993, Malmquist 1992, Snorrason *et al.* 1994). High trophic specialization towards benthic or pelagic niches has also been observed in experimental feeding and growth studies of sympatric fish morphs (Malmquist 1992, Schluter 1993, 1995). Limnetic morph of three-spined stickleback is inferior in benthic feeding and opposite is true for benthic morph in pelagic feeding (Schluter 1993).

Heritability of morphological traits is generally higher than life history, behavioural or physiological traits (Mosseau & Roff 1987). As morphological traits of sympatric forms can be related to the efficiency of resource use and fitness (Schluter 1995), sympatric forms may have mechanisms preventing hybridization. This is relevant, since artificially produced hybrids are viable (Svärdson 1970, McPhail 1984, 1992, Schluter 1996a, Hatfield & Schluter 1999). Different reproductive mechanisms between sympatric forms could prevent hybridization. Sympatric morphs of Arctic charr may differ in age and/or size of sexual maturity, spawning place and/or time (Skúlason *et al.* 1989, Klemetsen *et al.* 2002). In three-spined stickleback morphs, assortative mating reduces possibility of hybridization during spawning season and in addition hybrids are inferior in resource use compared to pure forms (Schluter 1993, 1995, Nagel & Schluter 1998, Hatfield & Schluter 1999, Vamosi *et al.* 2000). Despite of the reproductive isolation mechanisms, introgressive hybridization could have played significant role in fish evolution (Himberg 1970, Svärdson 1970, 1979, Lu *et al.* 2001).

## **1.2 Whitefish**

The distribution of whitefish is wide in Europe. It appears in polymorphic populations especially in the northern parts of its distribution area (Svärdson 1979). In Europe, two major mtDNA lineages exist, one in northern Europe and the other in southern Fennoscandia and central Europe (Bernatchez & Dodson 1994). Sympatric forms of whitefish and lake whitefish may have evolved after multiple invasions of different lineages or intralacustrine divergence of a single lineage (Bernatchez *et al.* 1999, Douglas *et al.* 1999, Lu *et al.* 2001). The continuous existence of sympatric forms throughout time usually includes niche segregation between forms (Lindsey 1981, Amundsen 1988). Sympatric forms may differ for example in habitat use, food selection and growth (Svärdson 1979, Bergstrand 1982, Amundsen 1988). Morphological differentiation of sympatric whitefish forms is often related to the number of gillrakers. In postglacial lakes, gillraker distribution of whitefish usually

follows patterns of mono-, bi- or trimodality (e.g. Himberg 1970, Svärdsön 1979, Amundsen 1988, Sandlund *et al.* 1995, Amundsen *et al.* 2004a, 2004b).

The level of divergence between sympatric whitefish forms is variable and has caused considerable confusion in taxonomic considerations (Himberg 1970, Himberg & Lehtonen 1995). Sympatric whitefish are usually divided into forms by counting the number of gillrakers, which have a high hereditary component (Svärdsön 1970, 1979). Gillrakers are considered to be one of the most stable and reliable of the morphological characters (Lindsey 1981) supporting their use in identification. Furthermore, field data often suggests correlation between gillraker number and feeding. Sparsely rakered whitefish forms are usually benthivores, whereas densely rakered whitefish forms are planktivorous (Lindström & Nilsson 1962, Svärdsön 1979, Bergstrand 1982, Amundsen 1988, Amundsen *et al.* 2004a, 2004b). This gives preliminary assumption that morphometric traits, at least number of gillrakers, should be related to feeding efficiency of whitefish forms. Morphometric divergence can be strong, as identification of sympatric forms in the field can be possible due to distinct differences in gillraker number, space and length (Amundsen 1988, Amundsen *et al.* 2004a).

Morphological differentiation between sympatric forms should be high, if they continuously use distinct pelagic or benthic niches (Schluter 2000b). This has been clearly observed with other fish lineages, such as sympatric Arctic charr and three-spined stickleback morphs (e.g. McPhail 1984, Snorrason *et al.* 1994). Sympatric whitefish forms show more pronounced variance in gillraker number than most of the limnetic and benthic morphs in other fish lineages (Svärdsön 1979, Amundsen 1988, McPhail 1993, Bernatchez *et al.* 1999, Saint-Laurent *et al.* 2003). Gillraker number has been considered as a standard method in whitefish identification throughout decades, but other morphometric or meristic traits has been considerably less explored for sympatric whitefish (but see Svärdsön 1950, Amundsen *et al.* 2004a).

In various distantly related fish lineages, the limnetic and benthic morphs share available resources (Schluter & McPhail 1993, Robinson & Wilson 1994). However, little is known about availability of food resources in different habitats, which should have effect of profitability of the use of pelagic or benthic habitat. Furthermore, for fish, profitability of certain habitat should influence on growth and might also affect the life history. Resource competition between sympatric morphs of three-spined stickleback is shown to decrease as divergence proceeds (Pritchard & Schluter 2001). This suggests that if whitefish forms are highly specialized to use of distinct niches, their food and habitat overlap should be low. Segregation of sympatric morphs usually includes both diet and habitat component (Larson 1976, Amundsen 1988, Skúlason *et al.* 1999). In most of the studies, data of habitat use and diet of sympatric morphs concern only distribution and diet of morphs in pelagic and benthic habitat during certain time of day. Little attention has been paid on the diel and seasonal habitat use and diet of sympatric whitefish forms.

Predation is an important structuring force in freshwater communities and most likely influences to the divergence of sympatric morphs (Lima 1998, Vamosi 2002). In three-spined sticklebacks, predation may even intensify divergence of morphs (Rundle *et al.* 2003). In addition, risk of predation may differ between habitats of sympatric morphs. Pelagic habitat is considered to contain higher predation risk due to lack of refuge than other habitats (Werner *et al.* 1983, Werner & Hall 1988, L'-Abée-Lund *et al.* 1993). This suggests that predation may have impacts on the predator avoidance behaviour of prey *i.e.* possibilities to use certain food resources (Lima 1998). Whitefish is known to be important prey item for piscivores (Amundsen 1994, Næsje *et al.* 1998, Bøhn *et al.* 2002). However, importance of



different whitefish forms in predators diets and impacts of predation on their habitat use and migrations have been less explored (but for predation see Næsje *et al.* 1998).

Polymorphic whitefish is widely recognized in the northern hemisphere and in some cases even morphologically distinguishable in the field (Amundsen 1988, Amundsen *et al.* 2004a). Field data of sympatric whitefish forms suggest rather strong reproductive isolation via differences in spawning times or places, and furthermore, one of the strongest morphometric traits related to feeding, number of gillraker, is heritable (Svärdson 1970, 1979). Sympatric whitefish forms may represent the early stage of speciation being not full biological species as artificially produced hybrids of whitefish forms are viable (Svärdson 1970, 1979). For evolutionary point of view, sympatric whitefish forms give opportunity to study mechanisms involved in their divergence.

### 1.3 Main objectives of this thesis

This study was performed in Lake Muddusjärvi, northern Finland. Lake Muddusjärvi is a subarctic lake inhabited by ten fish species, of which polymorphic whitefish is the most numerous one. Perspective of one lake gives a good opportunity to reveal various aspects of the ecology of sympatric whitefish forms. Lake Muddusjärvi is known to be inhabited by sympatric whitefish forms at least during 1900's (Järvi 1928, Toivonen 1960, Sarjamo *et al.* 1989). This suggests that this lake has constant food and habitat availability for persistent existence of sympatric whitefish forms. Closely related species, in this case sympatric whitefish forms, lower their niche overlap by segregating in habitat, food or time (Ross 1986). Thus, habitat and food segregation is likely to exist between sympatric whitefish forms. If habitat and food segregation between sympatric whitefish forms is strong, it could also have induced morphological divergence between them especially as these sympatric forms have been recognized for decades. Following to these niche segregation and morphometric suggestions the main objectives in the whitefish part were:

1. To evaluate the level of morphological divergence of the whitefish forms (I)
2. To investigate niche segregation between the whitefish forms by the examination of the diet and the habitat use (II, III)

Fish fauna of Lake Muddusjärvi is known to be dominated by whitefish, but also piscivorous brown trout (*Salmo trutta* L.), Arctic charr, burbot (*Lota lota* (L.)) and pike (*Esox lucius* L.) coexist in the lake (Sarjamo *et al.* 1989). Dominance of whitefish in fish fauna implies possible importance in piscivores diet. If sympatric whitefish forms show niche segregation, they should confront unequal risk of predation. Pelagic habitat use should include the highest risk of predation due to lack of refuges (Werner *et al.* 1983, Werner & Hall 1988, L'-Abée-Lund *et al.* 1993). This suggests that sympatric whitefish forms could have different predator avoidance behaviour during different times of day and/or season. Also sympatric whitefish forms may differ in their vulnerability to predation if their growth is different. To reveal answers to these questions the main objectives in the predation part were:

3. To reveal the level of persistence in habitat and food segregation of the whitefish forms different times of day and season (III)
4. To explore predation impacts of brown trout and Arctic charr on the whitefish forms (IV)
5. To evaluate the importance of whitefish forms in the diet of piscivores and to estimate the vulnerability of whitefish forms (V)

## 2. Materials and methods

### 2.1 Study area

The oligotrophic Lake Muddusjärvi is situated in the northern Finland (69°N, 27°E) and has a total surface area of 48 km<sup>2</sup> (Fig. 1). It is 146 m above sea level and belongs to the Paatsjoki catchment area, which discharges its waters to the Ice Sea. Two humic rivers discharge their waters into Lake Muddusjärvi making the water brownish (the average Secchi disc transparency 3 m). The lake morphometry is complex, including both shallow and deep areas. The main basin is deep (maximum depth 73 m), but the southern and northern bays are shallower. At shores, the bottom consists mainly of gravel, stones, and rocks, but also sandy shores exist. At the deeper areas coarse particulate organic matter transforms to fine mud. Aquatic vegetation is scanty. The ice-free period usually begins at late May to early June and lasts until late October-November. During the summer temperature in surface may reach 18-20 °C, but the maximum water column (0-20 m) temperature is lower (*circa* 12 °C).

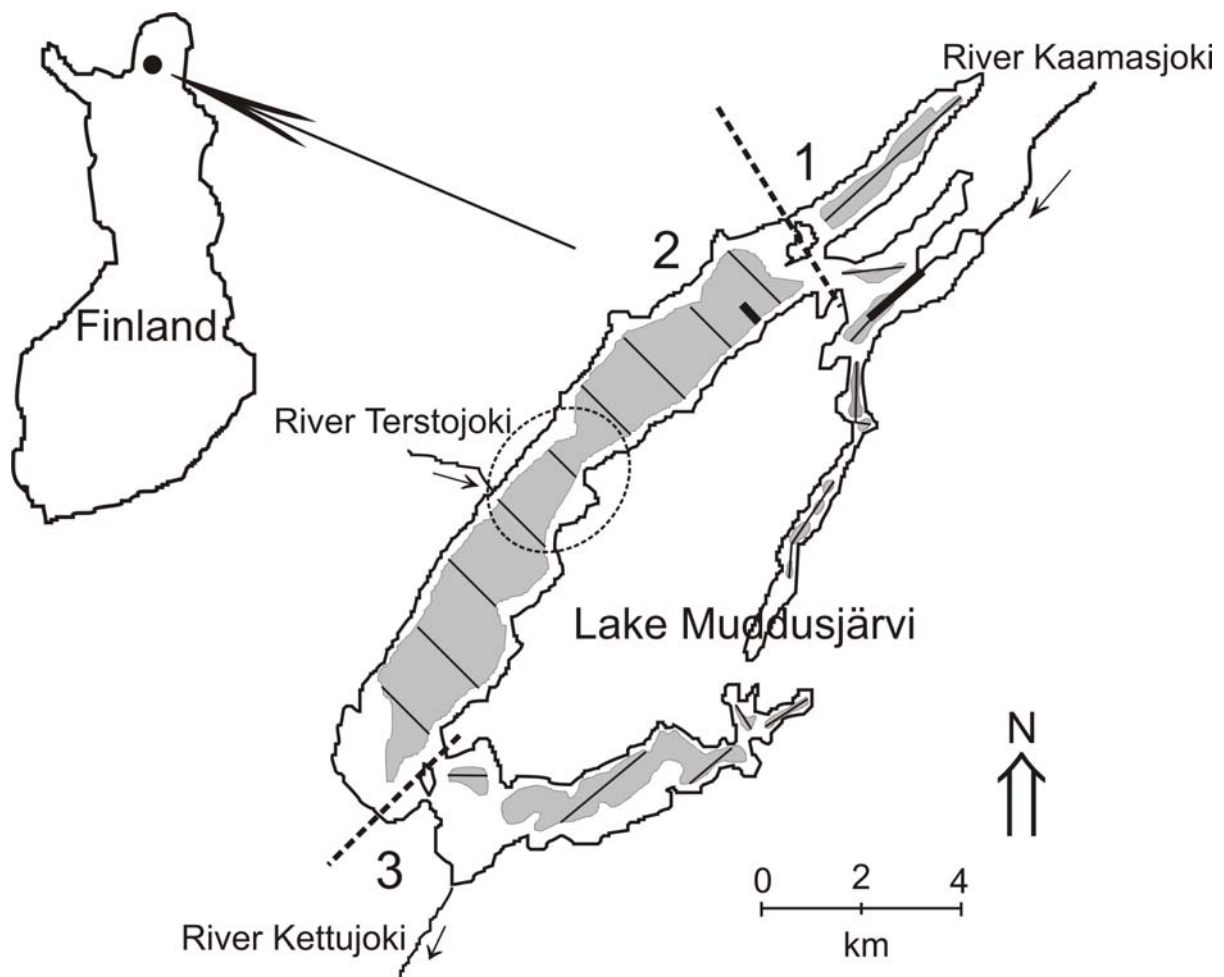


Fig.1. Map of Lake Muddusjärvi. Shaded areas indicate the pelagic zone (depth >6 m). Hatched ellipse indicates the location of the diel cycle study (paper III) and the 19 lines in the shaded areas indicate the echosounding transects. The lake is divided into three strata separated by bold hatched lines: 1 northern bays, 2 main basin, and 3 southern bays. Two bold lines in the northern part of lake indicate sampling transects of benthic macroinvertebrates (paper II).

The fish fauna of Lake Muddusjärvi consists of ten species: whitefish, Arctic charr, brown trout, grayling (*Thymallus thymallus* (L.)), perch (*Perca fluviatilis* L.), pike, burbot, minnow (*Phoxinus phoxinus* (L.)), three-spined stickleback and nine-spined stickleback (*Pungitius*

*pungitius* (L.)). Brown trout and Arctic charr stocks consist of both wild and stocked fish (Kahilainen & Lehtonen 2001, 2002a). Whitefish is the most numerous species in Lake Muddusjärvi.

## **2.2 Sampling methods**

### **2.2.1 Fishing**

Whitefish samples were caught with a set of eight gillnets (papers I-V). Depending on fishing year and period, 1-5 net series were used simultaneously. Single gillnet in this net series was 1.8 m high and 30 m long (mesh sizes 12, 15, 20, 25, 30, 35, 45 and 60 mm from knot to knot). Nets were tied together with random order. Predator species were sampled with two sets of monofilament gillnets (IV). A set consisted of five nets (each height 5 m and length 60 m, mesh sizes 35, 40, 45, 50, and 55 mm), which were tied together in random order. In 2000 (V), a minor proportion of the predator samples were caught with a slightly different net set also containing five nets made of twisted monofil (each 5 m high and 60 m long, mesh sizes 45, 50, 55, 60 and 65 mm). The fishing sites were randomized in each depth zone (littoral 0-10 m, profundal 10-20 m, and pelagial 0-10 m). Nets were anchored at both ends, and fishing depth was confirmed with an echosounder. Pelagic nets were set to desired fishing depth with floats.

Pelagic trawlings (III) were conducted with a small pair-trawl (5 m high, 8 m wide and cod-end mesh size 3 mm). Trawl was towed with two motorboats. The trawl was set to the desired depth (0-20 m) using iron weights apart from surface tows. Fishing depth and opening of the trawl were verified with an echosounder. Each trawl haul took 10-30 minutes and the average towing speed was 3.1 km/h.

Fish were removed from nets or trawl and cooled in ice. In the field, whitefish forms were identified according to appearance and gillraker morphometry. Small sparsely rakered whitefish (SSR) was distinguished by the large eyes, brownish back coloration and reddish fins. In addition, SSR has widely spaced and extremely short gillrakers. Gillraker tip is bent, especially in large specimens. Densely rakered whitefish (DR) and large sparsely rakered whitefish (LSR) have normal whitefish coloration including silvery sides, dark back and fins. However, gillraker morphometry is different: LSR has short and widely spaced gillrakers, whereas DR has long and densely spaced gillrakers. Gillrakers of LSR and SSR are unflexible, whereas gillrakers of DR are flexible. Each gillraker has small secondary teeth in the oral cavity side, but number of these teeth depends on whitefish form: SSR has lowest number, LSR intermediate and DR highest number of secondary teeth. The total length and weight of fish were measured with accuracy of 1 mm and 0.1 g. For predator species, stomachs were removed and frozen at  $-20^{\circ}\text{C}$ . Whitefish samples were frozen as whole at  $-20^{\circ}\text{C}$  prior to measurements.

### **2.2.2 Echosounding**

Acoustic data were collected with a SIMRAD EY-500 –echosounder (III), which was equipped with a split-beam transducer ES120-7F (operating frequency 120 kHz and beam opening angle  $7^{\circ}$  at -3 dB level). The transducer was mounted on a towed body, which was lowered to a depth of 0.6 m in the left side of the boat. Pulse duration was set to 0.3 ms. Echosounding equipment was calibrated with a standard copper sphere (target strength -40.4 dB).

The area of the diel cycle study was located in the main basin (depth 6-40 m) of Lake Muddusjärvi (Fig. 1). Echosoundings were conducted along 1-3 fixed transects at 1-2 hour intervals. Fish species composition was studied using trawlings in the pelagial and gillnettings in the epibenthic zones during the day and at night. Temperature (°C) in the water column was recorded from the surface down to a depth of 25 m during the study periods. The diel cycle study was conducted to reveal possible differences in whitefish habitat use and also to find the most suitable time for the pelagic fish abundance estimation. This is the time when fish are absent from the “blind zones” of the echosounder (close to bottom or surface) and not aggregated into dense shoals (Appenzeller & Leggett 1992).

Seasonal fish density in >6 m deep areas was estimated along 19 echosounding transects on 5-9 September 2000, on 14-17 June 2001, and on 8-11 August 2001. According to the results of the diel cycle studies, nighttime was selected for estimation of pelagic fish density in every study occasion. Systematic sampling with equidistant transects at intervals of 1500 m was applied (Fig. 1). The location of the first transect was randomized. On each night, trawl hauls were conducted in pelagic areas and gillnetting in epibenthic areas to assess species composition and length distributions. Fishing was carried out in all bays and main basin including pelagic and benthic depth zones.

### **2.2.3 Benthic macroinvertebrates**

Two sampling transects were used to estimate abundance, biomass and diversity of benthic macroinvertebrates (II). These transects were situated in two different slope types in the northern part of Lake Muddusjärvi (Fig. 1). Whitefish form samples were caught in the vicinity of these benthic macroinvertebrate transects. Sampling was made in June and August with the Ekman grab (collecting area of 272.3 cm<sup>2</sup>). Three replicates were taken from each sampling depth. Benthic macroinvertebrates were sieved immediately through 0.5 mm mesh size net. After sieving, the sample was preserved in 96% ethanol.

## **2.3 Measurements**

### **2.3.1 CPUE and length distributions**

Catch per unit of effort (CPUE) was calculated as the number of fish per set of eight nets in a 12-hour period (II, IV, V). In paper III, gillnet CPUEs were calculated as the number of whitefish per gillnet series per one hour and trawl CPUEs as number of whitefish per minute of trawl haul. The CPUEs (log-transformed) were analyzed using the analysis of variance (ANOVA) (IV, V). The analyzed factors; depth, form and their interactions (depth×form) were included into the ANOVA model (V). Pairwise comparisons of CPUE were studied with Tukey's HSD test. Average length differences between whitefish forms in gillnet catches were analyzed with ANOVA and pairwise comparisons were made with Tukey's HSD test (V). In paper II, intraform CPUEs of LSR and SSR in epibenthic depth zones 0-10 m and 10-20 m were compared with Mann-Whitney U-test separately at each month. Differences of all statistical analyses were considered significant if  $P < 0.05$ .

### 2.3.2 Age and growth

For age determination, both otoliths (sagitta) and 10-20 scales behind the ventral fins were taken (II, IV). Scale impressions were printed on soft polycarbonate slides with a roller press. Otoliths were burnt and cracked through the nucleus. To improve the reliability, both otoliths (burnt and unburnt) and scales were used for age determination.

Back-calculated growth was determined from scales (Kahilainen & Lehtonen 2002b). The most symmetric scale was chosen from each fish. The Monastyrsky method was used for back-calculation (Bagenal & Tesch 1978; equations 1 and 2).

$$L = aSb \quad (1)$$

where  $L$  is the length of the fish at capture (cm),  $a$  is a constant and  $b$  is a growth coefficient.

$$L_i = \left( \frac{S_i}{S} \right)^b L \quad (2)$$

where  $L_i$  is the length of the fish at formation of the  $i$ :th annulus (cm),  $L$  is the length of the fish at capture (cm),  $S_i$  is scale radius at age  $i$ ,  $S$  is the total scale radius, and  $b$  is a growth coefficient. Back-calculated length at age was tested with ANOVA (II). Pairwise comparison of length-at-age between whitefish forms was performed with Tukey's HSD test.

### 2.3.3 Morphometric and meristic analyses

The gillrakers on the first right branchial arch were counted under a preparation microscope. The average gillraker number between whitefish forms was compared with Student's  $t$ -test (II, III) or ANOVA (I, summary). The relationship between gillraker number and whitefish length was analyzed with linear regression (II, summary). In paper III, gillraker distributions were presented for three habitats: pelagic, shallow (<10 m) epibenthic zone and deep (>10 m) epibenthic depth zone. Comparisons of gillraker distributions between different depth zones were made using Kolmogorov-Smirnov test.

Morphologic and meristic measurements were conducted of 254 field-identified adult whitefish (I). Four meristic counts and eleven morphological measurements were made (Fig. 2). According to field identification, sample sizes for SSR, LSR and DR were 80, 84 and 90, respectively. The whitefish length ranges in the analyses for SSR, LSR and DR were 10.1-36.2, 10.1-43.6 and 11.1-38.9 cm. Morphological measurements of whitefish body traits were made with dial calliper (at precision of 0.1 mm) and gillraker traits were measured under preparation microscope. Meristic counts were made under preparation microscope, using 16-fold magnification. The average gillraker space was calculated as the length of gillarch divided by the number of gillrakers.

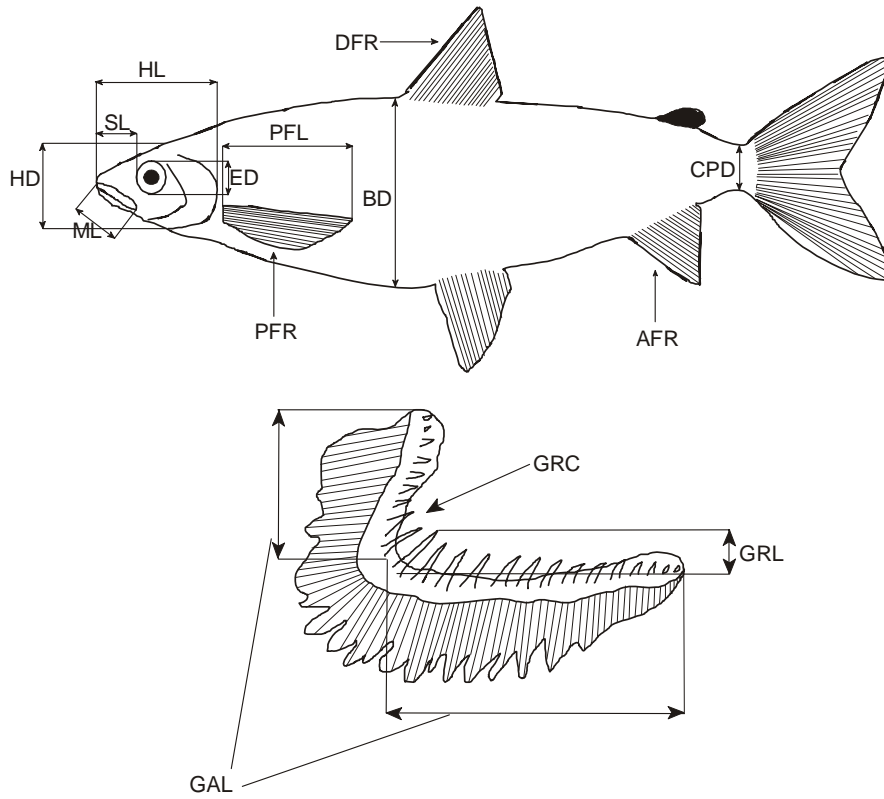


Fig. 2. Morphometric measurements and meristic counts made from whitefish samples of Lake Muddusjärvi. Arrows indicate morphometric distance measured. Abbreviations for morphometric measurements: GRL=gillraker length (length of the longest gillraker), GAL=gillarch total length, GRS=gillraker space (gillarch total length/gillraker number), ED=eye diameter, HL=head length, HD=head depth, SL=snout length, ML=maxillary length, PFL=pectoral fin length, BD=body depth, CPD=caudal peduncle depth. Abbreviations for meristic counts: GRC=gillraker count, PFR=pectoral fin ray count, AFR=anal fin ray count, and DFR=dorsal fin ray count.

Morphological data were first log-transformed (I). Morphological measurements were then size-adjusted to the average length of all whitefish samples. The size-adjustment was made with the allometric formula (Thorpe 1975),

$$X_i = 10^{Y_i} \quad (3)$$

where  $X_i$  is size-adjusted morphometric measurement and  $Y_i$  is the logarithm of adjusted morphometric measurement.

$$Y_i = \log_{10} M_i - b(\log_{10} L_i - \log_{10} L_{tot}) \quad (4)$$

where  $b$  is the pooled regression coefficient of  $\log_{10}M_i$  against  $\log_{10}L_i$ ,  $M_i$  is the morphometric measurement of  $i$ th whitefish,  $L_i$  is the total length of  $i$ th whitefish,  $L_{tot}$  is the average total length of all whitefish samples.

Meristic counts were examined as raw data. First morphometric and meristic differences between sexes in each whitefish form was analysed with pairwise t-tests. Body depth was significantly higher in females for LSR and DR (t-tests,  $p < 0.01$ ), but no other significant differences was found, and thus both sexes was pooled in subsequent analysis. Morphological measurements and meristic counts of whitefish forms were analysed univariately with ANOVA and pairwise comparisons between the forms were conducted using the Tukey's HSD test.

Data were examined multivariately with discriminant function analysis (DFA) using SPSS version 10.0 (I). Morphological (size-adjusted) and meristic measurements were analysed separately due to heterogeneity of the variances. To ensure, that size-adjustment did not bias the results, DFA was completed also with residual values (Reist 1985, 1986, Fleming *et al.* 1994). Both analyses gave similar results, and only those results obtained with the allometric method were used. DFA was performed with the stepwise method in which the variable was included in the analysis until the discriminant power was not further improved. The variables with F-value >1 were considered to contribute to the DFA (Lu & Bernatchez 1999, Saint-Laurent *et al.* 2003). A scatterplot of canonical scores in two-dimensional space was used for detection of groups. The statistical significance of differences between the whitefish groups was also tested using Multi-Response Permutation Procedures (MRPP) with Euclidean distance measurement (Berry *et al.* 1983, Biondini *et al.* 1985). It is a non-parametric procedure for testing the significance of possible differences between a priori classified groups. In the analysis, average distances for whitefish groups were estimated, and the difference between expected and observed delta was tested. In MRPP, test statistic A (chance-corrected within-group agreement) is a descriptor of within group homogeneity compared to random expectation. If A=0, heterogeneity within groups equals expectation by chance. When A=1, all items are identical within groups. MRPP was done using program PC-ORD version 4 (McCune & Mefford 1999).

### 2.3.4 Diet analyses of whitefish

The point method (Hynes 1950) was used for stomach content analysis (II, III). The stomach was removed and all food items were identified to family or order level. Stomach fullness was visually estimated on a scale of 0-10, where 0 represented an empty stomach and 10 an extended full stomach. The relative contribution of various food items to stomach fullness was estimated.

In paper I, whitefish stomach was removed and wet weight method was used (Windell & Bowen 1978). Food items were identified to family or order level and wet weight (accuracy of 0.01 g) of each category was measured. The proportion of each food category of total stomach contents was calculated for all whitefish forms.

Intra- and interform diet-overlap (I, II) between different length groups of whitefish forms was calculated with Schoener's (1970) index:

$$\alpha = 1 - 0.5 \left( \sum_{i=1}^n |P_{xi} - P_{yi}| \right) \quad (5)$$

where  $P_{xi}$  is the proportion of food item  $i$  used by length group  $x$  and  $P_{yi}$  is the proportion of food item  $i$  used by length group  $y$ , and  $n$  is the number of prey categories. A value of zero indicates no overlap, and a value of 1.0 suggests complete overlap. Diet-overlap value 0.6 or higher was considered biologically significant (Wallace 1981).

Body length of zooplankton in whitefish stomachs was measured from undeteriorated individuals, of which 30 randomly selected specimens was measured, if possible (I). Five main taxa were *Bosmina* sp., *Daphnia* sp., *Eurycerus* sp., Cyclopoida and Calanoida. Differences in the average length of zooplankton (all taxa pooled) in the stomach between different whitefish forms were examined with ANOVA and pairwise comparisons with Tukey's HSD test. The relationships between gillraker number, space and length and the average length of zooplankton (all taxa pooled) in the stomach was examined with Spearman

correlation. All whitefish samples were pooled in this analysis to examine correlation between morphology (gillraker) and zooplankton length.

### **2.3.5 Diet analyses of piscivores**

Prey categories in the stomach of piscivores were identified under a preparation microscope. Whitefish forms were identified according to appearance and gillraker morphometry as in gillnet catches, but if preyed whitefish form was strongly deteriorated, it was classified as unidentified whitefish. Wet weight method (Windell & Bowen 1978) was used for diet content analysis (IV), where each food category was measured with an accuracy of 0.01 g, and its proportion of the total wet weight of the stomach contents was calculated.

The total length of each prey fish was measured with an accuracy of 1 mm. Whitefish was the most numerous prey species found in the stomachs of piscivores. Occasionally whitefish had been digested in stomachs so that the total length was impossible to measure directly. If the direct measurement was impossible, the whitefish length was estimated from the total length of otolith (sagitta), using a linear regression (Kahilainen & Lehtonen 2001):

$$y = 3.36x + 0.52 \quad (6)$$

where  $y$  is whitefish length and  $x$  is otolith length. Relationship between predator and prey length was studied with linear regression (IV, V). If the predator had many fishes in the stomach the mean length of prey was used in the analysis (IV, V). In order to test differences in predator-prey relationships between brown trout and Arctic charr, slopes of regression equations were analysed with Student's t-test. The relative abundance of whitefish forms in catches and in predator stomachs were compared with Kolmogorov-Smirnov test. To estimate the age groups vulnerable to predation, the maximum and minimum lengths of whitefish eaten were compared to back-calculated growth curves for the three whitefish forms (Kahilainen & Lehtonen 2002b).

The length at the shift to piscivory was examined with a logistic regression model (V). If the predator stomach contained fish remains it was considered piscivorous and a value of 1 was given. If the predator stomach contained invertebrate but no fish remains the value was 0. Empty stomachs were excluded from the analyses. The proportion of piscivorous fish of each species was analysed with the logistic regression:

$$y = \frac{\exp(\alpha + \beta L)}{1 + \exp(\alpha + \beta L)} \quad (7)$$

where  $y$  is the occurrence of fish in the stomach recorded as 0 or 1, and  $L$  is the total length of the predator. Constants  $\alpha$  and  $\beta$  were estimated from the data. In this analysis, predator species was considered to have shifted to piscivory at length when the probability of finding fish in the diet was  $\geq 50\%$ .

### **2.3.6 Whitefish density calculations**

In the density estimation of whitefish in the pelagic areas, echosounding transects were divided into circa 500 m long elementary sampling distance units (ESDUs), whereas in the diel cycle studies the whole transects worked as sampling units. In this study, the "blind zones" excluded from fish density calculations were 0-2 m layer below surface and 0.5 m



layer above the bottom. Fish densities of ESDUs were computed with EP 500 –software, which uses  $40 \log R$  time-varied gain (TVG) function for estimating target strength (TS) of single targets and  $20 \log R$  TVG function for summing up the echo integral from multiple targets (*i.e.* from fish shoals). The program computes the fish density assuming the TS-distributions of fish in shoals and fish detected as single targets to be identical. Based on TS-distributions and species-specific length distributions of trawl catches, TS threshold was set to  $-60$  dB and smaller targets were considered to be noise. The only fish species in the study area of which TS is probably lower than  $-60$  dB is nine-spined sticklebacks (the average total length 34 mm in trawl catches). Integration threshold was set to  $-65$  dB based on thresholding with different values (Eckmann 1998). Brown trout and nine-spined sticklebacks were the only other species caught in the pelagic areas and their relative abundance was low (0.1% of catches). Thus, the pelagic fish density could be treated as whitefish density.

Fish density in the pelagic areas (depth  $>6$  m) was computed with post-stratified sampling (Cochran 1977), lake basins as strata. Lake Muddusjärvi was divided into three strata: 1 northern bays, 2 main basin, and 3 southern bays (Fig. 1). Fish density of  $>6$  m deep area within each stratum was computed as the weighted average of fish density values in ESDUs with ESDUs' lengths as weights. Weighted variance of average density in stratum  $h$ ,  $Var(\bar{y}_h)$ , was computed using the equation (Shotton & Bazigos 1984):

$$Var(\bar{y}_h) = \frac{\sum_{i=1}^n [(y_i - \bar{y})^2 * l_i]}{\sum_{i=1}^n l_i * (n-1)} \quad (8)$$

where  $y_i$  is the fish density in  $i$ th ESDU,  $\bar{y}$  is the average fish density,  $l_i$  is the length of  $i$ th ESDU and  $n$  is the number of ESDU's.

Variance of average fish density in the whole study area,  $Var(\bar{y})$ , was computed using the equation (Cochran 1977):

$$Var(\bar{y}) = \sum_{h=1}^L \left[ \left( \frac{A_h}{A} \right)^2 * Var(\bar{y}_h) \right] \quad (9)$$

where  $A_h$  is the area of  $h$ th stratum,  $A$  is the study area and  $L$  is the number of strata. The approximate 95% confidence limits for fish density were calculated on the basis of Poisson distribution (Jolly & Hampton 1990):

$$\text{The end points of confidence limits} = \bar{y} \left( 1 + \frac{Var(\bar{y})}{\bar{y}^2} \right) \pm 2\sqrt{Var(\bar{y})} \quad (10)$$

The variance estimate, and hence also the confidence limits will be biased if correlation between successive ESDUs is high ( $>0.25$ ) (Williamson 1982). Therefore, the validity of the variance estimate was studied with Pearson correlation analysis.

Differences in fish density estimates for day and night within each study period (June, August and September) and differences in nighttime pelagic whitefish density estimates between study months were compared using Mann-Whitney U-test (Conover 1980).

### 2.3.7 Benthic macroinvertebrate analysis

Most of the benthic macroinvertebrates were identified to family, but a few groups were identified only to order level (II). All macroinvertebrates were counted and biomass (wet weight) was measured to the nearest mg. Statistical tests were performed similarly as for the whitefish CPUE data (II), where littoral zone and profundal zone included depths <10 m and 10-20 m, respectively. Benthic macroinvertebrate abundance and biomass between littoral and profundal were compared with Mann-Whitney U-test.

## 3. Results

### 3.1 Morphometric and meristic differences between whitefish forms

Gillraker distribution, combined from Lake Muddusjärvi whitefish samples during 1998-2001, showed strong trimodality (Fig. 3). The average number of gillrakers, gillraker range and number of samples for SSR were 16.7, 12-20 and 820, for LSR 22.9, 17-28 and 1509, and for DR 34.6, 27-41 and 1983, respectively. The average number of gillrakers was significantly different (ANOVA,  $F_{2, 4309}=32598$ ,  $P<0.00001$ ) and all whitefish forms differed significantly (Tukey's HSD tests,  $P<0.00001$ ). In linear regression analysis, length ranges were for SSR 8.1-36.2 cm, for LSR 6.9-43.6 cm and for DR 5.1-38.9 cm (Fig. 3). Linear regression equations between length and gillraker number were for SSR  $y=0.030x+16.151$ ,  $R^2=0.011$ ,  $P<0.05$ , for LSR  $y=-0.002x+22.914$ ,  $R^2=0.00003$ ,  $P=ns.$ , and for DR  $y=-0.025+34.943$ ,  $R^2=0.004$ ,  $P<0.05$ .

Univariate method (ANOVA) for morphological measurements and meristic counts revealed significant differences ( $P<0.05$ ) between whitefish forms (I). The highest F-values were observed for gillraker count, space and length, in which all of the whitefish forms differed from each other (Tukey's HSD tests,  $P<0.05$ ). Number of gillrakers (I-III) and length of gillraker were lowest for SSR and highest for DR, whereas the values of LSR were intermediate. Gillraker space was largest for SSR, intermediate for LSR and smallest for DR. High F-values were observed also for eye diameter and head length, which were also significantly different (ANOVA,  $P<0.05$ ). SSR had largest eye diameter and head length (Tukey's HSD tests,  $P<0.05$ ).

In stepwise DFA for morphological measurements, gillraker space and length entered in the analysis first (I). Next six variables minimizing Wilks' Lambda were eye diameter, gillarch length, head depth, head length, snout length and pectoral fin length. Within these eight entered variables two canonical discriminant functions were used. Eigenvalues for function 1 (explained variance 91.2%) and 2 (8.8%) were 13.23 and 1.28, respectively. In the scatterplot figure, three separate groups were observed indicating SSR, LSR and DR (Fig. 4). Three whitefish forms could be distinguished with eight morphological measurements with an accuracy of 99.2%. In MRPP analysis, the average distances (Euclidean) for SSR, LSR and DR were 7.34, 6.26 and 4.90, respectively. Observed delta (6.12) was significantly smaller ( $P<0.00001$ ) than expected delta (7.81) and chance-corrected within-group agreement (A) was 0.21.

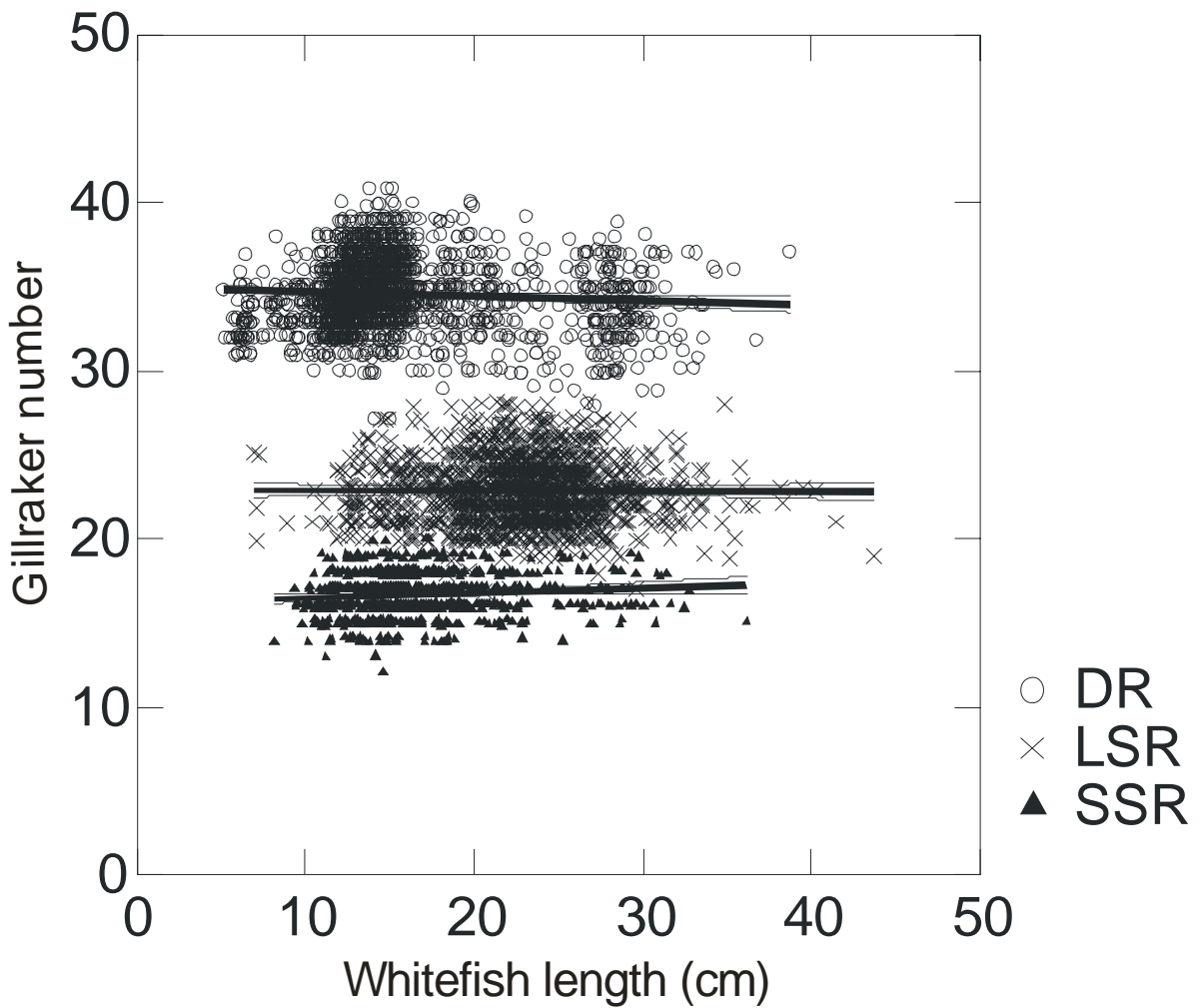
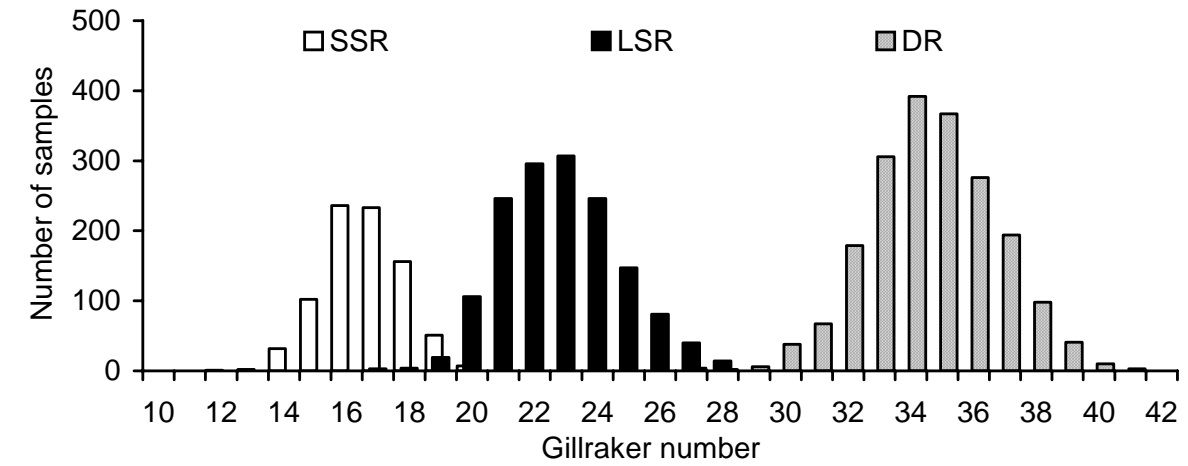


Fig. 3. The gillraker distribution (upper figure) and linear regression (with 95% confidence intervals) between whitefish length and gillraker number (lower figure) of Lake Muddusjärvi whitefish forms during 1998-2001 (n=4312). Abbreviations: SSR=small sparsely rakered, LSR=large sparsely rakered and DR=densely rakered whitefish.

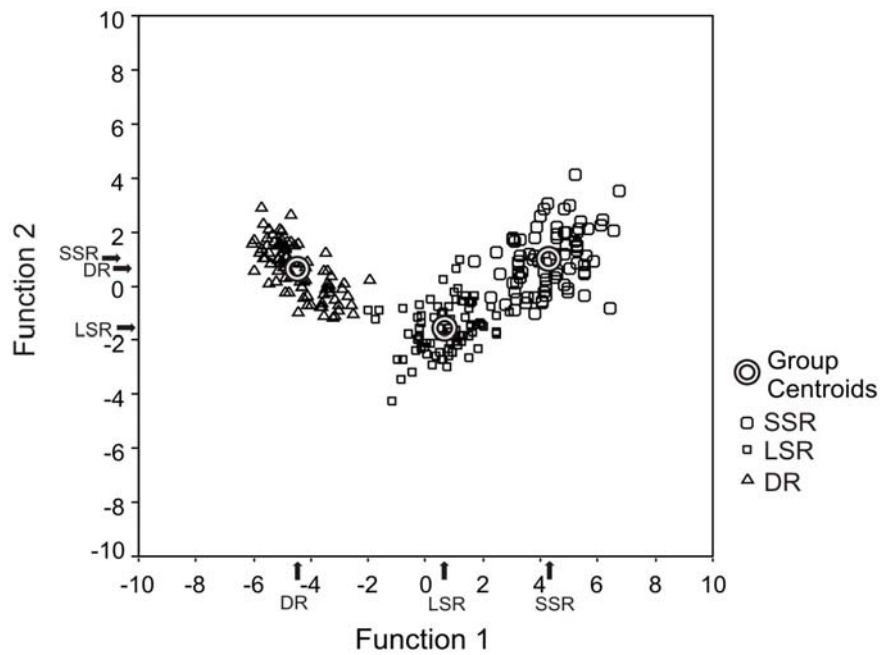


Fig. 4. DFA scatterplot of morphometric discriminant scores of Lake Muddusjärvi whitefish samples (DR=densely rakered, LSR=large sparsely rakered and SSR=small sparsely rakered whitefish). Arrows indicate the group centroids in function 1 and 2.

Stepwise DFA for meristic data revealed that the number of gillrakers was the most important variable and entered to the analysis first (I). All other meristic counts entered to stepwise DFA too (I). Function 1 (explained 98.5% of variance) and 2 (1.5%) had eigenvalues of 15.77 and 0.23, respectively. Three whitefish forms were identified in the scatterplot figure (Fig. 5) and detectability of whitefish to form was 98.8%. According to MRPP, the average distances (Euclidean) for SSR, LSR and DR were 2.55, 3.08 and 3.06. Observed delta (2.91) was significantly smaller ( $P < 0.00001$ ) than expected delta (8.795) and A was 0.66, respectively.

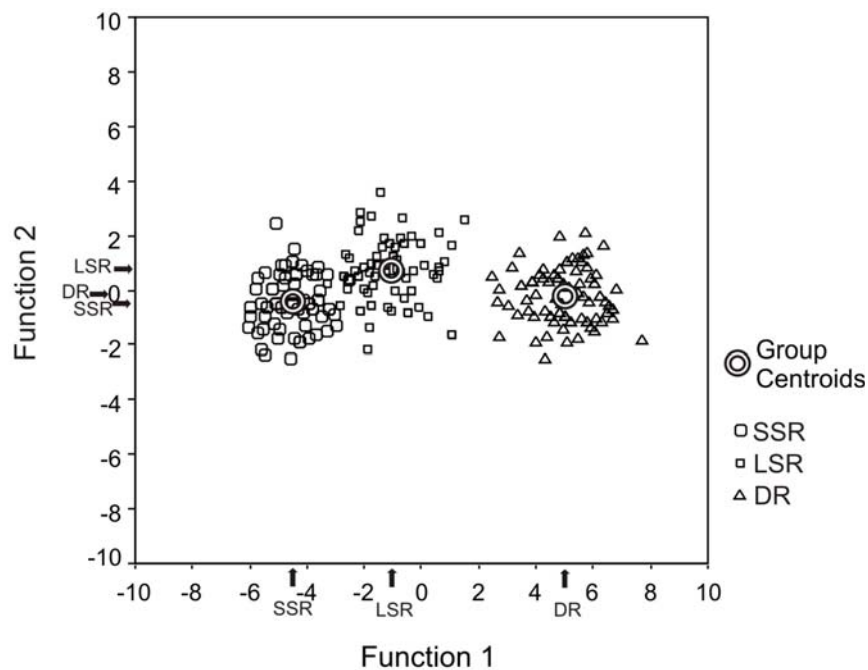


Fig. 5. DFA scatterplot of meristic discriminant scores of Lake Muddusjärvi whitefish samples (DR=densely rakered, LSR=large sparsely rakered and SSR=small sparsely rakered whitefish). Arrows indicate the group centroids in function 1 and 2.

### 3.2 Habitat segregation between sparsely rakered whitefish forms

Habitats of sparsely rakered whitefish forms were segregated: LSR dwelled mainly in shallow <10 m areas, whereas SSR preferred depths >10m (Fig. 6, II). In June-August, CPUE's of SSR in the depth zone 10-20 m were significantly higher than those in the depth zone 0-10 m (Mann-Whitney U-test,  $P<0.05$ ). In contrast, CPUE's of LSR in June-August were significantly higher in <10 m than in >10 m deep areas (Mann-Whitney U-test,  $P<0.05$ ). The abundance and biomass of benthic macroinvertebrates were highest in the littoral zone, decreasing towards the profundal in both transects and both study months (Fig. 6). The abundance and biomass were higher in depths <10 m than in depths 10-20 m in June and August. This difference was statistically significant (Mann-Whitney U-test,  $P<0.05$ ) in both transects in August and in transect 2 in June.

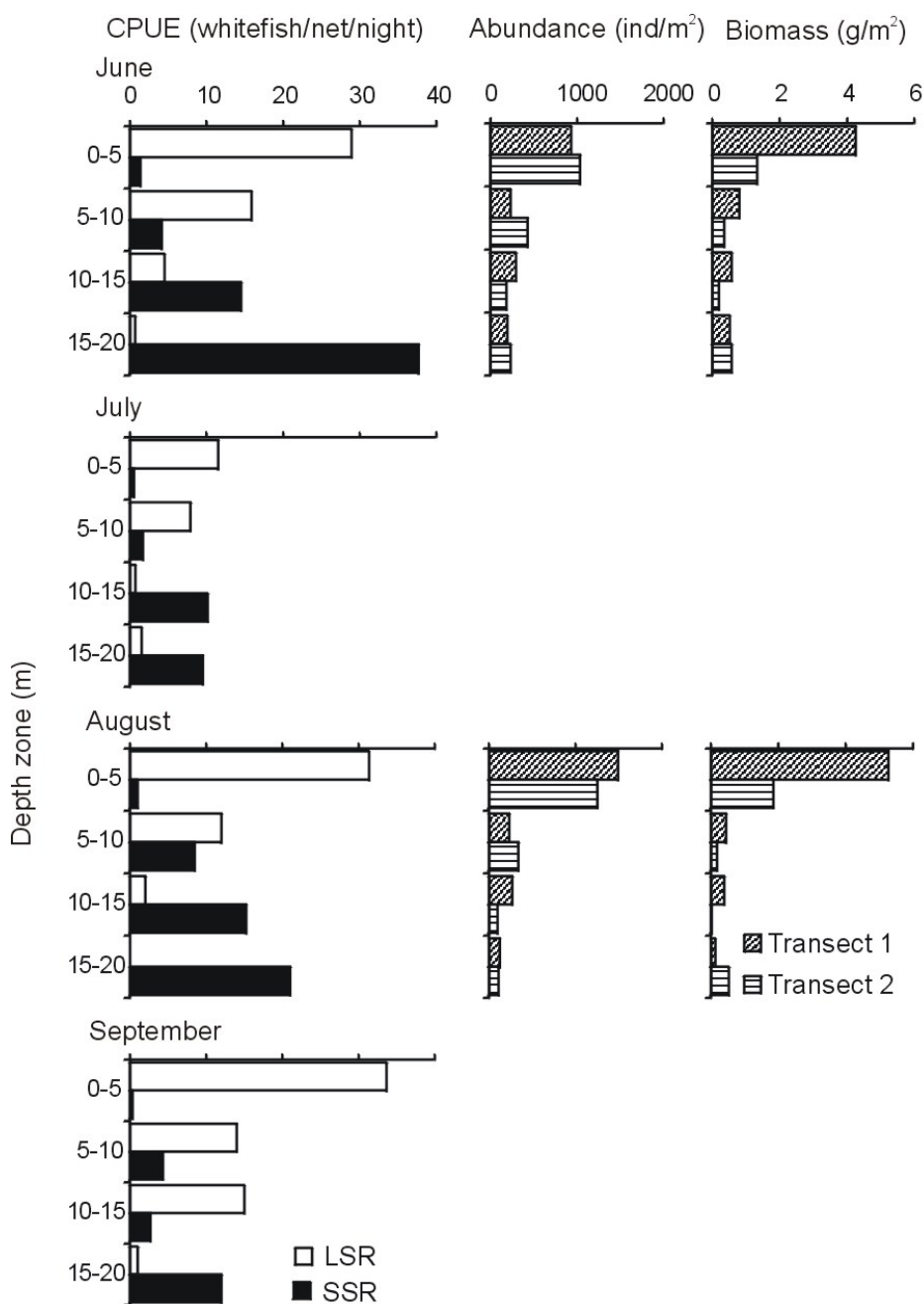


Fig. 6. CPUE of small sparsely rakered (SSR) and large sparsely rakered (LSR) whitefish in epibenthic depth zones from June to September (left). Abundance and biomass (wet weight) of benthic macroinvertebrates in June and August (right).

### 3.3 Diel and seasonal habitat segregation between whitefish forms

In Lake Muddusjärvi, whitefish forms inhabited both pelagic and epibenthic habitats (III). However, seasonal and diel differences in habitat use were evident. In June, during the continuous daylight of the polar region, no clearly distinguishable night exists. At this time, light intensity was lowest at 00.00-02.00, which was nominally considered as the night in this study. According to the echosounding surveys, fish were concentrated close to the bottom both during the day and at night (Fig. 7). However, at night, fish ascended slightly above the bottom and fish density in the pelagial was significantly higher (Mann-Whitney U-test,  $P < 0.05$ ) than during the day (III). In June, the water temperature was low ( $< 10\text{ }^{\circ}\text{C}$ ) with no thermal stratification (Fig. 7).

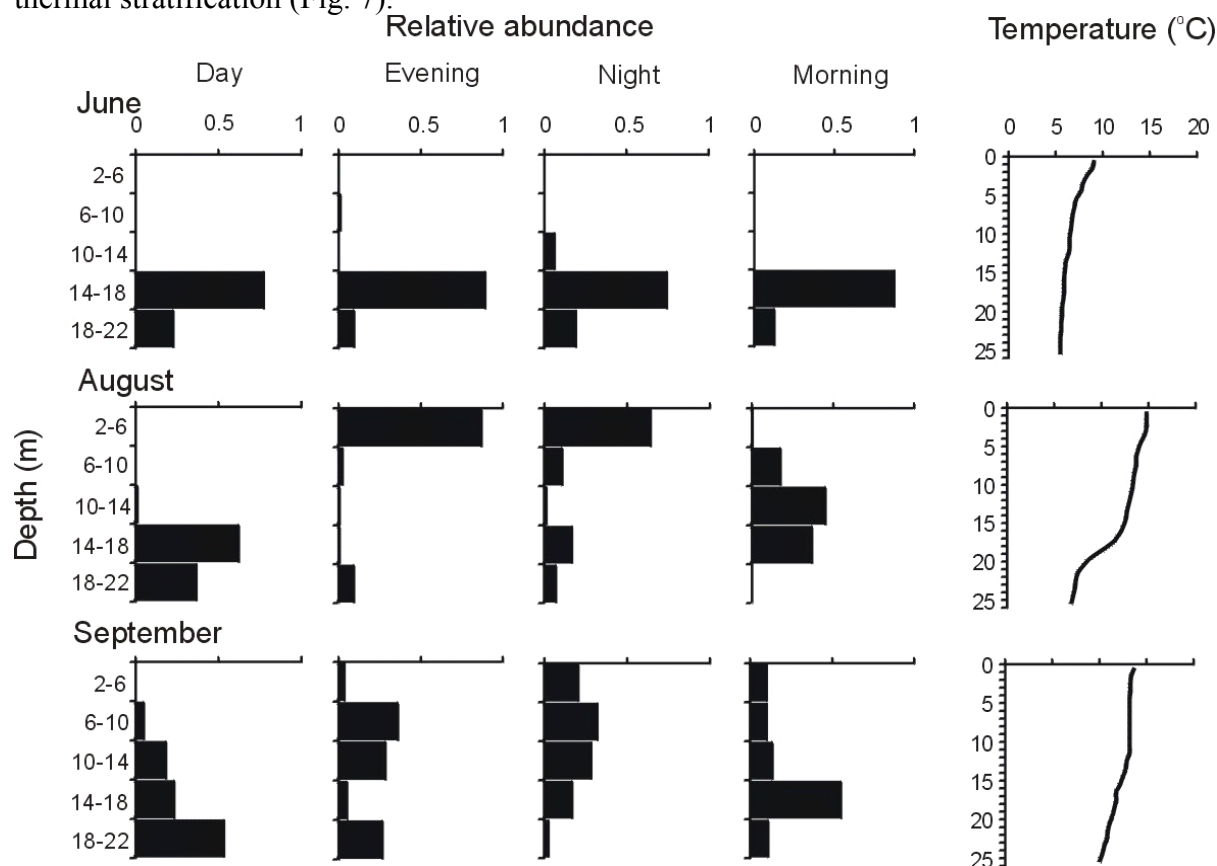


Fig. 7. Vertical distribution of whitefish (relative abundance) at different time of the day in June, August and September. In the right, the temperature profile in the water column in the study months.

In August, the period of broad daylight was still long, but a noticeable night existed at 23.00-03.00. Most of the whitefish used epibenthic habitats during the day. In addition, some shoals were observed above the bottom. At dusk, whitefish shoals partially dispersed and fish ascended to midwater and the surface. At night, relative fish density was highest at depths of 2-6 m (Fig. 7) and fish density in the pelagial was significantly higher ( $P < 0.05$ ) than during the day (III). As light intensity increased at dawn, whitefish descended towards the bottom. In August, the surface water temperature was  $14.8\text{ }^{\circ}\text{C}$  decreasing to  $6.8\text{ }^{\circ}\text{C}$  at depth of 25 m and a thermocline was observed at a depth of 18-20 m (Fig. 7).

In September, a distinct night existed, the darkest period being at 22.00-04.00. During the day, fish used mainly epibenthic habitats, but some fish shoals were detected in the vicinity of the bottom. In the evening, whitefish shoals dispersed and ascended to midwater and the surface. At night, relative fish density was highest at depths of 2-14 m (Fig. 7) and pelagic fish density was significantly higher ( $P < 0.05$ ) than during the day (III). In September, the

temperature was fairly homogenous throughout the water column: surface temperature was 13.7 °C decreasing to 10 °C at a depth of 25 m (Fig. 7).

The fishing and gillraker distribution data supported hydroacoustic data of whitefish vertical distribution (III). SSR and LSR were absent from the pelagic zone during the day and at night in all study periods (Fig. 8). CPUEs of LSR were high in the shallow (<10 m) epibenthic zone, whereas CPUEs of SSR were highest in the deep (>10 m) epibenthic zone (Fig. 8). In June, the pelagic fish density was low according to the echosounding, a conclusion that was also supported by extremely low CPUEs of pelagic trawl during the day and at night (Fig. 8). Only a few DR whitefish and brown trout were caught. Most of the whitefish dwelled close to the bottom, where all whitefish forms were caught both during the day and at night (Fig. 8). DR whitefish was the most numerous whitefish form in the gillnet catches both in the shallow and deep epibenthic zone.

In August, pelagic day CPUEs were low and only a few DR were caught. At night pelagic CPUE of DR was high (Fig. 8). The average length of DR in pelagic trawl catches was 11.1 cm (n=7134) and 99% of the catch consisted of DR <15 cm long. In September, the situation was close to that in August: pelagic day CPUEs were low and only DR were caught. At night, pelagic CPUE of DR was high, and a few brown trout were also caught. In September, the average length of DR in pelagic trawl catches was 12.8 cm (n=1404), and 95% of DR were <15 cm long.

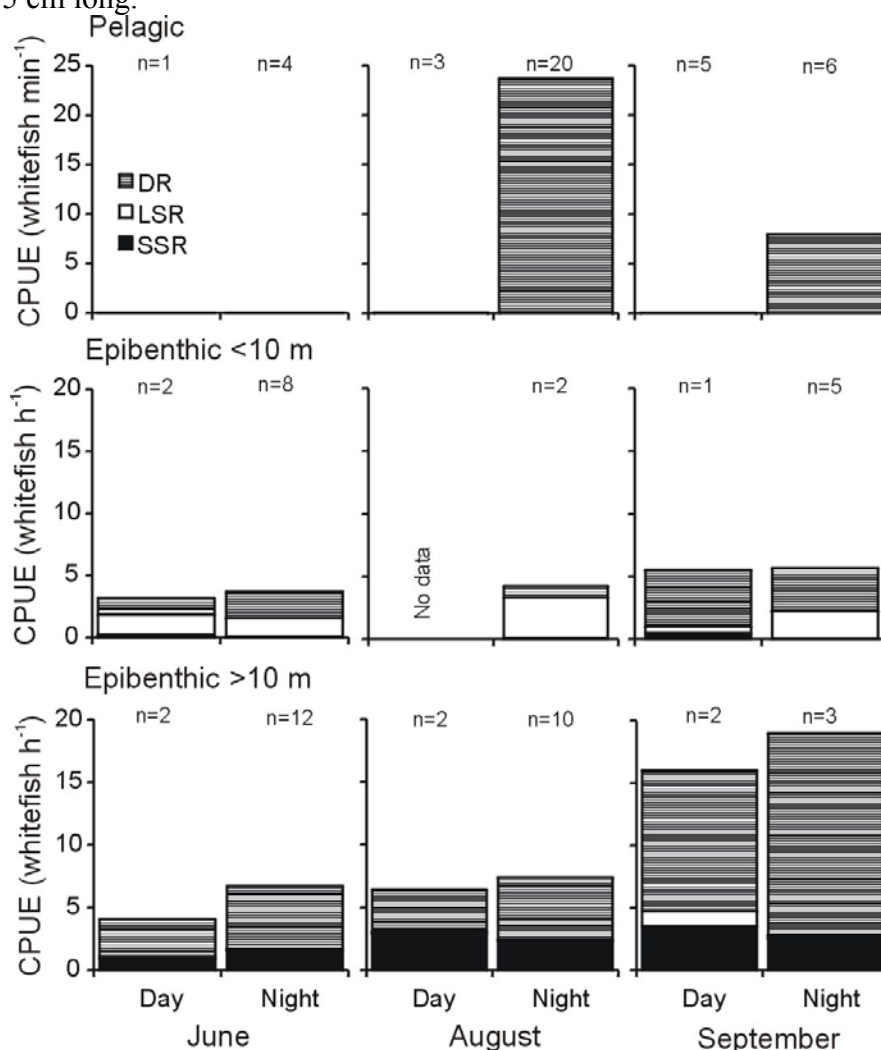


Fig. 8. Catch per unit of effort (CPUE) of SSR whitefish, LSR whitefish and DR whitefish calculated from pelagic trawl and epibenthic gillnet catches during the day and at night in June, August and September. Number of fishing occasions (n) during the day and at night is shown in each figure.

### 3.4 Diet of the whitefish forms

Whitefish forms differed in food selection during all study periods (I, II, III). Both LSR and SSR consumed mainly benthic macroinvertebrates both in different times of day and season, but in different habitats: LSR in shallow and SSR in deep epibenthic zone (Fig. 9)(I, II). In contrast to the SSR and LSR, DR stomachs contained mainly pelagic food items, such as zooplankton, adult insects and pupae (Fig. 9, I). Whitefish forms had distinct diet segregation during open water season. Diet-overlap index values were low ( $<0.60$ ) between whitefish forms (I). However, high ( $>0.60$ ) diet-overlap values were observed between different length groups of single whitefish form (II).

LSR used various benthic macroinvertebrates including Trichoptera, Ephemeroptera, *Sialis* sp., Chironomid larvae, *Valvata* sp., *Lymnea* sp. and also epibenthic *Eurycerus* sp. (Fig. 9, I, II). SSR consumed a narrower range of benthic macroinvertebrates such as Diptera (mainly Chironomid larvae) and *Pisidium* sp., but also Copepoda and *Eurycerus* sp. especially in September (Fig. 9, I, II). Both sparsely rakered whitefish forms used almost exclusively benthic food resources (LSR 83-100% and SSR 77-100% of stomach contents) in all diel and seasonal study periods. Similar preference towards benthic diet was observed also during summers 1998 and 1999 (I, II).

In contrast to SSR and LSR the diet of DR was dominated by pelagic food items. Benthic food items were consumed by DR only in June. The proportion of pelagic food items in the diet of DR during June was 20-85% depending on the length-group. The DR population consisted mainly of small-sized ( $<20$  cm) fish consuming mostly zooplankton, of which *Bosmina* sp. and Copepoda were dominant taxa (Fig. 9). The proportion of zooplankton in the diet decreased with increasing DR size and food selection shifted towards other pelagic food items, such as surface insects (including pupae and adults). During August and September, the proportion of pelagic food items in the diet of DR was 97-100%, except for one length group (day, 20.0-29.9 cm) in which pelagic food items comprised only 60% of the food composition. DR preferred pelagic food items also during 1999 (I).

Specialization towards benthic or pelagic food items was observed in the size of digested zooplankton. If sparsely rakered whitefish forms consumed zooplankton, usually only large sized zooplankton species were predated. In contrast, DR consumed frequently small sized zooplankton. The average zooplankton lengths in stomachs of SSR, LSR and DR were 1.69, 1.60 and 0.55 mm (I). The average zooplankton length in stomach differed between all whitefish forms (ANOVA,  $F_{2,1783}=2670.45$ ,  $P<0.0001$ ) being the highest in SSR and the lowest in DR stomach (Tukey's HSD tests,  $P<0.001$ ). Zooplankton length in whitefish stomach was significantly correlated with gillraker traits. Gillraker number range in correlation analysis was 15-39 including all whitefish forms (I). Zooplankton length was negatively correlated with gillraker number (Spearman correlation,  $r_s=-0.73$ ,  $P<0.001$ ,  $n=119$ ). Zooplankton length was positively correlated with gillraker space (Spearman correlation,  $r_s=0.81$ ,  $P<0.0001$ ,  $n=119$ ) and negatively correlated with gillraker length (I, Spearman correlation,  $r_s=-0.60$ ,  $P<0.0001$ ,  $n=119$ ).

### 3.5 Habitat use and diet of brown trout and Arctic charr

Arctic charr and brown trout were the most abundant salmonid piscivores consuming whitefish in Lake Muddusjärvi (IV). Habitats of brown trout and Arctic charr were partially segregated. Brown trout occupied pelagic areas, where brown trout CPUEs in June-September were considerably higher than those of Arctic charr.



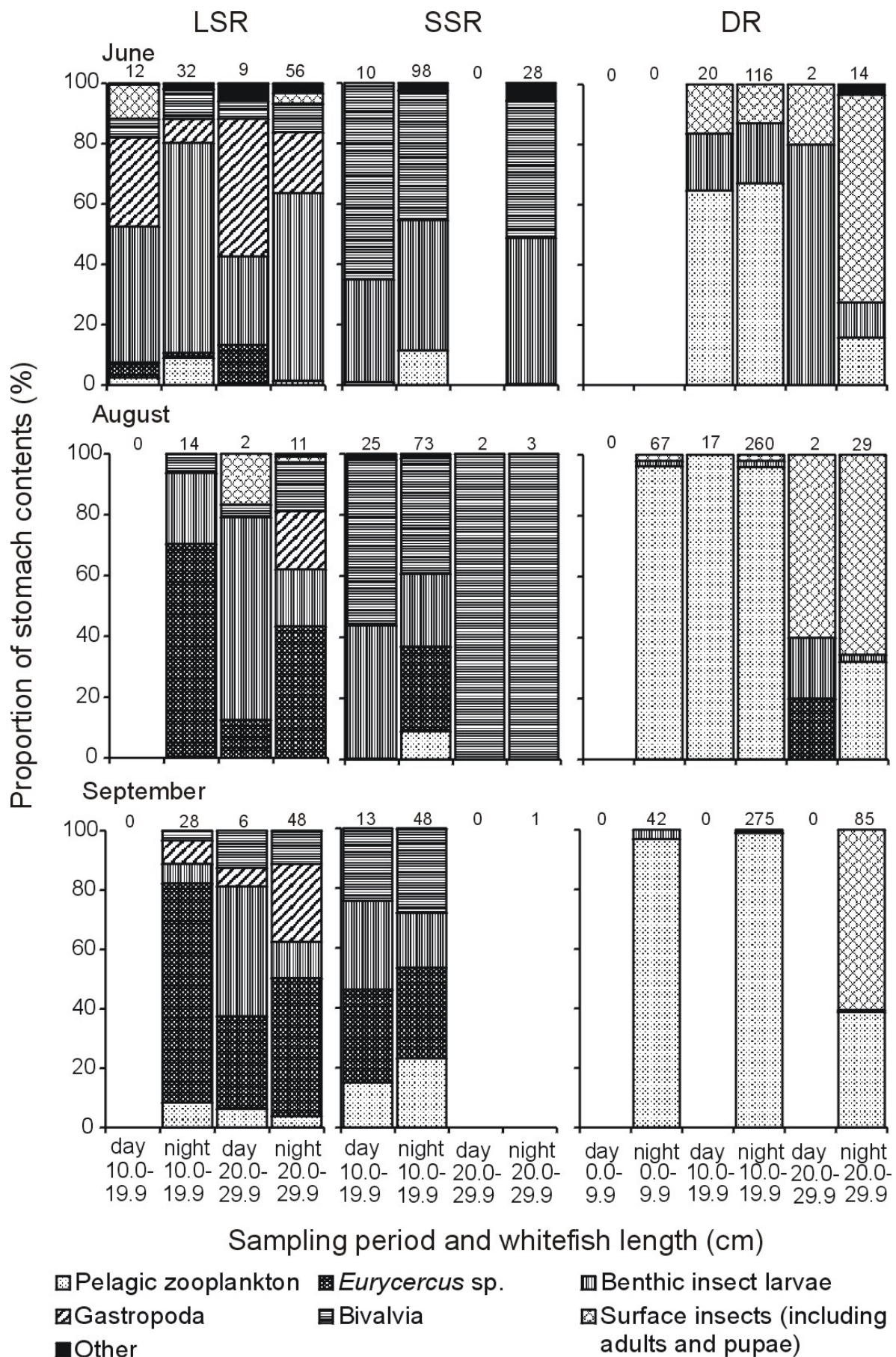


Fig. 9. Diet composition of large sparsely raked (LSR), small sparsely raked (SSR) and densely raked (DR) whitefish in Lake Muddusjärvi during the day and at night in study months. Number of studied stomachs is indicated above the bars.

In epibenthic (0-20 m) areas, both species were found and no clear habitat segregation was observed (Fig. 10). The influence of depth on predator (brown trout and Arctic charr) CPUEs in June-August was significant (IV). The most important factor in the ANOVA model was the interaction of depth and species, which had a significant influence on CPUEs in June-September (IV). CPUEs of brown trout in the pelagic 0-10 m were significantly higher than those of Arctic charr in June-September (Tukey's HSD test  $P < 0.05$ ). Only whitefish form using pelagic zone was DR, whereas LSR and SSR used only epibenthic depth zones (Fig. 10).

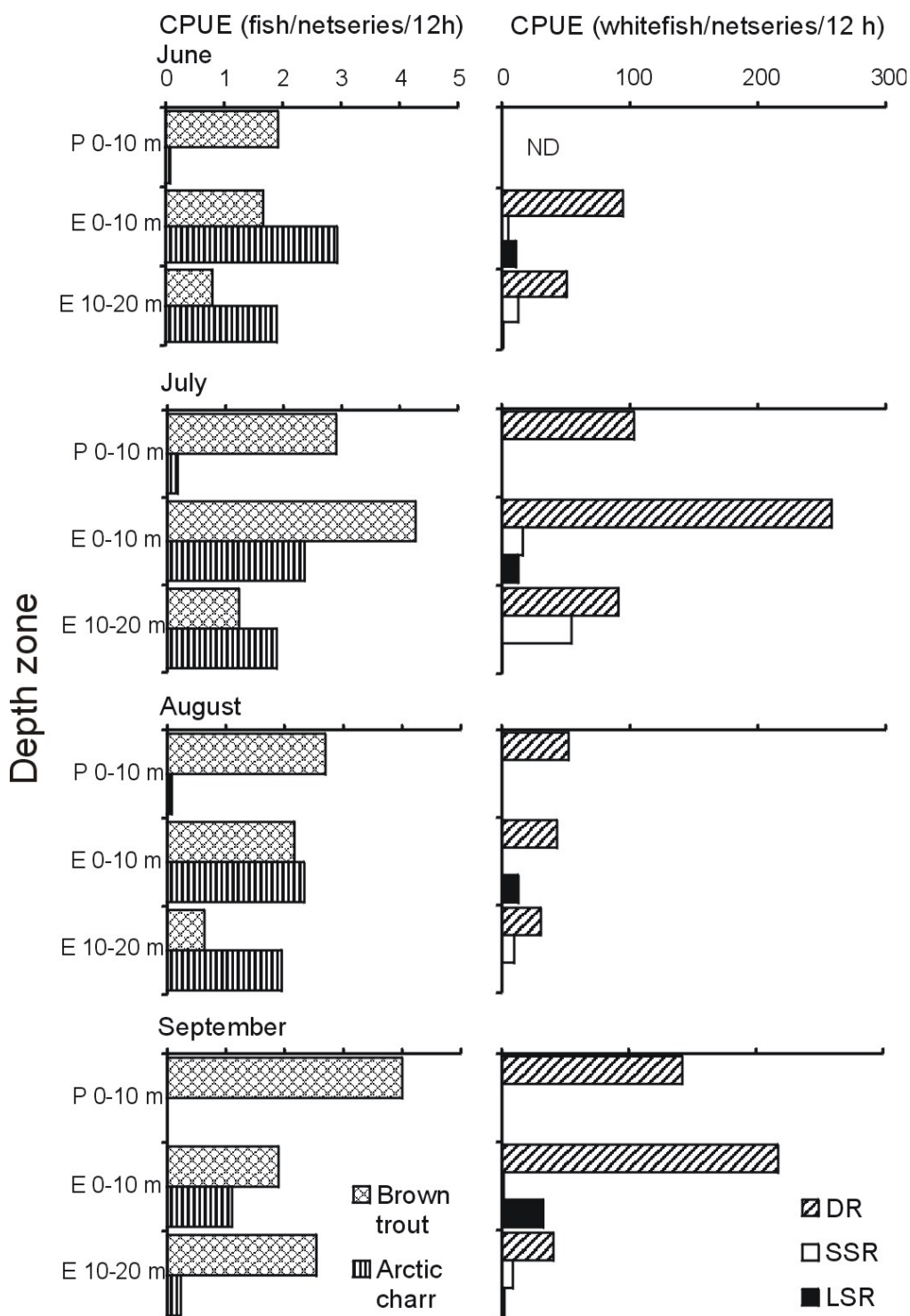


Fig. 10. In the left, CPUEs of brown trout and Arctic charr in different depth zones are given (P=pelagic, E=epibenthic). In the right, CPUEs of whitefish forms (DR=densely rakered, SSR=small sparsely rakered and LSR=large sparsely rakered whitefish) are given. ND means no data available.

Brown trout and Arctic charr >30 cm fed almost exclusively on whitefish (Fig. 11). Small-sized (<30 cm) individuals of both species consumed also invertebrates, especially in early summer. Towards autumn, all length groups of both species were piscivorous. Both species fed mainly on DR whitefish (Fig. 11). A minor proportion of identified whitefish was LSR, but SSR whitefish was not found in the stomachs of brown trout and Arctic charr (Fig. 11).

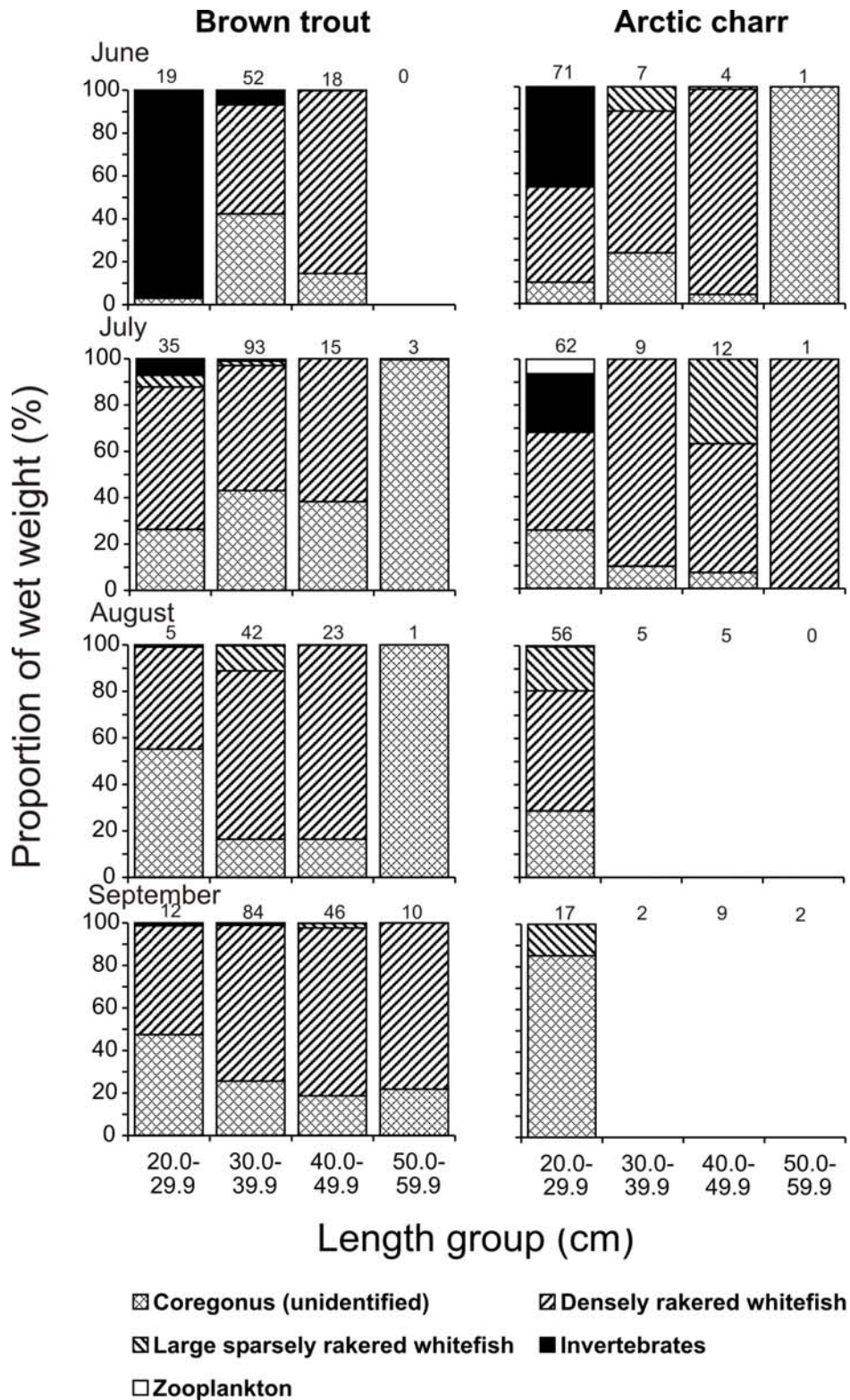


Fig. 11. Food composition of brown trout and Arctic charr in June-September 1999. Number of studied stomachs is shown above the bars.



### 3.6 Piscivory, prey selection, and habitat use of predator species

Whitefish was the most important prey for all predator species (V). All the piscivores fed mainly on the DR, which was also the most abundant whitefish form in prey gillnet catches (V). However, the relative abundance of prey species in gillnet catches and pike stomachs was different (Kolmogorov-Smirnov test,  $P < 0.05$ ). Pike had a wider range of species in the stomach than was observed in prey gillnet catches. For other predator species, the difference between the relative abundance of prey fish catch and predator diet was not significant ( $P > 0.05$ ). Relative abundances of prey species in pike and burbot stomachs were significantly different from those in brown trout or Arctic charr stomachs ( $P < 0.05$ ).

Whitefish was the dominant species in prey gillnet catches (94% of numerical catch). DR constituted 78% of the whitefish catch, while the proportions of LSR and SSR were 14% and 8% (V). The length distributions of whitefish in gillnet catches were distinct: DR and SSR were small-sized, whereas LSR attained a larger size (V). The average lengths of DR, SSR and LSR were 13.9 cm, 15.5 cm and 22.1 cm in gillnet catches, respectively (V). The average length between whitefish forms was different in the gillnet catches (ANOVA,  $F_{2,10699} = 5077.9$ ,  $P < 0.0001$ ), with all three whitefish forms also differing significantly (Tukey's HSD tests,  $P < 0.05$ ).

The habitats of the whitefish forms were partly segregated; DR was caught in all available epibenthic and pelagic habitats, whereas LSR and SSR were collected mainly in epibenthic habitats (Figs. 6, 8 and 12). The depth $\times$ form interaction was an important source of variation in the ANOVA model ( $F_{4,348} = 50.6$ ,  $P < 0.0001$ ). The CPUEs of DR were higher than those of LSR and SSR in the pelagic zone (Tukey's HSD test  $P < 0.05$ , Fig. 12). The CPUE of DR was higher than that of SSR in the shallower epibenthic zone (0-10 m) and higher than that of LSR in the deeper epibenthic zone (10-20 m) ( $P < 0.05$ ). The habitats of LSR and SSR were segregated in epibenthic habitats: the CPUE of LSR was significantly higher than of SSR in the epibenthic 0-10 m zone ( $P < 0.05$ ), whereas the CPUE of SSR in the epibenthic 10-20 m depth zone was higher than of LSR ( $P < 0.05$ ).

In the ANOVA model, predator CPUEs were significantly influenced by species ( $F_{3,1112} = 167.5$ ,  $P < 0.0001$ ), depth ( $F_{2,1112} = 24.8$ ,  $P < 0.0001$ ) and depth $\times$ species interaction ( $F_{6,1112} = 23.9$ ,  $P < 0.0001$ ). CPUEs of brown trout were higher than of other species (Tukey's HSD test,  $P < 0.05$ ) and CPUEs of Arctic charr were higher than of burbot or pike ( $P < 0.05$ ). Predator CPUEs were highest in the 0-10 m epibenthic and lowest in the 0-10 m pelagic zone ( $P < 0.05$ ). All predator species used both epibenthic and pelagic habitats, but their CPUEs differed (Fig. 12). CPUE of brown trout in the pelagic were higher than those of other species ( $P < 0.05$ ). Brown trout and Arctic charr CPUEs were higher than those of pike or burbot in both epibenthic zones ( $P < 0.05$ ). CPUE of Arctic charr was higher than that of brown trout in the deep epibenthic zone (10-20 m), and lower than that of brown trout in the shallow (0-10 m) epibenthic zone ( $P < 0.05$ ). Pike and burbot were caught mainly in epibenthic habitats, but their CPUEs were not significantly different in any of the depth zones ( $P = ns$ ).

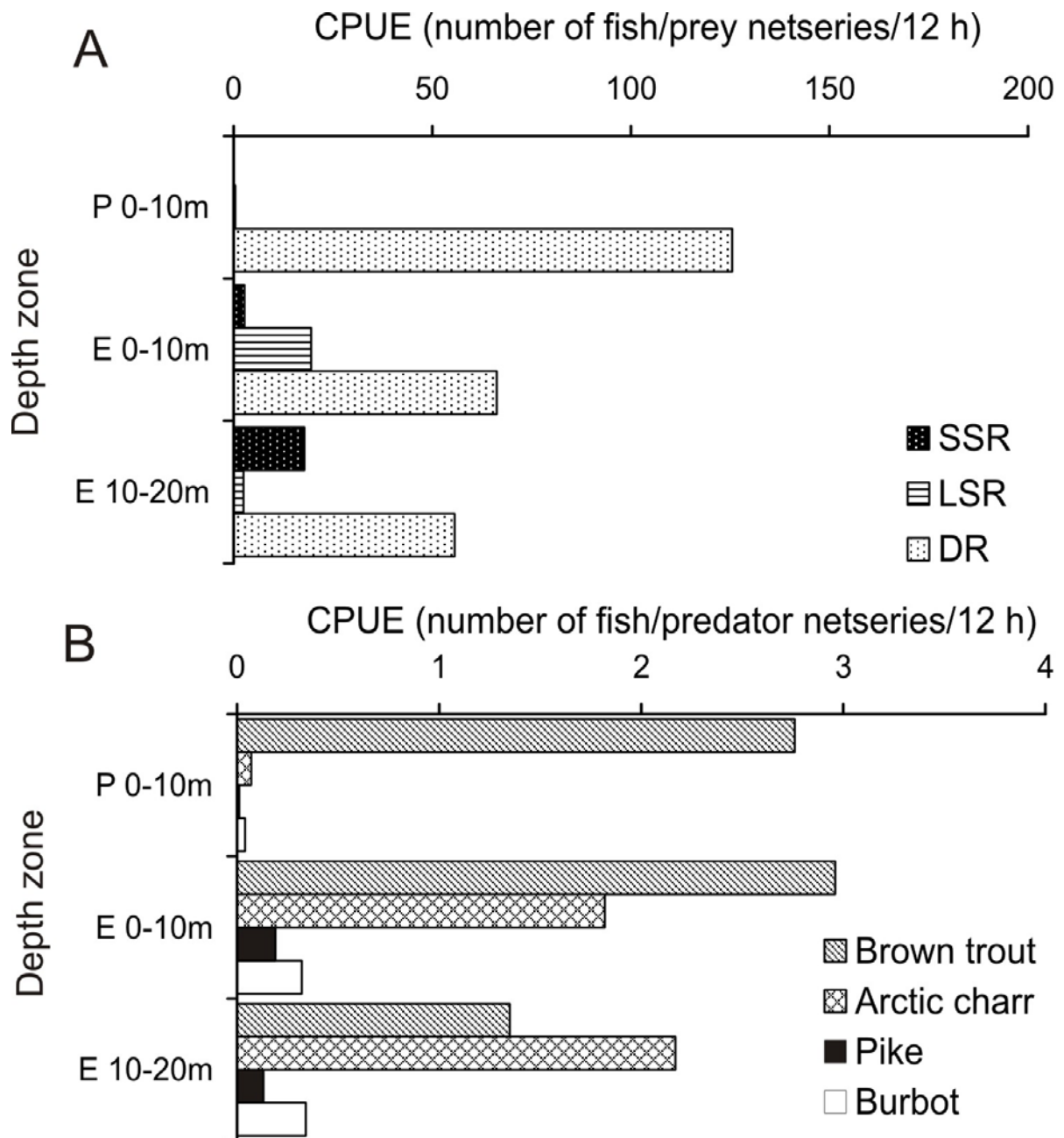


Fig. 12. A) CPUE of whitefish forms (SSR=small sparsely rakered, LSR=large sparsely rakered, and DR=densely rakered whitefish) in the epibenthic (E) and pelagic (P) habitats. B) CPUE of predators in the epibenthic and pelagic habitats.

The probability of predator species preying on fish increased in concert with the predator length ( $V$ ). Pike had the lowest length (19.3 cm), at which the probability to prey on fish was 50%. However, only three pike had preyed on invertebrates. Burbot, Arctic charr and brown trout fed frequently on invertebrates, except for the largest individuals. Burbot, Arctic charr and brown trout shifted to piscivory at lengths of 22.1 cm, 25.7 cm and 26.4 cm, respectively. Pike and burbot preyed upon a wider length range of prey than other species (Fig. 13). Statistically significant positive regression slopes were observed between predator and prey length for all species ( $P < 0.001$ ). After the shift to piscivory, the average prey length of Arctic charr increased fastest (Fig. 13).

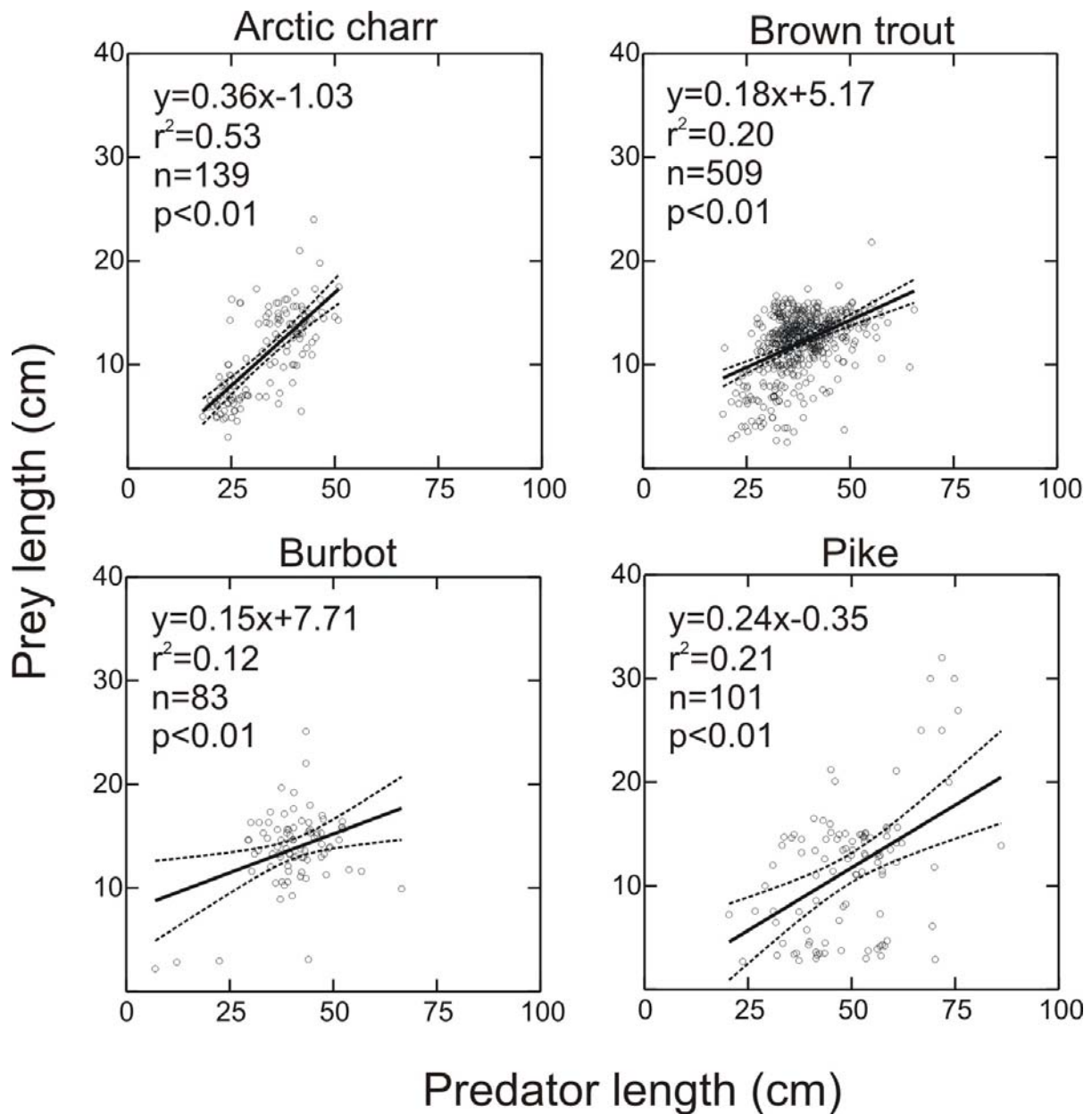


Fig. 13. Predator and prey length of piscivorous species in lake Muddusjärvi presented with linear regression lines and their 95% confidence intervals. Regression equations, coefficients of determination ( $r^2$ ), risk levels ( $p$ ) and number of samples ( $n$ ) are shown in each figure.

### 3.7 Growth of whitefish forms and vulnerability to predation

Growth of the three sympatric whitefish forms was different (Fig. 14). LSR was the fastest growing and SSR the slowest growing form, growth of DR settling between the two preceding forms. Whitefish forms differed in back-calculated growth (ANOVA,  $P<0.05$ ), and the length-at-age between forms was different from age 1 onwards (Tukey's HSD tests,  $P<0.05$ ). The length range of whitefish prey in brown trout stomachs was 2.9-20.0 cm, in Arctic charr 3.0-24.0 cm, in burbot 6.6-25.1 cm and in pike 5.9-32.0 cm. According to the whitefish growth curves, the vulnerability to predation between whitefish forms differed distinctly (Fig. 14). All whitefish forms were vulnerable to pike predation during the first ten years of life. LSR attained a refuge size for burbot, Arctic charr and brown trout predation at the age of 5-7, whereas slow growing SSR was vulnerable to predation by all piscivorous

species during the first 10 years of life (Fig. 14). The most frequently predated whitefish form, DR, reached a refuge size from predation by brown trout and Arctic charr at the age of 7 and 10 years (Fig. 14). However, pike and burbot were able to consume DR for at least the first ten years of life.

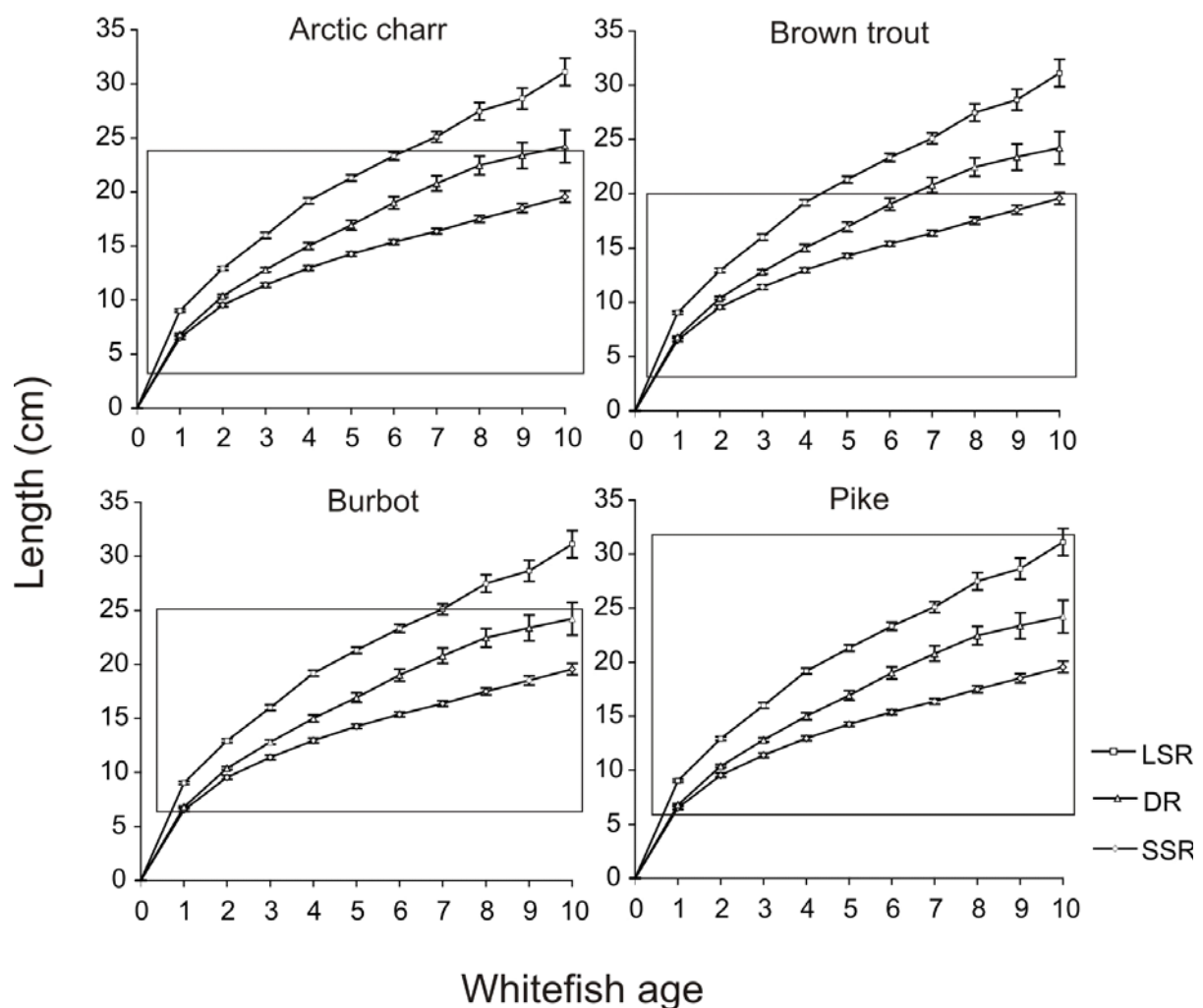


Fig. 14. The average back-calculated length-at-age of three whitefish forms with 95% confidence intervals (LSR= large sparsely rakered, DR=densely rakered, and SSR=small sparsely rakered whitefish). Rectangles indicate vulnerable age groups of whitefish forms to predation by different predator species.

## 4. Discussion

### 4.1 Resource polymorphism in postglacial lakes

Lake Muddusjärvi is inhabited by three morphometrically distinct whitefish forms, which show clear niche segregation (I-III). Two whitefish forms are specialized to the littoral and the profundal habitat and one whitefish form to the pelagic habitat (II, III). Specialization to benthic or pelagic niches is typical also for other polymorphic fish populations. Polymorphic Arctic charr, three-spined stickleback and lake whitefish in postglacial lakes are among the most studied cases of specialization to pelagic and benthic resources (Bodaly 1979, Malmquist *et al.* 1992, Schluter & McPhail 1992, Rogers *et al.* 2002). Arctic charr in Lake Thingvallavatn, Iceland, exists in four morphs of which two are benthivorous, one planktivorous and one piscivorous (Malmquist *et al.* 1992). Interspecific competition is low

in Lake Thingvallavatn, as only sparse populations of brown trout and three-spined stickleback exist in the lake (Malmquist 1992, Skúlason *et al.* 1999). Polymorphic three-spined sticklebacks are found in British Columbian lakes, where cutthroat trout *Oncorhynchus clarki* (Richardson) is the only other species found in these lakes (Schluter & McPhail 1992). Interspecific competition between cutthroat trout and three-spined sticklebacks is not likely, as cutthroat trout is the predator species feeding on sticklebacks (Vamosi 2002, Rundle *et al.* 2003). In northern America, normal and dwarf forms of lake whitefish co-occur in some of the postglacial lakes, but the planktivorous dwarf form is absent if strong zooplankton competitors, ciscoes (*Coregonus artedii* complex), are present (Bodaly 1979, Lindsey 1981, Bernatchez *et al.* 1999).

There are few possible reasons for polymorphism of whitefish in Lake Muddusjärvi. The absence of strong interspecific competitors, such as vendace *Coregonus albula* (L.) (Svårdson 1976, Bøhn & Amundsen 2001), and presumably also cyprinids and ruffe *Gymnocephalus cernuus* (L.), may promote the divergence of whitefish population via higher niche availability. This refers the possibility that divergence of sympatric morphs could be intralacustrine and may have arisen via ecological opportunity *i.e.* high availability of open niches (Skúlason & Smith 1995, Schluter 2000b). Whitefish is an abundant species in lakes of this region (Sarjamo *et al.* 1989), and it presumably has dominance over other sympatric species, such as perch and salmonids. Furthermore, predation by piscivorous salmonids may intensify divergent selection and trophic specialization of sympatric forms, indicated in three-spined stickleback studies (Vamosi 2002, Rundle *et al.* 2003). In Lake Muddusjärvi, brown trout and Arctic charr are the main salmonid predators of whitefish forms feeding them at different intensities (III-V). Risk of predation is especially high for the pelagic DR (III, IV). Thus, it has to be a highly specialized planktivore to attain the size of sexual maturity. Lower survival of limnetic morph compared to benthic morph in presence of predators, is documented for three-spined stickleback (Vamosi & Schluter 2002). High specialization is probably needed for SSR, as well. Predation risk is most plausibly lowest in the profundal (V), but SSR has to be a specialized benthic feeder as the profundal is a poorly illuminated habitat where food resources are scarce (II). The littoral habitat offers abundant benthic food resources for LSR, but attains also high predator densities (II, V). Despite of high predator abundance, LSR attains the fastest growth of the sympatric forms, reaching refuge size from predation the earlier than other forms (V).

The highest number of sympatric whitefish forms is apparently found in deep and morphometrically complex lakes (Svårdson 1979). Lake Muddusjärvi is a large and deep lake, offering a vast number of both pelagic and epibenthic areas for whitefish. Because of this complexity, benthic forms have an opportunity to use separate habitats: LSR uses littoral (<10 m) habitat, SSR dwells at deeper (>10 m) profundal habitat and DR utilizes both pelagic and epibenthic habitats (II-III). Most of the lakes in this region are inhabited by only one allopatric form, with gillraker distributions close to LSR (Sarjamo *et al.* 1989, Lehtonen & Niemelä 1998, Amundsen *et al.* 2004b). Interestingly, the allopatric populations of either SSR or DR have not been documented. This is similar to lakes in the northern America, where the normal form of the lake whitefish is rather common in lakes, but the dwarf morph is not present without the normal form (Bodaly 1979, Lindsey 1981, Pigeon *et al.* 1997). In large northern Scandinavian lakes, where the distinct pelagic niche is available the sympatry of LSR and DR is rather common, whereas SSR seems exist with LSR and DR only in the large and deep lakes (Toivonen 1960, Amundsen 1988, Sarjamo *et al.* 1989, Kahilainen & Lehtonen 2002b, Amundsen *et al.* 2004b).



## 4.2 Morphological divergence of whitefish forms

The morphometric and meristic results of this study indicated that the whitefish population of Lake Muddusjärvi can be divided into three forms. Gillraker distribution was distinctly trimodal indicating SSR, LSR and DR. Furthermore, regression analysis shown, that gillraker number did not change considerably with increasing whitefish length. These results suggest that number of gillrakers stabilize at early age, most plausibly at the age of 0+ and at the length of <10 cm as suggested in earlier studies (Lindström 1962, 1989). Thus, it is unlikely that whitefish belongs to one form at early age and size and to another at later age and size. Also other morphological differences between Lake Muddusjärvi whitefish forms were distinct as detection with DFA could be made with an accuracy of 99.2% (I). This is an exceptionally high detectability compared to a closely related species; lake whitefish (Chouinard *et al.* 1996, Bernatchez *et al.* 1999). Distinct morphological differentiation was plausibly a consequence of a high trophic specialization of the whitefish forms in Lake Muddusjärvi. This was indicated in morphometric DFA, where all entered traits were related to feeding specialization.

Morphological differences related to trophic specialization should be pronounced if morphs continuously prefer particular food and habitat resource (McPhail 1984, 1992, Snorrason *et al.* 1994, Skúlason *et al.* 1999). The most pronounced differences between the whitefish forms of Lake Muddusjärvi were observed in gillraker, head and pectoral fin traits, which are related to food selection and efficiency of resource use (Svärdson 1979, Janssen 1980, Webb 1984). In addition, the mouth position correlates with feeding and gillrakers: the pelagic form has pointed snout and mouth opens forward, whereas the mouth of the benthic forms open downwards. In polymorphic postglacial fish populations, the pelagic form has more gillrakers, which are longer and densely spaced (Schluter & McPhail 1993). Gillraker number and length were highest for the pelagic form DR, decreasing towards the littoral LSR and being lowest for the profundal dwelling SSR. This was in accordance with the food selection of these forms, of which DR was the only form frequently using small-sized zooplankton, whereas the two sparsely rakered forms exclusively consumed benthic macroinvertebrates (I-III). This segregation is stable, because no changes were found in food and habitat selection patterns of whitefish forms between consecutive years (Kahilainen & Lehtonen 2002b, Lehtonen & Kahilainen 2002, II- IV).

The other morphological traits observed for pelagic forms are slender body form and smaller size (Malmquist 1992, McPhail 1993, Bernatchez *et al.* 1999). In univariate analysis of morphometric data, body depth was highest for the profundal SSR and lower for LSR and DR in Lake Muddusjärvi (I). DR consumes mainly pelagic food items (zooplankton, surface insects and insect pupae), which requires a continuous swimming effort. Slender body form most plausibly minimizes energy demand for searching and handling of energetically poor prey, such as zooplankton. In aquarium, DR feeds on zooplankton swimming slowly and attacking at short distances (Kahilainen K., personal observation).

Profundal dwelling SSR has the highest body depth, the longest pectoral fins and the largest diameter of eye (I). These traits could be related to feeding in deep and poorly illuminated profundal areas, where good maneuvering abilities with large pectoral fins and presumably higher visual abilities with large eyes are advantageous (Webb 1984, Schliewen *et al.* 2001). In aquarium, benthic feeding tactic of SSR is distinct: it uses large pectoral fins for quick turns and takes considerable amounts of benthos at each strike (Kahilainen K., personal observation). The other benthic form, LSR, has shorter and smaller pectoral fins and it has lower maneuvering abilities than SSR. Also, attack tactics differ as LSR uses more visual feeding than SSR, which is possible in well-illuminated littoral habitats. In aquarium, LSR

takes eyesight to benthic prey and determinedly attacks it without taking a large amount of benthos simultaneously (Kahilainen K., personal observation).

The role of the gillrakers is important in zooplankton retention and fish species with large number and long gillrakers are efficient planktivores (Janssen 1980, Gibson 1988). It has been suggested that gillrakers are mechanical sieves retaining zooplankton larger than the interraker spacing (Drenner *et al.* 1984). Despite of this, smaller-sized zooplankton than the gillraker space is frequently found in stomachs of planktivorous whitefish (Seghers 1975, Langeland & Nøst 1995) as was observed in Lake Muddusjärvi as well (I). Sanderson *et al.* (1991) found that gillrakers of blackfish, *Orthodon microlepidotus* (Ayres) forms a barrier to waterflow guiding it to mucus covered roof of oral cavity and there after retention of zooplankton. This has not been performed with whitefish, and the role of gillrakers is therefore still unclear. However, the increase in gillraker number and length of the morphs specialized to planktivory has been documented for many species (Bodaly 1979, McPhail 1984, Malmquist 1992, Schluter & McPhail 1992, Snorrason *et al.* 1994) suggesting that gillrakers have importance in zooplankton retention efficiency, even though they may not be mechanical sieves that retain zooplankton.

Long and densely spaced gillrakers of DR may improve the efficiency of sieving or directing the water current. The gillrakers of DR are flexible and have numerous secondary teeth along the gillraker. Interestingly, this is valid only for the pelagic form, because gillrakers of sparsely rakered whitefish forms are unbending and have less secondary teeth along gillraker. Trophic specialization of whitefish forms was observed in their selection of pelagic zooplankton. Two sparsely rakered whitefish forms only seldom consumed pelagic zooplankton, whereas DR used exclusively small-sized pelagic zooplankton (I). DR was the most specialized planktivore and was able to consume frequently the smallest zooplankton specimens (I). The gillraker structure of sparsely rakered forms is rational, because these forms use mainly benthic food, which is partly buried in sand, gravel or mud. After a strike, benthos is removed between gillarches and gillrakers and the food items are retained (Kahilainen K., personal observation). Benthic material (sand or mud) is probably more easily removed via less numerous and inflexible than through long, densely spaced and flexible gillrakers. The profundal benthivore SSR dwells in the lowest light intensities and it takes high amount of benthic material as bycatch (Kahilainen, K. personal observation). This feeding tactic most plausibly requires especially low number of gillrakers. On the contrary, littoral benthivore LSR uses well-aimed attacks taking only minor amounts of benthic material and has higher number of gillrakers.

#### **4.3 Niche segregation between whitefish forms**

In Lake Muddusjärvi, sympatric whitefish forms showed distinct habitat segregation. The habitat selection of a fish species is influenced by many interacting factors. Water temperature and light are usually important abiotic factors, while predation and food distribution are prominent biotic factors influencing the habitat selection of fish (Clark & Levy 1988, Werner & Hall 1988, Becker & Eckmann 1992, Beauchamp *et al.* 1999). In Lake Muddusjärvi, observed water temperatures were suitable for whitefish in the whole water column and should not restrict habitat selection. Preferred temperature range for whitefish is between 8-15 °C (Alabaster & Lloyd 1980). Diel vertical migrations of fish and zooplankton are induced by changes of light intensity during dusk and dawn (Lampert 1989, Appenzeller & Leggett 1995, Beauchamp *et al.* 1999). In Lake Muddusjärvi, diel migration of whitefish started as continuous daylight ceased, but only densely rakered and planktivorous DR showed a clear diel cycle ascending to pelagial at dusk (III).

Observed pattern of migrations by DR (III) supports earlier suggestions that vertical migration of planktivorous whitefish with densely spaced gillrakers intensifies towards autumn (Skurdal *et al.* 1985, Hammar 1988). Most of the migrating DR consisted of small-sized (<15 cm) fish, which fed almost exclusively on zooplankton and grew slowly (Kahilainen & Lehtonen 2002b, Lehtonen & Kahilainen 2002). The lack of vertical migration in June was presumably related to the continuously high light intensity and low zooplankton densities. The density of pelagic zooplankton (Copepoda, Cladocera) in June 1998 was <4 ind l<sup>-1</sup> increasing to 12 ind l<sup>-1</sup> in August (Kahilainen *et al.* unpublished). As zooplankton density increased in concert with temperature towards autumn, DR shifted to partly pelagic habitat use. In the Norwegian Lake Mjøsa, a part of the whitefish population shifted from epibenthic to pelagic feeding areas during the summer (Næsje *et al.* 1991). This habitat switch of large-sized (length 25-35 cm) whitefish occurred when the abundance of pelagic zooplankton increased. Whitefish remained in the pelagic zone until zooplankton abundance decreased in autumn (Næsje *et al.* 1991). In Lake Muddusjärvi, DR shifted to use the pelagic area as zooplankton density increased, but used this habitat only at the lowest light intensities during the night (III).

When two or more closely related species, in this case whitefish forms, with a preference for a similar niche occur sympatrically, they may avoid competition by segregating in food, habitat or time (Ross 1986). In Lake Muddusjärvi, habitats of the whitefish forms were segregated: LSR used mainly depths <10 m, SSR depths >10 m and DR dwelled both epibenthic and pelagic habitats (II, III). An ontogenetic habitat shift was not observed for sympatric whitefish forms in Lake Muddusjärvi (II, III, Kahilainen *et al.*, unpublished) in contrast to Lake Mjøsa, where habitat shift led to food segregation between different size-classes of monomorphic whitefish (Sandlund *et al.* 1992). This suggests that in lakes with polymorphic whitefish, habitat resources are strictly divided and thus possibilities to ontogenetic habitat shifts may be limited. Furthermore, habitat choice of whitefish forms may also have genetic basis indicated in the study on dwarf and normal lake whitefish ecotypes (Rogers *et al.* 2002). Hybrids of the lake whitefish were intermediate of their parents in habitat use (Rogers *et al.* 2002). If this is valid for whitefish too, hybrids should fall between parent niches, reducing their fitness in nature as indicated with three-spined stickleback morphs (Vamosi *et al.* 2000).

In Lake Muddusjärvi, both LSR and SSR fed mainly on benthic macroinvertebrates and semibenthic zooplankton (*Eurycercus* sp.) (II). In Lake Muddusjärvi, the diversity of benthic macroinvertebrates was highest in the littoral zone where also large insect larvae as well as *Lymnaea* sp. and *Valvata* sp. were present. Practically the only available benthic food resources for whitefish in the profundal were small-sized *Pisidium* sp. and Diptera, other benthic macroinvertebrate species being absent or scarce. This was reflected in ontogenetic food shifts of whitefish forms in Lake Muddusjärvi: LSR was able to shift to larger food items as fish length increased, whereas all length groups of SSR used small-sized food items. Shift to larger food items is presumably important for both forms, because neither of them changed habitat as length increased. Thus, the higher growth rate of LSR was probably due to higher availability of food resources in the littoral and consumption of energetically more rewarding food items. In addition, light intensity is lower in the profundal than in the littoral habitats and thus feeding efficiency of SSR may be reduced.

In absence of strong interspecific competitors, whitefish forms have shared available food and habitat resources in Lake Muddusjärvi. Food competition between whitefish forms is unlikely to be present anymore, because of their distinct habitat and food segregation (Kahilainen & Lehtonen 2002b, II, III). Diet-overlap index in June-September between

whitefish forms was always  $<0.60$ , which has been considered as a limit for biological significance (Wallace 1981). Similarly to our field observation, strength of resource competition between sympatric morphs of three-spined stickleback decreases as divergence proceeds (Pritchard & Schluter 2001). If both genetic and ecological mechanisms strengthen habitat segregation between sympatric morphs (Schluter 1993, 1995, Rogers *et al.* 2002), intraform diet-overlap presumably has strong influence on the growth of whitefish forms (II, Kahilainen *et al.* unpublished). In Lake Muddusjärvi, intraform diet-overlap plausibly decreases especially the growth of SSR, since ontogenetic habitat shifts are absent and scarce food resources in profundal limits the possibility for ontogenetic food shifts (II). High intraform diet-overlap values ( $>0.60$ ) were more frequently observed for SSR than LSR. For DR, intraform diet-overlap between age groups is high during summer (Kahilainen *et al.* unpublished) suggesting negative effect on growth. Taken collectively, in Lake Muddusjärvi, intraform diet-overlap is higher than interform diet-overlap.

#### 4.4 Prey selection of predators and predation impacts on whitefish forms

Lake Muddusjärvi is inhabited by several potential predator species influencing to prey communities (V). Generally, postglacial lakes with sympatric morphs are species poor ecosystems and number of predator species is low (Malmquist 1992, Schluter & McPhail 1992, McPhail 1993). For predator species, the relative abundance of prey species is an important factor determining prey selection (Diana 1979, Mann 1982, Vøllestad *et al.* 1986, Hughes 1997). Predation is often directed towards the most abundant and available prey species (Garman & Nielsen 1982, Amundsen 1994, Næsje *et al.* 1998, Bøhn *et al.* 2002). In Lake Muddusjärvi, all predator species preyed on whitefish, which was the most abundant prey species. However, the relative abundance of the whitefish forms differed in predator stomachs. DR was the most numerous whitefish form in the lake and in the stomachs of predators. High predation pressure most plausibly influences to life history of DR: most specimens reach sexual maturity early, in length of 12 cm and age of 3 years (Lehtonen & Kahilainen 2002, Kahilainen *et al.* unpublished).

According to the gillnet catches, brown trout and Arctic charr were the most abundant predators in Lake Muddusjärvi. DR was the main prey for these salmonids (IV), but despite their similar food selection, their habitats were partly segregated. The most pronounced difference between the habitat uses of the predators was in the pelagic zone, which only brown trout occupied frequently. In the pelagial, habitat overlap between predator and prey was strongest for brown trout and DR. Habitat selection of fish is considered to be a trade-off between costs and benefits of different habitats (Lima & Dill 1990). Diel migration of prey species is often a consequence of changes in risk of predation and food availability between different habitats (Clark & Levy 1988). Prey species could avoid the high risk of predation in pelagic areas by utilizing them only at night, when the foraging ability of visual predators is lowered (Beauchamp *et al.* 1999). The pelagial has been considered to be an area of high predation risk, because of the lack of refuges (Werner *et al.* 1983, L'-Abée-Lund *et al.* 1993). In Lake Muddusjärvi, diel vertical migration of DR is probably a consequence of the high predation risk in the pelagic induced by brown trout, which use the pelagic habitats in June-September (IV). Brown trout consume almost exclusively DR, which does not reach refuge size until the length of  $>20$  cm (V). The migrating DR population was mainly comprised of vulnerable-sized ( $<15$  cm) fish. Brown trout is a visual predator, but feeding efficiency of prey fish at different light intensities is currently unknown. Vogel & Beauchamp (1999) studied reactive distance of piscivorous lake trout, *Salvelinus namaycush* (Walbaum) to salmonid prey (5.5-13.9 cm) at different light intensities. In clear water, reactive distance of lake trout was 100 cm at light level of 17.8 lux decreasing to 25 cm at light level of 0.17 lux.

Assuming a similar trend of reactive distances as for lake trout, the feeding efficiency of brown trout should be dramatically reduced at night lowering the predation risk of DR.

Sparsely rakered forms did not use pelagic zone and dwelled benthic habitats all times of day and season (III). Epibenthic habitats offer refuge areas for LSR and SSR, which at least partly explain their minor importance in the diet of predators (V). Predator species dwelling in the epibenthic habitats used sparsely rakered whitefish as a prey, but life histories of LSR and SSR suggest that their importance is low in the diet of piscivores. LSR reach sexual maturity at large size and rather high age: length of *circa* 23 cm and at age 6-7 years (II). LSR forages in profitable littoral areas and may also reach size refuge from predation (II, V). Burbot and pike used epibenthic habitats, but the pelagic zone was practically avoided. This is understandable, as these specialist predators are not able to chase prey continuously, but need ambush sites found in epibenthic areas (Hart 1997, Pääkkönen 2000). Pike stomach contents supported the expectation of littoral habitat use, because pike preyed also upon LSR (V). Burbot was caught in both littoral and profundal areas, although burbot should prefer profundal habitat in summer due to its preference for low temperatures (Vøllestad 1992, Lehtonen 1998). Burbot is less dependent on light in chasing prey (Lehtonen 1998), and thus might use deeper profundal feeding habitats than observed in this study (Guthruf *et al.* 1990). According to the stomach contents, burbot was the only predator frequently consuming SSR. However, SSR may not confront high predation induced mortality, as this form commonly reach age of >15 years and the maximum observed age was 30 years (Kahilainen & Lehtonen 2002b). In addition, the age and length of SSR for sexual maturity was *circa* 6-7 years and 15 cm suggesting low predation pressure in the profundal (II). The aquarium experiments suggest that also predation avoidance behaviour of SSR may be the most efficient of the sympatric forms, as SSR is able to use its large fins for quick escape movements (Kahilainen, K., personal observation).

The vulnerability of whitefish forms to predation was different (V). Prey consumption by predators is limited by their gape size (Damsgård 1995, Mittelbach & Persson 1998). Prey fish species reach a refuge size; at the length at which predators are not able to swallow them due to the gape size limitations (Nilsson & Brönmark 2000). In Lake Muddusjärvi, the smallest whitefish eaten by predators was approximately 3 cm, and the largest one 32 cm (V). Slow growth rate of prey species induces a higher probability of death because of the longer period of time spent vulnerable to predation (Werner *et al.* 1983). Slow growing SSR was vulnerable to predation by all predator species during the first ten years of life, whereas LSR was able to reach refuge size from brown trout, Arctic charr and burbot predation. Despite of the differences in the growth of whitefish forms, predator species consumed mainly DR.

## 5. Conclusions

Three sympatric whitefish forms of Lake Muddusjärvi were morphologically divergent indicated especially in traits related to feeding. High morphological divergence was supported by distinct niche segregation of sympatric whitefish forms. Pelagic dwelling densely rakered whitefish (DR) was planktivorous, whereas littoral large sparsely rakered whitefish (LSR) and profundal small sparsely rakered whitefish (SSR) were benthivorous. Morphological traits were correlated with feeding environment of whitefish forms, benthivores having low number of short, widely spaced gillrakers and planktivore having the highest number of long and densely spaced gillrakers. The fastest growing form, LSR dwelled in littoral habitat where the benthic food resources were highest. In contrast, the slowest growing SSR dwelled in the profundal habitats, where benthic food resources were

scarce. Intermediately growing form, DR, consumed zooplankton, which availability was high only during short period in mid-summer. Furthermore, the risk of predation induced by pelagic brown trout limited the ability of DR to use zooplankton resources. To decrease the risk of predation, DR performed diel vertical migrations during autumn ascending to pelagial at dusk and descending to vicinity of bottom during dawn. As whitefish is a visual forager, the feeding efficiency of DR was most plausibly lowered during night. SSR and LSR used epibenthic habitat during all study periods.

Whitefish was the main prey species for all predators. Brown trout and Arctic charr used almost exclusively DR as a prey, but specialist piscivores, burbot and pike, consumed also other species and whitefish forms. Two sparsely rakered whitefish forms dwelled in epibenthic habitats offering also refuge areas and these forms were in minor importance in predator species diet. The slowest growing SSR did not reach size refuge from predation, but was the least predated whitefish form most plausibly due to profundal habitat use. LSR and DR were able to reach the size refuge from brown trout predation. Arctic charr, burbot and pike were able to predate DR at first ten years of whitefish life.

## 6. Future research

In the future, field research will concentrate on lake ecosystems inhabited by allopatric and sympatric whitefish populations. Study will give insights to resource use in ecosystems with no specialized forms and specialized sympatric whitefish forms. Study will include at least components of morphological divergence, resource use, and predator-prey interactions. High specialization of sympatric whitefish forms suggest more efficient resource use compared to the lakes with allopatric whitefish. This should be detected also in morphometric analysis, where specialized sympatric forms (especially pelagic planktivore and profundal benthivore) should be clearly distinguished from allopatric populations. If there are distinct differences between allopatric and sympatric populations this should have impact on prey populations. Zooplankton prey should show higher predator avoidance behaviour and have smaller average size in lakes with specialized planktivore *i.e.* in lake with sympatric whitefish forms.

This study arose many questions for experimental research. Sympatric whitefish forms showed high persistence in their niche use during study years. High trophic and morphological specialization of sympatric forms suggests differences in feeding efficiency and behaviour. Field data suggest that the feeding efficiency of whitefish forms differs between pelagic and benthic food items. The pelagic form, DR, should be inferior in feeding benthic food and superior in feeding pelagic food items. Opposite should be true for benthic whitefish forms. Furthermore, feeding efficiency should also depend on light intensity, which differs between the habitats of whitefish forms. The profundal form, SSR, should be specialized forager in dark and LSR in well-lighted littoral conditions. In addition, feeding efficiency of DR with zooplankton in light and dark conditions is unknown. Feeding efficiency is closely related with predator avoidance behaviour of pelagic DR. Thus, also the predator-prey interactions should also gain experimental interest.

High morphological divergence of whitefish forms suggests also reproductive isolation between them. First, detailed genetical approach is needed to investigate level of reproductive isolation between whitefish forms in the same lake. Second, divergence patterns (migration, intra-lacustrine radiation) of morphometrically similar whitefish forms in different lakes should be examined. Later heritability of morphological traits should be also studied experimentally with cross-breeding experiments with sympatric whitefish forms. This study would give answers to many questions of mechanism in whitefish divergence, such as

fertilization success and embryonic mortality rate between pure and hybrid crosses. In later stage, study would reveal possible differences in the resource use efficiency between pure and hybrid crosses in the benthic and pelagic environment. Conclusive study with experimental cross-breeding would enlighten also heritability of growth, habitat use and feeding behaviour.

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