Empirical evaluation of phenotype–environment correlation and trait utility with allopatric and sympatric whitefish, *Coregonus lavaretus* (L.), populations in subarctic lakes

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Adaptive phenotypic divergence of sympatric morphs in a single species may have significant evolutionary consequences. In the present study, phenotypic impacts of predator on zooplankton prey populations were compared in two northern Finnish lakes; one with an allopatric whitefish, *Coregonus lavaretus* (L.), population and the other with three sympatric whitefish populations. First, we examined whether there were phenotypic associations with specific niches in allopatric and sympatric whitefish. Second, trait utility (i.e. number of gillrakers) of allopatric and sympatric whitefish in utilizing a pelagic resource was explored by comparing predator avoidance of prey, prey size in environment, and prey size in predator diet. The allopatric living large sparsely rakered (LSR) whitefish morph, was a generalist using both pelagic and benthic niches. In contrast, sympatric living whitefish morphs were specialized: LSR whitefish was a littoral benthivore, small sparsely rakered whitefish was a profundal benthivore and densely rakered (DR) whitefish was a pelagic planktivore. In the lake with allopatric whitefish, zooplankton prey did not migrate vertically to avoid predation whereas, in the lake with sympatric whitefish, all important prey taxa migrated significantly. Trait utility was observed as significantly smaller size of prey in environment and predator diet in the lake with DR whitefish than in the lake with only LSR whitefish. © 2007 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2007, **92**, 561–572.

ADDITIONAL KEYWORDS: adaptive radiation – diel vertical migration – gillraker – niche segregation – resource polymorphism – speciation – zooplankton.

INTRODUCTION

Resource polymorphism is considered to emerge in novel environments such as newly-formed lakes or remote islands (Skúlason & Smith, 1995; Schluter, 1996). In these environments, interspecific predation and competition is usually low and the amount of open niches high, promoting divergence of amphibians, birds, and fishes (Smith & Skúlason, 1996). In some cases, divergence of sympatric ecotypes has been related to the theory of adaptive radiation, which is the diversification of a common ancestor into divergent morphs or forms utilizing two or more niches through morphological, life historical, and physiological specialization (Schluter, 2000). Recently, coregonids have been suggested to be one of the candidate organisms in the study of adaptive radiation (Bernatchez, 2004) but the evidence of trait utility and phenotype–environmental correlations of different morphs is still scarce for this taxon.

Phenotype–environment correlation and trait utility are closely related to foraging niche (Schluter, 2000). For example, in Darwin's finches, beak sizes are strongly correlated with specific feeding habitat and fitness (Lack, 1947; Price *et al*., 1984). In fish, mouth and head shape are correlated with feeding

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environment with higher trait utility in niche specific morphology (Malmquist, 1992; Schluter, 1993). Adaptive significance of phenotype–environment correlation and trait utility is pronounced in particular, if the same selected traits influence reproductive isolation (Rundle & Schluter, 2004). Evolutionary young polymorphic fish populations in the northern hemisphere are ideal model organisms for empirical evaluation of the adaptive significance of phenotypic evolution.

Whitefish, *Coregonus lavaretus* (L.), is a widely distributed species in Europe appearing as polymorphic populations especially in the northern part of its distribution area (Svärdson, 1979). In European whitefish, two major mitochondrial DNA (mtDNA) lineages exist, one in the northern Europe and the other in the southern Fennoscandia and central Europe (Bernatchez & Dodson, 1994). According to the mtDNA results, allopatric and sympatric whitefish populations in the northern Scandinavian lakes have evolved from the northern ancestor lineage within a maximum time period of approximately 10 000 years after the last Ice Age (Bernatchez & Dodson, 1994; Østbye *et al.*, 2005a).

In whitefish, the number of gillrakers is a genetically based phenotypic trait used to discriminate between sympatric morphs, forms or ecotypes (Svärdson, 1979). Phenotype–environment correlation has been suggested between the number of gillrakers and feeding niche of sympatric whitefish morphs: densely rakered (DR) morphs being more planktivorous and sparsely rakered morphs more benthivorous (Bergstrand, 1982; Amundsen *et al.*, 2004a). In northern Scandinavian lakes, whitefish is usually the most abundant fish species and divergence has been parallel: allopatric populations have only one low rakered whitefish morph and sympatric populations have the same low rakered and a high rakered morph of whitefish (Amundsen, 1988; Lehtonen & Niemelä, 1998; Amundsen *et al.*, 2004a). As the number of gillrakers in allopatric and sympatric populations closely follow similar pattern in different lakes (Lehtonen & Niemelä, 1998; Amundsen *et al.*, 2004a), chance is not a likely explanation for their divergence (Schluter & McPhail, 1992). Furthermore, differences in whitefish populations cannot be explained by different environment (Schluter, 2000) because allopatric and sympatric whitefish populations inhabit lakes in similar geographical and climatic areas.

Despite a rather extensive literature of polymorphic fish populations, little is known about the impacts of different phenotypes on prey populations. However, such impacts may have an essential role in fish divergence inducing the generally observed pelagic and benthic niche segregation between sympatric morphs (Schluter & McPhail, 1993; Robinson & Wilson, 1994),

which may ultimately lead to reproductive isolation. In the present study, we investigated the consequences of the phenotypic divergence of allopatric and sympatric whitefish in two subarctic lakes. First, we investigated any phenotype–environment correlation (i.e. whether a certain phenotype associated with a specific niche in allopatric and sympatric lakes). Second, we assessed whether trait utility in terms of morphological specialization (i.e. higher number of gillrakers) has a stronger impact in prey populations by comparing zooplankton size and predator avoidance behaviour in lakes with allopatric or sympatric whitefish populations. If the higher number of gillrakers is related to more efficient pelagic resource use, it should be observed in the form of smaller prey size in the environment (water column) and pronounced predator avoidance behaviour of the prey (i.e. larger amplitude of diel vertical migrations of zooplankton).

MATERIAL AND METHODS

STUDY SITES

Oligotrophic Lake Muddusjärvi, hereafter L. Muddus (total surface area = 48 km^2, maximum depth = 73 m) is situated in northern Finland (69°00′N, 27°00′E). Secchi disk transparency is approximately 3 m. The fish fauna of L. Muddus consists of ten species: whitefish, Arctic charr [*Salvelinus alpinus* (L.)], brown trout (*Salmo trutta* L.), grayling [*Thymallus thymallus* (L.)], perch (*Perca fluviatilis* L.), pike (*Esox lucius* L.), burbot [*Lota lota* (L.)], minnow [*Phoxinus phoxinus* (L.)], three-spined stickleback [*Gasterosteus aculeatus* (L.)], and nine-spined stickleback [*Pungitius pungitius* (L.)]. Whitefish is the most numerous species in L. Muddus, dividing into three morphs according to gillraker distribution (Kahilainen *et al.*, 2004). Two morphs are sparsely rakered and one morph is DR. The DR morph is the most numerous and dwells in both pelagic and epibenthic zones, whereas the sparsely rakered morphs dwell only in epibenthic areas (Kahilainen & Lehtonen, 2002, 2003; Kahilainen *et al.*, 2004). Large sparsely rakered (LSR) whitefish use shallow littoral habitats and small sparsely rakered (SSR) whitefish use deep profundal habitats (Kahilainen, Lehtonen & Könönen, 2003).

Lake Kilpisjärvi, hereafter L. Kilpis (69°03′N, 20°49′E) is located in northern Finland and has a total surface area of 37 km^2 and a maximum depth of 57 m (Tolonen, 1997). L. Kilpis is oligotrophic and Secchi-disk transparency is approximately 10 m. Altogether, eight fish species are found in L. Kilpis: whitefish, Arctic charr, grayling, brown trout, burbot, pike, minnow and alpine bullhead (*Cottus poecilopus*

Heckel). Whitefish is the numerically dominant species in L. Kilpis fish fauna and occurs as a monomorphic population (Tolonen, 1997).

HABITAT USE OF WHITEFISH

In both lakes, experimental gillnetting was conducted during September 2002, in the vicinity of our zooplankton sampling station during the day and night, with a set of eight nets each having a length of 30 m and height of 1.8 m. The gillnet set was randomly combined from eight nets having mesh sizes 12, 15, 20, 25, 30, 35, 45 and 60 mm (from knot to knot). Altogether, three net series were used simultaneously in the pelagic and benthic zone. Catch per unit effort (CPUE) was calculated as number of whitefish/gillnet series h^{-1} and used as indicator of whitefish diel habitat use. In L. Kilpis, the whitefish population consist of a single morph and thus all whitefish were pooled in the CPUE analysis. In L. Muddus, the three whitefish morphs were identified in the field according to differences in appearance and morphology of gillrakers (Kahilainen & Østbye, 2006). After identification, the total length and weight were measured with an accuracy of 1 mm and 0.1 g, respectively.

Whitefish habitat use during day and night was also examined with vertical hydroacoustics. Acoustic data were sampled with a SIMRAD EY-500 echosounder, which was equipped with a split-beam transducer ES120-7F. The equipment and settings are given in detail in Kahilainen et al. (2004).

In both lakes, three echosounding transects (in vicinity of zooplankton sampling stations) were sampled at noon and midnight. The vertical distribution of whitefish was studied with echo integrals (area backscattering strength, s_a) from two water layers: pelagic (from 3 m below the surface to 2 m above the bottom) and benthic zone (from 0.2 m to 2 m above the bottom). The s_a values were calculated using EP 500-software (Lindem Data Acquisition, 1995). They should indicate vertical distribution accurately because s_a values are linearly proportional to fish density (MacLennan & Simmonds, 1992) and the proportion of other fish species was negligible (4–6%) in catches from both lakes. In L. Muddus, pelagic fish targets are > 99% of DR whitefish and the remaining proportion consists of brown trout according to extensive seasonal and diel echosounding, pelagic trawling, and gillnetting study (Kahilainen et al., 2004). Sparsely rakered morphs, LSR and SSR whitefish, dwell only on benthic habitats (i.e. 'the bottom blind zone' of echosounder) and thus their density can not be estimated with echosounding (Kahilainen et al., 2004). Differences between the day and night whitefish proportions in pelagic and benthic zones were compared with the Mann–Whitney U-test.

GILLRAKER AND DIET ANALYSES

The number of gillrakers was determined from the first brancial gill arch under a preparation microscope. The average number of gillrakers between whitefish morphs was compared using the analysis of variance (ANOVA) and pairwise comparisons were made with Tukey's HSD tests. The stomach was removed and food categories were identified to order or family level. The diet was analysed using the wet weight method (Windell & Bowen, 1978), in which different food categories were weighted separately and their contribution to the total wet weight of stomach contents was calculated. In the diet analysis, size-adjustment was made by dividing each food category wet weight by whitefish total wet weight. Zooplankton body length of the main taxa (Bosmina spp., Daphnia spp., Cyclopoida and Calanoida) in each whitefish stomach was measured from 30 randomly selected and undeteriorated individuals under a preparation microscope.

ZOOPLANKTON SAMPLING

In both lakes, zooplankton were sampled at noon (12.00 h) and midnight (00.00 h). Water depth in the sampling stations in L. Muddus and L. Kilpis was 12 m and 14 m, respectively. Samples were taken from surface to bottom at 1-m intervals using a tube sampler (length 1 m, volume 7.1 L). Three replicates were taken with the distance between sampling points being approximately 15–20 m. Samples were immediately sieved through a zooplankton net (mesh size 50 μm) and preserved with 5% formalin solution.

Zooplankton samples were later analysed in the laboratory using a light microscope. In L. Muddus, the most abundant species in the samples were *Bosmina coregoni*, *Bosmina longispina*, *Bosmina longirostris*, *Daphnia cristata*, *Daphnia longiremis*, *Cyclops scutifer* and *Eudiaptomus graciloides*. In L. Kilpis, the most abundant species included the previous ones, but also *Daphnia longispina* and *Daphnia cuculata*. The total number of individuals per sample was counted and zooplankton body length (for *Daphnia* spp. as eye length, i.e. length from centre of eye to root of tail spine) was measured from the first 30 specimens. Pelagic zooplankton specimens collected from the water column were pooled into four main taxa: Cyclopoida, Calanoida, *Bosmina* spp. and *Daphnia* spp. The average length [transformed with $\log(x + 1)$] of zooplankton in the lakes and in whitefish stomachs were compared with ANOVA (separately for each taxa) and pairwise comparisons were made with Tukey's HSD tests.

Zooplankton density in the water column during day and night was calculated as number of specimens per litre. Zooplankton densities through the water
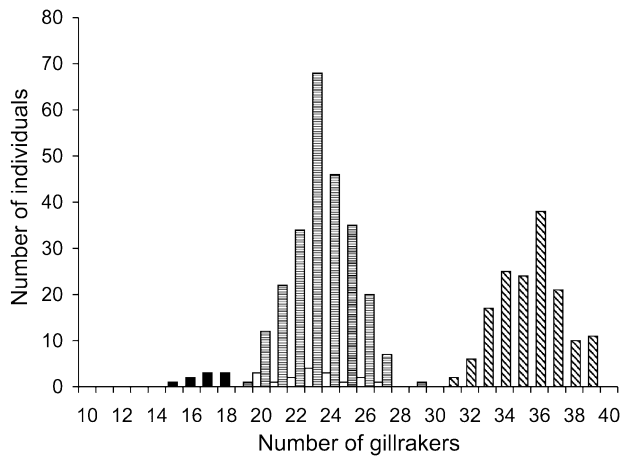
Figure 1. Gillraker distribution of allopatric large sparsely rakered (LSR) (▤) whitefish in Lake Kilpisjärvi and sympatric small sparsely rakered (SSR) (■), LSR (□) and densely rakered (DR) (▨) whitefish in Lake Muddusjärvi.

column were calculated using 2-m high layers. For statistical analyses, we calculated the proportion of zooplankton density in each depth layer relative to that of the whole water column. Proportions were normalized with arcsine squareroot transformation (arcsin $\sqrt{x}$). Comparison between the daytime and night-time vertical distributions was made with ANOVA separately for each lake and taxon. Pairwise comparisons were made with Tukey's HSD tests.

RESULTS

GILLRAKER NUMBER OF ALLOPATRIC AND SYMPATRIC WHITEFISH

Gillraker distribution of whitefish was unimodal in L. Kilpis and trimodal in L. Muddus (Fig. 1). In L. Kilpis, the average gillraker number of allopatric LSR whitefish was 23.4 ($N = 246$). In L. Muddus, the average gillraker numbers of sympatric whitefish morphs were: SSR whitefish 16.9 ($N = 9$), LSR whitefish 23.1 ($N = 17$) and DR whitefish 35.4 ($N = 154$). The average number of gillrakers between whitefish morphs differed significantly (ANOVA, $F_{3,422} = 1595$, $P < 0.001$). Gillraker number within phenotypes (allopatric and sympatric LSR whitefish), did not differ significantly (Tukey's HSD test, $P = $ not significant), but both of these differed from other whitefish morphs ($P < 0.001$).

DIEL HABITAT USE OF PREDATOR AND PREY

In L. Kilpis, a part of the whitefish population migrated to the pelagic at dusk, but the major part remained benthic both during the day and night
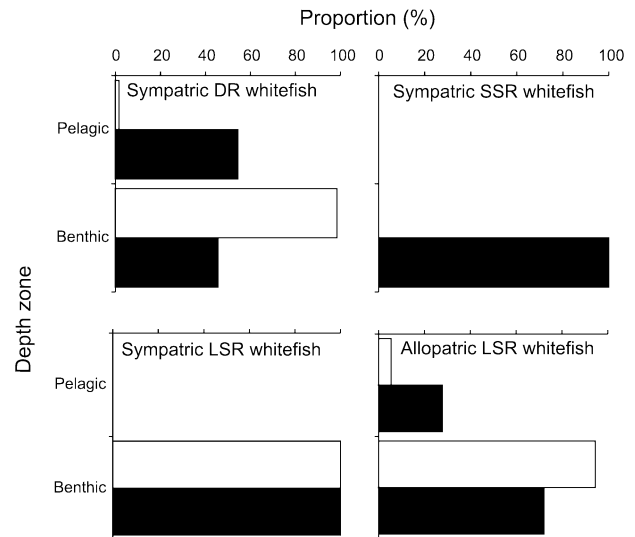

Figure 2. Proportion of whitefish caught in pelagic and benthic habitats during the day (□) and night (■) calculated from gillnet catch per unit effort in Lake Muddusjärvi and Lake Kilpisjärvi.
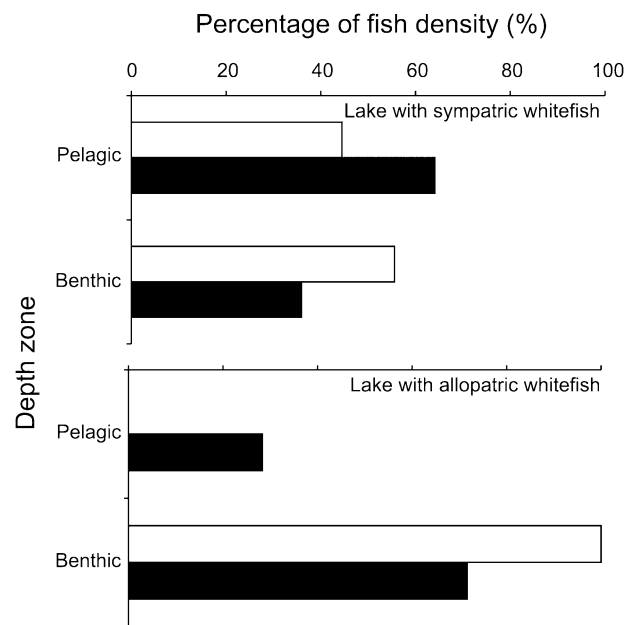

Figure 3. Whitefish distribution in pelagic and benthic habitats during the day (□) and night (■) calculated from hydroacoustic data in Lake Muddusjärvi (upper) and Lake Kilpisjärvi (lower).

(Fig. 2). This was even more pronounced in the acoustic survey (Fig. 3). At night, some whitefish used the pelagic habitat, but most remained benthic (Fig. 3). Pelagic fish density at night was significantly higher than in daytime (Mann–Whitney U-test, $P < 0.05$),

whereas no significant difference between day and night was observed in the benthic layer. In L. Muddus, the LSR and SSR whitefish were only caught in the benthic habitat (Fig. 2). In daytime, almost all DR whitefish were caught from benthic habitats but, at night, a major part was caught from the pelagic (Fig. 2). This was identified also in acoustic data: a major part of DR whitefish were benthic during the day and pelagic at night (Fig. 3). Pelagic fish density at night was significantly higher than in daytime (Mann–Whitney U-test, $P < 0.05$).

There were pronounced differences in diel vertical migrations of zooplankton prey between lakes (Fig. 4). In L. Kilpis, zooplankton did not migrate (Fig. 4, Table 1; ANOVA, time × depth interaction, P = not significant). In contrast, apart from *Daphnia* spp., all zooplankton prey migrated in L. Muddus (Fig. 4, Table 2; ANOVA, time × depth interaction, $P < 0.001$). In the daytime, both copepods and cladocerans had the highest abundance in the vicinity of surface or midwater, whereas, during the night, zooplankton migrated downwards in the water column (Fig. 4). The daytime distribution in the surface layer was significantly higher (Tukey's HSD test's, $P < 0.05$) than the night-time distribution for *Bosmina* spp. (depth layer: 3–4 m), Calanoida (depth layer: 1–2 m, 3–4 m) and Cyclopoida (depth layer: 3–4 m). In contrast, the night-time distribution in deep water was significantly higher (Tukey's HSD test's, $P < 0.01$) than in the daytime distribution for *Bosmina* spp. (depth layer: 11–12 m), Calanoida (depth layer: 11–12 m), and Cyclopoida (depth layer: 9–10 m and 11–12 m).

PREDATOR'S DIET AND PREY SIZE

In L. Kilpis, allopatric LSR whitefish used both pelagic and benthic prey (Table 3). The most frequent pelagic zooplankton taxa from LSR stomachs were bosminids and cyclopods, whereas benthic prey includes especially bivalves and gastropods. In contrast, sympatric LSR and SSR whitefish used almost exclusively benthic prey in L. Muddus. Copepods consumed by SSR whitefish consisted of Megacyclops, whose habitat is related to benthic zone similarly to that of cladoceran *Eurycercus* sp. No specimens of either Megacyclops or *Eurycercus* sp. were found in the pelagic zooplankton samples. DR whitefish almost exclusively used pelagic zooplankton prey (Table 3). Foraging niches of sympatric whitefish diverged to two benthivores (SSR and LSR whitefish) and one planktivore (DR whitefish), whereas allopatric LSR was generalist using both pelagic and benthic diet.

Both allopatric and sympatric whitefish exhibited size selective zooplankton predation (Fig. 5, Tables 4, 5). In both lakes, the average size of zooplankton was larger in whitefish stomach compared to the lake
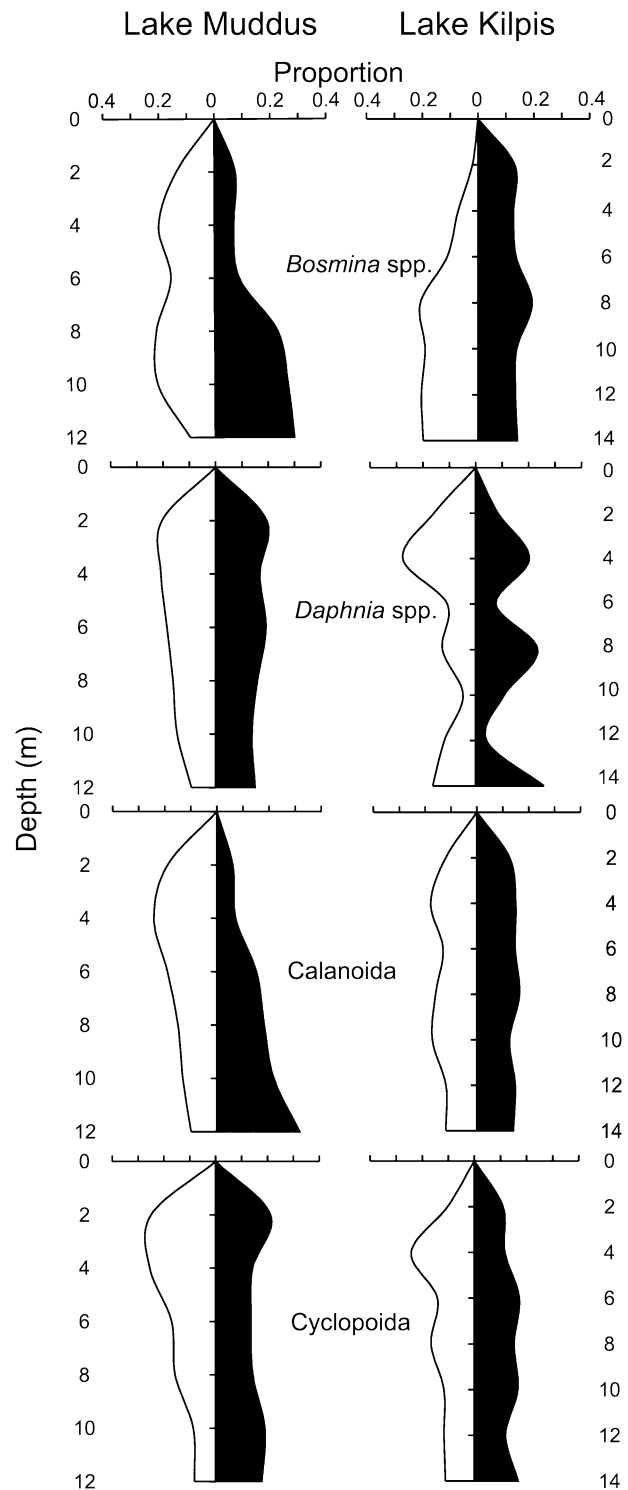

Figure 4. Zooplankton vertical distribution at noon (□) and at midnight (■) in Lake Muddusjärvi (left) and Lake Kilpisjärvi (right).

Table 1. Analysis of variance of the effects of time (day or night), depth, and their interactions on prey vertical distribution in the lake with allopatric whitefish (Lake Kilpisjärvi)

Source of variation	SS	d.f.	MS	F	P
Bosmina spp.					
Time	0.0016	1	0.0016	0.1743	0.6794
Depth	0.1840	6	0.0306	3.3137	0.0136
Time × depth	0.1231	6	0.0205	2.2172	0.0710
Daphnia spp.					
Time	0.0001	1	0.0001	0.0097	0.9219
Depth	0.4248	6	0.0708	3.7863	0.0069
Time × depth	0.1678	6	0.0279	1.4955	0.2159
Calanoida					
Time	0.0001	1	0.0001	0.0360	0.8507
Depth	0.0185	6	0.0031	0.8934	0.5131
Time × depth	0.0144	6	0.0024	0.6947	0.6558
Cyclopoida					
Time	0.0007	1	0.0007	0.0906	0.7655
Depth	0.0415	6	0.0069	0.8129	0.5689
Time × depth	0.0709	6	0.0118	1.3866	0.2545

Analysis of variance was calculated for each prey group separately.
d.f., degrees of freedom.

Table 2. Analysis of variance of the effects of depth, time (day or night), and their interactions on prey vertical distribution in the lake with sympatric whitefish (Lake Muddusjärvi)

Source of variation	SS	d.f.	MS	F	P
Bosmina spp.					
Time	0.0012	1	0.0012	0.5883	0.4505
Depth	0.1619	5	0.0323	15.5424	< 0.001
Time × depth	0.2005	5	0.0401	19.2452	< 0.001
Daphnia spp.					
Time	0.0000	1	0.0000	0.0414	0.8404
Depth	0.0573	5	0.0114	6.3163	0.0007
Time × depth	0.0182	5	0.0036	2.0031	0.1145
Calanoida					
Time	0.0005	1	0.0005	0.1381	0.7133
Depth	0.0409	5	0.0081	1.9573	0.1218
Time × depth	0.2911	5	0.0582	13.9160	< 0.001
Cyclopoida					
Time	0.0004	1	0.0004	0.3669	0.5503
Depth	0.0844	5	0.0168	13.9394	< 0.001
Time × depth	0.1040	5	0.0208	17.1757	< 0.001

Analysis of variance was calculated for each prey group separately.
d.f., degrees of freedom.

(Fig. 5, Tables 4, 5; Tukey's HSD tests $P < 0.01$). The average size of *Bosmina* spp., Cyclopoida and *Daphnia* spp. was also different between lakes (Table 5), being significantly higher in L. Kilpis than in L. Muddus ($P < 0.001$). This was also reflected in zooplankton length in whitefish stomachs: the average length of *Bosmina* spp. and Cyclopoida was significantly higher in allopatric LSR whitefish

Table 3. Diet composition and the principal foraging niche (pelagic/benthic) according to diet of sympatric and allopatric whitefish in Lake Muddusjärvi and Lake Kilpisjärvi

	Lake Muddusjärvi			Lake Kilpisjärvi
	SSR	LSR	DR	LSR
Pelagic prey				
Bosmina spp.	–	–	70.3	47.9
Daphnia spp.	–	–	0.5	–
Calanoida	–	–	15.3	–
Cyclopoida	10.6	–	12.7	0.5
Chironomid pupae	–	–	–	–
Terrestrial insects	–	–	0.9	2.6
Benthic prey				
Chironomid larvae	2.6	39.5	0.3	5.7
Water mites	–	9.7	–	–
Bivalves	32.6	14.3	–	0.9
Gastropods	–	–	–	16.2
Cottus poecilopus	–	–	–	0.3
Eurycercus sp.	54.2	36.5	–	25.9
Proportion of pelagic prey (%)	10.6	0.0	99.7	51.0
Proportion of benthic prey (%)	89.4	100.0	0.3	49.0

LSR, large sparsely rakered whitefish; DR, densely rakered whitefish; SSR, small sparsely rakered whitefish.
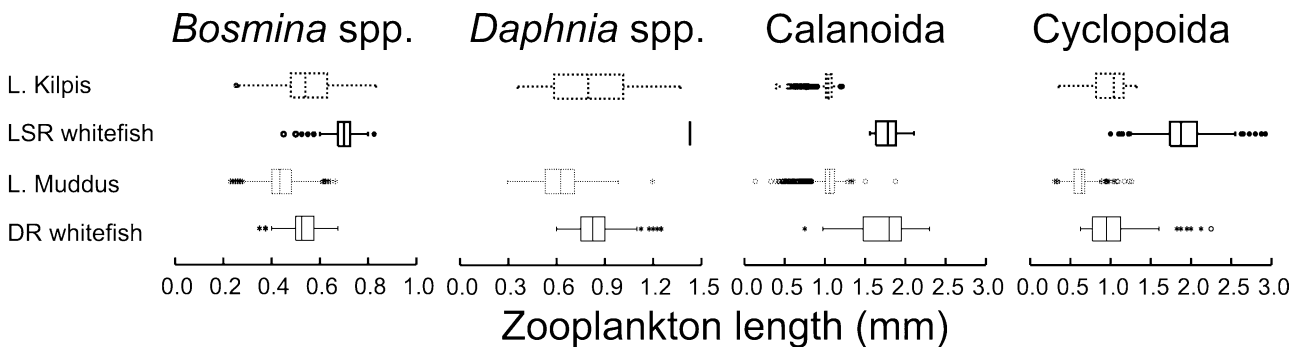

Figure 5. Zooplankton lengths in study lakes, allopatric large sparsely rakered (LSR) whitefish and sympatric densely rakered (DR) whitefish stomach presented as a box plots. The boxes indicate the range of central values (50%) between the first and third quartile, whereas the centre vertical lines indicate the median value of samples. For zooplankton sample sizes, average lengths and statistical significance, see Tables 4 and 5.

stomachs than sympatric DR whitefish stomachs ($P < 0.001$).

DISCUSSION

We found phenotype–environment correlation between gillraker number and feeding niche in the sympatric whitefish lake, but not in the allopatric whitefish lake. Trait utility of DR whitefish was observed in the form of smaller size of zooplankton in the environment and diet than in the lake with allopatric LSR whitefish. An effect of trait utility was also observed in the behaviour of prey populations: DR whitefish predation induced stronger avoidance behaviour of zooplankton in terms of diel vertical migration than allopatric LSR whitefish predation.

The number of gillrakers is a key trait differentiating polymorphic fish populations in the northern hemisphere (Schluter & McPhail, 1993; Robinson & Wilson, 1994). Differences in the gillraker morphology of polymorphic fish are comparable with the divergence of beak size in birds and hind-limb length in

Table 4. The mean size ± standard error of zooplankton in the water column and whitefish stomach

	Lake Muddusjärvi	Sympatric DR	Lake Kilpisjärvi	Allopatric LSR
Bosmina spp.	0.439 ± 0.001 (2327)	0.529 ± 0.001 (2823)	0.546 ± 0.002 (884)	0.695 ± 0.001 (1333)
Daphnia spp.	0.616 ± 0.003 (1312)	0.850 ± 0.015 (77)	0.809 ± 0.012 (127)	1.425 (1)
Calanoida	1.020 ± 0.004 (1031)	1.707 ± 0.012 (110)	1.009 ± 0.003 (1503)	1.783 ± 0.055 (6)
Cyclopoida	0.612 ± 0.004 (1289)	1.008 ± 0.017 (99)	0.971 ± 0.009 (339)	1.908 ± 0.013 (180)

The number of samples is presented in parenthesis.
DR, densely rakered whitefish; LSR, large sparsely rakered whitefish.

Table 5. Analysis of variance of the effects of sampling source (Lake Kilpisjärvi and Lake Muddusjärvi water columns, allopatric LSR whitefish and sympatric DR whitefish stomach) on the average length of zooplankton

	SS	d.f.	MS	F	P
Bosmina spp.	22.96	3	7.65	4310.06	< 0.001
Daphnia spp.	2.61	3	0.87	126.92	< 0.001
Calanoida	9.41	3	3.13	688.40	< 0.001
Cyclopoida	59.57	3	19.85	2617.69	< 0.001

Each prey group was analysed separately.
d.f., degrees of freedom.

lizard ecotypes (Lack, 1947; Boag & Grant, 1981; Losos, Warheir & Schoener, 1997), with all traits governing the efficiency of resource use. A general pattern of gillraker divergence in postglacial lakes is that the higher number of gillrakers is related to a pelagic niche and the lower number to a benthic niche (Schluter & McPhail, 1993; Robinson & Wilson, 1994). In whitefish, gillraker divergence, ranging from 12 to 55 gillrakers, is even more pronounced than in most of the other polymorphic fish lineages (Svärdson, 1979; Amundsen, 1988; McPhail, 1993; Bernatchez, Chouinard & Lu, 1999; Kahilainen *et al*., 2003; Saint-Laurent, Legault & Bernatchez, 2003). A distinct pattern in gillraker number was found in sympatric whitefish morphs, where the number of gillrakers decreased in the epibenthic depth gradient: deep water benthivores, SSR whitefish, had the lowest number of gillrakers and shallow water benthivores, LSR whitefish, had an intermediate number of gillrakers (Kahilainen *et al*., 2003; present study). Towards the pelagic niche, the number of gillrakers increased: pelagic DR whitefish had the highest number of gillrakers (Kahilainen *et al*., 2004; Kahilainen, Alajärvi & Lehtonen, 2005; present study). In contrast, the allopatric LSR whitefish used all pelagic and benthic niches and had an intermediate number of gillrakers.

The function of gillrakers in feeding and correlation with specific niche use is essential in under-standing this trait's contribution in fish divergence. Particulate feeding planktivores, including white-fish, are size selective and the feeding efficiency depends on species (Confer *et al*., 1978; Lazzaro, 1987; Langeland & Nøst, 1995). The most efficient planktivorous species have a high number of long gillrakers and are able to consume small-sized zooplankton species and individuals (Eggers, 1977; Janssen, 1980; Lazzaro, 1987; Gibson, 1988; Langeland & Nøst, 1995). This is especially evident for sympatric whitefish: gillrakers of DR morphs are long and tightly packed, whereas gillrakers of sparsely rakered morphs are short and widely spaced (Amundsen, Bøhn & Våga, 2004b; Østbye *et al*., 2005b; Kahilainen & Østbye, 2006). The function of the gillraker apparatus is not yet fully understood (Seghers, 1975; Drenner *et al*., 1984; Sanderson, Cech & Patterson, 1991), but the implication of an increasing number and length of gillrakers in whitefish is a decrease of prey size in fish diet (Kahilainen & Østbye, 2006). This is further supported by the present study, which indicated that the increasing number of gillrakers in whitefish induced a decrease in size of the most important prey species. According to Sanderson *et al*. (2001), gillrakers function as a crossflow filter directing small food particles, such as zooplankton, to the oesophagus of fish. Thus, the long and densely spaced gillrakers of DR whitefish may be more effi-

cient crossflow filters to small zooplankton than the short and widely spaced gillrakers of LSR whitefish (Kahilainen & Østbye, 2006).

The higher feeding efficiency with long and numerous gillrakers governs the profitability of pelagic habitat use and a specialized planktivore may force other less efficient fish species to use alternative niches (Svärdson, 1976; Robinson *et al*., 1993; Bøhn & Amundsen, 2001). In the presence of an efficient planktivore (DR whitefish), less specialized pelagic foragers such as LSR and SSR whitefish may not be able to utilize zooplankton resources at all (Kahilainen *et al*., 2003; present study). In the allopatric lake, where zooplankton were large and did not migrate, a part of LSR whitefish also utilized this resource. However, the generalist behaviour of LSR whitefish was observed as a less pronounced diel vertical migration, in which the major part of the population utilized only the benthic niche typical for its morphology.

Predation is the main factor inducing avoidance mechanism (i.e. the diel vertical migration of zooplankton; Zaret & Suffern, 1976; Stich & Lampert, 1981; Lampert, 1989). Zooplankton seek refuge from visual fish predation, performing diel vertical migrations towards the depths with a low density of planktivorous fish (Gliwicz, 1986; Lampert, 1993), and this was observed in the lake with the efficient planktivore DR whitefish. For zooplankton prey, migration is a trade-off between grazing opportunities and the risk of death (Lampert, 1989). Migration increases energetic costs and lowers grazing time but reduces probability of death (Lampert, 1993). The results suggest that migration was a viable predator avoidance tactic in the lake with sympatric whitefish, but not in the lake with allopatric whitefish. This indirectly infers profound differences in the feeding efficiency between LSR and DR whitefish. The results refer that the feeding ability of LSR whitefish on small zooplankton prey was limited and predation risk induced by LSR whitefish may not be sufficient to induce diel vertical migration of zooplankton. Taken together, the results indicate that whitefish divergence has ecosystem level consequences, both reducing prey size and inducing prey migrations.

The ability of LSR whitefish to use both benthic and pelagic prey suggests that this morph may be the closest phenotype to ancestor whitefish inhabiting northern lakes after the last glacial retreat. Field studies strongly imply that morphologic specialization, higher number, and long gillrakers are required for efficient foraging of small-sized prey in pelagic habitat, and that gillraker number is a likely trait under natural selection (Lindsey, 1981). Such foraging morphology related feeding efficiencies are not rare in nature. For example, beak morphology of

Geospiza sp. significantly influences the handling time of seeds (Grant & Grant, 1996). The evolutionary importance is pronounced as the same selected foraging traits are the basis of reproductive isolation (Ratcliffe & Grant, 1983; Podos, 2001).

Foraging traits divergence in whitefish may involve several mechanisms, including phenotypic plasticity, allopatric speciation, and intralacustrine radiation (West-Eberhard, 1989; Bernatchez, 2004; Østbye *et al*., 2005a). According to recent mtDNA and nDNA results obtained in polymorphic northern whitefish populations, the last alternative is likely and the divergence is strongly related to resource segregation (Østbye *et al*., 2006). Resource competition is one plausible initial reason for whitefish divergence after the Ice Age because whitefish are known to produce overcrowded stocks especially in subarctic lakes (Amundsen, 1988; Amundsen *et al*., 2002). In these situations, resource competition is presumably very high and disruptive selection may favour extreme phenotypes over the most abundant ones (Bolnick, 2004). In whitefish, this can be related to divergence of gillraker distributions, in which resource competition may split a population into different phenotypes, if alternative profitable and competitively underutilized habitats exist (e.g. the pelagic). For example, competition within allopatric LSR whitefish population may favour individuals with a higher number of gillrakers via higher survival of adults and their offspring because they are more efficient at feeding on smaller prey, such as pelagic zooplankton (Kahilainen & Østbye, 2006). If accumulation of reproductive isolation via resource competition (Dieckmann & Doebeli, 1999) in whitefish is valid, future generations of specialized pelagic phenotype will decrease available zooplankton size in the lake environment and reduce generalist possibilities to use pelagic habitats.

The reproductive isolation mechanisms in whitefish are traditionally related to size assortative mating and differences in spawning time and place (Svärdson, 1979), which are all likely influenced by resources. Reproductive isolation between morphs of diverging species can be formed as a by-product of resource use and/or adaptive morphological specialization to use these resources (Bush, 1969; Podos, 2001; Nosil, Crespi & Sandoval, 2002). In polymorphic fish, pelagic morphs are usually smaller sized than benthic morphs (Schluter & McPhail, 1992; Bernatchez *et al*., 1999; Amundsen *et al*., 2002), which implies that specialization to a pelagic niche may have a general correlation with small size. One possible reason for the small size of pelagic morphs is the lower energy content of pelagic prey (i.e. usually zooplankton) compared to that of benthic macroinvertebrates (Cummins & Wuycheck, 1971), which likely

results in a slower growth rate and smaller size at sexual maturity. Assuming the size assortative mating observed in many fish species (Foote, 1988; Ros, Zeilstra & Oliveira, 2003; Boughman, Rundle & Schluter, 2005), resources may cause reproductive isolation via spawning with a similar sized mate within sympatric pelagic and benthic morphs. Resources can also indirectly influence to differentiation in spawning time, as seasonal pelagic and benthic prey availability may differ. In the case of northern whitefish, pelagic zooplankton, especially cladocerans, is available only limited timeframe during summer (Kahilainen *et al*., 2005), whereas benthic macroinvertebrates are available more continuously in different seasons (Kahilainen *et al*., 2003). DR whitefish spawns first of the sympatric morphs, which could be related to a rapid decrease in zooplankton availability when the water temperature lowers in September (Kahilainen *et al*., 2005). Benthivorous morphs do not face such a sharp decline of prey resources and they spawn later. In whitefish, reproductive isolation may thus be a result of resource-based size assortative mating and temporal isolation. The final outcome of resource competition-induced divergence and resource-based reproductive isolation is a lake with sympatric LSR and DR whitefish. However, detailed genetic sampling is needed to confirm the divergence patterns of whitefish populations in the present study.

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