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Parallel evolution of ecomorphological traits in the European whitefish *Coregonus lavaretus* (L.) species complex during postglacial times

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Abstract

The extensive phenotypic polymorphism in the European whitefish has triggered evolutionary research in order to disentangle mechanisms underlying diversification. To illuminate the ecological distinctiveness in polymorphic whitefish, and evaluate taxonomic designations, we studied nine Norwegian lakes in three watercourses, which each harboured pairs of divergent whitefish morphs. We compared the morphology and life history of these morphs, documented the extent of genetic differentiation between them, and contrasted the niche use of sympatric morphs along both the habitat and resource axes. In all cases, sympatric morphs differed in the number of gill rakers, a highly heritable trait related to trophic utilization. Individual growth rate, age and size at maturity, diet and habitat use also differed between morphs within lakes, but were remarkably similar across lakes within the same morph. Microsatellite analyses confirmed for all but one pair that sympatric morphs were significantly genetically different, and that similar morphs from different lakes likely have a polyphyletic origin. These results are most compatible with the process of parallel evolution through recurrent postglacial divergence into pelagic and benthic niches in each of these lakes. We propose that sparsely and densely rakered whitefish sympatric pairs may be a likely case of ecological speciation, mediated in oligotrophic lakes with few trophic competitors.

Keywords: adaptive radiation, gill rakers, life history, local adaptation, resource polymorphism, sympatric speciation

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Introduction

A major objective in evolutionary biology is to illuminate ecological and evolutionary forces responsible for population divergence and adaptation, which may ultimately result in speciation (Schluter 2000; Dieckman *et al*. 2004). Efforts to partition historical contingency from evolutionary processes have been particularly rewarding (Taylor & McPhail 2000; Hendry *et al*. 2002; Saint-Laurent *et al*. 2003; Fraser & Bernatchez 2005). The importance of historical factors is implicit in the secondary contact zones of allopatrically evolved taxa (Lu *et al*. 2001; Turgeon & Bernatchez 2001, 2003), whereas past or current evolutionary forces are most evident in cases of sympatric speciation (Pigeon *et al*. 1997; Douglas *et al*. 1999; Schliewen *et al*. 2001). In either scenario, introgressive hybridization may either facilitate or constrain adaptive diversification (Seehausen 2004). Polymorphic freshwater fishes in recently deglaciated areas are useful model organisms for the studies of intra- and interlake population divergence, and niche adaptation, in combination with the fishes' evolutionary history.

Ecological speciation is the process by which barriers to gene flow evolve between populations due to divergent

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selection, where food competition and niche adaptation are driving mechanisms (Schluter 1994, 2000; Bolnick 2004). Such a process requires a source of divergent selection (environmental differences, sexual selection, or ecological interactions), a build up of reproductive isolation (pre- or post-zygotic), and a link between divergent selection and accumulation of reproductive isolation (Rundle & Nosil 2005). If reproductive isolation between independent pairs of sympatric populations evolves as a replicated response to similar divergent selection pressures, it is termed parallel speciation (Funk 1998; McKinnon *et al*. 2004). Under a divergence-with-gene-flow scenario, adaptive divergence proceeds as a balance between selection and gene flow where populations accumulate differences over time (see Rice & Hostert 1993; Liou & Price 1994; Hendry & Taylor 2004; Schluter *et al*. 2004). Thus, the exchange of gametes between populations climbing different peaks on the adaptive landscape could constrain or enhance their optimal specialization (e.g. Saint-Laurent *et al*. 2003; Gavrilets 2004; Seehausen 2004). Theoretical models suggest that sympatric divergence is possible under, e.g. density-dependent selection and assortative mating (e.g. Drossel & McKane 1999, 2000; Dieckmann *et al*. 2004). Moreover, the support for ecological speciation in laboratory (Rice & Hostert 1993) and nature is accumulating (see Schluter 2000; Bernatchez 2004; Coyne & Orr 2004).

The independent evolution of the same trait in closely related lineages, termed parallel phenotypic evolution (Futuyma 1986), is a common feature in several adaptive radiations that occurred in northern freshwater fishes following postglacial colonization (Taylor 1999; Schluter 2000; Bernatchez 2004). Here, selection pressures result in the same trait expression due to similar niche tracking across populations or species (Schluter *et al*. 2004). However, independence is a subjective matter with regard to genealogy. For instance, evolutionary transitions may reflect the adaptive appearance or removal of liable ancestral trait states. The convergence of form and function within the genus *Coregonus* apparently represents some cases of homoplasy, i.e. where trait similarities are not simply due to genealogy (Bernatchez 2004; Politov *et al*. 2004; Douglas *et al*. 2005; Østbye *et al*. 2005a, b). The complex evolution of phenotypic diversity in whitefish has led to taxonomic confusion and has resulted in a multitude of currently used nomenclatures (Berg 1962; Kottelat 1997; Svärdson 1998).

The European whitefish *Coregonus lavaretus* (L.) species complex comprises both allopatric and sympatric populations differing in morphology, life history, niche use, and genetic identity (Svärdson 1957, 1979; Douglas *et al*. 1999; Kahilainen *et al*. 2004; Østbye *et al*. 2005a, b). The number of gill rakers, which apparently has a high additive genetic component and temporal stability even when transferred to new environments, has traditionally been used for designating whitefish species (Svärdson 1950, 1970; Himberg 1970; Sandlund 1992; Hermida *et al*. 2002). However, as this trait is also associated with diet acquisition, variation in gill-raker numbers may at least partly be influenced by natural selection. The mean number of gill rakers in European populations ranges between 18 and 55 (e.g. Berg 1962; Svärdson 1998). Typically, fish with many and long gill rakers are pelagic with a zooplankton diet, while fish with few and short rakers eat zoobenthos (Bergstrand 1982; Amundsen *et al*. 2004a, b; Kahilainen *et al*. 2004). Thus, there may exist a conflict between their systematic recognition (i.e. nomenclature) and evolutionary history based on this trait.

In north Norway, several lakes harbour whitefish populations characterized by a bimodality in gill-raker numbers and morphology, composing a sparsely and a densely rakered morph (Amundsen 1988; Amundsen *et al*. 2004a, b). These sympatric pairs are ecologically distinct with regard to habitat- and diet-choice and also growth trajectories, but their population genetic structure is unknown (Amundsen 1988; Amundsen *et al*. 1999, 2003, 2004a, b). A recent phylogeographic study revealed the occurrence of a single mitochondrial DNA (mtDNA) clade in this region (Østbye *et al*. 2005b), which was also common to most of northern Europe, as shown by Bernatchez & Dodson (1994). This unique model system enables us to evaluate relative roles of historical identity, phenotypical distinctness and ecological parameters in ‘replicate’ geographical sets of sparsely and densely rakered whitefish morphs on their adaptive diversifications. The combination of such data is indeed needed in order to infer potential early steps in an adaptive radiation and may reveal the very conditions upon which speciation acts. To date, few studies in fishes have fully integrated information from ecology, morphology and life history onto a genetic framework in order to jointly address ecological speciation.

Here, we sampled nine north Norwegian lakes in three watercourses which harboured a pair of divergent whitefish morphs. Their genetic identity was screened using microsatellites to test the null hypothesis of no reproductive segregation of intralacustrine morphs, to assess correspondence between a priori taxonomical designation and genetic identity, and to illuminate their origin. We also contrasted niche use of sympatric morphs along the habitat- and resource axis, and assessed life-history traits and morphological specialization to infer whether the data supported an ecological basis for the sympatric differentiation. The joint evaluation of these parameters was important in suggesting the presence or absence of similar selection pressures being responsible for ecomorphological parallelism. By using these ecomorphological measures, and reproductive segregation, our goal was to find the most likely evolutionary scenario for intralacustrine polymorphism, testing the hypotheses: (i) secondary contact of allopatric lineages, (ii) simultaneous colonization of divergent lineages, or (iii) parallel evolution of intra-lacustrine morphs. Finally, these data and hypotheses were all used in interpreting the likelihood of ecological speciation being a major force behind the apparent adaptive diversification.

Materials and methods

Study sites and sample collection

We sampled nine lakes hosting pairs of sparsely rakered and densely rakered European whitefish (Amundsen 1988; Amundsen *et al*. 2004a, b). In the following, we use only morph classification as their genetic and taxonomic status is still debated. Lakes were situated in the Pasvik (3 lakes), Tana (2) and Alta (4) watercourses in a flat subarctic landscape in northern Norway (see Fig. 1, Table 1). These lakes are oligotrophic, with some humic impact, 1.2–25.0 km^2, maximum depths of 15–36 m, altitude 21–374 m above sea level (m a.s.l.), with 4–7 fish species in addition to European whitefish. Fish were sampled during August and September 1981–1999 using bottom and floating gill-net series of eight mesh sizes (10–45 mm) in pelagic and benthic areas. Body length, age (by surface reading otoliths submerged in glycerol), sex, and maturity were scored. The first left gill arch was stored in 95% EtOH for measurements and DNA extraction. Stomach contents were collected from morph-subsets in seven of the lakes.

Gill-raker numbers

Fish were assigned in the field to the two morphs by a visual evaluation of the general gill-raker morphology (i.e. based on length, breadth and distance between gill-rakers), which were later confirmed in the laboratory by counting the gill-raker number on the first left gill-arch (see Amundsen 1988; Amundsen *et al*. 2004a). The sparsely and densely rakered whitefish displayed an almost nonoverlapping gill-raker distribution in all lakes (Fig. 2). Given our preclassification and sorting of fish into morphs in the field and in the laboratory, and the lack of samples from distinct spawning populations (as such populations are currently unknown), we merely describe differences between a *priori* morphs instead of testing this trait statistically. The functional prediction is that fish with many gill rakers comprise a dense gill-raker apparatus, and may forage more efficiently on smaller prey items such as zooplankton than will fish with few rakers (which may be more efficient on larger benthic prey), although the mechanism is unresolved (Robinson 2000; Kahilainen & Østbye 2006).

Life-history patterns

Length-at-age, asymptotic length (L_∞) and Broodie's growth coefficient (K) were estimated using the nonlinear von Bertalanffy growth model on the observed data (Bagenal 1978), while length- (Lm) and age-at-maturity (Am), i.e. the point where 50% of the population reach maturity, were estimated by nominal logistic regression (see Trippel & Harvey 1991). Nonoverlapping 95% confidence interval (95% CI) of the estimates was considered significantly different. Finally, a Welch analysis of variance (ANOVA) was applied for testing age distribution differences between the morphs within these lakes. If the pelagic niche offers a lower energetic income per effort than the benthic niche, then we may expect a lower age and size at maturity for the whitefish populations utilizing the pelagic zones than for whitefish populations preferring the benthic zones. Also, predation regimes will likely act on selection of life-history trajectories.

Table 1 The geographical locations, lake characteristics, and the current fish fauna of the nine study lakes in north Norway

Latitude (North)	Longitude (East)	Locality	Watercourse	Altitude (m a.s.l.)	Area (km^2)	Max depth (m)	St	Tt	Pf	Ll	Pp	El	Pu	Sa
69°14′N	29°12′E	Vaggatem	Pasvik	51	15.0	35	x	x	x	x	x	x	x	–
69°13′N	29°14′E	Ruskebukt	Pasvik	52	5.3	15	x	x	x	x	x	x	x	–
69°33′N	30°07′E	Skrukkebukt	Pasvik	21	6.6	36	x	x	x	x	x	x	x	–
69°21′N	24°01′E	Vuoddasjavri	Tana	334	2.7	24	x	x	x	–	–	x	–	–
69°38′N	25°19′E	Iddjajavri	Tana	275	10.4	30	x	x	x	x	–	x	–	–
69°08′N	22°47′E	Stuorajavri	Alta	374	25.0	30	x	–	x	x	x	x	–	x
69°04′N	23°11′E	Njallajavri	Alta	304	2.1	30	x	–	x	x	x	x	–	x
69°08′N	23°22′E	Vuolgamasjavri	Alta	304	1.2	18	x	–	x	x	x	x	–	x
69°32′N	23°42′E	Ladnetjavri	Alta	265	3.3	32	x	x	x	x	–	x	x	–

St, brown trout (*Salmo trutta*); Tt, arctic grayling (*Thymallus thymallus*); Pf, Eurasian perch (*Perca fluviatilis*); Ll, burbot (*Lota lota*); Pp, minnow (*Phoxinus phoxinus*); El, pike (*Esox lucius*); Pu, nine-spined stickleback (*Pungitus pungitus*); Sa, arctic charr (*Salvelinus alpinus*). Vendace (*Coregonus albula*) recently (1989) colonized the Pasvik watercourse (not natural).

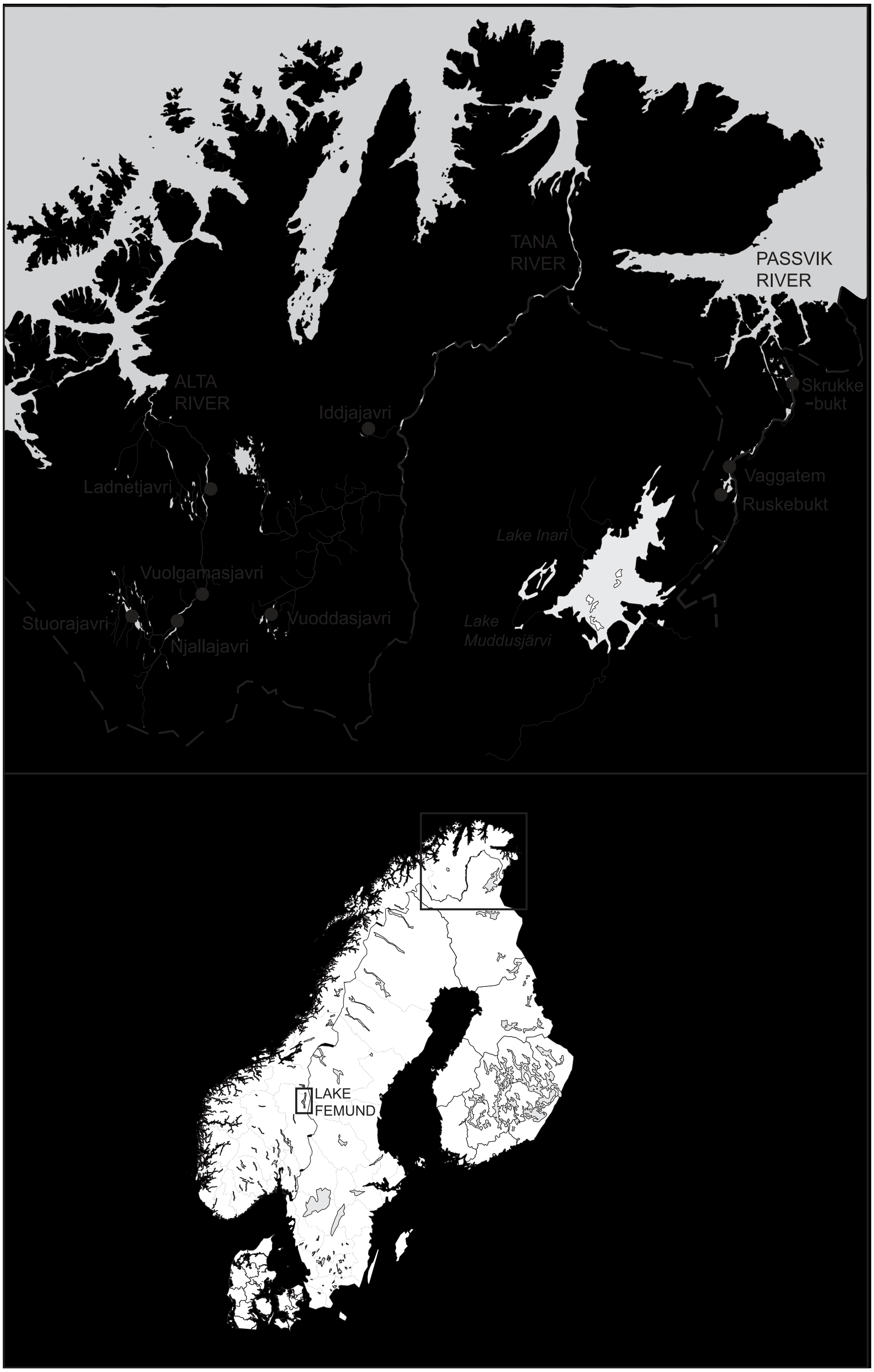

Fig. 1 Whitefish localities in the Pasvik, Tana and Alta watercourses, northern Norway. Position of Lake Femund, which was used as an outgroup, is indicated.

Habitat use

We used Fisher's exact 2×2 test to compare occurrence of morphs in the pelagic vs. the benthic habitat. In addition, to contrast interlake differences, we used a nominal logistic analysis on the whole data set nesting populations in morph and lakes. Moreover, as a scaled estimate of habitat use by the two morphs, we estimated catch per unit effort

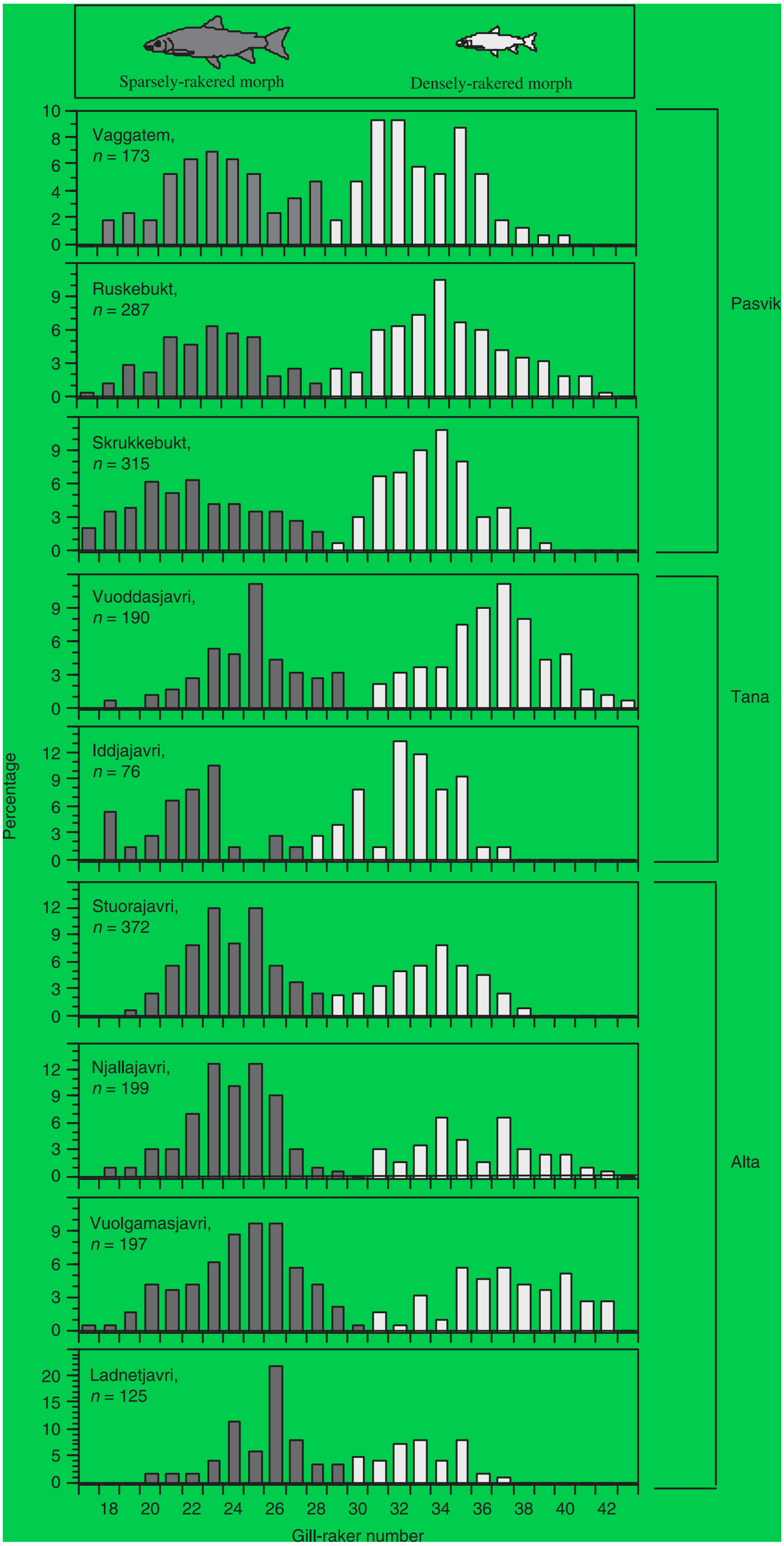

Fig. 2 Gill-raker distribution (%) in lakes (dark grey = sparsely rakered morphs, light grey = densely rakered morphs). Sample size, lakes and watercourses are given.

($CPUE$ = number of fish caught per 100 m^2 gill-nets per night), where the differences in these two habitats were analysed using an ANOVA. The habitat overlap between these two morphs in each of the lakes (wherever possible) was quantified by Schoener's (1970) D, which varies from 0 (i.e. no habitat overlap) to 1 (total overlap). If morphology is associated with foraging acquisition, we expect to find that different morphs are unequally distributed in these two niches which hold different prey items.

Diet composition

Diet preference in the two morphs was calculated using volumetric-percentage diet composition of six prey categories: zooplankton, surface insects, chironomid pupae, benthic crustaceans, insect larvae and molluscs, and tested by ANOVA. Total number of stomachs analysed was 987. Diet breadth was quantified applying Levins' (1968) index (B), where B varies from 1 (a single food category) to 6 (equal representation of the six food categories). Difference in diet breadth (B) between morphs was tested by an ANOVA, while diet overlap of morphs was estimated by Schoener's D (as above). As we have not sampled stomachs in both the pelagic and benthic niches, but rather in the 'lake' (i.e. based on a mixed subset of fish), we may assume (or predict) that the two morphs that forage on different prey items will reflect different niche preference.

Specialization and divergence

In order to compare similarity of morphs across lakes in these traits, we constructed a dendrogram using JMP 5.0 (SAS 2002) (Ward's method; standardized cluster distance values; geometric x-scale) based on the morphology (*gill raker numbers*), life history (L_∞, K, Lm, Am), habitat preference ($CPUE$ in benthic and pelagic habitat), and diet in morphs from six applicable lakes (based on all the data in Fig. 3, Table 2). If there exists a pattern in these diverse parameters grouping our a priori morphs separately, this supports a prediction that phenotypically similar fish in lakes have the same life history and ecology, and also that sympatric morphs behave as ecoguilds.

Genetic analysis

DNA was extracted from the gill-lamellae using the phenol/chloroform procedure (Sambrook *et al*. 1989). Six microsatellites were analysed; *SsBgIIIM*.26 (Goodier & Davidson; GenBank Accession no. U10051), *Cocl-23* (Rogers *et al*. 2004), *C2-157* (Turgeon *et al*. 1999), *Bwf1* (Patton *et al*. 1997), *Bwf2* (Patton *et al*. 1997), and *C1-g* (Turgeon *et al*. 1999). Mapping data confirm that these loci are on separate linkage groups (Rogers *et al*. 2004). Details regarding PCR amplification and microsatellite scoring are given by Østbye *et al*. (2005a). Genetic variation was described as microsatellite allele frequency, observed heterozygosity (H_O), expected heterozygosity (H_E), and pairwise F_{ST} using GENEPOP 3.3 (Raymond & Rousset 1995). Allelic richness, i.e. allele number corrected for sample size (El Mousadik & Petit 1996), was estimated using FSTAT 2.9.3 (Goudet 1995). Deviation from Hardy–Weinberg equilibrium was tested by the exact (probability) test for each locus and population (Guo & Thompson 1992), and P-values were corrected using the sequential Bonferroni method for each locus ($\alpha = 0.05$; $k = 18$). In order to test for the presence of null alleles in our data and to estimate their frequencies, we used MICRO-CHECKER (Van Oosterhout *et al*. 2004).

Population differentiation was estimated using the log-likelihood based exact test on contingency tables of genotypes (rather than on the genes as deviation from H-W equilibrium was found). Tests were made across populations, and between pairs of populations, using GENEPOP 3.3, and combined across loci.

Genetic relationship between populations was assessed by constructing a neighbour-joining tree using the D_A genetic distance matrix (Nei *et al*. 1983), and statistical support for nodes were obtained from 1000 bootstrap iterations performed in PHYLIP 3.5 (Felsenstein 1993). Four whitefish populations representing four morphs in Lake Femund, southern Norway (Østbye *et al*. 2005a, b) were used as genetic outgroups. We performed a Bayesian analysis of population structure in BAPS 4.0 (Corander *et al*. 2003, 2006; Corander & Marttinen 2006) using the '*Clustering of groups of individuals*', and then '*Admixture based on mixture clustering*' option to graphically evaluate concordance between Bayesian clustering and genetic distance dendrogram. This approach can detect hidden population structure within samples or between geographical locations, even without any a priori assumptions of population structure.

Distribution of allelic variation was quantified by variance components of Φ statistics by analysis of molecular variance (AMOVA) in ARLEQUIN 2.000 (Excoffier *et al*. 1992; Schneider *et al*. 2000). Variance components were estimated for three levels, namely: (i) between the three rivers, (ii) between the nine lakes, and (iii) between the two morphs. Finally, we analysed the distribution of private alleles between the rivers, lakes and populations, using rarefaction (Hurlbert 1971) and a hierarchical sampling design as implemented in HP-RARE 1.0 (Kalinowski 2005). This rarefaction procedure accounts for unequal number of populations and sample size and estimates allelic richness and private allelic richness in a hierarchical balanced design (see Kalinowski 2004, 2005).

The predictions under a scenario of ecological speciation would be that sympatric morphs are partially or fully

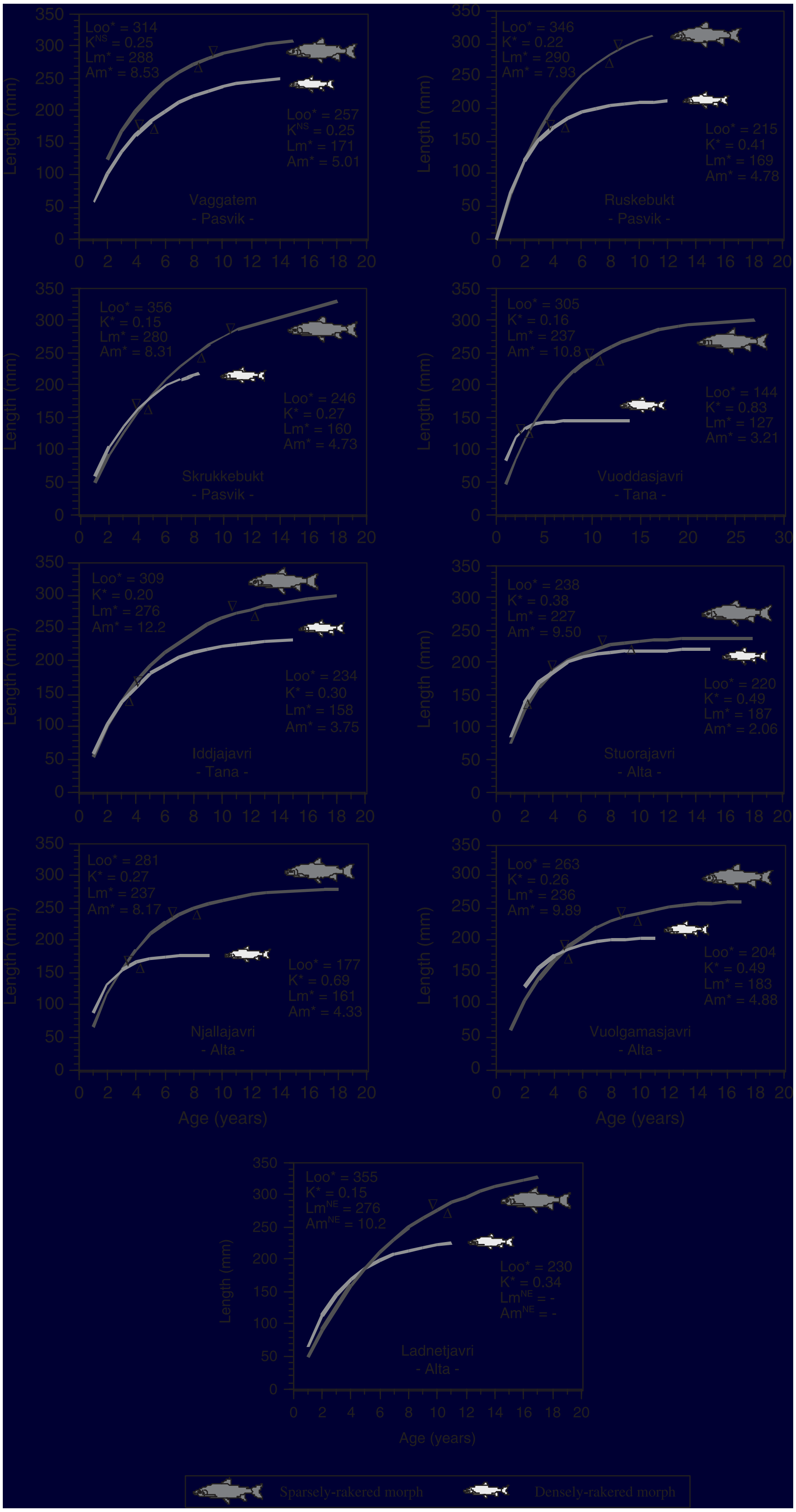

Fig. 3 Life-history parameters of the densely and sparsely rakered morphs with $L\infty$, asymptotic length, and K, Broodie's growth coefficient, Am (triangle), age-at-maturity, and Lm (inverse triangle), length at maturity. * denotes a significant difference, NS, not significant based on the 95% CI, and NE, insufficient data.

Table 2 The diet composition in percentage, diet breadth (B_{diet}), diet overlap (D_{diet}), habitat overlap ($D_{habitat}$), and *CPUE* (catch per unit effort: see Material section for details) in the benthic and pelagic environments for sparsely rakered (SRM) and densely rakered whitefish morphs (DRM)

Location Morph	Water-course	N diet	Zoo-plankton	Surface insects	Chironomid pupae	Benthic crustaceans	Insect larvae	Mollusca	B_{diet}	D_{diet}	$D_{habitat}$	*CPUE* benthic	*CPUE* pelagic
Ruskebukt	Pasvik									0.14	0.58		
SRM		22	1.6	10.6	4.2	2.1	18.3	63.1	2.25			7.9	2.2
DRM		36	85.1	0.6	0.0	4.3	5.0	5.0	1.37			12.1	5.8
Skrukkebukt	Pasvik									0.29	0.47		
SRM		31	16.1	3.4	0.0	27.7	21.6	31.2	4.04			17.8	1.4
DRM		17	46.8	0.0	0.0	4.6	48.6	0.0	2.19			5.0	38.6
Vuoddasjavri	Tana									0.22	0.35		
SRM		60	7.1	5.2	6.7	63.8	11.4	5.7	2.30			17.2	0.9
DRM		79	80.5	7.6	8.5	1.9	1.4	0.0	1.51			5.0	16.9
Stuorajavri	Alta									0.37	0.53		
SRM		119	30.6	24.9	2.5	4.8	17.3	19.9	4.38			9.9	0.7
DRM		123	93.4	6.6	0.0	0.0	0.0	0.0	1.14			0.3	25.0
Njallajavri	Alta									0.49	0.13		
SRM		119	16.9	0.2	17.0	22.4	30.0	13.5	4.63			19.8	0.2
DRM		73	7.3	1.5	61.1	28.2	1.9	0.1	2.18			0.8	16.5
Vuolgamasjavri	Alta									0.39	0.18		
SRM		116	15.6	21.8	8.5	12.8	22.5	18.7	5.52			11.5	0.3
DRM		78	60.0	38.4	0.8	0.0	0.1	0.7	1.97			1.4	1.0
Ladnetjavri	Alta									0.23	0.19		
SRM		81	0.0	14.1	13.8	15.3	26.6	30.1	4.47			9.8	0.6
DRM		33	0.0	91.6	8.4	0.0	0.0	0.0	1.18			0.6	3.6

reproductively segregated, and that they also are more genetically related to each other than to similar morphs in other lakes.

Results

Gill-raker numbers

In all lakes, the sparsely and densely rakered whitefish morphs showed differences in the number of gill rakers with estimated overall means (± SE) of 23.9 ± 0.3 and 36.1 ± 0.3, respectively (Fig. 2). The number of gill rakers was similar across all lakes in sparsely rakered morphs (22.5–25.6) and densely rakered morphs (32.9–36.8). Thus, the trajectories of gill-raker number divergences were similar in different lakes.

Life-history patterns

Length-at-age was significantly different between sympatric morphs (Fig. 3), with the densely rakered morphs consistently attaining a lower asymptotic length ($L\infty$; population range 144–257 mm) and a higher growth coefficient K (0.27–0.83) than sparsely rakered morphs ($L\infty$, 238–390 mm; K, 0.15–0.38). Large and significant differences further existed for body-length- at-maturity (Fig. 3), where the densely rakered morph had a lower length at maturity (Lm; population range 127–187 mm) than sparsely rakered morphs (227–290 mm). Age distributions were significantly different (Welch ANOVA, $P < 0.05$) between sympatric morphs in all lakes, where the densely rakered morphs (population range in means 3.67–8.30) were younger than the sparsely rakered morphs (4.69–9.53 years). Age-at-maturity differed significantly between morphs (Fig. 3), with densely rakered morphs maturing at between 2.1 and 5.0 years, and sparsely rakered at between 7.8 and 12.2 years.

Habitat use

Habitat use differed significantly between morphs in all the nine lakes ($R^2 = 0.02$–0.69, $N = 140$–910, all $P < 0.002$), with sparsely-rakered morph being more often caught in the benthic area (mean of 88.8%) than in pelagic areas (11.2%), while the densely rakered morphs were caught less often in benthic areas (25.7%) than in pelagic areas (74.3%). The nominal logistic analysis ($R^2 = 0.37$, $N = 2860$, $P < 0.0001$) supported that morphs used different habitats (Wald $\chi^2 = 571.2$, $P < 0.0001$), but also that the proportion of morphs in the two habitats varied between lakes (Wald $\chi^2 = 264.5$, $P < 0.0001$). The habitat overlap ($D_{habitat}$) in pelagic and benthic areas ranged between 0.13 and 0.58, with a mean of 0.28 in seven of the nine lakes (Table 2). *CPUE* data confirmed this pattern (Table 2), with more of the sparsely rakered morphs (mean *CPUE* = 13.4) than densely rakered morphs (3.6) caught in the benthic areas ($R^2 = 0.58$, $N = 14$, $P = 0.002$). In contrast, densely rakered morphs (mean *CPUE* = 15.3) were more frequent in the pelagic areas than sparsely rakered morphs (0.9) ($R^2 = 0.42$, $N = 14$, $P = 0.013$).

Diet composition

Sympatric morphs had different diet composition in all lakes (Table 2). The sparsely rakered morphs ate less zooplankton (12.6% vs. 53.3%) and more molluscs (26.0% vs. 0.8%) than densely rakered morph ($R^2 = 0.51$, $N = 14$, $P = 0.004$). For surface insects, chironomid pupae, benthic crustaceans, and insect larvae, however, no significant differences were observed ($P > 0.05$). The diet breadth (B_{diet}) was significantly smaller ($R^2 = 0.64$, $P = 0.0006$) in densely rakered morphs (mean 1.60, range 1.14–2.19) than in sparsely rakered morphs (3.94, 2.25–5.52) (Table 2). The diet overlap (D_{diet}) was typically low between morphs with mean of 0.30, and range of 0.14–0.49 across lakes.

Specialization and divergence

A dendrogram constructed from the composite morphological and ecological measures, suggested only two distinct branches (Fig. 4), each one representing one of the two morphs. Also, populations from the same watercourse did not cluster together.

Genetic analysis

The six microsatellite loci were variable in all samples, except the *C2-157* locus in Lake Ladnetjavri (Table 1; Alta watercourse) where both sparsely rakered and densely rakered morphs featured only one allele (Table 3). Deviation from Hardy–Weinberg proportions was common among tests within locus/sample with eight tests and six populations remaining significant after a sequential Bonferroni correction (Table 3). All but one of these cases showed a significant deficiency of heterozygotes, and four observed at the *Cocl-23* locus. There were no significant patterns among the morphs or locations in deviation from HW equilibrium.

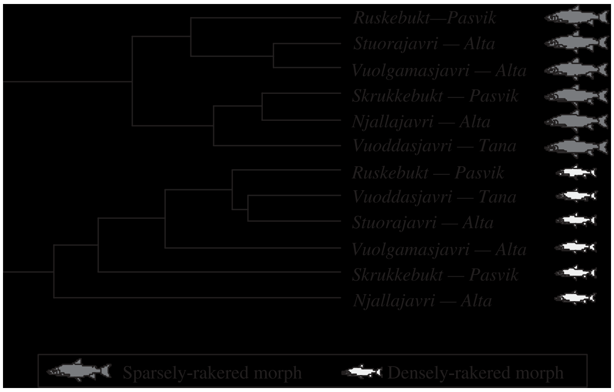

Fig. 4 Dendrogram based on morphology (gill-raker numbers), life history ($L\infty$, K, Lm, Am), habitat preference (*CPUE* in benthic and pelagic habitat), and diet use (percentage occurrence) in morphs from six of the nine lakes in three watercourses.

Null alleles were suggested in nine locus-x-population combinations out of a total of 106 tests. Two populations had two significant null-allele loci; both were densely rakered whitefish in Lake Vuoddasjavri and Lake Vuolgomasjavri, respectively. The locus-specific presence of null alleles was; *C1-g* (2 cases), *Cocl-23* (2), *SsBgIIIM.26* (1), *Bwf2* (2), *C2-157* (2), and *Bwf1* (0). The difference between observed allele frequencies and the adjusted allele frequencies, following null allele estimation, was minor in most cases and exceeded one standard deviation of the allele frequency estimate in only nine out of 75 adjustments of allele frequencies. Null alleles therefore were considered unlikely to substantially impact on the following results.

The total genetic variability within samples showed a significant geographical pattern, with allelic richness (*Ar*), observed heterozygosity (H_O) and expected heterozygosity (H_E) decreasing ($P < 0.001$ in all cases) from the easternmost watercourse (Pasvik; *Ar*: H_O: H_E estimates of 9.14: 0.81: 0.82) through Tana (6.57: 0.64: 0.66) to the westernmost watercourse (Alta; 4.32: 0.49: 0.51). There was no significant difference in the level of genetic variability between sparsely and densely rakered morphs ($P > 0.60$), although the former showed a higher expected heterozygosity than the latter in seven of the nine lakes (see Table 3).

In all but one lake, the two morphs were significantly genetically differentiated based on genotypic frequency differences (after Bonferroni corrections) with a pairwise F_{ST} from 0.010 (Vuolgamasjavri) to 0.075 (Ladnetjavri) (the Alta watercourse). In Lake Iddjajavri (the Tana watercourse), morphs were not significantly different ($P = 0.22$).

A dendrogram based on microsatellite genetic distances (Fig. 5), and including the outgroup from Lake Femund, showed that the major branches corresponded to the four watercourses. In Lake Vuolgamasjavri and Iddjajavri, sparsely and densely rakered morphs clustered together in their respective lakes with moderate bootstrap support. Two triplets of lakes were evident, where there was only low support for further genetic resolution; the first being Lake Njallajavri, Ladnetjavri and Stuorajavri, and the second being Lake Vaggatem, Skrukkebukt and Ruskebukt. Additional support for this scenario came from the Bayesian clustering analysis, which suggested a total of seven genetic groups (see Fig. 5a, b). In the Alta River, populations grouped as follows: (i) Stuorajavri sparsely (S) and densely rakered morphs (D) + Njallajavri S and D + Ladnetjavri S and D, (ii) Vuolgomasjavri S and D. In the Tana River, two

Table 3 Genetic variability at six microsatellite loci in sympatric pairs of sparsely rakered (SRM) and densely rakered whitefish morphs (DRM) estimated as number of alleles at each locus (A), allele richness (Ar), range of allele size in bp (R), observed heterozygosity (H_O), and gene diversity (H_E). All the loci deviating significantly from Hardy–Weinberg equilibrium are marked as * after sequential Bonferroni adjustment of significance levels. The overall Ar estimate is the arithmetic mean of Ar of all loci within each of the 18 populations

Location	Morph (N tot)		*SsBgIIIM.26*	*Cocl-23*	*Bwf2*	*C1-g*	*C2-157*	*Bwf1*	Overall
Vaggatem	SRM (20)	A	10	11	6	17	7	7	56
		Ar	9.1	10.1	5.6	15.0	7.0	6.6	8.90
		R	155–207	158–302	155–165	190–302	127–157	217–229	—
		H_O	0.800	0.850	0.700	0.900	0.900	0.550	0.783
		H_E	0.796	0.850	0.626	0.917	0.846	0.755	0.798
	DRM (18)	A	9	10	4	17	9	8	57
		Ar	8.3	9.6	4.0	16.4	8.9	7.9	9.18
		R	155–207	258–296	155–161	192–250	127–157	217–229	—
		H_O	0.611	0.889	0.389	0.833	0.944	0.667	0.722
		H_E	0.639	0.864	0.562	0.958	0.881	0.810	0.786
Ruskebukt	SRM (21)	A	10	11	7	10	10	7	55
		Ar	8.9	9.8	6.3	9.3	9.3	6.7	8.38
		R	155–203	258–302	151–163	194–238	127–159	209–229	—
		H_O	0.762	0.700	0.810	1.000	0.524	0.619	0.736
		H_E	0.789	0.821	0.786	0.875	0.846	0.781	0.816
	DRM (24)	A	3	11	9	15	11	8	57
		Ar	3.0	10.3	7.8	12.2	9.4	7.5	8.37
		R	155–201	258–300	151–169	196–240	127–159	215–229	—
		H_O	0.235	0.958	0.875	0.833	0.708	0.750	0.810
		H_E	0.318	0.895	0.813	0.886	0.863	0.810	0.822
Skrukkebukt	SRM (70)	A	15	21	10	21	15	8	90
		Ar	9.5	12.7	7.3	11.2	9.5	6.7	9.75
		R	155–201	258–306	149–167	188–264	127–169	209–229	—
		H_O	0.759*	0.871	0.783	0.929	0.800	0.783	0.823*
		H_E	0.797	0.900	0.818	0.875	0.861	0.785	0.841
	DRM (45)	A	15	14	11	25	12	9	86
		Ar	9.5	9.6	8.2	16.1	8.2	6.9	9.48
		R	155–207	250–300	149–167	178–248	123–167	217–233	—
		H_O	0.854	0.822	0.867	0.889	0.911	0.800	0.857*
		H_E	0.753	0.810	0.781	0.933	0.816	0.790	0.815
Vuoddasjavri	SRM (34)	A	5	10	4	15	10	5	49
		Ar	3.9	7.8	4.0	10.4	8.1	4.5	6.45
		R	155–203	190–300	155–161	194–238	127–155	217–229	—
		H_O	0.676	0.824	0.647	0.824	0.765	0.647	0.730
		H_E	0.576	0.740	0.631	0.822	0.782	0.618	0.695
	DRM (33)	A	7	8	5	16	9	9	54
		Ar	5.3	6.7	4.2	11.2	7.3	6.8	6.92
		R	155–203	258–294	153–163	190–248	127–155	212–229	—
		H_O	0.303	0.636*	0.424	0.758	0.606	0.667	0.566*
		H_E	0.440	0.712	0.598	0.749	0.723	0.625	0.641
Iddjajavri	SRM (26)	A	3	8	5	13	7	8	44
		Ar	2.5	7.3	4.9	11.4	6.2	6.8	6.52
		R	155–197	258–300	153–161	204–238	127–161	217–233	—
		H_O	0.091	0.652	0.731	0.739	0.560	0.783	0.599
		H_E	0.090	0.745	0.740	0.863	0.639	0.652	0.628
	DRM (24)	A	3	10	6	11	7	5	42
		Ar	3.0	8.4	5.6	11.0	6.2	4.3	4.2
		R	155–201	258–300	153–163	194–238	127–155	219–229	—
		H_O	0.235	0.478*	0.833	0.813	0.792	0.739	0.661*
		H_E	0.318	0.772	0.766	0.848	0.716	0.581	0.675
Stuorajavri	SRM (58)	A	7	10	4	8	3	5	37
		Ar	4.9	6.0	3.2	5.6	1.6	3.2	4.08
		R	155–207	256–296	153–161	216–234	127–161	203–229	—
		H_O	0.667	0.603*	0.534	0.638	0.034	0.431	0.484
		H_E	0.646	0.729	0.476	0.639	0.034	0.477	0.498

Table 3 *Continued*

Location	Morph (N tot)		*SsBgIIIM.26*	*Cocl-23*	*Bwf2*	*C1-g*	*C2-157*	*Bwf1*	Overall
	DRM (52)	A	6	7	4	8	5	3	33
		Ar	3.9	4.7	2.8	8.9	2.7	2.5	4.25
		R	155–203	258–294	155–163	216–258	123–153	219–227	—
		H_O	0.571	0.692	0.269	0.700	0.115	0.462	0.466
		H_E	0.592	0.603	0.271	0.654	0.112	0.463	0.446
Njallajavri	SRM (32)	A	5	9	3	4	4	6	31
		Ar	4.5	7.4	2.5	3.3	3.0	4.9	4.27
		R	155–203	258–296	155–161	216–234	127–157	219–233	—
		H_O	0.625	0.867	0.438	0.400	0.063*	0.500	0.479
		H_E	0.583	0.800	0.479	0.518	0.152	0.495	0.501
	DRM (22)	A	4	6	3	6	2	6	27
		Ar	3.5	5.8	3.0	5.8	1.7	5.4	4.20
		R	155–201	258–292	155–161	216–234	127–131	219–231	—
		H_O	0.667	0.750	0.455	0.667	0.045	0.600	0.520
		H_E	0.526	0.749	0.415	0.596	0.045	0.637	0.485
Vuolgamasjavri	SRM (42)	A	7	8	5	10	5	8	43
		Ar	4.8	86.1	4.7	7.2	3.8	5.9	5.42
		R	155–205	250–296	153–161	214–254	131–155	203–231	—
		H_O	0.750	0.675	0.643	0.615*	0.341	0.500	0.586*
		H_E	0.602	0.733	0.656	0.757	0.304	0.587	0.605
	DRM (46)	A	7	5	8	11	4	4	39
		Ar	4.9	4.6	4.5	8.3	2.8	3.5	4.77
		R	155–203	258–292	153–191	214–236	131–149	217–229	—
		H_O	0.652	0.756	0.217*	0.556*	0.174	0.500	0.474*
		H_E	0.646	0.624	0.591	0.801	0.164	0.580	0.567
Ladnetjavri	SRM (24)	A	4	7	4	5	1	6	27
		Ar	3.8	6.5	3.8	4.0	1.0	5.1	4.03
		R	155–201	258–296	155–163	216–234	131	217–229	—
		H_O	0.762	0.750	0.667	0.458	0.0	0.625	0.539
		H_E	0.629	0.793	0.583	0.492	0.0	0.611	0.516
	DRM (24)	A	5	8	3	8	1	3	30
		Ar	4.3	6.7	2.9	6.6	1.0	2.7	4.03
		R	155–203	248–290	155–165	216–232	131	219–227	—
		H_O	0.348	0.522*	0.375	0.500	0.0	0.364	0.348
		H_E	0.432	0.693	0.322	0.495	0.0	0.531	0.407

groups were evident: (iii) Vuoddasjavri S and D, (iv) Iddjajavri S and D. In the Pasvik River, one group was found: (v) Vaggatem S and D + Ruskebukt S and D + Skrukkebukt S and D. Finally, in the Trysil River, two groups were resolved: (vi) Kvernvika and (vii) Vestfjorden + Tufsinga + Hallsteinvika. The Bayesian admixture analysis based on the prior clustering analysis graphically revealed moderate degrees of past, or present, gene flow among populations (Fig. 5).

In the AMOVA, the first analysis (all $P < 0.00001$) showed that 10% of the variation was distributed among the three rivers and 3.3% among populations within rivers. The second analysis (all $P < 0.00001$) showed that 8.5% of the variation was distributed among lakes and 2.3% of the variation between morphs. Finally, in the third analysis, 0% of the variation was distributed among the two morphs ($P = 0.76$), while 10.8% was distributed within the two morphs across lakes ($P < 0.00001$).

The distribution of private allelic richness followed the same general pattern as the distribution of molecular variance. When samples were standardized by rarefaction to 32 genes per sample, two morphs per lake and two lakes per watercourse, the private allelic richness varied from 4.9 in the Pasvik watercourse to 1.4 in the Tana and 0.8 in the Alta watercourses (averages across six loci). On a lower hierarchical level, lakes in the Pasvik watercourse had more private alleles (1.4–2.5) than most other lakes (< 0.6), with Lake Vuoddasjavri (1.1) in the Tana as a possible exception. Outside the Pasvik watercourse, Lake Vuoddasjavri was the only location where a private allele was shared by the two morphs. An alternative hierarchy, where the morphs were placed at the highest level, gave similar average

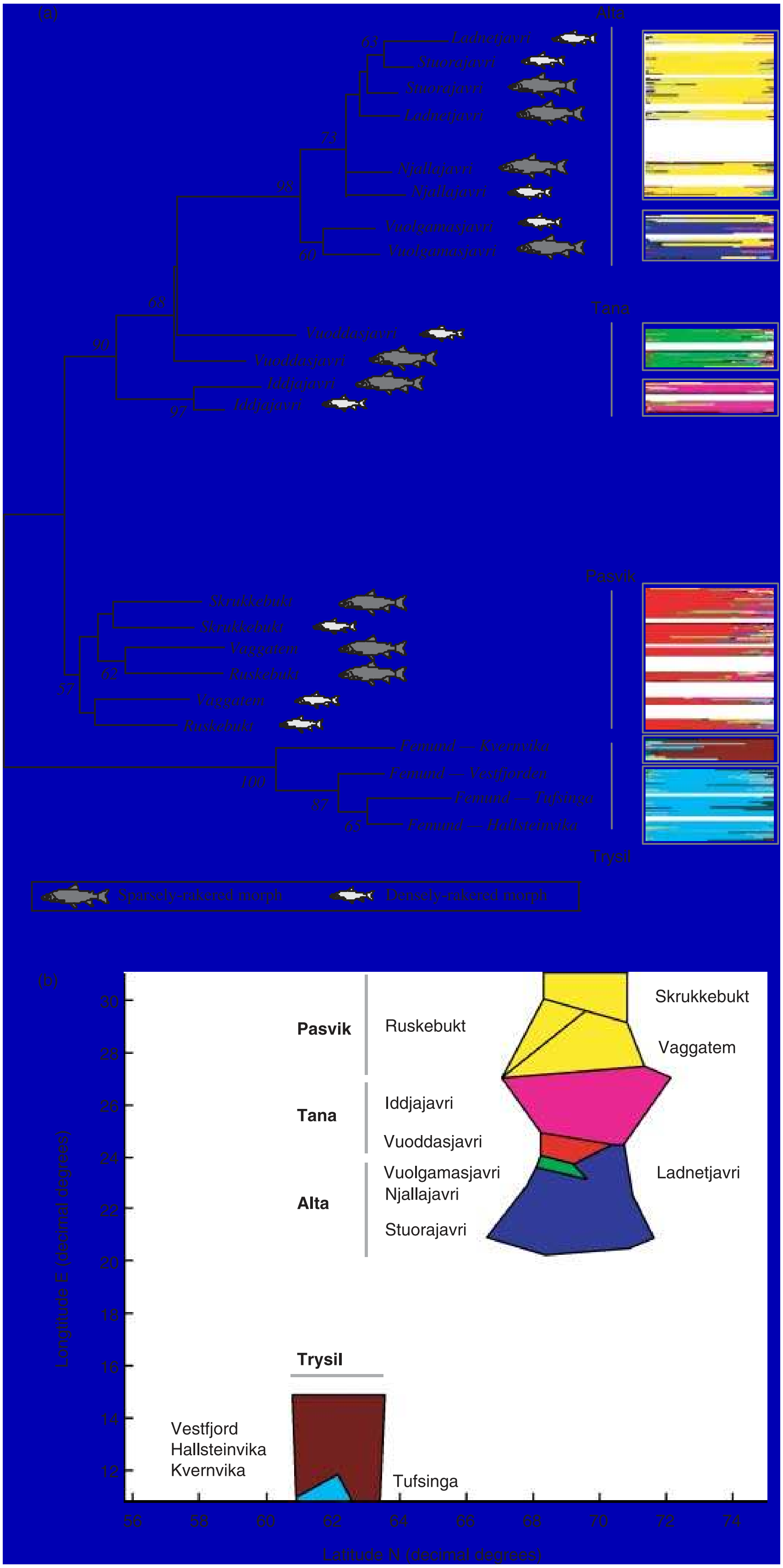

Fig. 5 (a) Neighbour-joining tree based on genetic (D_A) distance between populations. Bootstrap support (%) is based on 1000 runs. Colour bars on the right hand side are from the Bayesian admixture analysis; different colours are different genetic groups. (b) The Bayesian analysis of population structure onto a grid of geographical coordinates of the a priori 22 populations analysed. Watercourses are supplied. Note that colours in (a) and (b) are not identifying the same genetic groups.

values for private allelic richness for sparsely rakered and densely rakered morphs (3.0). Whereas significances are difficult to attach to these numbers (Kalinowski 2004), they suggest that evolution by morph has a more recent history than evolution by watercourse (and possibly, lakes) in this area.

Discussion

The sparsely rakered and densely rakered whitefish morphs were characterized by an almost nonoverlapping distribution of gill-raker numbers with very few intermediate individuals, and were found in sympatry in a number of lakes in northern Norway. The sparsely rakered morph had consistently fewer gill rakers than the densely rakered morph across lakes. Life history differed between morphs, with sparsely rakered morphs attaining a larger body size, and being larger and older at sexual maturity. Moreover, the smaller age range seen in the densely rakered morph likely suggests differential survival between morphs. The sparsely rakered morphs preferred the benthic zone, eating zoobenthos, while densely rakered morphs mainly ate zooplankton in the pelagic zone. The ecomorphological analysis clustered morphs in two separate branches, suggesting apparent 'monophyletic' origin of morphs. In contrast, genetic analysis indicated reproductive segregation of sympatric morphs, and clustered morphs together within watercourses (and partly, within lakes), thus supporting the parallel evolution and likely polyphyletic origin of these morphs. By combining genetic, phenotypic and ecological data, this revealed that sympatric and divergent whitefish morphs have likely arisen postglacially due to specialization for divergent foraging niches under influence of gene flow and resource competition. Our approach makes a joint evaluation of such parameters for inferring adaptive diversification of morphs. By gaining similar data from biogeographically 'independent' systems within the *Coregonus lavaretus* × *Coregonus clupeaformis* species complexes, general features of evolution can be supported.

Evolutionary scenarios behind sympatric morphs

Three main hypotheses may explain the sympatric occurrence of two morphs within several lakes: (i) secondary contact of two allopatrically evolved species, (ii) co-immigration of two ancient species/morphs, and (iii) a postglacial intralacustrine evolution of morphs. The three hypotheses may not be mutually exclusive.

If intralake polymorphisms stem from secondary contact of two allopatrically evolved species, we would expect to find that ecologically similar morphs cluster together on the microsatellite tree, and the presence of two mtDNA lineages reflecting their ancient history. There was no support in the microsatellite distance tree for a monophyletic origin of morphs. On the contrary, divergent morphs grouped together in their respective lakes and watercourses. This claim was also supported by the Bayesian analysis, which supported the microsatellite tree with regard to differentiation into watercourses. In addition, this analysis suggested moderate to high admixture of populations/morphs in close proximity. In an mtDNA phylogeographic survey (Østbye *et al*. 2005b), only the 'North European clade' was found in the study area. A 'South European clade' dominates in central Europe, reflecting a different glacial refugial occupation with few descendants in northern Fennoscandia. Alternatively, the merging of two such lineages through strongly sex-biased introgression, and purging of unfit hybrids, and/or lineage sorting through genetic drift could result in a single mtDNA lineage. However, this is unlikely to have occurred with equal magnitude in each of these lakes, although one cannot rigorously rule out the possibility that it could also have predated the colonization of these lakes.

Second, the occurrence of sympatric morphs could be due to one single colonization event of two ancient species/morphs immigrating simultaneously. Support for such a scenario could be that a within-lake origin of trait differences is unlikely due to insufficient time for divergence, that these morphs are remarkably similar across localities, and that traits are old and temporally stable. However, moderate to high heritability (h^2) (range: 0.30–0.70) have been reported for morphometric, meristic and life-history traits (Svärdson 1970; Mousseau & Roff 1987; Hatfield 1997), as well as for behavioural traits (Klemetsen *et al*. 2002; Rogers *et al*. 2002). This suggests that natural selection can be efficient in matching the environmentally dependent adaptive landscape. Indeed, the rate of divergence can be fast between salmonid populations that segregated only recently, even within less than 50 generations ago (e.g. Hendry & Kinnison 1999; Koskinen *et al*. 2002; Roberge *et al*. 2006). Similarity of morphs between lakes is expected if similar selection pressures prevail (e.g. Schluter 2000). Moreover, closely related species tend to vary in the same way phenotypically, which further implies that parallel inheritance of adaptive traits may lead to a genetic bias in ecological transitions (Schluter *et al*. 2004; Colosimo *et al*. 2005; Derome *et al*. 2006). Also, similarity of morphs may be due to pleiotropy in the genetic architecture, resulting in a collective inheritance of traits (Albertson *et al*. 2003; Derome *et al*. 2006), suggesting the presence of intertrait developmental constraints to evolutionary trajectories. The alternative suggestion that polymorphic traits may be ancestral and labile, appearing only when adaptive, cannot be easily ruled out. However, solitary densely rakered whitefish morphs are almost nonexisting in allopatry (at least in Fennoscandia), which suggests that it has evolved from the common sparsely rakered morph. Indeed, gill-raker distributions in the latter morph are 'constant' when comparing monomorphic and dimorphic lakes (Amundsen *et al.* 2004b), which supports an argument of this morph being the ancestral phenotype.

Third, if the occurrence of sympatric morphs is due to postglacial intralacustrine divergence, one would expect to find only one mtDNA lineage, and genetic clustering of divergent morphs in their respective lakes or watercourses on the microsatellite distance tree, as were indeed observed. This tree suggested a single colonization event into the Pasvik watercourse, with subsequent stepwise colonization into the Tana and Alta watercourses, with Tana and Alta watercourses only having alleles being a subset of those found in the Pasvik watercourse. The glacial geology also supports such a colonization route, as the Weichselian ice covered the northwestern areas prior to *c.* 9000 BP, with an earlier deglaciation of the northeastern parts of Fennoscandia (see Andersen & Borns 1994; Berglund *et al.* 1996). Based on an mtDNA survey, Østbye *et al.* (2005b) suggested that the main clade that colonized Fennoscandia, had a demographic inference of restricted gene flow/dispersal but with some long distance dispersal, and an estimated population expansion 11 700–5800 BP (based on 1–2% sequence divergence per million years), with an extremely small female effective population size (*Ne*). These conditions fit our results from the northern Norwegian watercourses, suggesting that a rapidly colonizing front lost genetic diversity, and yet, could colonize and successfully utilize these diverse habitats. The results of Østbye *et al.* (2005b) also suggested that the gill-raker diversity was associated with the youngest events (0-level clades, that is haplotypes) on the nested mtDNA hierarchy, thus implying a recent origin of divergence in gill-raker numbers, which is possible given a high heritability.

Further support for our interpretations as given above stems from the AMOVA analysis and the rarefaction analysis of private alleles. First, the results from our AMOVA analysis are very similar to Douglas *et al.* (1999) who studied polymorphic whitefish systems across lakes in the European Alps. We found that 8.5% of the variation was distributed among lakes and 2.3% of the variation between morphs while Douglas *et al.* (1999) had values of 4.7% and 4.7%, respectively. We also found that no significant part (0%) of the variation could be partitioned between morphs and that 10.8% was partitioned within morphs across lakes, being similar to Douglas *et al.* (1999) who found values of 0.8% (not significant) and 8.3%. In Lake Femund, Østbye *et al.* (2005a) found a higher component of variance (3.9%) between four morphs than among populations within morphs (2.8%). The higher geographical component than morphologically based component suggests that sympatric whitefish morphs in northern Norway are polyphyletic, with reproductive isolation building up after a postglacial colonization. The rarefaction analysis adds to these evaluations as sympatric morphs tended to have the same allelic richness and private allelic richness, while larger differences were observed between the three watercourses. Thus, a parallel recent polyphyletic origin of sympatric morphs seems plausible.

This study confirms that sympatric and morphologically divergent whitefish populations commonly occur in the whitefish evolutionary lineage associated with the North European mtDNA clade (see also Østbye *et al.* 2005b). In the whitefish lineage associated with the South European clade, Douglas *et al.* (1999) studied polymorphic whitefish in several lakes in the European Alps, and also suggested a scenario of multiple parallel origins of sympatric morphs. Polymorphic whitefish also exists in the contact zones between these lineages, but are apparently not contingent upon their genetical history (Østbye *et al.* 2005b), nor do these populations display increased divergence there, further implying that phenotypic divergence is not ancestral in *Coregonus* lineages. More support for a selection-driven, intralacustrine, adaptive divergence can be sought by a comparison with the North American lake whitefish (*C. clupeaformis* Mitchill) systems where sympatric morphs exist both within single mtDNA lineages, and in secondary contact zones of glacial mtDNA lineages (Bernatchez *et al.* 1996; Pigeon *et al.* 1997; Lu *et al.* 2001; Bernatchez 2004). Clearly, the parallel evolution of ecomorphological traits appears to be a generalized phenomenon within both the European whitefish and North American lake whitefish evolutionary lineages.

Ecological speciation in North Norwegian whitefish?

During the ecological speciation process, barriers to gene flow are predicted to evolve as a by-product of adaptation to divergent niches, where density-dependent resource competition and optimality in niche occupation are likely to be driving mechanisms. However, whether adaptive divergence constrains gene flow, or vice versa, whether gene flow constrains the level of adaptive divergence (Hendry & Taylor 2004) cannot be resolved in our study. If selection favours adaptation to divergent niches, we would expect an association between trait value and niche, that traits reflect functional adaptation, and that divergent traits in sympatric morphs are replicated across similar lakes (Jastrebski & Robinson 2004). Our data suggest that there is an association between trait values and niche use as reflected in the divergent habitat- and diet preference of sympatric morphs. With regard to functionality of apparent adaptive traits, we have no direct data, but lend support from studies which suggest adaptive values of, e.g. the gill-raker apparatus (Robinson & Wilson 1994; Schluter 2000; Østbye *et al.* 2005a; Kahilainen & Østbye 2006). As such, our data suggest that evolution has repeatedly favoured the same trait combinations in different lakes with regard to divergent niches as morphs are strikingly similar between lakes. Our genetic data support this suggestion. The results from morphology, life history, habitat and diet use of the North Norwegian sympatric whitefish morphs, show strong similarities with other northern freshwater fish species which harbour sympatric morphs (Bodaly 1979; Mann & McCart 1981; Robinson & Wilson 1994; Gillespie & Fox 2003).

Diet and habitat patterns are difficult to evaluate as they are often studied during limited periods of time and in small parts of the home-range of a population. Yet, our data showed a consistent pattern with sparsely rakered morphs using benthic niches, and densely rakered morphs mainly utilizing pelagic niches, but also benthic niches to a lesser degree. Thus, adaptation to a pelagic or benthic environment may not strictly preclude use of the opposite niche when needed. In general, monomorphic whitefish stocks are commonly characterized as a sparsely rakered diet- and habitat generalists in benthic and pelagic areas, while dimorphic stocks partition pelagic and benthic niches (Amundsen *et al*. 2004a, b). In lakes with more morphs, a further dissection of niches has occurred presumably due to natural selection matching a higher complexity of lake ecosystems (Bergstrand 1982; Kahilainen *et al*. 2004). Also, parasite data as ecological markers of former trophic niche support the ecological diversification of sympatric whitefish morphs in, e.g. Stuorajavri (Petersson 1971; Knudsen *et al*. 2003).

The repeated patterns of sympatric divergence observed in this study suggest that antagonistic ecological selection in the two niches is strong enough to be effective despite potential for gene flow between morphs. In support to this, Lu & Bernatchez (1999) observed an increased phenotypic divergence associated with increased reproductive isolation in the lake whitefish. Potentially important factors for build-up of reproductive isolation may be prezygotic factors such as distance between spawning sites (isolation by distance), spawning time (isolation by time), and mate-choice (see Kawecki & Ebert 2004; Hendry & Day 2005). Moreover, Rogers & Bernatchez (2006) provided evidence of a genetic basis for increased embryonic mortality followed by asynchronous emergence, which indicated that intrinsic and extrinsic post-zygotic mechanisms are not mutually exclusive in the formation and maintenance of reproductive isolation but may be jointly promoting population divergence in North American sympatric lake whitefish ecotypes. Here, however, we would not expect the evolution of pronounced intrinsic post–zygotic barriers because the origin of these populations is much younger than in the case of sympatric lake whitefish ecotypes which are derived from a history of secondary contact between older lineages. In such a case, ecological selection is more likely to act negatively on hybrids being mal-adapted to both niches (Schluter 2000, 2003; Coyne & Orr 2004; Rogers & Bernatchez 2006). Indeed, the low intermediate frequency of fish in the joint gill-raker distribution of sympatric whitefish morphs in all our lakes, suggests that intermediate fish may be less fit ecologically, or the occurrence of assortative mating within lakes, thus driving these morphs apart. Strong indications for rapid evolution of assortative mating based on body size are found in recently evolved cichlid taxa (see, e.g. Schliewen *et al*. 2001; Dieckmann *et al*. 2004).

Resource competition has been suggested as the driving mechanism behind adaptive niche segregation in ecological speciation, although empirical support for this is relatively scarce. In the Pasvik watercourse, introduced vendace *Coregonus albula* displaced the densely rakered pelagic whitefish morph to the benthic habitat increasing its competition with the sparsely rakered benthic whitefish (Amundsen *et al*. 1999; Bøhn & Amundsen 2001, 2004; Bøhn *et al*. 2004). In northern America, sympatric lake whitefish morphs are not found in lakes with pelagic zooplanktivore lake cisco *Coregonus artedii* (Bernatchez 2004). Even within vendace, and the least cisco (*C. sardinella*), resource and habitat partitioning is evident for sympatric populations, likely mediated through competition (Mann & McCart 1981; Schulz *et al*. 2006). In the absence of a specialist, the European whitefish seems to partition available niches in a way as to occupy the competitors' ecological function. Fennoscandian whitefish range from monomorphic, to sympatric polymorphic stocks with two, three or four morphs (Svärdson 1957; Bergstrand 1982; Kahilainen *et al*. 2004; Østbye *et al*. 2005a, b). This pattern can be interpreted as character release, with a subsequent widening of niche. Amundsen *et al*. (2004b), comparing Norwegian lakes, showed that this may be a likely mechanism, as the resource partitioning and habitat diversification did increase in dimorphic lakes when compared to monomorphic systems. It is not known what are the consequences of such resource competition on the diverging whitefish populations with regard to physiology or overall fitness (but see Trudel *et al*. 2001; Derome *et al*. 2006).

Taxonomical considerations

Our results suggest that the traditional habit of naming whitefish species strictly based on phenotype is misleading from an evolutionary standpoint since the very same species/morphs apparently evolved in parallel several times. In the phylogeographical study of Østbye *et al*. (2005b), similar gill-raker groups were found in the North- and South European mtDNA clades, which also suggested that similar gill-raker numbers evolved in parallel due to selection. Also, a polyphyletic origin of North American lake whitefish (Lu *et al*. 2001), as well as evidence that Alpine whitefish of the South European mtDNA clade actually represent species flocks with an intralacustrine origin (Douglas *et al*. 1999, 2005), add serious concern to the validity of nomenclature used. Clearly, the traditional taxonomy and nomenclatural settings within the genus *Coregonus* need to be revised using both molecular and ecomorphological data (Kottelat 1997).

Conclusion and prospects

In summary, our results provide evidence for parallel and rapid postglacial divergence of partly reproductively isolated sympatric whitefish morphs specialized to differential occupation in the pelagic and benthic niches in each lake. We suggest that the sparsely and densely rakered whitefish sympatric pairs likely represent replicated events of ecological speciation, i.e. parallel evolution within a single evolutionary lineage, mediated in lakes with few trophic competitors. Future research directions of these populations should target the genetic basis for parallel diversification of whitefish morphs by means of functional genomics approaches, including QTL mapping and analyses of gene transcription, and to document the effects of genomic introgression on adaptive differentiation. These studies should remain embedded into a strong ecological framework.

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