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# Contrasting niche-based variation in trophic morphology within Arctic charr populations

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## ABSTRACT

**Hypothesis:** The opportunity for inter-individual niche differences in contrasting resource environments can induce divergent natural selection in trophic morphology within single gene pools.

**Organisms:** Arctic charr (*Salvelinus alpinus*) caught in the littoral and pelagic habitats of two neighbouring sub-arctic lakes.

**Field sites**: Two post-glacial lakes (Fjellfrøsvatn and Lille Rostavatn, North Norway) of similar size and physical structures, but with different fish diversities (two and six species, respectively).

**Methods:** Analysis and comparison of trophic niche (habitat and diet usage) and trophic morphology (body form and head structure) data from individual fish. Only immature charr 19–25 cm long were used to reduce the effects of allometric growth and secondary sex traits.

**Conclusions:** The utilization of multiple resource types has facilitated incipient steps towards the evolution of polymorphism in one lake, but not in the other. In Fjellfrøsvatn, individual specializations in benthivore and planktivore diet niches are correlated with inter-individual morphological differentiation. In contrast, the Arctic charr in Lille Rostavatn were restricted to zooplanktivory, and distinct morphological diversification was absent. We conclude that the two lakes have dissimilar opportunities for individual niche specialization and evolution of polymorphism.

*Keywords*: adaptive trophic morphology, feeding, incipient speciation, polymorphism, post-glacial fish, *Salvelinus alpinus*.

## INTRODUCTION

Pelagic and littoral morphs with dietary specialization on plankton and benthos constitute a recurrent pattern of resource polymorphism in lacustrine post-glacial fishes (Skúlason and Smith, 1995; Taylor, 1999; Schluter, 2001). Recent theoretical models suggest that resource competition

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in the presence of a trade-off associated with resource exploitation can lead to adaptive diversification for different resource types and subsequent segregation of a population into the above specialized forms (Dieckmann and Doebeli, 1999; Schluter, 2000; Bolnick, 2004; Doebeli *et al.*, 2005). In vertebrates, the first stages of incipient speciation are suggested to involve divergence in trophic behaviour [e.g. dietary and habitat selection (West-Eberhardt, 1989; Skúlason *et al.*, 1999)], usually followed by subsequent adaptive modifications in morphology (Skúlason *et al.*, 1999; Streelman and Danley, 2003). Individual specialization to a narrow trophic niche may facilitate selection for specific favourable trophic traits (Bolnick *et al.*, 2003), and may be an initial step in incipient trophic diversification and subsequent adaptive speciation from a single population gene pool (Ackermann and Doebeli, 2004). Differences in feeding behaviour and trophic morphology (head structures related to feeding) within a population may thus represent an early phase in the evolution of polymorphism (Skúlason and Smith, 1995; McLaughlin, 2001; Swanson *et al.*, 2003), and individual differences within single populations can be of great adaptive importance in morph formation and speciation (Wilson, 1998). In the present study, we compared the morphology of two populations of Arctic charr (*Salvelinus alpinus*) from littoral and pelagic habitats in their lakes. The main objective was to examine whether inter-individual resource specializations were associated with niche-dependent adaptations in body form and trophic morphology, and thus represent an initial step in sympatric morph formation.

Divergence in morphology is common in northern post-glacial freshwater fish populations and often represents adaptive responses related to littoral or pelagic habitat specialization (Robinson and Parsons, 2002). Arctic charr populations are excellent model organisms for studying adaptive divergence because they provide many cases with different degrees of incipient speciation (Gislason *et al.*, 1999; Skúlason *et al.*, 1999). Polymorphic populations are often segregated along the littoral–pelagic habitat axis (Sandlund *et al.*, 1992; Adams *et al.*, 1998; Skúlason *et al.*, 1999; Jonsson and Jonsson, 2001; Klemetsen *et al.*, 2003a). Genetic differences in trophic behaviour and ecomorphological traits between sympatric charr morphs have been observed (Skúlason *et al.*, 1993; Mikheev *et al.*, 1996; Adams *et al.*, 1998; McLaughlin, 2001; Adams and Huntingford, 2002a, 2002b; Klemetsen *et al.*, 2002, 2006; Sacotte and Magnan, 2006). Monomorphic populations are also known to utilize both the pelagic and the littoral zones (Klemetsen *et al.* 1989, 2003a, 2003b; Langeland *et al.*, 1991) and individual charr are able to specialize in trophic niches over long periods (Amundsen, 1995; Curtis *et al.*, 1995; Knudsen, 1995; Knudsen *et al.*, 1996, 2004). Diet and habitat specialization triggers the evolution of niche-specific foraging tactics and adaptations in trophic morphology [e.g. zooplanktivorous versus benthic foragers (see Futuyma and Moreno, 1988; Bjøru and Sandlund, 1995; Schluter, 2000)].

Here, we examine the possible existence of inter-individual, niche-based differentiation in trophic morphology of Arctic charr in contrasting resource environments (the littoral and pelagic habitats) in two lakes where the charr populations differ in their resource utilization. In one lake (Fjellfrøsvatn) individual charr segregate in benthivorous and zooplanktivorous niches (Knudsen 1995), whereas in the other lake (Lille Rostavatn) the entire charr population is planktivorous (P.-A. Amundsen and R. Knudsen, unpublished data). The lakes are situated 5 km apart at the same elevation and in the same type of landscape, but in separate tributaries of a common watercourse. The physico-chemistry and morphometry of the two lakes are similar, whereas fish community composition differs markedly, with only two fish species present in Fjellfrøsvatn compared with six species in Lille Rostavatn. Different niche opportunities in the two lakes should promote the evolution of distinct morphological patterns in the two Arctic charr populations. We predicted a stronger niche-based divergence in the trophic morphology of the Arctic charr in Fjellfrøsvatn, where individual fish specialize in either benthivorous or planktivorous trophic niches, than in Lille Rostavatn, where most individual Arctic charr are planktivorous regardless of habitat utilization.

## MATERIALS AND METHODS

Fjellfrøsvatn (69°05′N, 19°20′E, 125 m above sea level) and Lille Rostavatn (69°00′N, 19°35′E, 102 m above sea level) are sub-arctic lakes located in separate tributaries of the Målselv watercourse in Troms County, North Norway. Both lakes are situated in mixed-forest landscapes dominated by Scots pine *Pinus silvestris* and birch *Betula pubescens*. The lakes are dimictic and oligotrophic with respective surface areas of 6.5 and 12.9 km$^2$ and maximum depths of 88 m and 92 m. Both lakes have well-developed pelagic, littoral, and profundal zones, with the profundal (>20 m depths) extending over about two-thirds of the surface areas. Helophyte and floating leaf vegetation is largely absent, but some beds with submerged charophytes *Nitella* sp. occur in the 5–12 m depth zone. The only fish species present in Fjellfrøsvatn are Arctic charr and brown trout (*Salmo trutta*). Brown trout consisted of 28.9% of the total littoral catches ($n = 761$) during the ice-free season (June to November) in a standard test-fishing with multi-mesh gillnets (see later) for four nights each month in all main lake habitats: littoral (<15 m depth), pelagic (>30 m depth), and profundal (>25 m depth) zones. A separate reproductively isolated morph of charr has been found in Fjellfrøsvatn (Klemetsen *et al.*, 1997; Knudsen *et al.*, 2006), but, being confined to the profundal zone of the lake, should not interfere with the objective of the present study. In contrast, Lille Rostavatn holds a fish community of six species. The two predominant species are Arctic charr and burbot (*Lota lota*), which consisted of 41% and 53.6%, respectively, of the total fish catch ($n = 130$) in the littoral zone. The burbot occurs only in the benthic habitat along with four less frequent species: brown trout, Atlantic salmon parr (*Salmo salar*), grayling (*Thymallus thymallus*), and minnows (*Phoxinus phoxinus*). Arctic charr was the only species caught in the pelagic zone in both lakes.

Mature Arctic charr develop secondary sex traits (Skarstein and Folstad, 1996). To limit this source of variation in our study, we restricted the morphological analyses to immature individuals. Immature Arctic charr were sampled from the littoral and pelagic habitats in Fjellfrøsvatn [$n = 72$; length: 21.5 ± 1.9 cm (mean ± standard deviation), range 18.9–25.1 cm; age: 5.2 ± 0.7 years, range 4–7 years] and Lille Rostavatn ($n = 68$; length: 21.6 ± 1.7 cm, range 18.9–25.0 cm; age: 3.4 ± 1.1 years, range 2–6 years) using multi-mesh gillnets (10, 12.5, 15, 18.5, 22, 26, 35, and 45 mm, knot to knot) in October 1997. Care was taken to use the same length ranges in both lakes, and we sampled narrow size ranges to reduce possible influences of allometric growth. The fish were measured (fork length) and then aged by surface reading of otoliths (Kristoffersen and Klemetsen, 1991). Each fish was individually photographed under identical light conditions using Kodak 64 ASA EPR Ectachrome film. The photographs were later digitized using the Kodak Photo CD-system, and morphological measurements were made using UTHSCSA Image Tool for Windows (Version 2.0). To determine body form and trophic morphology, 26 measurements (Fig. 1) were taken from the digitized photographs. Each photograph was separately calibrated to a common scale.

Prey items in the stomach contents of individual fish were identified and their relative volumetric contributions to total stomach fullness estimated according to Amundsen (1995). The food items were categorized as limnetic prey (zooplankton and pleuston) or benthic

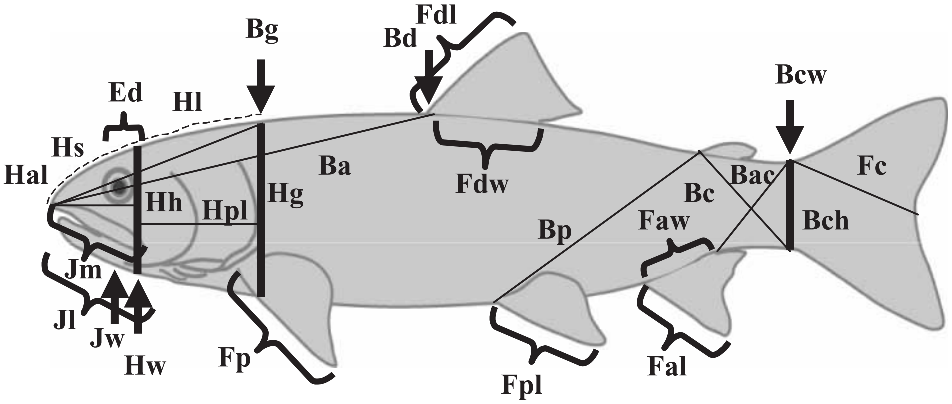


**Fig. 1.** Morphological characteristics measured from the left side of Arctic charr. Measurements with an arrow indicate where the width (maximum) was taken: (1) lower jaw length (Jl); (2) lower jaw width (Jw); (3) upper jaw length (Jm); (4) eye diameter (Ed); (5) head width (Hw); (6) head height (Hh); (7) head height behind gills (Hg); (8) posterior head length (Hpl); (9) head length (Hl); (10) anterior head length (Hal); (11) snout length, head curvature from the snout to back of the gills (Hs); (12) anterior body length from the snout to the dorsal fin (Ba); (13) ratio: Hs/Hl (Hc); (14) posterior body length from the anal fin to the adipose fin (Bp); (15) caudal height (Bch); (16) caudal peduncle length, from the adipose fin to ventral caudal height (Bc); (17) caudal peduncle length, anal fin to dorsal caudal height (Bac); (18) body width at gills (Bg); (19) body width at dorsal fin (Bd); (20) caudal body width (Bcw); (21) caudal fin length (Fc); (22) pectoral fin length (Fp); (23) dorsal fin length (Fdl); (24) dorsal fin width (Fdw); (25) pectoral fin length (Fpl); (26) anal fin length (Fal); (27) anal fin width (Faw).

prey (benthic crustaceans, molluscs, and insect larvae). Individual charr were categorized as belonging to either zooplanktivorous or benthivorous ecotypes based on the dominance (>50%) of limnetic or benthic prey in the stomach contents. Diet data of charr from other seasons in Fjellfrøsvatn are given by Knudsen (1995) and Klemetsen *et al.* (2003b) and in Lille Rostavatn by Knudsen *et al.* (2006).

Here, we defined trophic morphology as head and jaw structures, and body morphology as different body measurements and fin sizes according to Adams *et al.* (1998). To analyse variation in body shape, we first standardized for body size by dividing each morphometric measurement by fork length. We checked the validity of this length standardization by comparing results of statistical analyses with those obtained after an allometric standardization (Reist, 1986; following an analysis of covariance – see Hendry and Taylor, 2004). Statistical results were consistent, confirming the reliability of ratios of traits to body length (presented here). The morphometric variables, chosen on the basis of functional considerations corroborated by experimental and comparative research on salmonids, were expected to be collinear due to correlational selection. We explored morphological differences among and within lakes by discriminant analysis, grouping individuals within a lake by habitat used. Following discriminant analysis among lakes, we used analyses of variance to determine whether the morphological variables that contributed to group separation differed significantly between lakes. We used principal component analysis to study the covariation between standardized morphometric measurements within lakes. The relationship between morphometry and habitat use within each lake was first investigated indirectly using the scores for the first two principal components in two-way analyses of variance with factors habitat and sex. The frequency distributions of scores for the first and second principal components were inspected by diagnostic plots to check for bimodality, to obtain an additional indication of the extent of morphological separation between ecotypes. To test the modality of principal component scores, we used Hartigan's Dip test (Hartigan and Hartigan, 1985). The association between resource use and morphometry within lakes was further analysed using direct multivariate methods. We used linear discriminant analysis to provide a measure of morphometric separation among habitats. Finally, we modelled morphometry as a function of diet using redundancy analysis (RDA), a direct ordination technique that first relates the response variables to the explanatory variables by regression, and then performs a (constrained) ordination on the predicted values of the response variables (Legendre and Legendre, 1998). The RDA models were tested by Monte Carlo permutation. We performed the above analyses using the statistical softwares R and CANOCO (Ter Braak and Smilauer, 2002).

## RESULTS

The diet of Arctic charr caught in both the pelagic and littoral habitats in Lille Rostavatn was dominated by zooplankton (93% of total diet; Fig. 2). The cladoceran *Daphnia* sp. contributed 92% of the zooplankton. Only two of 37 charr from the littoral zone had a dominance (>50%) of benthic prey (*Gammarus lacustris*) in their stomachs, whereas the pelagic charr had exclusively consumed zooplankton. The pelagic charr in Fjellfrøsvatn had also predominantly eaten zooplankton (92.8% of total diet), and were all classified as zooplanktivores on the basis of a dominance (>50%) of limnetic prey (cladocerans, copepods, and some pleuston) in their stomachs. In contrast, benthic prey dominated the diet of the Fjellfrøsvatn charr in the littoral zone (Fig. 2). Only seven fish (11.7%) from the littoral catches were classified as zooplanktivores, with a mean of 84% zooplankton in their stomachs. The other Arctic charr were classified as benthivorous fish by the dominance (>50%) of benthic prey (*Gammarus*, insect larvae, molluscs, and chydorids) in their stomachs, and had a mean of 91.3% benthos in their diets.

There were clear differences in morphology of Arctic charr between Lille Rostavatn and Fjellfrøsvatn (Fig. 3). Arctic charr from Fjellfrøsvatn had larger eye diameters ($F_{1,138} = 102.2$, $P < 0.01$), longer pectoral fins ($F_{1,138} = 79.8$, $P < 0.01$), and greater head depths ($F_{1,138} = 28.9$, $P < 0.01$) than charr from Lille Rostavatn. The charr in Lille Rostavatn had slightly larger anal fins ($F_{1,138} = 29.2$, $P < 0.01$) than those in Fjellfrøsvatn. The morphological variables that discriminated between lakes also partly distinguished fish according to habitat used along the second discriminant axis.

Morphometric measurements were highly collinear within lakes. The first two principal components accounted for about 46% and 50% of total morphometric variation in Fjellfrøsvatn and Lille Rostavatn, respectively (Fig. 4). Some morphological variables separated the fish in both lakes, including head length and depth, and anterior body length. The main sources of morphometric variation were fin and jaw length in Lille Rostavatn and several body form measurements in Fjellfrøsvatn.

In Fjellfrøsvatn, both the first and second discriminant axes based on Arctic charr morphology allow a significant separation of groups of fish that use different diets (e.g. benthos and zooplankton). A linear discriminant analysis (LDA) correctly predicted group affiliation for 92% of benthivorous and zooplanktivorous ecotypes. Sample scores for the first principal component differed markedly between habitats ($P < 0.01$; Figs. 5 and 6), but

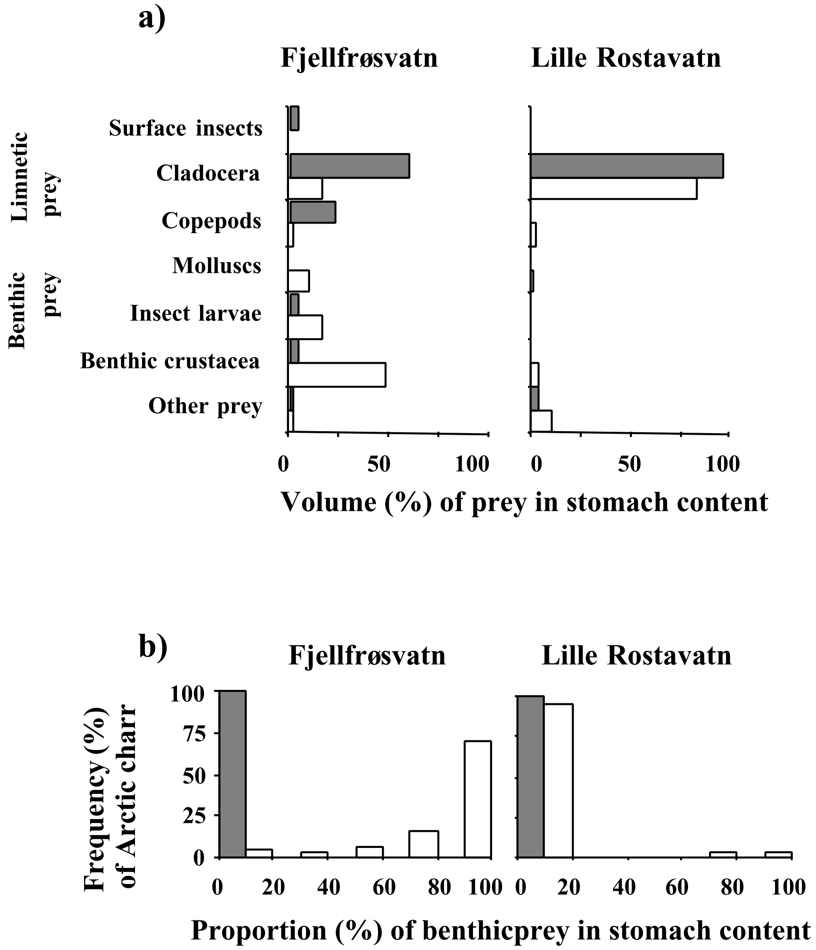


**Fig. 2.** (a) Diet composition (relative volumetric contributions) and (b) proportion of benthic prey in stomachs of Arctic charr caught in littoral (open bars) and pelagic habitats (grey bars) in Fjellfrøsvatn and Lille Rostavatn.

showed only minor differences between the sexes ($P = 0.36$; Fig. 5). Sex seemed to contribute more to the morphological variation captured by the second principal component, the difference between the sexes being contingent on the habitat used ($P = 0.057$; Fig. 5). A LDA correctly predicted habitat and sex group affiliation for 84% of the charr.

In Lille Rostavatn, the differences in morphology between habitats were much less pronounced for the first principal component and absent for the second (Figs. 5 and 6). Morphological differences between the sexes were detected only for the first component ($P < 0.03$; Fig. 5). A LDA correctly predicted habitat and sex group affiliation for 88% of the charr. The Dip test did not detect multimodality of principal component scores in either of the lakes.

Multivariate modelling (RDA) of charr morphology as a function of diet data produced different results in the two lakes (Fig. 7). In Fjellfrøsvatn, diet contributed significantly to

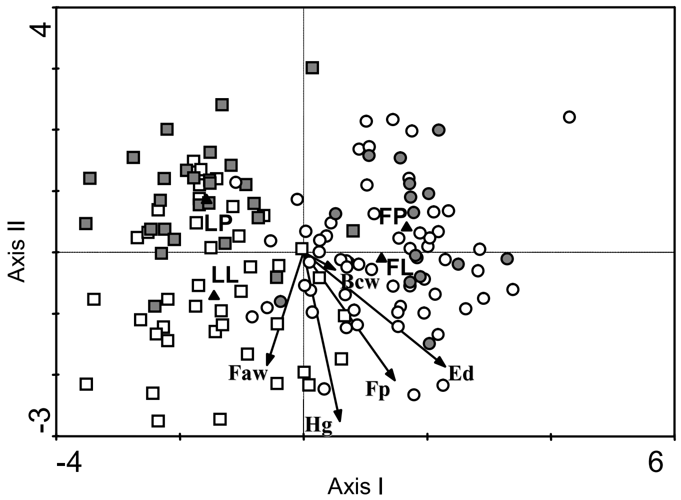


**Fig. 3.** First two discriminant axes showing morphological separation of Arctic charr from different lakes (Fjellfrøsvatn, circles; Lille Rostavatn, squares) and habitats (L = littoral, open symbols; P = pelagic, grey symbols); mean scores marked for each group. For abbreviations of morphological measurements, see Fig. 1.

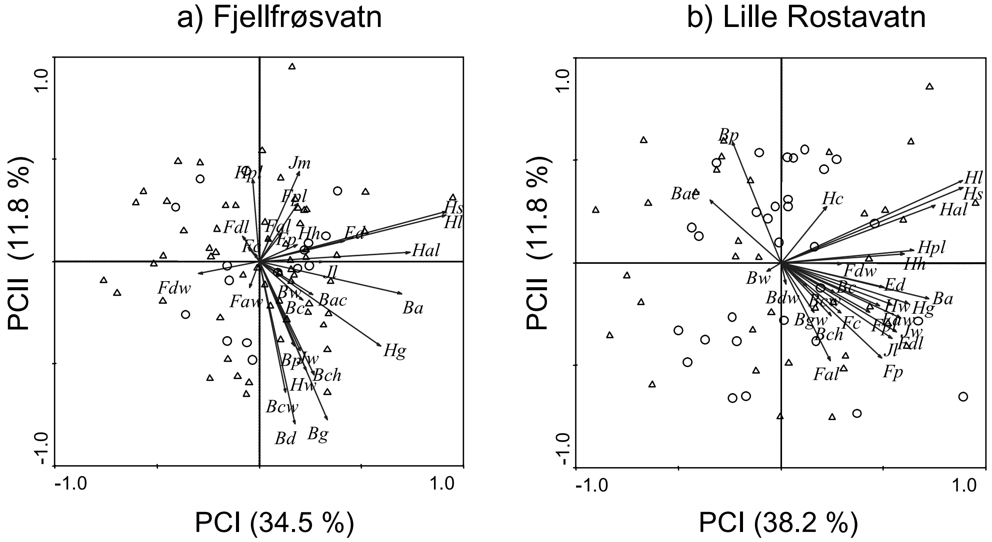
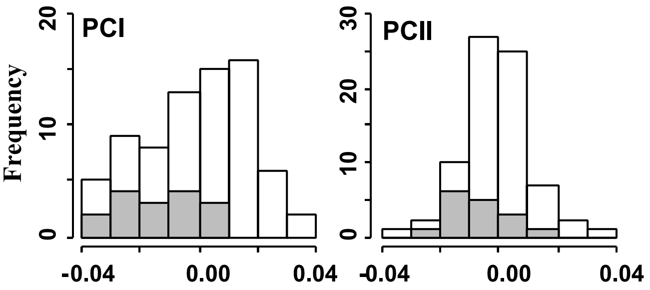


**Fig. 4.** Principal component analysis of Arctic charr morphology from (a) Fjellfrøsvatn and (b) Lille Rostavatn as a function of habitat (littoral = triangles, pelagic = circles). For abbreviations of morphological measurements, see Fig. 1.

variation in morphology (Monte Carlo test, $P = 0.002$). The first ordination axis separates littoral benthic prey (on the left) from pelagic prey (on the right). This diet gradient is significantly correlated (Monte Carlo test, $P = 0.008$) with several morphological variables, including variables that characterize trophic morphology. Fish feeding on littoral benthic

**a) Fjellfrøsvatn**



**b) Lille Rostavatn**

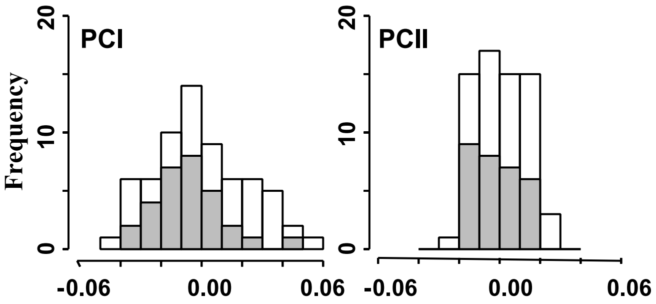


**Fig. 5.** Frequency distributions of scores for first and second principal components of Arctic charr morphology grouped by habitat used (pelagic fish in grey) in (a) Fjellfrøsvatn and (b) Lille Rostavatn.

prey have longer and broader jaws and heads, and broader bodies and longer posterior bodies (length from pelvic to anal fin). In Lille Rostavatn, variation in morphology was not significantly associated with Arctic charr diet (Monte Carlo test: axis I, $P = 0.256$; all axes, $P = 0.09$).

## DISCUSSION

Our results confirmed that morphology differed between Arctic charr populations in the two lakes. These pronounced inter-lake differences in morphological traits may represent adaptations to the local ecological and environmental conditions in each individual lake system as suggested by Gislason *et al.* (1999). Resource-based phenotypic differences within the populations varied from slight in Lille Rostavatn to large in Fjellfrøsvatn. In Lille Rostavatn, all specimens examined were zooplanktivorous, and the morphological differences between Arctic charr caught in littoral and pelagic habitats were insignificant. In Fjellfrøsvatn, in contrast, the differences in trophic morphology of charr confirmed the existence of benthivorous and zooplanktivorous ecotypes of fish within the same population. Diversification in benthivorous and zooplanktivorous diet niches associated with the littoral and pelagic habitats, respectively, is commonly found in other Arctic charr

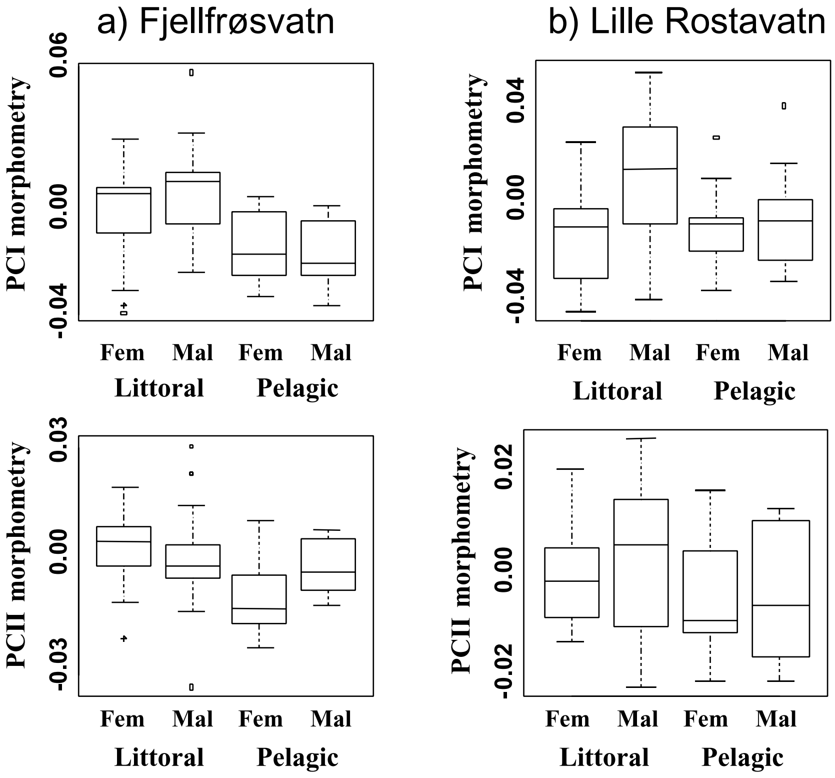


**Fig. 6.** Boxplots relating first and second principal components of Arctic charr morphology to resource used and sex in (a) Fjellfrøsvatn and (b) Lille Rostavatn. Fem = female, Mal = male.

lakes (Klemetsen *et al.*, 1989, 1997, 2003a; Langeland *et al.*, 1991; Bjøru and Sandlund, 1995) and among other post-glacial fishes (Skúlason and Smith, 1995; Bourke *et al.*, 1997; Dynes *et al.*, 1999; Taylor, 1999; Schluter, 2001; Bernatchez, 2004).

Divergences in the body form and trophic morphology of post-glacial fishes are thought to be specializations to pelagic and littoral habitats (e.g. Webb, 1984; Robinson and Parsons, 2002). The environmental conditions in the two lakes studied are uniform, as both have large pelagic habitats and littoral zones of similar relative sizes and physical structures. Thus, the lack of significant morphological differences between littoral and pelagic Arctic charr in Lille Rostavatn suggests that adaptations to environmental conditions *per se* are not sufficient to evolve divergence in morphological traits. This lake holds a complex fish community with a dense population of benthos-feeding burbot (54% of total catch) and co-occurring Atlantic salmon parr, minnows, brown trout, and grayling all feeding almost exclusively on benthos (P.-A. Amundsen and R. Knudsen, unpublished data). Thus, even Arctic charr caught in the littoral zone had obviously been forced to feed on planktonic cladocerans due to a high diet competition for zoobenthos. When co-occurring with benthivorous competitors, the Arctic charr often specialize in their population niche and become zooplanktivorous (Langeland *et al.*, 1991; Klemetsen *et al.*, 2003a). Strong interspecific competition tends to narrow both the population and the individual diet niche (e.g. Putman and Wratten, 1984; Bolnick *et al.*, 2003). Polymorphism in post-glacial fishes may arise from intraspecific resource competition, causing divergent intra-population

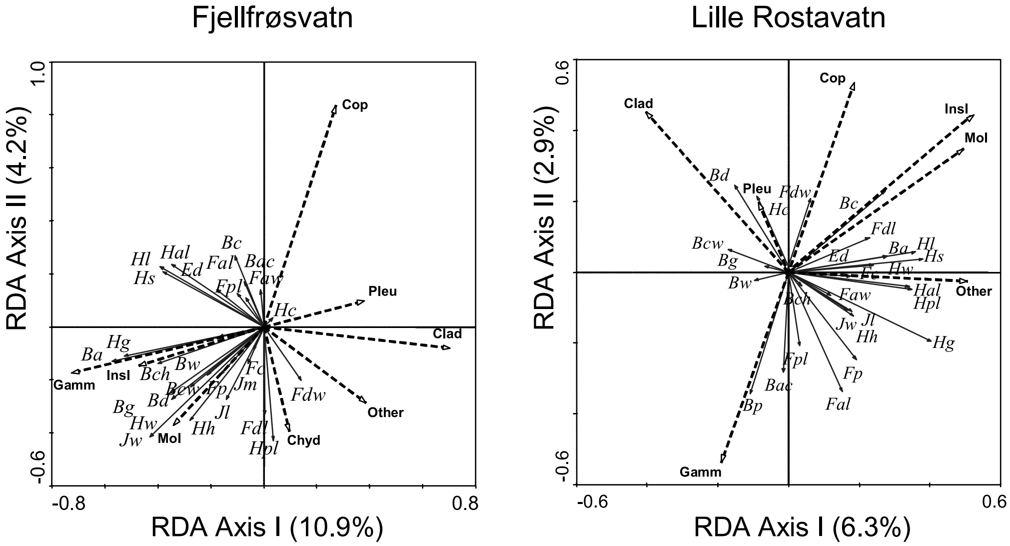


**Fig. 7.** Multivariate modelling (RDA) of morphological traits as a function of diet in Arctic charr from (a) Fjellfrøsvatn and (b) Lille Rostavatn. Biplots display explanatory variables (prey items, dotted arrows) and response variables (morphological traits). For abbreviations of morphological measurements, see Fig. 1.

selection pressure (Smith and Skúlason, 1996; Schluter, 2000). In Lille Rostavatn, strong interspecific food competition probably interrupts this development; the Arctic charr are restricted to a narrow zooplanktivorous diet niche with no space for exploiting multiple resource types, and thus exhibit little differences in morphological traits within the population.

In Fjellfrøsvatn, the diet niche of the charr population was wide compared with Lille Rostavatn, but the individual niches were generally narrow with specialization into benthivory or planktivory. Strong intraspecific competition may cause such patterns with a widening of the population niche but narrowing of the individual trophic niches (Giller, 1984; Putman and Wratten, 1984; Amundsen, 1995; Bolnick *et al.*, 2003). Consequently, significant differences in ecomorphological traits were found between benthivorous and zooplanktivorous Arctic charr. The benthivorous ecotype had a deeper body form and larger and broader jaws and head shape than the zooplanktivorous ecotype. Such traits are suggested to be favourable when feeding on large, hard-bodied and/or swift-moving prey (e.g. *Gammarus*, molluscs, caddis flies) in the littoral habitat (Webb, 1984; Ehlinger, 1990; Mittelbach *et al.*, 1999; Robinson and Parsons, 2002; Parsons and Robinson, 2007). The planktivorous charr had more slender bodies, which represents a typical adaptation to steady swimming (cruising) in the pelagic zone searching for smaller and less mobile cladoceran prey. Thus, the differences in body form and trophic morphology observed between the Arctic charr ecotypes can be explained functionally and appear to be related to niche preferences of individual fish.

Behavioural diversification is believed to be an important initial step in the development of resource polymorphism because it is flexible, with a subsequent manifestation in morphological traits (West-Eberhardt, 1989; Schluter, 1996; Skúlason *et al.*, 1999). Trophic behaviour seems to have both plastic and genetic components (McLaughlin, 2001; McCairns and Fox, 2004). Thus, the observed divergence in morphology between ecotypes should be expected if the trophic behaviour of individual Arctic charr is consistent over a period of time (Robinson and Parsons, 2002; Bolnick *et al.*, 2003). In Fjellfrøsvatn and elsewhere, strong relationships between habitat use, dietary niche, and infection of trophic-transmitted helminths among individual Arctic charr and other post-glacial fishes indicate persistent trophic behaviour involving long-term habitat use and individual feeding specialization (Curtis *et al.*, 1995; Knudsen, 1995; Knudsen *et al.*, 1996, 2003, 2004; Wilson *et al.*, 1996). Individual feeding specialization of Arctic charr has also been found in experimental studies (Amundsen *et al.*, 1995). A few zooplankton feeders were caught in the littoral zone and their morphology was closely associated with the planktivorous specimens caught in the pelagic habitat, indicating long-term individual feeding specialization. Similar divergence in trophic morphology associated with a narrow dietary niche (benthivorous vs. zooplanktivorous) was found within a littoral perch population (Svanbäck and Eklöv, 2002). This suggests that the differences in morphology are strongly associated with an individual dietary niche separation into planktivorous and benthivorous ecotypes promoted by an initial diversification in trophic behaviour with respect to habitat selection and foraging specialization.

Theoretical models suggest that resource competition can lead to adaptive diversification into forms specialized to multiple resource types and subsequently to a speciation (Schluter, 2000; Bolnick, 2004; Doebeli *et al.*, 2005; Polechova and Barton, 2005). Adaptive diversification is more likely to occur when there is a strong trade-off associated with the resource gradient (Ackermann and Doebeli, 2004; Rueffler *et al.*, 2007). A cost could, for example, occur if each individual consumer specialized in a narrow range of resources that it acquires most effectively, and morphology favouring benthivory could then be in conflict with morphology favouring zooplanktivory. Such trade-offs have been found between genetically separated morphs (Robinson and Wilson, 1994; Schluter, 1993, 1996, 2000) and within single populations (Robinson *et al.*, 1996; Smith and Skúlason, 1996; Svanbäck and Eklöv, 2003; Proulx and Magnan, 2004). Thus, the mechanisms that give rise to and maintain the differences in morphology between benthivorous and planktivorous ecotypes are most likely related to trade-offs in foraging efficiency on different resource types.

Phenotypic plasticity may play a significant role in the early stages of polymorphisms in Arctic charr and among other post-glacial fishes (Wimberger, 1994; Mittelbach *et al.*, 1999; Robinson and Parsons, 2002; Adams *et al.*, 2003; Andersson, 2003; Adams and Huntingford, 2004; Alexander and Adams, 2004; Jastrebski and Robinson, 2004; Andersson *et al.*, 2005; Olsson and Eklöv, 2005). In Arctic charr (Adams and Huntingford, 2004) and brook charr, *S. fontinalis* (Peres-Neto and Magnan, 2004), trophic morphology can respond to diet preferences of fish, and plasticity and genetic factors operate simultaneously as neither one alone can explain all variations. The modern view is that phenotypic plasticity often has a genetic basis (Agrawal, 2001; Albertson *et al.*, 2005; Svanbäck and Eklöv, 2006). The divergence in morphological traits between ecotypes resembles inter-morph differences related to separated habitat niches of distinct Arctic charr morphs (Skúlason *et al.*, 1993; Adams and Huntingford, 2002a, 2002b; Klemetsen *et al.*, 2002). Such co-occurring morphs differ in life-history traits, morphologies, habitat and diet niches (see reviews by Jonsson and Jonsson, 2001; Klemetsen *et al.*, 2003a), and several are reproductively isolated (Klemetsen *et al.*, 1997; Adams *et al.*, 1998) and genetically dissimilar (Gislason *et al.*, 1999; Westgaard *et al.*, 2004; Wilson *et al.*, 2004). Differences in trophic behaviour and morphology of some sympatric pairs of Arctic charr have been shown to be heritable (Skúlason *et al.*, 1993; Adams and Huntingford, 2002a, 2002b; Klemetsen *et al.*, 2002, 2006). Similarly, indications of a genetic basis for divergent morphology in single populations have been found in Arctic charr (Gislason *et al.*, 1999) and brook charr (Dynes *et al.*, 1999; Sacotte and Magnan, 2006). Thus, both a genetic and a plastic basis of the observed behavioural and morphological divergence found between Arctic charr ecotypes in Fjellfrøsvatn is highly plausible.

In most theoretical studies, assortative mating is an important component in the incipient divergence between morphs (Schluter, 2000; Dieckmann and Doebeli, 2004). Sexual dimorphism was unevenly expressed among charr in the two lakes. In Lille Rostavatn, where morphological traits showed insignificant variation in relation to ecological traits, substantial sexual dimorphism was established. In Fjellfrøsvatn, however, the benthivorous and planktivorous ecotypes had profound discrepancies in ecomorphological traits, whereas sexual dimorphism was expressed only slightly. This corresponds to model studies of adaptive speciation by Bolnick and Doebeli (2003), implying that assortative mating based on ecological traits is less likely to occur if strong sexual dimorphism has been developed, and suggests that assortative mating related to ecological traits could be present in Fjellfrøsvatn, but is less likely to occur in Lille Rostavatn. The observed larger, more robust body form and head of the benthivorous compared with the planktivorous males of Arctic charr and variability in secondary sex traits in coloration (Skarstein and Folstad, 1996) may play significant roles in mate choice as found between benthic and limnetic ecotypes and sympatric morphs of three-spine sticklebacks (Nagel and Schluter, 1998; Boughman, 2001; Boughman *et al.*, 2005). Furthermore, spatial and temporal barriers are important mechanisms in reproductive isolations between ecotypes (Schluter, 2000). The existence of niche-based assortative mating at distinct spawning sites is possible, and may reduce gene flow among ecotypes and thus increase the likelihood of divergence through differential adaptation in morphology. However, there is a high need for supplementary studies addressing both potential genetic differences and assortative mating between ecotypes in the present systems.

In conclusion, we found profound differences in the development of trophic polymorphisms in the two lakes studied. In the species-poor fish community in Fjellfrøsvatn, individual charr showed differences that linked habitat, diet, and morphology to polymorphic ecotypes. In the more species-rich Lille Rostavatn with strong interspecific resource competition, no such differences were present. A tentative conclusion is that an incipient development of adaptations along the benthic–pelagic resource axis is taking place in Fjellfrøsvatn, but not in Lille Rostavatn where only pelagic food resources were utilized. Fjellfrøsvatn also holds a reproductively isolated and genetically distinct profundal morph of Arctic charr (Klemetsen *et al.*, 1997, 2002, 2006; Westgaard *et al.*, 2004; Wilson *et al.*, 2004; Knudsen *et al.*, 2006). In his book on adaptive radiation, Schluter (2000) asked whether evolution beyond the two-niche stage could be predicted for post-glacial lakes, and remarked that few examples exist where the three-niche stage may incorporate the two-niche stage as a sub-set. Fjellfrøsvatn may provide such a case, with the separation of the profundal morph being definitely older than the incipient benthic–pelagic polymorphism discussed in the present study. The contrasting results from these two neighbouring lakes support the general hypothesis that access to multiple resource types and subsequent niche specialization are central for the development of repetitive radiation of fishes in young post-glacial lakes. The evolution of polymorphic benthic and limnetic ecotypes is also highly dependent on the availability and structure of prey resources in other circumpolar fish families (e.g. Østbye *et al.*, 2006; Landry *et al.*, 2007).

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