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Parallel divergence of sympatric genetic and body size forms of Arctic charr, *Salvelinus alpinus*, from two Scottish lakes

COLIN E. ADAMS[1]*, ALASTAIR J. WILSON[2]† and MOIRA M. FERGUSON[2]

[1]*Fish Biology Group, Scottish Centre for Ecology and the Natural Environment, Institute of Biomedical and Life Sciences, Rowardennan, Glasgow G63 0AW, UK*
[2]*Department of Zoology, University of Guelph, Guelph, Ontario, N1G 2W1, Canada*

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F_{ST} and R_{ST} estimates for Arctic charr from six microsatelite markers collected from two neighbouring Scottish lakes, Loch Maree and Loch Stack, confirm the presence of two distinct genetic groupings representing separate populations within each lake. In both lakes, there was also a clear body size dimorphism, with large and small body size forms that segregated according to genetic grouping. There was evidence of only subtle foraging ecology differences between morphs, with the small body size morph in both lakes being more generalist in its foraging in the summer (consuming mostly plankton but also some macrobenthos) than the large body size morph, which specialized on planktonic prey. Trophic morphology (head and mouth shape) did not differ significantly between morphs (although the small sample size for Maree makes this a preliminary finding). Cluster analysis of the microsatelite data and the presence of private alleles showed that morphologically similar forms in different lakes were not genetically similar, as would be expected under a multiple invasion hypothesis. Thus, the data do not support a hypothesis of a dual invasion of both lakes by two common ancestors but instead suggest an independent origin of the two forms in each lake. Thus parallel sympatric divergence as a result of common selection pressures in both lakes is the most parsimonious explanation of the evolutionary origin of these polymorphisms.

ADDITIONAL KEYWORDS: evolution – phenotypic plasticity – polymorphism.

INTRODUCTION

The Arctic charr *Salvelinus alpinus* (L.) is highly polytypic. It displays a very high degree of phenotypic variation between populations (Johnson, 1980; Behnke, 1984; Alexander & Adams, 2000; Alekseyev *et al.*, 2002; Adams *et al.*, 2007) and, less commonly, but still widespread, sympatric polymorphic populations have been reported (Nyman, Hammar & Gydemo, 1981; Hindar & Jonsson, 1982; Nordeng, 1983; Klemetsen *et al.*, 1985, 2003a, 1997; Snorrason *et al.*, 1989; Savvaitova, 1995; Adams *et al.*, 1998; Fraser, Adams & Huntingford, 1998). Frequently, sympatric morphs express variation in morphological and/or behavioural traits that have a functional role in foraging (Fraser *et al.*, 1998; Adams & Huntingford, 2002a; Klemetsen *et al.*, 2006). Such polymorphisms often show a clear correlation with variability in foraging ecology both in the wild (Malmquist, 1992; Snorrason *et al.*, 1994; Adams *et al.*, 1998; Klemetsen *et al.*, 2003a; McCarthy *et al.*, 2004) and in experimental trials (Skúlason *et al.*, 1993; Adams & Huntingford, 2002a; Klemetsen *et al.*, 2006).

A recent study of the molecular genetic structure of lake-resident Arctic charr, from 43 sites across northwestern Europe, identified ten sites where there was significant within-lake genetic structuring, indicative of putative genetically distinct sympatric populations. Seven of these sites are in Iceland and three in Scotland (Wilson *et al.*, 2004). One of the Scottish

*Corresponding author. E-mail: c.adams@bio.gla.ac.uk
†Current address: Institute of Evolutionary Biology, University of Edinburgh, Edinburgh EH93JT, UK

sites (Loch Rannoch) is known to support three sympatric morphs of Arctic charr that differ in feeding ecology and in inherited elements of trophic morphology (Adams *et al.*, 1998; Adams & Huntingford, 2002b, 2004; Alexander & Adams, 2004).

In the present study, we examine the patterns of genetic and phenotypic variation in the two remaining Scottish populations showing evidence of genetic substructuring (Wilson *et al.*, 2004; Adams *et al.*, 2007). Specifically, we test the hypothesis that sympatric genetic variants identified by microsatellite analysis also show differences in functional phenotypic traits.

MATERIAL AND METHODS

Study sites

Loch Stack, Sutherland, Scotland (58°20′N, 4°54′W) has an area of 2.56 km^2, with a maximum depth of 33 m and mean depth of 10.9 m (Murray & Pullar, 1910). Loch Maree, Wester Ross (57°39′N, 5°24′W) is larger at 28.6 km^2 and deeper at 112 m maximum depth and 38.2 m mean depth (Murray & Pullar, 1910). Both lakes are in north-western Scotland and both drain westward into the North Atlantic. Both are accessible to anadromous salmonids. Loch Maree is 2.9 km from the sea and Loch Stack 6.4 km from the sea. The two lakes drain into the sea 75 km apart and thus it could reasonably expected that they would be subject to similar invasion processes during post-glacial colonization by arctic charr.

Collection of fish

Arctic charr were collected from Loch Maree and Loch Stack during mid-summer (June to September 1998) using multi-panel Nordic gill nets, which comprise 12 panels of 5–55 mm knot-to-knot mesh. These nets are nonselective for salmonids within the modal size range 45–495 mm fork-length (Jensen & Hesthagen, 1996). Nets were set overnight in the pelagic, profundal (deepest area), littoral (less than 7 m depth) and sub-littoral (7 to 10 m depth) on the bottom of the loch; floating pelagic nets were set from the surface. A total of 30 nets were set in Loch Maree and ten in Loch Stack. Collected fish were killed and the adipose fin removed and stored in ethanol for genetic analysis. The fish were then frozen within 6 h of collection at –18 °C.

Genetic structuring within and among lakes

Genetic analysis of individuals sampled from Loch Stack and Loch Maree was conducted as part of a larger study of population genetic structure of arctic charr across Europe (Wilson *et al.*, 2004), and this provided evidence of two genetically distinct groups within each lake. Full details of the laboratory protocols and statistical analyses are presented elsewhere (Wilson *et al.*, 2004). In summary, genomic DNA was extracted from adipose fin tissue and individuals were genotyped at six microsatellite loci (Loch Stack, $N = 70$; Loch Maree, $N = 31$) revealing high levels of genetic diversity. Across loci, mean allele number was 11 and 13.7, and expected mean heterozygosities were 0.71 and 0.77, for Loch Stack and Loch Maree, respectively. Samples from both lakes showed evidence of significant departures from Hardy–Weinberg proportions caused by heterozygote deficits ($P < 0.001$; Wilson *et al.*, 2004). This pattern is consistent with intra-lacustrine genetic sub-structuring (i.e. the Wahlund effect), a conclusion further supported by previous analyses using STRUCTURE, version 2 (Pritchard, Stephens & Donnelly, 2000) indicating the presence of two genetic populations within each of these lakes (Wilson *et al.*, 2004).

In the present study, the data were reanalysed using the clustering method of STRUCTURE, but with no a priori assumption about the genetic structuring. Thus, the clustering method was applied to the set of all individuals from both lakes, with the number of genetic populations (K) determined from posterior probabilities of K (assuming a uniform prior on $K = \{1,2,3,4,5,6\}$). In all cases, the MCMC scheme employed a burn-in period of 100 000 steps and a chain length from 250 000 to 1 000 000. Convergence of Ln Pr($X|K$) was assessed from multiple ($N = 6$) runs at each value of K from 1 to 6. The estimated log probability of the data was found to be highest for $K = 4$ (with subsequent reductions for $K = 5, 6$), and, thus, we proceeded with a model of four genetic populations represented in the full set of sampled individuals.

All individuals were assigned to a most-likely population, arbitrarily denoted A, B, C, and D, based on estimates of Q (the membership coefficient) generated with STRUCTURE. Relationships among the four putative populations, were further characterized by generating multilocus estimates of pairwise F_{ST} and R_{ST} (i.e. its equivalent under a stepwise mutation model of microsatellite evolution) using ARLEQUIN, version 3.01 (Excoffier, Laval & Schneider, 2005). Significance was determined using permutation tests (1000 permutations). Finally, we also visualized the genetic relationships among the set of all individuals by constructing a Neighbour-joining (NJ) tree using Rousset's (2000) measure of genetic distance between individuals (a) estimated using SPAGeDi, version 1.2 (Hardy & Vekemans, 2002).

Morphometric analysis

A significant number of fish sampled were subject to damage by eels (*Anguilla anguilla*) and nets and

could not be used for morphometric analysis. A total of 32 fish from Loch Stack and 12 fish from Loch Maree were included in morphometric analysis. To determine head morphology, fish from the sample from each lake were defrosted overnight, weighed (±0.1 g), measured (fork-length, ±1 mm) and photographed in lateral view (tip of the snout to the end of the pectoral fins) on a suitable scale. Eleven linear morphometric measures of the head (eye diameter, anterior head length, posterior head length, head length, snout length, maxillary bone length, snout to maxillary length, maxillary width, lower jaw length, head depth at the jaw, head depth at the operculum) and pectoral fin length were made (these measurements are identical to those illustrated in fig. 3 in Adams *et al.* (2007), to which reference should be made for additional detail). A full account of the techniques employed are given elsewhere (Adams & Huntingford, 2002a, b; Adams *et al.*, 1998, 2003).

These linear head morphometric variables were strongly correlated with fish size (fork-length). To test for differences in morphology between groups, each linear morphological variable was regressed on fork-length and derived residuals used as a measure of the morphological variable independent of body size (Reist, 1986; Adams *et al.*, 2003, 2006).

Principal component analysis was used to derive principal component scores for each fish from the size corrected morphometric variables. Differences in component scores and morphological mesures between genetic groups within sites were subsequently tested using analysis of variance. Multiple comparisons were corrected for using Bonferoni correction. For clarity, the *P*-value equivalent of the corrected probability is presented.

Foraging

The diet of each fish in the present study was assessed from stomach contents. Stomachs were removed by dissection from charr for which morphometric data were collected and placed in 70% ethanol. Invertebrate prey were identified to family. Fish with empty stomachs ($N = 6$) were not analysed further.

RESULTS

Genetic structure

Based on $K = 4$ genetic populations, estimates of Q generated with STRUCTURE showed high assignment probabilities of individuals to one of the four populations (Fig. 1).

Thus, across all individuals, mean Q for the most likely population was 0.945. Of the 101 individuals included 29, 41, 24, and seven fish were assigned to populations A to D, respectively. Furthermore, it was found that all individuals of populations A and B originated in Loch Stack, whereas those assigned to C or D were from Loch Maree. Thus, our analysis confirmed prior expectations of differences between lakes and two genetic populations within each of these lakes (Wilson *et al.*, 2004). Visual inspection of allele frequencies (not shown) revealed that private alleles were present (for at least one microsatellite marker) in all four genetic groups assigned.

Within lakes, the genetic structure was further confirmed by large, and highly significant, estimates of F_{ST} and R_{ST} between Stack populations (A and B), and between Maree populations (C and D) (Table 1). Similarly, significant differentiation was found in pairwise comparisons across lakes. This structuring was also reflected in the topology of the NJ tree (Fig. 2) in which individuals grouped to form population specific clusters. A single exception to this is that the cluster containing the seven members of population D (from Loch Maree) also contained one individual sampled from Loch Stack (and assigned to population A).

Variation in morphology between genetic variants

Loch Stack

Genetically-defined populations of charr from Loch Stack differed significantly in size. Population B individuals were significantly longer (fork-length: $P < 0.001$; Fig. 3A) and heavier ($P < 0.001$, Fig. 3B) than those of population A. There was only minimal overlap in length range (fork-length: Stack A, 100–219 mm; Stack B, 139–243 mm) and weight range (weight: Stack A, 13–114 g; Stack B, 35–168 g); however, only a single Stack population A fish was larger than 143 mm length and weighed more than 37 g.

Head morphometrics measures were taken for nine Loch Stack A and 23 Stack B genetic variants. The first and second principal components from PC analysis (PC1 and 2) accounted for 73% and 8% of variation, respectively, in the 12 morphometric variables. PC scores for PC1 and PC 2, however, did not differ significantly between A and B population individuals from Loch Stack (Table 2). Similarly, univariate analysis of each of the 12 morphological variables of head shape showed no evidence of any between group variation in head morphology, nor in pectoral fin length (Table 2).

Loch Maree

The populations from Loch Maree also differed significantly in size. Population D individuals were significantly longer (fork-length: $P < 0.002$; Fig. 3A) and heavier ($P < 0.001$; Fig. 3B) than those of population

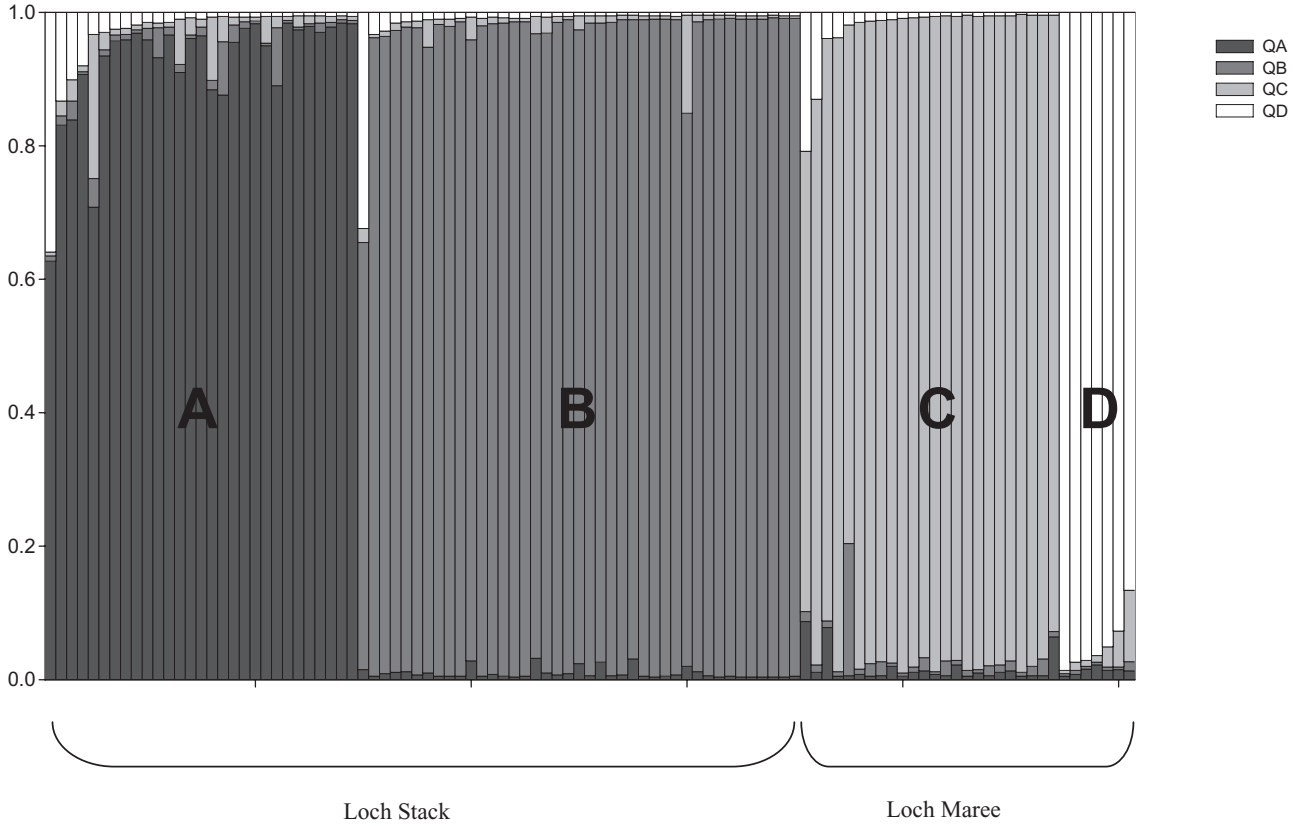

Figure 1. Results of cluster analysis performed in STRUCTURE under a model of four genetic populations. Each column shows membership coefficients (Q) for each of four populations (A, B, C, and D). Individuals are assigned to most likely population based on Q. All individuals assigned to populations A and B were sampled from Loch Stack; all those assigned to populations C and D were sampled from Loch Maree.

Table 1. Pairwise estimates of F_{ST} (below the diagonal) and R_{ST} (above the diagonal) between genetic variants within and between lakes

	Stack A	Stack B	Maree C	Maree D
Stack A	–	0.353	0.358	0.221
Stack B	0.180	–	0.091	0.398
Maree C	0.095	0.140	–	0.439
Maree D	0.191	0.283	0.168	–

All values are significantly greater than zero at $P < 0.001$ based on permutation tests (permutation number = 1000).

C (Fig. 3). There was limited overlap in body size between variants (Fork-length range: Maree C, 7–48 mm; Maree D, 30–263 mm; weight range: Maree C, 93–153 g; Maree D, 137–255 g).

Morphology measures were available for only seven population C and five population D fish. PC1 and PC2 of the 12 morphometric variables recorded from charr from Loch Maree accounted for 62% and 16.0% of total explained variance, respectively. PC scores did not differ significantly between A and B populations from Loch Maree for either PC1 or PC2 (Table 2). Similarly, univariate analysis of each of the 12 morphological variables showed no evidence of significant differences (Table 2). However, these analyses are based on small sample size and should be regarded as tentative.

FORAGING

One thousand three hundred and fifty-two prey items were recorded from 28 charr from Loch Stack. Organisms originating from the pelagic (*Cladocera* and *Chironomidae* pupae) dominated the diet of both populations (A and B) (Fig. 4). However, the frequency of prey groups differed significantly between populations, primarily as a result of a greater proportion of benthic insect prey in stomachs of population A individuals ($P < 0.001$). The 351 prey items recovered from Loch Maree charr were also dominated by pelagic organisms (*Cladocera*, *Copepoda*, and *Chironomidae* pupae). Loch Maree populations also differed in the frequency of dietary items ($P < 0.001$).

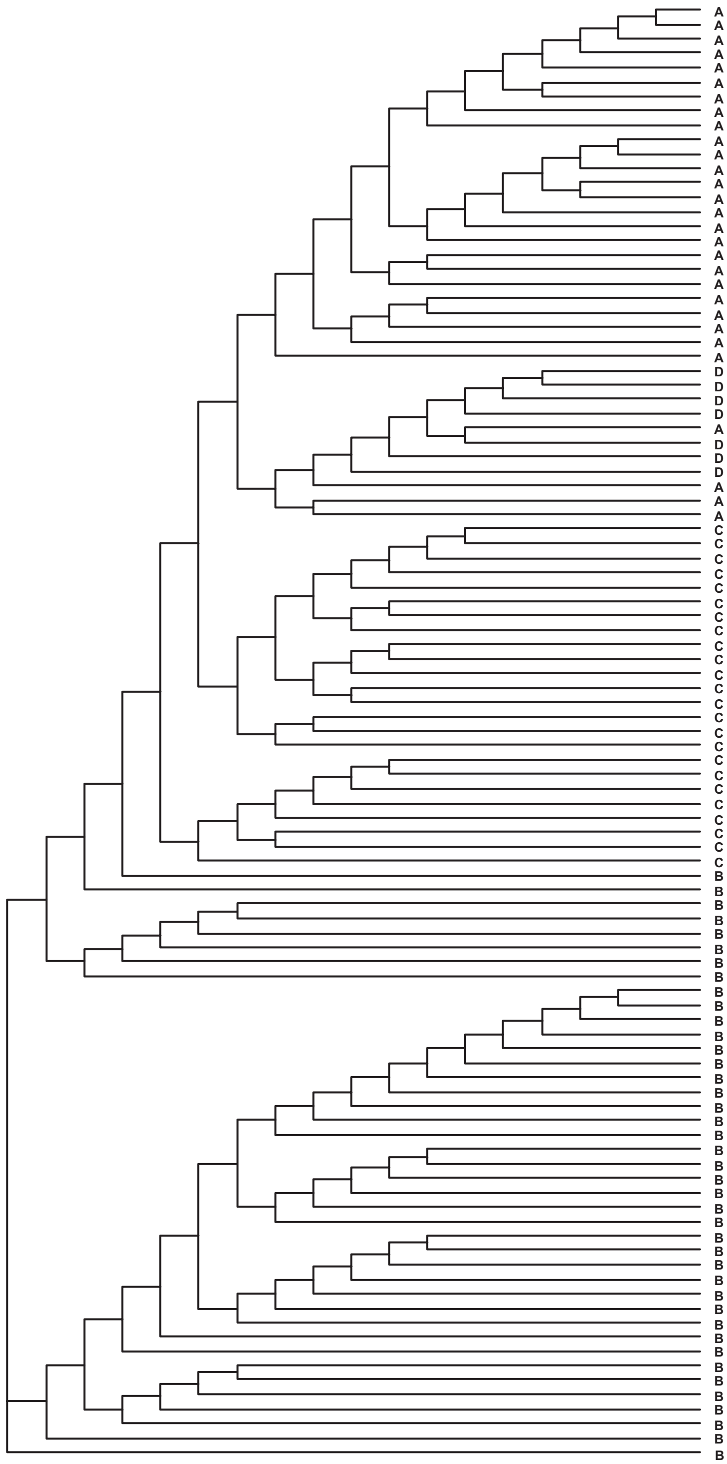

Figure 2. Unrooted Neighbour-joining tree for 101 individuals based on genetic distance between individuals (a) estimated from six microsatellite loci. Also indicated are assignments to genetic populations (A, B, C, and D) based on cluster analysis (see text). Note relative branch lengths are not to scale.

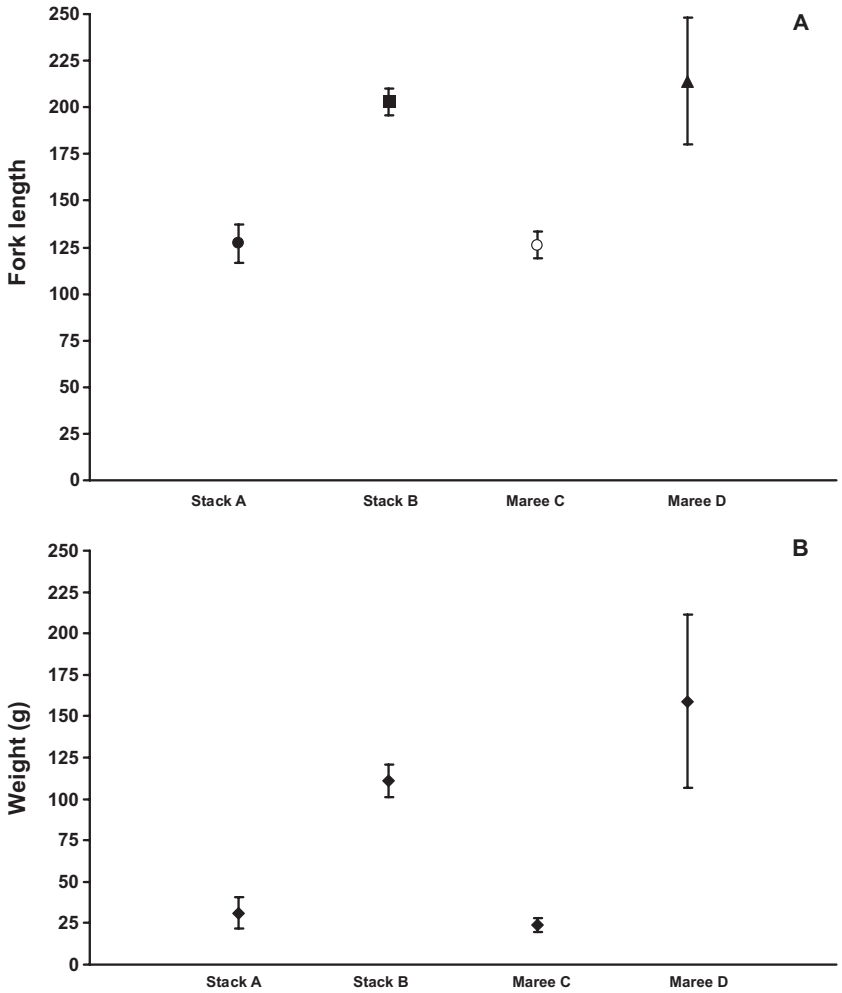

Figure 3. Variation in size between genetic variants of Arctic charr from Loch Stack and Loch Maree. A, fork-length (mm) (Loch Stack morphs: $F_{1,30} = 49.0$, $P < 0.001$; Loch Maree morphs: $F_{1,16} = 18.5$, $P = 0.001$. B, weight (g) (Loch Stackmorphs: $F_{1,30} = 22.8$, $P < 0.001$; Loch Maree morphs: $F_{1,16} = 18.1$, $P < 0.001$).

The diet of individuals from population C contained a significant number of benthic living *Piscidium* sp. not seen in individuals in population D. Also notable in the diet is that three individuals of Maree population D contained material resembling fish farm food pellets.

DISCUSSION

There is clear evidence of significant genetic structuring within the arctic charr in the two lakes examined in the present study. It should be noted that sample size is modest for Loch Maree (and especially for population D) and, although there is strong evidence of genetic differentiation between populations C and D, quantitative estimates of F_{ST} and R_{ST} should be treated with appropriate caution. Nevertheless, pairwise estimates of F_{ST} and R_{ST} were not substantially larger in across-lake comparisons than between genetic variants within lakes (Table 1). Thus, F_{ST} and R_{ST} data and the presence of private alleles confirm the results of Wilson *et al.* (2004) showing that there are two clearly distinct genetic populations in both Loch Maree and Loch Stack. This conclusion is additionally supported by cluster analysis of individuals and by the topology of the NJ tree (Fig. 2) in which individuals cluster into four discrete populations (with only one exception)

Evidence of further structuring within lakes is supported by morphology comparisons. Charr in Loch Stack showed a clear body size dimorphism that segregated according to genetic grouping (Fig. 3). There was a similar body size dimorphism in Loch Maree despite a relatively small sample size. There was also evidence of foraging differences between the two body size morphs. In Loch Stack, both small and large

Table 2. Mean and standard error of 11 head morphology measures (eye diameter, anterior head length, posterior head length, head length, snout length, maxillary bone length, snout to maxillary length, maxillary width, lower jaw length, head depth at the jaw, head depth at the operculum) and pectoral fin length and PC1 and PC2 scores derived from principal component analysis of all 12 morphological measures for two genetic variants from Loch Stack and Loch Maree and test of significance (analysis of variance)

	Loch Stack							Loch Maree						
	A		B					C		D				
	Mean	SE	Mean	SE	*F*	d.f.	*P*	Mean	SE	Mean	SE	*F*	d.f.	*P*
ED	0.24	0.16	–0.11	0.11	3.42	1,26	0.08	0.09	0.25	–0.12	0.28	0.32	1,10	0.58
AHL	0.33	0.21	–0.13	0.30	0.86	1,26	0.36	0.17	0.39	–0.16	0.56	0.20	1,10	0.66
PHL	0.06	0.21	–0.02	0.43	0.01	1,26	0.91	0.15	0.40	–0.21	1.15	0.14	1,10	0.72
ML	0.37	0.34	–0.14	0.66	0.22	1,26	0.64	0.25	0.74	–0.35	1.64	0.16	1,10	0.69
SL	0.28	0.17	–0.11	0.14	2.33	1,26	0.14	–0.03	0.18	–0.04	0.50	0.03	1,10	0.87
ML	0.09	0.21	–0.03	0.36	0.04	1,26	0.84	0.27	0.50	–0.38	0.81	0.58	1,10	0.46
SML	0.37	0.22	–0.14	0.46	0.47	1,26	0.50	0.24	0.67	–0.34	0.79	0.34	1,10	0.57
MW	0.13	0.06	–0.05	0.10	1.26	1,26	0.27	0.04	0.10	–0.06	0.19	0.26	1,10	0.62
LJL	0.49	0.24	–0.19	0.57	0.53	1,26	0.47	0.15	0.44	–0.21	1.38	0.10	1,10	0.75
HDJ	0.27	0.23	–0.10	0.44	0.26	1,26	0.61	0.16	0.40	–0.23	0.71	0.30	1,10	0.59
HDO	0.45	0.58	–0.18	0.56	0.43	1,26	0.52	0.14	0.62	–0.19	0.83	0.12	1,10	0.74
PFL	–0.27	0.52	0.01	0.78	0.00	1,26	0.98	0.41	0.70	–0.57	1.42	0.53	1,10	0.48
PC1	0.28	0.14	–0.11	0.26	0.89	1,26	0.36	0.15	0.30	–0.21	0.57	0.36	1,10	0.56
PC2	0.23	0.28	–0.09	0.24	0.57	1,26	0.45	0.09	0.16	–0.13	0.78	0.13	1,10	0.73

P-values quoted include a Bonferroni adjustment for multiple tests.
All values are significantly greater than zero at $P < 0.001$ based on permutation tests (permutation number = 1000).

morphs consumed mostly plankton but the small morph also consumed significant amounts of benthic living insect larvae, not seen in the large morph (Fig. 4). Similarly, in Loch Maree, the two populations differed significantly in their dietary items. The majority of prey consumed by both populations comprised plankton; however, individuals of the small morph also consumed a significant proportion of benthic living prey: *Piscidium* sp. and *Chironomidae* larvae. However, the conclusions made for this latter group, based on the relatively small sample size employed in the present study, should be regarded as provisional.

These differences in diet are relative subtle compared with the clearly distinct foraging of sympatric morphs from lakes elsewhere (Snorrason *et al.*, 1989, 1994; Adams & Maitland, 1998, 2007). However, Klemetsen *et al.* (2003b) have reported similarly subtle dietary differences between sympatric charr morphs from Fjellfrøsvatn in Norway. The recorded prey of the large morph from Loch Maree points to one possible route through which phenotypic structuring may have occurred. Three individuals of this morph from Loch Maree contained remnants of fish farm food pellets in their stomachs. Fish farm pellets provide a high energy food source and if abundant, and if the Loch Maree D population were able to access this food source but population C could not, then this could potentially result in accelerated growth in the D population compared with C, and thus also in the body size structuring of populations recorded in Loch Maree. It is impossible to determine whether this mechanism could be operating in Loch Maree in the present study.

Trophic morphology has been found to discriminate between sympatric populations of arctic charr described elsewhere and, in many cases, there is a clear logical link between variation in mouth and head shape and foraging specialisms (Skúlason *et al.*, 1993; Adams & Huntingford, 2002b; Klemetsen *et al.*, 2002). By contrast, in the present study, the two body size morphs did not differ significantly in trophic morphology in either Loch Stack or Loch Maree, despite the use of highly sensitive multivariate statistical techniques; however, the very small sample size for morphological analysis of charr from Loch Maree make this a preliminary conclusion only. Variants of charr from these lakes have been recognized previously. Regan (1909) affords full species status to *Salvelinus maxillaris* from Loch Stack; Kottelat & Freyhof (2007) reassert this nomenclature but only record *maxillaris* from Loch Maree (the basis for this

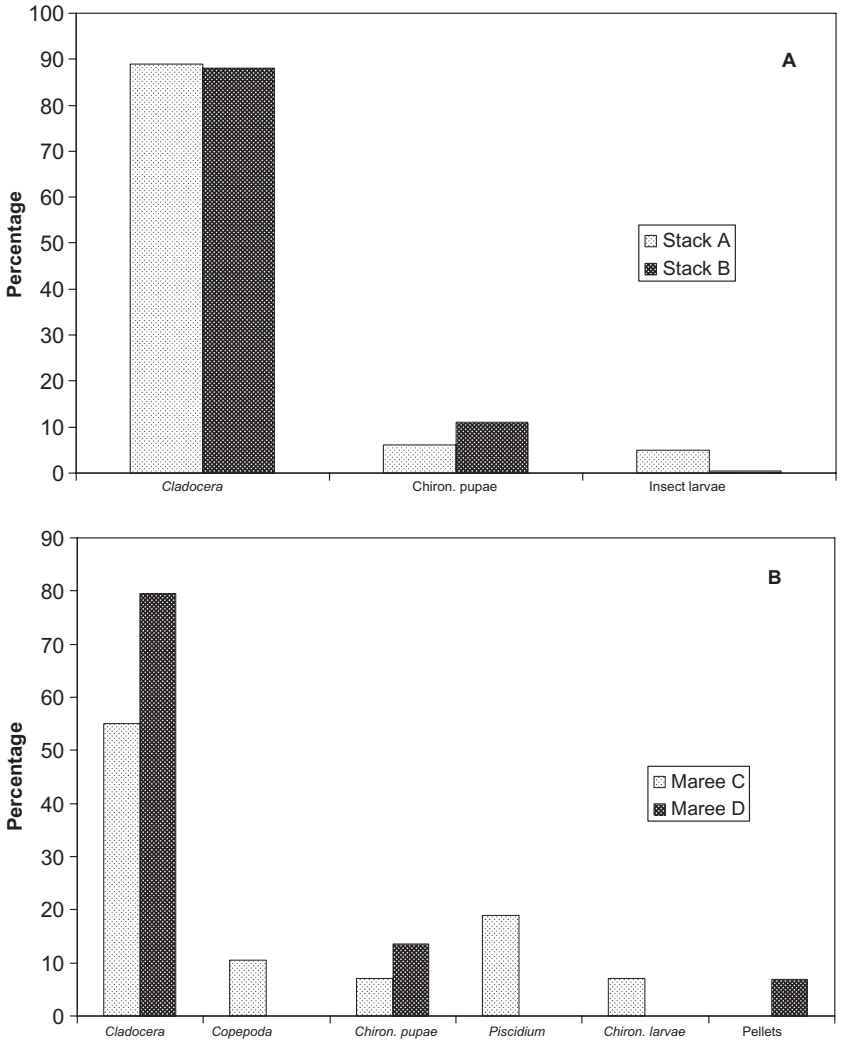

Figure 4. The percentage of prey items by number comprising macrobenthos in the stomachs of small body size and large body size charr from Loch Stack ($\chi^2 = 35.7$, d.f. = 2, $P < 0.001$) and the large body size and small body size charr from Loch Maree ($\chi^2 = 36.5$, d.f. = 4, $P < 0.001$).

is uncertain). In addition to *maxillaris*, Kottelat & Freyhof (2007) nominally identify two more full species of charr from Loch Maree (*Salvelinus* sp. slender and *Salvelinus* sp. large-eye). However, in the absence of a comprehensive review of Scottish charr, the evidence for this taxonomy in these two lakes is slim (for a more complete review of the status of species, see Adams & Maitland, 2007)).

There was no clear evidence of any spatial segregation in habitat use between the two populations in either lake. In Loch Stack, individuals of both populations were caught at the same time in the same gill net in four out of six occasions when there were more than one charr in a net and in Loch Maree on three out of five occasions.

The pattern of morphometric and genetic data presented suggests a probable evolutionary origin for the polymorphisms described in the present study. Despite that it is highly likely that both Maree and Stack were subject to similar post-glaciation colonization processes, the existence of private alleles, and the lack of genetic similarity between superficially similar morphs from different lakes, makes it improbable that the two body size morphs originated as two separate invasions of two common ancestral forms that were genetically and morphologically distinct.

The most logical and parsimonious explanation is that the body size variation and genetic structuring described in the present study evolved in sympatry independently in each lake. There is now a strong theoretical basis underpinning the evolutionary divergence in sympatry (Turner & Burrows, 1995; Diekmann & Doebeli, 1999). However, there is a paucity of empirical examples from nature. Where sympatric

divergence has been described previously, the best examples have been in freshwater fish in high latitude systems (sticklebacks *Gasterosteus aculeatus* in Canada: Rundle *et al.*, 2000; Boughman, Rundle & Schluter, 2005; arctic charr in Iceland: Gíslason *et al.*, 1999), suggesting that the combination of low species diversity and relative isolation in recently colonized post-glacial fresh waters may promote sympatric divergence (Schluter, 1996).

The parallel evolution of similar traits in different lakes implies that charr in both Stack and Maree are responding to similar selection pressures, although what these selection pressures comprise is not clear from the present study.

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