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Genomic underpinnings of head and body shape in Arctic charr ecomorph pairs

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Abstract

Across its Holarctic range, Arctic charr (*Salvelinus alpinus*) populations have diverged into distinct trophic specialists across independent replicate lakes. The major aspect of divergence between ecomorphs is in head shape and body shape, which are ecomorphological traits reflecting niche use. However, whether the genomic underpinnings of these parallel divergences are consistent across replicates was unknown but key for resolving the substrate of parallel evolution. We investigated the genomic basis of head shape and body shape morphology across four benthivore–planktivore ecomorph pairs of Arctic charr in Scotland. Through genome-wide association analyses, we found genomic regions associated with head shape (89 SNPs) or body shape (180 SNPs) separately and 50 of these SNPs were strongly associated with both body and head shape morphology. For each trait separately, only a small number of SNPs were shared across all ecomorph pairs (3 SNPs for head shape and 10 SNPs for body shape). Signs of selection on the associated genomic regions varied across pairs, consistent with evolutionary demography differing considerably across lakes. Using a comprehensive database of salmonid QTLs newly augmented and mapped to a charr genome, we found several of the head- and body-shape-associated SNPs were within or near morphology QTLs from other salmonid species, reflecting a shared genetic basis for these phenotypes across species. Overall, our results demonstrate how parallel ecotype divergences can have both population-specific and deeply shared genomic underpinnings across replicates, influenced by differences in their environments and demographic histories.

KEYWORDS
ecomorphology, fish, genomics, parallel evolution, population genomics, QTL

Colin E. Adams and Kathryn R. Elmer are joint senior authors.

1 | INTRODUCTION

Parallel evolution is an evolutionary process and outcome by which similar phenotypes arise and are established in multiple independent populations in separate environments (Bolnick et al., 2018; Elmer & Meyer, 2011; Schluter, 1996). These replicate evolutionary outcomes suggest that similar environments impose similar selective pressures on organismal phenotypes, with only a small number of phenotypic solutions favoured in that context. However, replicate populations often show deviations from what could be described as strict parallel evolution (Bolnick et al., 2018). These instances of non-parallelism can be driven by a range of factors (Elmer & Meyer, 2011; Oke et al., 2017; Stuart et al., 2017). While replicates can exist in similar environments, particular spatial and temporal selection pressures can and do vary even in environments that seem equivalent (Oke et al., 2017). The extent of parallelism can be influenced by a range of ecological factors (Landry et al., 2007; Riesch et al., 2016). For example, ecomorphs of three-spine stickleback (*Gasterosteus aculeatus*) that show higher divergence in diet also show high divergence in ecologically relevant traits (Berner et al., 2008; Kaeuffer et al., 2012). Furthermore, the extent of contemporary gene flow and differing demographic histories can directly influence the extent of parallelism seen (Hendry, 2017; Langerhans & DeWitt, 2004; Weber et al., 2021). Replicates may also find alternative solutions to the same functional problem resulting in deviations from strict parallelism (Alfaro et al., 2004).

While the existence of parallel phenotypes is well established in natural populations (Oke et al., 2017; Siwertsson et al., 2013), the extent to which those are associated with similarly shared genomic underpinnings is rarely examined (Magalhaes et al., 2021; McGirr & Martin, 2018; Ravinet et al., 2016). Indeed, the appearance of the same phenotypes through parallel evolution does not mean that the same genomic processes underpin those similar evolutionary outcomes across replicates (Conte et al., 2012; Elmer & Meyer, 2011). Similar phenotypic outcomes could result from alternative genetic pathways with multiple genes influencing a single phenotype, known as polygenicity (Láruson et al., 2020). This might arise because of differing demographic histories (Elmer et al., 2014) and variable genetic backgrounds (Arendt & Reznick, 2008; Kowalko et al., 2013), while relative effect size and hard and soft selective sweeps can also influence the genomic pathways used (Láruson et al., 2020; Pritchard et al., 2010). Similarly, the involvement of alternative splicing, differential gene expression or post-translational modifications can also result in phenotypic parallelism through different molecular mechanisms (Filteau et al., 2013; Jacobs & Elmer, 2021; McGirr & Martin, 2018).

One classic example of parallel evolution is the replicated divergence across northern freshwater lakes of distinct trophic specialists, also known as ecomorphs or ecotypes. These occur abundantly in salmonid fishes in recently glaciated lakes, such as lake whitefish (*Coregonus clupeaformis*) (Landry et al., 2007), lake trout or lake charr (*Salvelinus namaycush*) (Baillie et al., 2016) and Arctic charr (*Salvelinus alpinus*) (Doenz et al., 2019; Jensen et al., 2017). In Arctic charr, ecomorphs are associated with divergence along the depth axis and ecological niche, typically forming pelagic and benthic foraging specialists (Elmer, 2016; Klemetsen, 2010). Two key traits involved in this divergence are head shape and body shape, both having functional significance; head shape being important for foraging and prey specialization and body shape important for swimming behaviour and niche use (Adams & Huntingford, 2002; Skoglund et al., 2015). Additionally, ecomorphs often differ in other complex traits such as body size, colouration and spawning time (Garduño-Paz et al., 2012; Jonsson & Jonsson, 2001).

Previous research on benthivorous–planktivorous ecomorph pairs of Arctic charr has shown that individual traits related to head shape, such as eye diameter, can show a strong degree of parallelism across replicates; however, the extent of parallelism is highly variable across individual traits (Adams et al., 2008; Jacobs et al., 2020). Research into benthic ecomorphs in Iceland has shown that while these ecomorphs are morphologically similar across locations, they are distinguishable in several characteristics, most prominently in head shape, suggesting some specialized adaptations to their local environment (Sigursteinsdóttir & Kristjánsson, 2005). Genomic analysis to date suggested limited genetic parallelism across lakes, with many differences in demography and colonization history across the breadth of the Arctic charr distribution (Brachmann et al., 2022; Jacobs et al., 2020; Salisbury et al., 2020). However, this previous research on parallelism between Arctic charr ecomorphs focused on the patterns of the genomic response to selection such as outlier loci, which are known to have high rates of false positives and false negatives (Excoffier et al., 2009; Kelley et al., 2006; Narum & Hess, 2011) and are indirect approaches to exploring adaptive divergence in morphology, strongly influenced by evolutionary genomic and demographic histories (Ravinet et al., 2017). Therefore, to properly understand the genomic underpinnings of key phenotypes, we need to apply different approaches that identify loci associated with phenotypic differences through genome-wide association studies (GWAS) in Arctic charr and determine the extent to which these are shared across ecomorph pairs (Elmer, 2016).

Because of their vital role in foraging and swimming, the genetics of head and body morphology have been explored as QTL studies in many fish species, including salmonids (Boulding et al., 2008; Küttner et al., 2014; Laporte et al., 2015; Smith et al., 2020). For example, in lake whitefish, as many as 138 different quantitative trait loci (QTLs) related to body shape have been identified, implying that the trait is highly polygenic in this species (Laporte et al., 2015). In other species, body shape has been found to be less polygenic, with a small number of QTLs identified related to benthic–limnetic differences between ecomorphs of lake trout (Smith et al., 2020) and a single region that differentiates ecomorphs in Atlantic cod (*Gadus morhua)* (Hemmer-Hansen et al., 2013). However, the extent to which parallel phenotypes have the same genomic underpinnings across replicates seems to vary greatly between species and locality. Studies in three-spine

stickleback, rainbow trout (*Oncorhynchus mykiss*) and sockeye salmon (*Oncorhynchus nerka*) all suggest that while some genetic variation that underlies morphological variation can be shared across replicates, this is rarely the case across the species' entire range and the degree of genetic parallelism that is shared is often low (Fang et al., 2020; Larson et al., 2019; Weinstein et al., 2019). Often only a few key genes or loci are shared across replicates, and in some cases, they underlie morph differentiation in multiple species (Jacobs et al., 2017; Salisbury & Ruzzante, 2021).

In this study, we investigated the genomic underpinnings of head and body shape morphology in replicate ecomorph pairs of Arctic charr across four independent lakes in Scotland. First, we determined the extent of phenotypic parallelism in head and body shape morphology across ecomorph pairs. We examined these two traits separately as they are known to involve different axes of ecological specialization and can have different genetic bases (Boulding et al., 2008; Küttner et al., 2014; Smith et al., 2020). Second, we investigated the genome-wide underpinnings of these phenotypes by identifying SNPs strongly associated with head shape variation and body shape variation. We then evaluated the genomic organization of these head- and body-shape-associated SNPs, specifically to determine if they were distributed widely across the genome, co-localized in genes or genomic regions or within known salmonid QTLs. To do this, we updated and augmented an existing QTL database (Jacobs et al., 2017) and mapped this to the orthologous location in the *Salvelinus* sp. genome. Third, we examined evolutionary genomic background by analysis of selection on those loci we found to be associated with head shape and body shape. Shared signals of selection and elevated differentiation and divergence in independent ecomorph pairs would suggest similar processes across evolutionary replicates. Finally, we synthesized the findings to identify shared genomic underpinnings and similarities in phenotypic divergence between head and body shape, as two physically interlinked components of ecomorphology.

2 | MATERIALS AND METHODS

2.1 | Study populations

Fish populations were examined from four lakes in Scotland: Loch Awe, Loch Dughaill, Loch na Sealga and Loch Tay (Figure 1a). Each of these lakes is found in different river systems and has distinct demographic histories and contemporary differentiation, as revealed by previous genetic structuring analysis (Jacobs et al., 2020; Maitland & Adams, 2018) and thus represent independent replicates. Each lake contains two ecomorph populations, one benthivorous and the other planktivorous, with each lake representing an ecomorph pair (Garduño-Paz et al., 2012; Hooker et al., 2016; Jacobs et al., 2020). Explicitly, we investigated the similarities in divergences of head and body shape between the two different ecomorphs across pairs. Short-read genomic data (ddRADseq NCBI short-read bioproject: PRJNA607173) and fish photographs were drawn from previous research (Jacobs et al., 2020) and reanalysed here.

2.2 | Morphological analyses

To investigate patterns in head morphology and body shape separately, landmarks for head (16 landmarks) and body shape (14 landmarks) were placed using *ImageJ v1.50i* (Schneider et al., 2012) (Figure 1e,f). Raw linear measurements for each individual, including fork length, can be found as part of Jacobs et al. (2020). To allow us to cover the whole-body shape of each individual, several markers related to head shape were retained in the body shape analysis. As such, the head and body shape analyses are not completely independent but are focused on each specific phenotype and use a distinct set of landmarks. In total, 341 individual fish were landmarked for head shape (Awe_Bn=37, Awe_Pl=31, Dughaill_Bn=43, Dughaill_Pl=54, naSealga_Bn=42, naSealga_Pl=20, Tay_Bn=41, Tay_Pl=73) and 335 were landmarked for body shape (Awe_Bn=34, Awe_Pl=30, Dughaill_Bn=43, Dughaill_Pl=54, naSealga_Bn=42, naSealga_Pl=19, Tay_Bn=40, Tay_Pl=73). Separate analyses were run for head shape and body shape to allow for comparisons between the two phenotypes.

General procrustes analysis (GPA) was performed to standardize the orientation and remove the isometric effect of size on shape for each individual using *geomorph v3.0.7* (R package) (Adams & Otárola-Castillo, 2013). Following this procedure, shape data were standardized for any residual size effects using the log of centroid size to correct for allometry after determining all lake ecotype populations had parallel slopes using the *procD.allometry()* function (Klingenberg, 2016). Size-corrected data then were used in all subsequent analyses. Principal component analyses (PCA) using the *plotTangentSpace* and *arrayspecs* functions with plots made in *ggplot2 v3.3.5* (R package) (R Core Team, 2021; Wickham, 2016).

Analysis of variance (ANOVA) models were used to determine the relative contributions of parallel and non-parallel aspects of the morphological divergence across ecomorph pairs (Langerhans & DeWitt, 2004). Our ANOVA models (ANOVA model: PC ~ ecomorph + lake + ecomorph × lake) were run for PC1, as it explained the most variance in shape. The *EtaSq* function in the *BaylorEdPsych v0.5* (R package) (Beaujean, 2012) was used to estimate the effect size of each model term. In our model, the ecomorph term represents the parallel or shared term, the ecomorph*lake interaction is the non-parallel (non-shared) term and the lake term represents unique evolutionary history.

Phenotypic trajectory analyses (PTA) were performed on the procrustes scores using the *trajectory analysis* function in *geomorph* to look at the extent and direction of phenotypic change between ecomorphs. Magnitude of divergence is described by the length of trajectories (L) while the angle between trajectories (θ) describes their direction in phenotypic space. This approach allows us to determine how parallel the trajectories of each ecomorph pair are

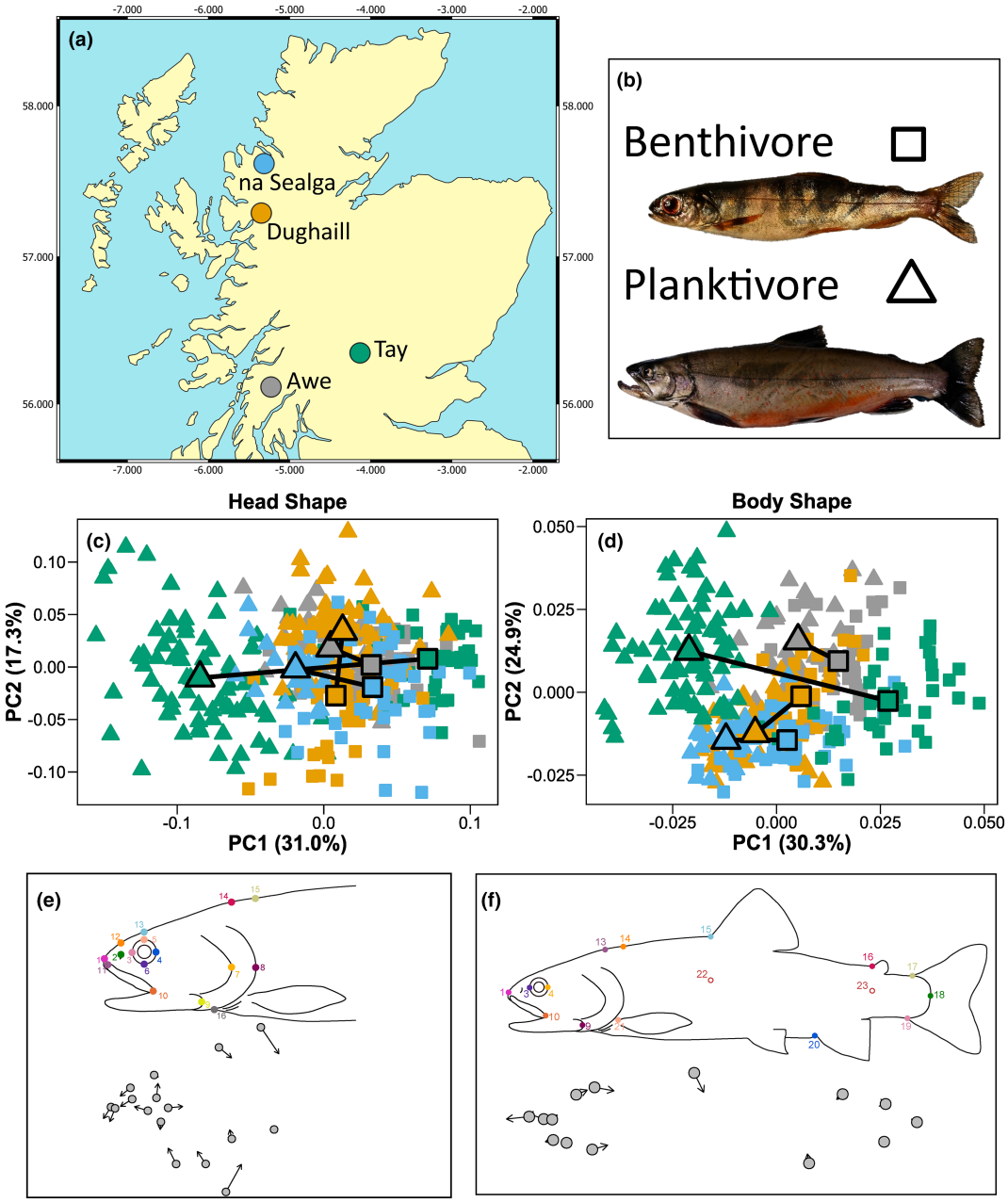

FIGURE 1 Sample locations and morphological analysis. (a) Map of Scotland showing the sampling locations of Arctic charr. (b) Pictures showing an example ecomorph pair, here from Loch Tay. Principal component analysis for landmark analysis for head shape (c) and body shape (d). Individuals are coloured by lake with larger points representing the mean values for each ecomorph with a line connecting means in each pair. Vector plots display how head shape (e) and body shape (f) morphology changes across PC1 with diagrams showing where each landmark was placed on the fish for each phenotype. Grey points show landmark positions at the minimum PC1 score and vectors show how landmark positions change at the maximum PC1 score.

to one another by using the difference in phenotypic trajectory length (ΔL_P) and the direction of phenotypic trajectories (θ_P), where P is either head shape (Head) or body shape (Body) (See Stuart et al., 2017). The significance of differences in trajectory lengths and differences in trajectory direction was assessed using 1000 permutations (Adams & Collyer, 2013; Stuart et al., 2017). Phenotypic divergence between ecomorphs in different lakes was considered to be parallel if the direction and/or magnitude of phenotype change did not differ significantly between the pairs ($p > .05$).

2.3 | Population genomics

Filtered 75 bp reads for each individual, generated via ddRAD-seq from Jacobs et al. (2020) and accessed from ddRADseq NCBI short read bioproject: PRJNA607173, were mapped using *bwa mem* and *SAMtools* using settings described in that paper to the *Salvelinus* sp. genome from NCBI (ASM291031v2). The number of reads per individual ranged from 1 to 3.5 million. RAD loci were built in the *gstacks* module of *Stacks v2.53* (Rochette

et al., 2019) for 200 individuals (Awe large-effect loci_Bn=26, Awe_Pl=29, Dughaill_Bn=28, Dughaill_Pl=27, naSealga_Bn=18, naSealga_Pl=20, Tay_Bn=21 and Tay_Pl=31). Biallelic SNPs were retained in the *populations* module of *Stacks* if they met the following criteria: present in 66% of all individuals in each population and across all populations, a minimum minor allele frequency of 0.05 and a maximum observed heterozygosity of 0.5. Each ecomorph within a lake was considered to be a discrete population (Jacobs et al., 2020). The script filter_hwe_by_pop.pl filters out sites outside Hardy–Weinberg equilibrium within populations using a *p*-value of .001 (available at https://github.com/jpuritz/dDocent). *vcftools v0.1.13* (Danecek et al., 2011) was used to filter to a minimum coverage of 5× and a maximum of 50×. A total of 13,071 SNPs were retained for analyses at mean genotyping rate of 74.8%. A principal component analysis was performed to identify the major axes of genetic variation using *SNPRelate v1.22.0* (R package) (Zheng et al., 2012).

2.4 | Genotype–phenotype association analyses

To determine the association between genotypes and phenotypic variation in head or body shape, we ran linear mixed models (LMMs) in *Gemma v0.98.1* (Zhou & Stephens, 2012). Univariate and multivariate LMMs with Wald's test were run using PCs 1–5 for head shape and body shape as each explained more than 5% of the total variance (Figure S1), the SNP dataset generated for the population genomics analyses and lake of origin as a co-variate (Zhou & Stephens, 2014). Missing genotypes were imputed using *LinkImpute v1.1.4* (Money et al., 2015) and a relatedness matrix was generated using *Gemma* and included in the models to correct for population structure. Changes in allele frequency after imputation were checked with 85% of SNPs showing less than a 5% change in allele frequency. We determined significant associations using Bonferroni-corrected *p*-values (.05/7329 unlinked SNPs) from Wald's tests. The number of unlinked SNPs was determined by LD pruning the full SNP dataset using the snpgdsLDpruning function in *SNPRelate*. Bayesian sparse linear mixed models (BSLMM) (Zhou et al., 2013) were run using PC 1–5 variables to determine how much of the phenotypic variation is explained by the SNPs in our dataset (PVE), secondly how much of that variation is explained by large-effect loci (PGE) and finally, how polygenic each phenotype is (ρ). Manhattan plots were made using *CMplot v4.0* (R package) (https://github.com/YinLiLin/CMplot).

We subsequently determined if SNPs showing significant associations with head shape or body shape morphology were found within annotated genes in the *Salvelinus* sp. reference genome using *BEDtools v2.27.1* (Quinlan & Hall, 2010). The functions of genes containing, or ±1 kbp of, associated SNPs were investigated using GO term overrepresentation analysis (ORA) and gene set enrichment analysis (GSEA). These analyses were run using *topGO v2.40.0* (R package) (Alexa & Rahnenfuhrer, 2020) with all genes containing any RAD loci as the full comparison dataset. Results were summarized using *REVIGO* (Supek et al., 2011) before visualization in *Cytoscape v3.91* (Shannon et al., 2003).

2.5 | Comparisons to known QTLs

Using existing information on the genetics of important phenotypes from other salmonid species, we mapped a database of 1338 QTL markers to the *Salvelinus* sp. genome. This was based on a previously published database of QTLs involved in traits related to morphology and life history, derived from a range of salmonid species and previously mapped to the *Salmo salar* genome (Jacobs et al., 2017). Additionally, a literature search was conducted up to April 2021 to augment the existing database with more recently published QTLs. This literature search was conducted on Web of Science and Google Scholar using the search terms 'QTL', 'quantitative trait loci', 'salmonid' and the common and scientific names for rainbow trout, Atlantic salmon, Arctic charr, lake whitefish, Chinook salmon, coho salmon, brook trout and lake trout. QTL marker sequences were gathered for 17 different phenotypes: body length, body shape, body weight, Fulton's condition factor, directional change, disease resistance, embryonic development, gill rakers, growth rate, hatching time, head shape, parasite resistance, salinity tolerance, sexual maturation, smolting, spawning time and upper-temperature tolerance (Table S1).

Following Jacobs et al. (2017), the strategy of mapping the QTL-linked markers to the *Salvelinus* sp. genome depended on the QTL marker type: RAD loci were mapped using *Bowtie2 v2.4.4* and the *very sensitive* preset; microsatellite primer sequences, which are shorter, were mapped using *Bowtie v1.3.1* allowing for three mismatches. QTLs for which the flanking markers mapped to different chromosomes were removed. Redundant QTLs, that is, where two QTLs for the same trait from the same species mapped to the same location, were removed only keeping the QTL with the higher PVE or LOD score (following Jacobs et al., 2017). For QTLs, where more than one marker was reported, we attempted to map all markers. Position values for the QTLs markers were then compared to positions of the phenotype-associated SNPs using *BEDtools*, with a cut-off of ±100kbp. This value was used so that we could consider SNPs within the range to be proximal to a QTL peak while also accounting for the large size of many of the QTLs in the database. In total, we successfully mapped 669 QTL-linked sets of markers to the *Salvelinus* sp. genome after removing redundant QTLs (Table S2).

2.6 | Genomic response to selection

We investigated if the phenotype-associated SNPs identified in our analyses showed signals of genomic differentiation potentially caused by response to selection and if those signals were replicated across ecomorph pairs. To test this, for each ecomorph pair, we

compared F_{ST} and D_{XY} values for phenotype-associated SNPs to a random background subset of SNPs. This random subset was 100 SNPs randomly selected from the whole dataset and the mean F_{ST} and D_{XY} values for those SNPs were calculated. This was repeated 10,000 times and the means for F_{ST} and D_{XY} were taken across all permutations. These permuted values were then compared to the empirical mean F_{ST} and D_{XY} values for the phenotype-associated SNPs using the *t.test* function in R.

2.7 | Analyses of recombination rate variation

To test the effect of the recombination landscape on phenotype–genotype association, we first estimated recombination rates using the published Arctic charr linkage map ($N = 3636$) (Christensen et al., 2018) using *MareyMap v1.3.6* (Siberchicot et al., 2020). RAD loci from the linkage map were aligned to the *Salvelinus* sp. reference genome with Bowtie2 (Langmead & Salzberg, 2012) using the *-very-sensitive* setting. Loci were kept if they were uniquely mapped to one location, mapped to the same chromosome as all other loci on their linkage group and followed the orientation of the linkage map (i.e. not reversed). The filtered dataset was used to estimate the recombination rate across each chromosome using a spline algorithm. Spar values were varied for each chromosome from 0.5 to 0.9, depending on chromosome size, to best fit the data (Berloff et al., 2002). Subsequently, *WindowScanR v0.1* (available at: https://github.com/tavareshugo/WindowScanR) was used to summarize recombination rate values in 1 MB windows along the genome. All SNPs were assigned to these windows using *BEDtools*. A random subset of 100 SNPs was then selected and the mean recombination rate for those SNPs was calculated based on their windows. This was repeated 10,000 times to generate a background mean recombination rate, which was then compared to the mean recombination rate of the phenotype-associated SNPs (based on their windows) using a *t*-test.

3 | RESULTS

3.1 | Ecomorph divergence in head shape

For head shape, the benthivore and planktivore ecomorphs were separated across PC1 (31% variance explained), except from Loch Dughaill where the ecomorphs separate along PC2 (17.3%) (Figure 1c). Individuals with a positive PC1 score had shallower heads with larger eyes than those with negative PC1 scores (Figure 1e). For PC2, a more positive score suggested a longer head shape. The benthivore ecomorphs generally have a more negative PC2 score, suggesting their heads are shorter than the planktivore ecomorphs (Figure S2).

We compared the magnitude and direction of phenotypic change for head shape between the ecomorphs across pairs to determine how similar the divergences were, through a phenotypic trajectory analysis (PTA). We found that for all pairwise comparisons, the angle of difference in phenotypic trajectories (θ) was significantly different ($p < .05$) (Table 1). Similarly, almost all differences in trajectory lengths between ecomorphs pairs (ΔL) were significantly different with the exception of the Awe versus na Sealga comparison. These results suggest that head shape morphology is variable across lakes. While the ecomorph term explained the most variance along PC1 in our ANOVA model ($PC \sim ecomorph + lake + ecomorph \times lake$) ($\eta^2_{Eco} = .595$), the ecomorph × lake interaction term explained a similar amount of variance ($\eta^2_{Eco*Lake} = .568$), suggesting that the effect of lake environment and/or evolutionary history strongly impacts the direction and magnitude of head shape divergence between ecomorphs

TABLE 1 Phenotypic trajectory analysis comparisons across ecomorph pairs for head shape and body shape.

Phenotype	Ecomorph pair comparison	ΔL (magnitude of change)	*p*-Value	θ (Direction of change)	*p*-Value
Head shape	Awe–Dughaill	0.0347	.003	67.51°	.001
	Awe–na Sealga	0.0032	.777	65.74°	.002
	Awe–Tay	0.0901	.001	57.29°	.007
	Dughaill–na Sealga	0.0379	.002	78.37°	.001
	Dughaill–Tay	0.0554	.001	100.56°	.001
	na Sealga–Tay	0.0933	.001	47.88°	.027
Body shape	Awe–Dughaill	0.0097	.004	92.48°	.001
	Awe–na Sealga	0.0013	.726	55.27°	.004
	Awe–Tay	0.028	.001	39.64°	.038
	Dughaill–na Sealga	0.011	.001	70.65°	.001
	Dughaill–Tay	0.0183	.001	79.24°	.001
	na Sealga–Tay	0.0293	.001	34.20°	.118

Note: The difference in trajectory length, the magnitude of change and between ecomorph pair is indicated by ΔL. The angle between trajectories is indicated as θ. The significance values are provided for each comparison.

and that there are unique elements of divergence in head shape across lakes (Table S3).

3.2 | Genomic regions associated with head shape

To determine the genomic variation underpinning head shape, we performed a genome-wide association analysis (GWAS) on a set of 13,071 SNPs (PCA of ecomorph and lake variation shown in Figure S3). Using the PC scores from the head shape analysis (PCs 1–5), a Bayesian sparse linear mixed model (BSLMM) showed that the proportion of phenotypic variance in head shape explained by genetic variation (PVE_{Head}) in the SNP dataset was 0.62 with the proportion of phenotypic variance explained by large ('sparse') effect loci (PGE_{Head}) was 0.82. This is supported by the ρ (rho) value for head shape that suggests that the head shape phenotype is controlled largely by a few large-effect loci ($\rho_{Head} = 0.792$).

Applying linear mixed models to identify SNPs highly associated with head shape variation found a total of 82 SNPs (66 SNPs mapped on 27 of 39 chromosomes and 16 mapped to unanchored scaffolds) that showed a significant association with variation in head shape (Bonferroni-corrected p-value <.05; Figure 2a) with these SNPs broadly distributed across the genome.

3.3 | Genomic differentiation at SNPs associated with head shape

We investigated whether these head-shape-associated SNPs were highly diverged between the ecomorphs in all lakes, consistent with shared genomic bases for these phenotypes or whether they were specific to certain populations suggesting the deployment of different genetic pathways leading to the similar phenotypes across pairs. We found a total of three SNPs that were diverged in all four lakes (Figure 3a).

We aimed to identify if those SNPs associated with head shape showed signs of response to divergent or positive selection in all four lakes. Mean genetic differentiation (F_{ST}) and absolute divergence (D_{XY}) between ecomorphs in lochs Dughaill and Tay were

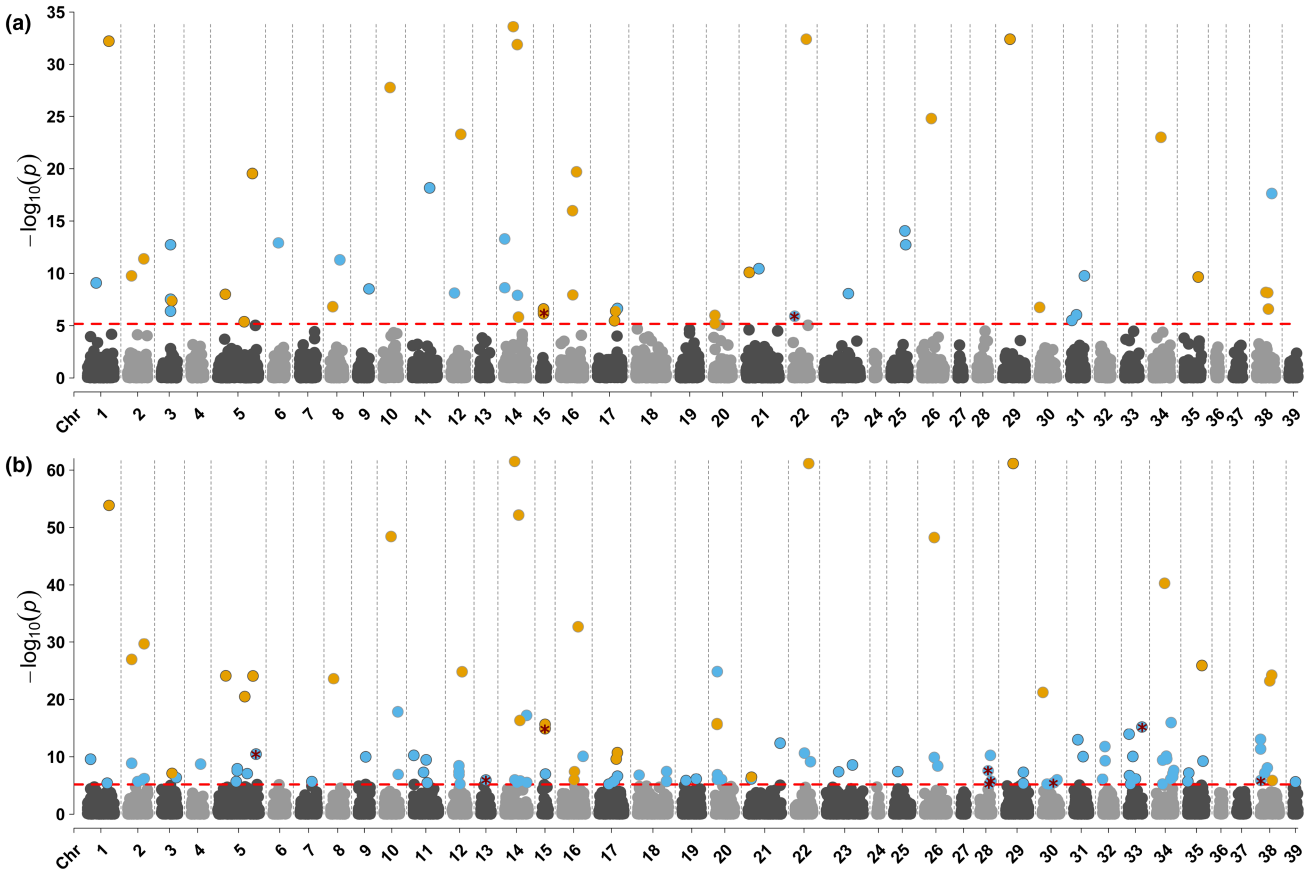

FIGURE 2 Manhattan plots for genomic location of SNPs highly associated with morphology. (a) Shown are 67 SNPs associated with head shape across the four lakes of two ecomorphs of charr. (b) Shown are 144 SNPs associated with body shape. SNPs associated with head or body shape are highlighted in blue; SNPs associated with both head shape and body shape are highlighted in orange (38 SNPs). Red asterisk indicates SNPs shared across all four ecomorph pairs for head shape ($N = 2$) and body shape ($N = 9$). SNPs on unanchored scaffolds are not pictured.

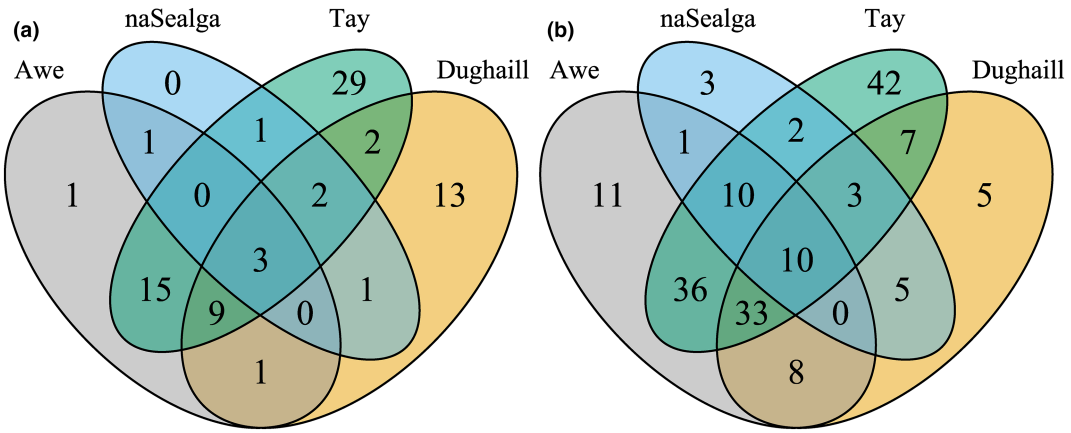

FIGURE 3 Venn diagram of SNPs associated with head shape (a) and body shape (b) and how they are shared across each combination of different lake pairs.

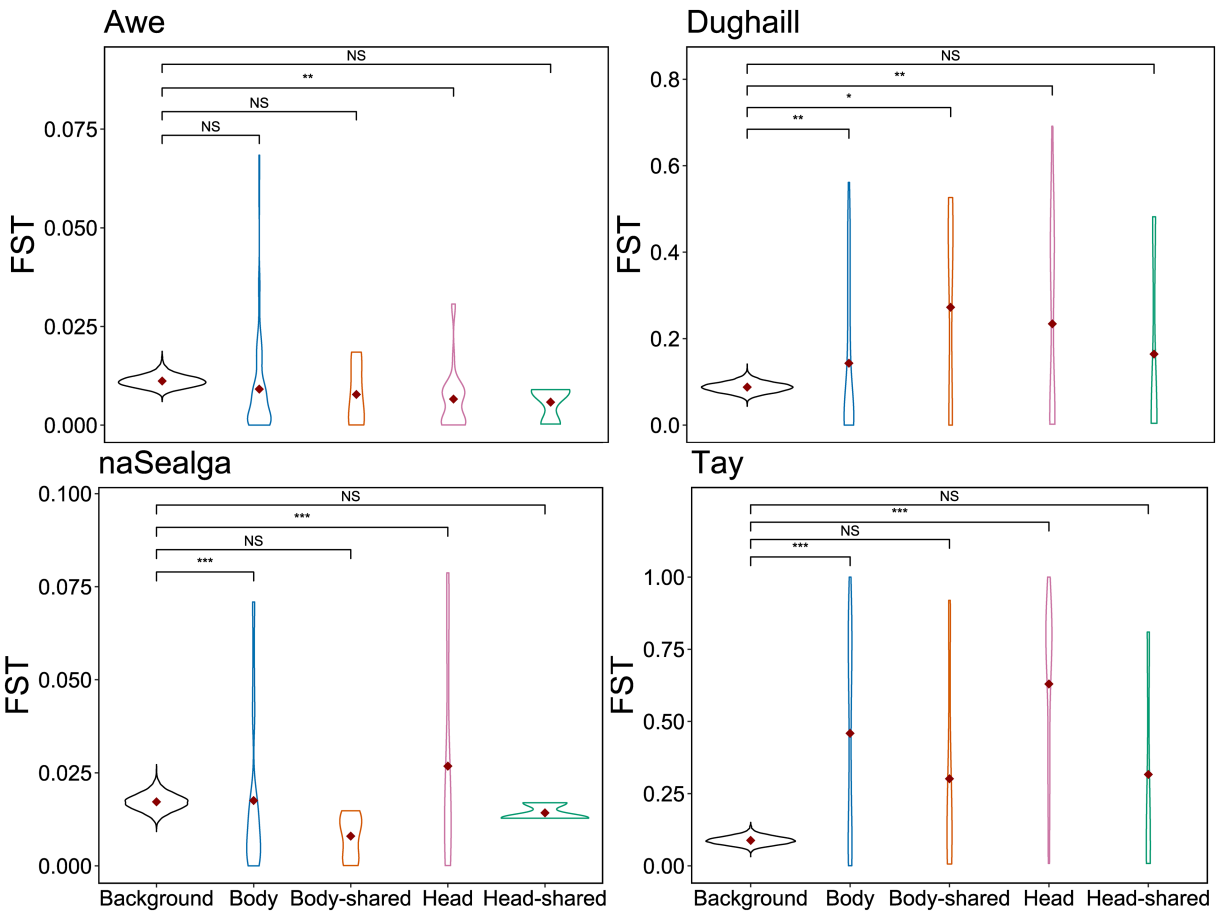

FIGURE 4 Genetic differentiation (F_{ST}) between ecomorphs at each lake for different associated SNP datasets. Body refers to all SNPs associated with body shape and head refers to all SNPs associated with head shape. Body-shared dataset is just the body shape SNPs found in all four ecomorph pairs and head-shared is the equivalent for head shape SNPs. Background SNPs refer to a randomly selected background subset of SNPs used for comparisons. Red diamonds are the mean value for that dataset. Significance of difference in means is indicated by NS ($p > .05$), * ($p < .05$), ** ($p < .01$) and *** ($p < .001$).

elevated among associated SNPs when compared to the background (Figures 4 and 5, Table S4). F_{ST} and D_{XY} were significantly lower than background between ecomorphs in Loch Awe for the associated SNPs. There was no significant difference in F_{ST} or D_{XY} between associated SNPs and the background in na Sealga. These results suggest that the SNPs associated with head shape are not similarly responding to, or are under selection, across all lakes. These patterns were not influenced by linkage because

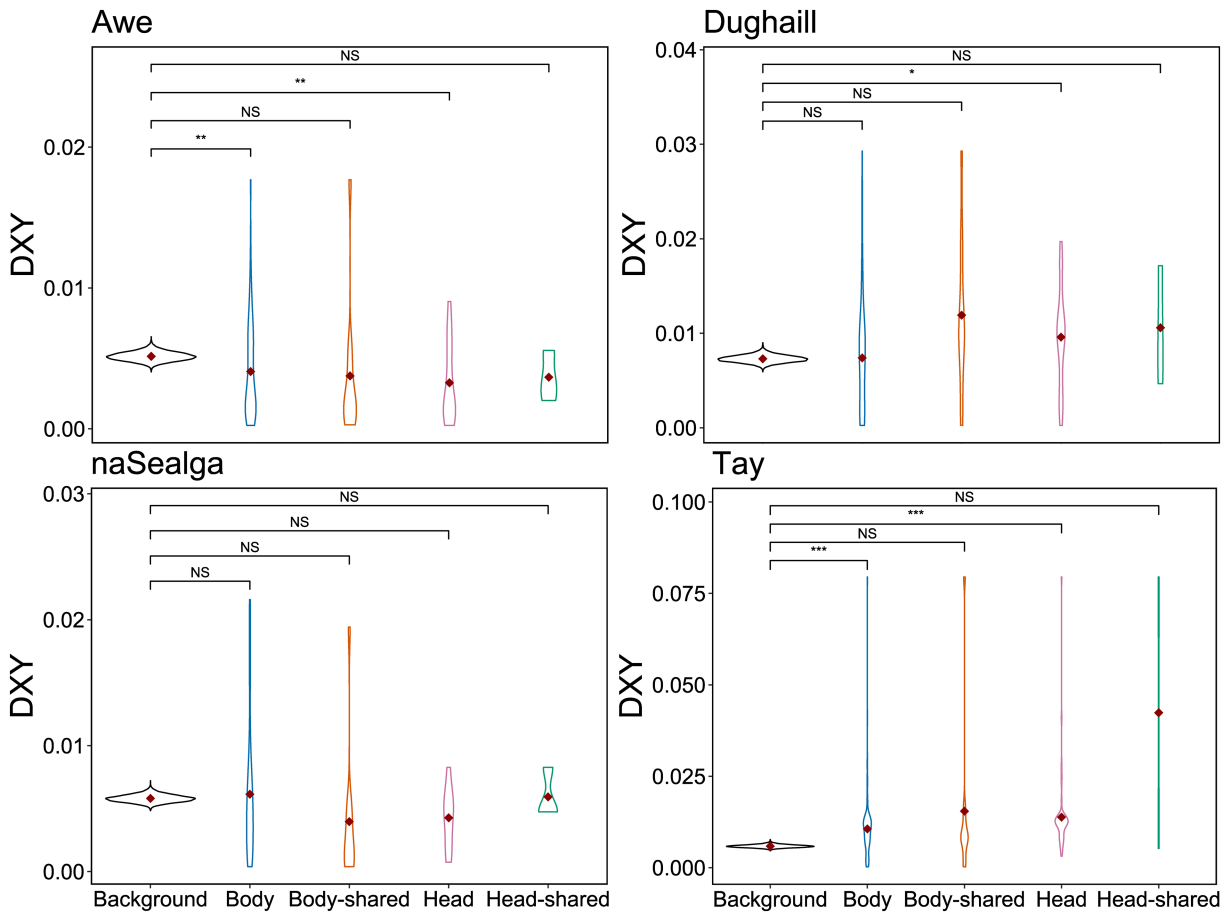

FIGURE 5 Absolute divergence (D_{XY}) between ecomorphs at each lake for different associated SNP datasets. Body refers to all SNPs associated with body shape and head refers to all SNPs associated with head shape. Body-shared dataset is just the body shape SNPs found in all four ecomorph pairs and head-shared is the equivalent for head shape SNPs. Background SNPs refer to a randomly selected background subset of SNPs used for comparisons. Red diamonds are the mean value for that dataset. Significance of difference in means is indicated by NS ($p > .05$), * ($p < .05$), ** ($p < .01$) and *** ($p < .001$).

recombination rates for genomic regions around head-shape-associated SNPs did not differ significantly from genomic background (Figure S4).

3.4 | Genes and QTLs associated with head shape variation

Focusing on the location of the head-shape-associated SNPs relative to known genes in the charr genome, we found that 38 of the 82 SNPs were located within annotated genes (Table S5). GO term analyses found that the genes containing head-shape-associated SNPs showed overenrichment for GO terms related to odontogenesis (GO:0042476) and cranial skeleton system development (GO:1904888) among other processes and functions (Table S6) when compared to all genes containing SNPs in our dataset.

To examine if any of these genomic associations were shared across other species, we compared the positions of the head-shape-associated SNPs to QTL markers from across salmonid species. We found that three of the head-shape-associated SNPs were found within ±100,000 bp of the peak positions of two mapped QTLs (Table 2). These two QTLs were previously found to be associated with body shape morphology in lake trout and lake whitefish (Laporte et al., 2015; Smith et al., 2020).

3.5 | Ecomorph divergence in body shape

For body shape, all four ecomorph pairs showed separation along PC1 (30.3%) (Figure 1d); however, the pair from Loch Dughaill diverged in a different direction, along PC2 (24.9%). Individuals with a positive PC1 score (e.g. the benthivore morphs at Awe, na Sealga and Tay) have shallower, more elongated body shapes (Figure 1f). The patterns across PC2 suggest that a more positive score is associated with a deeper body (Figure S5).

In the PTA, we again found that all differences in the magnitude of phenotypic change between the pairs (ΔL) were significant with the exception of the Awe-na Sealga comparison (Table 1). When comparing angle of difference in trajectories (θ), we found all angles between pairs were significant with the exception of the na Sealga–Tay comparison

TABLE 2 Table of associated SNPs found within ±100 kbp of salmonid QTLs mapped to the *Salvelinus* sp. genome.

SNP phenotype	QTL species	QTL marker	QTL type	Chromosome	SNP position	QTL position
Head and Body	*C. clupeaformis*	Cocl_BS_096	Body shape	NC_036838.1	46,764,741	46,685,809
Head and Body	*S. namaycush*	Sna_BS_069	Body shape	NW_019942687.1	358,354	361,478
Head and Body	*S. namaycush*	Sna_BS_069	Body shape	NW_019942687.1	358,355	361,478
Body	*S. alpinus*	Sal_BW_053	Body weight	NC_036871.1	32,030,838	31,993,282
Body	*S. namaycush*	Sna_BS_092	Body shape	NC_036854.1	21,330,886	21,293,280

Note: Which phenotype the SNP is associated with, its position and position of QTL marker in question are all indicated. The QTL type and species of origin are indicated. QTL name refers to the designation the QTL was given in the whole QTL database found in Table S1.

(Table 1), suggesting body shape may show some parallelism across lakes. The ecomorph term in the ANOVA model (η^2_{Eco}=.63) for body shape (PC1) explained the most variation which indicates some shared elements of body shape across lakes (Table S3).

3.6 | Genomic regions associated with body shape

A BSLMM found that the proportion of phenotypic variance in body shape explained by the SNP dataset (PVE_{Body}) was 0.82, the proportion of phenotypic variance explained by large ('sparse') effect loci (PGE_{Body}) was 0.39 and the ρ (rho) value (ρ_{Body}) was 0.425. By analysis with LMMs, we found 180 SNPs significantly associated with body shape variation (144 SNPs mapped to 34 chromosomes and 36 SNPs mapped to unplaced scaffolds) (Figure 2b). We found that 10 of these SNPs were present in all 4 ecomorph pairs (Figure 3b) and broadly distributed across the genome (on 7 chromosomes).

3.7 | Genomic differentiation at SNPs associated with body shape

For F_{ST}, we found that the body-shape-associated SNPs had a higher mean value than the background at Loch Dughaill and Tay (Figures 4 and 5, Table S4) but no notable difference at Loch Awe or na Sealga. D_{XY} was significantly higher at Tay for the associated SNPs while it was significantly lower at Loch Awe. There was no significant difference in D_{XY} between associated SNPs and the background at Loch Dughaill and na Sealga. The mean recombination rate in regions containing body shape SNPs did not differ from the background (Figure S4).

3.8 | Genes and QTLs associated with body shape

Relative to known genes in the *Salvelinus* sp. genome, 89 of the body-shape-associated SNPs were located within annotated genes (Table S5). The body-shape-associated genes showed overrepresentation for genes involved in skeletal system (GO:0001501), face (GO:0060324), eye (GO:0060041, GO:0001745) and mouth development (GO:0060021) among other processes and functions (Table S6). We found five SNPs in close proximity to four known QTLs (Table 2). These QTLs were previously found to be associated with body shape morphology in lake whitefish, body weight in Arctic charr and body shape morphology in lake trout (Laporte et al., 2015; Norman et al., 2011; Smith et al., 2020).

3.9 | Comparisons between head shape and body shape

We found in our PTA that comparisons in head shape showed greater mean differences in the magnitude and direction of phenotypic change (ΔL_{Head}=0.053±0.035 SD, mean θ_{Head}=69.87°±17.54 SD mean) compared to body shape (mean ΔL_{Body}=0.016±0.011 SD, mean θ_{Body}=61.62°±22.63 SD) (Table S7). Both our PTA and ANOVA suggest that body shape shows more elements of shared divergence than head shape; however, both phenotypes show substantial deviations from strict parallelism across lakes.

Our association analyses indicated a significant shared genetic basis behind body shape and head shape. Fifty of the SNPs found in our study appeared associated both with head and body shape morphology (212 SNPs identified: 32 SNPs associated with head shape, 130 associated with body shape and 50 associated with head and body shape), which exceeds random expectation (hypergeometric test; $p=6.633e^{-16}$). Of these head- and body-shape-shared SNPs, 38 mapped to 20 chromosomes and 12 mapped to unplaced scaffolds (Figure 2). These SNPs show overrepresentation for terms related to brain (GO:0030900, GO:0021575) and heart development (GO:0003007), and regulation of cell shape (GO:0008360) among other processes (Table S6). With a number of SNPs shared between both head and body shape, two of the QTLs we identified as near-associated SNPs were near SNPs shared for both phenotypes. These QTLs related to body shape in lake trout and lake whitefish respectively (Table 2) (Laporte et al., 2015; Smith et al., 2020).

This shared genetic basis is reflected in the PTA, which showed that there was a positive linear relationship when comparing trajectory lengths for head shape and body shape across lakes. Specifically, pairs in which the ecomorphs have diverged to a similar extent in head shape have also diverged to a similar extent in body shape (adjusted R^2=.99, p<.001) (Figure 6). A similar positive relationship was seen

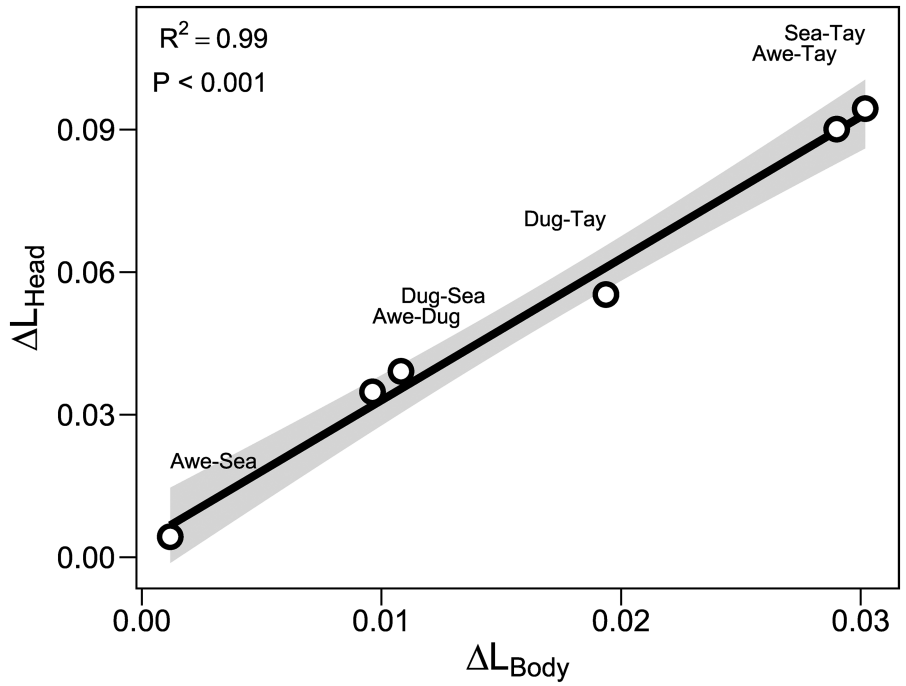

FIGURE 6 Correlation between the magnitude of difference in trajectory lengths between head shape (ΔL_{head}) and body shape (ΔL_{Body}) in each sympatric ecomorph pair within each lake and compared pairwise between ecomorph pairs across all lakes (lakes Awe, Dughaill [Dug], Na Sealga [Sea] and Tay).

when comparing differences in the direction of phenotypic change, although this was non-significant (adjusted $R^2 = .29$, $p = .154$) (Figure S6).

4 | DISCUSSION

Through our analyses, we identified genomic regions that underlie head shape and/or body shape morphology in ecomorph pairs of Arctic charr. Of these phenotype-associated SNPs, many (approximately one quarter: 50 of 212) were shared between head and body shape. The extent and direction of divergence in head and body shape morphology were positively correlated, suggesting a shared developmental basis for the two phenotypes. The SNPs we found associated with each phenotype were often found in genes related to morphology or anatomical development. Indeed, independently previously identified QTLs in the genomic region of body- or head-associated SNPs were often those related to morphology.

We found limited parallelism in shape morphology and genomic underpinnings with many population-specific patterns in the divergence of head and body shape morphology between ecomorphs across pairs. Many of the phenotype-associated SNPs were not present in all four pairs likely due to polygenic genomic architectures and the incomplete representation of the genome in our approach. The phenotype-associated SNPs that were found to be shared were not highly diverged in all pairs and did not appear to be under the same selective pressures. Body shape in particular appears to be rather polygenic allowing for the genomic underpinnings of the phenotypes to vary across lakes.

4.1 | Limited parallelism in head and body shape divergences across replicates

While previous work on parallelism in these pairs suggested substantial phenotypic parallelism in some linear traits related to head shape (Jacobs et al., 2020), our more sensitive geomorphometric approach to describe shape suggests considerable phenotypic variation across replicated ecomorphs in multivariate space for both head shape and body shape.

The lack of phenotypic parallelism between Loch Dughaill and the other ecomorphs pairs may arise from its ecological distinctiveness compared to the others. While benthivore morphs typically occupy the shallow littoral zone of lakes as they do at the other three lakes in our study, the benthivore morph at Loch Dughaill is a 'profundal' benthivore and as such utilizes a much deeper part of the lake environment and the lake has a smaller area (Hooker et al., 2016; Jonsson & Jonsson, 2001). The divergence we see between the ecomorphs at Loch Dughaill, as indicated by the PCA, is in line with other 'profundal' charr morphs found across the Holarctic, with the benthivore ecomorph having a deeper head and body than the planktivore morph (Klemetsen, 2010; Skoglund et al., 2015). This is the inverse pattern of the more common benthivore–planktivore divergence where the benthivore morph has the shallower, longer head and body shape that is seen in the other three ecomorph pairs (Garduño-Paz et al., 2012).

Evidence for the parallel evolution of head and body shape morphology across ecomorphs has been shown in previous studies of Arctic charr (Adams et al., 2008; Kristjánsson et al., 2012; Saltykova et al., 2017). However, even disregarding the notably

distinct Dughaill ecomorph pair, the other three ecomorph pairs show limited evidence of parallelism in shape morphology despite the parallel evolution of ecomorphs themselves. Evolutionary divergence and thus phenotypic trajectories are influenced by the interaction between environmental variation and adaptive genetic variation. As a result, repeated ecomorph divergences often have very different phenotypic trajectories for key components of phenotypes, as seen in three-spine stickleback (Stuart et al., 2017). Thus, the lack of strict parallelism seen in our study is likely the result of known differences in the evolutionary histories of these pairs and differing selective pressures in their local environments, for example, from differences in their ecosystems or diets (Jacobs et al., 2020). Parallelism can also be generated by other mechanisms, such as differences in gene expression, post-translational modifications and/or alternate splicing (Filteau et al., 2013; McGirr & Martin, 2018). Indeed, differences in splicing and gene expression patterns showed parallel patterns across ecomorph pairs in a study on three of the ecomorph pairs we investigated (Jacobs & Elmer, 2021) and provided explanations of alternative adaptive paths.

Of the two traits we tested, head shape had longer phenotypic trajectory lengths and greater angles, suggesting that the ecomorphs are more differentiated in head shape from one another and that head shape has evolved in more distinct directions across lakes. Head shape is well recognized as an important phenotype for foraging and prey specialization, while body shape is important for swimming behaviour and habitat complexity in these and other fishes (Adams et al., 1998; Skoglund et al., 2015; Webb, 1984). The considerable divergence in head shape between ecomorphs within lakes suggests different prey specializations (Garduño-Paz et al., 2012; Hooker et al., 2016) while their body shapes and therefore perhaps swimming behaviours are more subtly different. The high trajectory angles for head shape suggest notable differences in foraging across lakes, whether that be due to the lake environments or the actual species available as prey (Garduño-Paz & Adams, 2010). For both traits, Loch Tay and Dughaill showed notably higher trajectory lengths than Awe and na Sealga and more evolutionary divergence, also seen in the ecomorphs' genomic divergence (F_{ST} ~ 1% between ecomorphs in Awe and na Sealga vs. 9% in Dughaill and Tay) (Table S8). This reflects likely what were previously inferred to be recent sympatric divergences of ecomorph pairs in Awe and na Sealga, while Tay and Dughaill each have complex histories of divergence and secondary contact between colonizing lineages (Fenton et al., 2023; Jacobs et al., 2020).

4.2 | Genomic underpinnings of head and body shape across lakes

From our total of 212 SNPs that showed high associations with head and/or body shape (Figure 2), we found more SNPs associated with body shape than for head shape. Head shape was controlled by more large-effect loci relative to body shape and may suggest that head shape is controlled by fewer genes/pathways. In both cases, these will be an underestimate of actual associations because we have reduced representation of the genome captured. We found that for both head and body shape only a small number of associated SNPs were diverged between ecomorphs in all four pairs (Figure 3). This is in line with what has been suggested both in other Arctic charr studies and other salmonid species, in which genetic differentiation between ecomorphs is largely non-parallel across pairs bar at a few key genes (Brachmann et al., 2022; Salisbury et al., 2020; Salisbury & Ruzzante, 2021). Further to previous work, we found that the SNPs shared across pairs were not highly differentiated between ecomorphs in all pairs, suggesting that while present, they are not critical to underlying the phenotypic differences in each pair (Figure 4). These results also suggest that the genomic underpinnings of each phenotype vary across the lakes, likely contributing to the phenotypic differences we see between pairs. The polygenic genomic underpinnings of both phenotypes, as indicated by the numbers of associated SNPs identified, indicate that there are multiple pathways that can achieve the same phenotypes, hence the lack of high divergence for the same SNPs across all lakes (Salisbury & Ruzzante, 2021).

Loch Dughaill and in particular Loch Tay often showed notable high genomic divergence between ecomorphs for many of the associated SNPs for each trait. Additionally, the associated SNPs for both traits showed high D_{XY} values compared to the background subsets at both of these lakes. While increased levels of D_{XY} or F_{ST} compared to genomic background can be indicative of positive selection (Bamshad & Wooding, 2003), they might also be expected for loci resisting introgression following secondary contact (Cruickshank & Hahn, 2014), as is likely the case in Loch Tay and Loch Dughaill (Jacobs et al., 2020). The associated SNPs we found are widespread across the genome (Figure 2) indicating these are not single-linked regions of divergence as found in studies on Atlantic cod and rainbow trout (Hemmer-Hansen et al., 2013; Pearse et al., 2019) but instead are diffused and highly polygenic, similar to patterns for body shape in lake whitefish (Laporte et al., 2015).

4.3 | Functional genomic regions for head and body shape

Roughly half of the associated SNPs identified for head and/or body shape were found within or proximal to an annotated gene in the charr genome. A number of the GO terms that appeared as significantly overrepresented or enriched in our study have been identified in other studies investigating adaptive divergences or parallel evolution in various fish species. Odontogenesis (GO:0042476), sensory perception of sound (GO:0007605), blood vessel remodelling (GO:0001974), response to muscle activity (GO:0014850), ventricular trabecula myocardium morphogenesis (GO:0003222), common-partner SMAD protein phosphorylation (GO:0007182), cellular response to ethanol (GO:0071361) and neuromuscular synaptic transmission (GO:0007274) have shown

significance in other Arctic charr studies investigating ecomorph divergence (Guðbrandsson et al., 2019; Salisbury et al., 2020). The GO terms for associative learning (GO:0008306), regulation of cell shape (GO:0008360) and UDP-glucuronate biosynthetic process (GO:0006065) also appear in overrepresented groups in a study on the divergence of a sympatric lake whitefish species pair (*Corgeonus clupeaformis*) in the USA (Hebert et al., 2013). Finally, in pupfishes (*Cyprinodon* sp.), the divergent expression of a number of genes involved in cranial skeletal system development was seen between different trophic specialists with the GO term for this process (GO:1904888) significant in our study (McGirr & Martin, 2018). Differences in ossification rate have been related to adaptive morphological differentiation in other freshwater fish and the overenrichment or overexpression of genes related to formation of various bones in our study indicates a similarly important role in adaptive divergences between ecomorphs of Arctic charr (Esin et al., 2018). Indeed, previous work has noted the importance of differences in bone structure and sizes between different ecomorphs of Arctic charr (Jónsdóttir et al., 2023; Kapralova et al., 2015). These functional genomic links warrant further research.

The QTL database that we have developed allows us to explore whether rapid replicated diversification of ecomorphs in different salmonid species is underlined by the use of the same functional regions as has been previously suggested for salinity tolerance (Jacobs et al., 2017; Norman et al., 2012). Our results suggest that this is true to some extent with QTLs related to body shape in lake trout and whitefish found in proximity to SNPs that we identified as being associated with phenotypic differences in Arctic charr ecomorphs. While we only identified a small number of QTLs located near the associated SNPs, this is in line with other work which suggests that shared basis for ecomorph divergence across species may be limited (Salisbury & Ruzzante, 2021). This QTL marker database will be a valuable resource for future salmonid research in charr and other species.

5 | CONCLUSION

Our results indicate differences in head and body shape responses to ecological selection regimes across four replicate lakes. These differing responses are likely enabled through the use of largely different genetic bases across independent replicate ecomorph pairs. Specifically, we found that only a small number of SNPs were shared across all four pairs, suggesting limited genetic parallelism with these shared SNPs under varying selective pressures across lakes. We found that head and body shape morphology have a level of shared genetic underpinnings in Arctic charr and that the genetics of these phenotypes are shared to an extent across different salmonid species. Our analyses highlight the complexity of the evolutionary genetics that underlie parallel phenotypes across replicates. Furthermore, we demonstrate the power of using population replicates to resolve fundamental genetic and evolutionary patterns from the noise of local variation.

AUTHOR CONTRIBUTIONS

KRE and AJ conceived the study with input from CB and CA. Read mapping and landmarking were done by AJ. Data analyses were performed by SF with analytics support from AJ. SF wrote the original draft with support from KRE and all authors contributed to subsequent versions of the manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors report that there are no competing interests to declare.

OPEN RESEARCH BADGES

This article has earned an Open Data badge for making publicly available the digitally-shareable data necessary to reproduce the reported results. The data is available at https://doi.org/10.5525/gla.researchdata.1502

DATA AVAILABILITY STATEMENT

The SNP VCF file, landmark data and the QTL database are available on the University of Glasgow's data repository along with the scripts. See Enlighten DOI: https://doi.org/10.5525/gla.researchdata.1502

BENEFIT SHARING STATEMENT

Benefits from this research accrue from the sharing of our data and results on public databases. The QTL database is made public and shared.

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