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Ontogenetic and ecotypic variation in the coloration and morphology of rainbow trout (*Oncorhynchus mykiss*) in a stream–lake system

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Alternative ecotypes of diverse animal taxa exhibit distinct, habitat-specific phenotypes. Rainbow trout (*Oncorhynchus mykiss*), a salmonid fish, exhibits stream-resident (fluvial), lake-migrant (adfluvial) and ocean-migrant (anadromous) ecotypes throughout its range. We investigated the coloration, and morphology associated with swimming performance of wild, native non-anadromous rainbow trout in connected stream and lake habitats of a south-west Alaskan watershed to assess if they exhibited phenotypic diversity consistent with the presence of alternative fluvial and adfluvial ecotypes. Colour differences among rainbow trout of different size classes and habitats (stream or lake) indicated ecotype-specific pathways, diverging at the same point in ontogeny and resulting in different terminal coloration patterns. Specifically, lake-caught fish exhibited distinct silvering of the body, whereas stream-caught fish displayed banded coloration when small and bronze colour when larger. The morphology of lake-caught rainbow trout also differed from that of stream-caught fish in features associated with swimming performance, and they exhibited both shared and unique morphological patterns compared to sympatric *Salvelinus* species in those habitats [Dolly Varden (*S. malma*) in streams, and Arctic char (*S. alpinus*) in the lake]. Greater morphological variation within stream- than lake-caught rainbow trout, and their limited overlap in morphology, suggested population-specific partial migration. This study highlights the intraspecific diversity of migratory behaviour and how conservation of particular phenotypes depends on managing both for genotypes and for habitats.

ADDITIONAL KEYWORDS: adfluvial – coloration – ecotype – fluvial – morphology – *Oncorhynchus mykiss* – ontogeny – partial migration – rainbow trout.

INTRODUCTION

Animals occurring across a gradient of environmental conditions or in distinctly different habitats may experience disruptive selection, leading to the emergence and maintenance of multiple ecotypes (i.e. alternative habitat-specific forms of the same species: Weissing *et al.*, 2011). Intraspecific ecotypes of diverse taxa exhibit distinct phenotypes suited to their respective habitats, including differences in coloration and morphology (western brook lamprey (*Lampetra richardsoni*): Beamish, 1987; walking stick (*Timema cristinae*): Nosil, 2007; grey wolf (*Canis lupus*): Schweizer *et al.*, 2016; bottlenose dolphin (*Tursiops truncatus*): Fruet *et al.*, 2017). Phenotypic differentiation among ecotypes may have a significant genetic basis (Liedvogel *et al.*, 2011) or be primarily due to phenotypic plasticity (Adams & Huntingford, 2004). The ecological and phenotypic distinctiveness of ecotypes may lead to assortative mating and further promote adaptive divergence within a species (Maan & Seehausen, 2011).

In salmonids and other groups of fishes, resident and migrant individuals from the same population constitute alternative ecotypes in a phenomenon known as partial migration (Jonsson & Jonsson, 1993; Chapman *et al.*, 2012). Most salmonids spawn in streams, and their progeny may reside in the natal stream network (fluvial), migrate to a lake (adfluvial) or migrate to an ocean (anadromous) (Quinn, 2018). The proportion of residents to migrants within a population is controlled by differences in growth potential and mortality risk between the natal and non-natal habitats (Pavlov & Savvaitova, 2008; Chapman *et al.*, 2011); migrants typically achieve greater asymptotic sizes and fecundity but experience lower survival rates (Jonsson & Jonsson, 1993). Movement to

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*Corresponding author. E-mail: marosteg@uw.edu a new habitat by migrant salmonids exposes them to different ecological challenges (*sensu* Liedvogel *et al.*, 2013) and is associated with their phenotypic change (Jonsson & Jonsson, 1993). Migrant and resident salmonids exhibit morphological divergence consistent with swimming in standing vs. flowing water (Varian & Nichols, 2010; McKinney *et al.*, 2014). Similarly, migrants exhibit silver coloration appropriate to the pelagic environment whereas residents typically remain darkly coloured with numerous spots, providing camouflage in streams (Nakano *et al.*, 1990; Tanguy *et al.*, 1994; Tsiger *et al.*, 1994; Behnke, 2002).

Oncorhynchus mykiss commonly exhibit fluvial and adfluvial ecotypes, both commonly referred to as rainbow trout, and an anadromous ecotype, known as steelhead, throughout their native range from north-west Mexico to western Alaska in the eastern Pacific Ocean and along the Kamchatka Peninsula in the western Pacific Ocean (Behnke, 1992). The species almost invariably spawns in streams, and the migrant ecotypes typically rear there for one or more years prior to initial migration into the ocean (Busby *et al.*, 1996) or a lake (Arostegui & Quinn, 2019). In partially migratory populations, the resident fluvial ecotype is sympatric with stream-rearing juveniles of either of the two migrant ecotypes (adfluvial or anadromous) prior to their outmigration (Pavlov & Savvaitova, 2008; Holecek & Scarnecchia, 2013; Arostegui & Quinn, 2019). However, although the fluvial and anadromous ecotypes of *O. mykiss* have been well studied (e.g. Nichols *et al.*, 2008; Ohms *et al.*, 2014), less is known of the adfluvial ecotype, despite its common occurrence.

There is an inversion on the fifth chromosome of the rainbow trout genome (hereafter referred to as 'Omy05') and its two haplotypes are associated with phenotypic expression of migratory behaviour; the ancestral haplotype is associated with migration and the rearranged haplotype with residency (Pearse *et al.*, 2018). The ancestral haplotype has typically been associated with anadromy; however, adfluvial rainbow trout in a natural lake (Arostegui *et al.*, 2019) and reservoirs (Pearse *et al.*, 2014; Apgar *et al.*, 2017; Leitwein *et al.*, 2017) also exhibit an increased frequency of this haplotype relative to trout in tributary streams. The genetic differentiation of rainbow trout among habitat types in a natural stream–lake system, at both the Omy05 inversion and numerous outlier loci (Arostegui *et al.*, 2019), strongly suggests disruptive natural selection maintaining fluvial and adfluvial ecotypes in partially migratory populations. The alternative scenario, that all rainbow trout found in streams and lakes are different ontogenetic stages of a single, adfluvial ecotype in fully migratory populations (i.e. all juveniles occurring in streams that survive eventually migrate to the lake, and thus there are no lifelong residents in streams), is less parsimonious.

The purpose of this study was to investigate the coloration and body morphology associated with swimming in wild, native rainbow trout in connected stream and lake habitats of a south-west Alaskan watershed to assess if they exhibited phenotypic diversity consistent with the presence of alternative fluvial and adfluvial ecotypes. We also compared the phenotypic differentiation of rainbow trout among these habitat types with the differentiation of a sympatric pair of phylogenetically distinct char species specialized to these habitats [Taylor *et al.*, 2008: streams – Dolly Varden (*Salvelinus malma*); lakes – Arctic char (*S. alpinus*)], to determine if their patterns of divergence were shared and indicative of parallel evolutionary responses. Specifically, rainbow trout and Dolly Varden in streams were expected to exhibit morphologies favouring sustained swimming performance (e.g. streamlined bodies and short fins that reduce drag) whereas rainbow trout and Arctic char in the lake were expected to exhibit morphologies favouring unsteady swimming performance (e.g. posteriorly deep bodies that increase acceleration and long fins that increase turning stability) (*sensu* Langerhans, 2008).

MATERIAL AND METHODS

STUDY SITE

Iliamna Lake, draining into Bristol Bay (Alaska) via the Kvichak River, is the largest in the state, with a surface area of 2622 km^2, volume of 1151 km^3 and maximum depth > 300 m (Burgner *et al.*, 1969). The watershed, like others in Bristol Bay, supports no steelhead (Behnke, 1992) but supports many breeding populations of rainbow trout, and trout are managed with protective fishing regulations. The system has only native fish species (Bond & Becker, 1963), and has no history of habitat alteration, hatchery propagation or transplantation that might affect the evolutionary ecology or population structure of the fish. The pristine condition of the ecosystem makes Iliamna Lake and its tributaries an appropriate site in which to study the phenotypic diversity of rainbow trout.

SAMPLING

In August 2015–2018, rainbow trout (N = 73) and Arctic char (N = 40) were sampled together from the littoral zone of Iliamna Lake at beaches of three islands (Woody, Fuel Dump and Porcupine), and Finger Bay beach on the lake's shoreline (Fig. 1). These sites are used for spawning by sockeye salmon (*Oncorhynchus nerka*; Demory *et al.*, 1964) and for foraging by rainbow trout and Arctic char (Arostegui & Quinn, 2018). Rainbow trout (N = 105) were also

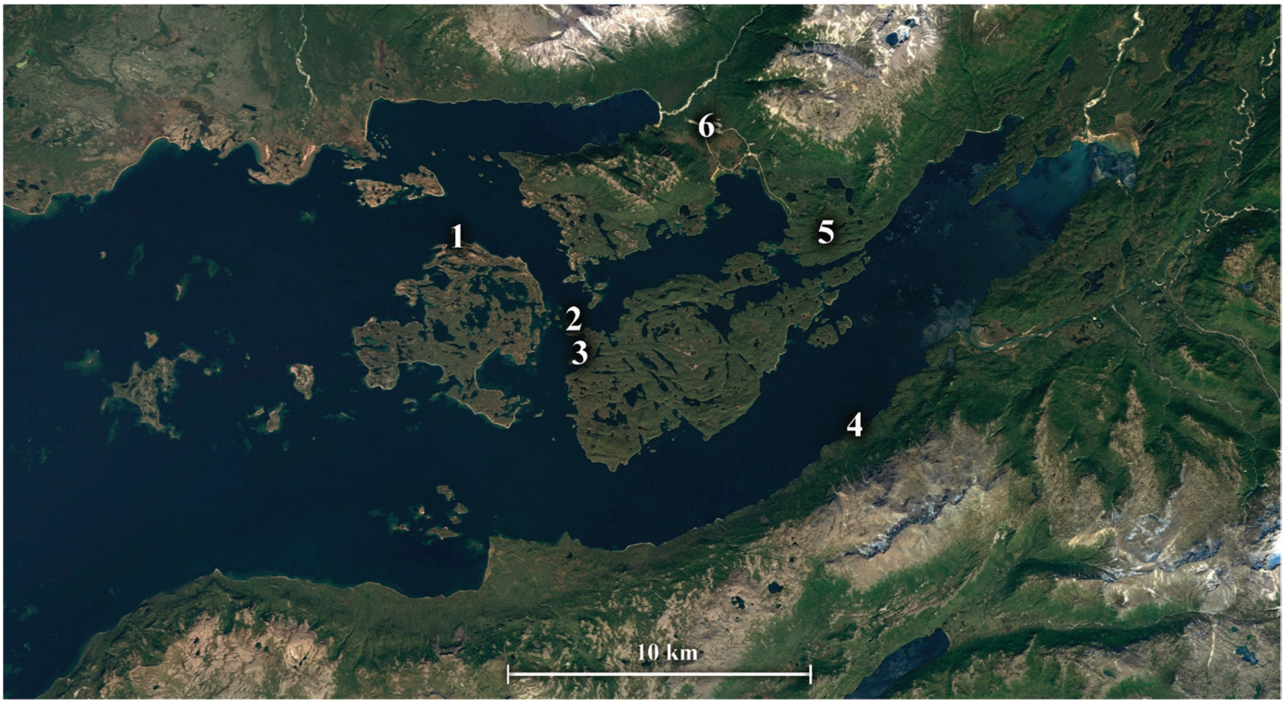

Figure 1. Map of the eastern end of Iliamna Lake. Study sites are indicated by numbers: 1, Woody Island; 2, Fuel Dump Island; 3, Porcupine Island; 4, Finger Bay; 5, Russian Creek; 6, Pedro Ponds system. Satellite image produced with Google Earth Pro using data from Image Landsat/Copernicus.

sampled in Russian Creek (Fig. 1), which supports a population nearly fixed for the rearranged Omy05 haplotype (i.e. with a genetic predisposition for stream-residency; Arostegui *et al.*, 2019), in August 2015, 2017 and 2018. Dolly Varden (N = 25) were sampled in the Pedro Bay system (Fig. 1), a complex of small ponds and streams supporting a small-bodied fluvial population (Denton *et al.*, 2009, 2010), in August 2018. Arctic char in Iliamna Lake are monomorphic (Woods *et al.*, 2013) and exhibit genetic, meristic and morphological distinction from Dolly Varden in the Pedro Ponds system (Taylor *et al.*, 2008).

Fish were sedated in a solution of AQUI-S anaesthetic, then measured for fork length (mm) and placed on a flat, white board for imaging of their left side. A camera was mounted on a tripod and levelled relative to the board to ensure the same imaging angle for all photos. After imaging, fish were recuperated in fresh water and released at the capture site.

Coloration pattern

Rainbow trout were classified by their images into four coloration patterns ('banded', 'intermediate', 'silver' and 'bronze'; Fig. 2). The first three designations ('banded', 'intermediate' and 'silver') were defined by Negus (2003) and used by Holecek *et al.* (2012) for the description of anadromous and adfluvial *O. mykiss* undergoing the parr–smolt transformation; and we added the fourth designation ('bronze') to describe fish not matching the other three categories. 'Banded' trout exhibited parr marks over their entire bodies. 'Intermediate' trout exhibited parr marks towards the tail, but those near the head were no longer visible. In 'silver' trout, parr marks were either not visible or were pale and exclusively on the caudal peduncle, and the fish were bright silver with little or no spotting laterally. 'Bronze' trout displayed no parr marks or only pale marks exclusively on the caudal peduncle and were faded bronze with minimal to widespread spotting laterally. Differences in mean fork length between rainbow trout of each coloration pattern were assessed with Welch's one-way ANOVA and Games–Howell post-hoc tests. The prevalence of silver streaks on caudal fin rays, an open-water camouflage present in certain adfluvial and anadromous salmonids (e.g. Edo *et al.*, 2005; Markevich *et al.*, 2018), was determined by inspecting fish photos (Fig. 2C). All cameras used in the classification of coloration patterns employed the sRGB IEC61966-2.1 colour profile.

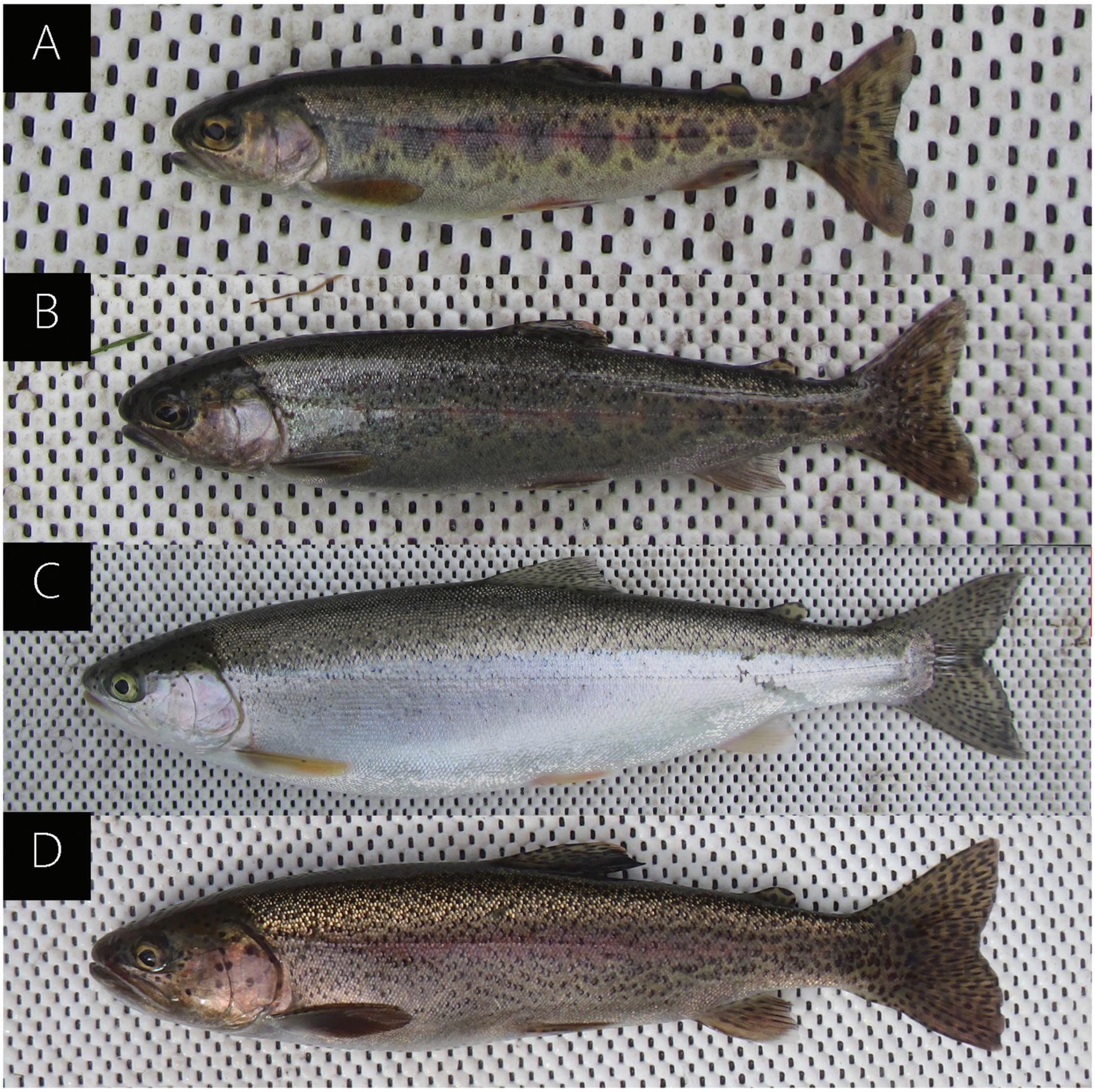

Figure 2. Coloration patterns of rainbow trout: A, banded – 113 mm fork length (FL); B, intermediate – 195 mm FL; C, silver – 393 mm FL; D, bronze – 277 mm FL. Note the silver streaks on the central caudal fin rays in C.

MORPHOLOGY

We used linear character measurements in a multivariate framework to assess divergence in morphology between rainbow trout collected in the lake and stream, and to compare those patterns with those observed in sympatric *Salvelinus* species. For this analysis, we used the largest subset of the photographs taken with a single camera, a Canon Powershot D20, to avoid any potential bias in morphological comparison of specimens among cameras with different optical properties. This camera used a focal length of 5 mm, no flash and automatic exposure settings to account for variable, natural lighting. Photos of rainbow trout captured in the lake (N = 50), rainbow trout captured in the stream (N = 33), Arctic char (N = 40) and Dolly Varden (N = 25) were loaded into the ImageJ program, where the following standardized linear measurements were taken in pixel distance: fork length, post-orbit length, pectoral fin length, anal fin length, caudal peduncle length, caudal peduncle depth and body depth (Fig. 3). Measurement of external features from standardized photos paralleled the methods of Keeley *et al.* (2007); the known fork length of each fish (in pixels and mm) was used to convert between distance in pixels and millimetres for the other features. Character measurements (mm) were $\log_{10}$ transformed to normalize and standardize the data. The measurements of interest were selected to investigate differences in body shape characteristic of

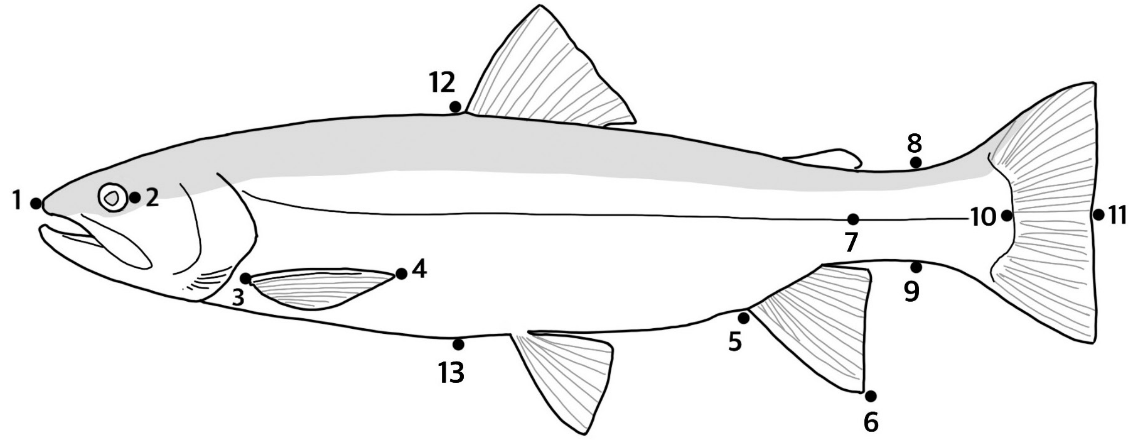

Figure 3. Linear morphological measurements: 1–11, fork length; 2–10, post-orbit length; 3–4, pectoral fin length; 5–6, anal fin length; 7–10, caudal peduncle length; 8–9, caudal peduncle depth; 12–13, body depth. Artwork by Brandon Li.

fishes experiencing divergent water flow conditions; morphological changes enhancing sustained swimming (e.g. streamlined bodies and short fins that reduce drag) are predicted in stream habitats whereas those enhancing unsteady swimming (e.g. posteriorly deep bodies that increase acceleration and long fins that increase turning stability) are predicted in lake habitats (*sensu* Langerhans, 2008).

Allometric trajectories of morphological features may be shared or discrete at the intraspecific level (Simonsen *et al.*, 2017; Esin *et al.*, 2018) and can change throughout ontogeny (Meyer, 1987; Wainwright *et al.*, 1991). Thus, we used a model comparison framework to identify (1) which groups of fish to combine or separate and (2) what type of regression to use when accounting for allometric changes of pectoral fin length, anal fin length, caudal peduncle length, caudal peduncle depth and body depth. Three different models were compared for each character measurement of rainbow trout: (1) *null* – one linear allometric trajectory shared by fish in the lake and stream (suggesting a shared genetic basis); (2) *distinct* – two linear allometric trajectories, one specific to fish in the lake and a second specific to fish in the stream (suggesting genetic differentiation); and (3) *segmented* – one non-linear allometric trajectory with a change in slope corresponding to an ontogenetic shift from stream to lake habitat (suggesting a plastic change in phenotype). Only the *null* and *distinct* models were tested for *Salvelinus* species, as the two species occupy different habitats in this system (Taylor *et al.*, 2008: streams – Dolly Varden; lakes – Arctic char). The linear regressions of the *null* and *distinct* models were conducted following Ostberg *et al.* (2009) and Brenkman *et al.* (2014), using the equation from Thorpe (1976). The threshold regression of the *segmented* model was conducted with the *exact* maximum-likelihood estimate approach of Fong *et al.* (2017). In all three models, we regressed character length against post-orbit length, instead of fork length, to remove any potential bias from caudal fin damage (Pakkasmaa & Piironen, 2001b) and sexual dimorphism in head size that is typical of mature salmonids (e.g. Beacham, 1984; Merz & Merz, 2004; Janhunen *et al.*, 2009). Model selection was done with the Akaike information criterion (AIC) and the parameters of the model with the lowest AIC were then used to size-adjust the corresponding morphological feature. Adjusting the size ($\log_{10}$ mm) of each morphological feature to the size predicted by the feature-specific, model-selected regression at a particular post-orbit length yielded the size-adjusted dataset for each individual fish. Size adjustment accounts for allometry and permits direct morphological comparison among fish of different sizes and at different stages of ontogeny (Thorpe, 1976). The mean post-orbit length of all fish (across species) was used as the transformation target.

Two linear discriminant analyses (LDAs) of the size-adjusted data for pectoral fin length, anal fin length, caudal peduncle length, caudal peduncle depth and body depth were used to assess morphological divergence (1) among *O. mykiss* captured in different habitats and (2) among *Salvelinus* species, and thereby compare the degree of parallelism in habitat selection on specific morphological features. In such cases, where only two groups of fish are being compared at once, LDA reduces the multivariate dataset into a single linear discriminant function that minimizes within-group and maximizes among-group dissimilarity. Reclassification rates of the fish into the correct habitat or species grouping were calculated using jackknife validation of the linear discriminant function unique to each of the two LDAs. Model validation via the jackknife procedure reduces bias in estimates of model predictive performance (Olden *et al.*, 2002). LDA was conducted with the 'lda' function from the 'MASS' package in R (Ripley *et al.*, 2015).

To compare results with the two LDAs, principal component analyses (PCAs) using the same size-adjusted data were performed separately for *O. mykiss* captured in different habitats, and the two *Salvelinus* species. LDA relies upon a priori group classification while PCA assumes no a priori classification (Fleming *et al.*, 1994). The PCAs used a correlation matrix and were conducted with the 'prcomp' function from the 'stats' package in R (R Core Team, 2016). Monte Carlo permutation testing of the principal component eigenvalues was conducted with the 'ordi.monte' function from the 'BIOSTATS' R collection (McGarigal 2016).

RESULTS

Coloration pattern

All rainbow trout classified as banded or bronze, and most classified as intermediate, were sampled in the stream, whereas those classified as silver were almost exclusively sampled in the lake (Table 1). Mean fork length was significantly different between rainbow trout with different coloration patterns (Welch's one-way ANOVA: $F = 101.9$, $P < 0.001$), with all pairwise comparisons being significant ($P < 0.05$). The order of increasing length was banded, intermediate, bronze and then silver trout, but trout began to be classified as bronze or silver at a similar size (Fig. 4; Table 1). Silver streaks were not present on the caudal fin rays of any Dolly Varden, banded, intermediate or bronze rainbow trout, but were visible on 67.5% of Arctic char and 39.7% of silver rainbow trout.

Morphology

For rainbow trout, the *distinct* model (two linear allometric trajectories, one specific to fish in the lake and a second specific to fish in the stream) had the lowest AIC for all morphological measurements (Fig. 5; Table 2). However, the *segmented* model (one non-linear allometric trajectory with a change in slope corresponding to an ontogenetic shift from stream to lake habitat) scored nearly as well as the *distinct* model for four of the five morphological measurements (dAIC: 0.2–1.7). For *Salvelinus* species, the *distinct* model (two linear allometric trajectories, one for Arctic char and one for Dolly Varden) had the lowest AIC for pectoral fin length, anal fin length, caudal peduncle depth and body depth, whereas the *null* model (one linear allometric trajectory with a constant slope shared by Arctic char and Dolly Varden) had the lowest AIC for caudal peduncle length (Fig. 5; Table 2).

The LDA of size-adjusted *O. mykiss* captured in lake vs. stream habitats revealed intraspecific morphological divergence (Fig. 6). The linear discriminants with the greatest contributions to their separation were (in decreasing order) body depth, pectoral fin length and caudal peduncle length (Table 3). Canonical structure

Table 1. Proportion of rainbow trout with different coloration patterns in the stream and lake (% of individuals within habitat type) and mean fork length (FL, mm) of each across habitat types

Coloration pattern	Stream	Lake	Mean FL (range)
Banded	40.0	0.0	134 (56–198)
Intermediate	38.1	4.1	183 (103–329)
Bronze	19.0	0.0	256 (206–405)
Silver	2.9	95.9	301 (188–555)

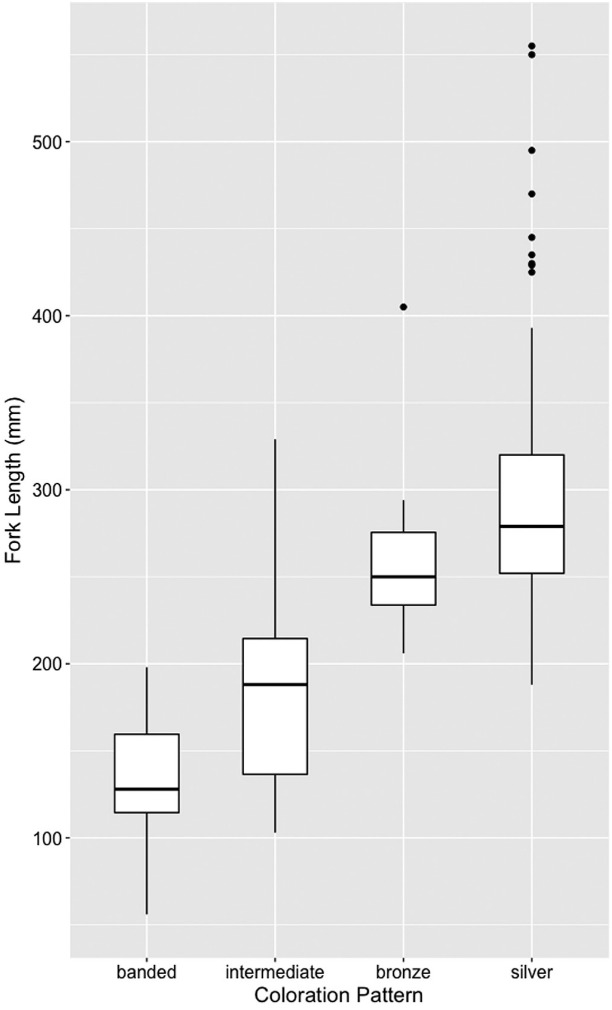

Figure 4. Boxplot of rainbow trout fork length (mm) by coloration pattern.

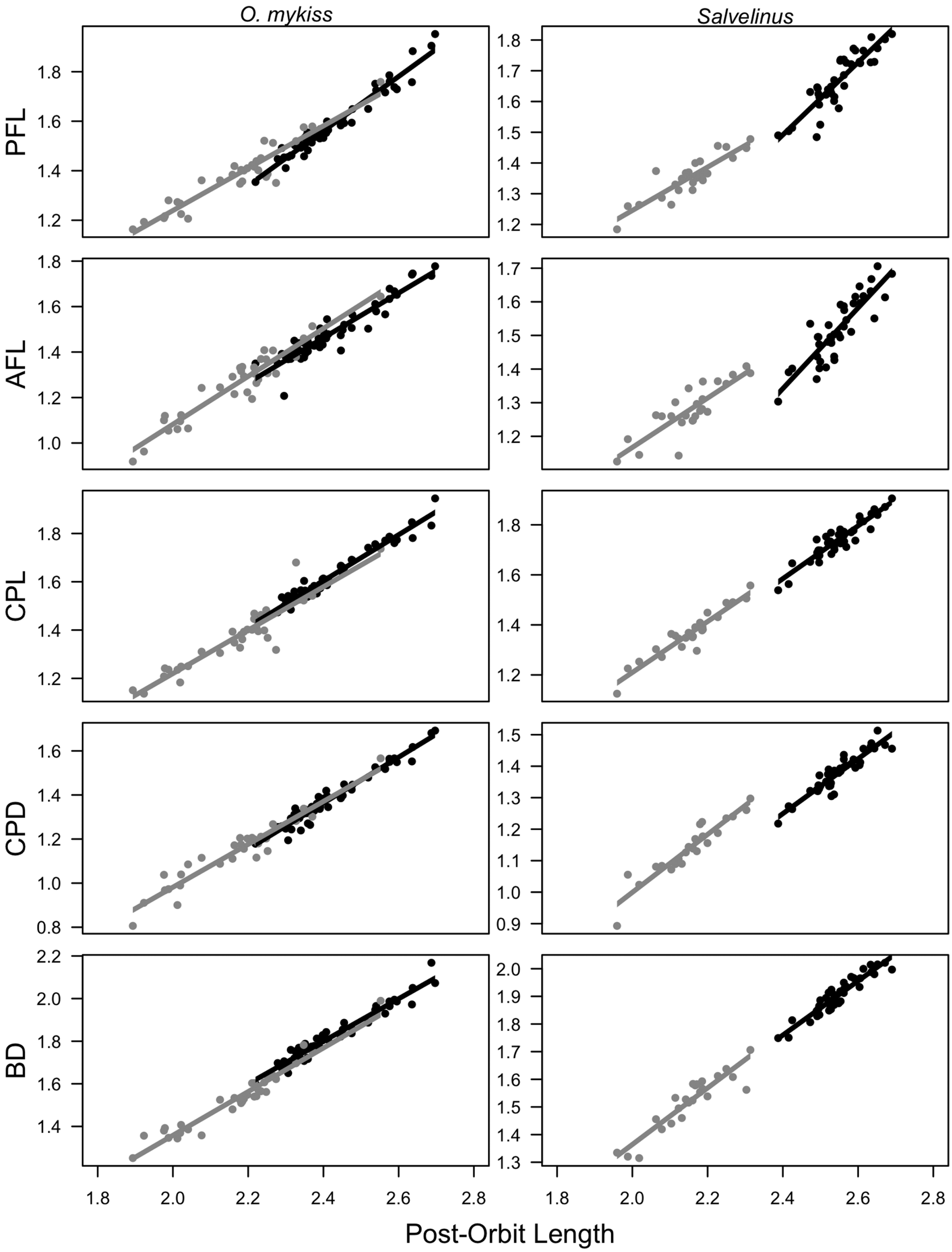

Figure 5. Model-selected relationships of post-orbit length with morphological characters ($\log_{10}$-transformed). Colour coding: *O. mykiss* – stream (grey)/lake (black); *Salvelinus* – Dolly Varden (grey)/Arctic char (black). Morphological features: PFL, pectoral fin length; AFL, anal fin length; CPL, caudal peduncle length; CPD, caudal peduncle depth; BD, body depth.

Table 2. Model comparison results for allometric trajectories of the linear character measurements; the model with the lowest AIC value for each morphological feature is highlighted in grey

	O. mykiss Habitats			*Salvelinus* Species	
Morphological feature	Null	Distinct	Segmented	Null	Distinct
Pectoral fin length	−288.4	**−316.6**	−315.1	−219.7	**−232.4**
Anal fin length	−271.6	**−273.3**	−273.1	−192.6	**−213.1**
Caudal peduncle length	−310.4	**−332.0**	−311.5	**−269.8**	−266.9
Caudal peduncle depth	−319.5	**−323.0**	−321.3	−254.4	**−282.3**
Body depth	−320.0	**−327.6**	−326.4	−266.8	**−270.0**

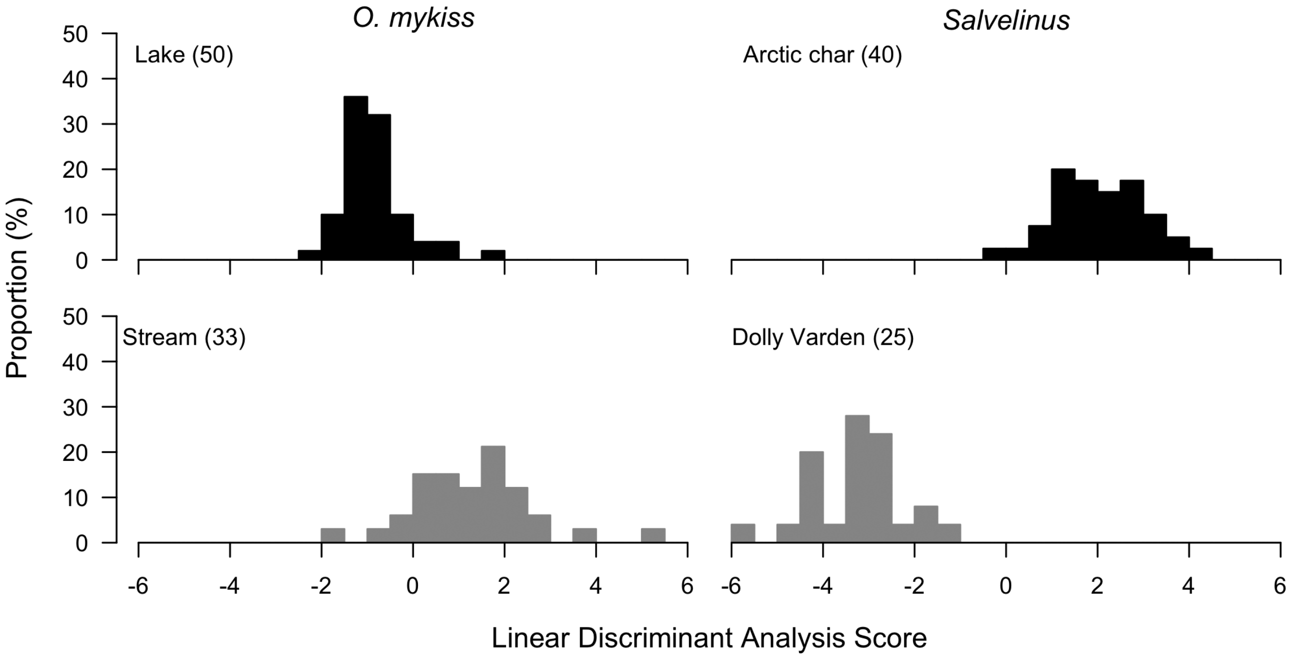

Figure 6. LDA scores for rainbow trout sampled in lake and stream habitats, and Arctic char and Dolly Varden. The sample size of each group is given in parentheses.

correlations of trout LDA scores with the discriminant variables revealed a positive relationship with pectoral fin length, anal fin length and caudal peduncle depth, but a negative relationship with caudal peduncle length and body depth (Table 3). Therefore, lake-caught rainbow trout, with a negative LDA score distribution (Fig. 6), generally had shorter pectoral and anal fins, a shallower but longer caudal peduncle, and a deeper body than stream-caught rainbow trout.

The PCA of size-adjusted *O. mykiss* data produced similar results to the LDA. The eigenvalues of principal components (PC) 1 and 2 were both significant (Monte Carlo permutation test; $P < 0.05$) and explained 32.6% and 24.8%, respectively, of the variance. The variables with the greatest eigenvector coefficients on and structure correlations with PC1 were (in decreasing order) anal fin length, pectoral fin length and caudal peduncle depth, whereas only body depth exhibited a high eigenvector coefficient on and correlation with PC2 (Table 4). Lake-caught rainbow trout exhibited significantly greater PC1 (two-sample *t*-test; $T = 4.41$, $P < 0.001$) and PC2 scores ($T = 4.03$, $P < 0.001$) than stream-caught trout. Thus, lake-caught rainbow trout generally exhibited shorter pectoral and anal fins and a shallower caudal peduncle (i.e. greater PC1 scores), and greater body depth (i.e. greater PC2 scores) than stream-caught trout.

Univariate comparisons, among size-adjusted trout captured in different habitats, identified all morphological features as being significantly different

Table 3. Coefficients of linear discriminants and canonical structure correlations for the variables used in the LDAs of morphology among *O. mykiss* captured in different habitats (lake vs. stream) and *Salvelinus* species (Arctic char vs. Dolly Varden)

	O. mykiss Habitats		*Salvelinus* Species	
Morphological feature	Coefficient	Correlation	Coefficient	Correlation
Pectoral fin length	19.9	0.569	4.3	−0.646
Anal fin length	2.1	0.541	−13.1	−0.906
Caudal peduncle length	−17.2	−0.403	1.7	−0.080
Caudal peduncle depth	10.5	0.217	−32.3	−0.975
Body depth	−28.6	−0.615	0.5	−0.198

The coefficients identify how each variable contributes to the separation of the categorical groups along the linear discriminant axis (greater absolute values indicate greater contribution to the separation of the groups). The correlations show the relationship (positive or negative) between each variable and the fish scores along the linear discriminant axis (greater absolute values indicate stronger relationships).

Table 4. Eigenvector coefficients and structure correlations for the variables used in the PCAs of morphology of *O. mykiss* captured in different habitats (lake and stream) and *Salvelinus* species (Arctic char and Dolly Varden)

	O. mykiss Habitats				*Salvelinus* Species			
	PC1*		PC2*		PC1*		PC2	
Morphological feature	Coefficient	Correlation	Coefficient	Correlation	Coefficient	Correlation	Coefficient	Correlation
Pectoral fin length	−0.584	−0.746	−0.115	−0.128	−0.538	−0.846	0.019	0.021
Anal fin length	−0.603	−0.770	−0.368	−0.410	−0.580	−0.913	0.040	0.043
Caudal peduncle length	0.099	0.127	−0.121	−0.135	−0.040	−0.062	0.779	0.825
Caudal peduncle depth	−0.529	−0.676	0.418	0.465	−0.579	−0.910	0.092	0.098
Body depth	−0.069	−0.088	0.814	0.906	−0.190	−0.299	−0.619	−0.656

The coefficients identify how each variable relates to the principal component (greater absolute values indicate stronger relationships). The correlations show the relationship (positive or negative) between each variable and the fish scores along the principal component (greater absolute values indicate stronger relationships). An asterisk (*) denotes a principal component with a significant eigenvalue.

in mean size (mm) except caudal peduncle depth (Table 5). While permutational multivariate analysis of variance (perMANOVA) indicated that the lake- and stream-caught groups of trout were significantly different in morphology ($F = 12.5$, $P < 0.001$), there was a small amount of overlap along the linear discriminant axis (Fig. 6) reflected by an 81% jackknife reclassification rate (94% of lake-caught trout were correctly reclassified, whereas only 76% of stream-caught trout were correctly reclassified) and there was partial overlap in the PCA ordination (Fig. 7).

The LDA of size-adjusted *Salvelinus* species revealed complete morphological distinction of Arctic char and Dolly Varden (Fig. 6). The linear discriminants with the greatest contributions to separation of the species were (in decreasing order) caudal peduncle depth and anal fin length (Table 3). Canonical structure correlations of *Salvelinus* LDA scores with the discriminant variables revealed a negative relationship with caudal peduncle depth, pectoral and anal fin length, and body depth, but essentially no relationship with caudal peduncle length (Table 3). Therefore, Arctic char, with a positive LDA score distribution, generally have shorter pectoral and anal fins, shallower caudal peduncles and bodies, but caudal peduncles similar in length to Dolly Varden.

Table 5. Size-adjusted means (mm) of the linear character measurements from the *O. mykiss* captured in different habitats (lake vs. stream) and *Salvelinus* species (Arctic char vs. Dolly Varden), set to a transformation target of 226 mm post-orbit length (~283 mm fork length)

	O. mykiss Habitats			*Salvelinus* Species		
Morphological feature	Lake	Stream	*P*	Arctic char	Dolly Varden	*P*
Pectoral fin length	32.3	34.8	<0.001	27.3	31.2	<0.001
Anal fin length	26.1	28.5	<0.001	19.3	26.7	<0.001
Caudal peduncle length	36.3	34.5	<0.05	35.8	36.2	0.54
Caudal peduncle depth	20.6	21.2	0.15	16.2	21.1	<0.001
Body depth	56.6	52.5	<0.001	51.8	53.1	0.15

P-values are from Welch's two sample *t*-test. Grey shading indicates which group exhibited a significantly greater mean value for that specific morphological feature (shading is not present for comparisons that are not statistically significant).

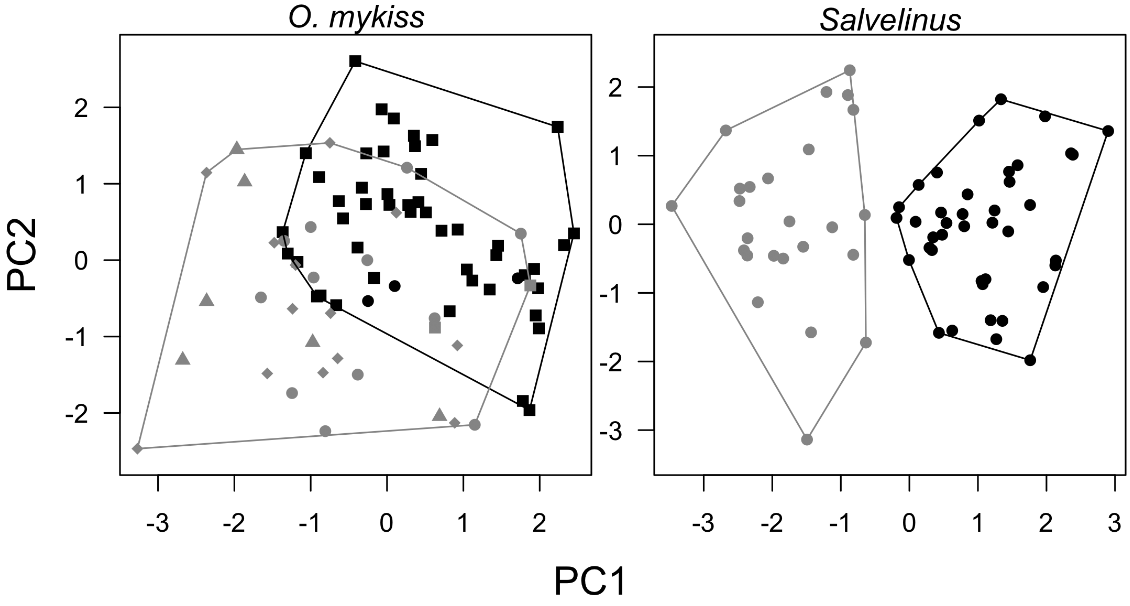

Figure 7. PCA ordination of rainbow trout sampled in lake and stream habitats (*O. mykiss*), and Arctic char and Dolly Varden (*Salvelinus*). Colour coding: *O. mykiss* – stream (grey)/lake (black); *Salvelinus* – Dolly Varden (grey)/Arctic char (black). In the *O. mykiss* PCA, symbols denote the coloration pattern assigned to each rainbow trout: banded (diamond), intermediate (circle), bronze (triangle), silver (square).

The PCA of size-adjusted *Salvelinus* species data produced similar results to the LDA. The eigenvalue of PC1 was significant (Monte Carlo permutation test; $P < 0.001$) and explained 49.4% of the variance, whereas that of PC2 was not significant (Monte Carlo permutation test; $P > 0.05$) but explained 22.5% of the variance. The variables with the greatest eigenvector coefficients on and structure correlations with PC1 were (in decreasing order) anal fin length, caudal peduncle depth and pectoral fin length, whereas caudal peduncle length and body depth were the variables that exhibited the highest eigenvector coefficients on and correlations with PC2 (Table 4). Arctic char exhibited significantly greater PC1 scores (two-sample *t*-test; $T = -14.64$, $P < 0.001$) than Dolly Varden, but similar PC2 scores (two-sample *t*-test; $T = 0.55$, $P > 0.05$). Thus, Arctic char generally had shorter pectoral and anal fins, and shallower caudal peduncles and bodies (i.e. greater PC1 scores) than Dolly Varden.

Univariate comparisons, among size-adjusted *Salvelinus* species, identified pectoral fin length, anal fin length and caudal peduncle depth, but not caudal peduncle length or body depth, as being significantly different (Table 5). A significant perMANOVA result ($F = 97.4$, $P < 0.001$), 100% jackknife reclassification rate from the LDA and no overlap in the PCA ordination

(Fig. 7) supported the complete morphological distinction of the two *Salvelinus* species.

DISCUSSION

Rainbow trout in the Iliamna Lake system exhibited disparate coloration and morphology consistent with ontogenetic and ecotypic variation. The distribution of coloration patterns with respect to fish size and habitat indicated the presence of sympatric adfluvial and fluvial ecotypes that undergo ontogenetic changes in colour resulting in different terminal colorations suited to their respective habitats. The morphology of lake-caught rainbow trout was distinct from that of stream-caught fish in features associated with swimming performance, and the observed divergences exhibited shared and unique patterns compared to sympatric *Salvelinus* species in those habitats. Greater morphological variation within stream- than lake-caught rainbow trout, and their limited overlap in morphology, suggested population-specific partial migration.

Ecotype-specific coloration

Disparate frequencies of the rainbow trout coloration patterns observed among size classes and habitats were consistent with our hypothesis of phenotypically distinct adfluvial and fluvial forms, as we found evidence of two ecotype-specific coloration trajectories during ontogeny. Ocean- or lake-migrant salmonids produced in sympatry with stream-residents are often distinguishable at the (sub)adult stage by their divergent coloration patterns; migrants are bright silver laterally whereas residents are darker (e.g. *S. leucomaenis*: Nakano *et al.*, 1990; *O. masou*: Tsiger *et al.*, 1994; *O. clarkii*: Eek & Bohlin, 1997). The silver lateral coloration of migrant salmonids, a widespread trait in the family, is part of the parr–smolt transformation, when stream-rearing juveniles with parr marks increase the deposition of guanine in their skin and thereby cover their parr marks with silver coloration suited to the pelagic environment of a lake or ocean (e.g. *O. mykiss*: Negus, 2003; Holecek *et al.*, 2012; *O. tshawytscha*: Beckman *et al.*, 2000; *S. trutta*: Schulz, 1999; *S. salar*: Birt & Green, 1986; Piironen *et al.*, 2013). The presence of banded rainbow trout exclusively in the study stream, intermediate rainbow trout almost exclusively in the study stream and silver rainbow trout almost exclusively in Iliamna Lake, together with their progressively greater mean sizes, are consistent with an ontogenetic change in the coloration of an adfluvial form of rainbow trout.

However, we also identified dark, bronze individuals in the study stream but not in the lake; they had lost their parr marks and were significantly larger than intermediate and banded trout. These bronze trout were of a size range (206–405 mm fork length) corresponding to an approximate age range of 3–6+ years old, which largely overlaps with that of silver trout caught in this study (2–7+ years old; Table A1) and are ages beyond which most anadromous and adfluvial *O. mykiss* in other systems have already migrated (Kwain, 1971; Busby *et al.*, 1996; Holecek *et al.*, 2012). In addition, rainbow trout began to be classified as silver or bronze at a similar size (Fig. 4), indicating diverging coloration pathways at the same point in ontogeny. The greater maximum (and average) size of silver trout than bronze trout is consistent with the larger asymptotic size of adfluvial than fluvial salmonids in sympatry (Robillard *et al.*, 2011; Holecek & Scarnecchia, 2013). We note, however, that the body size of the bronze trout may have been, in part, a function of the small stream where they were sampled; large-bodied, fluvial rainbow trout occur in a large river of a nearby system (Meka *et al.*, 2003). Lastly, the loss of parr marks by silver and bronze rainbow trout is in accordance with a study of adfluvial and fluvial strains of brook trout (*Salvelinus fontinalis*) in Lake Superior where adfluvial individuals exhibited greater skin reflectance than fluvial counterparts although both life history types exhibited increased skin reflectance throughout development (McKinney *et al.*, 2014).

Thus, the distribution of coloration patterns among rainbow trout in different size classes and habitats suggests that parr in streams may follow one of two ecotype-specific coloration pathways during ontogeny that are specific to either the lake (banded, then intermediate and then silver as adfluvial trout) or the stream (banded, then intermediate and then bronze as fluvial trout). In addition, guanine streaks on caudal fin rays, a trait shared by many salmonids in open-water habitats such as anadromous Sakhalin taimen (*Hucho perryi*; Edo *et al.*, 2005) and adfluvial longhead char (*Salvelinus malma*; Markevich *et al.*, 2018), were solely found on silver rainbow trout and Arctic char in Iliamna Lake but not on rainbow trout of any other coloration pattern nor Dolly Varden in streams.

Note that the coloration of rainbow trout varies among populations and subspecies; therefore, the results from our study may not be applicable in all systems. For example, fluvial adults of the coastal rainbow trout (*O. m. irideus*), the subspecies sampled in our study, are not described as exhibiting parr marks, whereas certain other subspecies retain them as adults (e.g. *O. m. newberrii*, *O. m. aguabonita*) (Behnke, 2002). Similarly, the absence or reduction of parr marks occurs in fluvial adults of some but not all subspecies of cutthroat trout (*O. clarkii*) (Behnke, 2002). Other studies investigating rainbow trout coloration in lake/reservoir tributaries in Idaho and Minnesota, USA, did not find a coloration pattern parallel to our bronze category (darkly coloured and spotted but with minimal or no parr marks); however, they worked with different subspecies (or transplants and hatchery strains thereof) and focused on sampling juvenile migrants (Negus, 2003; Holecek *et al.*, 2012).

SHARED AND UNIQUE DIVERGENCE IN MORPHOLOGY

Rainbow trout and *Salvelinus* species in the lake and stream habitats exhibited shared divergence in fin morphology, with shorter pectoral and anal fins in the lake and longer fins in streams. This pattern is consistent with intraspecific differences in coho salmon (*Oncorhynchus kisutch*; Swain & Holtby, 1989), spotted galaxias (*Galaxias truttaceus*; Humphries, 1990) and pumpkinseed sunfish (*Lepomis gibbosus*; Brinsmead & Fox, 2002) in lake and stream habitats, as well as interspecific differences among lake-rearing and stream-rearing salmonids in sympatry (Pakkasmaa *et al.*, 1998; Taylor *et al.*, 2008). Shorter fins reduce drag during sustained swimming (Webb, 1984) and may benefit the physiological performance of fishes cruising in the pelagic zone of a lake (e.g. Proulx & Magnan, 2002, 2004). Larger paired and median fins increase drag but increase stability, positioning and manoeuvrability (Webb, 1975, 1982; Standen, 2005) of fishes in streams. Intraspecific comparisons of salmonids among streams often show a positive relationship between flow velocity and fin length (Riddell & Leggett, 1981; Beacham, 1984; Beacham *et al.*, 1989; Drinan *et al.*, 2012; Westley *et al.*, 2012).

Rainbow trout and *Salvelinus* species also exhibited shared divergence in caudal peduncle depth; fish in the lake tended to have narrower caudal peduncles than their stream counterparts, contrary to flow-morphology predictions (Langerhans, 2008). As with shorter fins, a shallower caudal peduncle may minimize drag and energy expenditure for sustained swimming by rainbow trout and Arctic char in the pelagic environment (Proulx & Magnan, 2002, 2004; Robinson & Parsons, 2002). In contrast, a deeper caudal peduncle may increase unsteady swimming performance (Webb, 1982) for rainbow trout and Dolly Varden in streams and indicate increased caudal muscle mass (Eniutina, 1954; Imre, 2002), consistent with the positive relationship between flow velocity and caudal peduncle depth documented in salmonids of other systems (Keeley *et al.*, 2005, 2007; Pavey *et al.*, 2010, 2011).

While caudal fin coloration, fin morphology and caudal peduncle depth exhibited shared divergence among stream–lake pairs of salmonids in the Iliamna Lake watershed, unique patterns were observed in body depth and caudal peduncle length. Rainbow trout in the lake had significantly deeper bodies and longer caudal peduncles than their counterparts in the stream, which is largely consistent with flow-morphology predictions for enhanced unsteady swimming performance in lentic waters via increased posterior body area, and for improved sustained swimming performance in lotic waters via body streamlining (Webb, 1982; Langerhans, 2008). Greater body depth in lower velocity waters is commonly observed in fishes, including centrarchids (Brinsmead & Fox, 2002), cyprinids (Haas *et al.*, 2010; Collin & Fumagalli, 2011; Franssen, 2011), cichlids (Theis *et al.*, 2014) and numerous salmonids (e.g. Riddell & Leggett, 1981; Bowen & Marchetti, 2015), whereas elongation of the caudal peduncle is less common but known from percids, atherinopsids and fundulids (Krabbenhoft *et al.*, 2009). Contrary to the patterns in rainbow trout, Dolly Varden in stream habitat tended to have deeper bodies than lacustrine Arctic char, and they did not differ in caudal peduncle length. The morphology of drift-feeding salmonids in streams reflects the tradeoff between sustained and unsteady swimming performance (Bisson *et al.*, 1988), and deeper bodies (as seen in Dolly Varden) and shorter caudal peduncles (as seen in stream-caught rainbow trout) are associated with increased prey capture success in other drift-feeding fishes (Rincón *et al.*, 2007).

The shared and unique patterns of phenotypic differentiation among rainbow trout and *Salvelinus* species in lake and stream habitats may highlight how different phenotypic pathways can reflect lineage-specific constraints to plasticity and yield similar habitat-specific performance solutions. Sympatric species may exhibit contrasting morphological divergence patterns among habitat types for a subset of features (Pakkasmaa & Piironen, 2001a; Brinsmead & Fox, 2002; Krabbenhoft *et al.*, 2009; Franssen *et al.*, 2013). These unique responses may result from lineage-specific constraints to phenotypic diversity (Witte *et al.*, 1990; Robinson & Parsons, 2002), where the status of certain traits as fixed or plastic varies among species. For example, the shared allometric trajectory for caudal peduncle length among the *Salvelinus* species but not among rainbow trout in the lotic and lentic waters of the Iliamna Lake watershed suggests this is a fixed trait in the former lineage and plastic in the latter. Although morphological divergence patterns among habitat types are not all shared, they may constitute alternative solutions to the same selection pressures (Langerhans *et al.*, 2003). Additionally, while changes to a single morphological feature cannot simultaneously optimize both unsteady and sustained swimming performance, independent modification of multiple morphological features may enable simultaneous performance optimization (Langerhans, 2008). Thus, although rainbow trout and Arctic char in Iliamna Lake, and rainbow trout and Dolly Varden in its tributaries exhibit substantial ecological overlap (Denton *et al.*, 2009, 2010; Woods *et al.*, 2013; Arostegui & Quinn, 2018), they display some differences in their habitat–morphology relationships.

POTENTIAL SOURCES OF MORPHOLOGICAL DIVERSITY IN *O. MYKISS*

Rainbow trout in lakes are adfluvial, but those in connected streams may include both pre-migrant juveniles and fluvial residents if the population is mixed. In the Iliamna Lake system, several lines of evidence indicate that rainbow trout do not enter the lake in their first year of life but later, primarily at age 2 years or older. Multi-year sampling in the littoral zone with beach seines yielded no rainbow trout fry whereas young-of-the-year Arctic char were collected (H. Rich, Jr & T. P. Quinn, unpublished data). A stable isotope study suggested a minimum size at outmigration of ~150 mm fork length, based on the size of the smallest trout sampled exhibiting a benthic lacustrine δ^{13}C signature (Arostegui & Quinn, 2018). Additionally, the youngest trout we collected in the lake were age 2 years (Table A1), although we cannot rule out entry by some younger fish.

Therefore, morphological variation among rainbow trout in streams and lakes may be attributable to an ontogenetic change in the direction of habitat-specific plastic morphological responses. This hypothesis suggests that there is a shared allometric trajectory that changes in slope at the time of migration. Thus, trout in streams (both individuals of the fluvial ecotype and pre-migratory adfluvial individuals) are morphologically different from adfluvial trout in lakes because they have not experienced the lake environment where different environmental conditions would induce a novel plastic response. Under experimental conditions, jaguar guapote (*Parachromis managuensis*) diverged and then converged in trophic morphology when their diets were switched (Meyer, 1987). Similarly, the slope of allometric trajectories for pharyngeal muscles in pumpkinseed sunfish changed when they began consuming snails (Wainwright *et al.*, 1991).

An alternative hypothesis is that the morphological variation among habitats represents divergence among genetically distinct fluvial and adfluvial ecotypes, with allometric relationships that differ throughout life. The stream population of rainbow trout we sampled is nearly fixed for the rearranged haplotype of an inversion complex on Omy05, which is associated with stream-residency. In contrast, the rainbow trout in the lake exhibit a much higher frequency of the ancestral haplotype, which is associated with migration (Pearse *et al.*, 2018; Arostegui *et al.*, 2019). Genetic studies of partially anadromous populations of *O. mykiss* have identified numerous quantitative trait loci associated with body coloration and morphology during the parr–smolt transformation (Nichols *et al.*, 2008; Hecht *et al.*, 2012), including loci within the region of the inversion complex (Miller *et al.*, 2012). Others have identified substantial differences in gene expression (particularly on Omy05) between anadromous and fluvial *O. mykiss* ecotypes as early as hatching, throughout development, and at the time of the major phenotypic changes associated with the parr–smolt transformation (Hecht *et al.*, 2014; McKinney *et al.*, 2015). The heritability of body morphology in rainbow trout is further highlighted by hybridization experiments with cutthroat trout; hybrids demonstrated morphology and swimming performance intermediate to those of the parent species (Hawkins & Quinn, 1996; Seiler & Keeley, 2007).

The ontogenetic and ecotypic hypotheses are not mutually exclusive, as the morphological variation among rainbow trout sampled in lakes and streams may reflect both disparate plastic responses (among fluvial and adfluvial ecotypes in their respective habitats as well as among the stream- and lake-rearing stages of the adfluvial life history) and heritable differences in morphology (among ecotypes). For example, exposure to identical environmental conditions reduced phenotypic dissimilarity among genetically distinct populations of Arctic char (Alexander & Adams, 2004) and the inverse could augment dissimilarity. However, a common-garden experiment by Keeley *et al.* (2007) revealed that, on average, only 7% of the morphological variation among stream and lake populations of rainbow trout was attributable to phenotypic plasticity whereas 53% was attributable to genetic differentiation, highlighting the primacy of genetics in the species' phenotypic diversity. Future studies should assess the intrapopulation phenotypic diversity of individuals with different Omy05 inversion genotypes, and explicitly test to what degree the morphological divergence among migrant and resident ecotypes is the result of departures in allometry after migration due to plasticity as well as disparate allometric trajectories prior to migration that are genetically determined.

PARTIAL MIGRATION

Patterns of morphology and coloration among rainbow trout caught in stream and lake habitats indicated partially migratory populations consisting of adfluvial and fluvial individuals in sympatry. First, there was greater variation in the LDA scores of the stream-caught rainbow trout from Russian Creek than of the lake-caught trout (Fig. 6), even though the lake-caught trout probably represent a mixture of populations that may exhibit morphological variation associated with spawning in different natal streams of varying environmental conditions (Pakkasmaa & Piironen, 2001b). Second, there was overlap of the lower tail of the stream-caught trout LDA distribution with the mode of the lake-caught trout LDA distribution (Fig. 6); the LDA scores of silver individuals in the stream-caught group (−1.93 to −0.21) occurred exclusively in this lower tail and did not overlap with those of bronze individuals in the stream-caught group (0.38–3.51). Similarly, there was partial overlap of the stream- and lake-caught trout in the PCA ordination but none of the bronze stream-caught trout occurred in this area of overlap whereas all of the silver stream-caught fish did (Fig. 7). Third, incorrect reclassifications from the LDA were disproportionately of stream-caught trout into the lake-caught group. Lastly, there were more than six bronze for every silver rainbow trout caught in the stream, but no bronze individuals were caught in the lake (Table 1).

Together, these results indicate that Russian Creek is a partially migratory population consisting predominantly of the fluvial ecotype but producing some adfluvial fish. This is consistent with the rarity of the ancestral, migration-associated Omy05 inversion haplotype in this population and the substantial genetic differentiation of this population from the mixture of adfluvial individuals in the lake (Arostegui *et al.*, 2019). Different tributary streams may contribute unequally to the sum of adfluvial individuals in a stream–lake system (e.g. brook trout: D'Amelio & Wilson, 2008; Elias *et al.*, 2018), and we did not sample the streams thought to be the primary sources of adfluvial rainbow trout (e.g. Russell, 1977). While population-level differences in morphology may be confounding, as morphological variation among populations within an ecotype can exceed the variation among ecotypes at small spatial scales (Keeley *et al.*, 2005), our results suggesting partial migration in rainbow trout (and the morphological distinction of migrants and residents) are consistent with the morphological divergence of migrant and resident roach (*Rutilus rutilus*) among and within populations (Chapman *et al.*, 2015).

CONCLUSION

Phenotypic diversity of rainbow trout in a stream–lake system is the result of both ontogenetic and ecotypic variation, reflecting the phenomenon of partial migration in which a single population may produce both a fluvial ecotype that remains resident in streams and an adfluvial ecotype that migrates to a lake. This intraspecific diversification in migratory behaviour has a genetic basis (Arostegui *et al.*, 2019), is linked to habitat heterogeneity (*sensu* Herbold *et al.*, 2018), and may increase population stability via the portfolio effect (*sensu* Schindler *et al.*, 2010). Thus, conservation of partially migratory populations must manage for both the underlying genotypes (Elmer, 2016) and the environmental conditions (Wilson *et al.*, 2008) maintaining alternative migrant and resident ecotypes.

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COMPETING INTERESTS

We declare no conflicts of interest.

AUTHOR CONTRIBUTIONS

M.C.A. conducted analyses and drafted the manuscript. M.C.A. and T.Q. provided project funding, conducted fieldwork, and contributed to study design and manuscript refinement.

REFERENCES

Adams CE, **Huntingford FA. 2004.** Incipient speciation driven by phenotypic plasticity? Evidence from sympatric populations of Arctic charr. *Biological Journal of the Linnean Society* **81:** 611–618.

Alexander GD, **Adams CE. 2004.** Exposure to a common environment erodes inherited between-population trophic morphology differences in Arctic charr. *Journal of Fish Biology* **64:** 253–257.

Apgar TM, **Pearse DE**, **Palkovacs EP. 2017.** Evolutionary restoration potential evaluated through the use of a trait-linked genetic marker. *Evolutionary Applications* **10:** 485–497.

Arostegui MC, **Quinn TP. 2018.** Trophic ecology of nonanadromous rainbow trout in a post-glacial lake system: partial convergence of adfluvial and fluvial forms. *Canadian Journal of Zoology* **96:** 818–826.

Arostegui MC, **Quinn TP. 2019.** Reliance on lakes by salmon, trout, and charr (*Oncorhynchus, Salmo*, and *Salvelinus*): an evaluation of spawning habitats, rearing strategies, and trophic polymorphisms. *Fish and Fisheries* **20:** 775–794.

Arostegui MC, **Quinn TP**, **Seeb LW**, **Seeb JE**, **McKinney GJ. 2019.** Retention of a chromosomal inversion from an anadromous ancestor provides the genetic basis for alternative freshwater ecotypes in rainbow trout. *Molecular Ecology* **28:** 1412–1427.

Beacham TD. 1984. Age and morphology of chum salmon *Oncorhynchus keta* in southern British Columbia. *Transactions of the American Fisheries Society* **113:** 727–736.

Beacham TD, **Murray CB**, **Withler RE. 1989.** Age, morphology, and biochemical genetic variation of Yukon River Chinook salmon. *Transactions of the American Fisheries Society* **118:** 46–63.

Beamish RJ. 1987. Evidence that parasitic and nonparasitic life history types are produced by one population of lamprey. *Canadian Journal of Fisheries and Aquatic Sciences* **44:** 1779–1782.

Beckman BR, **Larsen DA**, **Sharpe C**, **Lee-Pawlak B**, **Schreck CB**, **Dickhoff WW. 2000.** Physiological status of naturally reared juvenile spring Chinook salmon in the Yakima River: seasonal dynamics and changes associated with smolting. *Transactions of the American Fisheries Society* **129:** 727–753.

Behnke RJ. 1992. *Native trout of western North America*. Bethesda: American Fisheries Society Monograph 6.

Behnke RJ. 2002. *Trout and salmon of North America*. New York: The Free Press & Chanticleer Press.

Birt TP, **Green JM. 1986.** Parr-smolt transformation in female and sexually mature male anadromous and nonanadromous Atlantic salmon, *Salmo salar*. *Canadian Journal of Fisheries and Aquatic Sciences* **43:** 680–686.

Bisson PA, **Sullivan K**, **Nielsen JL. 1988.** Channel hydraulic, habitat use, and body form of juvenile coho salmon, steelhead, and cutthroat trout in streams. *Transactions of the American Fisheries Society* **117:** 262–273.

Bond CE, **Becker CD. 1963.** *Key to the fishes of the Kvichak River system*. Seattle: University of Washington, Fisheries Research Institute Circular 189.

Bowen HL, **Marchetti MP. 2015.** Ecomorphological plasticity of juvenile fall-run Chinook salmon (*Oncorhynchus tshawytscha*) in perennial and ephemeral streams. *Environmental Biology of Fishes* **99:** 67–78.

Brenkman SJ, **Duda JJ**, **Kennedy PR**, **Baker BM. 2014.** A legacy of divergent fishery management regimes and the resilience of rainbow and cutthroat trout populations in Lake Crescent, Olympic National Park, Washington. *Northwest Science* **88:** 280–304.

Brinsmead J, **Fox MG. 2002.** Morphological variation between lake- and stream-dwelling rock bass and pumpkinseed populations. *Journal of Fish Biology* **61:** 1619–1638.

Burgner RL, **DiCostanzo CJ**, **Ellis RJ**, **Harry Jr. GY**, **Hartman WL**, **Kerns Jr. OE**, **Mathisen OA**, **Royce WF. 1969.** Biological studies and estimates of optimum escapements of sockeye salmon in the major river systems in southwestern Alaska. *Fishery Bulletin* **67:** 405–459.

Busby PJ, **Wainwright TC**, **Bryant GJ**, **Lierheimer LJ**, **Waples RS**, **Waknitz FW**, **Lagomarsino IV. 1996.** *Status review of west coast steelhead from Washington, Idaho, Oregon, and California*. NOAA Technical Memorandum NMFS-NWFSC-27. Seattle: National Marine Fisheries Service.

Chapman BB, **Brönmark C**, **Nilsson J-Å**, **Hansson L-A. 2011.** The ecology and evolution of partial migration. *Oikos* **120:** 1764–1775.

Chapman BB, **Hulthén K**, **Brodersen J**, **Nilsson PA**, **Skov C**, **Hansson LA**, **Brönmark C. 2012.** Partial migration in fishes: causes and consequences. *Journal of Fish Biology* **81:** 456–478.

Chapman BB, **Hulthén K**, **Brönmark C**, **Nilsson PA**, **Skov C**, **Hansson LA**, **Brodersen J. 2015.** Shape up or ship out: migratory behaviour predicts morphology across spatial scale in a freshwater fish. *The Journal of Animal Ecology* **84:** 1187–1193.

Coggins Jr. LG. 1994. Precision of ages estimated from scales for rainbow trout in Bristol Bay, Alaska. Alaska Department of Fish and Game. Fishery Data Series No. 94–26.

Collin H, **Fumagalli L. 2011.** Evidence for morphological and adaptive genetic divergence between lake and stream habitats in European minnows (*Phoxinus phoxinus*, Cyprinidae). *Molecular Ecology* **20:** 4490–4502.

D'Amelio S, **Wilson C. 2008.** Genetic population structure among source populations for coaster brook trout in Nipigon Bay, Lake Superior. *Transactions of the American Fisheries Society* **137:** 1213–1228.

Demory RL, **Orrell RF**, **Heinle DR. 1964.** Spawning ground catalog of the Kvichak River system, Bristol Bay, Alaska. U.S. Fish and Wildlife Service Special Scientific Report - Fisheries No. 488.

Denton KP, **Rich HB Jr**, **Moore JW**, **Quinn TP. 2010.** The utilization of a Pacific salmon *Oncorhynchus nerka* subsidy by three populations of charr *Salvelinus* spp. *Journal of Fish Biology* **77:** 1006–1023.

Denton KP, **Rich HBJr**, **Quinn TP. 2009.** Diet, movement, and growth of Dolly Varden in response to sockeye salmon subsidies. *Transactions of the American Fisheries Society* **138:** 1207–1219.

Drinan TJ, **McGinnity P**, **Coughlan JP**, **Cross TF**, **Harrison SSC. 2012.** Morphological variability of Atlantic salmon *Salmo salar* and brown trout *Salmo trutta* in different river environments. *Ecology of Freshwater Fish* **21:** 420–432.

Edo K, **Kawaguchi Y**, **Nunokawa M**, **Kawamula H**, **Higashi S. 2005.** Morphology, stomach contents and growth of the endangered salmonid, Sakhalin taimen *Hucho perryi*, captured in the Sea of Okhotsk, northern Japan: evidence of an anadromous form. *Environmental Biology of Fishes* **74:** 1–7.

Eek D, **Bohlin T. 1997.** Strontium in scales verifies that sympatric sea-run and stream-resident brown trout can be distinguished by coloration. *Journal of Fish Biology* **51:** 659–661.

Elias A, **McLaughlin R**, **Mackereth R**, **Wilson C**, **Nichols KM. 2018.** Population structure and genomic variation of ecological life history diversity in wild-caught Lake Superior brook trout, *Salvelinus fontinalis*. *Journal of Great Lakes Research* **44:** 1373–1382.

Elmer KR. 2016. Genomic tools for new insights to variation, adaptation, and evolution in the salmonid fishes: a perspective for charr. *Hydrobiologia* **783:** 191–208.

Eniutina RI. 1954. Local stock of pink salmon in the Amur basin and neighbouring waters. *Voprosy Ikhtiologii* **2:** 139–143.

Esin EV, **Markevich GN**, **Pichugin MY. 2018.** Juvenile divergence in adaptive traits among seven sympatric fish ecomorphs arises before moving to different lacustrine habitats. *Journal of Evolutionary Biology* **31:** 1018–1034.

Fleming IA, **Jonsson B**, **Gross MR. 1994.** Phenotypic divergence of sea-ranched, farmed, and wild salmon. *Canadian Journal of Fisheries and Aquatic Sciences* **51:** 2808–2824.

Fong Y, **Huang Y**, **Gilbert PB**, **Permar SR. 2017.** chngpt: threshold regression model estimation and inference. *BMC Bioinformatics* **18:** 1–7.

Franssen NR. 2011. Anthropogenic habitat alteration induces rapid morphological divergence in a native stream fish. *Evolutionary Applications* **4:** 791–804.

Franssen NR, **Harris J**, **Clark SR**, **Schaefer JF**, **Stewart LK. 2013.** Shared and unique morphological responses of stream fishes to anthropogenic habitat alteration. *Proceedings of the Royal Society B* **280:** 20122715.

Fraser CM. 1916. Growth of the spring salmon. *Transactions of the Pacific Fisheries Society* **1915:** 29–39.

Fruet PF, **Secchi ER**, **Di Tullio JC**, **Simões-Lopes PC**, **Daura-Jorge F**, **Costa APB**, **Vermeulen E**, **Flores PAC**, **Genoves RC**, **Laporta P**, **Beheregaray LC**, **Möller LM. 2017.** Genetic divergence between two phenotypically distinct bottlenose dolphin ecotypes suggests separate evolutionary trajectories. *Ecology and Evolution* **7:** 9131–9143.

Haas TC, **Blum MJ**, **Heins DC. 2010.** Morphological responses of a stream fish to water impoundment. *Biology Letters* **6:** 803–806.

Hawkins DK, **Quinn TP. 1996.** Critical swimming velocity and associated morphology of juvenile coastal cutthroat trout (*Oncorhynchus clarki clarki*), steelhead trout (*Oncorhynchus mykiss*), and their hybrids. *Canadian Journal of Fisheries and Aquatic Sciences* **53:** 1487–1496.

Hecht BC, **Thrower FP**, **Hale MC**, **Miller MR**, **Nichols KM. 2012.** Genetic architecture of migration-related traits in rainbow and steelhead trout, *Oncorhynchus mykiss*. *G3* **2:** 1113–1127.

Hecht BC, **Valle ME**, **Thrower FP**, **Nichols KM. 2014.** Divergence in expression of candidate genes for the smoltification process between juvenile resident rainbow and anadromous steelhead trout. *Marine Biotechnology* **16:** 638–656.

Herbold B, **Carlson SM**, **Henery R**, **Johnson RC**, **Mantua N**, **McClure M**, **Moyle P**, **Sommer T. 2018.** Managing for salmon resilience in California's variable and changing climate. *San Francisco Estuary and Watershed Science* **16**. Retrieved from https://escholarship.org/uc/item/8rb3z3nj.

Holecek DE, **Scarnecchia DL. 2013.** Comparison of two life history strategies after impoundment of a historically anadromous stock of Columbia River redband trout. *Transactions of the American Fisheries Society* **142:** 1157–1166.

Holecek DE, **Scarnecchia DL**, **Miller SE. 2012.** Smoltification in an impounded, adfluvial redband trout population upstream from an impassable dam: does it persist? *Transactions of the American Fisheries Society* **141:** 68–75.

Humphries P. 1990. Morphological variation in diadromous and landlocked populations of the spotted galaxias, *Galaxias truttaceus*, in Tasmania, south-eastern Australia. *Environmental Biology of Fishes* **27:** 97–105.

Imre I. 2002. Phenotypic plasticity in brook charr: changes in caudal fin induced by water flow. *Journal of Fish Biology* **61:** 1171–1181.

Janhunen M, **Peuhkuri N**, **Piironen J. 2009.** Morphological variability among three geographically distinct Arctic charr (*Salvelinus alpinus* L.) populations reared in a common hatchery environment. *Ecology of Freshwater Fish* **18:** 106–116.

Jonsson B, **Jonsson N. 1993.** Partial migration: niche shift versus sexual maturation in fishes. *Reviews in Fish Biology and Fisheries* **3:** 348–365.

Keeley ER, **Parkinson EA**, **Taylor EB. 2005.** Ecotypic differentiation of native rainbow trout (*Oncorhynchus mykiss*) populations from British Columbia. *Canadian Journal of Fisheries and Aquatic Sciences* **62:** 1523–1539.

Keeley ER, **Parkinson EA**, **Taylor EB. 2007.** The origins of ecotypic variation of rainbow trout: a test of environmental vs. genetically based differences in morphology. *Journal of Evolutionary Biology* **20:** 725–736.

Krabbenhoft TJ, **Collyer ML**, **Quattro JM. 2009.** Differing evolutionary patterns underlie convergence on elongate morphology in endemic fishes of Lake Waccamaw, North Carolina. *Biological Journal of the Linnean Society* **98:** 636–645.

Kwain W-H. 1971. Life history of rainbow trout (*Salmo gairdneri*) in Batchawana Bay, eastern Lake Superior. *Journal of the Fisheries Research Board of Canada* **28:** 771–775.

Langerhans RB. 2008. Predictability of phenotypic differentiation across flow regimes in fishes. *Integrative and Comparative Biology* **48:** 750–768.

Langerhans RB, **Layman CA**, **Langerhans AK**, **Dewitt TJ. 2003.** Habitat-associated morphological divergence in two Neotropical fish species. *Biological Journal of the Linnean Society* **80:** 689–698.

Lee RM. 1920. *A review of the methods of age and growth determination in fishes by means of scales*. London: Ministry of Agriculture and Fisheries. Fishery Investigations Series 2 Volume **4**.

Leitwein M, **Garza JC**, **Pearse DE. 2017.** Evolutionary ancestry and adaptive evolution of anadromous, resident, and adfluvial rainbow trout (*Oncorhynchus mykiss*) in the San Francisco bay area: application of adaptive genomic variation to conservation in a highly impacted landscape. *Evolutionary Applications* **10:** 56–67.

Liedvogel M, **Akesson S**, **Bensch S. 2011.** The genetics of migration on the move. *Trends in Ecology & Evolution* **26:** 561–569.

Liedvogel M, **Chapman BB**, **Muheim R**, **Åkesson S. 2013.** The behavioural ecology of animal movement: reflections upon potential synergies. *Animal Migration* **1:** 39–46.

Maan ME, **Seehausen O. 2011.** Ecology, sexual selection and speciation. *Ecology Letters* **14:** 591–602.

Markevich G, **Esin E**, **Anisimova L. 2018.** Basic description and some notes on the evolution of seven sympatric morphs of Dolly Varden *Salvelinus malma* from the Lake Kronotskoe Basin. *Ecology and Evolution* **8:** 2554–2567.

McGarigal K. 2016. *BIOSTATS: a collection of R functions written to aid in the statistical analysis of ecological data sets*. Available at: http://www.umass.edu/landeco/teaching/ecodata/labs/ecodata_labs.html. Accessed 24 June 2019.

McKinney GJ, **Hale MC**, **Goetz G**, **Gribskov M**, **Thrower FP**, **Nichols KM. 2015.** Ontogenetic changes in embryonic and brain gene expression in progeny produced from migratory and resident *Oncorhynchus mykiss*. *Molecular Ecology* **24:** 1792–1809.

McKinney GJ, **Varian A**, **Scardina J**, **Nichols KM. 2014.** Genetic and morphological divergence in three strains of brook trout *Salvelinus fontinalis* commonly stocked in Lake Superior. *PLoS One* **9:** e113809.

Meka JM, **Knudsen EE**, **Douglas DC**, **Benter RB. 2003.** Variable migratory patterns of different adult rainbow trout life history types in a southwest Alaska watershed. *Transactions of the American Fisheries Society* **132:** 717–732.

Merz JE, **Merz WR. 2004.** Morphological features used to identify Chinook salmon sex during fish passage. *The Southwestern Naturalist* **49:** 197–202.

Meyer A. 1987. Phenotypic plasticity and heterochrony in *Cichlasoma managuense* (Pisces, Cichlidae) and their implications for speciation in cichlid fishes. *Evolution* **41:** 1357–1369.

Miller MR, **Brunelli JP**, **Wheeler PA**, **Liu S**, **Rexroad CE 3rd**, **Palti Y**, **Doe CQ**, **Thorgaard GH. 2012.** A conserved haplotype controls parallel adaptation in geographically distant salmonid populations. *Molecular Ecology* **21:** 237–249.

Nakano S, **Maekawa K**, **Yamamoto S. 1990.** Change of the life lake cycle of Japanese charr following artificial construction by damming. *Nippon Suisan Gakkaishi* **56:** 1901–1905.

Negus MT. 2003. Determination of smoltification status in juvenile migratory rainbow trout and Chinook salmon in Minnesota. *North American Journal of Fisheries Management* **23:** 913–927.

Nichols KM, **Edo AF**, **Wheeler PA**, **Thorgaard GH. 2008.** The genetic basis of smoltification-related traits in *Oncorhynchus mykiss*. *Genetics* **179:** 1559–1575.

Nosil P. 2007. Divergent host plant adaptation and reproductive isolation between ecotypes of *Timema cristinae* walking sticks. *The American Naturalist* **169**, 151–162.

Ohms HA, **Sloat MR**, **Reeves GH**, **Jordan CE**, **Dunham JB. 2014.** Influence of sex, migration distance, and latitude on life history expression in steelhead and rainbow trout (*Oncorhynchus mykiss*). *Canadian Journal of Fisheries and Aquatic Sciences* **71:** 70–80.

Olden JD, **Jackson DA**, **Peres-Neto PR. 2002.** Predictive models of fish species distributions: a note on proper validation and chance predictions. *Transactions of the American Fisheries Society*, **131:** 329–336.

Ostberg CO, **Pavlov SD**, **Hauser L. 2009.** Evolutionary relationships among sympatric life history forms of Dolly Varden inhabiting the landlocked Kronotsky Lake, Kamchatka, and a neighboring anadromous population. *Transactions of the American Fisheries Society* **138:** 1–14.

Pakkasmaa S, **Piironen J. 2001a.** Water velocity shapes juvenile salmonids. *Evolutionary Ecology* **14:** 721–730.

Pakkasmaa S, **Piironen J. 2001b.** Morphological differentiation among local trout (*Salmo trutta*) populations. *Biological Journal of the Linnean Society* **72:** 231–239.

Pakkasmaa S, **Ranta E**, **Piironen J. 1998.** A morphometric study on four land-locked salmonid species. *Annales Zoologici Fennici* **35:** 131–140.

Pavey SA, **Nielsen JL**, **MacKas RH**, **Hamon TR**, **Breden F. 2010.** Contrasting ecology shapes juvenile lake-type and riverine sockeye salmon. *Transactions of the American Fisheries Society* **139:** 1584–1594.

Pavey SA, **Sutherland BJG**, **Leong J**, **Robb A**, **von Schalburg K**, **Hamon TR**, **Koop BF**, **Nielsen JL. 2011.** Ecological transcriptomics of lake-type and riverine sockeye salmon (*Oncorhynchus nerka*). *BMC Ecology* **11:** 31.

Pavlov DS, **Savvaitova KA. 2008.** On the problem of ratio of anadromy and residence in salmonids (Salmonidae). *Journal of Ichthyology* **48:** 778–791.

Pearse DE, **Barson NJ**, **Nome T**, **Gao G**, **Campbell MA**, **Abadía-Cardoso A**, **Anderson EC**, **Rundio DE**, **Williams TH**, **Naish KA**, **Moen T**, **Liu S**, **Kent M**, **Minkley DR**, **Rondeau EB**, **Brieuc MSO**, **Sandve SR**, **Miller MR**, **Cedillo L**, **Baruch K**, **Hernandez AG**, **Ben-Zvi G**, **Shem-Tov D**, **Barad O**, **Kuzishchin K**, **Garza JC**, **Lindley ST**, **Koop BF**, **Thorgaard GH**, **Palti Y**, **Lien S. 2018.** Sex-dependent dominance maintains migration supergene in rainbow trout. *bioRxiv* Available at: https://www.biorxiv.org/content/biorxiv/early/2018/12/22/504621.full.pdf.

Pearse DE, **Miller MR**, **Abadía-Cardoso A**, **Garza JC. 2014.** Rapid parallel evolution of standing variation in a single, complex, genomic region is associated with life history in steelhead/rainbow trout. *Proceedings of the Royal Society B* **281:** 20140012.

Piironen J, **Kiiskinen P**, **Huuskonen H**, **Heikura-Ovaskainen M**, **Vornanen M. 2013.** Comparison of smoltification in Atlantic salmon (*Salmo salar*) from anadromous and landlocked populations under common garden conditions. *Annales Zoologici Fennici* **50:** 1–15.

Proulx R, **Magnan P. 2002.** Physiological performance of two forms of lacustrine brook charr, *Salvelinus fontinalis*, in the open-water habitat. *Environmental Biology of Fishes* **64:** 127–136.

Proulx R, **Magnan P. 2004.** Contribution of phenotypic plasticity and heredity to the trophic polymorphism of lacustrine brook charr (*Salvelinus fontinalis* M.). *Evolutionary Ecology Research* **6:** 503–522.

Quinn TP. 2018. *The behavior and ecology of Pacific salmon and trout*, *2nd edn*. Seattle: University of Washington Press.

R Core Team. **2016.** *R: a language and environment for statistical computing*. Vienna: R Foundation for Statistical Computing. Available at: http://www.R-project.org/.

Riddell BE, **Leggett WC. 1981.** Evidence of an adaptive basis for geographic variation in body morphology and time of downstream migration of juvenile Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences* **38:** 308–320.

Rincón PA, **Bastir M**, **Grossman GD. 2007.** Form and performance: body shape and prey-capture success in four drift-feeding minnows. *Oecologia* **152:** 345–355.

Ripley B, **Venables B**, **Hornik K**, **Gebhardt A**, **Firth D. 2015.** *MASS: support functions and datasets for Venables and Ripley's MASS. R package version 7.3–45*. Available at: https://cran.r-project.org/web/packages/MASS/index.html.

Robillard MM, **Casselman JM**, **McLaughlin RL**, **Mackereth RW. 2011.** Alternative growth histories in populations of Lake Superior brook trout: support for partial migration. *Biological Conservation* **144:** 1931–1939.

Robinson BW, **Parsons KJ. 2002.** Changing times, spaces, and faces: tests and implications of adaptive morphological plasticity in the fishes of northern postglacial lakes. *Canadian Journal of Fisheries and Aquatic Sciences* **59:** 1819–1833.

Russell R. 1977. Rainbow trout life history studies in lower Talarik Creek-Kvichak drainage. *Alaska Department of Fish and Game* **18:** 48.

Schindler DE, **Hilborn R**, **Chasco B**, **Boatright CP**, **Quinn TP**, **Rogers LA**, **Webster MS. 2010.** Population diversity and the portfolio effect in an exploited species. *Nature* **465:** 609–612.

Schulz UH. 1999. Downstream migration of European lake trout, *Salmo trutta f. lacustris* L., and resident brown trout, *Salmo trutta f. fario* L., progeny in a Lake Constance affluent river. *Fisheries Management and Ecology* **6:** 187–194.

Schweizer RM, **vonHoldt BM**, **Harrigan R**, **Knowles JC**, **Musiani M**, **Coltman D**, **Novembre J**, **Wayne RK. 2016.** Genetic subdivision and candidate genes under selection in North American grey wolves. *Molecular Ecology* **25:** 380–402.

Seiler SM, **Keeley ER. 2007.** Morphological and swimming stamina differences between Yellowstone cutthroat trout (*Oncorhynchus clarkii bouvieri*), rainbow trout (*Oncorhynchus mykiss*), and their hybrids. *Canadian Journal of Fisheries and Aquatic Sciences* **64:** 127–135.

Simonsen MK, **Siwertsson A**, **Adams CE**, **Amundsen PA**, **Præbel K**, **Knudsen R. 2017.** Allometric trajectories of body and head morphology in three sympatric Arctic charr (*Salvelinus alpinus* (L.)) morphs. *Ecology and Evolution* **7:** 7277–7289.

Standen EM. 2005. Dorsal and anal fin function in bluegill sunfish *Lepomis macrochirus*: three-dimensional kinematics during propulsion and maneuvering. *The Journal of Experimental Biology* **208:** 2753–2763.

Swain DP, **Holtby LB. 1989.** Differences in morphology and behavior between juvenile coho salmon (*Oncorhynchus kisutch*) rearing in a lake and in its tributary stream. *Canadian Journal of Fisheries and Aquatic Sciences* **46:** 1406–1414.

Tanguy JM, **Ombredane D**, **Baglinière JL**, **Prunet P. 1994.** Aspects of parr-smolt transformation in anadromous and resident forms of brown trout (*Salmo trutta*) in comparison with Atlantic salmon (*Salmo salar*). *Aquaculture* **121:** 51–63.

Taylor EB, **Lowery E**, **Lilliestråle A**, **Elz A**, **Quinn TP. 2008.** Genetic analysis of sympatric char populations in western Alaska: Arctic char (*Salvelinus alpinus*) and Dolly Varden (*Salvelinus malma*) are not two sides of the same coin. *Journal of Evolutionary Biology* **21:** 1609–1625.

Theis A, **Ronco F**, **Indermaur A**, **Salzburger W**, **Egger B. 2014.** Adaptive divergence between lake and stream populations of an East African cichlid fish. *Molecular Ecology* **23:** 5304–5322.

Thorpe RS. 1976. Biometric analysis of geographic variation and racial affinities. *Biological Reviews of the Cambridge Philosophical Society* **51:** 407–425.

Tsiger VI, **Skirin NI**, **Krupyanko KA**, **Kashkin VV**, **Semenchenko AY. 1994.** Life history forms of male masu salmon (*Oncorhynchus masou*) in South Primor'e, Russia. *Canadian Journal of Fisheries and Aquatic Sciences* **51:** 197–208.

Varian A, **Nichols KM. 2010.** Heritability of morphology in brook trout with variable life histories. *PLoS One* **5:** e12950.

Wainwright PC, **Osenberg CW**, **Mittelbach GG. 1991.** Trophic polymorphism in the pumpkinseed sunfish (*Lepomis gibbosus* Linnaeus): effects of environment on ontogeny. *Functional Ecology* **5:** 40–55.

Webb PW. 1975. Hydrodynamics and energetics of fish propulsion. *Bulletin of the Fisheries Research Board of Canada* **190:** 158.

Webb PW. 1982. Locomotor patterns in the evolution of actinopterygian fishes. *American Zoologist* **22:** 329–342.

Webb PW. 1984. Body form, locomotion and foraging in aquatic vertebrates. *Integrative and Comparative Biology* **24:** 107–120.

Weissing FJ, **Edelaar P**, **van Doorn GS. 2011.** Adaptive speciation theory: a conceptual review. *Behavioral Ecology and Sociobiology* **65:** 461–480.

Westley PAH, **Conway CM**, **Fleming IA. 2012.** Phenotypic divergence of exotic fish populations is shaped by spatial proximity and habitat differences across an invaded landscape. *Evolutionary Ecology Research* **14:** 147–167.

Wilson CC, **Stott W**, **Miller L**, **D'Amelio S**, **Jennings MJ**, **Cooper AM. 2008.** Conservation genetics of Lake Superior brook trout: issues, questions, and directions. *North American Journal of Fisheries Management* **28:** 1307–1320.

Witte F, **Barel CDN**, **Hoogerhoud JC. 1990.** Phenotypic plasticity of anatomical structures and its ecomorphological significance. *Netherlands Journal of Zoology* **40:** 278–298.

Woods PJ, **Young D**, **Skúlason S**, **Snorrason SS**, **Quinn TP. 2013.** Resource polymorphism and diversity of Arctic charr *Salvelinus alpinus* in a series of isolated lakes. *Journal of Fish Biology* **82:** 569–587.

Appendix

Table A1. Summary statistics of length-at-age data for rainbow trout caught in Iliamna Lake (*N* = 77) and tributary streams (*N* = 88). The age of each trout was determined by counting the number of annuli on scales collected from an area above the lateral line on a diagonal between the posterior edge of the dorsal fin and anterior edge of the anal fin (Coggins, 1994). Length-at-age for previous years was determined with the Fraser–Lee model of back-calculation (Fraser, 1916; Lee, 1920). These length-at-ages largely come from different rainbow trout than those used in this coloration/morphology study but are from many of the same sampling locations and, thus, provide representative data. Note that age 0+ fry (≥33 mm fork length) were sampled in streams but not included in this table

Habitat-of-capture	Age	*N* (at capture)	*N* (back-calculated)	Mean	SD	Min.	Q1	Median	Q3	Max.
Lake	1	0	77	82.5	9.2	65.1	76.1	80.4	88.7	108.0
	2	13	77	134.3	19.3	95.9	121.9	131.6	144.7	192.9
	3	25	64	190.3	29.6	128.8	172.4	185.5	207.6	295.9
	4	17	39	257.8	46.9	174.8	219.8	254.5	289.5	369.1
	5	13	22	316.0	40.7	255.3	284.0	315.0	352.0	392.7
	6	7	9	390.7	50.5	299.1	371.8	383.8	426.9	448.0
	7	2	2	493.3	22.5	477.4	485.4	493.3	501.3	509.2
Stream	1	58	88	74.4	8.0	56.4	69.3	74.2	78.8	95.6
	2	15	30	122.1	15.9	96.4	106.1	123.4	136.2	147.3
	3	12	15	176.2	25.4	135.1	165.0	171.9	192.6	228.6
	4	1	3	247.6	21.3	235.1	235.4	235.6	253.9	272.2
	5	2	2	314.0	14.7	303.5	308.7	314.0	319.2	324.4