Nonanadromous Life History Diversity of Rainbow Trout (*Oncorhynchus mykiss*)

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Abstract

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Rainbow trout (*Oncorhynchus mykiss*) is a salmonid species, native to Pacific Ocean drainages in North America and eastern Russia, which exhibits fluvial (stream-resident), adfluvial (lake-migrant), and anadromous (ocean-migrant) ecotypes. The differentiation of fluvial and anadromous individuals in sympatry is well-studied, whereas comparatively little research has focused on the adfluvial form and its distinction from fluvial individuals in sympatry. Thus, the purpose of this dissertation was to investigate the ecological, genetic, and phenotypic diversity of nonanadromous rainbow trout in a natural stream-lake system to better understand the differentiation of fluvial and adfluvial individuals in sympatry, the basis of residency versus migration in this species, and the role of lakes in salmonid diversification. Rainbow trout were sampled in the lake (thus, by definition, adfluvial) and in several tributary streams (where adfluvial and fluvial individuals may co-occur), and were examined for a variety

of features to develop a holistic understanding of the behavior, ecology, and evolution of these life history pathways.

Stomach contents and stable isotopes revealed disparate trophic ecology among rainbow trout in connected stream and lake habitats, suggesting both an ontogenetic shift in the diet of adfluvial fish as well as divergence in diet between adfluvial and fluvial ecotypes. Rainbow trout in streams fed primarily on aquatic insects, while those in the lake largely consumed snails and amphipods; however, partial trophic convergence among trout in these two habitats occurred when they incorporated the marine nutrient subsidy of spawning sockeye salmon eggs. Stable isotope data suggested that the minimum size of migration from stream to lake habitat by adfluvial fish was ~150 mm fork length, suggesting a juvenile stream-rearing period of a year or more prior to lake entry. Dietary niche comparisons with sympatric *Salvelinus* species suggested a greater degree of dietary overlap between rainbow trout and Dolly Varden (*S. malma*) in streams than between rainbow trout and Arctic char (*S. alpinus*) in the lake, which may increase the relative fitness benefits of migration over residency for rainbow trout.

Restriction site-associated DNA sequencing revealed an association between habitat type (stream or lake) and a chromosomal inversion in the rainbow trout genome as well as numerous single nucleotide polymorphisms, supporting the genetic divergence of adfluvial and fluvial ecotypes in sympatry. Rainbow trout in streams were nearly fixed for the rearranged haplotype of the Omy05 inversion, whereas trout in the lake exhibited a markedly higher frequency of the ancestral, anadromy-associated haplotype. The functions of outlier genes with nonsynonymous mutations among stream- and lake-caught trout paralleled those documented in studies of fluvial and anadromous *O. mykiss*, highlighting the migratory nature of the adfluvial ecotype even though it is nonanadromous. Structure was present at both non-outlier and outlier loci among and within streams supporting populations nearly fixed for the rearranged Omy05 haplotype (i.e., with a genetic predisposition for stream-residency), highlighting the roles of local adaptation and genetic drift via spatial isolation in population divergence.

Assessment of lateral coloration patterns and multivariate analyses of body shape of rainbow trout from stream and lake habitats over a range of body sizes revealed ontogenetic and ecotypic variation in coloration and morphology. Color differences among trout of different size classes and habitats indicated ecotype-specific pathways resulting in different terminal coloration patterns; banded parr in streams transitioned to either a silver coloration suited to pelagic waters in the lake (when adfluvial) or bronze coloration suited to confined cover in streams (when fluvial). The morphology of lake-caught rainbow trout was distinct from that of stream-caught trout, and their morphological differentiation exhibited many shared but some unique patterns compared to sympatric Dolly Varden in streams and Arctic char in the lake. Patterns of morphological variation in rainbow trout among and within habitats suggested the presence of partial migration, in which both fluvial and adfluvial individuals are produced from the same population.

A review of the spawning behaviors, rearing strategies, and trophic polymorphisms in lakes among 16 species of salmonids from the genera *Oncorhynchus*, *Salmo*, and *Salvelinus* identified a negative association between the extent of reliance on lakes and the degree of anadromy. *Oncorhynchus* exhibits the least lake reliance, *Salmo* an intermediate level, and *Salvelinus* the greatest; opposite of the anadromy spectrum identified in previous studies. Lakes support life history forms, reproductive ecotypes, and trophic morphs unique to lacustrine habitat, and also support anadromous and fluvial salmonids by providing spawning, rearing, overwintering, and/or summer refuge habitat. Adfluvial and anadromous salmonids exhibit similar migration-associated traits and behaviors including the parr-smolt transformation, sex-biased partial migration, and the presence of precocious ‘jack’ males.

TABLE OF CONTENTS

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GENERAL INTRODUCTION

Partial migration is a widespread phenomenon in birds, fishes, and other animals in which certain individuals in a population remain resident while others migrate, representing alternative life history pathways (Chapman *et al.* 2011). These migratory alternatives result in different fitness tradeoffs, particularly regarding growth opportunity and mortality risk. Residents are generally smaller at sexual maturity but more likely to survive to that point than migrants; however, the increased size of migrants is associated with increased female fecundity and male breeding opportunity (e.g., in fishes: Jonsson and Jonsson 1993). The ratio of migrants to residents within a population is influenced by a variety of environmental factors, including the differences in food availability, competition, and predation risk among the natal and alternative foraging habitats (Chapman *et al.* 2012). In addition, there is a genetic basis for partial migration, with the expression of migrant or resident behavior being influenced by heritable traits (Pulido 2011); offspring tend to exhibit the same life history as their parents (Phillis *et al.* 2016), though considerable variation exists in the strength of genetic control. Partial migration enhances population abundance and stability; the use of resources in different habitats by migrants and residents reduces intraspecific competition and results in both greater population size and resilience to environmental variability (Vélez-Espino *et al.* 2013).

The intraspecific diversity in habitat use resulting from partial migration in fishes poses notable considerations for conservation planning and resource management. Fishes may reside exclusively in one habitat type or another, freely move between multiple types, and reproduce in one or more types (Lucas and Baras 2001). Use of marine versus fresh water and flowing versus standing water can induce phenotypic plasticity, evolutionary diversification, and population structure (e.g., Jones *et al.* 2012; Franssen *et al.* 2013). Thus, it is important to study the extent to which the resident and migrant population components utilize the various habitats, and any underlying genetic basis to their behavioral differences, to better inform conservation and management efforts aimed at their recovery and sustainability.

Salmonid fishes are characterized by their intraspecific diversity associated with partial migration (Jonsson and Jonsson 1993). Throughout their native Asian, European, African and North American ranges, many salmonid species and population segments are threatened or endangered, and their persistence is dependent on the diversity of their stocks (Schindler *et al.* 2010) and/or the habitat use patterns of their resident and migrant forms (Campbell *et al.* 2019). Salmonid fishes follow four primary life histories; fluvial (spawning in and residing in streams or migrating within river systems), adfluvial (spawning in streams and migrating to lakes), lake-resident (spawning in and residing in lakes), and anadromous (spawning in fresh water and migrating to the ocean). Species in the family span the range from exclusively migratory (e.g., pink salmon) to exclusively resident (e.g., Mexican golden trout), but most occur along the gradient occurring between those two extremes and exhibit partially migrant populations (Jonsson and Jonsson 1993). In partially migrant populations of salmonids, the migrant form may be anadromous, which is particularly well-studied (Rounsefell 1958; Quinn and Myers 2004; Spares *et al.* 2015), or adfluvial, which is comparatively understudied in certain species (Olsson and Greenberg 2004; Olsson *et al.* 2006).

The rainbow trout (*Oncorhynchus mykiss*) is a partially migrant salmonid species native to Pacific drainages in North America and eastern Russia, which predominantly exhibits fluvial, adfluvial, and anadromous life history types (Behnke 1992). Several recent studies have investigated the phenotypic differentiation and genetic divergence of fluvial and anadromous forms in sympatry (e.g., Nichols *et al.* 2008; McKinney *et al.* 2015; Baerwald *et al.* 2016). Most notably, there is an inversion on the fifth chromosome of the *O. mykiss* genome that reduces recombination, resulting in alternative haplotypes of co-adapted alleles that are associated with migration to the ocean or residency in streams (Pearse *et al.* 2018). In contrast, far less research effort has focused on the distinction of adfluvial rainbow trout from fluvial individuals in sympatry and has largely been limited to altered systems where the 'adfluvial' individuals were recently anadromous until damming blocked their ocean migration and forced them into an artificial reservoir (Holecek *et al.* 2012; Holecek and Scarnecchia 2013). Other studies investigating adfluvial fish were conducted in systems where they experienced hatchery introgression and hybridization with introduced strains of rainbow trout (Pearse *et al.* 2014; Pearse and Garza 2015; Leitwein *et al.* 2017), and these genetic interactions hinder interpretation of those results. Therefore, the limited work explicitly comparing the differentiation of the migrant adfluvial form from the other life history types is largely confounded by anthropogenic influences.

The purpose of this dissertation is to investigate the ecological, phenotypic, and genetic diversity of nonanadromous rainbow trout in a natural stream-lake system, to better understand the differentiation of fluvial and adfluvial individuals in sympatry and the basis of residency versus migration in this species. The Bristol Bay drainage in southwest Alaska supports fluvial and adfluvial forms of rainbow trout (Meka *et al.* 2003; Schwanke and Hubert 2003), but no anadromous individuals (known as 'steelhead' – Behnke 1992) even though the ocean is accessible. The drainage was formerly covered by the Cordilleran ice sheet at least 10000 years ago and must have been colonized in the post-glacial period by anadromous ancestors (McCusker *et al.* 2000) that ultimately evolved into the extant nonanadromous populations. One such system is the Kvichak River basin containing Iliamna Lake, the largest in the state (Burgner *et al.* 1969). This system hosts an entirely native fish fauna (Bond and Becker 1963), has protective fishing regulations for rainbow trout in stream and lake habitats, and has had no habitat alteration, hatchery propagation, or transplantation of nonnative trout. These attributes make Iliamna Lake and its tributaries an appropriate system, devoid of confounding anthropogenic factors, in which to study the ecological and phenotypic diversity of nonanadromous rainbow trout, as well as determine if there is also a genetic basis for migration into lakes parallel to that for migration into marine waters. Comparing results from these studies of rainbow trout with those of other species from the genera *Oncorhynchus*, *Salmo*, and *Salvelinus*, will facilitate a greater understanding of lake use within the family and inform habitat protection central to the continued viability of healthy salmonid populations globally.

This dissertation is comprised of four chapters; the first three describing original research conducted on Iliamna Lake rainbow trout, and the fourth reviewing the variation in use of lakes by salmonids as a family. The first chapter, published as Arostegui and Quinn (2018), described the trophic ecology of rainbow trout in connected streams and lakes to determine the extent of diet segregation among fluvial and adfluvial forms. The second chapter, published as Arostegui *et al.* (2019), investigated the genomic architecture underlying migratory behavior in nonanadromous rainbow trout to determine if fluvial and adfluvial ecotypes exhibit genetic divergence and if that divergence parallels that documented between fluvial and anadromous ecotypes. The third chapter compared the coloration and body shape associated with swimming performance of nonanadromous rainbow trout among stream and lake habitats to determine if they exhibit phenotypic diversity consistent with the presence of alternative fluvial and adfluvial ecotypes. The fourth chapter, published as Arostegui and Quinn (2019), compared spawning behaviors, rearing strategies, and trophic polymorphisms in lakes among 16 species of salmon, trout, and charr from the genera *Oncorhynchus*, *Salmo*, and *Salvelinus* to assess the relative extent of reliance on lakes within this family. Together, these four chapters are intended to advance our knowledge of nonanadromous life history alternatives in rainbow trout and the role of lakes in the ecological and genetic diversification of salmonids.

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CHAPTER 1

Trophic ecology of nonanadromous rainbow trout in a post-glacial lake system: partial convergence of adfluvial and fluvial forms

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ABSTRACT

The rainbow trout (*Oncorhynchus mykiss* Walbaum, 1792) is one of many salmonid species exhibiting a gradient of life histories including fluvial (stream-resident), anadromous (ocean-migrant), and adfluvial (lake-migrant) forms, the last of which is less extensively studied than the other two. Our goal was to determine the extent of diet segregation between fluvial and adfluvial rainbow trout. We collected stomach content and stable isotope data on rainbow trout sampled in stream and lake habitats in a southwestern Alaska watershed during summer, and compared them to data on sympatric stream- and lake-specialist char species (*Salvelinus malma* Walbaum, 1792 and *S. alpinus* Linnaeus, 1758*,* respectively). Rainbow trout in streams fed largely on aquatic insects while those in the lake ate primarily benthic snails and amphipods. The trophic segregation of stream-resident and lake-migrant rainbow trout mirrored but was less extreme than the divergence of lotic Dolly Varden (*S. malma*) and lentic Arctic char (*S. alpinus*) in the same system. Spawning sockeye salmon (*Oncorhynchus nerka* Walbaum, 1792) provided a nutrient subsidy in the form of eggs that supported rainbow trout in both stream and lake (littoral) habitats, causing their isotopic signatures to converge. This study augments knowledge of partial migration and trophic divergence within populations.

INTRODUCTION

Within populations of some migratory species, individuals may reside in a single habitat or migrate among habitats; such populations are referred to as displaying partial migration (Dingle 1996; Pulido 2011). This dichotomous behavior occurs in diverse taxa, and differences in prey resources, competition, predation risk, and abiotic factors can result in dramatic differences in growth, survival, and population dynamics between migrants and non-migrants (Chapman *et al.* 2011). In fishes, partial migration appears to result from interactions between environmental conditions and genetic controls that ultimately cause differential growth and survival between migrants and residents (Jonsson and Jonsson 1993; Chapman *et al.* 2012*a*,*b*).

In salmonid fishes, the prevalence of resident and migratory strategies may be controlled by the energetic profitability of foraging in a given habitat (Forseth *et al.* 1999; Morinville and Rasmussen 2003). Certain individuals may experience food limitations and seek resources elsewhere while others satisfy their requirements and remain resident, leading to partial migration within the population (Olsson *et al.* 2006; Chapman *et al.* 2011). The various life histories followed by salmonids represent a gradient of migration that balances fitness trade-offs between potential size at reproduction, fecundity in females, breeding opportunity in males, and mortality (Holecek and Scarnecchia 2013; Boel *et al.* 2014).

Most salmonids spawn in streams, and when their progeny emerge from the gravel they can reside within their natal stream or river (fluvial), migrate to a lake (adfluvial) if one is accessible, or migrate to the ocean (anadromous) if it is accessible (Quinn 2005; Holecek and Scarnecchia 2013). Brook trout, *Salvelinus fontinalis* Mitchill, 1814 (Morinville and Rasmussen 2003; Robillard *et al.* 2011), brown trout, *Salmo trutta* Linnaeus, 1758 (Olsson and Greenberg 2004; Charles *et al.* 2006), cutthroat trout, *Oncorhynchus clarkii* Richardson, 1836 (Trotter 1989;

Gresswell *et al.* 1994), and other species display all three life histories, highlighting migratory variation as a fundamental aspect of salmonid diversity. The tendency to migrate or not may be displayed within a given breeding population and it also varies among breeding populations, as each is subjected to a different regime of selection based on the capacity for growth and risk of mortality in its respective habitats.

Although adfluvial behavior is well studied in other salmonids (Jonsson 1985; Huckins *et al.* 2008; Gresswell 2011), less is known of the ecology of adfluvial rainbow trout, *Oncorhynchus mykiss* Walbaum, 1792 (Northcote 1969; Irvine 1978) despite the species' wide native range around the Pacific Rim, from northwest Mexico to southwest Alaska and the Kamchatka Peninsula in eastern Russia, and extensive introductions around the world (MacCrimmon 1971; Behnke 1992; Quinn 2005; Casal 2006). The best-known types are the anadromous (steelhead) and fluvial forms (Ohms *et al.* 2014; Baerwald *et al.* 2016) but adfluvial forms also exist and can co-occur with fluvial forms (Holecek and Scarnecchia 2013).

Stream and lake habitats provide different prey resources, and may therefore promote the diversity of the species through adaptive evolution or phenotypic plasticity (Bateson 2015). Rainbow trout ecotypes may diverge in habitat use, diet, morphology, age at maturity, fecundity, spawning timing and other aspects of their life histories (Keeley *et al.* 2005; Matala *et al.* 2009; Holecek and Scarnecchia 2013). Reproductive isolation and genetic differentiation of rainbow trout ecotypes occurs at varying degrees (McPhee *et al.* 2007; Baerwald *et al.* 2016), highlighting how this intraspecific diversity manifests along the gradient between genetically distinct forms representing separate populations and environmentally determined forms representing a single integrated population. Expanding knowledge of organisms with various life history forms or ecotypes, such as the rainbow trout, is important for their conservation both below the species level of classification and for the species as a whole (Keeley *et al.* 2007).

Determining feeding ecology, which is an integral part of the distinction between ecotypes, can be difficult because adfluvial rainbow trout may move back and forth between stream and lake habitats. Diet analysis indicates prey consumed in the immediate past but provides no information about the preceding period. Dual stable isotope analysis of $\delta^{15}N$ and $\delta^{13}C$ is a complementary method for evaluating life history diversity through trophic position and habitat. The $\delta^{15}N$ signature of consumers, derived from their diet, indicates trophic position due to a 2-5‰ stepwise enrichment of the isotope with every increase in trophic level (Minagawa and Wada 1984; Post 2002). The $\delta^{13}C$ signature indicates the relative contributions of various terrestrial and aquatic sources of primary production to a consumer's diet, and typically undergoes enrichment of 1‰ or less per trophic level (Rau 1980; Post 2002). Salmonids may eat the same prey in the same habitats, different prey in the same habitats, the same prey in different habitats, or different prey in different habitats, representing the varying degrees of ecotypic overlap and separation (Robillard *et al.* 2011).

This study investigated the trophic ecology of wild, native nonanadromous rainbow trout in a large Alaskan lake where they occupy both lake and stream habitats during the same time of year, testing several alternative hypotheses. First, these fish might represent distinct ecotypes deriving their nutrition largely or exclusively from their respective habitats. Second, all trout might move freely between lake and stream habitats as a single mixed ecotype. Finally, some intermediate level of distinction might occur, perhaps related to fish size or specific feeding opportunities. To evaluate these alternatives, we compared the stomach contents and stable isotope profiles of rainbow trout sampled in lake and stream habitats to each other, and to sympatric Arctic char, *Salvelinus alpinus* Linnaeus, 1758 and Dolly Varden, *Salvelinus malma* Walbaum, 1792. In this system these two species of char are habitat specialists: Arctic char in the lake and Dolly Varden in streams (Taylor *et al.* 2008; Denton *et al.* 2010), thus providing values against which the rainbow trout could be compared.

METHODS

Study Site

The study was conducted in Iliamna Lake, which drains via the Kvichak River into Bristol Bay, southwest Alaska. The lake, with a surface area of 2622 km^2 and volume of 1151 km^3, is the largest in the state (Burgner *et al.* 1969), and its associated tributaries host an entirely native fish fauna (Bond and Becker 1963). As in other Bristol Bay basins, steelhead are absent (Behnke 1992) but nonanadromous rainbow trout are abundant and widely distributed in stream and lake habitats. This system has had no habitat alteration such as dams or land-use practices affecting the stream or lake environments, no history of hatchery propagation or transplants of non-native trout, and very protective fishing regulations. All of these attributes make it suitable for studying trophic ecology and life history variation in rainbow trout.

Fish Sampling

Rainbow trout, Dolly Varden, and Arctic char were sampled in the eastern end of Iliamna Lake from July-September in 2015 and 2016 (Fig. 1). Collection methods included stick seining in smaller streams, beach seining in the lake, and hook-and-line angling in the lake and larger streams. Fish were held in a solution of AQUI-S anesthetic for 1-3 minutes, depending upon size, until they were unresponsive to handling. The fish were measured for fork length (mm) and lower lobe caudal fin clips were removed and placed within vials containing 95% ethanol for stable isotope analyses. A subset of rainbow trout also underwent gastric lavage; stomach contents were saved for later classification. Fish were then held in fresh water until they recuperated and were released at the site of capture.

Rainbow trout were collected in stream (*n* = 123), stream mouth (*n* = 20), and lake (*n* = 80) habitats, with an overall range in fork length from 58 – 565 mm. Habitats were defined as follows: stream – more than 0.30 km upstream of the stream/lake transition, stream mouth – less than 0.30 km upstream of the stream/lake transition, lake – in the lake proper. Stream rainbow trout were sampled at Russian, Roadhouse, Mink, Canyon, and Chinkelyes creeks, including its confluence with the Iliamna River. Stream mouth rainbow trout were sampled at Russian, Knutson, and Lonesome Bay creeks. Lake rainbow trout were sampled at Porcupine Island, Flat Island, Woody Island, and Finger Bay sites.

Dolly Varden were collected in stream and stream mouth habitats (*n* = 30 combined, fork length range: 76 – 375 mm) including Canyon, Mink, Lonesome Bay, and Russian creeks. Arctic char were collected exclusively in lake habitats (*n* = 29, fork length range: 130 – 580 mm), including Porcupine, Flat, and Woody islands. Dolly Varden and Arctic char were distinguished by morphological differences, validated with genetic analysis (Taylor *et al.* 2008).

Stomach Contents

A total of 79 rainbow trout from stream, stream mouth, and lake habitats had their stomach contents identified to the taxonomic Order (except for snails at the Class level). Insects were further identified to the developmental stage (larvae, pupae, adult or nymph, adult depending on the order) and dipterans were further identified to the family level. Nineteen trout with empty stomachs were excluded from the following diet comparisons. Diet categories occurring in < 5% of the 60 remaining rainbow trout were excluded from the quantitative transformations and analyses. Sockeye salmon (*Oncorhynchus nerka* Walbaum, 1792) eggs were a very common diet item in stream and lake habitats but, unlike the insects and other invertebrates, their consumption depended on date rather than habitat (diet samples collected prior to spawning by salmon could not include eggs). Consequently, as our goal was to compare the more fundamental differences in prey selection between habitats without the confounding effect of date, we excluded eggs from diet analyses but report those data separately. Rainbow trout with no data from any of the remaining diet categories were excluded (e.g., a trout with only eggs in its stomach would be excluded), reducing the sample size to 55 individuals. A Jaccard distance matrix was computed from the proportion data (# of specific item/ # of all items) of the 16 diet categories to assess the similarity of diets between individual rainbow trout.

Overall analysis of similarities (ANOSIM) and post-hoc multiple comparisons (Bonferroni-corrected $\alpha = 0.017$) of the diets of rainbow trout sampled in lake ($n = 22$), stream ($n = 25$), and stream mouth ($n = 8$) habitats were conducted on the Jaccard distance matrix. Nonmetric multidimensional scaling (NMDS) with three dimensions was conducted on the same distance matrix to elucidate differences in rainbow trout diets across habitats. Goodness of fit of the NMDS results was tested with a stress function, where values range between 0 and 1 and lower values indicate a better fit to the data (Kruskal 1964). Both NMDS and significance testing of individual diet category vectors used 5000 permutations.

Stable Isotope Sample Processing

Rainbow trout, Dolly Varden, Arctic char, and diet end member (prey item) samples were drained of ethanol, freeze-dried for 24 h, cut or ground into small pieces, weighed (0.350 - 0.650 mg) with a microbalance, and packed into tin capsules for processing at the University of Washington (UW) IsoLab, Seattle. Isotope values were presented as the difference (in parts per thousand, ‰) between the isotope ratios of a sample and sockeye salmon standard where $\delta^{15}N$ or $\delta^{13}C = ([R_{\text{sample}} / R_{\text{standard}}]-1) \times 1000$, with $R = {}^{15}N/{}^{14}N$ or ${}^{13}C/{}^{12}C$ (Post 2002).

All fin clips from rainbow trout, Dolly Varden, and Arctic char had C:N ratios < 1.1 and were not lipid-normalized (Post *et al.* 2007). Diet end members were processed whole, and since the predators in our study consume entire prey items (sockeye salmon eggs, aquatic and terrestrial invertebrates) we did not normalize the end members to account for tissue-specific lipid concentrations. Storage of consumer fin clips and prey items in ethanol may have slightly shifted their $\delta^{13}C$ values, but effects are inconsistent (Sarakinos *et al.* 2002).

Rainbow Trout Trophic Ecology

Rainbow trout (n = 223) were classified *a posteriori* into trophic and habitat use groups via cluster analysis of their $\delta^{15}N$ and $\delta^{13}C$ signatures, rather than *a priori* by the habitat where they were sampled. We chose this analytical approach because the habitat where a fish was found is not necessarily where it acquired most of its resources (Huckins *et al.* 2008), and it might have only recently arrived there. Rainbow trout fin clips have an ~13-day turnover rate for $\delta^{15}N$ (Heady and Moore 2013), and a study of another fish species demonstrated that $\delta^{15}N$ and $\delta^{13}C$ in caudal fin tissues exhibit nearly identical half-lives (Suzuki *et al.* 2005). Thus, our classification of rainbow trout from their dual isotope signatures reflects their foraging and habitat use prior to that ~13-day period.

The dual isotope data were z-score standardized and their dissimilarity calculated with a Manhattan distance matrix. Within-group dispersion was minimized with Ward's linkage method (Strauss and von Maltitz 2017). The number of clusters to retain was determined by assessing Jaccard cluster stability and which solution most appropriately accounted for differences in $\delta^{13}C$ between habitat-specific prey and $\delta^{15}N$ between sockeye salmon eggs and other diet components. General cluster diagnostics included calculation of the agglomerative coefficient and cophenetic correlation. Differences between rainbow trout clusters in terms of fork length (mm) were assessed with a Kruskal-Wallis test and post-hoc multiple comparisons.

Trophic segregation and marine-subsidy utilization by rainbow trout occupying different habitats was assessed with Bayesian mixing models (Stock and Semmens 2013), incorporating uncertainty (Moore and Semmens 2008) and residual error (Parnell *et al.* 2010), which provide population-level diet compositions derived from the dual isotope data. Fork length (mm) was included in the models as a continuous variable (Francis *et al.* 2011) to account for any size-related differences in the isotope signatures. Mixing models were run for each rainbow trout cluster using three chains of length 3,000,000 with a burn in of 1,500,000 and thinning of 500. Diet end members were selected based on the stomach content analyses and included sockeye salmon eggs, stream aquatic invertebrates/ hymenopterans, and lake benthic invertebrates. The isotopic variance of each end member was included in the model to enable the Bayesian algorithm to recognize and use these distributions while estimating consumer diet compositions. We utilized average (+/- 1 SD) $\delta^{15}N$ and $\delta^{13}C$ trophic fractionations of 3.40 +/- 0.98 and 0.39 +/- 1.30, respectively (Post 2002), for all three end members.

Diet End Members

Mean values and variances for the diet end members included in the mixing model were quantified by combining prey items and sampling over a range of locations and summer dates. Isotope data for end members came from our own collections within the Iliamna Lake system, except for sockeye salmon eggs that were sampled over a 3-week period from the nearby Wood River system (Moore and Semmens 2008). Aquatic snails (Genera *Stagnicola* Jeffreys, 1830 and *Gyraulus* Charpentier, 1837) were collected over a 2 - 3 week period from rainbow trout stomach contents and the littoral zone of the lake. Additional snails from Denton *et al.* (2010) were included in the sample. Amphipods (Genus *Gammarus* Fabricius, 1775) were collected from rainbow trout stomach contents. Aquatic snails and amphipods (n = 9 each, 18 total) were isotopically similar and so were averaged to form the "lake benthic invertebrates" end member. Aquatic worms (Phylum Annelida) and insects (Orders Diptera, Plecoptera, Ephemeroptera, Trichoptera), sampled with standardized methods in each of four streams across a two week period (n = 2 for each stream, 8 total), were processed together as an isotopic average of "stream invertebrates". Terrestrial insects (Order Hymenoptera) sampled from rainbow trout stomach contents (n = 2 insects) were averaged with stream invertebrates to form the "stream aquatic invertebrates/ hymenopterans" end member because they were isotopically similar (n = 8 stream invertebrate + 2 terrestrial insect samples = 10 total).

Computation

All analyses were performed in program R (R Core Team 2016). Distance matrix calculations, ANOSIM, NMDS, and ordination vector significance testing were conducted with the 'vegdist', 'anosim', 'metaMDS', and 'envfit' functions, respectively, from the 'vegan' package (Oksanen *et al.* 2016). Z-score standardization was conducted with the 'data.stand' function from the ‘BIOSTATS’ R collection (McGarigal 2016). Ward clustering, tree cutting, and cophenetic correlation were calculated with the ‘hclust’, ‘cutree’, and ‘cor’ functions, respectively, from the ‘stats’ package (R Core Team 2016). The clustering agglomerative coefficient was calculated with the ‘coef.hclust’ function from the ‘cluster’ package (Maechler *et al.* 2016). Jaccard cluster stability was conducted with the ‘clusterboot’ function from the ‘fpc’ package (Hennig 2015). Kruskal-Wallis tests and post-hoc multiple comparisons were performed with the ‘kruskal.test’ function in the ‘stats’ package and the ‘kruskalmc’ function in the ‘pgirmess’ package, respectively (Giraudoux 2015; R Core Team 2016). Bayesian mixing models were run with the ‘MixSIAR’ package (Stock and Semmens 2013).

RESULTS

Rainbow Trout Trophic Ecology

Only 16 of 33 diet items (excluding sockeye salmon eggs) were present in 5% or more of the stomachs of rainbow trout sampled in stream, stream mouth, and lake habitats combined (n = 60 containing prey). These items included different developmental stages of various aquatic insects (Diptera - Simuliidae, Chironomidae; Plecoptera; Ephemeroptera; Trichoptera), terrestrial insects (Hymenoptera), other unidentified insects, water mites (Hydracarina), aquatic snails (Gastropoda), and amphipods (Gammaridae; Table 1). Of those 60 trout, 5 were excluded from further analysis because they had none of the 16 common diet items in their stomachs. The 55 rainbow trout with at least one of the 16 common diet items present in its stomach exhibited different diets among habitats (ANOSIM: $R = 0.227$, $p < 0.001$). The diets of rainbow trout sampled in streams were significantly different from those sampled in stream mouths ($R = 0.235$, $p = 0.004$) and lakes ($R = 0.225$, $p < 0.001$), but the latter two did not differ from each other (R =

0.117, *p* = 0.061). Of the 16 common diet items, seven were identified by NMDS (stress = 0.057) as significantly contributing to the differences among habitats (Table 1). Stream fish diets were primarily differentiated by higher proportions of larval and adult simuliids, and hydracarina (Fig. 2; Table 1). Stream mouth fish diets exhibited higher proportions of ephemeroptera nymphs and unidentified insects (Fig. 1; Table 1). Lake fish diets were distinguished by the nearly exclusive occurrence of aquatic snails and exclusive occurrence of amphipods (Fig. 2; Table 1).

Fish were conspicuously absent from the rainbow trout diets, with only a single unidentifiable specimen found in the stomach of one trout sampled in the lake. In contrast to the scarcity of fishes, sockeye salmon eggs were a dominant food item in all habitats once salmon had commenced spawning. From the first day on which sockeye salmon eggs were documented in a rainbow trout stomach to the end of the study, salmon eggs were found in 32% of stream, 100% of stream mouth, and 100% of lake rainbow trout stomachs. Rainbow trout as small as 98 mm consumed salmon eggs and over 400 eggs were found in the stomach of a 515 mm trout. Additionally, two fish also consumed red fruits (watermelon berry - *Streptopus spp.* Michaux, red currant – *Ribes spp.* Linnaeus) that resembled and likely were mistaken for sockeye salmon eggs.

Diet analyses were complemented with dual isotope signatures that identified four distinct clusters of rainbow trout (agglomerative coefficient = 0.99; cophenetic correlation = 0.50; Fig. 3). Clusters 1-3 had Jaccard stabilities of 0.59-0.67, indicating patterns in the data, and cluster 4 had a stability value of 0.88, indicating a highly stable cluster (Hennig 2015). Clusters 1 and 2 included fish that were sampled in all three habitats, had similar fork lengths, and exhibited δ^{13}C values primarily in the range between lake benthic invertebrates and sockeye salmon eggs (Table 2; Fig. 3). Cluster 1 fish exhibited less enriched δ^{15}N and a greater range of δ^{13}C values than those in cluster 2. Clusters 3 and 4 included fish that were almost exclusively sampled in stream habitats, had similar fork lengths, and exhibited δ^{13}C values primarily in the range between stream aquatic invertebrates/ hymenopterans and sockeye salmon eggs (Table 2; Fig. 3). Cluster 3 fish exhibited more enriched δ^{15}N and δ^{13}C values than those in cluster 4. Fish in clusters 3 and 4 were significantly shorter (fork length) than those in clusters 1 and 2 (Kruskal-Wallis: $\chi^2 = 50.7$, $p < 0.001$; Table 2).

Isotope mixing models revealed differences in rainbow trout diet contributions among clusters (Table 3). Cluster 1 diets consisted primarily of sockeye salmon eggs and secondarily of lake benthic invertebrates. Cluster 2 diets consisted primarily of lake benthic invertebrates and secondarily of both stream aquatic invertebrates/ hymenopterans and sockeye salmon eggs. Fish in clusters 1 and 2 primarily represent the transition from lake benthic invertebrates directly or indirectly (incorporating stream aquatic invertebrates/ hymenopterans) to sockeye salmon eggs (Fig. 3). Clusters 1 and 2 included fish collected in all three habitats, but 96.25% of fish collected in the lake were in these two clusters (Table 2). Cluster 3 diets consisted primarily of sockeye salmon eggs and secondarily of stream aquatic invertebrates/ hymenopterans. Cluster 4 fish almost exclusively ate stream aquatic invertebrates/ hymenopterans. Fish in clusters 3 and 4 primarily represent the direct transition from stream aquatic invertebrates/ hymenopterans to sockeye salmon eggs (Fig. 3).

Dolly Varden and Arctic Char Isotope Space

Dolly Varden, all of which were collected in stream and stream mouth habitats, exhibited δ^{15}N and δ^{13}C values generally along the axis between stream aquatic invertebrates/ hymenopterans and sockeye salmon eggs (Fig. 4). Arctic char, exclusively from the lake, exhibited $\delta^{15}N$ and $\delta^{13}C$ values largely within the polygon created by the variances for lake benthic invertebrates, threespine sticklebacks *Gasterosteus aculeatus* Linnaeus, 1758, and sockeye salmon eggs (Fig. 4).

DISCUSSION

Ecotype Classification

Our sampling indicated that the Iliamna Lake watershed supports rainbow trout that drift-feed largely on aquatic insects in streams and those that forage primarily on benthic prey (snails and amphipods) in the lake prior to spawning by sockeye salmon. The dietary differences between stream-resident and lake-migrant rainbow trout in separate habitats exhibits many similarities to the divergence of lotic Dolly Varden and lentic Arctic char in this system. Returning sockeye salmon provide an annual subsidy of nutrients (Kline *et al.* 1993) to both stream-resident and lake-migrant trout, supporting their life history diversity and residency within the freshwater ecosystem, and causing some convergence of their trophic position as salmon eggs were highly prevalent in and constituted a substantial proportion of the rainbow trout diets in both habitats.

Cluster assignment revealed that 59.44% of trout captured in streams or at stream mouths exhibited isotopic signatures strongly associated with lake benthic invertebrates (i.e. assignment to clusters 1 or 2), suggesting recent movement from the lake to streams by a portion of the fish classified as adfluvial based on isotope values. In contrast, only 3.75% of trout captured in the lake exhibited an isotopic signature suggestive of sustained stream resource use (i.e. assignment to clusters 3 or 4), suggesting little movement from streams to the lake by fish in mid- to late-summer. These disparate results show that rainbow trout in the Iliamna Lake watershed do not constitute a single ecotype that freely mixes between habitats, but instead represent two primary ecotypes, one of which resides and forages in streams (fluvial) and the other that primarily forages in the lake (adfluvial). All these rainbow trout are spawned in streams and fish that are fluvial in a given year may transition to an adfluvial life history at a later age. The adfluvial life history could represent two separate forms in Iliamna Lake; one that occupies and primarily forages in the lake except when returning to streams to spawn (lacustrine) and a second that forages primarily in streams and utilizes the lake as a migratory corridor (intertributary-migrant). The former has been documented in lakes of the Alagnak River system (Meka *et al.* 2003) and the latter in lakes of the Wood River system (Bentley *et al.* 2015), both part of the Bristol Bay drainage.

We note that the cluster assignments of a few fish may improperly indicate one life history and habitat use pattern or another. Fish at the extremes of the $\delta^{13}C$ range represent clear examples of divergent stream and lake resource use behavior, however those in the middle nearer to the average sockeye salmon egg value are harder to discretize as both stream-resident and lake-migrant trout may acquire similar isotopic signatures when in separate habitats utilizing the same marine-derived resource. Three large (380-450 mm) and potentially lake-migrant fish were assigned to cluster 3, which is within the stream portion of the $\delta^{13}C$ range. This may arise if lake-migrant fish enter a stream mouth (where all three were sampled) and consume exclusively insects for an extended period of time before sockeye salmon begin spawning. These fish in addition to other lake-migrants potentially being incorrectly assigned to this group due to their heavy consumption of sockeye salmon eggs, are likely responsible for the slight consumption of lake benthic invertebrates estimated by the mixing model for cluster 3 that otherwise appears to be comprised primarily of stream-resident trout. Similarly, 10 small (< 125 mm) fish sampled in streams were assigned to clusters 1 and 2, which are within the lake portion of the $\delta^{13}C$ range. This may arise through stream-specific differences in invertebrate composition, and therefore isotopic signature, in addition to quick shifts in invertebrate isotopic signature (Gratton and Forbes 2006) due to assimilation of salmon-derived resources (Kline *et al.* 1990). Finally, it is important to note that our sampling in the lake was limited to the littoral zone in the vicinity of spawning salmon. Sampling in other littoral areas of the lake with beach seine nets over multiple years did not yield any rainbow trout (Harry Rich, Jr. and Thomas Quinn, unpublished data) so they seem concentrated around spawning salmon in late summer but we had no way to sample the deep, open water of this large lake.

Ecotype Prevalence and Tradeoffs

The prevalence of migratory rainbow trout may be due to limited food availability in streams (Pavlov and Savvaitova 2008; Pavlov *et al.* 2008) arising from both intra- and inter-specific competition. Partial migration enables portions of a population to utilize distinct habitats and food resources, which results in competitive release between conspecifics (Chapman *et al.* 2011). In the case of coastal river systems where habitat and prey resources are scarce, stream-resident or fluvial ecotypes may constitute a small proportion of the local rainbow trout population compared to the estuarine or fully anadromous forms (Pavlov *et al.* 2008; McPhee *et al.* 2014). The abundance of fish with lacustrine isotopic signatures suggests that the lake-migrant life history strategy is common among rainbow trout in the Iliamna Lake watershed. Stream-residency by rainbow trout may limit their maximum size due to potentially low energetic returns from drift-feeding (Dodrill *et al.* 2016), which is further exacerbated by numerous conspecifics and other species competing for the same prey and foraging territory.

Additionally, as drift-feeding fish such as salmonids grow, their energetic demands increase the needed territory size, so these small streams may not be able to support many large trout (Keeley and Grant 1995).

Outmigration after a year or more of stream rearing is characteristic of adfluvial salmonids (Nowak *et al.* 2004; Holecek and Scarnecchia 2013). Based on the smallest fish with a strongly benthic lacustrine δ^{13}C signature (-16.4), it appears that outmigration in Iliamna Lake begins at ~150 mm. This is consistent with the length-at-age for the youngest rainbow trout (age 2) in eight British Columbia lakes that, in terms of means, ranged from 128 – 215 mm (Nilsson and Northcote 1981). The change in habitat from stream to lake, and in life history type from resident to migratory (Zimmerman *et al.* 2003), may provide the newly adfluvial fish in Iliamna Lake with more abundant food resources enabling greater size for both sexes and, subsequently, increased fecundity for females and competitive ability on spawning grounds for males (Quinn 2005). While lake-migrant behavior exposes rainbow trout to predation from resident harbor seals *Phoca vitulina* Linnaeus, 1758 (Hauser *et al.* 2008), residence in small streams such as Russian and Roadhouse creeks (mean widths: 4.1, 4.3 m and depths: 0.14, 0.39 m) would also carry risk, as brown bears *Ursus arctos* Linnaeus, 1758 forage extensively on adult sockeye salmon and large trout would be vulnerable. Thus a combination of foraging opportunities and predation risk may drive the combination of fluvial and adfluvial patterns in this system.

Adfluvial Foraging Behavior

Adfluvial rainbow trout in Iliamna Lake relied upon benthic prey rather than fish prior to the onset of sockeye salmon spawning. In a study of 34 native rainbow trout populations across British Columbia, Keeley *et al.* (2005) found a large piscivorous morph exclusively in lakes

>10,000 ha in surface area also containing kokanee (nonanadromous sockeye salmon). Iliamna Lake is >260,000 ha and, while it contains no kokanee, it supports lake-rearing juvenile sockeye salmon, albeit at low densities (Rich *et al.* 2009), as potential prey. Yet, we documented only a single instance of piscivory. Russell (1977) similarly found a low frequency of occurrence of fish prey (pond smelt *Hypomesus olidus* Pallas, 1814 = 7%, sockeye salmon fry = 2%, threespine stickleback = 1%) when sampling rainbow trout returning to Lower Talarik Creek in the northwest portion of Iliamna Lake. However, at the outlet of the lake, Berejikian (1992) documented rainbow trout consuming sockeye salmon smolts, but only when smolts were migrating to the ocean in late spring. Although threespine sticklebacks, and coastrange *Cottus aleuticus* Gilbert, 1896 and slimy sculpins *Cottus cognatus* Richardson, 1836 are abundant in the littoral zone in mid to late summer (data not shown), rainbow trout predominantly consumed snails and amphipods, and secondarily insects, in the lake during that time. Predation on benthic prey besides aquatic insects and annelids is uncommon in rainbow trout, with exceptions occurring in introduced populations in Marion Lake, British Columbia, Canada (Efford and Mathias 1969), Lake Benmore, New Zealand (McCarter 1986) and both Flaming Gorge Reservoir and the Green River, Utah-Wyoming, USA (Haddix and Budy 2005; Vinson and Baker 2008). The consistent use of benthic resources in Iliamna Lake suggests that it is not merely a body of water that rainbow trout transit to find another stream or river in which to feed or spawn, but is itself significant to their foraging ecology and development as adfluvial fish (Huckins *et al.* 2008).

Adfluvial trout in other Bristol Bay lakes move tens of kilometers between streams to forage (Meka *et al.* 2003; Bentley *et al.* 2015). In the Wood River system, Bentley *et al.* (2015) documented 6-12 fold increases of resident fish densities (including rainbow trout) in late June and July in streams with spawning sockeye salmon. Adfluvial rainbow trout that enter streams prior to the arrival of sockeye salmon drift-feed on the available aquatic and terrestrial insects until spawning begins (Scheuerell *et al.* 2007) or reenter the lake and move between tributaries to locate higher densities of salmon (Eastman 1996; Ruff *et al.* 2011; Bentley *et al.* 2015). Bentley *et al.* (2015) suggested that the inter-tributary migrants in Lake Nerka did not feed in the lake and only used it as a migration corridor. However, a number of large adfluvial fish in Iliamna Lake entered streams in late summer still exhibiting lacustrine isotopic signatures, suggesting that either typically lacustrine trout enter streams to feed during salmon spawning season (Meka *et al.* 2003) or that intertributary-migrants thoroughly forage on benthic invertebrates while slowly transiting the large lake to the next stream.

In certain lake systems there are also sockeye salmon spawning on mainland beaches and, in the unique case of Iliamna Lake, island beaches as well (Blair *et al.* 1993) that allow adfluvial rainbow trout to take advantage of the salmon-subsidy within the lake. All beach spawning by sockeye salmon in Iliamna Lake occurs at the east end, yet there are large-bodied and apparently adfluvial rainbow trout populations tens of km farther west in the lake (Russell 1977), suggesting that beach spawning sockeye salmon may provide bonus resources but are not a prerequisite for adfluvial behavior. If in a given summer few salmon return to a particular stream, the growth rate of resident trout will be limited whereas adfluvial trout can take advantage of salmon resources in another stream or in lake habitats where sockeye salmon densities are high. The substantial use of salmon-derived resources by rainbow trout (Russell 1977; Kline *et al.* 1993; Scheuerell *et al.* 2007) highlights the importance of this subsidy to the development of both stream-resident and lake-migrant life history stages. The life history diversity of sockeye salmon spawning in streams, rivers, and along island and mainland beaches supports that of rainbow trout residing in or migrating to those heterogeneous habitats.

Interspecific Dietary Niche Comparisons

Stream-resident and adfluvial rainbow trout exhibited varying degrees of niche overlap with sympatric Dolly Varden and Arctic char. Rainbow trout and Dolly Varden co-occurring in tributaries to Iliamna Lake both primarily consumed aquatic and terrestrial insects, shifting almost exclusively to salmon-derived resources once they were available (Denton *et al.* 2009; Denton *et al.* 2010; Jaecks and Quinn 2014). In contrast, both rainbow trout and Arctic char in Iliamna Lake (often caught simultaneously) consumed snails and sockeye salmon eggs, but rainbow trout also ate amphipods and insects while Arctic char ate sticklebacks and other fishes (Denton *et al.* 2010; Woods *et al.* 2013). In the Iliamna Lake watershed, stream-resident rainbow trout and Dolly Varden broadly overlapped in trophic niche whereas adfluvial rainbow trout and Arctic char only partially overlapped, suggesting that the former pair experiences a greater degree of interspecific competition for resources in their shared, confined habitat. This potential disparity in interspecific competition would favor the migration of rainbow trout from streams into the lake where more diverse prey are available.

Our study, confined to a single lake, could not capture the full range of foraging opportunities for rainbow trout. Foraging in lakes is likely affected by physical features such as thermal stratification, bathymetry, and shoreline development, and by biotic features such as the prey, competitor, and predator communities. Such diverse factors affect the development of multiple morphs of Arctic char in Iceland, for example (Woods *et al.* 2012). Nevertheless, the results from only one section of this lake revealed aspects of rainbow trout ecology that may occur elsewhere, and the similarities and differences in rainbow trout differentiation in other lakes can be contrasted to those found in Iliamna Lake.

Conclusion

Adfluvial behavior represents an understudied but important migratory alternative, along with the more widely-studied stream-resident and anadromous forms, exhibited by rainbow trout (Holecek and Scarnecchia 2013). Migration into lakes and utilization of lacustrine resources (as distinguished from movement between streams flowing into a lake) is a widespread salmonid pattern (Gresswell *et al.* 1994; Olsson and Greenberg 2004; Robillard *et al.* 2011), but many river systems occupied by rainbow trout do not have lakes and therefore the adfluvial ecotype is not always present. Such life history diversity increases long-term population productivity and stability for species utilizing a variety of environmentally variable habitats (Schindler *et al.* 2010). The ecotypic composition of rainbow trout in Iliamna Lake and others has been pondered for decades (Behnke 1972), and in this study we documented the ecological segregation and trophic specialization of rainbow trout occupying stream and lake habitats. Both of these ecotypes heavily rely upon the annual sockeye salmon subsidy, suggesting the possibility for further divergence in the absence of this temporary superabundance of food. Future work describing adfluvial versus stream-resident trout should assess divergence in length-at-age, morphology, and adaptive genetic expression to better understand the evolutionary history and trajectory of distinct rainbow trout ecotypes.

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TABLES

Table 1 – Mean proportion (by number) of different taxa in the rainbow trout (*Oncorhynchus mykiss*) diets (n = 55 total) in each of three habitats and NMDS results. MDS1 and 2 are the variable loadings on each derived axis and r^2 is the coefficient of determination for the linear correlation of each diet category as a function of the axis scores. Significant diet categories are those explaining the majority of the variance among fish. Significance levels are designated as follows: <0.05 (*), <0.01 (**), <0.001 (***).

	Mean Proportion by Habitat			NMDS Results		
Diet Category	Stream	Stream Mouth	Lake	MDS1	MDS2	r^2
Simuliidae larvae	0.338	0.018	0.010	-0.462	-0.887	0.211**
Simuliidae pupae	0.009	0.018	0.000	0.246	-0.969	0.007
Simuliidae adults	0.248	0.062	0.072	0.046	-0.999	0.328***
Chironomidae larvae	0.062	0.000	0.047	0.992	-0.126	0.015
Chironomidae pupae	0.016	0.000	0.139	-0.921	0.389	0.064
Chironomidae adult	0.058	0.136	0.027	0.741	-0.672	0.071
Plecoptera nymphs	0.033	0.000	0.000	0.264	-0.964	0.052
Plecoptera adults	0.139	0.000	0.000	0.189	-0.982	0.056
Ephemeroptera nymphs	0.042	0.419	0.000	0.992	0.130	0.231**
Trichoptera larvae	0.032	0.031	0.024	-0.181	0.983	0.069
Trichoptera adults	0.002	0.000	0.039	-0.722	0.692	0.013
Hymenoptera adults	0.020	0.025	0.033	-0.082	0.997	0.087
Hydracarina	0.014	0.000	0.045	-0.043	-0.999	0.199***
Unidentified insects	0.072	0.291	0.309	0.623	0.782	0.583***
Aquatic snails	0.040	0.000	0.183	-0.913	0.408	0.619***
Amphipods	0.000	0.000	0.072	-0.705	0.710	0.116*

Table 2 – Cluster assignment of rainbow trout (*Oncorhynchus mykiss*) sampled in stream, stream mouth, and lake habitats based on their dual isotope ($\delta^{15}N$ and $\delta^{13}C$) signatures. Fork length (mean +/- 1 standard deviation for each cluster) is provided; superscripts indicate clusters that did not differ significantly based on Kruskal-Wallis post-hoc multiple comparisons.

	Habitat				
Cluster	Stream	Stream Mouth	Lake	Cluster Total	Fork Length (mm)
1	40	5	19	64	313 +/- 124[a]
2	28	12	58	98	273 +/- 91[a]
3	46	3	3	52	187 +/- 85[b]
4	9	0	0	9	151 +/- 31[b]
Habitat Total	123	20	80		

Table 3 – Diet contribution estimates from Bayesian mixing models (MixSIAR) of the dual isotope ($\delta^{15}N$ and $\delta^{13}C$) data for the four clusters of rainbow trout (*Oncorhynchus mykiss*). Medians (5th-95th percentiles in parentheses) of the posterior end member contributions are shown.

	Diet End Members		
Cluster	Stream Aquatic Invertebrates/ Hymenopterans	Sockeye Salmon Eggs	Lake Benthic Invertebrates
1	0.021 (0.003-0.056)	0.562 (0.500-0.615)	0.414 (0.366-0.469)
2	0.232 (0.145-0.334)	0.165 (0.035-0.268)	0.603 (0.526-0.690)
3	0.249 (0.186-0.335)	0.646 (0.552-0.723)	0.104 (0.028-0.173)
4	0.912 (0.366-0.988)	0.075 (0.005-0.392)	0.008 (0.000-0.227)

FIGURES

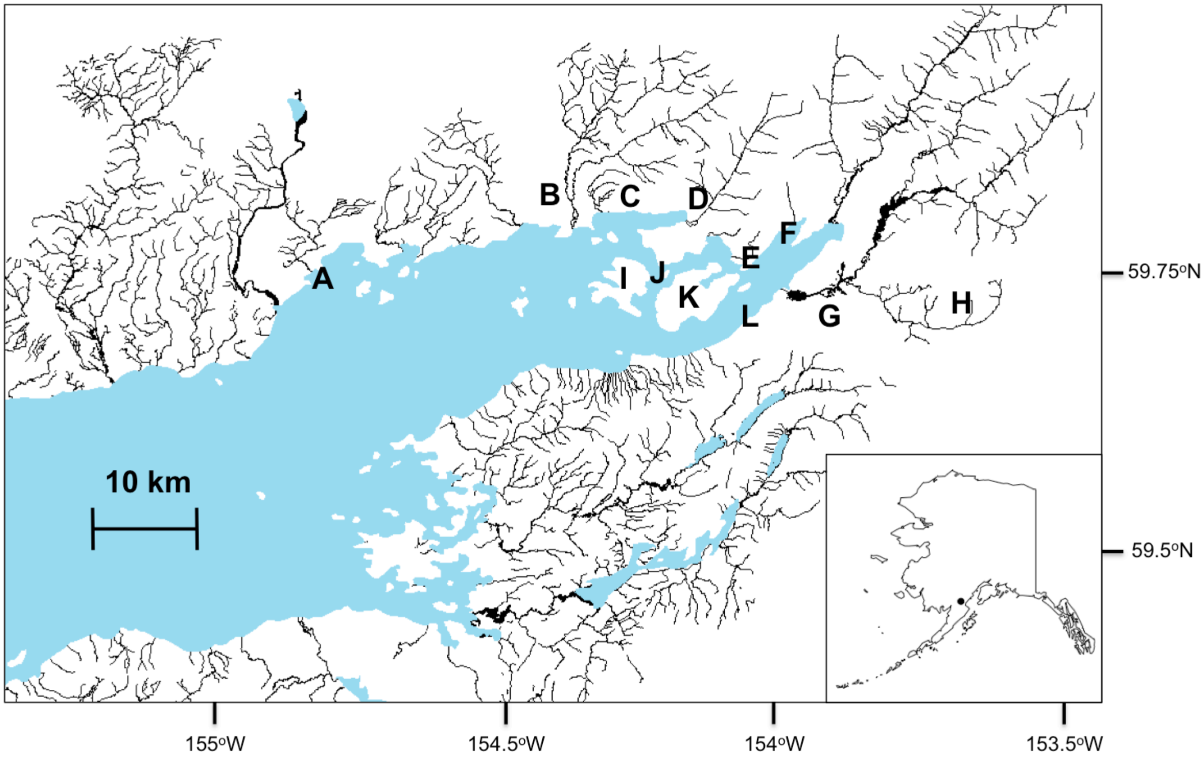

Figure 1 – Iliamna Lake (east end) map. The location of the lake in southwest Alaska is marked on the inset state map. Letters indicate sampling sites: A – Roadhouse Creek, B – Canyon Creek, C – Mink Creek, D – Knutson Creek, E – Russian Creek, F – Lonesome Bay Creek, G – Iliamna River, H – Chinkelyes Creek, I – Woody Island, J – Flat Island, K – Porcupine Island, L – Finger Bay. Certain stream features have been removed to clarify the location of the sampling sites. Colour version online.

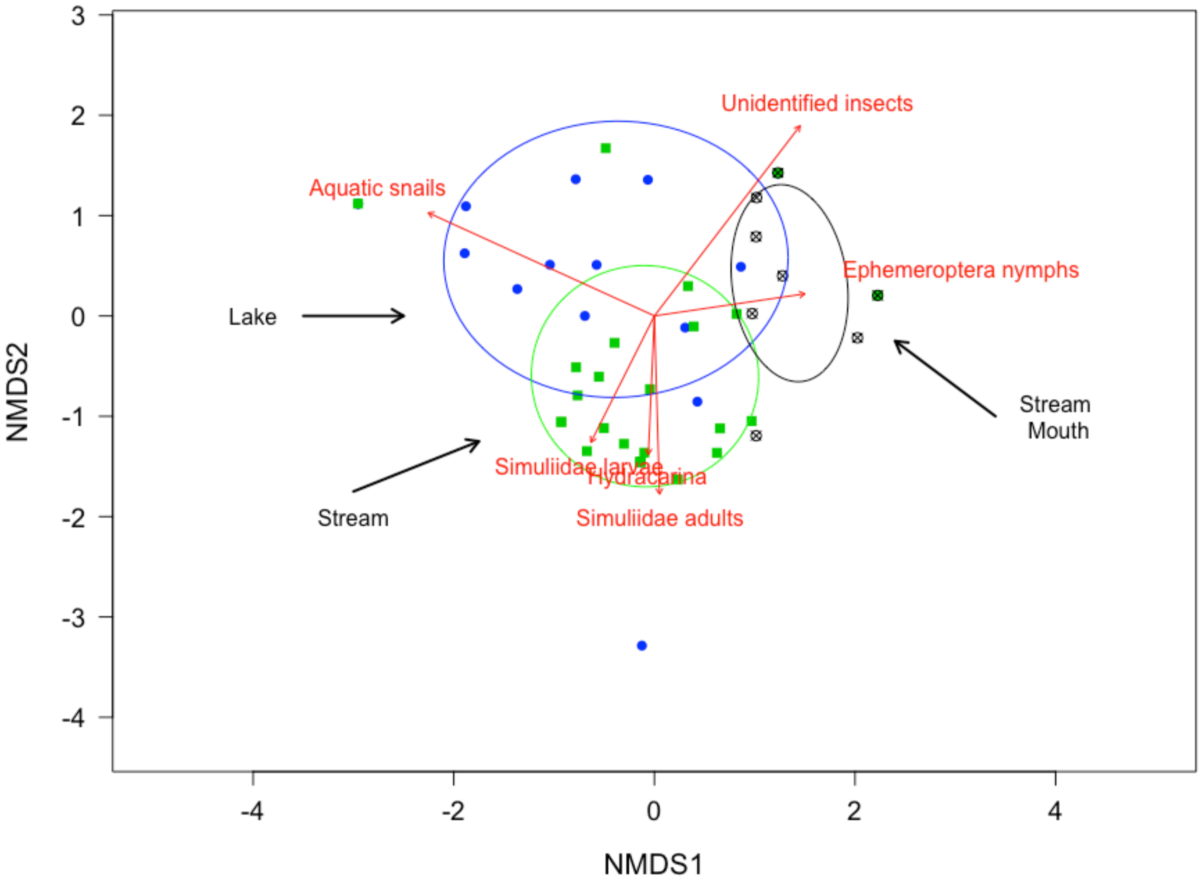

Figure 2 – Biplot of NMDS 1 and 2 for diets of rainbow trout (*Oncorhynchus mykiss*) sampled in different habitats. Individual fish and the ellipse (CI = 0.50) for each habitat group are color and symbol coded: stream (green, filled square), stream mouth (black, empty crossed circle), lake (blue, filled circle). Significant diet items (those explaining the majority of the variance among fish) and their vector loadings (Table 1) are indicated in red. Colour version online.

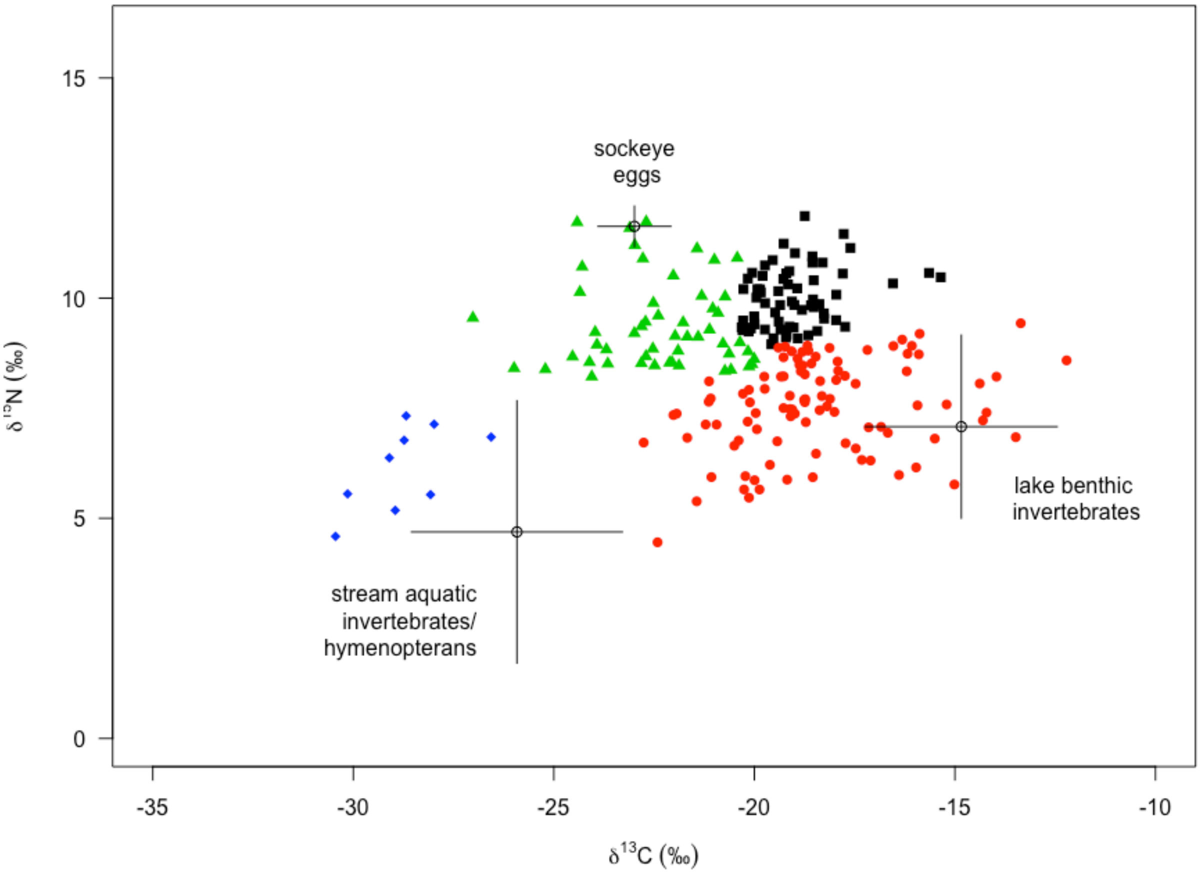

Figure 3 – Biplot of δ^{15}N and δ^{13}C for rainbow trout (*Oncorhynchus mykiss*) sampled in stream, stream mouth, and lake habitats. Consumer δ^{15}N and δ^{13}C values are decreased by 3.40 and 0.39, respectively, to account for fractionation and better present the consumer values relative to the isotopic polygon defined by the end members and their variances. Individual fish are color and symbol coded by cluster assignment: 1 (red, circle), 2 (black, square), 3 (green, triangle), 4 (blue, diamond). Diet end member values (mean +/- 1 SD) are included. Colour version online.

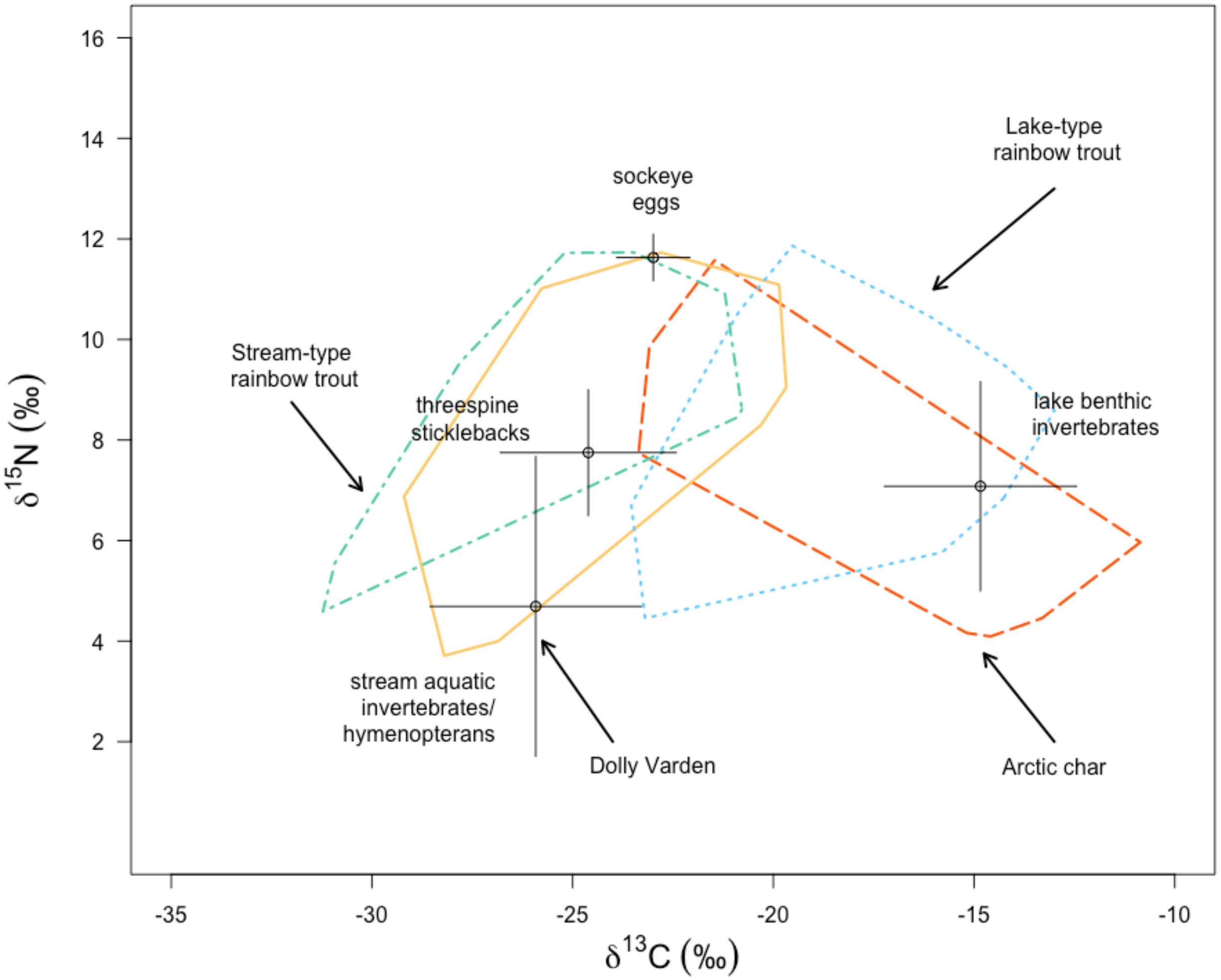

Figure 4 – Biplot of $\delta^{15}N$ and $\delta^{13}C$ for rainbow trout (*Oncorhynchus mykiss*), Dolly Varden (*Salvelinus malma*), and Arctic char (*Salvelinus alpinus*). Consumer $\delta^{15}N$ and $\delta^{13}C$ values are decreased by 3.40 and 0.39, respectively, to account for fractionation and better present the consumer values relative to the isotopic polygon defined by the end members and their variances. Convex hulls for each species and rainbow trout ecotype are color and line coded: Dolly Varden (orange, solid), Arctic char (red, long dash), stream-type rainbow trout (clusters 3 and 4; green, dash dot), lake-type rainbow trout (clusters 1 and 2; blue, short dash). Diet end member values (mean +/- 1 SD) relevant to each species and rainbow trout ecotype are included. The data for threespine sticklebacks (*Gasterosteus aculeatus*) come from Denton *et al.* (2010), but are not lipid-normalized here. Colour version online.

CHAPTER 2

Retention of a chromosomal inversion from an anadromous ancestor provides the genetic basis for alternative freshwater ecotypes in rainbow trout

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ABSTRACT

Migratory behavior patterns in animals are controlled by a complex genetic architecture. Rainbow trout (*Oncorhynchus mykiss*) is a salmonid fish that spawns in streams but exhibits three primary life history pathways: stream-resident (fluvial), lake-migrant (adfluvial), and ocean-migrant (anadromous). Previous studies examining fluvial and anadromous *O. mykiss* have identified several genes associated with life history divergence including the presence of an inversion complex within chromosome 5 (Omy05) that appears to maintain a suite of linked genes controlling migratory behavior. However, adfluvial trout are migratory without being anadromous, and the genetic basis for this life history has not been investigated from evolutionary perspectives. We sampled wild, native nonanadromous rainbow trout occupying connected stream and lake habitats in a southwest Alaskan watershed to determine if these fish exhibit genetic divergence between fluvial and adfluvial ecotypes, and if that divergence parallels that documented in fluvial and anadromous *O. mykiss*. Data from restriction site-associated DNA (RAD) sequencing revealed an association between frequencies of both the Omy05 inversion complex and other single nucleotide polymorphisms (SNPs) with habitat type (stream or lake), supporting the genetic divergence of fluvial and adfluvial individuals in

sympatry. The presence of a genetic basis for migration into lakes, analogous to that documented for anadromy, indicates that the adfluvial ecotype must be recognized separately from the fluvial form of *O. mykiss* even though neither is anadromous. These results highlight the genetic architecture underlying migration and the importance of chromosomal inversions in promoting and sustaining intraspecific diversity.

INTRODUCTION

Migration is a vital and characteristic behavior in diverse animal taxa, enabling them to exploit superior rearing and breeding sites when environmental conditions are most favorable (Baker 1978; Dingle 1996). Migratory behavior varies among individuals and populations (Liedvogel *et al.* 2011), often as partial migration whereby certain individuals migrate and others remain resident (Chapman *et al.* 2011a). There is a significant genetic component to the variation in migratory behavior (Liedvogel *et al.* 2011), and migrants often develop different phenotypes from residents (Jonsson and Jonsson 1993). Environmental conditions including food availability (Olsson *et al.* 2006), density-dependence (Marco-Ruis *et al.* 2013), and predation risk (Chapman *et al.* 2011b) may also influence whether individuals or populations tend to migrate or remain resident (Chapman *et al.* 2011a). Genetic and environmental components influencing migration may interact in the form of conditional strategies, whereby a specific threshold to migration is inherited (e.g., size or body condition), and the environmental conditions not only exert selection pressure on the threshold trait itself but also affect the likelihood of an organism surpassing that threshold (Pulido 2011; Phillis *et al.* 2016).

Salmonid fishes exhibit a variety of migration behaviors including fluvial (stream-resident or migratory within river systems), adfluvial (migrating between streams and lakes), and anadromous (migrating between freshwater and marine habitats) life histories (Quinn 2018). The prevalence of partial migration varies within and among populations and among species (Jonsson and Jonsson 2011; Quinn 2018), but some species of the genera *Oncorhynchus*, *Salmo*, and *Salvelinus* exhibit all three life histories (e.g., *Oncorhynchus clarkii*, *O. masou*, *O. mykiss* – Christie 1970; Quinn and Myers 2004; *Salmo trutta* – Klemetsen *et al.* 2003; *Salvelinus confluentus*, *S. leucomaenis, S. malma* – Dunham *et al.* 2008).

Rainbow trout (*O. mykiss*) are native to Pacific Ocean drainages from northwest Mexico to western Alaska and the Kamchatka Peninsula of eastern Russia (Behnke 1992), and almost invariably spawn in streams where embryos incubate in gravel redds. Fry emerge and feed in the stream for a variable period of time before reproducing there or, alternatively, migrating to a lake or the ocean where they feed further prior to returning to their natal stream to spawn. The limited available information indicates that rainbow trout migrating to lakes exhibit similar physiology, coloration, and behavior to smolts entering the ocean (Holecek *et al.* 2012). Additionally, adfluvial rainbow trout exhibit lake-specific morphologies (Keeley *et al.* 2005) and divergent size-at-age, age-at-maturity, and trophic ecology from sympatric stream-residents (Holecek and Scarnecchia 2013; Arostegui and Quinn 2018). However, adfluvial rainbow trout are understudied in comparison to the anadromous (steelhead) and fluvial variants, particularly in the extent to which the genetic differentiation between fluvial and adfluvial fish parallels that between fluvial and anadromous rainbow trout/steelhead.

Comparisons of anadromous and fluvial *O. mykiss* have identified many quantitative trait loci (Nichols *et al.* 2008; Le Bras *et al.* 2011; Hecht *et al.* 2012; Hecht *et al.* 2015) and other loci under selection throughout the genome (Hale *et al.* 2013; Hecht *et al.* 2013) associated with life history variation. Divergence in gene expression (Hecht *et al.* 2014; McKinney *et al.* 2015) and epigenetic regulation (Baerwald *et al.* 2016) have also been documented. Most notably, there is suppressed recombination within chromosome 5 (hereafter referred to as Omy05 – Phillips *et al.* 2006) due to the presence of a chromosomal double-inversion maintaining a suite of linked genes controlling migratory behavior in *O. mykiss* (Pearse *et al.* 2018). Genetic studies of lake-migrant rainbow trout have been limited to assessments of local adaptation and drift of sympatric adfluvial populations (Wellband and Heath 2013a,b), and genomic variation and population structure of artificially adfluvial (and often hatchery introgressed) fish occupying reservoirs above dams (Pearse *et al.* 2014; Pearse and Garza 2015; Leitwein *et al.* 2017).

The ecological divergence of fluvial and adfluvial trout implies heritable variation but, to our knowledge, no previous study has evaluated the genetic divergence of these sympatric life history forms in a natural system. We sampled wild, native nonanadromous rainbow trout occupying connected stream and lake habitats in a southwest Alaskan watershed to determine if fluvial and adfluvial fish exhibit genetic divergence and, if so, whether their divergence is parallel to that documented among fluvial and anadromous *O. mykiss*. Single nucleotide polymorphism (SNP) data from restriction site-associated DNA (RAD) sequencing identified both the Omy05 inversion and other outlier loci associated with migratory behavior, supporting the genetic differentiation of adfluvial and fluvial individuals in sympatry.

METHODS

Study System and Sampling

Anadromous *O. mykiss* are absent from Bristol Bay drainages in southwest Alaska (Behnke 1992), but fluvial and adfluvial rainbow trout are common and widely distributed (Meka *et al.* 2003; Schwanke and Hubert 2003). We sampled rainbow trout from Iliamna Lake, which drains into Bristol Bay via the Kvichak River. Iliamna Lake is the largest lake in Alaska with a surface area of 2622 km^2, volume of 1151 km^3, and maximum depth over 300 m (Burgner *et al.* 1969). An entirely native fish fauna is present in the watershed (Bond and Becker 1963), and there are protective fishing regulations for rainbow trout, no history of habitat alteration, hatchery propagation, or transplantation. The intact nature of the ecosystem makes Iliamna Lake and its associated tributaries an ideal area in which to study the life history diversity of nonanadromous rainbow trout.

Rainbow trout were sampled in July-August at two tributary streams, to capture putatively fluvial fish, and one lake site, to capture putatively adfluvial fish, in the eastern half of Iliamna Lake (32 individuals per site) (Fig. 1). Stream collections occurred in 2015 at Russian Creek, a high gradient montane stream, and in 2016 at Roadhouse Creek, a low gradient wetland stream. Russian Creek has an approximately 1 m tall waterfall near its connection to the lake – but this feature does not constitute a complete barrier to migration because sockeye salmon spawn upstream – and Roadhouse Creek has no such feature. Sampling in Russian Creek occurred 1.1-2.8 km upstream of the lake; sampling in Roadhouse Creek occurred 0.3-1.4 km upstream of the lake. The lake collection occurred in 2016 at Woody Island, a foraging area for adfluvial rainbow trout (Arostegui and Quinn 2018), which is 11.5 km west of Russian Creek and 31.5 km east of Roadhouse Creek. The mouths of Russian and Roadhouse creeks are ~43 km apart. Rainbow trout in the Iliamna Lake system spawn in streams, but fish representing a wide range of sizes and ages occur simultaneously in both lake and stream habitats during the summer (Arostegui and Quinn 2018; Martin C. Arostegui, unpublished data). Seining in littoral areas of the lake over multiple years yielded no rainbow trout fry (Harry Rich Jr. and Thomas Quinn, unpublished data) and the estimated minimum size at lake entry is 150 mm (Arostegui and Quinn

2018). Rainbow trout captured at foraging areas in the lake are, by definition, adfluvial. In contrast, rainbow trout captured in streams may include lifelong fluvial fish and individuals that will eventually migrate to the lake, but we cannot determine whether or not any individual trout will migrate to the lake later in life.

Rainbow trout were captured with a combination of hook-and-line fishing and seining techniques. Fish were held in a solution of AQUI-S® anesthetic for 1-3 minutes until unresponsive to handling, measured for fork length (mm), and a tissue sample was taken from the lower lobe of the caudal fin and preserved in 95% ethanol. Fish were recuperated in freshwater and released at their site of capture. Sampling permits were obtained from the Alaska Department of Fish and Game and collection protocols were approved by the University of Washington's Institutional Animal Care and Use Committee.

RAD Sequencing

DNA was extracted using DNeasy (Qiagen, USA) following manufacturer's protocol. RADseq libraries were prepared using the modification of the RAD protocol described by Ali *et al.* (2016). DNA was digested with the *SbfI* enzyme and randomly sheared and size selection was done with the NEBNext kit using AMPure XP beads with a target insert size of 300-400bp; all individuals were uniquely barcoded. Sequencing was conducted on two lanes of an Illumina HiSeq 4000 with 96 individuals per lane and 100 bp paired-end reads. An initial round of sequencing was conducted after which samples were demultiplexed using the *process_radtags* module from *Stacks* version 1.46 (Catchen *et al.* 2013) to obtain the number of sequence reads per individual. A round of resequencing was then conducted where the proportion of DNA for each individual was adjusted for a targeted yield of 5 million total sequence reads per individual.

For both rounds of sequencing, default settings were used for *process_radtags* with the following exceptions: -c -q -r --filter_illumina -t 90.

Data Processing, Locus Filtering, and Genome Alignment

Sequence reads for each individual were processed through *Stacks* to obtain genotypes. Default settings were used for all *Stacks* modules with the following exceptions: *ustacks:* --model_type bounded --bound_high 0.01 -M 2 --gapped, *cstacks* -n 2. The *Stacks* catalog of loci and genetic variation was created using all samples. After running *Stacks*, individuals and loci were filtered to obtain the final data set. Individuals were ranked by genotype rate; retained individuals had genotype rates no lower than three percentage points below the population average. Following removal of low-quality individuals, loci with a genotype rate less than 80% were removed.

The filtered data were then run through *Genepop* version 4.1.0 (Rousset 2008) to obtain allele frequency and F_{ST} estimates. Loci with a minor allele frequency (MAF) of less than 5% were removed as these are likely uninformative for population genetic analysis (Roesti *et al.* 2012). Retained loci were then run through *HDplot* (McKinney *et al.* 2017) to identify paralogs, which are prevalent in the salmonid genome as a result of an ancestral whole-genome duplication (Ohno 1970; Macqueen and Johnston 2014). Paralogs were excluded from analyses of population structure due to genotyping uncertainty caused by insufficient read-depth (McKinney *et al.* 2018). Singleton (non-paralog) loci that passed genotype rate and minor allele frequency filters were aligned to the rainbow trout genome (v_1.0, NCBI: GCA_002163495.1) using bowtie2 (Langmead and Salzberg 2012) with end-to-end alignment.

Identifying Genome Inversion

Genomic inversions inhibit recombination, resulting in elevated linkage disequilibrium (LD), and should appear as regions of high LD within a chromosome. Pairwise LD between loci was estimated using the r-squared method in *Plink* (v1.07, Purcell *et al.* 2007). LD was visualized for each chromosome as a heatmap (R Development Core Team 2008). Genotypes for loci underlying regions of high LD were then visually examined to confirm the presence of the inversion complex identified by Pearse *et al.* (2018). Loci within the double-inversion were aligned against those of Pearse *et al.* (2014) to determine if any overlapped. Alleles for overlapping loci were compared to determine which haplotypes represented the ancestral (non-inverted) and rearranged (inverted) forms.

Admixture

We tested for admixture, with the 'snmf' function from the 'LEA' package for R using default parameters (repetitions = 10) (Frichot and Francois 2015), to determine if the rainbow trout from our three sampling sites were mixtures of populations. The 'snmf' function provides equally accurate ancestry coefficient outputs as the commonly used program *ADMIXTURE* but is computationally more efficient (Frichot *et al.* 2014). We found the Omy05 inversion (see Results: *Genomic Inversion*), so the admixture analysis was conducted twice, once including the loci within the Omy05 inversion and once without those loci, to determine if the inversion affected the estimated number of genetic clusters. Pairwise F_{ST} between populations was calculated with the method of Weir and Cockerham (1984) in *Genepop* (Rousset 2008).

Where substructure was present at a sampling site, relatedness was assessed to determine if the substructure was attributable to incidental sampling of families. Relatedness was estimated according to Ritland (1996), which makes no assumption of an outbred population (Wang 2017). Estimations were conducted with the *related* package in R (Pew *et al.* 2015) using non-outlier loci excluding those within the Omy05 inversion. Related individuals were retained to avoid biasing allele frequency and F_{ST} (Waples and Anderson 2017).

Identification, Annotation, and SNP Synonymy of Outlier Loci

Outlier loci were identified with *LFMM* version 1.6 and *Bayenv2*, both of which allow for testing of association between loci and environmental variables (Frichot *et al.* 2013; Günther and Coop 2013). In both programs, we incorporated the habitat where the rainbow trout were captured as an environmental variable in a binary format (stream = 0, lake = 1), following the procedure used by Bernatchez *et al.* (2016) for testing differentiation between "piscivorous" and "planktivorous" ecotypes of lake trout. The *LFMM* analysis was conducted twice, once with all loci and again with all loci excluding those within the Omy05 inversion, to assess the similarity of the outlier test results. The 'snmf' admixture results informed the number of genetic clusters in the *LFMM* analyses (K = 4, with and without the Omy05 inversion; see Results: *Admixture*). Default parameters were used (repetitions = 10), and the false discovery rate was controlled by multiple test correction (Benjamini and Hochberg 1995) as recommended by Frichot and François (2015). The *Bayenv2* analysis was similarly conducted twice, with all loci and then excluding those within the Omy05 inversion, and utilized the average of five independent runs (100000 iterations each) in both cases, as recommended by Blair *et al.* (2014). Allele frequencies of all loci excluding those within the Omy05 inversion were used to calculate a covariance matrix between populations that was used in the *Bayenv2* analysis; due to substructure within Roadhouse Creek this population was split into groups A and B and excluded a potential hybrid individual that could not clearly be assigned to either group (see Results: *Admixture*). Outliers were then identified as those SNPs occurring in the top 5% of the distribution for both Bayes factor and Spearman's ρ, as suggested by Günther and Coop (2013).

Outlier loci were annotated by comparing genome alignments with the positions of genes within the rainbow trout genome. CDS sequence from the rainbow trout genome was obtained from NCBI RefSeq: GCF_002163495.1. Outlier loci that occurred within a gene were then aligned to the CDS sequence for that gene to determine if the locus occurred in the coding or non-coding region of the gene; loci were given an annotation if they occurred within the coding region. If a locus occurred within the coding region of a gene, new variants of the CDS sequence were made to represent the allelic variation for each SNP. Open reading frames for these sequences were predicted with *OrfM* (v0.7.1, Woodcroft *et al.* 2016). These CDS allelic variants were then translated to protein sequence to determine if SNPs were synonymous or non-synonymous. We predicted 3'-untranslated region (UTR) regulatory elements to assess proximity to outlier loci using the program *UTRscan* (Grillo *et al.* 2010) for genes of interest.

Individual-Based Analysis

Individual-based principal component analyses (PCAs) were conducted with: 1) non-outlier SNPs identified when including the Omy05 inversion (n = 21492), 2) non-outlier SNPs identified when excluding the Omy05 inversion (n = 20623), 3) outlier SNPs identified when including the Omy05 inversion (n = 1442), and 4) outlier SNPs identified when excluding the Omy05 inversion (n = 1302) to assess structure at non-outlier loci, dissimilarity at outlier loci, and the effect of the Omy05 inversion on both. PCAs were conducted in R with *Adegenet* (Jombart 2008) and utilized the results of the *LFMM* outlier test.

RESULTS

RAD Sequencing and Genome Alignment

RAD sequence data were obtained from 88 individuals after filtering for read-depth (Woody Island: n = 28; Roadhouse Creek: n = 31; Russian Creek: n = 29). High-quality DNA from these fish yielded over 617 million reads, with a per individual read-depth that averaged > 6.7 million in each population (Table 1). Genotype-rate and MAF- filtering, in addition to removal of paralogous loci (duplicates and diverged duplicates), yielded 22934 singleton SNPs suitable for analysis (Table 2). A total of 19382 of the 21194 RAD tags (91%) that passed genotype rate and minor allele frequency filters aligned to a single position in the rainbow trout genome.

Genomic Inversion

Chromosome Omy05 contained a ~54 Mb region of high LD (Fig. 2), consistent with the location and size of the Omy05 inversion associated with life history variation in rainbow trout/steelhead in California and Oregon (Pearse *et al.* 2018). A total of 1009 SNPs (726 RAD tags) were contained within this region, 657 SNPs (511 RAD tags) of which had an LD of 1 indicating complete linkage. A total of 17 markers from this study aligned to those of Pearse *et al.* (2014) and contained the same SNP (Table S1). The most common haplotype in our dataset was the rearranged form of Omy05 (87.5%), and the least common was the ancestral form (12.5%). Omy05 rearranged/ancestral haplotype frequencies varied by sampling site – Woody Island (63.0%/37.0%), Roadhouse Creek (98.4%/1.6%), and Russian Creek (98.3%/1.7%). We found no evidence for an inversion on any of the other chromosomes.

Admixture

Of the 22934 SNPs that passed filtering criteria, 1369 exhibited a global $F_{ST} \geq 0.25$ with a maximum of 0.72 among sampling sites (Fig. 3). The 'snmf' admixture analyses revealed that four genetic clusters (K = 4) was either the highest likelihood solution (when excluding loci within the Omy05 inversion) or one of the two highest, nearly equal likelihood solutions (when using all loci). Downstream analysis revealed two clusters among fish sampled in Roadhouse Creek, suggesting substantial structure at non-outlier loci (see *Individual-Based Analysis*, Fig. 4b) and clarifying the admixture result of four genetic clusters sampled from three study sites. Thus, we divided Roadhouse Creek individuals into two groups (Roadhouse Creek A: PC2 > 50, n = 11; Roadhouse Creek B: PC2 < 10, n = 19), with one potential hybrid excluded (PC2 = 28.6). Pairwise F_{ST} was calculated for four groups: 1) Woody Island, 2) Russian Creek, 3) Roadhouse Creek A, and 4) Roadhouse Creek B. Notable structure was present among all four groups with Russian Creek consistently being the most genetically divergent (Table 3).

Within Roadhouse Creek A, the Ritland estimation of relatedness revealed two groups of potentially related individuals plus a single unrelated individual. Within Roadhouse Creek B, the estimation revealed five groups of potentially related individuals plus seven unrelated individuals (Fig S1).

Identification, Annotation, and SNP Synonymy of Outlier Loci

LFMM revealed 1443 outlier SNPs when including the loci within the Omy05 inversion, and 1302 outlier SNPs when excluding the loci within the Omy05 inversion, 1203 SNPs of which overlapped. Combining results from the two *LFMM* analyses yielded 1541 unique outlier

SNPs. *Bayenv2* revealed 58 outlier SNPs when including the loci within the Omy05 inversion, and 66 outlier SNPs when excluding the loci within the Omy05 inversion, none of which overlapped. Combining results from the two *Bayenv2* analyses yielded 124 unique outlier SNPs, nine of which overlapped with those identified by *LFMM*. Minimally overlapping results from these two outlier programs has been documented in empirical studies (e.g., Nadeau *et al.* 2016) and may be due to various factors including how population structure is controlled for, differences in power, false discovery rate, and false positive rate (de Villemereuil *et al.* 2014), and that the unit of analysis in *LFMM* is the individual whereas in *Bayenv2* it is the population (Lotterhos and Whitlock 2015). Combining the *LFMM* and *Bayenv2* outputs yielded 1656 unique outlier SNPs, 1472 (89%) of which aligned to a chromosome. Of the aligned outlier SNPs, 18% were located on Omy05, whereas only 1-5% were located on each of the other 28 chromosomes (Fig. S2).

Of the 1656 unique outlier SNPs combined from the *LFMM* and *Bayenv2* outputs (plus an additional 18 non-outlier SNPs that occurred within outlier genes), we eliminated those that could not be aligned to the genome, were within transposable elements, were synonymous, or were nonsynonymous but not annotated, leaving 33 nonsynonymous and annotated SNPs. These 33 SNPs included genes involved in osmoregulation, immune response, eye development/vision, cardiac development/contraction, nervous system development, lipid/fatty acid metabolism, spermatogenesis, bone formation, mRNA export/nuclear pore assembly, microtubule organization/mitotic progression, homologous recombination, autophagosome assembly, calcium ion bonding, iron ion binding, and DNA binding (Tables 4 and S2). Five of the 33 SNPs were located within the Omy05 inversion complex and exhibited high LD with pairwise r^2 values $\geq$ 0.95 (corresponding genes: *CAMSAP1B*, *RAI14*, *PATJ*, *TPR*, *ZNF644*). We also found an outlier locus with seven SNPs located in the 3'-UTR of a gene associated with osmoregulation (*PLEKHH2* - Patrakka *et al.* 2007; Perisic *et al.* 2012). The *PLEKHH2* locus was within 30 bp of a GY-box, a regulatory element known to affect gene expression (Kritikou 2005; Moncini *et al.* 2007).

Individual-Based Analysis

The stream- and lake-caught rainbow trout were divergent at non-outlier loci. Fish from Russian Creek were dissimilar from lake-caught and from Roadhouse Creek fish, and the Roadhouse Creek fish exhibited substructure suggesting two separate spawning populations (Fig. 4a). Exclusion of the non-outlier loci within the Omy05 inversion resulted in increased within-group similarity for all three sampling sites, although the substructure at Roadhouse Creek remained (Fig. 4b). Outlier individuals were present at Woody Island, as was expected for a sampling site in the lake where adfluvial trout originating from separate tributary populations could co-occur.

Ordination of outlier loci revealed distinct clusters of rainbow trout differentiated by their status as rearranged homozygotes, heterozygotes, or ancestral homozygotes for the Omy05 inversion (Fig. 4c). Rainbow trout sampled in the lake exhibited all three inversion genotypes (rearranged homozygote: n = 11, heterozygote: n = 12, ancestral homozygote: n = 4), whereas those sampled in Roadhouse and Russian creeks were all rearranged homozygotes except for one heterozygote in each stream. Exclusion of the outlier loci within the Omy05 inversion resulted in collapse of the inversion-driven structure, yielding three distinct clusters by sampling site (Fig. 4d). Within Roadhouse Creek, subpopulations A and B exhibited differentiation at outlier loci.

DISCUSSION

Nonanadromous rainbow trout in the Iliamna Lake system exhibited differentiation at outlier and non-outlier loci between lake- and stream-caught populations, populations in two different streams, and subpopulations within a stream despite the absence of complete physical barriers to movement. In addition, fish occupying distinct habitat types exhibited disparate haplotype frequencies of a chromosomal inversion. This highlights the potential for disparate selection pressures between and within habitats to facilitate population divergence and local adaptation (Maan and Seehausen 2011); these processes may be facilitated by the reduced recombination of co-adapted alleles that occurs within chromosomal inversions (Hoffman and Rieseberg 2008). The presence of genetic differentiation associated with migration into lakes, parallel to that documented for anadromy (e.g., Hale *et al*. 2013; Pearse *et al.* 2014), indicates that the adfluvial ecotype is a migratory alternative distinct from the fluvial form even though neither is anadromous. Thus, these results from *O. mykiss* suggest a shared genetic basis for migration in general (to lakes or the ocean) rather than the commonly discussed differentiation of anadromy versus nonanadromy.

The difference in frequency of the rearranged Omy05 haplotype between stream- and lake-caught rainbow trout, being nearly fixed among the former and less common among the latter, provides evidence for the divergence of fluvial and adfluvial ecotypes and further supports the characterization of this expansive block of linked and co-adapted alleles as a region exerting control over migratory behavior (Nichols *et al.* 2008; Miller *et al.* 2012; Pearse *et al.* 2014; Leitwein *et al.* 2017). Chromosomal inversions support genetic differentiation of alternative life history forms or ecotypes of diverse plant and animal taxa including monkey flower (*Mimulus guttatus* – Twyford and Friedman 2015), Hall's panicgrass (*Panicum hallii* – Lowry *et al.* 2015), Atlantic cod (*Gadus morhua* – Berg *et al.* 2016; Kirubakaran *et al.* 2016; Sodeland *et al.* 2016), threespine stickleback (*Gasterosteus aculeatus* – Jones *et al.* 2012), and rainbow trout (Pearse *et al.* 2014; Leitwein *et al.* 2017). The example of *O. mykiss* as a species exhibiting genetic divergence of multiple life history forms highlights the role of chromosomal inversions in promoting and sustaining intraspecific diversity (Rieseberg 2001). While inheritance of the rearranged Omy05 haplotype appears to increase the propensity for stream-residency (increased frequencies of the ancestral, anadromy-associated haplotype occur in adfluvial populations occupying reservoirs – Pearse *et al.* 2014; Apgar *et al.* 2017; Leitwein *et al.* 2017), the frequent occurrence of rearranged homozygotes in the lake indicated that environmental conditions influence whether an individual genetically predisposed to residency exceeds a conditional strategy threshold and becomes migratory (Pulido 2011; Phillis *et al.* 2016). While there is a northward latitudinal trend for increasing frequency of the rearranged Omy05 haplotype (Pearse *et al.* 2018), and similar latitudinal clines occur in other species (e.g., *Drosophila melanogaster* – Anderson *et al.* 2005), our results highlight how microgeographical variability in the frequencies of alternative inversion haplotypes may support distinct ecotypes in sympatry.

The post-glacial colonization of Alaskan watersheds by steelhead, and retention of the ancestral Omy05 haplotype among adfluvial individuals, suggests that the adfluvial ecotype is more similar to the anadromous ancestor whereas the fluvial ecotype is the most dissimilar locally. Lower genetic diversity in rainbow trout at the northern end of the species' range, in concert with the presence of numerous subspecies (e.g., golden trout – *O. m. aguabonita*) and related species (e.g., Gila trout – *O. gilae*) in the southern end of the distribution of *O. mykiss*, indicate a northward dispersal by anadromous fish after the recession of the Cordilleran ice sheet at least 10000 years ago (McCusker *et al.* 2000). Steelhead colonizing newly accessible habitat and encountering productive growing conditions in freshwater habitats could have experienced reduced selection pressure to migrate to the ocean (Quinn and Myers 2004), leading to the adaptation of adfluvial and fluvial individuals in post-glacial Alaskan watersheds as migration-related phenotypic traits were reduced. The presence of the rearranged and ancestral Omy05 haplotypes in Iliamna Lake (this study), California, and Oregon populations (Pearse *et al.* 2014; Leitwein *et al.* 2017) suggests that both haplotypes were propagated into numerous nonanadromous populations derived from anadromous colonizers. This parallels the consistency of genomic regions under divergent selection in multiple freshwater populations of threespine stickleback derived from oceanic populations (Hohenlohe *et al.* 2010), the presence of the same inversion architecture underlying alternative migratory ecotypes of Atlantic cod on opposite sides of the Atlantic ocean (Sinclair-Waters *et al.* 2018), and the repeated evolution of lake-type sockeye salmon and nonanadromous kokanee from an ancestral colonizing sea/river ecotype (Wood *et al.* 2008).

Most of the annotated, outlier genes with nonsynonymous SNPs in this study of sympatric stream- and lake-caught rainbow trout were functionally similar to those identified in studies of fluvial and anadromous fish. Most notably, two genes implicated in osmoregulation were identified as nonsynonymous outliers, and a third contained seven SNPs (*PLEKHH2* – Patrakka *et al.* 2007; Perisic *et al.* 2012) within the 3’-UTR where they may affect gene expression (Kritikou 2005; Moncini *et al.* 2007). The retention of genetic differences associated with osmoregulation, even though rainbow trout in the Iliamna Lake system do not enter marine waters, suggests that adfluvial fish inherit a suite of linked traits promoting migratory behavior including the ancestral capacity for adaptation to salt water. For example, formerly anadromous and now adfluvial *O. mykiss* isolated for 40+ years above a dam on Mann Creek, Idaho, exhibited elevated activity of gill Na^+/K^+ ATPase (an osmoregulatory protein – Folmar and Dickhoff 1980), more silver coloration than sympatric fluvial fish, and migrated in synchrony with steelhead emanating from unblocked areas of the same watershed (Holecek and Scarnecchia 2012). This matches divergent activity levels of Na^+/K^+ ATPase between anadromous and fluvial forms (Nichols *et al.* 2008; Hale *et al.* 2013). In addition, other annotated outlier genes in our study (Table 4) are associated with functions corresponding to those of outliers, QTL, or divergently regulated genes previously identified between fluvial and anadromous fish (Table 5). The numerous parallels in the functions of genes under divergent selection provide further evidence for the genetic differentiation of fluvial and adfluvial rainbow trout.

Genes involved in immune response are of particular interest, as they are under divergent selection between populations and ecotypes of numerous salmonid species (e.g., Tonteri *et al.* 2010; Kapralova *et al.* 2013; Larson *et al.* 2014; McKinney *et al.* 2016). In *O. mykiss*, divergence in immune response genes is not only documented between fluvial and anadromous fish (Martínez *et al.* 2011; Baerwald *et al.* 2016), but also between adfluvial populations in a lake system (Wellband and Heath 2013a,b) and between anadromous populations in a river basin (Micheletti *et al.* 2018). Rainbow trout in the Iliamna Lake watershed exhibited outlier SNPs in three immune response genes (Table 4), including one within *CXCL7*, an antibacterial protein (Krijgsveld *et al.* 2000). This matches Wellband and Heath's (2013a) discovery of *CXCL8* as a gene under divergent selection between adfluvial populations spawning in separate tributary streams (with disparate bacterial communities) of Babine Lake, British Columbia and Micheletti *et al.*'s (2018) identification of the *CXCL10*-like chemokine gene as an outlier among steelhead populations in the Columbia River basin, USA. The presence of outlier immune response genes associated with habitat type in our study of rainbow trout is consistent with divergent immunological response among alternative ecotypes of other taxa (e.g., threespine stickleback – Scharsack *et al.* 2007; Western terrestrial garter snake – Sparkman and Palacios 2009; African malaria mosquito – White *et al.* 2011).

The unexpected population structure within Roadhouse Creek may be related to landscape features and/or divergence in spawn timing. Brown trout (*Salmo trutta*) in a Norwegian stream system exhibited high gene flow between sections of the main stem, but low gene flow between the main stem and a tributary even though the two areas were separated by less than 600 m and had no barriers to migration (Carlsson *et al.* 1999). Roadhouse Creek splits into a tributary and main stem ~3.4 km upstream from its mouth and may support distinct spawning populations of rainbow trout above that junction. Genetic differentiation could also be related to spatial differences in environmental conditions (e.g., temperature) that sustain divergence of early and late spawning individuals (Ruff *et al.* 2011). While the genetic structure observed in Roadhouse Creek cannot, at this time, be attributed to a particular cause, our data do not suggest that it was due to the incidental sampling of families or the presence of adfluvial fish from another population entering the stream to feed (Arostegui and Quinn 2018). Estimates of relatedness excluded the possibility that groups A and B represented single families, and both groups included multiple individuals substantially smaller than the minimum estimated length at migration to the lake of 150 mm (Arostegui and Quinn 2018) and, therefore, likely were comprised of juveniles inhabiting their natal stream. A high degree of natal homing in rainbow trout (Shapovalov and Taft 1954; Lindsey *et al.* 1959) could support the strong substructure present within this creek, parallel to the precise homing (Halvorsen and Stabell 1990; Huusko *et al.* 1990; Arnesen and Stabell 1992) and microgeographical population structure (Ryman *et al.* 1979; Carlsson *et al.* 1999; Lemopoulos *et al.* 2018) in nonanadromous brown trout.

Residency enables trout in different streams to adapt to local environmental conditions and develop evolutionarily unique populations (Narum *et al.* 2010); however, low effective population size (N_e) in resident populations (Palm *et al.* 2003) and unequal gene flow from migrants to residents (Lemopoulous *et al.* 2018) can influence patterns of divergence across a watershed. There were disparate pairwise F_{ST} values between the Russian Creek population and Roadhouse Creek subpopulations (Table 3) that, given their spatial isolation and genetic architecture supporting stream-residency, are unlikely to establish gene flow. In addition, the Roadhouse Creek B subpopulation and Woody Island fish exhibited a considerably lower pairwise F_{ST} than did the Roadhouse Creek subpopulations with each other. This pattern of population differentiation suggests either (1) a greater degree of admixture between Roadhouse Creek subpopulation B and potentially stray adfluvial fish originating from other streams or (2) a faster rate of genetic drift in subpopulation A than B. Supporting scenario 1, studies of adfluvial salmonids (Lindsey *et al.* 1959; Fraser *et al.* 2004) identified asymmetric gene flow from populations with higher effective population size to those with lower N_e via stray spawners. Supporting scenario 2, low N_e, which is expected in a subpopulation of nonanadromous trout, enables more rapid genetic drift (Allendorf *et al.* 2013). Thus, we cannot be certain if the population structure we observed was attributable to asymmetric gene flow from populations with higher N_e to ones with lower N_e or divergent rates of genetic drift between populations of different N_e.

Conclusion

Our results highlight the genetic basis of migration, the role of chromosomal inversions in sustaining ecotypic diversity, and determinants of population structure. We demonstrated, for the first time, genetic differentiation of rainbow trout simultaneously occupying connected stream and lake habitats of a natural system, supporting the divergence of fluvial and adfluvial ecotypes in this species. A chromosomal inversion on Omy05 contains many genes exerting control over migratory behavior and its haplotypes were present at different frequencies between trout in streams and those that had migrated to a lake. The functions of annotated outlier genes between stream- and lake-caught fish paralleled those documented in studies of fluvial and anadromous *O. mykiss*, emphasizing the migratory nature of adfluvial fish even though they are nonanadromous. Structure at outlier loci was also apparent between and within streams supporting populations nearly fixed for the rearranged Omy05 haplotype (i.e., with a genetic predisposition for residency), indicating the role of local adaptation in population divergence supplemental to that caused by genetic drift through spatial isolation. Future work on species with alternative ecotypes should identify the environmental conditions driving variation in inversion haplotype frequencies at both micro- and macrogeographical scales to better inform their conservation in each system and evolutionarily significant unit.

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TABLES

Table 1. Summary information for sequence reads retained for each population after removing low quality individuals.

Population	Habitat	N	Fork Length (mm)	Total Reads	Average Reads Per Sample
Roadhouse Creek	Stream	31	51-229	228,098,654	7,358,021
Russian Creek	Stream	29	102-294	202,018,660	6,966,161
Woody Island	Lake	28	195-497	187,650,307	6,701,797

Table 2. Number of RAD tags and SNPs retained after filtering for genotype rate, minor allele frequency, and paralog status.

	Filtering Criteria		Paralog Status		
	80% genotype rate	5% MAF	Singletons	Duplicate	Diverged Duplicate
RAD tags	50,284	21,194	17,141	3,171	852
SNPs	133,896	29,571	22,934	5,361	1,239

Table 3. Pairwise F_{ST} between rainbow trout populations. Roadhouse Creek was split into subpopulations A and B due to substantial genetic structure between these sympatric groups of trout (see Results: *Admixture* for details).

Population	Woody Island	Roadhouse Creek A	Roadhouse Creek B	Russian Creek
Woody Island		0.1077	0.0325	0.0902
Roadhouse Creek A			0.0780	0.1761
Roadhouse Creek B				0.0991
Russian Creek				

Table 4. Annotated genes containing nonsynonymous outlier SNPs (or nonsynonymous non-outlier SNPs in outlier genes) identified by *LFMM* or *Bayenv2*. The number of nonsynonymous SNPs in each gene is indicated, and corresponding protein functions come from the associated citation. Note that certain genes have additional functions not included in this list. See Table S2 for chromosome, allele, and sequence information.

Gene	Protein	# SNPs	Function	Citation
WIZ	Protein WIZ	1	osmoregulation	Patrakka *et al.* 2007
ARHGDIA	Rho GDP-dissociation inhibitor 1	1	osmoregulation	Dovas & Couchman 2005
CXCL7	Platelet basic protein	1	immune response	Krijgsveld *et al.* 2000
BAG6	Large proline-rich protein BAG6	1	immune response	Binici & Koch 2014
OCLN	Occludin	1	immune response	Beeman *et al.* 2009
ZNF644	Zinc finger protein 644	2	eye development	Shi *et al.* 2011
PATJ	InaD-like protein	1	vision	Ranganathan & Ross 1997
TNNT2	Troponin T, cardiac muscle	2	cardiac contraction	Sehnert *et al.* 2002
ITPR3	Inositol 1,4,5-triphosphate receptor type 3	1	cardiac contraction	Garcia & Boehning 2016
CACNA1B	Voltage-dependent N-type calcium channel subunit alpha-1B	1	cardiac contraction	Ino *et al.* 2001
KDM6A	Lysine-specific demethylase 6A	1	cardiac development	Lee *et al.* 2012
DSP	Desmoplakin	1	cardiac development	Yang *et al.* 2006
DAG1	Dystroglycan	2	nervous system development	Saito *et al.* 2003
ASCL5	Achaete-scute homolog 5	1	nervous system development	Wang *et al.* 2017
ASPG	60 kDa lysophospholipase	1	lipid metabolism	Sugimoto & Yamashita 1994
EHHADH	Peroxisomal bifunctional enzyme	1	fatty acid metabolism	Zhao *et al.* 2010
RAI14	Ankycorbin	1	spermatogenesis	Qian *et al.* 2013
EPYC	Epiphycan	1	bone formation	Johnson *et al.* 1997
NXF1	Nuclear RNA export factor 1	2	mRNA export	Katahira *et al.* 2009
TPR	Nucleoprotein TPR	1	mRNA export	Bangs *et al.* 1998
AHCTF1	Protein ELYS	1	nuclear pore assembly	Rasala *et al.* 2006
CAMSAP1B	Calmodulin-regulated spectrin-associared protein 1-B	1	microtubule organization	Jiang *et al.* 2014
CEP95	Centrosomal protein of 95 kDa	1	mitotic progression	Kumar *et al.* 2013
BUB1	Mitotic checkpoint serine/threonine-protein kinase BUB1	1	mitotic progression	Cahill *et al.* 1998
MMS22	E3 ubiquitin-protein ligase substrate receptor MMS22	1	homologous recombination	O'Donnell *et al.* 2010
PACS2	Phosphofurin acidic cluster sorting protein 2	1	autophagosome assembly	Hamasaki *et al.* 2013
TCHH	Trichohyalin	1	calcium ion binding	Lee *et al.* 1993
LOC106583419	Prolyl 3-hydroxylase 3-like	1	iron ion binding	UniProt Consortium 2017
LOC108269134	Transcription initiation factor TFIID subunit 4-like	1	DNA binding	Shao *et al.* 2005

Table 5. Annotated genes identified as outliers between fluvial and anadromous rainbow trout in other studies. The study identifying the gene as an outlier is provided under *O. mykiss* citation, and the corresponding protein functions come from the associated function citation. Note that certain genes have additional functions not included in this list.

Gene	Protein	Function	*O. mykiss* Citation	Function Citation
RXRA	Retinoic acid receptor RXR-alpha	cardiac development	Nichols *et al.* 2008	Kastner *et al.* 1997
RSAD2	Radical S-adenosyl methionine domain-containing protein 2	immune response	Baerwald *et al.* 2016	Wang *et al.* 2012
CRYBB3	Beta-crystallin B3	vision	Baerwald *et al.* 2016	Lampi *et al.* 1997
NEUROD4	Neurogenic differentiation factor 4	vision	Baerwald *et al.* 2016	Inoue *et al.* 2002
ELVOL5A	Elongation of very long chai fatty acids protein 5	lipid metabolism	Hale *et al.* 2013	Morais *et al.* 2009
FADS2	Fatty acid desaturase 2	lipid metabolism	Hale *et al.* 2013	Cho *et al.* 1999
HES6	Transcription cofactor HES-6	nervous system development	Baerwald *et al.* 2016	Bae *et al.* 2000
NHLH2	Helix-loop-helix protein 2	nervous system development	Baerwald *et al.* 2016	Lipkowitz *et al.* 1992
PCDHGC5	Protocadherin gamma-C5	nervous system development	Baerwald *et al.* 2016	UniProt Consortium 2017
SPAG6	Sperm-associated antigen 16	spermatogenesis	Hale *et al.* 2013	Zhang *et al.* 2002
FSHB	Follitropin subunit beta	spermatogenesis	Hecht *et al.* 2014	Plant & Marshall 2001
TUBA1A	Tubulin alpha-1a chain	microtubule formation	Baerwald *et al.* 2016	Irobi *et al.* 2002
FIGN	Fidgetin	microtubule organization	Hale *et al.* 2013	Mukherjee *et al.* 2012
GEMIN2	Gem-associated protein 2	mRNA processing	Baerwald *et al.* 2016	Fischer *et al.* 1997

Table S1. Markers within the Omy05 inversion region that aligned to those of Pearse *et al.* (2014) and contained the same SNP. Life histories (i.e., fluvial, adfluvial, anadromous) are descriptors for the alleles they are putatively associated with in this study and Pearse *et al.* (2014). In both studies, the resident-associated (fluvial) alleles occur in the rearranged haplotype and the migrant-associated (adfluvial, anadromous) alleles occur in the ancestral haplotype. Asterisks (*) under the Note column indicate reverse complement alignments.

Locus	Tag	SNP	Omy05 Position	Fluvial Allele	Adfluvial Allele	Pearse Locus	Pearse Fluvial Allele	Pearse Anadromous Allele	Note
3595_56	3595	56	31675301	T	A	R40252	T	A	
38332_35	38332	35	34973485	T	A	R14589	T	A	
44000_33	44000	33	43270522	T	C	R14511	T	C	
22362_35	22362	35	44252219	T	C	R33010	A	G	*
8886_18	8886	18	46316422	G	C	R30015	G	C	
5192_47	5192	47	47337540	G	A	R24370	G	A	
8357_35	8357	35	51251690	A	C	R13730	A	C	
30553_38	30553	38	51334551	C	A	R24068	C	A	
55014_48	55014	48	51336354	G	A	R40342	C	T	*
69500_13	69500	13	52510201	T	C	R40580	T	C	
25806_49	25806	49	56162785	A	G	R33562	A	G	
28258_35	28258	35	63158900	C	T	R40319	C	T	
22284_19	22284	19	66281382	T	C	R18251	T	C	
16360_48	16360	48	73615367	A	G	R40152	A	G	
78208_24	78208	24	75699882	T	G	R23330	T	G	
69542_26	69542	26	79232694	A	C	R30220	A	C	
18901_19	18901	19	79714197	C	A	R34385	C	A	

Table S2. Chromosomal positions of the annotated, nonsynonymous outlier SNPs (or nonsynonymous non-outlier SNPs within outlier genes) from Table 4, including the base changes and sequences.

Gene	Tag	Chromosome	SNP	Alleles	Tag Sequence
LOC106583419	58258	omy02	61	A/C	TGCAGGACAGCTTCCTGTGTCTGCCGACATCGAGTACGAGTTTAGCACCCGGAACCCCTATAACTTCCTCCAGGTCGTCTACTGGAATGT
MMS22	54171	omy03	79	G/A	TGCAGGATGCTCCTTCTCAGTGCCGCCCCACGCGGGGTGGGCGTGGCCTCACAGGCCGCCAGCAGCACCGGGTGATTGGCTATGGCTCCA
KDM6A	18263	omy03	46	G/A	TGCAGGGACACTGCTCAGTCCCAGTCCCAGTCTCACCGCCCTTACACATGGATTGGCTAATCACATCCAGCAGGGGGCGGTGACCACCACGTACAG
TCHH	35004	omy03	45	A/C	TGCAGGAGGATAGAGGATGTCGTGTAGAGAGGCTGGGGGCTCAGGTTAAAGCCCTGGAGGAGGAGAGAGACCACCTCTTAGCTGAGATCA
DSP	24698	omy04	65	T/C	TGCAGGACAGTAGCGGCCAGCTGGTCCTCCTCACACACAGCCTGGACGAGGAGCAGAGGAGGAGGGGAGCATTGGAGGAGGAGAGGACCA
CACNA1B	13376	omy05	34	A/G	TGCAGGTCTGCAGGCTGGAGAGAAGCAAGAGGATGCTGACAACCAGAAGAACAGCCACAGAGCCAGCCAGGCAGGCCTGAACAGCAACAC
CAMSAP1B	26476	omy05	49	C/T	TGCAGGCACCACAAGCCTCCTAGAGTGTAGGGGGCGCTCTCCGAGCCATTGGGTGTGGTCTTTTGGGAGCTGCTGTTATTGGAGCAGTTG
OCLN	33810	omy05	61	G/C	TGCAGGGAGAGCTGGACATCATCAACAAGAGCCTGTCAGAGGTGGACAGAGAGCTGGATGAGCTGCAGGAGGGAAGCCCCCAGTTCCTGG
RAI14	45672	omy05	63	C/T	TGCAGGATGGCCTCAGCCCCCTGCTGCTGTCCGCCAGACACGCCCAGACAGAGGCGTGCGGCAACCTCCTGGACTGGGGAGCCGACGTCA
PATJ	5394	omy05	80	T/C	TGCAGGAGGTGTCGGATGAGGAGCCGGAGGAGCCAGCGCCCACGTACCCCAGCCACCAGGAGGAGATGCAGCAGGGGAGGGGAGGGGGGG
TPR	20968	omy05	23	C/G	TGCAGGGCCTGGGCCTTGGCTGCGTGGAGGGACTCCACGTCTGCAGCGTGGAGCATCATCTCACGCTCATACTTATCTTGTGCCTCTGAC
ZNF644	52084	omy05	22	C/T	TGCAGGAAGTCAGAGCCCCAAGCTGTTATCCGAAAGTCTCCATCCAAACGAAAAATGTCCACACCATTCCGCAACACTGTGGACAAGGTG
ZNF644	52084	omy05	28	C/T	TGCAGGAAGTCAGAGCCCCAAGCTGTTATCCGAAAGTCTCCATCCAAACGAAAAATGTCCACACCATTCCGCAACACTGTGGACAAGGTG
ASCL5	34878	omy07	71	A/G	TGCAGGGTCTGGTGGAGGGGCAGGGGAAAGGGAGAGAGGGGCATGAAGAGGAACAGGCATGCCACAGCCCCAGTTCTGCTCCATGTAGGA
BUB1	3674	omy08	36	A/C	TGCAGGAGGACCAGTTCCGCAGCATGCCAATGCATCCACATCAGACAGAGAACATTTTTGATGCTGGCTACCAGAGAACGGGTAATTCAA
PACS2	80794	omy09	75	A/G	TGCAGGGACCTGAAGGCACTCTTCAGGGTGTTCTTACCGCCCGTGTCACGCCGTTCCCCATCACGTCGCTTCTCCACCAGCGACGCCAGC
CXCL7	5003	omy11	54	C/T	TGCAGGAGTGGCTGGAGGTGTACACCTCGAGCTTCTCAATGTGAAGAGGTTTAACGTGGTTCACCAGTCCATTCAGACACAGGCACCGAG
WIZ	18689	omy12	16	T/A	TGCAGGATCACATGCAAGAGCACAGTCAGAGCAGGCCGGGGGCTGGCAGGAGGGAGCGCGGAGTGAAGGGCGCGCGATTTCGGTGCGTGG
CEP95	26074	omy13	7	A/T	TGCAGGATGAGCTGGAGGACAGGGCACCACTGGACACTGAGGAAGATGAGGAGGAAGAGACCTTCACGCAGCAGGACAGCTGGGCTCACA
ARHGDIA	47722	omy13	39	G/A	TGCAGGTCTCCAGGCTGGTCTGGCTGCTCTCTAGGCTCCCGAGGCCCAGGCGGAAGAAGGAAGAGTAGGCCGTGAGGGCAACGTCACTGA
NXF1	28084	omy14	67	C/G	TGCAGGGAGATGACGATGGTGTTGGAATGGGTTTGGATGTGTCTGCCGCTGGGAGCTCCACGTGAACGGACCAGATCCTGCAGCTGGGCT
NXF1	28084	omy14	70	T/C	TGCAGGGAGATGACGATGGTGTTGGAATGGGTTTGGATGTGTCTGCCGCTGGGAGCTCCACGTGAACGGACCAGATCCTGCAGCTGGGCT
TNNT2	47422	omy15	66	C/T	TGCAGGGAGAAGGCCAATGAGCTGTGGCAGTGGATGATGGAGTTGGAGGCGGAGAAGTTTGACCTCGGCGAGAAACTGAAGAAGCAGAAA
TNNT2	47422	omy15	68	G/C	TGCAGGGAGAAGGCCAATGAGCTGTGGCAGTGGATGATGGAGTTGGAGGCGGAGAAGTTTGACCTCGGCGAGAAACTGAAGAAGCAGAAA
LOC108269134	23715	omy16	8	A/C	TGCAGGCTCCAGGGACGCCCATGATGTCCCGTCAGGTGACCCCCACCATCACTAAGCAGGGCTCCACGGCCCAGACCACCGTCCAGGCCA
ITPR3	49779	omy16	61	A/T	TGCAGGTCTGGAGAGGGACAAGTTTGACAATAAAACGGTGTCTTTTGAGGAGCACATAAAGTTGGAACACAACATCTGGAACTACCTGTA
EPYC	60083	omy17	87	G/T	TGCAGGTGTAGTACTCGGAGGCTCTCAGGTAGTGGGACAGGGATGTAGTCCAGCTTGTTATCAGACAGATACAGGAACTCGAGCAGGCTC
DAG1	61137	omy17	69	T/C	TGCAGGAGGAGAAACCCCCACTGCCCCCGCCTGAGTACCCCAACATGACCAGTCCAGAGACCACCCCCCTGAACCAGGACCTTCTGGGGG
DAG1	61137	omy17	81	T/C	TGCAGGAGGAGAAACCCCCACTGCCCCCGCCTGAGTACCCCAACATGACCAGTCCAGAGACCACCCCCCTGAACCAGGACCTTCTGGGGG
BAG6	11385	omy18	40	T/G	TGCAGGGTTCTTCGGGGACCTGTTGTCTCTGGTGGGTCACAGTTTCTCCATGGTGGACATGGTGTTGTTACTCCACGGTAATGCCCAGCC
AHCTF1	58612	omy19	68	G/A	TGCAGGGTACAGGGGGTCTCCAGAACAGAGAGCTACTGATGATGCACTACCTGCAGCAGGCTAACTACGTCCCCGCCCTGCAGCTTAACC
ASPG	73545	omy19	62	T/A	TGCAGGCGCCCATGGAGGGCATTGTCCTGGAGACGTATGGTAGTGGAAACGCCCCTGATAACTGTGCTGACCTGCTTGAGGAGTTCCGAA
EHHADH	42259	omy22	7	T/G	TGCAGGATGCCATGGCCGCCGGGCCGGAAGACATCGACGCCATCTATGTGTTTGGGTACGGCTGGCCCCGGCACCACGGGGGACCCATGT

FIGURES

Figure 1. Map of Iliamna Lake and its location in the State of Alaska, USA. Study sites are indicated by circular symbols: Woody Island (blue), Roadhouse Creek (yellow), Russian Creek (grey). Satellite image produced with Google Earth using data from Image Landsat/Copernicus, SIO, NOAA, U.S. Navy, NGA, and GEBCO. In the inset map of the Pacific coast of North America, Alaska is shaded and Iliamna Lake is marked by a black circular symbol.

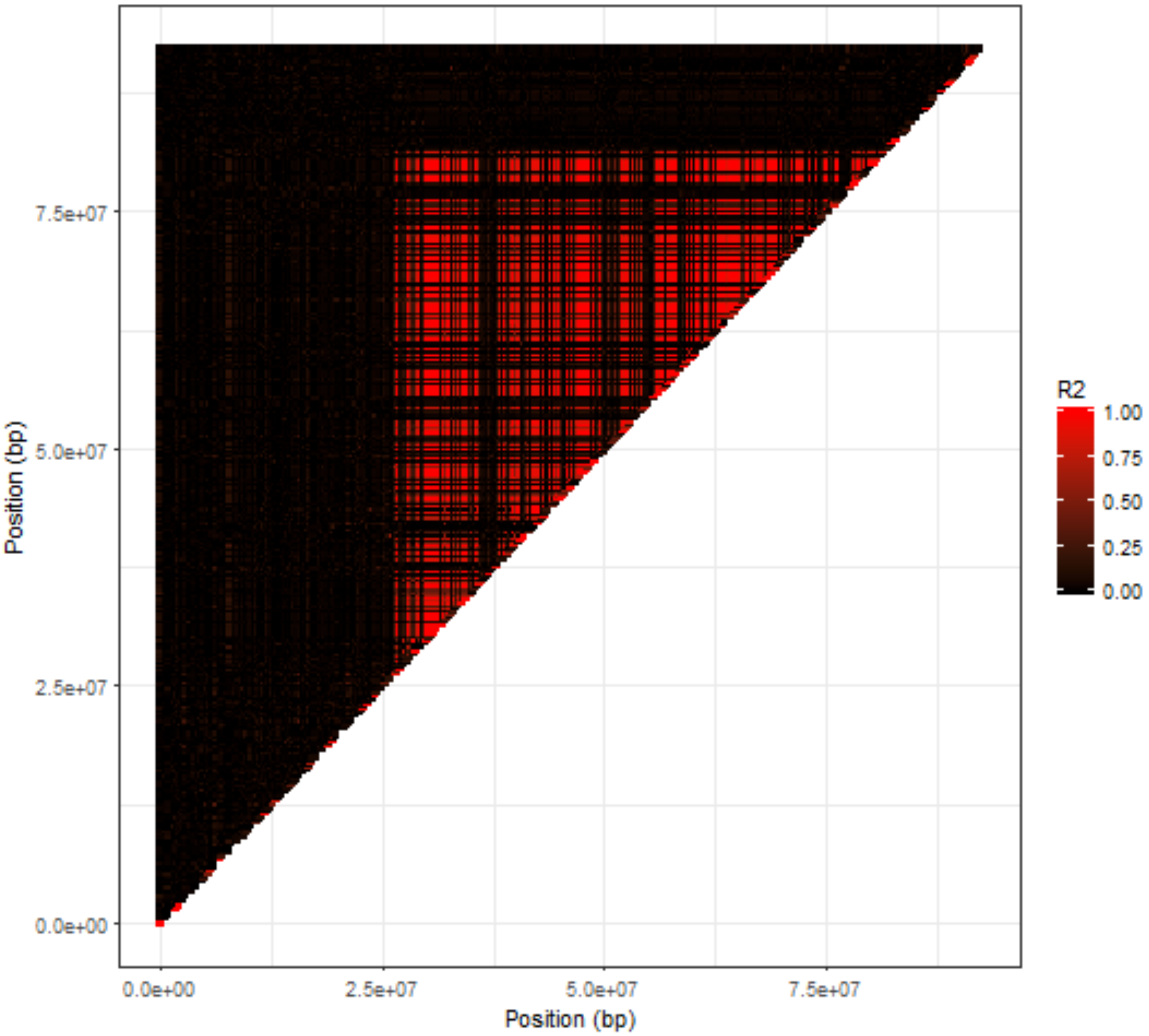

Figure 2. Plot of linkage disequilibrium (r^2) across chromosome Omy05. A value of 0 indicates no linkage and a value of 1 indicates complete linkage between a pair of markers. The linkage disequilibrium block spans ~54Mb. Genotypes for 511 RAD tags within this region show complete linkage, supporting the existence of a large genomic inversion.

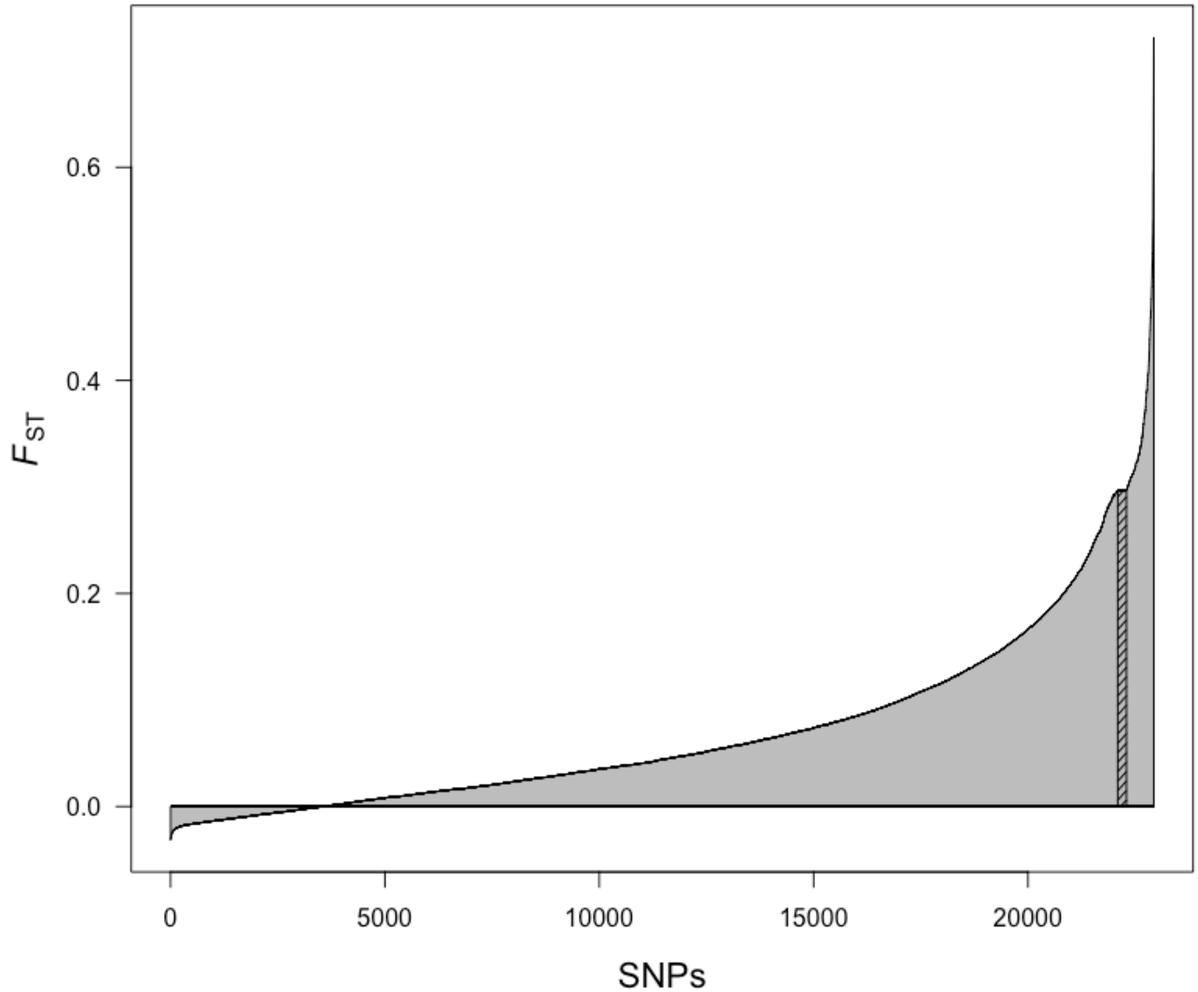

Figure 3. Global F_{ST} (among sampling sites) of genotype rate- and MAF-filtered singleton SNPs, including those within the Omy05 inversion (dashed area), rank ordered from lowest to highest.

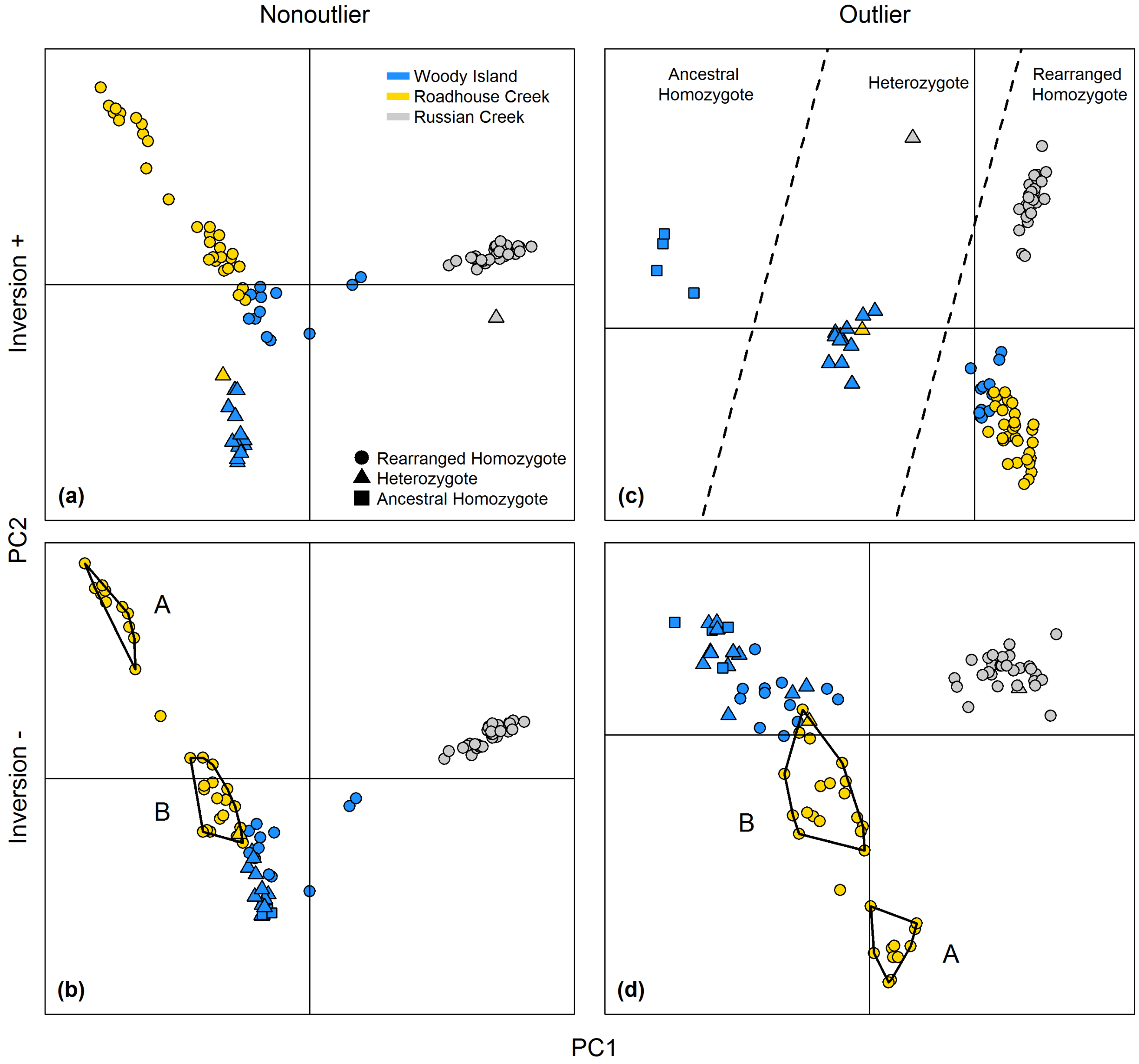

Figure 4. Individual-based PCAs of (a) non-outlier SNPs identified when including the Omy05 inversion [PC1: 7.4%, PC2: 5.1%], (b) non-outlier SNPs identified when excluding the Omy05 inversion [PC1: 7.5%, PC2: 4.1%], (c) outlier SNPs identified when including the Omy05 inversion [PC1: 13.5%, PC2: 5.1%], and (d) outlier SNPs identified when excluding the Omy05 inversion [PC1: 7.1%, PC2: 5.1%]. Sampling site and Omy05 inversion genotype legends are in panel (a). In panels (b) and (d), convex hulls indicate Roadhouse Creek subpopulations A and B, and the excluded individual is a potential hybrid. In panel (c), the dashed lines separate genotypes of the Omy05 inversion. The designation of SNPs as outlier or non-outlier loci comes from the *LFMM* analyses.

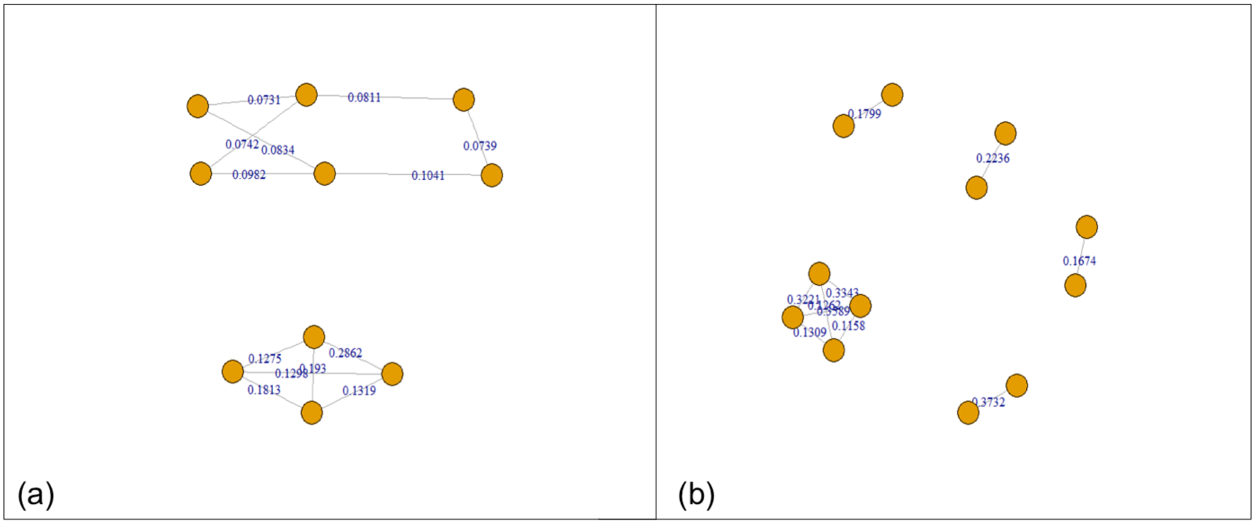

Figure S1. Network plots of rainbow trout individuals from Roadhouse Creek subpopulation A (a) and subpopulation B (b). The threshold for the coefficient of relationship was set at 0.0625 (equivalent to half-first cousins, first cousins once removed, and double second cousins). Individuals below the threshold were excluded from the plots (A: n = 1; B: n = 7).

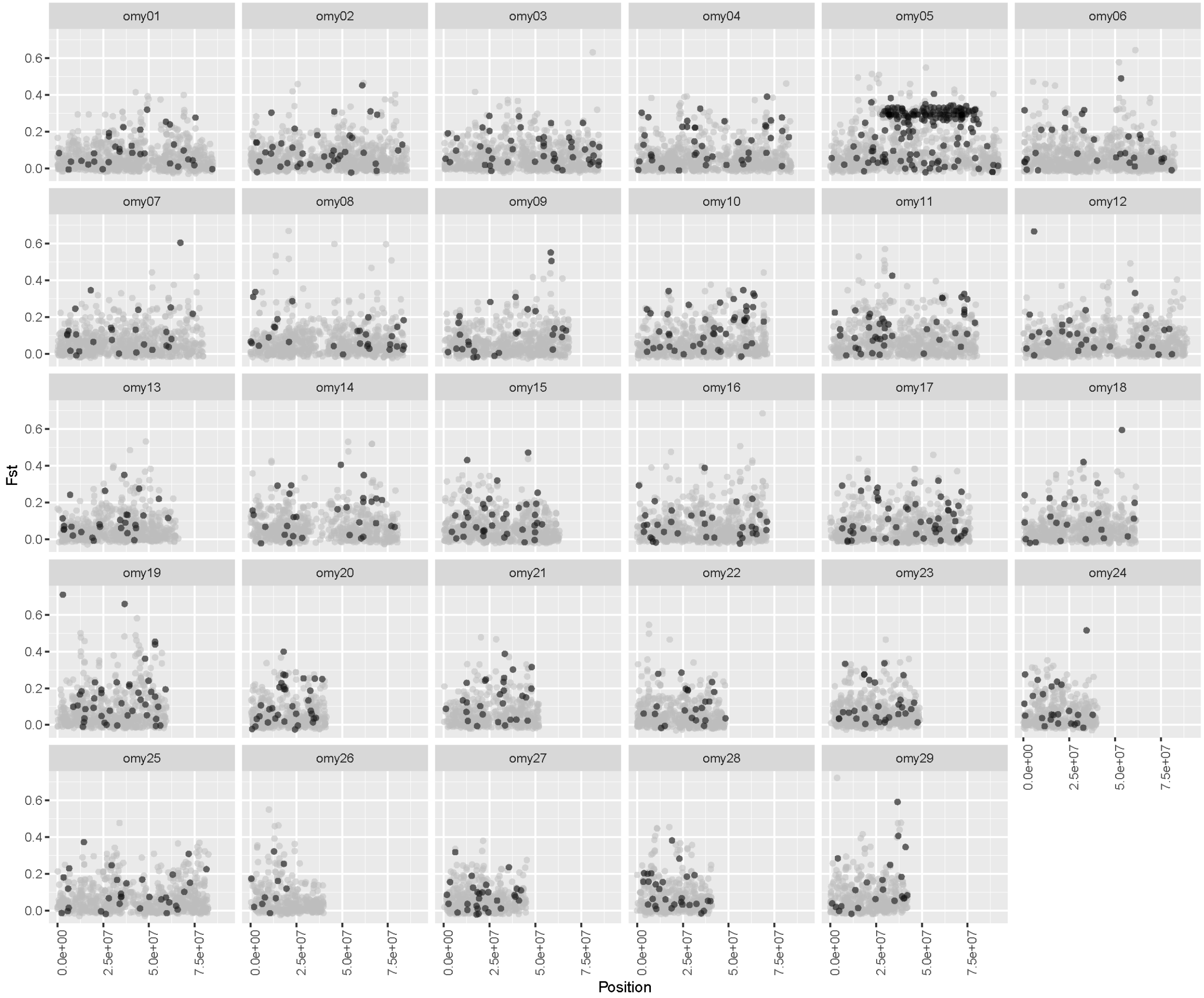

Figure S2. Genomic distribution of outlier SNPs (as designated by *LFMM* and/or *Bayenv2*). Outlier SNPs are in dark grey and non-outlier SNPs are in light grey.

CHAPTER 3

Ontogenetic and ecotypic variation in the coloration and morphology of rainbow trout in a stream-lake system

Arostegui MC, Quinn TP

ABSTRACT

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 nonanadromous rainbow trout in connected stream and lake habitats of a southwest Alaskan watershed to assess if they exhibited phenotypic diversity consistent with the presence of alternative fluvial and adfluvial ecotypes. Color differences among rainbow trout of different size classes and habitats (stream or lake) indicated the presence of 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 color when larger. The morphology of lake-caught rainbow trout was also distinct from that of stream-caught fish in features associated with swimming performance, and their morphological differentiation exhibited both shared and unique 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 behavior and how conservation of particular phenotypes depends on managing both for genotypes and habitats.

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 – Beamish 1987; walking stick – Nosil 2007; grey wolf – Schweizer *et al.* 2016; bottlenose dolphin – 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 and Huntingford 2004). The ecological and phenotypic distinctiveness of ecotypes may lead to assortative mating and further promote adaptive divergence within a species (Maan and 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 and 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 the differences in growth potential and morality risk between the natal and non-natal habitats (Pavlov and Savvaitova 2008; Chapman *et al.* 2011); migrants typically achieve greater asymptotic sizes and fecundity but experience lower survival rates (Jonsson and Jonsson

1993). The movement to 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 and Jonsson 1993). Migrant and resident salmonids exhibit morphological divergence consistent with swimming in standing versus flowing water (Varian and Nichols 2010; McKinney *et al.* 2014). Similarly, migrants exhibit silver coloration appropriate to the open pelagic environment whereas residents typically remain darkly colored with numerous spots in a pattern providing camouflage in streams (Nakano *et al.* 1990; Tanguy *et al.* 1994; Tsiger *et al.* 1994).

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 northwest 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 the initial migration into a lake or the ocean (Busby *et al.* 1996; Arostegui and Quinn 2019). In partially migrant populations, the resident fluvial ecotype is sympatric with stream-rearing juveniles of one of the two migrant ecotypes prior to their outmigration (Pavlov and Savvaitova 2008; Holecek and Scarnecchia 2013). However, while the fluvial and anadromous ecotypes are well-studied in *O. mykiss* (e.g., Nichols *et al.* 2008; Ohms *et al.* 2014) less is known of the adfluvial ecotype, despite its common occurrence.

There is a chromosomal inversion on the fifth chromosome of the rainbow trout genome (hereafter referred to as ‘Omy05’) with two alternative haplotypes associated with phenotypic expression of migratory behavior; 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, both at the Omy05 inversion and numerous outlier loci (Arostegui *et al.* 2019), strongly suggests disruptive natural selection maintaining fluvial and adfluvial ecotypes rather than just the segregation of different ontogenetic stages of a single ecotype and gene pool.

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 southwest Alaskan watershed to assess if they exhibited phenotypic diversity consistent with the presence of alternative fluvial and adfluvial ecotypes. In addition, we 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, *S. 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 favoring sustained swimming performance whereas rainbow trout and Arctic char in the lake were expected to exhibit morphologies favoring unsteady swimming performance (*sensu* Langerhans *et al.* 2008).

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 over 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 and 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 a beach on the lake's shoreline: Finger Bay (Fig. 1). These sites are used for spawning by sockeye salmon (Demory *et al.* 1964) and for foraging by rainbow trout and Arctic char (Arostegui and Quinn 2018). Rainbow trout (n = 105) were also 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 placed in a solution of AQUI-S anesthetic until sedated. Fish were 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 leveled 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 employed by Holecek *et al.* (2012) for the description of anadromous and adfluvial *O. mykiss* undergoing the parr-smolt transformation; 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 pales ones 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).

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. The 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: 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 followed the methods of Keeley *et al.* (2007). Character measurements were log10 transformed to normalize and standardize the data. The measurements of interest were selected to investigate differences in body shape characteristic of fishes experiencing divergent water flow conditions; morphological changes enhancing sustained swimming (cruising) are predicted in stream habitats whereas those enhancing unsteady swimming (maneuverability) are predicted in lake habitats (Langerhans *et al.* 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; Wainright *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 each linear character measurement. 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, 2) *distinct* – two linear allometric trajectories, one specific to fish in the lake and a second specific to fish in the stream, and 3) *segmented* – one non-linear allometric trajectory with a change in slope corresponding to an ontogenetic shift from stream to lake habitat. 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 – *S. malma*; lakes – *S. alpinus*). The linear regressions of the *null* and *distinct* models were conducted following Ostberg *et al.* (2009) and Brenkman *et al.* (2014), using post-orbit length instead of fork length in 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 and Piironen 2001b) and sexual dimorphism in head size that is typical of mature salmonids (e.g., Beacham 1984; Merz and 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. Size-adjustment accounts for allometry and permits direct morphological comparison of fish at different stages of ontogeny (Thorpe 1976). The mean post-orbit length of all fish was used as the transformation target.

Two linear discriminant analyses (LDA) of the size-adjusted data 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).

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 FL 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 ($p < 0.05$). In order of increasing length, there were 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 *S. alpinus* and one for *S. malma*) 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 *S. malma* and S. *alpinus*) had the lowest AIC for caudal peduncle length (Fig. 5; Table 2).

The LDA of size-adjusted *O. mykiss* captured in lake versus 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 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 the stream-caught rainbow trout. Univariate comparisons, among size-adjusted trout captured in different habitats, identified all morphological features as being significantly different in mean size (mm) except caudal peduncle depth (Table 4). While perMANOVA indicated that these two habitat-specific groups of trout were significantly different in morphology ($F = 12.5$, $P < 0.001$), the small amount of overlap along the linear discriminant axis (Fig. 6) was 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).

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. 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 4). Both a significant perMANOVA result ($F = 97.4$, $P < 0.001$) and a 100% jackknife reclassification rate 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 color 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 among size classes and habitats are consistent with ontogenetic changes in two ecotypes with distinct coloration trajectories. 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 and 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 2011, Holecek *et al.* 2012; *O. tshawytscha* - Beckman *et al.* 2000; *S. trutta* – Schulz 1999; *S. salar* – Birt and Green 1986; Piironen *et al.* 2013). The presence of banded parr exclusively in the study stream, intermediate rainbow trout almost exclusively in the study stream, silver rainbow trout almost exclusively in Iliamna Lake, and 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 FL) 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 (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 size of silver than bronze trout is consistent with the larger asymptotic size of adfluvial than fluvial salmonids in sympatry (Robillard *et al.* 2011; Holecek and Scarnecchia 2013). 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 in Lake Superior where adfluvial individuals exhibited greater skin reflectance than fluvial counterparts but 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 (Edo *et al.* 2005) and adfluvial longhead char (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. Not all silver rainbow trout exhibited this caudal pigmentation; however, its presence may identify adfluvial individuals outside of their characteristic lake habitat. For example, many adfluvial rainbow trout in Iliamna Lake enter tributary streams in late summer and early fall to opportunistically forage on the eggs of spawning sockeye salmon (Arostegui and Quinn 2018).

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 (Swain and Holtby 1989), spotted galaxias (Humphries 1990), and pumpkinseed sunfish (Brinsmead and 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 and Magnan 2002, 2004). Larger paired and median fins increase drag but increase stability, positioning, and maneuverability (Webb 1975; Webb 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 and 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, with fish in the lake tending to have narrower caudal peduncles than their stream counterparts in a pattern contrary to flow-morphology predictions (Langerhans *et al.* 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 (Robinson and Parsons 2002; Proulx and Magnan 2002, 2004). 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 exhibited 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 improved sustained swimming performance in lotic waters via body streamlining (Webb 1982; Langerhans *et al.* 2008). Greater body depth in lower velocity habitats is commonly observed in fishes, including centrarchids (Brinsmead and Fox 2002), cyprinids (Haas *et al.* 2010; Collin and Fumagalli 2011; Franssen 2011), cichlids (Theis *et al.* 2014), and numerous salmonids (e.g., Riddell and Leggett 1981; Bowen and 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 Arctic char in lake habitat and the two *Salvelinus* species exhibited no divergence in caudal peduncle length. The morphology of drift-feeding salmonids 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 and Piironen 2001a; Brinsmead and 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 and 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 *et al.* 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 and 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 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 (Harry Rich, Jr., and Thomas 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 $\delta^{13}C$ signature (Arostegui and Quinn 2018). Additionally, the youngest trout we collected in the lake were age 2 (Table A1), though 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 (*Lepomis gibbosus*) changed when they began consuming snails (Wainright *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, whereas the rainbow trout in the lake exhibit a heightened frequency of the ancestral haplotype, which is associated with migration (Pearse *et al.* 2018; Arostegui *et al.* 2019). Genetic studies on 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 hatch, 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 (*O. clarkii*); hybrids demonstrated morphology and swimming performance intermediate to those of the parent species (Hawkins and Quinn 1996; Seiler and 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 and Adams 2004) and the inverse could augment dissimilarity. However, Keeley *et al.* (2007) revealed in a common-garden experiment 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 migrant populations consisting of adfluvial and fluvial individuals in sympatry. Firstly, 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 likely represent a mixture of populations that may exhibit morphological variation associated with spawning in different natal streams of varying environmental conditions (Pakkasmaa and Piironen 2001b). Secondly, 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 – -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). Thirdly, incorrect reclassifications were disproportionately of stream-caught trout into the lake-caught group. Lastly, there was a high ratio of bronze to silver rainbow trout (~6.6:1) in the stream-caught group, but no bronze individuals in the lake-caught group (Table 1).

Together, these results indicate that Russian Creek is a partially migrant population consisting predominantly of the fluvial ecotype but producing the adfluvial ecotype at low frequency. 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 (D'Amelio and 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). However, 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).

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 behavior has a genetic basis (Arostegui *et al.* 2019), is linked with 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 migrant 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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TABLES

Table 1 – Proportion of rainbow trout with different coloration patterns in the stream and lake (% of individuals within habitat type) and mean fork length (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)

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**

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 versus stream) and *Salvelinus* species (Arctic char versus Dolly Varden). 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 a stronger relationship).

	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

Table 4 – Size-adjusted means (mm) of the linear character measurements from the *O. mykiss* captured in different habitats (lake versus stream) and *Salvelinus* species, set to a transformation target of 226 mm post-orbit length (~283 mm fork length). *P*-values are from Welch's two sample t-test. Grey highlights indicate which group exhibited a significantly greater mean value for that specific morphological feature (highlights are not present for comparisons that are not statistically significant).

	O. mykiss Habitats			*Salvelinus* Species		
Morphological Feature	Lake	Stream	*P*	*S. alpinus*	*S. malma*	*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

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 FL) 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

FIGURES

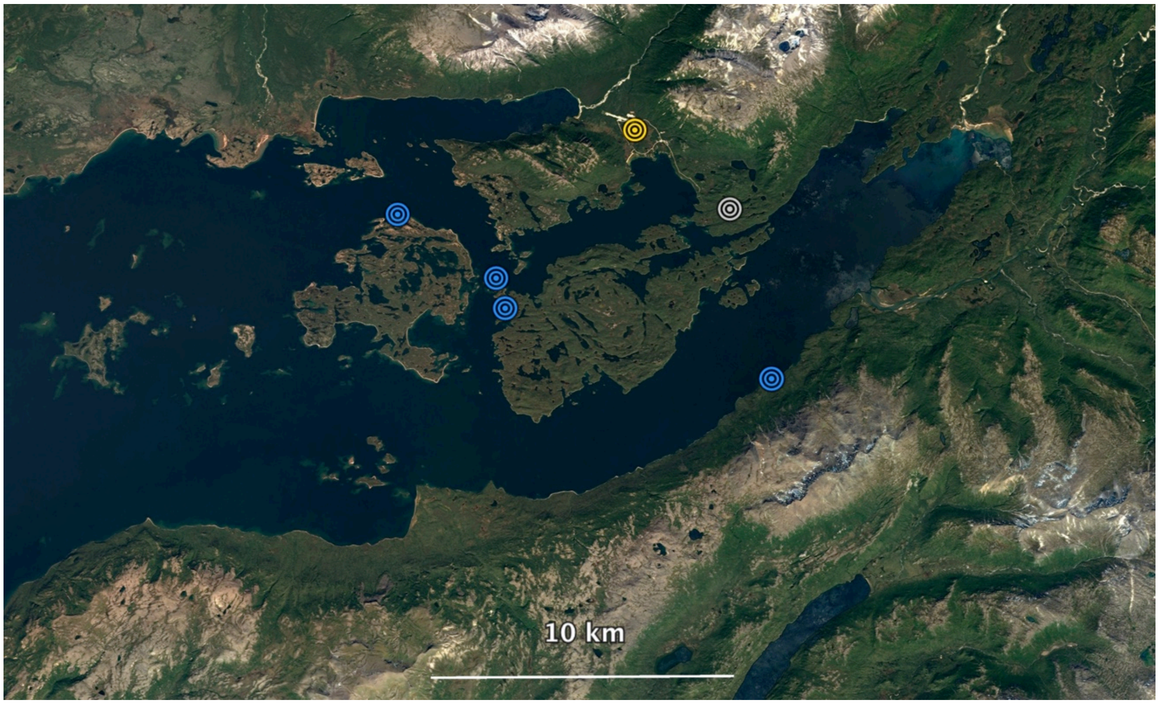

Figure 1 – Map of the eastern end of Iliamna Lake. Study sites are indicated by circular symbols: Woody Island, Fuel Dump Island, Porcupine Island, and Finger Bay (blue), Russian Creek (grey), and Pedro Ponds system (yellow). Satellite image produced with Google Earth Pro using data from Image Landsat/Copernicus.

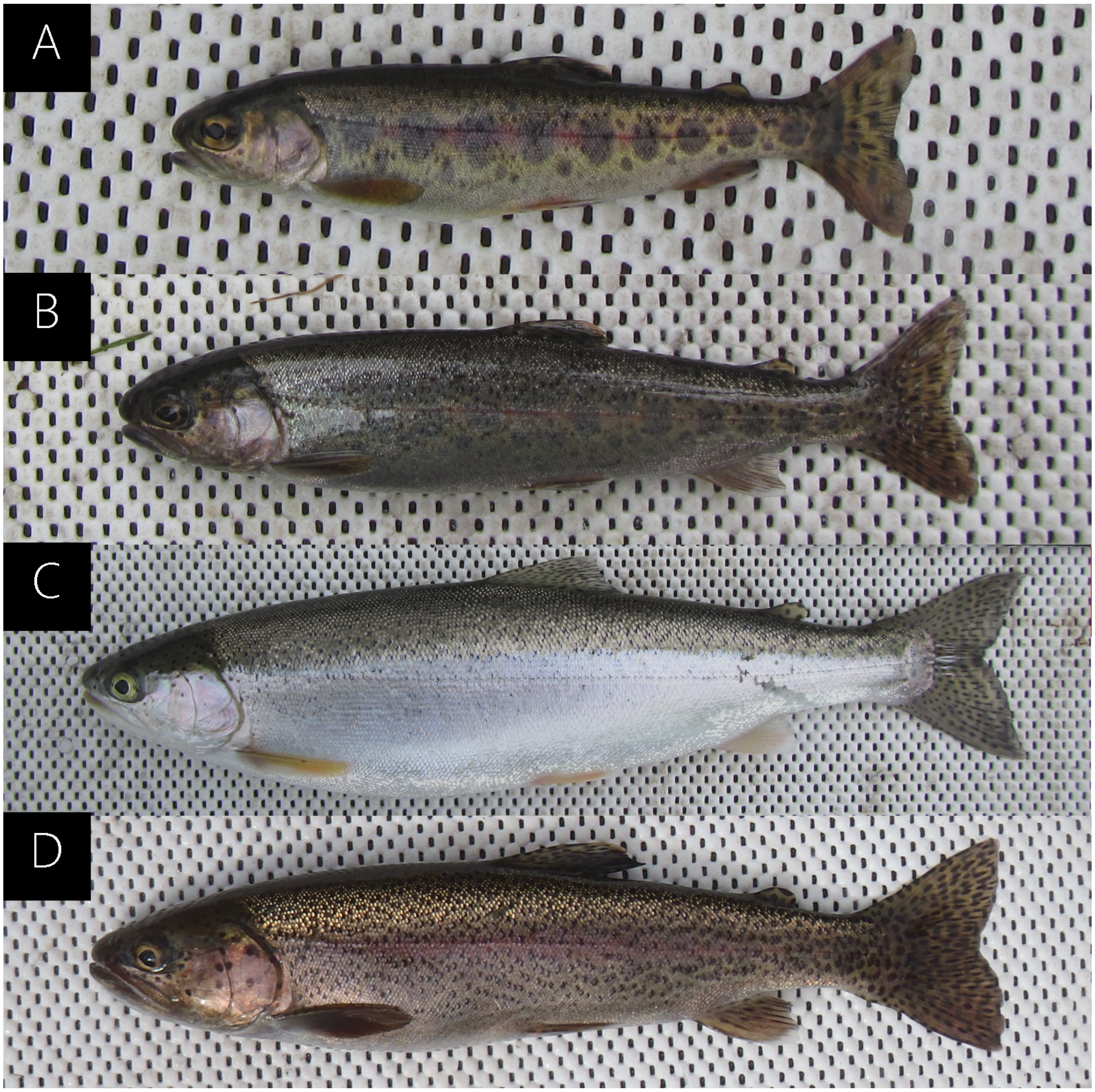

Figure 2 – Coloration patterns of rainbow trout; A) banded - 113 mm FL, B) intermediate - 195 mm FL, C) silver - 393 mm FL, D) bronze - 277 mm FL. Note the guanine streaks on the central caudal fin rays in C).

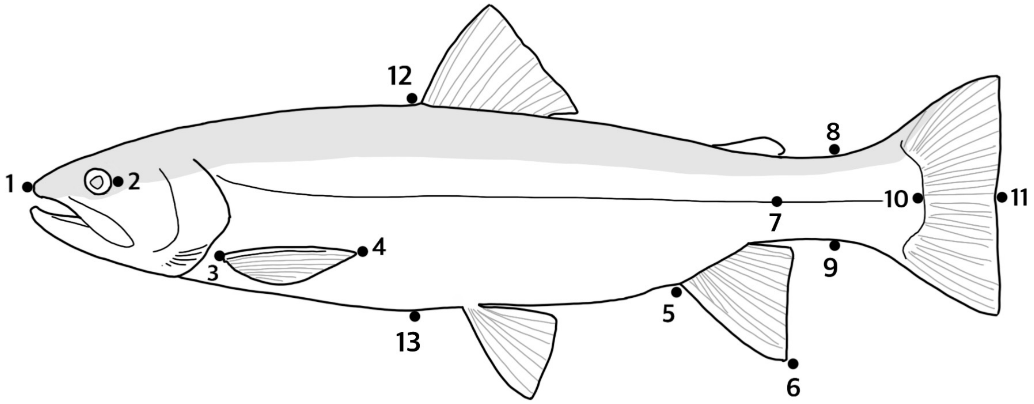

Figure 3 – Linear morphological measurements: 1-11 = fork length, 2-10 = post-orbit length, 3-4 = pectoral fin length, 5-6 = anal fin length, 7-10 = caudal peduncle length, 8-9 = caudal peduncle depth, 12-13 = body depth. Artwork by Brandon Li.

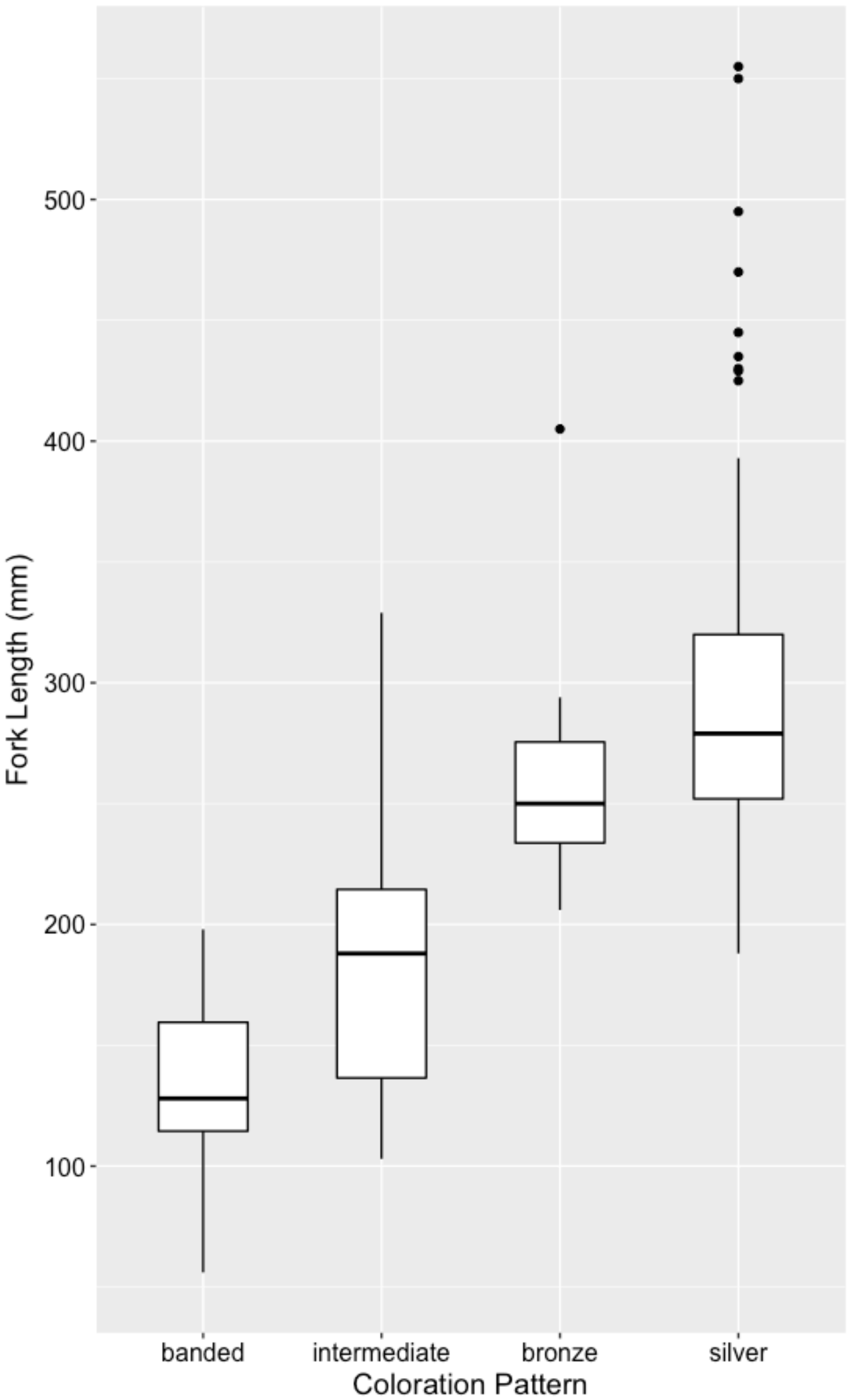

Figure 4 – Boxplots of rainbow trout fork length (mm) by coloration pattern.

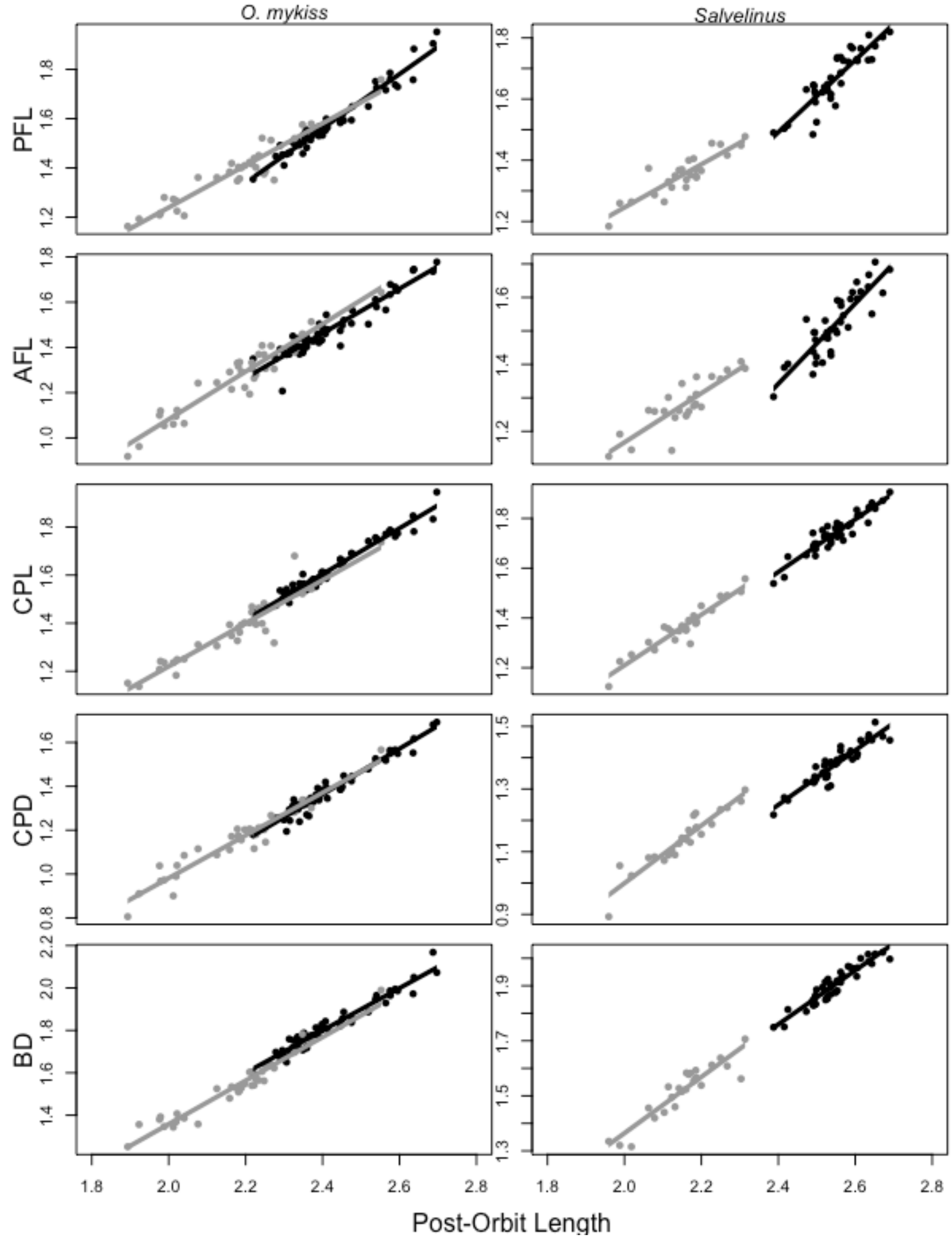

Figure 5 – Model-selected relationships of post-orbit length with morphological characters (log10 transformed). Color coding: *O. mykiss* – stream (grey)/lake (black), *Salvelinus* – Dolly Varden (grey)/Arctic char (black). Morphological features: PFL – pectoral fin length, AFL – anal fin length, CPL – caudal peduncle length, CPD – caudal peduncle depth, BD – body depth.

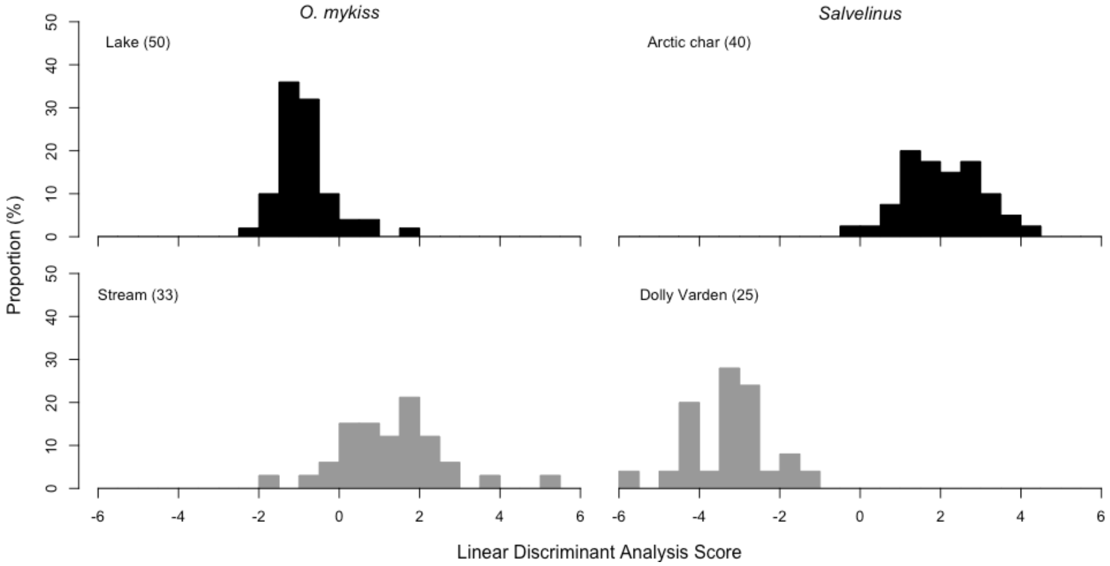

Figure 6 – LDA scores for rainbow trout sampled in lake and stream habitats, and Arctic char and Dolly Varden. The samples size of each group is in parentheses.

CHAPTER 4

Reliance on lakes by salmon, trout, and charr (*Oncorhynchus*, *Salmo*, and *Salvelinus*): An evaluation of spawning habitats, rearing strategies, and trophic polymorphisms

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ABSTRACT

Salmonid fishes may reside within or migrate between stream and lake habitats, or undergo anadromous migrations between fresh water and the ocean. While the degree of anadromy of salmonids has been thoroughly compared, no analogous review has examined the degree of lake use. To assess the extent of reliance on lake habitat in this family, we considered 16 species of salmon, trout, and charr from the genera *Oncorhynchus*, *Salmo*, and *Salvelinus,* comparing their 1) use of lakes as spawning habitat, 2) rearing strategies in lakes, and 3) occurrence and diversity of lacustrine trophic polymorphism. In identifying the primary life history patterns of each species and exploring the lesser-known lacustrine behaviors, we found that the extent of reliance on lakes exhibits a negative association with the degree of anadromy. *Oncorhynchus* rely least on lakes, *Salmo* to an intermediate level, and *Salvelinus* the most; opposite of the general prevalence of anadromy among these genera. Lakes are critical to adfluvial and lake-resident salmonids, but they also support anadromous and fluvial life histories by providing spawning, rearing, overwintering, and/or summer refuge habitat. Adfluviality, although a nonanadromous life history, consists of similar migration-related traits and behaviors as anadromy, including the parr-smolt transformation, sex-biased patterns of migration and residency, and the presence of precocious males. Lakes support life history variants, reproductive

ecotypes, and trophic morphs unique to lacustrine habitat. Therefore, conservation of salmonids is dependent on maintaining the diversity and quality of their habitats, including lakes.

INTRODUCTION

There is substantial inter- and intraspecific diversity in habitat use among fishes, which poses notable considerations for conservation planning and fishery management. In fresh water systems, where the primary habitat differentiation occurs along the stream-lake axis (Willis and Magnuson 2000; Seehausen and Wagner 2014), fishes may reside exclusively in streams or lakes, freely move between the two, spawn in one or both, or exhibit diadromy (Gross *et al*. 1988; Lucas and Baras 2001; Fausch *et al*. 2002). Furthermore, the use of lotic versus lentic waters may induce phenotypic plasticity (e.g., blacktail shiner, *Cyprinella venusta*, Cyprinidae – Franssen *et al.* 2013), evolutionary diversification (e.g., stream-lake pairs of three-spine stickleback, *Gasterosteus aculeatus*, Gasterosteidae – Deagle *et al.* 2012), and population structure (e.g., stream- and lake-spawning populations of walleye, *Sander vitreus*, Percidae – Strange and Stepien 2007). In addition to being important for the ecology and evolutionary biology of species, the extent to which species use both stream and lake habitats, and the connectivity of these population components, can be an important factor in their persistence and recovery (Campbell *et al.* 2019).

Species in the family Salmonidae, among the most extensively studied fishes in north temperate and boreal waters, may reside within or migrate between stream and lake habitats, following four primary life histories; fluvial (spawning in and residing in streams or migrating within river systems), adfluvial (spawning in streams and migrating to lakes), lake-resident (spawning in and residing in lakes), and anadromous (spawning in fresh water and migrating to the ocean). While the degree of anadromy of salmonids has been thoroughly compared (Rounsefell 1958; Quinn and Myers 2004; Spares *et al*. 2015), no such analogous review has examined the degree of lake use. Accordingly, the purpose of this paper is to compare the extent of reliance on lake habitat by the most widely studied salmonine taxa in their native Asian, European, African, and North American ranges, and thereby provide ecological information beneficial to their conservation and management.

We consider 16 species of salmon, trout, and charr from the genera *Oncorhynchus* (cutthroat trout – *O. clarkii*; pink salmon – *O. gorbuscha*; chum salmon – *O. keta*; coho salmon – *O. kisutch*; masu salmon – *O. masou*; rainbow trout – *O. mykiss*; sockeye salmon – *O. nerka*; Chinook salmon – *O. tshawytscha*), *Salmo* (Atlantic salmon – *S. salar*; brown trout – *S. trutta*), and *Salvelinus* (Arctic charr – *S. alpinus*; bull trout – *S. confluentus*; brook trout – *S. fontinalis*; white-spotted charr – *S. leucomaenis*; Dolly Varden – *S. malma*; lake trout – *S. namaycush*), comparing their 1) use of lakes as spawning habitat, 2) rearing strategies in lakes, and 3) occurrence and diversity of lacustrine trophic polymorphism. We identify the primary life history patterns of each species but also detail some lesser-known behaviors documented in lakes. We exclude studies of introduced populations, as the behavior in such systems often does not represent that expressed within the native range (e.g., adfluvial pink, Chinook, and coho salmon in the Laurentian Great Lakes –Wagner and Stauffer 1980, Carl 1982; rainbow trout spawning in previously fishless lakes of British Columbia – Northcote and Bull 2007). We include studies from dammed systems only when the life history expressed in that altered habitat is also known from natural populations (e.g., adfluvial masu salmon occur in both natural lakes and artificial reservoirs – Tamate and Maekawa 2000; Yamamoto *et al*. 2000). We do not consider distinct reproductive or trophic morphs to constitute separate species, and we treat *S. trutta* as a single species with five major evolutionary lineages (Bernatchez 2001). Within the genus *Oncorhynchus*, we exclude Gila trout (*O. gilae*) and Mexican golden trout (*O. chrysogaster*) because they only occur in headwater stream systems in their native range. We did not include species from the genera *Brachymystax*, *Hucho*, *Parahucho*, and *Salvethymus* due to a lack of relevant, published literature. It is important to note that many terms are applied in the literature to the various salmonid life histories, but their use is inconsistent. Our assessment of the life histories described in studies included in this review is based on the details provided in each paper but the terms we use when describing and categorizing a life history may not match those used in the paper(s) being cited.

We recognize that several forms of bias intrude into any review such as this. First, the different salmonid species share varying degrees of spatial overlap in their native ranges and, because the distribution of lakes is not random, they do not have equal opportunities to use lake habitats. Second, northern areas are vast and generally much less accessible to humans, so the opportunities to document unusual life history patterns are greatly reduced. This effect selectively affects the species found there, such as Arctic charr, which exhibit a latitudinal cline in the prevalence of anadromy (Rounsefell 1958). Consequently, the absence (or rarity) of documented cases of certain life history variants does not necessarily mean that they do not occur. Thus, an additional purpose of this paper is to encourage the documentation of such exceptional patterns, while still appreciating the broad differences among genera, species, and geographic regions. In each of the following interspecific comparison sections, the species least commonly spawning, rearing, or exhibiting trophic polymorphism in lakes are presented first and those most commonly doing so are presented last; species are grouped (irrespective of genera) according to their similarity in the extent and pattern of reliance on lakes.

INTERSPECIFIC COMPARISONS

Spawning Habitats

Salmonids spawn in stream, lake, and brackish-water habitats (Rounsefell 1958), but species differ in their relative use of each (Table 1). The development of embryos requires the flow of oxygenated water (e.g., Peterson and Quinn 1996; Greig *et al*. 2007), and streams are considered the typical spawning habitat for salmonids. In contrast, spawning in most areas of lakes is inhibited by a lack of water flow. Shoreline habitat used by lake-spawning salmonids is limited to areas with adequate flow of oxygenated water and appropriate substrate (Brabrand *et al*. 2002). Sufficient flow may be provided to shoreline spawning sites by groundwater upwelling from natural springs (Blanchfield and Ridgway 2005), groundwater from a proximate tributary penetrating through the lakeshore (Wilson 2014), or the gravity-driven pull of water at the transition from the lake to its outlet (Couturier *et al*. 1986). Less commonly, wind-driven currents may generate adequate flow for successful spawning near mainland or island shorelines (Leonetti 1997; Callaghan *et al*. 2016), or on deep reefs or bedforms (Riley *et al*. 2017) (Fig. 1). Areas of appropriate substrate may be determined by hydraulic processes and topography, as spawning sites must receive enough wave-action or current to prevent accumulation of fine particles but not so much that eggs become dislodged or physically shocked (Eshenroder *et al*. 1995; Marsden *et al*. 1995; Low *et al*. 2011). We found no examples of pink salmon, masu salmon, coho salmon, Chinook salmon, bull trout, or white-spotted charr spawning in lakes (Christie 1970; Savvaitova *et al*. 2007; Dunham *et al*. 2008; Quinn 2018); these species appear to be exclusively stream spawners, with the exception of pink salmon that also spawn in the intertidal zone of certain systems (Rounsefell 1958; Helle 1970).

Rainbow trout, cutthroat trout, Dolly Varden, and chum salmon almost exclusively spawn in streams, and lake-spawning populations represent rare exceptions. In Lake Crescent, Washington, USA, rainbow trout exclusively spawn in waters just above the lake outlet whereas cutthroat trout spawn in the outlet river, an inlet tributary to the lake, and along the lake's southwestern shoreline (Brenkman *et al*. 2014). In other systems, spawning by rainbow trout takes place in the flowing waters of the outlet, rather than in the lake itself (e.g., Lindsey *et al*. 1959; Schwanke and Hubert 2003). In Bull Run Lake, a montane system in Oregon, USA, cutthroat trout spawn in the lake's tributaries and on shoals of substrate in the lake; peak spawning in these two habitats is separated by 2-3 weeks (Saiget 2005). The only Dolly Varden known to spawn in lakes occur in geographically isolated systems on the Kamchatka Peninsula, eastern Russia. A derived population of Dolly Varden in Lake Dal'nee spawns in the littoral zone near the mouth of the only tributary (Esin *et al*. 2014). In contrast, the smallmouth and bigmouth morphs of Dolly Varden in nearby Lake Kronotskoe spawn in the profundal zone, whereas the other sympatric morphs spawn in the lake's many tributaries (Markevich *et al*. 2018). In North America, anadromous lake-spawning populations of chum salmon are known from the Kelly River lakes, Alaska, USA (James E. Seeb, University of Washington, pers. comm.) and Kluane Lake, Yukon, Canada (Wilson 2014). In Asia, chum salmon spawn on the beaches of lakes Peschanoe, Sopochnoe, and Lebedinoe on the Kuril Islands, Russia where they constitute a separate evolutionary lineage from sympatric river-spawners (Kaev and Romasenko 2003, 2010; Zhivotovsky *et al*. 2012).

Brown trout primarily spawn in streams but not uncommonly in lakes as well. Lake-spawning by brown trout is well studied in Norway (e.g., Jensen 1963; Andersen 1982; Brabrand *et al*. 2002), where redds are constructed along the mainland shore, or less commonly around an island (Barlaup *et al*. 1998). In western European systems, less numerous lake-spawning brown trout may co-occur with abundant stream-spawners (e.g., Ferguson and Taggart 1991; Matthews *et al*. 1997). Furthermore, derived populations of the *S. trutta* lineages spawn in the littoral, sub-littoral, and profundal zones of lakes in diverse regions such as the Italian Peninsula, Caucasus, Balkans, and Maghreb (e.g., Melotto and Alessio 1990; Savvaitova and Petr 1999; Sell and Spirkovski 2004; Doadrio *et al*. 2015).

Atlantic salmon and brook trout also primarily spawn in streams but not uncommonly in lakes. In many Newfoundland drainages, either anadromous *S. salar* or nonanadromous individuals (known as 'ouananiche') spawn in lakes, and the other life history form spawns in connected streams (Couturier *et al*. 1986; Claytor and Verspoor 1991), constituting genetically distinct populations segregated by spawning site (Birt *et al*. 1991; Verspoor and Cole 2005). Lake-spawning brook trout are found on the Avalon Peninsula of Newfoundland (Cowan and Baggs 1988) and in many lakes of the Laurentian Plateau (e.g., Curry and Noakes 1995; Blanchfield and Ridgway 1997), including large-bodied 'coaster' populations that spawn in bays of Lake Nipigon and Isle Royale, Lake Superior (Huckins *et al*. 2008).

Anadromous *O. nerka* (sockeye salmon) and the nonanadromous form (kokanee) spawn in both streams and lakes (Ricker 1938), and lake-spawning behavior is widely documented in East Asian and North American basins (e.g., Yegorova 1977; Bazarkin 1990; Burger *et al*. 1995; Whitlock *et al*. 2014). Three sympatric reproductive ecotypes of sockeye salmon in the Wood River lakes, Bristol Bay, Alaska exhibit genomic divergence associated with their river-, stream-, or mainland beach-spawning habitat (Larson *et al*. 2014, 2017), and to these three is added a fourth reproductive ecotype that spawns on island beaches in nearby Iliamna Lake (Blair *et al*. 1993; Gomez-Uchida *et al*. 2011) (Fig. 2). Similarly, genetic and morphological distinction of reproductive ecotypes of kokanee in Okanagan Lake, British Columbia is maintained by spatiotemporal isolation, as one form spawns in the lake a few weeks after the other spawns in tributaries (Taylor *et al*. 1997; Winans *et al*. 2003). The rarest and most unique reproductive ecotype of *O. nerka* is the black kokanee (treated as a separate species, *O. kawamurae*, by some authors), which is a darkly colored nonanadromous form that spawns in the profundal zones of lakes up to 300 m deep (Nakabo *et al*. 2011, 2014; Moreira and Taylor 2015) (Fig. 2).

Arctic charr and lake trout, the two species with the lowest degree of anadromy among those surveyed (Rounsefell 1958), predominantly spawn in lakes and rarely in streams. Lake spawning sites of Arctic charr are commonly shallow (Klemetsen *et al*. 2003; Low *et al*. 2011), however, when trophic morphs are present they sometimes segregate into littoral and profundal spawning zones (e.g., Alekseyev and Pichugin 1998; Skoglund *et al*. 2015; Knudsen *et al*. 2016). Additionally, morphs may segregate within the littoral zone, such as in Loch Rannoch, Scotland where one type spawns along shorelines unassociated with streams and the other type only spawns in the vicinity of an inlet (Walker *et al*. 1988). Relatively few Arctic charr populations spawn in streams or rivers, and those that do are almost exclusively either fluvial or anadromous (e.g., McCart 1980; Dempson and Green 1985; Jensen 1994); the only adfluvial population we identified is in Lake Frolikha, Transbaikalia (Gordeeva *et al*. 2015).

Lake trout broadcast spawn over a wide range of depths and substrates in lakes throughout their range in North America. In the Great Lakes, they most commonly spawn at shallow inshore sites near the mainland and islands (including algae beds), or at deep offshore sites over reefs and bedforms created by paleo-glacial activity (Kelso *et al*. 1995; Krueger and Ihssen 1995; Marsden *et al*. 1995; Riley *et al*. 2014, 2017). Stream-spawning by lake trout also occurs in select tributaries of lakes Nipigon and Superior (Dymond 1926; Loftus 1958). Recently, populations of lake trout were identified that exclusively spawn and reside in brackish-water drainage basins (1-11 psu) of the coastal Canadian Arctic (Kissinger *et al*. 2016, 2018).

Rearing Strategies

While some salmonids never enter a lake, others occupy lacustrine habitat for one or more life stage(s), representing a wide gradient of potential rearing strategies (phrases in quotations in this paragraph refer to rearing strategies displayed by the species listed in Table 2). By definition, fluvial fish do not rear in lakes, and anadromous populations may never enter a lake if their natal system is solely riverine or if they spawn downstream of a lake ("never"). Anadromous and otherwise fluvial fish may enter lakes only to overwinter without rearing there at other times of year ("overwinter only"). In systems where anadromous populations spawn upstream of a lake, fish may rear in transit, only foraging in the lake for a few weeks or months prior to entering marine waters ("rear in transit"). Anadromous fish may also rear in lakes from the fry to juvenile stage, migrating into the lake shortly after emergence or emerging from redds in the lake and rearing there for one or more years until they migrate to the ocean as juveniles ("fry to juvenile"). Additionally, anadromous fish may rear in lakes solely during the juvenile stage, spending the first year or more of life rearing in a natal stream before migrating to a lake and rearing for an additional year or more prior to ocean entry ("juvenile only"). Adfluvial fish may rear in lakes from the juvenile stage to maturity, spending the first year or more of life rearing in a natal stream before migrating to a lake and rearing until maturity ("juvenile to maturity [stream spawning]"). An alternative version of the preceding strategy occurs when fry emerge from redds in lakes and immediately migrate into a nearby tributary stream, rearing for a year or more before returning to the lake to continue rearing until maturity ("juvenile to maturity [lake spawning]"). Adfluvial and lake-resident fish may rear in lakes from the fry stage to maturity, with adfluvial fish entering the lake shortly after emergence and lake-residents emerging in a lake; both life history types then rear in the lake until maturity ("fry to maturity"). All species in this review facultatively rear and/or overwinter in lakes during at least one life stage, but the relative frequency of each strategy varies by species.

Pink and chum salmon typically do not rear in a lake, and exceptions are rare. Pink salmon fry transiting Lake Aleknagik, Alaska, USA rear there for up to a few weeks, growing 30-67% faster in fork length/day than sympatric sockeye salmon fry during that time (Robins *et al*. 2005). In lake systems of the Kuril Islands, Russia, the fry of river-spawning chum salmon begin feeding in coastal marine waters, whereas those of lake-spawning fish rear in the lake for a short period before entering the sea later that same year (Kaev and Romasenko 2010; Zhivotovsky *et al*. 2012; Zelennikov *et al*. 2016). Only one naturally adfluvial specimen has been recorded for pink salmon, a 2-yr old male that reared to maturity in Frazer Lake, Alaska, USA after fishways allowed colonization above what had been a barrier waterfall (Hennick *et al*. 1968). Similarly, an immature 4-yr old chum salmon was found in Langford Lake, British Columbia where it was likely trapped when the outlet stream dried up (Peden and Edwards 1976).

Most Chinook and coho salmon populations never rear in a lake, but some do so prior to becoming anadromous, and naturally-occurring adfluvial forms only occur in the latter species. When rearing in lakes, Chinook salmon pre-smolts typically only do so for a few months prior to ocean entry (e.g., Russell *et al*. 1980; Bendock 1989; Koehler *et al*. 2006; Tabor *et al*. 2011a,b), however, certain individuals feed in a lake for 1-5 years prior to seaward migration (Haw and Buckley 1963). An exceptional behavior of Chinook salmon occurs in a subpopulation in the Nanaimo River system, British Columbia; fry rear in streams for nearly a year but overwinter in lakes prior to outmigration (Carl and Healey 1984). Coho salmon that rear in lakes prior to becoming anadromous (Mason 1974; Blackmun *et al*. 1985; Ruggerone and Rogers 1992; Whitesel 1992) may enter as age 0+ fry and migrate to the ocean at age 1+ or older (Irvine and Johnston 1992; Kovach *et al*. 2014), and may therefore use lakes as both significant foraging and overwintering habitat (Russell *et al*. 1980; Swales *et al*. 1988; Quinn and Peterson 1996). Naturally adfluvial coho salmon occur in a few watersheds on both sides of the Pacific. In North America, adfluvial individuals (known as 'residuals') are the nonanadromous offspring of anadromous parents and occur within largely anadromous populations (Foerster and Ricker 1953; Ursitti 1989; Parkinson at al. 2016). In contrast, adfluvial individuals in eastern Russia, known as 'baydarka', primarily occur in naturally land-locked lakes where they constitute nonanadromous populations (Kurenkov *et al*. 1982).

White-spotted charr and masu salmon typically follow fluvial or anadromous life histories and do not use lacustrine habitat for rearing (*O. masou* - Tsiger *et al*. 1994, Morita and Nagasawa 2010; *S. leucomaenis* - Savvaitova *et al*. 2007). Naturally adfluvial white-spotted charr are only known to occur in Lake Peschanoe, Russia (Pichugin *et al*. 2006), whereas adfluvial masu salmon are present in at least five natural lakes in Japan (Osanai 1962; Yamamoto *et al*. 2000; Leonard *et al*. 2001; Kasugai *et al*. 2014). In adfluvial populations, white-spotted charr migrate into lakes at age 0+ and 1+ (Yamamoto *et al*. 1992), while masu salmon migrate at age 1+ and 2+ (Tamate and Maekawa 2000).

Dolly Varden are typically fluvial or anadromous and uncommonly adfluvial or lake-resident (Dunham *et al*. 2008; Taylor 2016). When adfluvial, Dolly Varden usually migrate to lakes after a year or more of stream-rearing (Esin *et al*. 2015; Markevich *et al*. 2017) and seldom enter as fry (Roos 1959; Bond *et al*. 2015). Dolly Varden display a rare version of this strategy in which some fry emerging from redds in a lake immediately migrate into a tributary stream where they rear for a year or more prior to re-entering the lake; the others emerge in the lake and remain lacustrine (Esin *et al*. 2014; only *S. fontinalis* and *S. alpinus* are also known to exhibit this behavior - Curry *et al.* 1997; May-McNally *et al.* 2015). Many anadromous Dolly Varden originating from a basin with a lake home, spawn in the natal river, and overwinter in that lake whereas many of those originating from basins without lakes home to their natal river to spawn but then leave and find a lake in a non-natal basin to overwinter (Armstrong 1970, 1974, 1984; Bernard *et al.* 1995).

Bull, rainbow, and cutthroat trout are commonly fluvial, adfluvial, or anadromous (Dunham *et al*. 2008; Quinn 2018), and exceptional instances of lake-resident populations only occur in the latter two species (e.g., Brenkman *et al*. 2014). Adfluvial bull and rainbow trout primarily first enter lakes at age 1+ or older (*S. confluentus* - Fraley and Shepard 1989, Mogen and Kaeding 2005, Sinnatamby *et al*. 2018; *O. mykiss* - Stables *et al*. 1990, Swales 2006, Holecek *et al*. 2012, Arostegui and Quinn 2018). In comparison, adfluvial cutthroat trout commonly enter lakes as both age 0+ fry and 1+ or older juveniles (Gresswell *et al*. 1994; Vinyard and Winzeler 2000; Nowak *et al*. 2004; Gresswell 2011). Fluvial bull trout (and other salmonids) that rear in streams may exclusively use a lake as a migratory corridor and/or as overwintering habitat (e.g., Bahr and Shrimpton 2004). Similarly, anadromous cutthroat trout migrate to lakes in natal or non-natal systems to overwinter (Armstrong 1971; Jones and Seifert 1997).

While Atlantic salmon, brook trout, and brown trout are commonly anadromous without having reared in lakes prior to smolting, and the latter two species are also commonly fluvial, these three species also include adfluvial and anadromous populations that rear in lakes during one or more life stages (Klemetsen *et al*. 2003; Huckins *et al*. 2008). Adfluvial or anadromous individuals may start rearing in lakes at age 0+ or older (e.g., *S. salar* - Hutchings 1986; *S. trutta* - Jonsson 1985, Matthews *et al*. 1997; *S. fontinalis* - Jardine *et al*. 2005, Huckins and Baker 2008); however, lake entry by fry seems to be rare in Atlantic salmon and brook trout (e.g., *S. salar* - Erkinaro *et al*. 1998, Gibson 2004; *S. fontinalis* - Wilder 1952, Huckins *et al*. 2008). Brook trout, brown trout, and Atlantic salmon are the only species identified in this review that sometimes rear in the natal stream for a year or more after emergence and then migrate to a lake where they rear for an additional year or more prior to becoming anadromous (*S. fontinalis* - Wilder 1952, Jardine *et al*. 2005; *S. trutta* - Jonsson 1985, Matthews *et al*. 1997; *S. salar* - Pepper *et al*. 1985, Hutchings 1986, O'Connell and Ash 1989, Halvorsen and Svenning 2000). Lake-resident populations of all three species, in which the full life cycle is completed in a lake, are uncommon but present throughout their native ranges (e.g., *S. salar* - Verspoor and Cole 2005; *S. fontinalis* - Huckins *et al*. 2008; *S. trutta* - Heggenes *et al*. 2009).

Anadromous sockeye salmon typically rear in lakes during at least one life stage, and nonanadromous kokanee are exclusively adfluvial or lake-resident. Stream- and lake-spawning individuals begin rearing in a lake at age 0+ (Ricker 1938). Anadromous fish rear in a lake for one or two years (and, rarely, more than two) prior to seaward migration as juveniles, and adfluvial and lake-resident kokanee rear in a lake until maturity without going to sea (Taylor 1999; Quinn 2018). Less commonly, anadromous populations originate from systems without lakes (or with limited lacustrine habitat) and the fry rear in streams and/or estuary areas prior to ocean entry (Gustafson and Winans 1999; Wood *et al*. 2008; Pavey *et al*. 2010, 2011; Simmons *et al*. 2013).

Arctic charr and lake trout predominantly follow a fully lake-resident life history but there are instances of other life history types and lake-rearing strategies (Klemetsen *et al*. 2003; Kissinger *et al*. 2016). Entirely fluvial populations of Arctic charr occur in isolated stream systems (McCart 1980), but we found no such examples in lake trout. Anadromous Arctic charr may migrate to the ocean as fry, rear in streams or lakes for over a year prior to initial ocean entry as juveniles, or exclusively utilize lakes as overwintering habitat (Moore 1975; Gyselman and Broughton 1991; Jensen 1994; Gyselman 1994; Mulder *et al*. 2018). In contrast, all anadromous lake trout rear in a lake for multiple years (up to 29) prior to the initial migration, and return to a lake to overwinter between annual ocean migrations (Swanson 2007; Swanson *et al*. 2010; Harris *et al*. 2014; Kissinger *et al*. 2016, 2018). In the rare adfluvial populations of lake trout and Arctic charr, it is unknown whether they migrate from the natal stream to a lake as age 0+ fry or age 1+ or older juveniles (*S. namaycush* - Dymond 1926, Loftus 1958; *S. alpinus* - Gordeeva *et al*. 2015).

Trophic Polymorphisms

Salmonids rearing in lakes often differ in morphology from conspecifics in streams (e.g., *O. kisutch* - Swain and Holtby 1989; *O. mykiss* - Keeley *et al*. 2005; *O. nerka* - Pavey *et al*. 2010) but species differ greatly in the occurrence and diversity of trophic polymorphism (Table 3). This term refers to sympatric ‘morphs’ of a species exhibiting distinct foraging habits, mouth and body morphology, adult size, and other associated traits (Smith and Skúlason 1996). Trophic morphs are differentiated from reproductive morphs by the primary source of selection; the former’s morphologies are determined by prey type and foraging environment characteristics (e.g., Ehlinger and Wilson 1988; Meyer 1989) whereas the latter’s are determined by spawning habitat characteristics (e.g., Quinn *et al*. 2001; Carlson *et al*. 2009; Larson *et al*. 2017). Trophic morphs may arise via phenotypic plasticity, whereby certain individuals in a population shift to a new foraging behavior (e.g., from invertivory to piscivory) and their morphology changes as they do so, or via evolutionary diversification, whereby morphs constitute genetically distinct populations maintained by reproductive isolation (Klemetsen 2010). The origin of sympatric morphs may be allopatric (separate colonization events by distinct genetic lineages) or sympatric (a single lineage that diverged after colonization) (Jonsson and Jonsson 2001). Among salmonids, trophic morphs almost exclusively occur in lakes, with a rare instance of riverine divergence occurring in lenok (*Brachymystax lenok* - Nakano 1999). We found no examples of trophic polymorphism in lakes in pink salmon, chum salmon, Chinook salmon, masu salmon, bull trout, white-spotted charr, or Atlantic salmon (Dunham *et al*. 2008; Klemetsen 2013), though we cannot rule out their existence.

Certain lakes support multiple life history forms of *O. mykiss* and *O. nerka*, or reproductive ecotypes of the latter, but only one lake for each of the two species has strong evidence of trophic polymorphism. Kootenay Lake, British Columbia supports two genetically distinct trophic morphs of rainbow trout; a larger, fast-growing, piscivorous form (known as the 'Gerrard' stock) that only spawns in the inlet Lardeau River, and a smaller, slow-growing, invertivorous form that spawns in other, diminutive tributaries (Taylor *et al.* 2019). In Lake Kronotskoe, Kamchatka, natural isolation of formerly anadromous spring and summer runs of sockeye salmon are thought to have yielded distinct kokanee populations with few or many gill-rakers that co-exist and exhibit distinct foraging habits (benthic vs pelagic), morphology, spawning age composition, and parasite loads, in addition to nearly full temporal- and partial spatial-isolation during spawning (Kurenkov 1978).

Lake Kronotskoe is also one of only two systems known to support sympatric lacustrine morphs of Dolly Varden. Five distinct morphs (white, longhead, nosed, smallmouth, and bigmouth) occur in sympatry (Markevich *et al*. 2018), and one of the morphs (nosed) exhibits three distinct submorphs (Markevich *et al*. 2017). These trophic morphs spawn at different sites in the lake and its tributaries, and are behaviorally segregated primarily by their occupation of the hypolimnion or epilimnion, and secondarily by their feeding habits (Markevich *et al*. 2018). In contrast, only two morphs (both littoral) occur in Lake Dal'nee, Kamchatka (Busarova *et al.* 2017). Where sympatric with bull trout or Arctic charr in North America, Dolly Varden tend to occupy streams and the other species occupies lakes (Taylor 2016). Thus, the rarity of lacustrine Dolly Varden morphs may be partially due to competitive exclusion from suitable lake habitats, as the species' native distribution largely overlaps with those of the other two species.

Brook trout display trophic polymorphism in at least five Laurentian Shield lakes but are limited to two sympatric forms. In all documented instances, brook trout diverged into pelagic and littoral morphs that primarily consume open-water or benthic prey, respectively (Bourke *et al*. 1997; Dynes *et al*. 1999; Marchand *et al*. 2003; Bertrand *et al*. 2008). The principal identifying character is the length of the pectoral fins (a genetically controlled trait); the littoral morph has longer fins that enhance its maneuverability near the bottom and the pelagic morph has shorter fins, better suited for cruising in open water (Proulx and Magnan 2002, 2004; Sacotte and Magnan 2006).

Trophic polymorphism of brown trout is common in lakes of northwest Europe, particularly Great Britain and Ireland, with the best-known form being the large, piscivorous 'ferox' trout. Small, young *S. trutta* forage on benthic macroinvertebrates in the littoral zones of lakes, but may gradually switch to a completely piscivorous diet, including cannibalism, once mouth gape-limitations have been surpassed (Grey 2001; Grey *et al*. 2002; Jensen *et al*. 2012). The exclusive consumption of fish enables ferox trout to delay sexual maturation and achieve greater size and age than typical brown trout in sympatry (Campbell 1971; 1979). In Scotland alone, 192 lakes are thought to currently or historically have ferox trout (Hughes *et al*. 2016). In Lough Melvin, Ireland, ferox co-occur with reproductively isolated and genetically distinct 'gillaroo' (littoral benthivore), and 'sonaghen' (pelagic planktivore) trophic morphs of *S. trutta* (Cawdery and Ferguson 1988; Ferguson and Taggart 1991; Fig. 3). Ferox trout in different systems of the British Isles are genetically more similar to each other than to sympatric brown trout (or gillaroo and sonaghen), apparently the result of independent post-glacial colonization by distinct lineages from multiple glacial refuges (Duguid *et al*. 2006; McKeown *et al*. 2010).

One of the most diversely polymorphic species is the lake trout, which exhibits two to four morphs in at least five lakes, differentiated by their trophic specialization, habitat occupancy, and mechanism of buoyancy regulation. Lake trout morphs most commonly emerge in large lakes where they become piscivorous or invertivorous and occupy shallow or deep habitats (Muir *et al*. 2016), indicating multiple parallel evolutionary events (Bernatchez *et al*. 2016). A shallow-water piscivorous form, referred to as the 'lean' morph, is slim-bodied with low lipid content, strongly contrasting with the 'fat' morph or 'siscowet', a deep-water piscivore that is deep bodied, high in lipids, and consumes different fish species (Zimmerman *et al*. 2006; Ray *et al*. 2007; Hansen *et al*. 2016). The 'humper' morph, an invertivore, occupies mid-water and exhibits lipid content intermediate to the lean and fat trout (Eschmeyer and Phillips 1965; Muir *et al*. 2016). These three morphs diverge in their relative use of hydrodynamic (swimming and gas bladder) and hydrostatic (lipid content) mechanisms of buoyancy regulation (*sensu* Eshenroder *et al*. 1999). In Lake Superior there is a fourth sympatric 'redfin' morph that is comparatively understudied (Muir *et al*. 2014). Unlike other systems where lake trout segregate into the shallow and deep habitats, Great Bear Lake, Canada supports four distinct shallow-water morphs (Chavarie *et al*. 2013).

Sympatric morphs of Arctic charr are widespread throughout the species' distribution and well documented in lakes of northwest Europe (Jonsson and Jonsson 2001; Klemetsen 2010), North America (Reist *et al*. 1995; O'Connell and Dempson 2002; Power *et al*. 2009; Woods *et al*. 2013), and eastern Asia (Alekseyev *et al*. 2002; Gordeeva *et al*. 2015). Most Arctic charr morphs are one of three types; normally sized planktivores (pelagic), dwarf benthivores (littoral or profundal), or large piscivores (Jonsson and Jonsson 2001; Gordeeva *et al*. 2015). Morphs diverging along the pelagic-benthic axis often constitute genetically distinct populations, whereas piscivorous morphs generally represent ontogenetic shifts by some individuals in a population (Klemetsen 2010). While most lakes with Arctic charr morphs support two or three distinct forms, Thingvallavatn, Iceland, with a complex lava bottom uncommon in other systems, is the only lake known to support four sympatric morphs; small and large benthivores, pelagic planktivores, and pelagic piscivores (Jonsson *et al*. 1988; Sandlund *et al*. 1992). The pervasive and diverse trophic polymorphism of Arctic charr, including virtually unpigmented, profundal dwarfs with degenerated eyes (Søreide *et al*. 2006; Klemetsen 2010), makes it one of the most phenotypically variable vertebrates (Klemetsen 2013).

DISCUSSION

Comparison of the Extent of Lake Reliance

In comparing the relative frequency of both the primary life history patterns and lesser-known lacustrine behaviors it is evident that, among species of the three genera considered in this review, the extent of reliance on lakes exhibits a negative association with the degree of anadromy. *Oncorhynchus* exhibits the least lake reliance, *Salmo* an intermediate level, and *Salvelinus* the greatest; opposite of the anadromy spectrum identified by Rounsefell (1958) and Spares *et al*. (2015). The semelparous species of the genus *Oncorhynchus* largely consist of anadromous species that either never or only rarely spawn in lakes, seldom rear in lakes, and do not exhibit trophic polymorphism. The primary exception is *O. nerka*, the lacustrine adaptations of which are unparalleled in the genus (Behnke 1972; Wood *et al*. 2008; Veale and Russello 2017). Rainbow and cutthroat trout (both iteroparous) represent additional exceptions to this pattern, as they commonly are adfluvial. Both species in the genus *Salmo* spawn in lakes (though not typically), often rear in lakes prior to becoming anadromous, and form adfluvial and, less commonly, lake-resident populations, but the widespread presence of trophic polymorphism in *S. trutta* makes it more lacustrine than *S. salar*. The genus *Salvelinus* includes the only species that predominantly spawn in lakes, naturally adfluvial or lake-resident populations of all species, and the highest occurrence and diversity of trophic polymorphism. The rarity of *S. alpinus* and *S. namaycush* populations that do not spend their entire lives in lakes, relative to populations in which the full life cycle is completed in a lake (Maitland 1995; Muir *et al*. 2016), confirms their status as the least anadromous (Rounsefell 1958) and most lacustrine.

The negative relationship between the degree of anadromy and the extent of lake reliance was not a given, as the less strongly anadromous species could have been more stream- than lake-reliant. Notably, while exclusively fluvial populations occur in many salmonid taxa, no species in this review that exhibits self-sustaining, nonanadromous populations fails to use lakes in at least part of its native range. For example, most species in this review exhibit fluvial populations but also exhibit adfluvial and/or lake-resident populations in sympatry or allopatry (e.g., *O. mykiss*, *S. trutta*, *S. fontinalis*). Nearly all nonanadromous populations of *S. salar* and *S. alpinus* are adfluvial or lake-resident; exclusively fluvial populations are exceptions (Klemetsen *et al.* 2003; Hutchings *et al.* 2019). In addition, all nonanadromous populations of *O. kisutch*, *O. nerka*, and *S. namaycush* are either adfluvial or lake-resident, and no fluvial individuals have ever been recorded. Chinook salmon is the only species we reviewed with naturally fluvial but not adfluvial or lake-resident individuals occurring in undammed systems of its native range; however, the nonanadromous individuals mature as fluvial male parr in largely anadromous populations and never constitute exclusively fluvial populations (e.g., Gebhards 1960; Taylor 1989; Foote *et al*. 1991; Mullan *et al*. 1992; Quinn 2018).

Lakes Support Anadromous and Fluvial Life Histories

Lakes differ from streams and rivers in a number of prominent aspects, including the reduction in flow (hence reduced energetic cost), thermal stratification (providing opportunity for more extensive behavioral thermoregulation), and persistence during low flow periods (in the summer when streams may dry, or winter when they may freeze). Lakes and streams also differ in the quantity, quality, and seasonality of food resources, and the communities of predators and competitors as well (Willis and Magnuson 2000; Keeley and Grant 2001). Consequently, the complex use of lakes by salmonids was not unexpected, but there were patterns in this spectrum of utilization, and sympatric salmonids often use lakes to very different extents.

While lakes are critical to the population health and stability of adfluvial and lake-resident populations of salmonids, they also support anadromous and fluvial life histories. Lakes provide rearing habitat (often superior to streams) for nearly all salmonid taxa prior to becoming anadromous. For example, Atlantic salmon parr rearing in lakes exhibited greater growth (Pepper *et al*. 1985; Hutchings 1986), body condition (Erkinaro *et al*. 1995; Dempson *et al*. 2004), and size-at-age (Erkinaro and Gibson 1997; Halvorsen and Svenning 2000; Jardine *et al*. 2005) compared to counterparts rearing in streams. Semelparous species that may rear for a year or more in freshwater (*O. tshawytscha*, *kisutch*, *nerka*) also utilize lakes as vital overwintering habitat prior to their sole oceanic migration (e.g., Carl and Healey 1984; Swales *et al*. 1988; Quinn and Peterson 1996). Iteroparous species (*O. clarkii*, *O. mykiss*, *Salmo* spp., *Salvelinus* spp.) may further depend on lakes as overwintering habitat between return spawning and oceanic foraging migrations (e.g., Bardonnet and Baglinière 2000; Klemetsen *et al*. 2003; Gruzdeva *et al*. 2015; Kissinger *et al*. 2018). Anadromous adults may also migrate back into fresh water and take refuge in lakes for months prior to spawning (e.g., *O. nerka* - Hodgson and Quinn 2002, Newell and Quinn 2005; *S. salar* - Reed *et al*. 2017), a pattern enabling such fish to avoid mortality at sea and/or unfavorable temperature or flow conditions in-stream during the summer (Quinn *et al*. 2016). While most fluvial salmonids never encounter or enter a lake, some utilize lacustrine overwintering habitat and spend the rest of their time rearing in streams (e.g., *S. trutta* - Jonsson 1985; *S. confluentus* - Bahr and Shrimpton 2004). Thus, lakes support the life history diversity of salmonids, including those predominantly occupying marine and /or fluvial waters.

Similarities of Adfluviality and Anadromy

Adfluvial salmonids exhibit migration-associated traits and behaviors similar to anadromous individuals, using lakes as 'miniature seas' although they are nonanadromous (Rounsefell 1958). The smolting process of adfluvial salmonids is parallel to that of adfluvial fish; most notably, they lose their parr marks and acquire silvery coloration suited to the open water environment (e.g., *S. salar* - Staurnes *et al*. 1992; *S. fontinalis* - McKinney *et al*. 2014; Fig.

4). In partially migrant nonanadromous populations, where individuals may either follow a fluvial or adfluvial life history, females exhibit a bias for migration and males for residency (e.g., *S. malma* – Maekawa and Onozato 1986; *S. leucomaenis* – Nakano *et al*. 1990; *O. clarkii* – Kaeding and Koel 2011; *O. mykiss* – Holecek and Scarnecchia 2013), following a pattern also seen in partially anadromous populations (e.g., *S. leucomaenis* – Yamamoto *et al*. 1999; *O. masou* – Morita and Nagasawa 2010; *O. tshawytscha* – Larsen *et al.* 2013; *O. mykiss* – Ohms *et al*. 2014). Furthermore, adfluvial populations may also contain the nonanadromous equivalent of 'jacks', sexually mature males that spawn at least a year younger than the youngest females in the population (e.g., *O. kisutch* - Kurenkov *et al*. 1982; *O. masou* - Yamamoto *et al*. 2000, Tamate and Maekawa 2004; *O. mykiss* - Holecek and Scarnecchia 2013). Adfluvial populations have emerged in numerous post-glacial systems in the last 15,000 years due to either natural isolation from the ocean (e.g., *O. nerka* - Kurenkov 1978; *O. kisutch* - Kurenkov *et al*. 1982) or experience of growing conditions favorable to nonanadromy (e.g., *O. mykiss* - Quinn and Myers 2004; *O. nerka* - Wood *et al*. 2008). In post-glacial systems colonized by anadromous ancestors, adfluvial fish represent a derived form (e.g., *O. mykiss* - Arostegui *et al*. 2019*; O. nerka* - Wood *et al*. 2008; *S. salar* - Nilsen *et al*. 2003; *S. trutta* - Lemopoulos *et al*. 2018). In the case of species with anadromous, adfluvial, and fluvial individuals (e.g., *S. trutta*), fluvial and adfluvial or fluvial and anadromous fish often co-occur but there is almost no evidence of all three life history types occurring in sympatry in a single, natural (undammed) system (see Jonsson 1985 for a possible exception). Coastal drainages are often devoid of lakes (precluding adfluviality) and many stream-lake systems are land-locked (precluding anadromy). In the reviewed stream-lake systems with marine access (where all three life histories could occur), only one of the migratory alternatives (adfluvial or anadromous) is documented as co-occurring with a resident fluvial form; however, it seems likely that there are systems in which the tradeoff between habitat-specific growth opportunity, migration difficulty, and mortality risk balance out and yield a life history triple point.

Life History Changes in Artificial Lakes

The construction of impassable dams fragments existing riverine habitat, creates new lacustrine habitat, and can cause salmonids to adopt a different, and sometimes novel, life history. A formerly anadromous, and currently adfluvial, population of redband trout (*O. mykiss gairdnerii*) persists above a dam on Mann Creek, Idaho, USA, where individuals continue to undergo a smolting process of increasing silver skin reflectance and gill Na^+/K^+ ATPase activity as they migrate into the reservoir where they rear until maturity (Holecek *et al*. 2012; Holecek and Scarnecchia 2013). Similarly, damming of the Uryu River, Hokkaido, Japan in 1943 led to the development of adfluvial populations of previously anadromous masu salmon that exhibit the same relationship between individual growth and parr-smolt phase differentiation as anadromous populations elsewhere (Osanai 1962; Tamate and Maekawa 2000, 2002). Chinook salmon populations spawning in rivers (once used by anadromous fish) above dams in California, Oregon, and Washington, USA also adopted adfluvial life histories (Romer and Monzyk 2014; Perales *et al*. 2015; Brenkman *et al*. 2017), a pattern not seen in any undammed system throughout the species' native range.

Impassable dams may not only force anadromous populations to become adfluvial, but also enable fluvial salmonids to transition to an adfluvial life history. Prior to the damming of the Joganji River and construction of the artificial Arimine Lake, Honshu, Japan in 1962, white-spotted charr in the system were exclusively fluvial and dwarfed. Afterwards, many white-spotted charr began migrating into the lake, where they achieved greater sizes and more silver coloration than sympatric fluvial fish prior to returning to tributaries to spawn (Nakano *et al*. 1990; Yamamoto *et al*. 1992; Maekawa *et al*. 1994). This case suggests that the reservoir provides greater feeding opportunities, size, and, therefore, fecundity benefits that outweigh the minimal migration cost and any potential increase in mortality.

Areas for Future Research

While there is substantial documentation of the phenotypic diversity in salmonids, more conservation genomic studies are needed to fully understand the genetic basis of alternative phenotypes. A substantial portion of the salmonid genome consists of residual tetraploid (duplicated) loci rather than typical diploid loci (Lien *et al.* 2016) due to an ancestral whole genome duplication event (Ohno 1970); however, such loci could not be included in genomic studies until recently due to analytical limitations (Limborg *et al.* 2016). Duplicated genes may acquire new functions, optimize pre-existing functions, and increase dosage benefits (Conant and Wolfe 2008), and are more responsive to selection pressures than diploid loci (Charlesworth 2009). Thus, duplicated genes disproportionately expand the adaptive capacity and potential phenotypic complexity of organisms with at least partially duplicated genomes (Freeling and Thomas 2006). Initial investigations of duplicated loci in *O. nerka* identified outliers of putative adaptive significance among migratory phenotypes (anadromous sockeye salmon and nonanadromous kokanee) and among reproductive ecotypes (stream-, river-, and beach-spawning sockeye salmon) (Limborg *et al.* 2017).

Another type of genomic feature increasingly recognized as promoting phenotypic diversity is a chromosomal inversion; this is a form of supergene in which hundreds or thousands of co-adapted alleles are inherited as one, rather than homogenized as typically occurs under conditions of high gene flow with non-inverted chromosomes (Rieseberg 2001). Alternative ecotypes of multiple plant and animal species are supported by chromosomal inversions (e.g., Hall's panicgrass, *Panicum hallii*, Poaceae – Lowry *et al.* 2015; Atlantic cod, *Gadus morhua*, Gadidae – Sodeland *et al.* 2016). Most recently, a large chromosomal inversion was characterized in *O. mykiss* in which one haplotype promotes stream-residency while the other promotes migration to the ocean (Pearse *et al.* 2018) or to lakes (Arostegui *et al.* 2019). Increasing the number of individuals sequenced and populations studied for each salmonid species will facilitate identification of duplicated loci, chromosomal inversions, and other genomic features influencing phenotypic expression.

Conclusion

Lakes provide spawning and rearing habitat for salmonids and support life history variants, reproductive ecotypes, and trophic morphs unique to lacustrine habitats. In addition to streams, estuaries, and oceans, lakes provide habitats where salmonids may diversify, facilitating local adaptation (Taylor 1991) and augmenting population and meta-population stability via the portfolio effect (Schindler *et al*. 2010). If the life history variants associated with lakes and streams represent phenotypically plastic responses to those conditions, then the stability of the population as a whole benefits from the buffering effect of each habitat, as they may be more or less productive under different environmental conditions. On the other hand, if the populations using the different habitats are discrete and reproductively isolated, then their conservation depends on the quality of and access to those habitats. In either case, fisheries management and habitat protection require a more complete appreciation of the extent of lake use by the fish, and the ecological and evolutionary basis of the different forms. There are strong links between habitat heterogeneity, trait diversity, population diversity, and resilience (Herbold *et al*. 2018), and habitat degradation may reverse speciation and reduce diversity of salmonids in lakes (Vonlanthen *et al*. 2012). Thus, the continued viability of healthy salmonid populations and the recovery of imperiled ones hinge upon our ability to maintain the quality and diversity of their habitats (McElhany *et al*. 2000), including lakes upon which they rely.

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TABLES

Table 1 – Spawning habitat use by salmonids, scored by frequency; (+++) - common, (++) – not uncommon, (+) – rare, (*) – exceptional. Within genera, species are ranked by the frequency of lake-spawning. Frequencies were determined qualitatively based on our assessment of the 350+ manuscripts read in the preparation of this review and paralleled the scoring system of Klemetsen (2013).

		Spawning Habitat		
Genus	Species	Brackish	Stream	Lake
Oncorhynchus	*gorbuscha*	+	+++	
	tshawytscha		+++	
	kisutch		+++	
	masou		+++	
	mykiss		+++	*
	clarkii		+++	*
	keta	+	+++	+
	nerka		+++	++
Salmo	*salar*		+++	++
	trutta		+++	++
Salvelinus	*leucomaenis*		+++	
	confluentus		+++	
	malma		+++	*
	fontinalis		+++	++
	alpinus		+	+++
	namaycush	*	+	+++

Table 2 – Rearing strategies of salmonids in lakes, scored by frequency; (+++) – common, (++) – not uncommon, (+) – rare, (*) – exceptional. Within genera, species are ranked from the least (top) to most (bottom) lake-reliant. Abbreviations of rearing strategies; N – never, O – overwinter only, RT – rear in transit, FJ – fry to juvenile, J – juvenile only, JM^S – juvenile to maturity [stream spawning], JM^L – juvenile to maturity [lake spawning], FM – fry to maturity. See the first paragraph of Interspecific Comparisons: *Rearing Strategies* for definitions of the rearing strategies. Frequencies were determined qualitatively based on our assessment of the 350+ manuscripts read in the preparation of this review and paralleled the scoring system of Klemetsen (2013).

		Rearing Strategies							
Genus	Species	N	O	RT	FJ	J	JM^S	JM^L	FM
Oncorhynchus	*gorbuscha*	+++		+					*
	keta	+++		+					*
	tshawytscha	+++	*	++	+				
	kisutch	+++			++				+
	masou	+++					++		
	mykiss	+++					+++		+
	clarkii	+++	+				+++		+++
	nerka	++			+++				+++
Salmo	*salar*	+++			+	++	+++		++
	trutta	+++	+		++	+	+++		+++
Salvelinus	*leucomaenis*	+++					*		*
	malma	+++	++				+	*	+
	confluentus	+++	+				+++		+
	fontinalis	+++				+		*	++
	alpinus	+	+		+			*	+++
	namaycush				+				+++

Table 3 – Occurrence of trophic polymorphism in lakes, scored by frequency; (+++) - common, (++) – not uncommon, (+) – rare, (*) – exceptional. Within genera, species are ranked first by the frequency of occurrence of trophic polymorphism and second by the maximum number of trophic morphs documented in a single lake. Frequencies were determined qualitatively based on our assessment of the 350+ manuscripts read in the preparation of this review and paralleled the scoring system of Klemetsen (2013).

		Trophic Polymorphism	
Genus	Species	Occurrence	Max # of Morphs
Oncorhynchus	*gorbuscha*		
	keta		
	tshawytscha		
	kisutch		
	masou		
	clarkii		
	mykiss	*	2
	nerka	*	2
Salmo	*salar*		
	trutta	+++	3
Salvelinus	*leucomaenis*		
	confluentus		
	malma	*	5
	fontinalis	+	2
	namaycush	+	4
	alpinus	+++	4

FIGURES

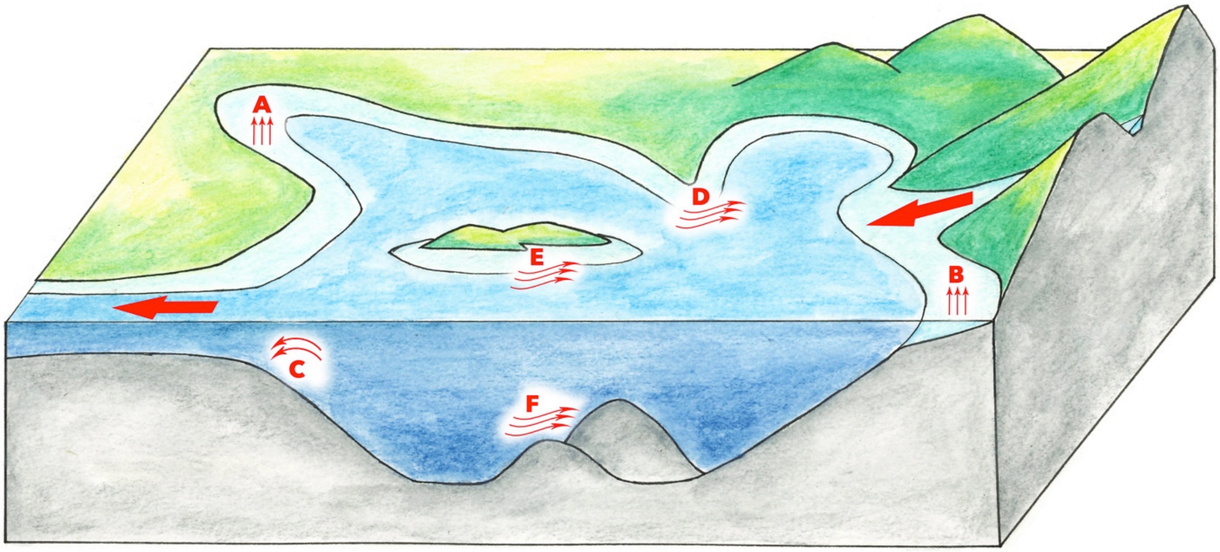

Figure 1 – Spawning sites used by salmonids in lakes. Littoral sites occur at (A) natural springs, (B) mainland shorelines proximal to an inlet tributary, (C) mainland shorelines proximal to an outlet, (D) mainland shorelines unassociated with a stream, and (E) island shorelines. Sub-littoral/profundal sites occur at (F) deep reefs/bedforms. Duplicate arrows at sites demarcate the source of water flow; upwelling groundwater (straight, upward), gravity-driven current (curved, downward), wind-driven current (wavy, horizontal). Single, bold arrows indicate the direction of inlet and outlet water flow. Artwork by Jason Ching.

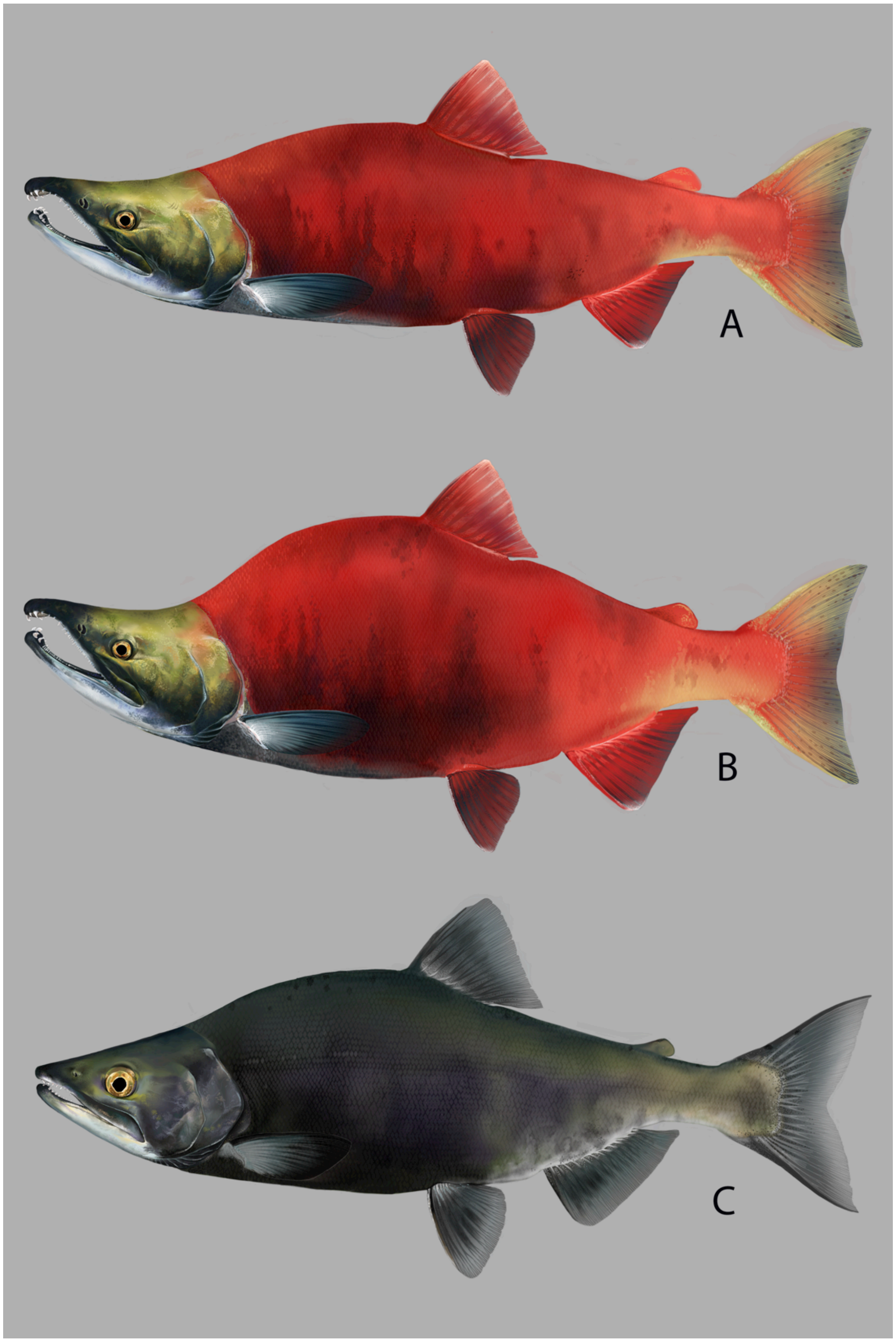

Figure 2 – Reproductive ecotypes of *Oncorhynchus nerka*, represented by males in spawning coloration and morphology; (a) stream-spawning sockeye salmon, (b) mainland beach-spawning sockeye salmon, (c) profundal-spawning black kokanee. River-spawning sockeye salmon are morphologically intermediate to (a) and (b), and island beach-spawning sockeye salmon are morphologically similar to (b). Artwork by Brandon Li.

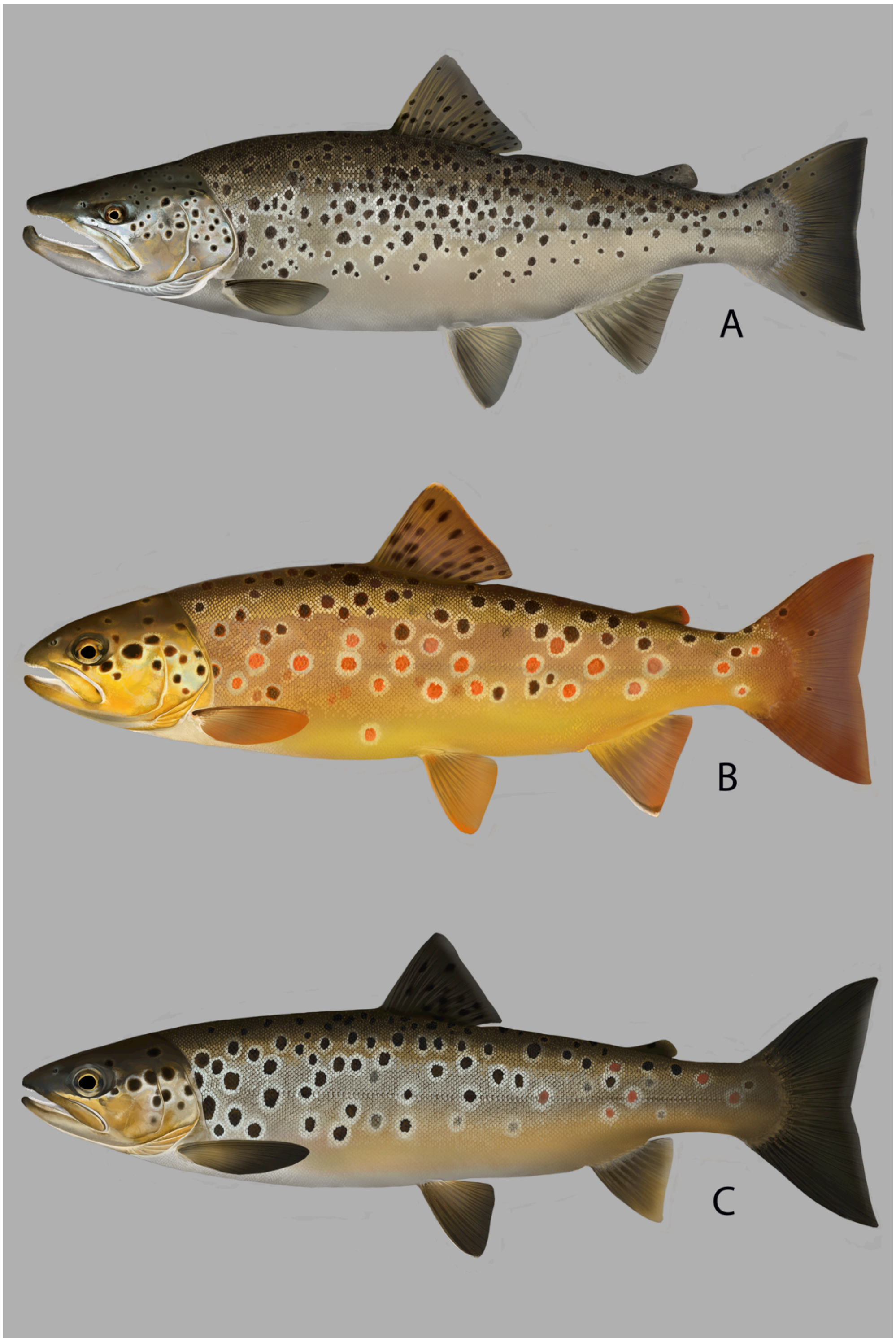

Figure 3 – Trophic morphs of *Salmo trutta*; (a) ferox – piscivore, (b) gillaroo – benthivore, (c) sonaghen – planktivore. The coloration and spotting patterns may vary among individuals and among populations in different lakes. Artwork by Brandon Li.

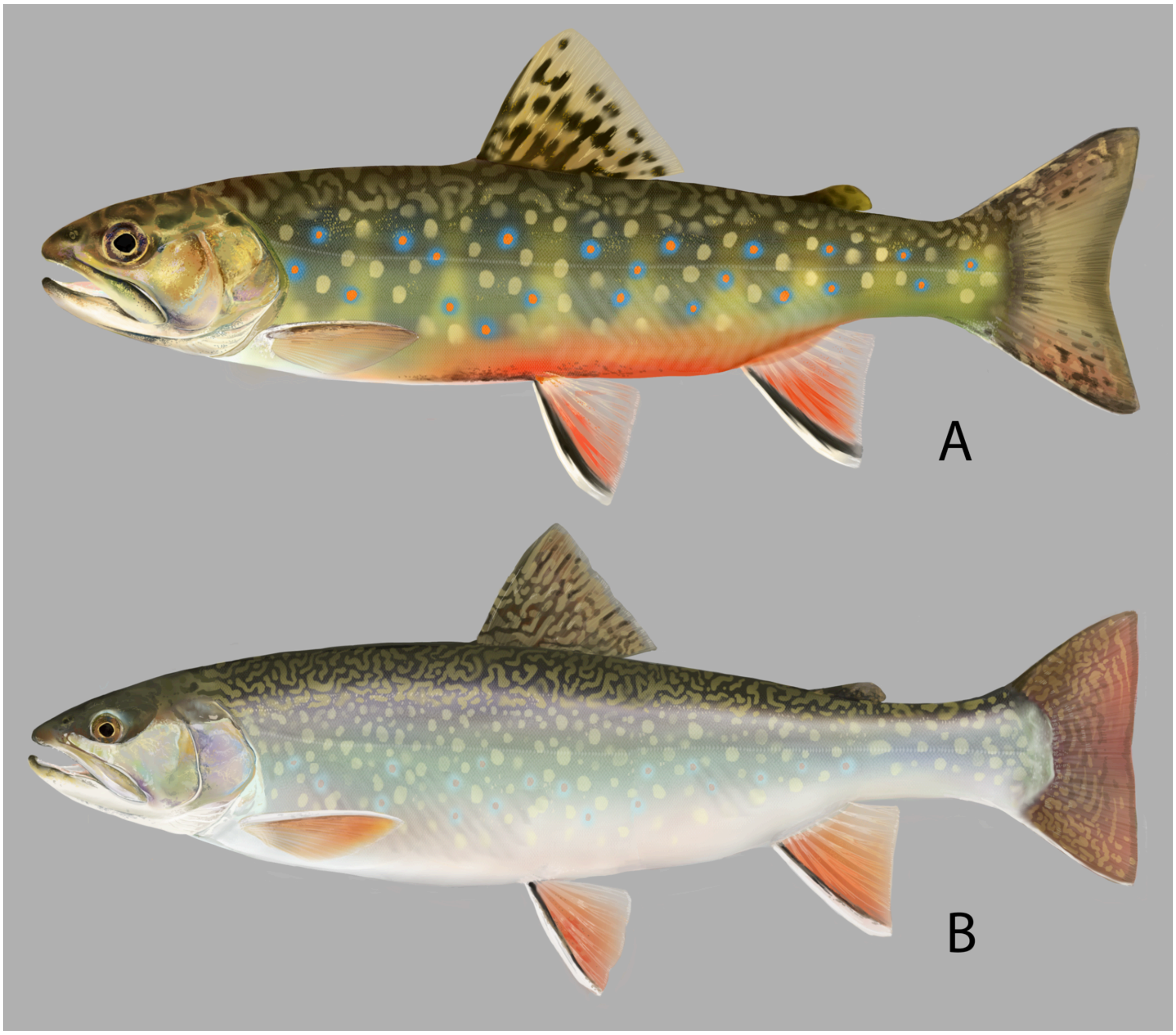

Figure 4 – Nonanadromous life history types of *Salvelinus fontinalis*, represented by individuals in non-spawning coloration and morphology; (a) fluvial and (b) adfluvial/lake-resident. The coloration and morphology may vary among individuals and among populations of the same life history. Artwork by Brandon Li.