



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

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

Arostegui, M. C.*, and Quinn, T. P.

School of Aquatic and Fishery Sciences, Box 355020, University of Washington
Seattle, WA 98195

*Corresponding Author:
marosteg@uw.edu
786-239-3595
ORCID: 0000-0002-9313-9487

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.

Keywords: Arctic char, diet, Dolly Varden, lake, *Oncorhynchus mykiss*, partial migration, rainbow trout, stable isotopes, stream

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 $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ is a complementary method for evaluating life history diversity through trophic position and habitat. The $\delta^{15}\text{N}$ 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 $\delta^{13}\text{C}$ 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 km² and volume of 1151 km³, 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 $\delta^{15}\text{N}$ or $\delta^{13}\text{C} = ([R_{\text{sample}} / R_{\text{standard}}] - 1) \times 1000$, with $R = {}^{15}\text{N}/{}^{14}\text{N}$ or ${}^{13}\text{C}/{}^{12}\text{C}$ (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 $\delta^{13}\text{C}$ values, but effects are inconsistent (Sarakinis 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 $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ 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 $\delta^{15}\text{N}$ (Heady and Moore 2013), and a study of another fish species demonstrated that $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ 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 $\delta^{13}\text{C}$ between habitat-specific prey and $\delta^{15}\text{N}$ 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 (\pm 1 SD) $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ 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 $\delta^{13}\text{C}$ values primarily in the range between lake benthic invertebrates and sockeye salmon eggs (Table 2; Fig. 3). Cluster 1 fish exhibited less enriched $\delta^{15}\text{N}$ and a greater range of $\delta^{13}\text{C}$ 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 $\delta^{13}\text{C}$ values primarily in the range between stream aquatic invertebrates/ hymenopterans and sockeye salmon eggs (Table 2; Fig. 3). Cluster 3 fish exhibited more enriched $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ 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 $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values generally along the axis between stream aquatic invertebrates/ hymenopterans and sockeye salmon eggs (Fig. 4). Arctic char, exclusively from the lake,

exhibited $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ 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 $\delta^{13}\text{C}$ 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 $\delta^{13}\text{C}$ 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 $\delta^{13}\text{C}$ 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 $\delta^{13}\text{C}$ 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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Conflict of Interest

We declare no conflict of interest.

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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 (***)

| Diet Category | Mean Proportion by Habitat | | | NMDS Results | | |
|----------------------|----------------------------|--------------|-------|--------------|--------|----------|
| | 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 ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) signatures. Fork length (mean \pm 1 standard deviation for each cluster) is provided; superscripts indicate clusters that did not differ significantly based on Kruskal-Wallis post-hoc multiple comparisons.

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

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

| Cluster | Diet End Members | | |
|---------|--|------------------------|-------------------------------|
| | 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) |

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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.

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 coded: stream (green), stream mouth (black), lake (blue). Significant diet items (those explaining the majority of the variance among fish) and their vector loadings (Table 1) are indicated in red.

Figure 3 – Biplot of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ for rainbow trout (*Oncorhynchus mykiss*) sampled in stream, stream mouth, and lake habitats. Consumer $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ 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 coded by cluster assignment: 1 (red), 2 (black), 3 (green), 4 (blue). Diet end member values (mean \pm 1 SD) are included.

Figure 4 – Biplot of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ for rainbow trout (*Oncorhynchus mykiss*), Dolly Varden (*Salvelinus malma*), and Arctic char (*Salvelinus alpinus*). Consumer $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ 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 coded: Dolly Varden (orange), Arctic char (red), stream-type rainbow trout (clusters 3 and 4; green), lake-type rainbow trout (clusters 1 and 2; blue). Diet end member values (mean \pm 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.

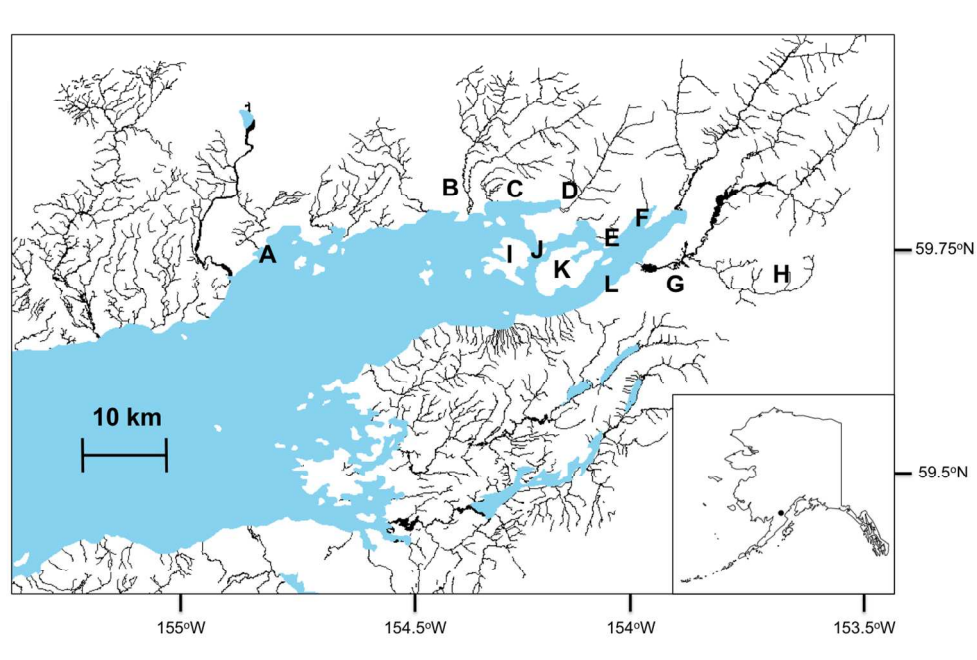


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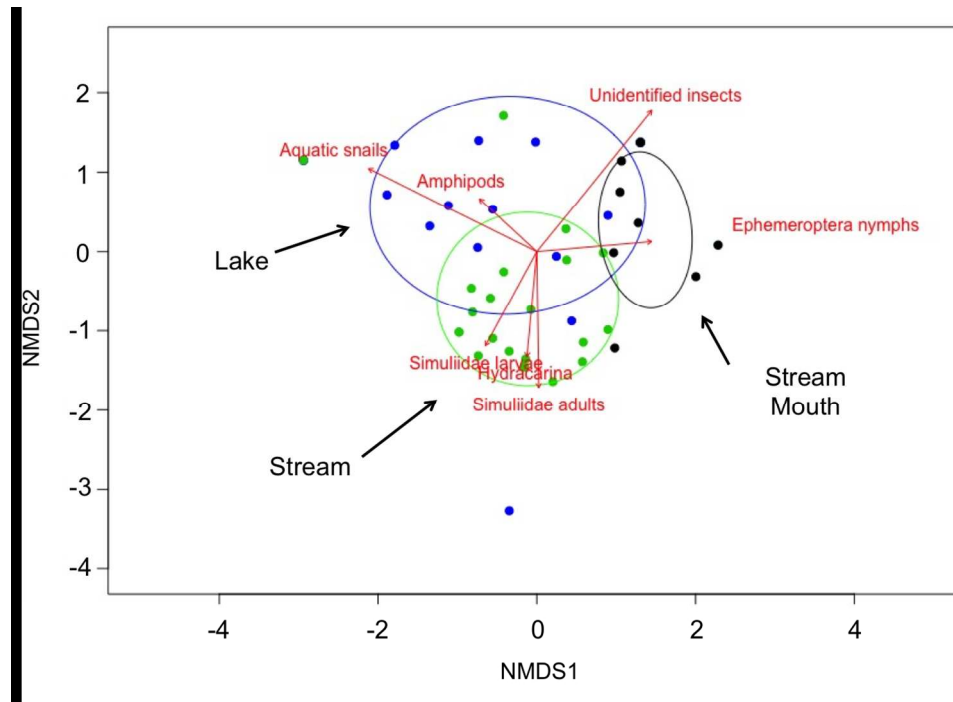


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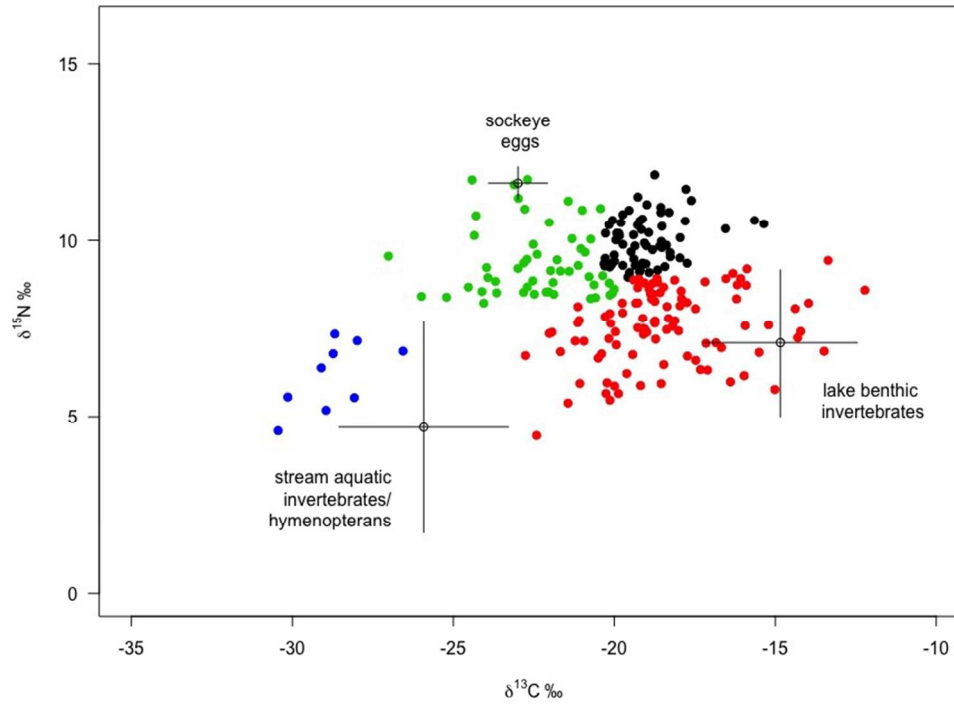


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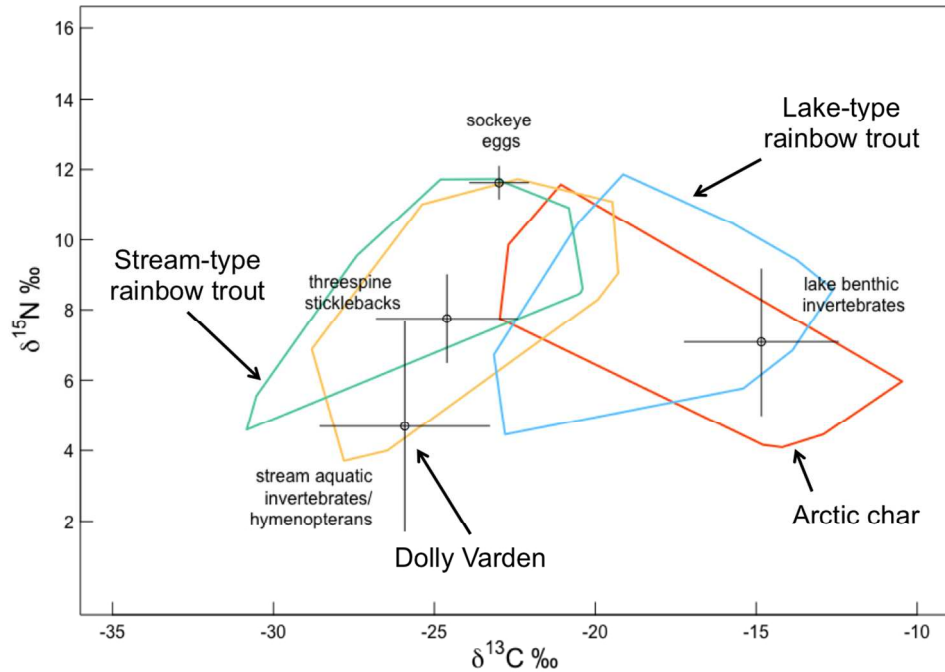


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