

Diversity of life history traits, growth, and lipid storage in migratory variants of steelhead and rainbow trout (*Oncorhynchus mykiss*) in Kamchatka, Russia

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Abstract

Partial migration in salmonids provides access to freshwater and marine feeding environments varying in productivity. To test the hypothesis that partial migration drives differences in growth and energy storage with differential consequences for females than males, we assigned *Oncorhynchus mykiss* sampled on the western Kamchatka Peninsula, Russia, to one of five life history contingents based on scale patterns. Stable isotopes, obtained from a subset of fish, indicated different foraging by fish showing oceanic and coastal anadromous life histories. In younger fish, body size was largest in anadromous fish feeding on the high seas, intermediate for those feeding in coastal environments, and smallest for nonanadromous fish feeding in rivers. Older fish converged on large (oceanic) and small (coastal and freshwater) body sizes. Somatic lipid content, also collected for a subset of fish, averaged 2.5% across all life histories. Percent lipid was highest in females of ocean and males of coastal and freshwater life histories. Taken together, migratory patterns predictably influenced growth but may limit compensatory lipid storage in females, especially for the rare life histories.

Résumé

La migration partielle chez les salmonidés donne accès à des milieux d'alimentation en eau douce et en mer de différentes productivités. Pour valider l'hypothèse selon laquelle la migration partielle est à l'origine de différences sur le plan de la croissance et du stockage d'énergie qui ont des conséquences différentes pour les mâles et les femelles, nous avons affecté des *Oncorhynchus mykiss* prélevés dans l'ouest de la péninsule du Kamtchatka (Russie) à un ou l'autre de cinq contingents de différents cycles biologiques, établis à la lumière des motifs d'écailles. Des analyses d'isotopes stables obtenues d'un sous-ensemble de poissons indiquent que les cycles biologiques océanique et côtier anadromes sont associés à différentes habitudes de quête de nourriture. Parmi les poissons plus jeunes, les plus grandes tailles du corps sont observées chez les poissons anadromes s'alimentant en haute mer, les tailles intermédiaires chez poissons anadromes qui s'alimentent dans des milieux côtiers, et les tailles plus petites chez les poissons non anadromes s'alimentant en rivière. Les poissons plus vieux convergent vers de grandes (océanique) et petites (côtier, eau douce) tailles du corps. La teneur en lipides somatique, également mesurée pour un sous-ensemble de poissons, est en moyenne de 2,5 % pour tous les cycles biologiques. Le pourcentage lipidique est le plus élevé chez les femelles de cycle biologique océanique et chez les mâles de cycles biologiques côtier et d'eau douce. Dans l'ensemble, les motifs migratoires influencent la croissance de manière prévisible, mais pourraient limiter le stockage compensatoire de lipides chez les femelles, particulièrement celles des cycles biologiques rares. [Traduit par la Rédaction]

Introduction

Partial migration occurs in populations where individuals express a mix of migratory and resident life histories (Lack 1943; Chapman et al. 2011) and is broadly observed among animal taxa (e.g., mammals—Avgar et al. 2013; fishes—Chapman et al. 2012; birds—Rankin and Burchsted 1992; Newton 2010). Partial migration is especially promi-

nent and well studied in salmonid fishes, where anadromy and freshwater residency bracket a range of patterns, including migrations within river systems and between rivers and lakes. Anadromous fish undergo marine migrations, often over long distances > 1000 km, before returning to fresh water to breed, whereas resident fish may complete their entire life cycle within their natal stream system, in some cases

without any substantial movement (Jonsson and Jonsson 1993; Hendry et al. 2004). Between these extremes, intermediate but often less well-studied migratory behaviors may be observed within freshwater systems (Northcote 2007, 2010; Arostegui and Quinn 2019) and to estuarine and nearshore marine waters rather than the open ocean (Pavlov et al. 2001; Pavlov and Savvaitova 2008; Pavlov et al. 2008). These intermediate behaviors are examples of differential migration—variation in the extent of migration rather than simply migratory versus nonmigratory patterns (Quinn 2021).

A central challenge for ecologists is to understand how physiology and the environment mediate partial migration (reviewed by Birnie-Gauvin et al. 2021). Although migration is linked to a large genomic region in some salmonids (Pearse et al. 2019; Arostegui et al. 2019b), the genetic basis of migration appears to be indirect and mediated by a variety of factors influencing the physiology of individual growth and development (Sloat and Reeves 2014; Kelso et al. 2020; Birnie-Gauvin et al. 2021). For example, the relationship between physiological traits and migratory tendency (i.e., reaction norm) differs between female and male salmonids (Sloat et al. 2014). Females are more likely to migrate than males (e.g., Morita and Nagasawa 2010; Ohms et al. 2014; reviewed by Quinn 2018) and store more energy as lipids prior to maturation (Lamperth et al. 2017). Compensatory lipid storage in females may help offset their higher costs of reproduction as compared to males (Hendry and Berg 1999; Fleming and Reynolds 2004).

In this study, we examined the consequences of different migratory patterns on life histories of *Oncorhynchus mykiss*, a widely distributed iteroparous species that exhibits partial migration across its native range from Kamchatka, Russia, to California, USA (Pavlov and Savvaitova 2008; Kendall et al. 2015). “Steelhead” and “rainbow trout” are the common North American names for anadromous and freshwater resident contingents of *O. mykiss*, respectively, whereas they are both called “mykizha” in Russia. Our study took place on the west coast of the Kamchatka Peninsula, Russia, where the species expresses diverse life history patterns within and among populations. Here, we use the term “contingent” to describe life histories as groups of migratory or resident individuals within a partially migratory population (Clark 1968; Chapman et al. 2012). The life history contingents in Kamchatkan rivers include the typical anadromous fish that migrates to the open ocean for feeding (Myers 2018) and the stream resident fish, both of which are well studied in North America (Behnke 2002). In addition, scale pattern analysis has detected more complex and intermediate growth patterns attributed to migration between rivers, estuaries, and coastal waters (Pavlov et al. 2001; Pavlov and Savvaitova 2008; Pavlov et al. 2008). Thus partial migration of these contingents is associated with a range of feeding environments from the most resource-rich and diverse open ocean (Daly et al. 2014) to coastal and freshwater environments, where *O. mykiss* appear to encounter prey in more limited and seasonal pulses (Kuzishchin et al. 2020b).

We hypothesized that differences among *O. mykiss* life histories are mediated by both their growth environment and physiological state. To examine this hypothesis, we synthe-

sized life history, demographic, and growth data previously collected for our study river (Pavlov et al. 2001; Pavlov and Savvaitova 2008; Kuzishchin et al. 2020b), applied genetic and stable isotope techniques to increase robustness of the data set, and analyzed new data on somatic lipid content. We predicted that life history contingents accessing the resource-rich oceanic environment would have faster growth and higher lipids than those associated with the more resource-limited coastal environments, which in turn would grow faster and store more lipids than those feeding in freshwater environments. Within each contingent, we predicted that females would have higher somatic lipid levels than males, and that younger (smaller) fish would have higher lipid levels than older (larger) fish.

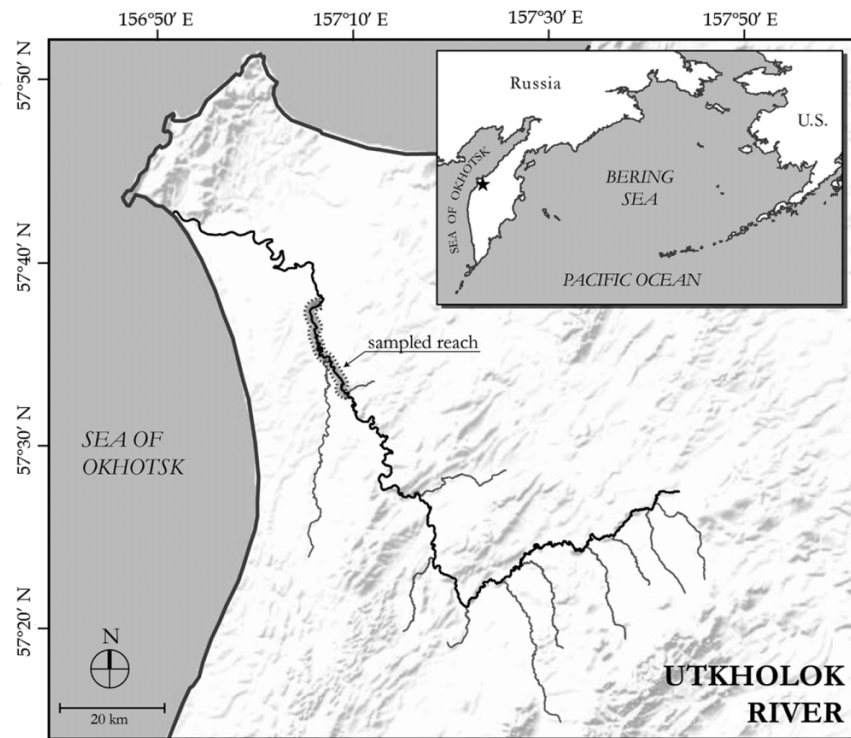
Materials and methods

Study area

We conducted this study in the Utkholok River (57°42'18.2"N, 156°52'57.3"E), which flows southwest 140 km from its headwaters on the Kamchatka Peninsula to the Sea of Okhotsk (Fig. 1). The river basin area is 1350 km², with a low gradient (5 m·km⁻¹), and base flows at the river mouth are 12 m³·s⁻¹ (Pavlov et al. 2005; Kuzishchin et al. 2020b). This tundra-type river is ice covered between November and April, with the lowest flows in the winter and highest flows in the spring, and is a meandering channel with tannic-colored water and limited riparian woody vegetation. Daily maximum water temperatures range from ~0 °C between November and April to 19 °C between June and August (M. Zimmerman, M. Sloat, K. Kuzishchin, M. Gruzdeva, unpublished data). Most anadromous *O. mykiss* enter the river in September and October and overwinter there, although some enter in May just before spawning (Kuzishchin et al. 2020a). All anadromous and resident contingents spawn in the spring (Savvaitova et al. 1999; Kuzishchin et al. 2007).

In Kamchatka, *O. mykiss* include at least five life history contingents (Pavlov et al. 2001; Pavlov and Savvaitova 2008). Life histories are assigned based on scale growth patterns (Kuzishchin et al. 1999; Pavlov et al. 2001; Savvaitova et al. 2005), and their migratory behavior has been further interpreted from otolith microchemistry, field sampling in the estuary and coastal waters, tagging and recapture, and parasite load. All begin life as juveniles, spawned in rivers, and later diverge in their movements and habitats; four migrate to sea and one remains in the river. First, there are the “typical” anadromous fish known as steelhead in North America (Busby et al. 1996; Myers 2018). After feeding in the river for several years, they migrate to the ocean, feed for 2–4 more years, return to the river for breeding, and may repeat the migration to sea and back for subsequent spawning seasons. Second, there are fish known as “half-pounders” in North America (Snyder 1925; Kesner and Barnhardt 1972; Savvaitova et al. 2005; Hodge et al. 2014) but what we call here is “anadromous B” fish for consistency with Russian nomenclature (Pavlov et al. 2001; Pavlov and Savvaitova 2008). These fish spend several years in the stream as juveniles prior to seaward migration, and they then make

Fig. 1. Map of the Utkholok River on Kamchatka Peninsula, Russia. Sampled area (dashed line) extended from tide water in the lower river to the upper limit of jet boat navigation, well upstream of the overwintering areas for migratory *Oncorhynchus mykiss*. Map was prepared using ArcGIS (version 10.7; ESRI, Redlands, California, USA). Streamlines were manually drawn and georeferenced using Google Earth imagery (earth.google.com/web/).



a brief marine migration (e.g., one summer) but return to the river for one winter, as documented from scales and parasite composition of fish captured during this first migration (Savvaitova et al. 2005). The next spring, they go to sea again for several years before returning to spawn as large-bodied adults, as documented through otolith Sr:Ca profiles ($n = 14$, K. Kuzishchin, unpublished data). The third “estuarine” contingent migrates to the estuary and nearshore environment for the summer, appearing in nearshore catches in the Sea of Okhotsk (K. Kuzishchin, unpublished data). Estuarine fish are thought to overwinter in deep sections of the estuary (Kuzishchin et al. 2020b) based on otolith Sr:Ca profiles ($n = 11$, K. Kuzishchin, unpublished data) and the observation that low temperatures (-0.1 to -0.5 °C) and high salinity (22–26 ppt) in the Sea of Okhotsk would be uninhabitable for salmonids between December and March. The fourth contingent, known as “riverine–estuarine” fish, similarly migrate to the estuary for the summer, but return to the river each year to overwinter (Kuzishchin et al. 2020b), a migration supported by otolith Sr:Ca profiles (Zimmerman et al. 2003) as well as tagging and index netting in the estuary and river (K. Kuzishchin, unpublished data). Lastly, stream residents (“riverine” fish in Russian nomenclature) complete their entire life cycle within fresh water.

Field data collection

Data collection was organized through the Kamchatka Steelhead Project, an angler-sponsored, scientific re-

search program organized by The Conservation Angler (headquarters in Everett, Washington, USA) and conducted in cooperation with the Wild Salmon Center (headquarters in Portland, Oregon, USA), the Russian Academy of Sciences, and Moscow State University as part of the US–Russia Agreement on the Environment (<https://www.fws.gov/international/wildlife-without-borders/russia/us-russia-environmental-agreement.html>). We analyzed data collected in September and October over seven years (1995, 1996, 2002, 2005, and 2016–2018). The seasonal timing of data collection spanned the fall river entry timing of anadromous *O. mykiss*, thus all four anadromous life history contingents included in this study were present in the study area at the time of sampling. Demographic and growth data were collected in all years, lipid content data were collected in 2016–2018, and isotope and genetic (sex identification) data were collected in 2017 only (Table S3).

Four to six anglers per week captured fish within a 16 km reach of river using fly fishing techniques (Fig. 1). Daily angling effort was distributed approximately equally over the study reach, and anglers were instructed to cover the entire habitat in each reach. Each captured fish was sampled for biological data, including sex, fork length, scales, and somatic lipid content. Twenty scales were collected from the area above the lateral line and posterior to the dorsal fin and used for the age and life history, genetic (sex identification), and stable isotope analyses. Each fish was tagged with a single numbered Floy® tag, photographed, and released alive

on site. Recapture of tagged fish in subsequent seasons validated scale age data and spawning checks. On the occasion that capture led to unintentional mortality, the gonads were inspected to confirm sex identification.

Our sampling methodology was designed to intercept fall migrating anadromous *O. mykiss* and likely underrepresented other components of *O. mykiss* diversity in the Utkholok River. For example, the gear used were unlikely to catch small, sexually mature male parr that occur in North American *O. mykiss* (Seamons et al. 2004; McMillan et al. 2012; Sloat and Reeves 2014). Moreover, the fall sampling precluded detection of a spring migrating anadromous *O. mykiss* recently described from the Utkholok River (Kuzishchin et al. 2020a). Finally, the spatial coverage of the sampling likely under-represented the relative abundance of riverine fish in the river.

Age and life history determination

Age, spawning history, and life history were evaluated for 867 fish sampled between 1995 and 2018. Age, spawning history, and life history determinations were based on examination of three–four scales with nonregenerated central zones. Scale imprints were made on acetate plates (Carver C-15 press, 200 mm Hg, 85 °C). Scale impressions were scanned and stored as digital files for analysis (7800 × 5232 pixels per inch, *.tiff) using an image-capture system consisting of a Leica DMLS microscope with the objectives of 2.5× to 10× magnification, a digital camera Canon X500-D, and ImageProPlus software. Further description of the methodology and scale images depicting each life history are provided in the supplemental materials (Supplement 1).

Following analysis methods established over five decades of research in Kamchatka (Kuzishchin et al. 1999; Pavlov et al. 2001; Kuzishchin et al. 2020b), we used scale pattern analysis to classify each fish into one of the five contingents. The total age of each fish at the time of capture was based on the number of years of growth inferred from annuli. Years in freshwater versus marine environments were inferred from spacing between annuli (Kuzishchin et al. 1999). Spawning history was inferred from spawning “checks” identified by the irregular wedging of the circuli on the distal part of the scale or the presence of unstructured wavy stripes without circuli (Kuzishchin et al. 1999). Since 1995, recaptures of tagged typical anadromous and riverine fish have been used to interpret and verify the interpretation of annual spawning checks from the scale patterns ($n = 1376$ tagged and 52 recaptures). Age at maturity for fish that had previously spawned was inferred from the number of growth years to the first spawning check. Age at maturity for anadromous contingents (typical anadromous, anadromous B) that had not previously spawned was the total age at the time of capture plus one, under the assumption that anadromous fish captured in the river during the fall would spawn the following spring. No age at maturity was inferred for riverine, riverine–estuarine, and estuarine contingents that did not have a spawn check (i.e., had not previously spawned) because we could not be certain they would spawn the following spring. As with all scale age analyses, there exists some uncertainty in individual calls; these errors were minimized by consistency in the

scale readers and protocols over the course of the research program. Importantly, all life history classification based on scales was done blind with respect to the data on fat content and stable isotopes (detailed below) to ensure complete objectivity.

Sex identification

Each fish’s sex was determined in the field based on such external features as jaw length and shape (e.g., presence of a kype in males), belly shape, and frayed tails in females caused by prior redd digging. We later used a genetic assay for a subsample of data from 2017 to corroborate and correct potential bias in field assignments of sex. These genetic tools independently verified the methods used to previously summarize sex ratios (Pavlov et al. 2001; Pavlov and Savvaitova 2008; Kuzishchin et al. 2020b), and increased the sample size of the riverine contingent for analyses of stable isotopes and somatic lipid content.

First, we validated a single nucleotide polymorphism (SNP) locus that is diagnostic of sex in North American *O. mykiss* (Brunelli et al. 2008) by genotyping 18 Utkholok River fish (1 female and 17 males) whose phenotypic sex was determined either by dissection or from fully developed secondary sexual characteristics. Genetic and field sex identification matched for all of these samples. We then used this assay to genotype 276 individuals collected in 2017, of which 273 (98.9%) were successfully genotyped. Agreement between genetic and field sex identification was 88.7%, with slightly better agreement for females (90.4%) than males (84.9%). Further detail on the genetic methodology is provided in the supplemental material (Supplement 2).

Stable isotopes

Stable isotopes provided an evaluation of feeding ecology that was independent of the scale growth patterns used to assign each life history. We investigated potential differences in trophic ecology among life history contingents with stable isotopes of carbon and nitrogen. The ratios of $^{13}\text{C}/^{12}\text{C}$ and $^{15}\text{N}/^{14}\text{N}$, known as the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values, measure the incorporation of carbon and nitrogen in a consumer from its diet (DeNiro and Epstein 1978; Minagawa and Wada 1984). A consumer’s $\delta^{13}\text{C}$ signature reflects that of its prey; therefore, consumers of prey with distinct $\delta^{13}\text{C}$ values will express different $\delta^{13}\text{C}$ values that can be used to infer trophic or habitat segregation (Rau 1980). A consumer’s $\delta^{15}\text{N}$ signature reflects its trophic level because there is a 2%–5% enrichment of the isotope with each increase in trophic level from the ecosystem baseline (Post 2002). The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ from scales of salmonids (e.g., Satterfield and Finney 2002; MacKenzie et al. 2011; Quinn et al. 2012) and other fishes (e.g., Wainright et al. 1993) have been used to reconstruct their feeding ecologies and conduct intra- and interspecific comparisons of diet composition, foraging location, and food web position.

Stable isotope analyses were conducted for 162 fish collected in 2017. Scale samples were lightly scraped to remove soft tissues and rinsed in deionized water to remove any remaining tissue. One scale per fish was processed from fish ≥ 400 mm long and two from smaller fish to ensure sufficient

sample mass. Original (i.e., nonregenerated) scales were selected for analysis to provide an isotopic signature integrated over each fish's life. The area between sequential annuli on a scale includes the isotopic signature of that particular year; the isotopic signature of a whole scale is, therefore, the signature of all years combined. The layers of lamellae in a scale are laid sequentially on top of each other and get larger with age, thus the isotopic signature of a whole scale is most heavily influenced by the most recent years of a fish's life (Hutchinson and Trueman 2006). Regenerated scales, identified by the presence of a large, irregularly shaped focus, reflect only the time since the original scale was lost and replaced and were only used if original scales were unavailable. The use of a lipid-deficient tissue, such as scales, from a lipid-rich consumer may result in an overly enriched $\delta^{13}\text{C}$ value in that tissue relative to the animal's whole body, which could bias interpretation (Arostegui et al. 2019a). However, all the fish measured exhibited <5% lipids (see the Results section), so any potential bias was likely to be negligible (Post et al. 2007). Scales were weighed to the nearest 0.001 mg, packed in tin capsules, and analyzed at the University of Washington IsoLab, Seattle, with a ThermoFinnigan MAT 253/Costech EA mass spectrometer. Isotope values were reported as the difference (in parts per thousand, ‰) between the isotope ratios of a sample and reference 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). Reference standards for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ were Alaskan sockeye salmon and glutamic acid. Measurement precision was estimated to be 0.04–0.15 for $\delta^{15}\text{N}$ and 0.03–0.08 for $\delta^{13}\text{C}$, depending on the sample.

Somatic lipid content

To quantify patterns of energy storage among life history contingents, we measured lipid content of the dorsal muscle tissue using a handheld microwave energy meter (Distell Fish Fatmeter, Model Number FM 692, Distell Inc., West Lothian, Scotland). This estimated water content and converted this value to percent lipids using the strong inverse relationship between the two components in the fish tissue (Crossin and Hinch 2005). The “Trout-1” setting of the meter was used, calibrated for *O. mykiss* by the manufacturer.

Lipid content was measured for 295 fish collected between 2016 and 2018. Eight readings were collected from each fish, four on each side of the body, scanning the dorsal muscle tissue above the lateral line, and the average value was calculated from these readings consistent with the manufacturer's instructions and with the methods used in similar research (Crossin and Hinch 2005; Lamperth et al. 2017).

Analysis

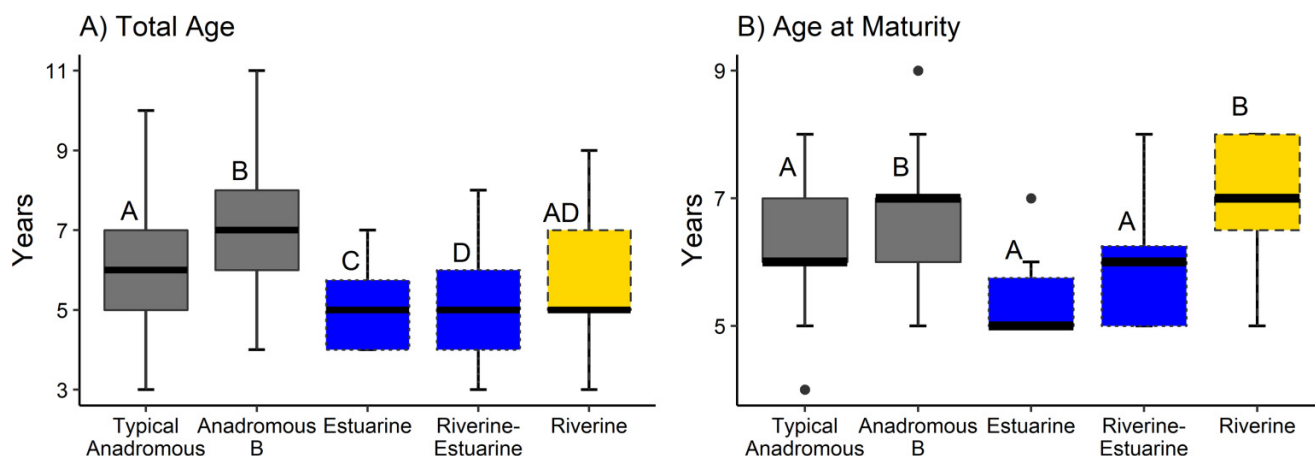
We compared demographic traits among life history contingents with a suite of nonparametric tests. To test for differences in total age and age at maturity, we used a Kruskal–Wallis test followed by Dunn's Kruskal–Wallis multiple comparisons test if ages differed among groups. To test for differences in proportion of females, we used a Fisher's Test of Independence followed with pairwise tests of independence for nominal data if the overall proportions differed

among groups. Pairwise comparisons were adjusted for multiple comparisons (Benjamini–Hochberg false discovery rate) and $\alpha = 0.05$ was used as the criterion for statistical difference. Analyses were conducted in R using the following packages: “stats” (R Core Team 2019), “FSA” (Ogle et al. 2020), “DescTools” (Signorell 2020), and “rcompanion” (Mangiafico 2020).

We assessed differences in stable isotopes ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) among life history contingents using a generalized least squares (GLS) models with a variance structure. The presence of heterogeneity was assessed through visual inspection of predictor variable values and confirmed via Akaike information criterion (AIC) selection among models of maximum complexity with and without variance structure. We tested life history, sex, and total age as covariates but excluded fork length, years in fresh water, and years in salt water due to collinearity. Moreover, sample sizes for some life history contingents were limited, so for this analysis we reclassified the five life history contingents into three aggregate categories: oceanic (typical anadromous and anadromous B), coastal (riverine–estuarine and estuarine), and fresh-water (riverine). For a GLS model, we first identified the optimal variance structure, then selected variables, and their potential interactions, based on the difference in AIC values, AIC weights, and significance of terms ($\alpha = 0.05$; Zuur et al. 2009). Pairwise comparisons among life history aggregates were conducted with Tukey multiple comparison tests using a Benjamini–Hochberg correction. Models were built and validated in R using the following packages: “stats” (R Core Team 2019), “nlme” (Pinheiro et al. 2016), “piecewiseSEM” (Lefcheck 2016), and “multcomp” (Hothorn et al. 2020).

We compared growth trajectories among life history contingents using length-at-age data as a proxy for growth. We fit length-at-age data with both linear and nonlinear models, and used the nonlinear approach after examining patterns in the residuals. We explored both the von Bertalanffy and Gompertz nonlinear growth models for the analysis and selected the von Bertalanffy based on visual inspection of the data (no sigmoidal relationship evident) but also because we lacked data points (total age 1–3 years) that would inform a sigmoidal shape to the curve. The von Bertalanffy equation was $L_a = L_\infty \{1 - \exp[-k(a - t_0)]\}$, where L_∞ is the asymptotic length, k is the growth coefficient, t_0 is a modeling artifact representing the age at which size was zero, and L_a is length at total age a (Beverton and Holt 1957). We set t_0 to a value of zero years (intercept at the origin) to allow the models to converge. We initially explored whether the parameters of the growth model differed by life history or sex. This analysis was done for each fixed effect separately because there were insufficient data to analyze both effects together. A difference was interpreted if the bootstrapped estimates for k and L_∞ were outside the 95% confidence intervals of other levels of the same fixed effect. Based on this initial exploration, growth model parameters differed among life histories but not between sexes. Therefore, we compared the full model with unique coefficients for each life history to reduced models that pooled coefficients of life history pairs. For this and other model selection analyses, we used AIC values and AIC weights (Wagenmakers and Farrell 2004) to evaluate model

Fig. 2. Total age (A) and age at maturity (B) for *Oncorhynchus mykiss* in the Utkholok River, Kamchatka, Russia. Age at maturity was estimated from repeat spawners only. Box plot shows median (horizontal line), quartile (box), range (line), and outlier (points) values for each life history. Letters depict pairwise differences ($\alpha = 0.05$). [Colour online.]



fit to the data. Models were built and validated in R using the following packages: “stats” (R Core Team 2019), “nlme” (Pinheiro et al. 2016), “nlstools” (Baty et al. 2015), and “FSA” (Ogle et al. 2020).

Finally, we compared somatic lipid content (% lipid) among life history contingents with a beta regression model. As with the stable isotope analysis, we compared three aggregate life history categories: oceanic, coastal, and freshwater. Sex and total age were also included as covariates in the model but fork length, years in fresh water, and years in salt water were excluded due to collinearity. We forward selected covariates and their potential interactions based on differences in AIC values, AIC weights, and significance of terms ($\alpha = 0.05$). We used pairwise comparisons and contrasts to further describe the effect of variables included in the final model. Models were built and validated in R using the following packages: “betareg” (Cribari-Neto and Zeileis 2010) and “emmeans” (Lenth 2020).

Results

Summary of field data

Of 867 *O. mykiss* in our sample, we determined the ages and life history contingent for 861 (99%) individuals, although sample sizes varied among the analyses (Table S3). Stable isotope and somatic lipid content data were collected in the recent years only for the purpose of testing growth and lipid storage hypotheses. Length, age, and sex data were collected in all years (Pavlov et al. 2001; Pavlov and Savvaitova 2008; Kuzishchin et al. 2020b) and were used for the demographic and growth analyses. A combination of field and genetic assignments classified sex for 822 fish, while 45 could not be classified using either method. Genetic assignment of sex increased the sample sizes of less common life histories (riverine and riverine–estuarine) for analyses of stable isotopes and somatic lipid content, as field calls for 22 of these individuals were inconclusive.

The data set included 55 different combinations of freshwater and saltwater ages; most anadromous fish (77%) spent 3 years (range: 2–5 years) in the river prior to saltwater entry. Typical anadromous fish were the most numerous contingent ($n = 650$, 75.5% of the sample), compared to the anadromous B ($n = 69$, 8.0%), estuarine ($n = 20$, 2.3%), riverine–estuarine ($n = 64$, 7.4%), and riverine ($n = 58$, 6.7%) contingents. For comparisons involving the three aggregate categories, the sample sizes were 719 (83.5%) oceanic, 84 (9.8%) coastal, and 58 (6.7%) freshwater fish.

Demographic traits

Total age of *O. mykiss* in our sample ranged between 3 and 11 years and differed among life history contingents ($\chi^2 = 66.5$, $df = 4$, $p < 0.001$); the anadromous B contingent was the oldest and the estuarine and riverine–estuarine fish were the youngest ages (Fig. 2A). Age of maturity, as determined from repeat spawners, ranged from 4 to 9 years and also differed among life histories ($\chi^2 = 50.1$, $df = 4$, $p < 0.0001$). Age of maturity generally formed two groups—an older group that included riverine and anadromous B fish and a younger group that included typical anadromous, estuarine, and riverine–estuarine fish (Fig. 2B).

Proportion of females ranged from 22% to 63% and differed among life histories ($p < 0.0001$; Table 1). The typical anadromous (58%) and anadromous B (63%) life histories were skewed toward females and did not differ from each other ($p = 0.57$). The estuarine (22%) and riverine (22%) life histories were skewed toward males and differed from the typical anadromous and anadromous B ($p < 0.007$). The riverine–estuarine (44%) contingent was also skewed towards males, higher than the riverine contingent ($p = 0.05$) but not different from the other life histories.

Stable isotopes and feeding environments

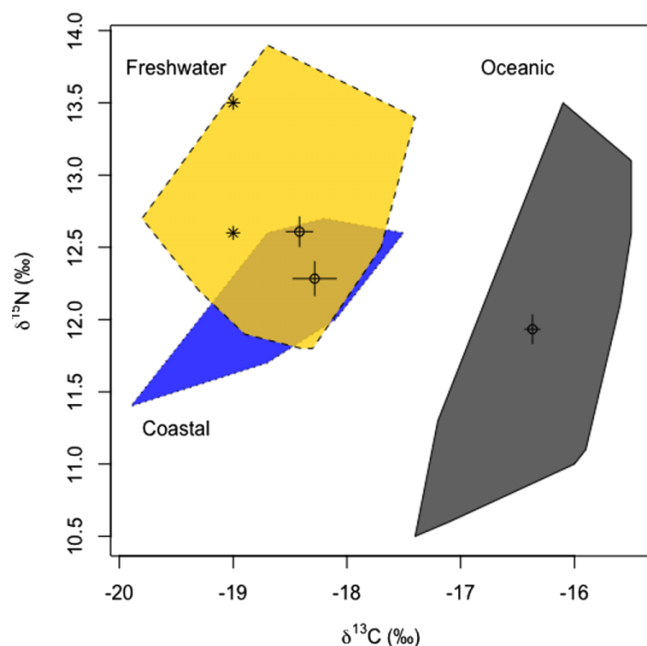
When $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ data were combined, the oceanic aggregate (typical anadromous and anadromous B) was distinct from the coastal (riverine–estuarine and estuarine) and fresh-

Table 1. Sex ratios and spawning statistics for five life history contingents of *Oncorhynchus mykiss* from the Utkholok River, Russia, 1995–2018.

Life history	Proportion repeat spawn (95% CI)	Median number repeat spawn (Range)	Proportion females (95% CI)
Typical anadromous	0.60 (0.56–0.64)	1.0 (1–6)	0.58 (0.54–0.62)
Anadromous B	0.62 (0.50–0.74)	2.0 (1–5)	0.63 (0.50–0.75)
Estuarine	0.35 (0.15–0.59)	1.0 (1–2)	0.22 (0.06–0.48)
Riverine–estuarine	0.20 (0.11–0.32)	1.5 (1–3)	0.44 (0.31–0.59)
Riverine	0.21 (0.11–0.34)	1.0 (1–3)	0.22 (0.12–0.36)

Note: The proportion of females and repeat spawners represent all samples. The number of repeat spawning seasons was calculated only for fish identified as repeat spawners.

Fig. 3. Isotope biplot of the life history aggregates (freshwater, coastal, oceanic) of *Oncorhynchus mykiss* in the Utkholok River, Kamchatka, Russia. Biplot includes convex hulls around the corresponding data and mean ± 1 SE for each life history aggregate ($\delta^{13}\text{C}$: Table 2—model 4; $\delta^{15}\text{N}$: Table 3—model 1). The asterisks indicate the two fish identified by scale readings as typical anadromous that, as outliers to the oceanic group, were excluded from further analysis. [Colour online.]



water aggregates, but considerable overlap occurred between the coastal and freshwater aggregates (Fig. 3). With respect to $\delta^{13}\text{C}$, the fish clustered in two distinct groups with only slight variation within groups, and there was an overall increasing cline that followed the presumed use of freshwater to salt-water feeding environments interpreted from scale growth patterns. One $\delta^{13}\text{C}$ group consisted of the fish classified

from scale reading as riverine (mean ± 1 SE: -18.4 ± 0.12 , $n = 23$), riverine–estuarine (-18.3 ± 0.18 , $n = 11$), and estuarine (-18.1 , $n = 1$), and the second group consisted of those identified as typical anadromous (-16.6 ± 0.05 , $n = 121$) and anadromous B (-16.6 ± 0.25 , $n = 6$). Two $\delta^{13}\text{C}$ values (-19.0) of fish identified as typical anadromous from scale data were outliers in the stable isotope data relative to the rest of the oceanic aggregate (≥ -17.4). Because they may have been misidentified during scale reading, the isotopic data were excluded from further analysis. Of the 162 samples, the $\delta^{15}\text{N}$ signatures of only 90 fish could be acquired due to oversaturation of the sensors in the mass spectrometer. There was no clear grouping by mean $\delta^{15}\text{N}$; instead, $\delta^{15}\text{N}$ decreased slightly with the presumed increasing use of salt-water feeding environments as interpreted from scale growth patterns: riverine (12.6 ± 0.09 , $n = 23$), riverine–estuarine (12.3 ± 0.13 , $n = 11$), estuarine (12.2 , $n = 1$), typical anadromous (12.0 ± 0.10 , $n = 51$), and anadromous B (11.45 ± 0.40 , $n = 4$). For the analysis of $\delta^{13}\text{C}$, a variance structure differing by life history aggregate improved model fit and necessitated the use of a GLS model. Forward selection identified two competing models according to AIC weight (Table 2), and we chose the most parsimonious model (model 4) of $\delta^{13}\text{C}$ as a function of life history aggregate and sex, with no interaction, for analysis. In this model of $\delta^{13}\text{C}$ (adjusted $R^2 = 0.73$), the fish with freshwater and coastal life histories did not differ significantly from each other ($t = -0.55$, $p = 0.581$), but both were significantly lower (more negative) than the oceanic fish (coastal vs oceanic— $t = 8.37$, $p < 0.001$; freshwater vs oceanic— $t = 14.38$, $p < 0.001$), and males were significantly lower than females ($t = -3.10$, $p < 0.01$) when aggregated across life histories. However, predicted difference in mean $\delta^{13}\text{C}$ was more than seven times greater among life histories than between sexes; oceanic fish exhibited a $\delta^{13}\text{C}$ value $1.79\text{‰} \pm 0.12\text{‰}$ or $1.66\text{‰} \pm 0.20\text{‰}$ greater than freshwater or coastal fish, respectively, whereas females exhibited a $\delta^{13}\text{C}$ value $0.23\text{‰} \pm 0.08\text{‰}$ greater than males. Relative to oceanic fish, the variance of $\delta^{13}\text{C}$ was 1.27 and 1.54 times greater in freshwater and coastal fish, respectively.

Table 2. Alternative generalized least squares models of $\delta^{13}\text{C}$ as a function of life history type (LH), sex, and total age.

Covariates	Model 1	Model 2	Model 3	Model 4	Model 5	Model 6	Model 7	Null
Intercept	X	X	X	X	X	X	X	X
LH	X			X	X	X	X	
Sex		X		X		X	X	
Total age			X		X	X		
LH \times sex							X	
df	158	159	159	157	157	156	155	160
ΔAIC	8.8	78.8	75.1	1.4	4.5	0.0	4.5	88.2
AIC_w	0.01	0	0	0.29	0.06	0.58	0.06	0

Note: Table includes degrees of freedom (df), difference in Akaike information criterion (ΔAIC) from the best model, and the relative likelihood that the model provides the best fit to the data (AIC weight, AIC_w). X indicates the variables included in each model. Data are *Oncorhynchus mykiss* from the Utkholok River in Kamchatka, Russia.

Table 3. Alternative generalized least squares (GLS) models of $\delta^{15}\text{N}$ as a function of life history type (LH), sex, and total age.

Covariates	Model 1	Model 2	Model 3	Model 4	Model 5	Null
Intercept	X	X	X	X	X	X
LH	X			X	X	
Sex		X		X		
Age			X		X	
df	85	86	86	84	84	87
ΔAIC	2.2	19.4	18.2	0.5	0	17.4
AIC_w	0.16	0	0	0.37	0.48	0

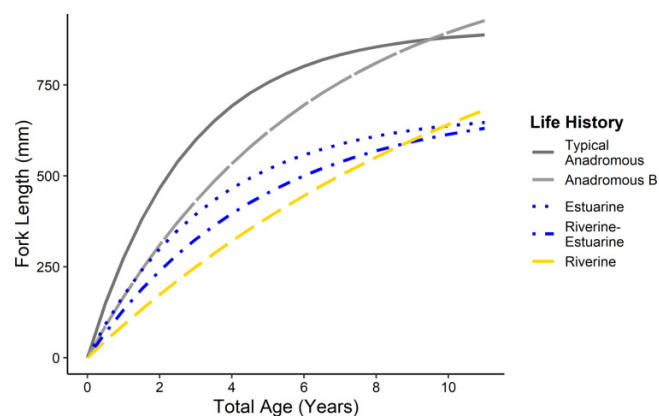
Note: Table includes degrees of freedom (df), difference in Akaike information criterion (ΔAIC) from the best model, and the relative likelihood that the model provides the best fit to the data (AIC weight, AIC_w). X indicates the variables included in each model. All GLS models include a variance structure that differed by life history. Data are *Oncorhynchus mykiss* from the Utkholok River in Kamchatka, Russia.

For the analysis of $\delta^{15}\text{N}$, a variance structure differing by life history also improved model fit and necessitated the use of a GLS model. Forward selection identified three competing models according to AIC weight (Table 3), and we chose the most parsimonious model (model 1) of $\delta^{15}\text{N}$ as a function of life history for analysis. In this GLS model (pseudo- $R^2 = 0.16$), the freshwater life history had marginally higher $\delta^{15}\text{N}$ values than the coastal aggregate ($t = 1.84$, $p = 0.066$), and both were significantly higher than the oceanic aggregate (coastal vs oceanic— $t = 2.28$, $p < 0.05$; freshwater vs oceanic— $t = 4.64$, $p < 0.001$). The predicted difference in mean $\delta^{15}\text{N}$ between the freshwater and oceanic samples was nearly twice that between the coastal and oceanic samples; freshwater fish exhibited a $\delta^{15}\text{N}$ value $0.62\text{‰} \pm 0.13\text{‰}$ greater than oceanic fish, and coastal fish exhibited a $\delta^{15}\text{N}$ value $0.35\text{‰} \pm 0.15\text{‰}$ greater than oceanic fish. The variance of $\delta^{15}\text{N}$ in oceanic fish was 1.72 times greater than in freshwater fish and 1.81 times greater than in coastal fish.

Length-at-age and growth trajectories

The growth model with unique coefficients for all five contingents (Fig. 4) provided the best fit to the data compared to alternate models with pooled coefficients among subsets of life histories (models 2–6; Table 4), and to the model with a single set of coefficients for all life histories combined (model 7). Growth coefficients were highest for typ-

Fig. 4. Length-at-age of *Oncorhynchus mykiss* in the Utkholok River, Kamchatka, Russia. Plot shows modeled growth curves fit to length-at-age data for each life history type with a von Bertalanffy growth model (Table 4—model 1, modeled parameter values in Table S4). Growth curves were derived from 3- to 11-year-old fish (98% between 4 and 9 years), and the fitted line may not accurately reflect the youngest ages (1–3 years). [Colour online.]



ical anadromous fish (median, 95% confidence interval: 0.37, 0.34–0.40) and estuarine (0.29, 0.11–0.61) contingents, intermediate for anadromous B (0.16, 0.12–0.20) and riverine–estuarine (0.17, 0.11–0.24) contingents, and lowest for river-

Table 4. Alternative von Bertalanffy growth curves fit to length-at-age data of *Oncorhynchus mykiss* from the Utkholok River, Russia.

Life history	Model 1	Model 2	Model 3	Model 4	Model 5	Model 6	Model 7
Typical anadromous	A	A	A	A	A	A	A
Anadromous B	B	A	B	B	B	B	A
Estuarine	C	B	B	C	C	A	A
Riverine–estuarine	D	C	C	C	D	C	A
Riverine	E	D	D	D	D	D	A
df	405	407	407	407	407	409	413
Δ AIC	0	123.3	35.8	15.8	23.7	247.0	1279.6
AIC _w	0.999	0.000	0.000	0.000	0.000	0.000	0.000

Note: Table includes degrees of freedom (df), difference in Akaike information criterion (Δ AIC) from the best model, and the relative likelihood that the model provides the best fit to the data (AIC weight, AIC_w). Letters indicate that coefficients for each life history were grouped (same letter) or fit separately (different letter).

Table 5. Alternative beta regression models of somatic lipid content as a function of life history (LH), sex, and total age (age).

Covariates	Null	Model 1	Model 2	Model 3	Model 4	Model 5	Model 6	Model 7
Intercept	X	X	X	X	X	X	X	X
Sex		X	X	X	X	X	X	X
Age			X	X	X	X	X	X
LH					X	X	X	X
Sex \times age				X				
Sex \times LH						X	X	X
Age \times LH							X	X
Sex \times age \times LH								X
df	285	284	283	282	281	279	277	274
Δ AIC	38.1	27.2	23.1	22.6	26.3	7.7	0	4.9
AIC _w	0.00	0.00	0.00	0.00	0.00	0.02	0.90	0.08

Note: Table includes degrees of freedom (df), difference in Akaike information criterion (Δ AIC) from the best model, and the relative likelihood that the model provides the best fit to the data (AIC weight, AIC_w). X indicates the variables included in each model. Data are *Oncorhynchus mykiss* from the Utkholok River in Kamchatka, Russia.

ine (0.08, 0.03–0.15) contingent. Modeled asymptotic lengths were greatest for anadromous B (1130 mm, 1006–1308 mm) and riverine fish (1121 mm, 767–2770 mm), intermediate for typical anadromous fish (902 mm, 882–922 mm), and shortest for estuarine (677 mm, 538–1169 mm) and riverine–estuarine fish (778, 625–1087 mm; Table S4).

Despite the differences in modeled asymptotic lengths, the actual lengths of the oldest anadromous B fish and typical anadromous fish were similar, and the actual lengths of the oldest riverine fish were comparable to the oldest estuarine and riverine–estuarine fish and 60% shorter than the oldest typical anadromous fish (Fig. 4, Fig. S5). Thus, the full modeled growth potentials of anadromous B and riverine life histories were not observed in our sample, although these asymptotic lengths did have high uncertainty due to small samples of older and larger individuals from each contingent.

Somatic lipid content and energy storage

Mean SLC of the entire sample was 2.5% ($\pm 0.78\%$, 1 SE), and mean values of the raw data were qualitatively similar among life history contingents (Table S5). The data were best fit by a model that included two interactions (life history by sex,

life history by age) and all main effects (sex, age, life history; Table 5). The best fit model had strong support in comparison to the null model (Δ AIC = 38.1) but explained just a fraction of the overall variability in somatic lipids (pseudo- $R^2 = 0.16$).

The SLC of females versus males differed among life history aggregates (Fig. 5). The SLC of oceanic fish was higher for females than males (z-ratio = -5.58 , $p \ll 0.001$) whereas the SLC of freshwater fish was higher for males than females (z-ratio = 2.66 , $p = 0.04$). For females, the mean SLC of oceanic aggregate was 1.4 times higher than both coastal and freshwater (z-ratio = 2.90 , $p = 0.02$) aggregates, but the SLC of coastal and freshwater aggregates did not differ from each other (z-ratio = -0.59 , $p = 0.98$). For males, the mean SLC of oceanic aggregate was 0.8 times lower than coastal and freshwater aggregates (z-ratio = -3.07 , $p = 0.01$), and the SLC of coastal and freshwater males also did not differ from each other (z-ratio = -0.76 , $p = 0.95$).

The relationship between SLC and fish age also differed among life histories (Fig. 6). Specifically, the relationship between SLC and total age of the freshwater aggregate differed from the oceanic aggregate (z-ratio = -3.24 , $p = 0.003$) and marginally differed from the coastal aggregate (z-ratio = 2.23 , $p = 0.07$). Freshwater aggregate SLC decreased with increased age (slope = -0.0042 , lower 95% = -0.0059 , upper 95% =

Fig. 5. Somatic lipid content of female and male *Oncorhynchus mykiss* in the Utkholok River, Kamchatka, Russia. Bar plot shows mean values and 95% confidence intervals for each life history aggregate (freshwater, coastal, oceanic) as predicted by a linear model (Table 5—model 6). Letters depict pairwise differences ($\alpha = 0.05$). [Colour online.]

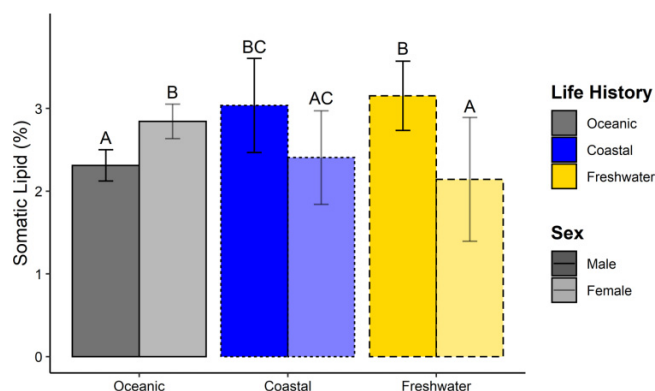
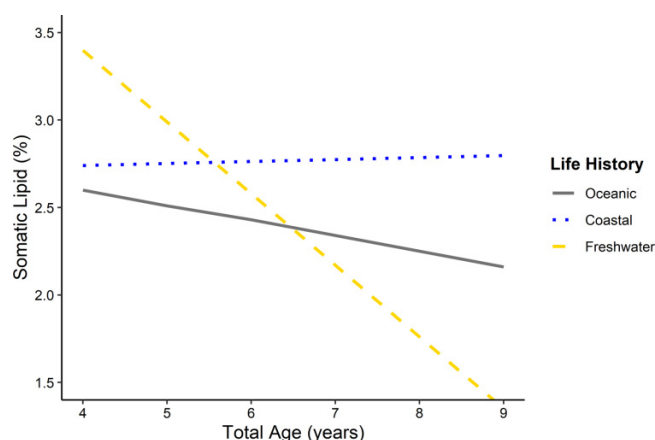


Fig. 6. Somatic lipid content versus total age of *Oncorhynchus mykiss* in the Utkholok River, Kamchatka, Russia. Plot shows modeled linear relationship between age and the percent of somatic lipid content for each life history aggregate (freshwater, coastal, oceanic; Table 5—Model 6). [Colour online.]



−0.0024); a 4-year-old freshwater fish had nearly twice the percent somatic lipid content as 9-year-old fish. In comparison, the SLC of coastal and oceanic fish was not correlated with age (i.e., confidence intervals of the slopes overlapped zero).

Discussion

The demographic traits of western Kamchatkan *O. mykiss*, as reported here and previously (Pavlov et al. 2001; Pavlov and Savvaitova 2008; Kuzishchin et al. 2020b), generally conform to patterns observed in other partially migratory salmonid populations. For example, migration enables greater size at maturation and disproportionately benefits females of anadromous compared to resident life histories (Jonsson and Jonsson 1993; Hendry et al. 2004). However, unlike much previous work on partially migratory *O. mykiss*, the western Kamchatkan populations provide information on contingents not

well documented in North America and offer rare comparative information on populations exposed to very little fishing pressure, habitat alteration, or hatchery production. The array of migratory contingents in our study system included not only the typical anadromous and resident (riverine) contingents but also three intermediate ones: the anadromous B life history, with a brief migration to sea at the half-pounder stage (Snyder 1925) prior to a more prolonged marine migration, and two migratory contingents that feed in combinations of river and coastal environments but not the open ocean. These five contingents represented increasing “degrees of anadromy” (sensu Rounsefell 1958; Quinn and Myers 2004) based on the extent to which they rely on marine resources, and these differences have had consequences for growth trajectories and energy storage.

Further, our study used genetic and stable isotope techniques to refine and verify western Kamchatkan *O. mykiss* data referenced for its exceptional diversity (Kendall et al. 2015). Genetic data indicated there has been minimal error in field identifications of sex in this volunteer angler program, and increased sample sizes of less common life histories for isotope and lipid content analyses in this study. Isotope results revealed differences in feeding ecology between anadromous oceanic (typical anadromous, anadromous B) versus coastal (estuarine, riverine) life histories, consistent with offshore and nearshore feeding environments for these anadromous contingents. Lipid content results revealed that energy storage in *O. mykiss* is complex and influenced by both growth environment and physiological state (sex and age); low explanatory power of our lipid content analyses indicates a need to investigate additional factors influencing energy storage.

Growth and demographics

Life history contingents associated with open-ocean feeding grew larger, consistent with the expected benefits of migration. Body size was the most divergent among contingents at age-4, the year following the onset of anadromy and preceding maturation for most fish in the study population (i.e., riverine < riverine–estuarine < estuarine < anadromous B < typical anadromous). Although this relative order in body size was never fully lost in subsequent years, differences among some contingents diminished with age, and fish converged on two general body size categories: larger oceanic contingents and smaller coastal and freshwater contingents (cf. Fig. 4).

Our sampling methods introduced several caveats to the growth comparisons. First, the angling method use to capture the fish was biased against the smallest fish (due to fly size and sampling location) and possibly the largest fish (due to difficulty in landing). Consequently, differences in size among the larger and smaller contingents may be even more pronounced than reported here. Lack of data points for the youngest age classes (total age 1–3 years) also means that the modeled sizes for the youngest ages are approximated. Given that the youngest ages shared a common freshwater growth environment prior to the onset of anadromy, their growth trajectories should be more similar to each other and the

divergence in growth trajectories associated with anadromy should be more pronounced than depicted by the growth curves fit to our data.

Life history contingents that initially grew faster also matured at younger ages, similar to patterns observed in other salmonids (Hutchings and Jones 1998; Siegel et al. 2018; Catterson et al. 2020). With the onset of maturation, energy allocation shifts towards storage and reproduction at the expense of somatic growth (e.g., Quinn et al. 2011). Thus, the convergence of body sizes at older ages was at least partly attributable to earlier maturation in faster growing contingents that provided slower-growing, later-maturing fish an additional year or more in which to prioritize energy allocation for growth. Comparisons between typical anadromous and anadromous B contingents exemplify this pattern. The anadromous B fish sacrificed a portion of the first year of ocean growth to overwinter in fresh water, were smaller during the first years of anadromy, and matured at older ages with a longer life span than the typical anadromous fish. These results are consistent with life history tradeoffs observed in the Klamath River, CA, one of the few other populations where both typical anadromous and anadromous B life histories are well documented (Hodge et al. 2014). Typical anadromous contingents in the Klamath River maintain a larger size at age than the anadromous B contingent, but anadromous B fish have higher survival and complete more spawning seasons (Hodge et al. 2014, 2016).

Because the growth benefits of migration are thought to favor female reproductive success in particular, we expected that the proportion of females in each life history contingent would increase with greater associated degrees of anadromy. For example, previous work in North American *O. mykiss* populations has found that anadromous fish are female-biased (e.g., 65% female; Ohms et al. 2014) and that resident contingents are often male-biased (e.g., McMillan et al. 2012; Rundio et al. 2012; Sloat and Reeves 2014). Our samples from the Utkholok River generally matched the expected female-to-male ratios: typical anadromous and anadromous B contingents were disproportionately female, the resident (riverine) contingent was disproportionately male, and the riverine–estuarine contingent, with an intermediate migratory strategy, had an approximately even sex ratio between female and male. However, the estuarine contingent was strongly male-biased thus deviating from this expected pattern. Interestingly, the female-to-male ratios of each contingent were similar to those estimated by Kuzishchin et al. (2020b), with the exception of the estuarine contingent. Kuzishchin et al. (2020b) included several more years of data and calculated a female-to-male ratio for the estuarine contingent that was slightly higher than the riverine–estuarine contingent. Based on this comparison to the larger data set, we conclude that sample size effects (just 20 of the 862 fish assigned to the estuarine life history) likely affected our estimate of this particular metric for the estuarine contingent.

Stable isotopes and feeding environments

Isotopic signatures of the Kamchatkan *O. mykiss* oceanic life histories were well within the range observed for scale tissue

of North American steelhead (Quinn et al. 2012; Lamperth et al. 2017) that feed offshore in the Pacific Ocean (Quinn and Myers 2004; Myers 2018) on energy-dense prey such as fishes and squid (Atcheson et al. 2012). However, the similarities in isotopic signatures between Russian and North American origin fish should be interpreted cautiously with respect to potential similarities in diet; there is substantial heterogeneity in $\delta^{15}\text{N}$ across the North Pacific at the base of the food web (Matsubayashi et al. 2020) and among pelagic prey at intermediate trophic levels (Madigan et al. 2021).

Stable isotopes distinguished the oceanic life histories from both coastal and freshwater life histories while showing less distinction between the coastal and freshwater life histories. The oceanic aggregate had less depleted $\delta^{13}\text{C}$ values compared to the coastal and freshwater aggregates, consistent with diets derived from marine versus terrestrial food webs (Fry and Sherr 1989; Romanuk and Levings 2005). In addition to revealing ecological separation, the $\delta^{13}\text{C}$ data provide independent support for the scale analysis used to assign oceanic versus coastal anadromous life histories, as classification of just a few individuals differed between the methods. Based on $\delta^{15}\text{N}$ values, freshwater and coastal life histories fed higher on the food chain than oceanic life histories. This may be explained by freshwater and coastal contingents feeding on eggs and tissues of anadromous salmon returning to spawn. Salmon eggs are a rich and favored food source for salmonids feeding in fresh water (e.g., Arostegui and Quinn 2018), and eggs retain maternal $\delta^{15}\text{N}$ values (sensu Fraley et al. 2020) that are effectively a trophic level above the marine prey of anadromous salmonids. Similarly, salmon carcasses and insects that scavenge them are also eaten by salmonids (e.g., Scheuerell et al. 2007; Jaacks and Quinn 2014).

Isotope signatures were less effective at differentiating between coastal and freshwater life histories, which was not entirely surprising given the observed dietary overlap among these life histories and the precision of our methodology. The coastal aggregate was dominated by samples from the riverine–estuarine life history contingent (Table S5) with presumed access to prey from both freshwater and estuarine food webs. Dietary overlap may also result from terrestrial-derived sources of carbon across freshwater, estuary, and nearshore habitats (Fry and Sherr 1989; Romanuk and Levings 2005) which would be available to freshwater and coastal contingents even if they fed in different locations. Further, salmon eggs, amphipods (Gammaridae, Amphipoda), and aquatic insect larvae (Trichoptera, Ephemeroptera, Plecoptera) are abundantly available to both freshwater and coastal contingents (Kuzishchin et al. 2020b), and consumption of seasonally pulsed resources may homogenize their isotopic signatures (Arostegui and Quinn 2018). Freshwater riverine fish are uniquely observed to consume small mammals, such as mice and shrew (K. Kuzishchin, personal observation), but the effect of this dietary source on isotopic signature is unknown. The lifetime-integrated isotopic signature of whole scales, as used in our analysis, did not capture short-term feeding habits that will be needed to further differentiate the freshwater and coastal contingents. A study of short-term feeding habitats will require isotopic signatures of fast turnover tissues (Heady and Moore 2013) or microchem-

istry of structures that retain the temporal record of an individual's feeding environment (Allen et al. 2009; Zimmerman et al. 2012).

Somatic lipid content and energy storage

Lipid content in the somatic tissue of Kamchatkan *O. mykiss* as they re-entered the river was substantially lower than adult Pacific salmon (Crossin and Hinch 2005; Quinn 2018) and also lower than adult summer steelhead (Penney and Moffitt 2014; Lamperth et al. 2017), a stream-maturing anadromous life history that returns to North American rivers 6 to 9 months prior to spawning (Quinn et al. 2016). However, the 2–3% somatic lipid content that we observed in Kamchatka was similar to that measured in North American adult winter steelhead, an ocean-maturing life history that spawns within a few weeks to a few months after entering fresh water (Lamperth et al. 2017). Many factors may account for these differences, including the stage of maturation, overwintering temperatures, and freshwater migration distances. For example, the migration distances (<100 km) and overwinter temperatures ($\sim 0^{\circ}\text{C}$; M. Zimmerman, M. Sloat, K. Kuzishchin, and M. Gruzdeva, unpublished data) of Kamchatkan *O. mykiss* are both minimal when compared to the typically long migrations and warmer stream temperature exposure of summer steelhead. For example, Penney and Moffitt (2014) found that summer steelhead lost 50% of their muscle lipids over an 800 km migration from the ocean and arrived at their natal site with an average of 2% muscle lipids, similar to anadromous *O. mykiss* SLC upon their fall arrival to the Utkholok River.

Lipids stored in muscle, visceral, and gonadal tissues of salmonid species provide energy for many physiological functions (Birnie-Gauvin et al. 2021). In *O. mykiss*, lipids stored in muscle tissue are highly correlated with total body lipids (Penney and Moffitt 2014), and the depletion of lipids stored in muscle tissue is well documented during migration and spawning of salmonids in general (Gilhousen 1980; Mesa and Magie 2006; Penney and Moffitt 2014). To control for seasonal variation, we measured lipid content of *O. mykiss* muscle tissue in the late fall, immediately preceding the winter fasting period shared by all life history contingents until spawning the following May (Savvaitova et al. 1999; Kuzishchin et al. 2007; Kuzishchin et al. 2008). Energetic costs of overwintering (Berg and Bremset 1998; Biro et al. 2004) and spawning (Hendry and Berg 1999; Fleming and Reynolds 2004) are substantial, and stored lipids are needed by all contingents for these events.

Contrary to our predictions, somatic lipid content did not differ substantially among life history contingents (cf. Table S4), despite their differences in growth and associated feeding environments. This result contrasts with lipid storage rates of anadromous versus resident mature individuals of other salmonid species, such as the higher percent lipid content observed in mature anadromous brown trout (*Salmo trutta*) compared to nonanadromous conspecifics from the same streams (Jonsson and Jonsson 1997). Of note, our study measured percent lipid content rather than total lipid content, and the total lipids available as energy reserves in our

study fish were likely to differ substantially among life histories due to differences in body mass (per Kuzishchin et al. 2020b). Assuming a similar muscle-to-body mass ratio among contingents, the oceanic life histories should have ~ 5 times more total lipids than the freshwater life history and the coastal life histories should have ~ 1.2 times more total lipids than the freshwater life history.

More subtle variation in lipid storage among the Kamchatkan life history contingents could be explained by a combination of the growth environment and the physiological state of individual fish (i.e., sex or age). Contrary to our predictions, males associated with the more resource-limited coastal and freshwater environments stored more energy as somatic lipids than did those associated with the open ocean. These differences may be explained by some threshold value of total lipids that males need for reproduction (Rowe et al. 1991; Sloat and Reeves 2014); small-bodied freshwater or coastal contingents may store lipids in higher proportions than large-bodied oceanic fish to achieve the total level of stored energy necessary for reproduction. Alternately, these differences may be a consequence of lower metabolic efficiency with smaller size (Brett 1995); small-bodied freshwater or coastal contingents with similar percent lipids as large-bodied oceanic contingents would not be able to fast as long, given similar temperatures and levels of activity.

Consistent with our predictions, females had higher somatic lipid content than males, but only in the ocean-feeding contingents. This allocation of stored energy may compensate for females needing more energy reserves than males for future gamete development and reproductive behaviors (Hendry and Berg 1999; Fleming and Reynolds 2004). However, the propensity of females to store more lipids than males, observed in both adults and juveniles elsewhere (Sloat and Reeves 2014; Lamperth et al. 2017), may be masked by energetic demands of female reproductive maturation that cannot be satisfied by available energy intake in resource-limited coastal and freshwater feeding environments. Males may not experience such severity in resource limitation as the energetic requirements of female gamete production are nearly an order of magnitude greater than those of male salmonids, after accounting for both proportion of body weight and energetic content (Fleming and Reynolds 2004).

For the freshwater contingent, somatic lipid storage of both females and males declined with age and further suggests that either compensatory lipid storage was most pronounced for the smaller individuals feeding in a resource-limited environment (Fernandes and McMeans 2019) or that the larger individuals found it increasingly difficult to meet their basic energy requirements through freshwater feeding. Larger and older fish in our sample were more likely to be repeat spawners, and there is a very short (4–5 months) feeding season to replenish energy between spawning and overwintering in the Kamchatkan rivers. In contrast, the lack of a correlation between somatic lipid content and age for coastal and oceanic contingents suggests that either the body size reached in the first years of anadromy exceeded that where compensatory storage is needed based on body size alone or that, regardless of size, these life histories can meet their

minimum energetic requirements and convert excess energy to lipids.

Implications

The Kamchatka Peninsula provides a unique setting to explore partial and differential migration in *O. mykiss* and to contrast residency with multiple types of anadromy in a location that has been largely untouched by human activities that otherwise complicate interpretation of life history patterns. Specifically, the rivers in this region have no dams to hinder migration, no large-scale habitat degradation, no *O. mykiss* hatchery production, and fishing for *O. mykiss* is limited to research conducted under scientific permits.

Salmonid diversity is associated with propensity to migrate, feed, and store energy in different environments. Our inclusion of the less-studied riverine–estuarine, estuarine, and anadromous B life histories revealed unique combinations of growth, demographics, and energy storage among the life history contingents. Mortality risks, also associated with life history tradeoffs in anadromous fishes (Jonsson and Jonsson 1993; Hendry et al. 2004), were not documented in this study as no survival data are currently available and remain a gap in our understanding of the system. Neither did we compare reproductive success among contingents, although previous behavioral and genetic studies suggest some level of interbreeding (Kuzishchin et al. 2007; McPhee et al. 2007; Kuzishchin et al. 2008).

When placed in context of *O. mykiss* across the species range, the diversity observed in Kamchatkan rivers is exceptional and raises many questions about how partial and differential migration is expressed among locations and under different conditions. Over five decades of study in Kamchatka, the relative proportions of each *O. mykiss* life history contingent varied among rivers (Pavlov et al. 2001) as well as within rivers over time (Savvaitova et al. 2002). Of note, contingents that are currently present yet rare in the Utkholok River (i.e., resident females, and the riverine–estuarine and estuarine contingents in general) were not observed at all in the earliest sampling that took place in 1970–1971 (Savvaitova et al. 2002; Kuzishchin et al. 2020b). We found that these rare life histories, such as females of the coastal and freshwater contingents, did not exhibit the expected compensatory lipid storage that would buffer them from uncertainties in future resource availability (Perrin and Sibly 1993; Varpe 2017), a finding consistent with growth and survival of these rare life histories being intermittently supported by certain growth environments. Further investigation of temporal changes in the growth environments and the capacity of the species to compensate for resource limitations is needed to better understand factors that maintain the exceptional diversity of *mykizha* on the Kamchatka Peninsula.

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Data availability

Fish, stable isotope, and genetic data and the R code are available from the corresponding author on reasonable request.

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Author contributions

All authors contributed to the study design and data interpretation. KK, MG, MZ, and MS contributed to field data collection. KK assigned life histories from scale pattern analysis.

MA analyzed stable isotope data. TS analyzed genetic data. MZ drafted the paper with contributions from all authors.

Competing interests

The authors declare there are no competing interests.

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Supplementary material

Supplementary data are available with the article at <https://doi.org/10.1139/cjfas-2021-0357>.

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