

Seasonal growth in juvenile steelhead

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**Seasonal variation in growth, consumption, and growth efficiency in overwintering juvenile steelhead**

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## Abstract

Food availability and thermal regimes can largely govern growth opportunities in fishes. In temperate regions, streams can exhibit summer temperatures that exceed the optima for coolwater-adapted species relative to the amount of available food, and there, spring and fall may confer better growing conditions, especially for larger size classes. We examined the relationship between growth, consumption, and growth efficiency across seasons in juvenile steelhead (*Oncorhynchus mykiss*) in their natal streams in Idaho, USA. Subyearling (0+) growth rates were higher in summer, whereas yearlings exhibited no statistically significant difference in growth between seasons. Consumption rates were overall lower in winter-spring but constituted a higher proportion of maximum consumption compared to summer and fall, indicating better food availability relative to metabolic demands. Net growth efficiencies were higher in winter-spring, but substantially more so than the proportion of maximum consumption. This suggests that overwinter growth performance was driven at least partly by higher growth efficiency, and the effect was most pronounced for yearling steelhead. The low proportions of maximum consumption for both age classes suggest that food was an overall limiting factor to growth, especially in summer when metabolic demands were highest. We discuss how temperature-based models can overestimate growth in the warmest parts of the year, and develop a simple conceptual model for the seasonal timing of juvenile growth. In anadromous populations, the outmigration of presmolts in spring can reduce the level of competition. For the individuals that remain in the river, growth in this period can be particularly important.

## 41 Introduction

42 Early growth performance can have important consequences for life-history expression and lifetime  
 43 fitness in fishes (Rose et al., 2001; Thorpe, 2007; Satterthwaite et al., 2010; Kendall et al., 2015). For  
 44 anadromous salmonids, growth during the first years in freshwater can influence the timing of  
 45 outmigration (Ward et al., 1989; Busby et al., 1996; Hartson & Kennedy, 2015), survival in freshwater  
 46 and at sea (Bond et al., 2008; Duffy & Beauchamp, 2011), and age at maturation (Vøllestad, Peterson,  
 47 & Quinn, 2004). Identifying the timing of juvenile growth can therefore give important insights into  
 48 the ecology of a population because it is shaped by life histories, environmental conditions,  
 49 community composition, and food availability (Thompson & Beauchamp, 2016; Quinn, 2018).

50 Factors that influence individual growth rates act directly or indirectly on the relationship between  
 51 energy intake and expenditure, and range from intrinsic individual characteristics such as physiology  
 52 and behavior (Metcalf, 1998; Reid, Armstrong, & Metcalf, 2011) to intraspecific competition,  
 53 environmental conditions, and food availability (Yamamoto, Ueda, & Higashi, 1998; Van den Avyle &  
 54 Hayward, 1999; Myrvoold Kennedy, 2015a; Spanjer et al., 2018). Which factor is more influential  
 55 depends on its magnitude and rank relative to the other factors under a given range of conditions  
 56 (Uthe, Al-Chokhachy, Shepard, Zale, & Kershner, 2019). For example, appetite in fishes generally  
 57 increases with water temperature up to some species-specific threshold (Wootton, 1999). Given  
 58 unlimited access to food, the temperature for which the scope for growth is optimal (i.e. the largest  
 59 difference between maximum consumption and energy expenditures) is relatively close to the  
 60 species' thermal tolerance (Brett, 1971; Wootton, 1999). However, food is most often limited in  
 61 natural settings due to fluctuating production and competition over what is available (Keeley, 2001;  
 62 Letcher et al., 2015; Myrvoold & Kennedy, 2015a). When the amount of food is limited and the  
 63 availability is unpredictable, the optimal temperature for growth is much lower because basal  
 64 metabolism and costs associated with processing the food also increase with temperature (Elliott,  
 65 1975; Hewett & Kraft, 1993).

66 Translated to geography, in cold environments (northern regions or high-altitude locations with a  
 67 short ice-free season) the summer temperatures may never exceed the optimal temperature under  
 68 an unpredictable and limited food supply. Consequently, there may be a positive relationship  
 69 between temperature, consumption, and growth over the restricted range of observed temperatures  
 70 in those areas because the effects of food limitation are less visible. In contrast, prolonged periods of  
 71 high water temperatures (> 18°C) typical of summers in lowland or temperate regions can prove  
 72 challenging for juvenile salmonids in streams, both directly through energetic stress and in  
 73 combination with other factors (Xu, Letcher, & Nislow, 2010; Letcher et al., 2015; Myrvoold &  
 74 Kennedy, 2015b; Ayllón et al., 2019; Kelson & Carlson, 2019). High water temperatures in the early  
 75 summer often coincide with the onset of summer baseflow conditions and the emergence of a new  
 76 cohort, so that increased competition and elevated metabolism may further decrease energy intake  
 77 and elevate energy expenditures (Nicola & Almodovar, 2004; McCarthy, Duda, Emlen, Hodgson, &  
 78 Beauchamp, 2009; Spanjer et al., 2019). Therefore, while the ice-free summer months (June, July,  
 79 and August) are important for growth performance at high latitudes and elevations (Borgstrøm &  
 80 Museth, 2005), spring and fall seasons may confer better conditions for growth in warmer climates  
 81 (Nicola & Almodovar, 2004; McCarthy et al., 2009; Tattam, Li, Giannico, & Ruzycki, 2017; Kelson &  
 82 Carlson, 2019). The optimal conditions for growth therefore depend critically on the seasonal timing

of temperature and prey availability, both of which are affected by landscape-scale features such as climate, elevation, and latitude.

Here, we study the growth performance of juvenile steelhead across seasons in the Lapwai Creek watershed in the Inland Pacific Northwest, USA. We have previously documented depressed growth rates due to intraspecific competition and high metabolic demands during the dry season from June to October (Myrvold & Kennedy, 2015a, b). Despite limited growth in summer and fall, overwintering yearling cohorts begin the subsequent summer substantially larger than expected based on summer and fall growth performance. Our first objective is to estimate the growth trajectories for overwintering juvenile steelhead to identify the timing of the mass accrual using a bioenergetics model. Next, we compare growth rates, consumption rates, and growth efficiency across seasons to elucidate the extent to which seasonal variation in growth performance was the result of high consumption rates or efficient use of energy. Finally, we develop a conceptual model for individual growth in relation to temperature, density, food availability, and stream area for anadromous populations in a similar physiographic setting.

## Methods

### Study area

The study was conducted in the 694 km<sup>2</sup> Lapwai Creek watershed of North-Central Idaho, United States (Figure 1). The study area and methods for obtaining data have been described in previous works (e.g. Myrvold and Kennedy 2015b, c), and will be briefly described here. Lapwai Creek is located between the Columbia River Plateau and Northern Rockies ecoregions (McGrath et al., 2002). The four tributaries drain through steep canyons before opening up to wider floodplains at their successive confluences. Coniferous forest dominates the high elevation (max. elevation 1530 m) and grassland and grain crops dominate the middle and lower elevations towards the confluence with the Clearwater River (elevation 237 m). The substrate is chiefly cobble-sized, and wetted channel widths during sampling ranged from 3 m in the upper study sites to 9 meters in the downstream sites. Mean annual precipitation is 490 mm, primarily from October through May (Myrvold & Kennedy, 2015c), and the mean annual discharge (1975 – 2018) was 2.2 m<sup>3</sup>s<sup>-1</sup> (obtained from USGS gauge 13342450). The hydrograph follows a typical snowmelt-driven pattern with a few rain-on-snow events occurring in spring, and stable baseflow conditions with very few rain-driven spates from mid-June through October (Myrvold & Kennedy, 2015a). The upper parts of the anadromous reaches freeze over during the coldest periods, whereas the mainstem remains mostly ice-free (K.M. Myrvold, *personal observation*). However, with predicted shifts in the form, amount, and timing of precipitation (Mote & Salathe, 2010; Vano, Nijssen, & Lettenmaier, 2015) it is likely that streams will enter baseflow earlier in the summer, and that periodic drying of stream beds will occur more frequently (Myrvold & Kennedy, 2018).

### Steelhead growth data

Lapwai Creek is a tributary to the Clearwater River and is designated as critical habitat for a wild steelhead population (NMFS, 2010). As part of a monitoring program to assess individual performance and population dynamics, we established an array of study sites representative of the physiographic variation in the watershed (Hartson & Kennedy, 2015; Myrvold & Kennedy, 2015b,c). Each study site was approximately 100m long, and key characteristics have been presented in previous publications (e.g., see Table 1 in Myrvold & Kennedy, 2015c). We visited each study site monthly from June to October in 2010, 2011, and 2012. In addition, we visited six of the uppermost study sites in May 2012. Fish were captured via three-pass depletion electrofishing using a Smith-Root LR-24 backpack electrofisher (Smith-Root Inc., Vancouver, Washington, USA). We measured fork length in millimeters and mass to the nearest 0.1g and tagged individuals larger than 65mm with a Passive Integrated Transponder (PIT). This allowed us to calculate the specific growth rates (referred to as *growth rate* in this article) of recaptured individuals between encounters (in the same year or in the subsequent year), expressed as the percent change in body mass per day.

Juvenile steelhead spend on average two years in their natal streams in the Lapwai Creek system but there is consistent variation among sites and some individual variation (Hartson & Kennedy, 2015; Caisman, 2015). Fish inhabiting the uppermost sites in each tributary tend to grow slower and outmigrate at a higher age than do fish in downstream sites, and fast-growing individuals tend to outmigrate earlier than their cohorts. In this paper we were interested in quantifying the growth rates of fish that remained in the study sites over winter (Figure 2). We tagged 3986 juvenile steelhead in 2010 and 2011, of which 133 were recaptured in subsequent years, i.e. had measurements of overwinter growth rates. Because we did not sample between October and May or June, we modeled the growth trajectories of these individuals using a bioenergetics model.

Temperature data

Stream temperatures were recorded every 30 minutes in each study site from 01 May 2010 through 2012 using HOBO TidbiT v2 temperature loggers (Onset Computer Corporation, Pocasset, Massachusetts, USA). The data were used in the bioenergetics modeling.

Bioenergetics model

We used Fish Bioenergetics 3.0 (“Wisconsin model”; Hanson, Johnson, Kitchell, & Schindler, 1997) to calculate consumption rates necessary to achieve a certain growth in a given thermal regime, and to simulate the growth trajectories on a daily time step during the period between encounters. Myrvold & Kennedy (2015b) used field data from the Lapwai Creek watershed to parameterize the model, and we use this model in the following analyses. The model was specified with Thornton & Lessem’s (1978) consumption equation, Kitchell et al.’s (1977) respiration equation, Elliott’s (1976) waste losses equation, predator energy density equation number 2 (Hanson et al., 1997), and subsequent improvements of the parameter set (Railsback & Rose, 1999). We used an energy density of 4324 J/g wet weight for the invertebrate prey (the main diet; Myrvold and Kennedy 2015b), and an energy density of 5763 J/g wet weight for steelhead (Glova & McInerney, 1977) – these values were used for all individuals in the current analysis. We used site-specific temperature data for each period and

specified the mass of the fish at the start and the end of the simulation run. For a given change in body mass between encounters, the bioenergetics model simulates the growth trajectory over the time period on daily time steps and outputs parameter values relevant to the energy budget for the fish. We note, however, that predator energy density tends to be overestimated for juveniles, which in turn leads to underestimates of consumption rates (Trudel, Tucker, Morris, Higgs, & Welch, 2005).

#### Consumption rates and growth efficiency

We were particularly interested in an individual's relative consumption rate, expressed as the proportion of maximum consumption ("P-value"; Hanson et al., 1997), and its growth efficiency. The P-value is the quotient between the modeled ration from a simulation and the maximum theoretical ration in a given time interval, such as the period between capture and recapture. An individual's growth efficiency in the same time interval is the quotient between the amount of energy allocated towards somatic growth and the total energy consumption. To obtain the amount of energy allocated towards growth we ran two simulations: one simulation reflecting the actual weight gain between capture and recapture to calculate the total ration, and one without any growth (by setting the end weight equal to the start weight) to calculate the ration necessary just to maintain its mass (Hewett & Kraft, 1993; Myrvold & Kennedy, 2015b). The difference between the two is the amount of energy allocated to growth. To calculate the growth efficiency we divided the ration allocated towards growth by the total ration.

#### Modeling overwinter growth trajectories

To assess the timing of mass accrual under a bioenergetics framework we simulated the average growth trajectories from October 15 to June 15 (as denoted in Figure 3). Subyearlings grew, on average, from 7.1g ( $n = 36$ ,  $SD = 2.3$ g) on the last sampling visit in year 1 to 25.8g ( $SD = 10.9$ g) on the first regular sampling visit in June the following year, whereas the yearlings for which we had recapture data grew from 19.8g ( $n = 9$ ,  $SD = 8.5$ g) to 49.5g ( $SD = 23.5$ g). The discrepancy in mean body mass between one-year old fish in June and in October owes to movement and migration: some of the fast-growing one-year old fish outmigrate in the fall following their second summer and would hence not be recaptured the following summer, and due to considerable movement throughout the year the composition of individuals in a given site is dynamic (Hartson & Kennedy, 2015). We specified the bioenergetics model with the same parameters as described above and conducted simulations for an example site (site UMU; mean = 4.5 °C,  $SD = 3.4$  °C) for both age classes.

#### Statistical analyses

The study design was clustered in both a longitudinal sense (observations nested within known individuals over time) and cross-sectional sense (comparison of individuals at given points in time, nested in discrete study sites). To account for the multilevel structure, we used linear mixed models (Raudenbush & Bryk, 2002). To find the average growth rate of subyearlings and yearlings and to

partition the variance among the different levels we first specified a variance components model (Raudenbush & Bryk, 2002). Here we have observations of growth rates nested within individuals taken at subsequent points in time:

$$growth_{ij} = \gamma_{00} + u_{0j} + r_{ij} ,$$

where growth rate  $i$  of fish  $j$  is related to a grand mean growth rate for all the individuals ( $\gamma_{00}$ ), an individual-level variance ( $u_{0j}$ ) around this mean, and a residual error within each individual ( $r_{ij}$ ), with  $u_{0j} \sim N(0, \tau_{00})$  and  $r_{ij} \sim N(0, \sigma^2)$ . We also assessed whether a three-level model structure was necessary by adding study site as a random effect in the variance components model (Myrvold & Kennedy, 2015a). There was no clustering at the level of study sites, and we consequently proceeded with the two-level model (Table 1).

We tested whether individual growth rates and growth efficiency differed between seasons. We defined summer as June-July, June-August, and July-August; fall as August-September, September-October, and August-October; and winter-spring as the period between October in one year and May or June the following year. To account for the paired observations within each individual we specified a mixed effects model with season as a categorical predictor variable with three fixed levels (summer, fall, and winter-spring) and individual as a random effect:

(eq. 1)

$$growth_{ij} = \beta_{0j} + \beta_{1j}season_{ij} + r_{ij}$$

To allow for individual-specific intercepts we can write

$$\beta_{0j} = \gamma_{00} + u_{0j} \text{ and } \beta_{1j} = \gamma_{10}$$

Substituting into equation 1, this becomes a linear mixed effects model

$$growth_{ij} = \gamma_{00} + \gamma_{10}season_{ij} + u_{0j} + r_{ij}$$

where  $u$  and  $r$  are random effects.  $r_{ij}$  is assumed  $N(0, \sigma^2)$  for growth rate  $i$  in fish  $j$ , and is the residual of growth rate  $i$  from the mean growth rate in fish  $j$  after controlling for season. Because of the categorical predictor variable, the value for the intercept was used to decode the values for the three levels of seasons. We conducted the same analysis for proportion of maximum consumption and growth efficiency.

All models were specified with the Kenward & Roger (1997) approximation of denominator degrees of freedom, an unstructured covariance matrix to allow for individual variation in growth trajectories, and maximum likelihood as the estimator. We used SAS v.9.4 Proc MIXED (SAS Institute, Cary, North Carolina, USA) for all the analyses. Finally, we assessed that model assumptions were met by visually examining the residual plots for all the models, obtained with the *ods graphics* command. Even though the proportion of maximum consumption and net growth efficiency are bound between 0 and 1, we only encountered a limited range of values for which a linear model was appropriate.

**Results**

The 133 individuals with overwinter growth histories were found in 10 sites (Appendix 1). These individuals were encountered 518 times and yielded 385 growth estimates (i.e. from one sampling visit to another), partitioned into 202 subyearling and 183 yearling growth histories. Only one individual moved between sampling sites (a subyearling tagged in site ULL in the summer of 2010 was recaptured in site ULU in July 2011). The individuals were primarily found in the uppermost study sites in each tributary (Figure 1), which corroborate earlier findings of later outmigration and greater site fidelity in the upper sites (Hartson & Kennedy, 2015).

#### Overwinter growth trajectories

The simulated growth trajectories for the average subyearlings and yearlings in example site UMU are shown in Figure 4. Some growth occurred in the remainder of October in both years and was relatively stagnant between the beginning of November and mid March both years. Most of the growth happened in the last month of the simulation. Subyearlings reached their average mass (16.5g) on May 15<sup>th</sup> (average for all simulations), and yearlings reached their average mass (34.7g) on May 14<sup>th</sup>, at which time 86% of the period had lapsed. The P-values (i.e. the proportion of maximum consumption) necessary to achieve this growth over the entire period were 0.372 in 2010-2011 and 0.363 in 2011-2012 for subyearlings and 0.376 and 0.367 for yearlings.

To show how temperature affected the growth trajectory in the bioenergetics model we plotted the thermograph and the specific growth rate together with the simulated subyearling mass (Figure 5). The simulated daily weight increments were closely, and positively, related to temperature in this temperature range.

#### Growth, consumption, and growth efficiency

We plotted the average values and associated standard deviations for specific growth rates (% body mass per day), P (proportion bound by 0 and 1), and growth efficiency (proportion bound by 0 and 1) for all the periods ( $n = 133$  individuals with 385 growth measurements; Figure 3). Qualitatively, subyearlings achieved the highest growth rates in their first summer and fall, and overall lower growth rates in the winter-spring period. Growth efficiency was consistently higher in the winter-spring period. Yearling growth rates were more variable throughout the different periods but were generally higher in the winter-spring period, and lower in summer and fall. Growth efficiency was substantially higher in the winter-spring period for both age classes.

In order to focus on the difference between seasons, we considered individuals with growth measurements within the narrow definitions of summer (June-July, June-August, and July-August), fall (August-September, August-October, September-October), and winter-spring (October-May and October-June). Sixty-three subyearlings yielding 118 growth histories and 60 yearlings yielding 125 growth histories satisfied these criteria. The discrepancies between numbers of individuals and growth histories owe to multiple growth histories for some individuals in summer (e.g. from June to July and July to August).



Subyearling growth rates were consistently higher in summer (mean 0.83% body mass per day) than in fall (mean 0.70% per day) and winter-spring (0.52% per day;  $n = 118$ ,  $F = 5.5$ ,  $d.f. = 118$ ,  $P = 0.005$ ). Inclusion of season as a factor in the model explained some 9% of the variance in growth rates (Table 2). For yearling steelhead there was no statistically significant difference in growth rates between summer (mean 0.24% body mass per day), fall (mean = 0.27%), and winter-spring (0.36% per day;  $n = 125$ ,  $F = 0.35$ ,  $d.f. = 125$ ,  $P = 0.70$ ). Inclusion of season as a factor variable in the model explained only 1% of the variance in yearling growth rates (Table 2). All the variance in the growth rates came from variation in an individual's growth rates, not from consistent variation among individuals.

Growth efficiency for subyearlings was highest in winter-spring ( $n = 118$ ,  $F = 91$ ,  $d.f. = 97$ ,  $P < 0.0001$ ). Inclusion of season explained 60% of the total variance in the data for subyearlings (64% of which at the residual level; Table 2). Similarly, yearling growth efficiency was higher in winter-spring (mean = 53%) than in fall (mean = 16%) and summer (mean = 9%;  $n = 125$ ,  $F = 14.5$ ,  $d.f. = 125$ ,  $P < 0.0001$ ). Inclusion of season explained 19% of the total variance, all of which at the residual level (Table 2).

Finally, we tested how the corresponding values for daily consumption rates and proportion of maximum consumption ("P-values") related to the pattern of higher growth efficiency in winter-spring. Daily average yearling consumption rates were significantly higher in summer (mean = 184 J/g/d,  $SE = 16$ ) than in fall (mean = 146 J/g/d,  $SE = 17$ ) and winter-spring (mean 91 J/g/d,  $SE = 15$ ;  $n = 125$ ,  $F = 22.5$ ,  $d.f. = 125$ ,  $P < 0.0001$ ). The corresponding proportions of maximum consumption were 0.202 ( $SE = 0.019$ ) in summer, 0.209 ( $SE = 0.020$ ) in fall, and 0.311 ( $SE = 0.018$ ) in winter-spring, which were significantly different ( $n = 125$ ,  $F = 17$ ,  $d.f. = 125$ ,  $P < 0.0001$ ). Hence, an overall lower absolute consumption rate in winter-spring constituted a higher proportion of maximum consumption and yielded higher growth efficiencies than in summer and fall. For subyearlings, daily average consumption rates were significantly higher in summer (mean = 321 J/g/d,  $SE = 5$ ) than in fall (mean 234 J/g/d,  $SE = 8$ ) and winter-spring (mean 110 J/g/d,  $SE = 7$ ;  $n = 118$ ,  $F = 135$ ,  $d.f. = 118$ ,  $P < 0.0001$ ). The corresponding proportions of maximum consumption were 0.198 ( $SE = 0.015$ ) in summer, 0.211 ( $SE = 0.0059$ ) in fall, and 0.328 ( $SE = 0.0056$ ) in winter-spring, which were significantly different ( $n = 118$ ,  $F = 203$ ,  $d.f. = 90.7$ ,  $P < 0.0001$ ). The higher consumption rates in summer yielded significantly higher growth rates, despite constituting a lower proportion of maximum consumption in summer relative to fall and winter-spring.

In discerning the extent to which consumption levels or growth efficiency were driving the observed variation in seasonal growth, our results show two main patterns. First, even though absolute consumption rates in winter-spring were overall lower, they constituted a higher P compared to that in summer for both age classes (Table 3). Similarly, the net growth efficiencies were higher in winter-spring than in summer and fall, but substantially more so than for P. For example, whereas yearling P was 54% higher in winter-spring than in summer, the net growth efficiency was 471% higher. This suggests that overwinter growth was driven chiefly by higher growth efficiency and to some extent by higher proportions of maximum consumption. Secondly, this manifested unequally among the age classes in terms of growth rates (Table 3). Whereas subyearlings grew faster in summer, there were no significant difference between seasons for yearlings. This could be due to high metabolic demands for larger fish in summer, that is, because the absolute demands could not be met as easily as for smaller individuals. Furthermore, the overall low proportions of maximum consumption for both age

classes in summer suggest that food is a limiting factor to summer growth under the prevailing thermal regime.

## Discussion

Seasonal growth patterns varied between age classes in the Lapwai Creek watershed. Whereas subyearling steelhead grew faster in their first summer and fall than in winter-spring, there was no statistically significant difference between seasons for yearling fish. Because we did not sample during the winter and spring, we did not have any growth measurements on regular intervals; however, bioenergetics simulations suggested that most of the body mass was accrued during May and early June. This owes partly to more efficient energy use over the entire winter-spring period, when fish were able to allocate a much higher fraction of their ration towards somatic growth. This suggests that spring might be particularly important for annual growth in areas where stream temperatures are high relative to the availability of food in the summer, especially for larger individuals.

Most studies on stream salmonid growth are conducted in summer and fall. There exist a handful of studies on the seasonal growth patterns in juvenile steelhead in temperate regions (Merz, 2002; Hayes et al., 2008; McCarthy et al., 2009; Thompson & Beauchamp, 2016; Tattam et al., 2017). Hayes et al. (2008) studied seasonal growth and life history of steelhead in a small coastal watershed in California. The watershed is characterized by mild winters (minimum average daily water temperature of 5.6 °C) and dry, mild summers (average temperatures 14-18 °C). Yearling fish achieved the highest growth rates in spring (0.50% body mass per day) and the lowest in summer and fall (0.0-0.20% body mass per day). These findings were similar to that of other studies on steelhead growth in California (Railsback & Rose, 1999; Merz, 2002). McCarthy et al. (2009) studied steelhead and rainbow trout growth and consumption in Northern California and reported overall fast growth in spring (March to May), and weight loss in summer. They attributed the pattern to overall higher consumption rates and closer-to-optimal temperatures for growth in spring than in summer. Recently, Tattam et al. (2017) documented the highest growth rates of the year in spring in juvenile steelhead in Central Oregon, an area with a similar temperature regime as the Lapwai Creek watershed. The average temperature in the spring season was 9 °C, which is lower than the reported optimal temperatures for growth (22 °C; Railsback & Rose 1999), suggesting that optimal temperatures for growth may depend on the season.

The same pattern of rapid growth in spring and slower growth in subsequent seasons has also been reported across species and genera in temperate rivers. Ebersole et al. (2006) found that juvenile coho in Oregon grew significantly faster in the spring (mean 0.84% body mass per day from mid-March through June) than winter (mean 0.58% body mass per day, December to March), and that spring growth rates did not differ among tributaries and mainstem rearing locations. Similar findings have been reported in Eastern North America. Horton, Letcher, Bailey, & Kinnison (2009) found that Atlantic salmon (*Salmo salar*) growth rate in Massachusetts was highly seasonal for all cohorts. The highest growth rates occurred in spring for age 1+ and 2+ fish, then decreasing through the subsequent seasons. Carlson, Hendry, & Letcher (2007) found that growth of sympatric brook trout

(*Salvelinus fontinalis*) and introduced brown trout (*Salmo trutta*) in West Brook, Massachusetts peaked in spring. This could result from higher drift densities in the spring and a sharp decline in drifting invertebrates in the subsequent seasons (Grade & Letcher, 2006).

Several field studies have compared seasonal growth rates with predictions from temperature models derived from laboratory studies of growth and consumption. Nicola & Almodovar (2004) found that brown trout in streams in Spain achieved their highest growth rates in spring. They compared these empirical growth rates with modeled growth rates from Elliott, Hurley, & Fryer's (1995) temperature-based growth model, which was based on ad libitum laboratory studies in Northwest England. Despite a limited and dynamic food supply, growth rates under natural conditions in Spain surpassed the modeled growth. It is uncertain whether this was because of a seasonal effect (for example that the laboratory studies were conducted in summer, when the optimal temperature for growth was higher; see discussion below), or genetic factors (e.g. that selection favors growth earlier in the year in Spanish populations). Similarly, Bacon, Gurney, Jones, McLaren, & Youngson (2005) studied the seasonal growth patterns of juvenile Atlantic salmon in Scotland and compared their field results to two temperature-based growth models for the species (Elliott & Hurley, 1997; Forseth, Hurley, Jensen, & Elliott, 2001). Bacon et al. found that most of the growth happened in a 10-week period in the spring at temperatures that were lower than what the models deemed necessary to achieve that level of growth.

Apart from misapplication of temperature-based growth models to systems for which they were not developed, the discrepancy between model predictions and field measurements of salmonid growth in temperate regions could result from two main factors. First, temperature-based models do not take into account the dynamic effects of season on growth efficiency. In a series of experiments, Averett (1969) investigated the effects of season on juvenile coho growth, consumption, and growth efficiency. He found that the optimal temperature for growth and growth efficiency depended upon season: fish achieved higher growth efficiencies at lower temperatures in April and May (range 5 – 14 °C) than in June-July (range 11 – 14 °C) and August-September (range 14 – 17 °C). At the lowest temperature treatments in the April-May experiment the growth efficiencies were high at low consumption rates, and declined sharply with increasing consumption rates, presumably due to a combination of increased costs of systemic dynamic action and increased activity costs (Averett, 1969). In other words, fish achieved no growth benefit from increasing their consumption rates, but grew well on a limited ration due to lower temperature-induced energy losses. In summer and fall, this relationship was shifted towards higher growth efficiency at higher temperatures, which were consistent with the thermal regime in their natal streams (Averett, 1969). The effects of thermal adaptation in local populations has received variable support. Jonsson, Forseth, Jensen, & Næsje (2001) and Forseth et al. (2009) found no evidence of growth-related adaptation to the prevailing thermal regimes in populations of Atlantic salmon and brown trout, respectively. However, Narum et al. (2013) found some evidence for thermal adaptation between populations of redband rainbow trout in Idaho. When subjected to high temperatures (from 17.0 to 28.5 °C), fish from relatively warmer desert environments exhibited lower heat shock protein response than fish from relatively colder mountain environments. This suggests that desert fish have maintained or developed mechanisms to cope with thermal stress (high temperatures in this case), but the relation to growth performance was not investigated.

Secondly, there is evidence that there is more food of higher quality available in spring. Grade & Letcher (2006) found the highest density of drift in April and June, and substantially lower densities in summer and fall. Benthic density showed an opposite pattern, with the highest values in summer and fall, and the lowest in winter and spring (Grade & Letcher 2006). Nakano & Murakami (2001) reported higher amounts of aquatic insects from December to July, and greater amounts of terrestrial invertebrates from July to September in Japan. Li, Gerth, Driesche, Bateman, & Herlihy (2016) reported a similar pattern in a coastal watershed in Oregon, and found that juvenile steelhead relied more on terrestrial invertebrates in summer. We do not have data on drift densities in the spring in Lapwai Creek. However, even if the amount of food were constant throughout the year, the lower metabolic demands during the typical temperatures in spring, and potentially the higher growth efficiency in this period, could explain why yearling growth rates in this period were comparable to those of summer (Myrvold & Kennedy 2015b).

In order to decouple the effect of season from temperature it is useful to compare growth rates between seasons with similar temperatures and photoperiods. Xu et al. (2010) provided a strong test of the effect of temperature and stream discharge on brook trout growth rates at different times of the year over 8 years in Massachusetts. Growth rates generally increased with water temperature in spring and winter but decreased with temperature in summer and fall within the same temperature range. Stream flow had a modulating effect through its control over temperature, but these effects were dynamic: growth increased with flow in cool summers but had no effect in the warmest summers. The effects of flow were not strong enough to affect the direction of the relationship between temperature and growth, but flow did affect the strength of the relationship (i.e. the slope of the regression). The effects of density on individual growth rates were also higher in summer than in spring (Xu et al., 2010).

Our simulations of overwinter growth trajectories suggested that most of the body mass was accrued at the end of the spring period (15. May to 15. June; figure 4). However, there is uncertainty in how well the temperature-dependent function of the bioenergetics model represents the ecology in the Lapwai Creek watershed. Given the results from other studies (Railsback & Rose, 1999; Merz, 2002; Hayes et al., 2008; McCarthy et al., 2009; Tattam et al., 2017) that have measured steelhead growth rates in spring we suspect that the modeled growth in our study was shifted more towards the end of the winter-spring period than what was actually the case. We attribute this to the distinct dry season, which represents metabolically stressful conditions in Lapwai Creek (Myrvold & Kennedy, 2015b).

Seasonality in food availability, temperature, and optimal temperatures for growth have been shown to affect size classes differently. Connolly & Petersen (2003) investigated the effects of overwinter temperature on different size classes of subyearling steelhead reared at different temperatures (3, 6, and 9 °C). All size classes grew faster at the highest temperature, but the small individuals benefited the most. The proportion of lipids decreased in the largest fish but increased overall in the smallest fish. Finally, Fulton's condition factor decreased for all size classes at the highest temperature but increased for all size classes at the lowest temperature. Relatively higher winter temperatures in concert with limited food availability could hence be physiologically more challenging for larger individuals (Connolly & Petersen, 2003). During high temperature conditions in summer, Breau, Cunjak, & Peake (2011) found physiological and behavioral differences between age classes of Atlantic salmon. Whereas subyearlings were feeding up to the highest temperature (28 °C) in the experiment, older fish experienced lactate buildup and ceased feeding at 24 °C. This shows that the

interactions between temperature, food, and fish size are complex, and that selection for certain traits and behaviors (e.g. movement between seasonal habitats) may vary throughout the species' range.

The level of competition for food and space can largely control individual growth opportunities (Quinn, 2018). During summer and fall, Myrvold & Kennedy (2015a) found evidence of density-dependent growth rates in subyearling steelhead in the Lapwai Creek watershed, whereas Myrvold & Kennedy (2015b) found that yearling growth was largely limited by food and high metabolism. However, winter mortality and the emigration of steelhead smolts during snowmelt in March and April (Hartson & Kennedy, 2015) will reduce the level of competition for the fish that remain in the rivers (Figure 2) at a time when food may be plentiful and growth efficiency is high. Hartson & Kennedy (2015) found that the probability of an individual outmigrating increased with density and the size of the individual relative to its conspecifics. Juvenile steelhead are territorial, and occupation of good feeding stations is to some extent linked to size (Keeley, 2001; Rundio & Lindley, 2019). This suggests that when the largest individuals outmigrate, the smaller individuals that remain in the river gain access to better feeding territories and can capitalize on the lower levels of exploitative and interference competition.

Because the release from competition coincides with a greater stream area, closer-to-optimal temperatures for growth efficiency, and potentially more food, the period between the start of spring runoff and summer baseflow might therefore be particularly important to yearling growth in locations such as Lapwai Creek. Based on these coinciding events we suggest a conceptual model for seasonal growth in juvenile steelhead that applies to temperate rivers with cold winters and long, dry summers (Figure 6). The model is clearly an oversimplification; however, it can be useful to help visualize the interrelationships between the main ecological components that can govern temporal growth patterns in juvenile stream salmonids.

With global climate change and increasing pressures on stream ecosystems, the suite of environmental conditions experienced by most steelhead populations will likely shift (Thompson & Beauchamp, 2016; Spanjer et al., 2018; Kelson & Carlson, 2019). Historically, the summer and fall discharge in the Lapwai Creek watershed has been influenced by gradual snowmelt and surface runoff until late June, and groundwater and spring releases until the return of precipitation in October. However, there is substantial inter-annual variation in the form of precipitation and timing of the runoff because the watershed lies in a transitional climatic zone and is topographically complex (Elsner et al., 2010; Mote & Salathe, 2010), and in addition, the changes in snow storage capacity due to logging and grazing have likely contributed to earlier snowmelt. Forecasting future streamflow and temperature is therefore complicated. The Lapwai Creek region showed some of the greatest sensitivity of streamflow to forecasted changes in precipitation and temperature in the Inland Northwest (Vano et al., 2015). The greatest decline in runoff was forecasted to occur in the warm season, which was largely driven by changes in the form of precipitation in the winter and an earlier runoff (Vano et al. 2015). In predicting the effects of climate change on the growth performance, life history choices, and population dynamics of salmonids it is important to have realistic models (Ayllón et al., 2019). As has been shown by others (Nicola & Almodovar, 2004; Bacon et al., 2005), this paper suggests that temperature-based growth models derived from trials in northern regions should be used with caution in temperate streams, which exhibit great annual temperature ranges and where summers pose energetically stressful conditions.

485

486

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496

497 **Ethical approval**

498 The sampling procedures were permitted as part of the Section 7 consultation for the Lewiston  
 499 Orchards Biological Opinion (NMFS 2010). The procedures were reviewed and approved by the Idaho  
 500 Department of Fish and Game and the University of Idaho Institutional Animal Care and Use  
 501 Committee.

502

503 **Data availability statement**

504 The data that support the findings of this study are available from the corresponding author upon  
 505 reasonable request.

506

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697 **Tables**

698 Table 1. Variance partitioning among the two levels (within individuals and among individuals) for 63  
 699 subyearlings and 60 yearlings with recapture histories in both summer (June, July, and August), fall  
 700 (August, September, and October) and the subsequent winter-spring season (October to May or  
 701 June).  $\rho$  is the intraclass correlation coefficient, i.e. the proportion of the total variance which is  
 702 attributable to each level. The P-value refer to the test  $H_0$ : estimate = zero. Also shown is the mean  
 703 value for growth rate, consumption, and growth efficiency for both age classes.

Response and age class	Level	Variance term	Estimate (SE)	$\rho$	P-value
SPECIFIC GROWTH RATE					
Subyearlings	Mean $\gamma_{00}$		0.642 (0.029)		<0.0001
	Residual	$\sigma^2$	0.100 (0.013)	100	<0.0001
	Individual	$\tau_{00}$	0.0 (-)	0	n/a
Yearlings	Mean $\gamma_{00}$		0.249 (0.038)		<0.0001
	Residual	$\sigma^2$	0.177 (0.022)	100	<0.0001
	Individual	$\tau_{00}$	0.0 (-)	0	n/a
PROPORTION OF MAXIMUM CONSUMPTION					
Subyearlings	Mean $\gamma_{00}$		0.253 (0.0063)		<0.0001
	Residual	$\sigma^2$	0.0046 (0.0006)	100	<0.0001
	Individual	$\tau_{00}$	0 (-)	0	n/a
Yearlings	Mean $\gamma_{00}$		0.212 (0.0054)		<0.0001
	Residual	$\sigma^2$	0.0036 (0.0005)	100	<0.0001
	Individual	$\tau_{00}$	0	0	n/a
GROWTH EFFICIENCY					
Subyearlings	Mean $\gamma_{00}$		0.437 (0.018)		<0.0001
	Residual	$\sigma^2$	0.0396 (0.005)	100	<0.0001
	Individual	$\tau_{00}$	0.0 (-)	0	n/a
Yearlings	Mean $\gamma_{00}$		0.146 (0.023)		<0.0001
	Residual	$\sigma^2$	0.066 (0.008)	92.2	<0.0001

	Individual	$\tau_{00}$	0.0 (-)	7.8	0.33
704	<hr/>				
705					

706 Table 2

707 Table 2. Parameter estimates for the effect of season on growth rates, consumption, and growth  
 708 efficiency. Shown for each age class are the growth rate estimates and standard errors for each  
 709 season and the estimates for the variance components.  $\rho_{\text{growth period}}$  shows how much of the  
 710 explainable variation at the residual level was explained by the inclusion of season as a factor, and  
 711 similarly,  $\rho_{\text{individual}}$  shows the effect on the individual level.

Response and age class	Variable	Parameter estimate (SE)	$\rho_{\text{growth period}}$	$\rho_{\text{individual}}$
SPECIFIC GROWTH RATE				
Subyearlings	Season_Summer $\gamma_{10}$	0.825 (0.035)		
	Season_Fall $\gamma_{10}$	0.697 (0.059)		
	Season_Winter-Spring $\gamma_{10}$	0.523 (0.047)		
	Random intercept $\tau_{00}$	0.0 (-)		n/a
	Residual $\sigma^2$	0.092 (0.0012)	8.5	
Yearlings	Season_Summer $\gamma_{10}$	0.240 (0.15)		
	Season_Fall $\gamma_{10}$	0.275 (0.15)		
	Season_Winter-Spring $\gamma_{10}$	0.356 (0.14)		
	Random intercept $\tau_{00}$	0.0 (-)		n/a
	Residual $\sigma^2$	0.176 (0.027)	0.6	
PROPORTION OF MAXIMUM CONSUMPTION				
Subyearlings	Season_Summer $\gamma_{10}$	0.198 (0.015)		
	Season_Fall $\gamma_{10}$	0.211 (0.0059)		
	Season_Winter-Spring $\gamma_{10}$	0.328 (0.0056)		
	Random intercept $\tau_{00}$	0.00024 (0.0006)		0
	Residual $\sigma^2$	0.0013 (0.0007)	83.5	
Yearlings	Season_Summer $\gamma_{10}$	0.202 (0.017)		
	Season_Fall $\gamma_{10}$	0.209 (0.020)		
	Season_Winter-Spring $\gamma_{10}$	0.311 (0.016)		
	Random intercept $\tau_{00}$	0 (-)		n/a

	Residual $\sigma^2$	0.0025 (0.0003)	32	
GROWTH EFFICIENCY				
Subyearlings	Season_Summer $\gamma_{10}$	0.310 (0.055)		
	Season_Fall $\gamma_{10}$	0.325 (0.024)		
	Season_Winter-Spring $\gamma_{10}$	0.642 (0.020)		
	Random intercept $\tau_{00}$	0.0017 (0.0023)		n/a
	Residual $\sigma^2$	0.0014 (0.0027)	64	
Yearlings	Season_Summer $\gamma_{10}$	0.093 (0.082)		
	Season_Fall $\gamma_{10}$	0.159 (0.085)		
	Season_Winter-Spring $\gamma_{10}$	0.531 (0.078)		
	Random intercept $\tau_{00}$	0.0 (-)		n/a
	Residual $\sigma^2$	0.054 (0.0068)	19	

712

713

714 Table 3

715 Table 3. Proportional differences between seasons for mean growth and consumption components.  
 716 Asterisks denote statistical significance ( $P < 0.05$ ) from the mixed-effects model.

<i>Age class</i>	<i>Component</i>	<i>Proportional difference</i>		
		<i>Winter/spring - summer</i>	<i>Winter/spring - fall</i>	<i>Fall - summer</i>
Subyearling	Specific growth rate (%BM per day)*	-37%	-25%	-16%
	Proportion of max. consumption (P) *	66%	55%	7%
	Net growth efficiency (%) *	101%	92%	5%
Yearling	Specific growth rate (%BM per day)	48%	29%	15%
	Proportion of max. consumption (P) *	54%	49%	3%
	Net growth efficiency (%) *	471%	234%	71%

717



**Figure captions**

Figure 1. Map showing the location of the study sites in the Lapwai Creek watershed. Overwintering juvenile steelhead with recapture histories were found in sites ULL, ULM, ULU, UML, UMM, UMU, USM, USU, UWM, and UWU.

Figure 2. Conceptual figure showing the fate of a steelhead cohort through three age classes in the Lapwai Creek watershed. The figure starts with the emergence of a new 0+ cohort (dotted line) in mid May (Taylor, Myrvold, & Kennedy, 2016). After a period of mass mortality, the cohort enters their first summer and begin establishing territories (Myrvold & Kennedy, 2015a). As individual demands for food and space increase, the cohort thins throughout summer and fall. The cohort (solid line) then enters the first outmigration period during the spring runoff in mid March to mid April. Few and only the fastest growing individuals outmigrate as subyearlings (Hartson & Kennedy, 2015). The cohort then begins its second summer (the first summer as 1+ yearlings), with less mortality than in its first summer (Caisman, 2015). A small fraction of the cohort will outmigrate in the fall (Hartson & Kennedy, 2015). There is less mortality in the cohort’s second winter (dashed line) leading up to the main outmigration period. Fish leave the watershed on the main spring runoff, the same discharge event their parents ascended upon approximately two years earlier (Caisman, 2015). This paper concerns the growth performance and energy allocation in those individuals that did not outmigrate or die, and that were encountered in two subsequent years.

Figure 3. Relationships between growth rate, P-value (the proportion of maximum consumption), and growth efficiency for a) subyearling and b) yearling steelhead recaptured at different time intervals. Periods with captures and recaptures in the same calendar year (e.g. from July to August, 2011) are denoted “same”, whereas periods with captures in one year and recaptures the following year (e.g. from October 2011 to May 2012) are denoted “next”. Asterisks indicate the periods used in the comparison between summer, fall, and winter-spring.

Figure 4. Simulated overwinter growth trajectories for average yearling (top) and subyearling (bottom) steelhead at site UMU (chosen as an example site) in two winter and spring seasons. Solid lines denote 2010-2011 and dashed lines denote 2011-2012. The start and end weights were the same across years, and the primary factor varying between the scenarios is the temperature regime. For example, yearling steelhead weighed 25.2g on 01 March 2011. On 01 March 2012 the same fish would have weighed 22.9g (9.1% less) due to a different thermal regime.

Figure 5. Simulated growth trajectory (solid black line) of an average subyearling steelhead in example site UMU from October 2010 to June 2011, growing from 7.1g to 25.8g. Most of the growth happened after early April and continued until the end on 15. June. Note the negative growth rate (dashed line, displayed on the secondary axis) during the cold periods in winter (temperature as solid grey line).

Figure 6. Schematic showing the relationships between the typical Lapwai Creek wetted stream area in a snowmelt year (blue line), the abundance of the steelhead cohort that enters their second or third summer (grey dashed line), the abundance of insect larvae in the drift (green line), the water temperature profile (red line), and the specific growth rates of the average overyearling individual (black dashed line). It highlights the saddle-shaped pattern of specific growth rates (percent change in body mass per day) as it relates to changes in abundance of steelhead and wetted area (proxies for intraspecific competition), food, and temperature (which controls appetite and metabolic demands) throughout a typical year. Based on our findings in the Lapwai Creek watershed we hypothesize that the best growing conditions for juvenile salmonids in temperate regions with a marked dry season occur in the spring and fall.

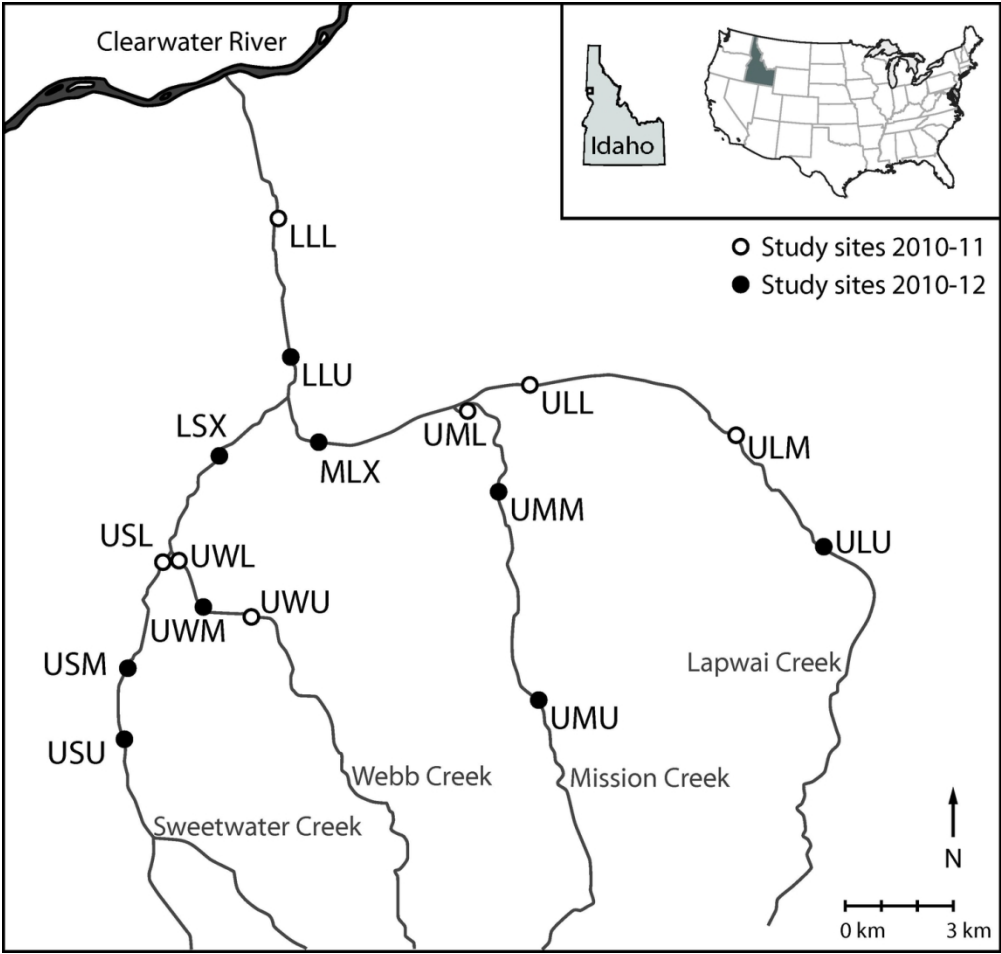
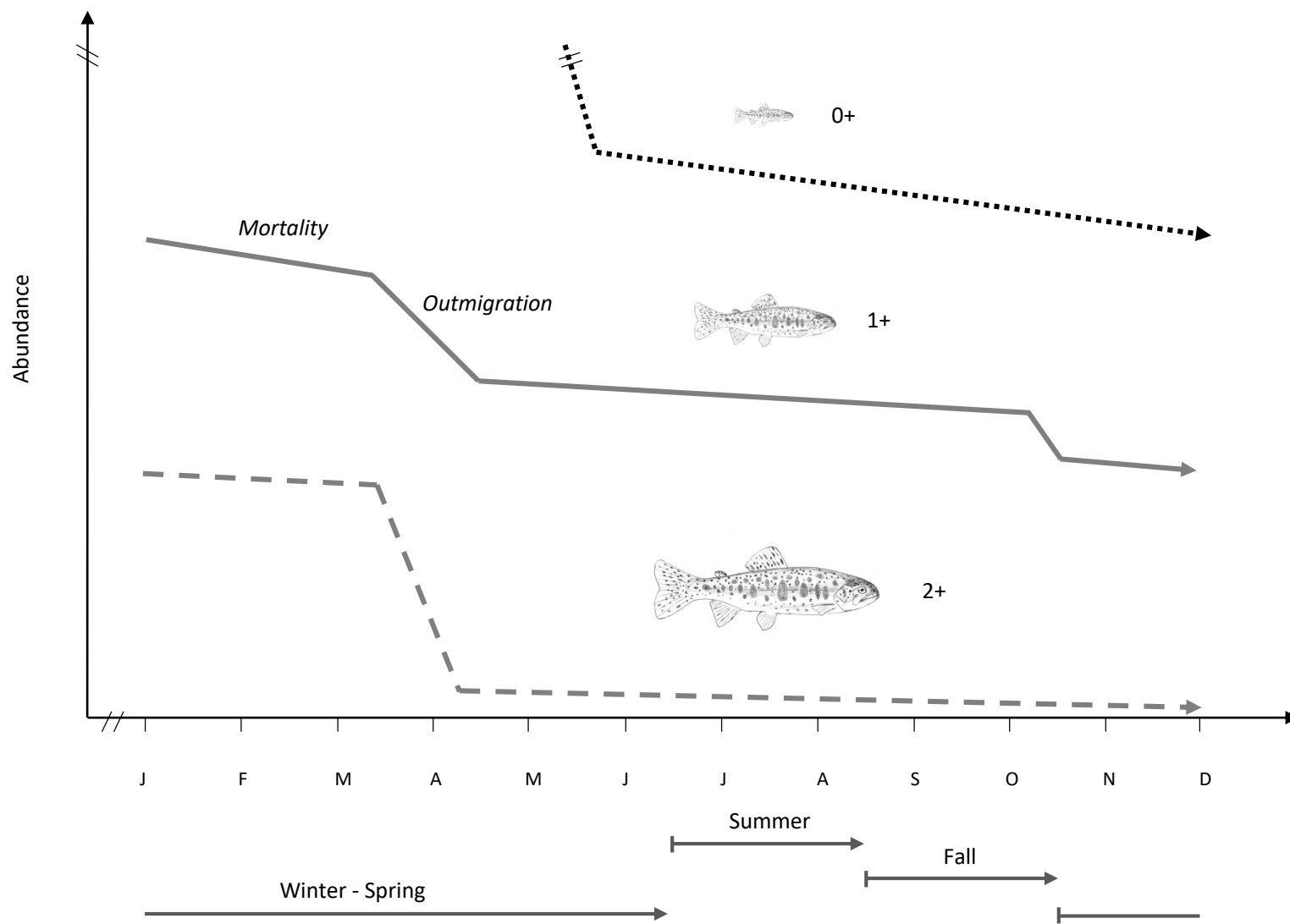
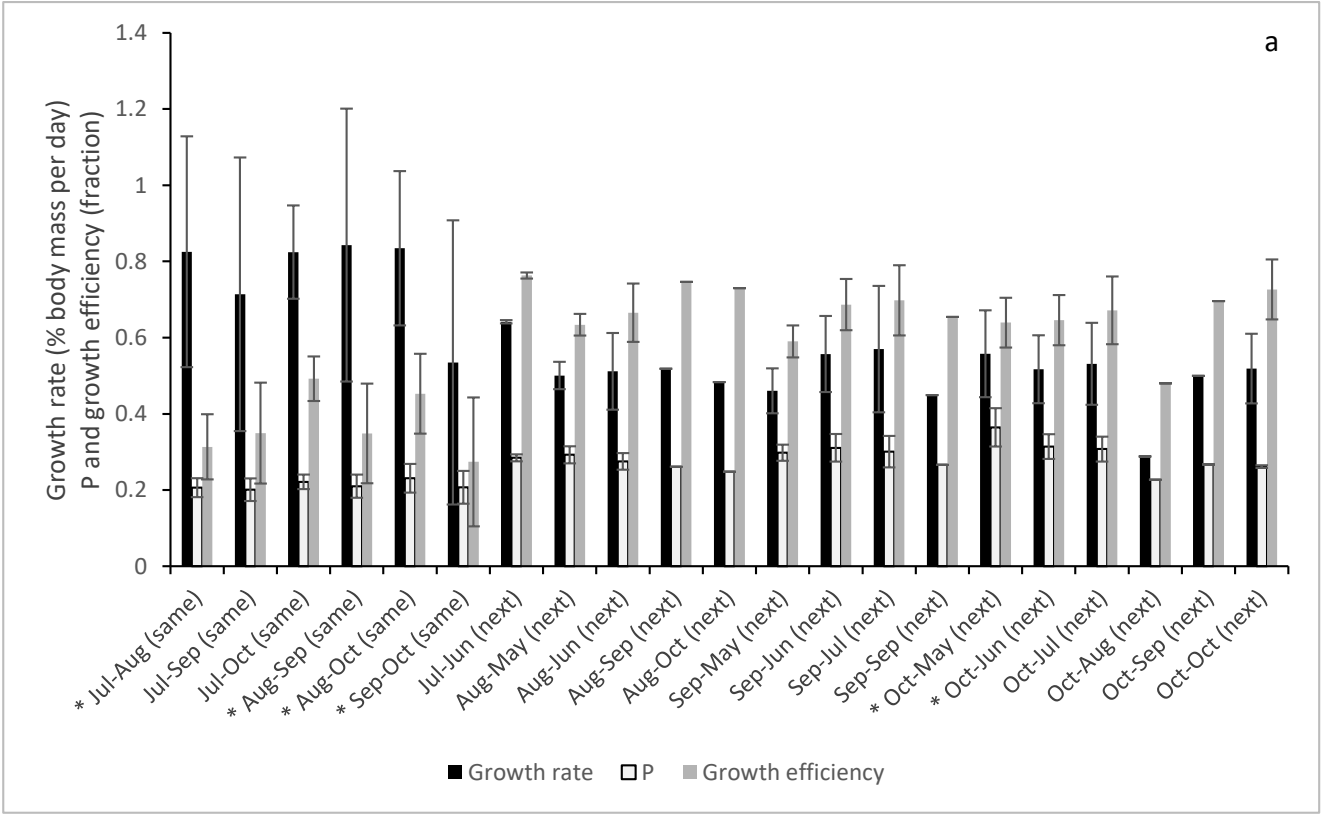
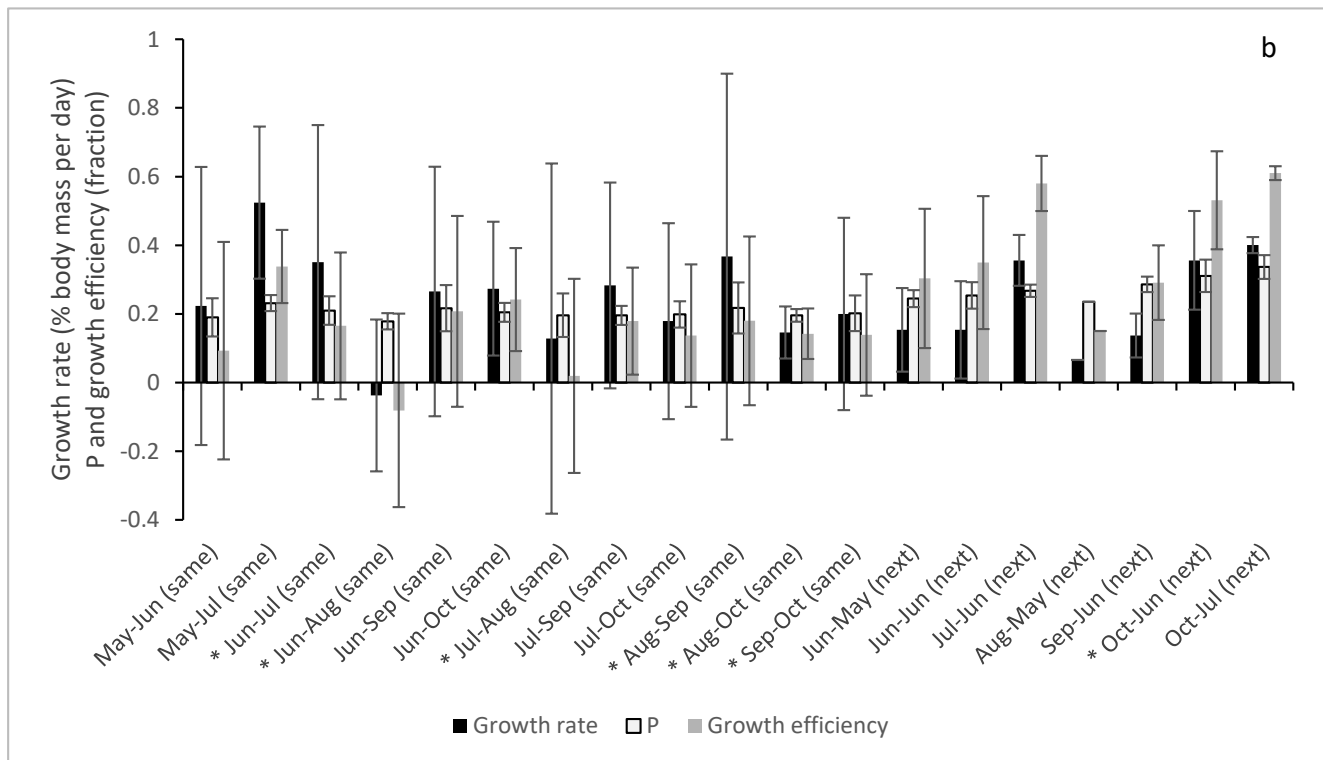


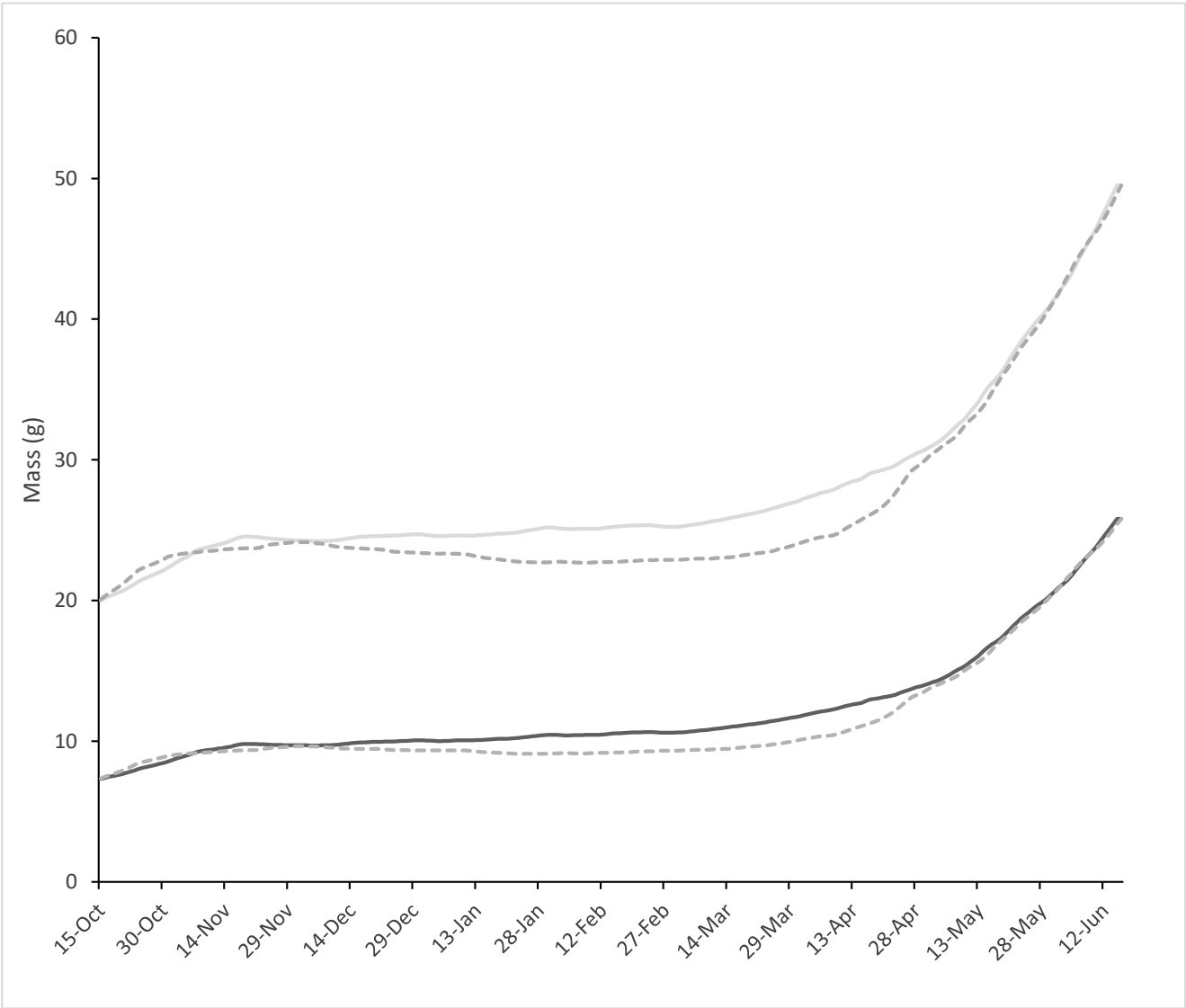
Figure 1. Map showing the location of the study sites in the Lapwai Creek watershed. Overwintering juvenile steelhead with recapture histories were found in sites ULL, ULM, ULU, UML, UMM, UMU, USM, USU, UWM, and UWU.

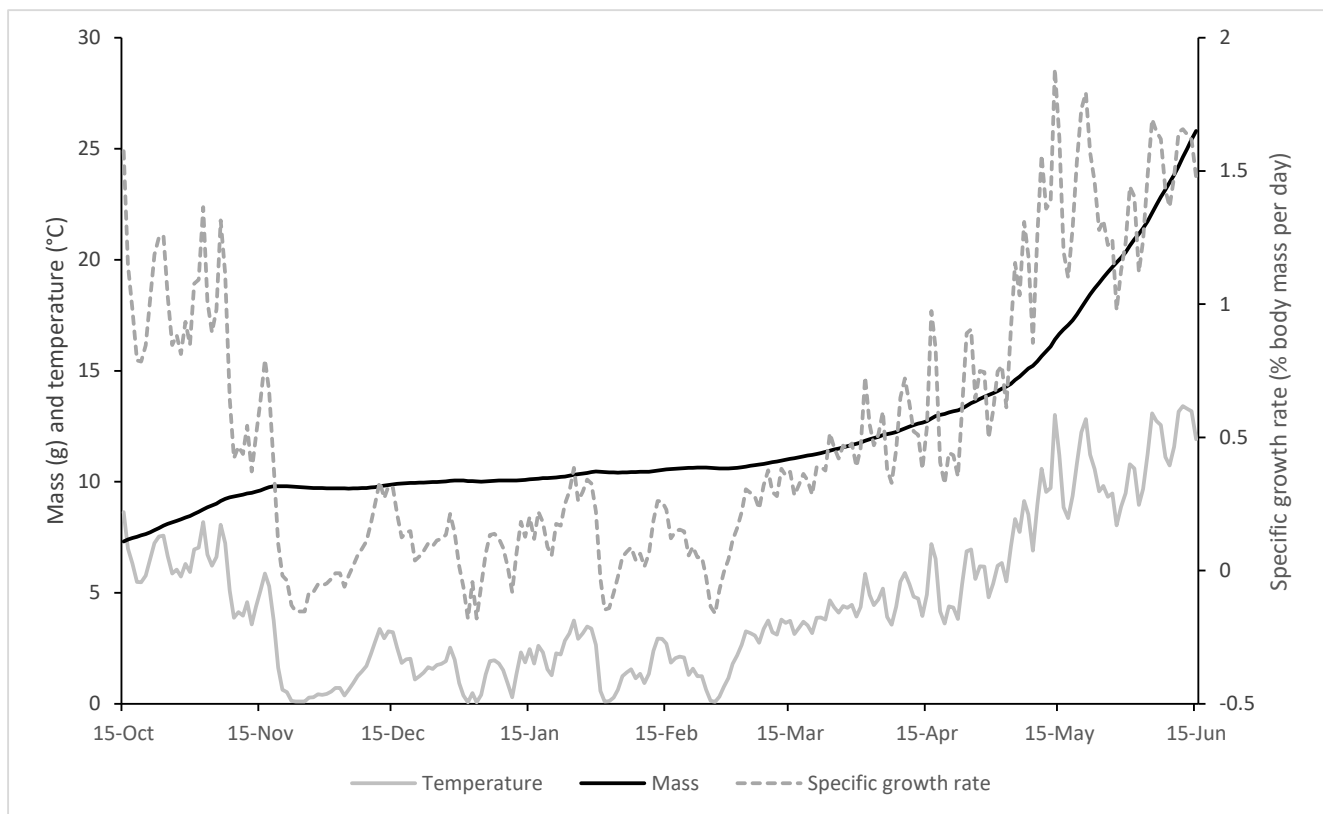
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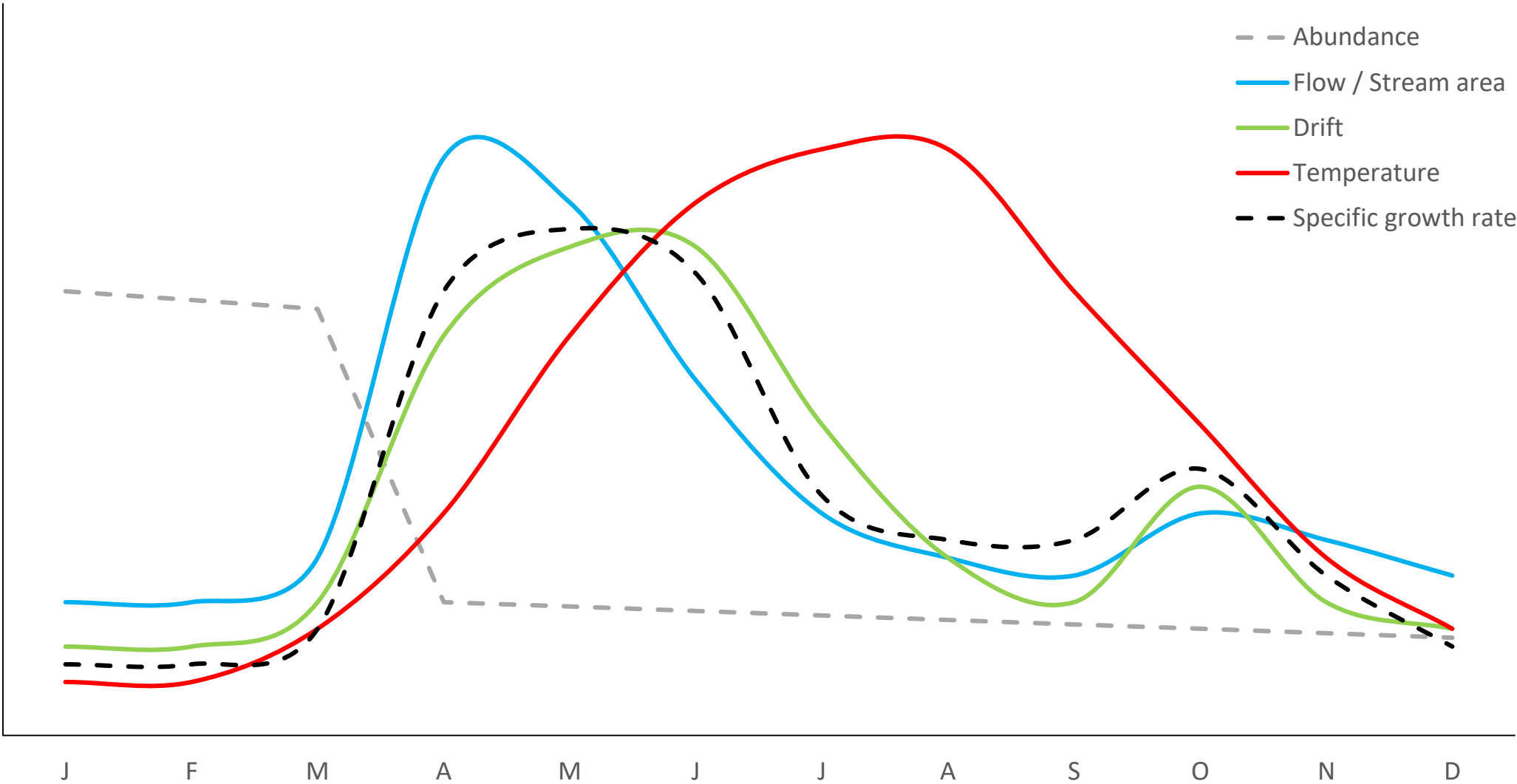












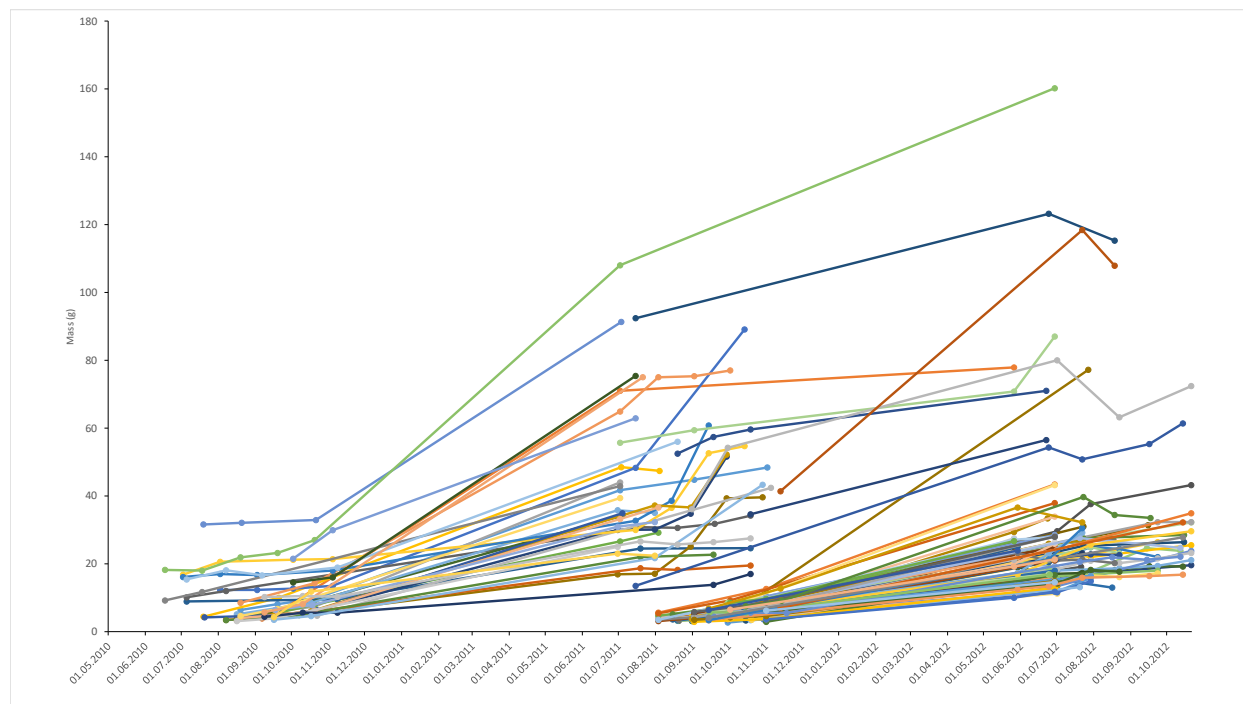


Figure A1. Raw data for the 133 individuals with overwinter recapture histories.