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33 ecosystem, intraspecific variation, life history, salmonid, seasonal subsidy

34 ABSTRACT

35 Life-history variation can contribute to long-term persistence of populations; however, it
36 remains unclear which environmental factors drive life-history variation within a population.
37 Seasonally recurring resource subsidies are common in nature and may influence variations
38 in recipient consumers' life-history traits. In this study, we experimentally demonstrated that
39 terrestrial invertebrate subsidies occurring early in the growing season facilitated consumer
40 individuals to adopt fast growth. In contrast, fewer consumer individuals adopted fast growth
41 when subsidies occurred late in the growing season. Consumer individuals that adopted fast
42 growth matured early at age-1, suggesting that the observed variation in life-history emerged
43 along with a fast-slow life-history continuum. The estimated survival probability was lower
44 in consumer individuals from the faster-growth cluster in the no-supply treatment, suggesting
45 a growth-survival trade-off. However, the growth-survival trade-off became unclear in the
46 early-supply treatment and even reversed in the late-supply treatment. As a result, the
47 frequency of consumer individuals maturing at age-1 was higher in the early-supply treatment
48 than in the late-supply treatment and no-supply treatment, implying a higher short-term
49 population growth with the early subsidies. Our findings highlight that seasonal ecosystem
50 linkages through resource subsidies help us understand how life-history variation can be
51 maintained within a population at the landscape scale.

INTRODUCTION

Life-history variation is fundamental for long-term persistence of populations and species (Schindler et al. 2010; Moore et al. 2014), community dynamics (Post et al. 2008; Weis and Post 2013), and ecosystem functions (El-Sabaawi et al. 2015). Individuals with distinct life histories contribute differently to population growth and thus population stability in temporally fluctuating environments (Hallgrímsson and Hall 2005); increasing fast-life individuals within a population result in increasing short-term population growth and probability of population recovery from environmental disturbance (Gamelon et al. 2014). In addition, population with higher life-history variation can be stable via asynchronous dynamics of individuals with different life-history that respond differently to environmental fluctuation (Moore et al. 2014). Furthermore, the effects of life-history variation can be scaled up to influence community dynamics and ecosystem functions by altering top-down (Post et al. 2008; Weis and Post 2013) and bottom-up regulation (El-Sabaawi et al. 2015). These ecological processes depend on the magnitude of life-history variation. However, the potential environmental drivers of life-history variation in natural populations remain unclear. Given that human activities cause substantial shifts and loss of intraspecific variation worldwide (Mimura et al. 2016), it is imperative to understand the drivers of life-history variation from basic (Clutton-Brock and Sheldon 2010) and applied ecological perspectives (Blanchet et al. 2020).

71 Seasonality of cross-ecosystem resource subsidies (Polis et al. 1997; Richardson and
72 Sato 2015) can be a potential driver of intraspecific life-history variation for consumers living
73 in connected open ecosystems. Previous studies have demonstrated that subsidies occurring
74 early in the consumers' growing season accelerate their seasonal growth, which in turn
75 enables juvenile consumers to capture seasonally limited reproductive windows at younger
76 ages (spiders: Marczak and Richardson 2008; lizards: Wright et al. 2013; stream fish: Sato et
77 al. 2016). Such an association between accelerated growth and early maturation, i.e., the
78 tendency toward fast life, suggests that early subsidies may increase the frequency of fast-life
79 individuals within a population. However, this may not be the case if individuals with
80 accelerated growth have lower survival rates than those with slow growth, i.e., growth–
81 survival trade-off (Stearns 1989; Mangel and Stamps 2001), and frequently die before
82 maturation. In addition, access to subsidies can be heterogeneous among individuals through
83 resource competition (Sato and Watanabe 2014; Sato et al. 2021) and niche variation (Kenny
84 et al. 2017). If growth–survival trade-off exists, individuals with limited subsidy access may
85 achieve same fitness as fast-life individuals by adopting slow life, i.e., slow growth and
86 maturity at older ages, resulting in no increase in fast-life individuals with the early subsidies.
87 Thus, the presence or absence of a growth–survival trade-off may determine the effects of
88 early subsidies on the frequency of fast-life individuals within a population. Testing these
89 mechanisms is fundamental to understanding how life-history variation emerges and is

maintained in seasonally coupled ecosystems. However, existing studies have focused largely on the population mean of life-history variation (Wright et al. 2013; Sato et al. 2016), which offers limited insights into how seasonal resource subsidies can mediate variations in life-history traits within a consumer population.

Streams and their surrounding forest ecosystems provide excellent models for studying resource subsidies and life-history variations among consumers (Richardson and Sato 2015). Specifically, salmonids in temperate streams preferentially consume terrestrial invertebrates from surrounding forests, and the seasonality of subsidies affects salmonid life-history traits, including growth, maturation, and migratory tendencies (Sato et al. 2016; Tanaka et al. 2023). The seasonal timing of terrestrial invertebrate inputs varies among streams in different forest types. When surrounded by deciduous trees, the input rates of terrestrial invertebrates commonly peak in early in the growing season (late spring toward early summer) of stream salmonid fishes (Nakano and Murakami 2001; Sato et al. 2011a; Inoue et al. 2013). In contrast, the peak timing of terrestrial subsidies can also naturally occur late in the salmonid growing season, i.e., late summer to early autumn, if riparian forests are dominated by conifer trees (Wipfli 1997) or when species interactions drive subsidy inputs, e.g., parasitic nematomorphs and nematodes manipulate their terrestrial invertebrate hosts to jump into streams (Sato et al. 2011a, b). Moreover, terrestrial invertebrate subsidies can be seasonally shifted or dampened by forest management, e.g., clear-cut logging and extensive

non-native conifer plantations (Inoue et al. 2013), or global climate change, e.g., warmer environments weaken the seasonality of resource subsidies (Larsen et al. 2016).

In this study, we tested whether the seasonal timing of terrestrial invertebrate subsidy supplies affects the life-history variation in a population of salmonid consumers in a temperate forest–stream ecosystem. For this, we examined a series of interrelated predictions (Figure 1). Prediction I: A greater proportion of fish individuals adopt a fast-growth strategy when subsidies are supplied early in their growing season than when supplied late or when no subsidy is supplied (Sato et al. 2016). Prediction II: Fast-growth individuals mature at younger ages than slow-growth individuals (Promislow and Harvey 1990; Sato et al. 2021). Prediction III-1: Fast-growth individuals have lower survival rates than slow-growth individuals, i.e., a growth–survival trade-off exists (Stearns 1989; Mangel and Stamps 2001). Prediction IV-1: If the growth–survival trade-off exists, fast-growth individuals maturing at age-1 have a lower survive rate, and the proportion of mature and immature individuals that survived until age-1 does not differ among experimental treatments. Alternatively, if the growth–survival trade-off does not exist (Hutchings 2006; Tymchuk et al. 2007), fast-growth individuals maturing at age-1 have higher survival rates than slow-growth individuals maturing at age-2 and older, it results in a greater proportion of mature individuals surviving in the early-supply treatments than those in the other treatments (Prediction III-2 and IV-2).

To examine these predictions, we conducted a large-scale field manipulation experiment that mimicked the seasonal timing and magnitude of subsidies in natural and artificial riparian forests, in conjunction with modern statistical analyses that quantify individual variations in life-history traits (Hamel et al. 2017). Although resource subsidies are known to affect the expression of life-history traits (Marczak and Richardson 2008; Wright et al. 2013; Sato et al. 2016, 2021), few studies have formally tested subsidy effects on variation in life-history traits in natural environments (but see, Tanaka et al. 2023). Our results provide one of the first empirical pieces of evidence that seasonal resource subsidies can be a potential driver of life-history variation within a consumer population in seasonally coupled ecosystems.

MATERIALS AND METHODS

Rationale of the experimental design

Our experiment controlled the timing and magnitude of seasonal subsidy supplies and evaluated their impacts on the life-history variation of red-spotted masu salmon *Oncorhynchus masou ishikawae* (hereinafter, masu salmon) in a Japanese temperate stream. To simulate real dynamics of subsidy inputs in our study system, we designed three treatments of subsidy addition: early-, late-, and no-supply treatment. In the study region, riparian vegetation originally consisted of deciduous trees, where the peak timing of subsidy

supplies occurred from late June to early August, corresponding with the early growing season of masu salmon (Sato et al. 2011a). However, extensive non-native conifer plantations (*Cryptomeria japonica* and *Chamaecyparis obtusa*) were developed around the study stream (57.1% conifer plantations within the drainage area), which has substantially reduced subsidy inputs (Sato et al. 2011b). In addition, conifer plantations potentially shift the timing of subsidy inputs to later in the growing season (Wipfli 1997). The early-supply treatment in our experiment mimicked subsidy inputs from deciduous riparian forests, whereas the late- and no-supply treatments (i.e., control) simulated seasonally shifted and reduced subsidies, respectively, in streams in extensive conifer plantations (Wipfli 1997; Inoue et al. 2013).

Study site and experimental procedures

The field experiment was conducted from June 2016 to October 2017 in a stream in an upper drainage of the Arida River system (34°04'N, 135°31'E) in the Wakayama Forest Research Station, Field Science Education and Research Center (FSERC), Kyoto University (Appendix S1: Figure S1). The stream is a typical mountain stream with step-pool morphology, i.e., gradient $\approx 12.9\%$, 3.0–5.2 m stream width, 0.067–0.112 m³/s in summer discharge, and gravel-dominated streambed. Stream-resident masu salmon and a small number of minnows, *Phoxinus oxycephalus jouyi*, are the only fishes inhabiting the stream.

We created three treatment reaches (early-, late-, and no-supply treatment), each with three replicates, resulting in nine experimental reaches within the study stream. The treatment reaches were randomly assigned to nine 122.8 ± 28.0 m reaches, each separated by > 20 m intervals. We did not adjust for the population density at the onset of the experiment. Although the natural density of masu salmon varied among experimental reaches at the onset of the experiment (age-0: 0.01–0.06 fish/m²; $\geq$ age-1: 0.06–0.14 fish/m²; Appendix S1: Figure S2), those densities are relatively low throughout the study period (age-0: 0.00–0.12 fish/m²; $\geq$ age-1: 0.04–0.18 fish/m²), compared with the densities reported in other populations (Kishi and Tokuhara 2012: 0.002–0.36 fish/m²; Saito et al. 2013: 0.25–0.68 fish/m²). Therefore, it is unlikely that these densities caused strong density-dependent effects on the life-history traits or, if any, had different density-dependent effects among experimental reaches, although local interference competition can be strong within a reach (Ward et al. 2007) (see Appendix S1 for more details). The reaches were not fenced off to retain the masu salmon in each treatment reach because it was not realistic to prevent the movement of fish by building a fence in running water for over two years. No immigration from either upper or lower stream of the experimental reaches was expected; i.e., no fish inhabited upstream of the upper end of the experimental reach, while there was a large weir that prevented fish from moving upstream at the lower end of the experimental reaches. In addition, we confirmed that the movement of fish across reaches was limited in the studied

population; only 12 out of 346 (3.5%) fish moved across reaches during the study period. We omitted individuals who moved across reaches from the analyses.

We emulated the early and late subsidies of terrestrial invertebrate input by adding mealworms (larvae of beetle *Tenebrio molitor*) to natural stream reaches over two discrete 60-day periods in 2016 and 2017. The early-supply treatment added mealworms to subsidy reaches from June to August, and the late-supply treatment added mealworms from August to October. The early- and late-supply treatments received mealworms at the same rate of 100 mg dry weight $\cdot$ m⁻² day⁻¹ by using 7–13 automatic fish feeders ($W \times H \times D = 6.8 \times 14.9 \times 8.7$ cm, $\approx$ 100 mL capacity for food; EHEIM GmbH & Co. KG., Deizisau, Germany) per reach. To spread mealworms naturally and evenly, automatic fish feeders were set $\approx$ 100 cm above the stream water surface on wooden stakes in the shallows at $\approx$ 10-m intervals, in each reach with subsidy supplies. Each feeder was set to randomly dispense mealworms four times during the daytime (6:00–17:00). This slow input of mealworms mimicked how masu salmon would encounter natural prey falling from the riparian vegetation (Sato et al. 2016). The natural input rates of terrestrial invertebrates were relatively low and expressed less obvious seasonality in the study reaches (< 30 mg $\cdot$ m⁻² day⁻¹; Appendix S2: Figure S1), compared with those reported in streams covered by natural deciduous forests (see below), probably because of previous deforestation and subsequent non-native conifer plantations, which are known to reduce terrestrial invertebrate inputs (Inoue et al. 2013). The total input rate

(mealworms + natural inputs of the terrestrial invertebrates) was comparable to the rates of peak terrestrial invertebrate inputs in temperate streams surrounded by natural and second-growth forests [136.1 ± 113.6 (mean $\pm$ SD; range 27–444) $\text{mg} \cdot \text{m}^{-2} \text{day}^{-1}$] (Inoue et al. 2013). Mealworms are ideal substitutes, i.e., body size and nutrient contents (Sato et al. 2016), for terrestrial invertebrate subsidies in our study system (Sato et al. 2016; Sato et al. 2021). In order to determine if masu salmon in reaches receiving no subsidy supply did not ingest mealworms flowing out of other reaches receiving subsidy supplies at the same time, we examined 112 fish captured across all treatment reaches for the presence/absence of mealworms in the stomach contents in 2016. Overall, we confirmed that many masu salmon in reaches receiving subsidy supplies ingested mealworms [81.3%, 13 out of 16 fish in August (in early-supply treatment reaches) and 89.0%, 65 out of 73 fish in October (in late-supply treatment reaches)], whereas almost no masu salmon in reaches receiving no supply of subsidies showed mealworm ingestion [0%, 0 out of 23 fish in August (in late- and no-supply treatment reaches) and 1.9%, one out of 54 fish in October (in early- and no-supply treatment reaches)]. .

Mark-recapture survey

Mark recapture surveys were conducted before and after the subsidy period (May, August, and October) and in early spring (March) in all reaches to track the life-history traits

(seasonal growth, survival, reproduction, and movement) of the studied masu salmon. Fish were captured using two-pass electrofishing with units operating at 250 V pulsed DC (LR-24; Smith-Root, Vancouver, WA, USA). Captured fish were anesthetized (clove bud; Seimi Laboratory, Kanagawa, Japan), measured (fork length to the nearest 1 mm and weight to the nearest 0.1 g), and individually marked with a unique color pattern of visible implant elastomer under the skin (North West Marine Technology, Inc. WA, USA). The captured location of each fish was recorded at 10-m intervals to estimate the probability of emigration from the study reaches for survival estimation. At the end of each subsidy period, we pumped the stomach contents of fish ($n > 5$) randomly selected from each study reach. The stomach samples were preserved in 70% ethanol and identified to distinguish their sources (mealworms, terrestrial, or aquatic invertebrates). These were then used to test whether experimental subsidy additions effectively increased the consumption rate (mg/100 mg wet mass of fish) of the studied masu salmon. Scales ($n < 10$ per fish) were sampled and preserved in 5% buffered formalin solution for age determination when the ages of the captured fish were unknown. In October, just before the spawning season, captured fish were judged as mature if they released sperm or eggs when the abdomen was softly pressed; otherwise, the fish were recorded as immature. All fish were released at their capture points after recovery from anesthesia.

The definition of life history

To evaluate the differentiation of life history among individuals, we examined growth trajectories and ages at first maturation because these life-history traits are tied to adaptive life history in many animals, such as the fast–slow life-history continuum (Promislow and Harvey 1990; Kozlowski 2006). We chose to primarily examine growth trajectories, in addition to simple growth rates during given periods, because our interest was to test whether quantitative differences in growth patterns were associated with different ages at maturity and generated discrete differences in life history (i.e., fast life vs. slow life). Focusing on growth rates during certain periods would regard individual differences in life history as simple variation around population means. While previous studies have often taken this approach and tested for differences between populations or groups, we consider that discrete life-history strategies might coexist within a population (Hamel et al. 2016; Shertzer et al. 2017). To evaluate whether distinct qualitative differences existed among individual life histories, we applied the finite mixture regression model that could test for multimodality in the distribution of growth trajectories (Hamel et al. 2017; see *Estimation of growth trajectories using the finite mixture model* for details).

Variation in ages at first maturation could appropriately define life-history variation in ages of reproduction in our study population, in which individual reproductive schedules were quite simple. Specifically, precocious males were rarely observed (2.8%), and almost all

masu salmon died after the spawning season at age-2 (95.6%). Fewer masu salmon (9.9%) were iteroparous, i.e., reproduce across multiple years during their lifespan. Furthermore, although sex-dependent life-history decisions are well-known in salmonids (Klemetsen et al. 2003; Kendall et al. 2015; Bourret et al. 2016; Beamish 2018), our preliminary analysis found that responses to seasonal subsidy inputs were similar between males and females (see Appendix S3). Therefore, we omitted sex dependence in life-history variation. To strictly test effects of subsidy additions, we confined our life-history evaluation to the 2016 cohort that had received experimental treatments since birth.

We could not determine the life history of individuals who died before the reproductive season at age-1. Thus, the variation of life histories we observed could have resulted from selection acting on intrinsic individual variations, e.g., genetic variations associated with life-history traits, or from plastic life-history decisions. This study could not distinguish between these processes causing subsidy effects on life-history variation.

Data analysis

Population-mean growth rate

We used generalized linear mixed models (GLMM; lme4 function in the R package ‘lmer’) (Bates et al. 2015) to test whether treatment, period, and their interaction affected the population-mean specific growth rate (SGR, see Appendix S1 for the formula) of masu salmon,

with a Gaussian distribution, and with individuals, stream sections (i.e., replicates) as random effects. In the analysis, the significant effects of the treatment and the interaction term do not simply mean the effects of the subsidy and its timing because, for example, fish in the early-supply treatment did not receive the subsidy in the late period. Therefore, we tested the effects of the subsidy and its timing by performing the post hoc tests by setting appropriate contrasts in GLMMs ($\text{SGR} \sim \text{groups}$; six unique groups of treatment $\times$ period). Specifically, to test the subsidy effect in the early period, we used the early-supply treatment in the early period as the contrast and tested its differences with the late-supply treatment in the early period and the no-supply treatment (control) in the early period. Similarly, to test the subsidy effect in the late period, we used the late-supply treatment in the late period as a contrast and tested its differences with the early-supply treatment in the late period and the no-supply treatment in the late period. In addition, to test the timing effect of the subsidy, we used the early-supply treatment in the early period as a contrast and tested its differences with the late-supply treatment in the late period. We conducted these analyses separately for the years 2016 ($n = 130$) and 2017 ($n = 138$), because the SGR was expected to be inherently lower for age-1 fish (year 2017) than for age-0 fish (year 2016).

Estimation of growth trajectories using the finite mixture model

We applied the finite mixture regression modelling approach that can quantify individual

variations in growth trajectories and statistically identify distinct growth clusters if present (Hamel et al. 2017). When the finite mixture regression model found multiple growth clusters, we further compared the number of growth clusters among early-, late-, and no-supply treatments (see more details in “*Treatment effects on proportional composition of growth clusters and maturation status at age-1*”).

Firstly, we modeled the expected body length of masu salmon at each sampling time point for each growth cluster using the von Bertalanffy equation with seasonally varying coefficients (Cloern and Nichols 1978). In the finite mixture regression model, we assumed that each fish was assigned a latent variable, i.e., an unobserved state (strategy) corresponding to a growth cluster. The latent variable is a set of four parameters ($L_{\max,cl}$, $L_{\min,cl}$, $a_{1,cl}$ and θ_{cl}) that fully describe the seasonal growth trajectory of a given growth cluster, as described in the following equation modifying Cloern and Nichols seasonal growth model:

$$L_{cl}(t) = L_{\max,cl} - (L_{\max,cl} - L_{\min,cl}) \cdot \exp\left[-a_{1,cl} \cdot (t - t_0) - \frac{180 \cdot a_{1,cl}}{\pi} \left(\cos\left\{\frac{\pi \cdot (t_0 + \theta_{cl})}{180}\right\} - \cos\left\{\frac{\pi \cdot (t + \theta_{cl})}{180}\right\}\right)\right]$$

where $L_{cl}(t)$ is body length at time t ($t = 0$ on January 1) for a given growth cluster (cl), $L_{\max,cl}$ is a maximum fork length of the growth cluster, $L_{\min,cl}$ is fork length at the time of recruitment (t_0) of the growth cluster, and $a_{1,cl}$ and θ_{cl} are the estimated parameters of

constant coefficients that determine seasonal dependence of body size growth.

Subsequently, to implement the finite mixture regression model, we utilized the FLXMRglm function in the R package ‘flexmix’ (Leisch 2004), where the expectation-maximization (EM) algorithm (Dempster et al. 1977) can be used for the parameter estimation. We used individual body size data collected from June of age 0 to October of age 1, seven time points in maximum. That is, 885 body-size data points from 334 individuals [2.65 ± 1.53 (mean $\pm$ SD; range 1–7) data per individual] were used to construct the model. If multiple growth strategies are included in the population instead of a single mean growth trajectory, the residuals should be biased. Therefore, clustering the residuals at each data point by individual using mixture regression model should allow for the estimation of growth trajectories of individuals with faster or slower than average growth.

In our finite mixture regression model, data points for individuals with multiple captures were initially used to classify them into different mean trajectories rather than a specific growth trajectory, meaning that parameter estimation was performed on independent data points. However, through repeated computations using the EM algorithm, data points for an individual were eventually adjusted to be classified into the same growth cluster.

Ideally, the mixture regression model would be performed by using only individuals captured multiple times. However, this approach limited the sample size (multiple capture, $n = 231$), making it difficult to achieve model convergence. Therefore, we also added

individuals with a single capture into the model to increase the amount of data for each sampling occasion. This largely increased the information about how large individuals are at specific times ($n = 103$ increase), which allowed for a more comprehensive analysis of seasonal growth patterns embedded in the studied population. However, with this approach, it becomes more difficult to capture unique growth trajectories as additional clusters. For example, it may underestimate the growth trajectories where individuals experience sudden body size increase during certain periods, leading to body size reversals within life histories. When checking the raw data, we did not observe many instances of such reversal of growth trajectories among individuals captured multiple times. Therefore, in this study, we decided to prioritize increasing the amount of data by using the full dataset.

We did not know *a priori* the number of growth clusters maintained in the studied population. Therefore, we applied model selection by developing the models with different numbers of growth clusters ($k = 1-6$). Both Akaike information criterion (AIC) and the Bayesian information criterion (BIC) were used to confirm the consistency of results by using the two criteria based on different parsimony principle (Hamel et al. 2017); competing models are considered different in predictive performance when the difference in AIC/BIC values are greater than two (Hamel et al. 2017).

Association of growth clusters with maturation at age-1

In the studied population, we previously found that competitively dominant individuals with fast growth were more likely to mature at age-1 than those with slow growth (Sato et al. 2021), which corresponds to the principle of the fast–slow life-history continuum (Promislow and Harvey 1990). Therefore, we examined whether the probability of age-1 maturation was higher among individuals in fast-growth clusters than among those in slow-growth clusters. In addition, the effect of growth clusters on the maturation decision might be larger in the early-supply treatment than in the late- or no-supply treatments because of timing-dependent life-history decisions (Sato et al. 2016). A generalized linear mixed model (GLMM; glmer function in the R package ‘lme4’), with a binomial error distribution and experimental reach ($n = 3$ replicates) as a random effect, was used to test whether the probability of maturation at age-1 was related to the growth clusters, treatments, and their interaction. The overdispersion and model fit were assessed by using ‘testDispersion’ in DHARMA package in R (Hartig 2024) and pseudo R^2 . The best model was selected by comparing models with different sets of fixed terms based on the log-likelihood ratio test (Jones et al. 2022).

Estimation of survival probabilities

The fitness trade-off is a well-known mechanism for maintaining life-history variation within a single population (Stearns 1989; Mangel and Stamps 2001). In this study, we predicted that the existence or absence of a growth–survival trade-off mediates life-history variation. To test

this prediction, true survival probabilities, i.e., corrected for permanent emigration and imperfect detection, were estimated for each unique combination of growth cluster and experimental treatment using a modified version of the Cormack-Jolly-Seber (CJS) model (Schaub and Royle 2014; Terui et al. 2017). In our experiment, survival estimates in classical CJS models can only represent “apparent” survival, as it is confounded with permanent emigration from an observation area. However, the modified CJS model can account for permanent emigration by integrating movement into observation processes. This modeling approach will be useful in the present study because the experiment was conducted in a stream, and permanent emigration of fish from the experimental reaches would inevitably occur. Our primary objective was to test whether a trade-off between growth clusters and survival could explain the life-history variation in each treatment. Therefore, we estimated the survival probability separately for the growth clusters and experimental treatments. The details of the survival estimates are shown in Appendix S4.

Treatment effects on proportional composition of growth clusters and maturation status at age-1

We used log-linear models for a contingency table (GLM with log-link function in R) to test whether the proportional compositions of growth clusters and maturation status at age-1 were, respectively, associated with the treatments (Dobson and Barnett 2018; Jones et al.

2022). We initially fitted a saturated model with three treatments (early-, late-, and no-supply treatments) and subsequently applied model simplification to analyze the treatment effects. Model simplification involves aggregating treatments with similar effects and likelihood ratio tests to determine whether simplification causes a significant loss of explanatory power (Slade et al. 2007; Fouks and Lattorff 2011; Jones et al. 2022). The simplified model was selected, for which no further simplification was justified (see Appendix S3 for more details). All statistical analyses were conducted using R 4.1.3 (R Core Team 2022).

RESULTS

A total of 54 stomach contents (six fish each in early-, late-, and no-supply treatment reaches in August, 12 fish in each treatment reach in October) were analyzed. In August, the total mass of all invertebrate consumption, i.e., aquatic and terrestrial invertebrates, and mealworms, by red-spotted masu salmon in reaches with subsidy supplies (early-supply treatment reaches) was, on average, 6.6 times higher than by those in reaches without subsidy supplies (late- and no-supply treatment reaches) (0.52 ± 0.34 mg/100 mg wet mass of fish in early-supply treatment reaches, and 0.08 ± 0.06 in late- and no-supply treatment reaches; Mann–Whitney U -test: $W = 70$, $p = 0.0004$). Likewise, in October, the total mass of all invertebrate consumption was 3.6 times higher in reaches with subsidy supplied (late-supply treatment reaches) than in reaches with not subsidy supplied (early- and no-supply treatment

reaches) (0.31 ± 0.37 in late-supply treatment reaches, and 0.09 ± 0.09 in early- and no-supply treatment reaches; Mann–Whitney U -test: $W = 213$, $p = 0.020$). Mealworms made up $97 \pm 3\%$ and $62 \pm 40\%$ of the total mass of consumption by masu salmon in August and October, respectively, and the consumption rate of mealworms was positively correlated with the total consumption rate in both periods (Spearman’s rank correlation, August: $r_s = 1$, $p = 0.0028$; October: $r_s = 0.95$, $p < 0.0001$).

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418 **Growth and age at maturity**

The specific growth rate differed significantly among treatment, period and their interaction (Appendix S1: Tables S2A and S2B). When subsidies were available (early- vs. late- or no-supply treatment in early period; late- vs. early- or no-supply treatment in late period), the specific growth rate was, on-average, 1.8–2.1 times higher in treatment reaches with subsidy supply than in those with no subsidies in 2016 [early period: early-supply (contrast) vs. late-supply or no-supply, $P < 0.03$; late period: late-supply (contrast) vs. early-supply or no-supply, $P < 0.07$; Appendix S1: Tables S3A and S4A) and 3.5–6.1 times higher in 2017 [early period: early-supply (contrast) vs. late-supply or no-supply, $P < 0.001$; late period: late-supply (contrast) vs. early-supply or no-supply, $P < 0.01$; Appendix S1: Tables S3B and S4B]. There was no significant difference in specific growth rate between the early-supply treatment in the early period and the late-supply treatment in the late period both in 2016 (df

= 6.15, 95% CI = -0.09–0.05, $t = -0.66$, $p = 0.53$; Appendix S1: Table S5A) and 2017 (df = 10.23, 95% CI = -0.08–0.02, $t = -1.12$, $p = 0.29$; Appendix S1: Table S5B), suggesting no timing effects of the subsidy-supply. However, the specific growth rate varied substantially among individuals within and across experimental reaches (Appendix S1: Figure S3). Three growth clusters (fast-, medium-, and slow) best explained this variation in the finite mixture regression model (Tables 1 and 2). The estimated seasonal growth trajectories based on the parameters for the best model is presented in Figure 2a. The frequency of individuals from the fast-growth cluster was higher in the early-supply treatment than in the late-supply treatment and no-supply treatment (Figure 2b; Appendix S3: Table S4; log-linear model, residual deviance = 3.9, df = 3).

The probability of maturation at age-1 was higher for individuals from the fast-growth cluster; 29 out of 39 fast-growth individuals (74%) matured at age-1, whereas only one out of 29 slow-growth individuals (3%) matured at age-1 (Figure 2c). The optimal GLMM model revealed that the growth cluster had a significant association with age at maturity, i.e., no significant association of subsidy timing or its interaction with growth clusters with the probability of maturation at age-1 was detected (Table 3).

Survival probability and its association with growth clusters

In the no-supply treatment, the estimated survival probability was the lowest in individuals

from the fast-growth cluster, suggesting a growth–survival trade-off. In contrast, the growth–survival trade-off became unclear in the early-supply treatment and apparently reversed in the late-supply treatment. The survival probability was similar among individuals from different growth clusters in the early-supply treatment; the survival probability was lower in slow-growth individuals than in fast-growth individuals in the late-supply treatment (Figure 3).

Life-history variation in age at maturity

The frequency of individuals maturing at age-1 was higher in the early-supply treatment than in the late-supply treatment and no-supply treatment (Figure 4; Appendix S3: Table S8; log-linear model, residual deviance = 1.0, $df = 2$). As a consequence, individuals maturing at age-1 and individuals maturing at age-2 and older were more evenly distributed in the early-supply treatment (% age-1 maturation: 47%) than the other treatments (28% in the late-supply treatment and 27% in the no-supply treatment).

DISCUSSION

Elucidating the mechanisms causing life-history variation is fundamental for understanding population persistence, community organization, and the regulation of ecosystem functions (Stearns 1992; Clutton-Brock and Sheldon 2010). However, the environmental drivers underlying life-history variation in natural populations in heterogeneous landscapes remain

poorly understood. In this study, we demonstrated that the seasonal timing and magnitude of resource subsidies mediate life-history variations in a consumer population. Although previous studies often demonstrated population-mean shifts in life-history traits in response to the magnitude (Yang et al. 2008; Yang et al. 2010) and timing of resource availability across ecosystem boundaries (Marczak and Richardson 2008; Wright et al. 2013; Sato et al. 2016), our results are distinct from those studies in documenting such life-history variation within a single population (but see Tanaka et al. 2023). Temporal matches between resource availability and consumer life-history events commonly regulate seasonal growth and maturation in many plants and animals (Durant et al. 2007). Given their ubiquitous nature, seasonal ecosystem linkages via resource subsidies might be a key factor regulating life-history variation in natural populations, and investigating these processes is crucial to fully understanding the mechanisms generating life-history variation in a heterogeneous landscape.

Timing-dependent emergence of growth clusters and their effects on maturation

The fast-growth cluster was more prevalent in the early-supply treatment than in the late- and no-supply treatment (Figure 2b), which supported Prediction I (Figure 1). The difference in resource availability between the subsidy periods would not explain this phenomenon. In contrast, the smaller proportion of fast-growth individuals in the no-supply treatment could be due to low resource availability. We added mealworms at the same rate in the early- and

late-supply treatments, and the natural input rates of the terrestrial invertebrate subsidy did not largely change from spring through autumn at the study site (Appendix S2: Figure S1). Furthermore, benthic invertebrate biomass in streams around the study region is known to decrease from late spring through autumn as many aquatic insects emerge from streams and become adults (Sato et al. 2011a), which is common in temperate forest streams (Kawaguchi and Nakano 2001; Nakano and Murakami 2001).

In salmonids (Thorpe et al. 1998), including the studied species (Silverstein and Shimma 1994), individuals that achieve rapid growth and gain lipid reserves early in the growing season can initiate gonadal development in spring and mature in autumn. If this reflects life-history adaptations to seasonal environments, growth acceleration induced by late subsidies may be too late for individuals to develop gonads before the reproductive season of the year. Matching the temporal window for maturation decision and the seasonal timing of the subsidy would facilitate individuals in the early-supply treatment to adopt a fast-growth strategy when they encountered high resource availability. However, some individuals exhibited the slow-growth strategy in the early- and late-supply treatments. These individuals would have limited access to subsidies through interference competition, which is well-known in salmonids (Nakano et al. 1995; Sato and Watanabe 2014; Sato et al. 2021). Another interesting finding is that the medium-growth clusters were statistically separated from the fast- and slow-growth clusters. Across a broad range of taxonomic groups (Bolnick et al.

2003), including salmonid fishes (Nakano 1995; Nakano et al. 1999a; Fausch et al. 2021), flexible niche shifts in response to resource availability and social hierarchy are common. Individuals who make flexible niche shifts might not gain better growth than fast-growth conspecifics with limited access to the subsidy but could gain better growth than slow-growth conspecifics. Consequently, these individuals may have adopted medium growth as a third growth strategy in the studied masu salmon.

Consistent with Prediction II (Figure 1), growth clusters were associated with subsequent maturation at age-1 (Figure 2c). This association corresponds to the fast–slow life-history continuum (Promislow and Harvey 1990). Specifically, individuals who adopted fast growth frequently matured early at age-1, while fewer medium- and slow-growth individuals achieved age-1 maturation. Along with the timing-dependent emergence of growth clusters and their effects on maturation at age-1, we argue that subsidy timing and magnitude mediated the emergence of life history within the masu salmon population.

Growth–survival trade-off and life-history variation

Trade-offs among life-history traits, such as growth, survival, and reproduction, are considered a leading cause of life-history variation within a population (Stearns 1989; Mangel and Stamps 2001; Christie et al. 2018). However, life-history trade-offs can be less pronounced depending on developmental stages (trade-offs can be less clear later in life;

Hutchings 2006) and competitive environmental conditions (faster-growth individuals can monopolize resources over slow-growth individuals without survival costs; Tymchuk et al. 2007). The magnitude of such a life-history trade-off, i.e., the growth–survival trade-off, may explain the proportional compositions of life-history traits among treatments. In accordance with Prediction III-2, growth and survival were not clearly associated in the early-supply treatment and were even positively related in the late-supply treatment. In contrast, a clear growth–survival trade-off was observed in the no-supply treatment, in line with Prediction III-1. The increase in fast-growth individuals resulted in an increase in the frequency of individuals maturing at age-1 in the early-supply treatment compared with those of the late- and no-supply treatment, probably because of the absence of the growth–survival trade-off (Prediction III-2 and IV-2). No such increase in individuals that matured at age-1 was found in the late-supply treatment, despite the positive association between growth and survival, because the late subsidies did not increase the frequency of fast-growth individuals compared with the no-supply treatment.

We cannot fully explain why the growth–survival trade-off was obvious in the no-supply treatment but not in the early- and late-supply treatments. However, the survival probability of slow-growth individuals was consistently lower in the early- and late-supply treatments than in the no-supply treatment, suggesting complex associations between growth and survival. Specifically, interference competition occurs for location to forage for drifting

invertebrates in salmonid fishes (Nakano 1995). Thus, the experimental increase in drifting terrestrial subsidies, i.e., mealworms, early in the masu salmon growing season may increase competition among individuals. This might increase the mortality cost associated with competition for slow-growth individuals, possibly masking the growth–survival trade-off in the early- and late-supply treatments. In fact, especially in the early-supply treatment, estimated survival probability of slow-growth individuals was rapidly decreased in the early period of 2016 (Appendix S4: Figure S2).

Another possibility is that the survival probability became similar among the growth clusters due to a process of the ideal free distribution (Boyce et al. 2016) within the early-supply treatment reaches. Specifically, individuals of the fast-growth cluster might compete each other to dominate preferred microhabitats for foraging on drifting mealworms, whereas individuals of the slow-growth cluster could occupy other microhabitats for primarily foraging on other food items (e.g., benthic invertebrates). Such microhabitat choice associated with flexible niche shifts is well-known in salmonids (Fausch et al. 1997; Nakano et al. 1999b) and may explain the unclear growth-survival trade-off in the early-supply treatments.

Furthermore, animals living in seasonal environments intrinsically have a strategy that allocates the acquired energy to growth early in the growing season and switches to allocation to storage late in the growing season, such as overwintering (Post and Parkinson

2001; Giacomini and Shuter 2013; Varpe 2017). Among individuals that received the late-supply treatment, winter survival (from October 2016 to March 2017) was lower for slow-growth individuals than for medium- and fast-growth individuals (Appendix S4: Figure S2). This might indicate that individuals with slow growth in the late-subsidy treatment faced limited opportunities for energy allocation and had reduced winter survival, causing a positive relationship between growth and survival in the late-supply treatment.

The above explanations might imply that slow-growth individuals would not be favored in the early- and late-supply treatments, and fast-growth individuals would dominate the population over time. However, we must recognize that slow-growth individuals might achieve fitness comparable to that of fast-growth individuals in the early- and late-supply treatments if other types of life-history trade-offs, such as the growth–reproduction trade-off (Christie et al. 2018), existed. For example, reproductive success in the same spawning ground would be higher in larger individuals that matured at age-2 than in smaller individuals that matured at age-1 due to size-dependent breeding competition. Elucidating the causal relationship between seasonal subsidies and the types and strengths of life-history trade-offs will be a crucial step in fully understanding the maintenance mechanisms of life-history variation within a population in seasonally coupled ecosystems (Siepielski et al. 2009).

Possible population stabilization due to life-history variation

Maintaining life-history variation within a population is fundamental for the long-term persistence of the population (Schindler et al. 2010; Moore et al. 2014). In this study, individuals maturing at age-1 (i.e., fast life) was observed more frequently in the early-supply treatment (% age-1 maturation = 47%) than in the late-supply (28%) and no-supply treatment (27%). Having those fast-life individuals within a population would result in increasing population productivity in short-term, which could help rapid population recovery after environmental disturbances, such as flooding that is often found around the study region (Sato 2006). In this aspect, the population stability would be higher in populations experiencing early subsidies than those having late subsidies or reduced subsidies. Empirically demonstrating this type of population stability, as well as others (such as portfolio effects: Schindler et al. 2010; Moore et al. 2014), via life-history variation will be a key for the comprehensive understanding of individual life-history decisions scale up to population-level life-history variation and population dynamics in seasonal environments.

Conclusions

In this study, we demonstrated that the seasonal timing of resource subsidies affects life-history variations within a consumer population in recipient ecosystems. Contrary to most studies focusing on the effects of subsidies on the population mean of life-history traits, acknowledging subsidy effects on variation in life history is crucial because life-history

601 variations are fundamental for the long-term persistence of populations and species
602 (Schindler et al. 2010; Moore et al. 2014). Consumer effects on species interactions and
603 ecosystem functions should be determined not only by population mean but also by variation
604 in their life-history traits (Bolnick et al. 2011; Des Roches et al. 2018; Raffard et al. 2019).
605 Given the ubiquitous nature of seasonal ecosystem linkages via resource subsidies (Polis et
606 al. 1997; Richardson and Sato 2015), ongoing global climate change and human-induced
607 environmental alterations that affect those subsidies can cause the loss of life-history
608 variation, which may result in unexpected changes in recipient ecosystems (Larsen et al.
609 2016). In forest–stream ecosystems, the conversion of broadleaf forests to conifer plantations
610 has raised concerns about reduction and seasonal shifts in resource subsidies (Wipfli 1997;
611 Ormerod et al. 2004; Inoue et al. 2013), which might have reduced variation in life history
612 within consumer populations, including salmonid fishes. The present study emphasizes the
613 need to understand the maintenance mechanisms of life-history variation in heterogeneous
614 landscapes, where seasonal subsidies govern the growth trajectory, age at maturity, and,
615 ultimately, life-history expressions of wildlife.

616

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References

- Bates, D., M. Maechler, B. Bolker, and S. Walker. 2015. Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software* 67:1–48.
- Beamish, R. J. 2018. The ocean ecology of Pacific salmon and trout. *American Fisheries Society* pp. 703–730.

- 639 Blanchet, S., J. G. Prunier, I. Paz-Vinas, K. Saint-Pé, O. Rey, A. Raffard, E. Mathieu-Bégné,
640 G. Loot, L. Fournet, and V. Dubut 2020. A river runs through it: The causes,
641 consequences, and management of intraspecific diversity in river networks.
642 *Evolutionary Applications* 13:1195–1213.
- 643 Bolnick, D. I., R. Svanbäck, J. A. Fordyce, L. H. Yang, J. M. Davis, C. D. Hulsey, and M. L.
644 Forister. 2003. The ecology of individuals: incidence and implications of individual
645 specialization. *The American Naturalist*, 161:1–28.
- 646 Bolnick, D. I., P. Amarasekare, M. S. Araújo, R. Bürger, J. M. Levine, M. Novak, V. H.W.
647 Rudolf, S. J. Schreiber, M. C. Urban, and D. A. Vasseur. 2011. Why intraspecific trait
648 variation matters in community ecology. *Trends in Ecology and Evolution* 26:183–192.
- 649 Bourret, S. L., C. C. Caudill, and M. L. Keefer. 2016. Diversity of juvenile Chinook salmon
650 life history pathways. *Reviews in Fish Biology and Fisheries* 26:375–403.
- 651 Boyce, M. S., C. J. Johnson, E. H. Merrill, S. E. Nielsen, E. J. Solberg, and B. Van Moorter.
652 2016. Can habitat selection predict abundance?. *Journal of Animal Ecology* 85:11–20.
- 653 Christie, M. R., G. G. McNickle, R. A. French, and M. S. Blouin. 2018. Life history variation
654 is maintained by fitness trade-offs and negative frequency-dependent selection.
655 *Proceedings of the National Academy of Sciences* 115:4441–4446.
- 656 Cloern, J. E., and F. H. Nichols. 1978. A von Bertalanffy growth model with a seasonally
657 varying coefficient. *Journal of the Fisheries Board of Canada* 35:1479–1482.

- 658 Clutton-Brock, T., and B. C. Sheldon. 2010. Individuals and populations: the role of long-
659 term, individual-based studies of animals in ecology and evolutionary biology. *Trends in*
660 *Ecology & Evolution* 25:562–573.
- 661 Dempster, A. P., N. M. Laird, and D. B. Rubin. 1977. Maximum likelihood from incomplete
662 data via the EM algorithm. *Journal of the Royal Statistical Society: Series B*
663 (Methodological) 39:1–22.
- 664 Des Roches, S., D. M. Post, N. E. Turley, J. K. Bailey, A. P. Hendry, M. T. Kinnison, J. A.
665 Schweitzer, and E. P. Palkovacs. 2018. The ecological importance of intraspecific
666 variation. *Nature Ecology & Evolution* 2:57–64.
- 667 Dobson, A. J., and A. G. Barnett. 2018. An introduction to generalized linear models. 4th ed.
668 CRC Press.
- 669 Durant, J. M., D. Ø. Hjernann, G. Ottersen, and N. C. Stenseth. 2007. Climate and the match
670 or mismatch between predator requirements and resource availability. *Climate Research*
671 33:271–283.
- 672 El-Sabaawi, R. W., M. C. Marshall, R. D. Bassar, A. López-Sepulcre, E. P. Palkovacs, and C.
673 Dalton. 2015. Assessing the effects of guppy life history evolution on nutrient recycling:
674 from experiments to the field. *Freshwater Biology* 60:590–601.
- 675 Fausch, K. D., S. Nakano, and S. Kitano. 1997. Experimentally induced foraging mode shift
676 by sympatric charrs in a Japanese mountain stream. *Behavioral Ecology* 8:414–420.

- 677 Fausch, K. D., S. Nakano, S. Kitano, Y. Kanno, and S. Kim. 2021. Interspecific social
678 dominance networks reveal mechanisms promoting coexistence in sympatric charr in
679 Hokkaido, Japan. *Journal of Animal Ecology* 90:515–527.
- 680 Fouks, B., and H. M. G. Lattorff. 2011. Recognition and avoidance of contaminated flowers
681 by foraging bumblebees (*Bombus terrestris*). *PLOS One* 6:e26328.
- 682 Gamelon, M., O. Gimenez, E. Baubet, T. Coulson, S. Tuljapurkar, and J. M. Gaillard. 2014.
683 Influence of life-history tactics on transient dynamics: a comparative analysis across
684 mammalian populations. *The American Naturalist* 184:673–683.
- 685 Giacomini, H. C., and B. J. Shuter. 2013. Adaptive responses of energy storage and fish life
686 histories to climatic gradients. *Journal of Theoretical Biology* 339:100–111.
- 687 Hallgrímsson, B., and B. K. Hall (Eds.). 2005. Variation: a central concept in biology.
688 Elsevier.
- 689 Hamel, S., J. M. Gaillard, N. G. Yoccoz, S. Albon, S. D. Côté, J. M. Craine, M. Festa-
690 Bianchet, M. Garel, P. Lee, C. Moss, D. H. Nussey, F. Pelletier, A. Stien, and T. Tveraa.
691 2016. Cohort variation in individual body mass dissipates with age in large
692 herbivores. *Ecological Monographs* 86:517–543.
- 693 Hamel, S., N. G. Yoccoz, and J. M. Gaillard. 2017. Assessing variation in life-history tactics
694 within a population using mixture regression models: a practical guide for evolutionary
695 ecologists. *Biological Reviews* 92:754–775.

- 696 Hartig, F. 2024. DHARMA: Residual Diagnostics for Hierarchical (Multi-Level / Mixed)
697 Regression Models. R package version 0.4.7. <http://florianhartig.github.io/DHARMA/>
- 698 Hutchings, J. A. 2006. Survival consequences of sex-biased growth and the absence of a
699 growth–mortality trade-off. *Functional Ecology* 20:347–353.
- 700 Inoue, M., S. Sakamoto, and S. Kikuchi. 2013. Terrestrial prey inputs to streams bordered by
701 deciduous broadleaved forests, conifer plantations and clear-cut sites in southwestern
702 Japan: effects on the abundance of red-spotted masu salmon. *Ecology of Freshwater*
703 *Fish* 22:335–347.
- 704 Jones, E., S. Harden, and M. J. Crawley. 2022. *The R Book*. 3rd ed. John Wiley & Sons.
- 705 Kawaguchi, Y., and S. Nakano. 2001. Contribution of terrestrial invertebrates to the annual
706 resource budget for salmonids in forest and grassland reaches of a headwater stream.
707 *Freshwater Biology*, 46:303–316.
- 708 Kendall, N. W., J. R. McMillan, M. R. Sloat, T. W. Buehrens, T. P. Quinn, G. R. Pess, K. V.
709 Kuzishchin, M. M. McClure, and R. W. Zabel. 2015. Anadromy and residency in
710 steelhead and rainbow trout (*Oncorhynchus mykiss*): a review of the processes and
711 patterns. *Canadian Journal of Fisheries and Aquatic Sciences* 72:319–342.
- 712 Kenny, H. V., A. N. Wright, J. Piovia-Scott, L. H. Yang, D. A. Spiller, and T. W. Schoener.
713 2017. Marine subsidies change short-term foraging activity and habitat utilization of
714 terrestrial lizards. *Ecology and Evolution* 7:10701–10709.

- 715 Kishi, D., and T. Tokuhara. 2012. Fish fauna in tributaries of the Hida River in southern Hida
716 Region. Report of Gifu Prefectural Research Institute for Freshwater Fish and Aquatic
717 Environments 57:1–10.
- 718 Klemetsen, A., P. A. Amundsen, J. B. Dempson, B. Jonsson, N. Jonsson, M. F. O'connell,
719 and E. Mortensen. 2003. Atlantic salmon *Salmo salar* L., brown trout *Salmo trutta* L.
720 and Arctic charr *Salvelinus alpinus* (L.): a review of aspects of their life histories.
721 Ecology of Freshwater Fish 12:1–59.
- 722 Kozłowski, J. 2006. Why life histories are diverse. Polish Journal of Ecology 54:585–605.
- 723 Larsen, S., J. D. Muehlbauer, and E. Marti. 2016. Resource subsidies between stream and
724 terrestrial ecosystems under global change. Global Change Biology, 22:2489–2504.
- 725 Leisch, F. 2004. FlexMix: A general framework for finite mixture models and latent class
726 regression in R. Journal of Statistical Software 11:1–18.
- 727 Mangel, M., and J. Stamps. 2001. Trade-offs between growth and mortality and the
728 maintenance of individual variation in growth. Evolutionary Ecology Research 3.
- 729 Marczak, L. B., and J. S. Richardson. 2008. Growth and development rates in a riparian
730 spider are altered by asynchrony between the timing and amount of a resource subsidy.
731 Oecologia 156:249–258.
- 732 Mimura, M., T. Yahara, D. P. Faith, E. Vázquez-Domínguez, R. I. Colautti, H. Araki, F.
733 Javadi, J. Núñez-Farfán, A. S. Mori, S. Zhou, P. M. Hollingsworth, L. E. Neaves, Y.

- 734 Fukano, G. F. Smith, Y. Sato, H. Tachida, and A. P. Hendry. 2017. Understanding and
735 monitoring the consequences of human impacts on intraspecific variation. *Evolutionary*
736 *Applications* 10:121–139.
- 737 Moore, J. W., J. D. Yeakel, D. Peard, J. Lough, and M. Beere. 2014. Life-history diversity
738 and its importance to population stability and persistence of a migratory fish: steelhead
739 in two large North American watersheds. *Journal of Animal Ecology* 83:1035–1046.
- 740 Nakano, S. 1995. Individual differences in resource use, growth and emigration under the
741 influence of a dominance hierarchy in fluvial red-spotted masu salmon in a natural
742 habitat. *Journal of Animal Ecology* 64:75–84.
- 743 Nakano, S., Y. Kawaguchi, Y. Taniguchi, H. Miyasaka, Y. Shibata, H. Urabe, and N. Kuhara.
744 1999. Selective foraging on terrestrial invertebrates by rainbow trout in a forested
745 headwater stream in northern Japan. *Ecological Research* 14:351–360.
- 746 Nakano, S., K. D. Fausch, and S. Kitano. 1999. Flexible niche partitioning via a foraging
747 mode shift: a proposed mechanism for coexistence in stream-dwelling charrs. *Journal of*
748 *Animal Ecology* 68:1079–1092.
- 749 Nakano, S., and M. Murakami. 2001. Reciprocal subsidies: dynamic interdependence
750 between terrestrial and aquatic food webs. *Proceedings of the National Academy of*
751 *Sciences of the United States of America* 98:166–170.
- 752 Ormerod, S. J., M. E. Jones, M. C. Jones, and D. R. Phillips. 2004. The effects of riparian

- 753 forestry on invertebrate drift and brown trout in upland streams of contrasting acidity.
754 Hydrology and Earth System Sciences 8:578–588.
- 755 Polis, G. A., W. B. Anderson, and R. D. Holt. 1997. Toward an integration of landscape and
756 food web ecology: the dynamics of spatially subsidized food webs. Annual Review of
757 Ecology and Systematics 28:289–316.
- 758 Post, J. R., and E. A. Parkinson. 2001. Energy allocation strategy in young fish: allometry
759 and survival. Ecology 82:1040–1051.
- 760 Post, D. M., E. P. Palkovacs, E. G. Schielke, and S. I. Dodson. 2008. Intraspecific variation in
761 a predator affects community structure and cascading trophic interactions. Ecology 89:
762 2019–2032.
- 763 Promislow, D. E. L., and P. H. Harvey. 1990. Living fast and dying young: A comparative
764 analysis of life-history variation among mammals. Journal of Zoology 220:417–437.
- 765 R Core Team. 2022. R: A language and environment for statistical computing. R Foundation
766 for Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>.
- 767 Raffard, A., F. Santoul, J. Cucherousset, and S. Blanchet. 2019. The community and
768 ecosystem consequences of intraspecific diversity: A meta-analysis. Biological Reviews
769 94:648–661.
- 770 Richardson, J. S., and T. Sato. 2015. Resource subsidy flows across freshwater–terrestrial
771 boundaries and influence on processes linking adjacent ecosystems. Ecohydrology

- 772 8:406–415.
- 773 Saito, T., T. Kanazawa, K. Morimoto, K. Nakamichi, N. Kawashima, K. Suzuki, and I.
774 Akagawa. 2013. Habitat selection and movements of *Oncorhynchus masou ishikawae* in
775 a mountain stream interrupted by several small dams. Journal of The School of Marine
776 Science and Technology, Tokai University 10:1–10.
- 777 Sato, T. 2006. Dramatic decline in population abundance of *Salvelinus leucomaenis* after a
778 severe flood and debris flow in a high gradient stream. Journal of Fish Biology 69:1849–
779 1854.
- 780 Sato, T., K. Watanabe, M. Kanaiwa, Y. Niizuma, Y. Harada, and K. D. Lafferty. 2011a.
781 Nematomorph parasites drive energy flow through a riparian ecosystem. Ecology
782 92:201–207.
- 783 Sato, T., K. Watanabe, N. Tokuchi, H. Kamauchi, Y. Harada, and K. D. Lafferty. 2011b. A
784 nematomorph parasite explains variation in terrestrial subsidies to trout streams in Japan.
785 Oikos 120:1595–1599.
- 786 Sato, T., and K. Watanabe. 2014. Do stage-specific functional responses of consumers
787 dampen the effects of subsidies on trophic cascades in streams?. Journal of Animal
788 Ecology 83:907–915.
- 789 Sato, T., R. W. El-Sabaawi, K. Campbell, T. Ohta, and J. S. Richardson. 2016. A test of the
790 effects of timing of a pulsed resource subsidy on stream ecosystems. Journal of Animal

- 791 Ecology 85:1136–1146.
- 792 Sato, T., R. Ueda, and G. Takimoto. 2021. The effects of resource subsidy duration in a
793 detritus-based stream ecosystem: A mesocosm experiment. *Journal of Animal Ecology*
794 90:1142–1151.
- 795 Schaub, M., and J. A. Royle. 2014. Estimating true instead of apparent survival using spatial
796 Cormack–Jolly–Seber models. *Methods in Ecology and Evolution* 5:1316–1326.
- 797 Schindler, D. E., R. Hilborn, B. Chasco, C. P. Boatright, T. P. Quinn, L. A. Rogers, and M. S.
798 Webster. 2010. Population diversity and the portfolio effect in an exploited species.
799 *Nature* 465:609–612.
- 800 Shertzer, K. W., J. Fieberg, J. C. Potts, and M. L. Burton. 2017. Identifying growth morphs
801 from mixtures of size-at-age data. *Fisheries Research* 185:83–89.
- 802 Siepielski, A. M., J. D. DiBattista, and S. M. Carlson. 2009. It’s about time: the temporal
803 dynamics of phenotypic selection in the wild. *Ecology Letters* 12:1261–1276.
- 804 Silverstein, J. T., and H. Shimma. 1994. Effect of restricted feeding on early maturation in
805 female and male amago salmon, *Oncorhynchus masou ishikawae*. *Journal of Fish*
806 *Biology* 45:1133–1135.
- 807 Slade, E. M., D. J. Mann, J. F. Villanueva, and O. T. Lewis. 2007. Experimental evidence for
808 the effects of dung beetle functional group richness and composition on ecosystem
809 function in a tropical forest. *Journal of Animal Ecology* 76:1094–1104.

- 810 Stearns, S. C. 1989. Trade-offs in life-history evolution. *Functional Ecology* 3:259–268.
- 811 Stearns, S. C. 1992. *The evolution of life histories*. Oxford University Press.
- 812 Tanaka, T., R. Ueda, and T. Sato. (2023). Seasonal ecosystem linkages contribute to the
813 maintenance of migratory polymorphism in a salmonid population. *Proceedings of the*
814 *Royal Society B* 290:20230126.
- 815 Terui, A., K. Ooue, H. Urabe, and F. Nakamura. 2017. Parasite infection induces size-
816 dependent host dispersal: consequences for parasite persistence. *Proceedings of the*
817 *Royal Society B: Biological Sciences* 284:20171491.
- 818 Thorpe, J. E., M. Mangel, N. B. Metcalfe, and F. A. Huntingford. 1998. Modelling the
819 proximate basis of salmonid life-history variation, with application to Atlantic salmon,
820 *Salmo salar* L. *Evolutionary Ecology* 12:581–599.
- 821 Tymchuk, W. E., L. F. Sundström, and R. H. Devlin. 2007. Growth and survival trade-offs
822 and outbreeding depression in rainbow trout (*Oncorhynchus mykiss*). *Evolution*
823 61:1225–1237.
- 824 Ueda, R., M. Kanaiwa, A. Terui, G. Takimoto, and T. Sato. 2025. Data from: Seasonal timing
825 of ecosystem linkage mediates life-history variation in a salmonid fish population.
826 Dryad. <https://doi.org/10.5061/dryad.gxd2547xv>
- 827 Varpe, Ø. 2017. Life history adaptations to seasonality. *Integrative and Comparative Biology*
828 57:943–960.

- 829 Ward, D. M., K. H. Nislow, J. D. Armstrong, S. Einum, and C. L. Folt. 2007. Is the shape of
830 the density-growth relationship for stream salmonids evidence for exploitative rather
831 than interference competition?. *Journal of Animal Ecology* 76:135–138.
- 832 Weis, J. J., and D. M. Post. 2013. Intraspecific variation in a predator drives cascading
833 variation in primary producer community composition. *Oikos* 122:1343–1349.
- 834 Wipfli, M. S. 1997. Terrestrial invertebrates as salmonid prey and nitrogen sources in
835 streams: contrasting old-growth and young-growth riparian forests in southeastern
836 Alaska, USA. *Canadian Journal of Fisheries and Aquatic Sciences* 54:1259–1269.
- 837 Wright, A. N., J. Piovia-Scott, D. A. Spiller, G. Takimoto, L. H. Yang, and T. W. Schoener.
838 2013. Pulses of marine subsidies amplify reproductive potential of lizards by increasing
839 individual growth rate. *Oikos* 122:1496–1504.
- 840 Yang, L. H., J. L. Bastow, K. O. Spence, and A. N. Wright. 2008. What can we learn from
841 resource pulses. *Ecology* 89:621–634.
- 842 Yang, L. H., K. F. Edwards, J. E. Byrnes, J. L. Bastow, A. N. Wright, and K. O. Spence.
843 2010. A meta-analysis of resource pulse–consumer interactions. *Ecological*
844 *Monographs* 80:125–151.

Tables

Table 1. Result of the model comparisons of the finite mixture regression models based on the Akaike information criterion (AIC) and the Bayesian information criterion (BIC). Bold font indicates the best model in terms of both AIC and BIC ($k = 3$).

Number of growth clusters (k)	AIC	BIC
1	−232.51	−208.59
2	−366.09	−318.24
3	−399.20	−327.42
4	−390.69	−294.98
5	−388.65	−269.01
6	−393.49	−273.85

Table 2. Estimated parameters for the best model ($k = 3$) of the finite mixture regression model. $L_{\min}$ and $L_{\max}$ are respectively fork length of red-spotted masu salmon at the time of recruitment and maximum fork length of each growth cluster; The a_1 and θ are coefficients for describing seasonal growth trajectories of each growth cluster.

Parameter	Growth cluster		
	Fast	Medium	Slow
$L_{\min}$	39.13	37.76	33.58
$L_{\max}$	394.57	756.84	273.37
a_1	0.0006	0.0002	0.0005
θ	-24.31	-15.67	-9.44

Table 3. Results of the GLMM ($\chi^2 = 47.34$, $df = 2$, $p < 0.001$, pseudo $R^2 = 0.33$, dispersion parameter = 1.03) model for the effect of growth clusters on the probability of maturation at age-1. In the model, the stream sections were incorporated as a random effect. No further clustering among growth clusters (i.e., medium + slow vs. fast; fast + slow vs. medium; fast + slow vs. slow) significantly improved the model fits (log-likelihood ratio tests: $p > 0.05$).

Variables	Estimate	SE	95% CI	<i>z</i>	<i>P</i>
(Intercept)	1.06	0.37	0.35–1.78	-	-
growth cluster (medium)	-2.65	0.53	-3.70–-1.60	-4.96	< 0.001
growth cluster (slow)	-4.4	1.08	-6.52–-2.28	-4.07	< 0.001

Figure captions

Figure 1. The predictions of effects of subsidy timing and availability on growth strategies (Prediction I), association between growth strategies and maturation age (Prediction II), a growth–survival trade-off (Prediction III), and its consequences for explaining the life-history variation (age-1 maturation or not; Prediction IV). In the study design, gray squares represent the mealworm subsidies that was experimentally added as early- and late-subsidies, respectively. In the Prediction I, an expected proportion of growth trajectories (F: fast-growth strategy, S: slow-growth strategy) in each treatment [(E: early-supply treatment, L: late-supply treatment, C: no-supply treatment (control))] is shown; the color represents slow (blue) and fast (red) growth trajectories. In the Prediction IV, expected proportional compositions of maturation status at age-1 (M: matured, IM: immatured) in each treatment are shown with (upper row) and without (lower row) growth–survival trade-off.

Figure 2. Estimated seasonal growth trajectories (a), proportional composition of growth clusters in each treatment (b), and their association with the proportion of maturation at age-1 (c). Dots in the panel (a) represent fork lengths of individual fish at each sampling occasion. Experimental periods in which subsidies were added are shaded. In the panel (b), number of individuals is represented above each bar. In the panel (c), M and IM indicate the matured

881 and immatured individuals, respectively.

882

883 **Figure 3.** Association between growth clusters and survival probabilities in each treatment.

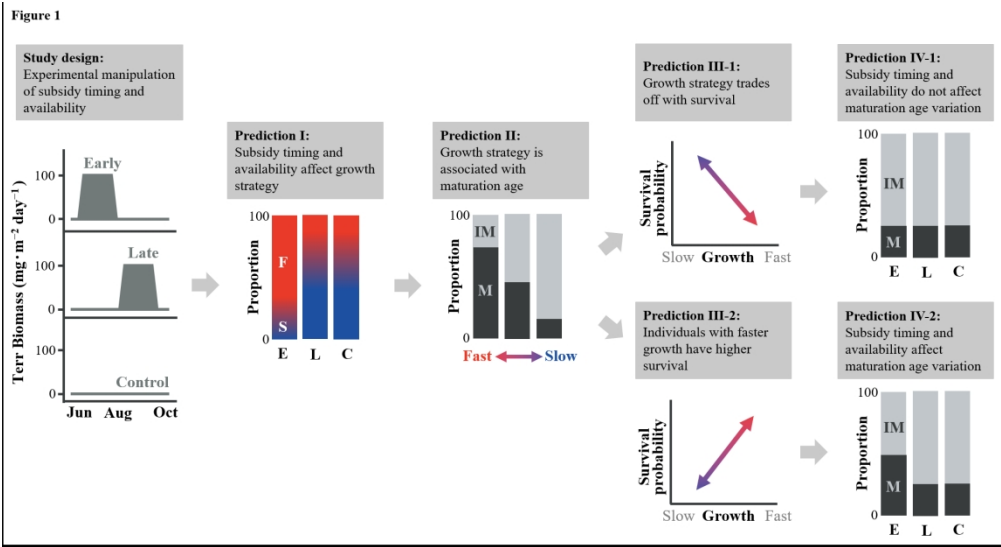
884 Dots represent the median of estimated survival probability until reproductive season at age-

885 1. Error bars represent 95% credible intervals.

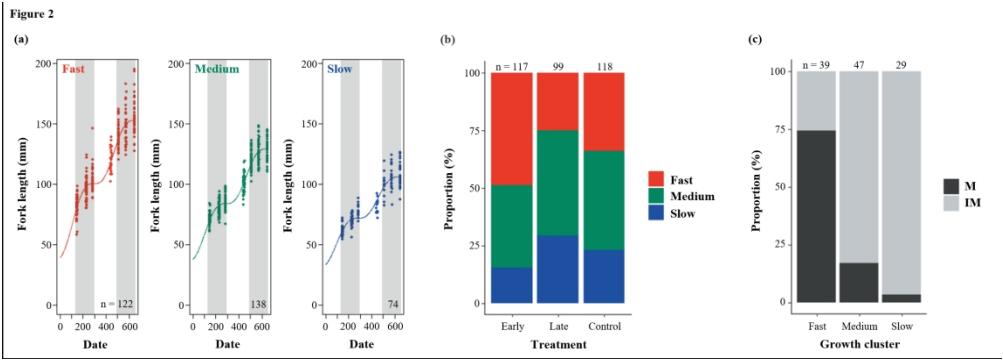
886

887 **Figure 4.** Proportional compositions of maturation status at age-1 in each treatment. M and

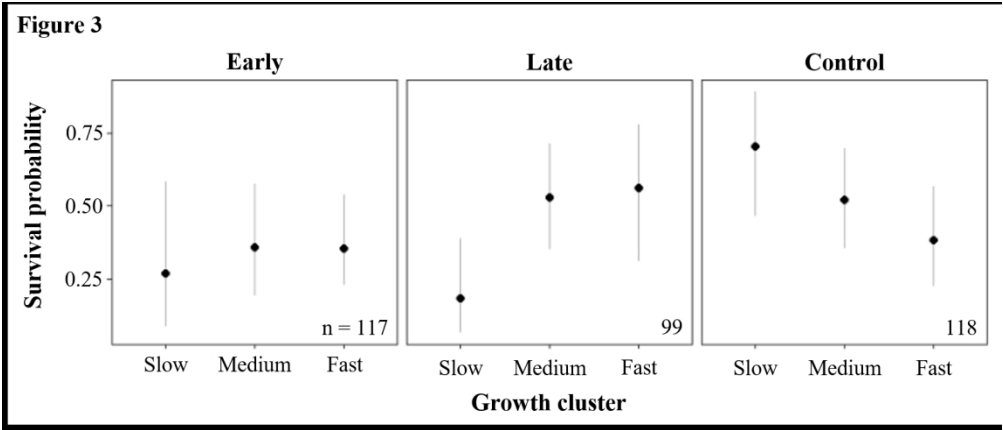
888 IM indicate the matured and immatured individuals, respectively.



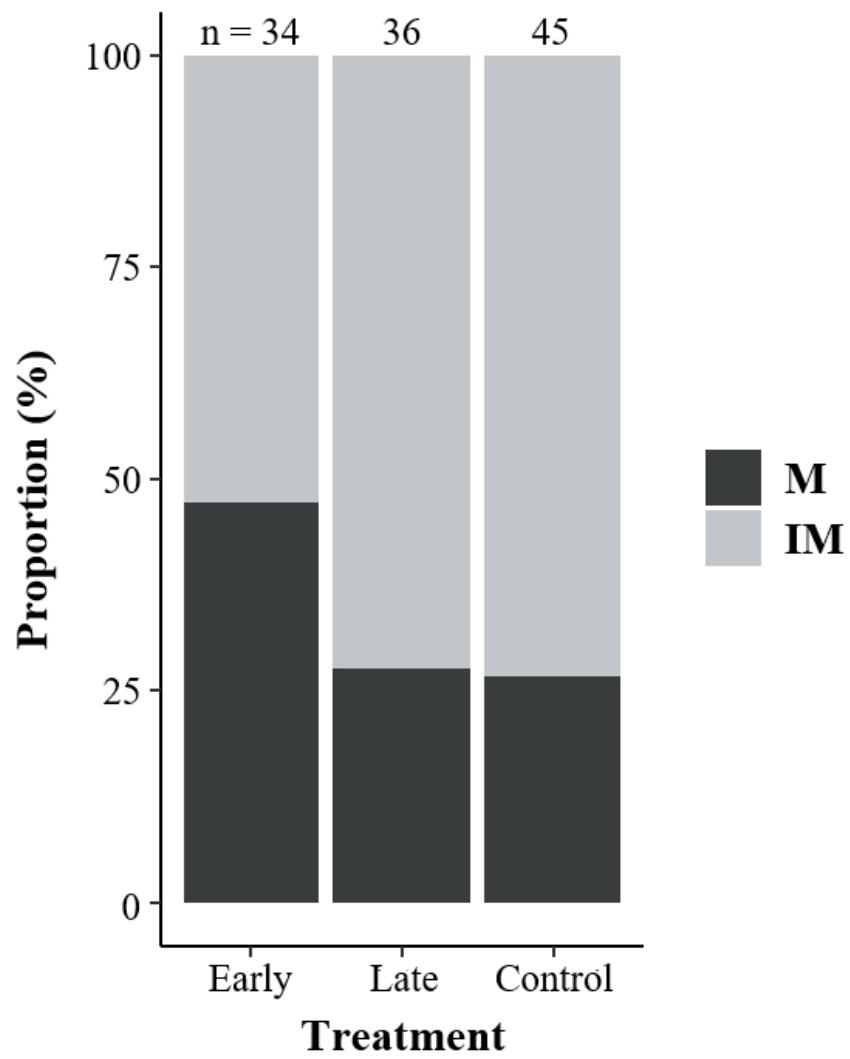
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Figure 4

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