

# Seasonal timing of ecosystem linkage contributes to maintaining life-history variation in a salmonid fish population

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February 10, 2023

## Abstract

Life-history variation can contribute to long-term persistence of populations, but it remains unknown what ecosystem properties maintain life-history variation within a population. Seasonally recurring resource subsidies are common in nature, but human-induced environmental changes, including global climate change, are causing temporal shifts and decline in those subsidies. We experimentally demonstrated that the terrestrial invertebrate subsidy occurring early in a growing season facilitated red-spotted masu salmon individuals to adopt a fast life, while the early-subsidy also maintained individuals that adopted a slow life. In contrast, the late-subsidy did not increase the fast-life individuals as much as the early-subsidy did. Consequently, the life-history variation was higher in the early-subsidy treatment than in late-subsidy treatment and no-subsidy control. The variation in life-history was not simply explained by the growth-survival trade-off. These results highlight the role of seasonal ecosystem linkages in maintaining life-history variation within a population and securing population stability at land-scape scale.

## INTRODUCTION

Maintaining life-history variation is fundamentally important for long-term persistence of populations and species (Schindler et al. 2010; Moore et al. 2014), community dynamics (Post et al. 2008; Weis & Post 2013) and ecosystem functions (El-Sabaawi et al. 2015). Individuals with distinct life-histories respond differently to temporally fluctuating environments (Hallgrímsson & Hall 2005), and the consequent asynchronous dynamics among life-history groups stabilizes aggregate dynamics over time. This statistical-averaging process, known as a portfolio effect (Schindler et al. 2015), can reduce the risk of population extinction and over-exploitation (Schindler et al. 2010). Furthermore, the effects of life-history variation can scale up to influence community dynamics and ecosystem functions by altering top-down (Post et al. 2008; Weis & Post 2013) and bottom-up regulations (El-Sabaawi et al. 2015). Those ecological processes should depend on the magnitude of life-history variation. However, what remains poorly understood is potential drivers of life-history variation in natural populations. Given human activities are causing substantial shifts and loss of intraspecific variations worldwide (Mimura et al. 2016), it is more imperative than ever to elucidate the drivers of life-history variation not only from basic (Clutton-Brock & Sheldon 2010) but also from applied ecological perspectives (Blanchet et al. 2020).

For consumers living in connected open ecosystems, seasonal flows of energy and materials across ecosystems (i.e., resource subsidies) (Polis et al. 1997; Richardson & Sato 2015) can be a potential key driver of intraspecific life-history variation. Previous studies have demonstrated that subsidies occurring early in consumers' growing season tend to facilitate consumers to adopt a fast life; early subsidies can accelerate

seasonal growth, which in turn allows juvenile consumers to mature and capture seasonally limited reproductive windows at young (spiders: Marczak & Richardson 2008; lizards: Wright et al. 2013; stream fish: Sato et al. 2016). However, utilization of subsidies can vary among individuals via resource competition (Sato & Watanabe 2014; Sato et al. 2021) and niche variation (Kenny et al. 2017), and individuals with limited subsidy supplies may benefit from adopting a slow life if life-history trade-offs exist between growth and survival (Stearns 1989; Mangel & Stamps 2001). Yet, current debates are focused largely on the emergence of a certain life-history as a population average (Wright et al. 2013; Sato et al. 2016) but have offered limited insights into how seasonal resource subsidies maintain the variation in life-history within a consumer population.

Here, we hypothesize that for salmonid consumers utilizing terrestrial resource subsidies in a temperate forest-stream ecosystem, a greater proportion of fish individuals adopt a fast life when subsidies are supplied early in their growing season (Figure 1-I) than when late or no-subsidy is supplied (Figure 1-II); as a consequence, early-subsidy will increase life-history variation (Figure 1-III). If this is the case, we further investigated the mechanism to maintain the life-history variation by testing if there is a trade-off between growth pattern (e.g., fast vs. slow) and survival (Figure 1-IV).

Seasonal timing of terrestrial invertebrate inputs may vary among temperate streams covered by different forest types and under ongoing climate changes. Where surrounded by deciduous trees, input rates of terrestrial invertebrates commonly peak in early in the growing season (late spring toward early summer) of stream salmonid fishes (Nakano & Murakami 2001; Sato et al. 2011a; Inoue et al. 2013). On the other hand, the peak timing of terrestrial subsidies can also naturally occur late in salmonids' growing season (i.e., late summer toward early autumn) if riparian forests are dominated by conifer trees (Wipfli 1997). Moreover, terrestrial invertebrate subsidies can be seasonally shifted or dampened by forest managements (i.e., clear-cut logging and extensive non-native conifer plantations; Inoue et al. 2013) and/or global climate change (Larsen et al. 2016).

Recent field evidence hints at the potential of subsidy timing in controlling life-history variation in subsidy consumers. In an experiment, early subsidies facilitated a population-level shift of salmonid individuals toward fast growth and young maturation (i.e., fast life), whereas late subsidies had no pronounced effects at population average (Sato et al. 2016). In addition, resource competition (Sato & Watanabe 2014; Sato et al. 2021) and niche variation (Kenny et al. 2017) can cause variable resource utilization among consumer individuals, potentially contributing to divergent life histories in consumers in seasonally coupled ecosystems.

To test our hypothesis, we integrate a large-scale field manipulation experiment that mimics the magnitude and seasonal timing of subsidies associated with natural and artificial riparian forests with elaborate statistical analyses that can quantifying individual variations in life-history traits. Although resource subsidies is known to affect life-history expressions (Marczak & Richardson 2008; Wright et al. 2013; Sato et al. 2016, 2020), few studies have formally tested their effects on the variation in life-history in natural environments. In addition, it has been increasingly recognized that statistical approaches that can quantify individual trajectories is crucial in life-history studies (Hamel et al. 2017), but few attempts have been made for wild populations. Our results have provided the first empirical evidence that seasonal resource subsidies can be a key driver of life-history variation in a consumer population in seasonally coupled ecosystems.

## MATERIALS AND METHODS

### Rationale of the experimental design

We designed the experiment to test the effects of the early-subsidy, late-subsidy and reduced-subsidy on the life-history variation of red-spotted masu salmon *Oncorhynchus masou ishikawae* (hereinafter, masu salmon) in a Japanese temperate stream. In the study region, a riparian vegetation originally consists of deciduous trees, and the peak timing of the subsidy occurs from late June to early August (Sato et al. 2011a), which corresponds to the early in the growing season for the studied masu salmon. However, extensive non-native conifer plantations (*Cryptomeria japonica* and *Chamaecyparis obtusa*) have been conducted around the study stream (57.1 % conifer plantation within the drainage area), which has substantially reduced the

magnitude of the subsidy in the studied stream (Sato et al. 2011b). In addition, the conifer plantation can potentially shift the subsidy timing toward late in the growing season (Wipfli 1997). The results from the early-subsidy treatment means how and in what extent the deciduous riparian forest can originally maintain life-history variation of recipient consumer fish, while their comparisons with the results for the reduced-subsidy (i.e., no-subsidy control) investigate the extent to which the extensive conifer plantation potentially cause loss of life-history variation. The comparison between the early- and late-subsidy tests whether shifts in riparian vegetation can increase or decrease the life-history variation that can be maintained within a population.

## Study site and experimental procedures

The field experiment was conducted from June, 2016 to October, 2017 in a stream in an upper drainage of Arida River system (34deg04'N, 135deg31'E), which drains a watershed within the Wakayama Forest Research Station, Field Science Education and Research Center (FSERC), Kyoto University. The stream is a typical mountain stream [i.e., gradient 16.5 %, 3.0–5.2 m stream width, 0.067–0.112 m<sup>3</sup>/sec in summer discharge, gravel-dominated streambed], and stream-resident masu salmon and a small number of minnows *Phoxinus oxycephalus jonyi* are the only fishes inhabiting the stream.

We created three treatment reaches (early-subsidy, late-subsidy and no-subsidy control) each with three replicates, resulting in nine experimental reaches. The treatment reaches were randomly assigned to nine 122.8 ± 28.0 m reaches, each separated by > 20 m intervals. We did not adjust the population density at the onset of the experiment. Although natural density of masu salmon varied among experimental reaches (age-0: 0.01–0.06 fish/m<sup>2</sup>; age-1: 0.06–0.14 fish/m<sup>2</sup>; Figure S2), those densities are relatively low compared with the densities reported in other populations (Kishi & Tokuhara 2012: 0.002–0.36 fish/m<sup>2</sup>; Saito et al. 2013: 0.25–0.68 fish/m<sup>2</sup>). Therefore, it is unlikely that these densities cause strong density-dependent effects on the life-history traits in this study (see more details in Supporting Information). The reaches were not fenced off to keep masu salmon in each treatment reach because it was not realistic to prevent movement of fish by building a fence in running water over two years. We confirmed that movements of fish across reaches were limited in the studied population [12 out of 346 (3.5 %) of fish moved across reaches]. We omitted individuals that moved across reaches from the analyses.

We emulated 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 time periods both in 2016 and 2017. Mealworms were added to subsidy reaches at the same rate from June to August as an early-subsidy treatment or from August to October as a late-subsidy treatment. In each subsidy treatment reach, the mealworms were added at a rate of 100 mg/m<sup>2</sup>/day by using 7–13 automatic fish feeders (W x H x D = 6.8 x 14.9 x 8.7 cm, 100 mL capacity for food; EHEIM Co. Ltd.) per reach. The natural input rates of the terrestrial invertebrates were relatively low in the study reaches (< 30 mg/m<sup>2</sup>/day; Figure 1-I) probably due to the previous deforestation and subsequent non-native conifer plantations that were known to reduce the 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 ± SD; range 27–444) mg/m<sup>2</sup>/day: Inoue et al. 2013]. Mealworms are ideal substitutes for the terrestrial invertebrate subsidy of our study system (Sato et al. 2016; Sato et al. 2021).

## Mark-recapture survey

Mark recapture survey was conducted each before and after the subsidy period (i.e., May, August, October) and early spring (i.e., March) to track the life-history traits, i.e., seasonal growth, survival, reproduction and movements, 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, Canada). Captured fish were anesthetized (clove bud: Seimi Laboratory, Kanagawa, Japan), measured (fork length to the nearest 1 mm and weighed to nearest 0.1 g) and individually marked by visible implant elastomer (North West Marine Technology, Inc. WA, USA). Captured location of each fish was recorded at 10-m interval to estimate the probability

of emigration from the study reaches for survival estimate. We pumped stomach contents of fish ( $n > 5$ ) that were randomly selected from each study reach at the end of each subsidy period. The stomach samples were preserved in 70 % ethanol and identified in order to distinguish their sources (mealworms, terrestrial or aquatic invertebrates). Scales ( $n < 10$  per fish) were sampled and preserved in 5 % buffered formalin solution for age-determination when captured fish were not known for their age. In October, just before the spawning season, captured fish were judged as matured if fish released sperm or eggs when we softly pressed the abdomen; otherwise, fish were recorded as immatured. All fish were subsequently released at their capture points after recovering from anaesthesia.

## The definition of life-history patterns

In this study, we focused on the growth trajectories and ages at maturity because those two life-history traits are tied to adaptive life-history variations in many animals, such as fast-slow life-history continuum (Promislow & Harvey 1990; Kozłowski 2006). In the studied population, 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 %) are iteroparous, i.e., reproduce multiple years during their lifespan. Therefore, we described the life-history of the studied masu salmon population by the combination of growth trajectory (e.g., fast vs. slow) and maturation status at age-1 (e.g., mature or immature). Sex-dependent life-history decision is well-known in salmonids (Klemetsen et al. 2003; Kendall et al. 2015; Bourret et al. 2016; Beamish 2018), but our preliminary analysis found responses to seasonal subsidies similar between male and female individuals (see Supporting Information). Therefore, we omitted sex-dependences from evaluation of life-history traits and proportional patterns of life-history variations. To strictly test the subsidy effects on life-history of masu salmon, we confined our life-history evaluation to the 2016 cohort that received the subsidy treatments since their birth.

We could not know life-history types of individuals that died before the reproductive season at age-1. Thus, the frequency of life-history types we observed could have resulted from selection acting on intrinsic individual variations (e.g., genetic variations associated with life-history traits) and/or from plastic life-history decisions such as those based on threshold traits. Present study could not distinguish the two processes in evaluating the effects of subsidies on life-history variation.

## Data Analysis

### Estimation of growth patterns using the finite mixture model

In some animals, body size divergence with age can be explained by a single growth trajectory with random variation among individuals (Haddon 2011). In other animals, in contrast, multiple distinct growth trajectories may better explain individual variation; that is, individuals may be classified into multiple groups (i.e., growth clusters) sharing different growth trajectories. To test the two possibilities, we used a finite mixture regression model 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-subsidy treatment, and no-subsidy control to test whether subsidy timing affected life-history variation in the study population.

To this end, we modeled the expected body length of masu salmon at each sampling timing for each growth cluster using the von Bertalanffy equation with seasonally varying coefficient (Cloern & Nichols 1978). In the finite mixture regression model, we assumed that each fish is assigned to a latent variable [i.e., an unobserved state (strategy) corresponding to a growth cluster]. The latent variable is a set of parameters that fully describes the seasonal growth trajectory of each growth cluster in the von Bertalanffy equation.

To implement the finite mixture regression model, we utilized FLXMRglm function in the R package ‘flexmix’, where the EM algorithm (Dempster et al. 1977) can be used for the parameter estimation. The 885 body-size data across 334 individuals [2.65  $\pm$  1.53 (mean  $\pm$  SD; range 1–7) data per individual] were used to construct the model. 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 number of growth

clusters ( $k = 1-6$ ). The Akaike Information Criterion (AIC) and the Bayesian Information Criterion (BIC) were used for the model selection; models both with  $\Delta \text{AIC} < 2$  and  $\Delta \text{BIC} < 2$  was considered to be an equivalent statistical support (Hamel et al. 2017). The details of the finite mixture regression model were shown in Supporting Information.

#### Association of growth clusters with maturation at age-1

Based on the previous study for the same masu salmon population (Sato et al. 2021) and along with the principle of fast-slow life-history continuum (Promislow & Harvey 1990), we hypothesize individuals of fast-growth clusters to have higher probabilities of maturation at age-1 than those of slow-growth clusters. In addition, the effect of growth cluster on the maturation-decision might be larger with the early-subsidy than with the late-subsidy and no-subsidy because of the timing dependent life-history decisions (Sato et al. 2016). Generalized linear mixed model (GLMM; glmer function in the R package ‘lme4’), with 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 interaction term was excluded from the final model if it did not significantly maximize the log-likelihood of the model in the log-likelihood ratio test (Crawley 2007).

#### Variation in life-history patterns

We classified life-history patterns as a combination of growth clusters (slow, medium, and fast) and maturation status at age-1 (mature, M or immature, IM); e.g., individuals grew fast and matured at age-1 are denoted as “Fast-M”. We tested whether the early-subsidy treatment induced higher variation in life-history patterns using the following two complementary approaches. First, Fisher’s exact test was used to examine if proportional composition of life-history patterns differed among treatments. When the treatment effect was significant, we further conducted pairwise comparisons with Bonferroni correction ( $\alpha = 0.017$ ). This approach cannot quantify the variation in life-history patterns *per se*. Therefore, we calculated the Shannon-Wiener diversity index ( $H'$ ) (Magurran 2004) to provide a statistically comparable metrics for the variation in life-history patterns. We pooled three replicates to calculate  $H'$  for each treatment due to low sample size of fish per replicate reach.

#### Estimation of survival probabilities

Fitness trade-off is a well-known mechanism to maintain life-history variations within a single population (Stearns 1989; Mangel & Stamps 2001). In this study, we hypothesized that individuals with faster growth experienced lower survival until their reproductive season at age-1, which underlies the generation of life-history variation of masu salmon. To test this hypothesis, true survival probabilities (i.e., corrected for permanent emigration) were estimated by a modified version of a Cormack-Jolly-Seber (CJS) model (Schaub & Royle 2014; Terui et al. 2017). Survival estimates in classical CJS models are called “apparent” survival, as it is confounded with permanent emigration from an observation area. The modified CJS model, however, 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 the permanent emigration of fish from the experimental reaches would inevitably occur. Our primary objective was to test whether the variation in life-history patterns in each treatment are explained by the trade-off between growth cluster and survival. Therefore, we estimated the survival probability separately for growth clusters and subsidy treatments. The details of the survival estimates were shown in Supporting Information.

## RESULTS

The total mass of all invertebrate consumption (i.e., aquatic and terrestrial invertebrates, and mealworms) by red-spotted masu salmon in subsidized-treatment reaches was, on average, 5.6 times higher than those in un-subsidized reaches in August [subsidized:  $0.52 \pm 0.34$  mg/100 mg mass of fish; un-subsidized (no-subsidy control + late-subsidy treatment):  $0.09 \pm 0.09$ ; Mann-Whitney  $U$ -test:  $W = 34, p = 0.009$ ] and 3.6 times higher in October [subsidized:  $0.31 \pm 0.37$ ; un-subsidized (no-subsidy control + early-subsidy treatment):  $0.09 \pm 0.09$ ; Mann-Whitney  $U$ -test:  $W = 213, p = 0.020$ ], respectively. Mealworms respectively made up

$97 \pm 3 \%$  and  $62 \pm 40 \%$  of the total mass of consumption by masu salmon in August and October, and the consumption rate of mealworms was positively correlated with the total consumption rate in both periods (Spearman rank correlation, August:  $r_s = 1$ ,  $p = 0.0028$ ; October:  $r_s = 0.95$ ,  $p < 0.0001$ ).

## Growth pattern and age at maturity

The specific growth rates of masu salmon did not differ between periods [(early in the growing season (June–August) vs. late in the growing season (August–October)] when they received no subsidy during the periods (GLMM<sub>gaussian</sub>, period:  $t = -1.24$ ,  $P = 0.24$ ; Figure S3; Table S2). When subsidies were supplied, their growth increased by 1.6 times higher, and the increase did not depend on the period they received subsidies (subsidy  $\times$  period:  $t = -0.29$ ,  $P = 0.77$ ). However, the specific growth rate varied substantially among individuals across experimental reaches. Three growth clusters (fast-, medium- and slow-growth clusters) best explained this variation in the finite mixture regression model (Table 1, 2; Figure 2a). The proportional composition of the growth clusters differed significantly among treatments (Fisher’s exact test:  $P < 0.01$ ), with only a significant difference in a pairwise comparison between early- vs. late-subsidy treatments (adjusted  $P < 0.001$ ) (Figure S4). Early-subsidies increased the proportion of individuals belonging to the fast-growth cluster (57 out of 117 fish, 49 %), while reducing that of the slow-growth cluster ( $n = 18$ , 15 %) (Figure S4). In no-subsidy control, individuals belonging to the medium-growth cluster were most common (51 out of 118 fish, 43 %), followed by the fast-growth (34 %) and slow-growth (23 %) individuals (Figure S4). Although the late-subsidy treatment supplied the same amount of subsidies as in the early-treatment, late-subsidies resulted in the composition close to that of the no-subsidy control, with a slightly larger representation of the fast-growth cluster (Figure S4).

Probability of maturation at age-1 was higher for individuals belonging to 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 %) did at age-1 (Figure 2b). The optimal GLMM model revealed that the growth cluster solely had a significant effect on age at maturity, i.e., no significant effects of the subsidy timing nor its interaction with growth clusters on the probability of maturation at age-1 were detected (Table S3).

## Variation in life-history patterns

We observed six different life-history patterns across treatment reaches (Figure 3). The proportional composition of the life-history patterns largely differed among treatments although it was not statistically significant (Fisher’s exact test:  $P = 0.11$ ) due to relatively small sample size. In the early-subsidy treatment, individuals that adopted fast life, i.e., fast-growth and matured at age-1 (Fast-M) were most common (11 out of 34 fish, 32 %), whereas the second common life-history pattern (7 fish, 21 %) was slow life, i.e., Slow-IM. Other life-history patterns, except for Slow-M ( $n = 1$ ), were evenly found in the early-subsidy treatment. In no-subsidy control, three life-history patterns (Fast-M, Medium-IM, and Slow-IM; 34 out of 36 fish, 94 %) dominated over the other three patterns. Among the three life-history patterns, relatively slower life-history patterns, i.e., Medium-IM ( $n = 15$ , 33 %) and Slow-IM ( $n = 14$ , 31 %), were found in similar proportions, while 20 % of fish ( $n = 9$ ) adopted Fast-M pattern. In the late-subsidy treatment, the three-dominant life-history patterns were the same as those observed in no-subsidy control, but the proportional composition differed largely between the two treatments. Specifically, Medium-IM was most common (18 fish, 50 %), while Fast-M (9 fish, 25 %) and Slow-IM (7 fish, 19 %) were the second- and third-common life-history patterns, respectively. Overall, the diversity of life-history patterns was highest in the early-subsidy treatment and lowest in the late-subsidy treatment (Shannon’s  $H'$ : early = 2.36, late = 1.75, control = 2.09).

## Survival probability and its association with growth clusters

In no-subsidy control, the estimated survival probability was lowest in individuals belonging to the fast growth cluster, suggesting a growth-survival trade-off. However, the growth-survival trade-off became unclear in the early-subsidy treatment and even disappeared in the late-subsidy treatment; the survival probability was similar among individuals belonging to the different growth clusters in the early-subsidy treatment; the survival probability was lower in the slow-growth individuals than the fast-growth individuals in the late-subsidy treatment (Figure 4).

## DISCUSSION

Elucidating the maintenance mechanisms of life-history variation is fundamentally important in ecology and evolutionary biology (Stearns 1992; Clutton-Brock & Sheldon 2010). However, it remains poorly understood what ecosystem properties increase or decrease life-history variation in natural environments. Here, we provide empirical evidence that the ecosystem linkage via seasonal resource subsidies can maintain life-history variation of consumers in recipient ecosystems. Another key implication from this study is that human-induced environmental changes may reduce the life-history variation through the temporal shifts and/or decline of seasonal resource subsidies. Our study suggests that such an indirect process through resource subsidies may underlie the ongoing loss of intraspecific variations in wildlife.

### Timing-dependent effects on life-history decision and its variation

Although our experimental subsidy increased the individual growth rate irrespective of timing, the fast-life history (represented by the fast-growth cluster and maturation at age-1) was prevalent in the early-subsidy treatment than in the late-subsidy treatment. This timing-dependent effects may reflect physiological constraints on the seasonally-determined onset of maturity. In salmonids (Thorpe et al. 1998) including the studied species (Silverstein & Shimma 1994), individuals achieving rapid growth and gaining lipid reserves early in the growing season can initiate gonad development and mature in autumn. Yet, growth acceleration induced by late subsidies may be too late for individuals to develop gonads before the reproductive season of the year. Arguably, this timing-dependent life-history decision facilitated individuals to adopt a fast life and suppressed the proportion of slow-life individuals in the early-subsidy treatment. In contrast, the late-subsidy was inefficient in inducing a fast life, resulting in many individuals expressing medium-growth and late maturation. In no-subsidy control, the reduced subsidy was not able to accelerate the seasonal growth important for inducing a fast life. Consequently, life-history variation was higher in the early-subsidy treatment than in the late-subsidy treatment and no-subsidy control.

Temporal match between resource availabilities and life-history decision windows commonly regulates seasonal growth and maturation in many plants and animals (Durant et al. 2007). Our study highlights that those phenological matching can occur across ecosystem boundaries and strongly regulate variations in life-history expression. Given the ubiquitous nature of seasonal ecosystem linkages, anthropogenic disturbances of seasonal resource subsidies at local and global scales (Richardson & Sato 2015; Larsen et al. 2016) may underlie the ongoing loss of intraspecific variations in wildlife.

### Maintenance mechanisms of life-history variation and their potential population consequences

Trade-offs among life-history traits, such as growth, survival and reproduction, is considered a leading cause that maintains life-history variation within a population (Stearns 1989; Mangel & Stamps 2001; Christie et al. 2018). In this study, individuals belonging to the fast-growth cluster tended to have lower survival rate until age-1 in the no-subsidy control, suggesting that the growth-survival trade-off partially explains the life-history variation in the no-subsidy control. However, such a trade-off was not found in the early- and late-subsidy treatments; the survival rate tended to be lower in the slow-growth cluster in both treatments. Two possible mechanisms may explain life-history variation despite the apparent lack of the growth-survival trade-off. First, slow-life individuals might achieve fitness similar to that of fast-life individuals in the subsidy treatments via other types of life-history trade-off, such as the growth-reproduction trade-off (Christie et al. 2018); reproductive success in a same spawning ground would be higher in slow-life individuals that matured at age-2 than fast-life individuals that matured at age-1 due to a size-dependent breeding competition. If this is the case, the life-history variation is stably maintained with the early-subsidy within a population. Second, spatial variation in resource subsidies may maintain life-history variation across space; i.e., fast-life individuals dominate in deciduous forested streams with early subsidies, whereas slow-life individuals would be prevalent in coniferous forested streams with late subsidies and/or reduced subsidies. As a consequence, life-history variation can be maintained at a basin scale (i.e., meta-population level). This can be the case in the studied masu salmon because many individuals complete their life-history within a stream (i.e., local population) that receives a given subsidy supply, but potentially move across streams (i.e., forming

meta-population).

Those maintenance mechanisms of life-history variation are highly relevant to whether the life-history variation potentially contributes to stabilizing population fluctuation at local population or meta-population levels. In salmonid fishes, individuals with distinct ages at maturity can respond differently to environmental fluctuations, such as large floods (Jensen & Johnsen 1999), and the consequent asynchronous dynamics among life-history groups can stabilize population fluctuations over time (Schindler et al. 2010; Moore et al. 2014). If the early subsidy can stably maintain life-history variation within a population, this stabilizing effect is expected to function at local population level. On the other hand, when given subsidies (early, late or reduced subsidies) associated with riparian forest types maintain a certain life-history in each stream (i.e., local habitat), the asynchronous dynamics among life-history groups can stabilize meta-population dynamics across streams within a river basin. Unravelling temporal and spatial variations in seasonal subsidies and their relevance with life-history variation within and among local populations will be a crucial step to fully understand the maintenance mechanisms of life-history variation and their population consequences across time and space.

### Limitation for the evaluation of life-history variation

While we successfully described the variation in life-history patterns until age-1 and its dependence with the timing and magnitude of the terrestrial subsidy, we might underestimate some of the life-history variations in the studied population. For instance, we could not evaluate (1) fish that matured at age-2 and older, and (2) fish that repeated reproductions (i.e., iteroparous individuals) in the 2-year field experiment. For the first limitation, because fewer fish (approx. 5 %) survived until reproductive period at age-3 in the studied population, individuals that did not mature at age-1 could be assumed to mature at age-2. For the second limitation, the iteroparous life-history was relatively uncommon (approx. 9.9 %) in the studied population. Taken together, we believe that potential underestimates of the life-history patterns would minimally affect the main argument of the present study.

### Conclusion

In this study, we demonstrated that seasonal timing of resource subsidies relative to consumer phenology can have pronounced effects on life-history variation in consumers in recipient ecosystems. Contrary to the most studies focusing the effects of subsidies on life-history traits as a population average, acknowledging the subsidy effects on the variation in life-history is crucial because life-history variations are fundamentally important for long-term persistence of populations and species (Schindler et al. 2010; Moore et al. 2014). Consumers' effects on species interactions and ecosystem functions should be determined by not only mean but variation of life-history traits of the consumers (Bolnick et al. 2011; Des Roches et al. 2018; Raffard et al. 2019). Furthermore, understanding relative contribution of life-history plasticity and genetic variation underlying such life-history variation can lead to answer two fundamental questions in ecology and evolution; how quickly individuals can respond to changing environments? and how it does maintain resilience at population level? Due to the technological development in molecular biology, the genetic and epigenetic mechanisms related to growth and age at maturity are being elucidated in wild organisms (Moran & Perez-Figueroa 2011; Barson et al. 2015; Therkildsen et al. 2019). Our study presents new insight into those studies by emphasizing the need to acknowledge environmental factors at landscape, where seasonal subsidies govern growth trajectory, age at maturity and ultimately life-history expressions of wildlife.

### Acknowledgements

We thank Shin Ukaji, Ryosuke Tanaka, Tatsuya Tanaka, Hiroki Tabuchi and Sean Naman for their substantial contribution to the preparation and maintenance of the field experiment and mark recapture survey. We also appreciate Atsushi Hasegawa, Hisaya Uenishi, Yoshikazu Asano, Ryo Arai, Jun Yanagimoto, Tomonori Katsuyama and Kae Matsuba for their assistance in conducting the experiment in Wakayama Forest Research Station. This work was supported by JSPS KAKENHI Grant Number JP 15H04422.

### References



- Barson, N. J., Aykanat, T., Hindar, K., Baranski, M., Bolstad, G. H., Fiske, P. et al. (2015). Sex-dependent dominance at a single locus maintains variation in age at maturity in salmon. *Nature*, 528, 405–408.
- Beamish, R. J. (2018). The ocean ecology of Pacific salmon and trout. *Am. Fish. Soc.*, pp. 703–730.
- Blanchet, S., Prunier, J. G., Paz-Vinas, I., Saint-Pe, K., Rey, O., Raffard, A. et al. (2020). A river runs through it: The causes, consequences, and management of intraspecific diversity in river networks. *Evol. Appl.*, 13, 1195–1213.
- Bolnick, D. I., Amarasekare, P., Araujo, M. S., Burger, R., Levine, J. M., Novak, M. et al. (2011). Why intraspecific trait variation matters in community ecology. *Trends Ecol. Evol.*, 26, 183–192.
- Bourret, S. L., Caudill, C. C., & Keefer, M. L. (2016). Diversity of juvenile Chinook salmon life history pathways. *Rev. Fish Biol. Fisheries*, 26, 375–403.
- Christie, M. R., McNickle, G. G., French, R. A., & Blouin, M. S. (2018). Life history variation is maintained by fitness trade-offs and negative frequency-dependent selection. *Proc. Natl. Acad. Sci. U.S.A.*, 115, 4441–4446.
- Cloern, J. E., & Nichols, F. H. (1978). A von Bertalanffy growth model with a seasonally varying coefficient. *J. Fish. Board. Can.*, 35, 1479–1482.
- Clutton-Brock, T., & Sheldon, B. C. (2010). Individuals and populations: the role of long-term, individual-based studies of animals in ecology and evolutionary biology. *Trends Ecol. Evol.*, 25, 562–573.
- Crawley, M.J. (2007). *The R Book*. John Wiley & Sons Ltd.
- Dempster, A. P., Laird, N. M., & Rubin, D. B. (1977). Maximum likelihood from incomplete data via the EM algorithm. *J. R. Stat. Soc. B Methodol.*, 39, 1–22.
- Des Roches, S., Post, D. M., Turley, N. E., Bailey, J. K., Hendry, A. P., Kinnison, M. T. et al. (2018). The ecological importance of intraspecific variation. *Nat. Ecol. Evol.*, 2, 57–64.
- Durant, J. M., Hjermann, D. O., Ottersen, G., & Stenseth, N. C. (2007). Climate and the match or mismatch between predator requirements and resource availability. *Clim. Res.*, 33, 271–283.
- El-Sabaawi, R. W., Marshall, M. C., Bassar, R. D., Lopez-Sepulcre, A., Palkovacs, E. P., & Dalton, C. (2015). Assessing the effects of guppy life history evolution on nutrient recycling: from experiments to the field. *Freshw. Biol.*, 60, 590–601.
- Haddon, M. (2011). *Modelling and quantitative methods in fisheries*. Second Edition. Chapman & Hall/CRC., pp. 217–230.
- Hallgrimsson, B., & Hall, B. K. (Eds.). (2005). *Variation: a central concept in biology*. Elsevier.
- Hamel, S., Yoccoz, N. G., & Gaillard, J. M. (2017). Assessing variation in life-history tactics within a population using mixture regression models: a practical guide for evolutionary ecologists. *Biol. Rev.*, 92, 754–775.
- Inoue, M., Sakamoto, S., & Kikuchi, S. (2013). Terrestrial prey inputs to streams bordered by deciduous broadleaved forests, conifer plantations and clear-cut sites in southwestern Japan: effects on the abundance of red-spotted masu salmon. *Ecol. Freshw. Fish.*, 22, 335–347.
- Jensen, A. J., & Johnsen, B. O. (1999). The functional relationship between peak spring floods and survival and growth of juvenile Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*). *Funct. Ecol.*, 13, 778–785.
- Kendall, N. W., McMillan, J. R., Sloat, M. R., Buehrens, T. W., Quinn, T. P., Pess, G. R. et al. (2015). Anadromy and residency in steelhead and rainbow trout (*Oncorhynchus mykiss*): a review of the processes and patterns. *Can. J. Fish. Aquat. Sci.*, 72, 319–342.

- Kenny, H. V., Wright, A. N., Piovia-Scott, J., Yang, L. H., Spiller, D. A., & Schoener, T. W. (2017). Marine subsidies change short-term foraging activity and habitat utilization of terrestrial lizards. *Ecol. Evol.*, 7, 10701–10709.
- Kishi, D., & Tokuhara, T. (2012). Fish fauna in tributaries of the Hida River in southern Hida Region. *Rep. Gifu Prefect. Res. Inst. Freshwat. Fish Aquat. Environ.*, 57, 1–10.
- Klemetsen, A., Amundsen, P. A., Dempson, J. B., Jonsson, B., Jonsson, N., O'connell, M. F. et al. (2003). Atlantic salmon *Salmo salar* L., brown trout *Salmo trutta* L. and Arctic charr *Salvelinus alpinus* (L.): a review of aspects of their life histories. *Ecol. Freshw. Fish*, 12, 1–59.
- Kozłowski, J. (2006). Why life histories are diverse. *Pol. J. Ecol.*, 54, 585–605.
- Larsen, S., Muehlbauer, J. D., & Marti, E. (2016). Resource subsidies between stream and terrestrial ecosystems under global change. *Glob. Change Biol.*, 22, 2489–2504.
- Magurran, A.E. (2004). *Measuring Biological Diversity*. Blackwells.
- Mangel, M., & Stamps, J. (2001). Trade-offs between growth and mortality and the maintenance of individual variation in growth. *Evol. Ecol. Res.*, 3.
- Marczak, L. B., & Richardson, J. S. (2008). Growth and development rates in a riparian spider are altered by asynchrony between the timing and amount of a resource subsidy. *Oecologia*, 156, 249–258.
- Mimura, M., Yahara, T., Faith, D. P., Vazquez-Dominguez, E., Colautti, R. I., Araki, H. et al. (2017). Understanding and monitoring the consequences of human impacts on intraspecific variation. *Evol. Appl.*, 10, 121–139.
- Moore, J. W., Yeakel, J. D., Peard, D., Lough, J., & Beere, M. (2014). Life-history diversity and its importance to population stability and persistence of a migratory fish: steelhead in two large North American watersheds. *J. Anim. Ecol.*, 83, 1035–1046.
- Moran, P., & Perez-Figueroa, A. (2011). Methylation changes associated with early maturation stages in the Atlantic salmon. *BMC Genet.*, 12, 1–8.
- Nakano, S., & Murakami, M. (2001). Reciprocal subsidies: dynamic interdependence between terrestrial and aquatic food webs. *Proc. Natl. Acad. Sci. U.S.A.*, 98, 166–170.
- Polis, G. A., Anderson, W. B., & Holt, R. D. (1997). Toward an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. *Annu. Rev. Ecol. Evol. Syst.*, 289–316.
- Post, D. M., Palkovacs, E. P., Schielke, E. G., & Dodson, S. I. (2008). Intraspecific variation in a predator affects community structure and cascading trophic interactions. *Ecology*, 89, 2019–2032.
- Promislow, D. E., & Harvey, P. H. (1990). Living fast and dying young: A comparative analysis of life-history variation among mammals. *J. Zool.*, 220, 417–437.
- Raffard, A., Santoul, F., Cucherousset, J., & Blanchet, S. (2019). The community and ecosystem consequences of intraspecific diversity: A meta-analysis. *Biol. Rev.*, 94, 648–661.
- Richardson, J. S., & Sato, T. (2015). Resource subsidy flows across freshwater–terrestrial boundaries and influence on processes linking adjacent ecosystems. *Ecohydrology*, 8, 406–415.
- Saito, T., Kanazawa, T., Morimoto, K., Nakamichi, K., Kawashima, N., Suzuki, K. et al. (2013). Habitat selection and movements of *Oncorhynchus masou ishikawae* in a mountain stream interrupted by several small dams. *J. Sch. Mar. Sci. Technol. Tokai Univ.*, 10, 1–10.
- Sato, T., Watanabe, K., Kanaiwa, M., Niizuma, Y., Harada, Y., & Lafferty, K. D. (2011a). Nematomorph parasites drive energy flow through a riparian ecosystem. *Ecology*, 92, 201–207.

- Sato, T., Watanabe, K., Tokuchi, N., Kamauchi, H., Harada, Y., & Lafferty, K. D. (2011b). A nematomorph parasite explains variation in terrestrial subsidies to trout streams in Japan. *Oikos*, 120, 1595–1599.
- Sato, T., & Watanabe, K. (2014). Do stage-specific functional responses of consumers dampen the effects of subsidies on trophic cascades in streams?. *J. Anim. Ecol.*, 83, 907–915.
- Sato, T., El-Sabaawi, R. W., Campbell, K., Ohta, T., & Richardson, J. S. (2016). A test of the effects of timing of a pulsed resource subsidy on stream ecosystems. *J. Anim. Ecol.*, 85, 1136–1146.
- Sato, T., Ueda, R., & Takimoto, G. (2021). The effects of resource subsidy duration in a detritus-based stream ecosystem: A mesocosm experiment. *J. Anim. Ecol.*, 90, 1142–1151.
- Schaub, M., & Royle, J. A. (2014). Estimating true instead of apparent survival using spatial Cormack–Jolly–Seber models. *Methods Ecol. Evol.*, 5, 1316–1326.
- Schindler, D. E., Hilborn, R., Chasco, B., Boatright, C. P., Quinn, T. P., Rogers, L. A. et al. (2010). Population diversity and the portfolio effect in an exploited species. *Nature*, 465, 609–612.
- Schindler, D. E., Armstrong, J. B., & Reed, T. E. (2015). The portfolio concept in ecology and evolution. *Front. Ecol. Environ.*, 13, 257–263.
- Silverstein, J. T., & Shimma, H. (1994). Effect of restricted feeding on early maturation in female and male amago salmon, *Oncorhynchus masou ishikawae*. *J. Fish Biol.*, 45, 1133–1135.
- Stearns, S. C. (1989). Trade-offs in life-history evolution. *Funct. Ecol.*, 3, 259–268.
- Stearns, S. C. (1992). The evolution of life histories. Oxford University Press.
- Terui, A., Ooue, K., Urabe, H., & Nakamura, F. (2017). Parasite infection induces size-dependent host dispersal: consequences for parasite persistence. *Proc. Royal Soc. B*, 284, 20171491.
- Therkildsen, N. O., Wilder, A. P., Conover, D. O., Munch, S. B., Baumann, H., & Palumbi, S. R. (2019). Contrasting genomic shifts underlie parallel phenotypic evolution in response to fishing. *Science*, 365, 487–490.
- Thorpe, J. E., Mangel, M., Metcalfe, N. B., & Huntingford, F. A. (1998). Modelling the proximate basis of salmonid life-history variation, with application to Atlantic salmon, *Salmo salar* L. *Evol. Ecol.*, 12, 581–599.
- Weis, J. J., & Post, D. M. (2013). Intraspecific variation in a predator drives cascading variation in primary producer community composition. *Oikos*, 122, 1343–1349.
- Wipfli, M. S. (1997). Terrestrial invertebrates as salmonid prey and nitrogen sources in streams: contrasting old-growth and young-growth riparian forests in southeastern Alaska, USA. *Can. J. Fish. Aquat. Sci.*, 54, 1259–1269.
- Wright, A. N., Piovia-Scott, J., Spiller, D. A., Takimoto, G., Yang, L. H., & Schoener, T. W. (2013). Pulses of marine subsidies amplify reproductive potential of lizards by increasing individual growth rate. *Oikos*, 122, 1496–1504.

## Figure legends

**Figure 1** . The hypothesized effects of subsidy timing (I) on life-history variation in the early-subsidy and late-subsidy treatments, respectively (II and III) and the growth-survival trade-off that may explain the life-history variation (IV). In the panel (I), seasonally asynchronous resource dynamics of aquatic invertebrate biomass (Aqua) and the terrestrial invertebrate subsidy (Terr) is shown; solid line represents the natural input rates of the terrestrial invertebrates in the study reach (mean  $\pm$  SD); dashed line shows aquatic invertebrate biomass measured in the nearby stream (Sato et al. 2011a), which is commonly observed seasonal pattern in temperate streams. Gray squares represent the mealworm subsidy that was experimentally added as early- and late-subsidies, respectively. In the panel (II), the expected life-history patterns (growth trajectory and age at maturity) were shown; the color represents slow (blue) to fast (red) growth trajectories, while the

thinness of arrows indicates the expected frequency of each life-history pattern, which is summarized in the panel (III). The life-history patterns and variation in no-subsidy control (reduced-subsidy in this study) were expected to be similar with those hypothesized in the late-subsidy along with the previous study (Sato et al. 2016; see more details in the main text).

**Figure 2** . Estimated seasonal growth trajectories (a) and their association with the proportion of maturation at age-1 (b). Dots in the panel (a) represent fork lengths of individual fish at each sampling occasion. In the panel (b), M and IM indicate the matured and immatured individuals, respectively.

**Figure 3** . Proportional compositions of life-history patterns in each treatment. The life-history pattern of individual is represented by a combination of the growth cluster (first term) and maturation status at age-1 (second character M = matured, and IM = immatured).

**Figure 4** . Association between growth clusters and survival probabilities in each treatment. Dots represent the median of estimated survival probability until reproductive season at age-1. Error bars represent 95 % credible intervals.

**Table 1**. Result of the model comparisons of the finite mixture regression models based on Akaike’s Information Criterion (AIC) and 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
<b>3</b>	<b>-399.20</b>	<b>-327.42</b>
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  $\vartheta$  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
$\vartheta$	-24.31	-15.67	-9.44



