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Hatch timing of two subarctic salmonids in a stream network estimated by otolith increments

Kevin A. Fitzgerald[1] | Matt R. Haworth[2] | Kevin R. Bestgen[2,3] | Collin J. Farrell[1] | Shunsuke Utsumi[4] | Osamu Kishida[5] | Hiromi Uno[6,7] | Yoichiro Kanno[1,3]

[1]Department of Fish, Wildlife, and Conservation Biology, Colorado State University, Fort Collins, Colorado, USA

[2]Larval Fish Laboratory, Department of Fish, Wildlife, and Conservation Biology, Colorado State University, Fort Collins, Colorado, USA

[3]Graduate Degree Program in Ecology, Colorado State University, Fort Collins, Colorado, USA

[4]Field Science Center for Northern Biosphere, Hokkaido University, Sapporo, Japan

[5]Tomakomai Experimental Forest, Field Science Center for Northern Biosphere, Hokkaido University, Tomakomai, Japan

[6]Center for Ecological Research, Kyoto University, Otsu, Japan

[7]Faculty of Environmental Earth Science, Hokkaido University, Sapporo, Japan

Correspondence
Yoichiro Kanno, Department of Fish, Wildlife, and Conservation Biology, Colorado State University, 1474 Campus Delivery, Fort Collins, CO 80523-1474, USA.
Email: yoichiro.kanno@colostate.edu

Abstract

Hatch timing in autumn-spawning stream salmonids is poorly understood in the subarctic region because snow cover prevents direct sampling of cryptic early life stages. Otolith micro-increment analysis was used to infer hatch dates of white-spotted charr *Salvelinus leucomaenis* (Pallas) and masu salmon *Oncorhynchus masou* (Brevoort) in a mainstem-tributary network in northern Japan. Accuracy and precision were validated by ageing hatchery individuals with known hatch date ranges. In July 2018, 93 wild young-of-the-year white-spotted charr and 81 masu salmon were collected and aged. Masu salmon hatched, on average, 24 days earlier (mean = February 8) than white-spotted charr (March 4), and hatch dates spanned a minimum of 2 months for each species. In masu salmon, hatch dates of individuals collected in the mainstem were nearly 3 weeks earlier than those in a tributary. This study provided knowledge on intra- and inter-specific variation in hatch timing of native salmonids in a subarctic stream network.

KEYWORDS
early life stages, larval fish, otolith increment analysis, Salmonidae, stream networks, subarctic region

1 | INTRODUCTION

Early life history ecology, in particular timing of hatch, is important in understanding population dynamics and community structure of stream salmonids. Larval stages are vulnerable to predation and physical disturbances, and their production is often regulated by annual variation in timing and magnitude of high flow events during egg incubation and post-hatch periods (Kovach et al., 2016). Timing of hatch influences variation in body size in early life stages (Yamamoto et al., 1997), which then mediates intra- and inter-specific competitive interactions (Blanchet et al., 2008; Peterson et al., 2004). Direct sampling of newly hatched fish is challenging in the subarctic region

because streams are typically covered with ice and deep snowpack when they hatch. Such was the case in this study area in northern Japan, in which hatch timing of two salmonids was inferred indirectly using otolith increments.

Increment analysis of otolith microstructure allows for retrospective estimation of hatch dates. Growth increments are deposited daily at hatch and enumerating the increments has been used to estimate hatch dates reliably in many species including salmonids (Radtke et al., 1996; Stevenson & Campana, 1992; Tsukamoto et al., 1989; Yamamoto et al., 1997). Although cold temperatures typically reduce increment widths, increments have been successfully used to determine fish ages in salmonids subject to near-freezing temperatures (Adams et al., 1992; Nielsen & Green, 1982; Radtke & Fey, 1996). This method readily applies to young-of-the-year (YOY) individuals collected when field sampling has become feasible, and the individuals have become large enough for efficient capture during a snow-free period.

Subarctic streams often harbour sympatric populations of native salmonids (Morita et al., 2011; Murdoch et al., 2020). Spawning time (Beechie et al., 2008; Heggberget et al., 1988) and egg incubation period (Sternecker et al., 2014) differ among sympatric salmonids, suggesting that hatch timing may also differ. However, information is scarce on inter-specific differences in hatch timing in subarctic streams. Hatch timing may also differ within species along latitudinal and elevational gradients (Coleman & Fausch, 2007; Jonsson & Jonsson, 2009). Much less is known about variation in hatch timing at finer spatial scales, although stream networks are heterogeneous environments in which abiotic factors shift abruptly, particularly at stream confluences (Benda et al., 2004).

Here, micro-increment analysis of otoliths was used to estimate daily age and infer hatch dates of two native land-locked salmonids, white-spotted charr *Salvelinus leucomaenis* (Pallas) and masu salmon *Oncorhynchus masou* (Brevoort), in a mainstem-tributary network in northern Japan. The study was conducted in one of the coldest regions of Japan, and snow cover over the stream until May precluded field sampling at the time of hatching and emergence. This necessitated otolith ageing to infer winter- and spring-time hatch dates of autumn-spawning white-spotted charr and masu salmon (Tsukamoto et al., 1989; Yamamoto et al., 1997). In northern Japan, masu salmon spawn a few weeks earlier than white-spotted charr where they occur in sympatry (Maruyama, 1981). Cumulative degree days to hatching are also shorter for masu salmon (386–440℃•day; Honjoh & Hara, 1984) than white-spotted charr (450–550℃•day; Saito et al., 1975). These suggest that distributions of hatch dates likely differ between the two sympatric salmonids occupying the study area. The field component of this study was preceded by a hatchery component using individuals with known hatch date ranges to validate age estimates and evaluate precision of age assignments among independent readers. Although otolith microstructural analysis has been applied successfully to infer hatch timing of both study species (Tsukamoto et al., 1989; Yamamoto et al., 1997), the age validation was deemed important because salmonids may deposit sub-daily increments on otoliths (Adams et al., 1992; Stevenson & Campana, 1992).

## 2 | METHODS

2.1 | Hatchery sampling

To validate daily age estimates and quantify variation among independent readers, hatchery fish with known hatch date ranges were aged. Samples were obtained from the Nikko Field Station, Fisheries Technology Institute, Japan Fisheries Research and Education Agency in Tochigi Prefecture, Japan. White-spotted charr were artificially spawned on 2 November 2018 and masu salmon were spawned on 25 October 2018 in the station, and fertilised eggs were reared in tanks where water temperature was kept at 9℃. Typical of hatchery operations, eggs were reared in single tanks and thus hatch date of each individual could not be known. Therefore, the median hatch date was estimated visually as the date in which approximately 50% of eggs had hatched in the tank. The median hatch date (i.e. known hatch date) was defined as 25 December for charr and 10 December for salmon. All fish hatched within ±1–2 week of the median hatch date. Fry were fed once daily after transition to exogenous feeding, which occurs following yolk sac absorption. Exogenous feeding began approximately 30 days after the median hatch date. On 14 March 2019, fifteen individuals of both species were euthanised and measured for body length (TL: 23.9–35.7 mm in white-spotted charr and 26.2–39.2 mm in masu salmon). All individuals were then stored in 85% ethanol solutions until processing in the laboratory.

2.2 | Field site

The field study was conducted in the mainstem of the Butokamabetsu River and its two unnamed tributaries (Trib1 and Trib2, hereafter) in the Hokkaido University Uryu Experimental Forest, Hokkaido, Japan (Figure 1). The study area was located in the subarctic region with the mean annual air temperature of 4.2℃ and annual precipitation of 1236 mm. Snow depth can reach approximately 3 m in winter (Aoyama et al., 2011), and snow cover typically extends until May. In 2018, when this study was conducted, snowmelt occurred in late April through May (Figure S1).

This study was conducted in two tributaries and a 520-m segment of the mainstem bounded by the tributaries. Trib1 was sampled along a 1-km segment, and Trib2 was sampled along a 140-m segment (Figure 1). The mainstem was approximately 10 m wide during summer base flow conditions and was wadeable except where deep pools occurred. The two tributaries were smaller in size (2 m wide each). Trib1 originated from a montane valley and transitioned into a meandering channel with fine substrates (i.e. gravel and sand) before flowing into the mainstem. Trib2 was in the floodplain of the mainstem and appeared to be a former side channel with sand and silt substrates. The upstream surface hydrological connection with the mainstem has been lost, although the connection may be re-established temporarily under extremely high-flow conditions. Trib2 contained primarily stagnant waters during summer base flow, but

FIGURE 1 Map of study area showing the mainstem Butokamabetsu River and two study tributaries (Trib1 and Trib2) in Hokkaido University Uryu Experimental Forest, northern Japan. Young-of-the-year samples were collected in the coloured segments (blue = mainstem, green = Trib1, and pink = Trib2). Lake Shumarinai is located approximately 5 km downstream of the study area, and a portion of populations of white-spotted charr and masu salmon move to Lake Shumarinai to express an adfluvial life history. Contour lines (grey) are based on a topographic map made available by the Geospatial Information Authority of Japan, the Ministry of Land, Infrastructure, Transport and Tourism
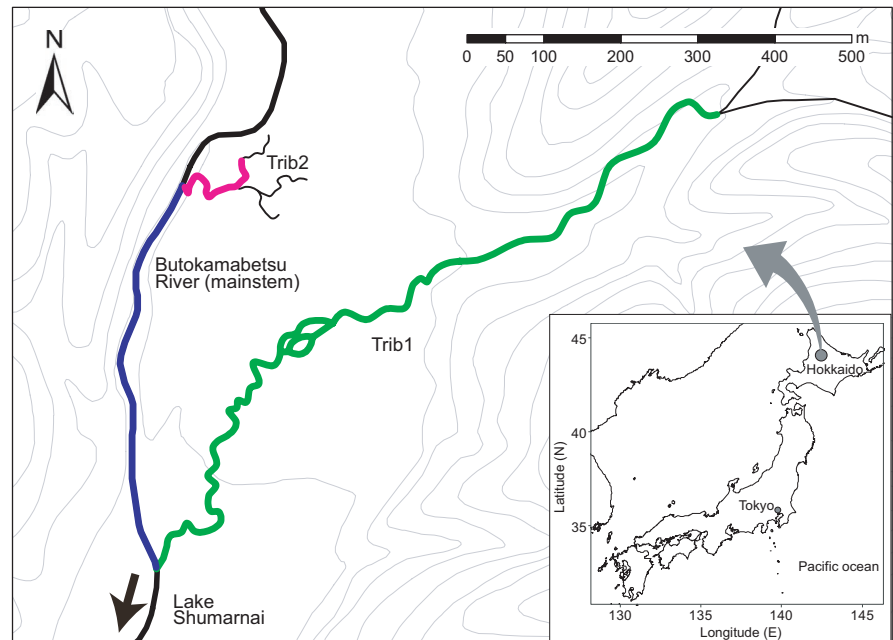
it was perennial. Daily mean water temperature ranged 4.7–13.1℃ in the mainstem, 5.6–12.4℃ in Trib1 and 5.3–14.0℃ in Trib2 from 19 May to 20 July, which covered a period beginning with peak snowmelt until YOY sample collections (measured every 30 min; Model HOBO TidbiT MX, Onset Computer Corp, Bourne, MA). Daily mean water temperature was significantly different among the three habitat locations (Repeated-measures ANOVA: F = 17.5, p < 0.001), although the small p-value may reflect large sample size (i.e. 63 days of observations).

White-spotted charr and masu salmon are native to the study area. Both species are landlocked and occur throughout the mainstem-tributary network, but YOY white-spotted charr were concentrated in Trib1 (Kanno et al., 2020). In both species, a portion of their populations (particularly females) displays an adfluvial life history (Tamate & Maekawa, 2004) by moving to Lake Shumarinai, a reservoir located 5 km downstream of the study area (Figure 1). Both species spawn in late summer and early autumn; masu salmon spawn between late-August and mid-September in the study area (Tamate & Maekawa, 2004) and white-spotted charr spawn a few weeks later. Sakhalin taimen *Parahucho perryi* (Brevoort), fluvial sculpin *Cottus nozawae* Snyder, Siberian stone loach *Barbatula toni* (Dybowski), Far Eastern brook lamprey *Lethenteron reissneri* (Dybowski) and redfin dace *Tribolodon* spp. were also collected in the study area.

2.3 | Field sampling

Young-of-the-year of both species were collected via backpack electrofishing on 22–25 July 2018. Sampling in Trib1 and Trib2 was part of a mark-recapture study (Kanno et al., 2020), in which a single backpack electrofishing unit (Model LR-24, Smith-Root Inc., Vancouver, WA) was used with pulsed direct current settings (300–400 V, 30–45 Hz and 25% duty cycle). In both tributaries,

20-m permanent sections were flagged and each section was sampled with a two-pass removal method. In Trib1, where YOY of both species were most abundant, up to three individuals of each species were randomly preserved per 20-m section to collect representative samples. In the mainstem habitat, two backpack electrofishing units were used to collect YOY. Upon capture, fish were measured for body length (TL, mm) and weight (g) and were preserved individually in an 85% ethanol solution. YOY could be readily distinguished from older individuals based on length–frequency histograms (Kanno et al., 2020), and their age in days was subsequently estimated by counting otolith increments. A total of 95 white-spotted charr and 85 masu salmon were collected in the mainstem-tributary network.

2.4 | Laboratory otolith analysis

Hatchery and wild samples were aged following Stevenson and Campana (1992). Both sagittal otoliths were removed from each individual under a low power stereo microscope (30× magnification; Model EMZ-5TR, Meiji Techno Co., Tokyo, Japan). A dissecting probe and scalpel were used to remove each sagittae from the otic capsule located at the posterior of the ventral surface of the skull (Vanderkooy et al., 2020). Otoliths were cleaned and laid flat on glass microscope slides and immersed in cyanoacrylate glue. After mounting, sagittae were first polished with 9-µm metallurgical lapping film and finished with 3-µm film until the otolith nucleus and increments were clear and readable under 30× magnification. The right-side sagittal otolith was read for age estimation unless it was damaged during the processing or otherwise hard to read. In that case, the left-side saggital otolith was read.

Polished otoliths were covered in immersion oil and viewed under a compound microscope (Carl Zeiss AZ, Jena, Germany). They were first observed using 100× magnification before enlarging to

200× magnification on the clearest transect to count increments. The view of the stage was projected onto a monitor using a camera (Excelis Model AU-600-HD) to photograph and enlarge the image of the otolith. For consistency, rings were counted along a transect at approximately 45 degrees to the longest axis of the otolith. Three readers independently counted daily increments of all hatchery fish blind of the known median age. Age estimates from three readers were averaged for each fish. Given the high precision (i.e. consistency) of age estimates among readers (see Results) and similarities of otoliths between wild and hatchery individuals (Figure S2), a single reader (K. Fitzgerald) estimated the age of all wild fish samples.

2.5 | Statistical analysis

Hatchery fish were used to evaluate accuracy and precision of age estimates. For accuracy, the median hatch date estimated from the increment counts was compared with the known median hatch date, or the date by which approximately 50% of eggs in rearing tanks hatched. Precision was quantified using the average per cent error (APE), which measures variability of age estimates among independent readers for a given otolith (Beamish & Fournier, 1981). Values of APE less than 5% are considered adequately precise for daily increment analysis of otoliths (Campana, 2001).

Welch t-tests were used to evaluate whether body length and hatch dates differed between wild white-spotted charr and masu salmon. To examine whether fish hatching earlier or later than the mean hatch date are represented equally, a Shapiro–Wilk test was used to evaluate whether distributions of hatch dates in each species deviated significantly from normal, and skewness of distributions was quantified.

Simple linear regression and Pearson correlation analyses were used to quantify the relationships between age and body length for each species taken from the wild. Welch t-tests were used to determine whether hatch dates differed among individuals collected in different habitat segments. Due to small sample sizes, this analysis compared only white-spotted charr collected in Trib1 versus Trib2, and masu salmon collected in the mainstem and Trib1. Statistical significance level was set at α = 0.05, and all analyses were conducted in Program R (R Core Team, 2020).

3 | RESULTS

3.1 | Validation with hatchery fish

Accuracy and precision of age estimates for hatchery fish read blindly were high. Of 15 individuals of each species processed, three white-spotted charr and one masu salmon were excluded from the analysis because their otoliths were damaged in the extraction or polishing process. Median estimated age based on otoliths was 79 days (hatch date: 25 December 2018) in white-spotted charr (range: 65–90 days) and 89 days (hatch date: 15 December 2018) in masu salmon (range:
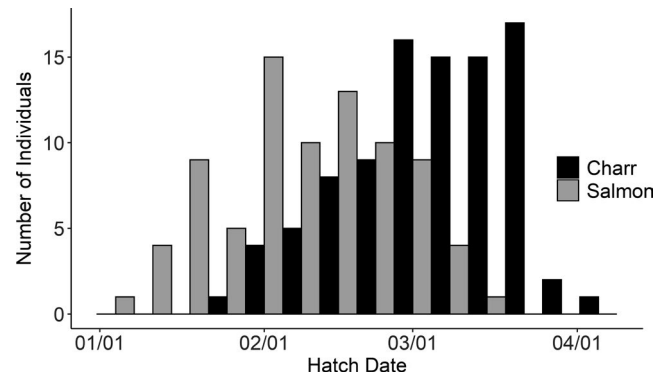

FIGURE 2 Distributions of hatch dates estimated by otoliths for white-spotted charr (N = 93) and masu salmon (N = 81)

80–105 days). For white-spotted charr, the median estimated hatch date, derived from otoliths, matched exactly with the known median hatch date based on tank observations. For masu salmon, the median estimated hatch date was 5 days later than the known median hatch date. Average per cent error across samples was 4.0% in white-spotted charr and 3.8% in masu salmon. Percentages <5% suggested that age estimates by three independent readers were repeatable (Campana, 2001).

3.2 | Ageing wild fish

Because some otoliths were damaged during preparation, 93 of 95 white-spotted charr individuals and 81 of 85 masu salmon individuals were aged. Mean total length of aged white-spotted charr was 55 mm (range: 44–67 mm), and aged masu salmon were larger at 70 mm (range: 53–87 mm). Body length differed between the species (Welch t-test: t = −15.9, p < 0.001). Age also differed significantly between species (Welch t-test: t = −9.1, p < 0.001). Mean estimated age was 141 days (range: 111–178) in white-spotted charr and 165 days (range: 135–199) in masu salmon. The mean estimated hatch date of white-spotted charr was 4 March, 24 days later than masu salmon (8 February). Distributions of hatch dates deviated significantly from normal in white-spotted charr (Shapiro-Wilk test: W = 0.97, p = 0.02), but not in masu salmon (W = 0.98, p = 0.18). Skewness was higher in white-spotted charr (0.44) than in masu salmon (0.10), and distributions of hatch dates were truncated in white-spotted charr because few late-hatching individuals were encountered (Figure 2). Hatch of white-spotted charr was estimated to be most common in March (59 individuals) followed by February (31 individuals). Only one individual hatched in April (Figure 2).

Regression analysis found significantly positive but weak relationships between age and total length in white-spotted charr (p < 0.001, adjusted r^2 = 0.26) and masu salmon (p = 0.02, adjusted r^2 = 0.06) indicating earlier-hatching individuals were larger (Figure 3). However, the high variation indicated by low adjusted r^2 values suggested that hatch date was just one factor that affected fish length. When the analysis was limited to only individuals collected in Trib1 (i.e. the same habitat from which most samples

FIGURE 3 Relationships between age in days estimated by otoliths and total length (TL) for white-spotted charr (adjusted R^2 = 0.26) and masu salmon (adjusted R^2 = 0.06). Black lines are derived using the least squares regression method with 95% confidence intervals for all samples. Colours indicate habitat segments where individuals were collected
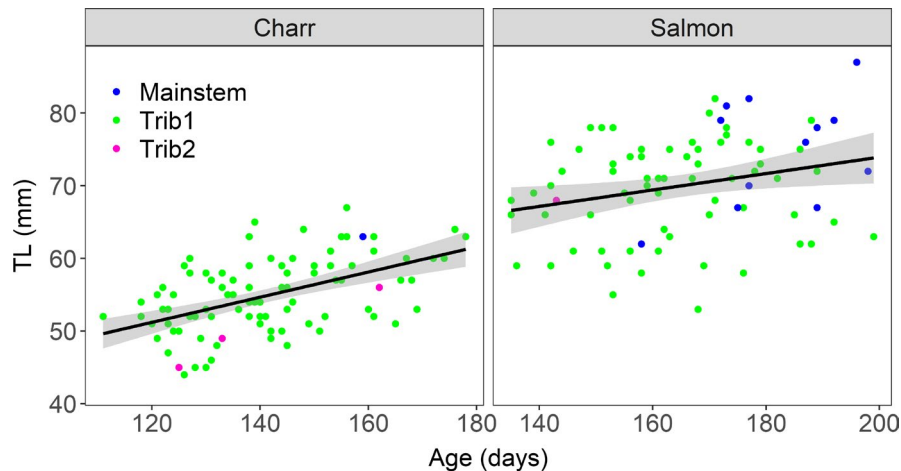

TABLE 1 Hatch dates and body length (TL) of white-spotted charr and masu salmon in the mainstem, Trib1 and Trib2, based on the increment growth analysis of otoliths

Species	Habitat	N	Mean hatch date (range)	Mean TL in mm (range)
White-spotted charr	Mainstem	1	16 February (NA)	63 (NA)
	Trib1	87	4 March (26 January–4 April)	55 (44–67)
	Trib2	5	9 March (10 February–20 March)	49 (45–56)
Masu Salmon	Mainstem	12	24 January (8 January–7 February)	75 (62–87)
	Trib1	68	11 February (7 January–12 March)	69 (53–82)
	Trib2	1	1 March (NA)	68 (NA)

Note: Samples were collected, and body length was measured in the field on 22–25 July, 2018.

were collected), age and total length were weakly positive in white-spotted charr (p < 0.001, adjusted r^2 = 0.22) but not in masu salmon (p = 0.32, adjusted r^2 < 0.01).

Mean hatch date of masu salmon was nearly 3 weeks earlier in the mainstem (24 January) than in Trib1 (11 February) (Table 1; Figure 4; Welch t-test: t = −5.2, p < 0.001). Mean hatch date of white-spotted charr collected in Trib1 and Trib2 did not differ (Welch t-test: t = −0.9, p = 0.42). Despite low sample size of white-spotted charr in the mainstem and masu salmon in Trib2, hatch dates appeared to be the earliest in the mainstem, followed by Trib1 and then Trib2 in both species (Table 1; Figure 4).

4 | DISCUSSION

High accuracy and precision of age validation for hatchery fish demonstrated that otolith increments were deposited daily, and the estimated hatch dates for wild fish are reliable at least for the comparison of hatch timing between species and among habitat segments. On average, masu salmon hatched 24 days earlier than white-spotted charr in the Butokamabetsu River system, and this likely resulted from their earlier spawning (Maruyama, 1981) and shorter cumulative degree days to hatching (Honjoh & Hara, 1984; Saito et al., 1975). Further, hatch dates also varied within species and spanned a minimum of 2 months for each species. Hatch dates of white-spotted charr in our study were a few weeks later than those of more southern populations in Japan (Yamamoto et al., 1997), reflecting the climate gradient among regions.

Distributions of hatch dates were normal in masu salmon, whereas they were truncated and deviated from normal in white-spotted charr because later-hatching individuals were absent in white-spotted charr. Only a single white-spotted charr individual was estimated to hatch after 1 April, although hatching of this species had peaked in March. Two potential reasons for this pattern are offered. First, mortality of later-hatching white-spotted charr may have been high due to high streamflows caused by snowmelt. In 2018, snowmelt started at the end of March and peaked in early- to mid-May (hydrograph in Figure S1). Snowmelt-driven high flows mobilise stream substrates, and early life stages of stream salmonids suffer high rates of mortality (Kanno et al., 2017; Kovach et al., 2016). The finding that the earlier-hatching masu salmon did not show a truncated distribution further supported this plausible mechanism because earlier hatching should have resulted in larger body size and better swimming abilities to withstand physical disturbances. Second, truncated distributions of white-spotted charr may have been a sampling artefact. Electrofishing is size-selective, and smaller individuals are typically underrepresented (Dolan & Miranda, 2003). However, this sampling bias is unlikely severe because YOY of spring-spawning Sakhalin taimen (20–30 mm TL) were captured in Trib1 during the July survey (Y. Kanno, *personal observation*), and their body size was smaller than the smallest individual of white-spotted charr collected (44 mm; Table 1). Additional research is warranted to evaluate whether early-life mortality depends on hatch date with particular reference to the timing of snowmelt-driven high streamflows.
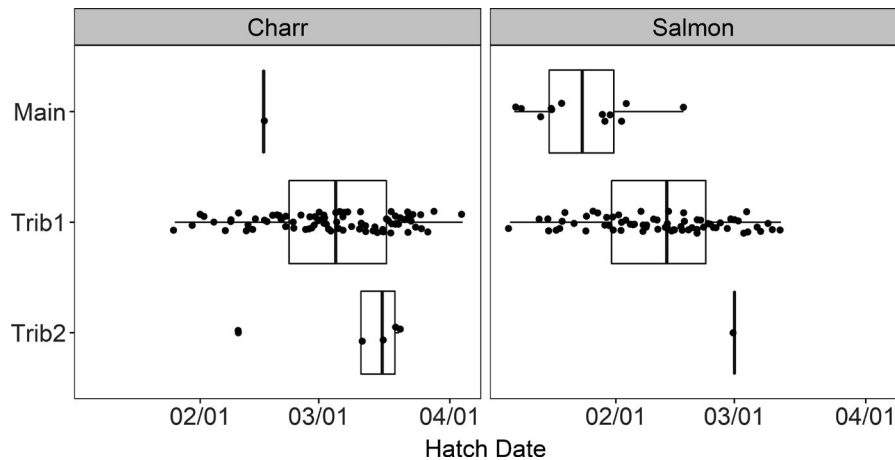
FIGURE 4 Box and whisker plots showing hatch date estimates of white-spotted charr and masu salmon collected in the mainstem, Trib1 and Trib2. Boxes indicate interquartile ranges with median shown by vertical lines inside the boxes. Whiskers extend 1.5 times the interquartile ranges from the upper and lower ends of boxes. Dots are raw data positioned to avoid overlaps. Sample size is one individual for white-spotted charr in the mainstem and masu salmon in Trib2

In masu salmon, hatch dates of individuals collected in the mainstem were nearly 3 weeks earlier than those collected in Trib1. This may be due to different spawning timing between the mainstem and tributary habitats (Henderson et al., 2000), different thermal regimes among habitats that result in heterogeneous accumulation of degree days for hatching (Uno, 2016), or both. An attempt was made to collect year-round temperature data, but data were not properly recorded due to a technical issue. Also, the available data could not distinguish whether the spatial pattern of hatch dates reflected true differences in hatch timing among habitats or is due to post-hatching movement of individuals. Propensity of fish to move downstream after hatching has been documented in masu salmon (Nagata et al., 1994), and it is possible that hatch timing is consistent among habitats but earlier-hatching individuals since moved to the mainstem. Natal origin and fidelity of early life stages can be investigated using genetic parentage and sibship assignments (Kanno et al., 2014) or otolith microchemistry (Heckel et al., 2020; Smith et al., 2011). An integrative approach using multiple methods is needed to understand spatial variation in hatch timing in the stream networks more fully. Spatial variation in population vital rates, including survival and growth, is also common in the mainstem-tributary networks (Letcher et al., 2015; Tsuboi et al., 2020), and a fuller understanding of how these demographic mechanisms and hatch timing differ by space is needed to explain why distributions of life stages and body size change in stream networks (Ebersole et al., 2009; Kanno et al., 2012).

Hatch date was only a weak predictor of summer-time body size in both study species, unlike previous studies (Tsukamoto et al., 1989; Yamamoto et al., 1997). Body size differed among individuals that shared the same hatch dates (Figure 3), and the result was similar when comparing body size and hatch dates among individuals from the same habitat (Trib1), which had the largest sample size (Table 1). These results suggested that body growth rates differed among individuals due to factors such as competition for food resources and inherent differences in metabolic rates (Grant & Imre, 2005; Metcalfe, 1986; Yamamoto et al., 1998), or individual variation in body size and energy reserves at hatch (Barneche et al., 2018; Jonsson & Jonsson, 1999). Water temperature can change within stream segments due to surface-groundwater interactions (Lowry

et al., 2007), which may also contribute to variation in somatic growth rates, otolith increment widths and periodicity of increment deposition (Radtke & Fey, 1996; Wright et al., 1990). Distributions of body size at early life stages may be maintained throughout subsequent life stages in stream salmonids (Letcher et al., 2011), and future work should investigate factors affecting initial size distributions at early life stages.

Otolith size and increment widths were not measured, but they might yield further insight as to why body size did not depend strongly on hatch date here. Differences in somatic growth may be reflected in otoliths where greater food availability and faster growth increase increment widths (Limm & Marchetti, 2009; Radtke & Fey, 1996; Wright et al., 1990; Yamamoto et al., 1998). Thus, increment width and otolith diameter may provide richer insights to early life history growth trajectories than the number of increments alone. However, otolith and somatic growth rates may become decoupled where an environmentally induced cessation of somatic growth is not accompanied by decreased growth in otoliths (Marshall & Parker, 1982; Wright et al., 1990). Future research should investigate the degree of linkage between somatic and otolith growth rates for fish in the subarctic, where stream ecosystems experience a rapid and major seasonal shift from spring to summer following snowmelt (Tockner et al., 2000).

Climate patterns in the arctic and subarctic regions are changing rapidly, with consequences on fisheries resources and their management (Murdoch et al., 2020). Earlier spring will likely affect early life stages of stream salmonids, but its mechanisms are potentially complex. If the timing of high streamflows due to snowmelt is indeed a key determinant of YOY recruitment (Kovach et al., 2016), climate change may negatively affect it by advancing the annual timing of high-flow events earlier and later-hatching species (i.e. white-spotted charr) or individuals may suffer higher mortality rates. At the same time, a warmer climate will accelerate hatch by reaching cumulative degree days earlier, and reduced snowpack may dampen the magnitude of high streamflows that mobilise stream substrate. Thus, impacts of climate change on YOY recruitment will depend on the interplay of these counteracting factors. Long-term monitoring of fisheries resources and abiotic conditions is crucial for understanding climate change impacts, and otolith increment analysis provides

a useful tool for documenting spatiotemporal changes in distributions of hatch timing.

Finally, two other management implications are highlighted from this study. First, the different timing of hatch between the two salmonids (i.e. 24 days apart on average) indicates that their early life stages may experience different effects of spring-time high stream flows (Kovach et al., 2016). This can lead to different recruitment patterns among sympatric species (Kanno et al., 2017), and where opportunities to manage flow exist (e.g. dams), high-flow events could be timed to favour early life stages of some species over others (Kiernan et al., 2012). Second, fish populations in a heterogeneous riverscape are more resistant and resilient in the face of disturbances (McCluney et al., 2014). Spatial variation in hatch timing in the mainstem-tributary network is yet another factor that generates spatially structured population dynamics. As the anthropogenic footprint on stream ecosystems increases, maintaining stream habitat heterogeneity and connectivity of riverscapes becomes more critical in conserving stream fishes (Fausch et al., 2002).

ORCID

Matt R. Haworth https://orcid.org/0000-0001-9363-7104
Kevin R. Bestgen https://orcid.org/0000-0001-8691-2227
Collin J. Farrell https://orcid.org/0000-0001-7591-6775
Shunsuke Utsumi https://orcid.org/0000-0003-1558-8073
Osamu Kishida https://orcid.org/0000-0002-2663-8155
Hiromi Uno https://orcid.org/0000-0002-9343-3061
Yoichiro Kanno https://orcid.org/0000-0001-8452-5100

REFERENCES

Adams, C.E., Murray, K.R. & Huntingford, F.A. (1992) The periodicity of primary increment formation in the otoliths of Arctic charr *Salvelinus alpinus* (L.). *Journal of Fish Biology*, 41, 515–520. https://doi.org/10.1111/j.1095-8649.1992.tb02679.x

Aoyama, K., Yoshida, T., Harada, A., Noguchi, M., Miya, H. & Shibata, H. (2011) Changes in carbon stock following soil scarification of non-wooded stands in Hokkaido, northern Japan. *Journal of Forest Research*, 16, 35–45. https://doi.org/10.1007/s10310-010-0204-y

Barneche, D.R., Robertson, D.R., White, C.R. & Marshall, D.J. (2018) Fish reproductive-energy output increases disproportionately with body size. *Science*, 360, 642–645. https://doi.org/10.1126/science.aao6868

Beamish, R.J. & Fournier, D.A. (1981) A method for comparing the precision of a set of age determinations. *Canadian Journal of Fisheries and Aquatic Sciences*, 38, 982–983. https://doi.org/10.1139/f81-132

Beechie, T., Moir, H. & Pess, G. (2008) Hierarchical physical controls on salmonid spawning location and timing. In: Sear, D. & DeVries, P. (Eds.) *Salmonid spawning habitat in rivers: Physical controls, biological responses, and approaches to remediation*. Bethesda: American Fisheries Society, pp. 83–101.

Benda, L., Poff, N.L., Miller, D., Dunne, T., Reeves, G., Pess, G. et al. (2004) The network dynamics hypothesis: How channel networks structure riverine habitats. *BioScience*, 54, 413–427. 10.1641/0006-3568(2004)054[0413:TNDHHC]2.0.CO;2

Blanchet, S., Loot, G., Bernatchez, L. & Dodson, J.J. (2008) The effects of abiotic factors and intraspecific versus interspecific competition on the diel activity patterns of Atlantic salmon (*Salmo salar*) fry. *Canadian Journal of Fisheries and Aquatic Sciences*, 65, 1545–1553. https://doi.org/10.1139/F08-079

Campana, S.E. (2001) Accuracy, precision and quality control in age determination, including a review of the use and abuse of age validation method. *Journal of Fish Biology*, 59, 197–242. https://doi.org/10.1006/jfbi.2001.1668

Coleman, M.A. & Fausch, K.D. (2007) Cold summer temperature limits recruitment of age-0 cutthroat trout in high-elevation Colorado streams. *Transactions of the American Fisheries Society*, 136, 1231–1244. https://doi.org/10.1577/T05-244.1

Dolan, C.R. & Miranda, L.E. (2003) Immobilization thresholds of electrofishing relative to fish size. *Transactions of the American Fisheries Society*, 132, 969–976. https://doi.org/10.1577/T02-055

Ebersole, J.L., Colvin, M.E., Wigington, P.J., Jr., Leibowitz, S.G., Baker, J.P., Church, M.R. et al. (2009) Hierarchical modeling of late-summer weight and summer abundance of juvenile coho salmon across a stream network. *Transactions of the American Fisheries Society*, 138, 1138–1156. https://doi.org/10.1577/T07-245.1

Fausch, K.D., Torgersen, C.E., Baxter, C.V. & Li, H.W. (2002) Landscapes to riverscapes: bridging the gap between research and conservation of stream fishes. *BioScience*, 52, 483–498. 10.1641/0006-3568(2002)052[0483:LTRBTG]2.0.CO;2

Grant, J.W.A. & Imre, I. (2005) Patterns of density-dependent growth in juvenile stream-dwelling salmonids. *Journal of Fish Biology*, 67, 100–110. https://doi.org/10.1111/j.1095-8649.2005.00916.x

Heckel, J.W., Quist, M.C., Watkins, C.J. & Dux, A.M. (2020) Life history structure of westslope cutthroat trout: inferences from otolith microchemistry. *Fisheries Research*, 222, 105416. https://doi.org/10.1016/j.fishres.2019.105416

Heggberget, T.G., Haukebø, T., Mork, J. & Ståhl, G. (1988) Temporal and spatial segregation of spawning in sympatric populations of Atlantic salmon, *Salmo salar* L., and brown trout, *Salmo trutta* L. *Journal of Fish Biology*, 33, 347–356. https://doi.org/10.1111/j.1095-8649.1988.tb05477.x

Henderson, R., Kershner, J.L. & Toline, C.A. (2000) Timing and location of spawning by nonnative wild rainbow trout and native cutthroat trout in the South Fort Snake River, Idaho, with implications for hybridization. *North American Journal of Fisheries Management*, 20, 584–596. 10.1577/1548-8675(2000)020<0584:TALOSB>2.3.CO;2

Honjoh, T. & Hara, T. (1984) *Aquaculture of masu salmon and red-spotted masu Salmon*. Japan: Midori Shobo (In Japanese).

Jonsson, B. & Jonsson, N. (2009) A review of the likely effects of climate change on anadromous Atlantic salmon *Salmo salar* and brown trout *Salmo trutta*, with particular reference to water temperature and flow. *Journal of Fish Biology*, 75, 2381–2447. https://doi.org/10.1111/j.1095-8649.2009.02380.x

Jonsson, N. & Jonsson, B. (1999) Trade-off between egg mass and egg number in brown trout. *Journal of Fish Biology*, 55, 767–783. https://doi.org/10.1111/j.1095-8649.1999.tb00716.x

Kanno, Y., Kulp, M.A., Moore, S.E. & Grossman, G.D. (2017) Native brook trout and invasive rainbow trout respond differently to seasonable weather variation: spawning timing matters. *Freshwater Biology*, 62, 868–879. https://doi.org/10.1111/fwb.12906

Kanno, Y., Letcher, B.H., Coombs, J.A., Nislow, K.H. & Whiteley, A.R. (2014) Linking movement and reproductive history of brook trout to assess habitat connectivity in a heterogeneous stream network. *Freshwater Biology*, 59, 142–154. https://doi.org/10.1111/fwb.12254

Kanno, Y., Vokoun, J.C., Holsinger, K.E. & Letcher, B.H. (2012) Estimating size-specific brook trout abundance in continuously sampled headwater streams using Bayesian mixed models with zero inflation and overdispersion. *Ecology of Freshwater Fish*, 21, 404–419. https://doi.org/10.1111/j.1600-0633.2012.00560.x

Kanno, Y., Yui, N., Mamiya, W., Sakai, R., Yabuhara, Y., Miyazaki, T. et al. (2020) A multistate mark-recapture approach to characterize stream fish movement at multiple spatial scales. *Canadian Journal of Fisheries and Aquatic Sciences*, 77, 1090–1100. https://doi.org/10.1139/cjfas-2019-0329

Kiernan, J.D., Moyle, P.B. & Crain, P.K. (2012) Restoring native fish assemblages to a regulated California stream using the natural flow regime concept. *Ecological Applications*, 22, 1472–1482. https://doi.org/10.1890/11-0480.1

Kovach, R.P., Muhlfeld, C.C., Al-Chokhachy, R., Dunham, J.B., Letcher, B.H. & Kershner, J.L. (2016) Impacts of climate variation on trout: a global synthesis and path forward. *Reviews in Fish Biology and Fisheries*, 26, 135–151. https://doi.org/10.1007/s11160-015-9414-x

Letcher, B.H., Coombs, J.A. & Nislow, K.H. (2011) Maintenance of phenotypic variation: repeatability, heritability and size-dependent processes in a wild brook trout population. *Evolutionary Application*, 4, 602–615. https://doi.org/10.1111/j.1752-4571.2011.00184.x

Letcher, B.H., Schueller, P., Bassar, R.D., Nislow, K.H., Coombs, J.A., Sakrejda, K. et al. (2015) Robust estimates of environmental effects on population vital rates: an integrated capture-recapture model of seasonal brook trout growth, survival and movement in a stream network. *Journal of Animal Ecology*, 84, 337–352. https://doi.org/10.1111/1365-2656.12308

Limm, M.P., & Marchetti, M.P. (2009). Juvenile Chinook salmon (*Oncorhynchus tshawytscha*) growth in off-channel and main-channel habitats on the Sacramento River, CA using otolith increment widths. *Environmental Biology of Fishes*, 85, 141–151. http://doi.org/10.1007/s10641-009-9473-8

Lowry, C.S., Walker, J.F., Hunt, R.J. & Anderson, M.P. (2007) Identifying spatial variability of groundwater discharge in a wetland stream using a distributed temperature sensor. *Water Resource Research*, 43, W10408. https://doi.org/10.1029/2007WR006145

Marshall, S.L. & Parker, S.S. (1982) Pattern identification in the microstructure of sockeye salmon (*Oncorhynchus nerka*) otoliths. *Canadian Journal of Fisheries and Aquatic Sciences*, 39, 542–547. https://doi.org/10.1139/f82-077

Maruyama, T. (1981) Comparative ecology on the fluvial forms of *Salmo (Oncorhynchus) masou* (Brevoort) and *Salvelinus leucomaenis* (Pallas) (Pisces, Salmonids). I. Structure of spawning redds and spawning sites in Kamidani. *River Yura. Japanese Journal of Ecology*, 31, 269–284 (In Japanese with English abstract.).

McCluney, K.E., Poff, N.L., Palmer, M.A., Thorp, J.H., Poole, G.C., Williams, B.S. et al. (2014) Riverscape macrosystems ecology: sensitivity, resistance, and resilience of whole river basins with human

alterations. *Frontiers in Ecology and the Environment*, 12, 48–58. https://doi.org/10.1890/120367

Metcalfe, N.B. (1986) Intraspecific variation in competitive ability and food intake in salmonids: consequences for energy budgets and growth rates. *Journal of Fish Biology*, 28, 525–531. https://doi.org/10.1111/j.1095-8649.1986.tb05190.x

Morita, K., Morita, S.H. & Nagasawa, T. (2011) Seasonal changes in stream salmonid population densities in two tributaries of a boreal river in northern Japan. *Ichthyological Research*, 58, 134–142. https://doi.org/10.1007/s10228-010-0201-3

Murdoch, A., Mantyka-Pringle, C. & Sharma, S. (2020) Impacts of co-occurring environmental changes on Alaskan stream fishes. *Freshwater Biology*, 65, 1685–1701. https://doi.org/10.1111/fwb.13569

Nagata, M., Nakajima, M. & Fujiwara, M. (1994) Dispersal of wild and domestic masu salmon fry (*Oncorhynchus masou*) in an artificial channel. *Journal of Fish Biology*, 45, 99–109. https://doi.org/10.1111/j.1095-8649.1994.tb01289.x

Nielsen, J.D. & Green, G.H. (1982) Otoliths of Chinook salmon (*Oncorhynchus tshawytscha*): daily growth increments and factors influencing their production. *Canadian Journal of Fisheries and Aquatic Sciences*, 39, 1340–1347. https://doi.org/10.1139/f82-180

Peterson, D.P., Fausch, K.D. & White, G.C. (2004) Population ecology of an invasion: Effects of brook trout on native cutthroat trout. *Ecological Applications*, 14, 754–772. https://doi.org/10.1890/02-5395

R Core Team (2020) *R: A language and environment for statistical computing.* Vienna, Austria: R Foundation for Statistical Computing.

Radtke, R.L. & Fey, D.P. (1996) Environmental effects on primary increment formation in the otoliths of newly-hatched Arctic charr. *Journal of Fish Biology*, 48, 1238–1255. https://doi.org/10.1111/j.1095-8649.1996.tb01818.x

Radtke, R.L., Fey, D.P., DeCicco, A.F. & Montgomery, A. (1996) Otolith microstructure in young-of-the-year Dolly Varden, *Salvelinus malma*, from American and Asian populations: resolution of comparative life history characteristics. *Arctic Institute of North America*, 49, 162–169. https://doi.org/10.14430/arctic1194

Saito, K., Kumazaki, T. & Tachikawa, W. (1975) Studies on the reproduction of Japanese common charr, *Salvelinus pluvius. Report of Gifu Prefectural Fisheries Experimental Station*, 21, 67–70 (In Japanese.).

Smith, N.G., Sullivan, P.J. & Rudstam, L.G. (2011) Using otolith microstructure to determine natal origin of Lake Ontario Chinook salmon. *Transactions of the American Fisheries Society*, 135, 908–914. https://doi.org/10.1577/T05-079.1

Sternecker, K., Denic, M. & Geist, J. (2014) Timing matters: species-specific interactions between spawning time, substrate quality, and recruitment success in three salmonid species. *Ecology and Evolution*, 4, 2749–2758. https://doi.org/10.1002/ece3.1128

Stevenson, D.K. & Campana, S.E. (1992) *Otolith microstructure examination and analysis.* Ottawa, ON: Canada Special Publication of Fisheries and Aquatic Sciences, p. 117.

Tamate, T. & Maekawa, K. (2004) Female-biased mortality rate and sexual size dimorphism of migratory masu salmon, *Oncorhynchus masou. Ecology of Freshwater Fish*, 13, 96–103. https://doi.org/10.1111/j.1600-0633.2004.00043.x

Tockner, K., Malard, F. & Ward, J.V. (2000) An extension of the flood pulse concept. *Hydrological Processes*, 14, 2861–2883. 10.1002/1099-1085(200011/12)14:16/17<2861:AID-HYP124>3.0.CO;2-F

Tsuboi, J., Morita, K., Koseki, Y., Endo, S., Sahashi, G., Kishi, D. et al. (2020) Spatial covariation of fish population vital rates in a stream network. *Oikos*, 129, 924–937. https://doi.org/10.1111/oik.07169

Tsukamoto, K., Seki, Y., Oba, T., Oya, M. & Iwahashi, M. (1989) Application of otolith to migration study of salmonids. *Physiology and Ecology Japan*, 1, 119–140.

Uno, H. (2016) Stream thermal heterogeneity prolongs aquatic-terrestrial subsidy and enhances riparian spider growth. *Ecology*, 97, 2547–2553. https://doi.org/10.1002/ecy.1552

Vanderkooy, S., Carroll, J., Elzey, S., Gilmore, J. & Kipp, J. (2020) *A practical handbook for determining the ages of Gulf of Mexico and Atlantic coast fishes*, 3rd edition, Ocean Springs, MS: Gulf States Marine Fisheries Commission Publication Number 300.

Wright, P.J., Metcalfe, N.B. & Thorpe, J.E. (1990) Otolith and somatic growth rates in Atlantic salmon parr, *Salmo salar* L: evidence against coupling. *Journal of Fish Biology, 36*, 241–249. https://doi.org/10.1111/j.1095-8649.1990.tb05599.x

Yamamoto, S., Shinomi, H. & Goto, A. (1997) The effect of birth date on growth of juvenile white-spotted charr *Salvelinus leucomaenis. Fisheries Science, 63*, 931–933. https://doi.org/10.2331/fishsci.63.931

Yamamoto, T., Ueda, H. & Higashi, S. (1998) Correlation among dominance status, metabolic rate and otolith size in masu salmon. *Journal of Fish Biology, 52*, 281–290. https://doi.org/10.1111/j.1095-8649.1998.tb00799.x

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.