



High rates of consecutive spawning and precise homing in Sakhalin taimen (*Parahucho perryi*)

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Abstract The frequency of reproduction and homing success are crucial in determining the lifetime reproductive fitness of iteroparous salmonids. We examined consecutive spawning and homing by Sakhalin taimen (*Parahucho perryi*), one of the least-studied iteroparous salmonids. The average consecutive return rate was 69.5%, the highest ever reported for an iteroparous salmonid. The consecutive return rates were highest for large spawners, females, and individuals with active inter-tributary movements in the preceding year. We estimated tributary-scale repeat homing rates to be 50–87%, which was significantly higher than expected by chance alone. The repeat homing rates were higher for spawners that entered tributaries with more abundant spawners in the preceding year, which is consistent with the pheromone hypothesis because the abundance of spawners in a tributary is expected to correlate to the concentration of chemical homing cues emanating from offspring in the following year. These extremely high consecutive return and homing rates likely facilitated local adaptation over evolutionary time scales and have contributed to population stability in this river system. These same traits, however, may impede species recov-

ery following habitat restoration efforts within the species historic range (e.g. dam barrier removal or improved passage) due to their limited rate of dispersal.

Keywords Sakhalin taimen · *Parahucho perryi* · Iteroparity · Repeat spawning · Homing · PIT tagging

Introduction

Repeat homing by iteroparous salmonids ensures that spawners find mates and that offspring survive in a proven, favorable habitat for incubation and juvenile rearing, thereby maximizing reproductive success and sustaining population-specific adaptations to that habitat (Lindsey et al. 1959; Leggett 1977; Binder et al. 2016). Unlike the semelparous Pacific salmon (genus *Oncorhynchus*), iteroparous salmonids can maximize their lifetime reproductive success (Bull and Shine 1979) by adjusting, for example, the timing and frequency of reproduction (Dutil 1986; Jonsson et al. 1991; Haraldstad et al. 2018) and seaward migration by adults and post-spawners (Bond et al. 2015; Gallagher et al. 2018). Repeat homing—the return of adults to spawn in subsequent breeding seasons at the location of previous spawning (McCleave 1967)—has been observed in a variety of species such as brook trout *Salvelinus fontinalis* (O'Connor and Power 1973), Arctic charr *S. alpinus* (Dutil 1986), Dolly Varden *S. malma* (Armstrong 1974), lake trout *S. namaycush* (Binder et al. 2016), brown/sea trout *Salmo trutta* (Shearer 1955; Tilzey 1977; Haraldstad et al. 2018), Atlantic

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salmon *Salmo salar* (Fleming 1998), rainbow trout/steelhead *Oncorhynchus mykiss* (Lindsey et al. 1959; Leider et al. 1986; Keefer et al. 2008), and cutthroat trout *O. clarkii* (McCleave 1967). However, relatively few studies have examined specific schedules of spawning migrations, the potential influence of prior spawning experience, and homing precision after a maiden spawn.

Sakhalin taimen (*Parahucho perryi*) is one of the largest, least studied, and most ancient salmonid species (Holčík et al. 1988). Listed in the IUCN Red List as Critically Endangered (Rand 2006), the species is currently found in about a dozen river systems in Hokkaido, Japan, and in rivers in the Russian Far East; there are at least 36 river systems in Japan where populations have been extirpated (Fukushima et al. 2011). It is a long-lived (>25 yr), spring-spawning, and iteroparous species that sexually matures at ages 7–8 (Zolotukhin et al. 2000). Populations may be resident, land-locked, or anadromous (Zimmerman et al. 2012). Age at first seaward migration ranges widely from 2 yr to >10 yr (Suzuki et al. 2011; Fukushima et al. 2019). Anadromous populations, however, out-migrate no farther than estuaries or a few kilometers from river mouths (Edo et al. 2005; Honda et al. 2010). After arriving in estuaries, adults spend most of their lives in brackish water and only return to fresh water during spawning migrations (Suzuki et al. 2011).

We investigated for the first time consecutive spawning and repeat homing by Sakhalin taimen in a river system in Hokkaido, Japan during a three year period. Our objectives were to (1) obtain biological data on Sakhalin taimen spawners including fish size, sex ratio, and spawning life (i.e., time spent on spawning grounds); (2) estimate the rate of consecutive spawning; (3) estimate the rate of repeat homing to tributaries; and (4) identify biological, behavioral, and environmental factors influencing consecutive spawning and repeat homing at the river and tributary scales, respectively. Lastly, we discuss the conservation implications of the homing ability in Sakhalin taimen.

Methods

Study area

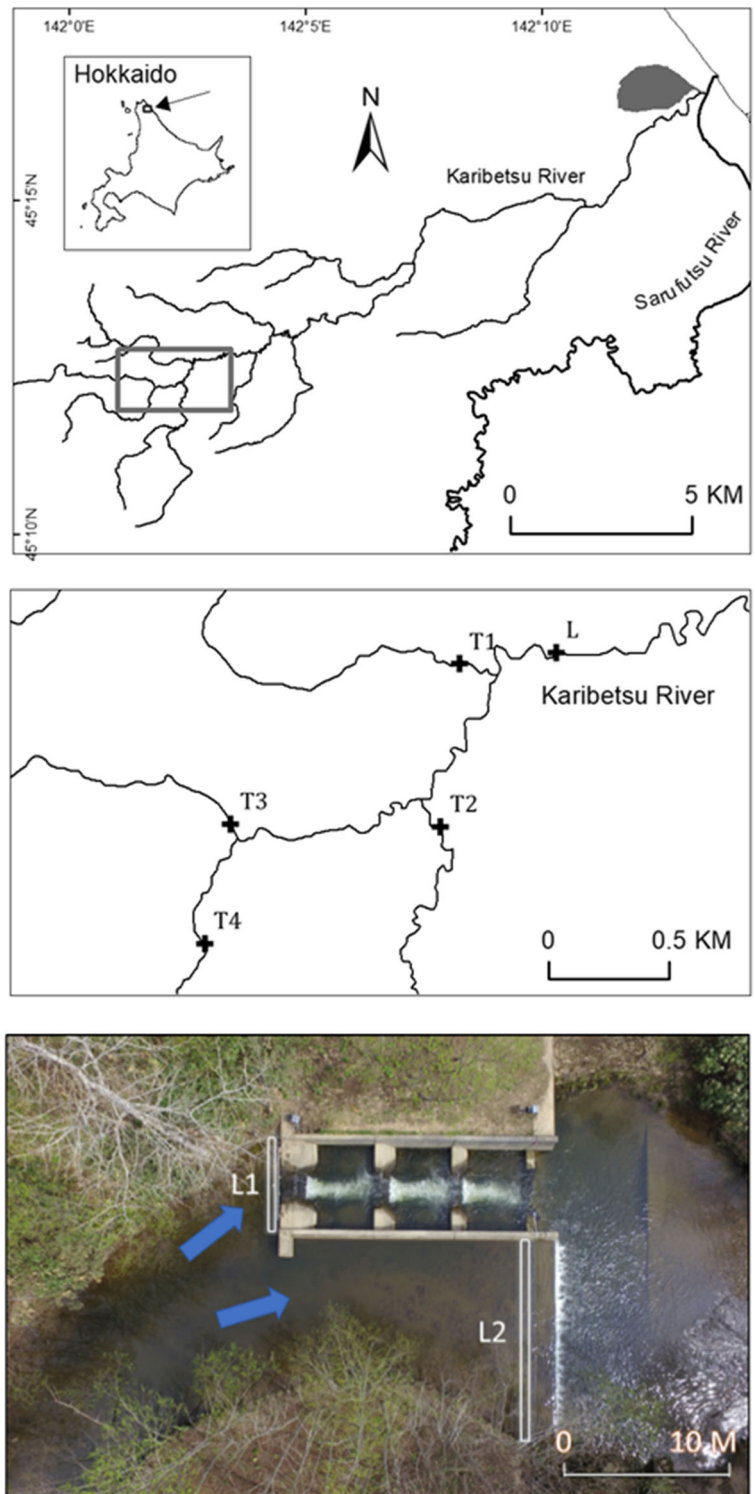
The Karibetsu River (watershed area = 83 km²) is the largest tributary of the Sarufutsu River (361 km²) and

empties into the outlet of a coastal lagoon near the Sarufutsu River mouth (Fig. 1a). Both rivers drain relatively pristine, gently sloping hills of 300–400 m in elevation that are densely vegetated with conifers and deciduous trees with dwarf bamboo (*Sasa* spp.) dominating the forest floor. Sakhalin taimen in the Sarufutsu River system are anadromous (Fukushima et al. 2019); adults are frequently captured in coastal set-nets near the river mouth (Edo et al. 2005; Suzuki et al. 2011). The Karibetsu River supports the runs of 335–425 Sakhalin taimen spawners each spring (Rand and Fukushima 2014), which is roughly one third of the entire spawning population of the species in the Sarufutsu River system (Fukushima 2001). The precise estimates of spawner counts in the previous studies and efficient PIT detection in this study were made possible largely due to the existence of a check dam (12-m wide across spillway, ~1.5-m elevation drop) constructed to control sediment load, and an associated 3-step fish ladder (15-m long, 5-m wide) through which all the up-migrating spawners pass (Fig. 1c). Other salmonids inhabiting the rivers include chum salmon (*O. keta*), pink salmon (*O. gorbuscha*), masu salmon (*O. masou*), and white-spotted char (*S. leucomaenis*), all of which exhibit anadromous life histories in the study area as well.

PIT detection system

Five PIT detection sites were established throughout the upper Karibetsu River (Fig. 1b). At the lowermost Site L, two PIT antennas were installed to cover the entire width of the mainstream (Fig. 1c): swim-through antenna L1 was installed at the upstream end of the fish ladder to detect up-migrants as well as down-migrating post-spawners, and swim-over antenna L2 was installed across the spillway of the check dam to detect post-spawners (Zydlowski et al. 2006). A single swim-through antenna was installed in each of 4 tributaries T1, T2, T3, and T4, near their confluences with the Karibetsu mainstream (Fig. 1b, Table 1). Hereafter, the same codes T1–T4 will also refer to detection sites or antennas in these tributaries. Antennas to detect half duplex PIT tags used in this study were constructed of 12-gauge, nylon-coated, stranded copper electrical wire housed in plastic tubing in the form of a loop. For the swim-over design, the entire loop was secured to the benthos. The swim-through design involved securing the lower loop to the benthos and supporting the upper loop just above the stream surface with ropes or cross-

Fig. 1 Map of the Karibetsu and Sarufutsu rivers. The grey rectangle is the area enlarged below (a). Locations of PIT detection systems (T1–T4 and L) installed in the Karibetsu River (b). Two antennas, L1 and L2, installed at Site L at the fish ladder and spillway, respectively (c)



channel pipes. Antennas were connected to a tuner and then to a reader (Oregon RFID, Portland, OR, USA), in which PIT signals that were scanned every 0.2 s while a tagged fish was inside the detection range were continuously recorded. The whole system was powered with two 12-V deep cycle marine batteries (ACDelco, Grand Blanc, MI, USA) connected in parallel, which were replaced every other day. All equipment was stored in a plastic, waterproof box, which was placed on the bank ~1 m above ground to prevent submersion during floods. The PIT signals recorded were wirelessly transferred using Bluetooth connection to a tablet PC on a daily basis. The detection systems were operated during two springs in 2018 (13 April – 8 May) and 2019 (11 April – 12 May). A marker tag, which was programmed to expose itself to the detection system every 15 min, was attached to each antenna to ensure that the systems were operational throughout these periods.

The PIT detection efficiency of antenna L1 was approximated by the number of up-migrating fish detected by this antenna divided by the total number of fish detected by any antennas in our array. Detection efficiency for antenna L2 could not be estimated because there were no reference detection records to compare to this antenna. The detection efficiencies of the tributary antennas T1–T4 were approximated as $(N_i + n_i)/2N_i$, where n_i is the number of fish that were detected on multiple passage events in tributary i and N_i is the total number of fish detected in that tributary, including n_i fish, regardless of the number of passage events. A tributary antenna was expected to detect each fish at least on two separate passage events when fish first entered the tributary, and a subsequent detection when the fish departed from the tributary. For identifying discrete passage events, a threshold of 7 s was established. High frequency detections (detections occurring at a frequency of less than 7 s) were grouped

together to represent a single passage event, while detections separated by a longer period of time (ranging from 3.6 h to 13 d, mean = 5.2 d) were considered distinct passage events. The 7 s time span is transient enough to encompass a single fish passage related to entry into or departure from a spawning tributary.

Fish sampling and tagging

Adult Sakhalin taimen were captured from pools below each step of the fish ladder using one cast net (mesh size 48 mm, 5.2 kg) at a time as the fish ascended through Site L (Fig. 1c) during the 2016, 2017, and 2018 migration periods. We believe there was no bias in the size or sex of fish captured with this method because, even though large males were more visible in clear water, fish sampling was conducted mostly during high flows with extremely poor visibility. While fish sampling in the first two years was preliminary with limited effort, the 2018 sampling was more thorough, covering the entire migration period and capturing a greater number of fish than previous years. Site L is located 22 river km upstream from the Sarufutsu River mouth and marks the approximate lower boundary of the species' spawning grounds in the Karibetsu watershed (Fukushima 2001). Thus, we defined spawning life of a given PIT-tagged fish as the period between the first and the last detections at this site.

Captured fish were anaesthetized using ~30 ppm eugenol solution (FA100, Pharma Animal Health Co., Ltd., Osaka, Japan), measured for fork length to the nearest 0.5 cm, sexed based on male nuptial body color characteristics, and tagged. The fish were internally tagged by surgically implanting a 23-mm PIT tag beneath the skin near the dorsal fin base and then released within an hour ~50 m upstream from Site L (i.e., above the dam), where they recovered from anesthesia in a holding pen. No mortality of captured fish was observed after tagging and release.

Data analysis

During the 2018 sampling season, we recaptured four fish tagged in 2016 or 2017. Using fork length measurements from the initial capture and recapture, we estimated an average growth rate of $24.7 \pm 1.3 \text{ mm}\cdot\text{yr}^{-1}$. Then, we used this estimate to predict fork lengths as of spring 2018 for individuals tagged in either 2016 or 2017 and detected in 2019, but not recaptured (and thus not re-

Table 1 PIT detection sites in the Karibetsu River

Site	Stream width (m)	Elevation (m)	Watershed area (km ²)	Distance (m)
L	17.6	25	24.72	0
T1	6.7	28	6.50	792
T2	8.4	32	8.78	1603
T3	3.7	38	2.96	2895
T4	5.9	43	5.83	3526

Distance was measured along river reaches from Site L

measured) in 2018. Hereafter, reported fish sizes refer to fork lengths observed in or predicted as of spring 2018.

Consecutive spawning or return was defined as individuals returning to the Karibetsu River to spawn during the two springs of 2018 and 2019 when PIT detection systems were operational. Specifically, adults detected by any antennas in both years were considered consecutive spawners at the river scale. Skip-year spawning can be defined as individuals that were captured and tagged before 2018, not detected in 2018, but detected in 2019. We did identify a few such individuals but could not evaluate them critically due to small sample sizes of both tag releases and detections. Also, individuals that strayed to other river systems including the Sarufutsu mainstream could not be tracked for this analysis because we did not install PIT detection systems outside the Karibetsu River.

Repeat homing and straying at the tributary scale were defined as individuals returning to the same tributary of the Karibetsu River during the 2 years (homed) or returning to different tributaries in the second year (strayed). Therefore, only consecutive spawners were included in the analysis of homing and straying. We could not confirm the natal origins of our PIT-tagged fish; hence, the term ‘repeat homing’ was used instead of ‘natal homing’ (sensu McCleave 1967). While determining whether a spawner repeatedly homed to the same tributaries or strayed into different tributaries was straightforward for most individuals, it was not the case for some individuals who returned to multiple tributaries in one or both years. An individual could be considered homed if it entered one tributary first before moving to another in 2018 and returned in 2019 to the tributary it first entered in 2018 (first-first, or FF). It could also be considered homed if it entered one tributary first in 2018 and entered the same tributary last (i.e., after entering another) in 2019 (first-last, or FL). Similarly, two other homing scenarios are possible: an individual could be considered homed if it entered one tributary last in 2018 and entered the same tributary first (last-first, or LF) or last (last-last, or LL) in 2019. For example, if a spawner returned to a single tributary of T1 in 2018 and two tributaries, first T1 and then T2, in 2019, we considered that this individual homed in both FF and LF scenarios but strayed in either the FL or LL scenario. Note that T1 in 2018 was treated as both the first and last tributary. Pearson’s chi-squared test was used to test if spawners returned to their home tributaries significantly more often than would be expected by chance alone.

Logistic regression analysis was performed to identify factors associated with consecutive return probability and homing probability at the river and tributary scales, respectively. For the river-scale analysis, the response variable was whether a spawner returned (1) or did not return (0), and for the tributary-scale analysis, whether it homed (1) or strayed (0). We adopted the LL scenario for the tributary-scale regression analysis for reasons described later. Biological and behavioral predictor variables were Length (fork length), Sex, Order (up-migration order of spawners passing through Site L in 2018 and 2019 for the river- and tributary-scale analyses, respectively), and Tributary (number of tributaries each fish entered in 2018). Environmental predictor variables were Watershed (watershed area of a tributary), Distance (distance from Site L to the tributary site), Elevation (elevation of the tributary site), and Spawner (number of PIT-tagged spawners that last entered the tributary in 2018). The environmental variables each had only four possible values corresponding to the four tributaries and thus were only tested in the tributary-scale analysis. Distance and Elevation were highly correlated ($r = 0.994$, $p = 0.006$), but the other combinations of tributary-specific variables were not. We used a forward stepwise variable selection procedure to identify the best model, in which no interaction terms were included. Models were ranked using Akaike’s information criterion corrected for small sample size (AIC_c) and compared using delta AIC_c (ΔAIC_c) and Akaike weights (w_i) (Burnham and Anderson 2002). All statistical analyses and tests were performed using R version 3.4.3 (R Development Core Team 2017) with a significance level of $\alpha = 0.05$.

Results

Summary of tag detections and tagged fish

Sixteen, 17, and 90 Sakhalin taimen were PIT-tagged in 2016, 2017, and 2018, respectively (Table 2). In 2018, the average fork length (\pm SD) of captured fish was 779 ± 93 mm (range 571–991 mm) for females and 726 ± 139 mm (range 487–1036 mm) for males. The sex ratio was 1.2 female per male.

Seventy-six fish tagged during the previous three seasons returned and passed Site L from 21 April to 5 May 2019. The majority (65 fish) passed downstream through this site after spending 5.6 ± 2.0 d (female;

mean \pm SD) and 10.4 ± 2.4 d (male) of spawning life upstream from Site L. It is unclear whether the remaining 11 fish were not detected when down-migrating through Site L, down-migrated after the termination of PIT detection operation, remained upriver as residents, naturally senesced, or were preyed upon. Most fish entered only one tributary of the Karibetsu River for spawning, but some entered two tributaries both in 2018 (12.4%) and 2019 (14.5%) (Table 3). Males were more likely to do so than females; two males (2.6%) entered three tributaries in 2019. Nine fish were not detected by any of the tributary antennas after passing through Site L in 2018, and two fish were also not detected by tributary antennas in 2019. At least two of the nine fish in 2018 did not spawn upstream of Site L or did not even pass antenna L1 because they were last detected by this antenna <2 h after first detection.

The detection efficiency of antenna L1 was 88.2%, and those of the tributary antennas were 94.4% (T1), 96.7% (T2), 100% (T3), and 100% (T4). The relatively low detection efficiency of antenna L1 was likely due to high stream discharge at Site L earlier in the season when some fish may have passed over the fish ladder outside the antenna's detection range.

Consecutive spawner return at the river scale

Of the 76 Sakhalin taimen detected in 2019, four, eight, and 61 fish (total $n = 73$) from the 2016, 2017, and 2018

Table 2 Numbers of PIT-tagged Sakhalin taimen released during 2016–2018 and those detected in the Karibetsu River in 2018 and 2019

Year	No. tagged	PIT detection		No. detected
		2018	2019	
2016	16	Yes	Yes	4
		Yes	No	2
		No	Yes	0
		No	No	10
2017	17	Yes	Yes	8
		Yes	No	1
		No	Yes	3
		No	No	5
2018	90	Yes	Yes	61
		Yes	No	29
Total		105	76	123

cohorts, respectively, had also returned in 2018 and three males from the 2017 cohort (fork length = 52.4, 85.9, and 82.4 cm) had not returned in 2018 (Table 2). Therefore, the consecutive return rate at the river scale was 69.5% (i.e., 73/105, the total number of fish tagged or detected in 2018), and the skip-spawning rate was 17.6% (i.e., 3/17, the total number tagged in 2017). There was no evidence of skip-spawners in the 2016 cohort because four of them that returned in 2019 had also returned in 2018 as part of six fish detected that year. The migration status for the 2016 cohort could not be determined in 2017 because the PIT detection system was not deployed that year.

The best model for consecutive return by Sakhalin taimen contained three variables of Sex, Length, and Tributary ($w_i = 0.65$; Table 4). This model indicates that the probability of consecutive return was higher for females (80.3% observed return rate as compared to 54.5% for males), large fish, and fish that entered more tributaries in 2018 (i.e., more active inter-tributary movements in the preceding year) (Table 5, Fig. 2).

Repeat homing and straying at the tributary scale

Of the 73 consecutive returners, 67 fish could be tracked to the four tributaries T1–T4 in both 2018 and 2019. Overall repeat homing rate under the LL scenario was 0.761 (Table 6), while rates under the other scenarios were 0.687 (FF), 0.701 (FL), and 0.746 (LF). Tributary-specific repeat homing rates (i.e., diagonals divided by the corresponding row sums in Table 6) were 0.867 (T1), 0.824 (T2), 0.500 (T3), and 0.625 (T4), which were significantly higher than rates expected by chance alone (i.e., 0.254, 0.463, 0.104, and 0.179, respectively; $\chi^2 = 80.00$, $df = 9$, $p < 0.001$).

Table 3 Numbers of Sakhalin taimen entering 0, 1, 2, and 3 tributaries during the 2018 and 2019 spawning seasons

Year	Sex	No. tributary			
		0	1	2	3
2018	Female	2	56	3	0
	Male	7	27	10	0
2019	Female	2	44	3	0
	Male	0	17	8	2

Table 4 Model selection results for river-scale return probability in Sakhalin taimen

Model	k	AIC _c	ΔAIC	w _i
1 ^a	1	131.16	10.1	0
1 + Sex	2	125.24	4.18	0.08
1 + Sex + Length	3	122.84	1.78	0.27
1 + Sex + Length + Tributary	4	121.06	0	0.65

^aIntercepts are denoted by 1. k = number of parameters, w_i = Akaike weight

The best model for repeat homing by Sakhalin taimen contained a single variable, Spawner (w_i = 0.97; Table 7). The stepwise procedure identified no additional variables that reduced AIC_c. Repeat homing probability was higher for individuals that returned in 2019 to tributaries where larger numbers of spawners entered in the preceding year of 2018 (p = 0.008, Table 8).

Discussion

Consecutive return at the river scale

The consecutive return rate we estimated for Sakhalin taimen (69.5%) is among the highest of those reported for iteroparous salmonids. Null et al. (2013) released 46 steelhead kelts (i.e., surviving post-spawners) with ultrasonic transmitters from a hatchery in the Sacramento River basin (California, USA) and observed that 41% of them returned to the hatchery the following year. Repeat return rates by steelhead are typically less than 10% along the Pacific coast of North America (Withler 1966; Leider et al. 1986; Keefer et al. 2008). Tilzey (1977) found that 25.7% of marked brown trout performed repeat spawning after one year and 10.6% did so

Table 5 Parameter estimates and their significance for the best model of river-scale return probability in Sakhalin taimen

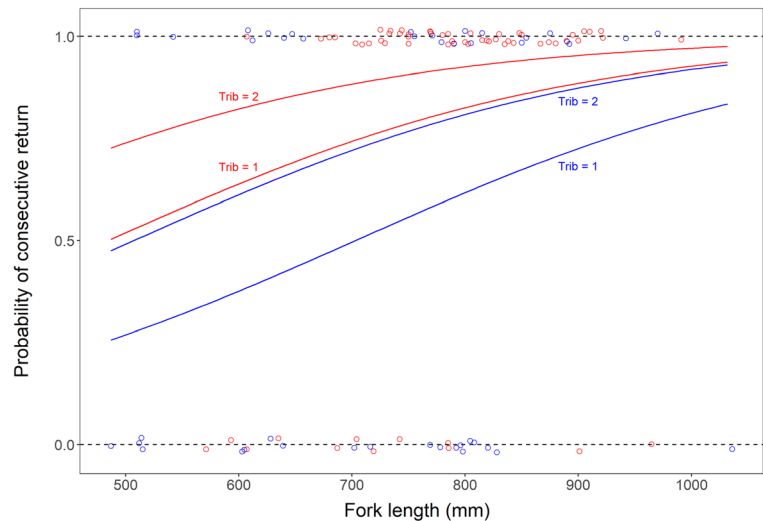
Variable	Coef	SE	z	p
Intercept	−3.35	1.83	−1.83	0.068
Sex	−1.08	0.47	−2.29	0.022
Length	0.01	0.00	2.31	0.021
Tributary	0.96	0.51	1.90	0.057

after two years. On average, 11% (range 0.7–42.5%) of Atlantic salmon spawners survive to reproduce another year (Fleming 1998). An adfluvial population of brook trout marked and released in two tributaries of a lake in Quebec, Canada, returned to the same streams at rates of 42.8% and 17.0% (O’Connor and Power 1973). Consecutive return rates reported for sea trout returning to a small Norwegian river (Haraldstad et al. 2018) were similar (max. 60%) to that reported in this study.

The high consecutive return rate of Sakhalin taimen is likely attributable to two characteristics of the population and river examined in this study. First, the Sakhalin taimen population in the Karibetsu River is located near the southern boundary of the species’ range (Rand 2006). Repeat spawning rates in anadromous salmonids tend to decrease at higher latitudes, where harsh conditions (e.g., lower temperatures and shorter growing seasons) make it difficult for individuals to regain enough energy to reproduce across consecutive years (Withler 1966; Jonsson and L’Abée-Lund 1993). Second, the relatively short distance from the river mouth to spawning grounds (25–30 km), coupled with the ocean-maturing life history of Sakhalin taimen in the Sarufutsu River system (Suzuki et al. 2011), help spawners conserve and provision enough energy during the growing season to support consecutive spawning migrations (Quinn and Myers 2004; Keefer et al. 2008; Penney and Moffitt, 2014). The observed high rate of consecutive spawning could also be due to high survival rates of Sakhalin taimen between breeding seasons, a likely explanation that warrants further investigation involving estimation of adult survival rates.

Consecutive return rates for Sakhalin taimen were significantly higher for females than males. This has been commonly observed in other iteroparous salmonids (Fleming 1998). Leider et al. (1986) attributed this phenomenon to the tendency of males to remain on spawning grounds much longer for reproduction and territorial defense. In fact, male Sakhalin taimen spawners spent two times longer in spawning streams than females in our study. The prolonged residence time of males on spawning grounds would potentially subject them to a higher risk of predation and other causes of mortality (Fleming 1998; Penney and Moffitt 2014). The males’ conspicuous nuptial coloration may also increase susceptibility to predation. In contrast, female Sakhalin taimen barely change their body color,

Fig. 2 Fork lengths of individuals that did and did not consecutively return at the river scale (red = female, blue = male). Predicted repeat return probabilities (lines) are indicated for females and males and for two levels of Tributary (number of tributaries fish entered in 2018). Data points (circles) have been vertically jittered for clarity



perform no nest guarding, and down-migrate immediately after spawning (unpublished data), making them less vulnerable to predation and allowing them to conserve energy.

Although males invest less energy into gonad development than females, the energetic costs of activity during the spawning period (e.g., courtship challenges, migration between tributaries) could create energy deficits that take more than 1 yr to recover, leading to a higher incidence of skip-spawning (Keefer et al. 2008). However, it is possible that three males that appeared to have skipped spawning in 2018 actually strayed to other spawning grounds that year within the Sarufutsu River basin. Post-spawners down-migrating from the Karibetsu and Sarufutsu rivers most likely co-mingle in estuarine and coastal areas prior to spawning in a subsequent year. Social interactions and conditioning during this period could result in individuals straying

to different spawning grounds from previous years (Secor 1999; Berdahl et al. 2017).

Consecutive return probabilities were higher in larger individuals. Relationships between repeat spawning and fish size are inconsistent in other studies. Larger sea trout had higher postspawning survival at sea due to size-biased predation on smaller fish by avian piscivores and other marine predators (Aarestrup et al. 2015; Haraldstad et al. 2018). Penney and Moffitt (2014) found a significant positive relationship between body size and white muscle protein content in steelhead kelts that had already depleted muscle lipids, suggesting that larger steelhead retain more energy during the spawning period compared to smaller conspecifics, which may allow large individuals to maintain a higher spawning frequency. Smaller summer-run steelhead (Keefer et al. 2008) and sea trout (Haraldstad et al. 2018) that had been PIT-tagged as post-spawners were also more likely to skip-spawn. However, large Atlantic salmon (Jonsson et al. 1991) and Arctic char (Dutil 1986) were less likely to spawn in consecutive years. The former

Table 6 Numbers of Sakhalin taimen returning to tributaries T1–T4 in 2018 (rows) and 2019 (columns) based on the last-last scenario

Site	T1	T2	T3	T4	Total in 2018
T1	13	0	1	1	15
T2	3	28	0	3	34
T3	0	2	5	3	10
T4	1	1	1	5	8
Total in 2019	17	31	7	12	67

Numbers of homed individuals are shown in bold

Table 7 Model selection results for tributary-scale homing probability in Sakhalin taimen

Model	k	AIC _c	ΔAIC	w _i
1 ^a	1	75.72	6.73	0.03
1 + Spawner	2	68.99	0	0.97

^aIntercepts are denoted by 1. k = number of parameters, w_i = Akaike weight

Table 8 Parameter estimates and their significance for the best model of tributary-scale homing probability in Sakhalin taimen

Variable	Coef	SE	z	p
Intercept	-0.44	0.60	-0.74	0.461
Spawner	0.08	0.03	2.67	0.008

species tended to spawn biennially rather than annually with increasing size. In the latter species, post-spawners required longer than 1 yr to restore expended energy following a spawning season; this recovery time became more protracted as the fish aged and grew larger.

Our study is the first to indicate that inter-tributary movement during a given spawning period may increase the likelihood of consecutive spawning in subsequent years. This tendency seems counter-intuitive given the energetic constraints described above. However, entering more tributaries would not necessarily require a large energetic investment, especially when the scale of movement is small, such as in this study. Individuals that enter more than one tributary per season could expose themselves to a variety of olfactory “bouquets” across multiple tributaries and thus could reinforce imprinting behaviors related to river-scale consecutive return. Youngson (1989) demonstrated that thyroxine, a hormone that is linked to olfactory imprinting, can be elevated in mature Atlantic salmon at the time of spawning. Our finding that consecutive return probability is positively correlated with fish size and inter-tributary movement by spawners is consistent with the hypothesis that olfactory imprinting may not be restricted to juvenile life stages but can play a role even at later life stages in larger, more experienced spawners.

Repeat homing and straying at the tributary scale

Repeat homing rates of Sakhalin taimen to the Karibetsu River tributaries ranged from 50% to 87%, which are among the highest reported in salmonids. The majority of tracked individuals, especially females, made one “choice” in selecting a spawning tributary, suggesting that they possess very finely tuned and precise homing abilities. Our measure of homing (the LL scenario) yielded the highest overall homing rate among the four scenarios and is consistent with a hypothesized “proving” (McCleave 1967) or “testing” (Keefer and Caudill

2014) behavior in which a fish may enter and reject alternative streams based on olfactory cues before finally entering its home stream. This theory posits the existence of cues (most likely chemical) that fish detect and use to select the tributary to which they imprinted earlier in life (Hasler and Wisby 1951). An alternative theory to explain salmonid homing behavior involves pheromone reception among conspecifics (Nordeng 1971, 1977). Although inter-tributary movements were more common among male spawners, neither the sex of a fish nor the number of tributaries it entered in 2018 explained homing success at the tributary scale. Instead, homing success to each tributary was best explained by the number of spawners that had ascended that tributary in the previous year of 2018. Because juvenile Sakhalin taimen tend to remain in their natal first-order spawning streams until age 1 or 2 (Fukushima et al. 2019), the number of juveniles in a tributary in a given year is related to the number of spawners that entered that tributary (i.e., the number of eggs deposited) in the previous year. This means that tributaries that had a large number of spawners would contain more chemical cues released from age-0 juveniles during the following year, helping parent spawners navigate efficiently towards their natal tributary.

Even though this study was not designed to reveal natal homing by Sakhalin taimen, we believe that the observed repeat homing was in fact the natal homing, considering that philopatry is a prevalent, fundamental life-history trait in anadromous salmonids (Keefer and Caudill 2014; Bett and Hinch 2015). Furthermore, although short freshwater residency by species like pink and chum salmon (Keefer and Caudill 2014) and dispersive juvenile movements (Hamann and Kennedy 2012) are often associated with less precise homing and higher straying, neither is the case for Sakhalin taimen (Suzuki et al. 2011; Zimmerman et al. 2012; Fukushima et al. 2019), rendering the observed high repeat homing more likely to be ‘natal’ homing rather than repeat homing to ‘non-natal’ locations.

Caution must be exercised, however, when interpreting our repeat homing results. Although homing rates tended to be greater for tributaries with higher spawner counts (e.g., T1 and T2), these tributaries also drained the largest watersheds with the most first-order spawning streams (Table 1). Thus, spawners entering T1 and T2 could have spawned in different first-order streams within their respective tributary watersheds

across the two years and still have been considered homed at the tributary scale. Thus, this spatial scale-dependence (Hamann and Kennedy 2012), or the confounding effect of watershed size, presents a challenge in elucidating causal relationships in the homing behavior; future work could overcome this issue experimentally by manipulating spawners in the field (e.g., Helle 1966; Ueda et al. 1998).

Conservation implications

Given the precise repeat homing of Sakhalin taimen, it is critical to identify, maintain, and restore important migratory corridors to and between existing historical spawning habitats. Outside the Sarufutsu river basin, the species has lost a significant portion of its range due to a number of factors, one of the most important of which is habitat fragmentation from dams, weirs, and numerous river structures such as culverts (Fukushima et al. 2011). A case study of the impacts of dam construction in a neighboring watershed offers some important insight into the conservation challenges that lie ahead. The Hokushin dam, built to create a drinking water reservoir, created a landlocked population of Sakhalin taimen. Through a study involving otolith microchemistry applied to bycaught mortalities, it was revealed that anadromy has persisted in this isolated population as progeny from reservoir tributaries emigrate over the dam spillway to reach the estuary (Fukushima et al. 2019). However, the mature Sakhalin taimen that return each spring are blocked by the dam and are unable to home to their natal streams or find alternate spawning grounds, presumably due to their strong natal site fidelity. The loss of the reproductive potential of these anadromous individuals has reduced the resilience of the landlocked population.

The extremely high propensity for consecutive spawning and repeat homing of Sakhalin taimen are likely to have been reproductively advantageous throughout much of the species' evolutionary history (Mobley et al. 2019). However, in the era of rapid environmental change and increasing fragmentation of riverine habitats (Fausch et al. 2010), such strong natal site fidelity may put the species at a disadvantage. One could argue that this fidelity contributed to some extent to the drastic range reduction of Sakhalin taimen in Japan (Fukushima et al. 2011), and in Russia (Zolotukhin et al. 2013). If individuals had strayed and colonized nearby habitats, the species might have been able to maintain meta-population dynamics through

dispersal to populations that may have experienced declines. Such meta-population dynamics can persist only if migratory links, or habitat connectivity, are preserved through concerted conservation efforts in pristine watersheds, or in more developed watersheds through bypassing existing barriers (e.g., Lusardi and Moyle 2017) or removing those that are more problematic (e.g., Quinn et al. 2017). Some efforts at improving river connectivity are currently underway in Hokkaido for Pacific salmon (e.g. Nakamura and Komiyama 2010), and there are now local efforts in the Sarufutsu watershed to repair or replace problematic culverts to improve passage conditions for Sakhalin taimen. Improving river connectivity needs to be an important component of future conservation planning for this species and other anadromous species in the region.

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Author's contributions Conceived and designed the investigation: M.F. and P.S.R., performed field work: M.F. and P.S.R., analyzed the data: M.F., wrote the paper: M.F. and P.S.R.

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Data availability The datasets generated during this study are available from the corresponding author on reasonable request.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethics approval Fish were collected under the Hokkaido Government permits No. 168 (2016), 201 (2017), and 191 (2018). Fish sampling protocol used in this study was approved by the Animal Care Committee of National Institute for Environmental Studies.

Consent for publication Not applicable.

Code availability Not applicable.

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