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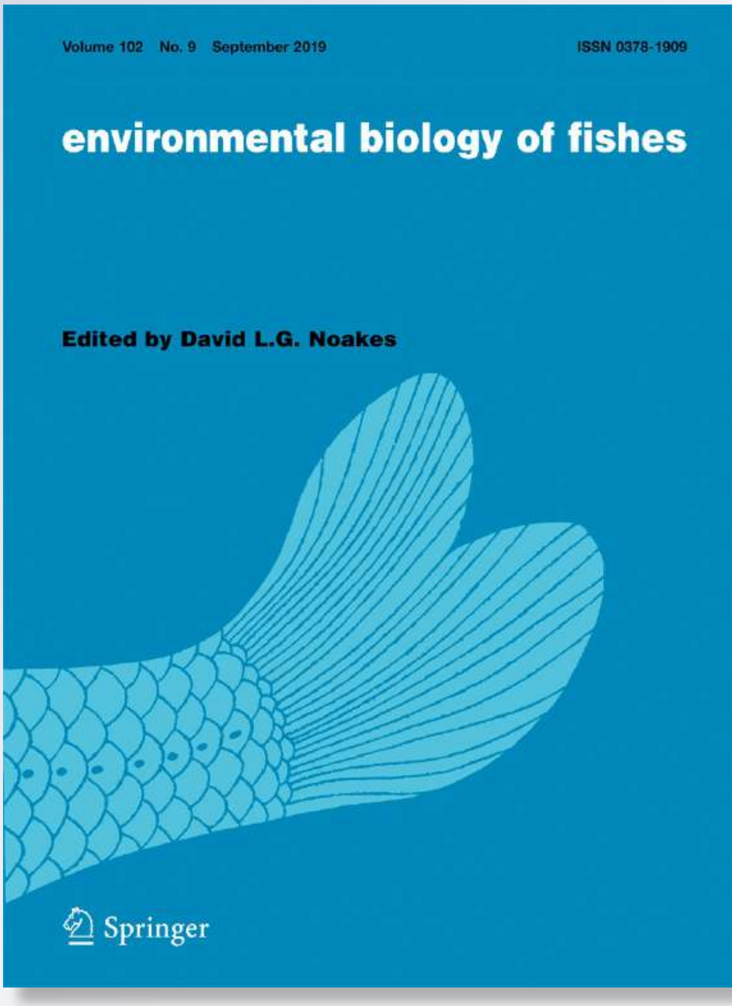

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Anadromy sustained in the artificially land-locked population of Sakhalin taimen in northern Japan

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Abstract The conservation of land-locked populations of migratory fishes is increasingly important in the era of dam removal and habitat reconnection. We used an otolith strontium (Sr) tracer ($^{87}Sr/^{86}Sr$) to test the hypothesis that a land-locked population of an endangered salmonine species, Sakhalin taimen (*Parahucho perryi*), retains the capacity for anadromy, and that some individuals out-migrate from the reservoir to the sea. Years later, these individuals return but are blocked by the migration barrier of the reservoir dam and are denied reproduction in their natal streams. Juvenile taimen collected from the reservoir and two nearby regions were classified based on their otolith Sr isotopic signatures to their regions of origin with an overall accuracy of 88%. When the same classifier was applied to ocean-caught adult taimen, we predicted some individuals had originated from the reservoir with high posterior probabilities (> 0.9). Whether the land-locked Sakhalin taimen can help sustain the metapopulation dynamics of the species at the watershed scale may depend on whether, and how soon, the disrupted migration pathway is restored.

Keywords Anadromy · Land-locked population · Dam · Sakhalin taimen · Otolith · Strontium isotope analysis

Introduction

Life history strategies in diadromous fishes are diverse within species and populations (Walther et al. 2011; Kendall et al. 2015; Hodge et al. 2016), yet this diversity has been substantially reduced by anthropogenic alterations to critical habitats, most notably by the loss of ecological connectivity through damming of rivers (Dauble and Watson 1997; Bunn and Arthington 2002). However, in a few cases, migratory phenotypes that had seemingly been lost due to dam construction have been found to have persisted over generations in isolated populations of rainbow/steelhead trout (*Oncorhynchus mykiss*) (Thrower and Joyce 2004), redband trout (*O. mykiss gairdneri*) (Holecek et al. 2012), and sockeye salmon (*O. nerka*) (Godbout et al. 2011). Furthermore, these phenotypes have even reappeared as resurgent diadromous populations once habitat connectivity is restored through barrier removal or modification (Pess et al. 2012; Quinn et al. 2017; Pearse and Campbell 2018).

Hokushin Reservoir supports a land-locked population of an endangered salmonine species, Sakhalin taimen (*Parahucho perryi*), in northern Hokkaido, Japan (Rand 2006). Sakhalin taimen are iteroparous (i.e., reproducing multiple times throughout life) and long-lived (lifespan >20 years), inhabiting Hokkaido, Japan and Far Eastern Russia (Holčík et al. 1988). Only a dozen Sakhalin taimen populations remain in Hokkaido.

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Three populations, including the one in Hokushin Reservoir, persist as adfluvial forms that have been land-locked above impassable dams for ~40–75 years, reproducing in inflowing tributary streams. Despite the overall at-risk status of the species, however, these adfluvial populations appear to be relatively stable in population size (Fukushima et al. 2011). However, repeated observations made at the dam site have recently called the viability of this population into question. Each spring dozens to hundreds of adult Sakhalin taimen have been observed just below the spillway of the dam, where they are blocked from migrating upstream. They remain there during their spawning season in late April through early May and eventually disappear downstream. This observation has led to a hypothesis that the above-dam taimen population has not been completely land-locked but retains anadromy, allowing individuals to emigrate from the reservoir, out-migrate to the sea, and return to the dam when mature, albeit without being able to reproduce in their natal streams.

The strontium isotope ratio ($^{87}Sr/^{86}Sr$) in otoliths is a reliable tracer to study fish movements because stream-specific Sr isotope ratios are seasonally stable (Kennedy et al. 2000; Muhlfeld et al. 2012; Brennan et al. 2015), yet they vary substantially among watersheds in association with lithology, specifically the geologic age and Rb/Sr ratios of bedrock (Walther and Thorrold 2009; Walther and Limburg 2012). Marine water has a globally uniform $^{87}Sr/^{86}Sr$ ratio of 0.70918 (Hodell et al. 1989), allowing researchers to trace diadromous fishes across salinity gradients (Kennedy et al. 2002; McCulloch et al. 2005; Crook et al. 2017). Importantly, there is no significant biological fractionation in isotope ratios during uptake from ambient water or dietary inputs (Kennedy et al. 2000; Barnett-Johnson et al. 2008); thus, measures of $^{87}Sr/^{86}Sr$ ratios in otoliths reflect ambient environmental conditions experienced by the fish.

Because salmonid otoliths start developing during oogenesis, Sr isotopes deposited in the otolith primordium reflect those in the egg yolk, which in turn reflect the maternal isotopic signature (Kalish 1990; Zimmerman and Reeves 2002). If a female spawner has an anadromous life and matures in marine water, her progeny would exhibit a Sr isotopic signature in the primordium that is close to the marine value. If, instead, she is a freshwater resident as in the case of land-locked populations, the signature in the primordium would differ from the marine value. After embryos hatch in natal streams, the alevins start to incorporate Sr isotopes contained in the ambient water onto new otolith layers that accrete over the maternally-influenced primordia. As a consequence, both the maternal and freshwater natal origins of salmonids can be evaluated by analyzing otolith Sr isotopes (Padilla et al. 2015; Hegg et al. 2019).

The objective of this study was to apply the otolith Sr isotope technique to predict the provenance and movements of Sakhalin taimen and to test the hypothesis that some individuals in the land-locked Hokushin Reservoir population retain an anadromous life history and undertake seaward migrations. To this end, we sampled juvenile Sakhalin taimen throughout two river basins, the Koetoi River on which the Hokushin Reservoir was built and the neighboring Sarufutsu River, to determine their maternal life history and natal streams of origin. We then applied the Sr-based classifier we developed using the juvenile Sakhalin taimen samples to adult otoliths sampled from ocean-caught individuals to determine their provenance.

Methods

Study area

The Koetoi and Sarufutsu rivers drain watersheds of 297 and 361 km^2, respectively, and originate in gently sloping hills approximately 300–400 m in elevation near the northern tip of Hokkaido (Fig. 1). Constructed in 1980 in the first-order tributary of the Koetoi River, the Hokushin Reservoir (capacity, 332 000 m^3; reservoir area, 71 ha; watershed area, 24.6 km^2) has supplied drinking water to ~35 000 residents in the city of Wakkanai. For this reason, the reservoir area has been protected from anthropogenic impacts by regulations prohibiting human access and activities such as recreational fishing, and by limitations on timber harvesting and land development in the watershed, all of which may have improved the conservation status of the Sakhalin taimen population.

Fish cannot pass upstream of the Hokushin Dam to enter the reservoir and its tributaries because the dam is not equipped with a fishway or other mitigation device. However, fish above the dam could potentially out-migrate from the reservoir through a 32-m high spillway (slope ~26 degrees from the horizontal plane) into a concrete pool (15 m wide, 60 m long, and 5 m deep) where what appear to be "anadromous" Sakhalin taimen spawners have been spotted as described above. Outside

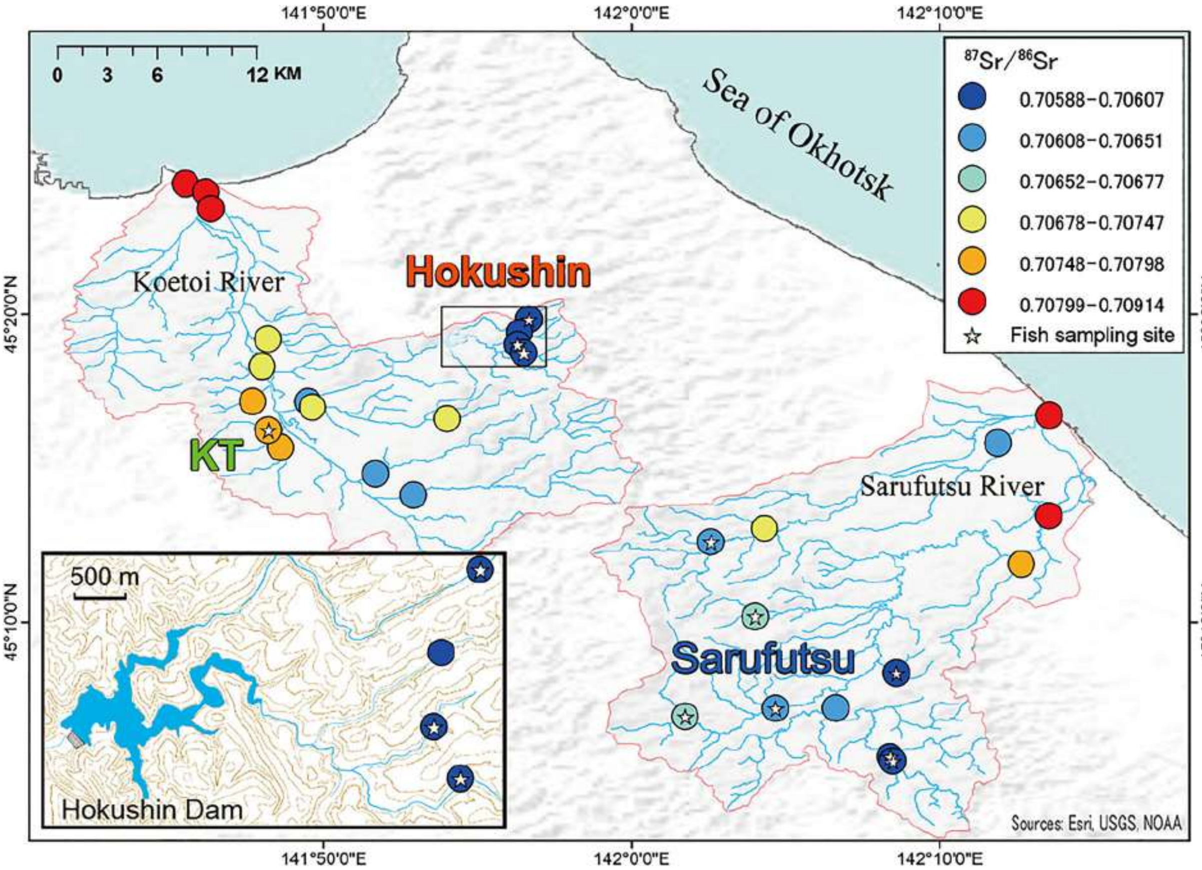

Fig. 1 Map of the Koetoi and Sarufutsu rivers showing observed river water strontium (Sr) isotope ratios. Inset shows a large-scale view of the Hokushin Dam area

the Hokushin watershed, taimen spawning streams are very limited in the Koetoi River because intensive flood prevention and agricultural development have severely degraded their historical spawning habitats owing to stream channelization and the construction of numerous river crossings (HRDB 2009). By contrast, the Sarufutsu River drains a relatively pristine landscape with few migration barriers and abundant riparian vegetation in the headwaters. The mouths of the Koetoi and Sarufutsu rivers are separated by 60 km of coastline. Both rivers support several other salmonine species, including chum salmon (*O. keta*), pink salmon (*O. gorbuscha*), masu salmon (*O. masou*), and white-spotted char (*Salvelinus leucomaenis*).

Water and fish sampling

All sampling sites for water and fish, except for those above the Hokushin Dam, are accessible for anadromous fish. A total of 31 sites were sampled for water in August 2016 at base flow conditions throughout the two river basins (Fig. 1). Each water sample was filtered in situ through a 0.2-μm syringe filter into a 15-mL acid-washed polypropylene tube, immediately mixed with ultrapure nitric acid (final nitric acid concentration, 1%), and refrigerated until analysis.

At 11 of the 31 sites, juvenile Sakhalin taimen were collected using a backpack electroshocker in a 100–200 m reach in June, July, and August of 2016 and 2017. The eleven sites were grouped into three regions: (*i*) "Hokushin" refers to three sites located in tributaries of the Hokushin Reservoir, (*ii*) "KT" refers to a single site in a tributary of the Koetoi River, and (*iii*) "Sarufutsu" refers to seven sites in the Sarufutsu River. KT is located in a short (< 5 km) first-order stream flowing eastward to connect to the Koetoi mainstem on its left bank; the stream is one of only a few spawning streams left for anadromous Sakhalin taimen in the river system. A total of 25 juvenile Sakhalin taimen (19 age-1 and 6 age-2 fish) were collected from the two rivers;

eight were from Hokushin, three from KT, and 14 from Sarufutsu (Table 1). The juvenile Sakhalin taimen collected were measured for total length to the nearest millimeter and weighed to the nearest gram. Adult Sakhalin taimen were caught as bycatch in gillnets or set nets by local fishermen in salt water within a 5-km radius of each river mouth; the fish were either dead or moribund when landed. All fish samples were kept frozen until otolith extraction for isotopic analyses.

Fish sampling was conducted with a permit issued by Hokkaido Government (no. 201). All applicable international, national, and institutional guidelines for the care and use of animals were followed.

Strontium isotopic analysis of water and otoliths

Prior to isotopic analysis, an aliquot of the pre-filtered water sample was transferred into a clean Teflon vial, evaporated to dryness on a hot plate, redissolved in 2 mL of 2 M HNO_3, and eluted through a Sr-specific resin (Eichrom Technologies Inc., Lisle, IL, USA). The sample was subsequently rinsed with both HNO_3 and HCl and conditioned with 1 mL of 2 M HNO_3, of which a 2-mL solution was loaded onto the cleaned resin, washed with 2 mL of 2 M HNO_3 to remove matrix elements such as Ca and Rb and purify Sr fractions, and eluted with 6 mL of 0.05 M HNO_3. The total procedural blank was ~0.1 ppb. The samples were analyzed for $^{87}Sr/^{86}Sr$ with multicollector inductively coupled plasma mass spectrometry (MC-ICP-MS) using a Nu Plasma II (Nu Instruments, Ltd., Wrexham, UK) at the National Institute for Environmental Studies, Japan and a Neptune Plus (Thermo Fisher Scientific, Bremen, Germany) at the University of Tokyo. Solution samples were introduced into the MC-ICP-MS using an Aridus II desolvating nebulizer (CETAC Technologies, Omaha, NE, USA). We corrected $^{87}Sr/^{86}Sr$ ratios for mass bias by normalizing to an $^{86}Sr/^{88}Sr$ value of 0.1194 after eliminating isobaric interferences from Kr and Rb (Jackson and Hart 2006). The mean (± 2SD) $^{87}Sr/^{86}Sr$ ratios in NIST SRM987 measured throughout the analyses were 0.71049 ± 0.00021 ($n = 14$) (Nu Plasma II) and 0.71029 ± 0.00006 ($n = 24$) (Neptune Plus). All data were externally normalized to an SRM987 $^{87}Sr/^{86}Sr$ value of 0.71034.

Sagittal otoliths of both juvenile and adult Sakhalin taimen were extracted using ceramic forceps. One of the otoliths was embedded in epoxy resin (Epofix; Struers Inc., Cleveland, OH, USA), sectioned in the transverse plane, and polished with 3-μm lapping film to expose the primordium. We measured $^{87}Sr/^{86}Sr$ ratios and the signal intensity of ^{88}Sr (V) as a proxy for Sr concentration (Phillis et al. 2018) along a core-to-edge otolith transect using the Neptune Plus MC-ICP-MS with a laser ablation-desolvating nebulizer dual sample intake system (LSX-213 G2+ equipped with a HelEX 2-volume cell, CETAC Technologies). The ablated material was carried by a He gas stream to the ICP where it was mixed with a desolvated aerosol carried by the Ar gas flow. Laser parameters were 8–15 Hz in repetition rate, 5 μm/s in scan speed, and 50 and 65 μm in beam diameter for juveniles and adults, respectively. The isobaric interference correction, mass bias correction, and $^{87}Sr/^{86}Sr$ normalization using the NIST SRM987 were made in the same manner as for the water samples. Analytical accuracy and precision were evaluated by analyzing four $CaCO_3$ standards that are expected to have the global marine $^{87}Sr/^{86}Sr$ value of 0.70918: coral high-Mg calcite WKY15–1, coral aragonite DH05Ishi-1, giant clam aragonite TS18MT-01, and flatfish otolith PO14SMN-01. The mean $^{87}Sr/^{86}Sr$ values (± 2 SD) of these standards obtained during the course of the analyses were 0.70922 ± 0.00014 ($n = 26$) for WKY15–1, 0.70919 ± 0.00008 ($n = 25$) for DH05Ishi-1, 0.70918 ± 0.00015 ($n = 25$) for TS18MT-01, and 0.70920 ± 0.00024 ($n = 25$) for PO14SMN-01.

We quantified isotopic signatures representing the maternal and natal freshwater origins of juvenile Sakhalin taimen by calculating the mean $^{87}Sr/^{86}Sr$ ratios at the otolith primordium (0–50 μm from the core) and edge region (0–50 μm from the rim), respectively. For adult otoliths, mean $^{87}Sr/^{86}Sr$ ratios were calculated for the primordium and a region 250–500 μm from the core to represent maternal and natal freshwater origins, respectively. The latter distance range encompasses the freshwater growth region at the juvenile stage but is outside the region influenced by maternal chemistry as shown later. All fish were aged by counting annuli shown in sectioned otolith samples under a transmitted light microscope.

Table 1 Summary of juvenile Sakhalin taimen sampled for otolith strontium isotope ratio analysis

Region	Total length (mm)	Weight (g)	Total collected
Hokushin	102 ± 21	11 ± 8	8
KT	103 ± 28	11 ± 8	3
Sarufutsu	110 ± 24	15 ± 10	14

Total length and weight are shown as mean ± SD

Data analysis

Linear discriminant function analysis (LDFA) was performed to classify juvenile otoliths into their geographical regions of origin (Venables and Ripley 1999). Classification accuracy was evaluated using a leave-one-out jackknife procedure. The estimated LDFs were then applied to isotopic data from adult otoliths to predict their provenance and corresponding posterior probabilities. Random noise was removed from laser transect data by applying loess smoothing with span size 0.2 (Cleveland 1979). Statistical analyses were performed in R version 3.4.3 (R Core Team 2017).

Results

River water $^{87}Sr/^{86}Sr$ ratios were consistently higher at lower elevations in both rivers, reaching a maximum near river mouths with a value close to the marine value (0.70918) and a minimum above Hokushin Reservoir in the Koetoi River (average, 0.70591) and at a site in the Sarufutsu River (also 0.70591, hereafter referred to collectively as the Hokushin value) (Fig. 1).

Sr isotopic signatures of juvenile otoliths

The $^{87}Sr/^{86}Sr$ profiles of Hokushin otoliths varied around the Hokushin value along the core-to-edge transect with substantial noise even after loess smoothing (Fig. 2). Three profiles from KT had isotope ratios (> 0.707) that substantially exceeded the Hokushin value. The isotope ratios of Sarufutsu otoliths were commonly elevated (0.708–0.709) at primordia but declined to 0.706–0.707 at distances over 250 μm from the otolith core. Apart from this initial decline and other variations attributable to random noise, the isotope ratios of individuals from the three regions remained stable, suggesting that the fish did not move out of their natal streams until captured.

A linear regression of otolith edge $^{87}Sr/^{86}Sr$ against river water ratios at fish sampling sites was highly significant ($p < 0.001$, $r^2 = 0.820$), but the slope of the regression line (0.788; 95% CI = 0.629–0.948) was slightly smaller than 1 (Fig. 3).

Juvenile taimen otoliths were classified according to core and edge $^{87}Sr/^{86}Sr$ ratios, producing an overall classification accuracy of 88% (Table 2). All individuals from Hokushin and KT were correctly classified, but two individuals from Sarufutsu were misclassified as being from Hokushin. One additional individual from Sarufutsu was misclassified as being from KT.

Provenance of adult taimen

Three and two adult Sakhalin taimen caught near the Koetoi (K1, K2, and K3) and Sarufutsu (S1 and S2) river mouths, respectively, were examined for their provenance and migration using otolith analysis (Table 3). Sex for K1 is unknown because internal organs were scavenged while in the net.

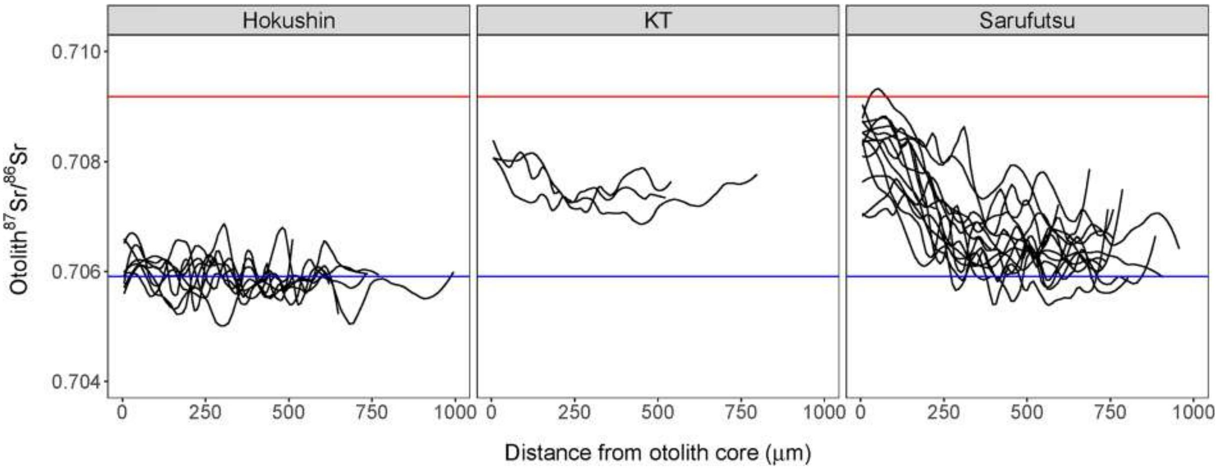

Fig. 2 Otolith core-to-edge $^{87}Sr/^{86}Sr$ ratios (black lines) of juvenile Sakhalin taimen otoliths sampled from individuals collected in the Hokushin ($n = 8$), KT ($n = 3$), and Sarufutsu ($n = 14$) regions. Red and blue horizontal lines indicate the global marine value (070918) and the Hokushin value (070591), respectively

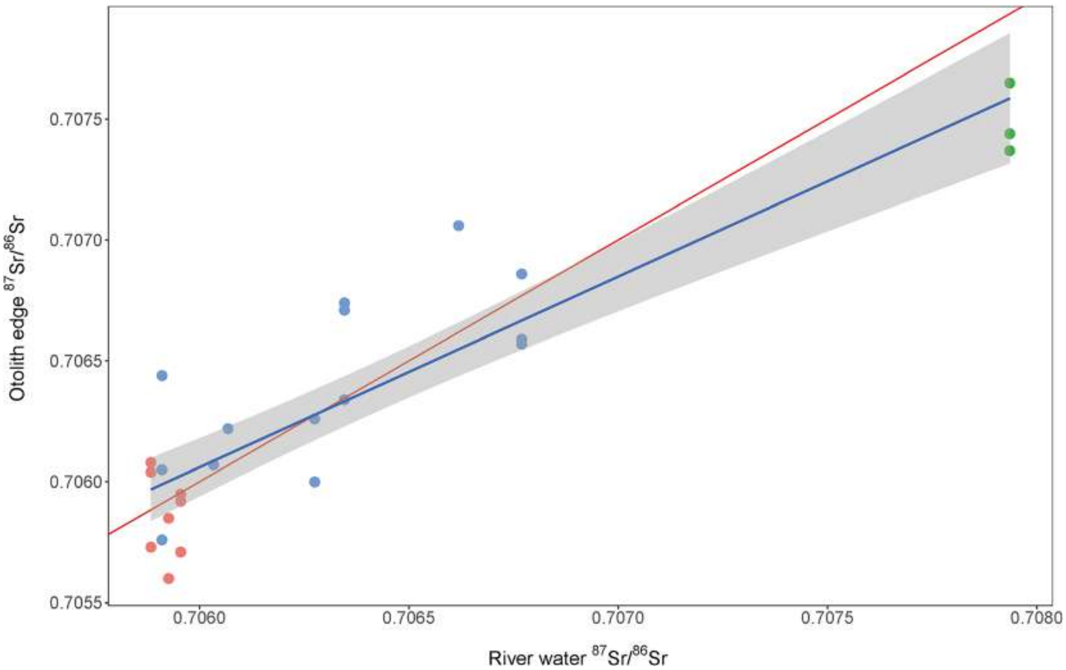

Fig. 3 Otolith edge $^{87}Sr/^{86}Sr$ plotted against river water isotope ratios for Hokushin (red), KT (green), and Sarufutsu (blue) samples. A linear regression (blue line) and a line with slope 1 and intercept 0 (red line) are also shown. The shaded area indicates a 95% confidence band around the regression line

The provenance of each adult taimen was predicted based on isotopic signatures of the otolith core and freshwater growth regions using the LDFA model fitted to juvenile otolith data (Fig. 4). The Koetoi adults were all predicted to be of Hokushin origin. K1 and K3 were given significantly high posterior probabilities of group assignment (0.989 and 1.000, respectively). In particular, the data point for fish K3 was close to those for the Hokushin juveniles and far away from those for the KT or Sarufutsu fish, corroborating its group assignment. In contrast, the K2 data point was close to the classification borders between Hokushin, KT, and Sarufutsu, and accordingly given a much lower posterior probability (0.618). S1 was misclassified as being of KT origin on the Koetoi River (0.695), whereas S2 was correctly classified as a Sarufutsu fish (0.871). Note that Fig. 4 shows fewer misclassifications of the juvenile data points than Table 2; the former shows classification results based on whole otolith analysis and the latter on leave-one-out jackknifed classification.

Table 2 Linear discriminant function analysis classification of juvenile Sakhalin taimen to three regions (Hokushin, KT, and Sarufutsu) based on strontium isotope ratios of the otolith core and edge

	Region assigned		
Region sampled	Hokushin	KT	Sarufutsu
Hokushin	8	0	0
KT	0	3	0
Sarufutsu	2	1	11

Predicted life histories

The core-to-edge $^{87}Sr/^{86}Sr$ profiles of adult otoliths varied markedly between the Hokushin and global marine values, but the variations differed considerably among individuals (Fig. 5). Isotope ratios in all profiles never exceeded the marine value but stabilized at slightly lower ratios (~0.7085) toward the time of capture. Of the Koetoi samples, the K1 and K3 profiles started with ratios around the Hokushin value. The K1 isotope profile then increased by 0.001 at age 2+ when the fish itself experienced considerable somatic growth for about a year, as inferred from a wider inter-annular distance. However, whether this rapid growth corresponded to marine habitation is unclear because the isotopic ratio

Table 3 Adult Sakhalin taimen analyzed for otolith strontium isotope ratios

ID	Sampling region	Season and year captured	Total length (mm)	Weight (g)	Age	Sex
K1	Koetoi	May, 2017	748	4315	9+	ND
K2	Koetoi	April, 2018	838	6510	12+	Female
K3	Koetoi	April, 2018	798	5140	11+	Female
S1	Sarufutsu	Fall, 2012	840	ND	16+	Female
S2	Sarufutsu	Fall, 2012	880	ND	25+	Female

ND no data

was relatively low (< 0.707). On the other hand, K3 consistently exhibited the Hokushin value from birth to age 5+, after which $^{87}Sr/^{86}Sr$ abruptly rose toward the marine value. In contrast, K2 started with a slightly higher isotope ratio at the primordium, which then decreased at age 2+ to the Hokushin value and bounced back toward the marine value afterwards. This fish appears to have spent a short period of time in brackish water before migrating into seawater at age 5+ because both $^{87}Sr/^{86}Sr$ and the signal intensity spiked a year earlier at age 4 + .

S1 appears to have out-migrated to salt or brackish water at age 2+, achieving considerable somatic growth. This individual, however, returned to and resided in freshwater for several years before migrating into seawater in later years (> 10+). By contrast, S2 showed the conspicuous maternal influence of anadromy at the primordium, as was commonly found in Sarufutsu juveniles (Fig. 2). This fish emigrated to the marine environment at the oldest age (15+) among the five adult Sakhalin taimen. Inter-annular distances revealed that in general, Sakhalin taimen from Koetoi grew much faster than those from Sarufutsu during their marine life stages. Note that K2 was 4 years younger than S1, but due to its faster growth, the two fish were similar in body size.

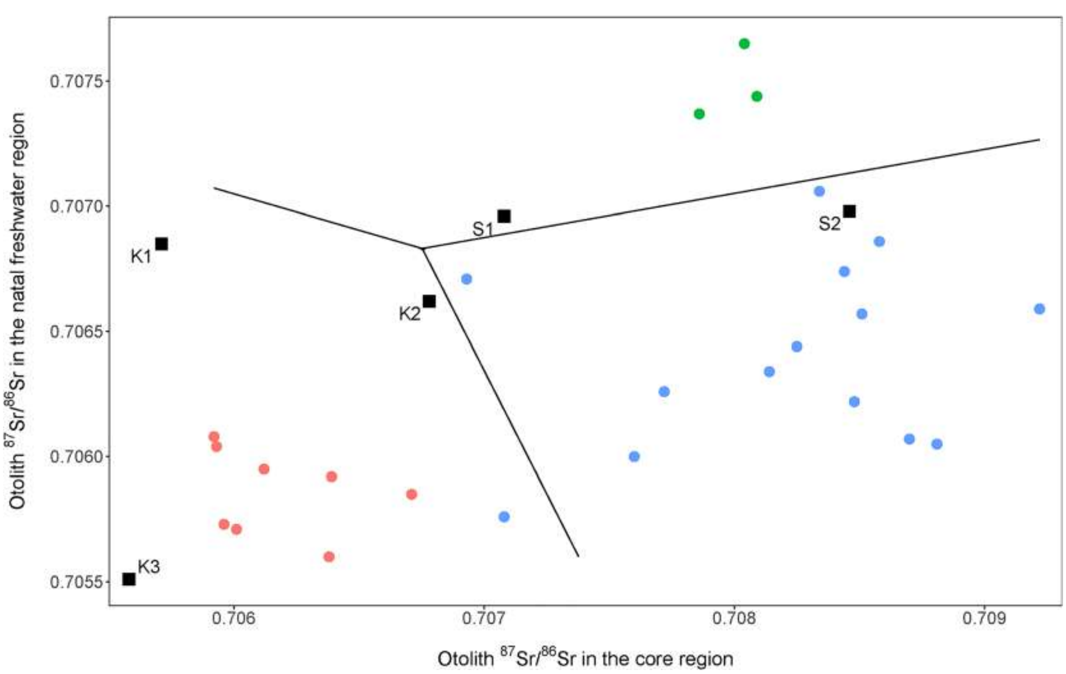

Fig. 4 Linear discriminant function plot showing juvenile otoliths originating from the Hokushin (red circles), KT (green circles), and Sarufutsu (blue circles) regions together with adult otoliths (black squares). Black lines delineate classification borders where posterior probabilities for adjacent groups become equal

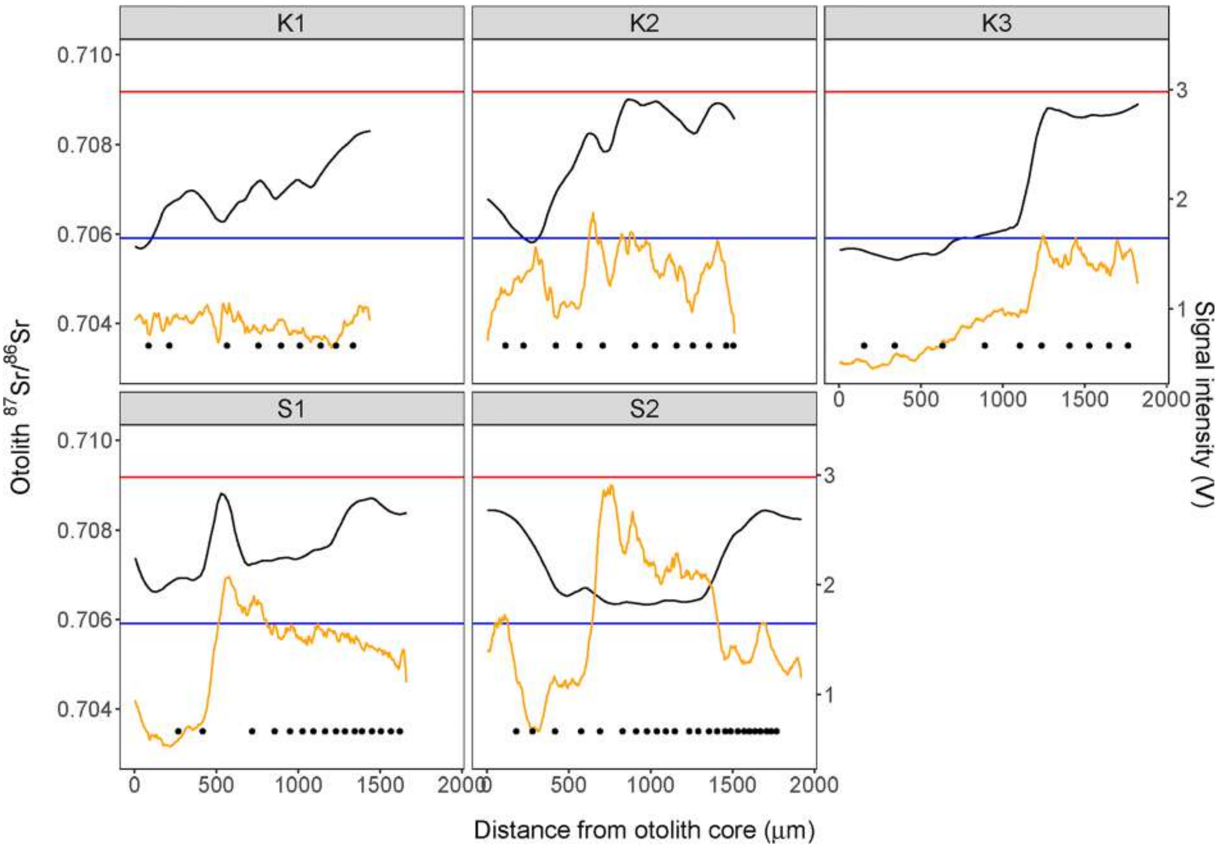

Fig. 5 Otolith core-to-edge $^{87}Sr/^{86}Sr$ profiles of adult Sakhalin taimen caught in the ocean in the Koetoi and Sarufutsu areas (black lines). The orange line shows ^{88}Sr signal intensity. Black dots on the bottom of each panel indicate annuli locations. Red and blue horizontal lines indicate the global marine value (0.70918) and the Hokushin value (0.70591), respectively. Refer to Table 3 for fish IDs

Discussion

Our otolith analyses verified that some individuals in the seemingly land-locked population of Sakhalin taimen in the Hokushin Reservoir still undertake anadromous migrations nearly 40 years after dam construction. Juvenile Sakhalin taimen collected above the dam commonly lacked a maternally-inherited marine signature at the otolith core because they were the progeny of freshwater-resident taimen in the reservoir. The same characteristic of a missing marine signature in the maternally-influenced primordium was recognized in some of the ocean-caught adults, providing strong evidence for their provenance in the Hokushin Reservoir.

The reappearance of anadromy in once land-locked populations has been documented in other salmonines. In British Columbia, Canada, adult sockeye salmon returned to rivers fragmented by hydroelectric dams for the first time in 90 years (Godbout et al. 2011). Two years earlier, the dams experimentally released water, and juvenile sockeye salmon (kokanee) land-locked in reservoirs unexpectedly out-migrated with the released water to the sea and returned as adults. The removal of hydroelectric dams on the Elwha River, Washington, USA, resulted in the resumption of anadromy and the expansion of foraging opportunities in bull trout (*S. confluentus*) after being almost entirely land-locked for over a century (Quinn et al. 2017). Rainbow trout transplanted to a lake in Alaska above large waterfalls in the 1920s continued to produce smolts that returned as adult steelhead to the base of the waterfalls 70 years later (Thrower and Joyce 2004). Adfluvial redband trout (a subspecies of rainbow trout) land-locked in a reservoir in southwestern Idaho for over 40 years retained the potential for anadromy and continued to undergo smoltification, although unlike in the present study the fish did not actually emigrate from the reservoir to undertake a seaward migration (Holecek et al. 2012).

In salmonids, maternal marine influences at the otolith core could be attenuated in progeny if the mother spends a prolonged time (> 6 months) in freshwater prior to spawning (Donohoe et al. 2008; Hegg et al. 2019), and therefore the lack of a marine signature at the otolith core may not necessarily indicate resident parentage. However, this is unlikely to explain the missing marine signature of adult Sakhalin taimen in this study. All juvenile otolith samples from the Sarufutsu River exhibited elevated maternal marine isotopic signatures at primordia, indicating they were the offspring of anadromous females. Although similar signatures were not obvious in juveniles from KT where anadromous taimen spawn, this is likely due to a high river water isotopic signature at this site (Fig. 1), which may have masked the presumed maternal marine signature of these individuals and made the profiles appear flat. Once Sakhalin taimen in Hokkaido become fully mature, their primary habitat shifts from fresh to brackish water. Thus, despite their iteroparous life history, otolith core-to-edge Sr/Ca profiles rarely exhibit distinct drops in elemental ratios that correspond to past freshwater spawning migrations (Arai et al. 2004; Honda et al. 2010; Zimmerman et al. 2012; but see Suzuki et al. 2011). Our observations and those of previous studies confirm that (*i*) the species in this area of Hokkaido consists primarily, or exclusively, of anadromous forms, and that (*ii*) the duration of their spawning migration is too short for spawners to uptake and transfer freshwater (as opposed to saltwater) signatures to their offspring. Consequently, the lack of maternal marine signatures in the otoliths of the ocean-caught adults (K1 and K3) would not be possible unless they originated from the Hokushin Reservoir where the only resident Sakhalin taimen occur in the area.

Contrary to our classification results, however, we doubt that all three adult Sakhalin taimen caught near the Koetoi River mouth originated from Hokushin. The otolith core signature of K2 started relatively high but subsequently declined to a value close to the Hokushin value, as if the fish had an anadromous mother. This is contradictory to its predicted Hokushin provenance because fish above the dam cannot have anadromous parentage. A possible explanation is that K2 is the progeny of an anadromous mother that spawned below the dam but in the same tributary before connecting to the Koetoi River. Note that even though the isotope ratio declined to the Hokushin value at age 2+, the ^{88}Sr signal intensity (a proxy for Sr concentration) was significantly higher than those exhibited by K1 and K3 during their natal rearing stages, further suggesting that Hokushin was not the likely natal origin of K2. Sakhalin taimen redds have been observed in the tributary between the dam and the confluence of the Koetoi River (Hokkaido Government 2014), although reaches in this section (~9 km) provide neither preferred spawning nor rearing habitats due to extensive channelization and revetment.

Despite our small sample size, our results were consistent with a high diversity of life histories among adult Sakhalin taimen. This was especially true in terms of the age at first seaward migration and the duration of freshwater and saltwater rearing. Two individuals appeared to have entered brackish or saltwater for the first time at age 2+ (K1 and S1), whereas one individual (S2) seemed to have done so at age 15+. Juvenile Sakhalin taimen have rarely been caught in the ocean, and the only records are of two smolts of ages 1+ and 2+ captured near the mouth of a small high-gradient stream on the Shiretoko Peninsula, Hokkaido (Komiyama and Takahashi 1988).

Otolith Sr isotopic signatures of the ocean-caught Sakhalin taimen did not fully reach the global marine value (0.70918), but instead stabilized at slightly lower values of 0.7080–0.7085. This may reflect the species' stronger reliance on brackish rather than seawater habitats, in contrast to fully anadromous salmonids like Pacific salmon, which migrate further offshore (Phillis et al. 2018; Hegg et al. 2019). Note that both the Koetoi and Sarufutsu rivers connect to large coastal lagoons with brackish water near the river mouths (Fig. 1). In fact, out of the twelve extant populations of Sakhalin taimen in Hokkaido, seven currently stable populations reproduce only in rivers connected to coastal lagoons or rivers above sizeable reservoirs, including the Hokushin population (Fukushima et al. 2011). Honda et al. (2010) caught adult Sakhalin taimen in Lake Akkeshi, a brackish lagoon in eastern Hokkaido (latitude: 43.0°N), and observed lower otolith Sr/Ca ratios ($<6.0 \times 10^{-3}$) than in saltwater-reared specimens, concluding that the sampled individuals had likely remained in the lagoon instead of migrating out to the sea. Arai et al. (2004) measured high otolith Sr/Ca ratios ($> 6 \times 10^{-3}$), representative of full seawater, in specimens from Lake Aynskoye in Sakhalin Island, Russia (latitude: 48.5°N) and suggested a latitudinal cline in the anadromy of Sakhalin taimen in which northern populations are more likely to undergo anadromous migrations (Gross 1987). However, Zimmerman et al. (2012) caught only resident and no anadromous Sakhalin taimen in the Koppi River and only one anadromous fish in the adjacent Tumnin River in the Russian Far East at sampling latitudes (48.5–49.3°N) that were equivalent to those of Arai et al. (2004). Both the Koppi and Tumnin rivers have no lagoons but drain watersheds 10–30 times larger than the rivers studied by Arai et al. (2004) or Honda et al. (2010). Therefore, the migration phenotypes of Sakhalin taimen appear to be governed by a complex set of factors including latitude, the presence or absence of brackish lagoons, and drainage size, all of which may collectively influence trade-offs in productivity between fresh and marine waters (Kendall et al. 2015).

We believe that the sea-run Sakhalin taimen whose otoliths were analyzed in this study were those that had been repeatedly blocked by the Hokushin Dam during past spawning migrations. This could have been more directly tested if we captured adults at the dam site and analyzed their otoliths to determine whether they had the Hokushin isotopic signature at their otolith cores and a marine signature near the edge; we chose not to do so to minimize the mortality associated with this study. Sakhalin taimen possess a very strong instinct to return to their natal streams over multiple years to spawn. Field observations of facial and body marks and scars have been used to identify the same Sakhalin taimen individuals repeatedly returning to the same stream reaches for spawning over multiple years (E. Komiyama, Wild Salmon Research Institute, pers. comm. 2018). This strong philopatric instinct, however, may hinder spawners stuck behind migration barriers from seeking alternative spawning streams and thereby sustaining metapopulation dynamics at the watershed scale (Pearse et al. 2009; Winans et al. 2015).

Our primary conservation concern is that the unidirectional migration of Sakhalin taimen out of the Hokushin Reservoir will remove genetic variations associated with anadromy from the semi-landlocked source population and promote selection against anadromy in the remaining above-dam population (Pearse et al. 2009; Hayes et al. 2012). The reservoir fish could be eventually replaced with those with a less migratory phenotype, and if so, the land-locked population may not be capable of reverting to anadromy even if downstream ecological connectivity is restored in the future. Whether and where adult Sakhalin taimen blocked by the migration barrier could spawn in the Koetoi basin is unknown. Equally unknown is the number of individuals emigrating from the Hokushin Reservoir relative to the population size remaining above the dam. Moreover, we lack an understanding of the migratory characteristics of the other two artificially land-locked Sakhalin taimen populations in Hokkaido. Further research is needed to address these questions to ensure the sustainability of these reservoir populations, which may be some of the few viable populations of Sakhalin taimen remaining in their historical range in Japan.

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