

# Spawning behaviour of Sakhalin taimen, *Parahucho perryi*, from northern Hokkaido, Japan

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**Abstract** A video camera mounted in an underwater housing and remotely operated was used to monitor the behaviour of five different Sakhalin taimen (*Parahucho perryi*), females and attendant males spawning in three coastal tributary streams in Northern Hokkaido, Japan. Based on three complete and two incomplete spawnings, we describe in detail for the first time the complete spawning behavioural repertoire of this species. The Sakhalin taimen was originally placed within *Hucho*, then removed from that genus based on morphological, life history and molecular data. Our study supports that removal—none of the behavioural traits we recorded clustered *Parahucho* with *Hucho* uniquely. Similarities between the two genera were all plesiomorphic traits that are widespread throughout the salmonines. The immediate behaviour right after spawning was found to be a major difference between *Hucho* and *Parahucho*. Like female *Oncorhynchus* and *Salmo*, Sakhalin taimen females cover their eggs by beats of their tails immediately after spawning. This is different from the “rest, then cover” behaviour shown by Siberian taimen

(*Hucho taimen*) as well as lenok (*Brachymystax lenok*), supporting again that the Sakhalin taimen be removed from *Hucho* and placed in its own genus.

**Keywords** Underwater video · Spawning act · Salmonines · Phylogeny

## Introduction

Sakhalin taimen, *Parahucho perryi*, is a salmonid fish inhabiting Far East Russia including the Sakhalin and Kuril Islands, and the northernmost island of Japan, Hokkaido (Edo et al. 2005). It is a long-lived and slow growing species; sexual maturity occurs at 6–8 years, with peak fecundity occurring at approximately 15 years (Zolotukhin et al. 2000). Like many other salmonids, it is iteroparous, spawning in the spring (Holčík et al. 1988) and diadromous; many populations migrate to the ocean during their adult feeding stage (Gritsenko et al. 1974; Edo et al. 2005).

The Sakhalin taimen was originally placed in *Hucho* based on morphological similarities with *Hucho hucho* (Kimura 1966; Holčík 1982; Holčík et al. 1988). It was then moved to *Parahucho*, a subgenus of *Hucho*, based upon differences in additional morphological traits, including the presence of basibranchial plate with teeth, shape of the frontal bones, fewer scales in the lateral line, fewer vertebrae, the presence of a hypoethmoid and the position of the supraethmoid; the latter two traits also distinguished it from *Brachymystax* (Matveev

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et al. 2007 and references therein). Vladykov and Gruchy (1972) suggested that *Parahucho* be removed from *Hucho* and elevated to genus status based on its unique morphological and karyotypic traits. More than three decades later, Crespi and Fulton (2004 and references therein) combined all available nuclear and mitochondrial DNA data using maximum parsimony, maximum likelihood and Bayesian analyses. Their total evidence study unambiguously placed *P. perryi* in a clade with *Salmo* + *Salvelinus* + *Oncorhynchus*. Distribution of SLMII SINEs provided further support for this classification (Matveev et al. 2007), as did genetic distance data; the divergence between *P. perryi* and either *Hucho* or *Brachymystax* is always significantly greater than the divergence between *Hucho* and *Brachymystax* irrespective of data type or method of calculating genetic distance (Shed'ko et al. 1996; Oleinik and Skurikhina and references therein).

To date then, morphological, life history and molecular data support the removal of the Sakhalin taimen from *Hucho*. We were curious to know whether behaviour also agreed with that assessment. Behavioural traits, particularly those displayed during breeding, have been used for decades to make taxonomic decisions and reconstruct phylogenetic relationships across a wide variety of taxa (Brooks and McLennan 2002 and references therein). We soon discovered that the only two manuscripts published in English about Sakhalin taimen spawning focused on the morphology and distribution of redds—elliptical areas of disturbed gravel containing the nests (Fukushima 1994; Edo et al. 2000). There were no accounts describing the actual behavioural characters involved from arrival on the spawning grounds to gamete release. To rectify this situation we videotaped five Sakhalin taimen females spawning in three coastal rivers of northern Hokkaido, Japan. Our goals for this study were twofold: (1) to provide as complete a description of the spawning sequence as possible and (2) to establish whether behavioural traits placed the Sakhalin taimen within *Hucho*, as originally described, or supported its more recent placement into *Parahucho*.

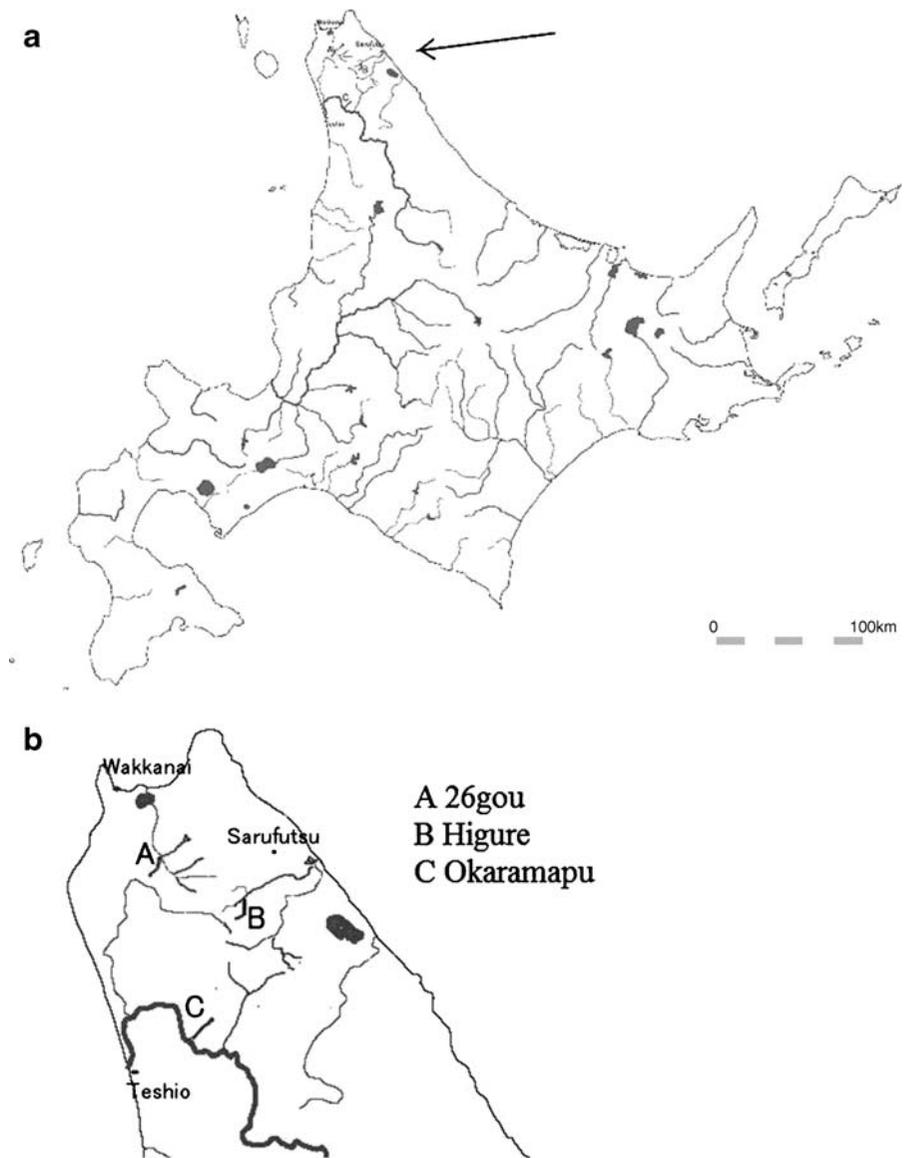
## Methods

A Sony TRV 900 colour digital video mounted inside an underwater housing was used to monitor

the mating activities of five females, associated with a variable number of males. Video signal from the camera was transmitted via cable to a digital recorder located outside the river. Recordings took place in northern Hokkaido at the Okaramapu, 26gou and Higure streams in April–May, 2007 (Fig. 1). The Okaramapu is a first order stream, flowing 5.5 km from its source at Onobunai Horonobe until it joins the Teshio River. From this point the river flows for another 35 km until reaching the Sea of Japan at Teshio town in Northwest Hokkaido. Females 1 and 2 were recorded in a stretch of the stream, average width 1–3 m, which traversed an open grass field. The 26gou is a first order stream flowing 3 km from its source in Numakawa until joining the Koetoi River. From this point the river flows for another 17.5 km until reaching the Sea of Japan at Wakkanai in North Hokkaido. Female 3 was recorded in a stretch of the stream, average width 1–1.5 m, which traversed an open grass field. The Higure is a first order stream flowing 7 km from its source at Mt Horosiri before joining the Karibetsu River. From this point the Higure-Karibetsu flows for another 25.5 km until reaching the Sarufutsu River and continues for another 0.5 km until reaching the Sea of Okhotsk at Hamasarufutsu in Northeast Hokkaido. Females 4 and 5 were recorded in a stretch of the stream, average width 2–3 m, flowing through a dense mixed forest formed by elm, alder, willow, Japanese oak and bamboo grass. White spotted charr, *Salvelinus leucomaenis* and masu salmon, *Oncorhynchus masou* inhabit the Okaramapu and 26gou, masu and pink salmon, *O. gorbuscha* are found in the Higure.

The camera was positioned approximately half a meter from the redds in which nesting females had previously been noted. Redds were located in tail pool areas with decreasing water depth ranging from 0.5–0.3 m and increasing flow velocity. Males and females presented no noticeable sexual dimorphism except for the difference in colouration, which was very pronounced; males were spotted on the anterior half of their body and red on the posterior half, while females were spotted overall. Behaviour was used to confirm sex. The fish slightly behind the other, intermittently performing *quivering* (courtship behaviour consisting of low amplitude and high frequency body vibrations from head to tail) was

**Fig. 1** Location of the three coastal rivers of this study in Northern Hokkaido



identified as the male, while the female was the fish that regularly performed *nest digs* (female turns on her side and excavates a depression in the gravel by beats of her tail). The number of female digs and male quiverings were recorded from the videotapes, as well as the number and characteristics of males around each female. The relative length of the nesting female and the males around her were only visual estimates to avoid disturbing the fish by trapping them for measurement. Males around female 4 were identified individually by facial and/or body marks or scars.

## Results

A total of 512 min of behavioural interactions, 843 quiverings (by 9 males) and 337 digs (by five females) were recorded. The following behaviours were identified from the videotapes:

*Probing* the female lies on the nest with her tail raised, pressing her anal fin into the gravel.

*Nest starting digs* high number of tail beats (7–14) per digging episode, female progresses upstream

while digging (1–2 m approximately), high tail beat intensity, visually judged according to the velocity with which the female repetitively flexed her tail and by the amount of gravel moved.

*Nest finishing digs* low number of tail beats (3–6) per digging episode, female concentrated the digging in one location, medium tail beat intensity.

*Egg covering digs* low number of tail beats (3–5) per digging episode, female progresses while digging (0.5–1 m approximately), low intensity tail beating.

*False spawning* female assumes the spawning position, gaping her mouth and trembling, but does not release eggs.

*Spawning act* pair releases gametes while trembling and gaping.

*Displacement quivering* male trembles his body away from the female. Differs from normal quivering by having a larger amplitude and shorter frequency.

*Lateral display* two males swim in parallel with their fins erected and their noses pointing upwards, often followed by one of the males turning and biting the opponent.

Female 1 was recorded at the Okaramapu stream on April 23 (N.44°55'54.95" E.141°55' 14.06"; Table 1). Recordings started at 13:06 with the female actively involved in *nest finishing digs* (concentrated in a single spot). A male, approximately the same length as the female, constantly approached her,

crossing over her dorsal area to alternate sides. At 13:14 the female started to repetitively perform *probings*. At 13:23 another male, about the same size as the guarding one, approached and was immediately chased away by the guarder. At 13:32 and 13:33 the female performed two *false spawnings*. The pair spawned at 13:34, the *spawning act* lasted for 11 s. The female performed her first *covering digs* with gentle beats of her tail 9 s after releasing her eggs. The male remained with the female after spawning until 13:38 when he left the area and never returned. Recordings ended at 14:02 with the female involved in building a new nest slightly upstream of the first one.

Female 2 was recorded at the Okaramapu stream on April 25 (15 m upstream from the preceding location; Table 1). Recordings started at 13:41 with the female actively involved in nest building using *nest finishing digs*. One male was recorded quivering and guarding her. At 13:51 and 14:01 the female performed her first two *false spawnings*. At 14:04 she performed the third and fourth *false spawnings* separated by 11 s. For unknown reasons the water suddenly turned brown and the pair left the area when, based on their behaviour, spawning was imminent.

Female 3 was recorded at the 26gou stream on April 27 (N 45°16'25.28" E 141°47'46.62"; Table 1). Recordings started at 12:55 with the female involved in the last stages of nest building (*nest finishing digs*). One male, approximately the same length as she, was present during the entire recording period. The pair spawned at 13:22, the spawning act lasted for 9 s. The female performed her first *egg covering digs* with gentle beats of her tail 5 s after spawning. The male remained with the female until recordings were ended

**Table 1** Recording history of 5 Sakhalin taimen nesting females at three rivers in northern Hokkaido

Female #	Location, date & time	Min recorded		# Digs		# Quivers		# Males
		b	a	b	a	b	a	
1	Okaramapu, April 23 13:06–14:02	28	28	28	19	84	0	1
2	Okaramapu, April 25 13:41–14:06	25	–	17	–	52	–	1
3	26gou, April 27 12:55–13:24	27	2	22	5	64	0	1
4	Higure, May 5 13:00–18:47 PM	346	–	183	–	568	–	5
5	Higure, May 6 17:23–18:19 PM	47	9	50	13	70	5	1
Total		473	39	300	37	838	5	10
		512		337		843		

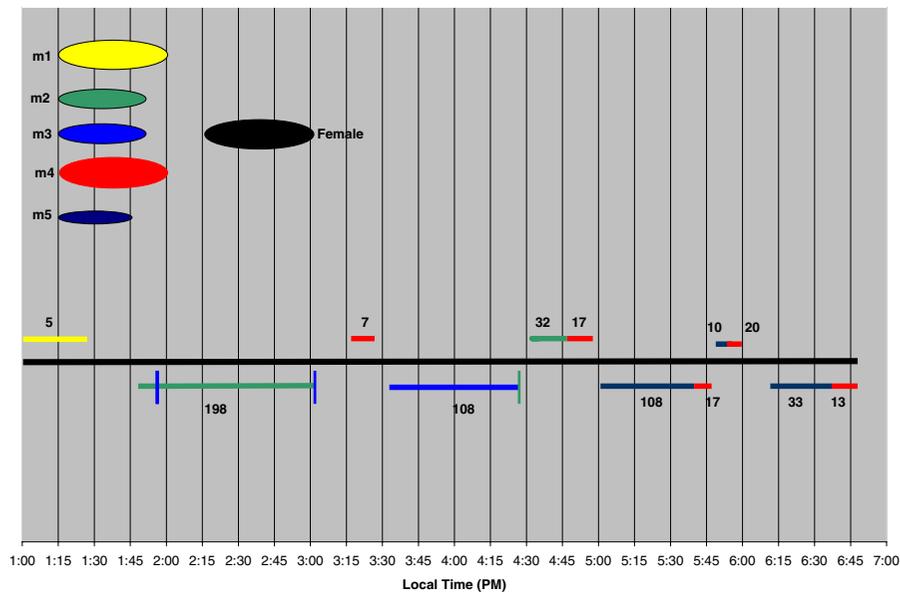
b = before spawning;  
a = after spawning

at 13:24 following a sudden decrease in water visibility to almost zero.

Female 4 was recorded at the Higure stream on May 5 (N 45°11'08.66" E 142°02'21.47; Table 1). Recording started at 13:00 and continued uninterrupted until 18:47 when light levels were too low to be captured by our camera. Five different males interacted with the female during this period (Fig. 2). The first male guarding the female (m1), remained passive for most of the time, only performing five quiverings over 25 min before leaving the area. Twenty minutes later a second male (m2) arrived and started to court the female. At 13:50 a third male (m3), approximately the same size as m2, approached and challenged m2. The two males frequently performed lateral threat displays and fought over the nest, leaving together twice to fight away from the nest. During the first of those absences another male (m4), about the same length as the female, approached and courted the female for 10 min, then left. Six minutes later, m3 returned and began guarding and courting. M2 returned 55 min later and the two males resumed their fight, leaving together for the second time. After 2 min m2 returned and resumed his role as guarding

male. M4 reappeared (80 min after his original departure) and chased away the smaller m2. From this point onwards the behaviour of m4 followed a similar pattern. He remained courting the female for short periods of time and then left voluntarily, returning at a later time (Fig. 2) and rapidly chasing away the small guarding male (m5) that had moved in during his absence.

Female 5 was recorded at the Higure stream on May 6 (N 45°11'16.31" E 141°02'16.27"; Table 1). Recordings started at 17:23 with the female alone performing *nest starting digs* (7–12 tail beats/digging episode) over a large area. At 17:33 a male of approximately the female's size arrived and remained courting and guarding her. At 17:36 the male left the area. He returned 13 min later and remained with the female for the rest of the recording period. From 17:50 onwards the female displayed *nest finishing digs* (concentrated in a single spot, low number [3–6] of tail beats). From 18:00 she performed repetitive *probing*s. From 18:06 to 18:09 the female performed a total of five *false spawnings*. The pair spawned at 18:10; spawning lasted 11 s. The female performed her first *covering dig* 12 s after spawning.



**Fig. 2** Recording history of female 4. Black horizontal line represents the female. Coloured lines represent each of the five courting males. Segments of black line with no coloured lines above or below represent time the female was alone at her nest. Vertical lines indicate fighting with another intruding male (i.e.

the vertical blue line crossing the green line before 14:00 indicates that m3 came to the nest while m2 was guarding; after some seconds or a few minutes of fights and displays m3 was expelled from the nest). The number of quiverings by each male is included

The male remained with the female and began to quiver her again 4 min later. Recordings ended at 18:19 because of low light levels with the female involved in building a new nest upstream from the previous one.

## Discussion

This is the first study to investigate Sakhalin taimen spawning behaviour based on underwater observations. Those observations indicated that the behavioural repertoire of Sakhalin taimen generally resembles that of other salmonines. Females invest their time building and testing their nests, while males invest their time guarding and courting nesting females (Groot 1996; Schroder 1981). As nest building progressed, female digging behaviour changed gradually from intense tail beats that moved the female forward while displacing large amounts of gravel to fewer tail beats concentrated in a single spot. As the nest approached completion, the female periodically tested its depth and condition by *probing* with her anal fin. The female could then either perform *false spawnings* (females 1 and 5) or move directly to spawning (female 3), during which both partners gaped and trembled while releasing gametes. The three females that were recorded spawning performed *egg covering digs* within 12 s of egg release. Females covered their eggs with a small number of gentle tail beats (3–5 beats per digging session) while progressing approximately 1 m along the redd, alternating her travelling direction to follow a V shape described for other Sakhalin taimen (Fukushima 1994; Edo et al. 2005).

Contrary to a previous study with Siberian taimen (Esteve et al. 2009), numerous male fights and several mate changes occurred in the redd area (Fig. 3). Apparently, unlike Siberian taimen which are thought to have the unusual strategy of pair bonding days or weeks before reaching the spawning grounds (Holčík et al. 1988; Witkowski 1988), pair formation in Sakhalin taimen follows the general salmonine pattern of occurring on the spawning grounds throughout the breeding season (Edo personal communication; our observations with female 4.). During lateral displays Sakhalin taimen males swim in parallel, pointing their noses upwards, which is similar to the display shown by sockeye (*Oncorhynchus nerka*) and pink salmon



**Fig. 3** Sakhalin taimen male bites a competitor. This interaction occurred in the nest area with the female present

(*O. gorbuscha*) (Esteve and McLennan 2007). On several occasions males were seen performing *displacement quiverings* away from the female. This behaviour, which is widespread throughout the salmonines, probably occurs when a highly motivated male is not getting sufficient feedback from his spawning partner. At no point during the study was either male digging (a behaviour commonly displayed by *Oncorhynchus*) or the presence of precocious maturing parr (present in *Salmo*, *Salvelinus* and some *Oncorhynchus* species: Esteve and McLennan 2007) observed.

Recordings with female 4 involved five different males, each at some point quivering and guarding her. Based on the behaviour of the first male (m1) and the female it is very likely that a *spawning act* occurred just prior to our recording. This suggestion is based on two observations. First, when recordings started female 4 was performing few tail beats per digging session, which gradually increased as time passed; a pattern that corresponds to the normal transition between *egg covering digs* and *nest starting digs*. Second, m1 performed very few quiverings even though he was with the female for 25 min. This pattern resembles that shown by female 5 and her partner, who performed 1.5 and 0.6 quiverings per minute pre- and post-spawning respectively (Table 1). Given that the rate of quivering has been shown to increase as spawning approaches in other salmonines (Tautz and Groot 1975; Gaudemar and Beall 1999; Berejikian et al. 2000), this low level of activity implies that spawning is still far off for female 4.

Coming in at the very beginning of a spawning cycle allowed us to observe competitive interactions between males as the female worked on her nest. As has been noted for other salmonids, fights occurred more often between same-sized opponents (m2–m3), larger males displaced smaller ones simply by chasing them away (m4 and m2, m5). The particular male guarding female 4 was very fluid, changing 12 times during the 345 min observation period. Within this fluid system, m4 seemed somewhat anomalous. He was large enough to monopolize the female, yet he repeatedly left her, returning to chase away smaller challengers. One possible explanation for this pattern is that males are capable of using the appearance of behaviours such as *nest finishing digs* and *probing* to assess how close a female is to spawning. If a female is in the initial—middle stages of nest building, it might pay the male to leave her every so often to search for and court a female that is closer to egg release. If m4 was indeed following this strategy, then he may have gained an unexpected benefit by leaving the female alone when she was not close to spawning—other males expended time and energy courting and quivering her. Overall, of the 291 min that the female was being guarded, m4 contributed only 17.2% of the total courtship (13% of the quiverings). When recordings ended, female 4 was performing *nest finishing digs*. Given that m4 was alone with her then, having chased m5 away, it is probable that he spawned with her. So, as long as a male can reliably predict when a female is getting close to spawning based on her behaviour, and if he is large enough to displace most challengers, he can move throughout an area visiting different females, leaving other smaller males to court each female in his absence, returning to spawn when a female's behaviour indicates that she is ready. This suggestion is, of course, based on very limited observations. In order to examine the idea further we need data from this and other salmonine species that engage in male–male competition for access to a nesting female.

None of the behavioural traits we recorded clustered *Parahucho* with *Hucho* uniquely. Similarities between the two genera were all plesiomorphic traits that are widespread throughout the salmonines (e.g., normal and displacement quiverings, nest diggings). This latter result is important because, prior to the advent of phylogenetic systematics, taxa were often clustered based on plesiomorphic traits since such traits made it look like the taxa were “similar”.

Plesiomorphies, however, provide no information about relationships among taxa within a clade because they evolved either before, or in, the ancestor of the clade (Brooks and McLennan 2002). The behaviour “cover eggs right after spawning”, however, clustered *Parahucho* with *Salmo* and *Oncorhynchus*, and separated it from *Hucho* and *Brachymystax*, whose females rest after spawning for approximately 3–5 min before covering their eggs and *Salvelinus*, whose females ventilate their eggs with strokes of their tail while maintaining a normal (not on their side) posture, (Esteve and McLennan 2008). This behaviour thus supports molecular, morphological and life history traits separating Sakhalin taimen from members of the *Hucho* family (Phillips et al. 1995; Kimura 1966; Zolotukhin et al. 2000).

*Parahucho perryi* is currently listed as critically endangered by the IUCN. Molecular analyses of both mitochondrial and nuclear genes have revealed that it is characterized by very low genetic diversity indices, translating into low values of mean heterozygosity within populations (Oleinik and Skurikhina 2008). This, combined with its slow growth rate and low fecundity, makes individual populations vulnerable to extirpation by anthropogenic influences such as over harvesting and habitat degradation, and this is exactly what is being observed at the moment; surveys indicate that population sizes are decreasing in Russia, while anecdotal observations report a similar trend in Japan (Rand 2006). Underwater video allowed us to compare spawning habitats in the three streams of this study. The Higure flows through a dense forest, free of human disturbance other than a controlled access, unpaved road that runs 25–50 m away from, and parallel to, the stream. This stream was the easiest of the three to film in, although it did suffer a little from reduced visibility produced by the heavy snow melt in northern Hokkaido at the end of April and early May. The Okaramapu and 26gou streams, on the other hand, traverse fields cleared for cattle grazing. This is a critical problem because removing trees and shrubs can lead to an increase in silt washed into the water during periods of intense rain and high flow (e.g., following snow melts: Jolicoeur et al. 2007 and references therein). This is exactly what was found in the Okaramapu and 26gou, in which sudden increases in turbidity forced us to stop recording either because the fish left or because visibility was reduced to virtually nothing. Not only

did the turbidity interfere with spawning, which is after all a very visually-based process, it also deposited silt, sand and other fine particles over the nests; something that has been shown to have detrimental effects on embryo survivorship in salmonids (Laponte et al. 2004 and references therein). The situation is even worse in 26gou because the stream has been artificially channelized along most of its length and thus lacks the normal succession of pools, riffles and glides typical of salmonid spawning grounds. Our observations thus provide an explanation for Rand's (2006) report that population sizes of Sakhalin taimen appear to be decreasing in Japan. If we are to reverse this trend we need conservation strategies informed by as much data as we can collect, particularly data concerning the spawning requirements and behaviours of this species. Our study represents a step in this process, one that we hope will stimulate future research on this enigmatic and endangered fish.

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