Conservation biology on endangered salmonid species Sakhalin taimen *Hucho perryi* inhabiting river basins of eastern Hokkaido.

(北海道東部の河川に生息する絶滅危惧サケ科魚種イトウの保全生物学)

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Contents

Abstract 4

Introduction 7

Study Area 10

Methods 14

1. Observations of spawning activities of Sakhalin taimen and rainbow trout and their interactions with rainbow trout 14

1.1. Estimation of number of redds per female 14

1.2. Observation of redd superimposition 14

1.3. Measurement of water velocity, water depth and pebble size on each redd 15

1.4. Species identification of each redd 16

1.5. Measurement of egg burial depth 17

1.6. Statistical analyses 18

2. Observation of hatch and behavior of Sakhalin taimen juveniles 18

3. Evaluation of factor threatening Sakhalin taimen 21

3.1. Estimation of distribution and abundance of Sakhalin taimen 21

3.2. Extraction of environmental variables accounting for distribution or abundance of Sakhalin taimen redds 22

3.3. Evaluating impacts of dams on Sakhalin taimen abundance 23

3.4. Statistical analyses 23

Results

1. Spawning activities of Sakhalin taimen females and their interaction with rainbow trout 24

2. Hatch and behavior of Sakhalin taimen juveniles 29

3. Abundance of Sakhalin taimen and environmental factors threatening them in eastern Hokkaido 30

Discussion

1. Impacts of introduced rainbow trout on Sakhalin taimen 34

2. Behavioral ecology of Sakhalin taimen juveniles in their natal stream 38

3. Population status and extinction risk of Sakhalin taimen 42

4. Factors threatening Sakhalin taimen 42

5. Possible pathways from grazing land to taimen's redd abundance 43

Conservation implications 45

Acknowledgements 46

References 47

Tables 63

Figures 72

Abstract

Sakhalin taimen, (*Hucho perryi*), is one of the largest (reaching up to 1.5 m and 40 kg) and most ancient salmonids in the world. They have been rapidly diminished in the last few decades, and listed under "Critically Endangered" in the IUCN red list. It is urgently required to know their behaviour, abundance and distribution of the species to avoid ongoing local extinction. However, little knowledge has been accumulated so far, although such information is critical for reasonable management and conservation. The present study was carried out in eastern Hokkaido where Sakhalin taimen was breeding in many tributaries of nine river basins until the 1960s but has been endangered to extinction since dairy farming were rapidly developed thereafter. First of all, to obtain the primary information of their ecology, I studied breeding activities of Sakhalin taimen in an upstream tributary of the Furen River which drains into the blackish waters of Lake Furen inhabited by this rare fish species throughout a year. In the spawning season from early April to early May, Sakhalin taimen female typically spawned at five different locations with pebble size (8−64mm in diameter), therefore, it was determined that five redds were made by one female spawner. In addition, number of females spawned could be estimated as one fifth of the observed redds

This tributary was also inhabited by another salmonid species rainbow trout which had been introduced in eastern Hokkaido especially since the 1970s, and I found that the spawning season of the two salmonid species were extensively overlapped with each other and the spawning activity of rainbow trout harmfully disturb the breeding of Sakhalin taimen. Much more than the introduced competitor rainbow trout, however, the drastic change of land usage in eastern Hokkaido has seriously damaged the habitats of Sakhalin taimen, and I analyzed the effects of the land use change on the abundance and distribution of Sakhalin taimen's redds in 64 tributaries of nine river basins in eastern Hokkaido, where Sakhalin

taimen was reported to be present in the 1960s. I walked through each tributary to search for Sakhalin taimen's redds (spawning nests) in their spawning seasons and also electrofished to capture newly emerged fry. The results suggest that as many as 75% of local populations have become extinct in the past five decades in this region. Based on redd count, estimated numbers of spawners were relatively abundant in two river basins (> 50 adults), extremely low (< 50 adults) in two river basins, and completely extinct in three river basins basins (no redd). Of 45 extinct subpopulations (tributaries), there is no migration barrier on 37(82%) tributaries.

Growth, migration, and density of Sakhalin taimen fry were studied in their natal stream of northernmost Japan. The fry emerged in the end of June and the beginning of July. Some of them stayed in the natal river for more than one year up to two years (residents) and the others migrated downstream (migrants) which began when water discharge increased. The migration occurred only at night, in particular shortly after the sunset. The residents captured by electrofishing were larger in both the fork length and fatness index than migrants captured by a drift sampler. The densities of residents were limited to some level. Thus, the carrying capacity of natal stream possibly regulates population densities, and so, this kind of stream is considered to be very important not only as a spawning habitat but also as a nursery habitat from the viewpoint of conservation of this species.

I investigated main factors depopulating the species in the same region, by correlating number of redds and environmental variables in 32 tributaries of two neighboring river basins. The livestock grazing is the most widespread land use in the study area at present. The land use of eastern Hokkaido has been dramatically changed from forest area and/or bushland to livestock grazing land since the 1960s. An information theoretic model suggested that the percentage of the watershed grazed, suitable spawning area, and the interaction of the two were important for Sakhalin taimen's persistence. This model also suggested that the cumulative level of livestock grazing in the past five decades has resulted in as many as 52.8% reduction of Sakhalin taimen redds. The rapid extinction of Sakhalin taimen populations in the study area was probably mainly due to the rapid expansions of livestock grazing area. Percentage of fine sediments within suitable spawning sites was positively related to percentage of the watershed grazed but negatively related to taimen's redd abundance. This result may suggests that sedimentation of silt and sand caused reduction in taimen's redd abundance, reducing egg incubation success because of soil washout from the adjacent grazing land.

To develop management strategies that minimize cumulative effects of livestock grazing on the endangered population, I forecasted the number of Sakhalin taimen's redds in response to simulated changes of percent grazing land based on the same model. Consequently, the increases in livestock grazing from 5% to 50% of the all study watershed grazed are predicted to reduce Sakhalin taimen redds from 13.9% to 63.7%. On the other hand, declines in livestock grazing from 5% to 50% of the basins are predicted to increase the abundance from 5.6% to 40%.

Habitat fragmentation by damming has serious consequences for freshwater ecosystems due to its 'barrier effects'. I assessed the effect of habitat fragmentation by damming on Sakhalin taimen in two tributaries that were not influenced by livestock grazing. Estimated number of redds in 20 years ago (immediately before dam constructions) were 147.6 and 3.4 redds, respectively, based on the model previously mentioned. The large difference between two basins enabled us not only to select more important tributary but also provide most reasonable management idea for increasing the population size in the whole river basin. The estimated redd abundance in one tributary was even much greater than the current redd abundance in the whole river basins. These estimations can be used to develop management strategies for conservation of the endangered species population.

In addition to the endangering effects of habitat fragmentations and watershed disturbances, invasive alien species can also be a serious threat to the conservation of freshwater fish. I document that spawning redd disturbance by artificially introduced rainbow trout (*Oncorhynchus mykiss*) on Sakhalin taimen redd. Sakhalin taimen and rainbow trout are the only spring-spawning salmonid species in Hokkaido. In 2006–2008, spawning activities of both these species were observed in a Hokkaido stream, and it was determined that their spawning periods overlapped during mid–late April. They also spawned at similar water velocities, depths, and substrate compositions. Although female Sakhalin taimen were larger than female rainbow trout, their egg burial depths were nearly identical. During the observation period, rainbow trout redds were approximately 5 times more abundant than Sakhalin taimen redds, and about 30% of the observed Sakhalin taimen redds were superimposed by rainbow trout redds. The high degree of spatial and temporal overlap in spawning, the similar egg burial depths of both species, and the high proportion of superimposed redds suggest that the introduced rainbow trout impact the endangered Sakhalin taimen in Hokkaido, and possibly, in other areas where the two species occur together.

As aforementioned, various threats to Sakhalin taimen population co-exist in eastern Hokkaido streams. However, river managers must consider practically about watershed management plan that minimize the threats to the taimen population in present situation.
To prevent them from extinction, it is urgently required to increase the population size. On the other hands, installing efficient fish ladders or removing dam is one of steps that provide immediate effect on increasing in taimen's redd in dam-installed tributary which is not influenced by watershed disturbances and have high level of potential spawning habitat.

Introduction

Since the industrial revolution in the 1700s, the numerous species have rapidly become extinct due to anthropogenic disturbance (Wilson 1992). And such extinctions are apparently ongoing every day (approximately 100 species per day) (IUCN 2009). It is one of the largest problems for humankind to rescue the endangered species from extinctions.

Sakhalin taimen (*Hucho perryi* or *Parahucho Perryi*) is the largest (reaching up to 1.5 m and 40 kg) and most ancient salmonid species in the world. They are distributed in Far East Russia including the Sakhalin and Kuril Islands, and the northernmost island of Japan, Hokkaido (Edo et al. 2005). They have long life spam up to over 20 years and grow slowly; sexual maturity occurs at 6–8 years, with peak fecundity occurring at age of about 15 years (Zolotukhin et al. 2000). It is iteroparous, spawning in the spring as well as many other salmonids, (Holčík et al. 1988) and diadromous; many populations go to the ocean (Gritsenko et al. 1974; Edo et al. 2005). In systematics, 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 on differences in additional morphological characteristics such as teeth, bones, and scales (Matveev et al. 2007). In addition to the morphological information, some researchers suggested that *Parahucho* should be removed from *Hucho* and elevated to genus status based on genetic differences in nuclear and/or mitochondrial DNA data (Oleinik and Skurikhina 2008; Crespi and Fulton 2004; Shed'ko et al. 1996). Therefore, Sakhalin taimen has become to be regarded as different from genus *Hucho* based on such information about morphological, life history and molecular characteristics in recent years (e.g. Estive et al. 2009; Shed'ko et al. 1996; Oleinik and Skurikhina 2008). In Hokkaido Island, Sakhalin taimen were reportedly present in over 42 River Basins in the 1960s; however, their distribution rapidly diminished to

24 river basins by 1980 (Fukushima 2008) and only 13 basins by 2008 (Edo 2007; present study). That is, 70% of the populations had gone extinct just during the past 50 years. At present, Sakhalin taimen is in danger of extinction, and has been listed under 'Critically Endangered' in the IUCN red list (IUCN 2006).

IUCN (1988) proposed four main factors of species extinction and decline: (1) habitat loss and fragmentation, (2) invasive species, (3) environmental pollution and (4) overexploitation. Although all these four may apply to Sakhalin taimen in Hokkaido, our understanding about the reason of rapid population declines is limited. In addition, the depopulating factor varies among species and, moreover, the extinction mechanism is closely linked to the species-specific behaviors and life histories of animals (Caro et al. 1998).

First of all, to obtain the primary information of their ecology in order to conserve an endangered species, I studied breeding activities of Sakhalin taimen in a tributary, which was also inhabited by another salmonid species rainbow trout (*Oncorhynchus mykiss*). Rainbow trout, whose native range stretches along the Pacific coast of North America and the Kamchatka Peninsula, have been introduced in 97 countries worldwide for recreational fishing purposes and as a food resource (Fausch 2007; Crawford & Muir 2008). The species has succeeded in establishing new populations in many areas (e.g., Crowl et al. 1992; Fausch et al. 2001; Pascual et al. 2002; Cambray 2003; Simon & Townsend 2003; Kitano 2004; Baxter et al. 2007; Crawford & Muir 2008), possibly because of their diverse life history forms, [e.g., anadromous (steelhead), fluvial, adfluvial, and resident (Van Velson 1974; Busby et al. 1996; Meka et al. 2003; Riva Rossi et al. 2004)] and their variable spawning timing (from November to July; Busby et al. 1996). Rainbow trout have hybridized with other rare species, such as inland cutthroat trout (*O. clarki*) (Allendorf & Leary 1988; Weigel et al. 2003), and have replaced native brook trout (*Salvelinus fontinalis*) throughout the long reaches of some southern Appalachian streams (Larson & Moore 1985). As a result, rainbow trout belong to the '100 of the world's Worst Invasive Species' list prepared by the International Union for the Conservation of Nature (IUCN) (IUCN 2000). In Hokkaido, rainbow trout were first introduced in the 1920s for use in aquaculture. By 1996, they were present in more than 70 catchments because of accidental or purposeful release into lotic and lentic environments (Takami & Aoyama 1999). Their invasion in Hokkaido is apparently continuing (Fausch et al. 2001). Before invasion by rainbow trout, Sakhalin taimen were only spring-spawning salmonids in Hokkaido and had not been exposed to interspecific competition with other native, fall- and/or winter-spawning salmonids, e.g., masu salmon (*O. masou*), pink salmon (*O. gorbuscha*), chum salmon (*O. keta*), and white-spotted charr (*Salvelinus leucomaenis*). Thus, I investigated the potential effects of introduced rainbow trout on the Sakhalin taimen population through redd superimposition (i.e. destruction of spawning nest) in a tributary of the Furen River, where these two salmonid species co-exist.

It is also crucial in the conservation biology of Sakhalin taimen to investigate the life history of newly emerged fry and juveniles. In many salmonids as well as other fish, the rate of mortality immediately after emergence from redds is very high, and so, this is the critical period of the life history for population regulation and growth (Ottaway *et al*. 1981; Elliott, 1986, 1987, 1994). Nonetheless, few ecological studies have been conducted in the juveniles of Sakhalin taimen. Therefore, the ecological studies in the period are needed. In this study, migration, growth and densities of Sakhalin taimen juveniles in their natal stream were surveyed for two years.

For developing action plan to rescue the Sakhalin taimen population from extinction, it is required to know precise population status at present, such as distributions and trends in abundance (Noss 1990) and to understand the causal factors in population declines.

Therefore, I also assessed the current distribution and abundance of the endangered Sakhalin taimen in eastern Hokkaido with extensive field survey, such as electrofishing and redd count.

I developed a statistical model to determine the factors affecting local tributary populations, especially focusing on human land use as potential factor. This model was further used for predicting past and future population status, which was very useful for population management. Based on these results, I discuss appropriate watershed management plans for conservation and restoration of the endangered Sakhalin taimen.

Study area

This study was made mostly in an area of Konsen region, eastern Hokkaido, and additionally in a tributary of Toikanbetsu River (one of numerous tributaries of Teshio River Basin), northern Hokkaido, Japan. Konsen region had been uncultivated due to its severe climate until the 1940s, and most of the land had been covered with peatlands, mires and mixed forests dominated by Japanese oak *Quercus crispula*, Japanese Alder *Alnus japonica*, Japanese White Birch *Betula platyphylla*, etc and floored with dwarf bamboos *Sasa senanensis.* Since the 1960s, western part of this area has been used by the Ground Self-Defense Force as The Yausubetsu Maneuver Area (1,680 km^2) or conserved as public forests (429 km^2). In contrast to the western part, eastern part of this area has rapidly been changed into broad grazing lands for domestic livestock especially since some agricultural laws were established in 1961 to promote the combination of small farms and the introduction of agricultural machinery. At present, the eastern part is extensively covered by dairy farmlands.

Thus, the study area in Konsen is now composed of relatively undisturbed forests, secondary forests, bamboo bushlands, grazing lands and some small residential areas, totally exhibiting a typical landscape in the Konsen region located in the Pacific coast climatic zone, with dry and chilly winters (mean temperature: −5.6°C in January) and cool and humid summers (17.9°C in August). According to the meteorological data at the Kushiro Meteorological Observatory (Japan Meteorological Agency 2008), the mean annual air temperature and mean annual precipitation are 6.0°C and 1,077 mm, respectively. Compared with other regions of Hokkaido, Konsen region has more foggy days in summer and lower snowfall, resulting in freezing of the peat soil in winter.

In this area, there are numerous low-gradient streams meandering through moor into the brackish waters (Lake Furen and Lake Akkeshi) and the Pacific Ocean. The stream beds are dominated by silt and sand with few pebbles and the streams drain through Konsen region underlaid by a volcanic stratum. The streams are inhabited by white-spotted charr, masu salmon, chum salmon, and pink salmon spawning in the autumn and/or winter and by Sakhalin taimen spawning in the spring. Five river basins of nine Konsen rivers surveyed in this study, i.e. The Furen, Yaushubetsu, Nishibetsu, Shunbetsu, and Tohoro Rivers) are also inhabited by introduced rainbow trout which spawn in the spring as well as Sakhalin taimen. In the 1940s, they were first introduced because of an accidental release from a fish-breeding pond which was connected with The Nishibetsu River. A rapid expansion of their distribution occurred particularly since the 1970s when additional rainbow trout were frequently released into the river for sport fishing purposes.

Populations of Sakhalin taimen have mainly been retained in mainstems of the river basins and brackish waters (Lake Furen and Lake Akkeshi), and only in the mating season, the adult males and females migrate to the upstream tributaries, and then Sakhalin taimen adults are easy to be discovered because of its large (>50 cm in total length) and brilliant-red colored body (in male) in small tributaries. After the adults finish spawning, they return to the above-mentioned habitats. I do not describe the location of the studied tributaries in detail to protect the critically endangered Sakhalin taimen (Category "Critically Endangered" in the IUCN red list) from fishing.

Observation of spawning activities of Sakhalin taimen and their interaction with rainbow trout were conducted in an upstream tributary of Furen River. The studied stream is sinuous with a low gradient (channel slope of about 0.65%), has a drainage area of 19.5 km^2, and is located at an average altitude of 70 m. The stream is 5–7 m wide and has a maximum depth of about 1 m. The surveyed reach was 6,380 m long and started at the stream mouth (lowermost of the surveyed reach). A preliminary survey revealed that there were no suitable salmonid spawning grounds upstream or downstream of the surveyed reach. At a fixed station near the stream mouth, daily water temperature and water discharge were monitored throughout the spring observation periods. The daily water temperature was recorded at hourly intervals using a data logger (Optic StowAway; Onset Computer Corp., Bourne, MA, USA). Water discharge was measured using the U.S. Geological Survey Mid-Section method (Orth 1983).

An additional study on the hatch and behavior of Sakhalin taimen juveniles was carried out in Seiwa Stream which is a tributary of the Toikanbetsu River, northernmost Hokkaido Japan (Fig. 9). Excluding the uppermost *ca.* 1 km reach where the stream is too narrow for Sakhalin taimen to migrate, this stream is *ca*. 3 km long and 1.5−3 m wide covered by a broad-leaved deciduous forests, dominated by alder *Alnus histuta* (Turcz), Wilows *Salix spp*, Japanese elm *Ulmusdavidiana* var. *japaponica* (Nakai), etc. and densely floored with dwarf bamboo *Sasa kurilensis.* Monthly mean air temperature ranges from −9.2 ºC (February) to 18.6 ºC (August) and annual precipitation is *ca.* 1241 mm at meteorological observatory of Teshio Research Forest, Hokkaido University, located about 10 km apart from Seiwa Stream.

The monthly mean water temperature in this stream ranges from 0ºC (December to March) to 15 ºC (June), and this stream was also inhabited by other fish such as masu salmon *Onchorhynchus masou*, fresh water sculpin *Cottus nozawae* (Snyder), brook lamprey *Lampetra reissneri* (Dybowski) and loach *Noemacheilus barbatula* toni (L.).

Methods

1. Observation of spawning activities of Sakhalin taimen and their interaction with rainbow trout

1.1. Estimation of number of redds per female

In spawning season from early April to late May 2005 and 2007, a weir was set up at two tributaries of the Bakanbeushi and Furen Rivers to count the number of Sakhalin taimen which had migrated to these streams for spawning. After they were released, I counted the number of their redds to estimate the mean number of redds constructed by one female in each stream

1.2. Observation of redd superimposition

In springs of 2006, 2007 and 2008, spawning activities of Sakhalin taimen and introduced rainbow trout were surveyed in an upstream tributary of the Furen River (Fig. 1), which drains into the brackish waters of Lake Furen. Redd construction and superimposition were surveyed almost every day throughout the overlapping spawning periods of Sakhalin taimen and rainbow trout. After one of the species had finished spawning, the surveys were continued to be performed almost every week until the other species finished spawning. During each survey, I walked along the river bank of the study reach and searched for spawning females and their redds. When a female spawner was observed, its body size was estimated by visually marking two stones on the stream bed. The distance between the selected stones was considered to be equal to the total body length of the spawner. After the female had left the area, the distance between the stones was measured (Maekawa et al. 1994; Taniguchi et al. 2000). The location of newly constructed redds was recorded by a differential global positioning system (Mobile Mapper Pro, Thales Navigation Inc., SanDimas, CA, USA). The redd was marked with four pegs stuck to enclose the redd tail. The shape and size (total length, and tail length and width) of the redds were recorded on a plan view of the redd. During each survey, redd superimposition was detected by examining the plan view. In this study, superimposition was defined as a disturbance of more than 50% in the tail area by a later spawner (Essington et al. 1998).

Sakhalin taimen and rainbow trout occasionally construct false redds which do not have egg pockets. For potential true redd, which are identified by their pit shape (V-shaped or not) or sizes (>140 cm in total length and >75 cm in tail width), the redd superimposition were recorded. In addition, I excavated the potential true redd, which had not been superimposed, to examine the probability that those actually have egg pockets. Results of the examination showed that the potential true redd for Sakhalin taimen could be distinguished from its false redds with 93% accuracy, while rainbow trout redds could also be distinguished from its false redds with 78% accuracy. On the other hand, a potential false redd for Sakhalin taimen could be distinguished from its true redd with 100% accuracy, while those for rainbow trout could be distinguished with 95% accuracy.

1.3. Measurement of water velocity, water depth and pebble size on each redd

At each redd, water velocity was measured 5 cm above the stream bed at two positions (A and T in Fig. 2) using a portable current meter (CR-7WP, Cosmo Riken Inc., Kashihara, Japan; as described by Tanida et al. 1985). Water depth was measured at four positions (A, P, T, and B in Fig. 2). In addition, substrate composition was determined by placing a 50 cm square metal grid (mesh size: 7 cm × 7 cm) on the stream bed adjacent to both sides of the redd tail and by classifying the diameters of 100 pebbles at the grid intersections into eleven categories (<2mm, 2–2.8 mm, 2.8–4 mm, 4–5.6 mm, 5.6–8 mm, 8–11.3 mm, 11.3–16 mm, 16–22.6 mm, 22.6–32 mm, 32–45.3 mm, 45.3–64 mm) using a template (US SAH-97; Wildco, Buffalo, New York, USA) according to methods described by Potyondy & Bunte (2002). In the present study, streambed substrate compositions were expressed as D50 (median diameter), which correspond to the 50th percentiles on the cumulative curve. These microhabitat measurements were conducted within seven days after a redd was first discovered.

1.4. Species identification of each redd

During the time of redd construction, the species present was immediately identified *in situ*. In the absence of spawner, the species of each redd was identified based on egg size, DNA sequencing or cultivation of eggs collected from one egg pocket per redd. When the accumulated daily water temperature reaches about 200ºC, the eggs are reported to be eyed and relatively tolerant to physical disturbance (Kawamula et al. 1996). Therefore, at that time, generally late May, all redds whose spawning species were unknown were excavated, and a few eyed eggs were collected from the upper area of each egg pocket for species identification. Based on species identification from DNA sequences (detailed in the next section) and on spawner observations undertaken in 2006, the diameter of eggs deposited by two salmonids were found to be 5.0–6.8 mm in Sakhalin taimen and 3.8–5.5 mm in rainbow trout. Therefore, in the 2007 and 2008 surveys, I considered eggs larger than 5.5 mm as those of Sakhalin taimen and those smaller than 5.0 mm as those of rainbow trout (Fig. 3. Species identification of medium-sized eggs from overlapping region (i.e., from 5.0 mm to 5.5 mm in diameter) was performed by egg cultivation as follows. Ten to twenty eyed eggs were collected from each egg pocket and reared in a mesh cage placed in flowing water drawn from a natural stream. Each eyed egg hatched to a fry after 50–60 days of cultivation. Sakhalin taimen and rainbow trout fry were discriminated from each other based on parr marks and body morphology.

DNA analysis: Prior to performing species identification by DNA analysis, new primers were developed by analyzing the control region of mitochondrial DNA extracted from eyed eggs of eight Sakhalin taimen and eight rainbow trout redds. A comparison of DNA sequences between the two fish species found relatively abundant substitutions in a 214-bp region, and the side sequences were used for developing new primers: OHCR-F1, GTATAATATTACATATTATGTATTTACCC and OHCR-R1, TGGTCGGTTCTTACTACATTAAG (Fig. 4). One and three haplotypes were observed from Sakhalin taimen and rainbow trout, respectively, and these sequence data were the same as the published data (Sakhalin taimen: position 161–373 in AY862364; Rainbow trout: position 3806–4019 in AY032631, position 15748–15961 in DQ288271, position 114–327 in AF044150). For species identification by DNA analysis, one eyed egg was collected from each redd and DNA was extracted from it; this DNA was amplified by PCR using the aforementioned primers. PCR was performed in 20 µl reaction volumes, which included 10× PCR buffer (Applied Biosystems, Foster city, CA, USA), 0.2 mM each dNTP, 3.0 mM $MgCl_2$, 0.5 µM of each primer, 0.3 units of *Taq* DNA polymerase (Applied Biosystems), and 1 µl of the DNA extract. The reaction conditions were 94°C for 10 min followed by 40 cycles of 30 s at 94°C, 30 s at 55°C, and 50 s at 72°C, and a final extension for 10 min at 72°C. PCR products were directly sequenced in forward and reverse directions using a BigDye Terminator kit (Applied Biosystems) and an ABI 3100 automatic sequencer (Applied Biosystems).

1.5. Measurement of egg burial depth

Egg burial depth has been considered as a criterion that indicates the robustness or vulnerability of the redds to superimposition and is correlated with spawner body size (DeVries 1997). Of all the redds excavated for species identification, 53 redds, including those of 8 Sakhalin taimen and 14 rainbow trout females, whose total length had been visually measured using the above-mentioned method, were excavated from the bottom of the egg pocket. Following the methods used by previous authors (e.g., Fukushima 1994; Elliott 1995; Edo et al. 2000), redds at the eyed egg stage were excavated, and all eggs were carefully collected from each egg pocket area. The eggs were placed in a hatchbox (Whitlock-Vibert; as described by Garrett & Bennett 1996) and the vertical distance between the surface of the stream bed and the bottom of the egg pocket was measured. Subsequently, with the exception of a few eggs collected for species identification, the eggs in the hatchbox were immediately returned to their natal pocket, which was then reburied to its original depth without adding silt and sand.

1.6. Statistical analyses

Two assumptions for parametic test, normality and homogeneity of variance were checked by Shapiro-Wilk normality test and F-test, respectively, and then a two-way ANOVA was performed to verify differences in median pebble size among redd locations along the stream or between the two species. Microhabitat uses were compared between Sakhalin taimen and rainbow trout using a complete-randomization test described by Manly (2006) with 10,000 iterations. In the randomization test, the number of variables (*n*) in the smaller groups was used to randomly select the values of an equal sample size from the larger group. The R computer package (R Development Core Team 2009; http:///www.R-project.org/) for Windows was used for statistical testing.

2. Observation of hatch and behavior of Sakhalin taimen juveniles

This additional observation was carried out in Seiwa Stream. In order to confirm the number of adult females and males that migrated into this stream, a weir was set up at the entrance of the stream for about 20 days from the end of April in 2004 and 2005 (Fig.9C). For the electrofishing of juveniles, 12 stations were set up along the stream (Fig.9C). Each station comprised of five pairs of pool and riffle and consequently exhibited reach length of

69−89 m. The reach width was measured at 10 points within each reach and the mean was used for calculating the area of the station. For the sampling of juveniles migrating downstream, a drift sampler was set up at lower end of this stream from late June to late August in 2004 and 2005 (Fig.9C). The entrance size of drift sampler was 50 ×50 cm. In mid May 2004, I surveyed the distribution of redds. Althogh there is a shape variation of redds and the number of egg pockets varies among different redds, I could correctly estimate the number of egg pockets from the number of V-shaped pot (Edo et al. 2000). In 2005, the riverbed was disturbed by a flood in the post-spawning season and the survey of redds was impossible. Since the fry of Sakhalin taimen emerge when the accumulated water temperature reaches 600 ºC-days (Kawamura et al. 1996), the beginning or end date of fry emergence was estimated from the following formula :

$$\sum_{j}^{x} \sum_{i}^{24} (T_{ij}/24) = 600 \quad \cdot \cdot \cdot \cdot 1)$$

where x is the estimated date of fry emergence, T_{ij} is water temperature (ºC) at i o'clock on j-th day from the beginning or the end of spawning season. The water temperature was recorded by a data logger (Optic Stow Away, Onset Inc.) near the mouth of this stream at one-hour interval.

From the estimated day of fry emergence in 2004 and 2005, I set up a drift sampler (mouth: 50×50 cm) at the lower end of this stream (Fig.9C) to collect juveniles migrating downstream. Furthermore, at intervals of two months from August to December in 2004 and from June to December in 2005, the density of fry was estimated at stations 1−12 by the three-pass removal method of Delury (1951). At each station, three replications of electrofishing with Model 12 Backpacker electrofisher, (Smith-Root Inc.) was conducted and the total number of juveniles at the station was estimated from the three numbers of collected fry using Capture Program (White *et al*. 1982). The density (no・m^{-2}) of fry calculated by $T/(L \cdot W)$ where T is the estimated number of fry and L and W are reach length and mean width at the station, respectively. This survey was completed within five days in the beginning of each month. I anesthetized all collected juveniles in the solution of 0.05% phenoxy-ethanol to measure fork lengths of those and sampled their scales to confirm their age (Fig.10).

For the fry collected in early August 2005, I also measured body weight to compare fatness index (*FI*) between the electrofished fry (residents) and the drift-sampled fry (migrants). According to Bohlin *et al*. (1994), fatness index (*FI*) was calculated as follows:

$FI = W_o - W_e$ ・・・・・・ 2)

where W_o is the log-transformed body weight and W_e is the log-transformed weight expected on a regression line between fork length and body weight of those was electrofished and drift-sampled. The length and weight are transformed into logarithm. The fry were released immediately after the counting and measurements of juveniles *in situ.*

In the season of fry migration, the water discharge was estimated by the U.S. Geological Survey Midsection method (Orth 1983). At the drift-sampling site (Fig.9C), a line transect was set up across the stream and the line was marked at intervals of 0.5 m. At each interval, velocity was measured using a portable current meter (Model CR-7WP, Cosmo-Riken Inc., Japan) at a point of 60% water depth from the bottom and the area (*A*) of water profile was calculated by $A = 0.5 (I_1 + I_2) / 2$ where I_1 and I_2 are water depth at both ends of the interval. The water discharge was estimated by $\Sigma V_i \cdot A_i$ where V_i is the velocity and A_i is the area of water profile at the *i*-th interval. Between station 1 and 12 there were eleven unsurveyed reaches. In order to estimate the total number of fry in the entire stream, the reach length (*L*) was measured by GPS (Mobile Mapper Office, Thales Inc.), the stream width was surveyed at five points in each unsurveyed reach and the mean (*W*) of the five values were calculated. The fry density (*D*) in the reach was represented by the mean of fry densities at the two neighboring stations. The number of fry in the reach was estimated by

$L \cdot W \cdot D$. The total number of fry in the entire stream was given by the total of all numbers of fry in all of the stations and unsurveyed reaches.

3. Evaluation of factors threatening Sakhalin taimen

3.1. Estimation of distribution and abundance of Sakhalin taimen

Prior to the present study, I interviewed local elderly fishermen and residents to reveal the distribution of tributaries where Sakhalin taimen had been spawning in the 1960s. Sakhalin taimen was recognized to have been spawning in a given tributary if (i) pairing or digging had ever been observed there, and/or (ii) at least one mature female or male had been captured there in the spawning season, April and May. As the result of the interviews, it was determined that Sakhalin taimen spawned in 64 tributaries of nine river basins in the 1960s: 17 of the Bekanbeushi River, 22 of the Furen River, three of the Yaushubetsu River, seven of the Nishibetsu River, six of the Tokotan River, four of the Shunbetsu River, one of the Tobikari River, two of the Tohoro River, and two of the Chashikotsu River. To estimate the present distribution and abundance of spawning sites, in each of the 64 tributaries Sakhalin taimen's redds were at least once searched in their spawning seasons in April and May from 2005 to 2008 and electrofishing was occasionally performed to capture newly emerged fry in the post-spawning seasons. A Sakhalin taimen female can not spawn and/or migrate upstream in water discharge less than approximately 0.04 $m^3 s^{-1}$ because of their large body. I walked up to this point of each tributary, and the total distance of my walk reached 495 km. In this survey, false redds could be discriminated from true redds based on its size and shape as shown in section 1.2. The location of newly constructed redd was recorded by a differential global positioning system (Mobile Mapper Pro, Thales Navigation Inc., SanDimas, CA, USA).

In order to reveal exact number of redds and estimate the number of spawners, I selected 34 of the 64 tributaries and recorded newly built redds at intervals of about seven days in the spawning season of 2008. In this selection of 34 study sites, only first- or second order tributaries (Strahler classification, Fig.15) were chosen from the Bakanbeushi, Furen, and Yaushubetsu Rivers. In these rivers, there were dams in 2 of the 34 tributaries. Moreover, in five tributaries of the Furen River and one tributaries of the Yaushubetsu River, rainbow trout's redds had been observed in previous surveys and species identification of each redd was conducted as shown in section 1.4.

3.2. Extraction of environmental variables accounting for distribution or abundance of Sakhalin taimen redds

At each of 34 tributaries where the number of redds was counted, I also surveyed the following environmental factors:

WF (water flow, m^3S^{-1}): To avoid the effect of seasonal fluctuation, I measured the water flow within nine days in early to mid May 2008 at lowermost point of each tributary using the US Geological Survey Method (Orth 1983).

SSA (suitable spawning area, m^2): In modification of the definition by Issak et al. (2007) for Chinook salmon (*Oncorhynchus tshawytscha*), a stream floor was defined as a site suitable for spawning by Sakhalin taimen if filled with the following conditions: 1) a crowd of φ 8−64 mm pebbles covered more than $1m^2$ area, with no cobble or boulders; 2) water depth was more than 6 cm; and 3) velocity was 20−90 cm/s. In each tributary, the suitable sites were looked for and SSA was given by the total area of all the suitable sites found within the tributary. D50 (median diameter of pebbles): On each tributary, a total of 15 transects evenly across the stream were set up at even intervals from the lowermost point and the pebble sizes were measured at two suitable spawning sites upward-nearest from each transect, by putting a 50 cm × 50 cm metal grid with 100 intersections at 7cm intervals and collecting a pebble (> 2 mm in diameter) on each intersection; viz a total of 100 pebbles were collected at each suitable spawning site. D50 was given by the median diameter of all pebbles (maximum: 100 pebbles × two sites × 15 transects = 3000 pebbles) collected in the tributary. PFS (percentage of fine sediments, %): In the survey of pebble size, some intersections of the metal grid were located on sand grains (< 2 mm in diameter). PFS was given by the percentage of intersections. RT (number of rainbow trout redds): Rainbow trout redds were distinguished from Sakgakin taimen redds in the manner shown in section 2.3., and RT was given by the number of rainbow trout redds found in the tributary. SS (stream slope, %), WA (watershed area, km^2) and PG (percentage of grazing land, %): Watershed is defined as entire area which contributes to providing water to the tributary. The three factors measured on topological map (1:25000). For each tributary, rise (RI) and run (RU) were measured and SS was given by 100 × RI/RU. The total area of grazing land (TAG) within the watershed was measured and PG was given by 100 × TAG/WA.

3.3. Statistical analyses

Poisson regression model with the random intercept of individual river was used to quantify relationship between mean number of taimen's redd and environmental variables. Environmental variables except fine sediment and proportion of the watershed grazed (i.e., D50, stream slope, suitable spawning site, water flow, watershed area and number of rainbow trout's redd) were log transformed prior to analysis below. Correlations among predictor variables were evaluated by paired correlation and tolerance value prior to inclusion in models to avoid colinearity. Water flow and watershed area were strongly correlated (r = 0.93) and their tolerance value was quite lower than 0.1, indicating that including these variables in the model is not recommended (Quinn and Keough 2002). I retained water flow as a predictor variable and excluded basin area from the following analysis. Because none of tolerance values of seven variables without basin area (i.e., fine sediment, D50, stream slope, suitable spawning area, water flow, proportion of the watershed grazed and number of rainbow trout's redd) were larger than 0.1, I conducted following analysis with these variables.

I conducted forward direction stepwise regression procedure in which Akaike's Information Criterion (AIC) was used to select the most parsimonious model. I started with the model which includes only suitable spawning area, not with the model including no predictor variables because this null model was not converged. Although the model including suitable spawning area has the second lowest AIC among seven models including only one predictor variable, I started with this model because starting with the lowest AIC model, that includes D50 as a predictor variable, the selected parsimonious model was not converged. Model fitting and stepwise procedure were conducted using R 2.9.2 (R development core team 2009) and its extension package, glmmML (ver 0.81-6; Broström 2009) and MASS (ver. 7.2−48; Venables and Ripley 2002), respectively. I refitted the parsimonious model, determined by stepwise regression procedure, in Bayesian statistic framework to predict change in mean number of taimen's redd associated with change in proportion of the watershed grazed at each stream with being the uncertainty of parameter estimation taken into account. The parameters were estimated by the Markov Chain Monte Carlo (MCMC) method in WinBUGS (Spiegelhalter et al. 2003), and then, 3,000 MCMC samples were obtained for each parameter. Using these samples and environmental data, I calculated the probability distribution of mean number of taimen's redd at each stream in cases where proportion of the watershed grazed becomes 5%, 10%, 20%, and 50% higher or lower than at present.

Results

1. Spawning activities of Sakhalin taimen females and their interaction with rainbow trout

In the spawning season from late April to late May 2005, 13 Sakhalin taimen females were captured at upstream reach of the weir which was set up in a tributary of the Bekanbeushi River and 70 redds were observed in upstream reach of the weir. In the spawning season from early April to mid-May 2007, 13 Sakahlin tamen females were captured in a tributary of the Furen River and 65 redds were observed in upstream reach of the weir. Additionally, in the Toikanbetsu River, northen Hokkaido, where I observed the hatch and behavior of juveniles, 12 Sakhalin taimen females were captured and 55 redds were found in the spawning season from late April to early May 2005. Thus, the mean number of redds per female was 70/13 = 5.4 in the Bekanbeushi River, 65/13 = 5.0 in the Furen River, and 55/12 = 4.6 in the Toikanbetsu River, suggesting that one Sakahlin taimen female constructs about five redds on the average and, in other words, the number of spawners could be estimated to be approximately one fifth of observed redds.

In the three-year surveys from 2006 to 2008 in a tributary of the Furen River, 364 redds were observed comprising 57 Sakhalin taimen and 267 rainbow trout redds: 15 and 93 in 2006, 20 and 89 in 2007 and 22 and 85 in 2008, respectively, indicating that the number of rainbow trout redds was about 5 times more than that of Sakhalin taimen in all of the three years (Table 2). As shown in Figure 3, spawning in both species started just after a strong freshet due to snow melt or rainfall in 2006 and 2007 but began in the absence of a freshet in 2008. The construction of new redds peaked shortly after the beginning of spawning and soon finished by early May in Sakhalin taimen, but continued until mid-May to early June in rainbow trout.

With the exception of the uppermost reach, which was dominated by rainbow trout, redds of both species were widely distributed along the reach in all the years (Fig. 4), indicating no interspecific separation of the stream reach for redd construction. Thus, microhabitat preferences were compared between the two species based on the pebble size, water velocity, and water depth data of each redd. The depth of the redds was 11–43.3 cm (mean: 23.9 cm ± 95% CL 2.2 cm, n = 52) in Sakhalin taimen and 10.5–41.5 cm (mean: 25.5 ± 95% CL 2.0, n = 61) in rainbow trout, with no statistically significant difference between the two species (Randomization test: $P > 0.05$; Fig. 5a). The water velocity above the redds was 31.8–85.3 cm/second (mean: 54.0 ± 95% CL 4.5, n = 50) in Sakhalin taimen and 16.4–77.7 cm/second (mean: 55.1 ± 95% CL 3.6, n = 61) in rainbow trout, with no significant difference between the two species (Randomization test: $P > 0.05$, Fig. 5b). Moreover, the D50 (median diameter) pebble size of the surface substrate adjacent to each redd was 8.21–12.66 mm (mean: 10.67 ± 95% CL 0.54) in Sakhalin taimen and 8.3−14.07 mm (mean: 10.73 ± 95% CL 0.6) in rainbow trout, with no significant difference between the two species (randomization test: $P > 0.05$). In addition, the D84 also was 14.6–21.06 mm (mean: 17.45 ± 95% CL 0.85) in Sakhalin taimen and 13.4–21.9 mm (mean: 17.42 ± 95% CL 1.05) in rainbow trout, with no significant difference between the two species (randomization test: $P > 0.05$).

Of the 364 redds observed in the springs of the three years from 2006 to 2008, 114 (31.3%) were superimposed by other spawners (Table 2). Excluding 40 unidentified species redds and 14 superimposers, 19 Sakhalin taimen redds were superimposed by other spawners: three by conspecific taimen 16 by other trout species, while 68 rainbow trout redds were superimposed by other spawners: 48 were conspecific trout and 14 were other Sakhalin taimen species (Table 2). Although Sakhalin taimen redds were more frequently superimposed by rainbow trout, a Fisher's exact test did not detected a significant difference, suggesting that both the species almost randomly disturbed the existing redds without showing any species-specific superimposition (Table 2). This test was also conducted for each year separately and no species-specific superimposition was detected in any year (Table 2).

Figure 8 shows the correlation between the total body length (x) and egg pocket depth (y) of eight Sakhalin taimen and 14 rainbow trout females. Among conspecific females, the egg pocket depth was significantly correlated with the total body length in both of Sakhalin taimen (y = 0.26x–1.5, R^2 = 0.73, P = 0.006) and rainbow trout (y = 0.32x + 2.87, R^2 = 0.54, P = 0.002), with larger females excavating deeper egg pockets. However, while the slope of the linear regression line were not significantly different between the two species (ANCOVA: F = 0.25, d.f. = 1, P = 0.62), the y-intercept of the line was significantly larger in rainbow trout than in Sakhalin taimen (F = 1.63, d.f. = 1, $P < 0.001$). This appears to be because the egg pocket depth was nearly equal in Sakhalin taimen (13–25 cm; mean: 17.4 ± 95% CL 3.3 cm, n = 8) than in the rainbow trout (11–23 cm; mean: 17 ± 95% CL 2.4 cm, n = 14) while the female total body length was much larger in Sakhalin taimen (58–117 cm; mean: 74.6 ± 95% CL 9.5 cm, n = 14) than in the rainbow trout (26–60 cm; mean: 40.5 ± 95% CL 2.9 cm, n = 36). Excavation of 53 redds over three years indicated that the egg pocket depths were nearly equal in Sakhalin taimen (13–32 cm; mean: 18.7 ± 95% CL 2.9 cm, n = 15) and rainbow trout (11–25 cm; mean: 17.0 ± 95% CL 1.1 cm, n = 38) with no significant difference between the two species (randomization test: $P > 0.05$).

2. Hatch and behavior of Sakhalin taimen juveniles

In 2004, 15 females and 13 males migrated into Seiwa Stream and spawning occurred from 1 to 7 May. I found a total of 55 redds and the number of redds with one, two, three, and four egg pockets were 35, 17, 2 and 1, respectively (Fig.9C). In 2005, only three females and seven males migrated into this stream and the spawning occurred from 7 to 13 May. It was evidently confirmed that the three females spawned around stations 7−12 but not around stations 1−6 at all. Although, the survey of redds was impossible because of the flood in post-spawning season, most, if not all, of the egg pockets did not seem to be damaged by the disturbance. The emergence season estimated from formula 1 was from 27 to 29 June in 2004 and from 29 June to 1 July in 2005.

Totals of 443 and 205 juveniles were electrofished at the 12 stations in 2004 and 2005, respectively. Estimated densities of the juveniles and total numbers of the juveniles are shown in Table 3. At stations 1−6 where spawning did not occur in 2005, no fry was collected. In 2004, no redds were constructed at stations 11 and 12 located at the lower end of the stream (Fig.9). Nonetheless, the density of fry was highest at two stations in August 2004, exhibiting downstream migration of some fry in this season. In October and December 2004, the fry density was almost homogeneous across the 12 stations. In June 2005, no juveniles were collected at uppermost stations, while a few juveniles were captured at lower stations. When compared between 2004 and 2005, the densities of juveniles at stations 7−12 in August were significantly higher in 2004 (Mann-Whitney's U-test: $u = 2.0$, $p = 0.01$) because the number of females was as many as 15 in 2004 but only three in 2005. However, densities in October and December were not different between the two years (Mann-Whitney's U-test: $u = 11.5$, $p = 0.29$, in October; $u = 7.5$, $p = 0.08$ in December).

The mean fork length of fry was 37.4 ± SE 0.1 mm in August 2004 and the fry grew up to

85.3 ± 1.8 mm in August 2005. It is notable that the coefficient of variation expanded with the growth of juveniles, probably reflecting the variation of nutritional condition among the residents. The oldest was a two-years-old juvenile which was collected in June 2005 and was 113 mm in the fork length (Fig.10D). Thus, while a few juveniles stayed in their natal stream more than one year up to two years, most juveniles migrated downstream before one year of age.

In mid July to early August 2004 and early August 2005, the downstream migrants were collected using a drift sampler with a 50×50 cm mouth to examine their daily activity. The drift sampler was set up during each quarter (six hours) of 24 hours from noon. Six replications of this sampling were conducted in the migration seasons of 2004 and 2005 (Fig.11). In all of the replications, the downstream migration occurred only at night, with no migrants from 6:00 to 18:00. In the night, the number of migrants was larger at 18:00−24:00 than at 0:00−6:00.

In addition to the survey of daily activity, the 24-hour sampling of migrants was conducted 20 times using the drift sampler in the migration season of 2005 and the water discharge was concurrently estimated for each sampling day (Fig.12). Even after the emergence in late June to early July, the fry stayed in the natal stream with rare occurrence of downstream migration for about one month. During this period the water discharge was below the level of 0.02 m^3s^{-1}. However, many fry started the downstream migration from 2 August when heavy rain covered the area of Seiwa Stream and the water discharge reached 0.13 m^3s^{-1}, suggesting that the increase of water discharge triggers the migration behavior of the fry. In 2004 when the water discharge constantly exceeded 0.05 m^3s^{-1} in the summer, the downstream migration started in early July (Fig.12), i.e. soon after the emergence of fry in late June. The migration season seems to depend on precipitation and varies from year to year.

In early August 2005, I collected 54 and 42 fry by electrofishing and drift sampler, respectively, and measured their fork length and body weight, and the fatness index was calculated. Pearson's correlation coefficient between fork length and fatness index was $r = -0.02$ which was not statistically significant ($p = 0.850$). The mean fork length was 40.9 ± SE 0.38 mm in the electrofished fry and 38.0 ± 0.78 mm in the drift-sampled fry. *T*-test suggests that the electrofished fry are significantly larger than the drift-sampled fry ($t = 3.516$, $p = 0.001$); thus, larger fry have higher probability to be residents than smaller fry. The mean fatness index was 0.096 ± SE 0.011 in the electrofished fry and 0.036 ± 0.014 in the drift-sampled fry. *T*-test indicates that the resident fry are significantly in better condition of nutrients than the migrants ($t = 3.440$, $p = 0.001$).

3. Abundance of Sakhalin taimen and environmental factors threatening them in eastern Hokkaido

In the surveys of 34 tributaries, I found 389 redds in eight of 17 tributaries of the Bekanbeushi River, 139 redds in eight of 22 tributaries of the Furen River, 25 redds in one of seven tributaries of the Nishibetsu River and 15 redds in one of six tributaries of the Tokotan River, and no redds nor adult Sakhalin taimen were observed in any of 45 tributaries of the Shunbetsu, Yaushubetsu, Tobikari, Tohoro, and Chashikotsu Rivers. Therefore, Sakhalin taimen population was regarded to be viable in the Bekanbeushi and Furen Rivers, enndangred in the Nishibetsu and Tokotan Rivers and extinct in other rivers surveyed. Based on the observation that the number of females was nearly equal to the one fifth of the number of redds, the number of spawners in the spawning season of 2008 is estimated to be 78 in the Bekanbeushi River, 28 in the Furen River, five in the Nishibetsu River, and three in the Tokotan River. If each Sakhalin taimen female breeds every two years as mentioned by Yamashiro (1965), number of adult females inhabiting each river basin is estimated to be 156 in the Bekanbeushi River, 56 in the Furen River, 10 in the Nishibetsu River, and six in the

Tokotan River (Table 4).

Sakhalin taimen population was extinct in 45 of the 64 tributaries surveyed, whereas 34 (75.5%) of the 45 tributaries did not have any migration barriers, i.e. dams, suggesting that there have been some serious causes for extinction other the construction of dams in eastern Hokkaido. In the watersheds where the 45 tributaries are distributed, dramatic expansion of of grazing lands have occurred in past five decades, especially from the 1950s to the 1980s. In contrast, all the seven tributaries in the watersheds of the Maneuver Area and public forests with no expansion of the grassland have consistently been used for spawning of Sakhalin taimen. Therefore, I analyzed the impact of the grazing land expansion on the populations of Sakhalin taimen, by analyzing the correlations between the number of redds (dependent variable) and eight environemetal factors (independent variables) using Poisson regression model. Table 6 shows the number of redds and values of eight environmental factors at the 34 tributaries surveyed in 2008.

Prior to the analysis of 32 dam-free tributaries by Poisson regression model, correlations among the eight environmental factors were calculated to exclude the effect of multicollinearlity. Based on the result (Table 7), I chose WF, SSA, D50, RT and PG as independent variables. The number of redds (NR) ranged from 0 to 169 and the poisson regression model showed that NR was correlated positively with SSA ($Z = 3.24$, $P < 0.001$) and SSA × PG interaction ($Z = 2.87$, $P = 0.004$) and negatively with PG ($Z = -3.71$, $P < 0.0001$) (Table 7), suggesting that the rapid expansion of grazing lands has occasionally caused local extinction of Sakhalin taimen populations. The significance of correlation between number of redds and SSA was enhanced when the 32 tributaries were divided into two groups A (N = 11) and B (N = 21) located in the watersheds where PG was less than and more than 40%, respectively: $r = 0.87$ $P < 0.001$ in group A; $r = 0.69$, $P < 0.001$ in group B

(Fig. 17), indicating that the suitable spawning area more remarkably affects the number of redds in the watersheds less covered with grazing lands.

From the topological maps issued in 1955, 1970, 1985 and 2002, the percentage of grazing lands (PG) was calculated for each of the 32 tributaries (Fig. 16). PG was nearly zero in 1955 in all the tributaries but rapidly increased from the 1960s to the early 1980s especially in such tributaries as ON, CR, NA, FR, KIS, etc., which are located in eastern part of Konsen region and show 60–90% of PG at present, while an increase of PG has been observed in KB, TA, KD, WFP, BK, FP and SI which are upstream tributaries of the Furen and Bekanbeushi Rivers and are all located in the Yausubetsu Maneuver Area.

From these patterns of PG increase, I estimated the decrease curve of NR in each tributary, using the Poisson regression model (Fig. 19). The total NR in all the 32 tributaries was estimated to be 1212 in 1955, suggesting that the total NR has decreased by 52% due to rapid expansions of the 32 watersheds during past 50 years (Fig. 19). Furthermore, the number of Sakhalin taimen redds in response to simulated increases or declines in percentage of the watersheds grazed (in 32 tributaries) at the level of 5%, 10%, 20% and 50% (those are considered to correspond to habitat degradation and improvement) were predicted. And as shown in Table 8, increases in livestock grazing from 5% to 50% of the all study watersheds grazed were predicted to result in declines of Sakhalin taimen redds from 13.9% to 63.7%. In contrast, declines in livestock grazing from 5% to 50% of the watersheds of 32 tributaries were predicted to result in increases in the abundance from 5.6% to 40% (Table 9). For planning the local management program to conserve the taimen population, I forecasted the extinction thresholds in response to simulated changes in the watersheds grazed area in each local breeding population at 14 tributaries which currently support the population in the basins.

Two dam-installed tributaries TA and SI had only eight and no redds and showed 3,168 m^2 and 32 m^2 of SSA and 0% and 0% of PG, respectively. When the two tributaries are plotted in the NR(y) < SSA(x) dimension, SI (PG > 40%) is close to the regression line $y = 0.0081x - 0.4959$ but TA (SSG<40%) is far from $y = 0.0464x + 0.0611$ on which SSA =3.168 m^2 corresponds to NR=147.6 (Fig. 18), indicating that dam construction considerably reduces the number of redds and TA would have had as many as about 150 redds if there had been no impacts of the dam. The expected number of 147.6 redds is larger than 139 redds actually observed in the entire Furen River. This estimation also suggests that TA has much higher priority than SI in dam destruction for the conservation of the endangered species Sakhalin taimen.

Discussion

At a smaller scale (i.e. within single tributary), I revealed a negative impact of introduced rainbow trout on Sakhalin taimen through redd superimposition. Sakhalin taimen is only the native Japanese salmonids that spawn in spring. Therefore, spawning disturbance by rainbow trout may be most serious for taimen compared to other Japanese native salmonids. This provides the first evidence that endangered taimen is suffering from introduced species.

In this dissertation, I assessed the current status of critically endangered Sakhalin taimen in eastern Hokkaido and revealed the factors affecting population decline. Of the 64 tributaries surveyed, Sakhalin taimen had gone extinct in 46 tributaries (71%) in the past 50 years. Increase in grazed area had significantly reduced the number of spawning redds, which is probably the main factor of population decline in eastern Hokkaido. Erosion dams also affected taimen populations in a few tributaries. This is the first study to quantitatively assess the impacts of land use on Sakhalin taimen abundance at a large scale (2284 km^2).

Here, I discussed these findings more detail and concluded with conservation implications for the critically endangered Sakhalin taimen.

1. Impacts of introduced rainbow trout on Sakhalin taimen

During the three years of observation, rainbow trout redds were about 5 times more abundant than Sakhalin taimen redds, and about 30% of the observed Sakhalin taimen redds were superimposed by rainbow trout. These results suggest that superimposition by the artificially introduced rainbow trout species is impacting the indigenous Sakhalin taimen species, which are rare and require urgent conservation in Hokkaido.

During the embryo stage of salmonids, redd superimposition seems to be a major mortality factor (Hayes 1987; Van den Berghe & Gross 1989). For instance, in New Zealand streams, introduced rainbow trout has been reported to superimpose 94% of the brown trout (*Salmo trutta*) redds, and occasionally, brown trout egg survival rates are reduced to less than 1% (Hayes 1987). As a result of such intensive superimposition by rainbow trout, one brown trout population has been extirpated (Scotts & Irvine 2000). Thus, rainbow trout have been reported to be a cause of serious damage to eggs deposited by an early spawner species through redd superimposition in oceanic streams where none of the indigenous salmonids inhabit. On the other hand, in other regions including the northern hemisphere, where numerous salmonids are native, such high levels of redd superimposition by rainbow trout on native salmonids have not been reported. Among the limited literature available on redd superimposition by rainbow trout, Taniguchi et al. (2000) reported that introduced rainbow trout superimposed redds constructed by two indigenous autumn spawners (13% of Dolly varden charr redds and 3% of white-spotted charr redds) in a southern Hokkaido stream. Over the three years of my study, as many as 28% of Sakhalin taimen redds were superimposed by introduced rainbow trout, while less than 6% of their redds were superimposed by conspecific Sakhalin taimen (Table 2). Moreover, the rate of superimposition by conspecific Sakhalin taimen is similar to that (about 10%) observed in another stream in central Hokkaido (Edo et al. 2000).

Redd superimposition by rainbow trout on Sakhalin taimen is considered to be due to four main reasons. First is the spawning time of rainbow trout, i.e., large numbers of rainbow trout spawn just after the main spawning period of Sakhalin taimen, a period when the uneyed embryos are vulnerable to physical shock. Second is the similarity in microhabitats used by the two species, i.e., similar microhabitats used by the two species can result in reuse of Sakhalin taimen redd sites by rainbow trout. Third is the higher abundance of rainbow trout spawner in an area where suitable spawning ground is limited. Fourth is the similarity in the depth of the egg pockets in the two species. These four reasons are discussed below in detail.

In the three observed spawning periods, spawning timing considerably overlapped between the Sakhalin taimen and rainbow trout. Such overlaps seem to enhance interspecific competition through occurrences such as redd superimposition between the two species. In many salmonid species, reproductive timing is considered to be affected by genetic adaptation (e.g., Siitonen & Gall 1989; Quinn et al. 2000) and phenological flexibility (Jonsson 1991). Although I have no information about the strain or population of the rainbow trout that had been introduced into the study area, there are rainbow trout populations in Hokkaido that spawn between January and April (Taniguchi et al. 2000) and others that spawn between April and June (Aoyama et al. 1999; present study). The overlap in the spawning timing between the two species can be partly attributed to the reproductive timing of the original rainbow trout strains that spawn in the same season even in other regions. Nevertheless, it may also be attributed to phenological flexibility, i.e., adaptation to environmental conditions such as water temperature, discharge, and the fluctuation (Jonsson

1991). In this study area, most streams are frozen until mid-March and freshets may suddenly occur in late March or early April due to the melting of snow and ice. If a spawner lays its eggs too early, the survival rate of the embryos may decline as a result of egg loss caused by a freshet, while if the eggs are laid too late, the resulting fry may be at a territorial disadvantage among earlier emerging fry (Einum & Fleming 2000; Carlson et al. 2004). In this study, spawning in both species started just after a strong freshet was produced due to snowmelt in both 2006 and 2007 (Fig. 5). Such a relationship between the initiation of spawning and water fluctuation has also been reported in other spring-spawning populations of Sakhalin taimen (Fukushima 1994) as well as in golden trout *O. mykiss aguabonita* (Knapp & Vredenverg 1996), redband trout *O. mykiss gairdneri* (Muhlfeld 2002) and in adfluvial rainbow trout (Holecek & Walters 2007).

In three years' survey, Sakhalin taimen and rainbow trout in this study stream began spawning when the daily average temperature exceeded 4ºC, which is similar to spawning water temperatures reported for Columbia River rainbow trout (Holecek & Walters 2007) and northern Hokkaido River Sakhalin taimen (Fukushima 1994), in spite of differences of fluctuation patterns in stream temperatures among three years, probably suggesting that the initiation of spawning in the two species reflected increasing water temperature in each year. Before and during peak discharge due to snowmelt, the temperature of the stream was probably too low for the two species to start spawning activities in the study stream, as mentioned in other rainbow trout populations (Holecek & Walters 2007; Muhlfeld et al. 2009). The relationships between spawning timing and an environmental cue may be a common characteristic of spring-spawning salmonids inhabiting streams where freshets occur due to spring snowmelt. In other words, the temporal overlap in spawning of both species is occurred probably because of their similar response to changes of the environmental cues such as water discharge and temperature.

In the present study, Sakhalin taimen and rainbow trout selected very similar microhabitats (water depth, velocity, and substrate composition) for their redd sites. The characteristics of microhabitat variables associated with the redds observed in this study were similar to other published values for adfluvial rainbow trout (Holecek & Walters 2007) and resident redband trout (Muhlfeld 2002). Of the physical variables assessed, substrate composition is considered to be a critical factor in spawning and embryo survival (Chapman 1988). As a result of geological and human influences, sediment particles that are appropriately sized for salmonid spawning were not abundant in the reach studied here. The stream bed was dominated by silt and sand with few pebbles because the stream originates in a volcanic stratum where there are few pebbles. In addition, intensive grazing by live stock within the catchment has led to a decrease in the spawning ground area due to sedimentation of silt and sand because of soil washout from the adjacent grazing land (K. Nomoto, unpublished data). This limitation of available habitat suitable for spawning and the large numbers of sympatric rainbow trout spawners may contributed to the increased rate of redd superimposition, because redd superimposition seems to attribute to the limited availability of spawning habitat (e.g., McNeil 1964, 1966; Hayes 1987; Ligon et al. 1995; Fukushima et al. 1998).

A critical question in this study is whether eggs deposited by an early spawner Sakhalin taimen die, after the redd has been superimposed by a later spawning, rainbow trout. To answer this question, egg burial depth was used as the criterion to determine the loss of Sakhalin taimen eggs due to redd superimposition by rainbow trout. Steen & Quinn (1999) reviewed published and unpublished data from different regions and compared regression lines (egg burial depth vs. female body length) among five salmonid species including Sakhalin taimen (data collected in northern Hokkaido rivers; Fukushima 1994). Their review indicated that Sakhalin taimen bury eggs at a relatively shallow depth for their body size compared with other salmonids such as rainbow trout, brown trout, Atlantic salmon (*S. salar*), and sockeye salmon (*O. nerka*). In the present study, Sakhalin taimen also buried eggs at a relatively shallow depth for their body size compared with the sympatric-spawning rainbow trout. Although egg burial depth is also reported to vary with changes in physical factors, such as water velocity and substrate composition (DeVries 1997), the egg burial depths of the two species observed here were within the ranges reported by previous researchers (for Sakhalin taimen, Edo et al. 2000: for rainbow trout, Crisp & Carling 1989). Their data were collected in a central Hokkaido river or British rivers, suggesting that the vertical overlap of egg burial depth observed here is probably attributable to a species-specific characteristics rather than related to local circumstances. Thus, if Sakhalin taimen redds in other streams are superimposed by rainbow trout redds, Sakhalin taimen eggs in those streams would also be affected as observed here.

However, I should take into consideration that the data presented here were derived from only one stream for three years. Additional observations in other regions or streams for longer periods will help determine the impacts of redd superimposition by rainbow trout on Sakhalin taimen. Such impacts may change according to changes in other factors such as biological (rainbow trout strain, body size, and abundance, etc.) and environmental (stream substrate composition, spawning ground availability, and water regime, etc.) conditions. Thus, further studies in other regions and streams are needed.

2. Behavioral ecology of Sakhalin taimen juveniles in their natal stream

Results suggest that there is a limited number of residents in Seiwa Stream for these two years, presumably exhibiting that effects of density dependency act as a regulation of population inhabiting Seiwa Stream. Such instances have been reported in several salmonids

(Elliott, 1986; Nakano & Nagoshi 1985; Mortensen, 1977). Elliott, (1986) noted that few fry of the brown trout emigrated out of the stream and therefore, population losses in spring and summer were chiefly due to mortality rather than migration. In contrast, a large proportion of Sakhalin taimen fry migrated downstream out of their natal stream, suggesting that population losses of those in the stream are in large part due to downstream migration.

This stream flows very gently, nonetheless, Sakhalin taimen juveniles rarely migrated upstream and mainly migrated downstream. This may be a characteristic behavior of the species contrary to other stream-dwelling salmonids in which precocious male appear, such as white spotted charr (Morita & Yamamoto. 2001), masu salmon (Nagata & Irvine 1997), coho salmon (Dittman et al. 1998), *etc*. Dittman et al. (1998) gave two instances of dispersal patterns of masu salmon and coho salmon juveniles and considered that differences of dispersal patterns of juveniles reflect those of life history. Similarly, such characteristic dispersal pattern of Sakhalin taimen juveniles probably reflect the life history of this species, for there are not any precocious males breeding as a parr or jack in Sakhalin taimen (present study).

In stream-dwelling salmonids, competitive ability among individuals is size-dependency. (Noakes 1980). It was confirmed that larger fish tend to be dominant and occupy efficient foraging microhabitat continuously (Fausch, 1984). Consequently, dominant fish grow more faster than subordinate fish (Metcalfe et al. 1989; Fausch, 1984). Meanwhile, subordinates that grow slowly tend to emigrate from there (Mason et al. 1965; Chapman, 1962). Results showed that standard error of fork lengths expands with growth of juveniles, suggesting probably that there was an interference competition for foraging microhabitat among Sakhalin taimen juveniles. Several authors have suggested that intraspecific aggressive interactions strongly influence population regulation of stream salmonids (Nakano & Nagoshi 1985; Elliott, 1990). Similarly, it is probable that an interference competition among juveniles plays an important role in regulating this population in the stream.

Downstream movement is primarily restricted to night in salmonid fry (Elliott, 1986; Crisp et al. 1991; Johnston et al. 1997). The results of this study indicate that the downstream migration of Sakhalin taimen fry also occurred only at night and greatest movement occurred in the first half of the night. Movement during dark may be a behavioral strategy to avoid predation (Johnston, 1997).

In 2005, patterns in the timing of juvenile Sakhalin taimen migration appeared to be influenced by fluctuation of water discharge in the stream, 2005. A rapid increasing of water discharge affects the dispersal pattern of salmonid fry (Ottaway *et al*. 1981; Heggenes & Traaen. 1988; Crisp, 1991; Johnston, 1997). In most salmonids, the peak of downstream migration exclusively occur immediately after the emergence period from redds (Johnston, 1997). There has never been such a precedent due to the shortage of water in summer like this case.

Significant differences were observed in the size and growth characteristics of drift-sampled fry compared to those of electrofished. Assuming that the electrofishing method was not size-biased, the migrants were shorter than those with established territories and exhibited different growth characteristics. In August 2004, many migrants may have been pushed out of their territories in Seiwa Stream by intra-specific competition and forced to seek new territories further downstream compared to those of 2005. Smaller fry are more susceptible than larger fry to downstream displacement (Ottaway & Clarke, 1981) and those in poor condition tend to drift greater distances than in good condition (Elliott, 1987).

Taylor (1986) equated migration with the behavioral movement relevant to population re-distribution and defined four kinds: randam dispersive, dynamic, homeostatic and social. Random dispersive migration is one-way, transported emigration without volition or control over the end point. Such a description might at first be thought applicable to the down stream-moving fry that were often in poor condition. However, as such movement occurred chiefly at night, the fry must have had some control over the start and finish of the movement. Therefore, this movement and most of the behavioral movements in this study are thought to belong to the second category; dynamic migration. This is defined as one-way, actively initiated emigration; the function is dynamic, non-random distribution. Elliott (1986) noted that a large proportion of brown trout fry that migrate downstream after emergence does not feed and eventually dies. A favorable habitat for fry are much abundant at the upper reach of the river than the lower in the Teshio River system, as many authors are mentioned (Bramblett et al. 2002; Charles *et al*. 2000), while, main-stem located at the lower reach are favorable for adults. Furthermore, the maximum burst velocity at which fry can keep their position is proportional to their body size, and the risk of predation is inversely proportional to their body size (Taylor et al. 1985). Although a follow-up survey of migrants was not conducted in the lower reach of Teshio River, These migrants from Seiwa Sream probably had a much higher mortality rate than residents in Seiwa Stream. From July to August when fry emerged from redds, the greatest downstream migration occurred. The effects of density dependency may have forced the smaller fry and those in worse condition to migrate downstream, those in this period were so small that costs of migration were probably higher, therefore, the larger ones tended to be the residents in their natal stream. Furthermore, residents grew there, and resumed downstream migration to benefit from growth in the post-wintering season when costs of migration probably became lower due to larger body size of them. They would have then gradually emigrated to larger scales of habitat located at the lower reach of the river to grow more faster. Thus, the carrying capacity of natal stream possibly regulates population densities, and so, this kind of stream is considered to be very important not only as a spawning habitat but also as a nursery habitat from the viewpoint of conservation of this species.

3. Population status and extinction risk of Sakhalin taimen in eastern Hokkaido

To estimate population abundance, I conducted redd count in 64 tributaries from the nine river basins where Sakhalin taimen was present in the 1960s. No spawning redd was observed in five of the nine river basins. Therefore, Sakhalin taimen had gone extinct in more than 50% of the studied basins in eastern Hokkaido. The estimated number of spawning females was more than 50 individuals in two river basins, but just and less than 10 individuals in the rest two basins. Demographic stochasticity and genetic deterioration should become significant when population size drops to 50 adults (Lande 1993). Therefore, of the nine river basins studied, only the two (22%) may have long-term viable populations. At the tributary level, Sakhalin taimen had disappeared in 46 tributaries (71%) in the past 30 years. This study provided the first quantitative and reliable evidence for population decline in endangered Sakhalin taimen.

4. Factors threatening Sakhalin taimen

Channelization is well known as an important factor decreasing stream-dwelling fishes in well-developed agricultural rivers (Portt 1986; Brookes 1988; Swales 1988). Furthermore, habitat fragmentation by damming is also well known to negatively affect on stream-dwelling salmonids due to its barrier effects (Nilsson & Berggren 2000; Morita & Yamamoto 2002). These, however, are unlikely in my study area. Of the 64 tributaries where Sakhalin taimen had been present until the 1960s, Sakhalin taimen became absent in 45 tributaries. All the 45 tributaries had not been channelized nor dammed. Therefore, most extinctions (82%) of

Sakhalin taimen in eastern Hokkaido should have been caused by other factors rather than channelizations and dams. Based on the Poisson regression model from the 32 tributaries (with no channelized and damming), expansion of glass land appeared to be the major factor decreasing the number of Sakhalin taimen redds. In stream ecosystems, principle mechanisms by which livestock grazing influences Sakhalin taimen redd abundances seems to have several different pathways discussed below.

5. Possible pathways to taimen's redd abundance from glass land

'Sediment pollution' has become a serious issue throughout the world. It has resulted from land use activities, such as farmland development (e.g., Allan et al. 1997; Nakamura et al. 1997; Nakamura & Yamada 2005), forestry activities (e.g., Platts et al. 1989; Nakamura et al. 2004; Ripley et al. 2005), mining (Hellawell 1986), and road construction (e.g., Barton 1977; Cline et al. 1982). Such pollution has been defined as fine sediments, with sand, silt, and/or clay particles smaller than 2 mm, an accumulation of fine sediment on riverbeds deleteriously influences habitats of fish, benthos, and periphyton (e.g., Berkman & Rabeni 1987; Watanabe et al. 2001; Yamada & Nakamura 2002; Yamada & Nakamura 2009). In eastern Hokkaido region, such pollution can probably explain a large proportion of rapid decline in Sakhalin taimen abundance in past five decades, because number of taimen's redd was positively associated with percentage of watershed grazed as well as percentage of fine substrate (< 2 mm) in each tributary.

In this study area, sediment pollution might affect redd abundance of Sakhalin taimen in three possible pathways, those are discussed below in detail. First, a decrease in permeability associated with accumulation of fine sediment (< 2 mm) lowered the survival rate of embryos by suffocation because the flux of DO that should be supplied to the embryo was severely limited (Yamada et al. 2009), although survival rate of eggs in redd was investigated in present study. Second, the accumulation of fine sand on streambed may have caused shrinkage of suitable spawning ground for salmonids (Opperman et al. 2005; present study), which are strongly associated with redd abundance of Sakhalin taimen (Fig. 17). Third, Sakhalin taimen juvenile usually feeds benthic invertebrates (Ephemeroptera *Baetis* sp. and *Ephemeroptera Ephemera* sp.) inhabiting above and/or below substrate gravels (Sagawa et al. 2003). It is also well known that sedimentation reduces abundance of benthic invertebrate species (Scrimgeour et al. 2000; Nagasaka et al. 2001; Infante et al. 2009). Therefore, the benthic invertebrates may rarely inhabit tributary intensively impacted by glass land due to excessive sedimentation. Sediment pollution may reduce number of Sakhalin taimen redds through reduction of benthic invertebrate which is principle prey of Sakhalin taimen juvenile.

In addition, the other two possible pathways are passing through water discharge and water quality, those are discussed below. Ishioka et al. (2004) compared water discharges among eight watersheds (including TK, TR, TS, CH and BE Stream) of Bekanbeushi River basin with different land use during base flow conditions and concluded that land use activities for livestock grazing reduces water discharge due to a decrease in the ability of the watershed to retain water. Therefore, shrinkage of suitable spawning habitat resulting from the decrease in water discharge might cause reduction in number of Sakhalin taimen redds in grazed tributary. Nagasawa et al. (1995) compared water quality in five watersheds (including HI and TR Stream) of Bekanbeushi and Furen River basin with different land use and reported that scattered manure on glass land increase NO_3-N in dairy farming basin. Such an increase in nitrogen accelerates disintegration of litter and dissolved oxygen consequently decrease in grazed stream (Niyogi et al. 2003).

Conservation implications

This study has several management implications for the conservation of endangered Sakhalin taimen. As aforementioned, various and complex threats to Sakhalin taimen population co-occur in eastern Hokkaido streams. To reduce extinction risk of eastern Hokkaido populations, it is required to relax negative impacts of glass land on Sakhalin taimen. For example, increasing riparian forest zone and reducing glass land is good to relax sediment pollution although the solution is inconsistent with reality because of existing social structure. If we cannot do the best plan, it is also good to install a buffer strip (ditch) in boundary between grass land and riverside, which can perform as a filter for sediment and nutrient pollution from glass land (Barling and Moore 1994). In addition, increasing a suitable spawning area by installing large pebbles may be good for increasing spawning success of Sakhalin taimen due to relax intra- and inter- specific (vs. rainbow trout) competition through redd superimposition.

In two dam-installed tributaries of Furen River Basin, estimated number of redds in 20 years ago (immediately before the dam installed) were 147.6 and 3.4 redds, respectively, based on the model as above mentioned. These estimations indicate that TA was much higher than SI in conservation priority for the Furen River population large based on difference in potential spawning habitat. In addition, the estimated redd abundance in one tributary (147.6) was even much greater than the present redd abundance in the entire Furen River Basin (139 redds). In other words, it was determined that damming by the Ministry of Defense in the past two decades has resulted in as many as about 50% reduction of Sakhalin taimen redds in the Furen River Basin. These estimations can be used for the action plan to increase the Furen River population size. On the other hands, increasing connectivity by removing dam, river manager had better to take one problem into consideration, for increasing connectivity in fragmented basin to reduce extinction risk on native species can enhance invasion by alien species that enter via corridor created, which can then increase extinction risk. Such dilemma is well known for salmonids especially in North America (as review in Fausch et al. 2009). In fact, number of rainbow trout redds increased in upstream reach as well as those of Sakhalin taimen after increasing connectivity by installing fish ladder on existing dam in a tributary of Furen River where both salmonids co-exist (Nomoto unpublished data). Based on the actual circumstances, it is required to monitor distribution and abundance of both salmonid redds in response to an increase in connectivity. Additionally, to reduce the deleterious impacts on Sakhalin taimen, we suggest that rainbow trout should not be released, neither purposefully nor accidentally, into catchments inhabited by Sakhalin taimen. Furthermore, removal of rainbow trout using efficient and reasonable methods such as electrofishing (as described by Peterson et al. 2008), may be needed especially in streams where Sakhalin taimen abundance is declining.

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Table 1.

Water depth, velocity, and pebble size at Sakhalin taimen and rainbow trout redds in the study stream. Values in parentheses are means ± 95% confidence limit. Randomization tests were performed for each value between the two species.

Species	Water depth (cm)	Velocity (cm/second)	Pebble size D50 (mm)
Sakhalin taimen	11.0–43.3 (23.9 ± 2.2) n = 52	31.8–85.3 (54.0 ± 4.5) n = 50	8.21–12.66 (10.67 ± 0.54) n = 17
Rainbow trout	10.5–41.5 (25.5 ± 2.0) n = 61	16.4–77.7 (55.1 ± 3.6) n = 61	8.30–14.07 (10.73 ± 0.60) n = 22
Randomization test	$P > 0.05$	$P > 0.05$	$P > 0.05$

Table 2.

Number of redds superimposed by conspecific or other salmonid species in 2006, 2007, and 2008. Fisher's exact test (F.E.T.) was performed for 2 × 2 contingencies (data in squares).

Speices spawned	No. of redds	No.(%) of total superimposed redds	Superimposed by			F.E.T.
			Unidentified	Sakhalin taimen	Rainbow trout	
2006						
Sakhalin taimen	15	5 (33.3%)	0	0	5	$P = 0.55$
Rainbow trout	93	26 (28%)	1	5	20	
Unidentified	11	7 (63.6%)	1	2	4	
2007						
Sakhalin taimen	20	8 (40%)	0	2	6	$P = 1$
Rainbow trout	89	23 (25.8%)	2	5	16	
Unidentified	14	10 (71.4%)	3	1	6	
2008						
Sakhalin taimen	22	6 (27.3%)	0	1	5	$P = 1$
Rainbow trout	85	19 (22.4%)	3	4	12	
Unidentified	15	10 (66.6%)	4	1	5	
Total						
Sakhalin taimen	57	19 (33.3%)	0	3	16	$P = 0.75$
Rainbow trout	267	68 (25.5%)	6	14	48	
Unidentified	40	27 (67.5%)	8	4	15	
Total	364	114 (31.3%)	14	21	79	

Table 3. Densities (N/100m) of Sakhalin taimen juveniles electrofished at each season in 2004 and 2005. Estimated number (N) of juveniles at stations 1−12 are shown in parentheses. Total number in the bottom row are estimated numbers of juveniles at all stations and unsurveyed areas,

St.	Area (100 m^2)	2004 Aug.		Oct.		Dec.		2005 June		Aug.		Oct.		Dec.	
1	2.1	8.7	(18.0)	3.4	(7.0)	2.9	(6.0)	0	(0)	0	(0)	0	(0)	0	(0)
2	2.5	9.3	(23.1)	3.6	(9.0)	1.2	(3.0)	0	(0)	0	(0)	0	(0)	0	(0)
3	1.9	10.5	(20.1)	2.6	(5.0)	3.1	(6.0)	0	(0)	0	(0)	0	(0)	0	(0)
4	2.1	4.3	(9.0)	4.8	(10.0)	2.4	(5.0)	0	(0)	0	(0)	0	(0)	0	(0)
5	1.8	17.4	(31.6)	6.6	(12.0)	3.9	(7.0)	0.6	(1.0)	0	(0)	0	(0)	0	(0)
6	1.9	14.8	(28.0)	6.9	(13.0)	3.7	(7.0)	0	(0)	0	(0)	0	(0)	0	(0)
7	2.1	9.1	(19.2)	1.4	(3.0)	1.4	(3.0)	0.5	(1.0)	6.1	(13.0)	6.1	(13.0)	3.8	(8.0)
8	1.9	10.6	(20.1)	4.8	(9.2)	2.1	(4.0)	2.1	(4.0)	11.1	(21.0)	7.4	(14.0)	4.8	(9.0)
9	2.2	14.2	(31.4)	2.7	(6.0)	2.7	(6.0)	1.4	(3.0)	7.7	(17.0)	4.5	(10.0)	2.7	(6.0)
10	2.1	13.3	(28.1)	5.2	(11.0)	1.9	(4.0)	2.8	(6.0)	4.7	(10.0)	3.3	(7.0)	2.4	(5.0)
11	2.1	26.8	(55.2)	2.4	(5.0)	1.9	(4.0)	2.4	(5.0)	8.3	(17.0)	2.9	(6.0)	1.5	(3.0)
12	1.9	36.6	(70.6)	6.8	(13.0)	2.1	(4.0)	3.1	(6.0)	9.9	(19.0)	4.2	(8.0)	3.1	(6.0)
Mean± SE		14.4±2.58		4.2±0.54		2.5±0.24		1.0±0.36		3.9±1.3		2.4±0.79		1.5±0.51	
Total		1058		332		193		74		332		233		147	

Table 4. Results of redd counts and estimated no. of female taimen and spawned in 2008.

River system	No. of redds	No. of females estimated (/Year)	Whole no. of females estimated (×2)
Bekanbeushi	**389**	**78**	**156**
Furen	**139**	**28**	**56**
Nishibetsu	**25**	**5**	**10**
Tokotan	**15**	**3**	**6**
Tohoro	**0**	—	—
Chashikotsu	**0**	—	—
Yaushubetsu	**0**	—	—
Shunbetsu	**0**	—	—
Tobikari	**0**	—	—
	568	114	228

Table 5. Comparison of mean characteristics between tributaries with and without Sakhalin taimen redds.

Variable	Taimen's redd observed (N = 14)			Taimen's redd not observed (N = 18)		
	Mean	SD	Range	Mean	SD	Range
Suitable spawning area (m^2)	1191	991	87–3420	95	124	5 – 409
Water flow ($m^3 s^{-1}$)	0.39	0.33	0.06–1.14	0.17	0.12	0.04–0.43
Stream slope	0.0069	0.0042	0.0022–0.0185	0.0072	0.0037	0.0145–0.0012
D50 of the pebbles (mm)	12.4	2.7	2.7–18	10.7	1.5	8.9–14.1
Percent fines	6.5	3.1	2.4–10.9	15.4	6	8.3–31.9
Percent grazed	25.6	29.2	0–84.5	65.2	13.6	38.1–85.1

Table 6. Number of Sakhalin taimen redd and values of eight environmental factors in 34 tributaries. NR: Number of Sakhalin taimen redds; PFS: Percentage of fine sediment (%); D50: median size of pebbles (mm); SS: Stream slope (%); SSA: Suitable spawning area (m^2); WF: Water flow ($m^3 S^{-1}$); WA: Watershed area (km^2); PG: Percentage of watershed grazed (%); RT: Rainbow trout. Tributaries are anonymous for protecting Sakhalin taimen from fishing.

Tributary	NR	PFS	D50	SS	SSA	WF	WA	PG	RT
Furen River									
NA	25	7.9	11.4	0.66	2029	0.49	27.2	69.7	85
KB	50	3.3	16.9	0.75	812	0.14	9.3	0.0	0
KD	6	3.2	15.8	0.86	113	0.06	5.5	0.0	0
FR	15	9.0	12.3	0.75	2144	1.14	35.0	84.5	25
WFR	8	9.1	11.8	0.23	1129	0.41	37.4	53.6	17
KM	0	12.5	10.1	0.48	25	0.32	14.1	55.0	10
MNK	0	13.0	9.7	0.90	21	0.04	2.6	80.8	0
NK	0	14.4	9.3	1.04	20	0.06	3.2	66.3	4
KF	0	27.3	9.7	0.30	5	0.41	21.6	68.9	0
TDN	0	14.1	9.7	0.51	12	0.10	6.6	80.7	0
KMR	0	15.5	9.7	0.42	15	0.16	6.9	54.4	0
RGA	0	17.0	12.6	1.27	42	0.07	2.5	76.9	0
RIA	0	13.7	9.8	0.91	15	0.05	3.3	58.4	0
NH	3	10.9	12.1	0.90	160	0.06	3.2	49.1	5
HD	0	11.7	11.8	0.60	324	0.14	8.9	70.4	2
KU	0	16.5	13.6	0.88	227	0.10	5.5	74.3	0
MN	0	10.6	14.1	0.51	176	0.18	6.2	85.1	3
TA	8	3.1	11.7	0.69	3168	0.27	19.3	0.0	0
SI	0	6.8	10.2	0.33	32	0.47	15.9	0.0	0
Bekanbeushi River									
WFP	169	2.4	10.7	0.35	3420	0.58	29.0	0.0	0
FP	75	4.3	10.8	0.47	1751	0.70	25.3	0.0	0
TK	15	9.0	9.9	0.27	104	0.24	16.9	23.7	0
ON	0	15.2	12.9	1.45	133	0.05	3.7	38.4	0
TR	50	6.6	11.3	0.72	1517	0.37	21.0	21.0	0
ST	10	10.1	10.0	0.70	87	0.07	10.1	14.8	0
SK	0	12.5	10.9	1.06	24	0.11	7.8	64.8	0
CB	0	12.2	10.1	0.74	30	0.17	9.0	38.1	0
BC	54	2.5	18.0	1.85	1138	0.12	6.6	16.6	0
BK	50	6.7	9.9	0.40	1084	0.70	31.8	0.0	0
CR	0	8.3	10.0	0.70	409	0.11	3.8	55.0	0
TRS	4	9.5	10.4	0.78	257	0.18	7.3	54.8	0
Yaushubetsu River									
YS	0	31.9	8.9	0.31	18	0.43	21.6	77.7	42
NKN	0	23.4	10.1	0.76	10	0.14	9.7	74.3	2
KIS	0	12.8	10.3	0.2	35	0.37	24.9	63.7	5

Table 7. Correlations among eight environmental factors. From this result, D50, SSA, WF, PG, and RT were chosen as independent variables to exclude the effect of multicollinearity in Poisson regression model.

Variable	PFS	D50	SS	SSA	WF	WA	PG	RT	Tolerance
PFS									0.27
D50	-0.48								0.57
SS	-0.16	0.43							0.37
SSA	-0.74	0.47	0.04						0.20
WF	-0.09	-0.15	-0.62	0.47					0.10
WA	-0.10	-0.16	-0.68	0.43	0.93				0.08
PG	0.65	-0.28	0.00	-0.49	-0.13	-0.24			0.32
RT	0.22	-0.10	-0.28	0.13	0.43	0.41	0.43		0.47

Table 8. Paramter estimates and significance levels for the Poisson regression best models predicting Sakhalin taimen redd abundance in individual watershed.

Parameter	Coefficient	SE	Z-value	P
Intercept	0.30	1.19	0.25	0.802
SSA	0.56	0.17	3.24	<0.001
PG	-13.55	3.65	- 3.71	<0.0001
SSA × PG	1.47	0.51	2.87	0.004

Table 9. Predicted numbers of Sakhalin taimen redds in response to simulated increases (habitat degradation; bottom) and declines (habitat improvement; top) in percentage of the 32 watershed grazed. Changes in number of taimen's redd relative to present number of taimen's redds were shown in parenthesis,

Habitat improvement			
⊿-5%	**⊿-10%**	**⊿-20%**	**⊿-50%**
563.7 (**+5.6%**)	608.7 (**+13.9%**)	658.1 (**+23.2%**)	743.3 (**39.9%**)
489.4-676	512.3-772.9	544-940.5	568.8-1517.5

Habitat degradation			
⊿+5%	**⊿+10%**	**⊿+20%**	**⊿+50%**
459.9 (**-13.87%**)	401.7 (**-24.8%**)	316.7 (**-40.7%**)	193.8 (**-63.7%**)
345.8-609.5	290.7-557	208.6-495	105.9-460.2

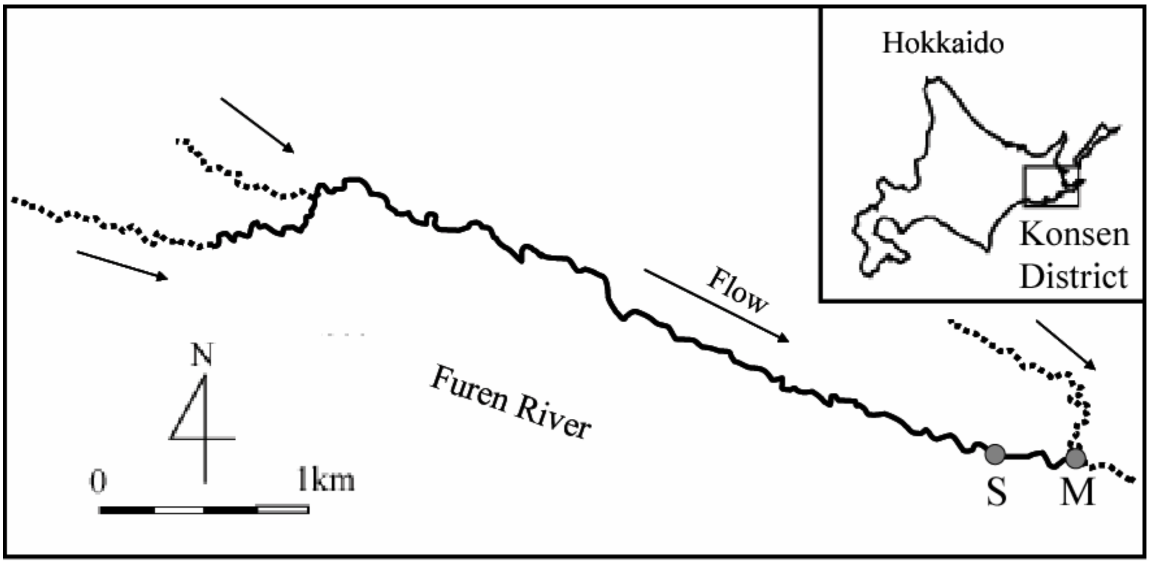

Fig. 1. A part of the Furen River located in Konsen District, Hokkaido, northernmost Japan. Study stream is shown by solid line. S: the station where water temperature and discharge were measured. M: stream mouth.

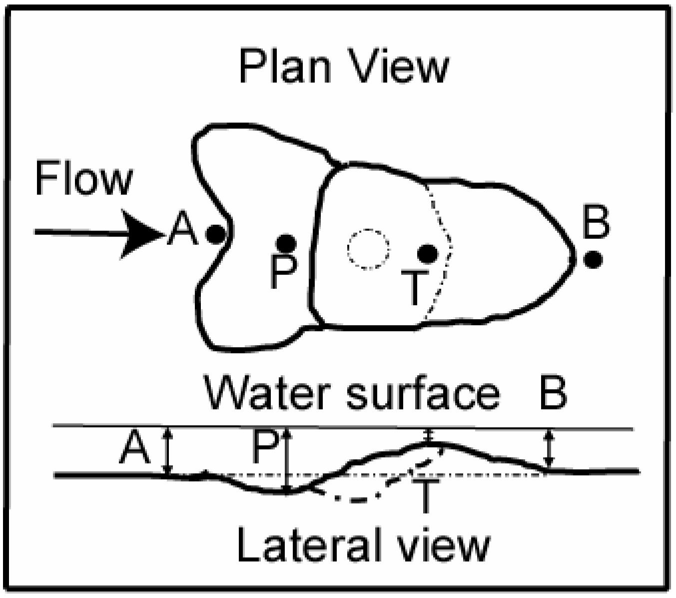

Fig. 2. Standard shape of redd. Water depth was measured at A (upstream of redd), P (pot), T (tail), and B (downstream of redd), and the depth of each redd was represented as the means of these four values. Water velocities were measured 5 cm above the stream bed at A and T and the velocity at each redd was represented as the means of the two values.

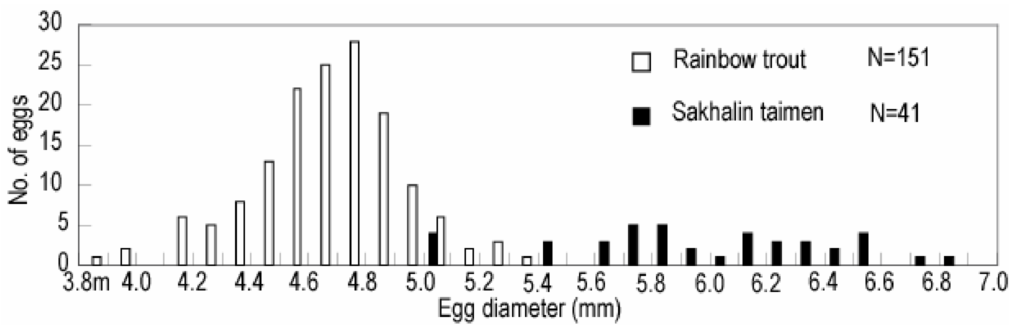

Fig. 3. Observed egg size of Sakhalin taimen and rainbow trout.

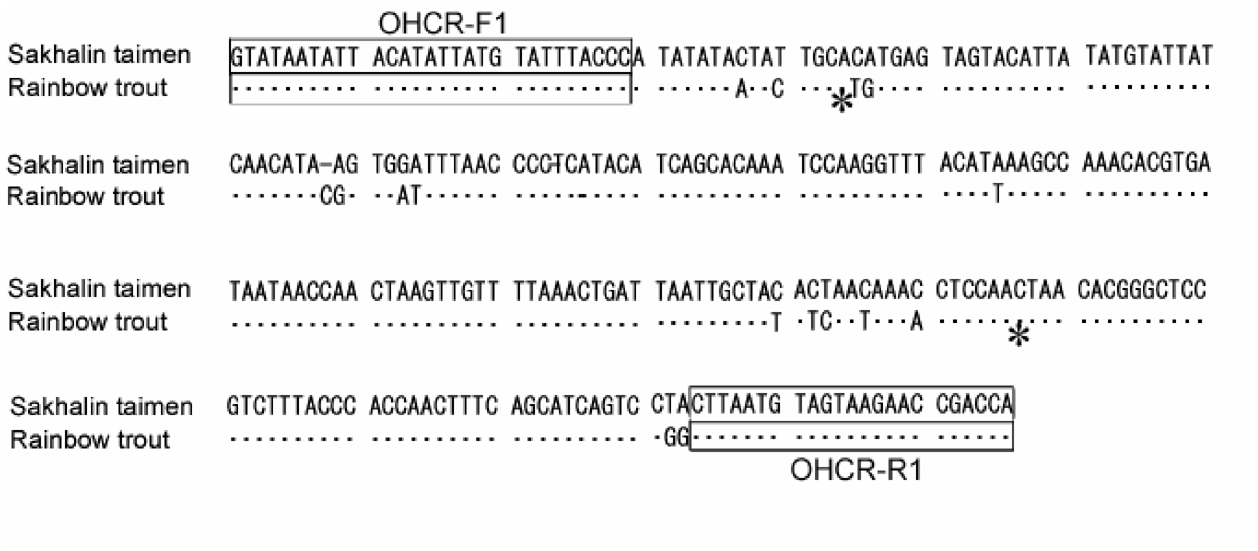

Fig. 4. Nucleotide sequences of a part of the control region (265–266 bp) from Sakhalin taimen and rainbow trout DNA amplified using primers OHCR-F1 and OHCR-R1. A eighteen-bp difference (17 substitutions and one deletion) was observed between the two species. Intraspecific variation was detected at two sites (*) in rainbow trout.

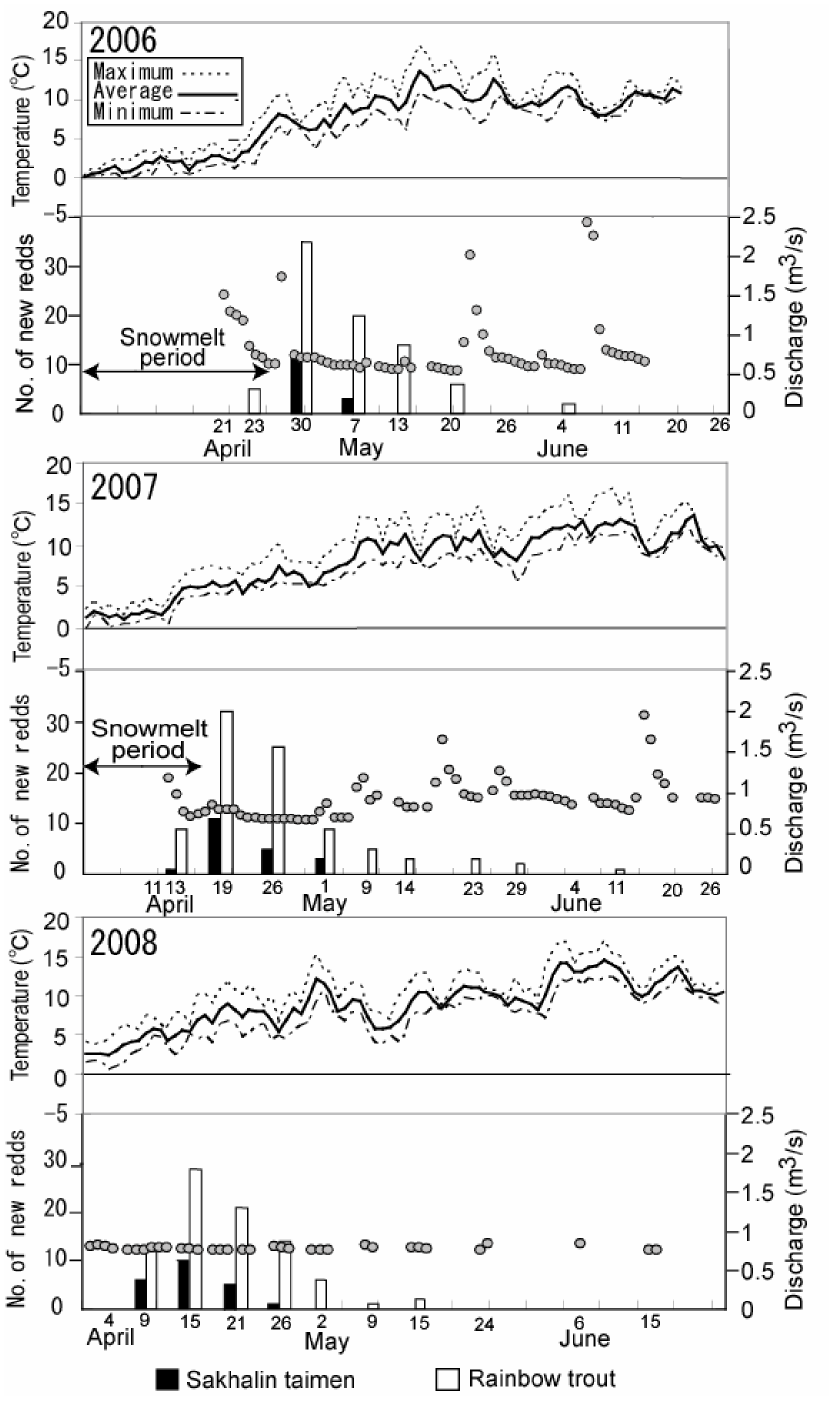

Fig. 5. Temporal fluctuation in water temperature and discharge as well as in the number of newly constructed redds during survey intervals of approximately one week in three spawning years. Bars represent redd counts and dots represent water discharge. Arrows indicate snowmelt periods an accumulation of snow observed at the riverside of the stream.

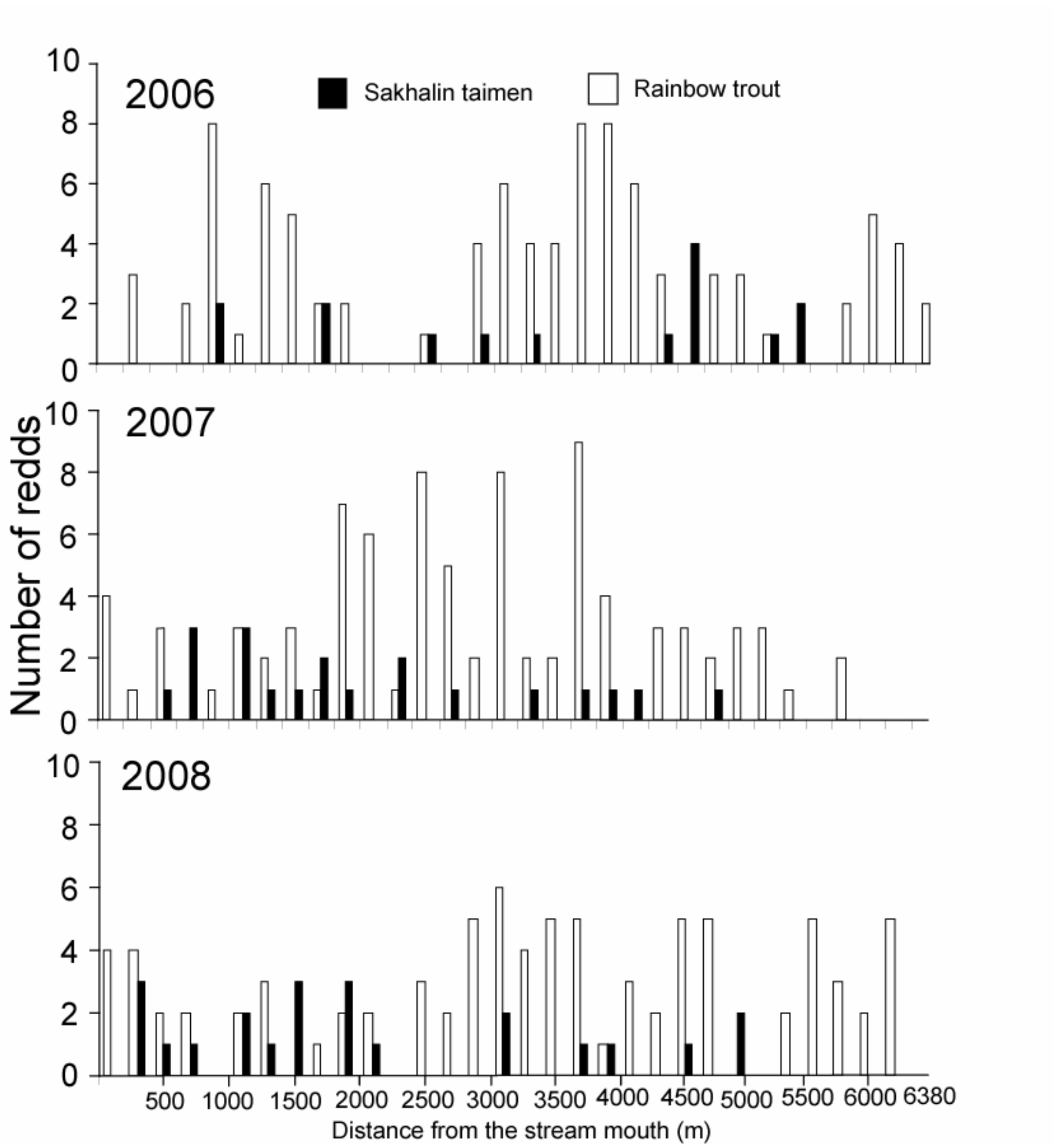

Fig. 6. Distribution of Sakhalin taimen and rainbow trout redds along the 6,380 m reach at intervals of 200 m during three spawning years.

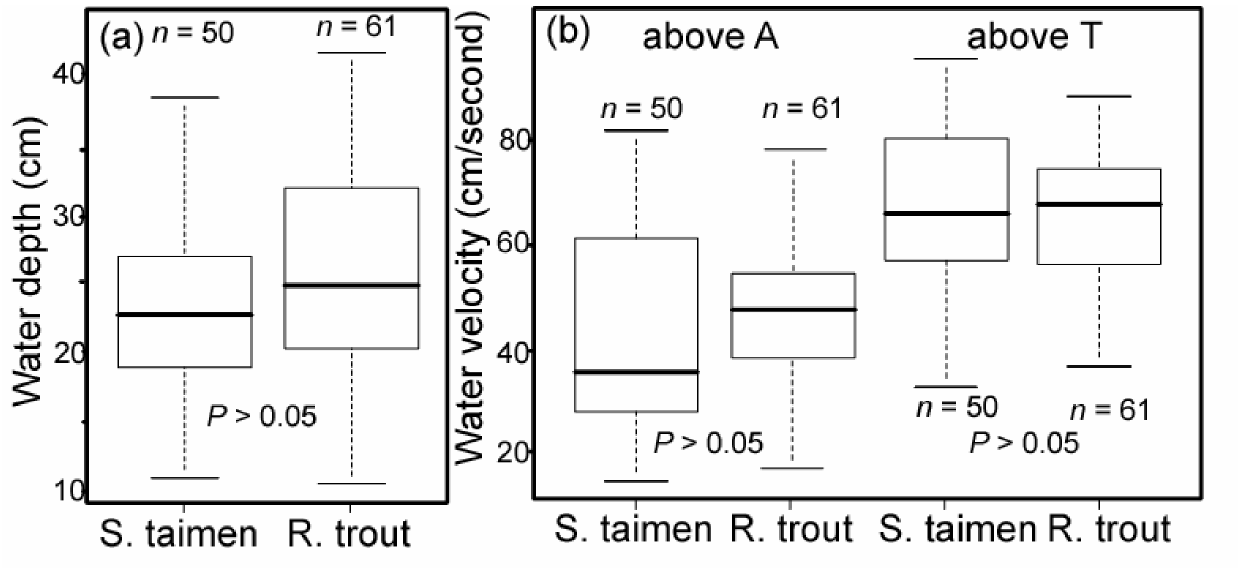

Fig. 7. Comparision of water velocities (a) and depths (b) at Sakhalin taimen and rainbow trout redds in the study stream. Median, quartile, and range are shown.

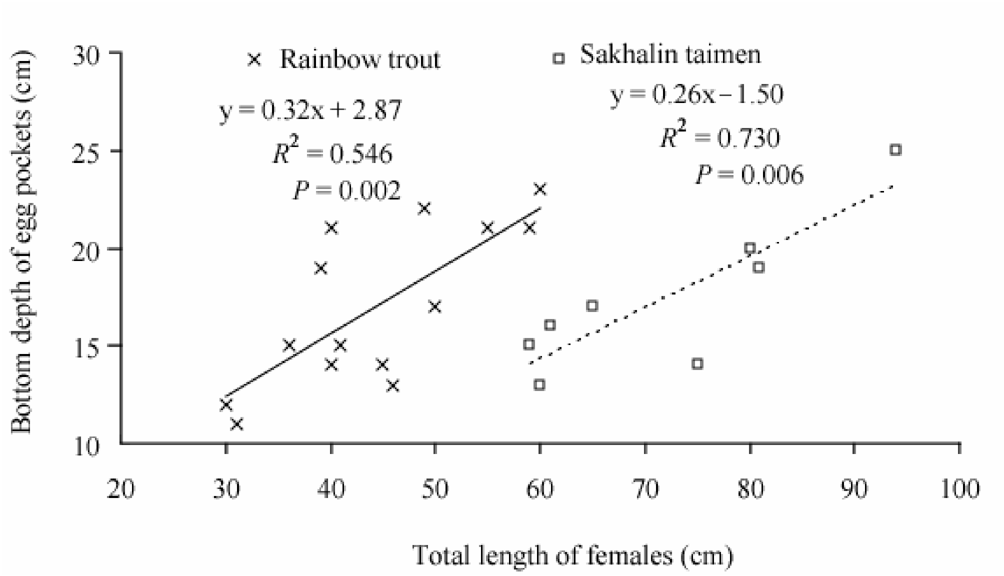

Fig. 8. Correlations between the egg pocket depth and total body length in female Sakhalin taimen and rainbow trout.

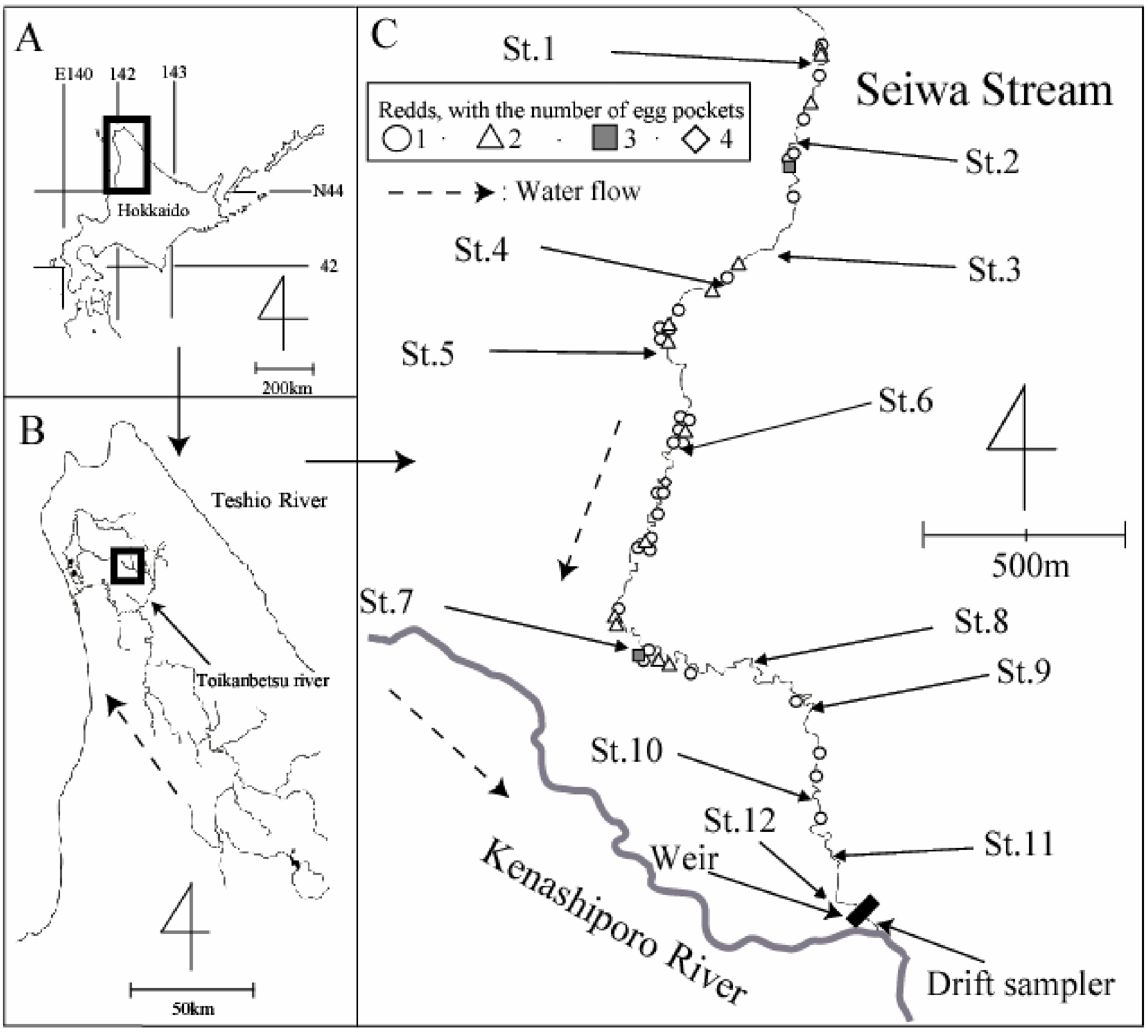

Fig. 9. Location of stidied stream (A, B) and distribution of redds with the number of egg pockets in Seiwa Stream, 2004 (C). St. 1−12: stations for electrofishing.

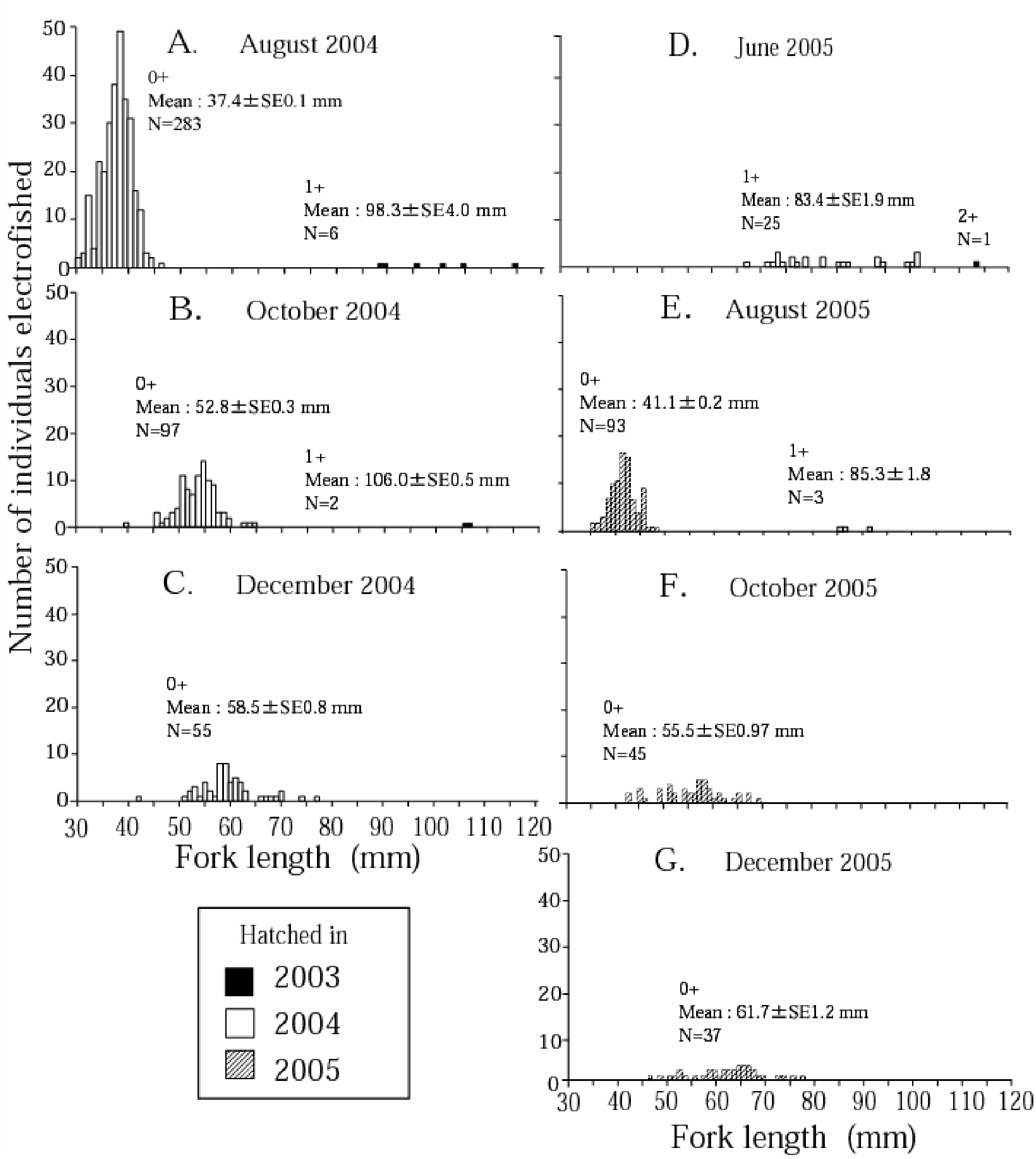

Fig. 10. Growth of juveniles electrofished in the post-hatch seasons in 2004 and 2005. Age was determined by the number of winter bands on scales.

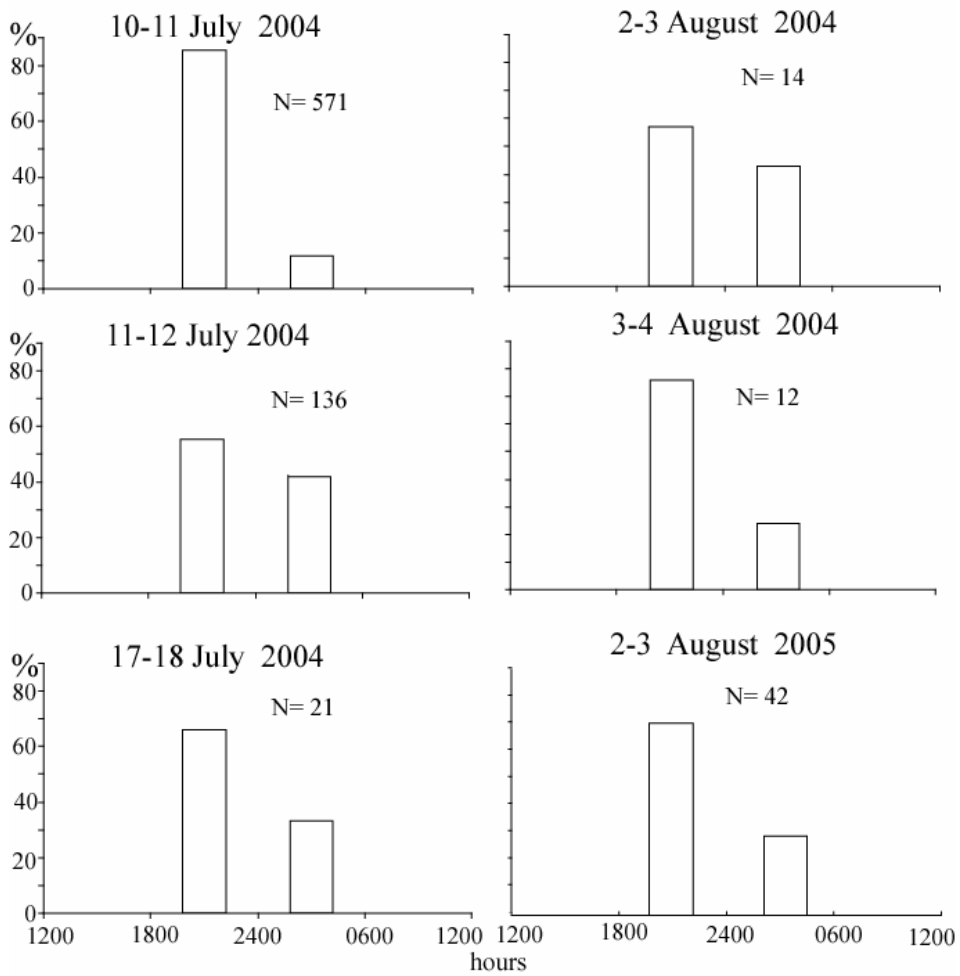

Fig. 11. Daily fluctuation in the number of downstream migrants (0+ fry) collected by a drift sampler. The sampling was conducted during each quarter (six hours) of 24 hours from noon. N: the number of individuals collected. Fry migrated only at night.

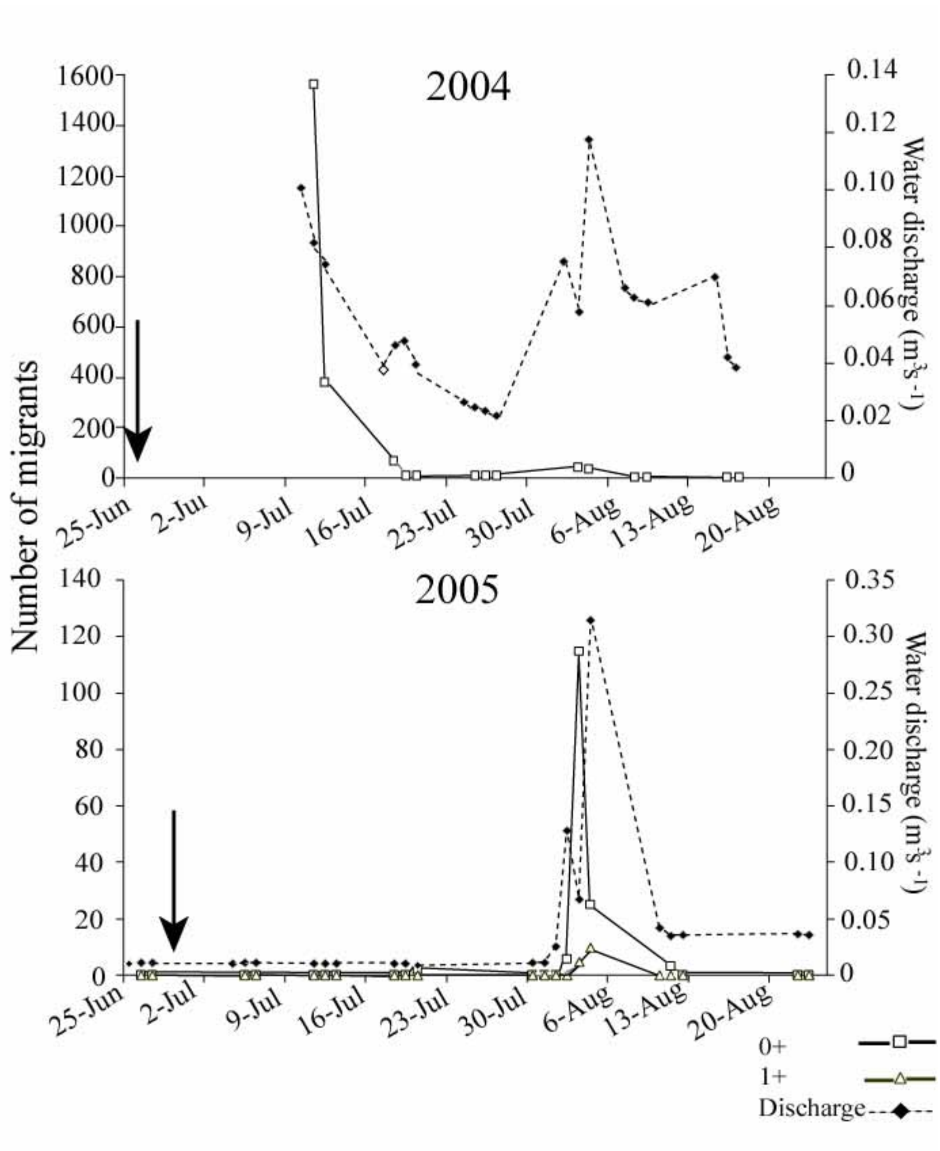

Fig. 12. Temporal fluctuation of water discharge and number of downstream migrants in the early emergent season, 2004 and 2005.

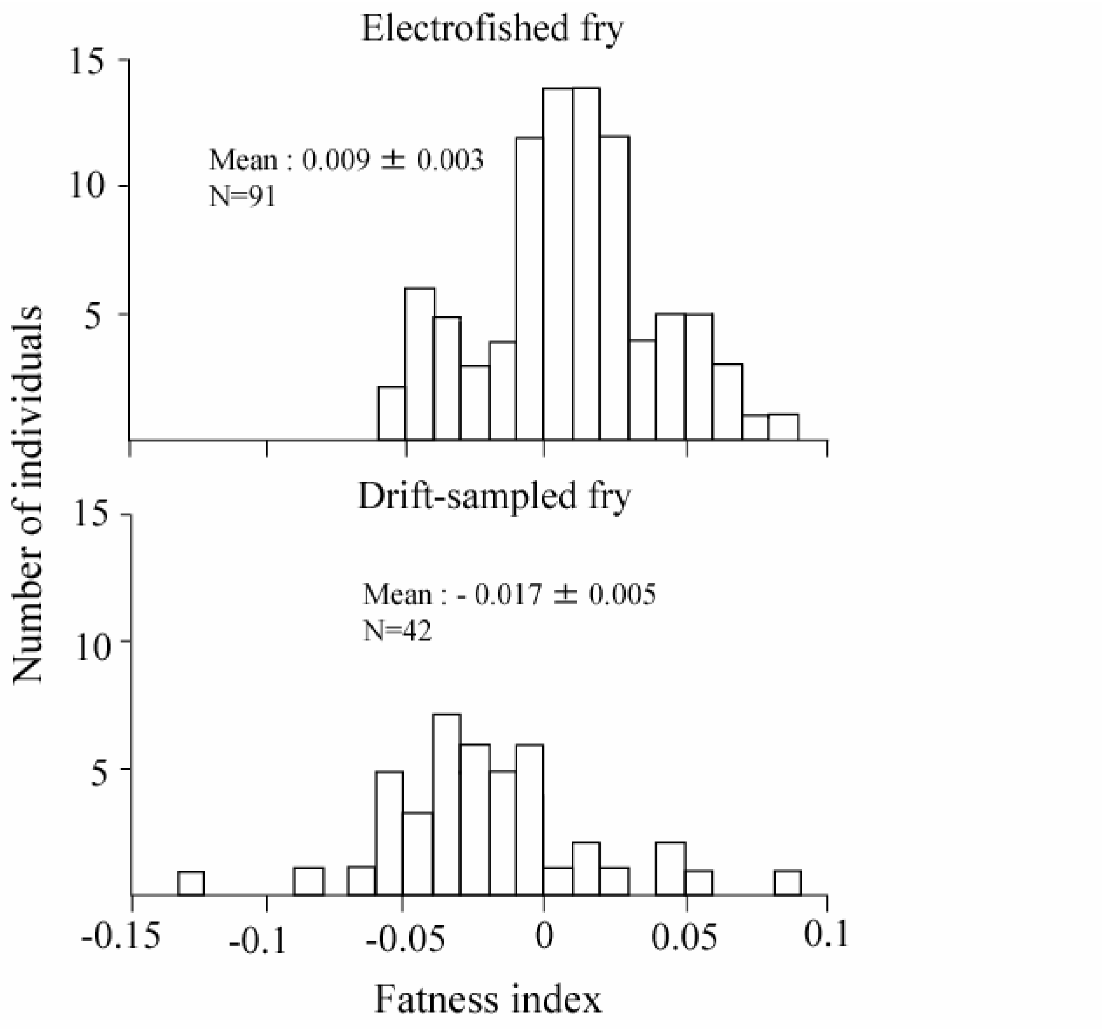

Fig. 13. Frequency distribution of fatness index in the electrofished and drift-sampled fry. The electrofished fry are significantly larger than drift sampled fry ($t = -4.74$, $p<0.001$)

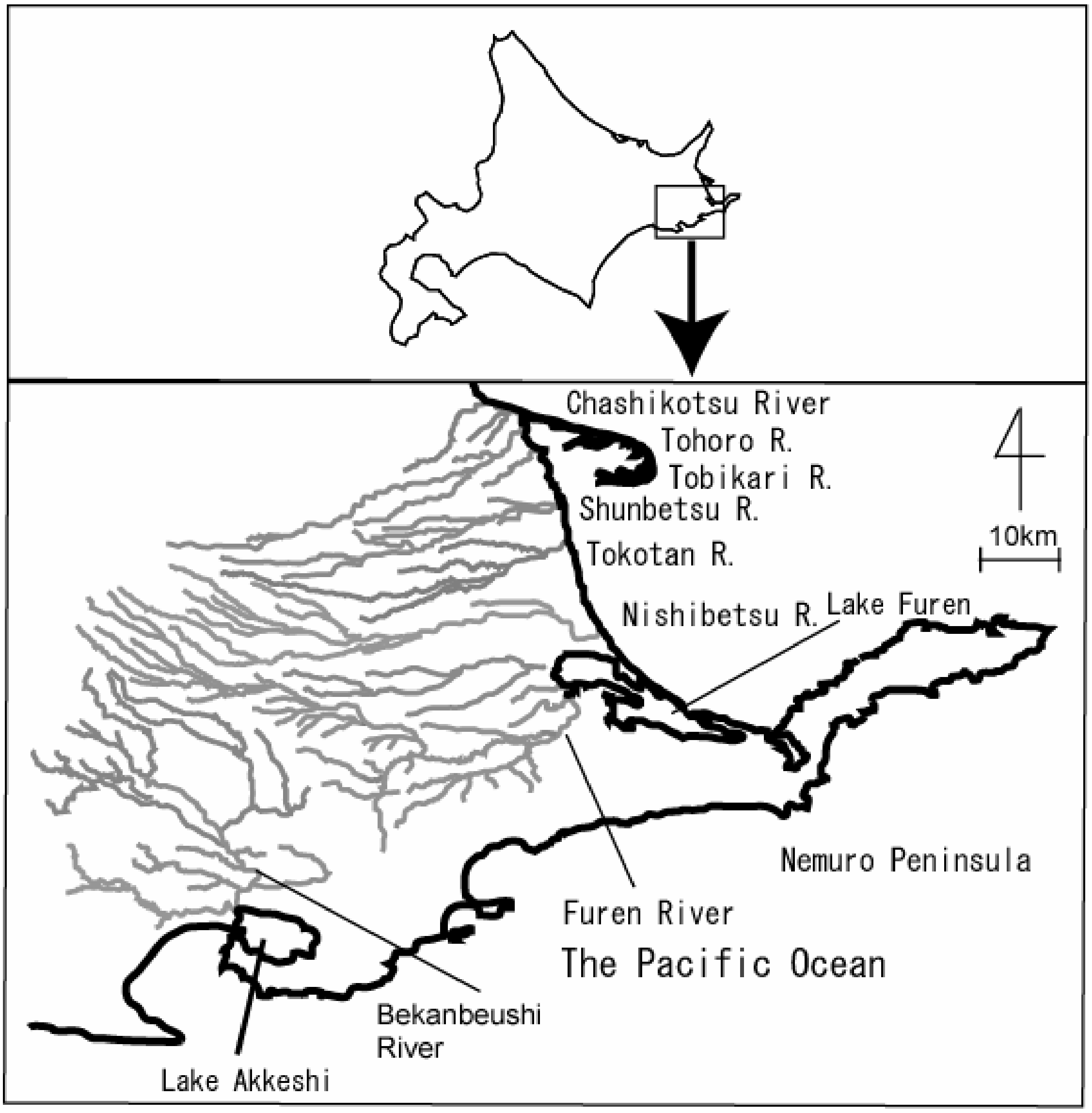

Fig. 14. Location of study river basins in eastern Hokkaido.

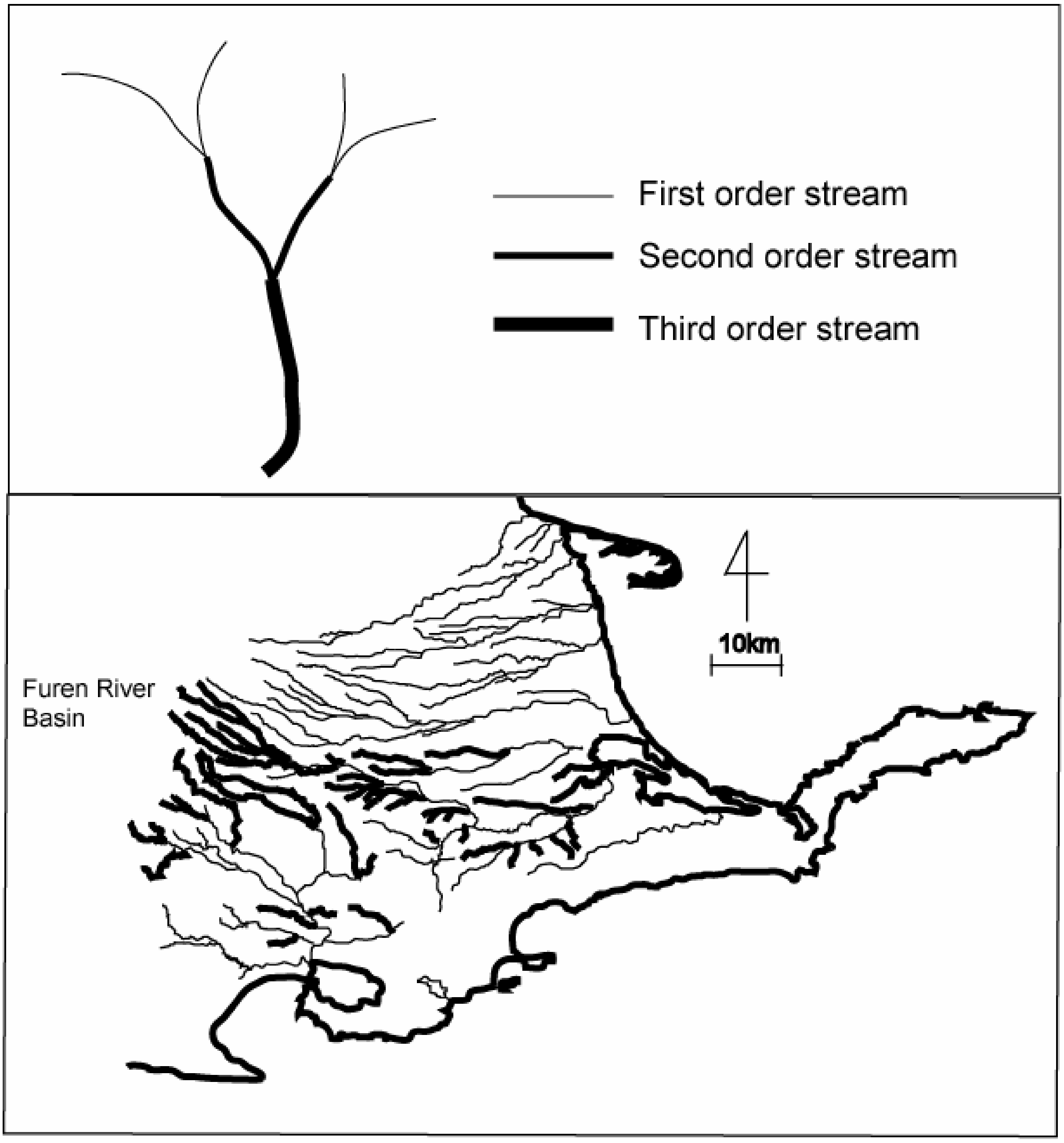

Fig. 15. Definition of these three orders of tributaries (A) and locations of the 34 study tributaries in eastern Hokkaido (B). Only first- and second-order tributaries were chosen as study tributaries (A).

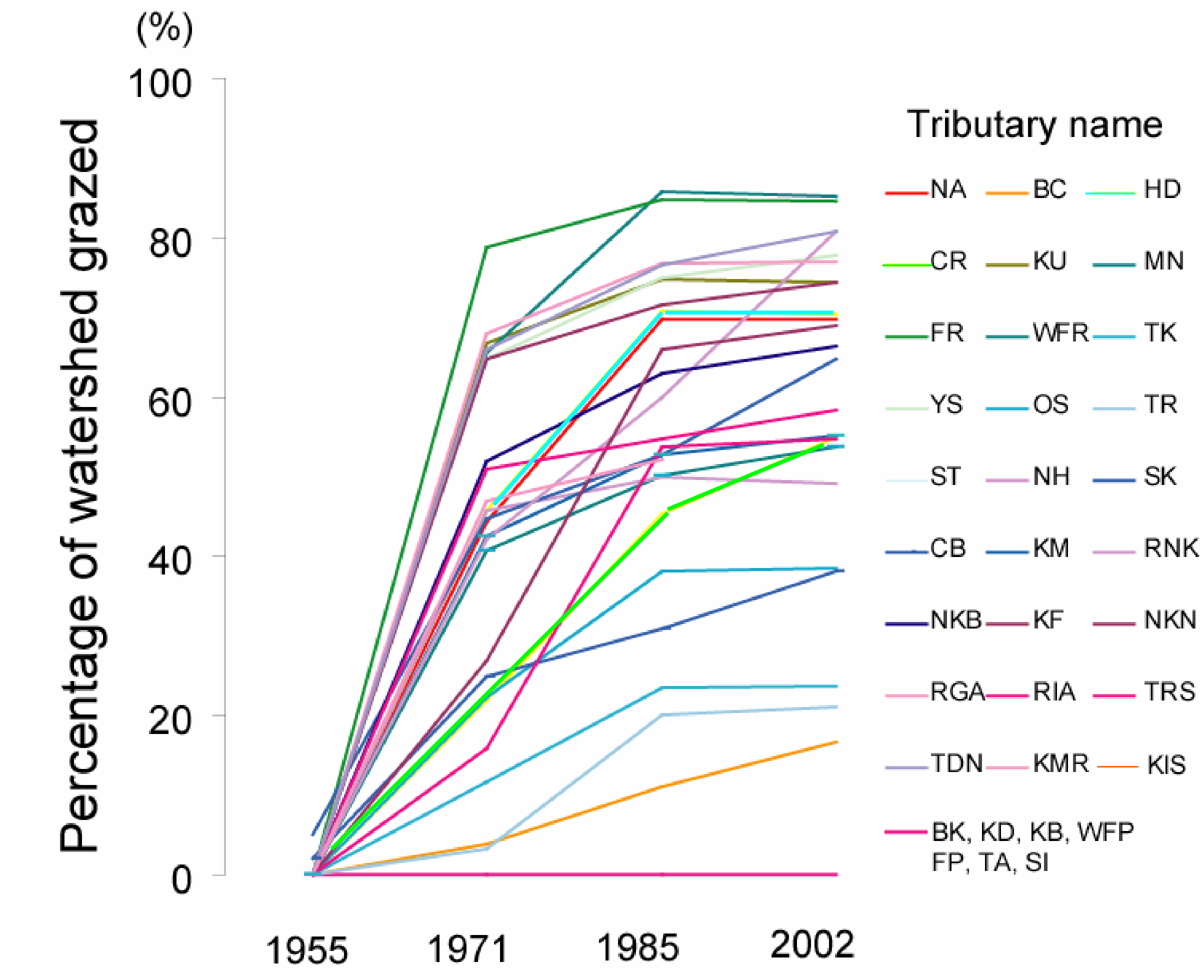

Fig. 16. Historical changes in percentage of grazing lands in watersheds of 32 dam-free and two dammed tributaries.

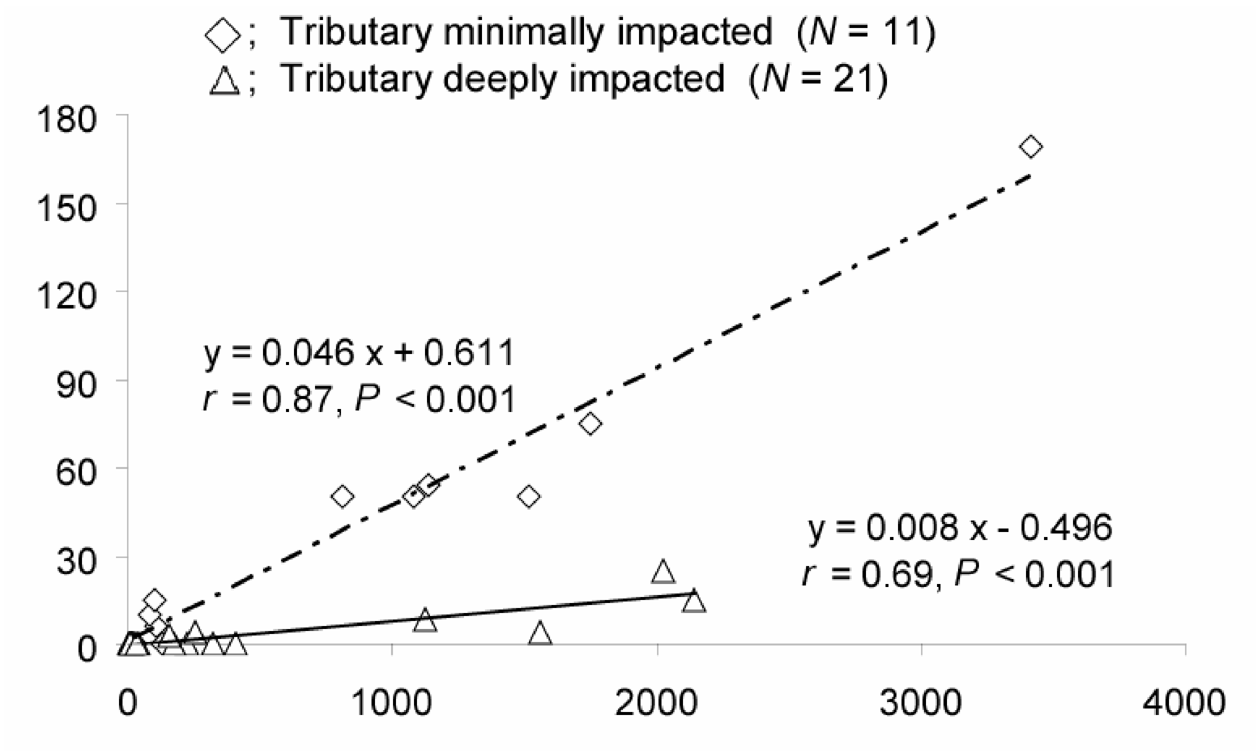

Fig. 17. The relationship between suitable spawning area and number of taimen redds in 32 dam-free tributaries. The tributaries are divided into two groups at the level of PG = 40%.

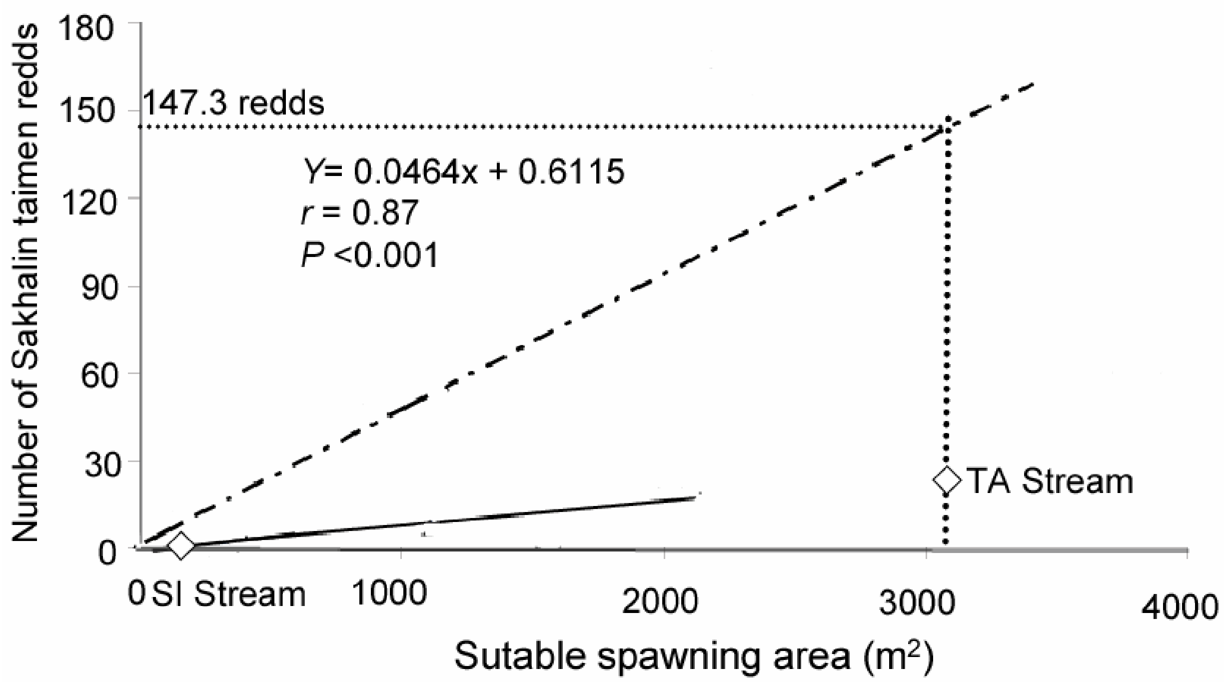

Fig. 18. Effects of dam construction on the number of Sakhalin taimen redd. Percentage of grazing land was less than 40% in TA Stream but more than 40% in SI Stream. In tributary TA, SSA = 3,168 m^2 corresponds to NR = 147.3 on the regression line y = 0.046x + 0.611.

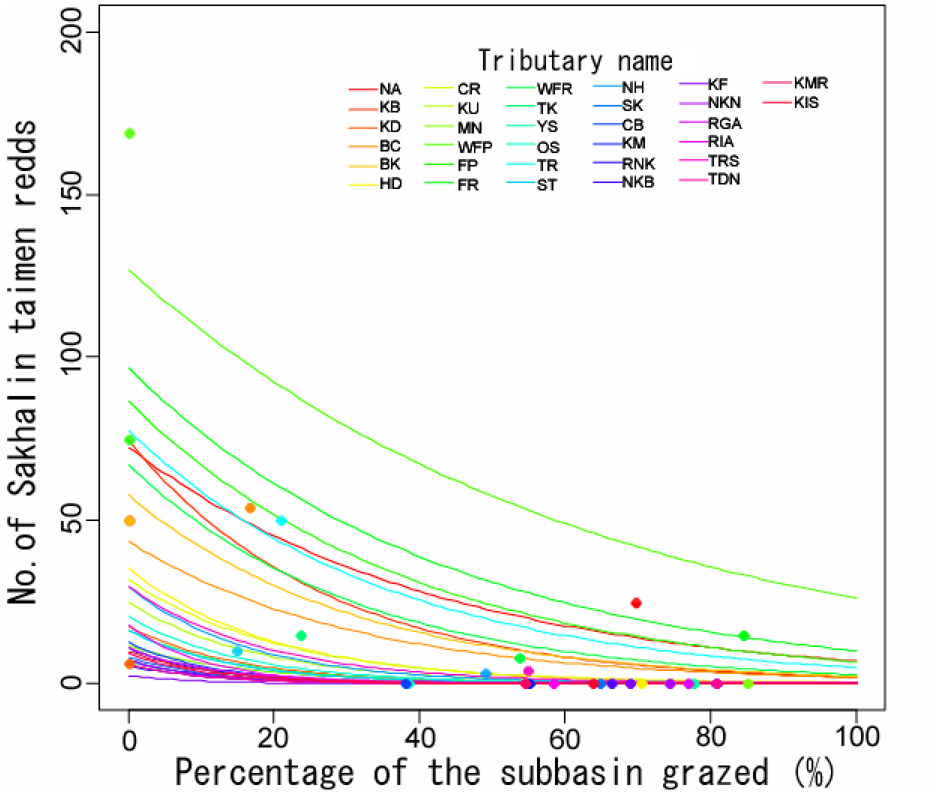

Fig. 19. Poisson regression model of the predicted numbers of Sakhalin taimen redds in response to simulated increasing of the percent livestock grazing in individual watershed. Each dot represents no. of taimen redds and percent livestock grazing in individual watershed, 2008.