Running head: Seasonal habitat use by *Hucho perryi*

Riverine environmental characteristics and seasonal habitat use by adult Sakhalin taimen (*Hucho perryi*) in the Bekanbeushi River system, Japan

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Abstract

The study identified seasonal habitat use by endangered adult Sakhalin taimen, *Hucho perryi* and the environmental characteristics of their habitats (water depth, amount of riparian forest, and meandering sinuosity). Fifteen adult *H. perryi* with acoustic tags were tracked by towing an acoustic receiver with a canoe in the Bekanbeushi River system in eastern Hokkaido Island, Japan during each month from late April to late November 2008. Individuals mainly used midstream (shallower than downstream) habitats in all seasons. These locations were generally characterized by relatively dense riparian forests and high sinuosity, indicating the presence of pools. In spring, individuals used habitats with less riparian forest cover compared to mean value of the river channel. From spring to autumn, adult *H. perryi* selected limnologically complex habitats with meandering channels. From summer to autumn, individuals selected habitats with more riparian forest cover. The inverse relationship between *H. perryi* detection and riparian forest area in spring was a result of seasonal defoliation in deciduous riparian forests.

Key word: Acoustic telemetry, Bekanbeushi River, Endangered species, River environmental characteristics, *Hucho. perryi*, Seasonal habitat

INTRODUCTION

Sakhalin taimen, *Hucho perryi* (Brevoort), is a salmonid fish that inhabits the Maritime Province of Siberia, Sakhalin, southern Kuriles, and Hokkaido Island (Kimura, 1966; Gritsenko *et al*., 1974). This is the only anadromous species among the five *Hucho* species and is the largest freshwater fish in Japan, reaching lengths >1.5 m (Gritsenko *et al*., 1974; Holicik *et al*, 1988). *H. perryi* is iteroparous and spawns in shallow upstream locations mainly from

April to May, after snowmelt, on Hokkaido Island (Fukushima, 1994, 2001; Edo *et al*., 2000; Esteve *et al*., 2009). As it grows, *H. perryi* uses more downstream habitats, eventually reaching coastal waters (Yamashiro, 1965; Kimura, 1966; Gritsenko *et al*., 1974; Kawamula *et al*., 1983; Sagawa *et al*., 2002, 2003; Arai *et al*. 2004; Edo *et al*., 2005; Mori & Nomoto, 2005; Honda *et al*., 2009; Honda *et al*., in press).

Due to its recent population decline, this species has been registered as Critically Endangered (CR) on IUCN's red list since 2006 (IUCN, 2009). Anthropogenic factors, such as recent river improvement projects, have been identified as causing this decline (Fukushima *et al*., 2008; Takami & Kawamula, 2008). The development of conservation programs for *H. perryi* is urgently needed.

Unfortunately, ecological information regarding the life history of *H. perryi*, including seasonal habitat use and habitat requirements, remains limited. The major rivers on Hokkaido Island in which *H. perryi* reside are generally associated with peat land. It is impossible to follow fish movements by visual observation because of low visibility in murky waters, except in shallower upstream areas. Therefore, most previous studies have referred to early life history and spawning ecology (Fukushima, 1994, 2001; Mori *et al*., 1997; Edo *et al*., 2000; Sagawa *et al*., 2003; Mori & Nomoto, 2005; Esteve *et al*., 2009) using ecological information from *H. perryi*. Information except for spawning season from adult fish is limited (Kimura, 1966; Gritsenko *et al*., 1974; Kawamula *et al*., 1983; Sagawa *et al*., 2002; Arai *et al*., 2004; Edo *et al*., 2005; Honda *et al*., 2009; Honda *et al*., in press). Generally, the presence of riffles and pools in rivers is important for riverine salmonids (Fausch & Northcote, 1992; Inoue & Nakano, 1994; Urabe & Nakano, 1998). Sagawa *et al*. (2002) indicated that adult *H. perryi* frequently inhabit large-scale pools in summer. Sagawa *et al*. (2002) studied the summer habitats of adult *H. perryi* in a tributary of the Teshio River in northern Hokkaido; they suggested that *H. perryi* primarily inhabit pools with large bottom areas and low flow velocities, which existed in locations with extensive riparian forest cover and highly meandering channels. Honda *et al*. (2009) tracked several adult *H. perryi* using acoustic telemetry from spring after spawning to winter and determined that adult fish migrated widely through the river system, from upstream areas to the estuary. Moreover, habitat use shifted to upper stream locations in the summer as water temperature increased. However, the Sagawa *et al*. (2002), study was limited to the summer months, and the focus was on pool environments. In Honda *et al*. (2009), the environmental characteristics of areas that adult *H. perryi* inhabited for long periods were not clarified because of a limited sample size.

The present study determined the seasonal environmental characteristics of the riverine habitats, which the adult *H. perryi* occupied for a relatively long time. The seasonal habitats of adult fish in the Bekanbeushi River system, eastern Hokkaido Island, were monitored by tracking more than ten fish with an acoustic receiver that was towed by a canoe. Using Geographic Information System (GIS) analysis, tracking data were compared with water depth, the tree density of riparian forests, and river sinuosity, several factors that Sagawa *et al*. (2002) hypothesized were closely related to *H. perryi* habitat use.

MATERIALS AND METHODS

STUDY SITE

Surveys were conducted in the Bekanbeushi River system (total basin area: 738.8 km^2), which flows in Akkeshi-cho and Shibecha-cho, Hokkaido (Fig. 1). In this river system, the main stream and tributaries, except for the Oboro and Obetsu rivers, were used as study sites. The study period spanned from the post-spawning season to just before the river froze: 25 April to 28 November 2008. Survey data were categorized by season: April–June, July–September, and October–November were defined as spring, summer, and autumn, respectively. In this study, the sites where fish were captured and released and their detected locations are not described for reasons of conservation. Location information is described using river domain blocks (areas).

The study sites were categorized into a total of six areas by considering channel length, junctions and tidal effects at the downstream end. Area 1 was located 30 km upstream from the river mouth, in terms of channel distance summed over the mainstream and any tributaries. The channel region from the border of area 1 to the two junctions between the Bekanbeushi River and the Toraibetsu (Chanbetsu) River was divided into upper (area 2) and lower (area 3) areas, and the lower border was 20 km from the river mouth. The downstream, was divided into three areas based on changes in the flow velocity with tidal fluctuations. Area 4 was the region extending from the Bekanbeushi River-Toraibetsu River junction to a point 8 km from the river mouth, where flow velocity did not change with the tide. Within the tide-affected area, the region that extended from the border of area 4 to the Bekanbeushi River-Chiraikaribetsu River junction was area 5, and the region from the junction to the river mouth was area 6. Riparian vegetation in areas 2–4 was comprised of an *Alnus–Flaxinus* association, an *Alnus* community, and a *Phragmites* class; riparian vegetation in area 5 was primarily comprised of the *Phragmites* class. In addition, the Chiraikaribetsu River was divided into two areas (upper: area 4, lower: area 5) at a point 6.8 km from the river mouth, where the river width decreases to less than half its greatest width.

FISH CAPTURE AND ACOUSTIC TAG ATTACHMENT

From 25 April to 3 May 2008, a net was set at the upstream end of a tributary in which *H. perryi* spawn, located ca. 51 km from the river mouth by channel length (area 1); 12 adult fish were captured (nine males and three females, Table I). The identity of each fish was described with regard to sex, fork length, and capture/release location. Fish were captured using a set net design with a seine net (1.0 m high × 28.1 m wide, mesh size: 40 mm). A fishway was placed along the riverbank. The entrance was located at the upstream side of the net to target *H. perryi* moving downstream. The sex of each fish was determined using physical characteristics and by pressing the abdomen to determine if unreleased gametes were present (Kawamula *et al*., 1996).

After anesthetizing (2-*phenoxyethanol* 0.04%, diluted with river water) the 12 captured fish, a small incision (ca. 1 cm) was made on each abdomen with a surgical knife, and an acoustic tag (Vemco V13-1L; www.vemco.com) covered with latex was inserted into each individual's abdominal cavity. The acoustic tags randomly transmitted a set of six pulses (69 kHz) once every 20–60 seconds for almost a year. A biodegradable line was used for suturing. After tagging, body length, fork length, total length, and body weight of each individual were measured. Measured individuals were immediately moved into a holding tank (60 cm long × 60 cm wide × 100 cm high) and held for more than 30 minutes. Individual fish were released immediately downstream of the net after they had recovered from the anesthetic.

Acoustic tags were also implanted in three additional adult *H. perryi* that had been caught by a set net fishery in Lake Akkeshi and had been held in a large fish tank in the market of the fisheries cooperative association of Akkeshi for several hours. These three fish were released at the nearby lakeshore after their recovery (Table I, Fig. 1).

In addition, Honda *et al*. (2009) reported that there is little chance of death for adult *H. perryi* from tagging stress in either laboratory or field studies.

TRACKING TAGGED FISH

Tagged fish were tracked using an acoustic receiver (Vemco VR2) that was towed behind a canoe in the river system. During the survey, the acoustic receiver's location was continuously recorded by a GPS receiver (Garmin eTrex Legend; www.germin.com). Because individual fish were continuously detected at ranges of 10–300 m in the channel, the center of the detection range was defined as a fish's position, with the stipulation that the location be within the channel. The acoustic receiver was towed in the river system from area 2 to area 6 at least once per month from late April to late November (see Appendix).

USE OF DETECTION DATA

A total of 25 stationary acoustic receivers were also deployed in the river system during the study [Honda *et al*. unpublished data, mean distance between receivers: 1363 ± 998 (S.D.) m]. When a fish was detected by a deployed receiver within three hours before or after the same fish was detected by the towed receiver, it was assumed the fish was actively migrating, and the detection was excluded from the analyses.

Fish positions were plotted monthly on a map (ESRI ArcGIS Vr. 9.2; www.esri.com), and an area spanning 400 m of channel length, centered on the fish's position, was defined as the occupied "habitat", based on the maximum detection range of the receiver. If two or more tagged *H. perryi* were present in the same 400-m channel segment, the 400-m segment centered on the multiple fish positions was defined as the occupied habitat. If an individual tagged fish was found several times in the same habitat segment within a single month, the individual was regarded as having stayed in that habitat, and the multiple detections were counted as a single occurrence.

ENVIRONMENTAL FACTORS AND METHODS FOR ANALYSIS

The environmental characteristics of *H. perryi* habitats were measured and recorded during the survey. Selected variables were river depth, tree cover of riparian forests and sinuosity as environmental characteristics; these factors are thought to be highly correlated with habitat use by adult *H. perryi* (Sagawa *et al.*, 2002). These environmental characteristics were compared between occupied habitats and all 400-m channel segments in each river area or in all river areas.

On 15–19 June, 16–17 July, and 18 and 20 August 2008, water depth was measured using a compact fishfinder (Honda Electronics HE-51C 4.3; www.honda-el.co.jp) attached to the canoe beam while traversing the river system from area 2 to area 6. Zigzag line transects were designed with multiple parallel lines within each subarea. Time was recorded from a radio-controlled clock that was captured by a digital video camera while waypoints were recorded on the GPS unit at ca. 7-m intervals. The mean depths of occupied habitats and all 400-m channel segments in each river area or in all river areas were calculated by interpolating depth through GIS analysis (normal kriging). The ratio of maximum to mean depth was also calculated as an index of pool existence at the habitat scale. This ratio was used for comparisons between occupied habitats and all segments in each river area or in all river areas, as were mean depth and maximum depth.

On 13 and 15 July 2008, the number of trees in riparian forests was counted along the river system from area 2 to area 6. Trees in riparian forests within 1 m of the river edge (on both sides of the river) were counted by visual observation along 40-m channel segments (20 m upstream and 20 m downstream) that were centered at points spaced at 100-m intervals along the channel length. Trees were classified into six groups based on diameter at breast height (dbh; 5, 10, 20, 30, 40, and 50+ cm), and the number of trees in each class was counted at each station. To minimize bias, measurements were taken by one person. The breast-height area of trees, calculated from dbh, was regarded as proportional to the projected area of tree cover for the river (Waring *et al.*, 1982). As a Riparian Forest Index (RFI), the number of trees in a riparian forest was used as an index of forest cover by:

$$RFI = 0.05^2 a + 0.1^2 b + 0.2^2 c + 0.3^2 d + 0.4^2 e + 0.5^2 f ,$$

where *a*–*f* represent the number of trees in each class. Mean values of RFI for each 400-m channel segment were calculated and used to compare occupied habitats with all 400-m channel segments in each river area or in all river areas.

Channel central points were connected by the longest straight line, and the number of lines was defined as the sinuosity index of a 400 m stretch (Sagawa *et al*., 2002). The 1/25000 map issued by the Geographical Survey Institute (Japan) was used for GIS analyses.

All environmental indices were compared between habitats and all 400-m channel segments in each river area or in all river areas; significance was tested at $\alpha = 0.05$ level by Mann-Whitney *U* tests to compare the difference between mean ranks for the variables.

RESULTS

RIVER ENVIRONMENTAL CHARACTERISTICS

The water depth and the sinuosity index were not different between areas 2 and 3, but mean RFI was smaller in area 3 (Table II). At the point where the Bekanbeushi, Toraibetsu, and Chanbetsu rivers diverge in area 4, the environment was characterized as being deeper, with a larger RFI and a smaller sinuosity index compared to area 3. The environment in area 5 was deeper, had a smaller RFI value and a smaller sinuosity index compared to area 4. Area 6, which consisted of the Bekanbeushi and Chiraikaribetsu rivers, was deeper and had a smaller sinuosity index than area 5. Trees were rarely found on the riverbank in area 6.

HABITAT OF ADULT *H. PERRYI*

Tagged fish were detected 468 times. Eleven tagged fish were detected across all areas, from areas 2 to 6. After excluding detections during migration, 66 habitat locations were found from areas 2 to 4 (see Appendix). All of the detections in area 2 involved the same fish (U741L), and they were all located ca. 50–100 m upstream from the border of area 3.

Therefore, these detections were pooled with the area 3 data. Two tagged individuals (F560R and F661R) remained in one location; they were found 20 times from July to November at a location in area 4. A large tree (dbh ca. 60 cm) had fallen perpendicular to the flow in this non-meandering area; considering the hydrographic disturbance to the habitat from the fallen tree, these data were excluded from the analysis. As a result, 24 habitat locations were found in area 3, and 22 locations were identified in area 4 (Table III).

SEASONAL CHANGES IN ENVIRONMENTAL CHARACTERISTICS

For each factor, total values were compared between occupied habitats and all 400-m channel segments in all river areas, and these are shown on Fig. 2. Mean depth of occupied habitats ranging 0.5–1.5 m was significantly shallower than that of all segments in all river areas [Fig. 2(a)], while there was no significant difference in maximum depth between occupied habitats and all segments [Fig. 2(b)]. For maximum depth/mean depth, mean RFI and sinuosity index, the values of occupied habitats were all significantly higher than those of all segments in all river areas ($P < 0.001$), no occupied habitat occurred in the river segments for which the maximum depth/mean depth, mean RFI and sinuosity index ranged between 1.0–1.1, 0 and 1–2, respectively [Fig. 2(c-e)].

Each environmental factor was also compared between occupied habitats and all 400-m channel segments (Table IV). Data pooled over all areas was compared to areas 3 and 4 where habitats occurred. Each combination of season and area as well as seasonal differences was analyzed (Table IV). To test for differences between occupied habitats and the all segments in river areas 3 and 4, the factor values for each area were standardized by dividing by the area’s mean value, because mean values of each factor in each area were not uniform (Table II); standardized values were used in statistical tests. Generally, there was no difference between occupied habitats and the all segments in river areas 3 and 4 in mean or maximum depth (Table IV). There were no significant differences between the maximum depth/mean depth ratio for occupied habitats and all segments in Areas 3 and 4 (Table IV). Except for spring in Area 3, there was a significant difference between the frequency distributions of RFI in occupied habitats and all river segments in Areas 3 and 4 (Table IV). For the sinuosity index, the values were significantly higher in occupied habitats than in all segments of Areas 3 and 4, except in autumn (Table IV).

DISCUSSION

In this study, persistence of adult *H. perryi* was only found in mid-stream (shallower than downstream) habitats, which are assumed to be seasonal territories. These habitats were characterized by a relatively large ratio of maximum depth against mean depth, highly meandering channels and high riparian forest cover. Also, compared to the whole channel in each river area, these habitats were characterized by highly meandering channels and high levels of cover from the riparian forest in summer and fall. These findings correspond to previous results, emphasizing the importance of river meandering and the existence of riparian forests for adult *H. perryi* (Sagawa *et al.*, 2002). Furthermore, this study evaluated seasonal changes in the environmental characteristics of their habitats.

H. perryi used habitats with sinuous channels and larger ratio of maximum depth against mean depth which indicates the existence of pool. These environmental conditions are likely correlated in natural settings; meandering rivers create a variety of horizontal flow velocities and provide vertical complexity in the channel (Morisawa, 1985; Harris *et al.*, 1995; Smith, 1998; Huggett, 2003). The importance of pools in river habitats has been suggested for several species of adult salmonids (Sagawa *et al.*, 2002; Baigún, 2003; Edo & Suzuki, 2003). Deeper pools help individuals hide from natural predators, such as eagles or bears (Power, 1987; Schlosser, 1987, 1988; Harvey & Stewart, 1991; Edo & Suzuki, 2003). In addition, the energy required to maintain position is expected to be lower in slow-flowing pools compared to riffles. Thus, the presence of pools associated with channel complexity is a key environmental characteristic of adult *H. perryi* territories. In spring, mean RFI values were smaller in occupied habitats than in the entire channel in each area. Because the study area is located in the subarctic zone, deciduous leaves, which shade the surface of the river, are absent in spring. The presence or absence of foliage influences the amount of cover a river has from sunlight. Water temperature can fluctuate widely because of differences in cover between the summer (July–September), when leaves are profuse, and winter to spring (November–May), when leaves are absent (Nakamura & Dokai, 1989). Studies have shown that riparian forests help supply terrestrial invertebrates as prey for salmonids (Hunt, 1975; Cada *et al*., 1987; Nielsen, 1992; Wipfli, 1997; Nakano *et al*., 1999). The quantity of terrestrial invertebrates that fall into a river is relatively small in spring (March–May), but can become large in summer (June–August; Kawaguchi & Nakano, 2001). The proportion of foraging on terrestrial invertebrates by rainbow trout (*Oncorhynchus mykiss*, Walbaum) that occurred in June–August was larger than in any other month (Kawaguchi & Nakano, 2001). Growth of prey and the presence of foliage in forests may seasonally alter the importance of riparian forests for *H. perryi*. Cover from riparian foliage helps individuals hide from terrestrial predators, as do pools (Shirvell 1990; Edo & Suzuki, 2003). Furthermore, Honda *et al*. (2009) suggested that adult *H. perryi* avoid open areas with high temperatures in downstream regions in summer. Adult *H. perryi* probably select habitats with high levels of riparian forest cover, which promise cooler environments with higher prey availability, from summer to autumn. In addition, fallen trees and drifting trees, which originate from riparian forests, provide pools and hiding places for salmonids (Urabe & Nakano, 1998; Nagayama *et al*., 2009). Although the data were excluded from the statistical analyses, two tagged fish remained near a large fallen tree for several months, suggesting that habitats can be created by occasional hydrographic events. Quantification of fallen trees and underwater habitat complexity should be addressed in future habitat assessments for *H. perryi*.

In recent years, declines in the habitats and species diversity of freshwater fishes have been noted. River channelization, flood control and/or water utilization, the loss of continuous structure consisting of shallows and pools, and floodplain area changes from river linearization have been regarded as the main reasons for these ecological patterns in fishes (Golden & Twilley, 1976; Swales, 1982; Takahashi & Higashi, 1984; Brooker, 1985; Brookes, 1985, 1988; Shimatani *et al*., 1994). Reductions in the complexity of riverine environments impact fish habitat availability and the socio-ecological costs required for the future sustainability of river basins. The present findings show that ecological complexity is essential in *H. perryi* habitats. Therefore, there is a need to maintain and recover natural channel environments, complete with horizontal and vertical complexity, for future conservation of the species. Vegetation in riparian zones should be considered with respect to seasonal movements and habitat selection by *H. perryi*. The conservation of riparian forests is important for the protection of seasonal habitats of *H. perryi* in the Bekkanbe-ushi River.

The methods used in this study were successful for examining the movements, and the environmental characteristics of selected habitats of adult *H. perryi*. However, methodological improvements are expected for future management. The accumulation of time-series data and additional surveys on biological aspects such as sex, age, and body size shall provide additional information and generate a detailed understanding of *H. perryi* ecology in the future. Moreover, to measure ecological characteristics in detail, new environmental factors, such as the effects of fallen trees or flow velocity, need to be considered. At the same time, the seasonal habitat use of *H. perryi* should be compared with prey distributions. Underwater objects, such as drifting trees, and prey availability should be included in future ecological surveys and habitat assessments. Finally, the management of endangered species requires spatial information without abundant *in situ* information. The integration of accumulated ecological information using GIS, as was done in this study, shall prove valuable for the conservation of suitable habitats for endangered freshwater fishes.

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Table I. Fish ID, measurements and tagging information for tagged adult *Hucho perry* captured at tributary upstream (ca. 51 km upstream from river mouth) of the Bekanbeushi River and Lake Akkeshi in Hokkaido, Japan.

Fish ID	Acoustic tag No.	Sex	Fork length (cm)	Body weight (kg)	Captured and released place	Released date
M699R	4726	Male	69.9	3.5	Tributary upstream	26 April
M520R	4652	Male	52.0	2.0	Tributary upstream	26 April
M566R	4722	Male	56.6	2.1	Tributary upstream	26 April
M839R	11753	Male	83.9	6.0	Tributary upstream	26 April
F815R	11756	Female	81.5	6.0	Tributary upstream	26 April
M595R	4723	Male	59.5	2.3	Tributary upstream	26 April
F560R	11754	Female	56.0	1.8	Tributary upstream	26 April
M605R	4725	Male	60.5	2.5	Tributary upstream	26 April
M476R	11757	Male	47.6	1.4	Tributary upstream	26 April
M563R	11755	Male	56.3	2.0	Tributary upstream	27 April
F661R	4724	Female	66.1	2.6	Tributary upstream	29 April
M529R	95	Male	52.9	1.7	Tributary upstream	3 May
U705L	96	Unknown	70.5	4.5	Lake Akkeshi	7 May
U741L	94	Unknown	74.1	5.0	Lake Akkeshi	9 May
U800L	98	Unknown	80.0	6.3	Lake Akkeshi	9 May

Upper cases “M”, “F”, “U”, “R” and “L” in fish ID show Male, Female, Unknown, River and Lake, respectively. Numbers in fish ID show fork length (mm) of each tagged fish.

Table II. Number (N) of 400-m channel segments, channel distance and means (± S.D.) of five environmental factors in each river area of the Bekanbeushi River system in Hokkaido, Japan.

	Area 2	Area 3	Area 4	Area 5	Area 6	All
N of 400-m channel segments	5	30	21	16	8	80
Channel distance (m)	2124	11665	6689	3417	3114	27009
Average of mean depth (m)	0.87 ± 0.10	0.87 ± 0.15	1.20 ± 0.26	1.67 ± 0.31	1.79 ± 0.46	1.21 ± 0.44
Mean maximum depth (m)	0.96 ± 0.06	1.09 ± 0.18	1.62 ± 0.46	1.92 ± 0.35	2.19 ± 0.44	1.50 ± 0.52
Mean of maximum depth/mean depth	1.12 ± 0.12	1.25 ± 0.12	1.33 ± 0.15	1.16 ± 0.10	1.24 ± 0.12	1.25 ± 0.14
Mean riparian forest index	0.45 ± 0.16	0.21 ± 0.15	0.42 ± 0.29	0.13 ± 0.17	0.00	0.24 ± 0.24
Mean sinuosity index	6.40 ± 0.89	6.80 ± 1.73	3.43 ± 1.36	1.94 ± 0.57	1.38 ± 0.52	4.38 ± 2.56

Table III. Number (N) of detected *Hucho perryi* and occupied habitats by season and river area of the Bekanbeushi River system in Hokkaido,

		Area 3	Area 4
Spring	N of detected fish	6	6
	N of habitat	7	7
Summer	N of detected fish	4	5
	N of habitat	12	10
Autumn	N of detected fish	3	3
	N of habitat	5	5
All	N of detected fish	7	9
	N of habitat	24	22

		Area 3	Area 4
Spring	N of detected fish	6	6
	N of habitat	7	7
Summer	N of detected fish	4	5
	N of habitat	12	10
Autumn	N of detected fish	3	3
	N of habitat	5	5

Table IV. Average standardized values (values of habitats / mean values in each river area of the Bekanbeushi River system in Hokkaido, Japan) and *P*-values of Mann-Whitney *U*-test between habitats of *Hucho perryi* and all 400-m channel segments in each river area, for five environmental factors in each season, each river area, and pooled over all river areas.

	Area 3 & 4						All season					
	Spring (n = 14)		Summer (n = 22)		Autumn (n = 10)		Area 3 (n = 24)		Area 4 (n = 22)		Area 3 & 4 (n = 46)	
	Mean ±	*P*	Mean ±	*P*	Mean ±	*P*	Mean ±	*P*	Mean ±	*P*	Mean ±	*P*
Mean depth (m)	1.03 ± 0.19	ns	0.95 ± 0.16	ns	1.03 ± 0.09	ns	1.00 ± 0.16	ns	0.99 ± 0.16	ns	0.99 ± 0.16	ns
Maximum depth (m)	1.09 ± 0.24	ns	0.96 ± 0.19	ns	1.06 ± 0.08	ns	1.02 ± 0.17	ns	1.03 ± 0.22	ns	1.02 ± 0.19	ns
Maximum depth/mean dep	1.05 ± 0.10	ns	1.02 ± 0.10	ns	1.04 ± 0.05	ns	1.02 ± 0.09	ns	1.04 ± 0.10	ns	1.03 ± 0.09	ns
Mean riparian forest index	0.96 ± 0.51	ns	1.40 ± 0.70	< 0.05	1.45 ± 0.51	< 0.05	1.07 ± 0.71	ns	1.50 ± 0.71	< 0.05	1.28 ± 0.63	< 0.05
Sinuosity index	1.38 ± 0.33	< 0.001	1.18 ± 0.26	< 0.05	1.18 ± 0.33	ns	1.15 ± 0.24	< 0.05	1.33 ± 0.34	< 0.05	1.24 ± 0.30	< 0.001

Each number in parenthesis shows number of occupied habitats. "ns" means not significant.

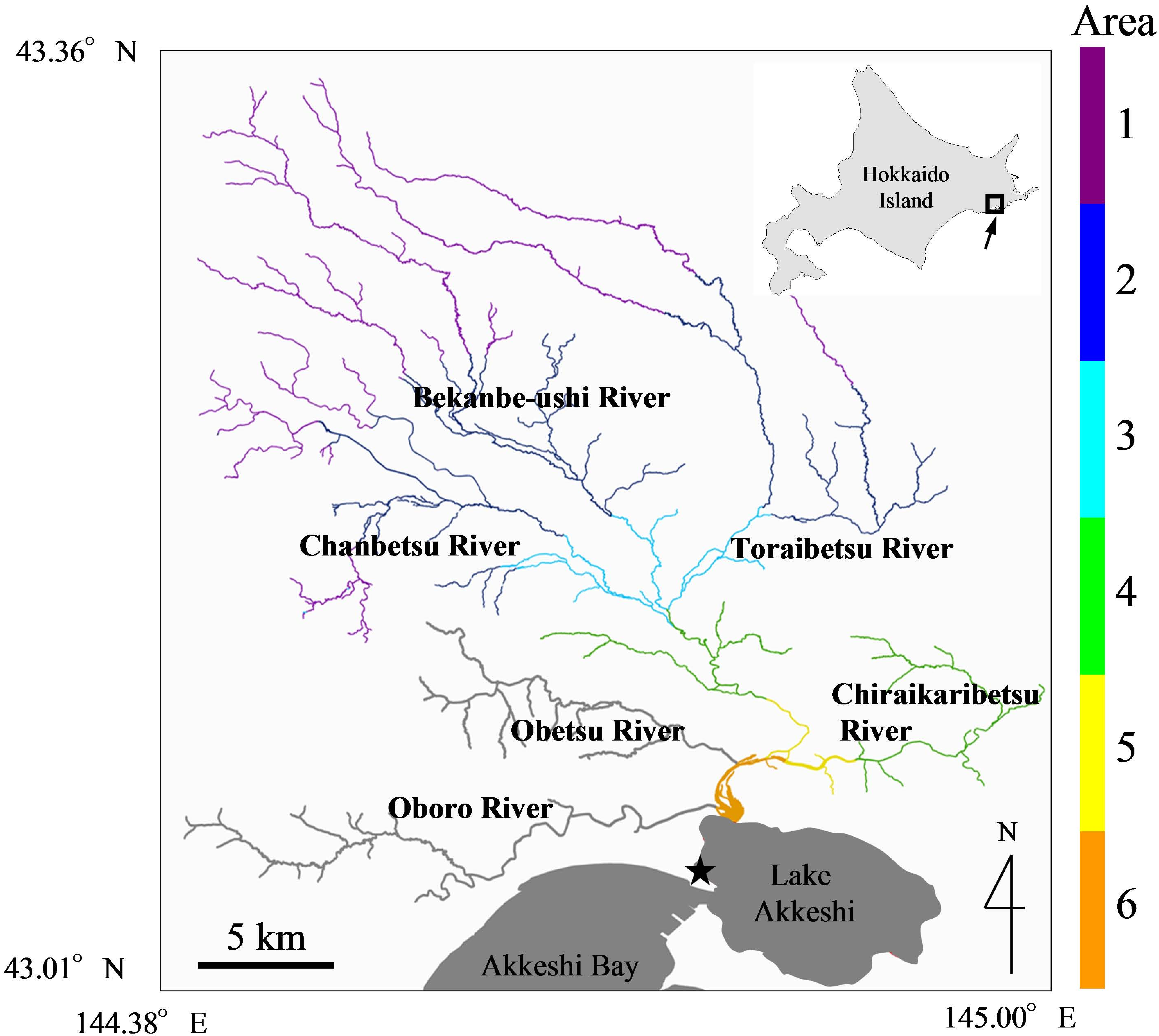
Appendix. Date (in 2008), area, and channel distance over which a receiver was towed by a canoe to detect tagged *Hucho perryi* in each river area of the Bekanbeushi River system in Hokkaido, Japan. Migrating fish are underlined.

Date	Areas	Distance a receiver towed (m)	Detected fish ID				
			Area 2	Area 3	Area 4	Area 5	Area 6
28 April	3-4	5812			M605R		
30 April	4-6	8783					
1 May	4-5	5556			M563R, F815R	M839R	
2 May	4-6	5743					
4 May	3-4	11368					
5 May	3-6	14444			M563R, F815R	M839R	
6 May	4-6	8632					
7 May	3-4	5812			M605R		
9 May	4-6	7263					M563R,
10 May	3-4	5812			M476R		
12 May	6	1520					U800L
13 May	4-6	8632			F815R	M839R	
14 May	3-6	14444		M476R	F815R, M563R	M839R	
15 May	2-4	11050					
19 May	2-4	13324		M605R, M699R, F560R,			
14 June	4-6	7263					
15 June	2-5	16606		M699R, U705L	M605R, M839R, F815R		
18 June	4-6	8632			M563R, F815R		
19 June	2-4	11050		U705L			
20 June	3-4	6957			F560R, F661R, M839R, M563R		
14 July	3-5	5556			M563R, F815R		
15 July	2-4	11050	U741L	U705L	U800L, M839R, F661R		
16 July	3-4	5812		M605R	M839R, F661R		
17 July	4-6	5743					
16 August	4-6	7263					
17 August	3-5	14019			M839R, U800L, F560R, F661R,		
18 August	4-5	7062			F815R		
19 August	2-5	16606	U741L	M699R, U705L	U800L, F560R, M839R, F661R,		
20 August	2-4	13386	U741L	M699R, U705L, M605R	M839R, F560R, F661R		
##########	4-6	7263					
##########	2-4	11050	U741L	M699R, U705L	U800L, F815R, F560R		
##########	3-4	6312		M605R	F815R, F661R, F560R, M563R		
16 October	3-6	14444			F815R, F661R,F560R	M563R	
17 October	4-6	7263					
18 October	2-4	11050			F815R, F661R, F560R		
19 October	2-4	9753		M699R, M605R			
##########	4-6	5743					
##########	3-5	12874		M605R	F661R, F560R, F815R	M563R	
##########	2-4	11050	U741L	M699R	F661R, F560R		
##########	3-5	11368		M605R	F661R, F560R, F815R		
##########	3-5	11368		M605R	U705L, F661R, F560R, F815R		
##########	4-5	5556			F815R, U705L		
##########	3-4	6612		M605R	F661R		
##########	3-4	6612			F560R, F661R		

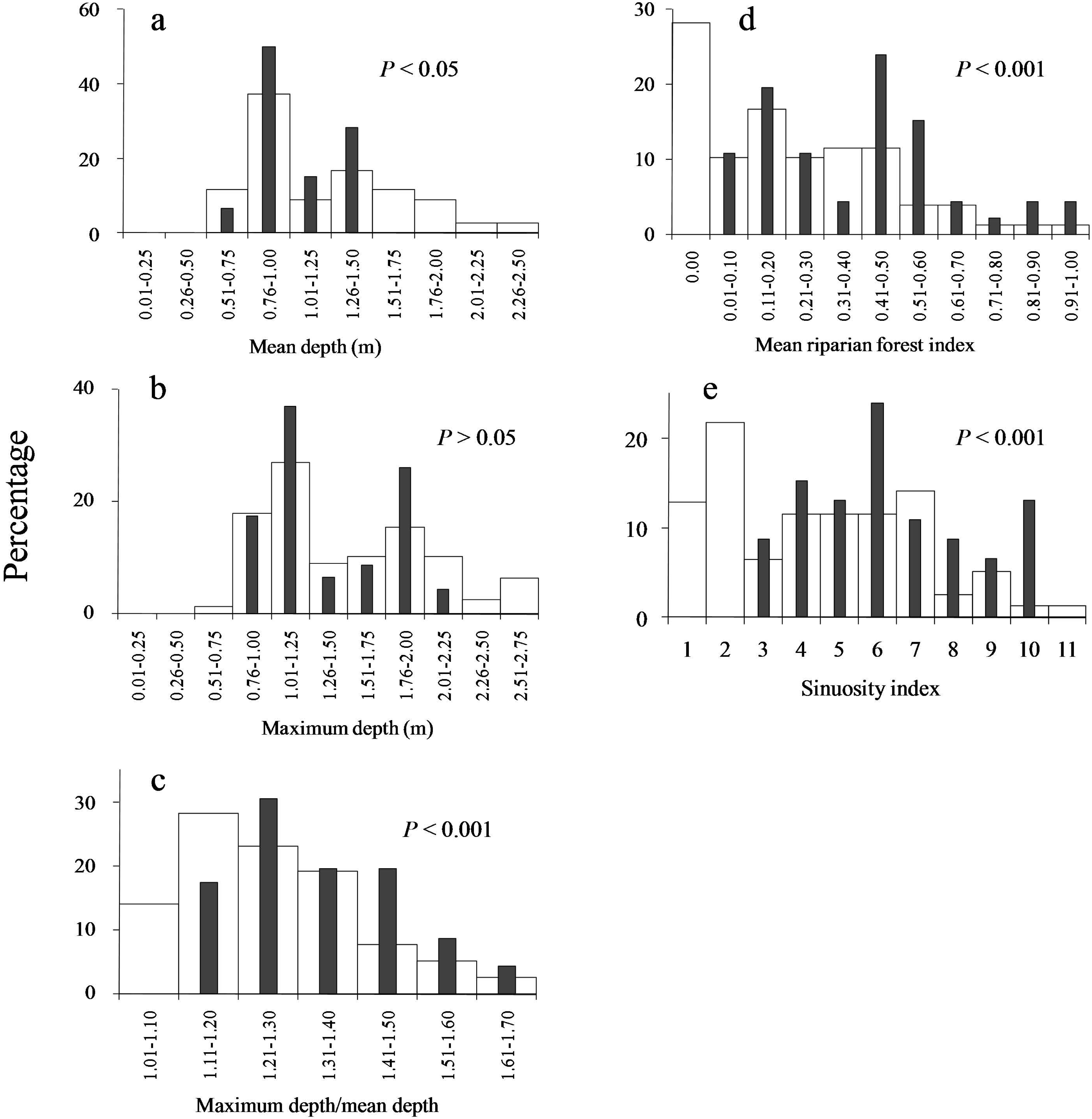
Figure caption

Fig. 1. Study site: The Bekanbeushi River system in eastern Hokkaido Island, Japan. Each area was colour-coded. Star indicates the location where three *Hucho perryi* that had been captured in Lake Akkeshi were released.

Fig. 2. Overlaid histograms of five environmental factors (a: mean depth, b: maximum depth, c: maximum depth/mean depth, d: mean riparian forest index, e: sinuosity index) between all 400-m channel segments in all survey areas (areas 2–6) of the study site (open bar, n = 78) and occupied habitats of adult *Hucho perryi* (filled bar, n = 46). *P*-values of Mann-Whitney *U*-test between those were shown.



Area
1
2
3
4
5
6
43.36° N
43.01° N
144.38° E
145.00° E
Hokkaido
Island
Bekanbe-ushi River
Chanbetsu River
Toraibetsu River
Chiraikaribetsu
River
Obetsu River
Oboro River
Lake
Akkeshi
Akkeshi Bay
5 km
N



Percentage
a
P < 0.05
0.01-0.25
0.26-0.50
0.51-0.75
0.76-1.00
1.01-1.25
1.26-1.50
1.51-1.75
1.76-2.00
2.01-2.25
2.26-2.50
Mean depth (m)
b
P > 0.05
0.01-0.25
0.26-0.50
0.51-0.75
0.76-1.00
1.01-1.25
1.26-1.50
1.51-1.75
1.76-2.00
2.01-2.25
2.26-2.50
2.51-2.75
Maximum depth (m)
c
P < 0.001
1.01-1.10
1.11-1.20
1.21-1.30
1.31-1.40
1.41-1.50
1.51-1.60
1.61-1.70
Maximum depth/mean depth
d
P < 0.001
0.00
0.01-0.10
0.11-0.20
0.21-0.30
0.31-0.40
0.41-0.50
0.51-0.60
0.61-0.70
0.71-0.80
0.81-0.90
0.91-1.00
Mean riparian forest index
e
P < 0.001
1
2
3
4
5
6
7
8
9
10
11
Sinuosity index