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Seasonal stream habitat of adult Sakhalin taimen, *Parahucho perryi*, in the Bekanbeushi River system, eastern Hokkaido, Japan

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Abstract – Behavioural tracking of endangered adult Sakhalin taimen (*Parahucho perryi*) by acoustic telemetry was conducted in the Bekanbeushi River system that flows through eastern Hokkaido in 2008–2010. A total of 39 tracked *P. perryi* showed extensive use of the river system, both upstream and downstream, regardless of the month or year. No tracked adult *P. perryi* stayed in the ocean for more than 1 day. Some of the fish (20%) dwelled in upstream habitat consistently from spring to autumn, while 40% of individuals showed wide utilisation of the entire upstream and downstream systems. Although 39.4% of tracked fish utilised two or more primary tributaries to the main river, 6.1% used only the main river system. Distinct variability was observed between individuals based on the proportion of time spent in each stream reach (up-, mid-, and downstream). A trend was observed in 2008 and 2010 showing that tracked fish moved to the upper stream reaches when water temperatures downstream increased. This trend was not observed in 2009 when the summer water temperature downstream was more than 2 °C below average when compared to 2008 and 2010. Our results suggest that adult *P. perryi* in the Bekanbeushi River system exhibit high behavioural plasticity, that is, the fish can select habitats based on their own individual requirements. Our results also demonstrate the importance of physical continuity among river reaches both upstream and downstream such that *P. perryi* does not experience barriers in moving to optimal habitats.

Key words: acoustic telemetry; endangered species; individual variability; *Parahucho perryi*; seasonal habitat

Introduction

Sakhalin taimen (*Parahucho perryi*) is a salmonid that inhabits the Maritime Province of Siberia, Sakhalin, southern Kuriles, and Hokkaido Island (Gritsenko et al. 1974; IUCN 2011). Sakhalin taimen was originally included in the genus *Hucho* but it has become recognised as a separate genus based on the phylogenetic divergence of mitochondrial DNA (Shed'ko et al. 1996). This species is the top predator in river ecosystems; it lives for more than 20 years and reaches at least 1.3 m in length (Zolotukhin et al. 2000). *P. perryi* is iteroparous (Yamashiro 1965; Kimura 1966), spawning in shallow upstream locations from March to June after snowmelt, and has an

anadromous form dissimilar to that of closely related *Hucho* species (Holčík et al. 1988).

Populations of *P. perryi* have been steadily declining owing to habitat degradation and activities such as river improvements aimed at flood control, agricultural land development and by-catch in the commercial salmon fishery (Rand 2006; Fukushima et al. 2011). Only seven river systems in Hokkaido now remain that support stable populations of *P. perryi* (Fukushima et al. 2011). The IUCN's (The International Union for the Conservation of Nature) Red List has classified *P. perryi* as Critically Endangered (CR) since 2006 (Rand 2006). To reestablish *P. perryi* populations, natural habitat needs to be restored and existing habitat must be protected. However, to do

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this, the preferred habitat and requirements of *P. perryi* must be understood.

Spawning ecology, particularly spawning habitat, has dominated the ecological studies published on *P. perryi* to date (Fukushima 1994, 2001; Mori et al. 1997; Edo et al. 2000; Yamada et al. 2008; Esteve et al. 2009; Nomoto et al. 2010). However, less is known about the habitat and behavioural ecology of *P. perryi* fry and juveniles. We know that floodplains are important (Mori & Nomoto 2005) and that fry and juveniles prefer low-flow sections of a river (Sagawa et al. 2003), but where fry and juveniles inhabit between upstream and estuary is largely unknown. With the exception of spawning season information, we also know little about adult *P. perryi*. Previous studies have focused on the anadromous form in either Sakhalin or Hokkaido (Arai et al. 2004; Edo et al. 2005; Honda et al. 2010a; Suzuki et al. 2011; Zimmerman et al. 2011). Although these studies verified the existence of anadromous fish in each region by analysing the microchemicals present in fish otoliths, the occurrence rate of anadromous fish, their first seaward-migrating age and seaward migration frequency or its timing have not been clearly revealed. Studies by Sagawa et al. (2002) and

Honda et al. (2009, 2010b) have reported on ecological aspects of *P. perryi* other than spawning season. For example, Sagawa et al. (2002) identified pools inhabited by adult *P. perryi* in a tributary of the Teschio River in northern Hokkaido and found that those pools were characterised by a reduced flow velocity, larger streambed and high (vegetation) cover compared to uninhabited areas. Honda et al. (2010b) identified seasonal habitats used by adult *P. perryi* for mid-to-long periods in the Bekanbeushi River system using acoustic telemetry. They classified these habitats as highly meandering, seasonal and densely vegetated with riparian plants providing thick shade in the summer and autumn. Acoustic telemetry in the same river system (Honda et al. 2009) revealed individual variability in the seasonal migration patterns and stream habitat use of five tagged *P. perryi*. Additionally, Honda et al. (2009) indicated that high water temperatures in the summer downstream triggered escape to upstream reaches, and Fukuda et al. (1992) reported increased mortality in captive *P. perryi* at water temperatures above 20 °C. However, these short and isolated studies are inadequate in comprehensively describing migration patterns and the environmental factors affecting them.

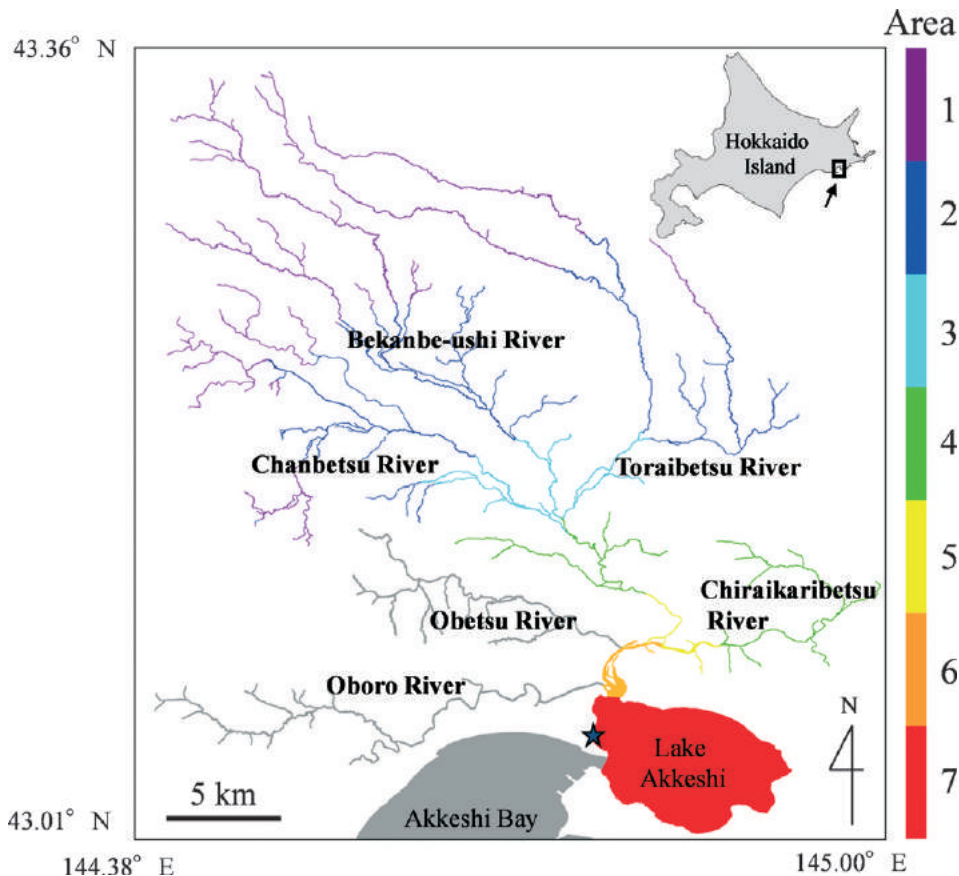


Fig. 1. Study site: The Bekanbeushi River system in eastern Hokkaido Island, Japan. Each area is colour-coded. The star indicates the location where *Parahucho perryi* captured in Lake Akkeshi were released.

Here, we described the behavioural ecology of adult *P. perryi* in the Bekanbeushi River system using acoustic telemetry as in Honda et al. (2009). By expanding the study area, we sought to quantify habitat use and variability and to explore differences in stream habitat use as determined by sex or body size. We also explored the influence of high summer temperatures on *P. perryi* habitat selection.

Methods

Study site

Surveys were conducted in the Bekanbeushi River system (total basin area: 738.8 km²) in eastern Hokkaido, Japan, from April to November 2008–2010 (Fig. 1). The main river (Bekanbeushi River) flows into brackish Lake Akkeshi (circumference: 24.8 km, maximum depth: 7.0 m, salinity: 25–30 psu; Hokkaido Institute of Environmental Sciences 2005). The lake is connected to the Pacific Ocean by Akkeshi Bay (Fig. 1). This basin has few artificial structures, and the dominant habitat in the lower reaches of the river basin is the Bekanbeushi wetlands (5277 ha), registered under the Ramsar Convention. Much of upstream habitat is also intact, given that the area has restricted access because of the presence of the Yausubetsu Japanese army training area (16,800 ha). According to Honda et al. (2010b), as one moves downstream, the Bekanbeushi River becomes deeper, less sinuous and has reduced amounts of riparian vegetation. The effectiveness of acoustic telemetry in targeting adult *P. perryi* in this river system has been confirmed previously (Honda et al. 2009, 2010b).

The entire Bekanbeushi River system was included in our study area except for the Oboro and Obetsu rivers (Fig. 1). The estuary of the Oboro River was initially selected as a study site in 2009 and 2010. In an effort to conserve remaining populations of *P. perryi*, the actual locations where fish were caught and released cannot be given. Rather, information on locations is described using river domain blocks (areas). The study sites were grouped into six areas based on channel length, junctions, and downstream tidal effects as in Honda et al. (2010b). Lake Akkeshi was included and categorised as area 7 (Fig. 1). Area 1 was located 30 km upstream of the river mouth, considering the total channel length summed over the main channel and tributaries. The region from the border of area 1 to the two junctions between the Bekanbeushi River and the Toraihetsu (Chanbetsu) River was divided into upper (area 2) and lower (area 3) areas. The lower border of area 3 was 20 km from the river mouth. Downstream reaches were divided into three areas based on changes in the flow velocity

from tidal fluctuations. Area 4 extended from the Bekanbeushi River–Toraihetsu River junction to a point 8 km from the river mouth, where the 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–Chiraihetsu River junction was deemed area 5, and the region from the river junction to the river mouth was designated area 6 (Fig. 1). In addition, the Chiraihetsu River was divided into two areas (upper: area 4 and lower: area 5) at a point 6.8 km from the river mouth, where the river width decreased to less than half its maximum. The estuary of the Oboro River was designated area 6. When the river system was divided into three stream habitat types, areas 1–3, 4–5 and 6–7 were defined as up-, mid- and downstream habitat, respectively. If only two classifications were used, areas 1–4 and 5–7 were the upper and lower reaches, respectively.

Fish capture and tag attachment

From late April to early May 2008–2010, 34 mature *P. perryi* were captured using a seine net design (1.0 m high × 28.1 m wide, mesh size: 40 mm) at the upstream end of a tributary in which *P. perryi* spawn, located 51 km from the river mouth (area 1) (Table 1). A fishway was placed along the riverbank with an entrance located at the upstream side of the net to target fish moving downstream. An additional, 11 adult *P. perryi* were caught by a local set-net fishery in Lake Akkeshi from the middle of April to the middle of May over the 3 years. In total, 45 fish were caught (15 each year); 23 fish were male and 11 each were female and unknown (Table 1). The sex of each fish was determined using physical characteristics and by pressing the abdomen to determine if unreleased gametes were present. Fork lengths (FLs) of tagged fish ranged from 46.0 to 83.9 cm, and the mean FL (\pm SD) was 62.7 ± 8.9 cm. The identity of each fish was described with regard to sex, FL, capture/release location and year tagged. A Vemco V13-1L acoustic tag (69.0 kHz, 13.0 mm diameter, 36.0 mm length; Vemco, Shad Bay, NS, Canada) was surgically implanted into abdominal cavity of all captured *P. perryi* using anaesthesia (2-phenoxyethanol 0.04%, diluted with river water) as in Honda et al. (2009, 2010b). Battery life and pulse varied between the two types of tag used. One randomly transmitted a set of six pulses once every 20–60 s lasting 439 days, the other sent pulses every 40–90 s, with power lasting 650 days. The tagged fish caught upstream were released just below the net after confirming recovery from anaesthesia, while the tagged fish caught in Lake Akkeshi were released at the nearby lakeshore following recovery (Fig. 1). Both laboratory and field studies

Table 1. Fish ID, measurements, and tagging information for tagged adult *Parahucho perryi* captured in an upstream tributary (51 km upstream from river mouth) of the Bekanbeushi River and in Lake Akkeshi in Hokkaido, Japan.

Fish ID	Sex	Fork length (cm)	Body weight (kg)	Transmission interval (once in: s)	Captured and released place	Released date	Date final detected
M699R08	Male	69.9	3.5	20–60	Tributary upstream	26 April 2008	20 November 2008
M520R08	Male	52.0	2.0	20–60	Tributary upstream	26 April 2008	None
M566R08	Male	56.6	2.1	20–60	Tributary upstream	26 April 2008	6 June 2008
M839R08	Male	83.9	6.0	20–60	Tributary upstream	26 April 2008	4 September 2008
F815R08	Female	81.5	6.0	20–60	Tributary upstream	26 April 2008	24 November 2008
M595R08	Male	59.5	2.3	20–60	Tributary upstream	26 April 2008	None
F560R08	Female	56.0	1.8	20–60	Tributary upstream	26 April 2008	28 November 2008
M605R08	Male	60.5	2.5	20–60	Tributary upstream	26 April 2008	26 November 2008
M476R08	Male	47.6	1.4	20–60	Tributary upstream	26 April 2008	19 May 2008
M563R08	Male	56.3	2.0	20–60	Tributary upstream	27 April 2008	23 November 2008
F661R08	Female	66.1	2.6	20–60	Tributary upstream	29 April 2008	28 November 2008*
M529R08	Male	52.9	1.7	20–60	Tributary upstream	3 May 2008	None
U705L08	Unknown	70.5	4.5	20–60	Lake Akkeshi	7 May 2008	24 November 2008*
U741L08	Unknown	74.1	5.0	20–60	Lake Akkeshi	9 May 2008	20 November 2008*
U800L08	Unknown	80.0	6.3	20–60	Lake Akkeshi	9 May 2008	17 September 2008
U593L09	Unknown	59.3	2.1	20–60	Lake Akkeshi	13 April 2009	24 November 2009
U627L09	Unknown	62.7	2.7	20–60	Lake Akkeshi	13 April 2009	29 November 2009*
U650L09	Unknown	65.0	3.0	40–90	Lake Akkeshi	20 April 2009	7 May 2009
U557L09	Unknown	55.7	1.8	20–60	Lake Akkeshi	24 April 2009	28 November 2009*
M663R09	Male	66.3	2.7	20–60	Tributary upstream	26 April 2009	27 November 2009*
F685R09	Female	68.5	2.8	20–60	Tributary upstream	26 April 2009	29 November 2009*
M606R09	Male	60.6	2.2	20–60	Tributary upstream	26 April 2009	27 November 2009*
M584R09	Male	58.4	1.9	40–90	Tributary upstream	26 April 2009	None
F585R09	Female	58.5	1.9	20–60	Tributary upstream	26 April 2009	27 November 2009*
F691R09	Female	69.1	2.9	40–90	Tributary upstream	29 April 2009	26 August 2009
M535R09	Male	53.5	1.6	20–60	Tributary upstream	29 April 2009	19 May 2009
F705R09	Female	70.5	3.1	40–90	Tributary upstream	1 May 2009	5 August 2009
M605R09	Male	60.5	1.9	20–60	Tributary upstream	1 May 2009	10 October 2009*
M585R09	Male	58.5	2.0	40–90	Tributary upstream	2 May 2009	None
U645L09	Unknown	64.5	2.9	40–90	Lake Akkeshi	7 May 2009	27 November 2009*
F618R10	Female	61.8	2.6	40–90	Tributary upstream	27 April 2010	17 June 2010
M705R10	Male	70.5	4.2	40–90	Tributary upstream	27 April 2010	12 May 2010
M514R10	Male	51.4	1.9	40–90	Tributary upstream	27 April 2010	24 November 2010
M510R10	Male	51.0	1.8	40–90	Tributary upstream	29 April 2010	20 May 2010
M460R10	Male	46.0	1.5	40–90	Tributary upstream	29 April 2010	None
M625R10	Male	62.5	2.8	40–90	Tributary upstream	1 May 2010	26 October 2010*
M462R10	Male	46.2	1.6	40–90	Tributary upstream	1 May 2010	26 May 2010*
M570R10	Male	57.0	2.3	40–90	Tributary upstream	2 May 2010	15 July 2010
M733R10	Male	73.3	4.5	40–90	Tributary upstream	3 May 2010	2 December 2010*
F638R10	Female	63.8	3.1	40–90	Tributary upstream	3 May 2010	24 November 2010
F708R10	Female	70.8	3.6	40–90	Tributary upstream	3 May 2010	5 June 2010
F632R10	Female	63.2	2.9	40–90	Tributary upstream	3 May 2010	14 May 2010
U725L10	Unknown	72.5	4.5	40–90	Lake Akkeshi	17 May 2010	2 December 2010*
U650L10	Unknown	65.0	3.8	40–90	Lake Akkeshi	19 May 2010	1 December 2010*
U668L10	Unknown	66.8	3.3	40–90	Lake Akkeshi	19 May 2010	2 December 2010*

M, F, U, R, and L in fish ID indicate male, female, unknown, river, and lake, respectively. Numbers in fish ID show the fork length (mm) of each tagged fish and year caught and released.

*Fish detected next year.

have noted a low probability of posttagging mortality from stress in adult *P. perryi* (Honda et al. 2009).

Tracking tagged fish

From 7 April to 19 May in the years 2008–2010, 25–28 stations were arrayed from area 1 to area 7, and a Vemco VR2(W) acoustic receiver was deployed at each station using sandbags, rope and a buoy (Table 2). Deployment of all receivers was completed

when tagged fish began to be released from upstream, by 26 April in all years with three exceptions (station 5 completed on 15 May in 2008, and stations 15 and 16 both completed on 19 May in 2009). Receivers were closely spaced in the junctions of rivers to adequately capture the movements of tagged fish in both the main channel and its primary tributaries. The detection range of receivers varied with changes in bed structure, flow velocity and water level. Although the detection range in area 1 was 30 m, that in area 6

Table 2. Station details and dates of deployed and recovered acoustic receivers during 2008–2010.

Station number	Channel length from the river mouth (m)	Area	Mainstream (M) or tributary (T)?	2008			2009			2010		
				Date deployed	Date recovered	Water temp. logger?	Date deployed	Date recovered	Water temp. logger?	Date deployed	Date recovered	Water temp. logger?
1	30607	1	T	21 April	27 November	Yes	14 April	26 November	Yes*	25 April	28 November	Yes
2	22264	2	T	21 April	27 November	Yes	14 April	26 November	Yes	25 April	28 November	Yes*
3	22224	2	M	21 April	27 November	Yes	10 April	27 November	Yes	24 April	1 June	Yes
4	18364	3	T	20 April	27 November	Yes	11 April	26 November		17 April	1 June	
5	17871	3	M	15 May	20 November		10 April	27 November		24 April	1 December	
6	16208	3	T				11 April	27 November		24 April	1 December	
7	14729	3	T	20 April	26 November	Yes	11 April	27 November	Yes	19 April	29 November	Yes
8	14441–14483	3	M	20 April	26 November	Yes	11 April	27 November	Yes	19 April	29 November	Yes
9	13901	4	M	20 April	26 November		10 April	27 November		19 April	29 November	
10	13604	3	T	20 April	26 November	Yes	11 April	27 November	Yes*	19 April	29 November	Yes
11	12958	4	M	20 April	26 November	Yes	10 April	27 November	Yes	19 April	29 November	Yes
12	11865	4	M	20 April	26 November		10 April	27 November		19 April	29 November	
13	11444	4	M				19 May	27 November				
14	11235	4	M	18 April	24 November					16 April	29 November	
15	10654	4	M				8 April	27 November				
16	9795	4	M				19 May	27 November				
17	9128	4	M	18 April	24 November	Yes	8 April	27 November	Yes	16 April	29 November	Yes
18	8285	4	T	19 April	23 November	Yes	9 April	29 November	Yes	17 April	31 May	Yes*
19	7553	5	M	18 April	24 November		8 April	27 November		16 April	29 November	
20	6744	5	T	19 April	23 November		9 April	29 November		08 April	2 December	Yes
21	6484	5	M	18 April	24 November							
22	5618–5883	5	M	18 April	24 November	Yes	8 April	27 November	Yes*	16 April	29 November	Yes
23	4494–4672	5	T	18 April	24 November		9 April	29 November		12 April	2 December	
24	4590	5	M	19 April	23 November		8 April	29 November		16 April	28 November	
25	3807–3895	6	M	19 April	23 November	Yes	8 April	29 November	Yes	12 April	2 December	Yes
26	2542	6	M	19 April	23 November		8 April	29 November		12 April	2 December	
27	1744	6	M	19 April	23 November							
28	1156	6	T				14 April	29 November	Yes	12 April	2 December	Yes
29	870–1022	6	M	19 April	23 November	Yes	9 April	29 November	Yes	12 April	2 December	Yes
30	0	7		23 April	25 November		13 April	29 November		23 April	1 December	
31	–2754	7										
32	–3471	7		21 April	25 November	Yes	13 April	30 November	Yes	23 April	1 December	Yes

*Incomplete data.

reached 500 m. In all cases, the minimum detection range was confirmed to cover the entire stream width. In total, 14–15 water temperature loggers (StowAway TidbiT Vr.1 or HOBO Pendant; Onset Computer Corporation, Bourne, MA, USA) were attached to receivers and recorded the ambient water temperature 1 m below the surface every 30 min (accuracy: ± 0.1 °C) (Table 2). Receivers and water temperature loggers were retrieved after obtaining data by the end of November. However, three station receivers (3, 4 and 18) deployed in 2010 were recovered early between 31 May and 1 June 2010 (Table 2).

An additional receiver was towed by canoe one or more times between area 2 and the end of area 6 in each study month in all years. Canoe location was logged using a Garmin etrex LEGEND or GPSMAP 60CSx Global Positioning System (GPS) (<http://www.garmin.com>) enabling fish locations to be determined in real time. Data obtained by the mobile receiver supplemented those captured by the static receivers. The total number of days that the mobile receiver was towed were 44, 45 and 43 in 2008, 2009 and 2010, respectively, and the respective mean \pm SD towed distances were 9.2 ± 3.5 , 9.2 ± 4.4 and 8.4 ± 3.6 km.

Use of detection data

Monthly data were categorised by season: April–June, July–September and October–November were defined as spring, summer and autumn, respectively, as in Honda et al. (2010b). Detection data recorded in the second year after fish release were not included in any analyses. Data gathered immediately following the ‘downward migration from spawning grounds’ defined in the following section were not used for any analyses except the following section.

Downward migration from spawning grounds

In this analysis, only data obtained from tagged fish released upstream were used. The completion of downward migration from spawning grounds was defined as the time when a fish was not detected by any receiver except for one within a day after the last detection by that same receiver. Any downward migration more than 10 days since a fish was released was not included in the analysis. Areas visited and time spent by each tagged fish during downward migration were counted and compared according to sex and body size (FL). To estimate the time of migration, the first detection of each fish at each station was extracted and instances counted. Those data were divided into dawn, day, dusk, and night, and their frequencies of occurrence were compared. Dawn and dusk were classified as 1 h before and after sunrise and sunset each day, respectively,

while day and night comprised the rest of the diurnal cycle.

Residence time

In this study, the ‘residence time’ in each area was estimated on either a monthly or individual basis to examine seasonal differences in stream habitat use by tagged fish. Residence time was calculated as the percentage of time that each tagged fish stayed in each area per day. Percentages for periods without detection were shared half and half between the area of detection before and the area of detection after the no detection period (Honda et al. 2009). Some upstream reaches were not captured by receivers; therefore, when a fish was detected at an uppermost station after two or more days since being detected (at the same station), the area the fish stayed was designated as an ‘unknown area’, except for the first and last day of the no detection period. For these 2 days, the location was assumed to be the last and next place detected, respectively, because of the low possibility for movement to other up- or midstream areas.

A missing receiver at station 30 in 2008 limited the monitoring of fish movements from area 6 to area 7. Therefore, in 2008, if a tagged fish was detected at station 29 after ≥ 1 h following detection at station 29, the area the fish stayed in for the no detection period was designated ‘unknown areas 6–7’ (including the estuary of the Oboro River) except for the first and last 30 min of the no detection period because of the probability that the fish moved to area 7. One hour was chosen (30 min on either side of no detection) because of the much higher frequency of movements in the estuary near the Bekaubeushi River mouth compared with mid- or upstream reaches (Honda, unpublished data). Similarly, when a tagged fish was detected at station 32 on the border between Lake Akkeshi (area 7) and Akkeshi Bay after ≥ 1 h since being detected at station 32, the area the fish stayed was designated ‘unknown areas 7–bay’ except for the 30 min on either side of the no detection period. Additionally, even though data following final detections were excluded, in cases when fish survival was confirmed in the second year following release and when the final detection location was known, the fish was considered to have remained in the area until the end of the study period in the first year.

The residence time was also calculated for each stream reach (up-, mid-, and downstream) and for the main channel and its primary tributaries (Toraibetsu, Chanbetsu, Chiraikaribetsu, and Oboro rivers). We also counted the number of primary tributaries each fish visited. To explore whether tagged fish released upstream appeared in nonspawning streams, the

channel between the uppermost reach of their spawning stream and the mouth of the Bekanbeushi River was defined as the ‘Spawning river’. We counted the number of spawning and nonspawning rivers visited by tagged fish. Nonspawning rivers were limited to primary tributaries of the main stream or of the spawning river that met with either the spawning river or the main channel in areas 4–6. To protect *P. perryi* populations, the residence time in each river or tributary are not shown, but numbers of tributaries each fish stayed in are given. Only fish tracked for more than 30 days during the study period were used for this analysis, and a visit or stay required ≥ 12 h in a particular tributary.

Individual variability

To verify individual variability among the three stream reaches where tagged fish visited, seasonal composition ratios of residence time in the three reaches were compared for each individual fish. In this analysis, we used data for fish tracked for more than half of each season. Pairwise comparisons for the proportion of stay in each reach in all seasons were conducted one by one for each tagged fish using R Ver. 2.12.2 (pairwise.prop.test), which is a free software environment maintained by the R Development Core Team (<http://www.r-project.org/>). To test for differences in the resulting proportions, Fisher’s exact test ($\alpha = 0.01$) was used. We then tabulated which comparisons were and were not statistically different. The maximum and minimum comparison results were then assessed using a chi-squared test. In addition, the maximum and minimum residence times in each stream reach were compared to differences in sex, body size, and released point using Mann–Whitney *U*-tests and Spearman rank correlation test.

Comparison with riverine water temperature

Simple logistic regression analyses were carried out to determine the presence or absence of escape behaviour to the upper reaches by tagged *P. perryi* based on changing water temperature using the methods in Honda et al. (2009). The mean daily maximum water temperatures at stations 25, 29 and 32 in the lower reaches, for which continuous 3 years of data were available, were used as an index of inhabitable water temperature for adult *P. perryi*. A model was derived with KyPlot 5.0 at $\alpha = 0.05$ (KyensLab Inc.; www.kyenslab.com) setting the mean daily maximum water temperature as the explanatory variable and the presence or absence of each tagged fish as a dependent variable such that

$$\log\{p/(1-p)\} = \beta_{1\chi} + \beta_0 \quad (1)$$

Table 3. Number of tracked *Parahucho perryi* in each final migrated area from the spawning ground according to sex, and its mean total migrated distance, mean total migrated duration, and mean migration speed.

Final migrated area	Number of tagged fish		
	Male	Female	All
1	3	2	5
2	1	1	2
3	8	3	11
4	2	3	5
5	1	1	2
Mean (\pm SD) total migrated distance (km)	35.7 \pm 7.3	35.6 \pm 8.2 ^{ns}	35.7 \pm 7.5
Mean (\pm SD) total migrated duration (days)	3.4 \pm 2.0	2.4 \pm 1.2 ^{ns}	3.0 \pm 1.7
Mean (\pm SD) migration speed (BL·s ⁻¹)	0.32 \pm 0.20	0.35 \pm 0.16 ^{ns}	0.33 \pm 0.18

ns indicates no significant difference between males and females by Mann–Whitney *U*-test ($\alpha = 0.05$).

where χ is the mean daily maximum water temperature and p and $1 - p$ are the probabilities of occurrence in the lower and upper areas, respectively. This analysis was carried out for the 2008–2010 study period. The same analysis using 3 years of summer data was also carried out.

Results

The numbers of tagged *P. perryi* detected one or more times were 12, 13 and 14 in 2008, 2009 and 2010, respectively. The total numbers of detections by all deployed receivers were 152,397, 310,547 and 143,848 in 2008, 2009 and 2010. The numbers of tagged fish tracked in mid-November or later each year were eight, eight and six (Table 1). Although three individuals (M605R09, M625R10 and M462R10) were finally detected at stations in areas 1, 3 and 3 on 10 October 2009, 26 October 2010 and 26 May 2010, respectively, because the survival of these individuals was confirmed the following year, they were assumed to have stayed in the upper channel or other areas lacking receiver coverage for the duration between detections.

Downward migration from spawning grounds

Downward migration from spawning grounds was observed in 25 of 34 tagged fish. Because three individuals (M605R09, F618R10 and M733R10) were first detected 161, 29 and 18 days following release at station 1, data from these three were excluded from this analysis. Downward migrations were completed over a wide range from areas 1 to 5; 11 fish (44%) finished migrations in area 3 (Table 3). Not only did 11 individuals complete their migration

Seasonal stream habitat of *Parahucho perryi*

Table 4. Number and standardised hourly rate of movements (first detections at each station) on downward migration from the spawning grounds during the four times of day (dawn, day, dusk, and night) recorded by all tracked *Parahucho perryi*.

Time zone	N of movements	Hourly rate of movements (estimated as 'Day' = 1.0)
Dawn	23	3.1
Day	45	1.0
Dusk	17	2.3
Night	49	1.7

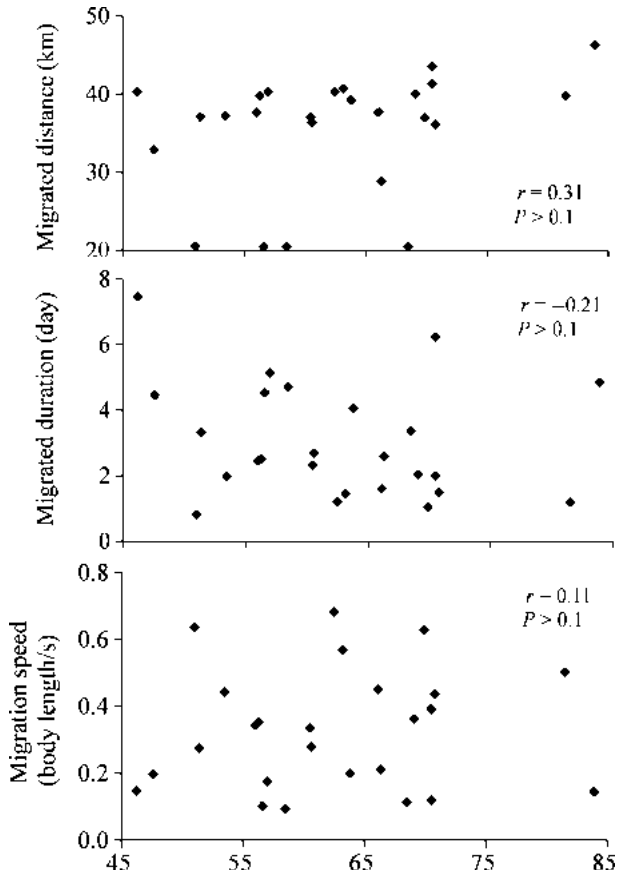


Fig. 2. Relationship between fork length and migrated distance, migrated duration or migration speed for tracked *Parahucho perryi* from the spawning ground to the final migrated locations ($N = 35$). Spearman rank correlation coefficient (r) and its P -value are shown on each graph.

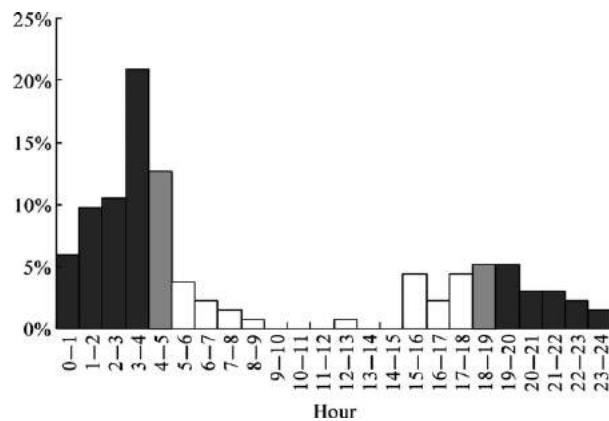


Fig. 3. Hourly rate of fish passing through each station (one station one time) on the migration from their spawning ground ($N = 134$) of the 25 tracked *Parahucho perryi*. White bars and dark grey bars show daytime and nighttime, respectively. Light grey bars indicate sunrise (04:05–04:21) and sunset (18:16–18:30).

in nonspawning rivers, an additional three individuals (12%) entered nonspawning rivers prior to completing downward migration. Mean (\pm SD) total migrated

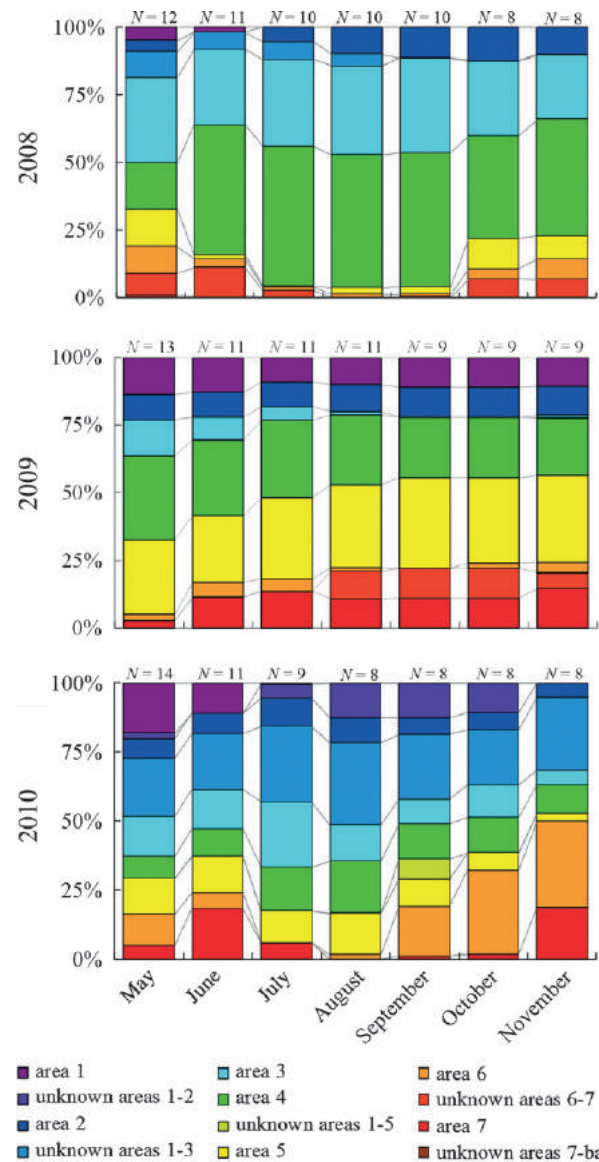


Fig. 4. Residence time in each area for each month by all tracked *Parahucho perryi* after completing downward migrations from their spawning ground from 2008 to 2010.

distance and mean total migration time were 35.7 ± 7.5 km and 3.0 ± 1.7 days, respectively. The wide range of distance travelled (20.5–46.3 km) and

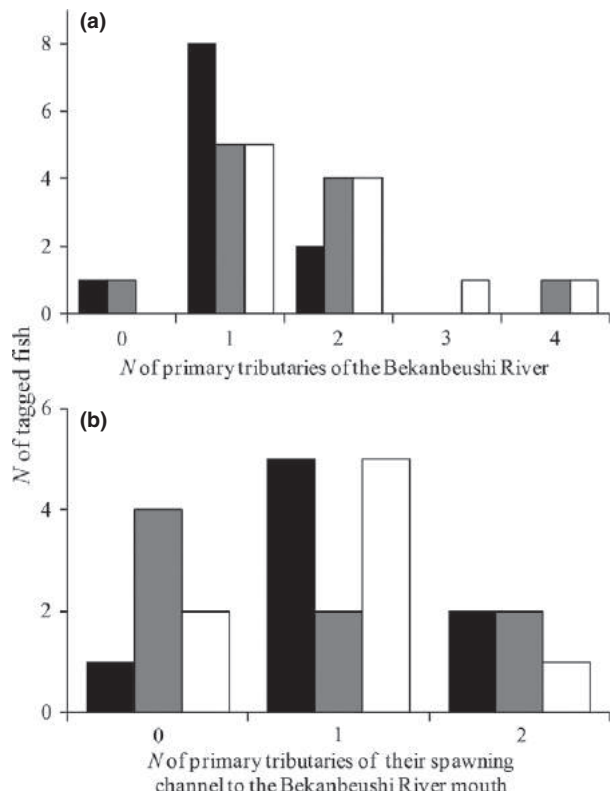


Fig. 5. Frequency counts of the primary tributaries of (a) the Bekanbeushi River (mainstream) and (b) the spawning river (channel between the spawning stream of *Parahucho perryi* and the Bekanbeushi River mouth) where each tracked *P. perryi* stayed (black: 2008, grey: 2009, white: 2010). The Oboro River is included in 2009 and 2010.

time taken (0.8–7.5 days) demonstrates individual variability (Table 3). Although no significant difference in either migrated distance or duration was observed between sexes, the mean total migration was 1 day shorter for females than males, and more males completed their migration in area 3 than females (Table 3). The differences observed in migrated duration and distance based on body size were not confirmed as statistically significant (Fig. 2). Little difference in migration speed was observed based on sex and body size (Table 3, Fig. 2). Although migration occurred at all time zones of day (Fig. 3), movement frequencies were particularly high from 01:00 to 05:00 h. Movement rates at dawn, dusk and night were 3.1, 2.3 and 1.7 times higher, respectively, than those during the day-time (Table 4).

Residence time

According to the monthly residence time in each area throughout 2008–2010, fish utilised the river system widely and visited both upstream and downstream reaches (Fig. 4). Two fish (M839R08 and U800L08)

are thought to have spent time (1.3 and 0.7 h, respectively) in Akkeshi Bay because their location was classified as ‘unknown areas 7–bay’ in this study. In 2008, the residence time in areas 3 and 4 was higher than that of other areas; the combined time spent in these two areas was 40% across all months (Fig. 4). The residence time in lower reaches decreased to <5% in the summer. While in 2009, the combined residence time in areas 4 and 5 occupied more than 50% of all months. Although the residence time in the lower reaches increased towards the end of the calendar year, no significant differences in the residence time were observed after August. According to detection data, fish U593L09 was thought to have stayed in area 6 from 1 August to 14 November 2009; however, owing to a long period without any detection, its location was reestimated as ‘unknown areas 6 and 7’. In 2010, the residence time in area 7 throughout June and November were both 20%, an increase over other months. The combined residence time in areas 6 and 7 increased in the autumn when the combined time in areas 1–3 gradually declined (Fig. 4).

Most of the tracked fish visited more than one primary tributary (Fig. 5). Specifically, 93.9% stayed in more than one primary tributary and 70.8% visited more than one tributary of their spawning river, whereas only 6.1% of fish stayed in the main channel and 29.2% stayed in their spawning river throughout the entire tracking period.

Some individuals (e.g., M699R08 and M605R09) did not change their area of stay over the entire study period, while other individuals (e.g., U705L08 and U725L10) changed their stay area in response to seasonal change (Fig. 6). The reaches in which fish stayed ranged widely from areas 1 to 7. Most individuals (78.8%) visited two or three stream reaches during the spring. Conversely, during the summer and autumn, many individuals remained in a single reach for the entire season (60.7% and 72.0% for summer and autumn, respectively) (Table 5). Of the 25 fish tracked from spring to autumn, 40.0% of individuals ($N = 10$) visited all three stream reaches, and 80.0% visited two or three different reaches ($N = 20$) (Table 5). The remaining 20% of individuals stayed in upstream reaches only. Results of pairwise comparisons for the proportion of time spent among the three stream reaches gave a higher number of combinations with significant differences than combinations with no significant differences (chi-squared test, $P < 0.01$; Table 6). Large variance was observed in all comparisons of the residence time with differences in sex, place of release and body size (Figs 7 and 8). Although no significant differences related to sex were found, residence times in the mid- and downstream reaches were slightly higher, and those in the upper reaches were lower for females than males

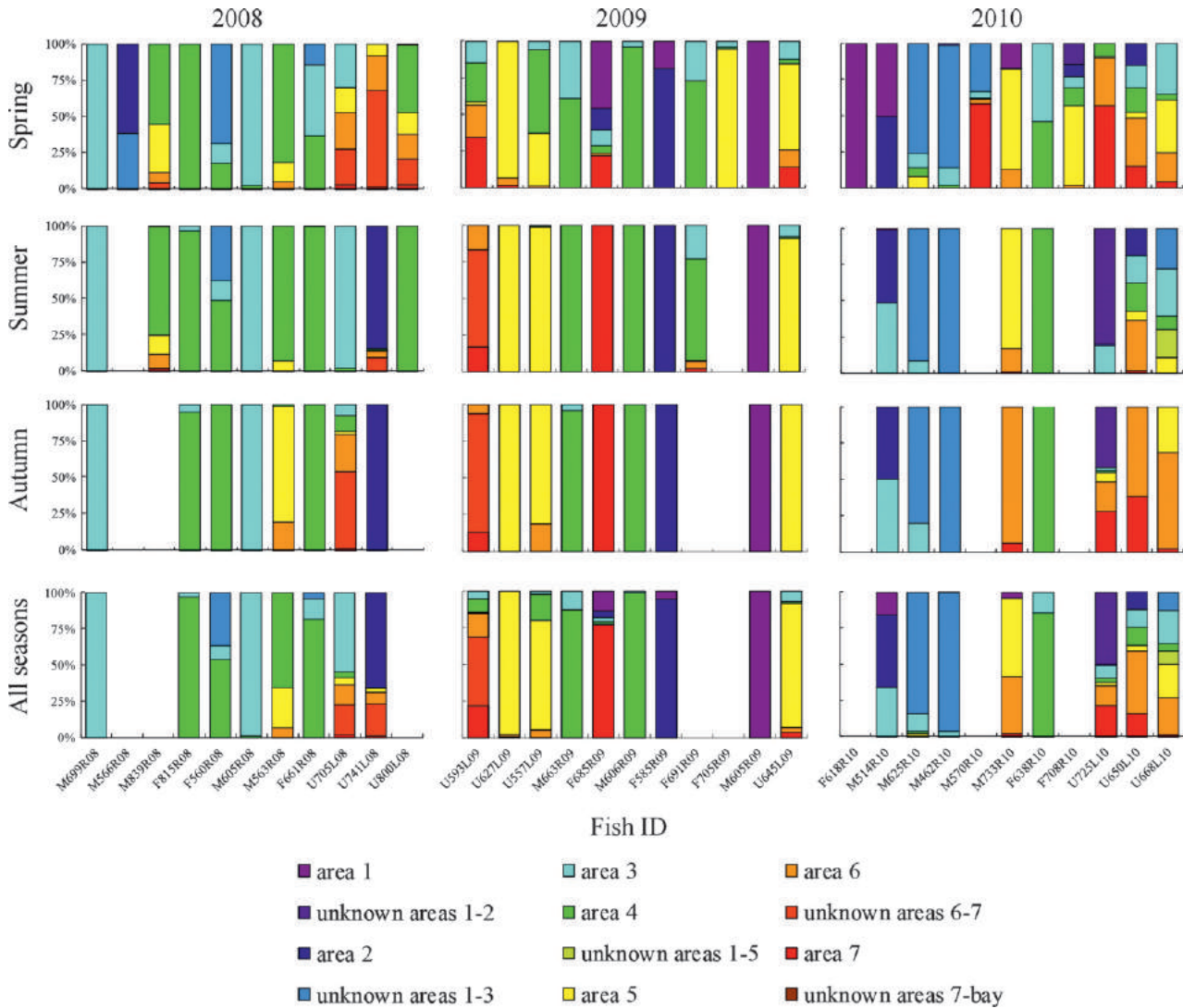


Fig. 6. Residence time in each area used by each tracked *Parahucho perryi* in each season or all seasons after completing the downward migration from their spawning grounds from 2008 to 2010.

(Fig. 7). Meanwhile, the spring and autumn residence time in downstream habitat for individuals released from Lake Akkeshi was significantly higher than that for individuals released upstream (Fig. 7). Additionally, although not all the significant differences were detected, smaller fish tended to stay upstream whereas larger fish preferred the mid- and downstream reaches from spring to autumn (Fig. 8).

Comparison with riverine water temperature

Water temperatures at the upper stations tended to lower than those at the lower stations throughout the study period, especially in 2008 and 2010 (Fig. 9). Simple logistic regression analysis showed that tracked fish moved away from lower areas when the mean daily maximum water temperatures increased in 2008 and 2010 (Fig. 10a,c). This trend was not detected in 2009 (Fig. 10b); however, it was

observed in the 3 years of summer data when tracked fish again moved out of certain reaches when the water temperature rose (Fig. 10d). The daily maximum water temperature in the lower reaches in summer 2009 fluctuated less than during the other two summers. The mean (\pm SE) differences in daily maximum temperature between summers 2008 and 2009, and between summers 2009 and 2010, were 2.0 ± 2.2 and 2.9 ± 2.2 °C, respectively (Fig. 11). The mean daily maximum water temperature in the lower reaches exceeded 20 °C in 6 days in 2009, 26 days in 2008 and 52 days in 2010.

Discussion

Previous telemetry research exploring the seasonal migration patterns and stream habitat use of *P. perryi* in the Bekanbeushi River system was conducted by Honda et al. (2009). However, specific details

Table 5. Number of tracked *Parahucho perryi* that stayed in each stream (up-, mid-, and downstream) habitat or plural stream habitats, total number, and percentage for one to three stream reaches where *P. perryi* stayed in each season and all seasons during 2008–2010.

Habitat	2008			2009			2010			2008–2010			Spring–Autumn			All
	Spring	Summer	Autumn	Spring	Summer	Autumn	Spring	Summer	Autumn	Spring	Summer	Autumn	2008	2009	2010	
	Number and its% for one to three stream habitats			Number and its% for one to three stream habitats			Number and its% for one to three stream habitats			Number and its% for one to three stream habitats			Number and its% for one to three stream habitats			
1	Upstream	2	2	3	2	2	2	2	2	6	8	8	1	2	2	5
	Upstream and midstream	3	4	1	4	1	3	1	0	10	6	2	4	2	2	8
	Midstream	1	2	2	0	4	0	1	1	1	7	6	0	0	0	0
	Midstream and Downstream	3	0	1	1	0	1	1	1	5	1	3	1	1	0	2
	Downstream	0	0	0	0	2	0	0	2	0	2	4	0	0	0	0
	All three streams	2	2	1	4	1	5	1	1	11	4	2	2	4	4	10
	<i>N</i>	3	4	5	2	8	7	5	6	7	17	18	1	2	2	5
	%	27.3	40.0	62.5	18.2	80.0	77.8	62.5	75.0	21.2	60.7	72.0	12.5	22.2	25.0	20.0
2	<i>N</i>	6	4	2	5	1	2	2	1	15	7	5	5	3	2	10
	%	54.5	40.0	25.0	45.5	10.0	22.2	25.0	12.5	45.5	25.0	20.0	62.5	33.3	25.0	40.0
3	<i>N</i>	2	2	1	4	1	0	1	1	11	4	2	2	4	4	10
	%	18.2	20.0	12.5	36.4	10.0	0.0	12.5	12.5	33.3	14.3	8.0	25.0	44.4	50.0	40.0

regarding stream habitat utilisation and its seasonality within the system had not previously been described. This study tracked a total of 39 adult *P. perryi*; 25 were tracked continuously from spring to autumn. We determined the preferred stream habitats and both the seasonal and individual variability. In addition to gaining information about downward migration from spawning grounds, we found that higher summer water temperatures in downstream reach triggered seasonal variation in stream habitat use.

Tagged *P. perryi* migrated from their spawning grounds to areas 1–5 (20–46 km) over periods of 1–7 days (Table 3). Although 44% of fish completed their migration in area 3, both the final area migrated to and the total migrated durations varied among individuals. For example, about half of the tracked fish visited nonspawning rivers. The fact that many tracked fish visited nonspawning rivers on their way to migratory destinations, or completed migrations in these rivers, suggests that fish might seek suitable habitat during their migration. The large variability in both areas visited and migration duration may support this hypothesis. Little difference not only in migrated duration and distance but also in migration speed was noted between males and females or among body sizes, suggesting that the large variability on their migratory patterns from spawning ground did not result from the difference in sex or body size.

Migration activity and movement from spawning grounds peaked around dawn and dusk and were higher at night than during the day (Fig. 3, Table 4). Downward migrations after spawning of iteroparous salmonid kelts have been previously reported for brown trout (*Salmo trutta*), Atlantic salmon (*Salmo salar*) and Arctic char (*Salvelinus alpinus*) (Bendall et al. 2005; Hubley et al. 2008; Jensen & Rikardsen 2008; Östergren & Rivinoja 2008). Hubley et al. (2008) tracked 27 *S. salar* kelts (48.5–76.7 cm total length) during downward migrations after spawning and reported migratory paths of 24 km up to coastal waters over periods of 3–32 days (mean: 14 days). Nocturnal migratory patterns in migration from spawning grounds have been identified in *S. trutta* kelts (Evans 1994; Bendall et al. 2005). Others have identified the postspawning habitat of some iteroparous salmonid species (Bendall et al. 2005; Hubley et al. 2008; Jensen & Rikardsen 2008) many of which (e.g., *S. salar* or *S. alpinus* kelts) prefer brackish and/or coastal waters. Conversely, cutthroat trout (*Oncorhynchus clarki*), bull trout (*Salvelinus confluentus*) and brook trout (*Salvelinus fontinalis*) kelts prefer to stay in rivers and exhibit a wide range of habitat preferences from upstream to downstream during their postspawning season (Jakober et al. 1998; Curry et al. 2002; Östergren & Rivinoja 2008).

Table 6. Number of tracked *Parahucho perryi*, the number of combinations, results of Fisher's exact test among combinations of tracked individuals as a test function of pairwise comparisons for proportions of the residence time in three stream (up-, mid- and downstream) habitats, and results of chi-square tests between the number of combinations with $P < 0.01$ and $P \geq 0.01$ by Fisher's exact test in each season or all seasons during 2008–2010.

	2008				2009				2010			
	Spring	Summer	Autumn	All season	Spring	Summer	Autumn	All season	Spring	Summer	Autumn	All season
No. of fish	11	10	8	8	11	10	9	9	11	8	8	8
No. of combinations	55	45	28	28	55	45	36	36	55	28	28	28
<i>The results of Fisher's exact test among combinations</i>												
$P < 0.01$												
<i>N</i>	49	36	22	25	47	33	28	29	49	22	24	18
%	89.1	80.0	78.6	89.3	85.5	73.3	77.8	80.6	89.1	78.6	85.7	89.3
$P \geq 0.01$												
<i>N</i>	6	9	6	3	8	12	8	7	6	6	4	3
%	10.9	20.0	21.4	10.7	14.5	26.7	22.2	19.4	10.9	21.4	14.3	12.0
<i>The results of chi-square tests between $P < 0.01$ and ≥ 0.01</i>												
χ^2	33.6	16.2	9.1	17.3	27.7	9.8	11.1	13.4	33.6	9.1	14.3	17.3
<i>P</i>	<0.001	<0.001	<0.01	<0.001	<0.001	<0.01	<0.001	<0.001	<0.001	<0.01	<0.001	<0.001

Postspawning habitats and the length of time required for the downward migration from spawning grounds varies depending on the species. Nighttime migration may help protect fish from predators such as eagles. For example, *P. perryi* tracked in this study avoided daytime movements, especially in upstream reaches with shallower waters and a narrower escape path.

If tagged fish were to have completed downward migration in the upper channel above station 1, at 20 km below the site of release, we would not have captured their movements because of the absence of a receiver along that upper stretch of channel. Considering the three individuals that first appeared at station 1, 10 or more days following release, a high probability exists that the upper channel above station 1 was also utilised as habitat throughout our study. Two fish (M733R10 and F618R10) may not have completed spawning by the time of release, despite that only fish moving downward were captured. Therefore, we cannot deny the possibility that those fish remained upstream and continued spawning. Previous records from the Sarufutsu River system in northern Hokkaido have shown that three female *P. perryi* (64.8–83.8 cm FL) stayed in an upstream tributary and spawned for over 5–8 days (Y. Tsuda, Kinki University, Wakayama, Japan, unpublished data).

After completing their migration from spawning grounds, fish dispersed widely and were found all the way from the upstream reaches to Lake Akkeshi. This movement continued until the end of November when the river began freezing (Fig. 4). No fish stayed in Akkeshi Bay for more than 1 day, indicating that a large amount of brackish water connected to the estuary may deter *P. perryi* although *P. perryi* populations in other river systems are known to show a distinct anadromous form (Arai et al. 2004; Suzuki

et al. 2011; Zimmerman et al. 2011). This finding confirms that of Kawamura et al. (1983) and Honda et al. (2010a), who suggested that most adult *P. perryi* in Lake Akkeshi do not move into Akkeshi Bay.

Throughout our tracking period, we found fish that changed habitat or stream reach across seasons and others that spent their entire time in a single stream reach (Fig. 6, Table 5). Additional individual variability was confirmed by the composition ratios for the residence time in each stream habitat determined for all seasons in all study years (Table 6). Owing to their high individual variability and their wide utilisation of the river system, *P. perryi* appears to be highly diversified and exhibits high behavioural plasticity. In this river system, upstream reaches have a more complex riverscape compared to downstream owing to increases in river sinuosity and the amount of riparian forest as it becomes narrower and shallower (Honda et al. 2010b; Honda, unpublished data). Therefore, life strategies including the foraging strategy of adult *P. perryi* may be different between upstream and downstream, and also midstream habitat which has intermediate characteristics based on the environmental differences. Probably, adult *P. perryi* can select their stream habitats depending on the conditions of individuals or on seasonal changes in their ambient environment. The two life history types (seaward migratory and freshwater resident) of salmonids are well known and are influenced by not only genotype but also growth condition (e.g., Heath et al. 1994; Silverstein et al. 1997; Thériault et al. 2007; Nichols et al. 2008; Wysujack et al. 2009). The life span of *P. perryi* is longer than that of other salmonid species and their habitats are limited to rivers or nearshore waters. Growth rates of *P. perryi* vary widely in accordance with their long life spans (Yamashiro 1965; Gritsenko et al. 1974). They are

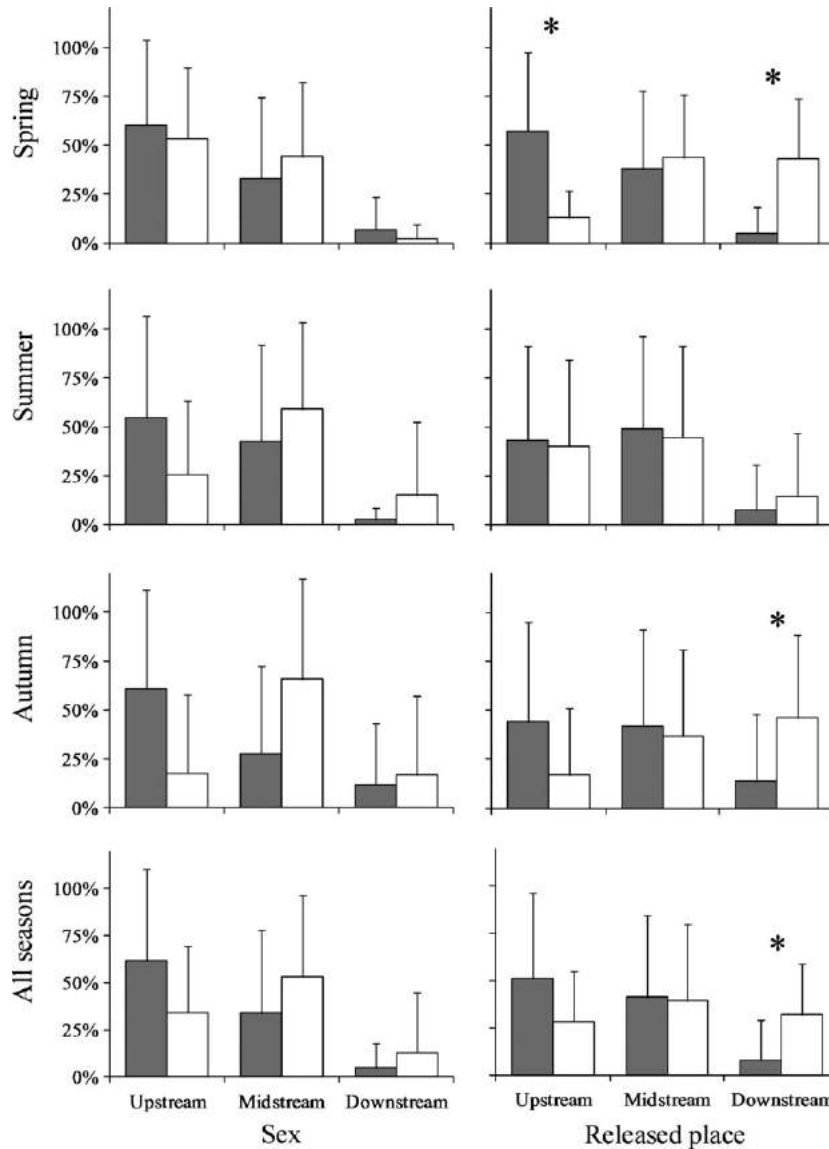


Fig. 7. Mean residence time in each stream habitat from 2008 to 2010: (left) between male (grey; $N = 13, 11, 10$ and 10 in order from top) and female (white; $N = 10, 7, 6$ and 6) *Parahucho perryi* and (right) between *P. perryi* released upstream (grey; $N = 23, 18, 16$ and 16) and *P. perryi* released in Lake Akkeshi (white; $N = 10, 10, 9$ and 9) in each season and for all seasons. Bars and * show standard deviations and a significant difference tested at $\alpha = 0.05$ by Mann–Whitney U test, respectively.

not faced with the alternative habitats of sea or river, but must choose a habitat over a narrower range between river and the connected coastal zone such that they can return to spawn. For this reason, this species may have acquired habitat flexibility. This sort of multiple migratory pattern has also been reported for the closely related species taimen (*Hucho taimen*). Gilroy et al. (2010) tracked 46 adult *H. taimen* for 5 years in Eg-Uur watershed, Mongolia, by radio and acoustic telemetry. They revealed that the taimen’s home range varied from 0.5 to 93.2 km (mean \pm SD, 23.0 ± 25.7 km) and that their migration patterns could be divided into four groups (restricted core home range, core range with seasonal departures, core range with separate seasonal range

and home range transfer). Similarly, Meka et al. (2003) studied the migration patterns of rainbow trout (*Oncorhynchus mykiss*) in the Alagnak River, Alaska, and reported three groups. The first group stayed in the river, the second group stayed in the lake, and the third group consisted of fish that migrated between the river and lake. Similar migratory patterns have also been observed in *S. trutta* and *O. clarki* (Schmetterling 2001; Zimmer et al. 2010). Multiple migratory patterns in river systems may characterise not only long-living salmonid species like *P. perryi*, but all salmonid species that widely utilise the river system. We also found that more tracked *P. perryi* stayed in two or three stream habitats in spring compared to summer or autumn when they moved less

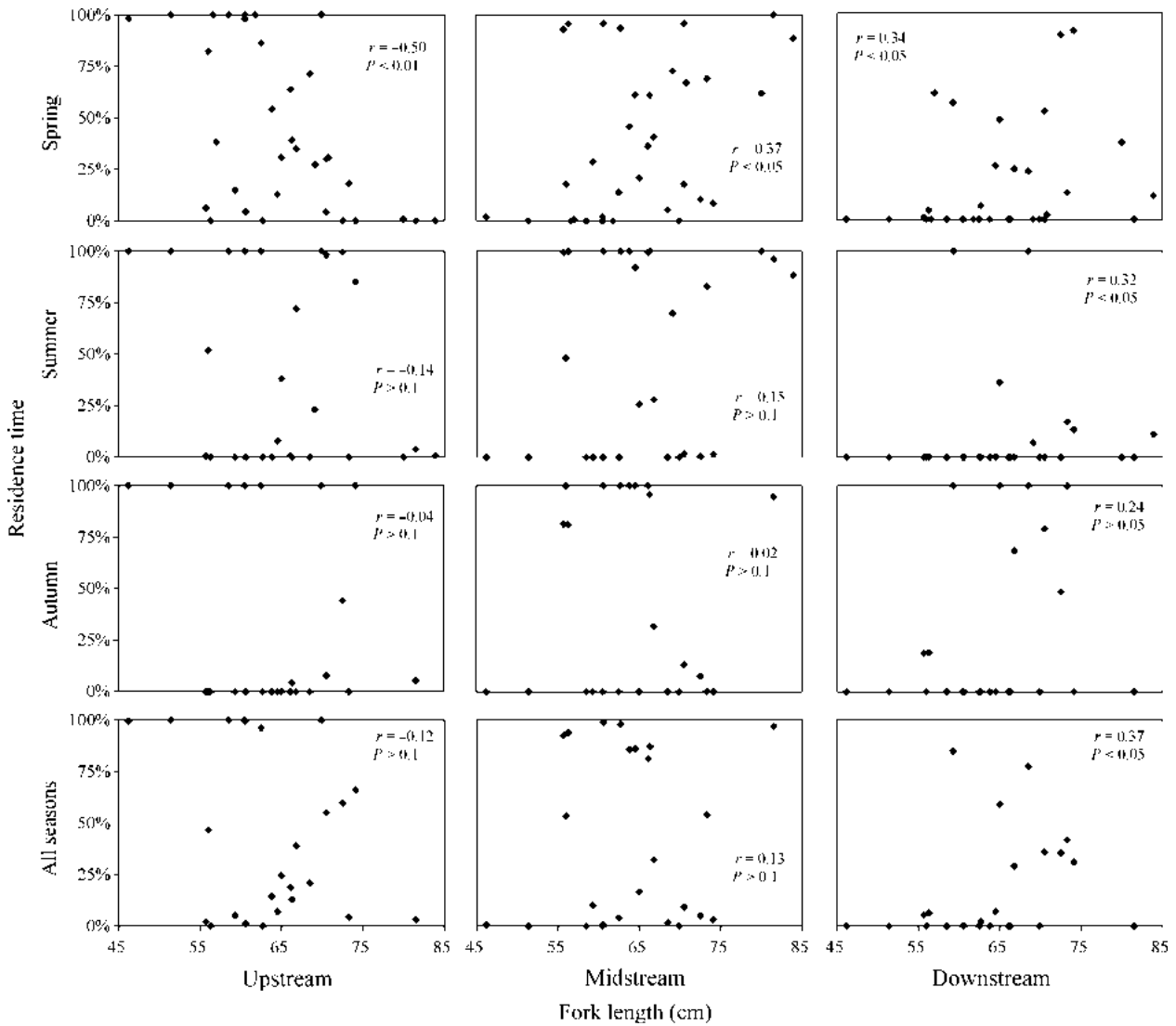


Fig. 8. Residence time of all tracked *Parahucho perryi* in each stream habitat from 2008 to 2010 in relation to fork lengths in each season and for all seasons ($N = 33, 28, 25$ and 25 from top down). Spearman rank correlation coefficient (r) and its P -values are shown on each graph.

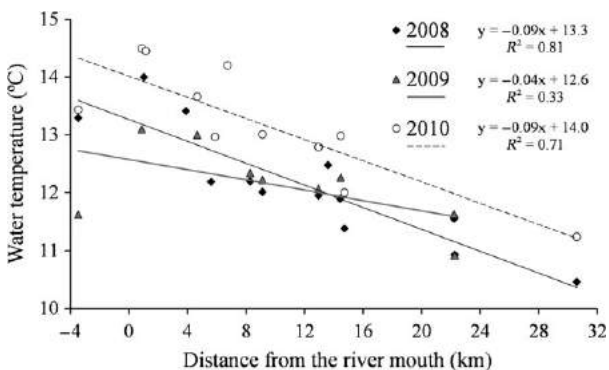


Fig. 9. Relationships between mean daily water temperatures in the study period recorded by each water temperature logger and their channel lengths from the Bekanbeushi River mouth during 2008–2010.

(Table 5). Gilroy et al. (2010) and Meka et al. (2003) also revealed that *H. taimen* and *O. mykiss* more widely utilised rivers and moved more frequently in the postspawning season than at other times of year. Overwintering and spawning utilise body strength and exhaust reserves; therefore, to recover in the spring, *P. perryi* may search for food and more desirable habitat leading to its variable movement within the river system.

Although differences in the residence time between males and females in each stream were not significant, females moved from upstream reaches to mid- and downstream reaches in the summer (Fig. 7). Additionally, smaller fish tended to stay upstream longer in spring, while larger fish tended to stay downstream longer throughout the study period

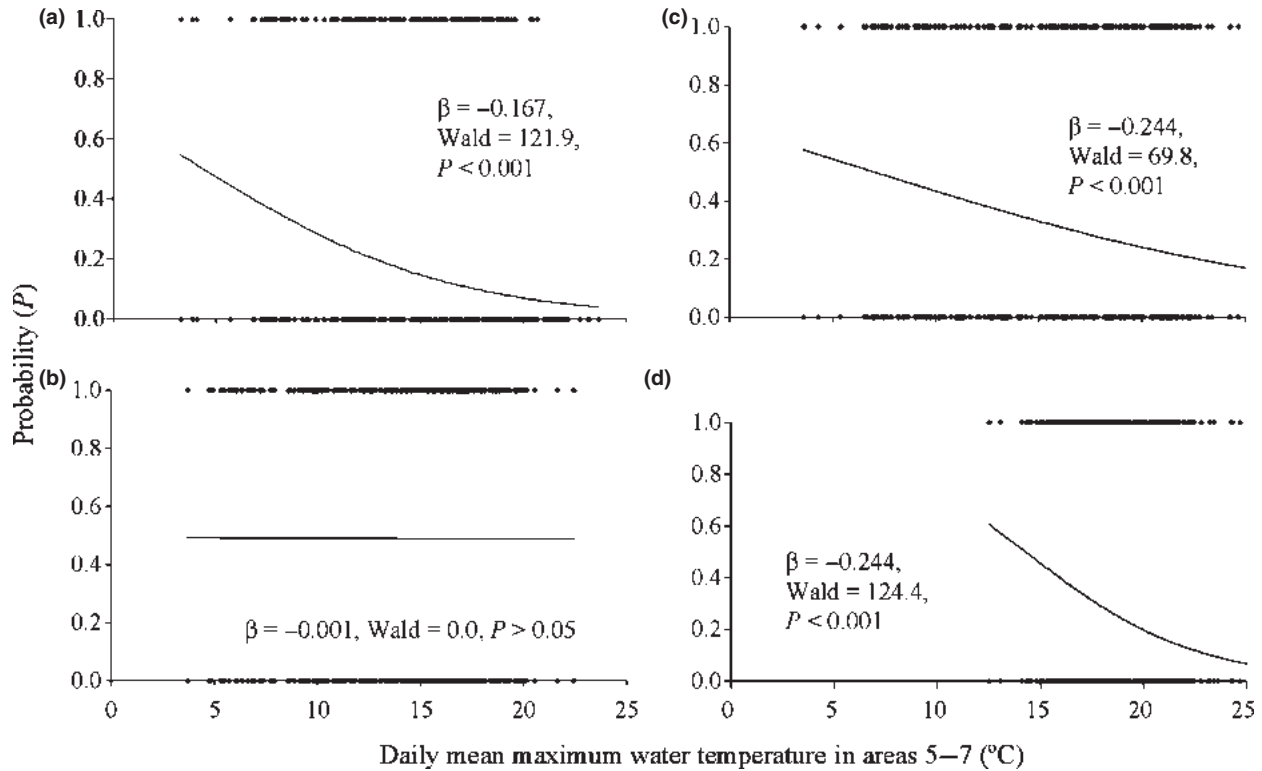


Fig. 10. Results of logistic regression analysis. Observed values (black dots) and expected values (solid lines) of probability that each tracked *Parahucho perryi* stays in lower areas (areas 5–7) in relation to the mean daily maximum water temperature: (a) 2008, (b) 2009, (c) 2010 and (d) summers from 2008 to 2010.

(Fig. 8). These findings may suggest that females expecting eggs in the following spring move to lower reaches to find food and that *P. perryi* individuals select stream habitat appropriate for their size and life cycle. Generally, salmonid females show anadromous form more than males (e.g., Yamamoto et al. 1999; Jonsson et al. 2001). *P. perryi* also shows the similar trend (Honda et al. 2010a). However, considering both insufficient data and large variances, more research is required to confirm these speculations. The trend that fish released from Lake Akkeshi stayed downstream with high frequency even in autumn may indicate that the fish had previously experienced downstream habitat and knew of its advantages. This sort of seasonal site fidelity of *P. perryi* has not been reported to date, and also that of other salmonid species has not been well studied (Clapp et al. 1990; Meka et al. 2003; Zimmer et al. 2010). The existence of fish such as U741L08, which stayed mainly in downstream reaches in the spring, but remained upstream from summer to autumn, means that fish that use downstream habitats in the spring do not always rely on the same habitat at other times of the year. Normally, these sex- and size-dependent and released place-based behaviours should be discussed together in related to their gonadal maturities, nutritional statuses and/or the distribution of food sources. Thus, further study regarding

those traits of adult *P. perryi* is required to draw definitive correlations.

We found that tracked *P. perryi* migrated to the upper reaches from lower reaches when water temperature in the lower reaches increased in the summer (Fig. 10). This trend was true in 2008 and 2010 when the summer water temperature was relatively high in the lower reaches, but not in 2009 when the water temperature remained low throughout most of the summer. Salmonids are known to avoid high water temperature because they are cold-water species (e.g., Bilby 1984; Torgersen et al. 1999; Baird & Krueger

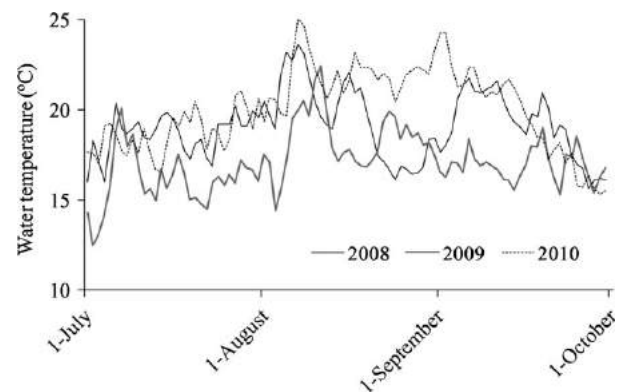


Fig. 11. Mean daily maximum water temperature in lower areas (areas 5–7) during each summer from 2008 to 2010.

2003). Curry et al. (2002) tracked 31 *S. fontinalis* (30.0–47.7 cm FL) in the Kennebecasis River, Canada, using both radio- and acoustic telemetry, and reported that many tracked fish remained upstream (50 km from the river mouth) where the mean daily water temperature was 0.6 °C lower downstream in prespawning summer. Additionally, Zimmer et al. (2010) tracked 43 *S. trutta* (34.0–59.6 cm FL) using radio telemetry in the Credit River, USA, and found that when water temperatures in the lower reach exceeded the 17.4 °C thermal preference for the species, the fish moved to upper reaches. Our results indicated that high water temperatures downstream is a trigger for adult *P. perryi* to move upstream, supporting the results of Honda et al. (2009). For adult *P. perryi*, the decision to move around in the lower reaches in hot summer probably comes with a risk as with other salmonid species (e.g., Berman & Quinn 1991; Matthews & Berg 1997). A water temperature of 20 °C is the speculated threshold temperature that triggers *P. perryi* to escape to cooler waters.

In this study, some tagged fish were not detected, and some tracked fish lost detection during the study period. Because *P. perryi* is an endangered species, missing fish cannot be ignored. Fish with no detection (all released from upstream) likely inhabited the area between the point of release and station 1; however, the possibility of either acoustic tag failure or fish death should not be overlooked. Some fish, such as M566R08, migrated downwards to area 2 after release in the middle of May and then migrated upstream back to area 1 around early June before losing contact. Similarly, F618R10, which was detected after release on 26 May at station 1 and then detected again at station 1 on 16 June, lost detection soon after. Conversely, M605R09 stayed in the upper channel before finally being detected at station 1 on 10 October. Moreover, F585R09 remained in areas 1 and 2 until 27 November. Fish whose detection signal was lost in the middle of the study period are assumed to have stayed upstream of station 1 or in Lake Akkeshi. Of all 17 fish whose detections were lost, three (U800L08, M535R09 and U650L09) were finally detected in the main channel, five were only detected at stations near the Beganbeushi River mouth or in Lake Akkeshi and nine were last detected by the uppermost reaches stations. The survival of three individuals (M605R09, M625R10 and M462R10) was not confirmed until the second year. Despite the possibility of acoustic tag failure, fish death or being fished, a high probability exists that the remaining 11 fish survived and stayed in channels that were not covered by receivers. However, this also indicates that the residence time in areas 1–3 and 6–7 (Fig. 4) may have been underestimated.

This study revealed the wide use of the Beganbeushi River system, from upstream to brackish Lake Akkeshi, by adult *P. perryi*. Not only did individuals use the main channel or their spawning rivers, many individuals also used multiple primary tributaries or nonspawning rivers. Moreover, some fish stayed from spring to autumn in one stream reach while other individuals used the river system more widely. Considering the above, adult *P. perryi* have high behavioural plasticity and their life forms show high variety in the pristine natural environment. Therefore, unless their migrations in the river system are blocked, or a region of habitat made unsuitable, they would occur everywhere regardless of upstream or downstream, making maximum use of the entire space in the long and short term. Therefore, the elimination of barriers that block migrations along stream habitats and their tributaries is absolutely essential to conserve this endangered species. The existence of barriers is known to be a threat for salmonid species with spawning grounds upstream (e.g., Hindar et al. 1991; Morita et al. 2009). Especially in Hokkaido, negative effects of habitat fragmentation caused by dams on several freshwater fishes including salmonid species were previously reported (Fukushima et al. 2007). Through this study, the importance of the connectivity among *P. perryi* habitats became more apparent. The ability to freely migrate back and forth in rivers is more important than anything else to *P. perryi*.

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