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1 **Movement patterns of adult Sakhalin taimen, *Parahucho perryi*, between stream**
2 **habitats of the Bekanbeushi River system, eastern Hokkaido, Japan**

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33 **Abstract** The behavior of endangered adult Sakhalin taimen *Parahucho perryi* was tracked
34 during 2008–2010 using acoustic telemetry in the Bekanbeushi River system, which flows
35 through eastern Hokkaido, Japan. Movement distances per unit time of tracked *P. perryi* were
36 compared between mid- and downstream habitats. Results indicated that movement distances
37 were significantly longer in downstream habitats during all seasons. The movement distances
38 in each stream decreased from spring to autumn. Moreover, tracked *P. perryi* exhibited
39 crepuscular movement patterns; however, patterns were less pronounced in downstream
40 habitats than in up- and midstream habitats. These findings strongly suggested that adult *P.*
41 *perryi* exhibit nearly distinctive movement patterns across stream habitats; thus, fish may
42 adopt different foraging tactics in each stream habitat. Fish moved more frequently in spring,
43 which included the post-wintering and post-spawning season, most likely to search for food
44 and more desirable habitat for recovery.

45

46 **Keywords** Acoustic telemetry · Crepuscular movement · Foraging tactics · *Parahucho perryi*
47 · Top predator

48

49 **Introduction**

50

51 The Maritime Province of Siberia, Sakhalin Island, the southern Kuril Islands, and
52 Hokkaido Island encompass the primary habitat of the salmonid species, Sakhalin taimen
53 *Parahucho perryi* (Gritsenko et al. 1974; Rand 2006), which has been classified under the
54 International Union for the Conservation of Nature (IUCN) Red List as Critically Endangered
55 (CR) since 2006 due to its drastic decrease over the past several decades (Rand 2006). In
56 addition to functioning as a top predator in river ecosystems, this species can reportedly live
57 for more than 20 years and reach at least 1.3 m in total length (Zolotukhin et al. 2000).
58 *Parahucho perryi* is an iteroparous species (Yamashiro 1965; Kimura 1966), spawning in
59 shallow upstream locations from March to June after snowmelt and displaying an anadromous
60 form that is distinct from its closely related *Hucho* species (Holčík et al. 1988).

61 To date, numerous studies worldwide have examined the behavioral ecology of riverine
62 fishes using telemetry methods to reveal migratory patterns and habitat uses (e.g., Gilroy et al.
63 2010; Hedger et al. 2010; Hahn et al. 2011). Generally, 24-h long-term tracking of fish
64 movements is possible when using multiple stationary receivers concurrently. Furthermore, if
65 the distances between stationary receivers are both constant and short enough to cover the
66 migration range of the target fish, the daily or monthly movement distances of the fish can be
67 roughly estimated without actual tracking. Moreover, recently even foraging strategies of
68 some riverine fishes have been beginning to be revealed based on their movement patterns
69 obtained by those telemetry methods (Hedgar et al. 2010; Schoby and Keeley 2011).

70 In recent years, several behavioral ecological studies have used acoustic telemetry to
71 examine adult *P. perryi* in the Bekanbeushi River system in eastern Hokkaido (Honda et al.
72 2009, 2010a, 2012). Honda et al. (2010a) documented the seasonal long-term habitat use of
73 adult *P. perryi* and classified their habitats as highly meandering and densely vegetated with

74 riparian plants providing thick shade in the summer and autumn. Meanwhile, in a study on the
75 seasonal stream habitats of adult *P. perryi* over 3 years, Honda et al. (2012) demonstrated that
76 adult fish widely utilized the river system from upstream to a brackish lake that connects to
77 the river mouth regardless of the mainstream or tributaries. These authors verified that *P.*
78 *perryi* individuals significantly varied in their use of each stream habitat: some fish remained
79 in one specific stream habitat throughout the study period from spring to autumn, whereas
80 others seasonally migrated between upper and lower reaches. In addition, high summer water
81 temperature in downstream habitats triggered the upward migration of this species (Honda et
82 al. 2012). Although Honda et al. (2012) successfully documented the broad-scale use of the
83 river system by adult *P. perryi* based on individual residence times in each stream habitat,
84 behavioral differences among the river habitats were not examined. Furthermore, although
85 crepuscular and nocturnal movement patterns of *P. perryi* were observed in post-spawning
86 migrations from upstream spawning grounds, such diel movement patterns after the spawning
87 season and seasonal differences therein were not reported.

88 Such behavioral ecological information would be beneficial for conserving an endangered
89 species such as *P. perryi* as well as the environments of its various habitats. In particular, if
90 behavioral differences exist among stream habitats, whether adult *P. perryi* remain within a
91 habitat may vary depending on the environment of the stream habitat. Thus, studying the
92 movement patterns of this species in each stream habitat is essential from a viewpoint of
93 conservation ecology. Here, we examined movement distances, diel movement patterns, and
94 seasonal differences therein in various stream habitats of adult *P. perryi* in the Bekanbeushi
95 River system using acoustic telemetry. We then discuss the presence or absence of various
96 foraging tactics across stream habitats.

97

98

99 **Materials and methods**

100

101 *Study site.* Surveys were conducted in the Bekanbeushi River system (total basin area: 738.8
102 km²) situated in eastern Hokkaido, Japan, from April to November during 2008–2010 (Fig. 1).
103 This river flows into the brackish Lake Akkeshi (circumference: 24.8 km, maximum depth:
104 7.0 m, salinity: 25–30 psu; Hokkaido Institute of Environmental Sciences 2005), which is
105 connected to the Pacific Ocean by Akkeshi Bay (Fig. 1). Few artificial structures exist within
106 this basin, and the dominant habitat in the lower reaches of the river basin is the Bekanbeushi
107 wetlands (5,277 ha), registered under the Ramsar Convention. Much of the upstream habitat is
108 also intact, as the presence of the Yausubetsu Japanese army training site (16,800 ha) restricts
109 access to the area.

110 The study area covered the entire Bekanbeushi River system except for the Obetsu and
111 Oboro rivers (Fig. 1), although the estuary of the latter river was initially selected as a study
112 site in 2009 and 2010. In an effort to conserve the remaining populations of *Parahucho perryi*,
113 the actual locations where fish were caught and released cannot be disclosed, although
114 information on these locations is described using river domain blocks (areas). The study sites
115 were grouped into seven areas according to channel length, junctions, and downstream tidal
116 effects (Fig. 1). Honda et al. (2012) presents more detailed information regarding
117 categorization of these areas.

118 *Fish tagging and tracking.* Thirty-four mature *P. perryi* were captured using a seine net
119 design (1.0 m high × 28.1 m wide, mesh size: 40 mm) at the upstream end of a tributary in
120 which *P. perryi* spawn, located 51 km from the river mouth (area 1) from late April to early
121 May 2008–2010 (Table 1). A fishway was placed along the riverbank with an entrance located
122 at the upstream side of the net to target only fish moving downstream. From the middle of
123 April to the middle of May, 11 adult *P. perryi* were additionally caught by a local set-net

124 fishery in Lake Akkeshi over the 3 years. The sex of each fish was determined by nuptial
125 coloration (i.e., the posterior half of bodies of males is more reddish than that of females;
126 Esteve et al. 2009) and by pressing the abdomen to determine if unreleased gametes were
127 present. Fork lengths (FLs) of tagged fish ranged from 46.0 to 83.9 cm, and the mean FL (\pm
128 SD) was 62.7 ± 8.9 cm. The identity of each fish was described with regard to sex, FL,
129 capture/release location, and year tagged. An acoustic tag (Vemco V13-1L; 69.0 kHz, 13.0
130 mm diameter, 36.0 mm length; www.vemco.com) was surgically implanted into abdominal
131 cavity of all captured *P. perryi* using anesthesia (2-phenoxyethanol 0.04 %, diluted with river
132 water) as in Honda et al. (2009, 2012). Battery life and pulse varied between the two types of
133 tag used. One randomly transmitted a set of six pulses once every 20–60 s lasting 439 days,
134 the other sent pulses every 40–90 s, with power lasting 650 days. After confirming recovery
135 from anesthesia, the tagged fish caught upstream were released just below the net, while the
136 tagged fish caught in Lake Akkeshi were released at the nearby lakeshore (Fig. 1). Both
137 laboratory and field studies have noted a low probability of post-tagging mortality from stress
138 in adult *P. perryi* (see Honda et al. 2009).

139 From April to November 2008–2010, 24–28 stations that harbored a VR2(W) (Vemco)
140 acoustic receiver were arrayed from area 1 to area 7 (Table 2). Tagged *P. perryi* were tracked
141 by these receivers during the study periods. Additional information about the receiver arrays
142 is described elsewhere (Honda et al. 2012).

143 *Use of detection data.* Monthly data were categorized by season, in which April–June,
144 July–September, and October–November were defined as spring, summer, and autumn,
145 respectively (Honda et al. 2012). Detection data recorded in the second year after fish release,
146 data regarding the “downward migration from spawning grounds,” and data recorded by a
147 towed receiver, all of which were obtained by Honda et al. (2012), were not used for any
148 analyses in the present study.

149 *Movement distances in areas 4–6.* Individual daily accumulated movement distances in
150 each of areas 4–6 in the mainstream of the Bekanbeushi River system were determined based
151 on the distances between receivers. Even movements between areas (e.g., between areas 3 and
152 4) were shared and counted based on the distance to the boundary. All stations used for the
153 estimation were shown in Table 2. Data for these areas were used in this analysis because
154 movements of all tagged fish were thoroughly monitored and the mean interval distances
155 between stations in each area did not differ greatly over the 3 years (Table 3). Covered
156 channel lengths in each area were 6,242, 3,888, and 3,090–3,292 m, respectively. According
157 to Honda et al. (2012), areas 4–5 and area 6 were located mid- and downstream within the
158 river system, respectively. Area 6 was wider and deeper than areas 4–5 because the channel of
159 the former contained both the mainstream and the Chiraikaribetsu River (primary tributary;
160 Fig. 1). In addition, some amount of riparian woods exists in areas 4–5, whereas forested
161 riparian areas are rare in area 6 (Honda et al. 2010a). The sinuosity index in area 4 was more
162 than twice higher than that in area 6 (Honda et al. 2010a). Meanwhile, due to these
163 environmental differences, the detection ranges of receivers at stations in lower areas were
164 assumed to be wider than those in upper areas (reviewed by Kessel et al. 2013).

165 The daily-converted total movement distance (DCTMD) was estimated for every
166 individual in each month based on the “residence time” in each of areas 4–6 in the
167 mainstream and was then compiled for seasons examined. Residence time, defined as the time
168 during which each tagged fish remained in each area, was calculated based on its detection
169 data (Honda et al. 2009, 2012). Time periods without detection were shared half and half
170 between the area of detection before and the area of detection after the no detection period
171 (Honda et al. 2009). Thus, the DCTMD represents the individual total movement distance in
172 each area which was divided by total residence time (d) there. The differences in monthly
173 DCTMDs among areas during the same season and among seasons in the same area were

174 tested using nonparametric multiple comparison analysis (Steel–Dwass test) with Ky Plot 5.0
175 (KyensLab Inc.; www.kyenslab.com) at $\alpha = 0.05$. Here, only monthly DCTMDs, which were
176 estimated using fish with more than 3 recorded days of residence time in each area and in
177 each month, were used in this analysis. Because some overlapping detections were recorded
178 between stations 23 and 25, any movement distances between station 25 and the boundary
179 between area 5 in the Chiraikaribetsu River and area 6 (i.e., 217 m) were not included due to
180 this uncertainty. Moreover, the lower boundary of area 6 was considered to occur at station 29
181 in this analysis because station 30 was absent in 2008. The time of continuous detections at
182 station 29 was included in the residence time of area 6. Here, two or more detections within
183 180 s (fish equipped with a transmitter having a 20–60-s transmission interval) or 270 s (fish
184 equipped with a transmitter having a 40–90-s transmission interval) were defined as
185 continuous detection, as in Honda et al. (2009), based on the very unlikely possibility of three
186 consecutive time transmissions (maximum transmission interval: 60 or 90 s) being missed
187 from one acoustic tag.

188 Furthermore, in order to determine the effect of the differences of detection ranges among
189 areas on movement distances, we assumed that the detection range of each acoustic receiver
190 in areas 5–6 were consistently 50 m and 100 m wider, respectively than that of area 4 (liberal
191 estimation) and that all fish movements in areas 5–6 were consisted of minimum distances
192 within the detection range of each receiver. We then carried out same analysis described
193 above but by shortening all movement distances by 100 m (50 m each side) in area 5 and 200
194 m (100 m each side) in area 6 and compared the obtained results between the two analyses.

195 *Diel movement patterns among stream habitats.* Assuming that tagged fish were moving
196 both outside and inside of the detection range at the beginning and end of a series of multiple
197 detections by each receiver, only the first and last detections were extracted and defined as
198 “movement” in this analysis. Areas 1–3, 4–5, and 6–7 were defined as up-, mid-, and

199 downstream habitats, respectively (Honda et al. 2012), while all movement data recorded by
200 all receivers in each stream habitat were divided into day, twilight, and night. The
201 standardized hourly rates of movement during these three time periods were also estimated.
202 Here, the time period for twilight was considered to be 4 h (2 h each around daily sunrise and
203 sunset), while day and night comprised the rest of the day. The timings of sunrise and sunset
204 were determined from data recorded at the Ota weather station (43.092°N, 144.780°E) of the
205 Japan Meteorological Agency (<http://www.jma.go.jp/jma/index>). Differences in movement
206 rates for all tagged fish among time periods in each season and during all seasons combined
207 were tested using Steel–Dwass tests ($\alpha = 0.05$). In this analysis, only fish that exhibited 10 or
208 more movements in each season or all seasons combined were used. All overlapping
209 detections and shuttle movements within 5 min between stations 23 and 25 were excluded
210 from the analysis because such detections were not likely to reflect actual movements.

211

212

213 **Results**

214

215 The numbers of tagged *Parahucho perryi* detected at least once were 12, 13, and 14 in 2008,
216 2009, and 2010, respectively. The numbers of tagged fish tracked in mid-November or later in
217 each year were eight, eight, and six, respectively (Table 1). More information on the basic
218 detection results and residence time in each area is available in Honda et al. (2012).

219 **Movement distances in areas 4–6.** The total accumulated residence times in areas 4, 5,
220 and 6 in the mainstream of the Bikanbeushi River system by all tracked fish in 2008–2010
221 were 1,611, 524, and 298 days, corresponding to total accumulated movement distances of
222 553, 378, and 1,417 km, respectively. The frequency of individual daily accumulated
223 movement distances of greater than 51 m in areas 4–5 was low, whereas the frequency of

224 movements of 0–50 m accounted for more than 70 % of all movements in these two areas
225 (Fig. 2). In addition, over 90 % of movement distances 0–50 m were recorded in 18–24 h of
226 daily accumulated residence time. On the other hand, movement distances of over 501 m
227 comprised more than 50 % of all movements in area 6, and the daily accumulated residence
228 time ranged widely from a few hours up to 24 h in this area (Fig. 2).

229 Mean monthly DCTMDs in each area increased toward downstream habitats regardless of
230 season (Fig. 3a). In particular, DCTMD significantly differed between areas 4–5 and area 6
231 during each season ($-4.80 \leq t \leq -2.37$, $P < 0.05$); mean distances in area 6 were 4.8–39.0
232 times higher than in areas 4–5 (Fig. 3a). This pattern was observed in many individuals; in
233 fact, even among individuals that were recorded in both areas 4 and/or 5 and area 6, 82 % of
234 fish (9 of 11) exhibited values of DCTMD in area 6 that were more than twice higher than
235 those in areas 4 and/or 5 throughout the study period.

236 The large variances of values of mean monthly DCTMD (Fig. 3) indicated that some
237 individuals differed considerably in movement distances. For example, F705R09 (fish ID, see
238 Table 1) remained in area 4 for a total of 11.6 days in the summer, but its DCTMD was 1,416
239 m, which was nearly five times higher than the mean value for the same season. In contrast,
240 even though U557L09 remained in area 6 for 7.1 days in the spring, its DCTMD was only 43
241 m (without treatment).

242 In addition, the monthly DCTMDs in spring were the highest of all seasons in all areas,
243 whereas values of DCTMD became significantly shorter from spring into autumn in areas 4 (t
244 = 3.93, $P < 0.05$) and 6 ($t = 3.25$, $P < 0.05$, Fig. 3a).

245 The trend did not differ between the results of detection-range-considered- (Fig. 3b) and
246 untreated analyses (Fig. 3a). Significant differences in the former were observed among same
247 areas and seasons as the latter ($-4.74 \leq t \leq 3.93$, $P < 0.05$, Fig. 3b).

248 **Diel movement patterns among stream habitats.** The mean individual standardized

249 hourly rates of movements during the twilight time period tended to be higher than those
250 during the day or night (Fig. 4). With the exception of upstream habitats in autumn when only
251 two fish were recorded, however, movements did not significantly differ between twilight and
252 day/night in downstream habitats during the summer ($t = -0.32$, $P = 0.95$, between day and
253 twilight; $t = 0.64$, $P = 0.80$, between night and twilight) or during all seasons combined ($t =$
254 -1.65 , $P = 0.22$, between day and twilight; $t = 2.25$, $P = 0.06$, between night and twilight; Fig.
255 4).

256

257

258 **Discussion**

259

260 The present study demonstrated that the movement patterns of adult *Parahucho perryi* varied
261 among stream habitats. Most fish tracked did not move long distances in midstream habitats
262 of the Bekanbeushi River; instead, fish in downstream habitats tended to exhibit much more
263 movement (Fig. 3) although their short-distance movements could not be monitored using the
264 current study design. Meanwhile, the comparison between the detection-range-considered-
265 and untreated analyses indicated that the differences of detection ranges among areas have not
266 affected greatly on the obtained results. Moreover, the daily accumulated residence time in
267 area 6 was shorter than that in areas 4–5 (Fig. 2). These results indicate that fish in areas 4–5
268 spent most of their time in the same area, whereas fish in area 6 did not and instead included
269 adjacent areas in their daily movement ranges. Only a limited number of studies of salmonids
270 have reported similar differences in movement patterns among river reaches (e.g., Young
271 1996; Zimmer et al. 2010). Zimmer et al. (2010) used radiotelemetry to track 43 brown trout
272 (*Salmo trutta*, 34.0–59.6 cm FL) in up- and midstream regions of the Credit River, which
273 flows into Lake Ontario. They found that the home range and displacement (km) of

274 individuals in upper reaches were small compared to individuals in lower reaches. These
275 authors suggested that the difference was caused by the presence of extensive riffle areas,
276 which deter movements, in upstream habitats, and because individuals in lower reaches
277 sought optimal water temperatures to avoid high temperatures in the area (Zimmer et al.
278 2010).

279 In the Bekanbeushi River system, the channels in upper reaches are more meandering and
280 are bordered by more dense riparian woods than those in the lower reaches (Honda et al.
281 2010a). Those channels also have few riffles even in upper reaches including area 4 because
282 of very low difference of elevation (the elevation at headstream of the mainstream is <150 m).
283 Such channels in the upper reaches are assumed to provide more woody debris and pools,
284 which are likely suitable for salmonid species including adult *P. perryi* to hide from both their
285 prey and predators such as eagles (Fausch and Northcote 1992; Sagawa et al. 2002,
286 Nagayama et al. 2009). In addition, riverine structures such as woody debris provide refuge
287 for prey species of *P. perryi* (Benke and Wallace 2003; Dolloff and Warren 2003). Therefore,
288 the upper reaches offer few advantages for adult *P. perryi* in terms of wide-range searching for
289 food; instead, ambush foraging tactics are likely to be more efficient to avoid energy costs. In
290 fact, adult *P. perryi* remained in specific habitats in up- and midstream habitats of the
291 Bekanbeushi River, particularly in areas with higher sinuosity and more dense riparian forests
292 for the mid- to long term (Honda et al. 2010a). In contrast, prey fish such as *Osmerus mordax*
293 *dentex*, *Hypomesus japonicas*, *Salangichthys microdon*, *Tribolodon hakonensis*, *Gasterosteus*
294 *aculeatus*, *Pungitius sinensis*, and *Gymnogobius urotaenia* are assumed to inhabit, either
295 seasonally or year-round, the downstream regions of the Bekanbeushi River (Mukai 2007; K.
296 Honda, unpublished data). Generally, most of these prey species form schools; therefore, in
297 these habits, cruising foraging tactics would likely be more efficient for adult *P. perryi* to
298 encounter schools of prey fish. In addition, even though the tidal effect on fish movements

299 was not taken into account in this study, area 6 was assumed to be more affected by tide than
300 areas 4–5. Both *P. perryi* and its preys may have moved along with tidal changes. The effect
301 of tide to fish movement patterns are reported in several other fish species (e.g., Childs et al.
302 2008; Sakabe and Lyle 2010), including some adult salmonids on their pre- and
303 post-spawning seasons (e.g., Bendall et al. 2005; Hubley et al. 2008). Sakabe and Lyle (2010)
304 revealed that *Acanthopagrus butcheri* in the Little Swanport Estuary in Tasmania exhibited
305 extensive tidal movements, with small-scale upstream movements during incoming tides and
306 downstream movements during out-going tides.

307 Ambush and cruising foraging tactics generally exhibit a trade-off relationship (O'Brien et
308 al. 1990). Furthermore, differences between the two tactics are closely related to different
309 alternative life history types of freshwater resident and seaward migrant salmonids (Elliott
310 1994; Yamamoto et al. 1999). The migratory ranges of *P. perryi* are generally limited up to the
311 connected coastal zone (Arai et al. 2004; Edo et al. 2005; Suzuki et al. 2011; Zimmerman et al.
312 2011). Among individuals of *P. perryi* from the Bekanbeushi River system, few fish are
313 thought to migrate into Akkeshi Bay (i.e., the ocean) from the brackish Lake Akkeshi
314 (Kawamura et al. 1983; Honda et al. 2010b, 2012). Because of their limited migratory ranges,
315 *P. perryi* may not face the rigid alternative choice between seaward migratory or freshwater
316 resident life histories. In fact, *P. perryi* in the study system exhibited large individual
317 variability in their use of seasonal stream habitats, and this variability did not appear to
318 exhibit remarkable seasonality or size- and/or sex-dependent patterns (Honda et al. 2012).
319 Therefore, it is not surprising that this species might adopt different movement patterns in
320 each stream habitat depending on individual requirements. With regard to the observed
321 individual differences in movement distances, we suspect that some fish may have tracked
322 prey fish even in area 4 and that large woody debris that provided suitable hiding places may
323 have existed even in area 6.

324 Movement distances of *P. perryi* significantly differed among seasons in each area, and
325 the tracked fish moved the farthest distances in spring (Fig. 3). Honda et al. (2012) reported
326 that the number of individuals that used multiple stream habitats was higher in the spring.
327 Similar increases in fish activity in the post-wintering/spawning season have also been
328 reported for other salmonid species (Meka et al. 2003; Gilroy et al. 2010). Overwintering and
329 spawning utilize body strength and exhaust reserves; therefore, to recover in the spring, *P.*
330 *perryi* may search for food and more desirable habitat, resulting in variable movement within
331 the river system.

332 In the present study, adult *P. perryi* exhibited crepuscular movement patterns (Fig. 4).
333 Endogenous circadian rhythms of salmonids fluctuate depending on differences in species,
334 growth stages, and external factors such as photoperiod or water temperature (e.g., Fraser et al.
335 1993; Alanära and Brännäs 1997; Metcalfe et al. 1999; Baldwin et al. 2002; Bendall et al.
336 2005). Similar crepuscular movement patterns have been reported in other salmonid species
337 (e.g., Douglas 1982; Ovidio et al. 2002); the purpose of active movements during twilight is
338 likely foraging (Boujard and Leatherland 1992). This particular time period may offer an
339 efficient foraging opportunity for adult *P. perryi* not only because prey may be less likely to
340 notice sudden attacks, but also because they can target both nocturnal and diurnal prey species
341 (Hobson 1972). Meanwhile, whether the high summer water temperatures in downstream
342 habitats (Honda et al. 2012) caused the lack of crepuscular movement patterns in fish in these
343 areas remains unclear. In the future, the actual swimming information which can be obtained
344 by such as acceleration data logger (see Tsuda et al. 2006) and electromyogram transmitter
345 (see Makiguchi et al. 2007) can be used to more clearly verify the differences of movement
346 patterns of *P. perryi* among different time periods and also among different stream habitats.

347 In Hokkaido, a main habitat of *P. perryi*, the loss of riverine heterogeneity due to river
348 developments such as channelization has resulted in marked uniformity of river channels over

349 the past several decades (Fukushima et al. 2005). For aquatic species such as *P. perryi* that
350 widely utilize the river system and exhibit nearly distinctive movement patterns across stream
351 habitats, reduced riverine heterogeneity would probably compromise their options for
352 foraging tactics. Thus, when conserving and restoring the habitats of *P. perryi*, barrier-free
353 physical connectivity among their habitats must be considered (Honda et al. 2012). Moreover,
354 conservation and restoration based on the original environmental characteristics of each
355 stream habitat should be a requirement.

356

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495

496 **Figure legends**

497

498 **Fig. 1** Study site: the Bekanbeushi River system in eastern Hokkaido Island, Japan. Each area
499 is color-coded. The *star* indicates the location where *Parahucho perryi* captured in Lake
500 Akkeshi were released. Figure reproduced from Honda et al. (2012), with permission from
501 John Wiley & Sons

502

503 **Fig. 2** Frequency of daily accumulated movement distances by each tagged *Parahucho perryi*
504 for each classified daily accumulated residence time in areas 4–6 in the mainstream of the
505 Bekanbeushi River system

506

507 **Fig. 3** Mean monthly daily-converted total movement distance (DCTMD) by each tagged
508 *Parahucho perryi* in areas 4–6 in the mainstream of the Bekanbeushi River system in each
509 season. **a** Untreated, **b** detection-range-considered by shortening all movement distances by
510 100 m (50 m each side) in area 5 and 200 m (100 m each side) in area 6. *Error bars* represent
511 standard deviations. Significantly different data are coded by *a*, *b*, or *c* among areas, and by *A*
512 and *B* among seasons ($P < 0.05$)

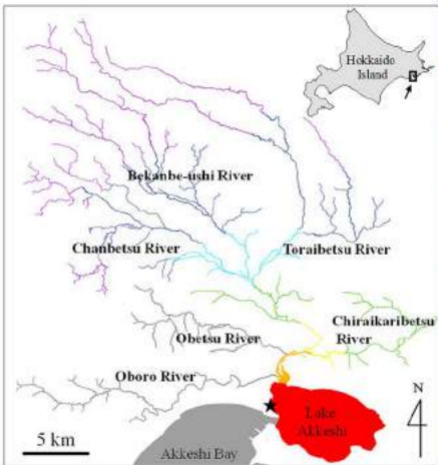
513

514 **Fig. 4** Standardized hourly rate of movements among three time periods by each tagged
515 *Parahucho perryi* among up- (areas 1–3), mid- (areas 4–5), and downstream (areas 6–7)
516 habitats in each season and in all seasons combined. Error bars represent standard deviations.
517 *White*, *gray*, and *black bars* indicate daytime, twilight, and nighttime periods, respectively.
518 Significantly different data are coded by *a*, *b*, or *c* ($P < 0.05$)

519

43.36° N

Area



1

2

3

4

5

6

7

5 km

N
4

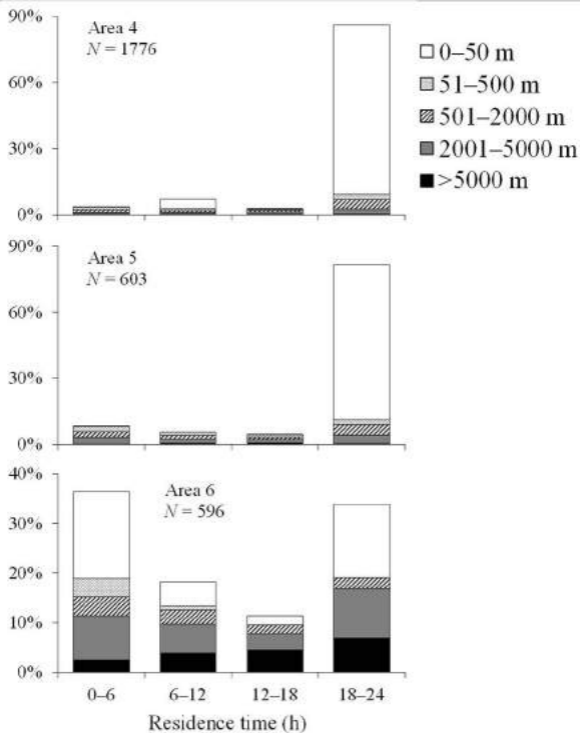
Akkeshi Bay

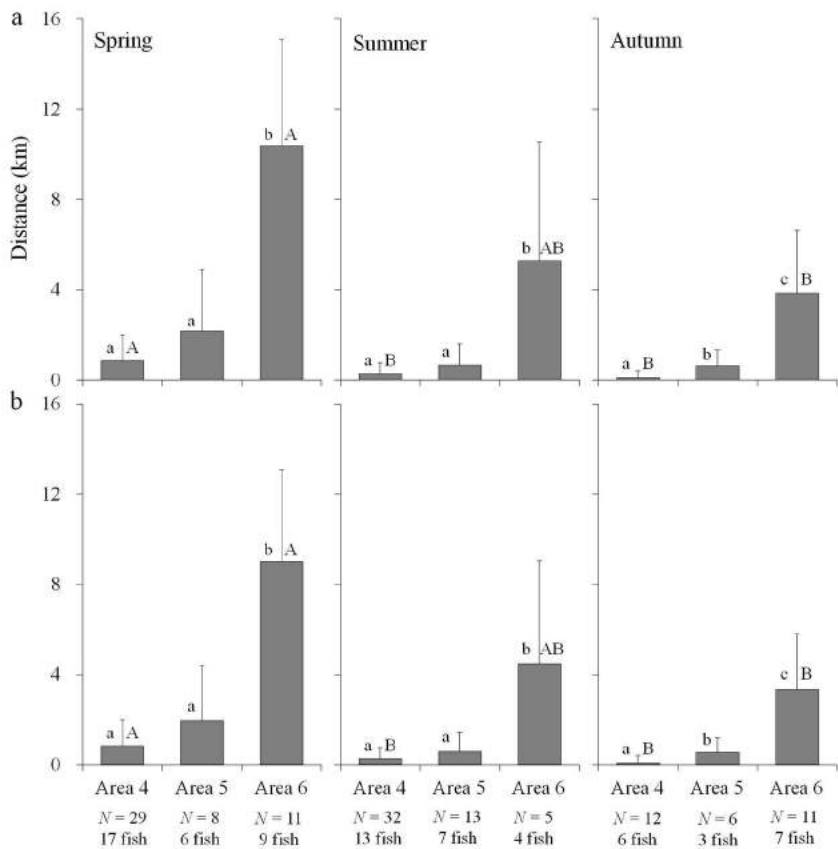
Lake Akkeshi

43.01° N

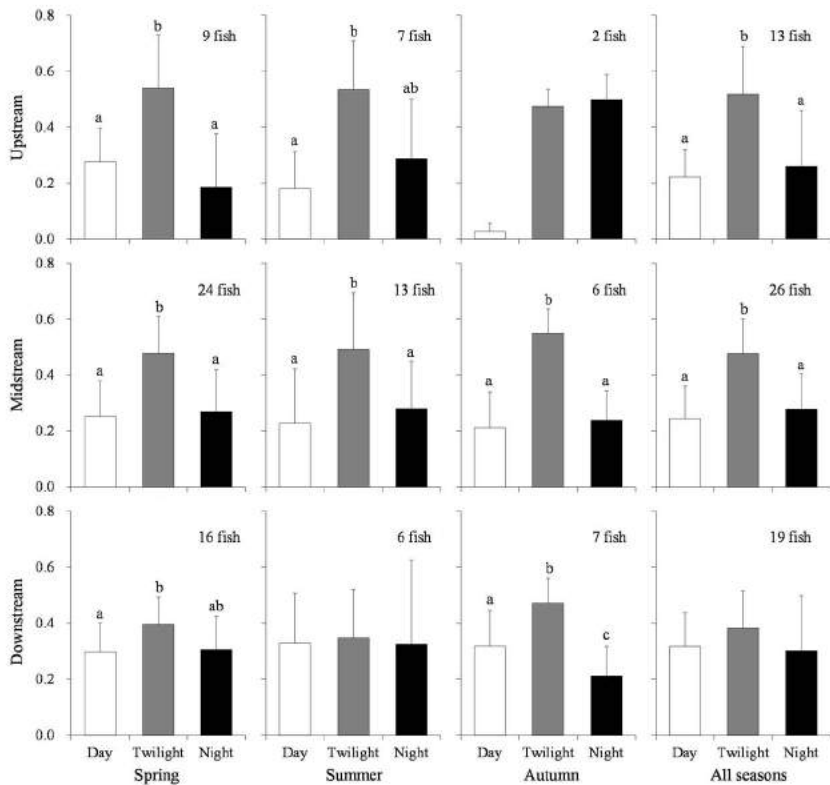
144.38° E

145.00° E





Standardized hourly rate of movement



1 **Table 1** Fish ID, measurements, and tagging information for tagged adult *Parahucho perryi* captured in an upstream tributary (51 km upstream
 2 from the river mouth) of the Bekanbeushi River and in Lake Akkeshi in Hokkaido, Japan. Table reproduced from Honda et al. (2012), with
 3 permission from John Wiley & Sons

4

Fish ID	Sex	Fork length (cm)	Body weight (kg)	Transmission interval (once in: s)	Capture and release location	Release date	Date of final detection
M699R08	Male	69.9	3.5	20–60	Tributary upstream	26 Apr 2008	20 Nov 2008
M520R08	Male	52.0	2.0	20–60	Tributary upstream	26 Apr 2008	Non
M566R08	Male	56.6	2.1	20–60	Tributary upstream	26 Apr 2008	6 Jun 2008
M839R08	Male	83.9	6.0	20–60	Tributary upstream	26 Apr 2008	4 Sep 2008
F815R08	Female	81.5	6.0	20–60	Tributary upstream	26 Apr 2008	24 Nov 2008
M595R08	Male	59.5	2.3	20–60	Tributary upstream	26 Apr 2008	Non
F560R08	Female	56.0	1.8	20–60	Tributary upstream	26 Apr 2008	28 Nov 2008
M605R08	Male	60.5	2.5	20–60	Tributary upstream	26 Apr 2008	26 Nov 2008
M476R08	Male	47.6	1.4	20–60	Tributary upstream	26 Apr 2008	19 May 2008

M563R08	Male	56.3	2.0	20–60	Tributary upstream	27 Apr 2008	23 Nov 2008
F661R08	Female	66.1	2.6	20–60	Tributary upstream	29 Apr 2008	28 Nov 2008 *
M529R08	Male	52.9	1.7	20–60	Tributary upstream	3 May 2008	Non
U705L08	Unknown	70.5	4.5	20–60	Lake Akkeshi	7 May 2008	24 Nov 2008 *
U741L08	Unknown	74.1	5.0	20–60	Lake Akkeshi	9 May 2008	20 Nov 2008 *
U800L08	Unknown	80.0	6.3	20–60	Lake Akkeshi	9 May 2008	17 Sep 2008
U593L09	Unknown	59.3	2.1	20–60	Lake Akkeshi	13 Apr 2009	24 Nov 2009
U627L09	Unknown	62.7	2.7	20–60	Lake Akkeshi	13 Apr 2009	29 Nov 2009 *
U650L09	Unknown	65.0	3.0	40–90	Lake Akkeshi	20 Apr 2009	7 May 2009
U557L09	Unknown	55.7	1.8	20–60	Lake Akkeshi	24 Apr 2009	28 Nov 2009 *
M663R09	Male	66.3	2.7	20–60	Tributary upstream	26 Apr 2009	27 Nov 2009 *
F685R09	Female	68.5	2.8	20–60	Tributary upstream	26 Apr 2009	29 Nov 2009 *
M606R09	Male	60.6	2.2	20–60	Tributary upstream	26 Apr 2009	27 Nov 2009 *
M584R09	Male	58.4	1.9	40–90	Tributary upstream	26 Apr 2009	Non
F585R09	Female	58.5	1.9	20–60	Tributary upstream	26 Apr 2009	27 Nov 2009 *
F691R09	Female	69.1	2.9	40–90	Tributary upstream	29 Apr 2009	26 Aug 2009

M535R09	Male	53.5	1.6	20–60	Tributary upstream	29 Apr 2009	19 May 2009
F705R09	Female	70.5	3.1	40–90	Tributary upstream	1 May 2009	5 Aug 2009
M605R09	Male	60.5	1.9	20–60	Tributary upstream	1 May 2009	10 Oct 2009 *
M585R09	Male	58.5	2.0	40–90	Tributary upstream	2 May 2009	Non
U645L09	Unknown	64.5	2.9	40–90	Lake Akkeshi	7 May 2009	27 Nov 2009 *
F618R10	Female	61.8	2.6	40–90	Tributary upstream	27 Apr 2010	17 Jun 2010
M705R10	Male	70.5	4.2	40–90	Tributary upstream	27 Apr 2010	12 May 2010
M514R10	Male	51.4	1.9	40–90	Tributary upstream	27 Apr 2010	24 Nov 2010
M510R10	Male	51.0	1.8	40–90	Tributary upstream	29 Apr 2010	20 May 2010
M460R10	Male	46.0	1.5	40–90	Tributary upstream	29 Apr 2010	Non
M625R10	Male	62.5	2.8	40–90	Tributary upstream	1 May 2010	26 Oct 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 Jul 2010
M733R10	Male	73.3	4.5	40–90	Tributary upstream	3 May 2010	2 Dec 2010 *
F638R10	Female	63.8	3.1	40–90	Tributary upstream	3 May 2010	24 Nov 2010
F708R10	Female	70.8	3.6	40–90	Tributary upstream	3 May 2010	5 Jun 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 Dec 2010 *
U650L10	Unknown	65.0	3.8	40–90	Lake Akkeshi	19 May 2010	1 Dec 2010 *
U668L10	Unknown	66.8	3.3	40–90	Lake Akkeshi	19 May 2010	2 Dec 2010 *

5

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

8 * Fish detected the following year

9

10 **Table 2** Station details and dates of deployed and recovered acoustic receivers during 2008–2010. Table modified and reproduced from Honda et
 11 al. (2012), with permission from John Wiley & Sons

Station number	Channel length from the river mouth (m)	Area	Mainstream (M) or tributary (T)	2008		2009		2010	
				Date deployed	Date recovered	Date deployed	Date recovered	Date deployed	Date recovered
1	30,607	1	T	21 Apr	27 Nov	14 Apr	26 Nov	25 Apr	28 Nov
2	22,264	2	T	21 Apr	27 Nov	14 Apr	26 Nov	25 Apr	28 Nov
3	22,224	2	M	21 Apr	27 Nov	10 Apr	27 Nov	24 Apr	1 Jun
4	18,364	3	T	20 Apr	27 Nov	11 Apr	26 Nov	17 Apr	1 Jun
5	17,871	3	M	15 May	20 Nov	10 Apr	27 Nov	24 Apr	1 Dec
6	16,208	3	T			11 Apr	27 Nov	24 Apr	1 Dec
7*	14,729	3	T	20 Apr	26 Nov	11 Apr	27 Nov	19 Apr	29 Nov
8*	14,441–14,483	3	M	20 Apr	26 Nov	11 Apr	27 Nov	19 Apr	1 Dec
9*	13,901	4	M	20 Apr	26 Nov	10 Apr	27 Nov	19 Apr	29 Nov
10*	13,604	3	T	20 Apr	26 Nov	11 Apr	27 Nov	19 Apr	1 Dec

11*	12,958	4	M	20 Apr	26 Nov	10 Apr	27 Nov	19 Apr	29 Nov
12*	11,865	4	M			10 Apr	27 Nov	19 Apr	29 Nov
13	11,444	4	M			19 May	27 Nov		
14*	11,235	4	M	18 Apr	24 Nov				
15*	10,654	4	M			8 Apr	27 Nov	16 Apr	29 Nov
16	9,795	4	M			19 May	27 Nov		
17*	9,128	4	M	18 Apr	24 Nov	8 Apr	27 Nov	16 Apr	29 Nov
18	8,285	4	T	19 Apr	23 Nov	9 Apr	29 Nov	17 Apr	31 May
19*	7,553	5	M	18 Apr	24 Nov	8 Apr	27 Nov	16 Apr	29 Nov
20	6,744	5	T	19 Apr	23 Nov	9 Apr	29 Nov	08 Apr	2 Dec
21*	6,484	5	M	18 Apr	24 Nov				
22*	5,618–5,883	5	M	18 Apr	24 Nov	8 Apr	27 Nov	16 Apr	29 Nov
23*	4,494–4,672	5	T	18 Apr	24 Nov	9 Apr	29 Nov	12 Apr	2 Dec
24*	4,590	5	M	19 Apr	23 Nov	8 Apr	29 Nov	16 Apr	28 Nov
25*	3,807–3,895	6	M	19 Apr	23 Nov	8 Apr	29 Nov	12 Apr	2 Dec
26*	2,542	6	M	19 Apr	23 Nov	8 Apr	29 Nov	12 Apr	2 Dec

28	1,156	6	T			14 Apr	29 Nov	12 Apr	2 Dec
29*	870–1,022	6	M	19 Apr	23 Nov	9 Apr	29 Nov	12 Apr	2 Dec
30*	0	7				13 Apr	29 Nov	23 Apr	1 Dec
31	-2,754	7		23 Apr	25 Nov				
32	-3471	7		21 Apr	25 Nov	13 Apr	30 Nov	23 Apr	1 Dec

12

13 * Stations that were used to estimate movement distances of each tagged fish in areas 4–6 in the mainstream of the Bekanbeushi River system

14

15

16 **Table 3** Channel distances (per station) and mean distances between stations among areas 4–6 in the mainstream of the Bekanbeushi River
 17 system during 2008–2010

	Area	2008	2009 and 2010
Covered channel distance (m)	4	6,242	6,242
	5	3,888	3,888
	6	3,090	3,242
Channel distance per station (m)	4	1,561	1,248
	5	972	1,296
	6	1,030	1,081
Mean (\pm SD) distance between stations (m)	4	1,591 \pm 593	1,193 \pm 247
	5	988 \pm 107	1,482 \pm 267
	6	1,437 \pm 118	1,469 \pm 288

18

19