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Interactions between fish and angler behaviour affect species-specific catchability of sympatric native charr and two introduced trout

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Running title: Catchability of endemic charr and introduced trout

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Abstract

Catchability is a key determinant of fishing pressure, and plays an important role in the management of recreational fisheries. We investigated the catchability of three sympatric salmonid species in a recreational fishery in Lake Shikaribetsu, Japan—the endemic Miyabe charr (*Salvelinus malma miyabei*), introduced masu salmon (*Oncorhynchus masou*), and introduced rainbow trout (*O. mykiss*)—using a combination of stock assessment and angler survey data. Catchability differed among species, angling gear, and the interaction between these two, even when a similar fishing gear was used. Because of its migratory behaviour and fishing gear restrictions, the catchability of Miyabe charr was the lowest of these species, which became lower as fish density was lower. Conversely, the density-dependent changes of the catchability were not detected in masu salmon which few anglers targeted specifically. Rainbow trout catchability by fly anglers was the highest, possibly because the fishing tactics of fly anglers targeting this species were tailored to its foraging behaviour. We regarded differences in catchability among these three salmonids to be related to differences in fish and angler behaviours. These results indicate that behavioural characteristics of both fish species and anglers can cause different fishing pressure in a single recreational fishery targeting multispecies fish via interspecific catchability, and they should be taken into account for their management.

Keywords: angling, catchability, conservation, Miyabe charr, recreational fishery

1. Introduction

Inland fish stocks are predominantly exploited by recreational fisheries, especially in industrialised countries (Arlinghaus et al., 2002; Cowx et al., 2010). Although recreational fishing is a leisure-based activity (in that it is not for economic profit), it plays an important role in enhancing the social and economic value of fish populations because of the high level of economic activity associated with it (Arlinghaus et al., 2002, 2017; Ditton et al., 2002). While recreational fishing can impact fish populations (Grimm, 2004) and even lead to population collapses because of poor angler self-control (Post et al., 2002), data from recreational anglers also can be used to monitor fish stocks (Vøllestad et al., 2009; Pinder et al., 2015; Yoshiyama et al., 2017) and contribute to their conservation. To achieve this, angling pressure must be managed to ensure sustainable recreational fisheries.

Recreational fisheries are integrated socio-ecological systems that involve interactions between human activity and fish behaviours (Arlinghaus et al., 2017). In this system, the catch is an important link between ecological (i.e. fish stock) and social (i.e. anglers) components (Johnston et al., 2013; Arlinghaus et al., 2017). The catch is a product of q (catchability coefficient), X (fishing effort) and N (fish density) (Hilborn and Walters, 1992), with fishing effort also dependant on the quantity of anglers and fishing gear. Assuming constant fishing effort and also constant population density N, q determines total catch. In recreational fisheries, multiple sympatric species are commonly targeted in single fisheries (e.g., Tsuboi et al., 2008, 2021; Hunt et al., 2014; Roth et al., 2018). In such a case, the impact on each fish stock by recreational fisheries can be different among fish species due to different species-specific catchability, although input fishing effort is the same. A lack of knowledge about catchability can lead to population

66 collapse, despite the fishing effort being known (Post et al., 2002; Erisman et al., 2011).
67 Therefore, evaluating species-specific catchability is essential for the management of
68 individual species in single recreational fisheries (Johnston et al., 2013; Tsuboi et al.,
69 2021).

70 Species-specific catchability is assumed to be determined by the nature of fish
71 ecology and their fisheries, including fish behaviour, fishing gear, and angler behaviour.
72 Vulnerability to angling is determined by a complex function of not only fish biology,
73 such as movement, foraging behaviour, and physiological traits, but also fishing gear
74 selectivity (Lennox et al., 2017). These biological traits and fishing gear selectivity can
75 differ among fish species, resulting in species-specific catchability. For example, Koeck
76 et al. (2019) found that rainbow trout were more vulnerable to angling than brown trout
77 when using natural bait, but no difference using an artificial lure. They assumed that this
78 result was due to physiological traits for stress-resilience. In addition, Tsuboi and Morita
79 (2004) reported that stream-dwelling charr was more vulnerable than sympatric rainbow
80 trout when using natural bait but less vulnerable when using artificial flies. They assumed
81 this difference in catchability was caused by the difference in foraging behaviour in charr
82 and rainbow trout and fishing gear selectivity (natural bait with sinker drift near the
83 bottom and artificial fly drift on the water's surface). Furthermore, an abiotic environment,
84 such as water temperature, can influence catchability through fish behaviour (Lennox et
85 al., 2017). In addition to this knowledge, angler behaviour can affect species-specific
86 catchability because they will optimise their fishing gear and tactics to target fish. In order
87 to understand species-species catchability, the relationship between fish, angler behaviour
88 and some environmental factors should also be considered.

89 Usually, catchability coefficient q is assumed to be invariable (i.e. catch- per- unit-

effort (CPUE) is proportional to fish density). However, it is known that the catchability coefficient can vary depending on fish density in the actual fishery (Hilborn and Walters, 1992; Erisman et al., 2011; Ward et al., 2013; Alós et al., 2019). Previous studies have reported that density dependence of catchability can be caused by both fish and angler behaviour. For example, when anglers target fish spawning aggregation, their catchability become higher as fish density decreases (Erisman et al., 2011). In addition, Ward et al. (2013) reported density dependence of catchability due to angler behaviour. When anglers prefer catching larger fish to catching more fish, their catchability can decrease as fish density increase, resulting in density-dependent catchability (Ward et al., 2013). In these cases, CPUE remains higher than the rate of decline of fish density, called "hyperstability". Conversely, CPUE can decrease greater than the rate of decline of fish density, called "hyperdepletion" (Hilborn and Walters, Alós et al., 2019). Hyperdepletion occurs when catchability increases faster than fish abundance increases (Hilborn and Walters, 1992; Ward et al., 2013; Alós et al., 2019). Alós et al. (2015) pointed out that fish behaviour plays a key role in the process of hyperdepletion in CPUE, but its mechanisms are less known than hyperstability (Alós et al., 2019). When catchability depends on fish density (i.e. hyperstability or hyperdepletion occur), CPUE may not accurately reflect fish density because CPUE is not proportional to fish density. Especially, hyperstability sometimes leads collapse of fish populations because CPUE cannot indicate decreasing fish population (Post et al., 2002; Erisman et al., 2011). Considering these previous studies, catchability is assumed to be determined by fish and angler behaviour and their complex interaction (Post, 2013; Ward et al., 2013; Lennox et al., 2017, Alós et al., 2019). Therefore, the relationship between catchability and its determinant such as fish behaviour and angler behaviour can help the management of the recreational fishery by

114 warning the hyperstability or hyperdepletion. However, direct estimation of the
115 relationship between CPUE and fish density is difficult.

116 Although recreational anglers sometimes target endangered species, if this fishing is
117 controlled then catch data can be used as a cost-efficient conservation tool (Granek et al.,
118 2008; Pinder et al., 2015; Cooke et al., 2016; Yoshiyama et al., 2017). For example,
119 recreational anglers have provided essential data for monitoring endangered fish
120 populations (Pinder et al., 2015; Yoshiyama et al., 2017), and by doing so the costs of
121 stock assessment have been reduced. However, sustainable fishing pressure is essential
122 to enhance the value of recreational fishery data for conservation (Cooke et al., 2016). To
123 achieve sustainable fishing levels, understanding the species-specific catchability of
124 target fishes is necessary for controlling fishing pressure.

125 Lake Shikaribetsu is a naturally dammed lake wherein the endemic, critically
126 endangered Miyabe charr *Salvelinus malma miyabei* inhabits (Maekawa, 1984). Miyabe
127 charr is listed as "Endangered" by the Ministry of the Environment (Japan Red List). Both
128 masu salmon *Oncorhynchus masou* and rainbow trout *O. mykiss* also inhabit Lake
129 Shikaribetsu (Maekawa, 1977), having been introduced into it (Hokkaido salmon
130 hatchery, 1981; Town of Shikaoi, 1994). These introduced trout are breeding naturally,
131 not stocked for more than 30 years (Hokkaido salmon hatchery, 1981). Recreational
132 anglers target these charr and trout in a single fishery that regulates the permissible fishing
133 periods (times of day, and dates), maximum number of daily anglers, and gear. The
134 recreational fishery in Lake Shikaribetsu has been used to effectively monitor and
135 conserve Miyabe charr (Yoshiyama et al., 2017, 2018). Populations of introduced masu
136 salmon and rainbow trout can also be monitored using angler catch data, because they
137 may threaten Miyabe charr through competition for food or hybridisation (Koizumi et al.,

2005; Baxter et al., 2007). Due to the different behaviour of target fish, catchability and density dependence can differ among target fish even if the similar fishing gear is used (e.g., Tsuboi and Endo, 2008; Tsuboi et al., 2021). Furthermore, angler behaviour due to their preference can affect catchability because recreational anglers in Lake Shikaribetsu have a species-specific preference (Yoshiyama et al., 2018). This background makes us assume that species-specific catchability is affected by fish and angler behaviour and their interaction. Evaluating species-specific catchability is required to assess these charrs and trout using catch data of anglers.

Here, we report the species-specific catchability of each of these species in Lake Shikaribetsu using a combination of stock assessment and angler survey data, and compare their catchability using different fishing gear (lures or flies). We attribute differences in catchability to differences in fish ecology, angler behaviour, and their interaction.

2. Methods

2-1. Study site

Lake Shikaribetsu, in the mountainous central Hokkaido Island, Japan (Fig. 1), has a surface area of 360.4 ha, an average depth of 56 m, and three small inlet streams and one outlet stream. Two of these inlet streams provide spawning habitat for Miyabe charr. Fishing in Lake Shikaribetsu is permitted only in its southern half (195.8 ha) (fishing is prohibited in the northern part and inlet streams throughout the year). The outlet stream was dammed in 1953 to regulate water levels for hydroelectric power generation (Maekawa, 1977).

Fishing is limited to 50 d annually, in two seasons: a “first stage” from early June to

early July (approximately 33 d), and a “second stage” from late September to early October (approximately 17 d). Fishing license sales are limited to 50 persons per day, with anglers usually having to advance book through a website or by telephone to purchase a license. Anglers are limited to using a single fishing rod, with gear restricted to an artificial lure or a fly with a single-barbless hook per rod. Anglers can use a rowing boat for fishing, but engines (combustion or electric) are prohibited, as are anchors. Fishing is limited to between the hours of 6:00 and 15:00 during the first stage. All anglers must return to the access point each day by 15:00. Although fishing is permitted from some areas of shoreline, anglers must approach these areas by boat. Since 2016 an additional onshore fishing area was established along the northeast shoreline, where anglers must approach via a ferry service. Approaching using their own lowing boat is prohibited.

Because only a single access point exists for Lake Shikaribetsu, the stock manager can regulate the numbers of daily anglers and collect all catch record sheets, upon which anglers must report all species, their size, and the location where they were caught. The daily bag limit is set at zero for Miyabe charr (i.e. catch-and-release is required), and a mix of up to 10 masu salmon and rainbow trout.

2-2. Estimating population size

Surveys of population size using tags have occurred for each salmonid species from early June to July 2015 and 2016. Procedures were followed detailed by Yoshiyama et al. (2017), in which tagging mortality and tag loss were assessed to be negligible. Because Lake Shikaribetsu is effectively a closed system, tagging can be used to efficiently estimate population size (Hokkaido fish hatchery, 1995; Yoshiyama et al., 2017). Each of

186 Miyabe charr, masu salmon, or rainbow trout was caught by lure or fly by a researcher
187 (first author) and management staff. Upon capture, the hook was removed, and a
188 numbered anchor tag (50 mm, Toska-Bano'k Co., Ltd., Tokyo) was inserted into the
189 dorsal musculature between the dorsal and adipose fin by tagging gun before release.
190 Tagging and handling techniques follow Brownscombe et al. (2017) and Yoshiyama et al.
191 (2017); deeply injured fish were not tagged. The release year was identified by tag colour.
192 Recapture records of tagged fish from anglers were collected using recapture record
193 sheets distributed with catch record sheets. Anglers were requested to record the length,
194 capture position, and tag number and its colour of any tagged fish on the recapture record
195 sheet.
196 Population size was estimated using tag-and-release data, the total catch of anglers,
197 and the number of tagged fish recaptured by anglers. The Schnabel method with an
198 adjustment for small sample size was first used to calculate population size, which
199 accuracy was confirmed by Yoshiyama et al. (2017). The model description of the
200 Schnabel method is as follows:
201

$$N' = \frac{\sum M_i n_i}{\sum m_i + 1}, \quad (1)$$

$$\mathrm{SE} = N' \sqrt{\frac{1}{\sum m_i + 1} + \frac{2}{(\sum m_i + 1)^2} + \frac{6}{(\sum m_i + 1)^3}}, \quad (2)$$

202

203 where N' is the population size from early June to July (first stage), M_i is the number of
204 tagged-and-released fish on day i, m_i is the number of recaptured tagged fish on day i,
205 n_i is the number of fish caught by all recreational anglers on day i, and SE is the standard
206 error (Begon, 1979). Using the result of population assessment by this method, fish

207 density N was calculated as follows:

208

$$N = \frac{N'}{S} \quad (3)$$

209

210 where N' is the estimated population size using the tagging method, and S is the lake water
211 surface area in which the estimated population resides. Since the movement of tagged fish
212 showed a different range by fish species (see the result), we used different values of lake
213 water surface area according to fish species following the movement of recaptured tagged
214 fish. The water surface area of the lake was calculated using ArcGIS version 10.2.2 (ESRI
215 Co. Ltd).

216

217 2-3. Angler survey

218 Interviews with randomly selected anglers were conducted to investigate their
219 behaviour, following procedures detailed by Yoshiyama et al. (2018). Anglers were asked
220 whether they had used a lure or fly, the catch of each species, and their primary target
221 species. Data regarding catch were also obtained during interviews because catch by
222 fishing gear was not sufficiently reported on mandatory catch record sheets. Since almost
223 all anglers started fishing within 1 hour from start fishing time (6:00 am), the interview
224 survey was started near 14:00, and the difference of fishing effort time is negligible across
225 the interviewed anglers.

226

227 2-4. Data analysis

228 In this study, the number of fish that anglers caught was used as catch, and the number
229 of anglers was used as fishing effort, respectively. Consequently, CPUE was calculated

as the number of fish per angler in a day. Because the relationship between total catch C, fishing effort X, and fish density N can be described by equation (4), the catchability coefficient q can also be described by equation (5) through the following transformation:

$$C = qXN \tag{4}$$

$$q = \frac{C}{X \cdot N} \tag{5}$$

Therefore, we used a log-linear model modifying catch-model analysing CPUE that uses catch data as the response variable with offset term (Maunder and Punt, 2004). We first tested for differences in catchability of species, fishing gear, and their interaction using a log-linear model with a Poisson distribution, as follows:

$$\frac{C}{(X \cdot N)} \sim \exp\left(sp + gear + sp \times gear\right) \tag{6}$$

where X is the number of anglers, N is fish density, *sp* is the targeted fish species (Miyabe charr or masu salmon or rainbow trout), and *gear* is gear type (lure or fly). The total catch of anglers was set as a response variable, and the product of the number of anglers and fish density (denominator of left hand) was set as the offset term. Data for total catch C and the number of anglers X were obtained from interviews. Model selection was performed based on information criterion. A model with the lowest criterion value was considered the best model, and any models whose criterion value was within 2 of the best model were also considered substantially supported models (Burnham and Anderson, 2002). This analysis was performed for rainbow trout data for only 2015 because too few

250 tagged rainbow trout were recaught in 2016 to estimate fish density.

251 While catchability can depend on fish density (Hillborn and Walters, 1992), it is also
252 affected by water temperature in Lake Shikaribetsu (Yoshiyama et al., 2017). Thus, we
253 looked for differences in catchability by year and water temperature for Miyabe charr and
254 masu salmon. For Miyabe charr, data for population size and angler catch in 2014 were
255 sourced from Yoshiyama et al. (2017, 2018). Data for water temperature were obtained
256 from logs recorded by management staff (Yoshiyama et al., 2017).

257 Differences in catchability by fishing year, gear type of anglers, and water
258 temperature were analysed using a generalised linear model with a negative binomial
259 distribution:

260

$$\frac{C}{(X \cdot N)} \sim \exp\left(year + gear + W.Temp + gear \times W.Temp\right) \qquad (7)$$

261

262 where X is the number of anglers, N is fish density, *year* is the opening year, *gear* is the
263 gear type of anglers (lure or fly), and *W.Temp* is water temperature. In this model, the total
264 daily catch of anglers was set as a response variable, and the product of the total number
265 of daily anglers and fish density (denomination of left hand) was set as an offset term.
266 Model selection was performed based on information criterion as same as above analysis.

267 Akaike's Information Criterion (AIC) or Bayesian Information Criterion (BIC) are
268 commonly used as information criteria in the model selection process. Comparing them,
269 AIC tends to select a more complex model than BIC with a large sample size (Schwarz,
270 1978). Therefore, we used BIC for model selection because the dataset for analysing the
271 difference in catchability among years has a relatively larger sample size (22 times greater
272 for Miyabe charr data and 16 times for masu salmon data) than that for analysing species-

273 specific catchability. All analysis about catchability was performed using R version 4.0.5
274 (R core team, 2021), with packages “MASS” and “MuMIn” (Venables and Ripley, 2002;
275 Bartoń, 2020).
276
277 **3. Results**
278 3-1. Population estimates: Miyabe charr
279 Of 450 Miyabe charr tagged and released from early June to July in 2015, 18 of 7092
280 caught by anglers during this same period were tagged fish. Of these, one was recaught
281 soon after release, which we excluded when calculating population size because our
282 model assumes that tagged fish can be recaptured by anglers from the day following
283 release. Accordingly, we estimated the population of Miyabe charr from early June to July
284 2015 to comprise 92,800 ± 23,250 fish (estimate ± standard error, Table 1a). No tagged
285 fish was recaptured twice in the year of its release.
286 Of 336 Miyabe charr tagged and released from early June to July 2016, 7 of 3088
287 fish caught by anglers were tagged. Accordingly, we estimated the population of this
288 species in 2016 to comprise 83,120 ± 34,080 fish (estimate ± standard error, Table 1a).
289 No tagged fish was recaptured twice in its year of release.
290 All tagged fish were identified by their reported tag number and had dispersed
291 throughout the lake (Figs. 2a, b), consistent with a study in 2014 (Yoshiyama et al., 2017).
292 For this reason, we assumed that our estimate for the Miyabe charr population size applied
293 to the entire lake. Because the surface area of Lake Shikaribetsu is 360.4 ha, we estimated
294 Miyabe charr density within it to be 257.5 ± 64.5 fish/ha in 2015 and 230.6 ± 147.8 fish/ha
295 in 2016 (estimate ± standard error, Table 1a). Additionally, we estimated the density of
296 Miyabe charr in 2014 to be 292.2 ± 143.5 fish/ha using data for population size (105,300

297 ± 51,700 fish) from Yoshiyama et al. (2017).

298

299 3-2. Population estimates: masu salmon

300 Of 67 masu salmon tagged and released in 2015, 8 of 938 that were caught by anglers
301 were tagged. Accordingly, we estimated the masu salmon population size for 2015 to
302 comprise 2,910 ±1,000 fish (estimate ± standard error, Table 1b). In 2016, 38 masu
303 salmon were tagged and released, of which 8 of 740 caught by anglers this year were
304 tagged. Accordingly, we estimated the population size of masu salmon in 2016 to
305 comprise 1,690 ±640 fish (Table 1b). No tagged fish was recaptured twice within the year
306 of its release.

307 Because 6 of the 8 tagged fish for which complete tag data were reported were caught
308 in 2015 and 2016 (for two fish, the tag number was not reported) had dispersed throughout
309 the lake (Fig. 3a,b), we assumed that our population estimate for this species, 7.5 ±2.8
310 fish/ha in 2015 and 4.7 ±1.8 fish/ha in 2016 (estimate ± standard error), applied to the
311 entire lake area.

312

313 3-3. Population estimates: rainbow trout

314 A total of 65 rainbow trout were tagged and released in 2015, but the anchor tag of
315 one fish accidentally detached when an angler caught and then released it. For this reason,
316 we reduced the total number of tagged-and-released fish to 64 after the day this incident
317 occurred. Of the 732 rainbow trout caught by anglers this year, 17 were tagged. Two
318 tagged rainbow trout individuals (#104 and #171) were recaptured twice, thus, the 17
319 recaptured tagged fish included 15 individuals. Accordingly, we estimated the rainbow
320 trout population in 2015 to comprise 1,620 ± 410 fish (estimate ± standard error, Table

1c). Because 12 recaptured tagged fish (10 individuals) with complete recorded tag number details had moved only short distances along the shoreline in the fishing area (Fig. 4a), we assumed that our estimate of population size applied only to the fishing area (southern half of the lake, 195.8 ha). Accordingly, we estimated the density of rainbow trout for 2015 to be 8.3 ± 2.1fish/ha (estimate ± standard error).

Of 42 tagged-and-released rainbow trout in 2016, only 3 individuals were recaptured (Table 1c), including 2 individuals from near where they were tagged and released (Fig. 4b). Thus, we did not use tag and recapture data for 2016 to estimate population size.

3-4. Results of angler survey, CPUE, and measurement of water temperature

The 398 anglers interviewed between 2015 and 2016 included 246 who had fished with lures (lure angler) and 107 who had fished with flies (fly angler) (Fig. 5), and 44 anglers that had fished with both lures and flies. We excluded data for these latter lures + fly anglers because the time allocated to each fishing style was not recorded. We also excluded data from one angler who used artificial bait.

Most lure anglers (204, 73%) targeted Miyabe charr; 55 (20%) anglers targeted rainbow trout (Fig. 6a). Similar numbers of fly anglers targeted Miyabe charr and rainbow trout (Fig. 6b), with 62 (48%) of 130 fly anglers targeting Miyabe charr and 61 (47%) targeting rainbow trout; 12 anglers targeted two or all species (e.g., Miyabe charr and rainbow trout, all target fish of Miyabe charr, masu salmon and rainbow trout). Anglers targeting multiple species were counted as having targeted each species (i.e. they were double counted).

Questionnaire responses in 2015 revealed 122 lure anglers to have caught 1592 Miyabe charr, 162 masu salmon, and 63 rainbow trout, and for 50 fly anglers to have

345 caught 285 Miyabe charr, 117 masu salmon, and 201 rainbow trout. The number of lure
346 anglers by their catch rate of Miyabe charr or masu salmon showed that anglers who
347 caught 1-5 fish were the highest frequency (Fig. 7a). In addition, more than 15 anglers
348 had more than 11 catch rate of Miyabe charr. That of rainbow trout showed that anglers
349 who caught no rainbow trout were the highest frequency. The number of fly anglers by
350 their catch rate of each targeted fish showed almost the same frequency as that of lure
351 anglers, except fly anglers who caught 1-5 rainbow trout was the highest (Fig. 7b). CPUEs
352 of Miyabe charr, masu salmon, and rainbow trout on lures were 13.0, 1.3, and 0.5
353 fish/angler-day, respectively, while those on the fly were 5.7, 2.3, and 4.0 fish/angler-day,
354 respectively (Table 2a).
355 In 2016, 124 lure anglers caught 719 Miyabe charr, 162 masu salmon, and 92 rainbow
356 trout, and 57 fly anglers caught 164 Miyabe charr, 100 masu salmon, and 157 rainbow
357 trout. The number of anglers by their catch rate of Miyabe charr of masu salmon in 2016
358 showed almost the same frequency as that in 2015 (Fig. 7c, d). CPUEs of Miyabe charr,
359 masu salmon, and rainbow trout on lures were 5.8, 1.3, and 0.7 fish/angler-day,
360 respectively, while those on flies were 2.9, 1.8, and 2.8 fish/angler-day, respectively
361 (Table 2b).
362 Water temperature ranged from 9 to 18 °C from June to July 2014-2017. The
363 minimum temperature was 9 °C, and the maximum was 18 °C. Water temperature was
364 the highest in 2014 (15.5 °C Tukey HSD test; $p<0.001$ for 2015 and 2016), and similar
365 to 2015 (13.1 °C) and 2016 (12.6 °C, Tukey HSD test; $p=0.549$).
366
367 3-5. Differences in catchability
368 Catchability coefficients of Miyabe charr, masu salmon, and rainbow trout on lures

were 0.051, 0.165, and 0.071 ha/angler, respectively, while those on flies were 0.022, 0.290, and 0.486 ha/angler, respectively. Analysis of catchability coefficients among target species revealed that a model including explanatory variables of species, angling gear, and their interaction had the lowest BIC value. (Table 3, Fig. 8). The catchability coefficient of Miyabe charr by lure anglers was higher than that for fly anglers, and that for masu salmon and rainbow trout was higher for fly anglers than it was for lure anglers (Table 4, Fig. 8).

The best model analysing Miyabe charr catchability included year, fishing gear, and water temperature as explanatory variables (Table 5a). The catchability coefficient decreased from 2014 to 2016, indicating that it was higher at higher fish densities (Table 6, Fig. 9). High water temperature negatively affected the Miyabe charr catchability coefficient (Table 6a), as reported by Yoshiyama et al. (2017); the catchability coefficient of Miyabe charr was also higher among lure anglers than fly anglers (Table 6a, Fig. 9).

The catchability coefficient of masu salmon differed significantly among fishing gears and water temperatures (Table 4b). High water temperature also negatively affected the masu salmon catchability coefficient (Table 4b), with that for fly anglers being higher than for lure anglers.

4. Discussion

We have reported the catchability coefficients of three sympatric salmonid species to differ by species and fishing gear. While it is known that catchability by angling can differ because of ecological factors and angler behaviour (Post et al., 2013; Ward et al., 2013; Lennox et al., 2017), we additionally consider the interaction between the two.

393 4.1 Species-specific catchability and its factor

394 4.1.1 Miyabe charr

395 Miyabe charr catchability on both lures and flies was the lowest of the three species
396 (lure; 0.05 ha/angler, fly; 0.02 ha/angler), likely because of Miyabe charr and angler
397 behaviours. Miyabe charr migrates between 0 and 20 m depth throughout the lake and
398 feeds on zooplankton (Kubo, 1968). Because boat motors and anchors are prohibited,
399 anglers targeting Miyabe charr must first locate and then remain at the point within the
400 range of a school while drifting on a rowboat, rendering this species more difficult to both
401 locate and catch. Anglers must also typically sink their lure or fly deeper in the water
402 column than they would if they were targeting other species, increasing the amount of
403 time required to present a lure or fly to a school of charr, particularly for fly anglers
404 (because lure fishing gear is more suitable for fishing deeper in the water column).
405 Consequently, Miyabe charr behaviour and fishing regulations contribute to its low
406 catchability. This result is consistent with a previous study on stream-dwelling Dolly
407 Varden (Tsuboi et al., 2021). Because Miyabe charr is a subspecies of Dolly Varden, they
408 might be less vulnerable to angling.

409 In addition to our result, previous records indicate that the catchability using natural
410 bait is much higher than that of artificial lures or flies. In 1995, there was no prohibition
411 on the use of natural bait and harvesting of Miyabe charr, and the average harvest of this
412 species was 5.88 fish/angler-day (Hirata, 1997). During this time, the estimated
413 population size of Miyabe charr was 13,880 fish (Hokkaido salmon hatchery, 1995).
414 Using these records, catchability in 1995 is estimated to be 0.15 ha/angler, 3 times higher
415 than in 2015. Additionally, catchability in 1995 could increase in the additional event fish
416 were caught-and-released or discarded. Consequently, Miyabe charr catchability on

417 natural baits would appear higher than on lures or flies. This result would be due to the
418 fishing technique that bait fishing can suspend the hook in the deep-water column that
419 Miyabe charr migrates easily.
420
421 4.1.2 Masu salmon
422 Masu salmon catchability (0.16 ha/angler) was the highest of the three species for
423 lure anglers, but its catchability was lower than for fly anglers (0.29 ha/angler). Because
424 questionnaire surveys revealed few anglers targeted masu salmon (lure anglers 8%, fly
425 anglers 3%), most masu salmon were probably "bycaught" when anglers were targeting
426 Miyabe charr or rainbow trout. Landlocked masu salmon were the most vulnerable of the
427 three species to being caught on a lure because their diet usually comprises small nekton
428 such as Japanese smelt *Hypomesus nipponensis* (Osanai, 1962). Additionally, anglers
429 targeting Miyabe charr might also accidentally hook masu salmon.
430 Landlocked masu salmon usually prefer water temperatures of ~15°C (Osanai, 1962),
431 which in Lake Shikaribetsu from early June to July usually occur at depths shallower than
432 5 m (Hokkaido salmon hatchery, 1973–75, 1977, 1981, 1982, 1987; NPO Hokkaido Trout
433 Fishing Union, unpublished data). Conversely, Miyabe charr usually inhabits waters near
434 the thermocline, typically between 5 and 15 m depth (Kubo, 1967). Because masu salmon
435 usually inhabit shallower water than Miyabe charr, they could be hooked by lure anglers
436 during lure retrieval from deeper waters. Because fly-fishing gear typically traces
437 shallower than lure-fishing gear, fly anglers might also accidentally hook masu salmon.
438 Therefore, masu salmon are more vulnerable to being bycaught by fly anglers than lure
439 anglers.
440

441 4.1.3 Rainbow trout

442 Rainbow trout catchability on flies (0.49 ha/angler) was the highest for all species
443 and gear combinations. We posit that this is because the fishing tactics of fly anglers are
444 tailored to the behaviour of rainbow trout. Almost half of all fly anglers targeted rainbow
445 trout migrating along the shoreline using artificial flies that resembled insects—the
446 primary prey of rainbow trout in Lake Shikaribetsu (Hokkaido salmon hatchery 1978).
447 Consequently, fly anglers could efficiently catch rainbow trout in shoreline areas,
448 resulting in a high catchability coefficient. Lure fishing may be less suitable for rainbow
449 trout because lures typically imitate nekton such as minnows. Rainbow trout are more
450 catchable than other salmonids (e.g., Koeck et al., 2019; Tsuboi et al., 2021), and they
451 might be more vulnerable to angling when gear types suit their diet. In addition, perhaps
452 the domestication effect based on catchable genetic traits to angling may remain over 50
453 years since introduction (Philipp et al., 2009; Lennox et al., 2017; Tsuboi et al., 2021).
454

455 4.1.4 Effect of uncertainty

456 When comparing catchability among species in this study, the effect of uncertainty
457 caused by population estimation should be considered. First, the catchability coefficient
458 varies depending on assumptions made when calculating fish density (i.e. the area of the
459 lake inhabited by the species). For rainbow trout, we calculated the population size for
460 the southern half of the lake's fishing area. Had we calculated this catchability coefficient
461 in the belief that the estimated population size corresponded to the entire lake, this
462 coefficient would be 1.8 times higher. However, rainbow trout catchability remains the
463 second highest for lure anglers and the highest for fly anglers. Therefore, we regard our
464 result as reasonable regardless of our assumption regarding the area inhabited by this

465 species to calculate fish density.

466 Second, our result includes uncertainty due to the small sample size of tagging
467 method. To assess this uncertainty, we re-analysed the difference in the catchability using
468 the dataset that the difference between three fish populations is the least within the
469 standard error of estimate (Miyabe charr; 69,550 fish, masu salmon; 3,910 fish, rainbow
470 trout; 2,030 fish respectively). As a result, its result was consistent with that of the original
471 dataset. Furthermore, this result was also invariable regardless of the assumption of the
472 area of the lake inhabiting the population. Therefore, our result about the difference in the
473 catchability by fish species was assumed to be robust for the uncertainty of tagging
474 method.

475 Third, the difference of catchability among target species can occur logistically
476 when the catch of anglers reaches the maximum number of fish they can catch in a day
477 because fish density differs among target species. For example, if the most anglers have
478 time to capture in a day is 10, regardless of fish species, catchability can be relatively low
479 for high-density fish when most anglers catch their maximum number of fish. However,
480 such a situation is unlikely in lake Shikaribetsu. Although bag limit is set in the regulation,
481 anglers can catch and release all fish with no limit during the fishing permitted time (6:00
482 – 15:00). In fact, a total of 34 (28%) lure anglers caught more than 15 Miyabe charr, but
483 few anglers caught more than 15 masu salmon or rainbow trout. These results indicate
484 that almost all anglers were not reached the maximum number of fish that anglers can
485 catch. Therefore, we assumed that the difference in catchability among fish species in our
486 study was caused by fish and angler behaviour, not logistical, due to maximum catch that
487 angler number of fish they can catch in a day.
488

489 4.2 Difference in catchability among years

490 4.2.1 Miyabe charr

491 The Miyabe charr catchability coefficient was high in a high fish-density year,
492 possibly because of fish and angler behaviours. Miyabe charr usually migrates throughout
493 the lake and forms schools, which anglers must first locate and then chase from a rowboat,
494 so the catchability of this species increases as fish density increases (the probability of an
495 angler encountering a school increases with fish density). This phenomenon is known as
496 "hyperdepletion," where catchability decreases as fish density decreases (Hillborn and
497 Walters, 1992). Hyperdepletion may benefit Miyabe charr stocks because fishing pressure
498 decreases when population levels are low, although an increase in CPUE does not
499 necessarily indicate a corresponding increase in the Miyabe charr population.

500 Our result that the catchability of Miyabe charr differed among years may remain
501 rather high uncertainty due to the wide range of standard error of the estimate. A
502 modelling approach is needed to clarify the relationship between catchability and fish
503 density (Hillborn and Walters, 1992; Alós et al., 2019). Therefore, more accumulation of
504 data about catch and population is needed to apply this approach. Nevertheless, our result
505 can suggest the possibility of hyperdepletion of CPUE of Miyabe charr for the stock
506 monitoring, because the mechanism constructing the catchability of Miyabe charr can be
507 assumed to cause hyperdepletion.

508

509 4.2.2 Masu salmon

510 Masu salmon catchability did not differ significantly over the years. A basic
511 supposition of stock assessment is that catchability is invariable, with CPUE being
512 proportional to fish density (Hillborn and Walters, 1992). This may apply to masu salmon

513 catchability because we believe that this species 1) migrates throughout the lake and does
514 not form large schools like Miyabe charr, which likely distribute uniformly all over the
515 lake and 2) most individuals are assumed to be bycatch from anglers targeting other
516 species, therefore anglers unlikely to aggregate to catch masu salmon. As a result, the
517 probability of encountering with lure/fly is assumed to increase as fish density becomes
518 high simply. These behaviours may make masu salmon catchability remain constant,
519 independent of fish density.
520
521 4.2.3 Effect of collinearity effect
522 When comparing the catchability of Miyabe charr and masu salmon over the years,
523 the co-linearity effect between each year and water temperature should be taken care of
524 to understand the result of the analysis. However, the co-linearity effect was assumed to
525 be negligible in our analysis. For Miyabe charr, catchability was the highest in 2014,
526 although high water temperature should reduce catchability. In addition, water
527 temperature in 2015 was similar to that in 2016, which can weaken the co-linearity effect
528 in the model analysing the catchability of masu salmon. Furthermore, the observed water
529 temperature was almost within the range that both Dolly Varden (Miyabe charr is a
530 subspecies of Dolly Varden) and masu salmon prefer for their feeding through each year
531 (Dolly Varden for 8-16℃ and masu salmon for under 24℃, Takami et al., 1997; Misawa
532 et al., 2006; Takami and Sato, 1998). Thus, the difference in water temperature among
533 years was less likely to influence the difference in catchability among the year.
534
535 4.3 Implications for managing endangered fish in a multispecies recreational fishery
536 In order to use recreational fishing as a tool to conserve endangered fish, fishing

pressure must be regulated at a low level (Cooke et al., 2016). Our study demonstrated that catchability among three sympatric salmonid fish could be different, although almost the same fishing gear is used in a recreational fishery. Therefore, the stock manager should use caution for species-specific catchability when endangered fish is included. Conducting stock assessment and collecting catch data of anglers is ideal for evaluating species-specific catchability. However, stock assessment such as tagging study will be difficult in the actual recreational fishery due to effortful and financial cost. Then, investigating factors affecting catchability can be an alternative tool to estimate species-specific catchability, although it may result in qualitative. Factors affecting catchability include not only the fish behaviour, such as migration and prey but also angler preference for targeting fish and detailed fishing tactics (Lennox et al., 2017). Considering this information and knowledge of previous studies about catchability may enable us to estimate relative interspecific catchability. Our result can also contribute to estimating catchability in another waterbody. Furthermore, a mechanistic understanding of how anglers catch fish through estimating catchability can contribute to finding the possibility of hyperstability or hyperdepletion effect. These effects can be a risk of misevaluation of population level using catch data (Post et al., 2002; Erisman et al., 2011; Post, 2013), nevertheless monitoring the population using catch data of anglers is a fundamental work of recreational fishery as a conservation tool (Granek et al., 2008; Pinder et al., 2015; Cooke et al., 2016; Yoshiyama et al., 2017). This finding can contribute to preventing the collapse of the population. Since recreational fisheries are integrated socio-ecological systems integrating fish ecology and angler behaviour (Arlinghaus et al., 2017), investigation based on wide comprehensive insight, including fish ecology, fishing gear and angler behaviour, is essential to controlling fishing pressure.

561

562 4.4 Conclusion

563 We demonstrated that differences in catchability of sympatric endemic charr and two
564 introduced trout are a consequence of interactions between fish and angler behaviour,
565 despite similarities in fishing gear. We report: 1) the catchability of endemic Miyabe charr
566 to be lower than that of introduced trout; 2) that caution must be exercised when
567 monitoring Miyabe charr population size using CPUE because the relationship between
568 CPUE and population size of Miyabe charr may not be proportional as basic theory; and
569 3), interactions between fish and angler behaviours cause that differences in species-
570 specific catchability. These results could enhance the work of the recreational fishery as
571 a conservation tool for the Miyabe charr population in Lake Shikaribetsu. Our findings
572 are the result of fisheries surveys involving the tagging of fish, and those of angler
573 behaviour. Understanding both fish ecology and angler behaviour is essential for the ideal
574 management of this recreational fishery.

575

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582

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Tables

Table 1 Summary of tag-and-release fish, number of caught fish by anglers, and estimated population size. The population size of rainbow trout in 2016 was not estimated due to few recaptured fish.

(a) Miyabe charr

Year	2015	2016
Tag-and-released fish	450	336
Number of caught fish by anglers	7,092	3,088
Number of recaptured fish	17*	7
Estimated population size	92,800	83,120
Standard error	±23,250	±34,080
Corresponding range of estimated population size (ha)	360.4	360.4
Fish density (fish/ha)	257.5	230.6
Standard error	±64.5	±147.8

*Additionary one Miyabe charr was recaught soon after release, which was not included for calculation.

(b) Masu salmon

Year	2015	2016
Number of tag-and-released fish	67	38
Number of caught fish by anglers	938	740
Number of recaptured fish	8	8
Estimated population size	2,910	1,690
Standard error	±1,000	±640
Corresponding range of estimated population size (ha)	360.4	360.4
Fish density (fish/ha)	7.5	4.7
Standard error	±2.8	±1.8

(c) Rainbow trout

Year	2015	2016
Number of tag-and-released fish	65	44
Number of caught fish by anglers	732	325
Number of recaptured fish	17	3
Estimated population size	1,620	-
Standardized error	±410	-
Corresponding range of estimated population size (ha)	195.8	-
Fish density (fish/ha)	8.3	-
Standardized error	±2.1	

Table 2 Number of anglers, catch by anglers, and CPUE by target fish and fishing gear in 2015 from the questionnaire.

(a) 2015

Fishing gear	No. of anglers (person)	Target fish	Catch	CPUE (fish/angler-day)
Lure	122	Miyabe charr	1,592	13.0
		Masu salmon	162	1.3
		Rainbow trout	63	0.5
Fly	50	Miyabe charr	285	5.7
		Masu salmon	117	2.3
		Rainbow trout	201	4.0

(b) 2016

Fishing gear	No. of anglers (preson)	Target fish	Catch	CPUE (fish/angler-day)
Lure	124	Miyabe charr	719	5.8
		Masu salmon	162	1.3
		Rainbow trout	92	0.7
Fly	57	Miyabe charr	164	2.9
		Masu salmon	100	1.8
		Rainbow trout	157	2.7

Table 3 Result of model selection analysing difference of catchability among the difference of catchability among Miyabe charr, masu salmon and rainbow trout. The best model and a model that has second lowest BIC value are shown.

Model	df	Log liklihood	BIC	delta*
Species + Gear + Species × Gear	6	-21.7	54.1	-
Species + Gear	4	-246.1	499.4	445.3

* delta shows difference of BIC value from the best model.

Table 4 Summary of the best model analysing the difference of catchability among Miyabe charr, masu salmon and rainbow trout.

Explanatory variables	χ^2 value	df	p-value	Reference level	coefficients	Standardized error
intercept	-	-	-	-	-3.81	0.06
Fishing gear	1014.1	2	<0.001	Lure	0.83	0.06
Target fish species	199.1	1	<0.001	Masu salmon	2.57	0.11
				Rainbow trout	3.09	0.09
Interaction	448.9	2	<0.001	Lure×masu salmmon	-1.39	0.14
				Lure×rainbow trout	-2.88	0.16

Table 5 Result of model selection analysing difference of catchability among year of (a) Miyabe charr and (b) masu salmon. The best model, model whose BIC value was within 2 from the best model, and full model are shown.

(a) Miyabe charr

Model	df	Log liklihood	BIC	delta*
Year + Gear + Water temperature	6	-484.0	997.4	-
Year + Gear + Water temperature + Gear × Water temperature	7	-482.7	999.7	2.31

(b) masu salmon

Model	df	Log liklihood	BIC	delta*
Gear + Water temperature	4	-235.1	488.4	-
Gear	3	-237.7	489.1	0.71
(null model)	2	-240.5	490.0	1.65
Year + Gear	4	-236.1	490.3	1.96
Water temperature	3	-238.8	491.3	2.92
Year + Gear + Water temperature + Gear × Water temperature	6	-234.2	495.6	7.27

* delta shows difference of BIC value from the best model.

Table 6 Summary of the best model analysing the difference of catchability among year of (a) Miyabe charr and (b) masu salmon.

(a) Miyabe charr

Explanatory variables	χ^2 value	df	p-value	Reference level	coefficients	Standardized error
intercept	-	-	-	-	-1.93	0.39
year	11.6	2	0.003	2015	-0.11	0.22
				2016	-0.78	0.23
Fishing gear	10.7	1	0.001	Lure	0.60	0.18
Water temperature	8.0	2	0.005	-	-0.14	0.03

(b) masu salmon

Explanatory variables	χ^2 value	df	p-value	Reference level	coefficients	Standardized error
intercept	-	-	-	-	0.39	0.56
Fishing gear	7.8	1	0.005	Lure	-0.64	0.23
Water temperature	5.4	2	0.020	-	-0.12	0.04

Figure captions

Fig. 1. Lake Shikaribetsu and lake fishing areas. A portion of the northeast shoreline which anglers can approach via a ferry service was established as an onshore fishing area in 2016.

Fig. 2. Movement of individually tagged Miyabe charr depicting tag numbers and intervals between release and recapture.

Fig. 3. Movement of individually tagged masu salmon. Fish of #803 was recaught during experimental angling in 2015 in an area in which recreational angling is prohibited.

Fig. 4. Movement of individually tagged rainbow trout. The callout boxes in grey indicate the second capture (# 104 and 171), and intervals from the first recapture.

Fig. 5. Number and proportion of anglers and their fishing gear in Lake Shikaribetsu.

Fig. 6. Number and percentage of most-targeted fish species by (a) lure and (b) fly anglers. Anglers targeting multiple species were counted as having targeted each species.

Fig. 7. The number of anglers by their catch rate of each target species, (a) lure anglers in 2015, (b) fly anglers in 2015, (c) lure anglers in 2016, (d) fly anglers in 2016.

Fig. 8. Catchability of Miyabe charr, masu salmon, and rainbow trout by fishing gear in 2015. Error bars represent standard error estimated from a log-linear model.

Fig. 9. Catchability and estimated fish density of Miyabe charr from 2014–2016, with the effect of water temperature standardised at 12°C. Error bars represent standard error of catchability estimated from a generalised linear model.

Fig. 1

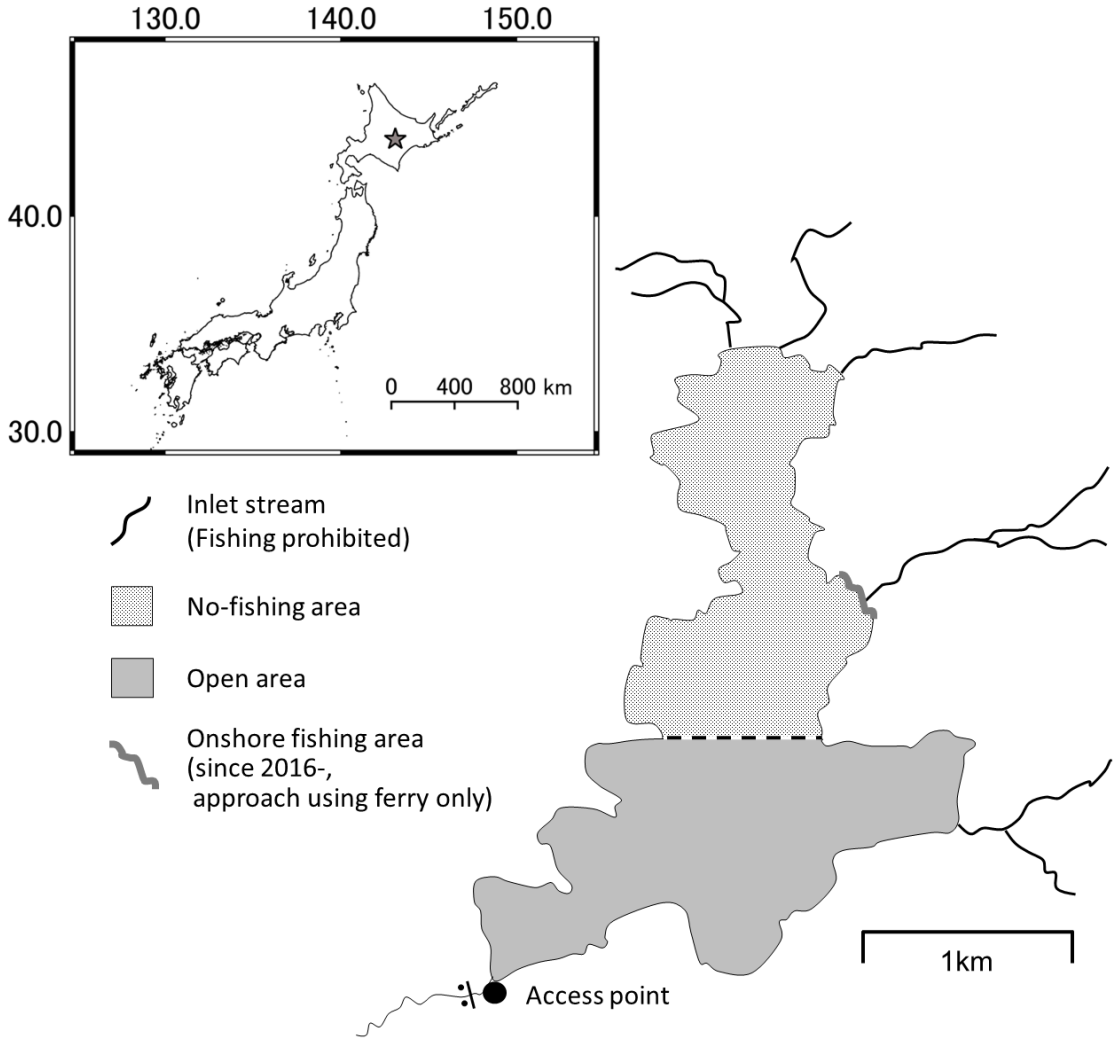
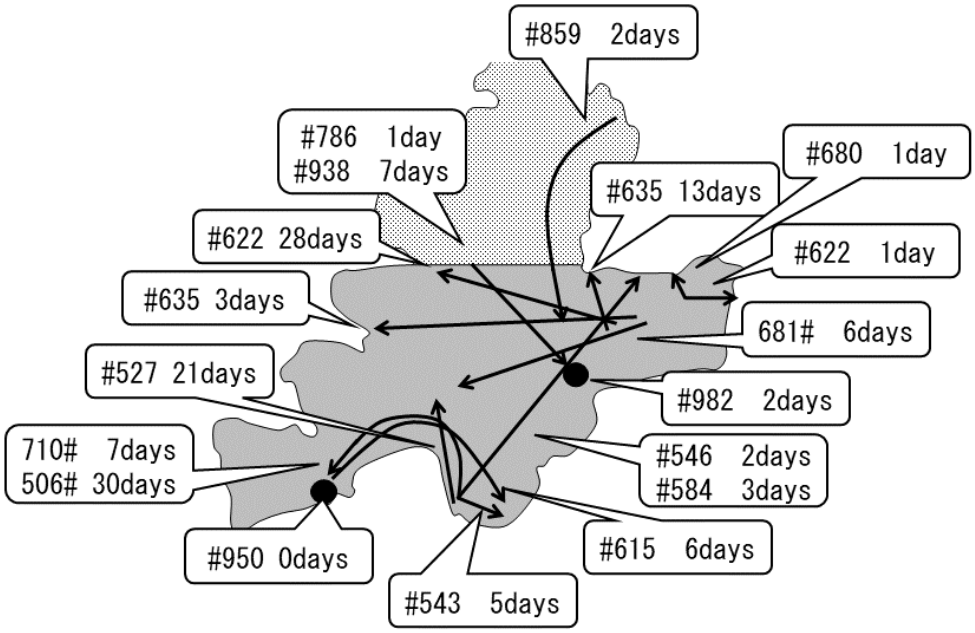

130.0
140.0
150.0
40.0
30.0
0 400 800 km
Inlet stream
(Fishing prohibited)
No-fishing area
Open area
Onshore fishing area
(since 2016-,
approach using ferry only)
1km
Access point

Fig.2

(a)2015



(b)2016

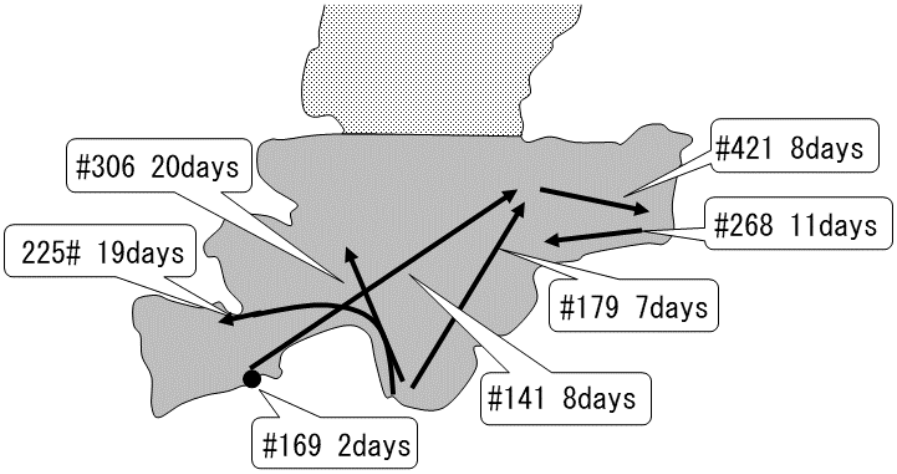
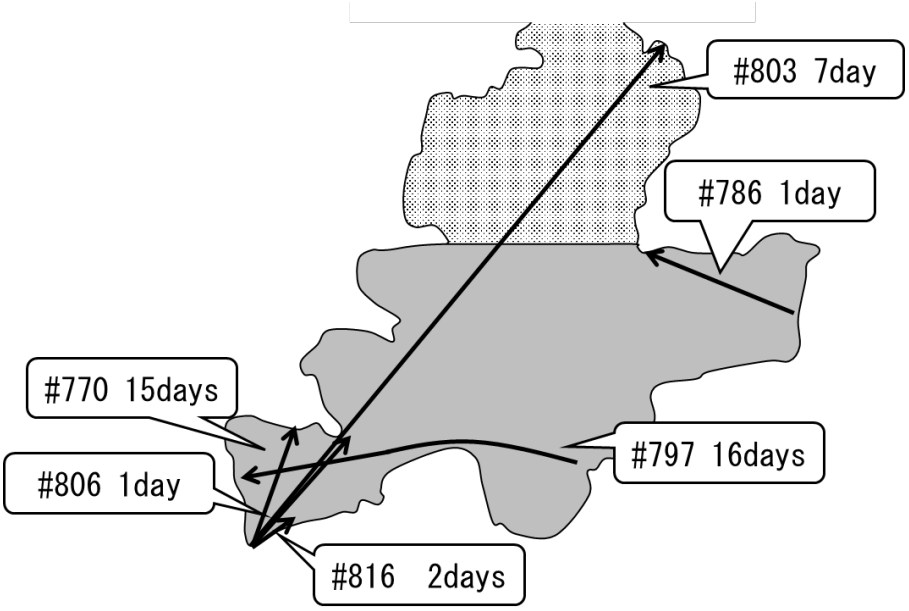


Fig. 3

(a) j2015



(b) 2016

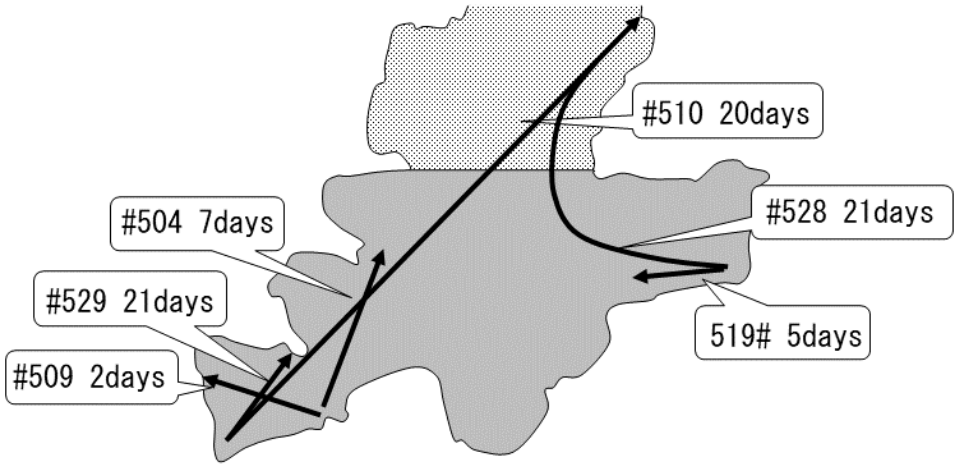
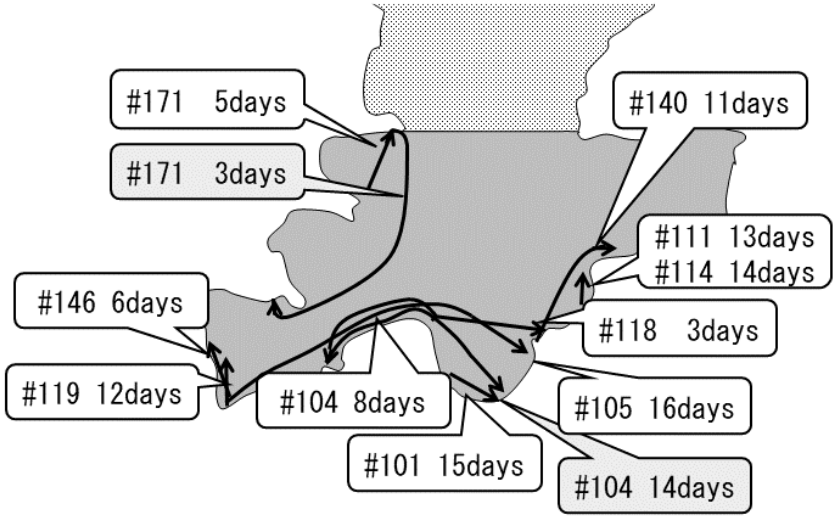


Fig.4

(a) 2015



(b) 2016

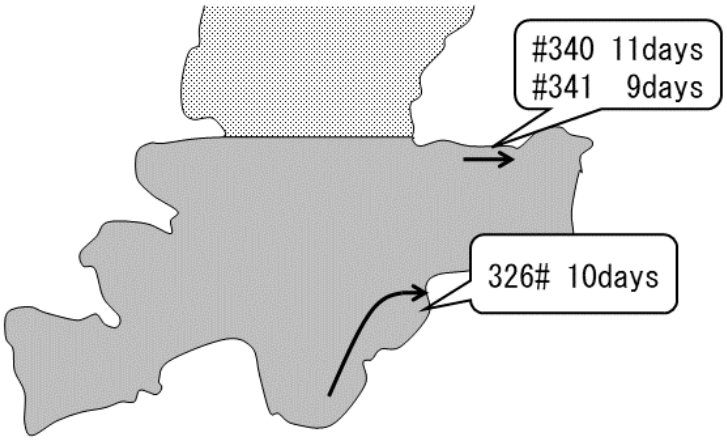


Fig. 5

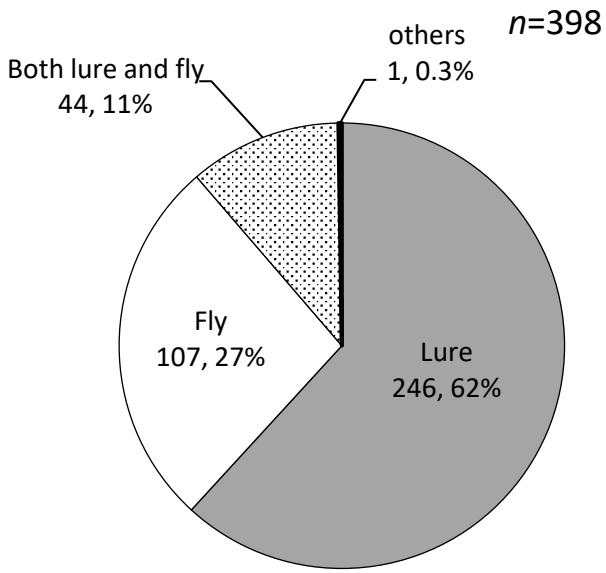


Fig. 6

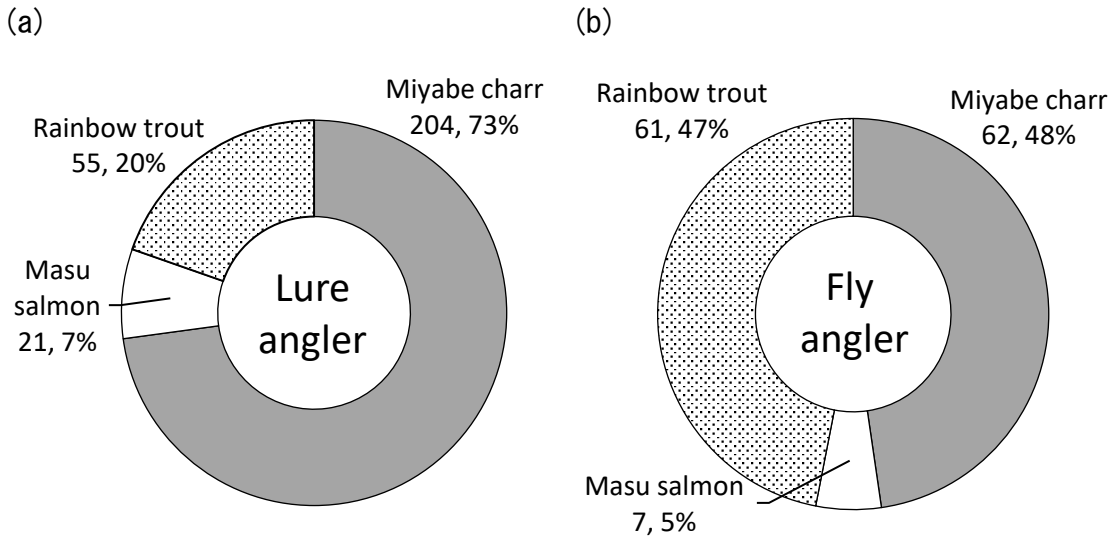

(a)
Miyabe charr
204, 73%
Rainbow trout
55, 20%
Masu
salmon
21, 7%
Lure
angler
(b)
Rainbow trout
61, 47%
Miyabe charr
62, 48%
Fly
angler
Masu salmon
7, 5%

Fig.7

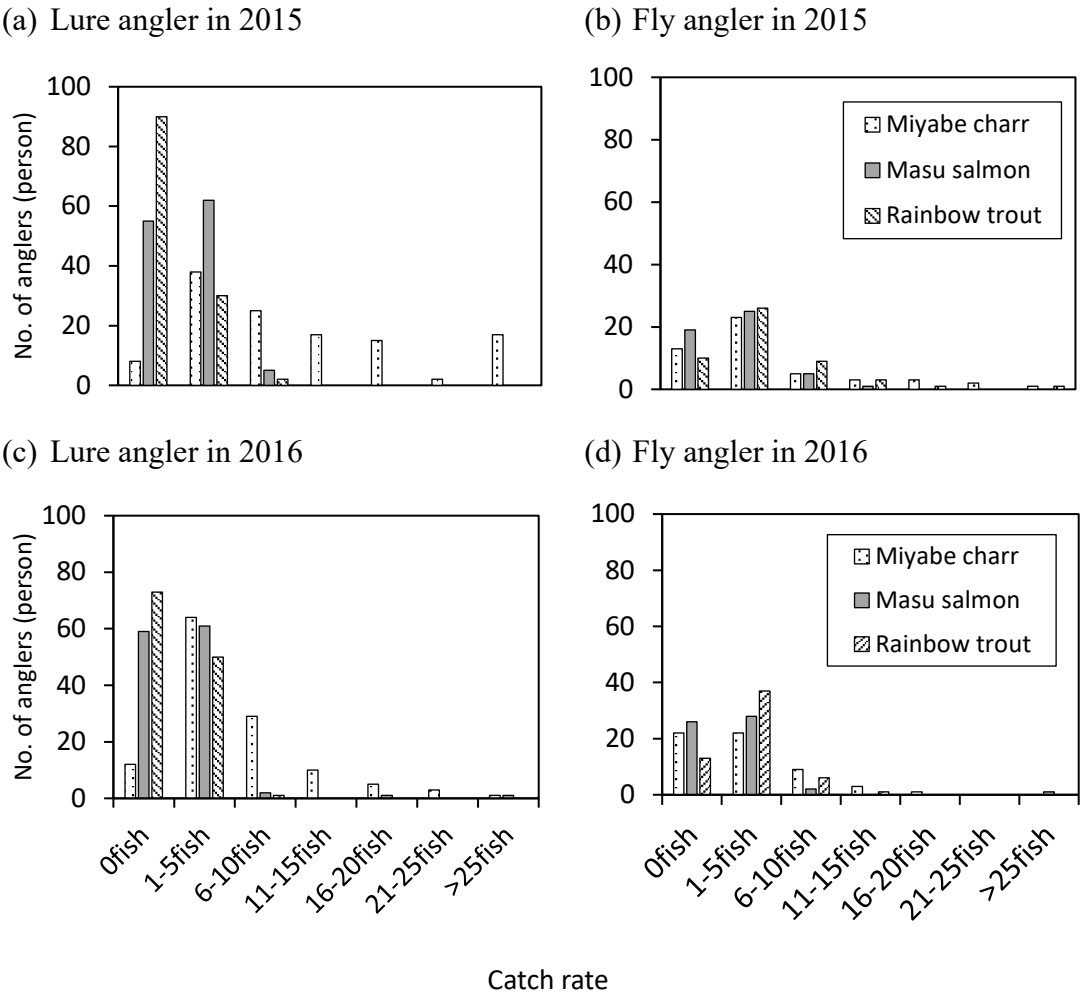

(a) Lure angler in 2015
(b) Fly angler in 2015
(c) Lure angler in 2016
(d) Fly angler in 2016
No. of anglers (person)
100
80
60
40
20
0
Miyabe charr
Masu salmon
Rainbow trout
0fish
1-5fish
6-10fish
11-15fish
16-20fish
21-25fish
>25fish
Catch rate

Fig. 8

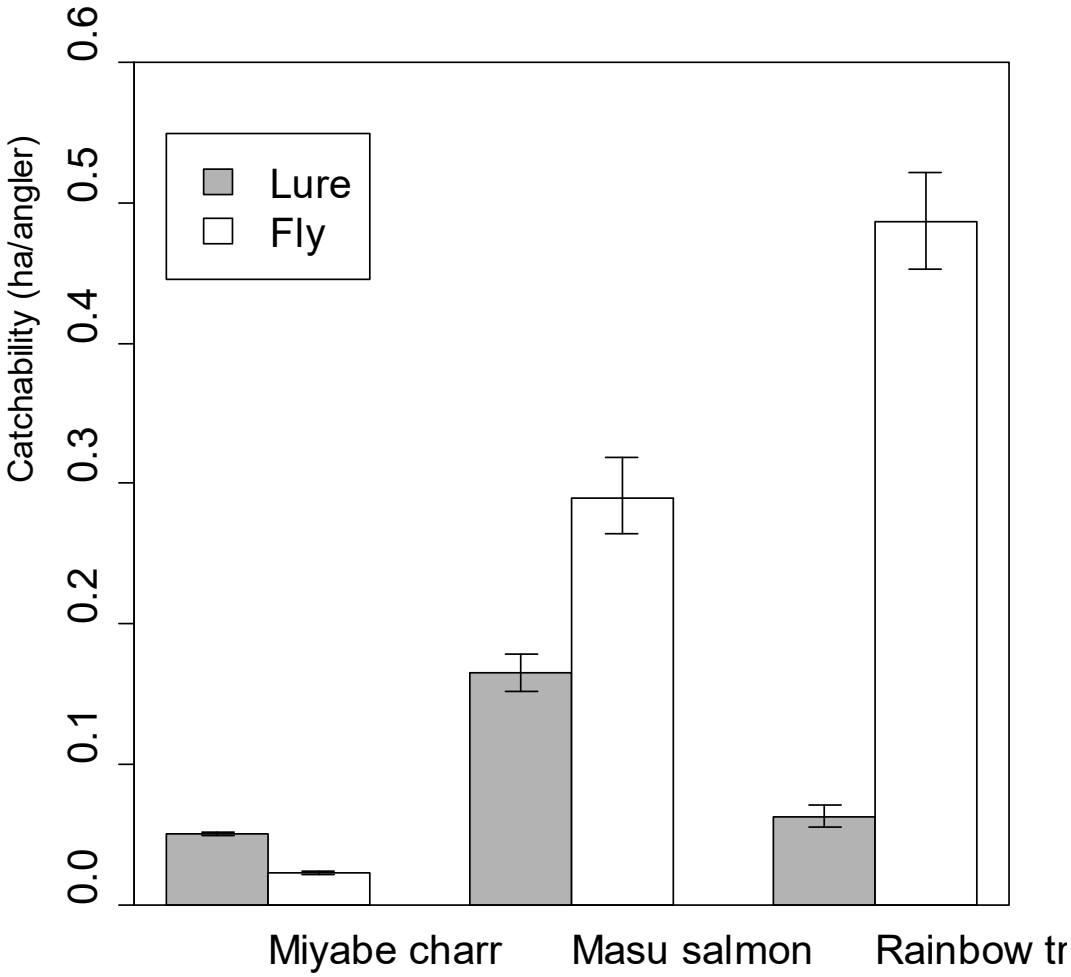
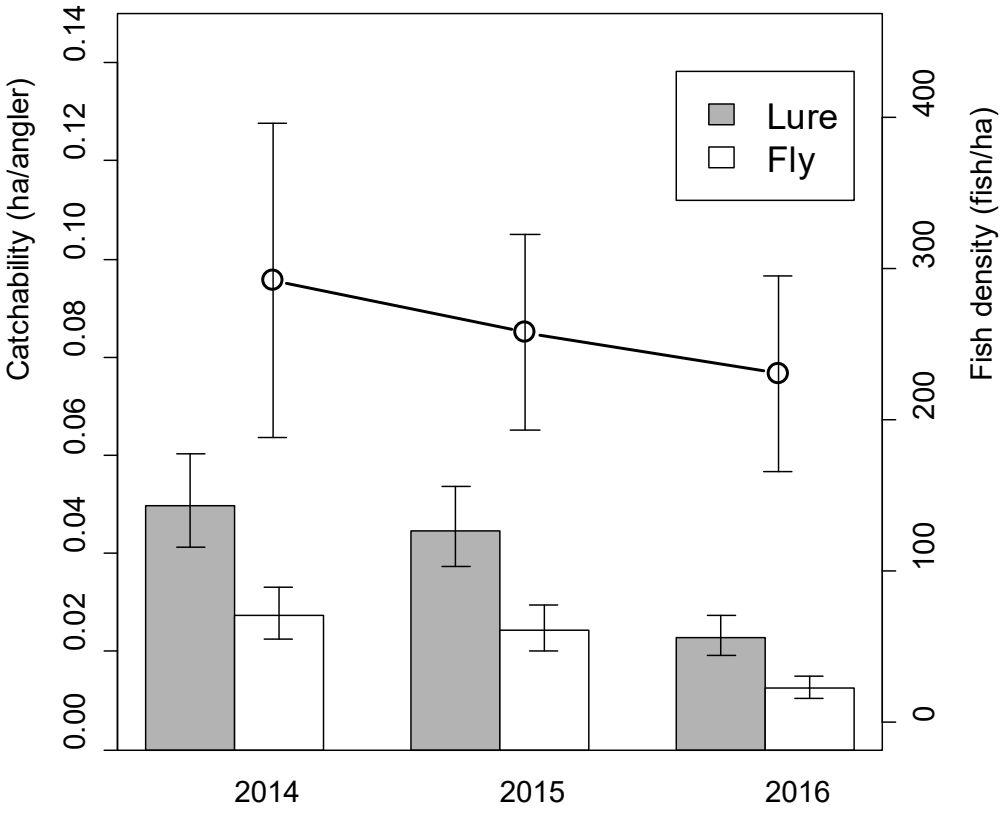

Catchability (ha/angler)
0.0
0.1
0.2
0.3
0.4
0.5
0.6
Lure
Fly
Miyabe charr
Masu salmon
Rainbow tr

Fig. 9


Catchability (ha/angler)
0.00
0.02
0.04
0.06
0.08
0.10
0.12
0.14
Fish density (fish/ha)
0
100
200
300
400
Lure
Fly
2014
2015
2016