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1	Ecological value of gravel pit ponds for floodplain wetland fish
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23	

24 ABSTRACT

25	1.	Floodplain wetlands support high biodiversity, but they have been degraded and
26		geographically fragmented due to human activities. Some types of human-created
27		waterbodies have received growing attention as alternative habitats for conserving
28		wetland biodiversity. Gravel pit ponds (GPPs) are human-created wetlands formed
29		when a gravel pit is excavated at or below the water table and filled with
30		groundwater. Differences in community structure among GPPs and floodplain
31		wetlands with respect to habitat characteristics are scarcely known, resulting in
32		insufficient evaluations of the ecological value of GPPs for floodplain wetland
33		species. In this study, we evaluated the ecological value of GPPs for wetland fishes
34		in floodplain landscapes.
35	2.	We surveyed fish abundance, community composition and ten environmental factors
36		in GPPs and two types of floodplain ponds (remnant ponds and river backwaters) to
37		clarify the biotic and abiotic differences among the pond types.
38	3.	Environmental factors were similar among the pond types, with only water
39		temperature and the distance from the main channel to the pond significantly lower
40		in river backwaters. The richness and abundance of native fish species did not differ
41		among the pond types, but species composition did. Rhynchocypris percnura
42		sachalinensis, Carassius sp., and Lethenteron sp. N (one of the two cryptic species
43		of Lethenteron reissneri) were selected as indicator species in GPPs, remnant ponds
44		and river backwaters, respectively.
45	4.	These results indicate that GPPs provide valuable habitats for wetland fishes in
46		floodplain landscapes and support regional gamma diversity. Since many species
47		inhabited the GPPs in this study, including red list species, appropriate management

48 of GPPs is important to conserve wetland fishes.

49 1. INTRODUCTION

Natural floodplain wetlands are among the most diverse and productive ecosystems on 50 51 Earth (Keddy et al., 2009; Kingsford, 2000; Tockner & Stanford, 2002). However, loss and degradation of floodplain wetlands have occurred around the world because of 52 human activities (Davidson, 2014; Hein et al., 2016; Kingsford, 2015; Reis et al., 2017; 53 Tockner & Stanford, 2002), including river regulation, river channelization, and 54 55 conversion to agricultural land (Fickas et al., 2016; Kingsford et al., 2016; Kuiper et al., 56 2014; Wilcock & Essery, 1991). The degradation of floodplains leads to a serious decline in the abundance of floodplain wetland species (Poff et al., 1997). Conservation 57 of remnant natural or seminatural wetlands is one possible measure for the mitigation of 58 59 biodiversity decline. However, this conventional measure cannot be applied to the areas 60 wherein remnant natural and seminatural wetlands are seriously decreasing due to land use development; therefore, alternative habitats should be considered to develop 61 62 conservation plans for wetland biodiversity. The utilization of human-created wetlands is an alternative measure for the 63 64 conservation of declining wetland biodiversity. Recent studies have shown that humancreated wetlands (e.g., channelized watercourses, flood-control basins, and drainage 65 66 pumping stations) function as habitats for wetland species (Chester & Robson, 2013; 67 Ishiyama et al., 2022; Yamanaka et al., 2020). Conserving various wetlands, including human-created wetlands, may increase the gamma diversity of wetland species in the 68 whole region because human-created waterbodies can support unique aquatic 69 70 communities (Ishiyama et al., 2016; Yamanaka et al., 2020). These ecological advantages of human-created wetlands can contribute to wetland species conservation. 71

72 Gravel pit ponds (GPPs) are a type of human-created wetland where gravel pits

73	are excavated at or below the water table, fill with groundwater and become artificial
74	lakes (Mollema & Antonellini, 2016). Most GPPs are located in urban or agricultural
75	settings (Mollema & Antonellini, 2016). Globally, the demand for sand and gravel is
76	increasing, largely due to urban expansion, infrastructural improvements and the
77	enhancement of coastal protection (Bendixen et al., 2019). Given the increased demand
78	for geomaterials, the construction of GPPs may continuously increase in the future.
79	Diverse organisms, such as fish, birds, plants, zooplankton, and macroinvertebrates,
80	inhabit GPPs (including gravel pit lakes) (Emmrich et al., 2014; Santoul et al., 2009;
81	Seelen et al., 2021; Søndergaard et al., 2018; Vucic et al., 2019; Zhao et al., 2016).
82	Previous studies on human-altered floodplain landscapes have examined the difference
83	in macrophyte community structures between GPPs and other pooled water bodies,
84	including artificial canals and natural lakes. For example, Seelen et al. (2021) have
85	suggested that GPPs have lower nutrient and chlorophyll-a concentrations, as well as
86	unique macrophyte communities, compared with pooled water bodies. However,
87	knowledge of the differences in community structure among GPPs and floodplain
88	wetlands with respect to habitat characteristics remains scarce; thus, the evaluation of
89	the ecological value of GPPs for floodplain wetland species is not sufficient. Species
90	composition in floodplain landscapes often differs among waterbody types (Ishiyama et
91	al., 2016), and the differences may contribute to the maintenance of gamma diversity.
92	Therefore, we should assess community structures and abiotic characteristics of GPPs in
93	floodplain landscapes by comparing them with other floodplain wetlands to deeply
94	understand the contribution of GPPs to regional aquatic biodiversity.
95	Freshwater fishes suffer severely from several human activities, including
96	agricultural activities, inland fisheries, habitat fragmentation, biological invasions, and

climate change (Allan et al., 2005; Barbarossa et al., 2021; Dudgeon, 2019; Gallardo et 97 al., 2016; Maitland, 1995; Reid et al., 2019; Weijters et al., 2009). Therefore, effective 98 99 conservation measures for freshwater fish are needed. This study aimed to evaluate the ecological value of GPPs for floodplain wetland fish by comparing abiotic and biotic 100 101 conditions among three types of waterbodies. In this paper, ecological value is defined 102 as the capacity of a habitat to support an abundance and diversity of organisms. We selected two floodplain ponds, a "remnant pond" and a "river backwater", in addition to 103 104 GPPs. Remnant ponds are permanent water bodies that include cut-off channels and 105 remnants of the back marsh (Yamanaka et al., 2020). River backwaters are slow-flowing 106 areas that are separated from the influence of the main channel (Moore & Gregory, 107 1988). We compared fish assemblages and environments among the three pond types 108 based on the hypothesis that GPPs function as important habitats for fish communities, 109 similar to other pond types, and contribute to an increase in gamma diversity in a 110 region. We predicted that each of the three pond types would provide habitats for unique fish species due to their different environments (e.g., water temperatures and distance 111 112 from the main channel).

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115 2. MATERIALS AND METHODS

116 **2.1 Study area**

117 Field surveys were conducted in the Tokachi Plain, Hokkaido, northern Japan. Since

118 1900, this region has been undergoing agricultural land expansion and river

119 channelization, and most of the wetlands have been converted to farmland. We

120 randomly selected five study sites for each pond type (Figure 1). All study ponds are

l lentic and connected to main channels through waterways, although some ponds are

122 connected to main channels only when the water level rises. The mean and range for the

area of each pond type are as follows: GPPs, 4349.8 (range 247–10746) m²; remnant

124 ponds, 4837.8 (range 548–10197) m²; and river backwaters, 396.6 (range 219–665) m².

125

126 **2.2 Environmental factors**

127 Abiotic surveys were conducted from July 20th to August 6th, 2021. All environmental 128 measurements and fish surveys were conducted during the same season and completed 129 within 30 days after the fish survey. We measured the dissolved oxygen content, 130 electrical conductivity, turbidity, water temperature, and pH at three points randomly 131 selected at each site using a portable water quality metre (WQC-24, DKK-TOA Corporation, Tokyo, Japan). These environmental factors were averaged for each pond 132 133 for data analysis. These measurements were taken within 5 h after sunrise. We also 134 measured water levels with a folding scale or a portable echosounder (Deeper Smart Sonar CHIRP⁺, Deeper, Vilnius, Lithuania) at 20 points in each site, at 10 points on the 135 shore and at 10 points in the centre of the water body, and then an average was 136 calculated for each position (i.e., centre or shore). Distance from the main channel 137 138 (excluding ditches) was measured as an indicator of connectivity using Google Maps 139 (https://www.google.co.jp/maps/) for remnant ponds and GPPs and a laser rangefinder (Tru-Pulse 200, Laser Technology Inc., Colorado, US) for river backwaters. 140

141

142 2.3 Fish

143 From July 7th to August 5th, 2021, fish surveys were conducted using one fyke net (0.4

144 m diameter, 2.0 m bag length, and 3 m wing length) and two minnow traps (0.25 m

145 width, 0.48 m length, and 0.25 m depth) at each site. The fyke net and minnow traps 146 were set up near shores covered by aquatic vegetation for 24 h. The collected fish were 147 anaesthetized with 2-phenoxyethanol and identified to the species level, and the abundance of each species was recorded. Then, all fish were released near the capture 148 149 sites. The collected fish were also categorized into native or nonnative species 150 according to the Hokkaido Blue List 2010 (Hokkaido, 2010), and the status of each fish 151 species was assessed according to national red lists (Ministry of the Environment, 152 2020). The samples from fyke net and minnow traps were pooled in each pond for data 153 analysis. Fish surveys were conducted at one or two ponds per day. The sampling effort 154 needed to comprehensively capture that community structure can vary among study 155 ponds. Prior to the statistical analyses, we compared the observed and estimated species 156 richness within each pond using an individual-based rarefaction curve (Colwell et al., 157 2012) to test whether the community in each pond was well represented by the sampling 158 data. The difference between the observed and estimated species richness within each pond was small (Figure S1; mean detection rate \pm SD, 95 \pm 8% [range 75–100%]). The 159 160 result suggests that the sampling effort used in this study was appropriate for capturing 161 the community structure.

162

163 **2.4 Data analysis**

Since candidate water bodies were very few and unevenly distributed spatially due to river regulation, river channelization, and conversion to agricultural land, our study sites for each of the pond types exhibited an aggregated pattern (Figure 1). Thus, we conducted a Moran's test to check for spatial autocorrelation of the abundance and species richness of native species among the study sites in each pond type. The results

showed no significant correlations among sites and suggested that spatial

autocorrelation does not occur in the present study design, and the samples can be

171 treated as independent.

We constructed generalized linear models (GLMs) to estimate the effects of 172 pond type on environmental factors, species richness and abundance. In the GLMs, we 173 174 used environmental factors, species richness and abundance as response variables and 175 pond type as an explanatory variable. Due to the fact that environmental factors were 176 comprised of non-negative continuous data, species richness was comprised of nonoverdispersed count data and abundance was comprised of overdispersed count data, we 177 applied a gamma distribution with a log link function, a Poisson distribution with a log 178 179 link function and a negative binominal distribution with a log link function in the 180 GLMs, respectively (Zuur et al., 2009). In the GLMs with species richness or 181 abundance as a response variable, native and nonnative species were used in separate 182 models. Second, we conducted pairwise comparisons using the constructed models to examine whether each environmental factor, species richness, and abundance 183 184 significantly differed among the pond types. *p*-values were corrected for pairwise 185 comparisons using the Holm procedure (Holm, 1979).

To compare species composition among the pond types, we ordinated species composition by nonmetric multidimensional scaling (NMDS). A dataset including both native and nonnative species was used for this analysis. In the NMDS analysis, we used the log-transformed species-abundance data and Bray–Curtis index as the length index. We tested whether the environmental factors were significantly correlated with NMDS ordination with 1000 permutations. Before the analysis, we calculated the variance inflation factors (VIFs) to avoid multicollinearity; the results showed that depth near

193	shore and depth in the centre had values over 5, which is the threshold indicative of
194	problematic collinearity for regressions (Sheather, 2009). Therefore, we removed the
195	depth in the centre, which had a lower R^2 than the depth near the shore, from our
196	analysis. Finally, the VIF for every variable was <5, suggesting that all variables were
197	suitable. Only environmental factors with significant correlation ($p < 0.05$) were fitted
198	and plotted on the given NMDS using the "ordisurf" function of the "vegan" R package
199	(Oksanen et al., 2020). We also conducted pairwise permutational multivariate analysis
200	of variance (pairwise PERMANOVA) to test for differences in species composition
201	among the pond types. <i>p</i> -values from pairwise PERMANOVA were corrected by using
202	the Holm procedure (Holm, 1979). The dispersion among the pond types was similar,
203	with no significant differences.
204	Furthermore, we used indicator species analysis to determine which species
205	were significantly associated with a specific pond type (Dufrene & Legendre, 1997).
206	Indicator species were determined based on significant <i>p</i> -values (< 0.05 , which was
207	computed by using 10,000 permutations).
208	All data analyses were conducted with R v. 4.2.0 (R Core Team, 2022) using
209	"emmeans" v. 1.7.4.1 (Lenth, 2022) for pairwise comparisons, "iNEXT" v. 2.0.20
210	(Chao et al., 2014) for rarefaction curve construction, "stats" v. 4.2.0 (R Core Team,

211 2022) and "MASS" v. 7.3.56 (Venables & Ripley, 2002) for GLM fitting, "vegan" v.

212 2.6.2 (Oksanen et al., 2020) for NMDS, "pairwiseAdonis" v. 0.4 (Martinez Arbizu,

213 2017) for pairwise PERMANOVA and "indicspecies" v. 1.7.12 (Cáceres & Legendre,

214 2009) for indicator species analysis.

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216

217 **3. RESULTS**

218 **3.1 Environmental factors**

219 Water temperature was lower in river backwaters than in other pond types (Figure 2e;

Table S1; Table S2), and the distance from the main channel to river backwaters was

shorter than that to other pond types (Figure 2f; Table S1; Table S2). Other

environmental factors did not significantly differ among the pond types (Figure 2a–d, g,
h; Table S1; Table S2).

224

225 3.2 Fish

We caught 12193 and 708 individuals representing 12 native and 4 nonnative species,

227 respectively. Regarding red list species, *Rhynchocypris percnura sachalinensis* was

228 mainly found in GPPs, Gymnogobius castaneus and Pungitius tymensis were found only

229 in remnant ponds, Lethenteron sp. N (one of the two cryptic species of Lethenteron

230 reissneri) and Salvelinus curilus were found only in river backwaters, and Lefua

231 *nikkonis* was present in all pond types (Figure S2; Figure S3; Table S3). Additionally,

one or two species were dominant in each pond type, i.e., *Gasterosteus aculeatus* in

river backwaters (Figure S2; Figure S3; Table S3). There was no significant difference

in species richness or abundance among the pond types except for the abundance of

nonnative species (Figure 3a–c; Table S4; Table S5). The nonnative species abundance

of remnant ponds was significantly greater than that of river backwaters (Figure 3d;

Table S4; Table S5). Species composition significantly differed among the pond types

238 (Figure 4a; Table 1). The stress value, which is an index of the fit of the reproduced

similarity matrix to the observed similarity matrix, was 0.11, suggesting that the

240 goodness of the fit was 'fair' (Kruskal, 1964). Turbidity, water temperature, distance

241	from the main channel, and depth near shore were significantly correlated with NMDS
242	ordination (Figure 4b-e; Table S6). While river backwaters and other pond types clearly
243	separated along the water temperature gradient and differed in distance from the main
244	channel (Figure 4c, d), no clear pattern was found in other factors. The indicator species
245	analysis showed that one species was a significant indicator for each pond type (Table
246	2): GPPs, Rhynchocypris percnura sachalinensis; remnant ponds, Carassius sp.; and
247	river backwaters, Lethenteron sp. N.

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- 249

250 4. DISCUSSION

251 The degradation of floodplains leads to a serious decline in the abundance of floodplain 252 wetland species (Poff et al., 1997). In the present study, we clarified the ecological value 253 of GPPs by comparing biotic and abiotic conditions among multiple pond types in 254 modified floodplain landscapes. We found that species composition differed 255 significantly among the pond types, although the richness and abundance of native 256 species did not differ. Indicator species also differed among the pond types. These 257 results support our hypothesis that GPPs function as important habitats for fish communities, similar to other pond types, and contribute to an increase in gamma 258 259 diversity in a region. Thus, appropriate management of GPPs is important to conserve 260 floodplain wetland biodiversity that is being lost.

It is possible that the unique fish communities in each pond type were formed by the occurrence of nonnative species and/or environmental factors. River backwaters have lower temperatures and shorter distances from the main channel than the other pond types, and these gradients explained the community structure of river backwaters.

265 The indicator species *Lethenteron* sp. N and several other species (*Salvelinus curilus* 266 and Oncorhynchus mykiss) that were found only in river backwaters prefer spring water 267 and/or cold water habitats (Hirano et al., 2020; Koizumi & Maekawa, 2004; Matthews & Berg, 1997). Therefore, the cold water in river backwaters may have caused the 268 formation of a unique community. Also, river backwaters exhibited the lowest nonnative 269 270 species abundance, which was significantly lower than that in remnant ponds. Invasion 271 by lentic or low-flow nonnative species may be prevented by flood disturbance (Ho et 272 al., 2013). Therefore, a high frequency of flood disturbance in river backwaters may cause a lower abundance of nonnative species. 273

274 Although GPPs and remnant ponds had more similar environments than we 275 predicted, their species composition and indicator species differed as predicted. In 276 GPPs, only one nonnative species (Misgurnus anguillicaudatus) was observed, although 277 no significant differences in the richness or abundance of nonnative species were found 278 between GPPs and remnant ponds. Since public access to the area near GPPs is prohibited, the release of nonnative species may have been prevented. Rhynchocypris 279 280 percnura sachalinensis (categorized as near-threatened) was the indicator species in 281 GPPs but not in remnant ponds with similar environments. The reason for this 282 difference may be the effect of nonnative species. Invasion by nonnative *Pseudorasbora* 283 parva, with an ecological niche similar to that of Rhynchocypris percnura 284 sachalinensis, can reduce the abundance of *Rhynchocypris percnura sachalinensis* (Ishiyama et al., 2020). Since Pseudorasbora parva inhabited three remnant ponds, the 285 286 abundance of Rhynchocypris percnura sachalinensis may have been low. In addition, deeper ponds probably function as refuges for *Rhynchocypris percnura sachalinensis* 287 from Pseudorasbora parva (e.g., Ishiyama et al., 2020); therefore, deeper GPPs created 288

by gravel mining may function as refuges for *Rhynchocypris percnura sachalinensis* if
the nonnative *Pseudorasbora parva* invades.

291 Our results showed that GPPs provide habitats for floodplain wetland fishes, including endangered species, and can help increase the gamma diversity of wetland 292 293 fishes in the studied region. Most species found in the studied ponds prefer lentic water and have a weak swimming ability (Ishiyama et al., 2014). Thus, if habitat 294 295 fragmentation by river alteration proceeds, dispersion of wetland fishes may be limited, 296 and populations may not be sustained. Conservation of existing GPPs may contribute to sustaining the habitat and populations of wetland fishes. However, the ecological value 297 298 of GPPs has been overlooked, and GPPs are disappearing in Japan. For example, GPPs 299 in some prefectures should be backfilled after mining projects due to past fatal water 300 accidents. GPPs often have steeper shores than natural lakes or ponds (Blanchette & Lund, 2016; Emmrich et al., 2014; Santoul et al., 2004); however, this structure is not 301 302 conducive to the growth of macrophytes (Søndergaard et al., 2018). Inshore macrophytes can serve as habitats for many organisms and increase overall biodiversity 303 304 (Santoul et al., 2004). Therefore, creating gently sloping shores for GPPs may be a 305 solution for biological conservation as well as the prevention of water accidents. 306 Our results indicated that GPPs have an important ecological role for 307 floodplain wetland fishes and can compensate for wetland loss. Although our study focused only on floodplain wetland fishes, various types of organisms inhabit GPPs 308 (including gravel pit lakes) (Emmrich et al., 2014; Santoul et al., 2009; Seelen et al., 309 2021; Søndergaard et al., 2018; Vucic et al., 2019; Zhao et al., 2016). Since ecological 310 values often differ among taxa (e.g., Yamanaka et al., 2020), it is important to clarify the 311 ecological value of GPPs for other floodplain wetland taxa in future studies. 312

314

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322

323 AUTHOR CONTRIBUTION STATEMENT

Conceptualization: TY. Developing methods: HN, TY, NI. Conducting the research, data
analysis, preparation figures & tables: HN, TY. Data interpretation, writing: HN, TY, NI,
FN.

327

328 DATA AVAILABILITY STATEMENT

329 Data used in this study will be made available by the authors upon reasonable request.

330

331 CONFLICTS OF INTEREST STATEMENT

332 None declared.

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TABLES

Table 1 Results of pairwise PERMANOVA.

Contrast	F	р
Gravel pit pond vs. Remnant pond	2.31	< 0.05
Gravel pit pond vs. River backwater	6.49	< 0.05
Remnant pond vs. River backwater	4.81	< 0.05

Table 2 Results of the indicator species analysis. Specificity is the probability that the

519 surveyed site belongs to the target site group given that the species has been found.

520 Sensitivity is the probability of finding the species in sites belonging to the site group.

521	Only spe	cies with	<i>p</i> < 0.05	are shown.
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Pond type	Species	Specificity	Sensitivity	р
Gravel pit pond	Rhynchocypris percnura	0.96	1.00	< 0.01
	sachalinensis			
Remnant pond	Carassius sp.	0.82	0.80	< 0.05
River backwater	Lethenteron sp. N	1.00	0.80	< 0.01

525 FIGURE CAPTIONS

526 **Figure 1** Map of the study area and representative landscapes of the surveyed ponds.

- 527 Figure 2 Differences in environmental factors among the pond types. The translucent
- 528 bars indicate 95% CIs. The circles denote each observed value. Different letters indicate
- significant differences in the pairwise comparison (p < 0.05).
- 530 Figure 3 Differences in species richness and abundance among pond types. The
- translucent bars indicate 95% CIs. The circles denote each observed value. Different
- big letters indicate significant differences in the pairwise comparison (p < 0.05).
- 533 Figure 4 Nonmetric multidimensional scaling (NMDS) of the fish community
- 534 structures in the surveyed pond types. (a) Site scores coded by pond types. (b-f) Contour
- 535 plots for each environmental factor. Greyscale bars in each panel indicate the range of
- 536 values for each environmental factor.



Gravel pit pond



Remnant pond



River backwater







