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The significance of meandering channel to habitat diversity and fish assemblage: a case study in the Shibetsu River, northern Japan

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Abstract

This study examined the structure and function of habitats for fish, the contribution to fish populations, and the effects of channel modification on habitats and fish populations in the lowland meandering Shibetsu River, northern Japan. Electrofishing and environmental measurements were conducted in bank areas of habitats constituting natural meandering and modified reaches. All types of habitats in a meandering reach highly contributed to the fish population(s). In particular, the contributions of lateral and wood habitats to fish populations were generally high, despite the low spatial extent of these habitats. The modified reach was simplified and had fewer types of habitats with uniform currents, and there was a low abundance of most fish within these habitats. Abundance of each fish group (taxa) was negatively affected by the changes to the habitats and/or channel shortening (i.e., decrease in the absolute abundance of habitat) due to river modification, which was implemented during 1950–1978. This study suggests that the recovery of all the habitat types is important in meander restoration and that the changes in habitat types and abundance should be examined in monitoring meander restoration and channel shortening.

Keywords: channel modification; habitat classification; lowland river; meander restoration; sinuous channel

Introduction

Natural rivers meander and form diverse longitudinal and cross-sectional profiles. Such diverse bathymetric features produce habitat heterogeneity, such as the repeated structures of pools and riffles and a lateral gradient of depth from shallow to deep areas, which are essential for aquatic organisms in rivers (Inoue and Nakano 1999; Rhoads et al. 2003; Nakano and Nakamura 2008). In addition, distribution of large woody debris are closely associated with the channel morphology of meandering rivers (Gurnell et al. 2002; Koehn et al. 2004; Lassettre et al. 2008) and provide essential habitats for aquatic organisms (Crook and Robertson 1999; Benke and Wallace 2003). However, many rivers have been channelized and straightened for purposes such as land development, navigation, and flood control, and the impact of such modification has been particularly intensive in lowland rivers with broad floodplains (Gore and Shields 1995), where a meandering channel with high sinuosity often develops. Although numerous studies have shown the detrimental effects of river channelization and straightening on aquatic organisms (Moyle 1976; Jurajda 1995; Rhoads et al. 2003), the effects of habitat alteration and those mechanisms in meandering rivers require further investigation.

The deterioration of freshwater ecosystems in lowland rivers has led to restoration projects such as the construction of meandering channels (Dahm et al. 1995; Friberg et al. 1998; Holubova and Lisicky 2001; Kondolf 2006; Pedersen et al. 2007a, b; Lorenz et al. 2009; Nakamura et al. 2014). The restoration of meanders is based on the paradigm that increasing habitat heterogeneity promotes recovery of biodiversity (Palmer et al. 2010). Indeed, some meander restorations have increased habitat heterogeneity in river reaches (Moerke et al. 2004; Pedersen et al. 2007b; Nakano and Nakamura 2008) and

43 enhanced the diversity and abundance of aquatic organisms such as fish and
44 macroinvertebrates (Lorenz et al. 2009; Nakamura et al. 2014), and similar positive
45 biological responses are expected at other sites in the future (Trexler 1995; Pedersen et
46 al. 2007b; Hauer et al. 2014). Conversely, a number of meander restoration projects
47 have failed to facilitate a significant recovery of target species and assemblages due to a
48 lack of understanding of key habitats, including floodplain waterbodies, and large-scale
49 factors that control features of river reach and segment such as sediment load (Holubova
50 and Lisicky 2001; Kondolf et al. 2001; Kawaguchi et al. 2005; Kondolf 2006).
51 Numerous studies have described the structure and function of natural habitats of fish in
52 various river systems (e.g., Murphy et al. 1989; Fausch and Northcote 1992; Inoue and
53 Nakano 1999; Peterson and Rabeni 2001; Beechie et al. 2005; Schwartz and Herricks
54 2008; Zeug and Winemiller 2008; Nagayama et al. 2012; Wolter et al. 2016). Most of
55 these studies also included parts of the habitat components which usually appear in
56 meandering channels. However, the entire distribution and composition of all habitats
57 along the meandering river have not been studied, which are indispensable for
58 understanding effects of channel modification and meander restoration on fish
59 assemblages and conserving fish diversity in river reach and segment scales.
60 The overall objectives of this study were to elucidate the structure and function of
61 habitats for fish in a meandering river by comparing meandering and modified reaches
62 to provide the practical knowledge required for the management and restoration of
63 meandering rivers. Our specific objectives were to (1) compare physical characteristics
64 among habitat types classified in meandering and modified channels, (2) describe use of
65 the habitat types by fish, (3) elucidate contributions of the habitat types to fish
66 abundance at the river reach scale, and (4) examine effects of channel modifications on

habitats and fish populations at the river reach scale.

Methods

Study area

Our study segment (23 km long in valley length) is located in the middle part of the Shibetsu River in Hokkaido, northern Japan (Fig. 1). The river is 77.9 km long and drains an area of 671 km^2. Natural coniferous and deciduous mixed forest covers the headwater basins, while pasture is the primary land cover in the middle to lower reaches where the river channel has been extensively modified and straightened (Hirai and Kuga 2005). There are some cut-off channels (artificial oxbow lakes) disconnected from the main river through channel straightening.

Two study reaches were established for our field survey: a natural meandering (NM) reach and a channelized, straightened (CS) reach (Fig. 1). The CS reach was set approximately 12 km downstream from the NM reach and approximately 3 km downstream from the nearest meandering reach in order to minimize the effects of passive immigration of fish from the meandering section to the CS reach on fish abundance. The entire NM reach is 2.33 km and 4.39 km long in valley length and river length, respectively (i.e., sinuosity index = 1.88). Here, the valley length and the river length are the straight-line and the watercourse distances from the upstream to the downstream end of the study reach, respectively. The NM reach retains natural meander bends, oxbow lakes, and riparian forests. No modifications of channel morphology have been conducted in the NM reach. In contrast, the CS reach has been modified and

91 straightened using concrete blocks as bank protection, and riparian trees are scarce
92 along the banks. The valley length and the river length of the entire CS reach are 1.86
93 km and 2.07 km, respectively (i.e., sinuosity index = 1.11). In both types of study reach,
94 the average bed slope is approximately 1/450, and the dominant bed material is pebble
95 (17–64 mm). The channel width is 10–20 m and 25–30 m in the NM and CS reaches,
96 respectively. The river lengths selected for both study reaches measured more than 50
97 times the length of channel width, to encompass all types of habitats and to enable the
98 characterization of fish fauna in the reaches (Bisson et al. 2006; Li and Li 2006).
99 The Shibetsu River has only two small weirs, and these are located in the lower part
100 of the study reaches. Because a wide passage for fish is constructed at the weirs,
101 anadromous fish such as salmon and lamprey are able to migrate upstream beyond the
102 weirs. The fish species observed in our study reaches were masu (*Oncorhynchus masou*)
103 and chum salmon (*O. keta*), Dolly Varden (*Salvelinus malma malma*), white spotted
104 char (*S. leucomaenis*), rainbow trout (*O. mykiss*), Siberian stone loach (*Noemacheilus*
105 *barbatulus toni*), sticklebacks [*Pungitius* sp. (Freshwater type), and *P. tymensis*], and
106 lampreys (*Lethenteron* spp.). Most of the lampreys observed were ammocoetes, and
107 probably consisted of three species (*L. kesseleri*, *L. japonicum*, and *L. reissneri*).
108 We conducted field surveys from late June to early September in 2006 and 2007
109 during the period of base flow. Water temperature ranged from 10.7 to 14.4 °C during
110 the surveys. As fish community composition can be dependent on season (Pander and
111 Geist 2010), the communities observed in this study might be limited by the study
112 period.
113
114 **Habitat classification**

115

116 Our study reaches were classified into habitat types based on the habitat classification
117 systems of channel-unit and subunit scales, and bank area (≤ 2 m from the bank) of each
118 habitat was investigated (Fig. 1). Habitat classification on a channel-unit scale, which is
119 a spatial scale with 10^0–10^1 channel widths (Grant et al. 1990) and is classified as a unit
120 regardless of its cross-sectional profiles of main channel, has been used in many studies
121 relating to fish habitat in small streams (Bisson et al. 1988; Hawkins et al. 1993; Bisson
122 et al. 2006). However, it could not be directly used in our study river, which was a
123 high-ordered meandering river, because of the difference in cross-sectional habitats
124 created by its asymmetrical cross-section with wide shallow and deep areas. To classify
125 these areas, another classification system on a subunit scale was also used. A subunit is
126 a patch within channel units (Grant et al. 1990; Sedell et al. 1990; Gregory et al. 1991).
127

128 *Natural meandering (NM) reach*

129

130 Ten types of habitat were identified in the NM reach: oxbow (OX), outer bend (OB),
131 inner bend (IB), run (RN), backwater (BW), side channel (SC), outer bend with large
132 wood (OB+W), inner bend with large wood (IB+W), run with large wood (RN+W), and
133 backwater with large wood (BW+W) (Fig. 1 and Table 1). The OX was a historic
134 meander bend that had been isolated from the main channel during the base flow. The
135 OB was a lateral scour pool created on the outer bend of a river channel. The IB was a
136 shallow area located on the inner bend. The RN was generally located between adjacent
137 channel bends across the river channel. The BW was found on the concave part of river
138 banks. The SC was a creek or a small channel connected to the main channel at its

uppermost and lowermost ends. When the OB, IB, RN, and BW contained one or more large pieces of wood measuring more than 15 cm in diameter and 1 m in length they were categorized as OB+W, IB+W, RN+W, and BW+W. In the NM reach, instream large wood was abundant, and the habitats containing large wood had evidently different environmental features from those without large wood. Therefore, instream large wood was considered as a category in our habitat classification.

Channelized, straightened (CS) reach

Four types of habitat were identified in the CS reach: an outer zone (OZ), inner zone (IZ), straight zone (SZ), and a straight zone with large wood (SZ+W) (Fig. 1 and Table 1). The OZ was a lateral scour pool formed at the outside of a moderately curved channel. The IZ was found inside of a moderately curved channel. The SZ was distributed between the curved parts of the channel and extended across the channel. When the SZ contained instream large wood it was categorized as SZ+W. Large wood was found only in the SZ in the CS reach.

Fish survey

Fish sampling was performed using a backpack electrofishing unit (Model 12, Smith-Root Inc., Vancouver, WA, USA) and was conducted using sampling quadrats (2 m wide and 4 m long) that were established in the bank area of the habitats. Each quadrat was established in an accessible area of the channel margin, at least 20 m apart from an adjacent quadrat. Fish sampling was not conducted in the mid-part of the river

163 channel because it was considered to be an ineffective practice in such an open area
164 (Beechie et al. 2005). One or two quadrats were set in each of the individual accessible
165 habitats in the NM reach. The number of sampling quadrats in each of the habitat types
166 was 6–15, with 110 quadrats in the NM reach and 37 quadrats in the CS reach in total
167 (Table 1). Because the individual habitats in the CS reach had a longitudinally long
168 distance, three or four quadrats were established in each of the individual accessible
169 habitats, except for in the SZ+W.

170 To minimize the dispersal of fish from the sampling quadrats, the size of quadrats
171 was set to allow the investigator to perform electrofishing from the outside of the
172 sampling quadrats by using a long pole (2.7 m). The electrofishing survey was
173 conducted by a three-person crew. Two people used dip nets and large D-shaped nets
174 (1.0 m wide, 0.8 m height, and 1.1 m depth), and the third used the electrofishing unit
175 and a dip net. Electrofishing in each quadrat terminated when no more fish could be
176 caught. We then classified each fish according to species or taxon; the number of each
177 fish species or taxon was counted and used to calculate the fish density in each type of
178 the habitats.

179 In our study, six groups of fish were identified based on taxon and age classes: age-0
180 and age-≥1 masu salmon, age-≥1 Dolly Varden, sticklebacks, lampreys, and Siberian
181 stone loach. The age-0 and age-≥1 masu salmon and Dolly Varden were <100 mm and
182 ≥100 mm in fork length, respectively, based on the study of Urabe et al. (2010) which
183 divided the age classes (age-0 and age-≥1) of masu salmon by a fork length of
184 approximately 100 mm. Sticklebacks and lampreys were identified at genus level.
185 Age-0 Dolly Varden, chum salmon, white spotted char, and rainbow trout were all
186 excluded from analysis because of their very small numbers.

187

188 **Environmental survey**

189

190 After sampling the fish, the depth, current velocity, and bed material of each sampling
191 quadrat were measured. A midline with a length of 4 m was established parallel to the
192 stream flow in each quadrat, where three measurement points were used at 1 m intervals
193 (with the middle measurement point as the center of the quadrat). The current velocity
194 was measured at a 60% depth from the water surface when the depth at the
195 measurement point was <60 cm, and at 20% and 80% depths when the depth was ≥60
196 cm (Gore 2006). The current velocity at a given depth was measured using a portable
197 electromagnetic current meter (Flow-MATE Model 2000; Marsh-McBirney Inc.,
198 Frederick, MD, USA). The depth and current velocity within each quadrat were
199 determined as the mean of the measurements from the three measurement points in the
200 quadrats, and the current variability was expressed as the coefficient of variation of the
201 three velocities recorded in each quadrat. The bed material was visually estimated
202 based on the dominant material size at the center point of the quadrat, and categorized
203 as (1) silt (grain size <0.062 mm), (2) sand (0.062–2 mm), (3) gravel (2–16 mm), (4)
204 pebble (17–64 mm), (5) cobble (65–256 mm).

205

206 **Survey of habitat distribution**

207

208 The distribution of habitats in the NM and CS reaches was investigated using the
209 differential global positioning system (DGPS). The investigator using the DGPS walked
210 along the edge of the river banks (both sides) and the side channels, and obtained line

211 data. The investigator also determined the habitat type adjacent to his position and
212 stored this information with the line data; therefore, the line data consisted of habitat
213 types (except for the OX). The lengths of each habitat were measured in ArcMap
214 (ArcEditor ver. 10.0; Esri Co., Redlands, CA, USA). The OX was traced along a
215 longitudinal midline of the oxbow lake based on aerial photographs, and its length was
216 then also measured in ArcMap. All the habitats were quantified using the length but not
217 the area, because fish sampling was limited to the marginal area of the channel.
218 Mid-channel lines were created using the above line data recorded along both sides of
219 the riverbank, and were then used to measure the river length of the NM and CS reaches
220 via ArcMap. The river length and the total lengths of each habitat type in the study
221 reaches were then used to calculate the length of each habitat type in a 1-km river
222 ("average habitat length in a 1-km river"). The valley lengths of the NM and CS reaches
223 were also measured, and the lengths of each habitat type in a 1-km valley ("average
224 habitat length in a 1-km valley") were calculated. These average habitat lengths and the
225 density of each fish group in each habitat type (refer to "Fish survey") were used to
226 estimate the total abundance of each fish group in a 1-km river/valley in the NM and CS
227 reaches. In addition, the proportions of "fish abundance in each habitat type in a given
228 length of reach" to "the total fish abundance in a given length of reach" were also
229 calculated for each fish group in the NM and CS reaches; these were used to assess the
230 relative importance of each habitat type for the abundance of each fish group. The
231 average habitat length was also used to calculate the relative proportion of each habitat
232 type in the NM and CS reaches.
233
234 **Temporal changes in river channel and oxbow lake in the study segment**

235

236 The line data of the river channel in this study segment (23 km long in valley length)
237 were generated for the years 1950, 1965, 1978, 1990, and 2005 by tracing the river
238 course in aerial photographs from each year in ArcMap. Subsequently, these line data
239 were separated into natural meandering and modified channel classifications, and the
240 lengths of each channel type were measured in ArcMap. The line data (longitudinal
241 midline) of natural and artificially disconnected oxbow lakes were also generated for
242 each year, and the lengths and the numbers of both oxbow lake types were measured
243 and counted.

244

245 **Data analysis**

246

247 Non-metric multidimensional scaling (NMS) and an analysis of similarities (ANOSIM)
248 (Primer 6 version 6.1.6, Primer-E Ltd.) were performed to detect differences in the
249 composition of fish assemblages between the different types of habitats. NMS is a
250 nonparametric ordination technique, and is one of the most robust methods used for
251 exploring biological community data (McCune 1994). We used the Bray-Curtis distance
252 measure and $\log_{10}(X+1)$-transformed fish density data to stabilize the variances. All
253 samples (N = 147) from the NM and CS reaches were used in these analyses.

254 Principal component analysis (PCA) was performed using four habitat variables
255 (current velocity, current variability, depth, and bed material) to examine any changes in
256 the habitats in relation to river modifications. The OX was excluded from PCA because
257 the environmental characteristics of the OX were obviously distinct from those of other
258 habitats. Therefore, there were only 141 samples used for PCA. Prior to using PCA, all

of the habitat variables were standardized to have mean 0 and standard deviation 1.

Results

Habitats in the NM and CS reaches

The first axis (PC1) explained 55.9% of the variance, and the second axis (PC2) explained 24.8% (Fig. 2). PC1 was positively correlated with current variability and negatively correlated with current velocity and bed material (Fig. 2). PC2 was negatively correlated with depth (Fig. 2). On the diagram of PCA ordination, the OZ, IZ, and SZ+W in the CS reach are shown to have distributions close to those of the OB, IB, and RN in the NM reach, respectively (Fig. 2). However, the SZ in the CS reach was found to be located at a distance from any of the habitats in the NM reach, and was characterized by a uniform and fast water current and large bed material (Table 1 and Fig. 2). No habitats in the CS reach were distributed close to the BW, SC, and habitats with large wood pieces (hereafter referred to as wood habitats) in the NM reach, which were characterized by diverse, but moderate current velocities (Table 1 and Fig. 2). In summary, the BW, SC, and wood habitats were specific habitats in the NM reach, and the SZ was a specific habitat in the CS reach.

In the NM and CS reaches, river length was 1.88 km and 1.11 km in a 1-km valley, respectively, and the habitat lengths combined both sides of the river banks in a 1-km river and in a 1-km valley were estimated (Table 1). The OX occupied 10% of the entire habitat length of the NM reach (Table 1). The lengths of the OB, IB, and RN exceeded 20% of the entire habitat length, the lengths of the BW and SC were each approximately

283 6%, and the total length of the wood habitats was approximately 12%, whether the OX
284 was included or not. In the CS reach, the SZ largely occupied the channel (42%), the
285 OZ and IZ were nearly 30% of the channel, and SZ+W was rare (2%; Table 1).
286
287 **Fish assemblages in the habitats**
288
289 Six habitat types without large wood in the NM reach were widely scattered in the
290 diagram of NMS ordination (Fig. 3a), and significant differences in assemblages were
291 found between those types, except for between IB and RN (Table 2). Age-0 masu
292 salmon and sticklebacks were abundant in the BW and SC, and lampreys abundance
293 was also high in the BW and relatively low in the SC (Fig. 4). There was a high
294 abundance of age-≥1 Dolly Varden in the OB. An overwhelming abundance of
295 sticklebacks was found in the OX, which was also a habitat for lampreys. Although
296 Siberian stone loach was found in all habitats (except for the OX) there was a relatively
297 high abundance of the species in the RN, SC, and OB+W. Age-0 masu salmon was also
298 relatively high in the RN and the IB.
299 Four wood habitats in the NM reach were seen to be clumped in the diagram of NMS
300 ordination (Fig. 3b), and no significant differences in the assemblages were found
301 between these habitats (Table 2). However, these wood habitats were significantly
302 different from most of the habitats without wood except for the SC. The IB+W, RN+W,
303 and BW+W were used by abundant age-0 masu salmon, sticklebacks, and lampreys (Fig.
304 4). These were similar groups to those found in the SC and BW, with no significant
305 difference in the assemblages found between the four wood habitats and the SC. Age-≥1
306 masu salmon was abundant particularly in the OB+W, although no significant difference

307 in assemblages was found between the OB+W and the other wood habitats.

308 Four habitat types in the CS reach were clumped in the diagram of NMS ordination
309 whether large wood was present or not (Fig. 3c), and no significant difference in
310 assemblages was found between the habitats, except for between the SZ and IZ (Table
311 2). Although age-0 masu salmon was most abundant fish groups in the CS reach, the
312 abundance was considerably lower than that found in the NM reach (Fig. 4). In the OZ,
313 SZ, and SZ+W, all fish groups were scarce (other than Siberian stone loach in the OZ).
314 Lampreys and Siberian stone loach were relatively abundant in the IZ, but other fish
315 groups were scarce.

316

317 **Relative importance of the habitats**

318

319 The contribution to total abundance of age-0 masu salmon in the NM reach was
320 relatively high in the IB (21%), RN (28%), and combined wood habitats (16%; Table 3).
321 The contribution to age-≥1 masu salmon abundance was 37%, 31%, and 24% in the OB,
322 RN, and combined wood habitats, respectively. The OB contribution to age-≥1 Dolly
323 Varden abundance was 80%. The OX contribution to sticklebacks and lampreys
324 populations was 89% and 33%, respectively. Among the lotic habitat types, high
325 contributions to the sticklebacks population were found in the BW (27%), combined
326 wood habitats (26.5%), and SC (19%), and high contributions to the lampreys
327 population were found in the BW (37%) and combined wood habitats (29.7%). The
328 Siberian stone loach population was highly dependent on the contribution from the RN
329 (46%). Among the wood habitats, the RN+W provided a relatively higher contribution
330 to all fish groups. In the BW, SC, and all wood habitats, the number of fish groups

found in each sampling quadrat was relatively high (Table 3).

In the CS reach, the contribution to age-0 masu salmon abundance was highest in the SZ (41%), and relatively higher in the IZ (32%) and OZ (23%; Table 3). Age-≥1 masu salmon and Dolly Varden were highly dependent on the OZ (masu salmon: 68%, Dolly Varden: 100%). Eighty-four percent of the lamprey abundance was found in the IZ. The contribution to the Siberian stone loach population was 51% in the IZ and 30% in the OZ. The SZ+W was used the least by all fish groups. Sticklebacks were not found in the CS reach. There were no differences in the number of fish groups found per sampling quadrat (Table 3).

Effects of channel modification on the habitats and fish assemblages

The abundances of each fish group in a 1-km river and in a 1-km valley were estimated in both the NM and CS reaches (Fig. 5). The OX was excluded in these estimations. The abundance of masu salmon, Dolly Varden, and sticklebacks in a 1-km river and in a 1-km valley were higher in the NM reach than in the CS reach, with distinctly high abundances in a 1-km valley length of the NM reach. Although lamprey abundance in a 1-km river was almost same between the reaches and loach abundance in a 1-km river was slightly lower in the NM reach than in the CS reach, those in a 1-km valley were higher in the NM reach than in the CS reach.

The study segment, a 23-km valley, used to have a natural meandering channel consisting of the natural habitats until 1950 (Fig. 6a). However, the study segment was considerably modified by 1978, with a reduction in the natural meandering channel to 35.7% of the original length. In contrast, the length of the modified channel started to

355 increase since 1965. The total channel length reduced to approximately 70% of the
356 original length by 1978, with a loss of approximately 25 km of the natural meandering
357 channel. Artificially disconnected oxbow lakes also occurred with river modifications,
358 temporarily increasing in 1965, and then gradually decreasing over time thereafter (Fig.
359 6b).
360
361 **Discussion**
362
363 **Fish habitat in the natural meandering reach**
364
365 Nine habitat types in the natural meandering (NM) reach were dispersed in the diagram
366 of PCA ordination, indicating that meandering reaches consist of physically diverse
367 habitats. Other than the four wood habitats that had similar fish assemblages, fish
368 assemblages were generally different among the habitat types, indicating that individual
369 habitats had different functions as fish habitat and essentially supported the fish
370 assemblage. The use of different types of habitats by different fish assemblages has
371 been reported in various river systems (e.g., Inoue and Nakano 1999; Peterson and
372 Rabeni 2001; Beechie et al. 2005; Schwartz and Herricks 2008; Wolter et al. 2016). The
373 present study showed such habitat use in all types of habitat that were classified within
374 the natural meandering reach, although the sampling period was limited from summer to
375 early autumn. Specific use of the OB by Dolly Varden is likely because this fish is a
376 drift feeder that intercepts drifting prey items in or near fast flow areas (Nakano et al.
377 1999). High abundance of age-0 masu salmon in the BW and SC can be attributed to the
378 preference of small drift feeders for moderate current habitats due to low swimming

379 ability (Nagayama et al. 2009). Sticklebacks distinctly used the BW, SC, and OX
380 because they belong to a taxon that prefers lentic or stagnant habitats (Kawaguchi et al.
381 2005; Nagayama et al. 2012). Because lampreys burrow into mud and sand (Sugiyama
382 and Goto 2002; Yamazaki 2007), this fish was abundant in the BW and OX. Although
383 Siberian stone loach, a benthic fish species which is also often observed in the run of
384 modified river channels (Inoue and Nakano 1994; Toyoshima et al. 1996), were
385 distributed in various habitats, abundance of this fish was relatively higher in the RN
386 and SC.

387 Fish assemblages were enhanced by the addition of wood. The four habitats with
388 wood generally had different fish assemblages from those without it, and they had a
389 similar ecological function to the side channel habitats used by diverse and abundant
390 fish assemblages. Preference for wood habitats by fish has been widely reported,
391 irrespective of naturally distributed and artificially installed wood, natural and altered
392 rivers, and season (e.g., Beechie et al. 2005; Nagayama et al. 2012; Pander and Geist
393 2016). The high availability of wood habitats is attributed to local habitat heterogeneity
394 with cover effects provided by wood structures (Lehtinen et al. 1997; Nagayama et al.
395 2009, 2012). In this study, moderate current velocity and high current variability were
396 observed in wood habitats.

397 At a certain distance of meandering reach, all the habitat types were found to highly
398 contribute to the fish population(s) of at least one group (taxon), indicating that high
399 fish abundance and diversity in the meandering reach were supported by all the habitat
400 types. In particular, the contributions of lateral (BW and SC) and wood habitats to fish
401 abundance were generally high, despite the low spatial extent of these habitats. Both the
402 wood and lateral habitats provide a nursery, refuge, and foraging habitats for juvenile

403 salmonids (Moore and Gregory 1988; Beechie et al. 2005; Nagayama et al. 2009) and
404 other fish species, including both lotic and lentic fishes (Lehtinen et al. 1997; Kume et
405 al. 2014). These relatively rare habitats are likely to be essential for fish populations and
406 assemblages in meandering channels. Other habitats such as OB, IB, and RN had large
407 spatial extent and thereby highly contributed to the populations of lotic fish in the
408 meandering reach.
409
410 **Habitat alteration and fish assemblage deterioration: comparison between the**
411 **natural meandering and modified reaches**
412
413 Although habitat types except for SZ in the modified reach had similar environmental
414 conditions to some habitat types in the meandering reach, the abundance of most fish
415 groups, other than the Siberian stone loach which is known as a generalist species
416 (Toyoshima et al. 1996), were lower in those of the modified reach. For example, the
417 OZ in the modified reach had currents that were too fast and uniform for all fish groups,
418 even for the Dolly Varden. A limited use of the SZ+W habitat by most fish might be
419 attributed to its simple structure, generally consisting of a single or two pieces of wood
420 arranged parallel to the flow direction (based on our observation): fish diversity
421 increases with increased size and complexity of wood structures (Nagayama et al. 2012).
422 Meanwhile, Siberian stone loach and lampreys were relatively abundant in the IZ in the
423 modified reach, probably because microhabitats suitable for these fish, such as mud and
424 pebble (Sugiyama and Goto 2002; Yamazaki 2007), were locally distributed within the
425 IZ.
426 The modified reach lacked the equivalent habitats resembling the environmental

conditions of the BW, SC, and wood habitats in the meandering reach, which were suitable habitats for most of fish groups. Instead, the SZ, which was characterized by fast and uniform currents and was not well used by any fish group, occupied 42% of the habitats in the modified reach. The simplification of habitat structure and composition is a common consequence of channel modification (Moyle 1976; Nakano and Nakamura 2008; Wyżga et al. 2014). In our study reach, the loss of lateral and wood habitats and the creation of the SZ were caused by channel straightening and bank protection. These modifications not only directly alter the lateral habitats but also prevent the creation of any new ones. Moreover, these modifications change the dynamic processes of large wood. Fluvial disturbances such as bank erosion enable the transportation of wood from riparian forests to the river (Nakamura and Swanson 2003). Meandering channels have numerous bank erosion sites at the outer bend of channels, which commonly retain wood; thus wood habitat is a typical component in meandering rivers (Gurnell et al. 2002; Ward et al. 2002; Koehn et al. 2004; Lassettre et al. 2008). However, wood recruitment is prevented in modified channels by bank protection, and wood retention sites are lost in relation to channel straightening.

The abundance of masu salmon, Dolly Varden, and sticklebacks in a 1-km river were obviously lower in the modified reach than in the meandering reach; this difference became even more distinct when comparing the abundance in a 1-km valley. This indicates that these fish are negatively influenced by both changes in the habitat types and shortening of the channel with river modification. In contrast, the abundance of lampreys in a 1-km river was almost equal in the two study reaches and the abundance of Siberian stone loach in a 1-km river was slightly higher in the modified reach than in the meandering reach. This indicates that these fish were not negatively influenced by

451 the changes in habitat types with the river modifications and that there were substitute
452 habitats for them within the modified reach. However, their abundances in a 1-km
453 valley were relatively higher in the meandering reach than in the modified reach. These
454 results mean that lampreys and Siberian stone loach were only negatively influenced by
455 channel shortening (i.e., decrease in the absolute abundance of habitat) with river
456 modification.
457 In the study segment, the river modification with channel straightening decreased the
458 amount of natural habitats and the total channel length from 1950 to 1978; this likely
459 caused a serious deterioration of some fish populations in the study segment.
460 Channelization of short river reaches does not necessarily have serious impact on fish
461 populations (Wyżga et al. 2014). In our study segment, however, long, continuous river
462 reach has been channelized and thus the impact on some fish populations is expected to
463 be more serious. The oxbow, which was used by overwhelmingly abundant sticklebacks,
464 was not found in the study CS reach. However, several artificial oxbow lakes, created
465 by past channel shortening, remained in the inter-levee zone of the 23-km study
466 segment, and abundant sticklebacks have been found there (Kawaguchi et al. 2005).
467 Such artificial oxbow lakes may highly contribute to the persistence of stickleback
468 populations in the study segment, because there were few habitats suitable for them in
469 the modified reach. However, the number and the amount of artificial oxbow lakes
470 gradually decreased over time in the study segment. This might be caused by landfill for
471 farmland development, sedimentation from surrounding areas, and drawdown of the
472 groundwater level followed by channelization (Ahn et al. 2009).
473
474 **Perspectives on meander restoration**

This study showed the significance of meandering channels to habitat diversity and fish assemblages through the comparison of habitat types and their ecological functions. Our findings indicate that what is important is not simply the reconstruction of a meandering channel but the recovery of habitat diversity and the dynamic processes that occur through channel meandering. There have been a number of meander restorations that were designed with the objective of creating a stable, single-thread, meandering channel with bank protection at the outer bends (Kondolf et al. 2001; Kondolf 2006). However, in meander restorations of this type, populations of lentic fishes (such as the sticklebacks in our study) may not recover due to the lack of wood and lateral habitats (which include inter-levee oxbow lakes). For example, pilot re-meandering, which was implemented in the Shibetsu River, resulted in poor recovery of lentic fishes due to the lack of backwater habitats, whereas large-sized masu salmon were found in naturally created wood habitats (Kawaguchi et al. 2005; Nagayama et al. 2008). Reconstruction of all the habitat types is needed for effective rehabilitation of meandering rivers. In particular, wood and lateral habitats, which are relatively rare and vulnerable to channelization, are important habitats for many fish species and should be reconstructed in the restored reach. Furthermore, successful meander restoration can be achieved by recovering fluvial processes which naturally create all the habitat types.

This study also suggests that when monitoring the effects of river modification or meander restoration on fish assemblages, both the changes in the habitat types and the total abundance of habitats should be examined. In this study, lampreys and Siberian stone loach were not negatively impacted by the changes in habitat types, but impacted by the decreases in the absolute abundance of habitats with channel straightening.

499 Although there are generalist species that can withstand highly altered stretches of river
500 (Toyoshima et al. 1996; Muller et al. 2011), this study suggests that even these species
501 cannot avoid the negative effects of shrinking habitats from the channel shortening in
502 meandering rivers.
503
504 **Acknowledgments**
505
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513
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684 Figure captions

685 **Fig. 1** Location and channel form of the study reaches in the 23-km study segment of
686 the Shibetsu River, Hokkaido, Japan, and pattern diagrams of the distribution of
687 habitat types in the natural meandering (NM) and channelized, straightened (CS)
688 reaches.

689 **Fig. 2** Principal component analysis (PCA) ordination of habitat variables of each type
690 of the habitats. Black and gray plots indicate the habitats of the natural meandering
691 (NM) and the channelized, straightened (CS) reaches, respectively, and are
692 expressed as mean with ± 1 standard error of each habitat for each axis. Percent of
693 variance explained by each principal component (PC) and factor loadings (> 0.5
694 and < −0.5) on each PC for each environmental variable are also shown. Please
695 refer to Table 1 for abbreviation of habitat types.

696 **Fig. 3** Non-metric multidimensional scaling (NMS) ordination of fish assemblages from
697 each habitat type. Plots are expressed as mean with ± 1 standard error of each
698 habitat for each axis. All habitats were used in NMS and are shown in separate
699 panels: **a** habitats without wood and **b** habitats with wood in the natural
700 meandering (NM) reach, and **c** all habitats in the channelized, straightened (CS)
701 reach. The stress value of the NMS plot was 0.11, indicating an acceptable level of
702 fit between dissimilarity and distance (Kruskal 1964). Please refer to Table 1 for
703 abbreviation of habitat types.

704 **Fig. 4** Abundance (mean + 1 standard error) of each fish group in each habitat type.
705 Black and gray bars indicate the natural meandering (NM) and channelized,
706 straightened (CS) reaches, respectively. Please refer to Table 1 for abbreviation of
707 habitat types.

Fig. 5 Estimated total abundance of each fish group in a 1-km river (black bar) and in a 1-km valley (gray bar) in the natural meandering (NM) and the channelized, straightened (CS) reaches. Oxbow (OX) is excluded from the estimation. The difference in fish abundance in a 1-km river between the NM and CS reaches is associated with the difference in habitat quality between the reaches (i.e., the effect of habitat change with river modification), and that in a 1-km valley is associated with the difference in habitat length between the reaches (i.e., the effect of channel shortening with river modification) as well as habitat quality.

Fig. 6 Temporal changes in **a** channel length (m), **b** oxbow length (m), and oxbow number (numeric characters within the bars) in the study segment from 1950 to 2005. Black and gray bars indicate natural meandering and modified channels in panel **a,** and natural and artificial oxbow lakes in panel **b**, respectively.

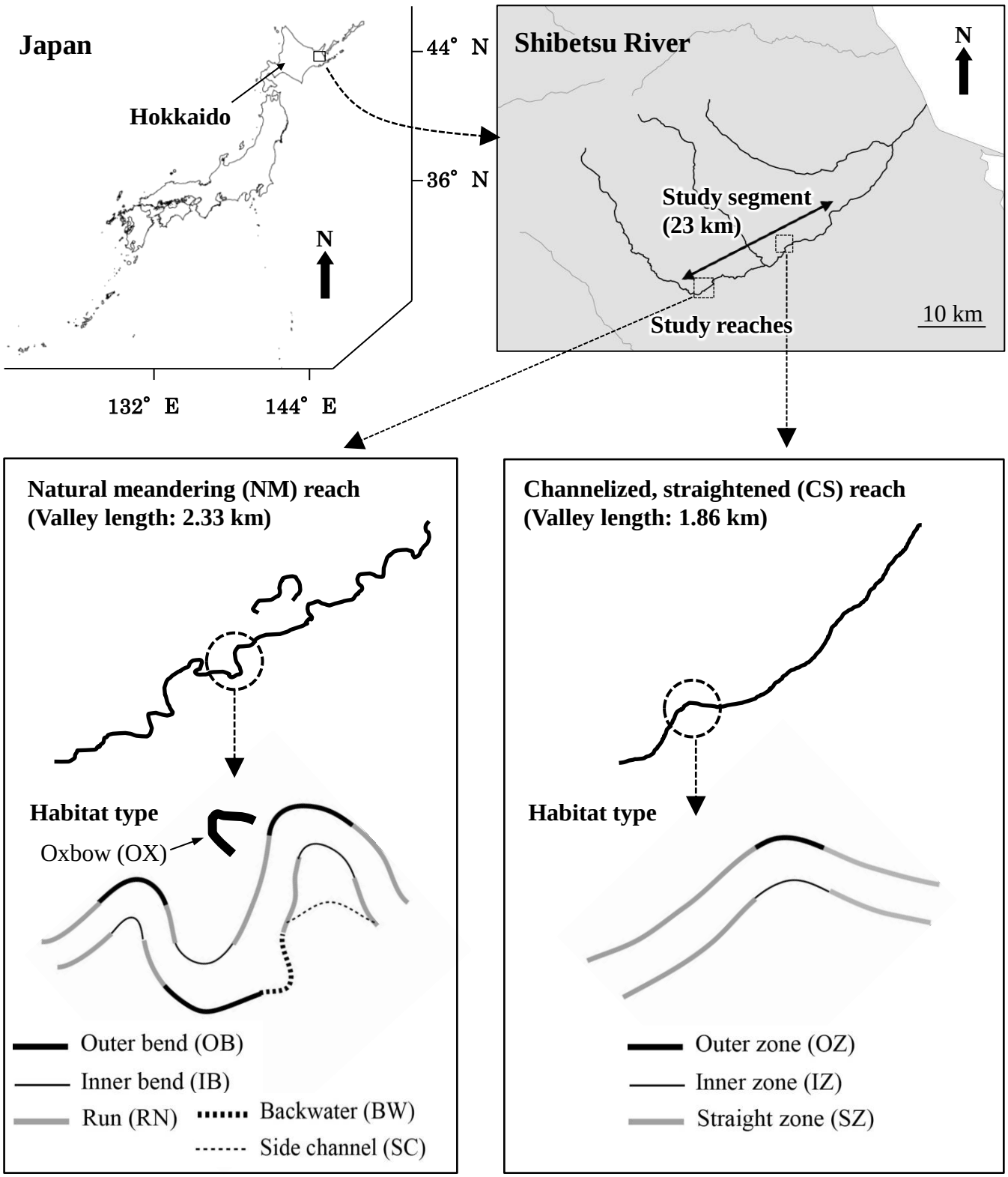

Figure 1 Nagayama & Nakamura

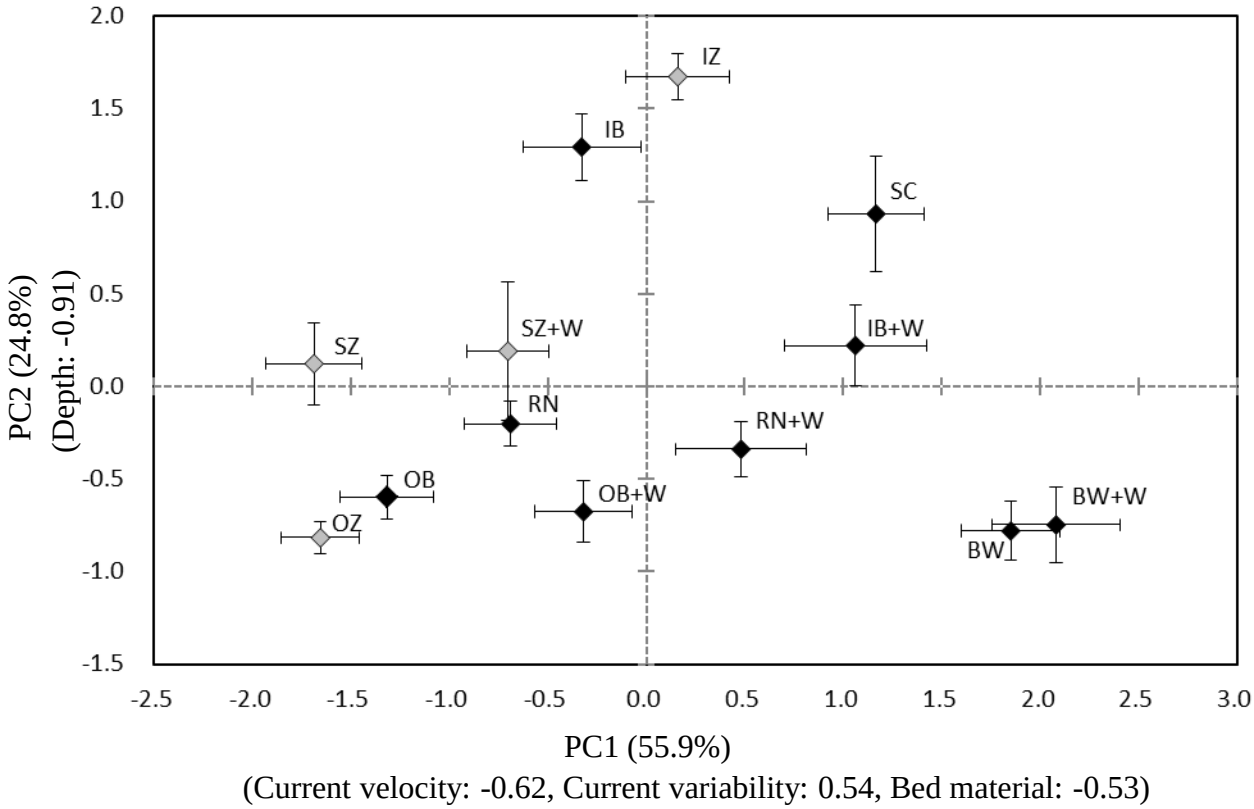

Figure 2 Nagayama & Nakamura

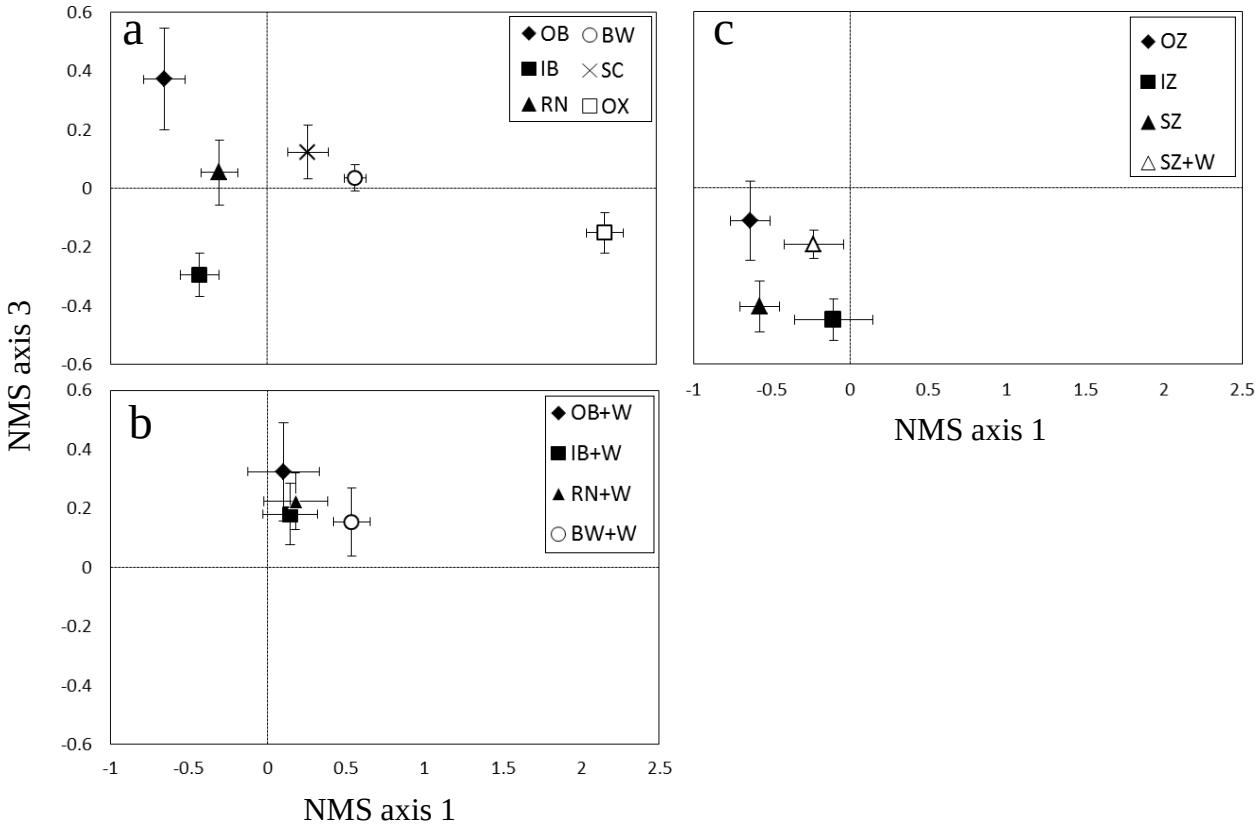

Figure 3 Nagayama & Nakamura

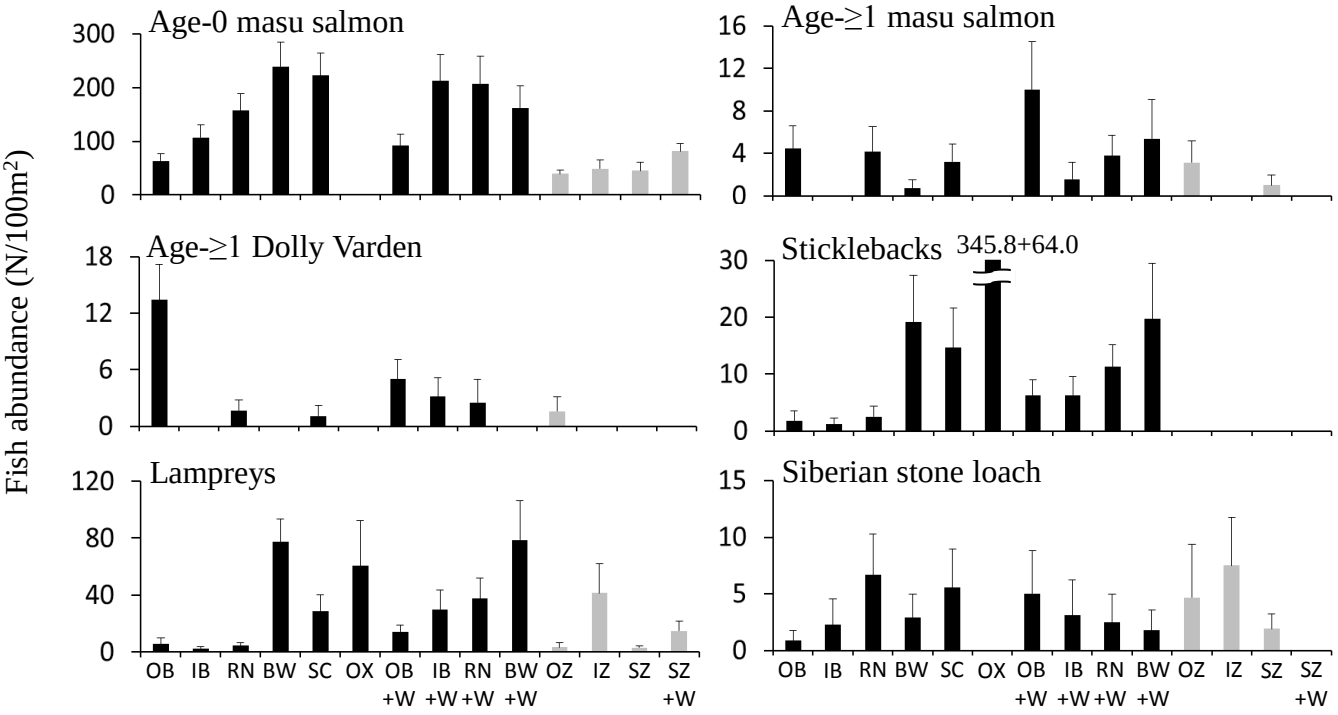

Figure 4 Nagayama & Nakamura

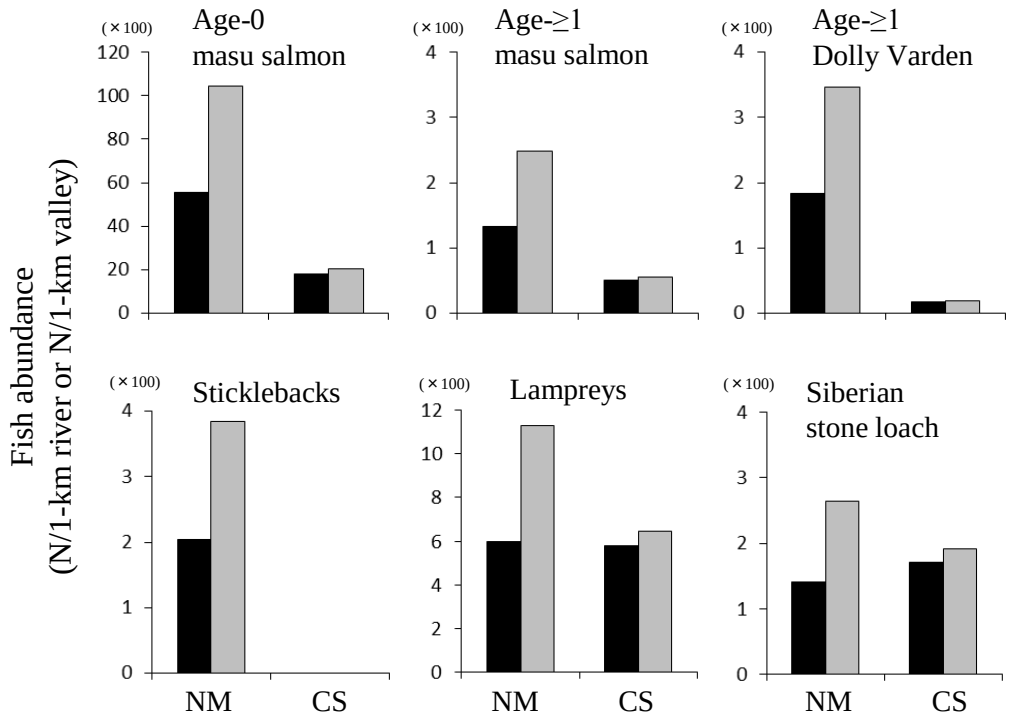

Figure 5 Nagayama & Nakamura

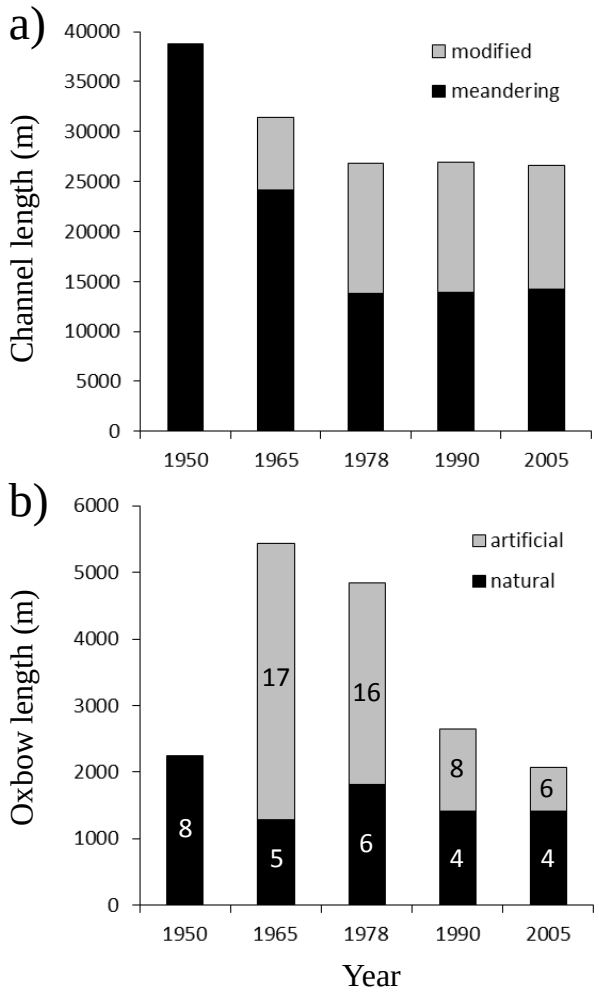

Figure 6 Nagayama & Nakamura

Table 1 The number of sampling quadrats, environmental variables (mean ± SD), average habitat lengths in a 1-km river and a 1-km valley, and occupancy of the habitats in the natural meandering (NM) and channelized, straightened (CS) reaches. The values of occupancy in parentheses indicate the values when the oxbow lake (OX) was excluded from the calculations. OB = outer bend; IB = inner bend; RN = run; BW = backwater; SC = side channel; W = wood; OZ = outer zone; IZ = inner zone; SZ = straight zone.

Reach	Habitat (number of sample)	Environmental variable				Average habitat length (m/1-km river)*	Average habitat length (m/1-km valley)*	Occupancy
		Current velocity (cm/s)	Current variability (%)	Depth (cm)	Bed material (1-5)			
NM reach	OB (n=14)	63.2±20.4	17.5±13.5	76.4±16.2	4.3±1.1	548.7	1034.1	0.23 (0.26)
	IB (n=11)	41.9±15.2	20.5±23.0	20.6±6.1	3.6±0.9	544.7	1026.4	0.23 (0.26)
	RN (n=15)	45.8±18.0	25.9±21.2	57.1±16.7	3.8±0.7	491.6	926.4	0.21 (0.23)
	BW (n=17)	10.7±7.8	45.2±27.8	52.0±21.6	1.5±1.0	141.7	267.1	0.06 (0.07)
	SC (n=12)	21.0±12.3	56.4±29.8	24.2±11.2	2.9±1.4	133.3	251.2	0.06 (0.06)
	OX (n=6)	0	0	38.2±10.9	1.0±0	248.1	467.5	0.10
	OB+W (n=10)	40.2±9.7	32.5±21.7	69.3±15.7	3.2±1.1	91.1	171.7	0.04 (0.04)
	IB+W (n=8)	22.2±10.0	64.5±41.8	35.5±11.7	2.5±1.1	23.7	44.6	0.01 (0.01)
	RN+W (n=10)	27.6±13.9	41.2±42.2	49.3±16.3	2.5±1.3	134.8	254.1	0.06 (0.06)
	BW+W (n=7)	9.0±5.7	52.3±28.0	47.6±14.2	1.3±0.5	23.7	44.6	0.01 (0.01)
CS reach	OZ (n=8)	76.8±27.1	9.5±4.9	81.0±9.4	3.8±0.5	543.4	605.9	0.27
	IZ (n=10)	27.9±10.4	21.4±8.3	16.7±6.1	3.9±1.1	586.8	654.3	0.29
	SZ (n=13)	61.6±21.3	6.3±4.5	50.4±22.9	4.2±0.6	831.2	926.9	0.42
	SZ+W (n=6)	44.0±13.7	19.6±16.4	48.2±24.4	3.8±0.4	38.6	43.0	0.02

* The habitat lengths include rounding errors.

Table 2 *P* values derived from analysis of similarities (ANOSIM) of fish assemblages among the habitats. NM reach = natural meandering reach; CS reach = channelized, straightened reach; OB = outer bend; IB = inner bend; RN = run; BW = backwater; SC = side channel; OX = oxbow lake; W = wood; OZ = outer zone; IZ = inner zone; SZ = straight zone.

Reach	Habitat	NM reach										CS reach			
		OB	IB	RN	BW	SC	OX	OB+W	IB+W	RN+W	BW+W	OZ	IZ	SZ	SZ+W
NM reach	OB														
	IB	0.013*													
	RN	0.020*	0.818												
	BW	0.001*	0.001*	0.001*											
	SC	0.001*	0.003*	0.003*	0.005*										
	OX	0.001*	0.001*	0.001*	0.001*	0.001*									
	OB+W	0.056	0.005*	0.034*	0.001*	0.187	0.001*								
	IB+W	0.008*	0.010*	0.303	0.011*	0.903	0.001*	0.829							
	RN+W	0.002*	0.008*	0.041*	0.020*	0.982	0.001*	0.450	0.954						
	BW+W	0.001*	0.001*	0.006*	0.207	0.902	0.001*	0.399	0.456	0.945					
CS reach	OZ	0.467	0.180	0.246	0.001*	0.002*	0.001*	0.061	0.016*	0.006*	0.002*				
	IZ	0.001*	0.257	0.017*	0.001*	0.001*	0.001*	0.001*	0.001*	0.001*	0.001*	0.331			
	SZ	0.005*	0.077	0.032*	0.001*	0.003*	0.001*	0.029*	0.045*	0.011*	0.011*	0.364	0.049*		
	SZ+W	0.242	0.430	0.823	0.003*	0.138	0.002*	0.343	0.257	0.130	0.009*	0.167	0.149	0.811	

* Significant difference in fish assemblages between the habitats.

Table 3 The contribution of habitats to the total abundance of each fish group estimated from fish abundance (N/100m^2) and actual area (m^2) of each habitat in each of the study reaches and the number (mean ± SD) of fish groups found in a sampling quadrat in each of the study reaches. The values in parentheses indicate the values when the oxbow lake (OX) was excluded from the calculations. OB = outer bend; IB = inner bend; RN = run; BW = backwater; SC = side channel; W = wood; OZ = outer zone; IZ = inner zone; SZ = straight zone.

Reach	Habitat	Contribution to total abundance of each fish group						Number of fish group
		Age-0 masu salmon	Age-≥1 masu salmon	Age-≥1 Dolly Varden	Sticklebacks	Lampreys	Siberian stone loach	
NM reach	OB	0.12	0.37	0.80	0.01 (0.10)	0.07 (0.10)	0.07	2.1 ± 1.0
	IB	0.21	0	0	0.01 (0.06)	0.03 (0.04)	0.17	1.4 ± 0.7
	RN	0.28	0.31	0.09	0.01 (0.12)	0.05 (0.07)	0.46	2.0 ± 0.8
	BW	0.12	0.02	0	0.03 (0.27)	0.24 (0.37)	0.06	2.8 ± 0.8
	SC	0.11	0.06	0.02	0.02 (0.19)	0.09 (0.13)	0.11	2.8 ± 1.0
	OX	0	0	0	0.89	0.33	0	1.5 ± 0.5
	OB+W	0.03	0.14	0.05	0.01 (0.06)	0.03 (0.04)	0.06	2.9 ± 1.1
	IB+W	0.02	0.01	0.01	<0.01 (0.01)	0.02 (0.02)	0.01	2.5 ± 1.2
	RN+W	0.10	0.08	0.04	0.02 (0.15)	0.11 (0.17)	0.05	2.7 ± 0.9
	BW+W	0.01	0.02	0	0.01 (0.05)	0.04 (0.06)	0.01	3.0 ± 0.8
CS reach	OZ	0.23	0.68	1.00	-	0.06	0.30	1.6 ± 0.9
	IZ	0.32	0	0	-	0.84	0.51	1.6 ± 0.7
	SZ	0.41	0.32	0	-	0.08	0.19	1.5 ± 0.7
	SZ+W	0.03	0	0	-	0.02	0	1.5 ± 0.5