Title	The significance of meandering channel to habitat diversity and fish assemblage: a case study in the Shibetsu River, northern Japan
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Citation	Limnology, 19(1), 7-20 https://doi.org/10.1007/s10201-017-0512-4
Issue Date	2018-01
Doc URL	http://hdl.handle.net/2115/72475
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Type	article (author version)
File Information	2017_Limnology_Nagayama&Nakamura_RG-1.pdf

An article prepared for **Limnology**

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 enhanced the diversity and abundance of aquatic organisms such as fish and macroinvertebrates (Lorenz et al. 2009; Nakamura et al. 2014), and similar positive biological responses are expected at other sites in the future (Trexler 1995; Pedersen et al. 2007b; Hauer et al. 2014). Conversely, a number of meander restoration projects have failed to facilitate a significant recovery of target species and assemblages due to a lack of understanding of key habitats, including floodplain waterbodies, and large-scale factors that control features of river reach and segment such as sediment load (Holubova and Lisicky 2001; Kondolf et al. 2001; Kawaguchi et al. 2005; Kondolf 2006). Numerous studies have described the structure and function of natural habitats of fish in various river systems (e.g., Murphy et al. 1989; Fausch and Northcote 1992; Inoue and Nakano 1999; Peterson and Rabeni 2001; Beechie et al. 2005; Schwartz and Herricks 2008; Zeug and Winemiller 2008; Nagayama et al. 2012; Wolter et al. 2016). Most of these studies also included parts of the habitat components which usually appear in meandering channels. However, the entire distribution and composition of all habitats along the meandering river have not been studied, which are indispensable for understanding effects of channel modification and meander restoration on fish assemblages and conserving fish diversity in river reach and segment scales.

The overall objectives of this study were to elucidate the structure and function of habitats for fish in a meandering river by comparing meandering and modified reaches to provide the practical knowledge required for the management and restoration of meandering rivers. Our specific objectives were to (1) compare physical characteristics among habitat types classified in meandering and modified channels, (2) describe use of the habitat types by fish, (3) elucidate contributions of the habitat types to fish 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 straightened using concrete blocks as bank protection, and riparian trees are scarce along the banks. The valley length and the river length of the entire CS reach are 1.86 km and 2.07 km, respectively (i.e., sinuosity index = 1.11). In both types of study reach, the average bed slope is approximately 1/450, and the dominant bed material is pebble (17–64 mm). The channel width is 10–20 m and 25–30 m in the NM and CS reaches, respectively. The river lengths selected for both study reaches measured more than 50 times the length of channel width, to encompass all types of habitats and to enable the characterization of fish fauna in the reaches (Bisson et al. 2006; Li and Li 2006).

The Shibetsu River has only two small weirs, and these are located in the lower part of the study reaches. Because a wide passage for fish is constructed at the weirs, anadromous fish such as salmon and lamprey are able to migrate upstream beyond the weirs. The fish species observed in our study reaches were masu (*Oncorhynchus masou*) and chum salmon (*O. keta*), Dolly Varden (*Salvelinus malma malma*), white spotted char (*S. leucomaenis*), rainbow trout (*O. mykiss*), Siberian stone loach (*Noemacheilus barbatulus toni*), sticklebacks [*Pungitius* sp. (Freshwater type), and *P. tymensis*], and lampreys (*Lethenteron* spp.). Most of the lampreys observed were ammocoetes, and probably consisted of three species (*L. kesseleri*, *L. japonicum*, and *L. reissneri*).

We conducted field surveys from late June to early September in 2006 and 2007 during the period of base flow. Water temperature ranged from 10.7 to 14.4 °C during the surveys. As fish community composition can be dependent on season (Pander and Geist 2010), the communities observed in this study might be limited by the study period.

Habitat classification

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

Natural meandering (NM) reach

Ten types of habitat were identified in the NM reach: oxbow (OX), outer bend (OB), inner bend (IB), run (RN), backwater (BW), side channel (SC), outer bend with large wood (OB+W), inner bend with large wood (IB+W), run with large wood (RN+W), and backwater with large wood (BW+W) (Fig. 1 and Table 1). The OX was a historic meander bend that had been isolated from the main channel during the base flow. The OB was a lateral scour pool created on the outer bend of a river channel. The IB was a shallow area located on the inner bend. The RN was generally located between adjacent channel bends across the river channel. The BW was found on the concave part of river 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 channel because it was considered to be an ineffective practice in such an open area (Beechie et al. 2005). One or two quadrats were set in each of the individual accessible habitats in the NM reach. The number of sampling quadrats in each of the habitat types was 6–15, with 110 quadrats in the NM reach and 37 quadrats in the CS reach in total (Table 1). Because the individual habitats in the CS reach had a longitudinally long distance, three or four quadrats were established in each of the individual accessible habitats, except for in the SZ+W.

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

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

Environmental survey

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

Survey of habitat distribution

The distribution of habitats in the NM and CS reaches was investigated using the differential global positioning system (DGPS). The investigator using the DGPS walked along the edge of the river banks (both sides) and the side channels, and obtained line data. The investigator also determined the habitat type adjacent to his position and stored this information with the line data; therefore, the line data consisted of habitat types (except for the OX). The lengths of each habitat were measured in ArcMap (ArcEditor ver. 10.0; Esri Co., Redlands, CA, USA). The OX was traced along a longitudinal midline of the oxbow lake based on aerial photographs, and its length was then also measured in ArcMap. All the habitats were quantified using the length but not the area, because fish sampling was limited to the marginal area of the channel.

Mid-channel lines were created using the above line data recorded along both sides of the riverbank, and were then used to measure the river length of the NM and CS reaches via ArcMap. The river length and the total lengths of each habitat type in the study reaches were then used to calculate the length of each habitat type in a 1-km river ("average habitat length in a 1-km river"). The valley lengths of the NM and CS reaches were also measured, and the lengths of each habitat type in a 1-km valley ("average habitat length in a 1-km valley") were calculated. These average habitat lengths and the density of each fish group in each habitat type (refer to "Fish survey") were used to estimate the total abundance of each fish group in a 1-km river/valley in the NM and CS reaches. In addition, the proportions of "fish abundance in each habitat type in a given length of reach" to "the total fish abundance in a given length of reach" were also calculated for each fish group in the NM and CS reaches; these were used to assess the relative importance of each habitat type for the abundance of each fish group. The average habitat length was also used to calculate the relative proportion of each habitat type in the NM and CS reaches.

Temporal changes in river channel and oxbow lake in the study segment

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

Data analysis

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

Principal component analysis (PCA) was performed using four habitat variables (current velocity, current variability, depth, and bed material) to examine any changes in the habitats in relation to river modifications. The OX was excluded from PCA because the environmental characteristics of the OX were obviously distinct from those of other 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

6%, and the total length of the wood habitats was approximately 12%, whether the OX was included or not. In the CS reach, the SZ largely occupied the channel (42%), the OZ and IZ were nearly 30% of the channel, and SZ+W was rare (2%; Table 1).

Fish assemblages in the habitats

Six habitat types without large wood in the NM reach were widely scattered in the diagram of NMS ordination (Fig. 3a), and significant differences in assemblages were found between those types, except for between IB and RN (Table 2). Age-0 masu salmon and sticklebacks were abundant in the BW and SC, and lampreys abundance was also high in the BW and relatively low in the SC (Fig. 4). There was a high abundance of age-≥1 Dolly Varden in the OB. An overwhelming abundance of sticklebacks was found in the OX, which was also a habitat for lampreys. Although Siberian stone loach was found in all habitats (except for the OX) there was a relatively high abundance of the species in the RN, SC, and OB+W. Age-0 masu salmon was also relatively high in the RN and the IB.

Four wood habitats in the NM reach were seen to be clumped in the diagram of NMS ordination (Fig. 3b), and no significant differences in the assemblages were found between these habitats (Table 2). However, these wood habitats were significantly different from most of the habitats without wood except for the SC. The IB+W, RN+W, and BW+W were used by abundant age-0 masu salmon, sticklebacks, and lampreys (Fig. 4). These were similar groups to those found in the SC and BW, with no significant difference in the assemblages found between the four wood habitats and the SC. Age-≥1 masu salmon was abundant particularly in the OB+W, although no significant difference in assemblages was found between the OB+W and the other wood habitats.

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

Relative importance of the habitats

The contribution to total abundance of age-0 masu salmon in the NM reach was relatively high in the IB (21%), RN (28%), and combined wood habitats (16%; Table 3). The contribution to age-≥1 masu salmon abundance was 37%, 31%, and 24% in the OB, RN, and combined wood habitats, respectively. The OB contribution to age-≥1 Dolly Varden abundance was 80%. The OX contribution to sticklebacks and lampreys populations was 89% and 33%, respectively. Among the lotic habitat types, high contributions to the sticklebacks population were found in the BW (27%), combined wood habitats (26.5%), and SC (19%), and high contributions to the lampreys population were found in the BW (37%) and combined wood habitats (29.7%). The Siberian stone loach population was highly dependent on the contribution from the RN (46%). Among the wood habitats, the RN+W provided a relatively higher contribution 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 increase since 1965. The total channel length reduced to approximately 70% of the original length by 1978, with a loss of approximately 25 km of the natural meandering channel. Artificially disconnected oxbow lakes also occurred with river modifications, temporarily increasing in 1965, and then gradually decreasing over time thereafter (Fig. 6b).

Discussion

Fish habitat in the natural meandering reach

Nine habitat types in the natural meandering (NM) reach were dispersed in the diagram of PCA ordination, indicating that meandering reaches consist of physically diverse habitats. Other than the four wood habitats that had similar fish assemblages, fish assemblages were generally different among the habitat types, indicating that individual habitats had different functions as fish habitat and essentially supported the fish assemblage. The use of different types of habitats by different fish assemblages has been reported in various river systems (e.g., Inoue and Nakano 1999; Peterson and Rabeni 2001; Beechie et al. 2005; Schwartz and Herricks 2008; Wolter et al. 2016). The present study showed such habitat use in all types of habitat that were classified within the natural meandering reach, although the sampling period was limited from summer to early autumn. Specific use of the OB by Dolly Varden is likely because this fish is a drift feeder that intercepts drifting prey items in or near fast flow areas (Nakano et al. 1999). High abundance of age-0 masu salmon in the BW and SC can be attributed to the preference of small drift feeders for moderate current habitats due to low swimming ability (Nagayama et al. 2009). Sticklebacks distinctly used the BW, SC, and OX because they belong to a taxon that prefers lentic or stagnant habitats (Kawaguchi et al. 2005; Nagayama et al. 2012). Because lampreys burrow into mud and sand (Sugiyama and Goto 2002; Yamazaki 2007), this fish was abundant in the BW and OX. Although Siberian stone loach, a benthic fish species which is also often observed in the run of modified river channels (Inoue and Nakano 1994; Toyoshima et al. 1996), were distributed in various habitats, abundance of this fish was relatively higher in the RN and SC.

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

At a certain distance of meandering reach, all the habitat types were found to highly contribute to the fish population(s) of at least one group (taxon), indicating that high fish abundance and diversity in the meandering reach were supported by all the habitat types. In particular, the contributions of lateral (BW and SC) and wood habitats to fish abundance were generally high, despite the low spatial extent of these habitats. Both the wood and lateral habitats provide a nursery, refuge, and foraging habitats for juvenile salmonids (Moore and Gregory 1988; Beechie et al. 2005; Nagayama et al. 2009) and other fish species, including both lotic and lentic fishes (Lehtinen et al. 1997; Kume et al. 2014). These relatively rare habitats are likely to be essential for fish populations and assemblages in meandering channels. Other habitats such as OB, IB, and RN had large spatial extent and thereby highly contributed to the populations of lotic fish in the meandering reach.

Habitat alteration and fish assemblage deterioration: comparison between the natural meandering and modified reaches

Although habitat types except for SZ in the modified reach had similar environmental conditions to some habitat types in the meandering reach, the abundance of most fish groups, other than the Siberian stone loach which is known as a generalist species (Toyoshima et al. 1996), were lower in those of the modified reach. For example, the OZ in the modified reach had currents that were too fast and uniform for all fish groups, even for the Dolly Varden. A limited use of the SZ+W habitat by most fish might be attributed to its simple structure, generally consisting of a single or two pieces of wood arranged parallel to the flow direction (based on our observation): fish diversity increases with increased size and complexity of wood structures (Nagayama et al. 2012). Meanwhile, Siberian stone loach and lampreys were relatively abundant in the IZ in the modified reach, probably because microhabitats suitable for these fish, such as mud and pebble (Sugiyama and Goto 2002; Yamazaki 2007), were locally distributed within the IZ.

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 the changes in habitat types with the river modifications and that there were substitute habitats for them within the modified reach. However, their abundances in a 1-km valley were relatively higher in the meandering reach than in the modified reach. These results mean that lampreys and Siberian stone loach were only negatively influenced by channel shortening (i.e., decrease in the absolute abundance of habitat) with river modification.

In the study segment, the river modification with channel straightening decreased the amount of natural habitats and the total channel length from 1950 to 1978; this likely caused a serious deterioration of some fish populations in the study segment. Channelization of short river reaches does not necessarily have serious impact on fish populations (Wyżga et al. 2014). In our study segment, however, long, continuous river reach has been channelized and thus the impact on some fish populations is expected to be more serious. The oxbow, which was used by overwhelmingly abundant sticklebacks, was not found in the study CS reach. However, several artificial oxbow lakes, created by past channel shortening, remained in the inter-levee zone of the 23-km study segment, and abundant sticklebacks have been found there (Kawaguchi et al. 2005). Such artificial oxbow lakes may highly contribute to the persistence of stickleback populations in the study segment, because there were few habitats suitable for them in the modified reach. However, the number and the amount of artificial oxbow lakes gradually decreased over time in the study segment. This might be caused by landfill for farmland development, sedimentation from surrounding areas, and drawdown of the groundwater level followed by channelization (Ahn et al. 2009).

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.

Although there are generalist species that can withstand highly altered stretches of river (Toyoshima et al. 1996; Muller et al. 2011), this study suggests that even these species cannot avoid the negative effects of shrinking habitats from the channel shortening in meandering rivers.

Acknowledgments

We are grateful for the supports of the fund for the "River Ecology Research Group of Japan" on the Shibetsu River, the River Fund in charge of the River Foundation, Japan, the Grants in Aid for Scientific Research (No. 19208013, No. 23248021, No. 26740048) from the Ministry of Education, Science, and Culture, Japan, and the Environment Research and Technology Development Fund (S9 and 4D-1201) from the Ministry of the Environment, Japan. We also thank our colleagues, particularly T. Seno and N. Ishiyama of Hokkaido University, for their assistance in conducting fieldwork.

References

Ahn YS, Nakamura F, Kizuka T, Nakamura Y (2009) Elevated sedimentation in lake records linked to agricultural activities in the Ishikari River floodplain, northern Japan. Earth Surf Proc Land 34:1650–1660

Beechie TJ, Liermann M, Beamer EM, Henderson R (2005) A classification of habitat types in a large river and their use by juvenile salmonids. T Am Fish Soc 134:717–729

Benke AC, Wallace JB (2003) Influence of wood on invertebrate communities in streams and rivers. In: Gregory SV, Boyer KL, Gurnell AM (eds) The ecology and management of wood in world rivers. American Fisheries Society, Symposium 37, Bethesda, Maryland, pp 149–177

Bisson PA, Montgomery DR, Buffington JM (2006) Valley segments, stream reaches, and channel units. In: Hauer FR, Lamberti GA (eds) Methods in stream ecology, 2nd edn. Academic Press, San Diego, California, pp 23–49

Bisson PA, Sullivan K, Nielsen JL (1988) Channel hydraulics, habitat use, and body form of juvenile coho salmon, steelhead, and cutthroat trout in streams. T Am Fish Soc 117:262–273

Crook DA, Robertson AI (1999) Relationships between riverine fish and woody debris: implications for lowland rivers. Mar Freshwater Res 50:941–953

Dahm CN, Cummins KW, Valett HM, Coleman RL (1995) An ecosystem view of the restoration of the Kissimmee River. Restor Ecol 3:225–238

Fausch KD, Northcote TG (1992) Large woody debris and salmonid habitat in a small coastal British Columbia stream. Can J Fish Aquat Sci 49: 682–693

Friberg N, Kronvang B, Hansen H, Svendsen LM (1998) Long-term, habitat-specific response of a macroinvertebrate community to river restoration. Aquat Conserv 8:87–99

Gore JA (2006) Discharge measurements and streamflow analysis. In: Hauer FR, Lamberti GA (eds) Methods in stream ecology, 2nd edn. Academic Press, San Diego, California, pp 51–77

Gore JA, Shields FD Jr. (1995) Can large rivers be restored? BioScience 45:142–152

Grant GE, Swanson FJ, Wolman MG (1990) Pattern and origin of stepped-bed morphology in high-gradient streams, Western Cascades, Oregon. Geol Soc Am Bull

102:340–352

Gregory SV, Swanson FJ, McKee WA, Cummins KW (1991) An ecosystem perspective of riparian zones: focus on links between land and water. BioScience 41:540–551

Gurnell AM, Piégay H, Swanson FJ, Gregory SV (2002) Large wood and fluvial processes. Freshw Biol 47:601–619

Hauer C, Mandlburger G, Schober B, Habersack H (2014) Morphologically related integrative management concept for reconnecting abandoned channels based on airborne LiDAR data and habitat modelling. River Res Appl 30:537–556

Hawkins CP, Kershner JL, Bisson PA, Bryant MD, Decker LM, Gregory SV, McCullough DA, Overton CK, Reeves GH, Steedman RJ, Young MK (1993) A hierarchical approach to classifying stream habitat features. Fisheries 18:3–12

Hirai Y, Kuga T (2005) The approach to nature restoration project for the Shibetsu River. Ecol Civil Eng 7:143–150 [In Japanese with English summary]

Holubova K, Lisicky MJ (2001) River and environmental processes in the wetland restoration of the Morava River. In: Falconer RA, Blain WR (eds) River basin management. WIT Press, Southampton, UK, pp 179–188

Inoue M, Nakano S (1994) Physical environment structure of a small stream with special reference to fish microhabitat. Jpn J Ecol 44:151–160 [In Japanese with English summary]

Inoue M, Nakano S (1999) Habitat structure along channel-unit sequences for juvenile salmon: a subunit-based analysis of in-stream landscapes. Freshw Biol 42:597–608

Jurajda P (1995) Effect of channelization and regulation on fish recruitment in a flood-plain river. Regul River 10:207–215

Kawaguchi Y, Nakamura F, Kayaba Y (2005) Effects of a re-meandering project on the physical habitats and fish in the Shibetsu River. Ecol Civil Eng 7:187–199 [In Japanese with English summary]

Koehn JD, Nicol SJ, Fairbrother PS (2004) Spatial arrangement and physical characteristics of structural woody habitat in a lowland river in south-eastern Australia. Aquat Conserv 14:457–464

Kondolf GM (2006) River restoration and meanders. Ecol Soc 11: Art. No. 42

Kondolf GM, Smeltzer MW, Railsback SF (2001) Design and performance of a channel reconstruction project in a coastal California gravel-bed stream. Environ Manage 28:761–776

Kruskal JB (1964) Multidimensional scaling by optimizing goodness of fit to a nonmetric hypothesis. Psychometrika 29:1–27

Kume M, Negishi JN, Sagawa S, Miyashita T, Aoki S, Ohmori T, Sanada S, Kayaba Y (2014) Winter fish community structures across floodplain backwaters in a drought year. Limnology 15:109–115

Lassettre NS, Piégay H, Dufour S, Rollet AJ (2008) Decadal changes in distribution and frequency of wood in a free meandering river, the Ain River, France. Earth Surf Proc Land 33:1098–1112

Lehtinen RM, Mundahl ND, Madejczyk JC (1997) Autumn use of woody snags by fishes in backwater and channel border habitats of a large river. Environ Biol Fish 49:7–19

Li HW, Li JL (2006) Role of fish assemblages in stream communities. In: Hauer FR, Lamberti GA (eds) Methods in stream ecology, 2nd edn. Academic Press, San Diego, California, pp 489–514

Lorenz AW, Jähnig SC, Hering D (2009) Re-meandering German lowland streams:

qualitative and quantitative effects of restoration measures on hydromorphology and macroinvertebrates. Environ Manage 44:745–754

McCune B (1994) Improving community analysis with the Beals smoothing function. Ecoscience 1:82–86

Moerke AH, Gerard KJ, Latimore JA, Hellenthal RA, Lamberti GA (2004) Restoration of an Indiana, USA, stream: bridging the gap between basic and applied lotic ecology. J N Am Benthol Soc 23:647–660

Moore KMS, Gregory SV (1988) Summer habitat utilization and ecology of cutthroat trout fry (*Salmo clarki*) in cascade mountain streams. Can J Fish Aquat Sci 45:1921–1930

Moyle PB (1976) Some effects of channelization on the fishes and invertebrates of Rush Creek, Modoc County, California. Calif Fish Game 62:179–186

Mueller M, Pander J, Geist J (2011) The effects of weirs on structural stream habitat and biological communities. J Appl Ecol 48:1450–1461

Murphy ML, Heifetz J, Thedinga JF, Johnson SW, Koski KV (1989) Habitat utilization by juvenile Pacific salmon (*Oncorhynchus*) in the glacial Taku River, Southeast Alaska. Can J Fish Aquat Sci 46: 1677–1685

Nagayama S, Kawaguchi Y, Nakano D, Nakamura F (2008) Methods for and fish responses to channel remeandering and large wood structure placement in the Shibetsu River Restoration Project in northern Japan. Landsc Ecol Eng 4:69–74

Nagayama S, Kawaguchi Y, Nakano D, Nakamura F (2009) Summer microhabitat partitioning by different size classes of masu salmon (*Oncorhynchus masou*) in habitats formed by installed large wood in a large lowland river. Can J Fish Aquat Sci 66:42–51

Nagayama S, Nakamura F, Kawaguchi Y, Nakano D (2012) Effects of configuration of instream wood on autumn and winter habitat use by fish in a large remeandering reach. Hydrobiologia 680:159–170

Nakamura F, Ishiyama N, Sueyoshi M, Negishi JN, Akasaka T (2014) The significance of meander restoration for the hydrogeomorphology and recovery of wetland organisms in the Kushiro River, a lowland river in Japan. Restor Ecol 22:544–554

Nakamura F, Swanson FJ (2003) Dynamics of wood in rivers in the context of ecological disturbance. In: Gregory SV, Boyer KL, Gurnell AM (eds) The ecology and management of wood in world rivers. American Fisheries Society, Symposium 37, Bethesda, Maryland, pp 279–297

Nakano D, Nakamura F (2008) The significance of meandering channel morphology on the diversity and abundance of macroinvertebrates in a lowland river in Japan. Aquat Conserv 18:780–798

Nakano S, Fausch KD, Kitano S (1999) Flexible niche partitioning via a foraging mode shift: a proposed mechanism for coexistence in stream-dwelling charrs. J Anim Ecol 68:1079–1092

Palmer MA, Menninger HL, Bernhardt E (2010) River restoration, habitat heterogeneity and biodiversity: a failure of theory or practice? Freshw Biol 55(suppl. 1):205–222

Pander J, Geist J (2010) Seasonal and spatial bank habitat use by fish in highly altered rivers – a comparison of four different restoration measures. Ecol Freshw Fish 19:127–138

Pander J, Geist J (2016) Can fish habitat restoration for rheophilic species in highly modified rivers be sustainable in the long run? Ecol Eng 88:28–38

Pedersen ML, Andersen JM, Nielsen K, Linnemann M (2007a) Restoration of Skjern

River and its valley: project description and general ecological changes in the project area. Ecol Eng 30:131–144

Pedersen ML, Friberg N, Skriver J, Baattrup-Pedersen A (2007b) Restoration of Skjern River and its valley – Short-term effects on river habitats, macrophytes and macroinvertebrates. Ecol Eng 30:145–156

Peterson JT, Rabeni CF (2001) The relation of fish assemblages to channel units in an Ozark Stream. T Am Fish Soc 130:911–926

Rhoads BL, Schwarts JS, Porter S (2003) Stream geomorphology, bank vegetation, and three-dimensional habitat hydraulics for fish in midwestern agricultural streams. Water Resour Res 39: Art. No. 1218

Schwartz JS, Herricks EE (2008) Fish use of ecohydraulic-based mesohabitat units in a low-gradient Illinois stream: implications for stream restoration. Aquat Conserv 18:852–866

Sedell JR, Reeves GH, Hauer FR, Stanford JA, Hawkins CP (1990) Role of refugia in recovery from disturbances: modern fragmented and disconnected river systems. Environ Manage 14:711–724

Sugiyama H, Goto A (2002) Habitat selection by larvae of a fluvial lamprey, *Lethenteron reissneri*, in a small stream and an experimental aquarium. Ichthyol Res 49:62–68

Toyoshima T, Nakano S, Inoue M, Ono Y, Kurashige Y (1996) Fish population responses to stream habitat improvement in a concrete-lined channel. Jpn J Ecol 46:9–20 [In Japanese with English summary.]

Trexler JC (1995) Restoration of the Kissimmee River: a conceptual model of past and present fish communities and its consequences for evaluating restoration success.

Restor Ecol 3:195–210

Urabe H, Nakajima M, Torao M, Aoyama T (2010) Evaluation of habitat quality for stream salmonids based on a bioenergetics model. T Am Fish Soc 139:1665–1676

Ward JV, Tockner K, Arscott DB, Claret C (2002) Riverine landscape diversity. Freshw Biol 47:517–539

Wolter C, Buijse AD, Parasiewicz P (2016) Temporal and spatial patterns of fish response to hydromorphological processes. River Res Appl 32:190–201

Wyżga B, Amirowicz A, Oglęcki P, Hajdukiewicz H, Radecki-Pawlik A, Zawiejska J, Mikuś P (2014) Response of fish and benthic invertebrate communities to constrained channel conditions in a mountain river: Case study of the Biała, PolishCarpathians. Limnologica 46:58–69

Yamazaki Y (2007) Microhabitat use by the larvae of cryptic lamprey species in *Lethenteron reissneri* in a sympatric area. Ichthyol Res 54:24–31

Zeug SC, Winemiller KO (2008) Relationships between hydrology, spatial heterogeneity, and fish recruitment dynamics in a temperate floodplain river. River Res Appl 24:90–102

Figure captions

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

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

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

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

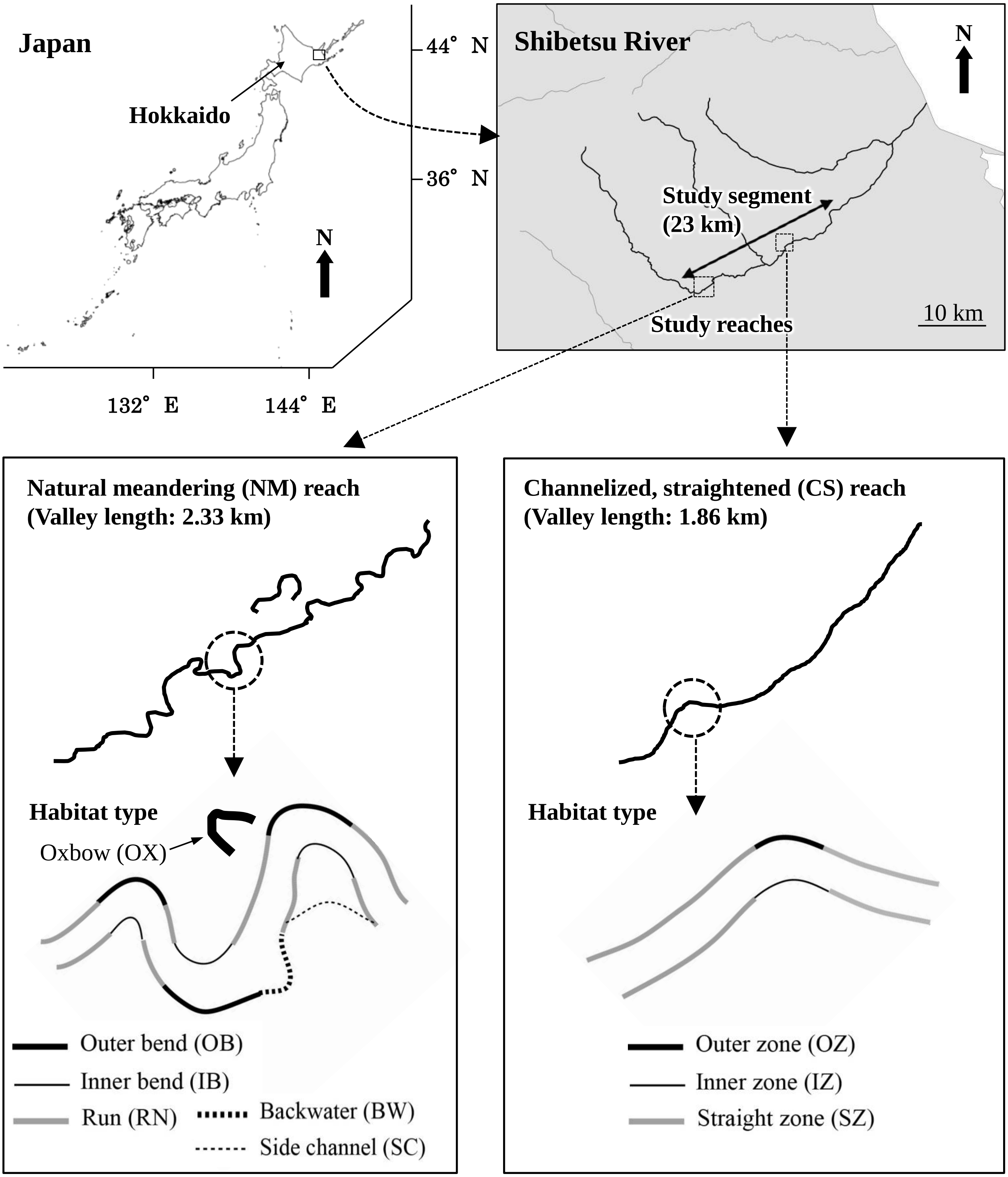

Figure 1 Nagayama & Nakamura

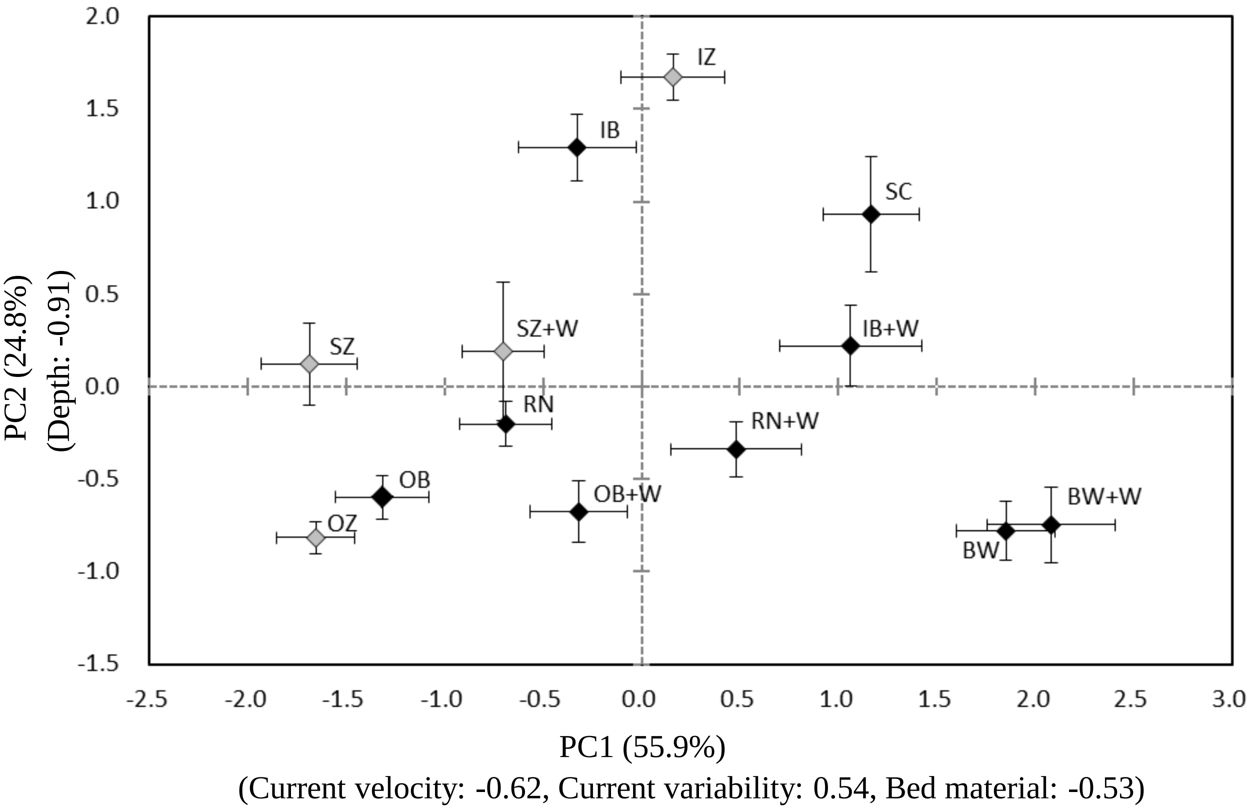

Figure 2 Nagayama & Nakamura

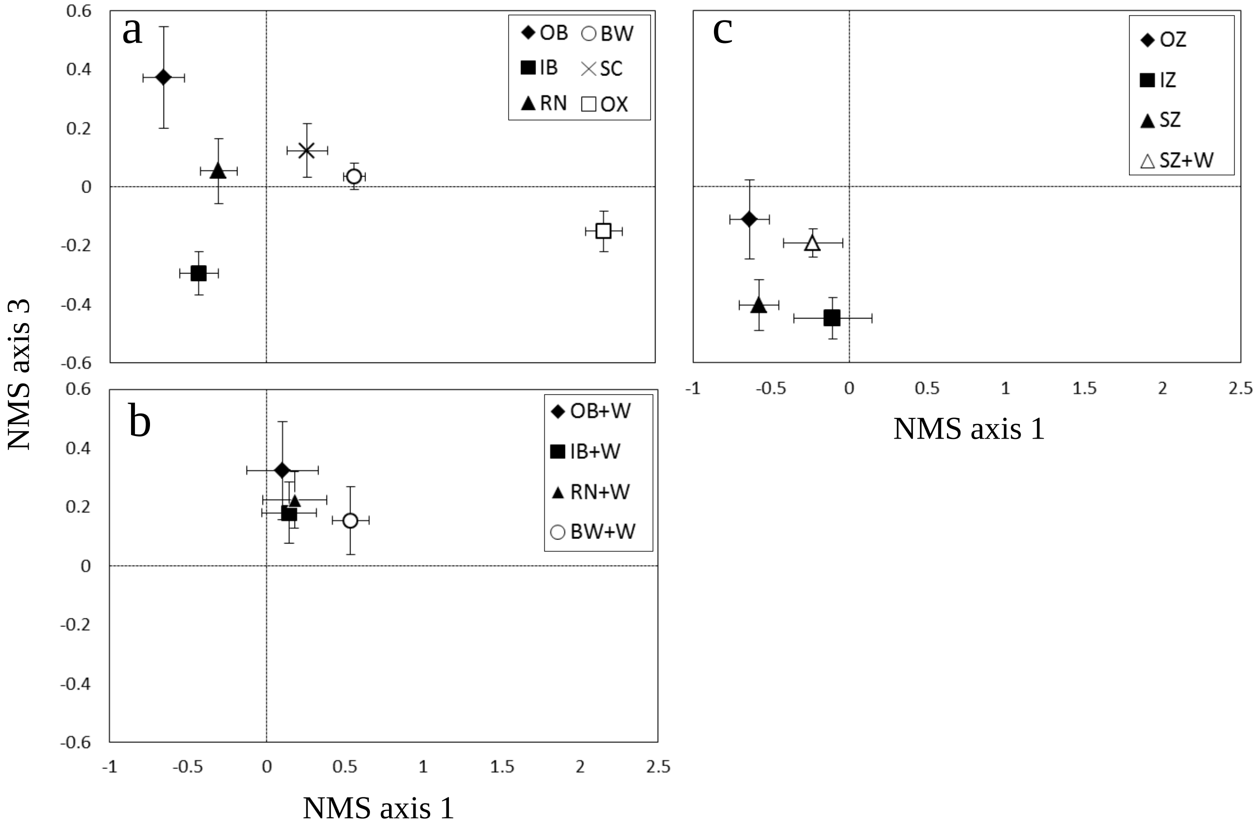

Figure 3　Nagayama & Nakamura

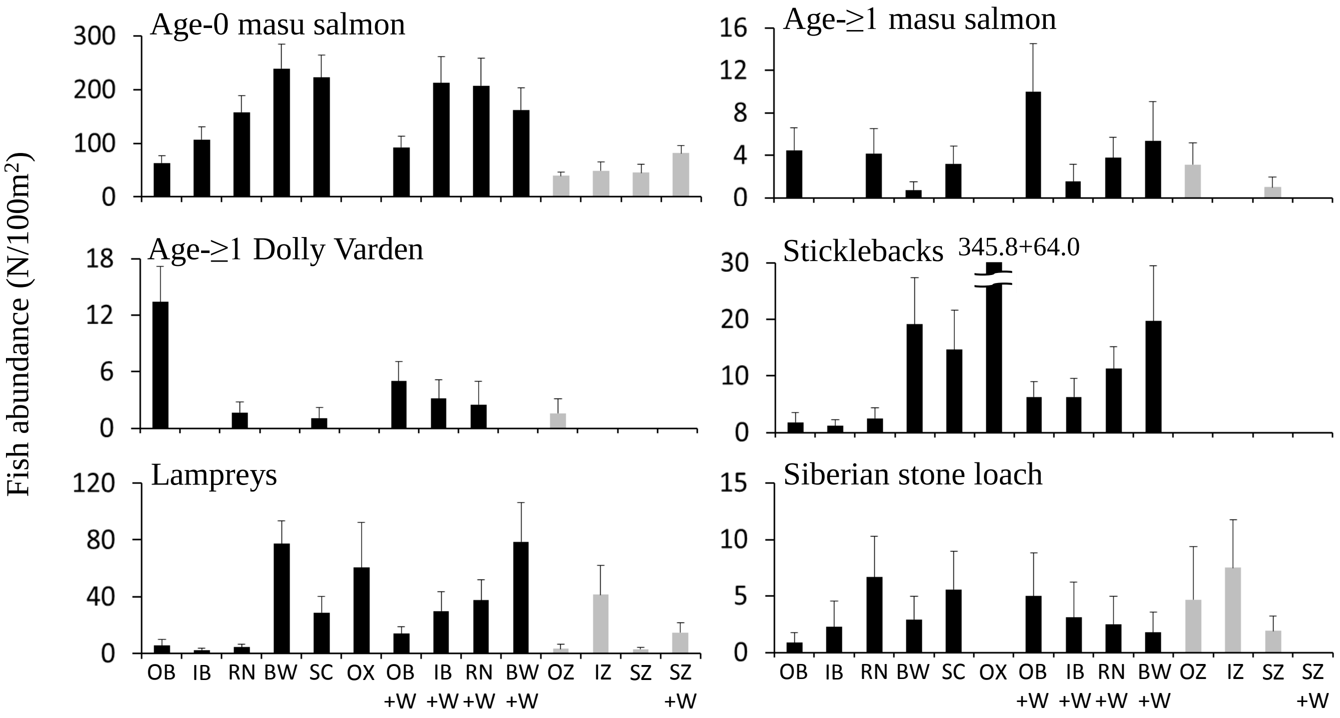

Figure 4 Nagayama & Nakamura

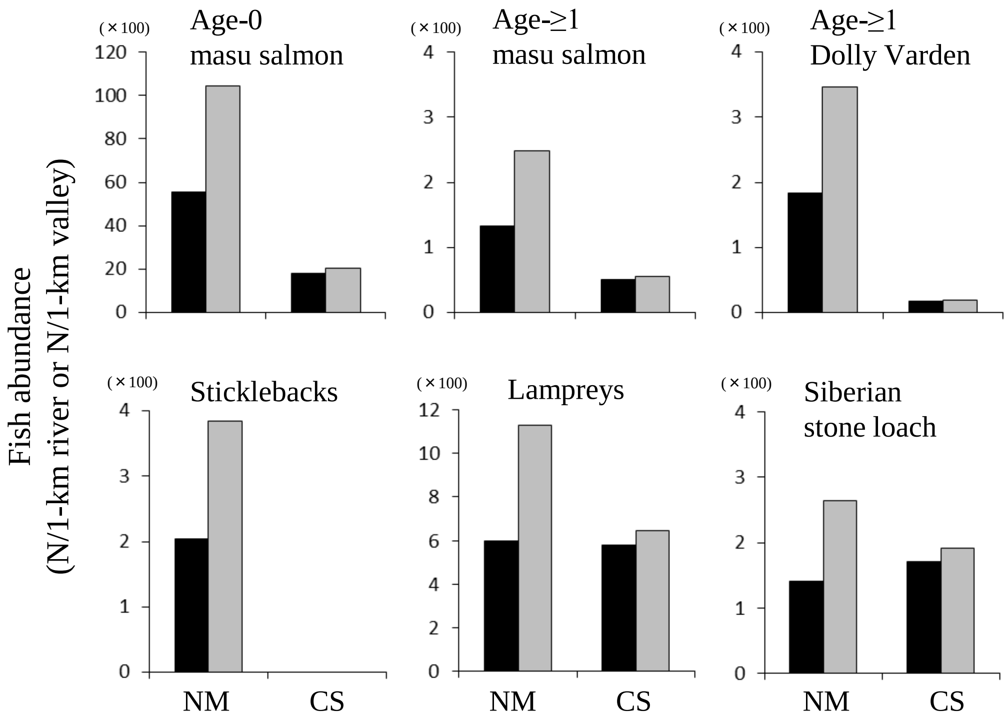

Figure 5 Nagayama & Nakamura

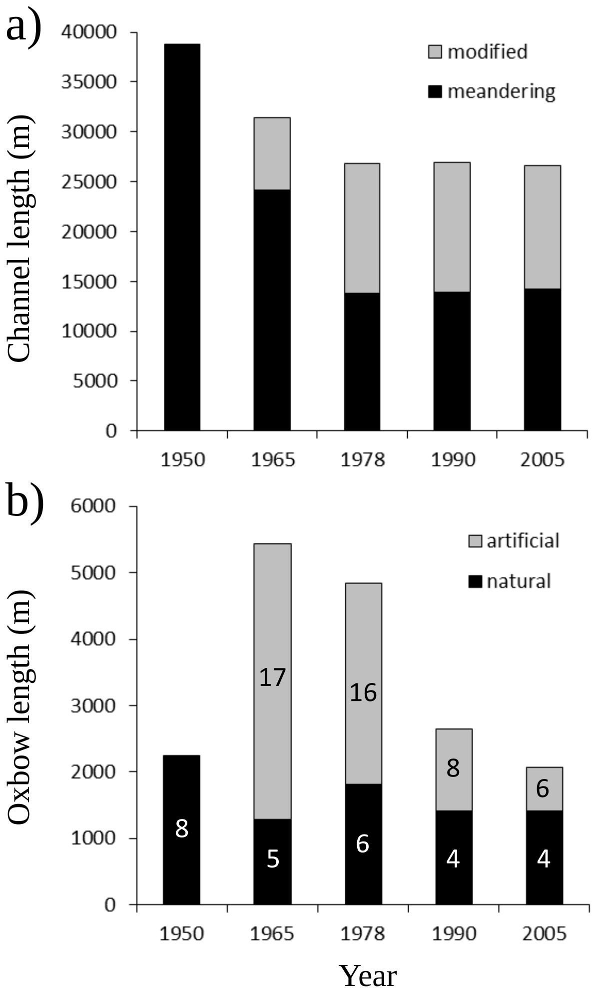

Figure 6 Nagayama & Nakamura

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