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Distribution and microhabitats of freshwater mussels in waterbodies in the terrestrialized floodplains of a lowland river

Shigeya Nagayama[1] · Morihiro Harada[2] · Yuichi Kayaba[3]

Abstract Even when anthropogenically altered, river floodplains continue to contribute to biodiversity. This study examined the distribution of freshwater mussels in relation to environmental factors in waterbodies in the terrestrialized floodplain of a lowland river. Mussels were captured, and environmental measurements were taken in November of 2013 and 2014 in quadrats established in three floodplain waterbodies (FWBs), which were isolated from the main river channel. Among the three FWBs, mussel abundance was highest in a shallow FWB (depth range 18–45 cm) that had intermediate conditions of mud depth and fine sediment rate. Mussel abundance showed a hump-shaped relationship with water depth (the peak 45–50 cm) and mud depth (the peak 8–12 cm). Mussel abundance was also negatively related to the abundance of benthic litter. Litter abundance was positively related to branch abundance and the presence of tree cover, and negatively related to the distance to tree cover, indicating that benthic litter was derived from riparian trees. Our results indicate that relatively shallow ($\leq$ 50 cm) FWBs with moderately accumulated mud, which are not scoured even during flooding, appear to be suitable habitats for mussels. Moreover, it is possible that riparian trees negatively impact mussel distribution in FWBs. Possible short-term measures for improving mussel habitat in FWBs may include the elimination of riparian trees and benthic litter.

Introduction

Floodplains consisting of ecotonal habitats are biodiversity hotspots along lowland rivers (Ward et al. 1999; Robinson et al. 2002; Tockner and Stanford 2002). The ecotonal nature of many floodplains and biological communities, however, has been altered by the terrestrialization of the floodplains, which is often associated with anthropogenically induced riverbed incision and flow regulation (Marston et al. 1995; Bravard et al. 1997; Negishi et al. 2008; Takahashi and Nakamura 2011). Terrestrialization accompanies an increase in the relative elevation of the floodplains to the water surface of the main channel, a decrease in inundation frequency, and an expansion of tree cover (Marston et al. 1995; Negishi et al. 2008). Despite terrestrialization and functional alteration, floodplains continue to provide vital habitats to many floodplain-dependent organisms and to contribute to biodiversity (Tockner and Stanford 2002).

The rapid suppression of terrestrialization is difficult because it often requires the recovery of dynamic natural processes, including sediment transportation and flow regimes (Marston et al. 1995; Takahashi and Nakamura 2011). Therefore, the potential role of terrestrialized floodplains as habitats should be understood to enable populations of organisms residing there to be sustained. In

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floodplain waterbodies (FWBs) that are isolated from the main river channel, environmental conditions and biological community composition vary along a gradient of hydrological connectivity (Tockner et al. 1998; Negishi et al. 2012a; Kume et al. 2014). Although the level of hydrological connectivity has been recognized as the most important factor in determining the distribution of aquatic organisms in FWBs, microhabitat conditions are also important in determining abundance within FWBs.

Unionid mussels, which are threatened in Japan (Negishi et al. 2008), North America, and Europe (Bogan 1993), reside in FWBs formed or left in terrestrialized floodplains along many large Japanese lowland rivers (Negishi et al. 2012a; S. Nagayama, unpublished data). An understanding of the habitat preferences of these mussels is an urgent need because their populations are declining, and they serve as indicators of habitat quality for other fauna (Aldridge et al. 2007; Negishi et al. 2013). High species richness, high abundance, and the occurrence of molluscs, including mussels, were found in the FWBs that frequently connect with a main channel during floods (Tockner et al. 1998; Negishi et al. 2012a). The high mussel abundance in such FWBs appeared to be related to the suppression of hypoxia that is associated with inundation (Negishi et al. 2012a). However, the microhabitats of mussels within FWBs have not been well examined, although there have been numerous studies in rivers (lotic habitat) (e.g., Lewis and Riebel 1984; Strayer 1999; Morales et al. 2006) and lakes (e.g., Cvancara 1972; Hayashi 1972; Samad and Stanley 1986).

The predominant factors that determine microhabitat conditions are different between FWBs and other systems (rivers and lakes). Microhabitat conditions within the FWBs are determined by the combined effects of lentic and lotic (inundation by flood) phases. Detritus, including litter derived from riparian trees, is known to be an influential factor on mussel occurrence in FWBs (Negishi et al. 2012a) and accumulates in FWBs during a lentic phase. During a lotic phase, the bathymetry of FWBs may be altered by flood water according to flooding intensity. An understanding of mussel responses to these habitat conditions that are characteristically formed in terrestrialized floodplains is required not only for short-term habitat improvement but also for future habitat management.

Our purpose was to examine the distribution of mussels in relation to environmental factors in the waterbodies in a terrestrialized floodplain of a lowland river. This study consists of two different investigations. First, mussel distribution was examined in relation to the environmental factors in three FWBs that had different bathymetric features. Second, microhabitat characteristics for mussels, including the metrics associated with riparian trees, were examined in a shallow FWB in which the mussels were most abundant among the abovementioned three FWBs.

Methods

Study site

The study was conducted in a lowland segment of the Kiso River in central Japan (drainage area of 5,275 km^2) (Fig. 1). The bed slope is approximately 0.025 %, and the flow rate calculated from the data of the last decade ranges from approximately 75 m^3/s of mean base flow to approximately 5,400 m^3/s of mean annual maximum (annual maximum during the last decade 11,054 m^3/s). Relatively high flows were observed in early summer from June to July (the *Baiu* season) and in early autumn from September to October (the typhoon season); from November to May, flows were relatively low and stable (Negishi et al. 2012b). Levees have been constructed along both sides of the segment studied, but floodplains and numerous FWBs are present in the interlevee zone. All FWBs become inundated, allowing them to connect to the main channel during floods of >3,200 m^3/s (Negishi et al. 2012a).

Until the 1970s, most of the interlevee floodplain was sand bars, but the terrestrialization followed by tree establishment has rapidly progressed since the 1980s, resulting in most of the floodplain being covered by trees (Negishi et al. 2008; Nagayama et al. 2015). With the terrestrialization of the interlevee floodplains, the FWBs became small but more abundant, with the number of
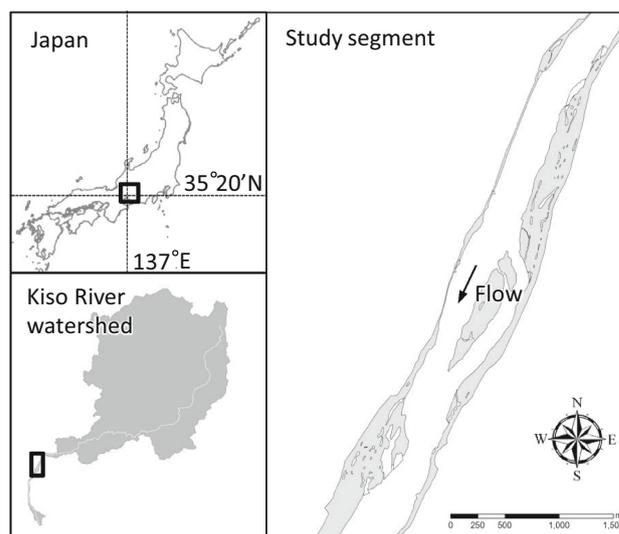
Fig. 1 Location of the study segment, in which floodplain waterbodies (FWBs 1–3) were located, in Kiso River, central Japan

FWBs isolated from the main channel increasing (Nagayama et al. 2015). Three isolated FWBs (FWBs 1–3), in which three taxa of mussels were present (*Unio douglasiae nipponensis*, *Lanceolaria grayana* and *Anodonta* spp.), were selected for this study. These FWBs had different bathymetric features. FWB 1 had a deep area of >100 cm, and FWBs 2 and 3 were relatively shallow (mostly <50 cm). Areas of FWBs 1, 2 and 3 were approximately 1800, 1100 and 1150 m^2, respectively. The inundation frequency (connectivity to the main channel) was 7.15 times a year in FWB 1, and 12 times a year in FWBs 2 and 3 based on the last decadal daily discharge of the study segment.

Data acquisition in the 2013 survey

Distribution and microhabitat surveys were conducted in the three FWBs (FWBs 1–3) on November 11 and 12, 2013. The water temperature in the FWBs was 10.4–14.8 °C during the daytime in the study period. Thirteen to 16 transects perpendicular to the longest axis of each FWB were established at 5-m intervals. Most transects had three quadrats (2 m × 2 m), but some had one or two quadrats, depending on the length of the transect (total number of quadrats in the three FWBs was 119). The quadrats were established at even intervals in each transect, according to the length of the transect, and the distance from the bank to quadrat was the same as the intervals between quadrats. Mussels were captured by disturbing 5 cm of the surface of the substratum by hand in quadrats with <60 cm depth and by using an iron winnow with a shaft (mesh size 1 cm) in quadrats with ≥60 cm depth. We could not find mussels visually because of the turbidity of the water in the FWBs. To reduce the number of mussels missed, we carefully looked for mussels in each subquadrat (1 m × 1 m) quartering a quadrat. On finding a mussel, we recorded the taxonomic identity and shell length to the nearest 0.1 mm; mussels were then released at the point of collection. Water depth and mud depth were measured in the middle of each quadrat. Mud depth was defined as the difference in height of the substratum surface before and after one person weighing approximately 75 kg stood on one foot. The sediment approximately 5 cm from the substratum surface was also sampled by hand (2–3 kg per sample) right next to the middle point of each quadrat and was taken to the laboratory to measure the fine sediment rate. The fine sediment rate was defined as the dry mass percentage of the silt and clay (≤0.075 mm) in the substratum samples. Dry sieving and hydraulic settling tests were employed according to the Japanese Industrial Standards A 1204 (JIS A 1204) to calculate the fine sediment rate. First, the substratum samples were dried, and the sediments of ≤2 and >2 mm were sieved. Second, the sediments of ≤2 mm were agitated in the water to disassemble individual grains and then the mixture was allowed to settle. Following that, the settled sediments were dried again, and the fine sediments were segregated with a 0.075-mm-mesh sieve. Finally, the fine sediments and all sediments in the sample were weighed.

Data acquisition in the 2014 survey

A microhabitat survey was conducted in FWB 2 on November 4, 2014, to examine the microhabitat characteristics for mussels, including the metrics associated with riparian trees. The water temperature in FWB 2 was 12.4 °C during the daytime on the study date. Six of 13 transects established for the 2013 survey were selected for the 2014 survey. Eleven to 19 quadrats (1 m × 1 m) were established, with even intervals between the quadrats in each transect, and the number of quadrats was the same as the integer part of the transect length (e.g., we established 10 quadrats in a transect that was 10.7 m long). The mussel survey in the quadrats was conducted using the same methods described for the 2013 survey. Four subquadrats (0.5 m × 0.5 m) were also established by quartering each quadrat. Water depth (cm) was measured in the middle of each subquadrat, and the mean of the four water depths in a quadrat was used. A handful of benthic litter was sampled at the middle point of each subquadrat, and the total wet weight of the four samples in a quadrat was used as the abundance of litter (g). Benthic litter was sampled by the right hand of the same person. The investigator stretched his palm and fingers, took it to bed surface of the sampling point, and clutched benthic litter. The litter samples collected in each quadrat were taken to the laboratory, and then they were washed with tap water to remove attached sand and mud, and were weighed using an electronic balance. The number of subquadrats that had tree branches of ≥1 cm in diameter and ≥10 cm in length in the litter samples was defined as the branch index in each quadrat (0–4). Mud depth (cm) was measured in the middle of each quadrat by the same method described above. The occurrence (presence/absence) of tree cover over the quadrats and the distance from the water surface of the quadrats to tree cover (m) were also recorded.

Statistical analyses

Spatial autocorrelation (Moran's correlogram) was examined using SAM 4.0 (Rangel et al. 2010), and other statistical analyses were conducted using R 3.2.2 (R Core Team 2015).

For the analysis in the 2013 survey (the total number of quadrats was 119 in the three FWBs), the Kruskal–Wallis test was performed to compare the environmental variables

(the water depth, mud depth, and fine sediment rate) and mussel abundance among the three FWBs. When a significant difference was detected, the variable(s) was compared between all pairs of FWBs using Mann–Whitney U tests. The statistical significance of the pairwise multiple comparisons was adjusted by the Holm method when appropriate.

We built a generalized linear mixed model (GLMM), in which the response variable was the total number of mussels of all taxa per quadrat and the explanatory variables were the three environmental variables, with a negative binomial error distribution and log-link function (package glmmADMB). Quadratic terms of each environmental variable were also used in building the model because parabolic relationships between the mussel abundance (response variable) and each environmental variable (explanatory variable) were expected. We incorporated individual FWBs and transects as nested random effects (transect < FWB) to account for differences among FWBs and transects. FWBs as a random effect were incorporated without assessment of spatial autocorrelation because individual FWBs obviously had specific habitat features that were not captured by our habitat environmental measurements (Bolker et al. 2009). Transects as a random effect were used because there was a possibility of spatial autocorrelation on a transect, but not between transects, based on the 2014 assessment (see below). The variables for which the 95 % confidence intervals (CI) did not include 0 were chosen as the influential variables.

For the analysis in the 2014 survey (the total number of quadrats was 85 in FWB 2), we also built a GLMM (package glmmML). A correlogram of Moran's I with 1000 permutations was constructed to assess the degree of spatial autocorrelation in the abundance data obtained from the quadratic surveys on mussels. The number of distance classes (k) used was 11. A significance level of $\alpha = 0.05$ was adjusted following the Bonferroni criterion (an adjusted significance level = α/k). As a result, the spatial autocorrelation was detected for a distance class smaller than the distance (5 m) between adjacent transects (see "Results"). We then incorporated individual transects as a random effect into a GLMM to account for differences among transects. The response variable was the total number of mussels of all taxa per quadrat, and the explanatory variables were the three environmental factors (the water depth, mud depth, and litter abundance). A quadratic term of the mud depth was also used in building the model because a parabolic relationship between the mussel abundance and the mud depth was expected. We used a Poisson error distribution and log-link function in building the model. Variables for which the 95 % CI did not include 0 were chosen as the influential variables.

In the data analyzed here, water depth was significantly correlated with litter abundance ($r = -0.78$). We therefore defined 'residual water depth' as the residuals of a linear relationship fitted between water depth and litter abundance to avoid multicollinearity. Residual water depth provides a relative measure of water depth, independent of litter abundance, in which positive values reflect deeper water than expected for a given litter abundance, whereas negative values reflect shallower water than expected (Vercken et al. 2011; Terui et al. 2014).

Using the data obtained from the 2014 survey, linear regression models were also constructed to detect the relations between litter abundance and branch index and distance to tree cover. The statistical significance of the models was tested using log-likelihood ratio tests ($\alpha = 0.05$). The Kruskal–Wallis test was also performed to compare the environmental variables (the water depth, mud depth, and litter abundance) of the quadrats used by the mussels among taxa and to compare the litter abundance between quadrats with and without tree cover. When a significant difference was detected, the variable(s) was compared between all pairs of taxa using Mann–Whitney U tests. The statistical significance of the pairwise multiple comparisons were adjusted by the Holm method when appropriate.

Results

Mussel distribution and microhabitat in the three FWBs (2013 survey)

The number of *U. douglasiae nipponensis*, *L. grayana*, and *Anodonta* spp. captured in the three FWBs was 294, 92, and 91, respectively. *U. douglasiae nipponensis*, *L. grayana*, and *Anodonta* spp. occurred in 59, 41, and 44 sampling quadrats (total 119, quadrats without mussels 34), respectively. The ranges of shell length of mussels captured were 10.8–81.4 mm for *U. douglasiae nipponensis*, 52.2–139.1 mm for *L. grayana*, and 39.3–133.4 mm for *Anodonta* spp. (Fig. 2).

The mussel abundance (N/m^2) of the total of three taxa was significantly highest in FWB 2 among the three FWBs (Table 1). In FWB 2, mussels were distributed in almost all of the sampling quadrats, and many individuals (>20) were observed in some quadrats (Fig. 3). FWB 2 had intermediate conditions of mud depth and fine sediment rate among the three FWBs and was shallow across the waterbody. Although FWB 3 was also shallow, the mud depth was lower than that in the other FWBs. In FWB 3, mussels were broadly distributed but scarce. FWB 1 was characterized by a greater water depth and a higher mud
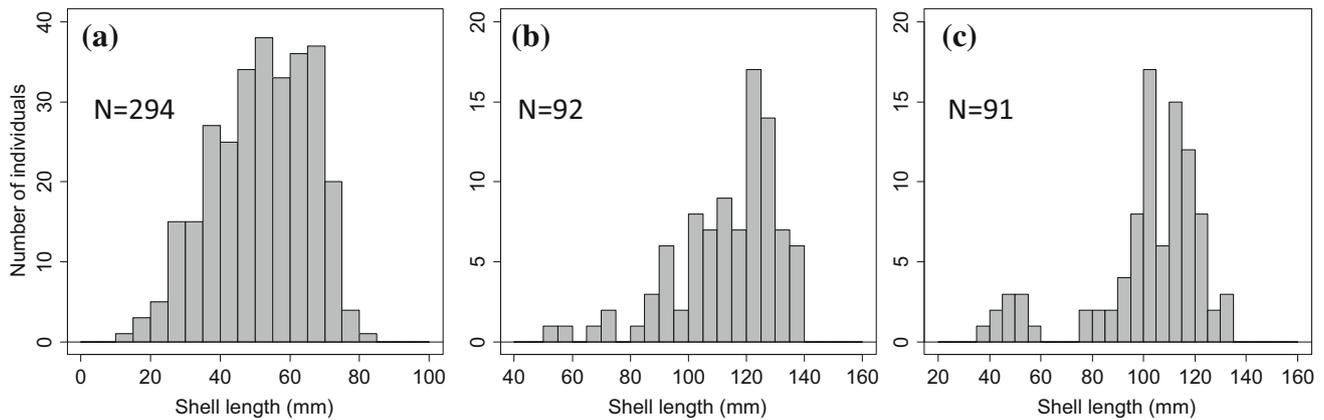
Fig. 2 Shell length of *U. douglasiae nipponensis* (**a**), *L. grayana* (**b**), and *Anodonta* spp. (**c**) captured in the three study FWBs in the 2013 survey

Table 1 Environmental conditions and mussel abundance in the study floodplain waterbodies (FWBs) observed in the 2013 and 2014 surveys

Variable	FWB 1		FWB 2		FWB 3	
	Mean ± SD	Range	Mean ± SD	Range	Mean ± SD	Range
2013 survey (the number of sampling quadrats: 46 in FWB 1, 37 in FWB 2, 36 in FWB 3, and 119 in total)						
Water depth (cm)	70.7 ± 32.0[a]	15.0–143.0	32.2 ± 7.3[b]	18.0–45.0	34.6 ± 5.8[b]	18.0–45.0
Mud depth (cm)	11.5 ± 7.2[a]	3.1–31.3	7.8 ± 3.3[b]	0–15.0	4.8 ± 5.2[c]	0–19.4
Fine sediment rate	0.30 ± 0.20[b]	0.03–0.75	0.40 ± 0.20[ab]	0.03–0.65	0.40 ± 0.10[a]	0.06–0.66
Mussel abundance (N/m^2)	0.3 ± 0.5[b]	0–1.8	2.5 ± 2.6[a]	0–13.3	0.3 ± 0.2[b]	0–0.8
2014 survey (the number of sampling quadrats: 85)						
Water depth (cm)			32.6 ± 9.3	14.5–50.3		
Mud depth (cm)			5.7 ± 3.2	0–15.0		
Litter abundance (g)			44.3 ± 81.5	0–548.0		
Mussel abundance (N/m^2)			2.6 ± 3.5	0–16.0		

Values accompanied by different alphabetical letters were statistically different by Mann–Whitney *U* tests after being adjusted by the Holm method

depth than those in the other FWBs. There were no mussels in deep quadrats (e.g., >100 cm) in FWB 1.

Water depth and mud depth were influential factors on mussel abundance (Table 2). Hump-shaped relationships between mussel abundance and these environmental variables were found. The peak of mussel abundance was expected in the intermediate habitat (water depth 45–50 cm, mud depth 8–12 cm) (Fig. 4). There were almost no mussels in quadrats with >80 cm depth.

Mussel microhabitat in a shallow FWB (2014 survey)

The number of *U. douglasiae nipponensis*, *L. grayana*, and *Anodonta* spp. captured in FWB 2 during the 2014 survey was 141, 33, and 45, respectively. *U. douglasiae nipponensis*, *L. grayana*, and *Anodonta* spp. occurred in 36, 19, and 34 sampling quadrats (total 85, quadrats without mussels 27), respectively.

A significant positive spatial autocorrelation was revealed for the smallest-distance class of 1.5 m (Appendix), indicating a spatial autocorrelation between adjacent sampling quadrats on a transect, but not between adjacent transects. Therefore, GLMM incorporating individual transects as a random effect was built. As a result, water depth and litter abundance were influential factors on mussel abundance (Table 3). Unlike the result of the 2013 survey, water depth showed a simple positive relationship with mussel abundance in the shallow FWB 2 with a maximum water depth of 50.3 cm (Fig. 5a). Conversely, litter abundance negatively related with mussel abundance (Fig. 5b).

There was a significant difference in water depths among quadrats occupied by different taxa: *U. douglasiae nipponensis* ($P = 0.007$) used deeper quadrats than *Anodonta* spp. (Fig. 6). Mud depth and litter abundance were not significantly different among taxa.

The litter abundance was positively correlated with the abundance of branches (branch index), negatively

Fig. 3 Contour map of the study floodplain waterbodies (FWB 1–3) and the sampling quadrats that are gradationally expressed based on the mud depth. *Numbers within squares* denote the total number of mussels in the sampling quadrats. Water depths (cm) are shown by *numbers along the contour lines*
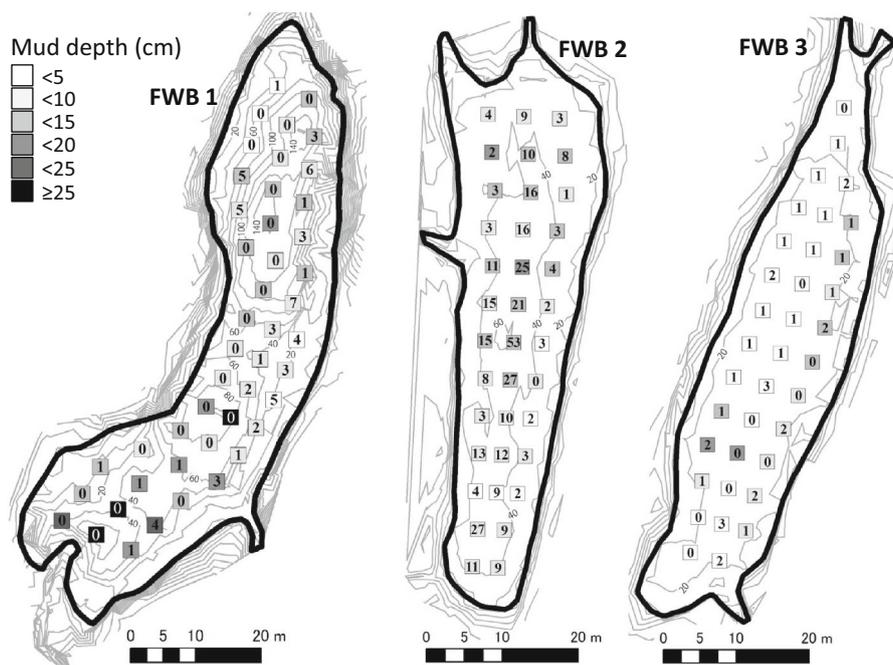
Table 2 Parameter estimates for the model predicting mussel abundance (N/quadrat) in the 2013 survey

Explanatory variable	Coefficient	SE	95 % CI
Water depth	**0.14**	**0.03**	**(0.08, 0.20)**
Water depth²	**−0.001**	**0.0003**	**(−0.0008, −0.002)**
FS rate	0.39	2.25	(−4.01, 4.80)
FS rate²	−1.24	3.08	(−7.29, 4.80)
Mud depth	**0.15**	**0.06**	**(0.03, 0.26)**
Mud depth²	**−0.007**	**0.003**	**(−0.01, −0.002)**

Bold typeface indicates variables for which the 95 % CI did not include zero

FS rate fine sediment rate, *Coefficient* standardized partial regression coefficient, *SE* standard error, *95 % CI* 95 % confidence interval

correlated with the distance to tree cover (cover distance), and was significantly higher in quadrats with tree cover than in quadrats without tree cover (Kruskal–Wallis test, $P < 0.001$) (Fig. 7).

Discussion

Despite anthropogenically induced alterations such as terrestrialization, floodplains continue to provide vital habitats to floodplain-dependent organisms, including threatened freshwater mussels (Tockner and Stanford 2002; Negishi et al. 2012a). However, an understanding of microhabitat use by freshwater mussels in isolated waterbodies in

Fig. 4 Relations between mussel abundance and water depth (**a**) and mud depth (**b**). Plots denote sampling quadrats (N = 119). The models are indicated by the *solid lines*. The fine sediment rate, which was not an influential factor on mussel abundance, is not shown
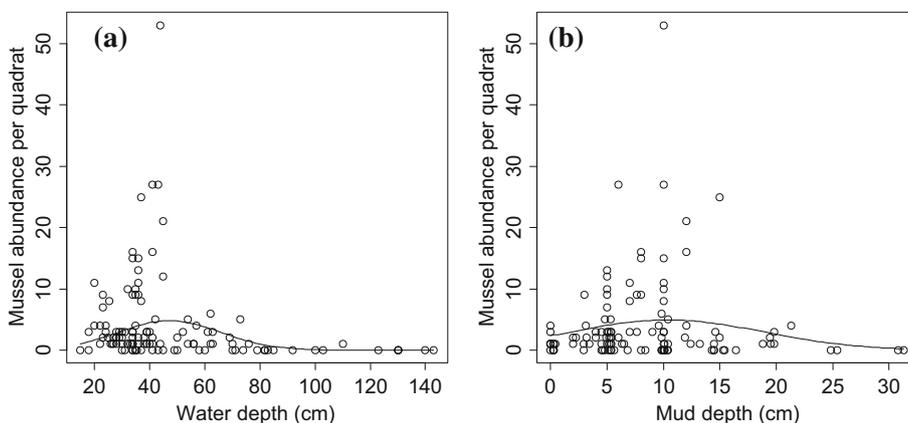
Table 3 Parameter estimates for the model predicting mussel abundance (N/quadrat) in the 2014 survey

Explanatory variable	Coefficient	SE	95 % CI
Residual water depth	**0.13**	**0.012**	**(0.11, 0.16)**
Litter abundance	**−0.007**	**0.002**	**(−0.010, −0.003)**
Mud depth	−0.11	0.08	(−0.27, 0.05)
Mud depth^2	0.004	0.006	(−0.008, 0.017)

Bold typeface indicates variables for which the 95 % CI did not include zero

Coefficient standardized partial regression coefficient, *SE* standard error, *95 % CI* 95 % confidence interval

terrestrialized floodplains has been scarce. This study suggests that mussel distribution and microhabitats in the FWBs are related to bathymetry and the accumulation of litter derived from riparian trees, although our results were based on only three FWBs.

Among the three FWBs, mussel abundance was highest in FWB 2 that had a lower water depth (mean ± SD $32.2 ± 7.3$ cm, range 18–45 cm) and intermediate conditions of mud depth and fine sediment rate. In addition, mussel abundance showed hump-shaped relationships with water depth (the peak 45–50 cm) and mud depth (the peak 8–12 cm) based on the combined data of the three FWBs, with almost no mussels inhabiting >80 cm depth. The hump-shaped relationship did not conflict with the result of a positive relationship between mussel abundance and water depth in the shallow FWB 2 with a maximum water depth of 50.3 cm. These results indicate the importance of FWBs with broad area of habitats characterized by intermediate conditions of water depth and mud accumulation for mussels.

The avoidance of deep areas (>80 cm) by mussels may be explained by the following two processes. First, hydraulic disturbance during flood inundation may prevent mussels from settling in deep areas. The distribution of
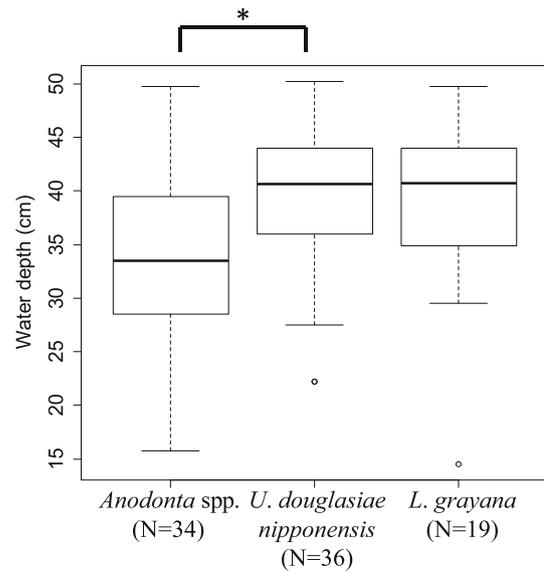
Fig. 6 A comparison of the water depths of the sampling quadrats used by each taxon. *Asterisk* indicates a significant difference between taxa by pairwise multiple comparisons after being adjusted by the Holm method. The mud depth and litter abundance, which were not significantly different among the taxa, are not shown

mussels in rivers was regulated by hydraulic power such as shear stress during floods (Howard and Cuffey 2003; Morales et al. 2006). The presence of a deep area within the FWBs implies that scouring of the bottom bed occurs during flood inundation. Mussels may be forcefully removed from the deep areas during floods. Second, the occurrence of hypoxia in the antecedent summer may prevent mussels from settling or surviving in the deep areas until autumn. Dissolved oxygen (DO) levels were seriously reduced in the bottom of a deep area in an irrigation pond with a maximum depth of 150 cm during the warmer seasons from April to September due to thermocline formation (Nagata 1985). In the deep areas where low DO levels occurred, mussels were not distributed (Nagata

Fig. 5 Relations between mussel abundance and residual water depth (**a**) and litter abundance (**b**). Plots denote sampling quadrats (N = 85). The models are indicated by the *solid lines*. The mud depth, which was not an influential factor on mussel abundance, is not shown
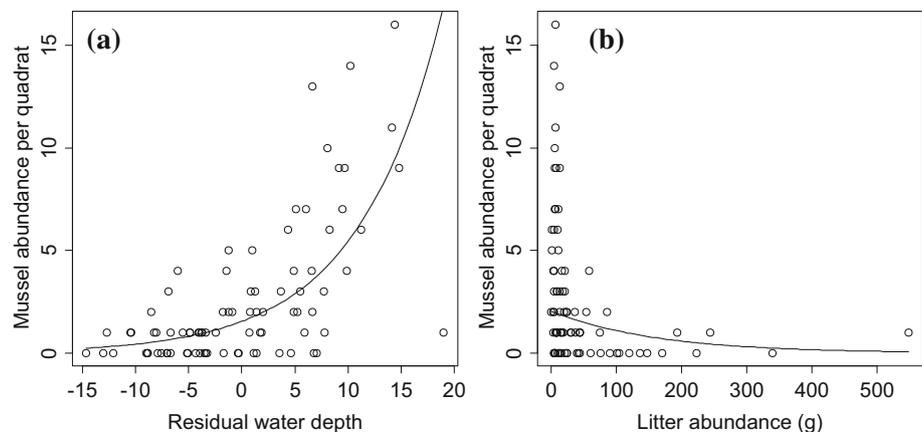
Fig. 7 Relations among litter abundance and branch index (**a**), cover distance (**b**), and presence/absence of tree cover (**c**). Plots in **a** and **b** denote sampling quadrats. A statistically significant regression model is indicated by the *solid line*. Two outliers (339 and 548 g) in the "presence" of tree cover are not shown in **c**
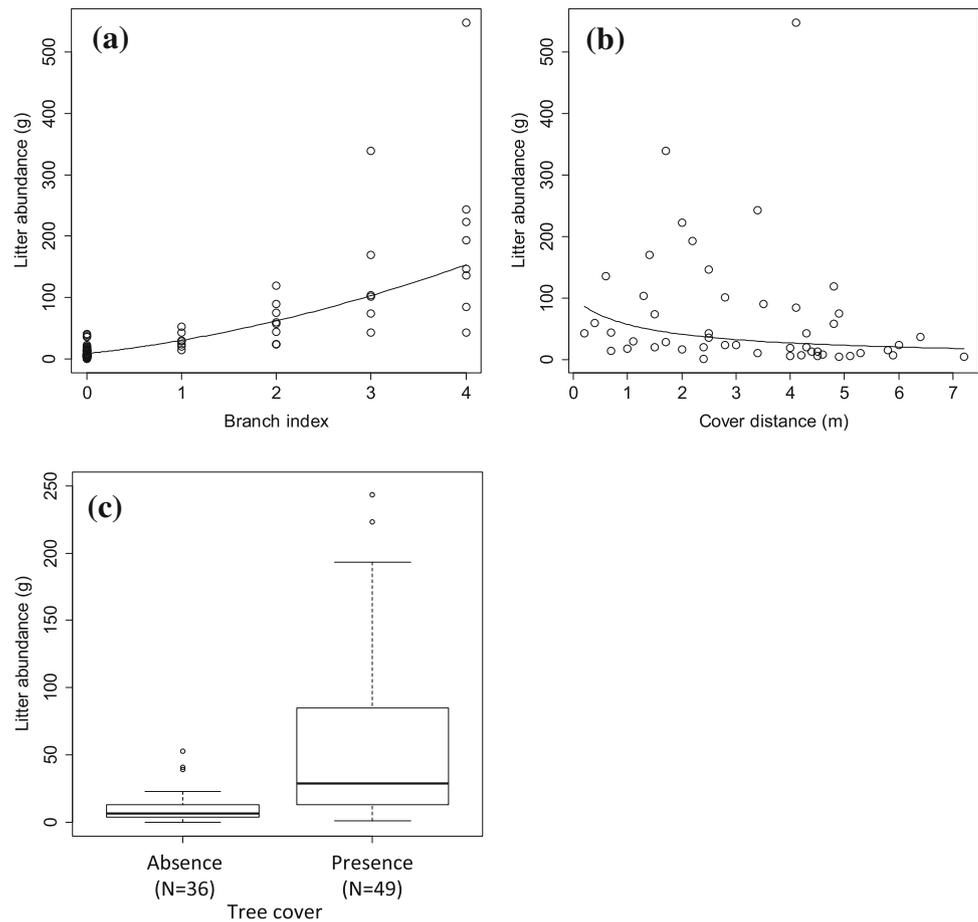
1985). Furthermore, hypoxia also occurred in the FWBs at a water temperature of >15 °C, limiting the growth of the mussels, and increasing mortality in the FWBs (Negishi et al. 2012a). In our study period, the water temperature was <15 °C (see "Methods") and hypoxia was unlikely to occur. Therefore, mussels may die in, or move away from, the deep area during summer, and cannot sustain their distribution in the deep area.

A hump-shaped relationship with mussel abundance and mud depth may indicate the unsuitableness of solid bottom bed and soft bottom bed due to excessive accumulation of mud. In our study FWBs, firm clay sediment was present under the accumulated mud. Mussels were absent on the bed where firm clay was exposed (i.e., mud depth was 0 cm). Mussel abundance was also considerably lower in habitats with a mud depth of >20 cm in this study, which may be associated with a negative effect of soft muddy substratum on the growth of mussels (Kat 1982).

Mussel abundance rapidly decreased with an increase in litter abundance. In addition, litter abundance was positively related to branch abundance and the presence of tree cover. The negative impact of benthic organic matter on mussel occurrence has also been previously

reported (Negishi et al. 2012a). Our results indicate that the microhabitat use by mussels in the FWBs was likely limited by accumulated litter falling from the riparian trees. In addition, the negative relationship between litter abundance and cover distance indicates the direct contribution of shrubs to benthic litter abundance along the shore line.

One possible cause of the negative relationship between mussel abundance and litter abundance may be hypoxia. Negishi et al. (2012a) attributed hypoxia to abundant benthic organic matter. Benthic organic matter may be abundant in the habitats covered by riparian trees even in summer when hypoxia often occurs. Although hypoxia was not likely in our study period (water temperature was <15 °C), hypoxia in the antecedent summer might limit the mussel distribution in autumn (our study period). Another mechanism of this negative impact may be the prevention of movement of the mussels by branch litter. Once a branch is provided in FWBs, it is likely retained and accumulated for a longer period than a leaf due to its immobility and resistance to decomposition. Therefore, the prevention of movement of the mussels by benthic branches may be sustained throughout the year and increase the

risk of mussel mortality due to hypoxia and drought. Alternatively, litter may cover the apertures of mussels and prevent mussels from engaging in feeding and respiration.

Although benthic organic matter (litter) possibly limits the mussel distribution and abundance in FWBs as stated above, the seasonality and duration of those impacts on mussels need to be examined in the future. In our study period (autumn), the abundance of leaf litter derived from riparian trees to FWBs is likely the highest in the year. The amount of benthic litter also varies throughout the year due to seasonal floods and decomposition. These temporal changes of benthic organic matter abundance need to be considered in a future study.

U. douglasiae nipponensis used deeper areas than the *Anodonta* spp. This may be explained by differences in mobility and tolerance among taxa. The mobility of *U. douglasiae nipponensis* was higher than that of *Anodonta* spp. (Kondo and Kano 1993). *U. douglasiae nipponensis* might move to a deeper area to avoid the risk of drought in shallow areas or to overwinter. The sampling date (November) was in a period when the water level is relatively low and stable (Negishi et al. 2012b) and when the water temperature gradually decreases. *Anodonta* spp. might have maintained their positions even though the water level was reduced. However, stranded individuals of *Anodonta* spp. might tolerate the severe conditions of the shallow areas that are associated with declining water level, which may explain the wide-range use of depth in this mussel.

Although the connectivity of FWBs with the main channel should be considered in priority to the local habitat conditions within waterbodies, this study suggests that the bathymetric features and riparian trees of waterbodies may also need to be considered in habitat management in terrestrialized floodplains. If the FWBs are artificially constructed to create additional habitats, they should have a broad area of ≤50 cm depth wider than the tree cover over the waterbodies. Also, waterbodies should be constructed in areas with moderate hydraulic conditions during floods to avoid bed erosion and the forceful removal of mussels. In the short run, the elimination of riparian trees, including shrubs and benthic litter, may be used as possible measures for improving habitat quality of existing waterbodies. However, under the hydrogeomorphic conditions of those regulated rivers along which the floodplains have terrestrialized, the re-establishment of riparian trees after deforestation is expected (Harada et al. 2015; Nagayama et al. 2015). Therefore, riparian trees in terrestrialized floodplains may have to be periodically eliminated to maintain the quality and quantity of habitats available for mussels. Over the long term, the restoration of hydrogeomorphic processes that suppress terrestrialization should be considered.

Appendix

See Table 4.

Table 4 Spatial correlogram of the abundance of mussels in FWB 2

Distance class	Spatial scale (distance: m)	Moran's I	P
1	**1.5**	**0.518**	**0.001**
2	3.5	−0.05	0.464
3	7.5	−0.04	0.304
4	12.5	−0.087	0.031
5	17.5	0.077	0.045
6	22.5	0.104	0.056
7	27.5	−0.18	0.009
8	32.5	−0.139	0.01
9	37.5	0.066	0.185
10	42.5	−0.102	0.642
11	47.5	−0.159	0.021

Bold typeface indicates significant spatial autocorrelation: statistical significance level was corrected with Bonferroni corrections ($\alpha = 0.05/11$; $\alpha = 0.0045$)

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