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Title: Unionoid mussels as an indicator of fish communities: a conceptual framework and empirical evidence

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Running head: Unionid mussels as fish indicator

Abstract

We tested the hypothesis that globally imperiled freshwater mussels (Order: Unionoida) can be used as an indicator of fish communities in lowland aquatic systems for relatively small geographic areas (i.e., <100 km²). The survey was conducted in 13 reaches within a network of agricultural drainage channels and in 9 floodplain backwaters in Central Japan. In each site, the fish community was examined on four seasonal occasions (spring to early summer, mid-summer, fall to early winter, and winter) and related to the mussel community. Total abundance, taxon richness, and diversity index were used to characterize fish communities. Mussel community variables predicted some aspects of fish communities, but such patterns were seasonally limited. In both systems, mussel community variables had no predictive power for the total abundance of fishes. In drainage channels, taxon richness of mussels was a good predictor of all fish community variables except for total abundance in early summer. In winter, mussel abundance predicted well the taxon richness of the fish community, while taxon richness predicted the diversity index of the fish community. In backwaters, mussel abundance was a good predictor of fish community variables except total abundance in mid-summer. A relatively minor portion (<23%) of fish–mussel relationships was attributable to direct commensalism between mussels and bitterlings. A conceptual framework was provided to help identify the mechanisms behind fish–mussel relationships. Our findings validated the use of mussels as an indicator of high-quality summer rearing habitats in backwaters and wintering and reproduction habitats of fishes in drainage channels.

Keywords: backwaters, fish, floodplains, drainage channels, surrogate, Unionoida

1. Introduction

Many aquatic species are endangered due to various human impacts throughout the world (Dudgeon et al., 2006). There is an urgent need to take effective conservation and restoration measures. One strategy is to identify groups of organisms whose distribution, abundance, or species richness indicate the conditions of other organisms in surrounding areas (Kremen, 1992). Prioritizations of conservation areas based on indicator organisms often facilitate regional conservation planning (Fleishman et al., 2000; Lawler et al., 2003). Various groups of aquatic animals such as fish and macroinvertebrates are proposed as ecological indicators of aquatic ecosystems (Niemi and McDonald, 2004; Carlisle et al., 2008).

Effective ecological indicators should be easily and routinely monitored while they capture the complexities of the ecosystem and are sensitive to environmental stresses having a low variability in response (Dale and Beyeler, 2001). Freshwater mussels (Order: Unionoida) meet these criteria (also see Aldridge et al., 2007). First, mussels can be relatively readily sampled and monitored compared with other taxa such as fish or macroinvertebrates for which quantitative assessments of community structures are often difficult, requiring specialized sampling techniques and expertise in taxonomy (Hauer and Lamberti, 2006). Second, mussels are among the most imperiled organisms in the world (Lydeard et al., 2004). About 70% of native species of freshwater mussels are currently considered endangered, threatened, or of special concern in North America (Williams et al., 1993) as well as in Japan (Kondo, 2008; Negishi et al., 2008b). Such a status implies that mussels are highly sensitive to environmental stresses with which aquatic ecosystems are threatened. Third, mussels have limited mobility (Schwalb and Pusch, 2007) and longevity spanning several

decades (Kesler and Downing, 1997); thus, local populations are unlikely to show high temporal variability under natural conditions.

Freshwater mussels capture complexities of aquatic ecosystems because they provide a wide variety of important ecological functions. For example, mussels mediate nutrient cycling and alter physicochemical characteristics of the sediment (Vaughn and Hakenkamp, 2001). There are lines of evidence in support of the idea that such mussel-mediated ecological processes could cause changes in the community structures of other organisms such as macroinvertebrates (Vaughn and Spooner, 2006; Vaughn et al., 2008). Furthermore, the occurrence and community structures of mussels could have direct implications for the characteristics of fish communities because of various symbiotic relationships. Mussels are obligate parasites on fish during the early stage of their life cycles with species-specific host choices (Wächtler et al., 2001). Besides, bitterlings (Family: Cyprinidae; Sub-family: Achelongnathinae) only occur in areas where they can use mussels as spawning substrates (Kitamura, 2007).

The suitability of freshwater mussels as indicators of aquatic organisms has been suggested in few previous studies. Aldridge et al. (2007) demonstrated that mussel abundance was positively related to the taxon richness of macroinvertebrates in UK rivers, although they provided limited discussion of the possible mechanisms behind such patterns. Watters (1992) reported a positive relationship between species richness of fishes and mussels for data sets from 37 systems whose drainage basin areas ranged from 10 to 530,140 km². This may reflect the premise that there is a higher probability of more diverse species of mussels with different host choices or life histories occurring sympatrically when more species of fishes are available. Species richness of both mussels and fishes decreases with a decreasing area (Watters, 1992); thus, whether such

positive relationships between community structures of fishes and mussels remain significant for a relatively small geographic areas (i.e., <100 km²) is questionable.

Presently, 36% of freshwater and brackish fish species are endangered in Japan with four species already extinct (Japanese Ministry of the Environment, 2007); thus, efficient management strategies for the conservation of fish communities and their habitats are greatly needed. The applicability of ecological indicators to conservation strategies at relatively small spatial scales is of great interest because the Japanese government is promoting the importance of conservation action at local levels (e.g., municipal governments) as an effective means of conserving nationwide biodiversity (Japanese Ministry of the Environment, 2008). In consequence, this study aimed to investigate the use of freshwater mussels as an ecological indicator for efficient identification of priority sites when conserving aquatic biodiversity in lowland systems. The specific objectives were (1) to test the relationships between the community structures of fishes and mussels and (2) to examine the relative contribution of commensalism through bitterling–mussel interactions to the value of mussels as an indicator of fish communities. First, we present a conceptual framework for what the community structures of mussels could indicate in aquatic ecosystems with particular reference to fishes and macroinvertebrates. The framework was developed to help understand potential mechanisms behind the relationships between mussels and fishes. Freshwater mussels occur in diverse aquatic habitats including lakes and rivers (Negishi et al., 2008b). Lotic species typically occur in areas where they are sheltered from harsh hydraulic conditions during floods. We examined two major lotic habitats for mussels in Japan: agricultural drainage channels and floodplain backwaters (Negishi et al., 2008b).

2. A conceptual framework

In this section, we present some relationships between mussels and biological, chemical, and physical factors to highlight important processes behind indicator roles of mussels for aquatic habitats (Fig. 1). Unionoid mussels are generally considered as primary consumers that filter-feed on fine organic matters in food webs (Vaughn and Spooner, 2006). Therefore, mussels do not directly affect other biological components such as fishes and macroinvertebrates through predator–prey interactions (Fig. 1A).

First, the occurrence of mussels could result in distinctive community structures of aquatic organisms through positive ecological processes such as ecosystem engineering, provision of habitat, and various symbiotic relationships with fishes (Fig. 1B). Mussels can filter drifting organic matter from the water column and transfer it as biodeposits (Nalepa et al., 1991). Howard and Cuffey (2006) demonstrated that the increase in deposited fine organic matter resulted in a greater biomass or abundance of groups of macroinvertebrates (also see Vaughn and Spooner, 2006). The growth of periphyton was enhanced on the shells of live mussels possibly through the increased nutrient supply by excretion products (Spooners and Vaughn, 2006; Vaughn et al., 2008). The surface of shells creates a habitat for periphyton and invertebrates (Gutiérrez et al., 2003). Such increased productivity of primary producers and invertebrate consumers may positively affect species diversity and productivity of fish consumers through a trophic cascade (Fig. 1A). Furthermore, bitterling species directly benefit from the presence of mussels through the provision of spawning substrates (Kitamura, 2007), and thereby mussels may increase the local species richness of the fish community.

Second, environmental factors that directly affect the local habitat quality of mussels may also affect other taxa (Fig. 1C). As a result, correlated responses along a

gradient of environmental conditions may appear even when there are weak interactions among taxa. The heterogeneity in physical environment such as variability in current velocity and substrate types are of great importance for the community structures of fishes and macroinvertebrates (Prenda et al., 1997; Heino, 2000). Species-specific microhabitat preferences of mussels may also exist, although there are mixed results for this hypothesis (Strayer and Ralley, 1993; Kitamura, 2007). Water quality is another potentially important factor that may directly limit organisms' presence through physiological stresses (Fig. 1D). Levels of chemical contaminants, dissolved oxygen (DO), and fine sediment can impair habitat quality of aquatic organisms including mollusks (Gagnon et al., 2004; Poole and Downing, 2004; Negishi et al., 2012b). Mussel's species-specific susceptibility to environmental changes such as increases in fine sediment load has been suggested (Brim Box and Mossa, 1999). With the loss of habitat heterogeneity and degradation of water quality, the impoverishment of community structures of mussels, macroinvertebrates, and fishes might coincide.

Third, environmental susceptibility of host fishes may act as a bottlenecking factor of mussel community structures through the control of reproductive success (Fig. 1B). The high abundance and taxon species of the local mussel community may be associated with the presence of diverse and abundant host fish species because the former benefits from the increased probability of finding suitable host species through parasitization (Watters, 1992; Vaughn and Taylor, 2000). The environmental factors that potentially limit the dynamics of host fishes include not only habitat heterogeneity or water quality at the local scale, but also habitat quality at the larger spatial scales (Fig. 1C and D). For example, the loss of dispersal pathways for the migrating host fishes, which would have negligible influence on local habitat conditions for mussels, may

cause indirect but strong bottlenecks on the reproductive success of mussels (Watters, 1996). Indirect influences of habitat conditions on mussels through host fish distribution may override the effects of direct influences of microhabitat environmental conditions (Vaughn, 1997; Haag and Warren, 1998; Vaughn and Taylor, 2000).

3. Materials and Methods

3.1 Study sites

The two study systems (drainage channels in rice paddies and floodplain backwaters along a large river) were located in the Nobi plain, which is one of the largest fluvial plains in Japan. Study sites in the respective systems were contained within a total area of 100 km^2.

3.1.1 Drainage channels

The survey was conducted in 13 reaches within a network of drainage channels, which joined the Nagara River, in Seki City, Gifu Prefecture (Fig. 2; also see Negishi and Kayaba, 2009; Nagayama et al., in press). The selected reaches were representative of those in the area, including a spectrum of conditions ranging from those with few channel modifications (earth channel) to those with a high level of modifications (concrete lining on beds as well as walls) (Figs. 2D and E). The selection of study reach was largely constrained by the locations of sites with resident unionoid populations of measurable abundance (four reaches with abundances of >5 individuals per square meter). Furthermore 2–3 reaches of different habitat conditions were selected near each of the mussel-present reaches based on site accessibility. The selected reaches were 50–5,000 m apart. Irrigation water was directed to neighboring rice paddy fields and drained to the irrigation channels and then to the river network downstream. Rice

cultivation typically starts in early May and continues until the end of September.

The study reaches had a perennial flow because either of surplus irrigation water from the river, groundwater recharge from adjacent paddy fields, and/or hill slopes provided base-flow throughout the year. During the cultivation period, additional flow was provided by irrigation water drained out from the paddy fields. On an average, base-flow rates were low ($<0.01 \text{ m}^3/\text{s}$) during the non-cultivation period but became as high as $0.08 \text{ m}^3/\text{s}$ during the cultivation period (Table 1). Water temperature ranged from $<5^\circ\text{C}$ in winter to $>30^\circ\text{C}$ in summer. DO was nearly at saturation point (Nagayama et al., in press), pH and conductivity ranged from 5.7–7.8 and 1.7–38.8 $\mu\text{S}/\text{cm}$, respectively. Conductivity was highly variable across reaches in February 2010, probably because geochemical signatures unique to each reach controlled local water quality with decreased irrigation water supply. More details about site characteristics and measurement methods are given in Nagayama et al. (in press). There were four species of unionoid mussels (*Inversidens brandti*, *Obovalis omiensis*, *Lanceolaria grayana*, *Pronodularia japonensis*) in the study reaches; six highly modified reaches were without resident mussels.

3.1.2 Floodplain backwaters

The survey was conducted in a 15-km lowland segment of the Kiso River in Japan (drainage area of $5,275 \text{ km}^2$, Fig. 2). The channel gradient was approximately 0.15%, and flow rate and water temperature of the main channel ranged from approximately $60 \text{ m}^3/\text{s}$ during the base-flow to approximately $5,000 \text{ m}^3/\text{s}$ during flood, and from 5°C in winter to $>28^\circ\text{C}$ in summer, respectively, within the study segment. The hydrograph is generally characterized by relatively high flows in early summer (the *Baiu* season from June to July) and in the typhoon season from September to October and by relatively

stable and low flows from November to May. Dikes run along both sides of the segment, but relatively extensive areas of the floodplain remain with large numbers of backwaters having stagnant water under base-flow conditions (also see Negishi et al., 2012).

Two types of backwaters exist on the basis of how they are connected to the main channel at base-flow conditions. Connected backwaters are perennially connected to the main channel having a surface connection regardless of flow rate, whereas isolated backwaters are connected with the main channel only when flow rate increases to certain levels. Nine backwaters were selected for the survey as representative of floodplain water bodies in the areas; both connected and isolated backwaters were included (Table 1; Figs. 2F and G). The study sites were selected such that they covered all possible combinations between backwater types and presence or absence of mussels with three replicates for each: (1) connected with mussels, (2) isolated with mussels, and (3) isolated without mussels (Negishi et al., 2012a, b). The backwaters were 300–12,000 m apart. Median (range) of water surface area and depth of each backwater were 1,151.2 (508.7–15,524.4) m² and 36.2 (25.8–50.6) cm, respectively. Water temperature ranged from approximately 6°C in winter to >30°C in summer. Daytime DO was almost at saturation point, although DO tended to be low in August 2009 because the relatively high temperature suppressed dissolution of oxygen and high respiration activity. pH and conductivity ranged from 6.1–8.0 and 4.8–24.6 µS/cm, respectively. More details about site characteristics and measurement methods are given in Negishi et al. (2012b). There were three taxa of unionoid mussels (*Unio douglasiae*, *Lanceolaria grayana*, and *Anodonta* sp.) in the study area.

3.2 Fish surveys

3.2.1 Drainage channels

Fish sampling was conducted in fall (September 15–17, 2009), winter (February 18–19), early summer (June 2–3), and mid-summer (August 17–18, 2010). Within each reach, two sub-reaches (a length of $10 \times$ channel widths) were set with a channel distance of at least $10 \times$ channel widths to each other. The upstream and downstream ends of sub-reaches were enclosed with gill nets (4-mm mesh) to prevent fish migration during surveys. The sub-reach was searched for fishes by conducting three passes of catches using triangular scoop nets (34-cm wide and 33-cm high mouth opening; 44-cm long; 2-mm mesh) aligned perpendicularly to the channel. Furthermore, specific areas such as those with a fast current and along the channel edge were thoroughly searched for fishes using scoop nets (up to 5 min). Specimens were identified to the species level using Nakabo (2002) and Stevenson (2002). *Carassius* spp., *Squalidus* sp., and *Rhinogobius* spp. were identified only to the genus level because they could not be identified to the species level *in situ*. Total numbers of taxa and individuals for each channel were calculated by pooling samples from two sub-reaches.

3.2.2 Floodplain backwaters

Fish sampling was conducted in spring (May 27–28), mid-summer (August 10–12), early winter (December 2–3, 2009), and winter (February 16–17, 2010). Fishes were collected using 2–10 stationary set-nets, each of which consisted of two leaded rectangular fence nets attached to a trap box (each fence net was 200-cm wide and 100-cm high; a trap box with an opening of 63×63 cm and 224-cm long; 4-mm mesh) in each backwater. The total number of nets for each site was proportional to the surface area. The set-net was installed perpendicular to the shoreline with one fence end fixed to the shore and the bottom to the bed. The nets were set at a minimum distance of 20 m from each other. After 10 min, three personnel disturbed the area adjacent to the net

opening along the shore (4×20 m) to chase fishes into the set-nets. Fish taxa were identified, enumerated, and released, as done for drainage channels. Total numbers of taxa and individuals for each backwater were calculated by pooling samples for respective backwaters.

3.3 Mussel surveys

3.3.1 Drainage channels

Surveys were conducted on September 15–17, 2009, prior to the fish surveys in each sub-reach. Mussels were collected in 3–9 belt-transects (50-cm long) laid out across the channel; the number of transects was proportional to the size of sub-reaches. Transects were thoroughly searched by disturbing 5 cm of the surface of the substrate; a 7-mm mesh sieve was used to collect individuals. The total area searched was recorded and individuals for each channel were calculated by pooling samples from two sub-reaches.

3.3.2 Floodplain backwaters

Surveys were conducted between January and May 2007 and 2008 within transects, which were laid out along the longest axis of each backwater, as part of a separate study (Negishi et al., 2012b). A total of 3–13 sampling points were set along the transect at equidistant locations with the total number of points being proportional to the length of the transect. The first and last points were at least 1.5 m from the surface water margins. Areas at sampling points (approximately 4 m^2) were thoroughly searched for 1 min by disturbing 5 cm of the surface of the substrate. As the survey progressed from one end of the transect to the other, survey personnel continued searching for mussels in the areas off the transect. Mussels collected from sampling points, and off-transect locations were pooled in each backwater. Time spent on all searches was recorded to calculate the numbers of individuals caught per unit effort.

3.4 Data analyses

Because two slightly different methods (time-based and area-based measurements) were used to quantify the abundance of fishes and mussels for backwaters and drainage channels, abundance was expressed in different ways for the two systems. The abundance in drainage channels was expressed as density (numbers of individuals caught per m² of searched bottom area), whereas the abundance in backwaters was expressed as catch per unit effort (CPUE; total numbers of individuals divided by the number of set-nets engaged for fish and by the total number of hours spent in searching for mussels). We quantified the abundance of mussels once in each system and used it to examine mussel–fish relationships on different sampling occasions. This was to minimize potential physiological stresses involved in repeated sampling (Haag and Commens-Carson, 2008) and mussels' limited mobility at the seasonal timescale (Negishi et al., 2011). Furthermore, in backwaters, large recruitments of juveniles were not observed during occasional qualitative observations in the period between mussel and fish surveys (personal observations, J.N. Negishi). To correct the taxon richness for fish abundances, we employed rarefaction to obtain the expected taxon richness using the Incidence-based Coverage Estimator (ICE) with 100,000 runs (Gotelli and Colwell, 2001). The Shannon–Wiener Index (H') was calculated to characterize the diversity of fish communities in each of the backwaters and drainage channels (Krebs, 1998). The calculations of taxon richness and H' were done using EstimateS ver. 8.2.0 (Colwell, 2009). In addition, rarity of fish taxon was calculated using the probability of occurrence of each taxon across sites and sampling occasions based on the method of Fleishman et al. (2000). We further calculated a rarity index, which indicates the degree to which a fish community consists of rare taxa, by summing rarity values of taxa

present in each site.

To examine the differences in fish community structures among sampling occasions, we performed one-way repeated-measures analysis of variance (ANOVA) with sampling occasion as the main factor and site identity as a repeated-measures factor on fish community variables. In addition, generalized linear models (GLMs) were generated separately for drainage channels and backwaters using abundance, taxon richness, H' , and rarity index of fish community as dependent variables. Abundance and taxon richness of mussels were included as independent variables with Gaussian error distribution and an identity link function. In these GLMs, all dependent and independent variables were standardized to have a value ranging from 0 to 1 so that the predictive power of relationships between community structures of fish and mussels were compared across different sampling occasions and two different systems. The best model was selected based on Akaike's Information Criterion (AIC; Akaike, 1974), and the statistical significance of the best models was tested using parametric bootstrap procedures (1,000 iterations for the residual deviance from null models). To examine the relative contribution of bitterlings to the fish–mussel relationships, GLMs were regenerated with fish community variables calculated after removing bitterlings from the dataset. Differences in the coefficient of determination in GLMs with and without bitterlings were interpreted as the contribution of bitterlings.

ANOVAs and GLMs were conducted using R 2.10.1 (R Development Core Team, 2008) with a significance level of 0.05. GLMs were fitted using the `glm` function in the MASS package. In ANOVAs, family-wise statistical significance was corrected for analyses on different fish metrics derived from the same community in each system (Bonferroni's method). In addition, variables were \log_{10} -transformed to improve

normality when appropriate. When there was a significant main effect in ANOVAs, multiple comparisons were made among groups using Bonferroni-corrected paired t-tests. The significance level for GLMs was corrected for analyses on different fish metrics derived from the same community at each sampling occasion (Bonferroni's method).

4. Results

A total of 2,785 and 4,292 individual fishes representing 20 and 24 taxa were collected in drainage channels and backwaters, respectively (Appendices 1 and 2). Nine and 13 taxa occurred exclusively in drainage channels and backwaters with 11 taxa found in both the systems. Among a total of six bitterling species collected, two and four species were observed exclusively in drainage channels and backwaters, respectively. In both systems, Cyprinidae numerically dominated fish communities, accounting for 52% and 89% of total numbers of fishes collected in drainage channels and backwaters. Pair-wise analyses on fish community variables showed that taxon richness and rarity index were highly correlated with each other in both systems ($n = 36$, $p < 0.001$, and $r > 0.98$ for drainage channel; $n = 52$, $p < 0.001$, and $r > 0.98$ for backwaters), and thus the latter was surrogated by the former for further analyses.

Except for the Shannon–Wiener diversity index in drainage channels, fish community variables differed among sampling occasions in both systems (one-way repeated-measures ANOVA, $p < 0.001$ in all cases). In drainage channels, total abundance and taxon richness showed relatively high values in mid-summer (August) and fall (September) with the highest in mid-summer when both water temperature and flow discharge were high (Tables 1 and 2). In backwaters, total abundance was the

highest in spring, intermediate in mid-summer, and relatively low in winter periods (December and February). In addition, taxon richness and diversity index were the highest in mid-summer (August) when temperature was the highest. In both systems, high abundance coincided with the high values of taxon richness, indicating the seasonal fluctuation of total abundance was partly caused by the inclusion of relatively rare taxa in the fish community.

On all sampling occasions in drainage channels and two occasions in backwaters, at least one fish community metric was modeled by mussel community variables (Tables 3 and 4). Among those models, statistically significant relationships were detected on two and one sampling occasion(s) in drainage channels and floodplain backwaters, respectively. In both systems, mussel community variables had no predictive power for the total abundance of fishes ($p > 0.45$ in all cases). In drainage channels, taxon richness of mussels was a good predictor of taxon richness and the diversity index of fish in early summer (June), exhibiting statistically significant positive relationships (Fig. 3). In winter (February), mussel abundance positively predicted the taxon richness well, whereas taxon richness of mussels was positively associated with the diversity index of the fish community. In floodplain backwaters, mussel abundance increased with an increasing level of taxon richness and diversity index of the fish community (Fig. 4).

Most of the significant fish–mussel relationships remained statistically significant even after the effects of bitterlings were removed (Tables 3 and 4). However, in June 2010, in drainage channels, the exclusion of bitterlings resulted in insignificant relationships between fish and mussels. On average, the presence of bitterlings accounted for 22.8% ($n = 4$) and 5.3% ($n = 2$) of significant fish–mussel community relationships in drainage channels and backwaters, respectively (Tables 3 and 4).

5. Discussion

We provided empirical evidence that mussel community characteristics can predict some aspects of fish communities for areas where local species richness of mussels is relatively low (<4). With the increased abundance or taxon richness of mussels, there was a statistically significant increase in taxon richness or diversity index in the fish community. Importantly, such significant positive relationships were observed in limited seasons in both systems: winter to early summer periods in drainage channels and the mid-summer period in floodplain backwaters. An additional analysis using data sets consisting of standardized community variables of fish and mussels pooled from different sampling occasions did not show statistically significant relationships in either system. Overall, our findings indicated that the use of mussels as indicators of fish community structure is limited to specific seasonal contexts for a geographic areas of $<100 \text{ km}^2$.

It is intuitively predictable that the occurrence and community structure of bitterlings and mussels are associated with each other given an obligate dependence of the former on the latter (Kitamura, 2007; Terui et al., 2011). Such direct commensalism accounted for a relatively minor portion ($<23\%$ in both systems) of the observed positive relationships between some community variables of fish and mussels. The decline of mussels is often concerned from the perspective of the conservation of bitterlings, which are also endangered due to poaching and degradation of mussel habitat (Negishi et al., 2008b; Kitamura et al., 2009). The current deterioration of mussel habitat is of great concern because mussels can be used as an indicator of fish communities as a whole, rather than for a particular group of fishes. Although

community-level attributes of mussels have been linked to those of fish or macroinvertebrates (Watters, 1992; Aldridge et al., 2007), possible mechanisms behind such patterns have not been well articulated (but see Vaughn and Taylor, 2000). Our conceptual model greatly helps to address the possible mechanisms behind the indicator roles of mussels for fish communities unaccounted for by bitterling species.

In floodplain backwaters, positive linear correlations between mussel abundance and fish community variables (i.e., taxon richness and diversity index) were significant only in summer when water temperature was highest. The habitat suitability of floodplain backwaters for mussels in the study area is determined by the average concentration of DO in summer which is mediated by the flood inundation frequency (Negishi et al., 2012a, b). The DO concentration serves as a strong determinant of aquatic community structures including fishes (Dodds, 2002). For example, with low oxygen levels, species sensitive to hypoxia are eliminated or the development of eggs and juvenile individuals are hampered. Therefore, the different characteristics of fish community structures along the gradient of mussel abundance in summer might also primarily result from local habitat constraints provided through low DO (Fig. 1D).

The strong gradient of DO concentration across floodplain backwaters occurred only during the warmest summer periods (Negishi et al., 2012b). Thus, it is conceivable that physiological stresses from hypoxia did not act as a strong bottlenecking factor on fish community organization in other seasons when DO levels were similar among backwaters. While mussel distribution across floodplain backwaters, which is preconditioned by the DO concentration in summer, changes little throughout the year, much more mobile fish could seasonally disperse across backwaters and the main channel. Consequently, we infer that the importance of DO as a controlling factor of

habitat suitability only in summer, and the differences in spatio-temporal scales at which different taxa respond to changing habitat environments resulted in the absence of association between community structures of fish and mussels in non-summer periods. These proposed mechanisms predict that the decreases in taxon richness and diversity of fish with decreasing mussel abundance would coincide with the exclusion and/or decreases in the abundance of relatively rare hypoxia-susceptible fish species. In fact, fish communities in backwaters with or without few resident mussels in mid-summer were low in taxon richness and were numerically dominated by common hypoxia-tolerant species such as *Pseudorasbora parva* (S. Nagayama, unpublished data). The summer period is important for fish growth because of abundant food resources and high metabolic rates. In backwaters, therefore, the abundance of mussels acts as an indicator of high-quality summer rearing habitat for fish communities including relatively rare species.

In drainage channels, significant relationships between fish and mussels were not observed in the warmest summer period, which contrasted with the patterns in the floodplains. This disparity could be explained by the differences in the environmental factors that limit the distribution of mussels between the two systems. DO level was nearly saturated even on nights during summer periods in drainage channels (Negishi and Kayaba, 2009). Relatively high DO is attributable to the shallow perennial lotic environment that maintains primary productivity within the channels at a relatively low level and precludes excessive detritus loading, both of which are key processes for high consumption of DO. Consequently, hypoxia was unlikely to be the limiting factor for mussel distribution in the drainage channels.

The degree of human alterations of channel structures such as straightening and

concrete-lining affects mussel occurrence and distribution in drainage channels (Negishi et al., 2008b). The within-channel habitat heterogeneity and sediment deposition, which both tend to decrease with an increasing level of human alterations, degrades habitat quality for mussels and fishes (Negishi et al., 2011; Nagayama et al., in press).

Therefore, the presence of fish–mussel relationships in seasons other than mid-summer might have resulted from the coincidental spatial distribution of fish and mussels along the gradient of local habitat conditions controlled by the level of human alterations of channels (Fig. 1C). Higher flow rates in irrigation periods are in general associated with greater water depth (Negishi and Kayaba, 2009), and could reduce the differences in terms of local habitat quality among sites by providing additional cover and habitat space (Nagayama et al., in press). Also, small vertical drops that are commonly present in drainage channel networks could become more passable because of the increased flow, allowing the immigration of species common in downstream areas. This hypothesis is supported by the observation that fish abundance and taxon richness were greatly increased during summer periods (Table 3). Thus, the absence of fish–mussel relationship in the mid summer may be attributable to the reduced importance of local habitat conditions in affecting fish community structures. Environmental conditions at spatially larger scales such as a connectivity to downstream areas that provide sources of migrating individuals are perhaps more important in accounting for fish community structures at the local scale (Vaughn and Taylor, 2000). Overall, mussel abundance or taxon richness could be indicative of high-quality habitat for fishes, particularly the taxa that depend on drainage channels for wintering and reproduction in early summer (also see Nagayama et al., in press).

6. Conclusions

Our findings indicate that the use of freshwater mussels has considerable merit when prioritizing habitat conservation areas for fishes even across a relatively small geographic area (<100 km²) with limited mussel taxon richness (<4 taxa). In floodplain backwaters, mussel abundance can serve as a useful tool that identifies important summer fish-rearing habitats. In contrast, mussels appear to indicate habitat potentially important for wintering and reproduction in drainage channels. Altogether, we infer that the decreases in abundance and taxon richness of mussels indicate not only the loss of habitat for bitterlings, but also the loss of important habitat for other fish species in lowland systems. Therefore, remaining areas with high abundance and/or taxon richness of mussels are proposed as good candidates for the conservation of aquatic fauna in regional planning. Importantly, we stress that the conservation of mussel habitat would not be sufficient for the conservation of the entire fish community. For example, wintering habitats in floodplain backwaters and summer rearing habitats in drainage channels were not identified based on mussel community structures. Ecological indicators are often criticized because a conceptual framework for what the indicator is indicating and appropriate identification of spatial and/or temporal scales for the indicator is lacking (Niemi and McDonald, 2004). Our findings are valuable because we not only provide the framework for what mussels indicate but also specify the spatio-temporal contexts for which this indicator could be effective.

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Figure captions

Fig. 1

A conceptual diagram showing the biological interactions and the direct or indirect effects of physico-chemical factors on biota. The arrows indicate the directions of major processes involved. Major pathways of energy through predator–prey interactions in food-webs including mussels (A); ecological interactions such as ecosystem engineering, provision of habitat, and commensalism (B); the processes associated with water quality such as DO, nutrient concentration, and levels of toxic substances and fine sediment (C); the processes associated with local physical habitat environments such as velocity, depth, and substrate characteristics (D). For the text explaining the relationships presented, see chapter 2 “A conceptual framework”.

Fig. 2

Japan islands with the geographic location of the study area (A), drainage areas of the rivers Nagara and Kiso (B), and points within the Nagara and Kiso river drainage area: areas including the drainage channels or the floodplain of backwaters of this study. Views of drainage channels: a least human-altered channel with abundant mussels (D) and a highly human-altered channel without mussels (E). View of floodplain backwaters: a frequently inundated backwater with abundant mussels (F) and a seldom inundated backwater without mussels (G).

Fig. 3

Relationships between community variables of fish and mussels in drainage channels in

central Japan in February and June 2010. Fish community scores differ among panels: taxon richness for the panels (A) and (C); Shannon–Wiener’s diversity index for the panels (B) and (D). Note that all variables are expressed as standardized scores ranging from 0 to 1. Solid lines indicate regression lines, and only statistically significant relationships are shown. The coefficient of determination and statistical significance (Bonferroni corrected level) are shown for each panel.

Fig. 4

Relationships between community variables of fish and mussels in floodplain backwaters in central Japan in August 2009. Fish community scores differ among panels: taxon richness for panel (A); and Shannon–Wiener’s diversity index for panel (B). Note that all variables are expressed as standardized scores ranging from 0 to 1. Solid lines indicate regression lines and only statistically significant relationships are shown.

Table 1. General characteristics of the study sites in drainage channels (n = 13) and floodplain backwaters (n = 9). Medians (with ranges in parentheses) for water temperature (Temp.), conductivity (Cond.), pH, chlorophyll a (Chlor.), DO, discharge, and water depth are presented. “—” denotes that the values were not applicable or available.

Occasions	Temp. (°C)	Cond. ($\mu\text{S}/\text{cm}$)	pH	Chlor. ($\mu\text{g}/\text{L}$)	DO (mg/L)	Discharge (m^3/s)	Water depth (cm)
<i>Drainage channels</i>							
September 2009	21.8 (19.6–23.2)	9.0 (5.6–12.7)	7.3 (5.7–7.8)	—	—	0.02 (0.002–0.17)	13.4 (4.9–23.7)
February 2010	7.9 (3.9–12.0)	7.6 (1.7–38.8)	7.3 (5.7–7.8)	—	—	0.003 (0.0003–0.04)	7.9 (2.9–12.6)
June 2010	22.0 (17.8–28.7)	7.2 (5.2–15.5)	6.8 (6.2–7.4)	—	—	0.03 (0.002–0.08)	11.7 (5.7–33.7)
August 2010	26.3 (21.9–30.0)	6.1 (2.0–16.5)	6.7 (6.2–7.1)	—	—	0.04 (0.002–0.08)	16.8 (8.7–31.6)
<i>Backwaters</i>							
May 2009	22.7 (17.1–30.8)	10.0 (6.0–19.8)	6.9 (6.8–7.2)	5.3 (0.4–22.1)	6.9 (9.5–16.3)	—	—
August 2009	23.2 (22.0–25.7)	7.4 (4.8–22.1)	6.6 (6.1–6.9)	9.1 (0.4–59.4)	7.0 (2.8–8.9)	—	—
December 2009	10.7(9.6–12.7)	8.9 (7.0–24.6)	6.9 (6.8–7.2)	3.4 (0.3–24.8)	9.9 (4.8–13.7)	—	—
February 2010	8.1 (6.0–9.7)	9.6 (6.3–20.5)	7.8 (7.6–8.0)	3.1 (0.5–23.7)	11.1 (9.8–12.5)	—	—

Table 2. Fish community characteristics in the drainage channels (n = 13) and floodplain backwaters (n = 9) in Central Japan. Medians (with ranges in parentheses) for total abundance, taxon richness, diversity index, and rarity index are shown. Measurements were made in September 2009 and February, June and August 2010 in drainage channels, whereas it was made in May, August, and December 2009 and February 2010 in backwaters. Values accompanied with different alphabetical letters were statistically different as a result of repeated-measures analysis of variance with sampling occasion as the main factor and site identity as a repeated-measures factor; the analyses were conducted separately for two systems.

	Drainage channels				Backwaters			
	Sept.	Feb.	June	Aug.	May	Aug.	Dec.	Feb.
Total abundance	3.0 ^a (0.4–9.5)	0.3 ^{bc} (0.0–6.3)	0.4 ^c (0.1–2.1)	2.0 ^{ab} (0.1–22.3)	33.7 ^a (8.6–210.3)	19.6 ^{ab} (7.3–64.5)	14.2 ^{bc} (0.1–35.0)	1.2 ^c (0.1–6.4)
Taxon richness	5 ^a (2–10)	2 ^b (0–9)	3 ^b (1–9)	6 ^{ab} (1–12)	8 ^{ab} (3–11)	8 ^a (4–13)	6 ^b (0–7)	2 ^c (1–3)
Shannon–Wiener index (H')	1.1 (0.3–1.8)	0.6 (0.0–1.8)	0.8 (0.0–1.8)	1.2 (0.0–1.9)	0.9 ^a (0.3–1.5)	1.1 ^a (0.5–1.9)	1.0 ^a (0.0–1.6)	0.4 ^b (0.0–0.9)

Table 3. Results of generalized linear models in drainage channels that tested the relationships between mussel community variables and fish community variables. Coefficient of determination was calculated for models with and without bitterling taxa included in fish community. Effects of bitterling were calculated as proportion of coefficient of determination explained by the bitterling taxa. Bold letters indicate statistical significance based on Bonferroni correction: *** < 0.001/3; ** <0.01/3; * <0.05/3. Because none of the mussel community variables were retained in the best models for H' in September 2009, total abundance in June 2010, and total abundance and H' in August 2010, they are not shown in the table.

Sampling occasions	Dependent variables (fish community)	Independent variables (mussel community)	Coefficient of determination (r^2)		Effects of bitterlings (%)
			With bitterlings	Without bitterlings	
September 2009	Total abundance	Taxon richness	0.19	0.15	22.9
	Taxon richness	Abundance	0.28	0.20	27.1
February 2010	Total abundance	Taxon richness	0.19	0.14	28.9
	Taxon richness	Abundance	0.50 ***	0.35 *	29.2
	H'	Taxon richness	0.42 *	0.38 *	8.0
June 2010	Taxon richness	Taxon richness	0.58 *	0.36 *	38.5
	H'	Taxon richness	0.30 *	0.26	15.6
August 2010	Taxon richness	Taxon richness	0.19	0.17	8.6

Table 4. Results of generalized linear models in floodplain backwaters that tested effects of mussel community variables on fish community variables as shown in Table 3. For total abundance and H' of the fish community in May 2009 and all fish community variables in December 2009 and February 2010, statistical tests were conducted but none of the mussel community variables were retained in the best models.

Sampling occasions	Dependent variables (fish community)	Independent variables (mussel community)	Coefficient of determination (r^2)		Effects of bitterlings (%)
			With bitterlings	Without bitterlings	
May 2009	Taxon richness	Abundance	0.26	0.21	19.5
August 2009	Total abundance	Abundance	0.31	0.38	-22.6
	Taxon richness	Abundance	0.59 *	0.53 *	10.2
	H'	Abundance	0.74 **	0.74 **	0.4

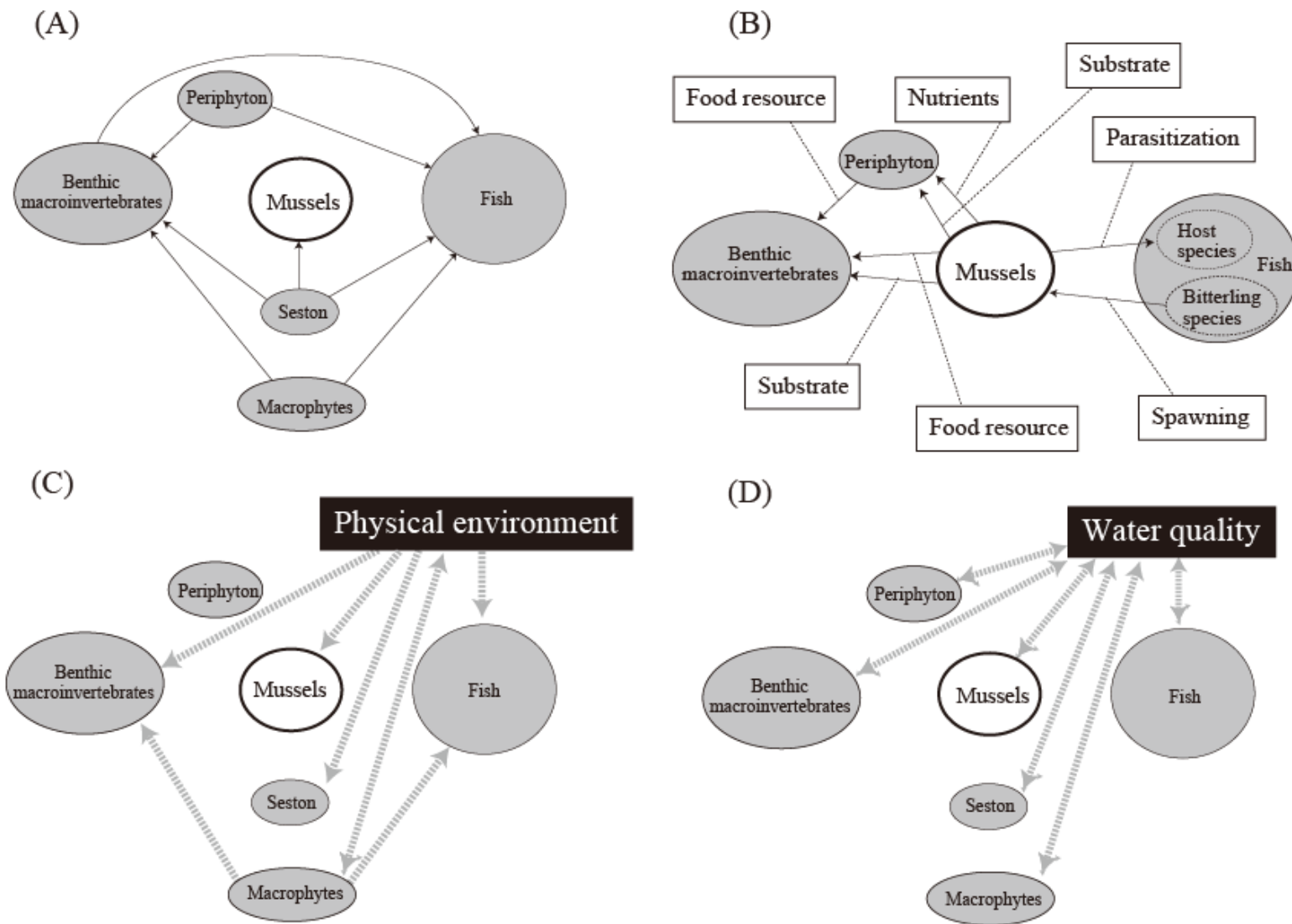


Fig. 1 Negishi et al.

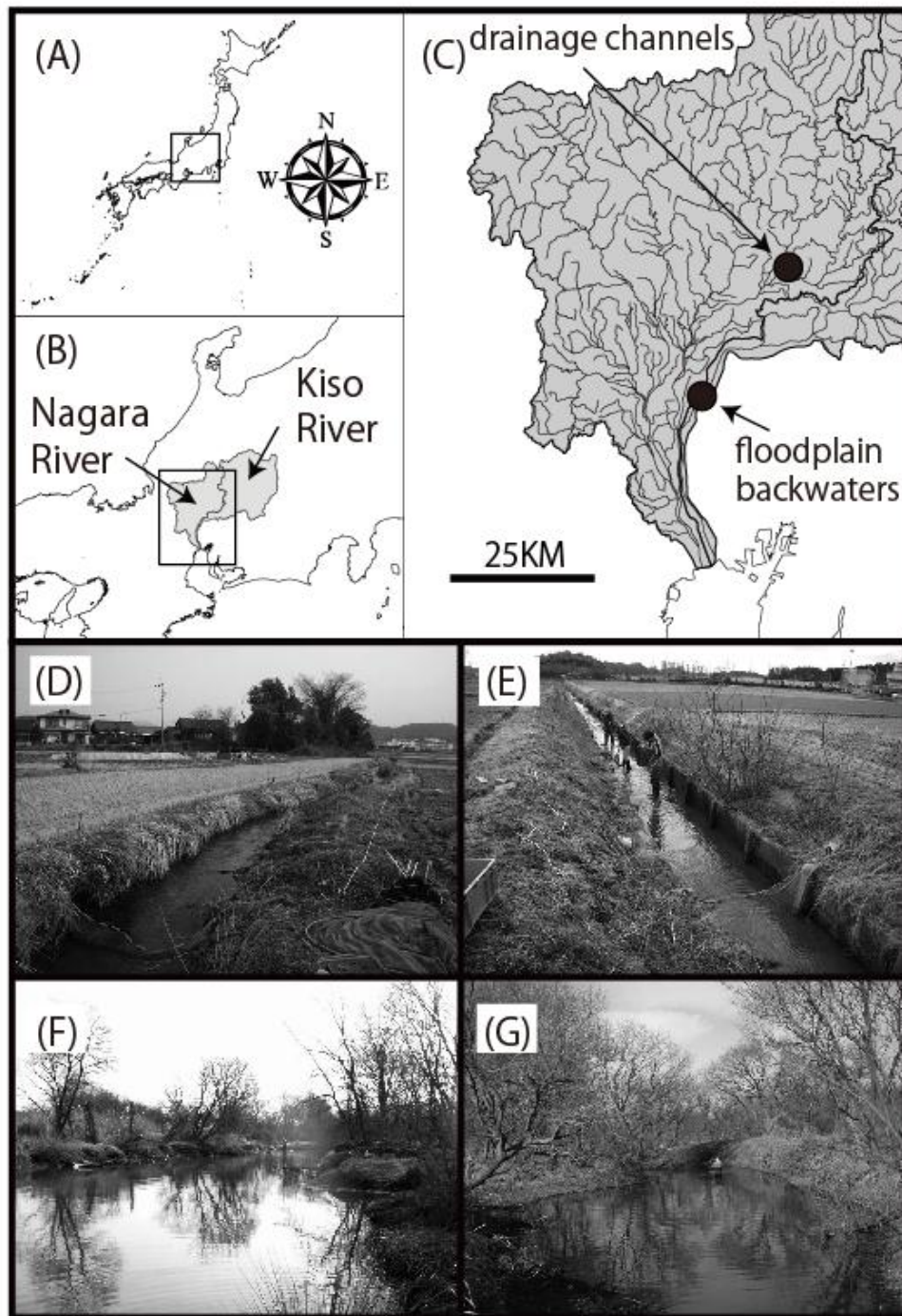


Fig. 2 Negishi et al.

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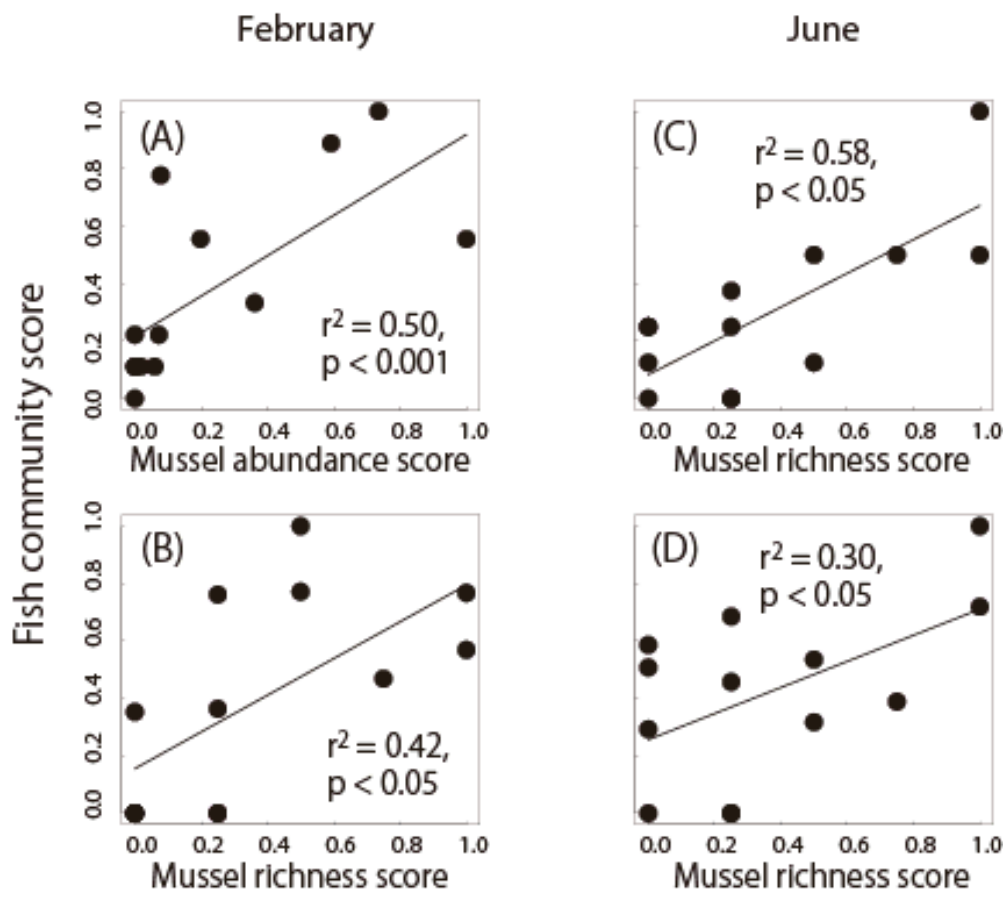


Fig. 3 Negishi et al.

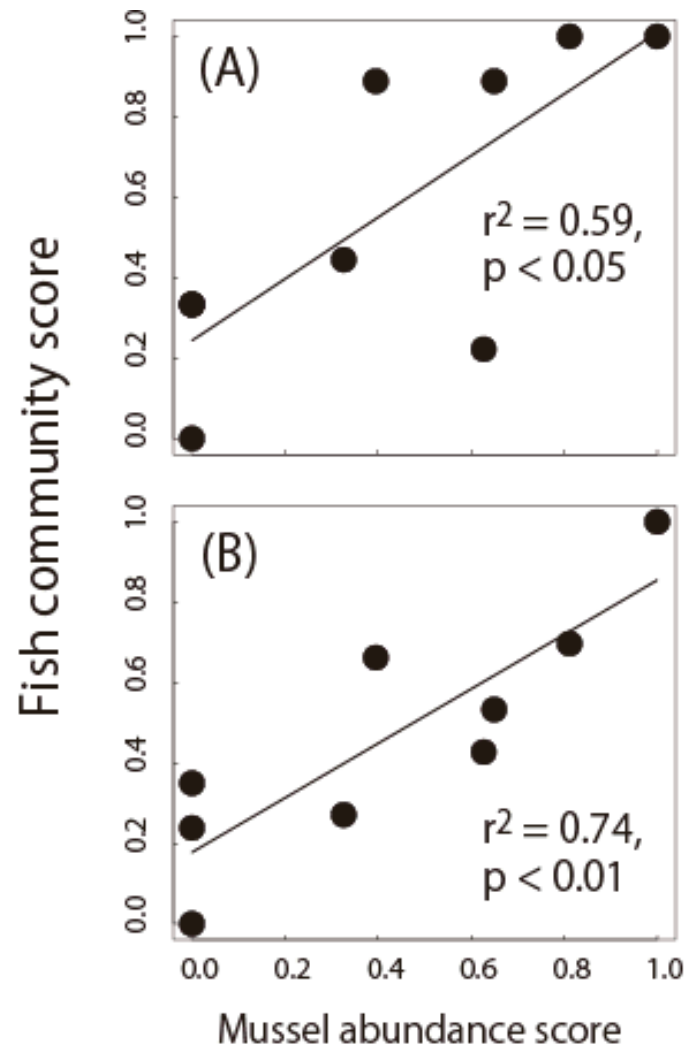


Fig. 4 Negishi et al.

Appendix 1. Species collected in drainage channels (n = 13). Species sorted by total numbers of individuals caught during the study (total counts). The percentage of each species constituting total counts (relative counts), average abundance across all sites and sampling occasions (abundance; individuals caught in m²), and rarity index of each species based on the probability of occurrence across sites and sampling occasions (rarity) are also shown. ‡Taxa exclusively found in drainage channels; other taxa were found in both the systems.

Family	Species	Total counts	Relative counts	Abundance	Rarity
Cobitidae	<i>Misgurnus anguillicaudatus</i>	697	25.03	0.65	0.25
Cyprinidae	<i>Tanakia limbata</i> ‡	541	19.43	0.38	0.48
Cyprinidae	<i>Zacco platypus</i>	444	15.94	0.24	0.62
Gobiidae	<i>Rhinogobius</i> spp.	332	11.92	0.31	0.25
Cyprinidae	<i>Nipponocypris sieboldii</i> ‡	193	6.93	0.13	0.77
Cobitidae	<i>Cobitis taenia striata</i> ‡	188	6.75	0.12	0.67
Cyprinidae	<i>Gnathopogon elongatus</i>	104	3.73	0.06	0.77
Adrianichthyidae	<i>Oryzias latipes</i>	74	2.66	0.19	0.81
Cyprinidae	<i>Tanakia lanceolata</i> ‡	69	2.48	0.04	0.75
Cyprinidae	<i>Pseudogobio esocinus esocinus</i>	35	1.26	0.01	0.85
Cyprinidae	<i>Carassius</i> spp.	29	1.04	0.05	0.88
Cyprinidae	<i>Nipponocypris temminckii</i> ‡	23	0.83	0.01	0.90
Cyprinidae	<i>Hemibarbus barbus</i>	15	0.54	0.01	0.83
Odontobutidae	<i>Odontobutis obscura</i> ‡	14	0.50	0.04	0.94
Cobitidae	<i>Cobitis biwae</i> ‡	11	0.39	0.02	0.90
Cyprinidae	<i>Phoxinus logowskii steindachneri</i> ‡	8	0.29	0.004	0.88
Centrarchidae	<i>Lepomis macrochirus</i>	3	0.11	0.002	0.94

Appendix 1. (Continued)

Family	Species	Total counts	Relative counts	Abundance	Rarity
Centrarchidae	<i>Micropterus salmoides</i>	2	0.07	0.001	0.96
Siluridae	<i>Silurus asotus</i> ‡	2	0.07	0.004	0.98
Cyprinidae	<i>Cyprinus carpio</i>	1	0.04	0.000	0.98

Appendix 2. Species collected in floodplain backwaters (n = 9). Species sorted by total numbers of individuals caught during the study (total counts). The percentage of each species constituting total counts (relative counts), average abundance across all sites and sampling occasions (abundance; individuals caught in each set-net), and rarity index of each species based on the probability of occurrence across sites and sampling occasions (rarity) are shown. † Taxa exclusively found in backwaters; other taxa were found in both systems.

Appendix 2. (Continued)

Family	Species	Total counts	Relative counts	Abundance	Rarity
Cyprinidae	<i>Rhodeus ocellatus ocellatus</i> †	2,228	51.91	67.52	0.25
Cyprinidae	<i>Pseudorasbora parva</i> †	825	19.22	25.00	0.28
Cyprinidae	<i>Zacco platypus</i>	298	6.94	8.76	0.33
Centrarchidae	<i>Lepomis macrochirus</i>	225	5.24	8.33	0.78
Cyprinidae	<i>Carassius</i> spp.	213	4.96	7.10	0.50
Adrianichthyidae	<i>Oryzias latipes</i>	174	4.05	5.80	0.69
Cyprinidae	<i>Gnathopogon elongatus</i>	82	1.91	2.83	0.64
Cyprinidae	<i>Abbottina rivularis</i> †	62	1.44	2.14	0.64
Gobiidae	<i>Rhinogobius</i> spp.	40	0.93	1.21	0.58
Cyprinidae	<i>Squalidus</i> spp. †	37	0.86	1.28	0.72
Cyprinidae	<i>Acheilognathus cyanostigma</i> †	32	0.75	1.19	0.81
Plecoglossidae	<i>Plecoglossus altivelis altivelis</i> †	12	0.28	0.44	0.86
Cyprinidae	<i>Hemibarbus barbus</i>	10	0.23	0.37	0.81
Gobiidae	<i>Gymnogobius urotaenia</i> †	10	0.23	0.36	0.92
Cyprinidae	<i>Acheilognathus longipinnis</i> †	9	0.21	0.32	0.92
Cyprinidae	<i>Biwia zezera</i> †	8	0.19	0.28	0.86
Cyprinidae	<i>Tribolodon hakonensis</i> †	7	0.16	0.26	0.97

Family	Species	Total counts	Relative counts	Abundance	Rarity
Cyprinidae	<i>Cyprinus carpio</i>	7	0.16	0.25	0.86
Centrarchidae	<i>Micropterus salmoides</i>	6	0.14	0.21	0.92
Cyprinidae	<i>Pseudogobio esocinus esocinus</i>	3	0.07	0.11	0.92
Cyprinidae	<i>Acheilognathus tabira tabira</i> †	1	0.02	0.04	0.97
Cyprinidae	<i>Sarcocheilichthys variegatus variegatus</i> †	1	0.02	0.04	0.97
Cobitidae	<i>Misgurnus anguillicaudatus</i>	1	0.02	0.04	0.97
Channidae	<i>Channa argus</i>	1	0.02	0.04	0.97