

# Connectivity and short-term flood interactively affect fish community composition in drainage ditches of paddy fields in an agricultural landscape

Hideyuki Iwamoto<sup>1</sup>, Daisuke Tahara<sup>2</sup>, and Takehito Yoshida<sup>3</sup>

<sup>1</sup>The University of Tokyo Graduate School of Arts and Sciences College of Arts and Sciences

<sup>2</sup>Research Center of Marine Bioresources, Fukui Prefectural University

<sup>3</sup>The University of Tokyo Graduate School of Agricultural and Life Sciences Faculty of Agriculture Department of Ecosystem Studies

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## Abstract

Community assembly can change over time following variations in connectivity among habitats. Previous studies have demonstrated the influence of seasonal pulse floods on community structures by facilitating species dispersal, but the effects of short-term flash floods have been poorly investigated. We investigated fish community structures before and after a short-term flood in drainage ditches of paddy fields in the Kita River basin, Japan. The study sites were classified into three connectivity types, “Transient” (connected only during the flood, with a temporally-disappearing vertical gap between drainage ditches and downstream rivers), “Connected” (always connected, without the vertical gap), and “Disconnected” (always not connected, with the vertical gap). The abundance of *Misgurnus anguillicaudatus*, the only species that dispersed from paddy fields to drainage ditches, increased after the flood irrespective of the connectivity types, although the total abundance of the other species significantly increased after the flood only in the “Transient” sites. The dissimilarity of species composition between the (n-1)-th and n-th surveys at each site was consistently low in the “Connected” and “Disconnected” sites, whereas it rose just after the flood and gradually declined in the “Transient” sites. Species composition was significantly different among the connectivity types, indicating that some fish species need stable connectivity even during the non-flood period. The results showed that the short-term flood facilitated fish dispersal from paddy fields by the increased water discharge and that from downstream rivers by the temporary removal of vertical gap, emphasizing the importance of hydrological connectivity for biodiversity conservation in an agricultural landscape.

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## Title

Connectivity and short-term flood interactively affect fish community composition in drainage ditches of paddy fields in an agricultural landscape

## The full names of the authors

Hideyuki Iwamoto<sup>1,4\*</sup>, Daisuke Tahara<sup>2,4</sup>, Takehito Yoshida<sup>3,41</sup> Department of General Systems Studies, University of Tokyo, 3-8-1 Komaba, Meguro, Tokyo 135-8902, Japan<sup>2</sup> Research Center of Marine Biore-sources, Fukui Prefectural University, 49-8-2, Katsumi, Obama, Fukui 917-0116, Japan

<sup>3</sup> Department of Ecosystem Studies, University of Tokyo, 1-1-1 Yayoi, Bunkyo, Tokyo 113-8657, Japan<sup>4</sup> Research Institute for Humanity and Nature, 457-4 Motoyama, Kamigamo, Kita-Ku, Kyoto 603-8047, Japan \*Corresponding author Email: iwamoto.freshwater@gmail.com ORCID id: <https://orcid.org/0000-0002-9695-4145>

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community assembly; river ecosystem; heavy rain; Bray-Curtis dissimilarity; temporal turnover;

## Abstract

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## Introduction

Metacommunity theories have emphasized that local communities are assembled not only through local processes related to environmental filtering and species interaction but also through regional processes based on species dispersal (Leibold et al., 2004). Connectivity is one of the most important factors affecting community assembly, which is defined as “the degree to which the landscape facilitates or impedes movement among resource patches” (Taylor et al., 1993). A decline in connectivity increases the effect of local niche-driven processes and decreases the mass effect that leads to the homogenization of community structure at adjacent localities due to high dispersal (Heino et al., 2015; Leibold et al., 2004). Moreover, connectivity can temporally fluctuate on various time scales, such as within a day and around a year in dynamic ecosystems (Zeigler & Fagan, 2014). As theoretical studies showed influences of time-varying connectivity on metapopulation and metacommunity dynamics (Aiken & Navarrete, 2014; Perry & Lee, 2019), it is one of the main issues to understand how this transient nature of connectivity drives community assembly and variations in community structures.

Previous studies in stream ecosystems have provided valuable insight into the dynamic mechanisms of community assembly. Among them, several studies demonstrated the effects of seasonal flow fluctuation on the

assembly of the aquatic community, mediated by temporal changes in local environmental conditions and connectivity, in tropical rivers (Arrington & Winemiller, 2006; Fernandes et al., 2014; Fitzgerald et al., 2017) and intermittent rivers (Crabot et al., 2020; Sarremejane et al., 2017). Seasonal pulse floods, which alternate wet and dry phases over several months gradually, increase the surface areas and connectivity of habitat patches, facilitating species dispersal. As a result, community assembly is more driven by the mass effect at the beginning of the flood, and then by the niche-driven mechanisms based on the species sorting at the end of the flood because species can track preferred environmental conditions (Datry et al., 2016; Fernandes et al., 2014; Sarremejane et al., 2017). The temporal pattern of assembly processes can be affected by the details of the flood regime, such as duration, frequency, intensity, and timing (Datry et al., 2016; Lepori & Malmqvist, 2009), though empirical studies have been limited to those on the seasonal pulse floods.

Short-term flash floods are another type of flood regime that potentially influences community assembly, and characterize temperate stream ecosystems with the expectation of an increase in magnitude and frequency with climate change (Ledger & Milner, 2015). Local physicochemical conditions and hydrological connectivity between habitats can dramatically change during short-term flash floods and then return to their original states after the floods. Although empirical studies are still scarce, Larsen et al. (2019) investigated benthic Chironomidae and Oligocheta communities in a dynamic river-floodplain ecosystem for over a year. They found that community structures were highly influenced by stochastic processes of dispersal shortly after flash floods and then affected by deterministic processes of species sorting during the stable hydrological period. In contrast to these taxonomic groups, different taxonomic groups such as fish can actively migrate in response to flood not only between habitats within a river floodplain but also between multiple rivers, such as between a mainstream and tributaries (Koizumi et al., 2013; Mori et al., 2018). It is thus expected that the short-term flood can change fish community structures of tributaries at a short time scale, depending on the degree of changes in connectivity between a mainstream and tributaries. However, few studies have examined this expectation by field surveys with a fine temporal resolution before and after a short-term flood, partly because of the difficulties in observing sporadic and unpredictable flood events (McLaughlin et al., 2013).

Drainage ditches of paddy fields are habitats where the short-term floods potentially influence fish community assembly. The modern drainage ditches with concrete revetments receive water from paddy fields and then drain to downstream rivers. Many fish species inhabit drainage ditches and immigrate from these adjacent water bodies. A few species resistant to dryness (e.g., mud loach) inhabit paddy fields and immigrate to drainage ditches, especially during a midsummer drainage practice of rice farming (Fujimoto et al., 2008), which is usually conducted in between mid-June and mid-July and makes paddy fields dry up for several days (Natuhara, 2013). On the other hand, some fish species move into drainage ditches from downstream rivers, when agricultural irrigation raises the water level of ditches enough for the species to spawn and grow up (Onikura et al., 2009; Saitoh et al., 1988). In this agricultural landscape, although a short-term flash flood is less likely to provide aftereffects on local environmental conditions of the ditches with concrete revetment (Nakano, 2017), it is likely to promote these fish immigrations by improving the hydrological connectivity. The rise in water level by the short-term flood enables fish species to move to drainage ditches by removing a vertical gap at a confluence that impedes the connectivity during non-flood periods (Minagawa, 2021). The short-term flood also increases water discharge from paddy fields and thus facilitates the fish immigration to ditches, as the midsummer drainage practice does. However, few studies have investigated fish community structures in drainage ditches during pre-flood and post-flood periods.

We investigated fish community structures in drainage ditches for a total of three months, once before and six times after a short-term flash flood, in the Kita River basin, Fukui Prefecture, Japan. To demonstrate how the short-term flood and connectivity influence fish community assembly, the following hypotheses were tested. (H1a) The short-term flood facilitates the drainage of water from paddy fields, resulting in the increase in the immigration of fish species from paddy fields to drainage ditches. In contrast, (H1b) the immigration from downstream rivers to drainage ditches depends on the degree to which the flood improves the connectivity by removing a vertical gap at a confluence. (H2) Temporal turnover of local community compositions sharply rises just after the flood depending on the degree of the improvement of connectivity,

and then gradually declines as time passes after the flood. Community compositions are highly determined by stochastic processes at the beginning due to the immigration during the flood (i.e., mass effect), and subsequently by deterministic niche-driven processes (i.e., species sorting) as the connectivity weakens. (H3) The connectivity between drainage ditches and downstream rivers during both the flood and non-flood periods influence the fish species distributions. The short-term flood relaxes the dispersal limitation of some fish species, while other species need stable connectivity due to their life history.

## Materials and methods

### Study sites

We set 16 study sites in drainage ditches with concrete revetments in the Kita River basin, Fukui Prefecture, Japan (Figure 1). These sites received water from adjacent paddy fields and, in some cases, upstream rivers via underground pipelines, and then drained water back to the Kita River (mainstream) directly or via connected tributaries. Each site was a segment of a drainage ditch with a length of 15m and within 600m away from the first confluence of downstream rivers (i.e., the Kita River or tributaries). There were vertical gaps of over 20 cm between the paddy outlets and the studied drainage ditches. These study sites did not dry up throughout the year. The width of the study sites varied from 0.55 to 1.65m, so their area ranged between 8.25 and 24.75 m<sup>2</sup>.

In the Kita River basin, heavy rain from the seasonal rain front resulted in a short-term flood event from the 7th to the 8th of July, 2020, which made the water level of the Takatsuka observatory reach the 12th highest level in the last decade, 5.44m (Figure 2a). Also, water levels of study sites during the flood rose  $56.5 \pm 13.4$ cm compared with pre-flood and returned to the original levels several days after the flood (Figure 2b). The first and second surveys were conducted several days before and after the flood, respectively, and then we conducted surveys approximately once in two weeks until the seventh survey in late September. We defined the connectivity to downstream rivers based on the presence/absence of a vertical gap of more than 20cm between the studied drainage ditches and the downstream rivers. Based on the connectivity to downstream rivers during the flood and non-flood period, study sites were classified into three connectivity types, namely “Transient”, “Connected”, and “Disconnected”. Four “Transient” sites usually had a vertical gap of more than 20cm between drainage ditches and downstream rivers but the gap disappeared during the flood, whereas ten “Connected” sites always had no vertical gap and two “Disconnected” sites always had the vertical gap even during the flood.

### Environmental measurement and fish sampling

In each survey, we measured nine environmental variables at each site to examine whether the flood changed local environmental conditions. At the center of each surveyed segment, we measured water depth and sediment depth with a measuring rod, as well as water temperature, dissolved oxygen, pH, and electrical conductivity by Multi-parameter Water Quality Checker (U-50; HORIBA, Kyoto). We also measured flow velocity as an average value of the measurements three times by a flow meter with an impeller (CR-7; Cosmo Riken, Tokyo). The coverage of terrestrial vegetations over ditches and submerged plant at the bottom of ditches were examined by visual observations.

We examined fish community compositions of study sites. At each end of a study site, a trap net (mesh size, 2 mm) was installed to prevent fish from migrating from and immigrating to the study site. An investigator collected fish for 15 min using an electrofisher (LR-24; SMITH-ROOT; USA) in one hand and a D-frame dip net (28 cm wide, 3 mm mesh) in another hand. After that, the investigator used only the D-frame dip net for 20 min to mainly collect benthic fish species. Collected fish were identified and counted in the field, whereas some fish individuals were too small to accurately identify at the level of genus and therefore were excluded from the data. All collected fish were immediately released back to their original ditches after counting.

Additionally, we recorded the presence of unionid species (freshwater mussels, family Unionidae). This is because some bitterling fish species (subfamily Acheilognathinae) spawn on the gills of these mussels and

therefore their presence in ditches is closely related to that of these unionid species (Nagayama et al., 2012; Terui et al., 2011).

## Statistical analysis

To statistically examine temporal changes of each environmental variable, we performed the Friedman test (Friedman, 1937), a nonparametric equivalent to the repeated measures ANOVA, in each connectivity type. As for each environmental variable, we grouped time-series values by surveys, calculated the ranks of sites within each survey, and analyzed to determine whether statistical differences existed in the ranks of sites among the seven surveys. We then used post hoc many-to-one exact multiple comparisons to test the equality of each post-flood survey (i.e., from the second to seventh one) against the pre-flood, first survey (Eisinga et al., 2017). The reasons why we did not conduct multiple comparisons of all pairs were because we were particularly interested in the difference between the pre-flood and post-flood surveys. Also, it should be noted that the statistical power of detection would be low for the "Disconnected" type as there were only two sites.

*M. anguillicaudatus* is the only species that disperse from paddy fields to drainage ditches in the Kita River basin according to our previous study (Iwamoto et al., 2022), so we separately considered the abundance of *M. anguillicaudatus* and that of all other species. We also performed a series of Friedman tests and then the post hoc multiple comparisons for temporal changes in these abundances for each connectivity type, as mentioned above. Additionally, to illustrate the temporal patterns, we calculated the relative difference in abundance between the first and the focal ( $n$ -th) surveys at site  $i$ , as  $(x_{in} - x_{i1})/\bar{x}_i$ .

We calculated the temporal turnover of fish species composition based on Bray–Curtis dissimilarity (Bray & Curtis, 1957) between the  $m$ -th and  $n$ -th surveys at each site (referred to as  $D_{m,n}$  hereafter), which can take account of both the presence/absence and the relative abundance of species. Particularly, we focused on the two kinds of temporal turnover,  $D_{n-1,n}$  (between the  $(n-1)$ -th and  $n$ -th) and  $D_{1,n}$  (between the first and  $n$ -th).  $D_{n-1,n}$  describes whether the turnover in species composition becomes greater or smaller over time, whereas  $D_{1,n}$  indicates whether the species composition during the post-flood period becomes different from or similar to that of the pre-flood as time passes. We conducted the Friedman test and then post hoc multiple comparisons to analyze whether there were significant differences between  $D_{1,2}$  and  $D_{1,n}$ , and between  $D_{1,2}$  and  $D_{n-1,n}$ .

To illustrate the fish species composition and their temporal changes, we performed a nonmetric multidimensional scaling (NMDS) analysis (Minchin, 1987) on a community matrix of the fish abundance of all 112 surveys (16 sites  $\times$  7 times) using the Bray–Curtis dissimilarity index. Moreover, we used a permutational multivariate analysis of variance (PERMANOVA) to clarify whether there are differences in fish community composition between connectivity types, conducting permutations constraining samples within each survey period (strata option within the `adonis2` function) to account for the effects of differences in time (Anderson, 2017).

All analyses were performed in R 4.1.2 (R Core Team, 2021). Friedman test and post hoc many-to-one exact multiple comparisons were constructed and computed using the `PMCMRplus` (Pohlert, 2021). Bray-Curtis dissimilarity, NMDS, and PERMANOVA were calculated and conducted with the `vegan` (Oksanen et al., 2020) package in R.

## Result

There were significant temporal changes in vegetation cover, water temperature, dissolved oxygen, pH, and electrical conductivity in "Transient" or "Connected" sites according to the Friedman test (Table S1). These temporal changes seemed to correspond with seasonal changes rather than the flood event, as post hoc multiple comparisons showed that there was no significant difference between the first (i.e., pre-flood) and the second surveys, and between the first and the third surveys (Table S2, Figure S1).

We recorded a total of 6895 fish individuals that belonged to 21 species (15 Cypriniformes, 1 Siluriformes, 4 Perciformes, and 1 Beloniformes) (Table S3). The mean abundance of fish species varied largely among study sites, and *Misgurnus anguillicaudatus* was the most dominant species, followed by *Tanakia limbata*, *Cobitis* sp. BIWAE type A and *Nipponocypris temminckii* (Table S3, Figure S2).

The abundance of *M. anguillicaudatus* changed over time significantly in the “Transient” and “Connected” sites, but did not in the “Disconnected” sites, according to the Friedman test (Table 1). Post hoc multiple comparisons demonstrated that the abundance in the first survey was significantly different from that in the second and third in the “Transient” sites and it was also different from that in the third in the “Connected” sites (Table 1). The abundance generally increased from the first to the second and third surveys, and then decreased in the fourth irrespective of the connectivity types (Figure 3a), as it reached the highest in the second or third at 12 sites (four “Transient”, six “Connected”, and two “Disconnected” sites). In contrast, although there were also significant temporal changes in the total abundance of species except for *M. anguillicaudatus* in the “Transient” and “Connected” sites, the difference compared with the first survey only existed in the third in the “Transient” sites (Table 1). The abundance in the “Connected” sites was generally high in the fourth and seventh surveys, while that in the “Transient” sites increased from the first to the third survey and then decreased in the fourth (Figure 3b).

The temporal turnover of fish species composition between the  $(n-1)$ -th and  $n$ -th surveys,  $D_{n-1,n}$ , was significantly changed as time passed only in the “Transient” sites (Table 2). Post hoc multiple comparisons verified that  $D_{1,2}$  was significantly different from  $D_{4,5}$ ,  $D_{5,6}$ ,  $D_{6,7}$  in the “Transient” sites. The temporal turnover was highest in the second survey (i.e., the dissimilarity between the first and second) and then decreased as time passed, while those in the “Connected” and “Disconnected” sites stayed at relatively low levels (Figure 4a). There was no significant change over time in the temporal turnover between the first and  $n$ -th survey,  $D_{1,n}$ , regardless of the connectivity types (Table 2). However, the mean of the temporal turnover was largest in the “Transient” sites (0.807), followed in order by the “Connected” (0.497) and the “Disconnected” sites (0.305) (Figure 4b).

Fish species composition was significantly different among the connectivity types (Figure 5), as confirmed by the PERMANOVA results ( $R^2 = 0.124$ ,  $p = 0.001$ ). *Pseudaspius hakonensis* and *Gnathopogon elongatus* belonging to Cyprinidae were representative species after the flood in the “Transient” sites, as newly observed in the second and third surveys in four and two “Transient” sites, respectively (Table S2, Figure 5, Figure S3a-d). *T. limbata* was one of the dominant species in the “Connected” sites (Table S3, Figure 5, Figure S3), as there were more than two individuals found only in seven “Connected” and one “Transient” sites during the entire period.

We recorded the presence of two unionid mussel species, *Pronodularia japonensis* only in five “Connected” sites and *Buldowskia iwakawai* in one “Transient”, two “Connected”, and one “Disconnected” sites (Table S3). Of the eight sites where *T. limbata* was dominant in the fish community, either *P. japonensis* or *B. iwakawai* occurred in five “Connected” and one “Transient” sites, and the other two sites where neither species was present shared the same confluence of the mainstream. Only in one “Disconnected” site, there was the unionid mussel species, but *T. limbata* was not observed.

## Discussion

No significant difference in local environmental variables was found between before and just after the flood (Table S1, Table S2, Figure S1), although the water level in drainage ditches actually rose during the flood (Figure 2b). Short-term floods often cause changes in environmental conditions within intact rivers, such as the modification of channel shape and depth, but the modern drainage ditches with concrete revetments have more constant width, shape and water depth (Nakano, 2017), indicating that changes in environmental conditions that continue well after the flood would be hard to occur. Therefore, the observed difference in fish community structure between before and after the flood was most likely to be derived from temporary changes in connectivity, rather than from environmental changes associated with the flood.

The abundance of *M. anguillicaudatus* increased significantly after the flood in the “Transient” and “Connected” sites, supporting the hypothesis (H1a), whereas the similar increase in the “Disconnected” sites was not significant probably due to their small number of sites (Figure 3a). The flood facilitated the discharge of water and the emigration of *M. anguillicaudatus* from paddy fields to drainage ditches, as the midsummer drainage practice of rice farming does usually in mid-June to mid-July in the study area (Fujimoto et al., 2008). The seasonal timing of the flood seems to be important because the abundance of *M. anguillicaudatus* in paddy fields commonly shows a peak at the end of the spawning season, which is before the midsummer drainage practice (Fujimoto et al., 2008; Tanaka, 1999). If the flood had occurred well after the midsummer drainage practice, the extent of the emigration of *M. anguillicaudatus* would have been more modest. It was also possible that *M. anguillicaudatus* moved from downstream rivers, but this was less likely to contribute to increasing the abundance. This is because the emigration of *M. anguillicaudatus* from paddy fields to drainage ditches widely observed around the midsummer drainage practice (Iwamoto et al., 2022), whereas the fish was observed at few points in downstream rivers during the summer in the studied Kita River basin (Matsumiya et al., 2001).

Effects of the flood on the immigration from downstream rivers to drainage ditches depended on the connectivity type with downstream rivers, supporting the hypothesis (H1b). The total abundance of fish species except for *M. anguillicaudatus* significantly increased after the flood only in the “Transient” sites, but it did not largely change between before and after the flood in the “Connected” and “Disconnected” sites (Figure 3b). The flood temporarily removed a vertical gap between drainage ditches and downstream rivers in the “Transient” sites, probably resulting in the immigration of fish species to drainage ditches. Many fish species used the temporary underwater path to actively immigrate to drainage ditches that serve as spawning and nursery habitats (Nakano, 2017). Additionally, fish species could evacuate from the disturbed downstream rivers during flood, as previous studies showed that fish species inhabiting a mainstream actively move into tributaries or backwaters for refuge when a flood increased flow discharge and turbidity in the mainstream (Koizumi et al., 2013; Mori et al., 2018; Sumida et al., 2019). Also, some fish species were likely to be passively swept away to drainage ditches by backflow of water from downstream rivers, which was expected to be caused by rapid rise of the water level in downstream rivers, although this backflow was not observed during this study. In contrast, there was little increase in the abundance of fish species other than *M. anguillicaudatus* in the “Connected” sites, although fish could have moved to drainage ditches at the “Connected” sites as well as at the “Transient” sites during the flood. This might be because fish species had already moved freely between downstream rivers and drainage ditches even before the flood in the “Connected” sites. We would also have failed to observe fish species that evacuated from a mainstream because our sampling of fish was done not during but several days after the flood for safety and practical reasons. Indeed, previous studies showed that some fish species that once moved to tributaries during a flood returned to a mainstream as soon as the flood settled (Koizumi et al., 2013; Mori et al., 2018).

The temporal turnover of fish species composition between the  $(n - 1)$ -th and  $n$ -th surveys (i.e.,  $D_{n-1,n}$ ) fluctuated over time depending the connectivity type, coinciding with the hypothesis (H2). The temporal turnover was consistently low in the “Connected” and “Disconnected” sites, whereas it rose just after the flood and gradually declined in the “Transient” sites (Table 2, Figure 4a). Local fish species composition in the “Transient” sites largely changed between before and right after the flood, resulting from the immigration of some fish species from downstream rivers (i.e., mass effect) that was limited before the flood. Although the “Transient” sites again lost the hydrological connectivity after the flood due to the vertical gap, the community compositions continued to fluctuate to some extent for around a month (Figure 4a). Moreover, the abundance of fish species in “Transient” sites reached their peak around three weeks after the flood rather than several days after the flood, and then declined and became stable a month after the flood (Figure 3). These results may indicate that fish species that once immigrated from downstream rivers migrated within networks of drainage ditches, and then returned to downstream rivers or died as time passed in the drainage ditches. After that, fish species composition was likely to approach the deterministic one that was influenced by local environmental conditions. The series of temporal changes occurred within around a month, which is relatively short compared to seasonal floods influencing fish communities (Fernandes et al., 2014) or

short-term floods determining invertebrate communities (Larsen et al., 2019). The rapid responses of fish communities derived from their high dispersal ability and longitudinally asymmetric connectivity that allowed immigration from drainage ditches to downstream rivers but prevented that of the opposite direction after the flood.

The temporal turnover between the first and  $n$ -th surveys (i.e.,  $D_{1,n}$ ) were generally higher in the “Transient” than in the “Connected” and “Disconnected” sites, and it showed little change as time passed irrespective of the connectivity type (Figure 4b). The reason why the species composition during the post-flood period did not become similar to that of the pre-flood should be partly because some fish individuals that immigrated from downstream rivers and paddy fields survived in drainage ditches. However, even after the final survey in late September, the species composition would further change due to the influence of water level decline during the agricultural off-season, so it would become similar to the pre-flood species composition in the following spring (Iwamoto et al., 2022).

The connectivity between drainage ditches and downstream rivers during both the flood and non-flood periods affected the distribution of some fish species, as hypothesized in (H3). *P. hakonensis* and *G. elongatus elongatus* newly appeared and their abundance rose in the “Transient” sites after the flood (Figure 5, Figure S3a-d), suggesting that the flood facilitated their immigration through improvement of the connectivity. These species seasonally immigrate from downstream rivers to drainage ditches in order to spawn and grow up during the irrigation flood (Moriyama et al., 2008; Saitoh et al., 1988; Takemura et al., 2011). Also, these species move during flood to the backwaters in low water channels, which is a semi-lentic habitat and functioned as a flow refugia (Denda et al., 2002). In contrast, *T. limbata* was one of the representative species in the “Connected” sites (Figure 5, Table S2), as well as *P. japonensis* that *T. limbata* often use as spawning beds (Inadome & Yamamoto, 2012; Kitamura, 2007). The continued connection with downstream rivers was likely to affect the distribution of *T. limbata* because the connectivity is also related to the suitable habitat of unionid mussels (Nagayama et al., 2012; Terui et al., 2011). The unionid mussels attach to the gills or fins of a host fish during their first larval stage (glochidia) (Negishi et al., 2008), so the hydrological connectivity affects their distribution through the influence on migration of host fish species. Indeed, previous studies showed that weirs in rivers limited the distribution of unionid mussels by preventing host fish species from moving upstream (Kuwahara et al., 2017; Watters, 1996). Negishi et al. (2014) also discussed the possibility that vertical gaps reduced the connectivity between drainage ditches and downstream rivers, and thus might have fragmented the mussel habitat by limiting movement of host fish with attached glochidia.

The present results also emphasize the importance of hydrological connectivity for biodiversity conservation in an agricultural landscape. Aquatic communities in rivers have been threatened because of the shrinking various waterbodies in floodplain by the modern river improvement (Nagayama et al., 2015) and because of increasing intensity and frequency of flood disturbance by ongoing climate changes (Ledger & Milner, 2015). Therefore, drainage ditches in an agricultural landscape can play more important roles as temporary refuges and seasonal habitats for spawning and growth as the drainage ditches somewhat resemble streamlets once existed in natural floodplains (Minagawa, 2021; Nakano, 2017). To secure their roles, it is desirable to recover the hydrological connectivity between drainage ditches and downstream rivers by removing vertical gaps (e.g. flap gates) that the modern river improvement and the drainage system construction for agriculture have created (Minagawa, 2021; Nakano, 2017). Moreover, the structures permitting backflow retention of flood from downstream rivers to paddy fields, such as the floodplain open levee system (*kasumi-tei*) (Taki et al., 2021; Teramura & Shimatani, 2021; Yamada et al., 2022), should allow drainage ditches and paddy fields to play a greater role as temporary refuges for fish in the event of severer flood than that observed in this study. In conclusion, our study demonstrated that the short-term flood and connectivity can influence interactively the process of fish community assembly in drainage ditches, and this understanding provides important insights into biodiversity conservation in an agricultural landscape.

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## Conflict of interest

The authors declare that there is no conflict of interest.

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## Tables and figures

Table 1. Results of the Friedman test and post hoc many-to-one exact multiple comparisons on temporal changes in the abundance of *Misgurnus anguillicaudatus* and that of all other species for each connectivity type. Post hoc multiple comparisons analyzed equality of each post-flood survey (i.e., from the second to the seventh one) against the pre-flood, first survey. The significant level of explanation and difference were shown in bold.

	Friedman test	Friedman test	Post hoc multiple comparisons ag
	$\chi^2$	$p$	2nd
<i>Misgurnus anguillicaudatus</i>	<i>Misgurnus anguillicaudatus</i>	<i>Misgurnus anguillicaudatus</i>	<i>Misgurnus anguillicaudatus</i>
Transient	<b>17.538</b>	<b>0.007</b>	<b>0.005</b>
Connected	<b>15.378</b>	<b>0.018</b>	0.111
Disconnected	10.036	0.123	-
Other species	Other species	Other species	Other species
Transient	<b>13.103</b>	<b>0.041</b>	0.732
Connected	<b>15.727</b>	<b>0.015</b>	1.000
Disconnected	9.214	0.162	-

Table 2. Results of the Friedman test and post hoc many-to-one exact multiple comparisons on the temporal turnover of fish species composition based on Bray–Curtis dissimilarity between the ( $n - 1$ )-th and  $n$  -th surveys ( $D_{n-1,n}$ ) and between the first and the  $n$  -th surveys ( $D_{1,n}$ ) for each connectivity type. Post hoc multiple comparisons analyzed equality of each temporal turnover against  $D_{1,2}$ , the temporal turnover between the first and the second survey. The significant level of explanation and difference were shown in bold.

	Friedman test	Friedman test
	$\chi^2$	$p$

	Friedman test	Friedman test
Between the $(n-1)$ -th and $n$ -th surveys	Between the $(n-1)$ -th and $n$ -th surveys	Between the $(n-1)$ -th and $n$ -th surveys
Transient	<b>14.714</b>	<b>0.012</b>
Connected	4.57	0.471
Disconnected	7.143	0.21
Between the first and $n$ -th surveys	Between the first and $n$ -th surveys	Between the first and $n$ -th surveys
Transient	4.712	0.452
Connected	6.914	0.227
Disconnected	4.857	0.434

## Figure legends

Figure 1. The study area showing the location of the Takatsuka observatory and the study sites of drainage ditches in the Kita River basin, Fukui Prefecture, Japan. Study sites were classified as three connectivity types, namely “Transient” (red), “Connected” (green), and “Disconnected” (blue).

Figure 2. The time-series water level at the Takatsuka observatory in the Kita River (a) and mean water levels of study sites (b) by three connectivity types, namely “Transient” (red), “Connected” (green), and “Disconnected” (blue). The grey vertical lines indicate the seven survey periods.

Figure 3. Mean  $\pm$  SE of the relative difference between the first and the focal ( $n$ -th) surveys in the abundance of *Misgurnus anguillicaudatus* (a) and that of all other species (b) by three connectivity types, namely “Transient” (red), “Connected” (green), and “Disconnected” (blue). The relative difference in the abundance between the first and the focal ( $n$ -th) surveys at site  $i$  is calculated by  $(x_{in} - x_{i1}) / \bar{x}_i$ . The vertical dashed line indicates the timing of the flood event.

Figure 4. Mean  $\pm$  SE of the temporal turnover of fish species composition based on Bray-Curtis dissimilarity between the  $(n-1)$ -th and  $n$ -th surveys ( $D_{n-1,n}$ ) (a) and between the first and the  $n$ -th surveys ( $D_{1,n}$ ) (b) by three connectivity types, namely “Transient” (red), “Connected” (green), and “Disconnected” (blue). The vertical dashed line indicates the timing of the flood event.

Figure 5. NMDS plot showing the variation of fish community composition across the study sites and the connectivity types to downstream rivers. Each point corresponds to the fish community observed at a survey of a site. Each cross represents fish species, and species names are shown only if they were observed at  $>15\%$  of surveys. Outlines encompass all the seven points or surveys for each site. Colors represent three connectivity types, namely “Transient” (red), “Connected” (green), and “Disconnected” (blue).

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