The Fishermen Were Right: Experimental Evidence for Tributary Refuge Hypothesis During Floods

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Fishermen often anecdotally report an unexpected increase of fish caught in small tributary streams during floods, presumably due to refuge-seeking behavior from the main stem. From a population perspective, this implies the significance of refuge habitats and connectivity for population viability against natural disturbances. Despite the plausibility, however, surprisingly few studies have examined the tributary refuge hypothesis, mainly due to the difficulty in field survey during floods. Here, we made use of a large-scale controlled flood to assess whether fishes move into tributaries during flooding in the main stem. A planned water release from the Satsunai River Dam located on Hokkaido Island in Japan rapidly increased the main stem discharge by more than 20-fold. Before, during, and after flooding censuses in four tributaries provided evidence of the refuge-seeking behavior of fishes from the main stem. For example, more than 10 Dolly Varden char, a salmonid fish, were caught in a tributary during the flood, even though almost no individuals were captured before or after the flood. The fish responded immediately to the flooding, suggesting the need for studies during disturbances. In addition, the likelihood of refuge movements varied among tributaries, suggesting the importance of local environmental differences between tributary and the main stem habitats. This is the first study to experimentally confirm the tributary refuge hypothesis, and underscores the roles of habitat diversity and connectivity during disturbances, even though some habitats are not used during normal conditions.

Key words: catastrophe, dam, habitat heterogeneity, stream network, metapopulation

INTRODUCTION

Habitats are not consistent entities. Under some conditions, such as natural disturbances, a favorable habitat may become suboptimal, whereas a habitat not used in normal conditions (i.e., a suboptimal or unsuitable habitat) may become suitable (e.g., Pickett and White, 1985). Individuals able to move freely between such habitats are as a result tolerant to changing environments. This explains in part why habitat heterogeneity and connectivity have recently received so much attention (Hanski, 1999).

River networks are highly relevant to habitat diversity and connectivity (Townsend, 1989; Fagan, 2002; Benda et al., 2004), as stream habitats are heterogeneous and dynamic even within very short time periods. Flooding as a result of heavy rain is one example of this heterogeneity. During flooding of the main stem, temporary habitats appear in off-channel floodplain areas (Ross and Baker, 1983; Cucherousset et al., 2007), which may support individuals seeking for refuges. It is remarkable how well freshwater organisms have adapted to natural disturbances (e.g., Lobón-Cerviá, 1996; Lytle and Poff, 2004; Kroon and Ludwig,

2010). Habitat diversity and connectivity may play significant roles in population viability in response to abrupt habitat changes (Townsend, 1989; Sedell et al., 1990; Peasons et al., 1992). Unfortunately, loss of connectivity and habitat heterogeneity, due to recent human activities, has resulted in population degradation in many freshwater species around the world (Pringle et al., 2000; Fagan, 2002; Morita and Yamamoto, 2002). It is urgent that we better understand the roles of habitat diversity and connectivity on species persistence in changing environments.

Small tributary streams may become important refuge habitats during floods or droughts (Sedell et al., 1990), as the impact of flooding or drought may be less severe in some, particularly spring-fed, tributaries (Power et al., 2000; Han et al., 2007). In fact, fishermen often anecdotally say (at least in Japan) that they unexpectedly catch many large fishes in small tributaries during floods, which is presumed to reflect refuge-seeking behavior against the flooded main stem. Despite the plausibility of this relationship, however, surprisingly few studies have examined the tributary refuge hypothesis (i.e., that fish move into tributaries for refuge during heavy floods in the main stem), mainly due to the difficulties in conducting field surveys during high floods. The limited observations that are available show weak evidence of fish seeking refuge in tributaries during floods (Harvery et al., 1999; Han et al., 2007; Koizumi et al., 2012). The only supporting evidence was provided by Nunn et al. (2010) in

a cyprinid-dominated floodplain tributary of a lowland river, where increases in water discharge are gradual. In this case, however, movements between the tributary and the main stem may not be a temporal refuge from a severe flood, but rather a seasonal migration initiated by the gradual increase in water flow (Nunn et al., 2010).

In this study, we experimentally tested for the first time the tributary refuge hypothesis using a large-scale flood control experiment on Hokkaido Island, Japan. Dam managers released a large amount of water from a reservoir to mimic a natural disturbance (i.e., controlled flood or managed flood, Molles et al., 1998) in a currently regulated river in an effort to recover ecosystem functions. The controlled flood rapidly increased the water discharge of the main stem by 20-fold (> 110 m^3/s), but not in the tributaries, making a field survey in the tributaries feasible. We sampled four tributaries immediately before, during, and after the flood to assess whether fishes move into the tributaries for refuge from the main stem. We discuss the results in terms of habitat diversity and connectivity as a possible mechanism for enhancing population persistence.

MATERIALS AND METHODS

A controlled flood was carried out in the Satsunai River in central Hokkaido, Japan during the 25th and 26th of June 2012 to recover ecosystem functions by mimicking a natural disturbance. The Satsunai River is 82 km long, and the Satsunai River Reservoir is located 20 km from the headwaters (43°10′ N; 143°30′ E, Fig. 1). After the construction of the dam in 1997, water discharge has been regulated to obtain low, consistent flows throughout the year of approximately 5–10 m^3/s. Consequently, flood disturbance events have been infrequent, and floodplain habitats have been replaced with more stable, forest environments (Takahashi and Nakamura, 2011). As a result, dam managers have tried to recover floodplain habitats, including the endangered floodplain willow (*Salix arbutifolia*), using controlled flooding.

The Satsunai River Dam released about 5 m^3/s of discharge
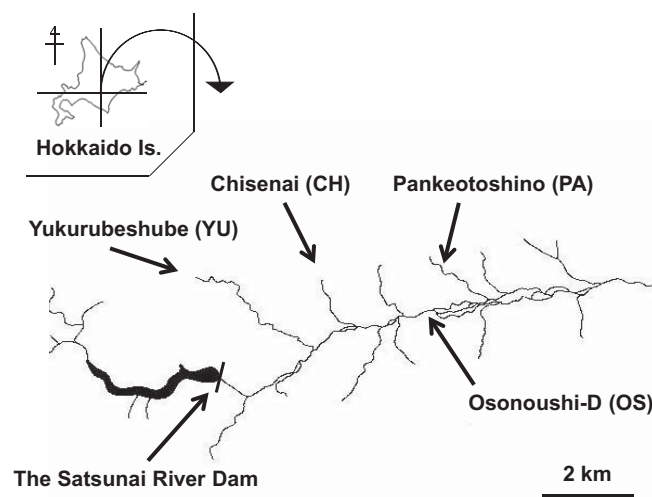

Fig. 1. Map of study sites. Locations of the Satsunai River Dam and four study tributaries (with abbreviation in parentheses) are indicated. Osonoushi-D is too small to describe on the map (located in the upper site). Water flows from left to right.

before the controlled flood. The dam was opened at 10:00 on 25 June 2012, and the peak release exceeded 112 m^3/s at 15:40 on the same day. Thus, water discharge increased by 20-fold within a single day (Fig. 2). This level of flooding was not uncommon in the past; it occurred, on average, five times a year before the dam was constructed (data from the Ministry of Land, Infrastructure and Transport, Japan). The controlled flood was completed at 12:40 on 26 June 2012, with 5–10 m^3/s discharge thereafter.

We conducted a population census in four tributaries of the Satsunai River (Fig. 1) on 23 June 2012 (before the flood), 25 June 2012 (during the flood), and 28 June 2012 (after the flood). The four tributaries, Yukurubeshube (YU), Chisenai (CH), Osonoushi-D (OS), and Pankeotoshino (PA), are located within 10 river kilometers (rkm) from the Satsunai River Dam. Each of the tributaries has a physical barrier, such as an erosion control dam and culvert, relatively close to the junction with the main stem (13–136 m). We sampled each tributary from the junction of the main stem to the physical barrier by using a backpack electrofisher (Smith-Root Inc., Vancouver, WA, USA). We could thus assume that most of the fish moving from the main stem would remain in the limited sections from the junction to the barrier, and also that few fish would move from above-barrier reaches, which enabled us to identify fish from the main stem easier. Some stream salmonids migrate into small tributaries for spawning (Koizumi et al., 2006), but the study period (June) is not the spawning season (generally autumn) and, therefore, the movement from the main stem can be considered to be refuge-seeking behavior. The mean length of surveyed reaches was 70.5 m (76 m in YU, 136 m in CH, 13 m in OS, and 57 m in PA, Table 1). All tributaries were relatively small (approximately 1–9 m in wetted width) and easy to conduct electrofishing due to the general lack of cover, such as deep pools and log jams. One- to three-pass electrofishing surveys were conducted in each tributary (Table 1). Because we wanted to complete sampling in all four tributaries within a 3-day timeframe, we could not standardize the number of passes (i.e., ideally three-pass electrofishing is needed for removal population estimates; Riley and Fausch, 1992) for each tributary for each sampling event. Thus, we report the total numbers of fishes captured for the minimum number of electrofishing passes during the three censuses (i.e., before, during and after the flood) in each tributary. We consider that the present sampling scheme provides useful information on refuge-seeking behavior for several reasons. First, because species composition and size structure generally differs between tributary and main stem habitats, it is often easy to identify immigrants from the main stem (e.g., Koizumi et al., 2012). Second, capture efficiency of mid-water (non-benthic) fishes, such as salmonids, should be high in this kind of tributary (i.e., small, open, less cover). Third, to minimize the variances in capture efficiency for each survey the same person (I. Koizumi) electrofished in the same manner in each tributary.

Fish captured were anesthetized with clove oil and measured for body size to the nearest 1 mm (fork length for salmonids, total length for other species). All fishes captured were released near the capture sites. Changes in species compositions among samples before, during, and after the flood were compared by chi-square test. The body size of each species in each tributary was also compared among samples before, during, and after the flood by ANOVA when sufficient samples were obtained (i.e., five or more individuals in each census). To investigate the effects of stream size on the degree of refuge movement, changes in the number of fishes (i.e., difference or ratio of total captures between samples before and during the flood) were correlated with stream size (i.e., length or surface area surveyed), although no statistical assessment was done due to small sample size (i.e., four tributaries). In the Satsunai River system, at least the following fish species have been found (I. Koizumi, personal observation): Dolly Varden char (*Salvelinus malma*), white-spotted char (*S. leucomaenis*), masu salmon (*Onchorynchus masou*), introduced rainbow trout (*O. mykiss*),
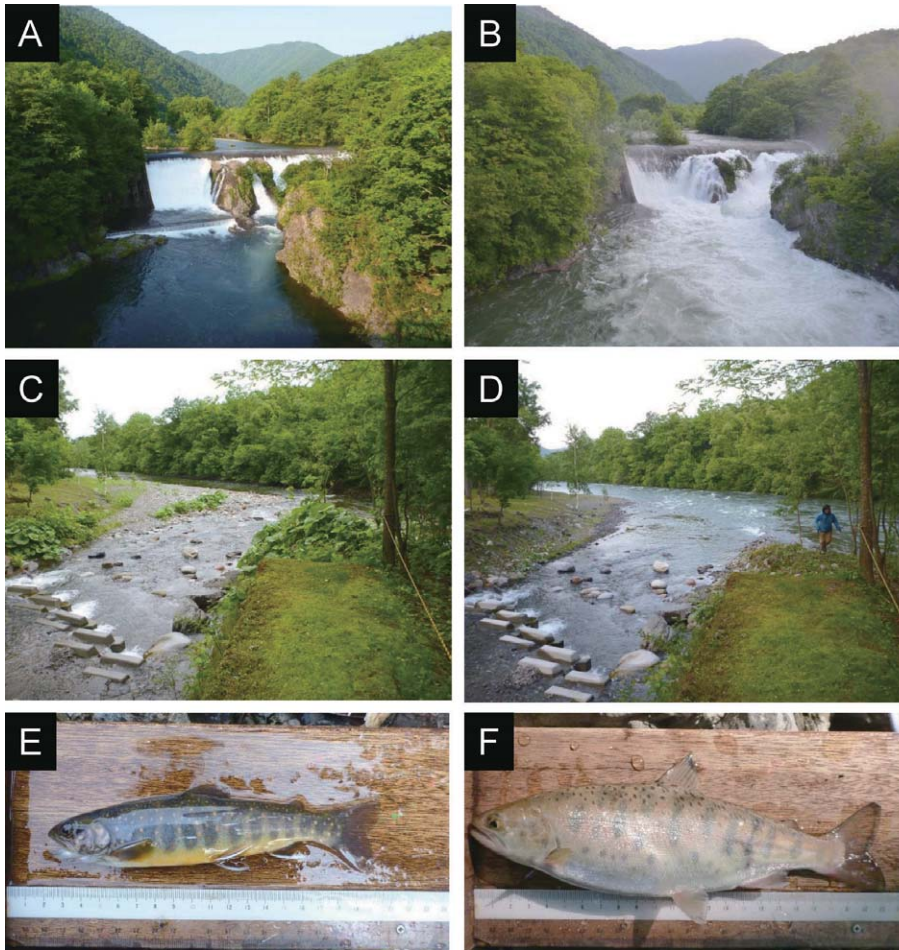
Fig. 2. The main stem of the Satsunai River (2.5 km downstream from the Satsunai River Reservoir) during **(B)** and after **(A)** a controlled flood. One of the studied tributaries (Yukurubeshube stream, 3 km downstream from the reservoir) before **(C)** and during **(D)** the flood. Fish captured only during the flood: **(E)** Dolly Varden char in Yukurubeshube stream (173 mm) and **(F)** masu salmon in Chisenai stream (220 mm).

freshwater sculpin (*Cottus nozawae*), brook lamprey (*Lampetra reissneri*), Siberian stone loach (*Barbatula barbatula toni*), nine-spine stickleback (*Pungitius pungitius*) and Japanese dace (*Tribolodon hakonensis*). The main stem of the Satsunai River is popular for fishing large rainbow trout (approximately 300–600 mm).

RESULTS

Two days before the controlled flood all four tributaries were dominated by freshwater sculpin (> 90%) with smaller numbers (< 10 individuals) of rainbow trout, brook lamprey, and Siberian stone loach (Table 1). All individuals were small, rarely exceeding 150 mm (i.e., freshwater sculpin: mean ± SD = 103.6 ± 20.1; range = 44–158 mm, n = 138, rainbow trout: mean ± SD = 134.8 ± 24.8; range = 108–170 mm, n = 9, brook lamprey: mean ± SD = 124.4 ± 14.1; range = 110–140; n = 5, stone loach: 115 mm, n = 1). No Dolly Varden char or masu salmon were collected in any tributary. During the flood, however, 11 individuals of relatively large Dolly Varden char (mean ± SD = 174.0 ± 18.4; range = 139–212 mm) were captured in Yukurubeshube (Fig. 2, Table 1). Interestingly, all but one individual disappeared from the tributary just two days after the flood. Similarly, a relatively large masu salmon (220 mm) and two rainbow trout (170 and 118 mm) were caught in Chisenai only during the flood

Table 1. Numbers of fish captured before, during, and after the controlled flood in four tributaries. The abbreviations of tributary names, lengths censused, and numbers of electrofishing passes are also described.

Tributary, length censused	Yukurubeshube (YU), 76 m reach			Chisenai (CH), 136 m reach		
	Before (2 pass)	During (2 pass)	After (2 pass)	Before (1 pass)	During (1 pass)	After (1 pass)
Dolly Varden char	0	11	1	0	0	0
Masu salmon	0	0	0	0	1	0
Rainbow trout	1	2	0	0	2	0
Freshwater sculpin	34	51	65	45	33	55
Brook lamprey	0	0	3	5	7	9
Siberian stone loach	1	2	10	0	0	0

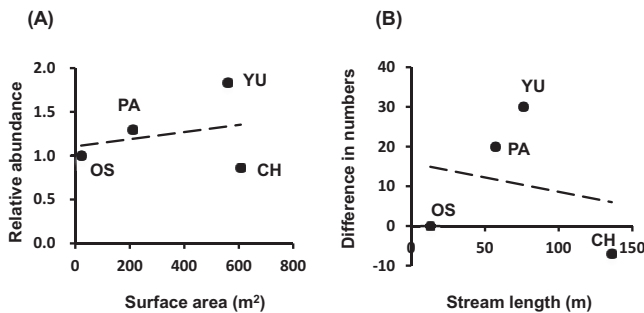| Tributary, length censused	Osonoushi-D (OS), 13 m reach			Pankeotoshino (PA), 57 m reach		
	Before (1 pass)	During (1 pass)	After (1 pass)	Before (2 pass)	During (2 pass)	After (2 pass)
Dolly Varden char	0	0	0	0	0	0
Masu salmon	0	0	0	0	0	0
Rainbow trout	0	0	0	8	4	2
Freshwater sculpin	1	1	3	58	77	48
Brook lamprey	0	0	0	0	1	1
Siberian stone loach	0	0	0	0	4	1

(A)

(B)

Fig. 3. The relationships between tributary size and degree of refuge movement. **(A)** Tributary size and refuge movement were calculated as surface area surveyed and the ratio of the number of fishes captured during the flood to those captured before the flood (i.e., relative abundance), respectively. **(B)** Tributary size and refuge movement were calculated as stream length surveyed and the difference between the number of fishes captured during the flood and those captured before the flood, respectively. Linear regression lines ($R^2 < 0.1$ in both cases) and tributary names are also indicated.

(Fig. 2). These results support the tributary refuge hypothesis. Another indication for the tributary refuge hypothesis was the Siberian stone loach whose numbers increased in Yukurubeshube (from one to ten) and Pankeotoshino (from zero to four) during and after the flood, although the numbers of fish caught were small. These were captured mostly in backwater areas near the junction of the main stem, where water currents were weak. Unlike salmonids, some of the stone loaches remained in the tributaries after the flood. In Yukurubeshube the number of sculpin increased nearly twofold (from 34 to 65 individuals) during and after the flood. Species compositions changed significantly before, during, and after the flood in Yukurubeshube ($\chi^2 = 28.7$, d.f. = 8, $P < 0.001$), whereas no significant change was detected in other tributaries (Chisenai: $\chi^2 = 9.1$, d.f. = 6, $P = 0.16$, Pankeotoshino: $\chi^2 = 8.5$, d.f. = 6, $P = 0.20$, Osonoushi-D: $\chi^2 = 1.6$, d.f. = 2, $P = 0.45$). Fish sizes were small (< 150 mm) also during and after the flood, except for some salmonids, as described above. No significant difference in body size was detected among samples before, during and after the flood (i.e., freshwater sculpin in YU: ANOVA, $F_{2, 147} = 0.64$, $P = 0.53$, freshwater sculpin in CH: $F_{2, 130} = 0.80$, $P = 0.45$, brook lamprey in CH: $F_{2, 18} = 0.87$, $P = 0.44$), except in freshwater sculpin in PA (ANOVA, $F_{2, 177} = 4.57$, $P = 0.01$). The difference in PA, however, was only trivial (mean body size: 103.1, 103.9, and 96.1 mm before, during, and after the flood, respectively) and, therefore, we did not consider it biologically meaningful. No clear pattern was observed between tributary size and the degree of refuge movement (Fig. 3).

DISCUSSION

This managed flood experiment supported the tributary refuge hypothesis, which had remained untested despite the well-known tales among fishermen and scientists' surmises (Sedell et al., 1990). For aquatic invertebrates, hyporheic zones (i.e., regions beneath or alongside stream beds) have been considered to serve as important refuge habitats during natural disturbances (see recent review on the "hyporheic refuge hypothesis" with some criticisms in Dole-Olivier,

2011); there has been little discussion, however, of the tributary refuge hypothesis for stream invertebrates, possibly due to lower swimming ability than fishes.

The present result, however, was a little surprising because several radio-telemetry studies have demonstrated that fishes are able to withstand catastrophic floods by using micro-refuges, such as large woody debris, boulders, or stream margins, in the main stem (Harvey et al., 1999; Makiguchi et al., 2009). In a small stream in Taiwan, all radio-tagged Formosa salmon (*Oncorhynchus formosa)* stayed in exactly the same focal points in the main stem during a catastrophic flood (Makiguchi et al., 2009). In addition, Koizumi et al. (2012) found no strong evidence of refuge movement during a severe flood (> 250 m³/s, 7–10 years recurrence) in another river system where the contrast of tributaries and main stem is higher than that in the Satsunai River system. The intensity of the present controlled flood was not uncommon in the past (i.e., five times a year) and boulders are abundant in the main stem of the Satsunai River. Therefore, we expected that fish would remain in main stem habitats during the flood, rather than seeking refuge in the tributaries.

The rapid fish response observed during our study may partly explain the difference between our results and previously reported results (Han et al., 2007; Koizumi et al., 2012). In Yukurubeshube and Chisenai, most salmonids were captured only during the flood, and few were captured two days before and after the flood. Pre- and post- disturbance comparisons are generally made over longer time periods (e.g., weeks or months). The present study underscores the importance for looking at what is happening during disturbances (see also Makiguchi et al., 2009), although such field surveys are generally very difficult.

The responses to the flood differed among fish species and tributaries. Many factors may account for the difference, such as species biological characteristics, community composition and density in the main stem, the amount of micro-refuges in the main stem, and the distances to the tributaries. For example, Osonoushi-D may be too small for a refuge habitat (1.7 m in mean width, 13 m long from the confluence to a culvert). The reason for no increase, rather decrease, of salmonids in Pankeotoshino is unknown, but may relate to the main stem habitats; this tributary flows into a side channel of the main stem where effects of the flood might have been less severe. Nunn et al. (2010) suggested in a lowland floodplain river that mid-water species, such as cyprinids, tend to move upstream during floods, whereas benthic species, such as bullhead and stone loach, move downstream in response to increased bed load. In the present study, salmonids (mid-water species) tended to move into tributaries (YU and CH), whereas freshwater sculpin and stone loach (benthic species) did not leave the tributaries. Body size may also be an important factor, as no large rainbow trout (approximately 300–600 mm) immigrated into the tributaries even though they were relatively abundant in the main stem (I. Koizumi, personal observation) and it may be that they are more tolerant to the flooding in the main stem. Overall, we could not determine the likely factor(s) affecting local differences in immigration tendency due to the lack of data in the main stem and also lack of replicates (i.e., tributaries studied). From a conservation viewpoint, it is

a challenge to determine which refuge habitats are most important during disturbances.

The number of immigrants was not particularly high in the tributaries, but these tributary refuges may still be of significance for population persistence or recovery. There are many other tributaries in the river system that could also provide refuge for fish escaping the flood, so even though small numbers of fishes use each individual tributary, the tributaries collectively could have a population-level effect. In addition, some tributaries may serve as better refuge habitats, and may accommodate greater numbers of immigrants. Fishes are generally fecund, producing hundreds or thousands of eggs per female. Therefore, even if populations in the main stem were severely affected by a flood, recovery from the disturbances may be possible even from the observed levels of immigration.

River connectivity has recently received much attention due to the accumulated knowledge of its roles in population persistence (Fagan, 2002; Koizumi, 2011) and also because of severe fragmentation by dams (Pringle et al., 2000; Morita and Yamamoto, 2002). The present study showed how connectivity between different habitats may increase population persistence. Moreover, some tributaries served as refuges even though they were not used in normal conditions. Metapopulation theory predicts the importance of vacant habitats that may be colonized in the future (i.e., vacant but suitable habitats) (Hanski, 1999); however, this study highlights how suboptimal or unsuitable habitats may also be important for conservation, as such habitats can function as temporal refuges during disturbances.

ACKNOWLEDGMENTS

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