Received: 13 April 2022 | Revised: 18 April 2023 | Accepted: 20 April 2023

DOI: 10.1002/rra.4148

RESEARCH ARTICLE

WILEY

Preferential behavior of *Tribolodon hakonensis* for fishways according to biological characteristics

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Abstract

In 2012, the fishway in the Miyanaka Intake Dam in Niigata Prefecture, Japan, was reconstructed and divided into three fishways (ice-harbor-, stair-, and rock-ramp-type) with different flow velocities and water depths. We conducted an adaptive monitoring survey in these fishways from 2012 to 2020, and 33 fish types were found, including migratory, swimming, small swimming, and benthic fishes. Many species displayed a preference for specific fishways. The run-up for *Tribolodon hakonensis* was studied to determine the effects of physical parameters such as body length, rush speed for instantaneous swimming, water temperature, and presence/absence of nuptial coloration on fishway preference. *T. hakonensis* with nuptial coloration had greater body length and higher rush speeds than those without it. They also preferred the ice-harbor fishway, whereas their shorter, uncolored counterparts preferred the stair and rock-ramp alternatives. The environmental conditions selected by *T. hakonensis* changed according to their growth stage, as did fishway preference. Changes in fishway environmental conditions may have influenced the observed differences in fishway populations. It was thus confirmed that developing fishways with different flow velocities and water depths is effective in supporting the various life stages of *T. hakonensis*.

KEYWORDS

fish length, fishway design, flow velocities, nuptial coloration, rush speed, *Tribolodon hakonensis*, water depth

1 | INTRODUCTION

Dams are necessary for the operation of hydroelectric power plants, but they impede fish movement in rivers (Dockery et al., 2020; Klopries et al., 2020; Nallaperuma & Asaeda, 2019). The electricity generated by hydroelectric power plants is indispensable to human society as a renewable energy source. Therefore, to minimize the negative impacts on river ecosystems, power generation companies install fishways on river-crossing structures such as dams and weirs (Da Silva et al., 2020; Gosselin et al., 2019; Harris et al., 2020; Hatry et al., 2016; Yoon et al., 2012) to protect the habitats of fish that run-up and move in rivers (Arsenault et al., 2022; Forcellini et al., 2022; Kynard et al., 1996; Onitsuka, 2012; Santos et al., 2021). Fishways aim to increase the connectivity of fragmented rivers (DVWK, Fisheries and Aquaculture Management Division, 2002; Larinier, 2001), and their effects on a wide variety of fish species have been validated through adaptive management with physical, biological, and hydraulic parameters (Boudreault et al., 2021; Castro-Santos et al., 2009; Gutfreund et al., 2018; Noonan et al., 2012; Romão et al., 2018).

Diverse types of fish live in rivers (Jarvis & Closs, 2019; Nepf et al., 2022), and their chosen environmental conditions can vary depending on their growth stage (McDonald & Nelson, 2021; Mulligan et al., 2021). Hydropower producers have designed various fishway formats to create environments that attract wide varieties of fish, including salmonids, which have commercial importance (Albayrak et al., 2020; Baki & Azimi, 2021; Branco et al., 2013; Harris et al., 2019; Kynard et al., 1996; Liu et al., 2019; Magaju et al., 2020; Marsden & Stuart, 2019; Moser et al., 2019; Syms et al., 2021; Tinoco et al., 2022; Zielinski et al., 2021). The shape of the fishway entrance is designed considering multiple constraints, such as the topography of the dam site, dam shape, and power station system (Amaral et al., 2020; Baumgartner et al., 2019; De-Miguel-Gallo et al., 2019; Gehrke et al., 2002; Kinsolving & Bain, 1993; Knapp et al., 2019; Moniz et al., 2020; Plesinski et al., 2020; Zobott et al., 2021). Moreover, various systems have been built to improve design efficiency (Gostner et al., 2021; Legleiter et al., 2019). Most fishways are primarily developed for fish that swim upstream; however, to cover the entire life cycle of fish, it is argued that fish that travel downstream should also be considered (Godinho & Kynard, 2009).

Migratory fish navigate across seas and along rivers, which are easily affected by human activities. These migrations include upstream migration of adults and fry, downstream migration, and in some instances, two-way migration (upstream and downstream), depending on the fish life stage. Fishways in Europe and the United States primarily focus on salmonid fish, which migrate upstream in rivers (O'Sullivan et al., 2021). Since fatigue decreases egg survival rates in such fish (Boudreault et al., 2021; Packman et al., 2021; Vogel et al., 1990), efficient consumption of stored energy is crucial during spawning and upstream swimming in unfavorable environments. Salmon run-up is affected by changes in flow rate; additionally, they exhibit a crowding effect, i.e., they are less susceptible to other environmental conditions when the population density is high. Furthermore, they select higher flow velocities when the difference in flow velocity is high (Banks, 1969; Mayama & Takahashi, 1977; Weaver, 1963). For fish with strong swimming abilities, the impact of confusion due to turbulent flow on the run-up exceeds that of the dissipating energy of a water stream provided by a notch (Kynard et al., 1996). Meanwhile, in Japan, fishways are often constructed considering various fishes, including freshwater and migratory fish (Miwa & Muraoka, 2012). Fishways worldwide are designed based on the types of fish that live in the target river to enable those fish to enter the fishway easily (Blank et al., 2021; Bunt, 2001; Mulligan & Palmer, 2019; Zhang et al., 2022).

Many *Tribolodon* species live in the Shinano river system in Japan, including *Tribolodon hakonensis* (a freshwater species that lives in the upper and middle streams), *Tribolodon brandtii maruta* (a downstream-descending species that primarily utilizes the downstream tidal zone), *Tribolodon brandtii* (found in the sea coastal zone except when traveling upstream to spawn), and *Tribolodon nakamurai* (an endemic species of the Agano river system). Owing to the popular "Tsukeba fishing" practice in the Nagano prefecture, approximately 100 tons of *T. hakonensis* are caught in the Shinano river system annually (Niigataken Naisuimen-gyogyokyodokumiai-rengoukai, 1991). The spawning season of *T. hakonensis* occurs in April to July. The spawning grounds of *Plecoglossus altivelis* are sand riverbeds, but *T. hakonensis* prefers gravel riverbeds in the middle reaches that have been washed and flushed during elevated river flow following rainfall events. Thus, the spawning ground for *T. hakonensis* is located upstream from the spawning ground for *P. altivelis* (Ito et al., 2003; Katano et al., 2010; Niigataken Naisuimen-gyogyokyodokumiai-rengoukai, 1991).

In the low-temperature upper reaches of the Shinano River, spawning begins in February (Niigataken Naisuimen-gyogyokyodokumiai-rengoukai, 1991). It takes approximately a week for the *T. hakonensis* eggs to hatch and approximately 10 days for the fry to emerge from the gravel. Subsequently, the size of the fry increases to 2–3 cm in 20–30 days and 5–10 cm in 1 year, and they mature in 2–4 years. *T. brandtii maruta* lives in rivers for 1 or more years before descending downstream. After living in the ocean for a few years, they travel upstream to spawn (Gudkov et al., 2010; Kawanabe, 1989).

During the spawning season, markers resembling acne occur on the heads and fins of *T. hakonensis*. In addition, the nuptial coloration (three red vertical bands) appears on the sides of their bodies. Although nuptial coloration primarily appears in males, it can be seen in females as well (Hatry et al., 2016), with nuptial coloration appearing in 80% or more of *T. hakonensis* (Atsumi & Koizumi, 2017). Nuptial coloration occurs in females (and males) to convey information regarding individuals' quality and maturity (Baldauf et al., 2011). Furthermore, the nuptial coloration of males influences their selection of females, and their diversity causes species differentiation (Miyagi & Terai, 2013).

The life span of *T. hakonensis* is 7–8 years (Honma, 1983). They are widely distributed from upstream to downstream in rivers, ponds, and artificial lakes; some even inhabit marine habitats, except during the spawning season. Consequently, they are not a target freshwater fish species compared with other migratory fish, although dams disrupt their spawning behavior.

Designing fishways to accommodate various fish species is becoming increasingly important in Japan. Although research regarding fishway structures and the corresponding behavior of *T. hakonensis* (Hayashida et al., 2000; Judes et al., 2021; McDonald & Nelson, 2021), i.e., rush speed and maintenance speed (Blaxter & Dickson, 1959; Brett, 1964; Gui et al., 2014; Lindsey, 1978; Montali-Ashworth et al., 2021; Namihira et al., 2008; Onitsuka et al., 2009), has been conducted, the mechanism used by *T. hakonensis* to select fishways has not been explored to date.

In this study, it was hypothesized that fish would select a fishway according to the flow velocity and water depth at the fishway entrance. We further hypothesized that this selection would be based on fish length and correlated swimming ability; however, we also investigated the possible role of fish shape and sexual maturity. As the Miyanaka Intake Dam (MID) fishway offers three varieties of fishway structures, we chose it to study the behavior of *T. hakonensis*. Since the establishment of the dam in 1939, large and small fishways have been established. In 2012, the fishway structure was improved, and a new rock-ramp fishway was established. The flow rates of the three fishways were changed by varying their flow velocity and depth, and traps were installed at the upstream ends of the fishways to catch the fish that ran up in each case. This allowed us to investigate the relationship between the fishway environment for upstream movement and the characteristics of fishes such as *T. hakonensis* and identify the mechanism used by fish to select fishways. The use of fishways by fish to move upstream has been extensively investigated in previous studies (Baki & Azimi, 2021). However, no long-term (309 days to 9 years) experiments have been conducted with different flow rates to confirm the hypothesis, including before and after fishway system improvements.

2 | MATERIALS AND METHODS

2.1 | Study site

The MID (37°3′58.445″ N, 138°41′50.321″ E) is the only hydroelectric power plant owned by a Japanese railway company (East Japan Railway Company). It was built in 1939 in the middle of the Shinano River. The dam is located 134 km from the river mouth of Niigata city. In this study, water was taken from the left bank of the MID. To eliminate the 11-m difference in elevation of the MID, a fishway was installed at the same time as the construction on the right bank (Figure 1). The length of the fishway was chosen to be 200 m to ensure an appropriate slope. The fishway folds in the middle, such that there are no water reduction sections directly below the dam, and its structure has been improved twice to accommodate the diverse fauna inhabiting the water in the vicinity of the Shinanogowa power plant.

In 1986, all boat channels were converted into stair-type channels. In 1999, a council was established to conduct studies to improve the water environment in the middle reaches of the Shinano River, as reported by Masumoto et al. (2022). The council conducted a fish habitat survey and confirmed that approximately 20 species of fish coexisted in the river. *T. hakonensis* is freely caught in Niigata Prefecture downstream of the MID. However, a permit from the governor is required for the capture of *T. hakonensis* in Nagano Prefecture upstream of the MID. The migration of *T. hakonensis*, which is recognized to be important in such upstream areas, was confirmed in the fishway of the MID (Masumoto et al., 2022).

2.2 | Fishway structure improvement

In 2009, improvement of the MID fishway structure was recommended. The purpose of the improvements was to prevent transverse waves and ensure continuity between the fishway and the river downstream. Continuity was ensured by changing the discharge method from the gate to eliminate circulation flow. To suppress shear waves, the width of the large fishway was reduced, and it was converted to an ice-harbor type. The top of the bulkhead was changed to a compound tri-arc shape, and the folded section was improved to a semicircle. Additionally, a new rock-ramp-type fishway, known as a "Seseragi fishway," was established to accommodate fish with low swimming power and benthic fish (Masumoto et al., 2022). To contribute to the fish habitat, the slope was designed to be gentle, and hydrostatic areas were provided on both sides of the main stream. Because the stair-type channel had exhibited no particular problems, it was relocated between the ice-harbor and rock-ramp types in its original shape. To prevent transverse waves and further improve the run-up environment, three fishways with different flow velocities and water depths were developed.

The specifications of the three fishways are outlined in Table 1. For the ice-harbor fishway, the flow velocity and overflow depth were set to support *P. altivelis* and *Oncorhynchus masou*. Additionally, to support *Oncorhynchus keta*, a higher flow velocity was partially realized by installing a 15-cm notch at the end of the wall that separated the pool. The flow velocity and overflow depth of the stair-type fishway were set to support small swimming fish (*Pseudorasbora parva*, *Gnathopogon elongates*, among others), whereas for the rock-ramp

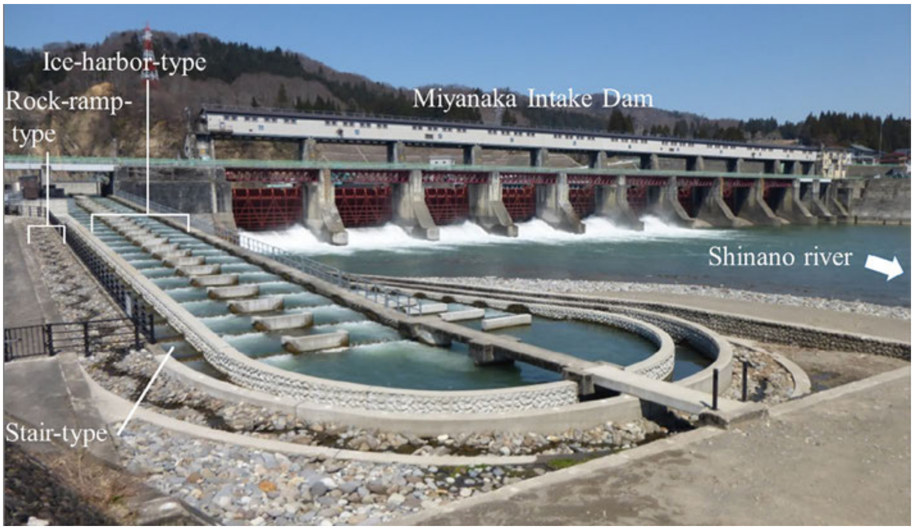

FIGURE 1 Fishways downstream of the Miyanaka Intake Dam. Three types of fishways with different flow velocities and water depths are installed on the side of the right bank. [Color figure can be viewed at wileyonlinelibrary.com]

TABLE 1 Fishway specifications.

	Flow velocity (m/s)	Overflow water depth (m)	Depth of cutout (m)	Slope (%)	Remark
Ice-harbor	1.06–1.56	0.24	0.39	6.6	–
Stair	0.89–1.10	0.13	–	6.6	–
Rock-ramp	0.18–0.33	0.08	–	5.0	2012–2014
	0.54–0.76	0.15			2015–

fishway, the parameters were set to support benthic fish with weak swimming abilities (*Cobitis biwae*, *Rhinogobius kurodai*, among others). The meandering channel promoted a gentle slope and low flow velocity in the rock-ramp fishway, which further supported these species. In 2015, considering the recommendations of the local fishery cooperative, the flow velocity and overflow depth of the rock-ramp fishway were modified to further improve the environment and ensure a stable habitat for benthic fish reproduction.

In the submerged area at the fishway entrance, the fish that reached the fishways could sense the flow differences among the three fishways. Therefore, the three fishways were made more effective by removing part of the sidewall in the submerged area at the fishway entrance. In particular, the wall between the stair-type fishway and the rock-ramp-type fishway was shortened significantly, enabling fish with slower swimming abilities to select fishways more easily. Consequently, based on their swimming abilities, fish that reached the fishway entrance could direct their courses toward other fishways with preferential flow velocities.

2.3 | Surveys before fishway improvement (2010) and during construction (2011)

A preliminary daily survey was conducted at MID in 2010 with the purpose of understanding the situation during the renovations in 2011 and implementing continuous monitoring from 2012 onwards. Based on existing literature, the presence of four nocturnal fish species was confirmed in the research area, including *Anguilla japonica*, *Pelteobagrus nudiceps*, *Silurus asotus*, and *Liobagrus reini* (Kawanabe, 2001). Nocturnal fish species are species that start their feeding activity at night rather than during migration. Therefore, nocturnal fish species are not only active at night but exhibit increased feeding activity at night. Therefore, by design, the survey was conducted only during the daytime to confirm the migration status of small fish, excluding bottom-dwelling fish. However, as a preliminary study to confirm the situation at the MID, surveys were also conducted at night. Because the rock-ramp fishway had not been set up by this point, the survey was carried out on the large and small stair-type fishways in 2010, using the same survey method as that after 2012. The 2010 survey was conducted from June 7 to 17. Between June 7 and 10, the nighttime survey was conducted from 5 PM on 1 day to 9 AM on the following day, continuing directly from the daytime survey. From June 11 to 17, the nighttime survey was conducted from 6 to 9 AM and 5 to 6 PM. In addition, considering the safety of the research team, nighttime surveys were conducted every 2 h from 8 PM to 6 AM, when the site was dark. From 2015 onwards, the daytime and nighttime survey periods were from 9 AM to 5 PM and 5 PM to 9 AM on the following day, respectively. During the construction period to improve the fishway structure, surveys were conducted over 17–28 May and 11–24 June 2011, only for the large fishway.

2.4 | Investigation based on adaptive management after fishway structure improvement

From 2012 to 2020, the three improved fishway structures, namely, the ice-harbor-, stair-, and rock-ramp-type fishways, were continuously monitored under adaptive management. The survey period was flexibly set according to the conditions, such as flooding and run-up time of *P. altivelis* every year between 6 June and 4 July, which includes the peak of *P. altivelis* run-up period based on the 2011 survey results. However, as the run-up time of *P. altivelis* changes according to the integrated river water temperature condition, the survey start date was shifted to 26 May 2016 as slightly higher water temperatures were observed that year. Therefore, the fish that ran up before 5 June were identified owing to the earlier start date of the 2016 survey. Furthermore, the investigations in 2011 (17–28 May), 2018 (from 2 June), and 2020 (from 25 May) began before 5 June according to the run-up time of *P. altivelis*. Results from 2011, before the construction of the rock-ramp fishway, were not included. Considering the impact of flooding on the survey, the survey period was extended to 10 July 2013 and 14 July 2017.

For data acquisition, a net cage was set up at the upstream end of the fishway to catch all the fish that ran upstream. All fish caught were released on the upstream side of the fishway, except for those that were to be disposed of in accordance with laws and ordinances. Fish that migrated up the fishway were counted by net cages and assessed on an hourly basis, as shown in Masumoto et al. (2022). Caught fish were identified, counted, photographed from the side for identification, and checked for the presence of *T. hakonensis* nuptial coloration. The survey hours between 2012 and 2014 were from 6 AM to 7 PM. Starting in 2015, the survey hours were changed, from 9 AM to 5 PM, considering the safety of the research team. A nighttime survey was conducted in 2017 to confirm that the trend remained unchanged from the 2010 nighttime survey results. These nighttime surveys were conducted twice, on June 24 and June 30 starting at 5 PM until 9 AM of the following day. Similar to 2010, the nighttime surveys were conducted every 2 h.

The relationship between *P. altivelis* and *T. hakonensis* catches (2012–2020) and environmental factors (i.e., the average river temperature, suspended solids [SS], and dam discharge) were analyzed by bivariate analysis taking the year as a factor. *P. altivelis* and *T. hakonensis* were selected owing to the high number of catches during the survey period. The water temperature and amount of SS were measured prior to analysis. The daily average water temperature was calculated from the water temperature, recorded hourly from the measurement results of the self-recording water thermometer temporarily installed on the fishway of the MID. The amount of SS was measured once a day at 12 noon by sampling the water at the catch point at the upstream end of the fishway. The amount of water released from the dam was based on the data from operations management. In the analysis of variance, individual data were assumed to be independent of each other, and a significance level of 5% was used for the analysis.

3 | RESULTS

3.1 | Confirmed species before fishway improvement

In 2010, 368 individuals from 11 species were caught during the daytime, while 183 individuals from 13 species were caught at night (Table 2). *A. japonica*, *Carassius auratus langsdorfii*, and *Hemibarbus labeo* were caught only during nighttime surveys. However, these were rare species with few catches. In this survey, *P. altivelis* and *T. hakonensis* dominated and detailed capture times were confirmed. As a result of the nighttime survey, 64 *T. hakonensis* individuals were caught between 5 and 7 PM, and 26 *T. hakonensis* individuals were caught between 8 and 11 PM. However, *T. hakonensis* were also caught during the entire nighttime survey period. Twelve *P. altivelis* individuals were caught between 5 and 7 PM, and 15 *P. altivelis* individuals were caught between 6 and 9 AM. No *P. altivelis* specimens were caught between 7 PM and 6 AM. *A. japonica*, which is classified as a nocturnal fish species, was caught only at night; by contrast, *P. nudiceps* moved not only at night but also during the day. As a result, since 2011, surveys have been conducted only during daytime as the number of catches during nighttime is lower than that during daytime.

As in the previous surveys, the dominant fish in the 2017 nighttime survey were *T. hakonensis* (61 individuals) and *P. altivelis* (16 individuals) (Table 3). *T. hakonensis* were caught during all nighttime survey hours. Four *P. altivelis* individuals were caught between 5 and 7 PM, and seven *P. altivelis* individuals were caught between 5 and 9 AM. Only five *P. altivelis* individuals were caught from 7 PM to 5 AM. In addition, rock-ramp fishways in MID are understood to be used mainly by bottom-dwelling fish, not only for swimming but also as habitat (Masumoto et al., 2022). In the nighttime survey in 2017, *Misgurnus anguillicaudatus*, *C. biwae*, and *Cottus pollux* were confirmed in rock-ramp fishways in addition to nocturnal fish species.

3.2 | Fish species composition according to fishway

The different types and populations (mean values) of fish caught during the survey period (2011–2020) are presented in Table 4. Despite being a dominant species, *O. keta* was not captured as the survey was conducted in June. Twenty-two types of non-bottom-dwelling fish and 11 types of bottom-dwelling fish, including *C. pollux*, *Rhinogobius kurodai*, and *C. biwae*, were captured during the 10-year period (2011–2020). For fish other than bottom-dwelling fish, small *Squalidus chankaensis biwae*, *P. altivelis*, *Opsariichthys platypus*, *T. hakonensis*, and

TABLE 2 Daytime and nighttime survey results for 2010.

Fish species		Day			Night		
		Total	Large	Small	Total	Large	Small
1	*Carassius auratus langsdorfii*	0	0	0	1	0	1
2	*Opsariichthys platypus*	27	6	21	7	5	2
3	*Rhynchocypris lagowskii*	1	0	1	1	0	1
4	*Tribolodon hakonensis*	177	173	4	121	117	4
5	*Sarcocheilichthys variegatus microoculus*	4	4	0	1	1	0
6	*Pseudogobio esocinus*	2	0	2	1	1	0
7	*Hemibarbus labeo*	0	0	0	2	2	0
8	*Squalidus*	9	0	9	7	1	6
9	*Plecoglossus altivelis*	86	63	23	27	19	8
10	*Oncorhynchus masou*	48	21	27	7	4	3
11	*Anguilla japonica*	0	0	0	1	0	1
12	*Pelteobagrus nudiceps*	4	1	3	5	0	5
13	*Cottus pollux*	9	4	5	1	1	0
14	*Rhinogobius fluviatilis*	0	0	0	1	0	1
–	*Rhinogobius*	1	0	1	0	0	0
	Total	368	272	96	183	151	32

TABLE 3 Nighttime survey results for 2017.

	Fish species	Day				Night			
		Total	Ih	St	Rr	Total	Ih	St	Rr
1	*Rhynchocypris lagowskii*	1	0	0	1	1	0	0	1
2	*Tribolodon hakonensis*	5	4	1	0	61	59	2	0
3	*Sarcocheilichthys variegatus microoculus*	0	0	0	0	1	1	0	0
4	*Pseudogobio esocinus*	1	1	0	0	2	1	1	0
5	*Plecoglossus altivelis*	77	74	3	0	16	15	1	0
6	*Salvelinus leucomaenis pluvius*	1	1	0	0	2	1	0	1
7	*Misgurnus anguillicaudatus*	0	0	0	0	2	0	0	2
8	*Paramisgurnus dabryanus*	0	0	0	0	3	0	0	3
9	*Cobitis biwae*	3	0	0	3	8	0	0	8
10	*Silurus asotus*	0	0	0	0	1	0	0	1
11	*Liobagrus reini*	1	0	0	1	3	0	0	3
12	*Cottus pollux*	0	0	0	0	2	1	0	1
13	*Rhinogobius kurodai*	5	0	0	5	2	0	0	2
	Total	94	80	4	10	104	78	4	22

Abbreviation: Ih: ice-harbor-type fishway; St: stair-type fishway; Rr: rock-ramp-type fishway.

O. masou in the run-up period were dominant. In the 2012 survey, 95% of captured individuals were small *S. chankaensis biwae*. Among bottom-dwelling fish, *C. biwae*, *C. pollux*, *R. kurodai*, and *L. reini* were predominately caught.

Approximately 10 individuals, particularly from swimming-type species, were recognized near the fishway entrance. Furthermore, some species stayed in the fishway for a long period of time and were not counted among the fish caught in the basket. Although the period from entering the fishway to entering the catch basket at the upstream end could not be measured in the present survey, the fraction of such fish seemed to be less than 5% of the total count as the survey was conducted for approximately 30 days.

3.3 | Nuptial coloring and fishway type for *T. hakonensis*

Caught *T. hakonensis* populations were divided according to the presence or absence of nuptial coloration and type of fishway in which they were captured (Table 5). Approximately 55.4% of *T. hakonensis* without nuptial coloration were caught in the stair-type fishway, while approximately 89.7% of *T. hakonensis* with nuptial coloration were caught in the ice-harbor fishway. No *T. hakonensis* with nuptial coloration was caught in the rock-ramp fishway.

3.4 | Relationship between fishway conditions and migration behavior of *T. hakonensis* according to nuptial coloration

The relationship between the number of *T. hakonensis* captures per hour and the presence or absence of nuptial coloration in the ice-harbor- and stair-type fishways is shown in Figure 2. The largest number of *T. hakonensis* was recorded between 2 and 4 PM (Jarvis & Closs, 2019). The results for the ice-harbor (Figure 2a) and stair-type (Figure 2b) fishways revealed large numbers of fish regardless of their nuptial coloration. Therefore, we concluded that there was no difference between the presence or absence of nuptial coloration and run-up time.

The *T. hakonensis* were divided into two groups based on the presence or absence of nuptial coloration from 2012 to 2020. Based on a bivariate analysis, we found that environmental factors, such as the average river temperature, SS, and discharge, do not affect *T. hakonensis*. For example, the presence of nuptial coloration did not show a significant correlation with the average river temperature, SS, and discharge ($p = 0.595$, $p = 0.946$, and $p = 0.961$, respectively). The absence of nuptial coloration showed a significant correlation only with the average SS ($p = 0.030$) and no significant correlation with the average river temperature or discharge ($p = 0.153$ and $p = 0.066$, respectively).

3.5 | Migration trends for commonly caught fish species

For the most commonly caught fish species, the run-up tendency for each fishway was summarized via one-way ANOVA using only the results from 2012 to 2020 when the three fishways were constructed (Table 6). The number of *T. hakonensis* caught in the ice-harbor fishway was significantly higher than those caught in the stair- and rock-ramp-type fishways ($p < 0.001$ and $p = 0.005$, respectively). *O. masou* used all three fishways, but *O. masou* running up in the fishway of MID is classified into cherry trout and cherry salmon. Cherry trout do not migrate to the sea and grow only up to ~0.2 m. Cherry salmon migrate to the sea, similar to *O. keta*, and grow to 0.3–0.7 m. They were distinguished here using common names because of their differences in body length and swimming ability. All cherry salmon used the

TABLE 4 Number of fish caught in each fishway during (2011) and after fishway renovation (2012–2020) for non-bottom-dwelling and bottom-dwelling fish.

(a) Non-bottom-dwelling fish

	Year	2011	2012–2020			
No.	Fish species	Fishway	Ice-harbor	Stair	Rock-ramp	Total
1	*Cyprinus carpio*	-	0.22	-	-	0.22
2	*Carassius auratus langsdorfii*	-	0.33	0.11	0.22	0.67
-	*Carassius*	-	-	-	0.56	0.56
3	*Rhodeus ocellatus*	-	-	-	0.33	0.33
4	*Opsariichthys platypus*	9.00	82.33	141.44	14.67	238.44
5	*Nipponocypris temminckii*	1.00	0.22	1.22	0.22	1.67
6	*Rhynchocypris lagowskii*	-	0.44	5.67	6.22	12.33
7	*Tribolodon nakamurai*	-	0.22	-	-	0.22
8	*Tribolodon hakonensis*	380.00	281.00	55.11	4.22	340.33
9	*Pseudorasbora parva*	-	-	-	2.11	2.11
10	*Sarcocheilichthys variegatus microoculus*	4.00	1.56	0.11	-	1.67
11	*Gnathopogon elongatus*	-	-	0.56	2.22	2.78
12	*Pseudogobio esocinus*	2.00	5.56	9.67	0.11	15.33
13	*Hemibarbus labeo*	4.00	7.11	0.44	0.11	7.67
14	*Squalidus chankaensis biwae*	4.00	3.33	44.56	-	47.89
-	*Cyprinidae*	-	0.44	0.56	-	1.00
15	*Plecoglossus altivelis*	208.00	1873.44	347.11	3.22	2223.78
16	*Salmo trutta*	1.00	1.44	-	0.22	1.67
17	*Salvelinus leucomaenis pluvius*	1.00	2.67	0.22	0.56	3.44
18	*Oncorhynchus mykiss*	2.00	1.44	0.11	-	1.56
19	*Oncorhynchus masou*	6.00	18.78	4.33	1.67	24.78
19–1	Cherry salmon	-	7.67	-	-	7.67
19–2	Cherry trout (without Cherry salmon)	6.00	11.11	4.33	1.67	17.11
20	*Lepomis macrochirus*	-	-	-	0.22	0.22
21	*Micropterus salmoides*	-	-	-	1.56	1.56
22	*Micropterus dolomieu*	-	2.11	0.78	0.11	3.00

(b) Bottom-dwelling fish

	Year	2011	2012–2020			
No.	Fish species	Fishway	Ice-harbor	Stair	Rock-ramp	Total
1	*Lethenteron sp*	-	-	-	0.11	0.11
2	*Anguilla japonica*	-	-	0.11	0.11	0.22
3	*Misgurnus anguillicaudatus*	-	-	0.11	1.00	1.11
4	*Cobitis biwae*	-	-	0.11	12.11	12.22
5	*Paramisgurnus dabryanus*	-	-	0.11	0.56	0.67
-	*Misgurnus*	-	-	0.11	-	0.11
6	*Pelteobagrus nudiceps*	5.00	0.89	1.44	0.56	2.89
7	*Silurus asotus*	-	0.56	-	-	0.56
8	*Liobagrus reini*	-	-	0.11	8.22	8.33
9	*Cottus pollux*	4.00	6.89	7.89	24.33	39.11
10	*Rhinogobius kurodai*	-	0.11	2.22	74.56	76.89
11	*Channa argus*	-	-	0.11	-	0.11

Note: Results from 2012 to 2020 are 8-year average values.

ice-harbor fishway ($p < 0.001$), and cherry trout used all three fishways, although significant differences were observed between the ice-harbor and rock-ramp fishways ($p = 0.051$). *P. altivelis* mainly used the ice-harbor fishway rather than the stair- and rock-ramp-type fishways ($p > 0.05$). *O. platypus* mainly used the stair-type fishway rather than the ice-harbor and rock-ramp types ($p > 0.05$ and $p = 0.039$, respectively). There was no significant trend in fishway usage for *S. chankaensis biwae*. Among five other non-bottom-dwelling fish, four species except *S. chankaensis biwae* used all three fishways.

3.6 | Fishway selection criteria according to species

As shown in Table 7, the body length ratios were established to determine the rush speed of fish such as *T. hakonensis*. The body length ratio was obtained by dividing the rush speed (m/s) by the body length (m); thus, the unit of the body length ratio was s^{-1}. Then, by multiplying the body length by the body length ratio (s^{-1}), the rush speed (m/s) corresponding to the body length was calculated (Jowett et al., 2021). There was a significant correlation between body length and rush speed. This is attributed to larger individuals having greater swimming abilities and therefore being better able to achieve higher velocities (Chida, 1995; Hirose, 1991; Koyama, 1965, 1978; Marshall, 1965; Morishita, 1996).

The relationship between the flow velocities of each fishway and the estimated rush speed was postulated, and the results were validated by *t*-tests. The average body length of *P. altivelis* that selected the ice-harbor-, stair-, and rock-ramp-type fishways was 100.0, 93.2, and 92.6 mm, respectively. *P. altivelis*, which is an anadromous migratory fish, is a semelparous species and spawns once a year. However, in the surveyed season, *P. altivelis* utilized the fishway to seek their habitat, not for spawning. All *P. altivelis* caught in this survey were fry with a strong desire to migrate upstream to more suitable habitats. Accordingly, *P. altivelis* at different life stages are not found at the same time in fishways and rivers, and *P. altivelis* chose the ice-harbor- and stair-type fishways rather than the rock-ramp-type fishway depending on their length-based lunge speed ($p > 0.05$ for both), as shown in Figure 3.

T. hakonensis, however, is an iteroparous species and lays eggs several times in its 7–8-year lifespan; therefore, different life stages of different sizes exist simultaneously in fishways and rivers. There was a significant difference in the length of *T. hakonensis* caught in the three fishways ($p < 0.05$), as shown in Figure 4.

TABLE 5 *T. hakonensis* fishway selection according to presence/absence of nuptial coloration.

Nuptial coloration		Ih	St	Rr	Total
No	Number	109	159	19	287
	Proportion (%)	38.0	55.4	6.6	100
Yes	Number	61	7	0	68
	Proportion (%)	89.7	10.3	0	100
Total (number)		170	166	19	355

Abbreviations: Ih: ice-harbor-type fishway; St: stair-type fishway; Rr: rock-ramp-type fishway.

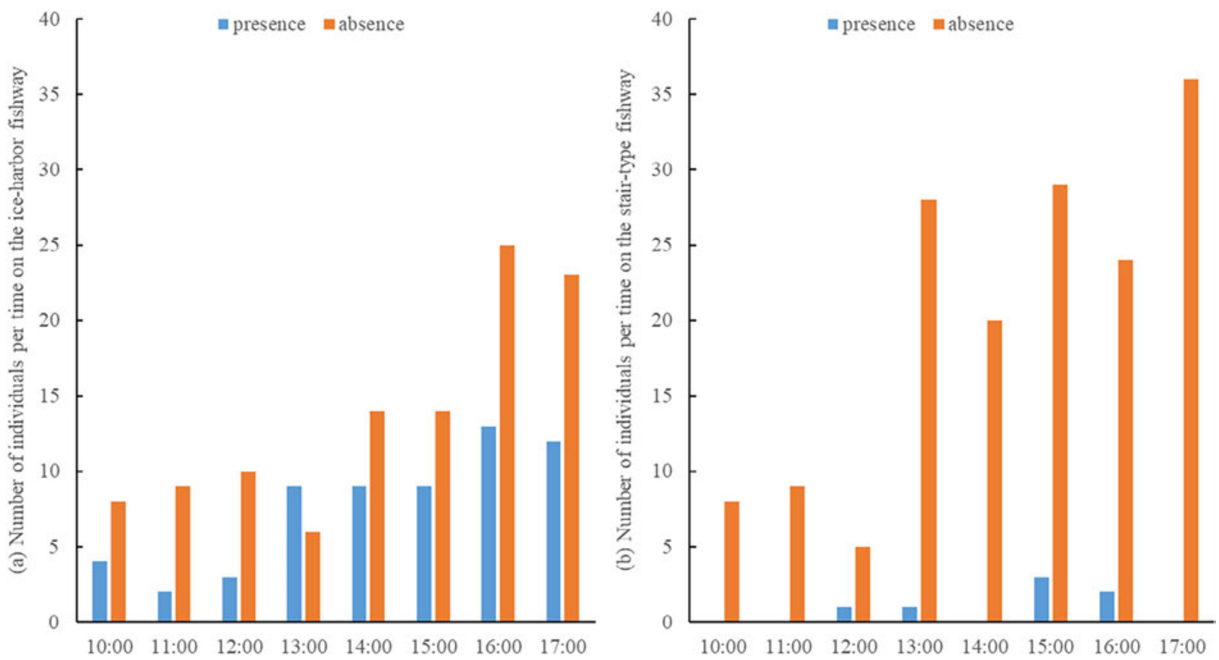

FIGURE 2 Number of individuals of *T. hakonensis* according to the presence or absence of nuptial coloration on the (a) ice-harbor-type and (b) stair-type fishways. A catch basket was placed in the water at 9 AM every morning, and the fish caught were counted hourly from 10 AM to 5 PM. [Color figure can be viewed at wileyonlinelibrary.com]

TABLE 6 Migration tendency in three fishways for dominant fish species via one-way ANOVA testing.

Scientific name	Ih versus St	Ih versus Rr	St versus Rr
Tribolodon hakonensis	$p < 0.001$	$p = 0.005$	$p > 0.05$
Oncorhynchus masou (Cherry salmon)	$p < 0.001$	$p < 0.001$	$p > 0.05$
Oncorhynchus masou (Cherry trout)	$p > 0.05$	$p = 0.051$	$p > 0.05$
Plecoglossus altivelis	$p > 0.05$	$p > 0.05$	$p > 0.05$
Opsariichthys platypus	$p > 0.05$	$p > 0.05$	$p = 0.039$
Squalidus chankaensis biwae	$p > 0.05$	$p > 0.05$	$p > 0.05$
Cobitis biwae	$p = 0.008$	$p = 0.008$	$p > 0.05$
Cottus pollux	$p > 0.05$	$p = 0.09$	$p > 0.05$
Liobagrus reini	$p > 0.05$	$p = 0.022$	$p = 0.024$
Rhinogobius kurodai	$p < 0.001$	$p > 0.05$	$p < 0.001$

Abbreviations: Ih: ice-harbor-type fishway; St: stair-type; Rr: rock-ramp-type.

TABLE 7 Adoption value and body length ratio calculated from the relationship between body length and rush speed.

Fish species	Body length (mm)	Rush speed (m/s)	Body length ratio	Adoption value	Literature
Plecoglossus altivelis	66	1.2	18	19	Hirose (1991)
	50–90	1.0–2.0	20		Koyama (1978)
Tribolodon hakonensis	70–100	1.0	10	10	Koyama (1965)
	150	1.6	10		Marshall (1965)
Oncorhynchus masou (Cherry salmon)	240–500	2–2.5	8.3–5	7	Morishita (1996)
Oncorhynchus masou (Cherry trout)	100	1.5	15	15	Chida (1995)
Opsariichthys platypus	80–100	1.0	10	10	Koyama (1978)

Note: When the rush speed differs depending on the body length, the body length ratio was calculated for each length and the average value was used as the adopted value.

O. masou, i.e., cherry salmon and cherry trout, run up the fishway for spawning; however, different life stages were recorded. As shown in Figure 5, cherry salmon were caught in the ice-harbor fishway, and the individuals had a rush speed exceeding the flow velocity set in the ice-harbor fishway. By contrast, cherry trout were caught in all three fishways. All cherry trout longer than 0.2 m were caught in the ice-harbor fishway; however, those shorter than 0.2 m did not significantly prefer this fishway. There was a significant difference between these results ($p < 0.05$, $df = 9$, $t = 2.262$).

O. platypus spawned once or twice in a year and ran up the fishway for spawning. As shown in Figure 6, *O. platypus* had a lower rush velocity than the flow velocity range set for each fishway. However, a clear preference for fishway was observed depending on whether the individuals strongly desired to spawn.

C. biwae, *L. reini*, and *R. kurodai* exhibited significant differences in preference between the ice-harbor and rock-ramp fishways by *t*-test ($p = 0.008$, $p = 0.022$, and $p < 0.001$, respectively). The average length of *C. pollux* in the ice-harbor-, stair-, and rock-ramp-type fishways was 73.9 (54–104), 70.5 (50–90), and 70.1 mm (52–85 mm), respectively. However, a significant difference between the selected fishways and the size of *C. pollux* was not recorded ($p = 0.09$).

4 | DISCUSSION

4.1 | Utilization of rock-ramp-type fishways by various fish

Rock-ramp-type fishways, because of their potential to assist the migration of multiple fish species, improve the connectivity of fish communities (Kupferschmidt & Zhu, 2017; Landsman et al., 2017). The existing rock-ramp-type fishways were considered to contribute to the migration of bottom-dwelling fishes, such as *C. pollux* (Knaepkens et al., 2004). However, the effect of rock-ramp-type fishways has not been adequately demonstrated in the literature (Beatty et al., 2007; Murry et al., 2019; Raabe et al., 2019; Richer et al., 2020; Stoller et al., 2016).

The results of this study showed that bottom-dwelling fish responded very well to the rock-ramp fishway. The rock-ramp fishway was mainly used by fish with a flat or plump body shape, which is typical of bottom-dwelling fish, while other fish have a streamlined body shape and mainly used the ice-harbor- or stair-type fishways. However, among non-bottom-dwelling fish, small-length individuals (including fry) with lengths less than 0.13 m also used the rock-ramp fishway. In addition, large bottom-dwelling fish, such as *S. asotus* and *P. nudiceps*, used the ice-harbor fishway. Therefore, it is considered

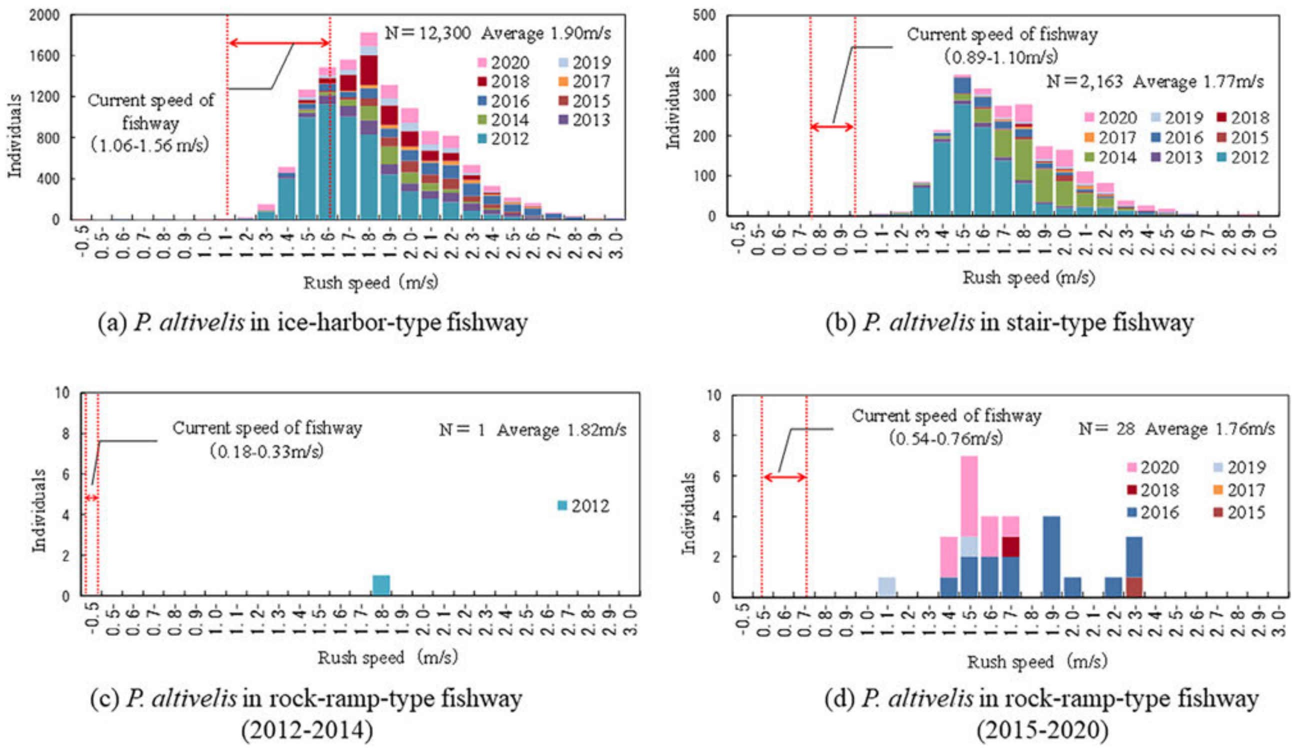

FIGURE 3 Relationship between range of flow velocity and number of catches of *P. altivelis* according to rush speed in the (a) ice-harbor-type and (b) stair-type fishway, as well as the rock-ramp-type fishway for (c) 2012–2014 and (d) 2015–2020. The overflow depth of the bulkhead was set according to the fish species targeted by each fishway; therefore, owing to the differing required flow rate, the flow velocity for each fishway also differed. [Color figure can be viewed at wileyonlinelibrary.com]

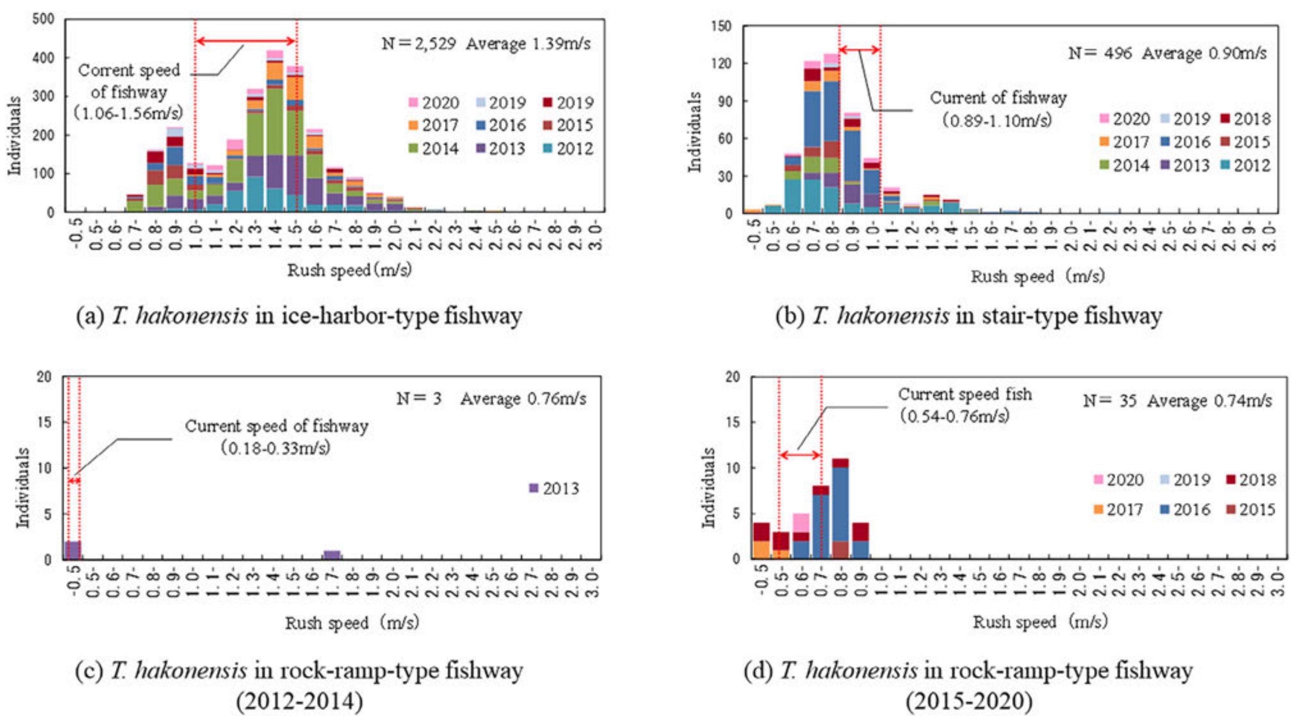

FIGURE 4 Relationship between range of flow velocity of three fishways and number of catches of *T. hakonensis* according to rush speed in the (a) ice-harbor-type and (b) stair-type fishway, as well as rock-ramp-type fishway for (c) 2012–2014 and (d) 2015–2020. [Color figure can be viewed at wileyonlinelibrary.com]

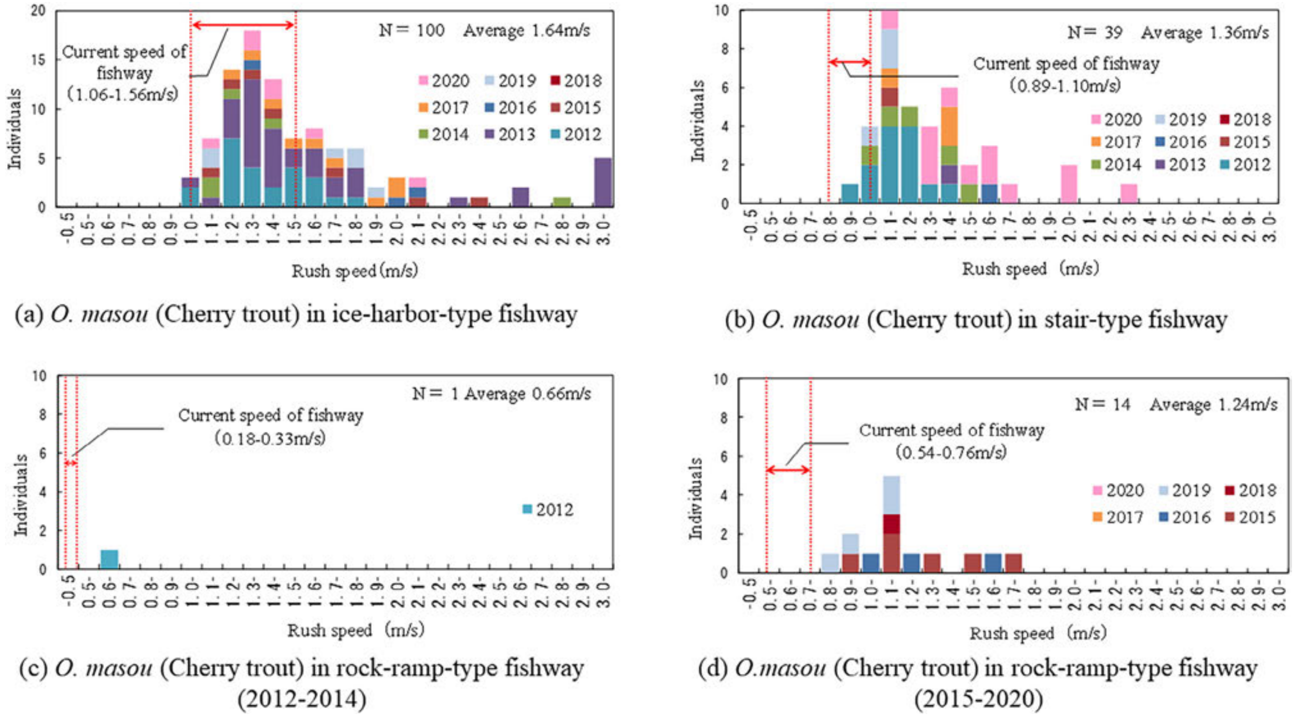

FIGURE 5 Relationship between range of flow velocity of three fishways and number of catches of *O. Masou* (Cherry trout) according to rush speed in the (a) ice-harbor-type and (b) stair-type fishway, as well as the rock-ramp-type fishway for (c) 2012–2014 and (d) 2015–2020. [Color figure can be viewed at wileyonlinelibrary.com]

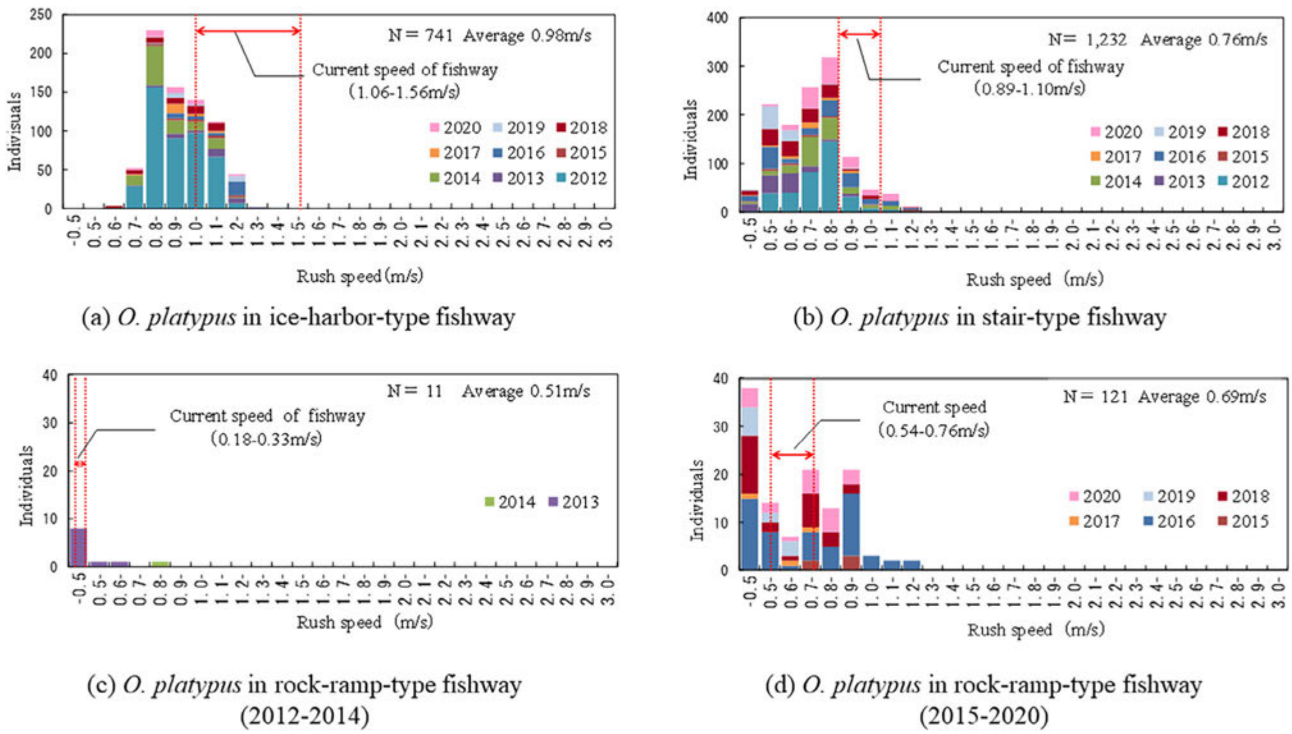

FIGURE 6 Relationship between range of flow velocity of three fishways and number of catches of *O. platypus* according to rush speed in the (a) ice-harbor-type and (b) stair-type fishway, as well as rock-ramp-type fishway for (c) 2012–2014 and (d) 2015–2020. [Color figure can be viewed at wileyonlinelibrary.com]

that the fishway is selected according to the swimming ability of the fish, related to its body length, regardless of body shape. Bottom-dwelling fish, such as *C. biwae*, *L. reini*, *C. pollux*, and *R. kurodai*, preferred the rock-ramp fishway. *O. masou* and *O. platypus* were all migrating upstream for spawning, and *P. altivelis* were all migrating upstream in search of suitable habitat. Therefore, the life stages of specimens were the same. These results indicate that the rock-ramp fishway, which can be passed with their swimming ability, is preferentially selected by these species. This was verified for *T. hakonensis*, which was hypothesized to have fishway selectivity according to both its life stage and body length.

4.2 | Average body length and fishway selection

Because *P. altivelis* is an annual fish, all *P. altivelis* that migrate upstream from the sea in search of habitat around June are juveniles. Salmonidae also migrate from the sea to upstream rivers to spawn. In contrast, *T. hakonensis*, which is not an annual fish, migrates not only for spawning but also for habitat (Katano et al., 2001). Therefore, fish moving upstream and downstream of the dam for habitat and fish going upstream to spawn were mixed. *T. hakonensis* migrating upstream for spawning show typical nuptial coloration (Atsumi & Koizumi, 2017).

Therefore, the average body length of *T. hakonensis* in each fishway was recorded along with the presence or absence of nuptial coloration. The mean length of *T. hakonensis* in the ice-harbor-type fishway was larger than that in the stair-type fishway ($p = 0.08$, $df = 29$, $t = 2.045$). The average length of *T. hakonensis* with nuptial coloration was significantly greater than that of *T. hakonensis* without nuptial coloration ($p < 0.05$, $df = 39$, $t = 2.023$). Furthermore, it was confirmed that individuals with nuptial coloration were larger in the ice-harbor- ($p < 0.05$, $df = 23$, $t = 2.160$) and stair-type fishways ($p < 0.05$, $df = 9$, $t = 2.262$).

The maintenance of fishways is costly, but managing them adaptively, considering the impacts upstream and downstream of dams and weirs, is important (Moore & Rutherfurd, 2017; Reimers, 1966). Furthermore, it is important to consider diverse fish and various life stages, not just salmon runs (Benitez et al., 2015). In this study, not only *T. hakonensis* with nuptial coloration but also many *T. hakonensis* without nuptial coloration were confirmed in the fishways of MID. In contrast to salmonids, river-dwelling fish can be affected by small barriers (Jones et al., 2021). Furthermore, fishways with lower current velocities and longer and continuous passages are needed for less active fish, such as bottom-dwelling fish and juveniles (Griffioen et al., 2022). Therefore, not only large fish with nuptial coloration but also small fish that do not have nuptial coloration should be considered. Stream continuity for fish migration and dispersal is also important to maintain diverse fish habitats (Kjærås et al., 2022; Pachla et al., 2022). Therefore, the fishways of MID have been improved and appropriately maintained to accommodate not only large fish with superior swimming ability but also small fish and bottom-dwelling fish with low swimming ability (Aoki et al., 2021).

4.3 | Fishway selection mechanism for *T. hakonensis*

The rush speed of *T. hakonensis* for each fishway in 2012–2020 was organized according to the presence or absence of nuptial coloration in Figure 7. In the ice-harbor fishway ($p = 0.043 < 0.05$, $df = 5$, $t = 2.571$), the average rush speed of the fish with nuptial coloration was 1.54 m/s, and 68.0% of the fish were within the design flow velocity range (1.06–1.56 m/s). Without nuptial coloration, the average rush speed of the fish in the ice-harbor fishway ($p = 0.005 < 0.05$, $df = 20$, $t = 2.086$) was 1.10 m/s, and 48.9% of the fish were within the design flow velocity range. In the stair-type fishway ($p = 0.368 > 0.05$, $df = 6$, $t = 2.447$), the average rush speed of fish with nuptial coloration was 1.38 m/s, and 5.1% of the fish were within the design flow velocity range (0.89–1.10 m/s). For fish without nuptial coloration, the average rush speed was 0.86 m/s, and 54.9% of the fish were within the design flow velocity range of the stair-type fishway ($p = 0.098 < 0.1$, $df = 2$, $t = 4.302$). In the initial design of the rock-ramp-type fishway, the average rush speed of fish with nuptial coloration was 1.74 m/s, which was within the design flow velocity range (0.18–0.33 m/s). For fish without nuptial coloration, the average rush speed was 0.27 m/s, and 100% of the fish were within the design flow velocity range (0.18–0.33 m/s) of the initial rock-ramp-type fishway (*t*-test not possible). Fish with nuptial coloration were not captured in the improved rock-ramp-type fishway. For fish without nuptial coloration, the average rush speed was 0.74 m/s, and 42.4% of the fish were within the design flow velocity range (0.54–0.76 m/s) of the improved rock-ramp-type fishway ($p = 0.098 < 0.1$, $df = 2$, $t = 4.303$).

In this study, sexually mature individuals with nuptial coloration had longer body lengths. Therefore, sexually mature individuals tended to choose the ice-harbor-type fishway, which was suitable for their body length and rush speed. Accordingly, sexually immature fish chose the stair-type fishway, while smaller fish used the rock-ramp fishway.

If the rush speed, which is proportional to body length, matches the current velocity in the fishway, it is thought that the fish can quickly run up the fishway without stress. The average length of *T. hakonensis* caught in the rock-ramp fishway was 74 mm, which was smaller than the average length of *T. hakonensis* caught in the ice-harbor- (139 mm) and stair-type fishways (90 mm). In addition, many *T. hakonensis* caught in the rock-ramp fishway were sexually immature.

O. platypus males also express nuptial coloration. However, the rock-ramp-type fishway was not characteristically selected by *O. platypus* because it did not have a long body length or a high rushing speed, even when it expressed nuptial coloration.

As outlined above, part of the wall at the entrance to the MID fishway was removed in 2015, making it easier for fish choose fishways and demonstrate a mechanism for preference according to the rushing speed and allowing fish to pass quickly.

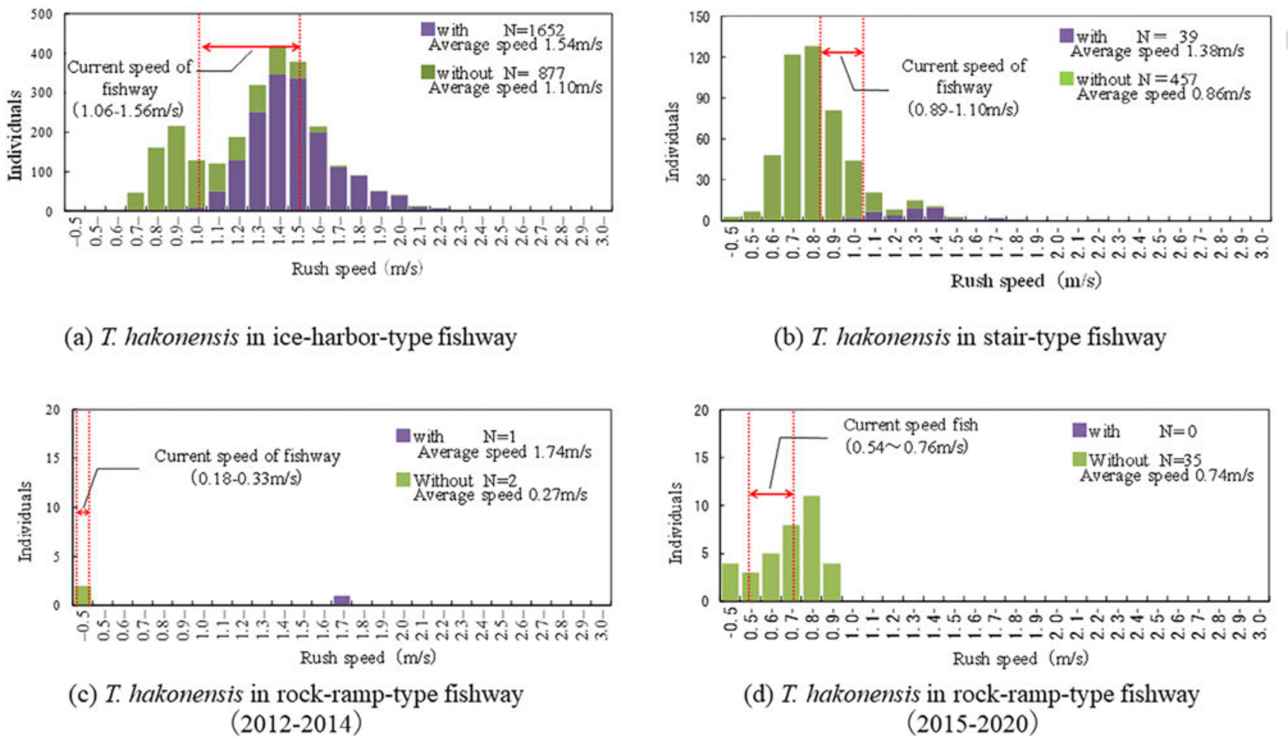

FIGURE 7 Population of *T. hakonensis* according to rush speed in the (a) ice-harbor-type and (b) stair-type fishways as well as rock-ramp fishways for (c) 2012–2014 and (d) 2015–2020, according to the presence or absence of nuptial coloration. The flow velocity range for each fishway and the rush speed range according to *T. hakonensis* body length were nearly the same. [Color figure can be viewed at wileyonlinelibrary.com]

4.4 | MID upstream contribution

Several types of fishways have been studied to assist fish in reaching upstream habitats (Helbig et al., 2021; Mensinger et al., 2021; Shahabi et al., 2023). However, no fishway suits all dams and weirs. Fishway types are selected to suit the environmental conditions (Mulligan et al., 2019; Tonkin et al., 2022; White et al., 2011), upstream and downstream topography and intake locations, characteristics of resident fish, commercially important fish species, and discharge from dams and weirs (Bunt, 2001; Halleraker et al., 2023; Lindberg et al., 2016; Nyqvist et al., 2017; Wilkes et al., 2018). Approaching the process considering all perspectives is important (García-Vega et al., 2023; Huuki et al., 2022; Morita, 2022; Ovidio et al., 2017; Prunier et al., 2023).

This study has clarified that the conditions for migrating upstream differ depending on the season and not only changes in the physical environment of rivers but also on ecological changes accompanying the growth of fish. In the Shinano River, almost all fish species that inhabit the main island in Japan were confirmed, and 55 species of fish have been identified, including *O. keta*, *P. altivelis*, and *O. platypus* (Shinanogawa River Office, 2017). The combination of the three fishways in the MID also responded to seasonal environmental changes (Masumoto et al., 2022). Utilization of a combination of fishways with different water depths and current velocities provides a range of conditions for fish to utilize. To contribute to the movement upstream from the MID of various small freshwater fishes, such as *P. altivelis*, *T. hakonensis*, *O. platypus*, and *O. masou*, the combination of fishways with different water depths and current velocities is important.

5 | CONCLUSIONS

T. hakonensis (which run up for spawning) with nuptial coloration and large body lengths preferred the ice-harbor-type fishway with a high flow velocity. *T. hakonensis* without nuptial coloration and with small body lengths preferred the stair-type fishway with a slow flow velocity or the rock-ramp-type fishway when its flow velocity was lower than that of the stair-type fishway. *T. hakonensis* displaying high run-up speeds were mostly individuals with nuptial coloration. These findings allowed us to evaluate the mechanism used by *T. hakonensis* for selecting fishways with different flow velocities. The environmental conditions selected by *T. hakonensis* changed according to their growth stage, and the MID fishways responded to changes in the environmental conditions. By allowing all fishes to run up a fishway without stress, regardless of fish life history, biodiversity and water usage can be harmonized. Elucidation of the mechanisms that enable the use of fishways by fish, such as *T. hakonensis*, regardless of their life history was performed in this study. While the study yielded useful findings, they are limited by including only fish caught in early summer. This does not guarantee equivalent effectiveness for migrating fish in late summer or fall. Verification with findings from other seasons will help clarify this mechanism further. Furthermore, the results of this study demonstrate that changing the fishway flow rate improves the fishway preference of the fish. Therefore, we suggest combining fishways with different flow velocities for efficiency. This study also confirms the necessity of learning the ecology of fish and continuing to work on the adaptive management of fishways for a range of different fish.

ACKNOWLEDGMENTS

We would like to thank the Ministry of Land, Infrastructure, Transport and Tourism, Shinanogawa River Office for providing data on fish ecology and the Miyanaka Intake Dam Fishway Structure Improvement Review Committee for their advice on fish ecology. We would like to thank Editage (www.editage.com) for English language editing.

DATA AVAILABILITY STATEMENT

All data generated or analyzed during this study are included in the article.

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How to cite this article: Masumoto, T., Nakai, M., Asaeda, T., & Rahman, M. (2023). Preferential behavior of *Tribolodon hakonensis* for fishways according to biological characteristics. *River Research and Applications*, 1–17. https://doi.org/10.1002/rra.4148