



Master thesis
 MSc Marine Biology

Does fishway passage success depend on individual phenotype? A study in three-spined sticklebacks (*Gasterosteus aculeatus*)



@Alexander Francis Lydon

Author: Loéva Martin-Podevin
 Supervisor: Dr Marion Nicolaus
 Collaboration: Peter Paul Schollema & Jeroen Huisman



Abstract

High numbers of artificial barriers such as dams, pumping stations and sluices are constructed worldwide to help us with several social and economic purposes. However, these structures can also block the migration of fish and prevent them from completing their life cycles. To mitigate this, fishways have been implemented to allow the safe passage of migratory fish species and restore river connectivity. Studies have shown that the passage success of fishways can vary between fish species based on their morphology, physiology and behaviour (fish length, swimming behaviour). Individuals of the same species or population can also display different phenotypic traits (fish length, personality); hence passage success is likely to also differ between individuals. This study aimed to investigate whether fishways can induce a phenotypic bias in exploration behaviour, fish length and timing of migration using three-spined sticklebacks (*Gasterosteus aculeatus*). To research this, fish were caught at two sampling sites in the Netherlands (n=191) and tested for their exploratory behaviour using passive transponder tags (PIT). Then, sticklebacks of known behavioural phenotypes were released in front of a fishway equipped with antennas to track their movements. The data gathered over five weeks allowed us to estimate the probability of passage success and detection at the entrance of the fishway, the latency to cross and be detected, weekly survival, resighting probabilities, and estimated passage success. Results show a mean passage success of 12% for tested sticklebacks (range 0-23% for all tagged sticklebacks released at Hongerige Wolf) with on average 5.4 days to cross the fishway after their release. Although passage success and latency to cross the fishway were not associated with variation in exploration behaviour and fish length, passage success was partly phenotype dependent for individual timing of migration. Timing of migration was a strong predictor of passage success with late migrants being more successful and faster at using the fishway. This temporal effect was not explained by an increased survival but more likely by an increase in temperature-driven activity as reflected by an increased resighting probability. Additional research is required to understand why the passage success of the fishway was moderate. Perhaps, this is explained by the lower swimming abilities of smaller fish species, stress, hydraulic conditions or water temperatures. Increased activity levels of sticklebacks near the fishway might have increased their vulnerability to predation hotspots that can emerge there. Therefore, future research should investigate the activity patterns of predators and fish near the fishway and study whether anti-predation boldness can predict fishway passage success. Additionally, analysing whether the effect of the timing of migration is strictly due to increased water temperatures or genetics would help improve the conservation of migratory fish. Overall, fishways should help restore river connectivity and conserve migratory fish species however, the efficiency of passage success requires further research (for non-commercially important species) and hydraulic adjustments in many cases.

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Introduction

Artificial barriers such as dams, pumping stations and sluices are important for water management worldwide. They offer protection from flooding and can provide hydropower, drinking water, and agricultural infiltration (Helmer, W, 2020). Globally, the number of artificial barriers has been increasing exponentially in the last few years. In 2020, a study reported the existence of at least 1.2 million barriers in 36 European countries with a mean density of 0.74 barriers per kilometre, within those, 15% were considered obsolete (Lehner *et al.*, 2011; Belletti *et al.*, 2020). A third of the Netherlands is below sea level, therefore, many artificial barriers have been constructed to protect its inhabitants. Dams and pumping stations have been used as a tool to reclaim over 350 000 hectares of land for Dutch agriculture (Lintsen, 2002). High numbers of artificial barriers can severely impair river connectivity by fragmenting aquatic habitats (Pringle, Freeman and Freeman, 2000; Geist, 2011). For example, artificial barriers can block the migrations of both diadromous (migration from the sea to freshwater to spawn) and catadromous (migration from freshwater to the sea to spawn) fish. However, these migratory species need to access different environments to reproduce, produce juveniles or forage to complete their life cycle (Larinier, 2001). To mitigate barriers, some species can evolve residency, however, this can result in lower spawning biomass and considerably negatively affect the population (Morita, Morita and Yamamoto, 2009). Other consequences of habitat fragmentation can include population loss, alteration of food webs, loss of biodiversity and local extinctions. To illustrate this, a study on European eels (*Anguilla anguilla*) revealed that in the last decades, glass-eel arrivals were lower than 2% compared to the 1960s likely due to anthropogenic barriers (van den Thillart, 2014). In 2008, the number of barriers that prevented eel migration increased to 4,671 pumping stations, 8,488 dams and 2,278 sluices. This increase severely impacted eel abundance and survival and in turn lowered commercial fisheries stocks (Drouineau *et al.*, 2018). Although barriers can greatly help humans in many different ways, they can be a serious threat to migratory fish species. Therefore, mitigating the detrimental effects of habitat fragmentation is essential to allow these species to complete their life cycles and sustain healthy populations.

There are two options to help restore river connectivity. The first one is to remove the structure of the barrier completely. The *Dam Removal Europe* project aims to demolish dams that are not in use anymore to reconnect rivers around Europe. The project believes that all artificial barriers, will eventually no longer serve their economic functions, and may become safety concerns. In such cases, decision-makers can either repair or demolish the structure (Helmer, W, 2020). Unfortunately, the removal of barriers can be difficult depending on a country's politics, economy and social and cultural awareness (Habel *et al.*, 2020). The second solution is to implement a fishway, to allow a safe upstream or downstream passage for migratory fish species by going around the barrier. Fishways can be made of a sloping channel partitioned by weirs, baffles, or vanes with openings for fish to swim in and out of the passage. Specific flow conditions are required for fish to navigate through the passage and attract them to the entrance. There are several types of fishways including vertical slots, denils, weirs and culvert fishways (Katopodis and Eng, 1992).

However, fishway passage success differs between different fish species. A meta-analysis showed that the mean upstream fishway passage efficiency of non-salmonid species was around 21.1% compared to 61.7% for salmonids species (Noonan, Grant and Jackson, 2012). The higher success of salmonids is likely due to their strong swimming abilities and to the design of the fishway, which targets adults of commercially important species (Webb, 1975). Another study comparing the use of denil fishways, by White suckers (*Catostomus commersoni*) and Smallmouth bass (*Micropterus dolomieu*) found different passage success rates. White suckers had a passage efficiency of 55% compared to 36% for Smallmouth bass. These values are

considered too low for the conservation of these declining species (Bunt, Katopodis and Mckinley, 1999). Lake sturgeons (*Acipenser fulvescens*) also had a moderate passage success of 36.4% for a vertical slot fishway in Canada (Thiem *et al.*, 2011). Overall, several studies on different species highlight that passage success differs between species and fishway structures (denil, vertical slot) around the world.

The differences between species in passage success can be linked to differences in their morphology, behaviour and physiology such as fish length, exploration behaviour and shape (Cooke and Hinch, 2013). Similarly, individuals within the same species can also differ in those traits and therefore could also have different success rates when crossing the fishway (Jolles *et al.*, 2019). Personality traits, for instance, are typically phenotypically integrated with morphological and physiological traits and could influence passage success. Personality traits can be defined as *consistent individual behavioural differences over time and/or across situations*. The word *consistent* does not imply that these individual behavioural differences will not change with age or environmental conditions, but rather that these individual differences are largely maintained across time or contexts. Personality traits can affect important ecological processes such as niche expansion, dispersal or social organisation (Réale *et al.*, 2007). In the event of crossing a fishway, individuals with higher levels of exploration and boldness might have a higher success as crossing an artificial structure can be perceived as risky and require high levels of exploration and individuals differ in risk-taking and exploratory behaviour. In comparison, individuals that fail to cross may congregate below the fishway in large numbers, increasing their susceptibility to predation (Peake, McKinley and Scruton, 1997).

In the literature, few studies have investigated the link between passage success and phenotypic variation at the individual level. For example, a study tested whether personality and eel length could predict passage success in 60 juvenile American eels (*Anguilla rostrata*) (Mensing *et al.*, 2021). The study focused on eel ladder fishways as juvenile eels are great climbers. The authors assessed three personality traits: exploration, boldness, and activity for all the juveniles through three laboratory experiments. The results showed that more exploratory juvenile eels were more likely to use the experimental ladder and that larger eels climbed faster through the fishway. Similarly, a study using 78 Brown trout (*Salmo trutta*) investigated whether individual personality differences (boldness, activity and exploration) could lead to differences in passage success (Lothian and Lucas, 2021). The results suggested that bolder individuals carried out fewer attempts and had an increased probability of passage success. Overall, both studies suggest that fishways could select for bolder, more exploratory, and larger individuals which can lead to serious ecological, evolutionary and conservation consequences for the species concerned. However, another study tested the effect of boldness on passage success in 276 Rainbow smelts (*Osmerus mordax*) found that 41.7% of fish entering the fishway passed successfully independently of their boldness scores (Landsman *et al.*, 2017). The author argues that high water temperatures and low river discharge were consistent predictors of successful passage and greater distances moved through the fishway. All of these studies provide mixed evidence regarding the existence of personality-related bias in the use of fishway and emphasise the need for further research on this topic.

Artificially selecting a non-random subset of individuals can have large consequences at the population, species and/or ecosystem level. A few direct consequences include loss of genetic diversity with, for example, more exploratory fish gaining an evolutionary advantage on other behavioural types if a higher fishway passage success gives them access to better/more habitats. Furthermore, a reduced genetic diversity can reduce a population's ability to persist in a changing environment and overall, decrease its resilience (Hughes *et al.*, 2008). Similarly, fitness consequences can include suboptimal resource acquisition, excessive energy expenditure to find and cross the passage, and higher exposure to predators at the entrance of the fishway (Merrick and Koprowski, 2017). Individuals that won't be able to cross the fishway might be left in an

unsuitable habitat with less food and mates, therefore decreasing their reproductive success. Similarly, if more exploratory individuals have higher passage success, they might outcompete other species and thus disrupt ecosystem functioning. Overall, migratory fish species that cannot successfully use fishways and complete their life cycles might face population decline. At the ecosystem level, other species rely on the migration of fish for food, for instance, the European eel in the Dutch commercial fishery (Kemper, 1995; van den Thillart, 2014).

The Three-spined stickleback (*Gasterosteus aculeatus*) is a good model species to study whether passage success at a fishway depends on individual phenotype. To start with, its variation in morphological and behavioural phenotypes has been widely studied since the 1930s. Sticklebacks have been shown to display a wide range of phenotypic variation in morphology, diet choice, shoaling, physiology, behavioural syndromes, and sexual signalling (Huntingford and Ruiz-Gomez, 2009). The variation in skeletal armour is a good example of phenotypic variation in the Three-spined stickleback. Marine sticklebacks are covered in a bony armour with three dorsal spines, two pelvic spines, and a continuous row of bony lateral plates. However, several freshwater populations have evolved a complete or partial loss of the pelvic skeleton with smaller dorsal spines and no pelvic structures (Peichel, 2005). Similarly, these changes can occur at a relatively fast pace. For instance, 50 years of isolation due to an artificial barrier was enough for individuals of a population of resident sticklebacks (landlocked) to become more active, aggressive, exploratory, and bolder compared to individuals from a migratory population (Ramesh *et al.*, 2021). This study will investigate individual phenotype from a population of migrant sticklebacks and their potential phenotype-dependent use of a fishway. The recent construction of this fishway (2020) enabled to reconnect a polder that was isolated for approximately 50 years.

Understanding the influence of phenotypic traits on passage success in migratory fish species is important for ecological, evolutionary and conservation purposes. Overall, this research will investigate whether fishway passage success depends on phenotypic traits such as exploration, fish length, and timing of migration. To answer this question, I will use three-spined sticklebacks (*Gasterosteus aculeatus*) and analyse the three following sub-questions: (a) What is the variation in fish length, exploration behaviour and timing of migration within the sampled population of stickleback migrants? (b) can successful fishway passage in the wild be predicted by phenotypic attributes (fish length, exploration behaviour and timing of migration)? (c) whether temporal variation in survival and resighting probabilities can explain temporal use of the fishway? I hypothesise that more exploratory, larger individuals and individuals that migrate later in the season will have a higher probability of passage success and a lower latency to cross the fishway as crossing the fishway will require high levels of exploration, strong swimming abilities that are found in larger fish and higher swimming velocities for later migrants to complete their spawning migrations in optimal conditions.

Methods

Study sites and field collection

Wild sticklebacks were caught at two sampling sites near the Eems-Dollard estuary in the province of Groningen in the Netherlands (Fig. 1). The first location was a sea lock (Nieuwe Statenzijl) equipped with a pumping station and a shipping lane where fish were caught using three cross nets in saltwater. The second location was a 50-year-old freshwater pumping station at Hongerige Wolf, it was approximately 5km from the first location where fish were sampled with two fyke nets. The fishway was also located at Hongerige Wolf (Fig. 1). The fishway was

constructed two years ago in 2020 and was officially opened in 2021. Wild sticklebacks were sampled at these two locations once a week for 5 weeks from the 3rd of March 2022 until the 31st of March 2022 during their spawning migration.

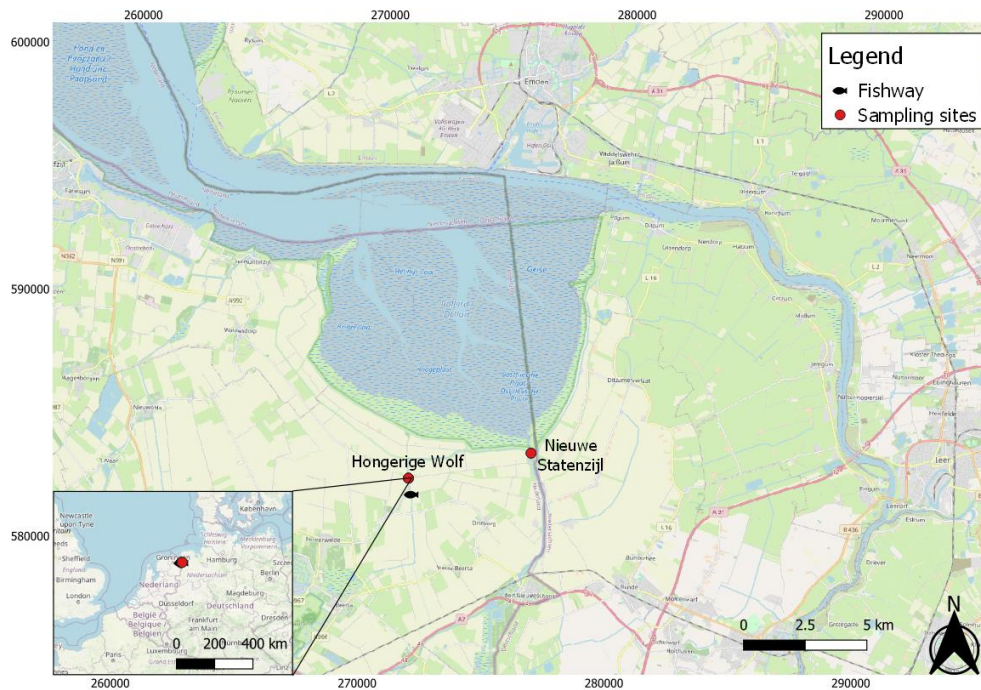


Figure 1. Sampling sites: Nieuwe Statenzijl and Hongerige Wolf near the Eems-Dollard estuary in the province of Groningen in the Netherlands. The fishway (black fish symbol) is located near the pumping station at Hongerige Wolf.

Individual identification

To identify individuals and study phenotype-dependent fishway use, a capture-mark recapture experiment was performed. Sticklebacks were caught (total: $n=1502$) at Nieuwe Statenzijl and Hongerige Wolf. Then, they were equipped with a passive transponder tag (PIT), measured and weighed ($n=888$). A subset was tested for their exploratory behaviour at the University of Groningen ($n=191$). All fish were released either immediately or 24/48 hours later near the fishway at Hongerige Wolf. The PIT tags allowed individual recognition and automated tracking of individual movements in the experimental set-up and in the fishway. Only individuals measuring above 5.5 cm from the beginning of their snout to the beginning of their caudal fin were selected for PIT-tagging. After this, a licensed member of the water management team equipped each individual with a passive transponder tag on the ventral side of the fish. During the procedure, a diluted anaesthetic was administered to minimise their pain and discomfort during the PIT-tag insertion which lasted approximately 10s.

Exploration test in the mesocosm

Upon arrival at the University, fish were fed blood worms and housed in semi-natural ponds or large buckets in groups of 20 individuals where they could acclimatise to their novel conditions. The first group had approximately 12 hours to acclimatise whereas the second group had approximately 24 hours to acclimatise. Water temperature in the ponds was recorded. Overall, 191 wild sticklebacks were tested in a mesocosm system at the University of Groningen. The

experimental mesocosm set-up consisted of 5 ponds connected (Fig. 2). The ponds were supplied with freshwater from a nearby waterway similar to what fish experienced inland. Exploration tests were conducted in batches of 20 individuals following the protocol developed by Ramesh *et al.*, 2021. Only one exploration test was run for each individual as pond crosses in this mesocosm system are highly repeatable; $R= 0.81$, a very high value as most repeatability factors in animal behaviour studies are approximately equal to $R= 0.37$ (Bell, Hankison and Laskowski, 2009). During acclimatisation, sticklebacks were placed in the first pond closed with a grid to prevent individuals from exploring the other ponds (Fig. 2). The next morning, the grid was removed before the start of the experiment and the fish were given 4 hours to explore their novel environment. Then, the data was saved automatically in the PIT-tag readers connected to each RFID antenna (Radio Frequency Identification) placed between the entrance and exit of the experimental set-up (Fig. 2). After the test, ponds were emptied to very low water levels to facilitate catching the fish and placing them back in a separate bucket before release into the wild. Another set of 20 individuals was subsequently tested if two groups of fish were caught that week. At the end of each exploration test, raw data was extracted with the PuTTY software from the PIT-tag readers. Then, the data was imported in RStudio 4.1.3 and the number of pond crosses, the number of unique ponds visited and the latency to reach the last pond (pond number 5) were calculated to measure exploration (Conrad *et al.*, 2011). Overall, the fish tested in the mesocosm were a representative sample of the population for their length and weight (Fig. 3). Hence, further statistical analysis was carried out.

In a few cases, the antennas failed to detect fish movements, for example, a few individuals were detected at the last antenna (pond number 5) but not at the second one (pond number 2). This can happen when there are too many fish moving together or standing still. Therefore, when missing, the latency to reach the last pond was estimated based on the minimum latency to reach the last pond (~ 2.717 min) of other individuals. Then, pond crosses and the unique number of ponds visited were adjusted to 4 and 5 respectively for individuals that were detected at the last pond. Additionally, a few individuals did not leave the first pond throughout the exploration test, therefore their latency to cross was set to 240min (4 hours).

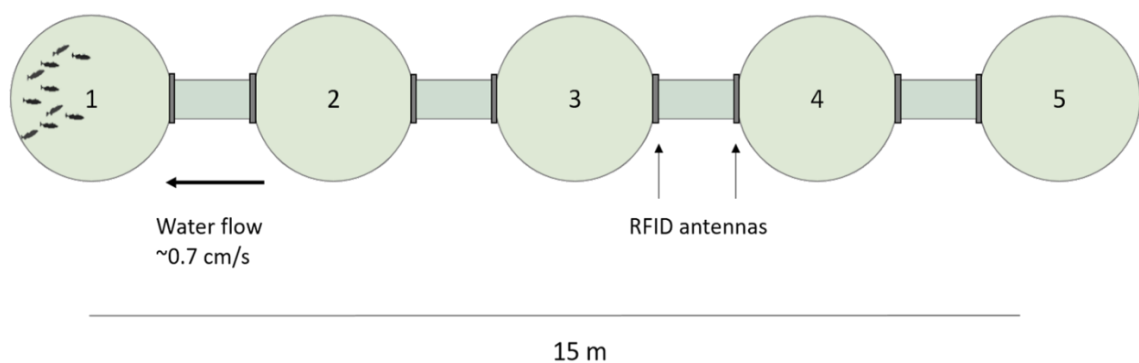


Figure 2. The mesocosm system for exploration tests. Five ponds were connected with 8 RFID antennas with a constant water flow of 0.7cm/s pumped for the waterway nearby.

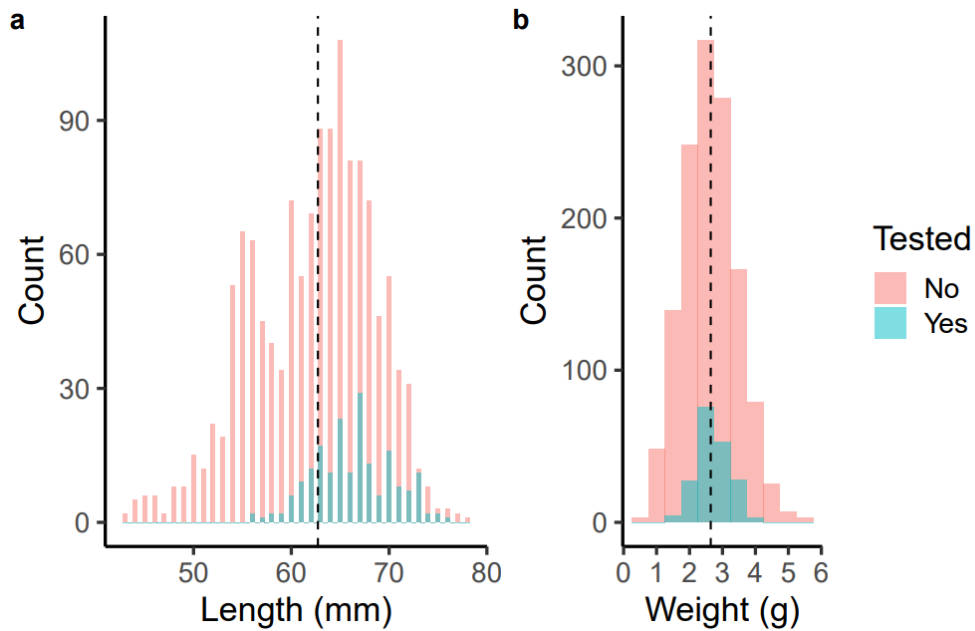


Figure 3. Length (mm) (a) and weight (g) (b) of all tagged sticklebacks ($n=888$) and tested individuals ($n=191$). Means are indicated by the black dashed line.

Passage success

Once the fish were tested in the mesocosm system, they were released at Hongerige Wolf in front of the fishway. In total, 191 tested sticklebacks were released at Hongerige Wolf with an additional 147 tagged sticklebacks (Table 1). Antennas at the entrance (number 4) and exit of the fishway (number 3) tracked the passage success of fish (Fig. 4). Fishway detections enabled to estimate the probability to cross the fishway, the probability to be detected at the entrance of the fishway, the latency to cross after release in the wild and the latency to be detected at the entrance of the fishway after release in the wild (see Appendix, Fig. S1). The probability and the latency to cross and being detected at the entrance of the fishway were calculated from the first detections at the entrance or exit of the fishway.

Table 1. Number of sticklebacks tagged and tested ($n=191$) and tagged and non-tested ($n=147$) released near the fishway at Hongerige Wolf. A few individuals died or lost their tags through the experiment hence the number of tested stickleback can be lower than 20 or 40 individuals. In total 338 individuals have been released at Hongerige Wolf during this year's migration season.

Release date	Number of tested individuals released ($n=191$)	The number of non-tested individuals released ($n=147$)
24/02/2022	0	26
05/03/2022	40	0
11/03/2022	20	0
19/03/2022	34	0
26/03/2022	37	21
31/03/2022	40	0
01/04/2022	20	100

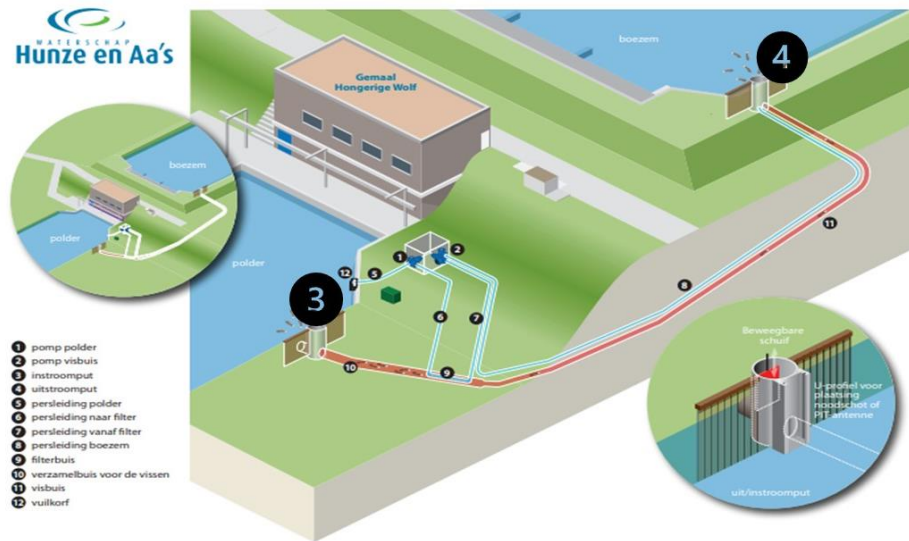


Figure 4. Fishway at Hongerige Wolf with antennas at the entrance (number 4) and exit (number 3) to track the movements and survival of the tagged stickleback.

Survival and resighting in the wild

The mark-recapture data allowed to estimate the weekly survival and resighting probabilities of tagged sticklebacks over 8 weeks. Survival probability (ϕ) was the probability that a fish caught at time x was alive at $x+1$ and resighting probability (p) was the probability that a fish caught at time x was alive and seen at $x+1$ (Sánchez *et al.*, 2017). It was important to differentiate between survival and resighting as resighting probability can be used to observe the level of activity of individuals near the entrance of fishway specifically. Furthermore, weekly survival estimates were used to calculate estimated population size and estimated weekly passage success. If sticklebacks have a high resighting probability near the entrance of the fishway and are not crossing the fishway, this might indicate that passage success is not easily accessible. Perhaps, passage success might vary with time depending on the biotic (predators) and abiotic (water temperature) conditions of each week.

Statistical analyses

All statistical analyses were run in RStudio 4.1.3 except for the survival analysis that was performed in the MARK program (White and Burnham, 1999). The main packages used in RStudio were namely: 'tidyverse' (Wickham and et al, 2019), 'lme4' (Bates *et al.*, 2014) and 'ggpubr' (Kassambra and Mundt, 2020).

First, the aim was to select the best proxy for individual exploration as multiple parameters were measured in the ponds (number of pond crosses, number of unique ponds visited and the latency to reach the last pond). A pairwise Spearman correlation matrix was used between the *number of pond crosses*, the *number of unique ponds visited* and the *latency to reach the last pond* (Table 2). This allowed to study the structure of exploration phenotypes. The results revealed that pond crosses, the number of unique ponds visited and the latency to reach the last pond were all strongly correlated ($-0.81 < R < 0.92$) (Table 2). *Pond crosses* and the *number of unique ponds visited* showed the strongest positive correlation with a coefficient of $R = 0.92$.

Consequently, *pond crosses* were selected to be used in further statistical analysis as a proxy for the exploration behaviour of the tested sticklebacks in the ponds. These results were checked by performing a Principal component analysis (PCA) that confirmed these traits were strongly correlated (See Appendix Fig. S2 and Table S1). Second, three generalized linear mixed models (GLMM) with a Poisson distribution were run to identify sources of variation in exploration (number of pond crosses). In these models, *water temperature* (measured in Celsius degrees at the beginning of each exploration test), *fishing method* (fyke vs. cross net, cross nets being used as a reference category), *length* (mm), *weight* (g), *acclimatisation time* (between the release in the mesocosm and the start of the exploration test) were fitted as fixed effects and 'test ID' (1-10; the 191 fish were tested in a total of 10 different batches) as a random factor with an observational level to control for overdispersion. To prevent collinearity, *fishing method* was fitted in the model without *fishing location* and *weight* without *length* as these variables were correlated. Model estimates (β) are provided with their 95% confidence interval. An effect was considered significant when the confidence intervals did not overlap with zero. None of the variables mentioned above explained significant variation in the exploration behaviour of sticklebacks in the ponds (Table 3). Therefore, we used *pond crosses* in further analyses without having to correct for these variables.

Table 2. Spearman correlation coefficient (R) and p-value of three behavioural variables from the pond system (n=191).

Variables (n=191)	Spearman correlation (R)	P-value
Pond crosses / Unique ponds	0.92	P< 0.001
Unique ponds / Latency antenna 8	-0.91	**
Latency antenna 8 / Pond crosses	-0.81	**

Note: ** indicates that the p-value is equal to 2.2e16

Table 3. Summary of the generalized linear mixed models (n=191) with confidence intervals (CI) and estimates of fixed effects (β).

Fixed effects	β	(95% CI)
Intercept	-5.96	(-12.66, 0.45)
Water temperature (°C)	0.20	(-0.22, 0.60)
Acclimatisation time (hours)	0.15	(-0.04, 0.34)
Length (mm)	0.03	(-0.04, 0.10)
Intercept	-0.85	NE
Weight (g)	0.33	NE
Intercept	-0.11	
Fishing method	0.35	NE

Notes: "NE" mean the confidence intervals were not estimable

To investigate whether successful passage could be predicted by the exploration, fish length and the timing of migration of individuals, the probability of crossing the fishway and the probability of being detected at the entrance of the fishway were analysed in generalized linear models (GLM) with a binomial distribution. Additionally, variation in the latency to cross or being detected at the entrance of the fishway was analysed with a GLM with a Gaussian distribution. The latencies were both log transformed to normalise the data and timing was converted in

February release date for a continuous format. Then, a survival analysis was run to study the temporal variation in the survival and resighting probabilities and estimate the population size of individuals alive and active near the entrance of the fishway and estimate weekly passage success. Survival rates were estimated using Cormack–Jolly–Seber (CJS) models (Lebreton *et al.*, 1992). CJS models using a logit-link function were run in the software MARK (White and Burnham, 1999). Akaike values (AICc) were used for ranking the fit of models to data. Models with a $\Delta\text{AICc} < 2$ were considered to fit the data equally well, and those for which the difference was >2 were considered to fit to the data less well. We ran all possible models with various patterns in ϕ and p [constant or affected by time (t)]. Survival rates and resighting rates were back transformed using the following formula $\exp(x)/(1+\exp(x))$. Furthermore, individuals that successfully crossed the fishway were removed from the analysis to not inflate the survival rates, however, it was assumed that the results were applicable to the entire sample size. Estimated weekly population size was calculated using the survival rates and the number of tagged individuals released every week. Passage success was estimated by dividing the number of individuals that crossed in a week by the estimated population size of the week. Spearman correlations were run to assess the relationship between estimated passage success and the survival and resighting probabilities.

Results

The goal of this study is to investigate whether fishways can induce a phenotypic bias, more specifically in exploration behaviour, fish length and timing of migration using the Three-spined stickleback as a model species. To answer this research question, the exploration behaviour of sampled sticklebacks was quantified in a mesocosm. The length of individuals of known exploration phenotype was measured and the timing of migration was estimated using fishing date over the sampling period (over 8 weeks).

Phenotypic variation in the ponds

Descriptive statistics were calculated based on the three variables measured during the exploration test in the mesocosm (*pond crosses, the number of unique ponds visited and the latency to reach the last pond*). On average, tested sticklebacks performed approximately 3.9 pond crosses, explored 2.9 ponds out of 5, and had a latency of 170.6 minutes to reach the last pond. Furthermore, sticklebacks tested in the mesocosm had on average a length of 66.3mm. Sticklebacks tested in the mesocosm showed inter-individual differences in their level of exploration. The measured *pond crosses, the unique number of ponds visited* and the *latency to reach the last pond* varied between individuals (Fig. 5). However, this variation can be classified as binary, for example, *the unique numbers of ponds visited* showed that most individuals either stayed in the first pond and did not explore at all or crossed all the ponds (Fig. 5).

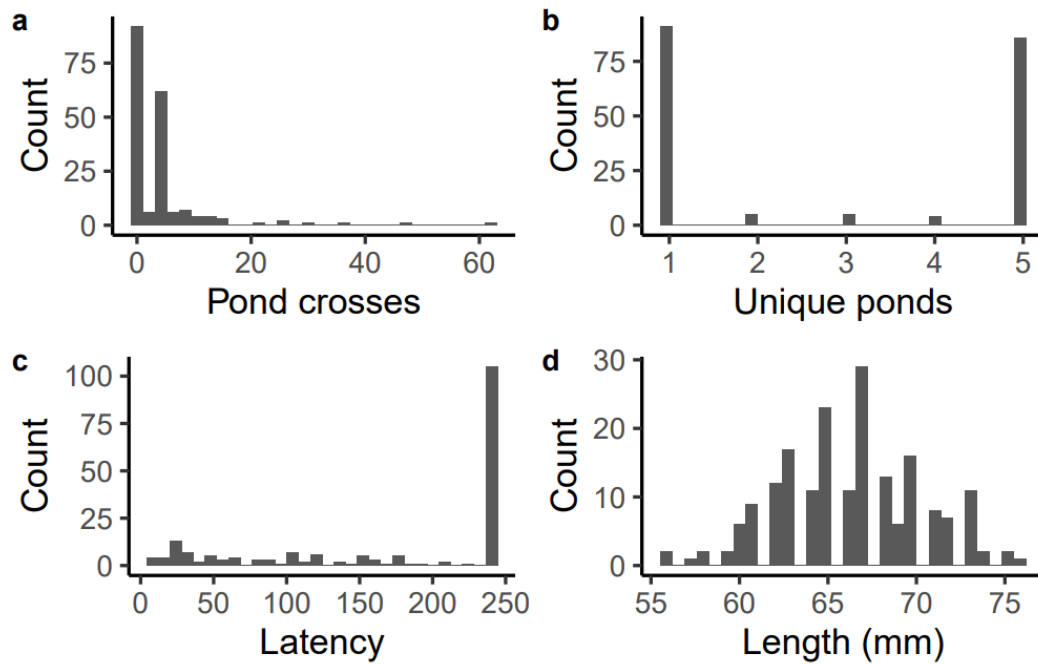


Figure 5. Frequency distributions of (a) pond crosses, (b) the unique number of ponds visited, (c) the latency to reach the last pond (minutes) and (d) length (mm) of tested sticklebacks (n=191).

Probability to cross and be detected

A total of 24 sticklebacks crossed successfully the fishway out of 191 tested individuals, representing approximately 12%. Similarly, a total of 43 sticklebacks crossed successfully the fishway out of 338 tagged individuals released at Hongerige Wolf, also representing 12%. For tested individuals (n=191), the result indicated passage success did not significantly covary with individual variation in exploration or fish length. Nonetheless, the probability to cross the fishway increased significantly with individual timing expressed in *February release date* (Fig. 6). Subsequently, individuals that arrived later in the spawning season, had a higher probability to cross the fishway compared to individuals that arrived earlier. However, when running the same models for all tagged individuals (n=888), the probability to cross the fishway successfully was not affected by timing. Similarly, the probability to cross the fishway did not increase with individual length (Table 4).

A total of 195 fish were detected at least once at the entrance of the fishway out of 888 individuals. For tested individuals (n=191), the results indicated that detection did not covary with exploration or fish length. Nonetheless, the probability to be detected at the fishway entrance covaried with timing expressed in *February release date* (Fig. 6). Individuals that arrived later in the spawning migration season, had a higher probability of detection at the entrance of the fishway compared to individuals that arrived earlier. Similarly, the probability to cross the fishway did not covary with length (Table 4). Furthermore, when running the same models for all individuals tagged (n=888), the probability of detection significantly decreased with the timing of migration (Table 4, Fig. 6). To summarise, passage success and probability of detection for both tested and non-tested sticklebacks were not influenced by length or exploration. The only variable that appeared to covary with passage success and detection was the timing of migration (*February release date*).

Table 4. Summary of the GLMs for the probability to cross the fishway and being detected at the entrance at least once with confidence intervals (CI) and estimates of fixed effects (β). Significant effects are denoted in bold.

	Probability to cross				Probability to be detected			
	Tested individuals (n=191)		Tagged individuals (n=888)		Tested individuals (n=191)		Tagged individuals (n=888)	
Fixed effects	β	(95% CI)	β	(95% CI)	β	(95% CI)	β	(95% CI)
Intercept	-2.00	(-9.83, 5.75)	-0.44	(-6.07, 5.12)	-0.89	(-6.11, 4.27)	1.49	(-1.37, 4.38)
Pond crosses	0.01	(-0.04, 0.06)	NA	NA	0.02	(-0.02, 0.07)	NA	NA
Length	-0.04	(-0.15, 0.07)	-0.04	(-0.12, 0.04)	-0.004	(-0.08, 0.07)	-0.008	(-0.05, 0.03)
Release date	0.05	(0.003, 0.10)	- 0.0006	(-0.03, 0.04)	0.03	(0.001, 0.06)	-0.04	(-0.06, -0.03)

Notes: the degrees of freedom for tested individuals: df=190 and tagged individuals: df=887.

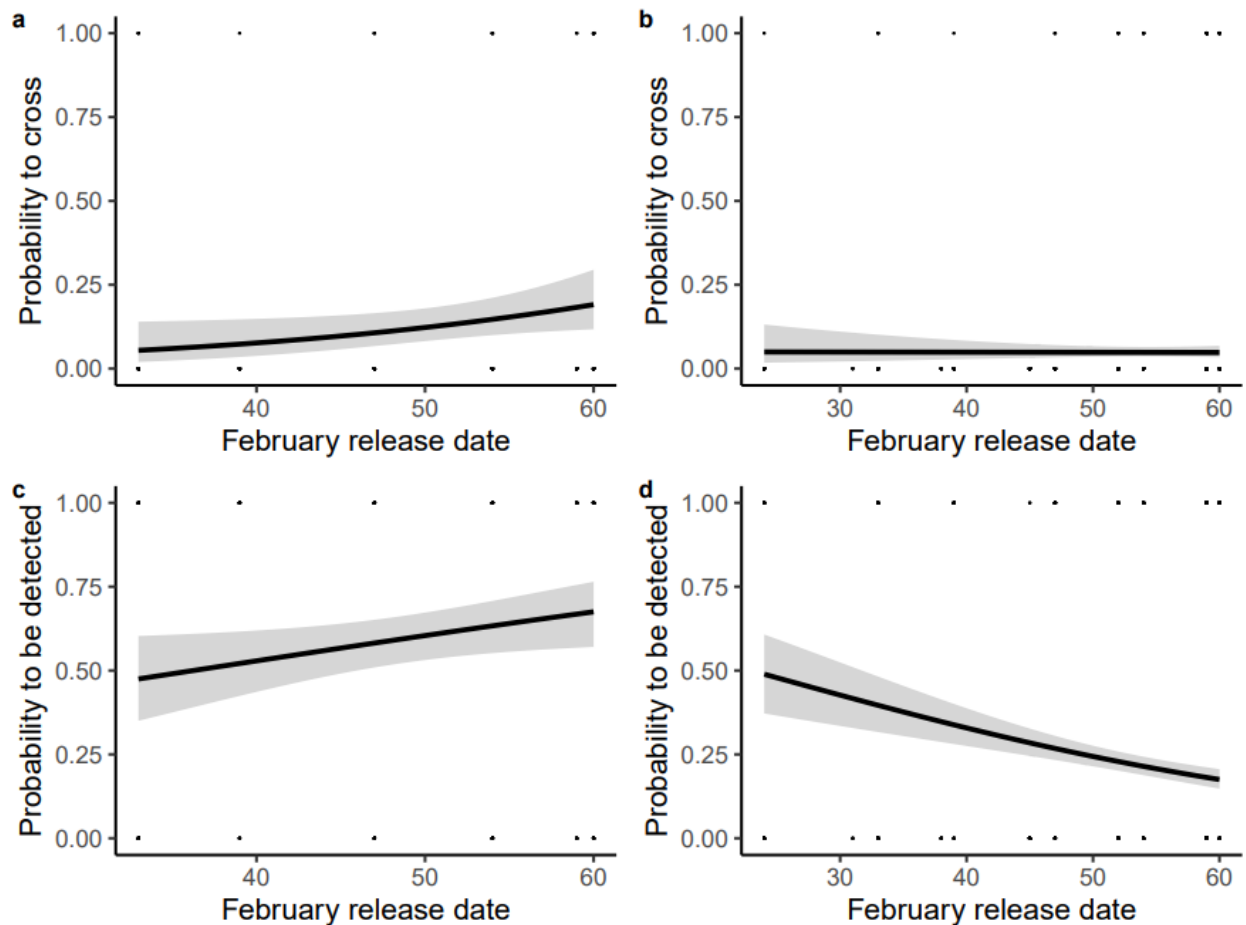


Figure 6. The probability of passage success and detection at the entrance of the fishway with the timing of migration expressed in February release date (95% CI; gray shading) for tested individuals (a,c; n=191) and tagged individuals (b,d; n=888).

Latency to cross and be detected

Individuals that crossed the fishway successfully (n=43), required an average of 5.4 days after their release in front of the fishway to cross successfully. Once finding the entrance of the fishway individuals required less than a day, approximately 0.4 days, the equivalent of 7 hours and 12 minutes to exit the fishway. For tested individuals (n=191), the latency to cross the fishway was not significantly associated with exploration and length. However, the latency to cross the fishway appeared to lower with later timing of migration. Later individuals in the season were faster to cross the fishway compared to earlier individuals (Table 5, Fig. 7). Additionally, for all individuals that were tagged (n=888), the latency to cross the fishway was not affected by fish length or exploration. Nevertheless, the timing of migration covaried with the latency to cross with later individuals crossing faster the fishway (Table 5). Individuals required approximately 4 days to find the entrance of the fishway after their release at Hongerige Wolf. For tested individuals (n=191), the latency to be detected at the entrance of the fishway was not affected by exploration or fish length (Table 5). However, it appeared that the timing of migration covaried with the latency to be detected with later individuals finding the entrance of the fishway faster compared to earlier individuals (Table 5). Additionally, for all individuals that were tagged (n=888), the latency of the first detection was not linked to variation in fish length or timing of migration. Moreover, the latency to cross the fishway and the latency to be detected at the entrance of the fishway for both tested and non-tested sticklebacks was not influenced by exploration or fish length. The only variable that appeared to covary with these latencies was timing of migration ('February release date').

Table 5. Summary of Gaussian linear model with log transformation for the latency to cross the fishway and being detected at the entrance at least once with confidence intervals (CI) and estimates of fixed effects (β). Significant effects are denoted in bold.

	Latency to cross				Latency to be detected			
	Tested individuals (n=191)		Tagged individuals (n=888)		Tested individuals (n=191)		Tagged individuals (n=888)	
Fixed effects	β	(95% CI)	β	(95% CI)	β	(95% CI)	β	(95% CI)
Intercept	5.98	(1.17, 10.80)	3.24	(-0.07, 6.55)	0.97	(-2.07, 4.02)	-0.28	(-2.62, 2.05)
Pond crosses	-0.01	(-0.05, 0.03)	NA	NA	-0.007	(-0.03, 0.02)	NA	NA
Length	-0.008	(-0.07, 0.06)	0.01	(-0.03, 0.06)	0.02	(-0.03, 0.06)	0.03	(-0.008, 0.06)
Release date	-0.07	(-0.11, -0.04)	-0.05	(-0.08, -0.03)	-0.02	(-0.04, -0.004)	-0.008	(-0.02, 0.005)

Notes: the degrees of freedom; for tested individuals' latency to cross (df=23) and latency to be detected (df= 112). For tagged individuals latency to cross (df=42) and latency to be detected (df=194).

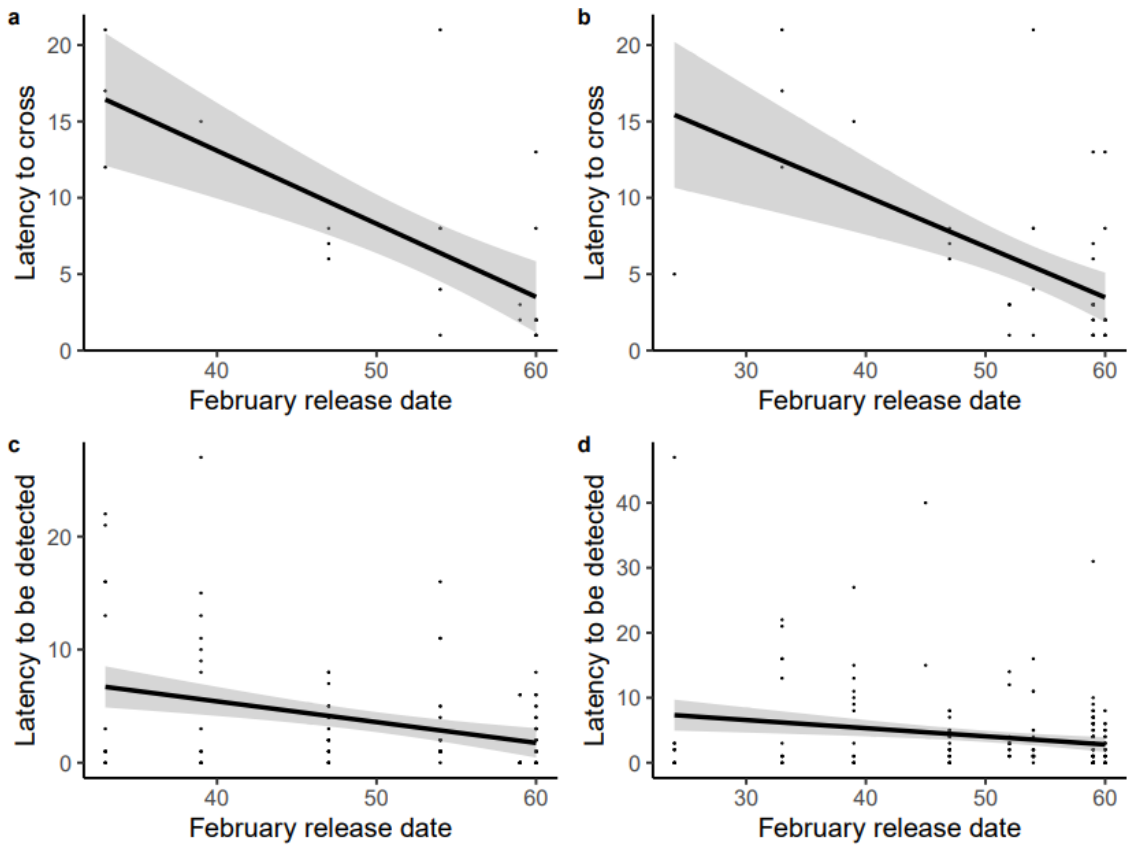


Figure 7. The latency of passage success and detection at the entrance of the fishway with timing of migration expressed in February release date (95% CI; gray shading) for tested individuals (a, c; n=191) and tagged individuals (b, d; n=888).

Survival analysis

The survival analysis revealed that the model with a survival probability (φ) and a re-sighting probability (p) dependent on time fitted best the dataset according to the Akaike Information Criterion (AIC= 760.4) (see Appendix, Table S2). It appeared that the survival rate peaked around the 4th week ($\beta = 0.7$) and then decreased until reaching the 8th week ($\beta = 0.2$) (Fig. 8). Similarly, resighting probability peaked until reaching the value of 1 and then stabilised. Overall, both parameters visually display temporal variation throughout the weeks. Interestingly, after the 6th week, the resighting probability increased whereas survival decreased. The estimated passage success rates also fluctuated weekly, ranging from 0% to 23.24% (Table 6). Overall, the increase in passage success with the timing of migration cannot be explained by an increase in survival probability later in the migration season.

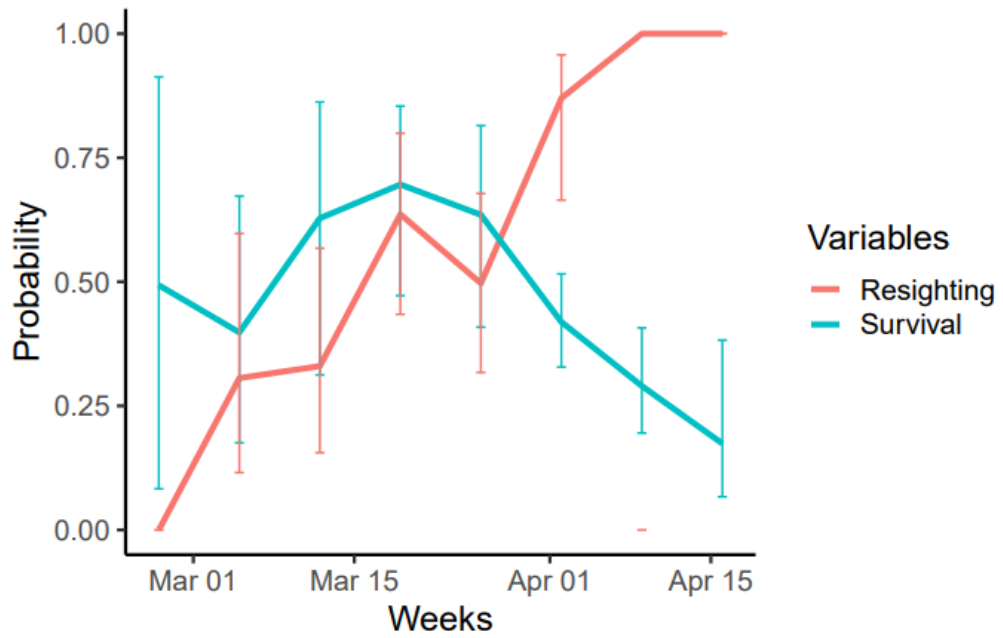


Figure 8. Weekly survival (a) and resighting probabilities (b) of tagged sticklebacks released at Hongerige Wolf (n=338) with 95% confidence intervals.

Table 6. Weekly survival (Φ) and resighting probabilities (P) logit back transformed, including 95% confidence intervals (CI), the number of individuals released, the number of individuals that crossed and estimated population size and passage success.

Week number	β (Φ)	95% CI	β (P)	95% CI	Number of individuals released	Number of individuals that crossed	Estimated population size	Estimated passage success %
1	0.49 3	(-2.40, 2.35)	0	(0, NA)	26	0	26	0.00
2	0.39 8	(-1.55, 0.72)	0.306	(0.115, 0.597)	40	1	52.83	1.89
3	0.62 8	(-0.79, 1.84)	0.330	(0.156, 0.568)	20	0	41.03	0.00
4	0.69 6	(-0.11, 1.77)	0.636	(0.435, 0.799)	34	1	59.76	1.67
5	0.63 5	(-0.37, 1.48)	0.497	(0.317, 0.678)	58	11	99.59	11.05
6	0.41 9	(-0.72, 0.06)	0.870	(0.665, 0.957)	40	24	103.29	23.24
7	0.29 0	(-1.42, -0.38)	1	(0,NA)	120	3	163.30	1.84
8	0.17 4	(-2.64, -0.48)	1	(1,1)	0	3	47.33	6.34

Discussion

This study aimed at investigating whether fishways can induce a phenotypic bias in exploration behaviour, fish length and timing of migration in three-spined sticklebacks. Study results show that fishway passage success was partly phenotype-dependent in terms of the timing of migration with later migrants having a higher probability to cross and a lower latency to swim through the fishway. However, passage success did not covary with the other two phenotypic traits studied: exploration and fish length. More exploratory and larger individuals did not have a higher probability of cross and a lower latency.

Low passage success

This study found a mean passage success of 12% (range 0%-23%) for three-spined sticklebacks. Although these values are low compared to findings on salmonid species, they are comparable to passage success rates of several non-salmonids species. In order to mitigate habitat fragmentation induced by artificial barriers, passage efficiency should allow 90% of migratory fish to cross the fishway successfully and rapidly (Noonan, Grant and Jackson, 2012). In this study, potential factors that could explain this low passage success rate include swimming abilities of small fish, poor hydraulic conditions of the fishway, stress of fish and water temperatures.

Although passage success was not higher for larger individuals, sticklebacks are overall a small species of fish; maximum length of 7.8cm in this study. Large size fish species are often associated with higher swim speeds and greater endurance (Videler and Wardle, 1991; Maynard, Kinnison and Zydlewski, 2017). A study on Alewives (*Alosa pseudoharengus*) and their movements through three different fishways revealed that fishways were size-selective with larger fish being able to pass the structures more easily than smaller fish (Andrews, 2014). Therefore, although no size bias in passage success was found, small size fish species might spend more energy swimming through the fishway depending on the hydraulic conditions of the fishway. Fishway design should include fish swimming capabilities to maximize passage efficiency (Oldani *et al.*, 2007). Several hydraulic conditions can prevent fish from crossing a fishway such as the entrance location and the attraction flow. In this study, sticklebacks spent approximately five days near the entrance of the fishway before deciding to cross. This may reveal either that the entrance of the fishway is inefficient or that the fish are reluctant to enter the fishway (Laine, Kamula, and Hooli, 1998). Hydraulic conditions near the fishway are key to allow safe upstream or downstream passage. A study found that when discharge regimes of a fishway were high, it was difficult for the fish to locate the entrance to the fishway and thus, delaying or preventing ascent. However, when discharge was low, it was difficult for fish larger to approach the entrance whereas when discharge was very low, the ascent was difficult for all size of fish (Jensen and Aass, 1995; Thorstad *et al.*, 2008; Landsman *et al.*, 2017). Another possible explanation for low passage success might be linked to stress. Possibly, the stress experienced during the handling procedure (PIT tagging, travelling to the University) might have prevented sticklebacks from successfully crossing the fishway. A study on Sockeye salmon (*Oncorhynchus nerka*) at a vertical slot fishway in British Columbia, found lower concentrations of Na⁺ ions observed in individuals that did not cross the fishway, maybe due to experienced stress and/or energy loss due to trying to cross the fishway (Pon *et al.*, 2009). However, individuals that did not travel to the University for exploration testing also showed a mean passage success of approximately 12%, therefore the PIT tagging, and fishing would be the potential sources of stress. Finally, water temperature is very important for successful fish passage. In a fishway in eastern Norway, the ascent of Brown trout (*Salmo trutta*) spawners was concentrated at temperatures of 12–14°C, although movement occurred at 6°C, which is

considered to be the minimum level for fish passage in Norway. Additionally, Landsman et al., 2021 found that higher water temperatures predicted successful passage and greater distances moved through the fishway for Rainbow smelt (*Osmerus mordax*). To summarise, low passage success might be explained by poor hydraulic conditions, lower swimming abilities of smaller fish species, stress or water temperatures.

Passage success is partly phenotype dependent

In this study, passage success was partly phenotype-dependent regarding the timing of migration but not for the exploration behaviour and the fish length of sticklebacks. The absence of bias in the exploration behaviour and in fish length for passage success and latency to cross corroborated with Landsman *et al.*, 2017 findings on Rainbow smelts (*Osmerus mordax*). Therefore, several individual phenotypes with different levels of exploration and fish length successfully crossed the fishway to continue their spawning migration. However, it is important to note that sticklebacks that were tagged had to have a length of 5.5cm, perhaps this selection did not capture all the variation in length and exploration behaviour as only tagged individuals were tested for their exploration behaviour and analysed with passage success. Nonetheless, PIT tags were the best option for this study to track sticklebacks in the wild. There was a phenotypic bias in the timing of migration for passage success with later migrants having a higher probability to cross compared to individuals that migrated earlier. This increase in the probability to cross, later in the season is not due to an increase in the survival probability, in fact, the results from the survival analysis show that the survival probability decreased later in the season.

Timing of migration and temperature driven activity levels

Changes in water temperatures can greatly influence poikilothermic fish in various ways, for example: increase their metabolic rates and thus, their energy balance and behaviour (locomotor and feeding behaviour) (Volkoff and Rønnestad, 2020). Studies have shown that fish are capable of detecting changes as low as 0.03°C (Beitinger and Fitzpatrick, 1979). During the migration season of this study, water temperatures varied from 5.14°C to 13.47°C and overall increased throughout the migration season (Fig. 9). A possible response to higher water temperatures is increased activity levels as metabolic rates increase, fish require to increase their food intake (Bartolini, Butail and Porfiri, 2015). Similarly, another response of fish to increased water temperature is the accelerated pace of migration (Jonsson, Jonsson and Hansen, 1991; Forsatkar *et al.*, 2016). Resighting probability is a good indication of the activity of individuals, as the survival analysis results showed, the resighting probability increased throughout the season similarly to water temperatures. The Spearman correlation test, results revealed that resighting probability and water temperature were strongly positively correlated ($R= 0.87$, $p= 0.0045$, Fig. 10). Increased water temperatures covary with increased resighting probability. Therefore, the link between the timing of migration and passage success found in this study could be explained by later migrants being more active and having a higher chance of crossing the fishway and crossing faster as a response to changes in metabolic rates induced by higher water temperatures. However, there was no correlation between weekly passage success and resighting probability (see Appendix, Fig. S3). To summarise, increased water temperatures during this study could have increased activity levels as indicated by an increased resighting probability that resulted in a higher and faster passage success. However, the origin of the timing of migration observed could also be due to genetics and not only to environmental factors.

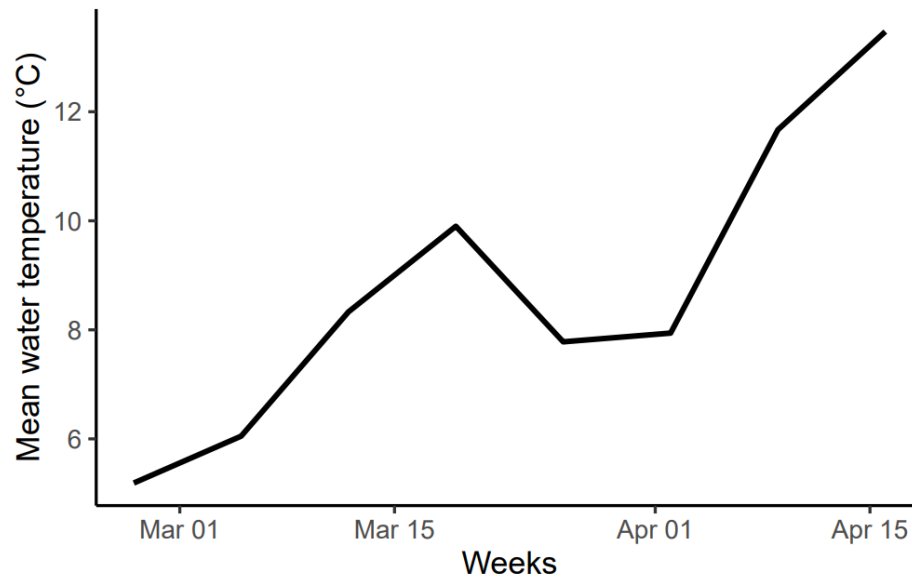


Figure 9. Mean weekly water temperature measured in degree Celsius at Westerdiep in the Netherlands during the migration season of three-spined sticklebacks (2022).

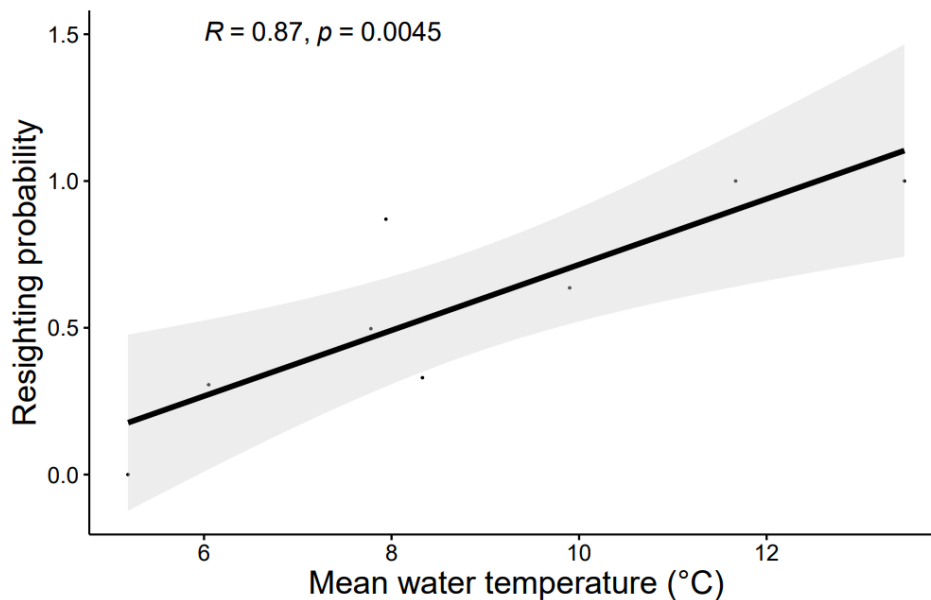


Figure 10. Correlation between mean water temperature in degree Celsius and resighting probability.

Higher vulnerability to predation hotspot

The presence of fishways can often generate predation hotspots near its entrance. A study on the abundance, distribution and time spent by predators near a fishway recorded at a dam in Brazil, revealed that predators aggregate near the fishway to forage for a maximum of 90 days (Agostinho *et al.*, 2012). The authors suggested that the high density of fish near the fishway and the presence of multiple predator groups with different foraging strategies created a perfect hotspot for predation. In our study, pikes and eels were caught in front of the fishway at Hongerige Wolf and tagged sticklebacks were detected through their ventral side. Therefore, it is likely that pikes and eels preyed upon sticklebacks and other fish trying to use the fishway. Additionally, these predators have different foraging strategies; pikes and eels prefer to forage

at night whereas perches forage mostly during the day (Sandström, 1999). Therefore, if there is a high abundance of predators that guard the entrance of the fishway day and night, it might be difficult for small species of fish such as sticklebacks to safely use the fishway. Higher activity near the fishway at higher temperatures could likely increase exposure to predators such as pikes and eels. This increased vulnerability could explain the results of the survival analysis, which revealed a lower survival probability of sticklebacks later in the migration season. To summarise, increased water temperatures during this study could have increased activity levels and resulted in a higher vulnerability to predators as indicated by a decrease in survival probability.

Conservation implications

Passage success is partly phenotype-dependent. On one side, the absence of phenotypic bias in the exploration behaviour and the length of three-spined sticklebacks is encouraging for the conservation of migratory species and river connectivity. On the other side, if passage success is dependent on the timing of migration, this might have several ecological and evolutionary consequences. Excluding certain phenotypes can have detrimental effects for the species and the ecosystem (Geist, 2011). Direct consequences include loss of genetic diversity with later migratory fish gaining an evolutionary advantage over earlier migratory fish as they complete their life cycles and increase their reproductive success. Fitness consequences include suboptimal resource acquisition assuming that individuals that cannot cross the fishway will be stuck in an unsuitable habitat with limited resources. Individuals that never crossed the fishway (88% of individuals in this study) were still detected for several weeks at the entrance of the fishway, this accumulation can alter the community of resident fish in the area where they are stuck and increase their vulnerability to predators (eels, pikes, perches) (Robert L McLaughlin *et al.*, 2013; van Leeuwen *et al.*, 2016). Unsuccessful sticklebacks might also use excessive energy to find the entrance of the fishway and attempt to cross. At the ecosystem level, sticklebacks are part of the food chain and several species prey on them such as Spoonbills (*Platalea leucorodia*), therefore, declines in small fish populations could impact their diet and have cascading effects. Unfortunately, all these consequences could also be applicable to other small migratory fish species.

Future recommendations

Further studies should investigate the activity patterns of tagged predatory fish (pikes, eels, perch) and compare the activity of sticklebacks near the entrance of the fishway. This could help to quantify the impact of predation on the passage success of sticklebacks. Perhaps individuals avoid the entrance of the fishway after a predator has been detected which could be interpreted as anti-predator boldness. This could be interesting to investigate whether passage success can be predicted using boldness behaviour, particularly as sticklebacks display consistent anti-predator boldness behaviour (Huntingford, 1976). This would support the results from Lothian and Lucas., 2021, showing that bolder individuals had an increased probability of passage success compared to shy individuals. Additionally, tracking the hydraulic parameters throughout the migration season in comparison to weekly passage success could reveal the importance of discharge regimes for small species of fish such as sticklebacks. Perhaps discharges at the pumping stations could explain why certain weeks had a passage success of 0%. Finally, studying the origin of the phenotypic bias in the timing of migration on passage success and assessing whether it is only environmentally or genetically driven (common garden experiment), might be beneficial for the conservation of migratory fish species. Overall, more interdisciplinary studies combining telemetry with disciplines like behaviour, physiology, genomics and experimental biology are needed to maximize passage efficiency and conserve migratory fish species (Roscoe and Hinch, 2010).

Conclusion

Overall mean passage success of the fishway at Hongerige Wolf was low, only 12% of individuals crossed. However, it is comparable to results from non-salmonid studies with values ranging from 0%-21% (Noonan, Grant and Jackson, 2012). This low passage success could be due to different factors including stress, water temperatures and the swimming abilities of small fish species (sticklebacks) that require more adapted hydraulic conditions (entrance location, attraction flow, discharge regimes) to cross the fishway. Passage success is partly phenotype-dependent for the timing of migration but not for the exploration and the length of sticklebacks. This bias in fishway use could have serious ecological and evolutionary consequences for the species including loss of genetic diversity, suboptimal resource acquisition and population decline. Further studies should investigate the activity patterns of predatory fish (pikes, eels, perch) and sticklebacks near the fishway while analysing whether anti-predation boldness can predict passage success. Additionally, studying the driver of the effect of the timing of migration (environmental or genetic) on passage success would help reinforce the conservation of migratory species. Overall, fishways should help restore river connectivity and conserve migratory fish species however, the efficiency of passage success requires further research (for non-commercially important species) and hydraulic adjustments in many cases.

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References

- Agostinho, A.A. *et al.* (2012) 'Fish ladders: safe fish passage or hotspot for predation?', *Neotropical Ichthyology*, 10(4), pp. 687–696. Available at: <https://doi.org/10.1590/S1679-62252012000400001>.
- Andrews, S.N. (2014) 'fishway efficiency and passage behaviour of alewife in three fishways on tantramar marsh near amherst, nova scotia', p. 112.
- Bartolini, T., Butail, S. and Porfiri, M. (2015) 'Temperature influences sociality and activity of freshwater fish', *Environmental Biology of Fishes*, 98(3), pp. 825–832. Available at: <https://doi.org/10.1007/s10641-014-0318-8>.
- Bates *et al.* (2014) 'Fitting Linear Mixed-Effects Models Using lme4.' *Journal of Statistical Software*, 67(1), 1–48. <https://doi.org/10.18637/jss.v067.i01>
- Beitinger, T.L. and Fitzpatrick, L.C. (1979) 'Physiological and Ecological Correlates of Preferred Temperature in Fish', *American Zoologist*, 19(1), pp. 319–329. Available at: <https://doi.org/10.1093/icb/19.1.319>.
- Bell, A.M., Hankison, S.J. and Laskowski, K.L. (2009) 'The repeatability of behaviour: a meta-analysis', *Animal Behaviour*, 77(4), pp. 771–783. Available at: <https://doi.org/10.1016/j.anbehav.2008.12.022>.
- Belletti, B. *et al.* (2020) 'More than one million barriers fragment Europe's rivers', p. 46.
- Bunt, C.M., Katopodis, C. and Mckinley, R.S. (1999) 'Attraction and Passage Efficiency of White Suckers and Smallmouth Bass by Two Denil Fishways', p. 11.
- Conrad, J.L. *et al.* (2011) 'Behavioural syndromes in fishes: a review with implications for ecology and fisheries management', *Journal of Fish Biology*, 78(2), pp. 395–435. Available at: <https://doi.org/10.1111/j.1095-8649.2010.02874.x>.
- Cooke, S.J. and Hinch, S.G. (2013) 'Improving the reliability of fishway attraction and passage efficiency estimates to inform fishway engineering, science, and practice', *Ecological Engineering*, 58, pp. 123–132. Available at: <https://doi.org/10.1016/j.ecoleng.2013.06.005>.
- Drouineau, H. *et al.* (2018) 'Freshwater eels: A symbol of the effects of global change', *Fish and Fisheries*, 19(5), pp. 903–930. Available at: <https://doi.org/10.1111/faf.12300>.
- Forsatkar, M.N. *et al.* (2016) 'Individual boldness traits influenced by temperature in male Siamese fighting fish', *Physiology & Behavior*, 165, pp. 267–272. Available at: <https://doi.org/10.1016/j.physbeh.2016.08.007>.
- Geist, J. (2011) 'Integrative freshwater ecology and biodiversity conservation', *Ecological Indicators*, 11(6), pp. 1507–1516. Available at: <https://doi.org/10.1016/j.ecolind.2011.04.002>.
- Habel, M. *et al.* (2020) 'Dam and reservoir removal projects: a mix of social-ecological trends and cost-cutting attitudes', *Scientific Reports*, 10(1), p. 19210. Available at: <https://doi.org/10.1038/s41598-020-76158-3>.
- Helmer, W (2020) 'Strategy - world fish migration foundation.' Available at: <https://worldfishmigrationfoundation.com/wp-content/uploads/2021/03/DRE-Strategy-2020-2030-v21juli-2020-WEB-SPREADS.pdf>.
- Hughes, A.R. *et al.* (2008) 'Ecological consequences of genetic diversity: Ecological effects of genetic diversity', *Ecology Letters*, 11(6), pp. 609–623. Available at: <https://doi.org/10.1111/j.1461-0248.2008.01179.x>.

- Huntingford, F.A. (1976) 'The relationship between anti-predator behaviour and aggression among conspecifics in the three-spined stickleback, *Gasterosteus Aculeatus*', *Animal Behaviour*, 24(2), pp. 245–260. Available at: [https://doi.org/10.1016/S0003-3472\(76\)80034-6](https://doi.org/10.1016/S0003-3472(76)80034-6).
- Huntingford, F.A. and Ruiz-Gomez, M.L. (2009) 'Three-spined sticklebacks *Gasterosteus aculeatus* as a model for exploring behavioural biology', *Journal of Fish Biology*, 75(8), pp. 1943–1976. Available at: <https://doi.org/10.1111/j.1095-8649.2009.02420.x>.
- Jensen and Aass (1995) 'Migration of a fast-growing population of brown trout (*Salmo trutta* L.) through a fish ladder in relation to water flow and water temperature'. *Regulated Rivers: Research & Management*, 10(2-4), pp. 217–228. Available at: <https://doi.org/10.1002/rrr.3450100216>.
- Jolles, J.W. *et al.* (2019) 'Personality, plasticity and predictability in sticklebacks: bold fish are less plastic and more predictable than shy fish', *Animal Behaviour*, 154, pp. 193–202. Available at: <https://doi.org/10.1016/j.anbehav.2019.06.022>.
- Jonsson, Jonsson and Hansen (1991) 'Energetic cost of spawning in male and female Atlantic Salmon (*Salmo salar* L.)'. *Journal of Fish Biology*, 39(5), pp. 739–744. Available at: <https://doi.org/10.1111/j.1095-8649.1991.tb04403.x>.
- Kassambra and Mundt (2020) 'Factoextra: Extract and Visualize the Results of Multivariate Data Analyses. R Package Version 1.0.7.' Available at: <https://CRAN.R-project.org/package=factoextra>.
- Katopodis, C. and Eng, P. (1992) 'introduction to fishway design', p. 71.
- Kemper, J.H. (1995) 'Role of the Three-Spined Stickleback *Gasterosteus Aculeatus* L. in the Food Ecology of the Spoonbill *Platalea Leucorodia*', *Behaviour*, 132(15–16), pp. 1285–1299. Available at: <https://doi.org/10.1163/156853995X00586>.
- Laine, Kamula, and Hooli (1998) 'Fish and lamprey passage in a combined Denil and vertical slot fishway', *Fisheries Management and Ecology*, 5(1), pp. 31–44. Available at: <https://doi.org/10.1046/j.1365-2400.1998.00077.x>.
- Landsman, S.J. *et al.* (2017) 'Fishway passage success for migratory rainbow smelt *Osmerus mordax* is not dictated by behavioural type', *River Research and Applications*, 33(8), pp. 1257–1267. Available at: <https://doi.org/10.1002/rra.3176>.
- Larinier (2001) 'Environmental Issues, Dams and Fish Migration.' FAO Fisheries Technical Paper, 419, 45-89.
- Lebreton, J.-D. *et al.* (1992) 'Modeling Survival and Testing Biological Hypotheses Using Marked Animals: A Unified Approach with Case Studies', *Ecological Monographs*, 62(1), pp. 67–118. Available at: <https://doi.org/10.2307/2937171>.
- van Leeuwen, C.H.A. *et al.* (2016) 'Mismatch between fishway operation and timing of fish movements: a risk for cascading effects in partial migration systems', *Ecology and Evolution*, 6(8), pp. 2414–2425. Available at: <https://doi.org/10.1002/ece3.1937>.
- Lehner, B. *et al.* (2011) 'High-resolution mapping of the world's reservoirs and dams for sustainable river-flow management', *Frontiers in Ecology and the Environment*, 9(9), pp. 494–502. Available at: <https://doi.org/10.1890/100125>.
- Lintsen, H. (2002) 'Two Centuries of Central Water Management in the Netherlands', *Technology and Culture*, 43(3), pp. 549–568. Available at: <https://doi.org/10.1353/tech.2002.0126>.
- Lothian, A.J. and Lucas, M.C. (2021) 'The role of individual behavioral traits on fishway passage attempt behavior', *Ecology and Evolution*, 11(17), pp. 11974–11990. Available at: <https://doi.org/10.1002/ece3.7964>.

- Maynard, G.A., Kinnison, M.T. and Zydlewski, J.D. (2017) 'Size selection from fishways and potential evolutionary responses in a threatened Atlantic salmon population', *River Research and Applications*, 33(7), pp. 1004–1015. Available at: <https://doi.org/10.1002/rra.3155>.
- Mensinger, M.A. *et al.* (2021) 'American eel personality and body length influence passage success in an experimental fishway', *Journal of Applied Ecology*, 58(12), pp. 2760–2769. Available at: <https://doi.org/10.1111/1365-2664.14009>.
- Merrick, M.J. and Koprowski, J.L. (2017) 'Should we consider individual behavior differences in applied wildlife conservation studies?', *Biological Conservation*, 209, pp. 34–44. Available at: <https://doi.org/10.1016/j.biocon.2017.01.021>.
- Morita, K., Morita, S.H. and Yamamoto, S. (2009) 'Effects of habitat fragmentation by damming on salmonid fishes: lessons from white-spotted charr in Japan', *Ecological Research*, 24(4), pp. 711–722. Available at: <https://doi.org/10.1007/s11284-008-0579-9>.
- Noonan, M.J., Grant, J.W.A. and Jackson, C.D. (2012) 'A quantitative assessment of fish passage efficiency: Effectiveness of fish passage facilities', *Fish and Fisheries*, 13(4), pp. 450–464. Available at: <https://doi.org/10.1111/j.1467-2979.2011.00445.x>.
- Oldani, N.O. *et al.* (2007) 'Is fish passage technology saving fish resources in the lower La Plata River basin?', *Neotropical Ichthyology*, 5(2), pp. 89–102. Available at: <https://doi.org/10.1590/S1679-62252007000200002>.
- Peake, S., McKinley, R.S. and Scruton, D.A. (1997) 'Swimming performance of various freshwater Newfoundland salmonids relative to habitat selection and fishway design', *Journal of Fish Biology*, 51(4), pp. 710–723. Available at: <https://doi.org/10.1111/j.1095-8649.1997.tb01993.x>.
- Peichel, C.L. (2005) 'Fishing for the secrets of vertebrate evolution in threespine sticklebacks', *Developmental Dynamics*, 234(4), pp. 815–823. Available at: <https://doi.org/10.1002/dvdy.20564>.
- Pon, L.B. *et al.* (2009) 'Physiological, energetic and behavioural correlates of successful fishway passage of adult sockeye salmon *Oncorhynchus nerka* in the Seton River, British Columbia', *Journal of Fish Biology*, 74(6), pp. 1323–1336. Available at: <https://doi.org/10.1111/j.1095-8649.2009.02213.x>.
- Pringle, C.M., Freeman, M.C. and Freeman, B.J. (2000) 'Regional Effects of Hydrologic Alterations on Riverine Macrobiota in the New World: Tropical–Temperate Comparisons', *BioScience*, 50(9), p. 807. Available at: [https://doi.org/10.1641/0006-3568\(2000\)050\[0807:REOHAO\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2000)050[0807:REOHAO]2.0.CO;2).
- Ramesh, A. *et al.* (2021) *Habitat fragmentation induces rapid divergence of migratory and isolated sticklebacks*. preprint. Ecology. Available at: <https://doi.org/10.1101/2021.08.20.457130>.
- Réale, D. *et al.* (2007) 'Integrating animal temperament within ecology and evolution', *Biological Reviews*, 82(2), pp. 291–318. Available at: <https://doi.org/10.1111/j.1469-185X.2007.00010.x>.
- Robert L McLaughlin *et al.* (2013) 'Unintended consequences and trade-offs of fish passage', *Fish and Fisheries* [Preprint].
- Roscoe, D.W. and Hinch, S.G. (2010) 'Effectiveness monitoring of fish passage facilities: historical trends, geographic patterns and future directions', *Fish and Fisheries*, 11(1), pp. 12–33. Available at: <https://doi.org/10.1111/j.1467-2979.2009.00333.x>.
- Sánchez, J.M. *et al.* (2017) 'Assessing the impact of extreme flooding on survival in a southern European population of White-throated Dippers *Cinclus cinclus*', *Bird Study*, 64(1), pp. 45–50. Available at: <https://doi.org/10.1080/00063657.2016.1270898>.
- Sandström, A. (1999) 'Visual ecology of fish - a review with special reference to percids', p. 38.

- Thiem, J. *et al.* (2011) 'Behaviour and passage success of upriver-migrating lake sturgeon *Acipenser fulvescens* in a vertical slot fishway on the Richelieu River, Quebec, Canada', *Endangered Species Research*, 15(1), pp. 1–11. Available at: <https://doi.org/10.3354/esr00360>.
- van den Thillart, G.E.E.J.M. (2014) 'European Eels: Dutch Fisheries, Culture and Eel Migration', in K. Tsukamoto and M. Kuroki (eds) *Eels and Humans*. Tokyo: Springer Japan (Humanity and the Sea), pp. 61–74. Available at: https://doi.org/10.1007/978-4-431-54529-3_4.
- Thorstad, E.B. *et al.* (2008) 'Factors affecting the within-river spawning migration of Atlantic salmon, with emphasis on human impacts', *Reviews in Fish Biology and Fisheries*, 18(4), pp. 345–371. Available at: <https://doi.org/10.1007/s11160-007-9076-4>.
- Videler, J.J. and Wardle, C.S. (1991) 'Fish swimming stride by stride: speed limits and endurance', *Reviews in Fish Biology and Fisheries*, 1(1), pp. 23–40. Available at: <https://doi.org/10.1007/BF00042660>.
- Volkoff, H. and Rønnestad, I. (2020) 'Effects of temperature on feeding and digestive processes in fish', *Temperature*, 7(4), pp. 307–320. Available at: <https://doi.org/10.1080/23328940.2020.1765950>.
- Webb, P.W (1975) 'Hydrodynamics and energetics of fish propulsion.' Bulletin—Fisheries Research Board of Canada, 190, 159.
- White, G.C. and Burnham, K.P. (1999) 'Program MARK: survival estimation from populations of marked animals', *Bird Study*, 46(sup1), pp. S120–S139. Available at: <https://doi.org/10.1080/00063659909477239>.
- Wickham and et al (2019) 'Welcome to the Tidyverse', *Journal of Open Source Software*, 4(43), p. 1686. [Preprint]. Available at: <https://doi.org/10.21105/joss.01686>.

Appendix

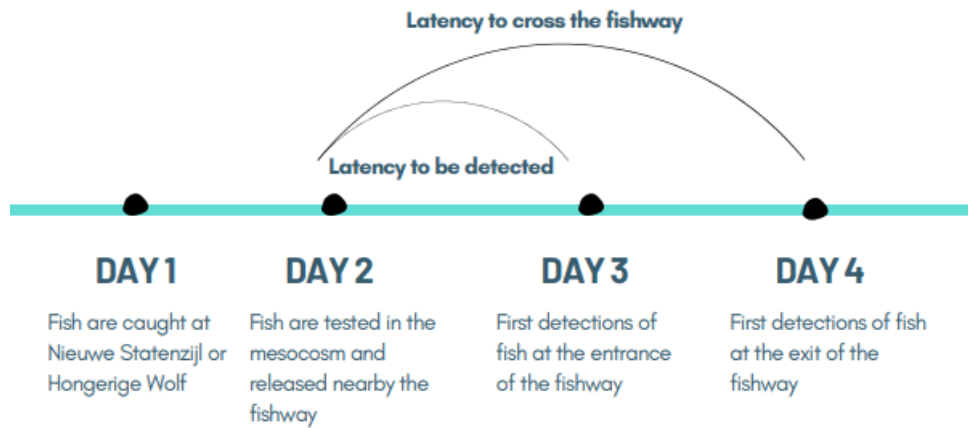


Figure S1. Timeline of an individual that crossed the fishway successfully. The latency to cross the fishway and being detected at the entrance are represented with arrows.

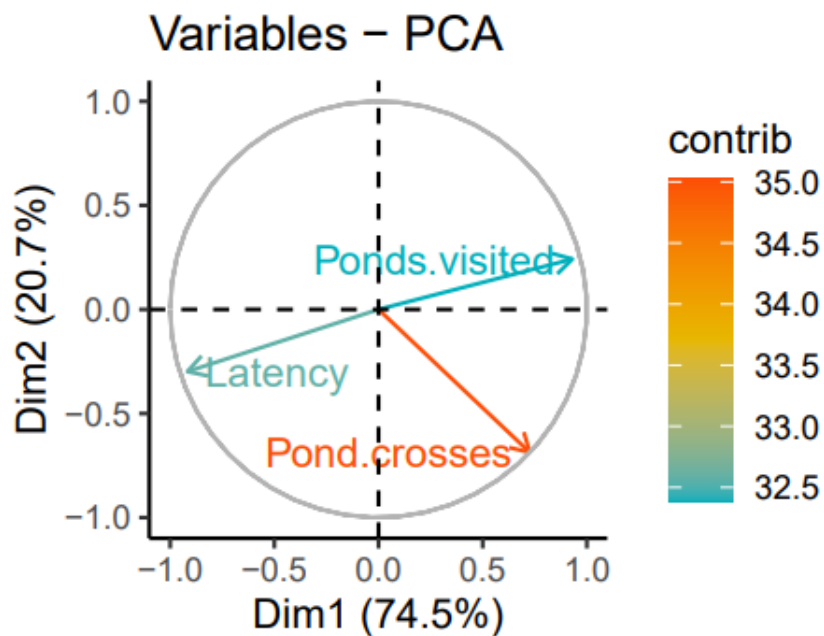


Figure S2. Principal component analysis coloured by contribution to the variation of the three variables (ponds visited, pond crosses and latency to reach the last antenna).

Table S1. Proportion of (pond crosses, number of unique ponds visited and latency to reach the last pond) found in each principal component.

	PC1	PC2	PC3
Pond crosses	-0.49	0.87	0.05
Number of unique ponds	-0.62	-0.30	-0.72
Latency antenna 8	0.61	0.38	-0.69

Table S2. Summary of the pre-defined models for the survival analysis in MARK. (t) is for time-dependent variables and (.) for non-time dependent variables.

Model	AICc	Model Likelihood	Deviance
{Phi(t) p(t) PIM}	760.3701	1	94.5367
{Phi(.) p(t) PIM}	769.4590	0.0106	114.1622
{Phi(t) p(.) PIM}	785.9747	0	128.5891
{Phi(.) p(.) PIM}	813.2050	0	172.277

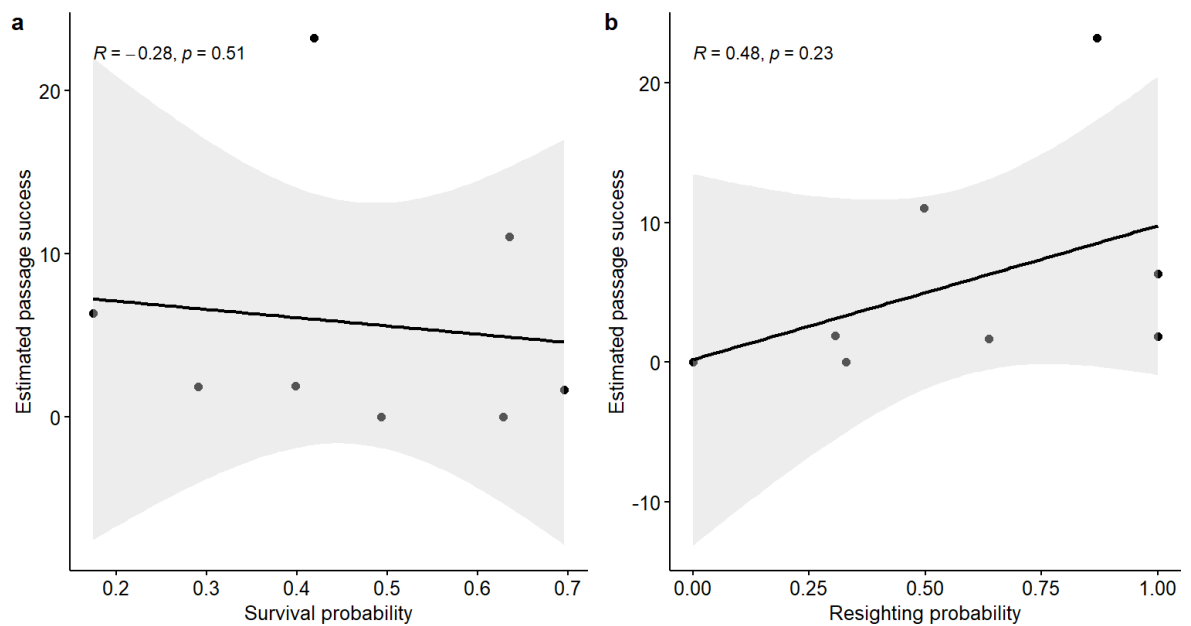


Figure S3. Correlations between survival probability and estimated weekly passage success (a) and resighting probability and estimated weekly passage success (b).