Near-natural Fish Bypasses in the Danube: Improving Downstream Migration, Connecting Tributaries, and Creating Habitats for Potamodromous Fish

Schabuss Michael[1], Zornig Horst[2], Petz-Glechner Regina[3], and Walter Reckendorfer[4]

[1]Universitat Wien Forschungsplattform Data Science Uni Vienna
[2]PROFISCH Mag. Schabuss Weissenbacher, Zornig OG
[3]Paris Lodron Universitat Salzburg Natur- und Lebenswissenschaftliche Fakultat
[4]Verbund Hydro Power GmbH

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Abstract

Fish passes, traditionally designed to facilitate upstream migration, are now increasingly recognized for their potential to support bidirectional fish movement and to improve habitat availability for potamodromous fish. This four-year study at the Ottensheim-Wilhering Hydro Power Plant on the Austrian Danube tracked the migration patterns of the common nase (*Chondrostoma nasus*) using five PIT tag antenna arrays installed in a 14 km long, near-natural bypass system, which integrates two natural tributaries. A total of 190 nase were tagged and released in the Danube upstream the hydro power plant, and fish movement data were collected from November 2020 to June 2024. A large percentage of the tagged individuals entered the fish pass from upstream. Over the years, many individuals utilized the bypass system for extended periods and were observed repeatedly visiting the fish pass, highlighting its role not just as a migration corridor but also as a spawning and feeding habitat. These findings underscore the multifunctionality of near-natural fish passes, which not only restore longitudinal connectivity but also provide critical habitats for various life stages of rheophilic fish. The study challenges the assumption that fish passes are ineffective for downstream migration and suggests that such systems can play a significant role in supporting potamodromous fish populations in highly regulated rivers like the Austrian Danube.

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Short running title: Fish Bypasses: Pathways and Habitats for Potamodromous Fish

Schabuss Michael [1], Zornig Horst [1], Petz-Glechner Regina [2] & Walter Reckendorfer[3]

[1] PROFISCH OG, A-1090 Vienna, Austria. E-mail: schabuss@profisch.at & zornig@profisch.at

[2] Umweltgutachten Petz OG, Neufahrn 74, A- 5202 Neumarkt am W., Austria. E-Mail: petz@umweltgutachten.at

[3] Verbund Hydro Power GmbH, Europaplatz 2, A-1150 Vienna, Austria. E-Mail: walter.reckendorfer@verbund.com

Corresponding author: Schabuss Michael, schabuss@profisch.at

ORCID ID (Michael Schabuss): https://orcid.org/0000-0002-9145-2058

Data Availability Statement

The datasets generated and analyzed during this study are available from the corresponding author upon reasonable request. Detection data from PIT-tagged fish, including movement patterns and habitat use, have been archived and can be provided for further research upon request.

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Conflict of Interest Disclosure

The authors declare no conflict of interest. The views and opinions expressed in this manuscript are those of the authors and do not necessarily reflect the positions of the European Union or VERBUND Hydro Power GmbH. Neither the European Union nor the granting authority can be held responsible for them.

Ethics approval statement

The care and use of experimental animals complied with Austian animal welfare laws, guidelines and policies as approved by Amt der Oberösterreichischen Landesregierung, Abt. Gesundheit, Ges-2016-445528/50-Bit and Ges-2016-445528/63-Bit.

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Abstract:

Fish passes, traditionally designed to facilitate upstream migration, are now increasingly recognized for their potential to support bidirectional fish movement and to improve habitat availability for potamodromous fish. This four-year study at the Ottensheim-Wilhering Hydro Power Plant on the Austrian Danube tracked the migration patterns of the common nase (*Chondrostoma nasus*) using five PIT tag antenna arrays installed in a 14 km long, near-natural bypass system, which integrates two natural tributaries.

A total of 190 nase were tagged and released in the Danube upstream the hydro power plant, and fish movement data were collected from November 2020 to June 2024. A large percentage of the tagged individuals entered the fish pass from upstream. Over the years, many individuals utilized the bypass system for extended periods and were observed repeatedly visiting the fish pass, highlighting its role not just as a migration corridor but also as a spawning and feeding habitat.

These findings underscore the multifunctionality of near-natural fish passes, which not only restore longitudinal connectivity but also provide critical habitats for various life stages of rheophilic fish. The study challenges the assumption that fish passes are ineffective for downstream migration and suggests that such systems can play a significant role in supporting potamodromous fish populations in highly regulated rivers like the Austrian Danube.

Keywords:

Potamodromous fish, fish pass, PIT tags, common nase, downstream migration, habitat connectivity, Austrian Danube.

Introduction:

Potamodromous fish spend their entire life cycles within freshwater environments and play a crucial role in maintaining the biodiversity and ecological balance of river ecosystems (Pennuto et al., 2018, Baras & Lucas, 2001). Their migratory behaviour is influenced by intrinsic factors such as age, life history stage, sexual maturity, or energy content, as well as extrinsic factors like temperature, season, presence of congeners (Castro-Santos & Haro, 2010; Lucas & Baras, 2000) and the availability of suitable habitats, including gravel banks and flood plain systems (Jungwirth et al., 1998, Reckendorfer, 2019).

The Danube River, one of Europe's most important watercourses, with its complex network of tributaries and variously connected flood plains provides a mosaic of diverse habitats for about 114 fish species along its entire river course (Sommerwerk et al., 2009, Schiemer et al., 2004, Schmutz & Jungwirth, 2022). However, since the 19th century, the Austrian section of the Danube has been heavily modified, with extensive straightening and disconnection from many of its natural floodplains and tributaries (Hohensinner et al., 2008, 2009 & 2013). The construction of hydroelectric power plants in the 20th century further disrupted the natural migratory patterns of Danube fishes (Kowall et al., 2024). Currently, 273 km, or 80 % of the Austrian Danube is impacted by 10 hydro power plants (Zauner et al. 2017). As a result of this regulation and damming, shallow gravel bank zones with bay structures, which are crucial habitats for rheophilic fishes, have been greatly reduced compared to the original river landscape of the Danube (Schiemer et al. 1991; Zauner & Schiemer, 1992; Keckeis et al., 1997). In recent decades, deficits in the fish fauna of the Austrian Danube have been documented, including, the absence or dysfunctional population structure of dominant species and an overall low fish abundance and biomass (Zauner et al., 2015, Zauner et al., 2017). These deficits cannot be addressed solely by restoring upstream longitudinal connectivity; they also require the creation of essential habitats, such as spawning grounds and nurseries, to support the Danube fish community (Schmutz, 2012, Koller-Kreimel 2017). According to a recent study, existing fish passes in Austria have improved passability by an average of 20% to 24%. However, longitudinal connectivity in the Austrian Danube system remains significantly disrupted (Kowall et al., 2024). To address this issue, the design of new fish passes should ideally incorporate not only longitudinal connectivity but also lateral connectivity and habitat availability (Kowall et al., 2024; Silva et al., 2017).

Traditionally, fish passes or fishways have been constructed to facilitate upstream migration, allowing fish to bypass barriers such as dams and weirs (Castro- Santos & Haro, 2010, Silva et al., 2017, Porcher & Travade, 2002) and it was assumed that they are unsuitable or quantitatively insignificant for downstream migration (Pelicice et al., 2015, 2020, Pelicice & Agostinho, 2012, Knott et al., 2023, Larinier & Travade, 2002, Eberstaller et al., 2001). Recent studies have begun to challenge this assumption, suggesting that fish passes may also support bidirectional movement, enabling potamodromous fish to migrate downstream (Reckendorfer et al., 2023, Petz-Glechner, 2009, Telhado et al., 2015, Unfer & Rauch, 2019, Sanz-Ronda et al., 2021, Celestino et al., 2019, Calles & Greenberg 2007).

Our study contributes to the evolving discourse on potamodromous fish migration by investigating the use of fish passes for downstream movement and the potential of bypass systems to serve as spawning and feeding habitats. Focusing on a specific case study at a run-of-river hydro power plant at the Austrian Danube, we employed PIT tags and detection arrays at the fish pass of the Hydro Power Plant Ottensheim-Wilhering. We used the common nase, *Chondrostoma nasus* , as an example for a frequently occurring, rheophilic potamodromous fish species in the Austrian Danube to examine if and how fish utilize the fish pass for downstream migration and to investigate their use of the additional habitats provided by the integration of two natural tributaries within the fish pass system.

Materials & Methods

Fish pass

As part of the LIFE project "LIFE+10 NAT/AT/016 - Netzwerk Donau", a near-natural bypass river was constructed at the Ottensheim-Wilhering power plant at the Austrian Danube between 2015 and 2016. This fish pass, stretching 14.2 km and designed to resemble a small river, has a discharge capacity of up to 20 m^3/s, with a bed width varying between 10 and 25 meters. It was integrated into the existing Aschach and

Innbach river systems, which were also restored within the project, thereby reconnecting the Danube with its tributaries (Figure 1). The bypass river enables fish to overcome a height difference of about 12 m, while simultaneously providing key habitats, now largely missing in the Danube, such as shallow shorelines & gravel banks, riffles and pools. The discharge in the bypass system follows that of the Danube, an upstream inlet structure ensures that the required volumes of water are maintained under varying flow conditions in the Danube.

During the construction of the bypass river, the focus extended beyond merely ensuring the passability of the hydropower plant (HPP) dam. A significant emphasis was placed on creating a natural gradient and restoring an original, furcating river landscape with its characteristic flow patterns and substrate conditions. The bypass system thus improves the habitat quality and availability, especially for rheophilic fish species of the Danube. Fish entering the bypass river from either upstream or downstream of the HPP can now utilize the restored sections of the Aschach and Innbach rivers. Additionally, the newly created sections of the bypass river provide migration routes and habitats for spawning, feeding, and juvenile nurseries.

Pit Tags & Antenna arrays

PIT tags (Passive Integrated Transponders) have been used for the individual tagging of fish since 1987 (McKenzie et al., 2012). As they are battery-free passive transmitters, they have an unlimited service life, allowing for the unique identification of individual fish throughout their entire lifespan (Connolly et al., 2008). This makes PIT tags particularly suitable for tracking fish individually over extended periods, ideal for large-scale studies (Greenberg & Giller, 2000; Roussel et al., 2004). For the investigation at the Ottensheim-Wilhering fish pass we used the FDX system from Biomark®, which is known for its high read rate of 30 scans per second, which enhances detection efficiency, especially for shoal-migrating species such as the potamodromous nase (*Chondrostoma nasus*) (Nagel et al., 2023). The tags (12.5 mm x 2.1 mm) were carefully implanted into the fish using syringes.

The PIT tags were read automatically and contactless using five permanently installed antenna arrays (Figure 1). These antennas were placed at strategic points in the bypass system: antenna #1 at the upper end and antenna #5 at the lower end of the bypass, covering the entire width of the watercourse. Antenna #2 was positioned in the upstream ramp connecting the bypass system with the Danube, approximately 1 km downstream of antenna #1, Antenna #3 was installed in the Aschach River, 125 m upstream of its confluence with the bypass channel, and antenna #4 in the Innbach River, 430 m upstream of its confluence with the bypass.

We analysed the antenna array data, including the date, time, and location (antenna #) of each fish detection from 18.11.2020 to 13.06.2024 to study the downstream migration and habitat use of the common nase (*Chondrostoma nasus*). Due to technical difficulties, Antenna #1 was not operational between 23.06.2023 and 01.02.2024.

To calculate the detection efficiency of the PIT Tag antenna arrays, it is necessary to know both the number of detected fish on an array and the number of fish present above or below this array, requiring data from at least two antenna arrays. The detection efficiency can then be determined using the method outlined by Zydlewski et al. (2006):

$$\mathrm{E1} = \mathrm{D}_{\text{common to }1+2} \;/\; (\mathrm{D}_{\text{unique to }2} + \mathrm{D}_{\text{common to }1+2})$$

E1 = Detection efficiency of antenna array #1

D = number of detected tags

The assumptions or necessary conditions for the calculation are as follows:

* The probability of detection on the first array is independent of the probability of detection on the second array

* The fish detected at the first array continues to swim in the direction of the next array

Detection efficiency can be calculated individually for Antennas #1 and #2. However, with additional arrays (#3-5) available to act as a secondary antenna array, there are alternative methods to calculate the overall efficiency.

Two different efficiencies were calculated: (i) the probability of detection during a single downstream passage over the Antennas #1 or #2, and (ii) the probability of being detected on Antennas #1 or #2 throughout the entire study period (2021-2024).

Binomial confidence intervals (CIs, 95%) for detection efficiencies were determined using the normal approximation or Wald method:

CI95 = 1.96 * SQRT((E1*(1-E1)/N), with $N = D_{\text{unique to }2} + D_{\text{common to }1+2}$.

We used the chi-square test (χ^2) to test whether differences in detection efficiency were related to the antenna arrays used in the calculation.

Fish

In our study, we used the common nase, *Chondrostoma nasus* , a potamodromous and highly specialized fish with distinct ecological and ontogenetic trophic niches (Reckendorfer et al. 2001, Hudson et al, 2014, Ovidio & Nzau Matondo, 2024). This species served as a surrogate for other common rheophilic fish species of the Austrian Danube such as Barbel (*Barbus barbus*) or ide (*Leuciscus idus*). Potamodromous fishes exhibit a cyclic sequence of migrations for feeding, refuge and reproduction across four habitat types (feeding, winter refuge, non-winter refuge and spawning) and show habitat-use patterns integrated with their life stages and body sizes (Thurow, 2016, Northcote 1984; Keckeis et al., 1997). In this section of the Austrian Danube, nase is a dominant species ("Leitart") and was very abundant until the beginning of the 20th century. Populations declined sharply in the 20th century, but in recent years a recovery has also been observed in restored sections of the Danube (Zauner et al., 2015). In spring, nase migrate to their spawning grounds (Penaz 1996), with spawning occurring between mid-March and late April at water temperatures from 9.6 to 10.8° C (Huber & Kirchhofer 1998; Melcher & Schmutz 2010). Suitable spawning habitats are shallow, fast flowing and gravelly streams (Panchan et al., 2022, Hauer et al., 2007, Kamler & Keckeis 2000). The larvae and juveniles of nase require different habitats than adults, favouring shallow, slow-flowing areas along the river shore (Keckeis et al. 1997, Kamler & Keckeis 2000, Penaz, 1996).

To investigate the migration through the fish pass and the movements within it, we captured a total of 190 nase (*Chondrostoma nasus*) in the impoundment above the HPP using boat electrofishing. The fish were tagged and subsequently released on November 18, 2020 into the Danube impoundment. Electrofishing, tagging, and handling of the fish were conducted in accordance with the Austrian Animal Welfare Guideline.

Data Analysis

The detection data were aggregated to the number of detections per day and analysed to monitor the movement patterns of individual fish over time. The primary analyses included: i) calculating the number of detections per fish ID per year to identify repeated entries; (ii) conducting a seasonal analysis of detections to determine the timing of migrations and habitat use; (iii) evaluating the duration spent in the bypass to assess its role as a habitat; and (iv) comparing detection locations to understand the utilization of different sections of the bypass.

For data collection, analysis, and presentation, we utilized MS Access®, MS Excel®, and Sigma Plot® software.

We used abacus or calendar plots to analyse the Pit Tag data to estimate the general locations of each nase. The frequency and distribution of detections over time provided insights into how often each individual was detected, how long it remained in the study area, and their movement patterns between antenna arrays. In an abacus plot, the x-axis represents time, while the y-axis lists tagged fish on individual lines, with detections displayed as dots.

Results

Detection efficiencies

The probability of detection during a single downward passage event at the top antenna (Antenna #1) ranged between 25.3±9.8 and 44.9±13.9% (mean+95% confidence limits), depending on the calculation method used, specifically which antenna array chosen as the second reference antenna in the Zydlewski et al. (2006) formula. The calculated values were not significantly different (χ^2-Test, $p > 0.05$) when using the different antennas (#2-5) for the calculations. Overall, we computed a mean detection probability of 34.8±14.2 % (Table 1). Similar calculations were performed for Antenna #2, reaching detection probabilities comparable to those of Antenna #1, ranging from 24.0% ± 9.7% to 38.7% ± 13.6%, with an overall mean of 31.4% ± 14.4% (Table 1). Again, the method used to calculate the detection efficiency had no effect on the calculated value (χ^2-Test, $p > 0.05$).

During the study period (2021-2024), the probability of a fish entering the fish pass system and being detected at the top Antenna #1 ranged from 52.4% and 74.6%, depending on which antenna was used as the secondary antenna (see methods), with an average detection probability of 65.4%. Using this probability, a total of 106 nase were calculated to have entered the system from the Danube reservoir above the HPP (69 nase detected at Antenna #1 / 0.654), representing 55.8% of the tagged fish. For Antenna #2 the detection probability ranged from 42.9% to 67.3% with an overall mean of 55.7%. Using this probability, it was again estimated that 106 nase entered the system from the reservoir (59 fish detected at Antenna #2 / 0.557).

Fish size & detection rates

Of the 190 nase tagged in November 2020, a total of 80 fish (42 %) was detected by at least one of the 5 antennas within the fish pass. Detection rates increased with fish size: 12 % of nase < 20 cm in total length were detected, this increased to 55 % for those between 20-30 cm, and 63 % for those from 30-40 cm, before decreasing to 44 % for nase larger than 40 cm (Figure 2). Consequently, while only a small proportion (12%) of juvenile nase (< 20 cm) were detected, a much higher percentage (59%) of adult nase (> 20 cm) were detected within the fish pass.

Antenna position & daily detection- numbers & -rates

Of the 80 nase that entered the fish pass from the Danube above the HPP between 18.11.2020 and 13.06.2024, a total of 69 individuals (86 %) were detected at the uppermost Antenna #1 at the “exit” of the fish pass (Table 3). At Antenna #2, positioned in the upstream ramp, approximately 1 km downstream of Antenna #1, 58 fish were detected. Antenna #3, situated in the Aschach River, recorded 48 nase, while Antenna #4, located in the Innbach River, detected 36 fish. Finally, 21 individuals were detected at the lowermost antenna, near the “entrance” of the fish pass below the HPP.

Throughout the study period 1.918 detections were recorded on antennas 1-5. Each detection was counted once per fish per antenna and day, though the same fish was counted multiple times if detected on different antennas on the same day. Table 3 summarizes the total number of detection days, the number of fish recorded, and the mean and maximum number of detection days for the years 2021-2024.

In 2021, the number of detection days was higher across all antenna arrays compared to subsequent years. Detection rates varied among antennas, with Antennas #1 and #2 consistently recording the highest number of unique fish (69 and 59 nase, respectively). In contrast, Antennas #4 and #5, located at the lower end of the bypass, had the fewest detection days throughout the study. Antenna #3, situated in the natural tributary Aschach, consistently registered the highest total and average detection days each year, especially in 2021. That year, it recorded 577 detection days from 41 individual fish, averaging 14 detection days per fish, with a maximum of 47 days for a single fish. This indicates significant ”traffic” at this key junction between the fish pass and the natural tributary.

First & last detections per year

Table 4 summarizes the locations (antennas) of the first and last detection of nase for each year from 2021 to 2024. In each year, the first and especially the last detections predominantly occurred at the most upstream antenna, Antenna #1, located at the exit of the fish pass. In 2021, a total of 78 individual fish were detected in the fish pass. The distribution of initial detections slightly decreased across the five antennas, with 24 fish detected first at Antenna #1 and 10 at Antenna #5. However, the final detections were predominantly at the uppermost Antenna #1, where 61 of the 78 fish (78 %) were last recorded that year. Similarly, in 2022, 34 of 42 fish (81%) were last detected at Antenna #1. This indicates that the majority of nase left the fish pass via upstream exit (= Antenna #1) into the Danube impoundment and spent the autumn and winter there after initially entering the fish pass via the same route. In 2023, although Antenna #1 was not operational from 23.06.2023 to 01.02.2024, data from the next closest antenna (Antenna #2) showed a similar trend, with a higher number of fish leaving the system at the upper end of the fish pass. Notably, 41 nase (51% of fish detected) exhibited a migration pattern of leaving the bypass system via Antenna #1 (or Antenna #2 during the period when Antenna #1 was not operational) in one year and returning via the same antenna in a subsequent year.

A notable number (9 individual nase) of last detections at Antenna #5 indicate that some fish are passing completely through the 14,2 km long bypass and exiting into the Danube downstream the HPP. Four nase were observed to have left the bypass system via Antenna #5 (last detection of the year at #5) and returned via Antenna #5 (first detection of the year at #5) in subsequent years.

The total number of fish entering and leaving the bypass system has declined over the years, with 78 nase recorded in 2021, 42 specimens in 2022, 32 fish in 2023, and 15 fish entering the system by mid-June 2024 (end of data analyses).

Residence time of nase within the bypass system

Table 5 presents the minimum, maximum, and mean (+/- SE) number of days that fish remained in the bypass, calculated based on the time between the first and last detection of each nase within each year. Throughout the study, individual fish were observed to stay in the bypass system for as short as 1 day. However, the mean residence time was initially very high averaging 101 days per year in 2021. This average residence time decreased to 90 days in 2022 and 2023. The maximum recorded residence time for a fish in the bypass system was 358 days in 2022.

Seasonality & fish size

Figure 3 illustrates the timing of the first and last detections of nase categorized by size class. The data indicate that larger individuals tend to enter the fish pass earlier in the season compared to juvenile fish. Additionally, nase of all size classes entered the fish pass earlier in 2022 and 2023 compared to 2021. This shift in timing correlates with water temperature data, which show that the mean temperature in the fish pass between February and June 2021 was approximately 0.94°C lower than in 2022 and 0.24°C lower than in 2023.

Seasonal use of the bypass system

An abacus plot visualizes the antenna detections of each individual nase (grouped by size) from 2021 to 2024 (Figure 4), enabling the tracking of fish movements within the bypass system over the years.

The plot reveals multiple detections of individual nase across different years, with noticeable clusters of detections starting around spring (March to May) each year, as fish enter the bypass. Continuous detections during the summer months (June to August) show that many fish remain in the bypass for extended periods. Detections in the autumn (September to November) and winter (December to February) indicate fish exiting the bypass.

A closer examination of the abacus plot shows that the majority of first and last detections of nase occur at the upstream Antenna #1 (brown dots), indicating that most fish enter and exit the fish pass from and to the Danube above the HPP Ottensheim. The peaks in detections, particularly during spring and summer, likely correspond with spawning migration and spawning periods. The high number of detections at Antennas #2-4, and especially at Antenna #3 (orange dots) and #4 (dark green dots) located at the natural rivers Aschach and Innbach, show that many fish use the fish pass not only to overcome the HPP dam or for spawning but also to remain within the bypass system throughout the growing season, from March to October.

The movement patterns indicate that fish are not merely passing through but are also exploring or utilizing various parts of the bypass, including the natural areas within it. Detections at Antenna #5 confirm downstream passage through the bypass.

It is evident that larger nase (> 20 cm) make extensive use of the bypass system (from 71 ind. in 2021 to 15 in 2024), while only 8 smaller fish (< 20 cm) entered the bypass in 2021 and none in subsequent years. These smaller fish also spent less time in the system.

Repeated use of the bypass system

As illustrated in the abacus plot, nase repeatedly utilized the bypass system throughout the four-year study period. 33 fish were detected in the bypass system during only one year of the study period (2021-2024), 20 individuals were detected in two years, 15 fish were detected in three years, and 12 nase visited the bypass every single year. Larger fish (> 30 cm in total length) were found to use the bypass system more than twice as often as smaller fish (< 30 cm) across multiple years.

Conclusion

Detection efficiencies

PIT tag systems are a well-established method for studying fish migration and movement (Schmidt et al., 2016; Lucas & Baras, 2000; O'Donnell et al., 2010; Sloat et al., 2011; Hodge et al., 2015). When analysing migration patterns based on antenna detections, it's important to account that detection efficiencies can vary due to changing abiotic factors, such as flow velocity and water depth at the antenna site. Aymes & Rives, (2009) showed that upstream movements were better detected than downstream movements. Nase, which have been tagged in the Danube downstream of the HPP Ottensheim and migrated upstream into the fish pass, showed a higher detection efficiency (approximately 60 %) (Reckendorfer, personal communication) than fish migrating downstream (24-45%, Table 1). The lower detection efficiency of fish moving downstream is probably due to the faster downstream movement of fish with the current, using the entire water column, compared to the slower, more bottom- oriented upstream movement against the current.

Fish size & detection rates

In this study, we found that detection rates increased with fish size: 12% of juvenile nase (<20 cm) were detected in the fish pass, compared to 59% of adult nase (>20 cm). Additionally, larger individuals tended to enter the fish pass earlier than juveniles. This aligns with documented behaviour of potamodromous species like nase, where larger adults typically move to spawning grounds earlier. For example, Kamler & Keckeis (2000) observed in the Austrian Fischa River that male nase (size 30-48 cm) often arrive at spawning sites before females (size 40-52 cm), occupying deep pools near the spawning area, with females arriving later and positioning upstream or downstream of the males, whereas small-sized fish were less numerous or even absent. Similarly, Penaz (1996) reported comparable behaviour. Epple et al. (2020) noted that adults were detected earlier in the year (March to April) and at lower water temperatures, while juvenile abundance peaked in August in fish bypass channels in the River Iller, Bavaria. Benitez et al. (2022) also found that juvenile nase used fish passes later in the year, from late June to early November. Apparently, juveniles use the fish pass for feeding during the growing season and enter the bypass system later in the year.

In addition to spawning migrations, nase use the fish pass at HPP Ottensheim throughout the year, depending on their size class. Meulenbroek et al. (2008) observed that nase in the 200 to 350 mm length class were underrepresented in a newly constructed fish bypass on the Danube in Vienna, while juveniles were found throughout the bypass, particularly in stagnant side arms and the pool pass. Larger individuals (>350 mm) were almost exclusively found in the meandering and straightened sections.

In our study, we found that fish repeatedly using the bypass and passing downstream were significantly larger than the average of all 190 tagged fish ($p = 0.005$). Previous research by Sanz-Ronda et al. (2021) showed that over 40% of tagged barbel in headwaters successfully found the exit of a slot bypass, with larger or more experienced fish showing an even higher success rate (>50%). Fish rely on spatial perception, using all senses and memory for orientation (Salena et al., 2021; Healy & Patton, 2022). This enables older and larger fish to learn and repeatedly find bypass entries (Reckendorfer et al. 2023). Kieffer & Colgan (1992) noted that fish can adapt to environmental changes and that homing behaviour is influenced by both brain development and experience. Similarly, Odling-Smee & Braithwaite (2003) suggested that fish may be predisposed to learn specific associations relevant to their navigational and migrational challenges.

During our 4-year study, larger fish (>250 mm at tagging in 2020) were detected twice as often (average 2.2 years) as smaller fish (average 1.1 years). This supports the hypothesis that larger, potentially more experienced fish may learn to use the bypass repeatedly over time. Especially considering that the upstream inlet structure, where the fish enter the fish pass from the Danube, is relatively small (2 x 5 m wide and 3.4 m high) compared to the Danube's width (around 320 meters) and is located within a monotonous rip- rap bank at the upper end of the impoundment with a reduced flow velocity.

The total number of fish entering and leaving the bypass system has steadily decreased over the years, from 78 nase in 2021 to 31 in 2023, and just 15 fish recorded entering the system by mid-June 2024. This decline is likely caused by natural mortality. Spindler (1993) reported an average annual mortality rate of 42% for nase in the Austrian Danube and its backwaters below Vienna. Therefore, it is not surprising to see a reduction in detections four years after tagging in 2020, especially given that only a few younger nase have been detected during the study period.

The use of fish pass for downstream migration

Most research on fish passes focuses on their role in upstream migration, with many studies suggesting that fish passes are either unsuitable for downstream migration or play a minimal role in this regard (Pelicice et al., 2015, Knott et al., 2023, Larinier & Travade, 2002, Agostino et al., 2011, Pelicice & Agostinho, 2012; Bravo-Cordoba et al., 2018; Birnie-Gauvin et al., 2019; Geist, 2021, Eberstaller et al., 2001). However, recent research has begun to recognize the importance of fish passes also for downstream migration of potamodromous fishes (Reckendorfer et al., 2023, Bravo-Cordoba et al., 2023, Sanz-Ronda et al., 2021, Celestino et al., 2019, Unfer & Rauch, 2019, Petz-Glechner, 2009, Telhado et al., 2015). Especially on the Austrian Danube, with 10 large HHPs on a river length of only 350 km, the installation of fish passes allowing bi-directional movement and ideally providing habitat, is essential to benefit fish populations. In particular nase, which suffer significant habitat loss in dammed stretches, require restored migration routes alongside improved habitat conditions in the main river and its tributaries (Panchan et al., 2022).

The fish bypass system at Ottensheim-Wilhering resembles a natural river, allowing fish to swim freely in both directions. This is shown by numerous fish entering the fish pass from upstream and hundreds of detections across the five antenna arrays throughout the year. The final annual detections of some nase at the lowest antenna (#5) indicate a complete downstream migration into the Danube below the HPP. Nevertheless, nase are likely to display strong homing behaviour, also regarding their wintering habitats (Ovidio & Nzau Matondo, 2024, Panchan et al., 2022). This drives them to migrate from the bypass system back upstream into the Danube during autumn and winter, as reflected by many last annual detections at Antenna #1, situated at the upper entrance of the bypass.

Our findings demonstrate that nase, though in relatively low numbers, successfully used the fish pass for a downstream passage into the Danube below the dam. These results align with other studies conducted on the Austrian Danube by Eberstaller et al. (2001) and Meulenbroek et al. (2018).

The (repeated) use of the fish pass as a suitable habitat

During our 4-year study, 51 % of nase, tagged in the Danube above the HPP, were detected within the fish pass. By analysing the detection patterns across the 5 antenna arrays and tracking individual fish over time, we observed that while some nase used the fish pass to overcome the HPP dam within a few days, the majority spent several weeks within the bypass system (average stay >86 days per year, with a maximum of 358 days in 2022).

This 14 km long, near-natural fish bypass, with its integrated tributaries, provides suitable habitats for spawning, as shown by elevated detection rates in spring. Spawning activities in the bypass have also been reported by Zauner et al (2017), the extremely high numbers of 0+ fish and feeding traces of juvenile nase within the fish pass reported by these authors indicates the use of the bypass as fish nursery. The high "traffic" at Antenna #3, located in the Aschach River, accounted for 48% of all detections in the system, highlighting the importance of a connection to natural tributaries.

Detection data also show that after entering the fish pass in spring from the Danube above the HPP, nase utilize the various habitats within the bypass system during summer before leaving the fish pass again via the upstream end to spend winter in the Danube. Thus, near-natural bypass rivers offer much more than just longitudinal connectivity; they provide valuable habitats for numerous fish species and life stages throughout the year. These habitats are very rare in degraded large rivers like the Austrian Danube and near natural fish passes which include natural tributaries, such as at the one at HPP Ottensheim, significantly support the potamodromous fish fauna of the main river and its tributaries.

In contrast to our study, investigations of nase migration through fish-bypass channels in the Iller River, Germany, revealed that most nase entered the bypass solely for spawning and left immediately afterward to migrate downstream (Epple et al., 2020). A telemetry study by Panchan et al. (2022) on the Austrian Danube found that 100% of nase exhibited distinct homing behaviour during the spawning season, returning to specific tributaries to spawn and migrating afterwards along the entire river stretch between two hydropower plants.

In our study, 47 of 80 nase (59%) were detected in the bypass system for more than one year, suggesting repeated use and homing behaviour. This aligns with Panchan et al. (2022), who observed nase returning, sometimes multiple times, to specific sites in the river and its tributaries after months of absence. The study also highlighted that Danube nase populations have a much larger home range compared to populations in smaller waters outside the reproductive period (Baras, 1997; Huber & Kirchhofer, 1998; Benitez et al., 2018; Ovidio et al., 2016).

Results of telemetry studies on the Austrian Danube by Wagner (2010) and Eschelmüller (2009) showed that nase exhibited an average total migration of 23.11 and 33.3 km respectively and a home range of 12.1 and 14.1 km. Migration behaviour varied seasonally: Winter showed the shortest migrations (4.9 km and 7.8 km), while prespawning (1st week in February to mid of April) recorded the longest distances (up to 10.8 km). Moderate migration activities were observed in summer and autumn. Individual nase have been observed to migrate distances up to 110 km, although this is less common. Historical data show that in the 1930s, when the Danube still had richly structured river sections, the migration distances of nase were significantly shorter than in recent years (Steinmann et al., 1937).

Meulenbroek et al. (2018) observed that the migration behaviour of nase and barbel, along with their multiple spawning activities within a nature-like fish pass at the HPP Freudenau on the Austrian Danube, is comparable to behaviour observed in natural streams and tributaries of the Danube (Keckeis et al., 1997, Ovidio & Philippart 2008; Melcher & Schmutz 2010). While artificially constructed systems can provide functional spawning grounds (Pander & Geist, 2016; Meulenbroek et al., 2018), large river-like bypasses that incorporate natural tributaries offer particularly suitable habitats for the rheophilic fish fauna of the Danube.

Our data showed that nase remained within the fish pass system for extended periods, averaging about three months each year, rather than simply passing through. Given the poor quality and limited availability of habitats in both the upstream and downstream areas of the Danube, it raises an important question: why would fish migrate along the monotonous main channel of the Danube when suitable habitats are available within the bypass system? This study indicates that bypasses serve a greater purpose than just passageways, offering significant potential to support potamodromous fish species in large rivers, as supported by other research (Quigley & Harper 2006; Calles & Greenberg 2007,2009, Tamario et al. 2018, Meulenbroek et al.

2018, Panchan et al., 2022).

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Data Availability Statement

The datasets generated and analyzed during this study are available from the corresponding author upon reasonable request. Detection data from PIT-tagged fish, including movement patterns and habitat use, have been archived and can be provided for further research upon request.

Tables

Table 1: Probability of detection during a single downward migration at the top antenna (antenna #1) using antenna arrays #2-5 as second antenna for calculation (SE=standard error, 95 % confidence limit).

	# Antenna used for calculation	No. of fish unique to antenna #1	No. of fish common to antenna #1 & 2	Total n
1	2	36	23	59
1	3	27	22	49
1	4	26	12	38
1	5	14	7	21
1	2 to 5	56	19	75
1	**Overall mean**			
2	3	30	19	49
2	4	25	13	38
2	5	15	6	21
2	3 to 5	57	18	75
2	**Overall mean**			

Table 2: Detections of individual nase, tagged in the Danube above HPP Ottensheim, at the 5 different antenna arrays in the fish pass (data from 18.11.2020 - 13.06.2024). + Antenna #1 was not in operation between June 23, 2023, and February 1, 2024.

Antenna #	**No. of fish**	**% of tagged**	**% of detected**
1+ (Exit = upstream end at ramp to Danube)	69	36,3	86,3
2 (within the upstream ramp)	59	31,1	73,8
3 (in the Aschach river above confluence with the bypass)	49	25,8	61,3
4 (in the Innbach river above confluence with the bypass)	38	20,0	47,5
5 (Entrance = downstream end of bypass)	21	11,1	26,3
Total	80	42,1	100

Table 3: Total detections, number of individual fish, mean and maximum number of days with individual fish detections from 2021 to 2024 across the five different antenna arrays in the fish pass (data from 18.11.2020 - 13.06.2024). + Antenna #1 was not in operation between 23 June 2023 and 1 February 2024.

year	**Antenna #1** tot. detect/ no. Ind/ mean det./max det. per fish	**Antenna #2** tot. detect/ no. Ind/ mean d
2021	149/66/2,3/11	147/51/2,9/13
2022	92/38/2,4/9	78/29/2,7/8
2023	37+/15+/2,5/9+	54/22/2,5/8
2024	4+/4+/1,0/1+	8/5/1,6/2
TOTAL	**282/69/4,1/26**	**287/59/4,8/19**

Table 4: Locations (antennas #1 –#5) of first and last individual fish detections for each year, data from 18.11.2020 - 13.06.2024, +Antenna #1 was not in operation between 23 June 2023 and 1 February 2024, ++ data were analysed just until 13 June 2024.

	2021	**2022**	**2023**	**2024**		
Antenna #	**First detection**	**Last detection**	**First detection**	**Last detection**	**First detection**	**Last dete**

	2021	**2022**	**2023**	**2024**		
1	24	61	16	34	11+	3+
2	17	0	9	5	2	17
3	15	5	8	0	11	5
4	12	6	6	2	5	3
5	10	6	3	1	2	3
total	**78**	**78**	**42**	**42**	**31**	**31**

Table 5: Minimum, maximum, mean (+/- Standard error SE) number of days fish stayed within the bypass (first versus last unique fish detection of each year between 18.11.2020 - 13.06.2024, + data were analysed just until 13 June 2024

Year	**Min. days**	**Max. days**	**Mean. days**	**+/- SE**
2021	1	264	101,0	6,6
2022	1	358	89,7	12,9
2023	1	286	90,4	15,7
2024+	1	125+	44,4+	11,4

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