Movement and habitat use of native and non-native small benthic fish in a high conservation value agricultural environment

Original
Movement and habitat use of native and non-native small benthic fish in a high conservation value agricultural environment / Ruffino, C.; Abba, M.; Candiotto, A.; Spairani, M.; Bovero, S.; Fenoglio, S.; Comoglio, C.; Nyqvist, D.. - In: JOURNAL OF LIMNOLOGY. - ISSN 1129-5767. - ELETTRONICO. - 84:(2025). [10.4081/jlimnol.2025.2216]

Publisher:
Page Press Publications

Published
DOI:10.4081/jlimnol.2025.2216

Movement and habitat use of native and non-native small benthic fish in a high conservation value agricultural environment

Carlo Ruffino,[1,2*] Margherita Abbà,[1,2]
Alessandro Candiotto,[3] Michele Spairani,[4]
Stefano Bovero,[5] Stefano Fenoglio,[1,2] Claudio Comoglio,[6]
Daniel Nyqvist[6,7]

[1]Department of Life Sciences and Systems Biology (DBIOS), University of Turin, Italy; [2]ALPSTREAM - Alpine Stream Research Center, Ostana (CN), Italy; [3]Individual firm Alessandro Candiotto, Predosa, Italy; [4]Flume Ltd., Gignod (AO), Italy; [5]"Zirichiltaggi" Sardinia Wildlife Conservation NGO, Sassari, Italy; [6]Department of Environment, Land and Infrastructure Engineering, Politecnico di Torino, Turin, Italy; [7]Department of Aquatic Resources, Institute of Freshwater Research, Swedish University of Agricultural Sciences, Drottningholm, Sweden

*Corresponding author: carlo.ruffino@unito.it

Key words: *Misgurnus*; *Cobitis*; *Gobiidae*; macrophytes; spring stream; telemetry.

Citation: Ruffino C, Abbà M, Candiotto A, et al. Movement and habitat use of native and non-native small benthic fish in a high conservation value agricultural environment. *J Limnol 2025;84:2216.*

Edited by: Pietro Volta, *CNR-IRSA Water Research Institute, Verbania-Pallanza, Italy.*

Contributions: DN, CC, MS, AC, SB, CR, conceptualization; DN, CC, MS, AC, SB, CR, MA, methodology; DN, MA, data analysis; DN, MA, CR, original draft preparation; CC, SF, project administration and funding acquisition; all authors, investigation, writing-review and editing. All authors have read and agreed to the published version of the manuscript.

Conflict of interest: the authors declare no conflicts of interest.

Funding: This research was funded by of the LIFE21-NAT-IT-LIFE Minnow Project: "Small fish, small streams, big challenges: conservation of endangered species in tributaries of the upper Po River", LIFE21-NAT-IT-LIFE-Minnow/101074559.

Institutional Review Board: the study was performed in accordance with "Servizio Caccia e Pesca della Provincia di Vercelli" D.D. n. 423 of 11 May 2023 and Prot. n. 11689/2024 dd 15 April 2024, "Ente di Gestione delle Aree Protette del Po Piemontese" Del. n. 67 dd 1 June 2023, and ISPRA (Istituto Superiore per la Protezione e la Ricerca Ambientale) Prot. n. 0009885-2023 of 24 February 2023), under the provisions of art. 2 of the national Decree n. 26/2014 (implementation of Directive 2010/63/EU).

Data Availability: the data presented in this study are available on request from the corresponding author.

Acknowledgments: this study was carried out within the scientific activities of the LIFE21-NAT-IT-LIFE Minnow Project: "Small fish, small streams, big challenges: conservation of endangered species in tributaries of the upper Po River", LIFE21-NAT-IT-LIFE-Minnow/101074559. We would like to thank Sara Vazzola and Marta Zoppi for their help about macrophyte identification, and Flavia Suraci, Ambra Alderighi, Camilla Brunet, Beatrice Allera, Nives Grasso, Andrea Merlin, and Alfredo Schiavon for assistance in the field, and Paolo Scagliotti and Edoardo Scagliotti for practical assistance.

Received: 12 February 2025.
Accepted: 18 June 2025.

Licensee PAGEPress, Italy
J. Limnol., 2025; 84:2216
DOI: 10.4081/jlimnol.2025.2216

ABSTRACT

Despite the considerable progress that has been made in the field of taxonomy and genetics of freshwater fish, there is still a paucity of knowledge regarding their ecology and behaviour. We used PIT-telemetry to study movement and habitat use of native and non-native benthic fish species in a spring fed irrigation stream, subject to seasonal macrophyte removal, in a rice field in North-Western Italy. This anthropogenically managed environment constitutes a habitat of high conservation value for some important endemisms, while hosting several non-native species. Fish were tracked both using manual tracking and stationary PIT-antennas, and telemetry data was complemented with catch data from electrofishing. The native *P. bonelli* and the non-native *M. anguillicaudatus* were tracked in sufficient numbers to allow quantitative analysis. While successfully tracked in the study area, both species were mostly stationary, but some fish registered movements in the study area of several hundred meters. *M. anguillicaudatus* showed a tendency of greater movements. With time, most fish disappeared from the study area, but no direct migratory movement was detected. *M. anguillicaudatus* showed a clear preference for macrophyte-covered substrates while *P. bonelli* were frequently tracked both among macrophytes and on gravel substrates. Electrofishing data showed higher fish abundance in reaches subject to only partial macrophyte removal (fish friendly management) compared to those subject to standard removal. Overall, movement seems to be an integral part of the ecology of benthic fish in this system where vegetation appears to structure their spatial behavior.

INTRODUCTION

Movement is an essential component of freshwater fish ecology, influencing a range of processes including habitat selection, population dynamics, prey-predator interactions, breeding success, and community structure (Petty and Grossman, 2004; Cooke *et al.*, 2022). Consequently, information on species movement patterns is crucial from several perspectives, for example for predicting the effects of environmental disturbances on a fish community

(Ovidio *et al.*, 2009), assessing the effectiveness of habitat restorations (Watz *et al.*, 2019), or designing non-native species control practices (Bajer *et al.*, 2011).

Studies of freshwater fish movements have increased greatly in the last decades (Gerking, 1953; Gowan *et al.*, 1994; Rodríguez, 2002), but most of them focused on few families of game fish such as salmonids (Höjesjö *et al.*, 2007; Frank *et al.*, 2012) and centrarchids (Gatz Jr. and Adams, 1994; Klinard *et al.*, 2018), while studies on non-game fish, particularly small benthic species are, with some exceptions, still scarce (Petty and Grossman, 2004; Ovidio *et al.*, 2009; Mitsuo *et al.*, 2013; Egger *et al.*, 2021). Previously, stream fish, except for strictly migratory species, were considered to be sedentary, inhabiting relatively short reaches of the river (Gerking, 1953). Over time, this paradigm, defined as the Restricted Movement Paradigm (Gowan *et al.*, 1994), has been challenged by studies highlighting the considerable movements of salmonids (Gowan *et al.*, 1994; Rodríguez, 2002). Benthic species are considered poor swimmers compared to pelagic and migratory ones (Langerhans and Reznick, 2010), and are still deemed to be primarily sedentary, despite the lack of studies investigating their movement behaviour.

Telemetry is a powerful and effective technology for studying movements, migration, and habitat use of individual fish (Cooke *et al.*, 2013; Thorstad *et al.*, 2013). In particular, PIT-telemetry has been demonstrated to be an effective method for studying small-sized fish, as it relies on the use of small electronic tags, Passive Integrated Transponder (PIT) tags. PIT-tags are glass-encapsulated microchips, typically 7-32 mm long, with a unique identification code that they transmit when activated by the electromagnetic field of a detection antenna. The absence of an internal battery has enabled a significant reduction in their size over time and makes them viable for long periods (Cooke *et al.*, 2013; Thorstad *et al.*, 2013). Tagged fish can be detected either by antennas installed at strategic sites, or with portable antennas, but in both cases the detection distance is relatively low (< 1m) (Thorstad *et al.*, 2013). PIT-telemetry has been used, for example, to estimate survival (Keeler *et al.*, 2007), migration (Schwinn *et al.*, 2017; Schiavon *et al.*, 2024), habitat use (Watz *et al.*, 2019), predation (Skov *et al.*, 2014), and behaviour (Závorka *et al.*, 2016) of fish, as well as to evaluate and refine fish conservation measures (Castro-Santos *et al.*, 1996; Watz *et al.*, 2019), and to map the movement of invasive species (Thorlacius *et al.*, 2015).

In North-Western Italy, spring-fed streams have been managed for irrigation purposes for hundreds of years, and have, with the draining of wetlands, become a biodiversity refuge harbouring a range of threatened species (Gomarasca, 2002). In fact, in the last two centuries, the agricultural landscape of the Po Valley has been subject to rapid change, with the banalisation of habitats, the mechanisation of cultivation practices and, especially, the progressive disappearance of natural wetlands. In this scenario, rice fields and their associate aquatic systems have assumed an increasingly important role as surrogate environments, often representing the only habitat in which lowland aquatic species populations can survive. Man-made irrigation streams require regular harvesting of macrophytes to keep water flowing and have experienced widespread deterioration or decay with the industrialization of agriculture (Gomarasca, 2002). Ongoing restoration efforts highlight their value as fish habitat (Gomarasca, 2002; EU, 2024), and the presence of several endangered fish endemisms, such as Italian golden loach (*Sabanejewia larvata* (De Filippi, 1859)), Po brook lamprey (*L. zanandreai* (Vladykov, 1955)), and Italian spring goby (*Orsinigobius punctatissimus* (Canestrini, 1864)), has been reported (Freyhof and Kottelat, 2007; Fortini, 2016). Despite the potentially high conservation value of this ecosystem, its ichthyofauna remains poorly studied, as do the effects of restoration interventions.

In addition to, and interacting with the loss of habitat, the introduction of non-native species is a huge concern for the conservation of freshwater fish (Dudgeon *et al.*, 2006; Baruch *et al.*, 2024), with predation, competition, hybridization, bioturbation, and parasite dynamics constituting some of a range of effects on the local ecosystems (Cucherousset and Olden, 2011; Carosi *et al.*, 2017; Zaccara *et al.*, 2020). In Italy, 47 non-native freshwater fish species have been reported, representing almost half of the total number of freshwater fish species (Rondinini *et al.*, 2022). These species are both new taxonomic arrivals, such as Wels catfish (*Silurus glanis* (Linnaues, 1758)) and pond loach (*Misgurnus anguillicaudatus* (Cantor, 1842)), and closely related sister species from across the Alps (Abbà *et al.*, 2024; Nyqvist *et al.*, 2024b). Despite their potential ecological impact, behavioral studies regarding non-native species from the Italian peninsula are almost lacking (Nyqvist *et al.*, 2022, 2024b).

In this study, we used PIT-telemetry to investigate the movement patterns of native and non-native small-sized benthic fish species in a spring-fed stream located within the rice fields of Vercelli, NW Italy. The objectives of our research were i) to quantify the movement of the benthic species in terms of linear range and movement rate, with a particular focus on comparing these parameters between native and non-native species; ii) to assess the habitat use of the species; and iii) to evaluate the effect of alternative management strategies (macrophyte removal) on the presence of the species. Our research focused on the most abundant benthic species in the study reach: the native Italian spined loach (*Cobitis bilineata* (Canestrini, 1866)) and Padanian goby (*Padogobius bonelli* (Bonaparte, 1846)), and the non-native *M. anguillicaudatus* (Cantor, 1842)) and Danubian spined loach (*Cobitis* cf. *elongatoides* (Băcescu & Mayer, 1969)).

METHODS

Study system

Roggia Marina (45.211999, 8.165367; WGS84) is a semi-natural spring fed stream located within the rice fields in the Vercelli Province, Italy (Fig. 1). The stream is used for irrigation of rice fields, and subject to removal of macrophytes and terrestrial vegetation once or twice per year. The substrate is composed mainly of gravel and silt with a large cover of aquatic macrophyte intermixed with limited artificialized stretches characterized by the presence of concrete and/or brick on the part of the bottom and banks. The watercourse has a width of 2-3.5 m, and a relatively uniform depth ranging from 0.4-1 m. At the start of the study, the discharge was estimated to 322 l/s. Although relatively stable over the year, water levels and water temperatures are influenced by precipitation, water regulation, and diel as well as seasonal temperature variation (Fig. 2).

The spring fed streams in the study area host a high diversity of fish species, including both endangered endemic and several non-native fish species. Of particular interest are *S. larvata* and

Lampetra zanandreai, both of which are abundant in some reaches of the Roggia Marina. Other native species include *P. bonelli*, *C. bilineata*, Italian chub (*Squalius squalus* (Bonaparte, 1837)), Italian riffle dace (*Telestes muticellus* (Bonaparte, 1837)), common minnow (*Phoxinus phoxinus* (Linnaeus, 1758)), North Italian roach (*Leucos aula* (Bonaparte, 1841)), and alborella (*Alburnus arborella* (Bonaparte, 1841)). Among the non-native species, *M. anguillicaudatus* is the most abundant but populations of *C.* cf. *elongatoides*, gudgeon (*Gobio gobio* (Linnaeus, 1758)), stone moroko (*Pseudorasbora parva* (Temminck & Schlegel, 1846)), European bitterling (*Rhodeus amarus* (Bloch, 1782)), eastern mosquitofish (*Gambusia holbrooki* (Girard, 1859)), crucian carp (*Carassius spp*.), and common carp (*Cyprinus carpio* (Linnaeus, 1758)) are also present (A. Candiotto, *personal observation*).

The macrophyte community in the study area is relatively rich and consists of both native and non-native species. The most abundant (area coverage) phanerogams are the invasive *Elodea nuttallii* (Planch., 1857) and *Elodea canadensis* (Michx., 1803) (*Supplementary material, Tab. S2*).

On 20 May 2024, a drone (Autel EVO II RTK; 17m height) was used to map the macrophyte coverage in the study area, a 300 m long rectilinear reach of Roggia Marina. Drone photos with a 1 cm resolution were converted to an orthophoto using a Structure from Motion algorithm. The orthophoto was then used to estimate the percentage of macrophyte cover in QGIS. The total study area and area covered by macrophytes were quantified by manually outlining polygons over the full stream and over macrophyte patches in the drone imagery.

The study area is part of a stream network subject to stream restoration efforts as part of the LIFE-Minnow project (European Commission, 2024). This includes the implementation of more fish friendly vegetation management as well as the active removal of non-native fish species; fish removal was not carried out in the study reach so as not to influence fish population dynamics. To quantify fish presence and movements in relation to the in-stream vegetation, a full and partial removal design was applied in the study reach towards the end of the study. The study reach was systematically divided into 12 sections of 25 m each to facilitate the management of the experiment and the vegetation removal design (Fig. 3).

PIT-telemetry

On 9 and 10 April 2024, the study reach was electrofished by wading upstream and fishing the entire stream width. Benthic fish captured were tagged with passive integrated transponders (PIT

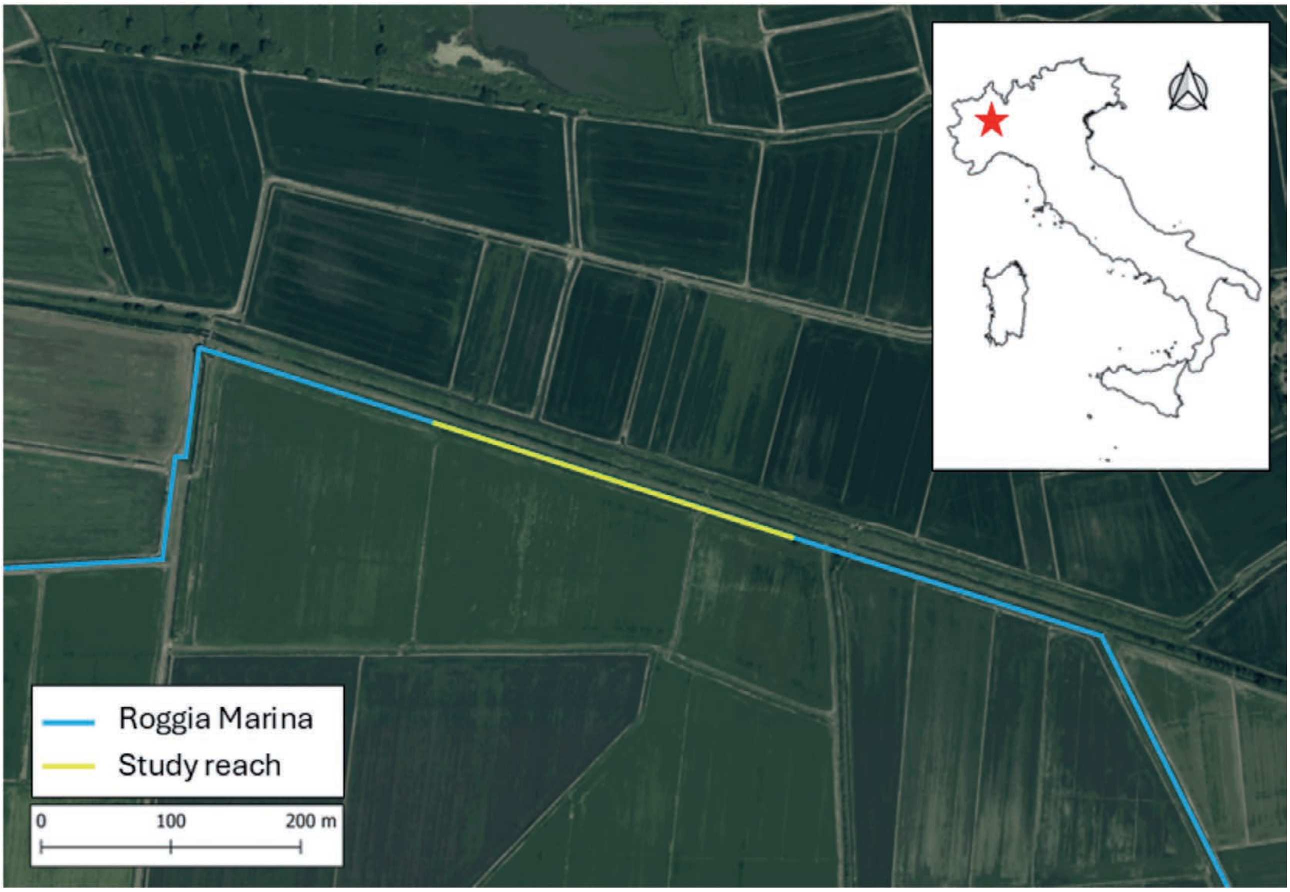

Fig. 1. Location of the study area in Northwest Italy, Piedmont Region, Vercelli Province. The study reach lies within the SAC (Special Area of Conservation) Palude di San Genuario (IT1120007). In light blue the Roggia Marina stream path, in yellow the study reach.

tags; Oregon RFID, USA; 12 × 2.1 mm; 0.10 g). Only healthy fish longer than 6 cm were tagged. Before tagging, fish were anesthetized (Aroma Labs, Kalamazoo, MI, USA; approximately 0.2 mL clove oil / L water). A small incision (2 - 3 mm) was made anterior of the pelvic fins, on the ventral side of the fish, slightly offset from the centre. The tag was then inserted and pushed forward into the body cavity of the fish (Nyqvist *et al.*, 2023, 2024a). All fish were measured for length and weight, and when possible, sexed. Tagged fish were left to recover in buckets filled with stream water before being released into the same study section where they were caught.

Tagged fish movements were monitored using stationary an-

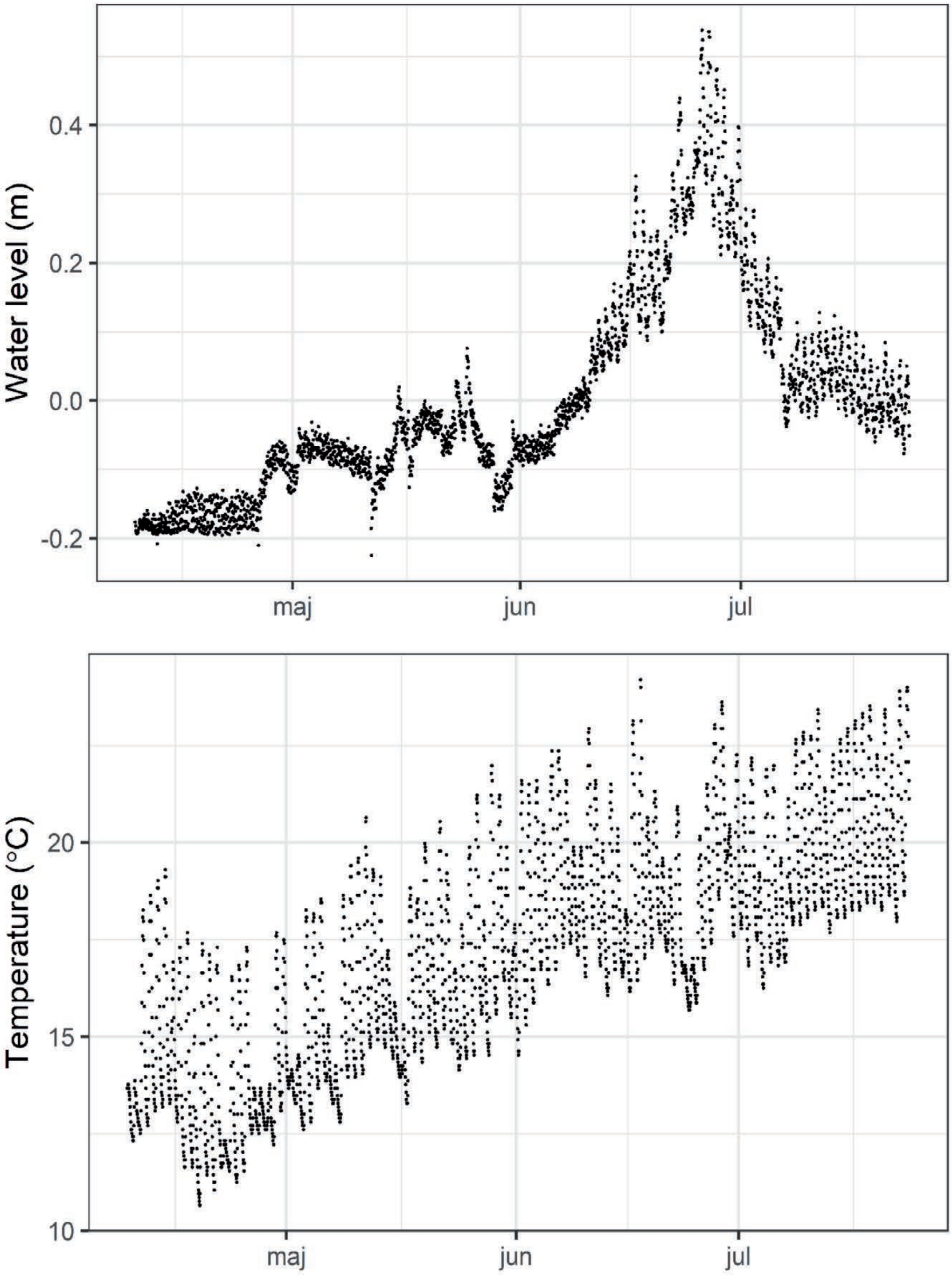

Fig. 2. Roggia Marina stream hourly water levels (m; above) relative to the mean water level and water temperature values (°C; below) during the study period (April-July 2024).

tennas and manual tracking. The stationary antenna network was active from 13 April to 10 July 2024 and consisted of two arrays (upstream and downstream), each composed of one reader (ORMR Multiple Antenna Reader, Oregon RFID) connected to four antennas (Fig. 3). Detection ranges of the stationary antennas were approximately 30-40 cm. This resulted in full coverage of the cross-section of the antenna but could potentially allow undetected passage above the antenna. To avoid disturbance to fish, trampling and damage to the substrate, manual tracking was conducted proceeding downstream from a small plastic boat, using a mobile backpack antenna (Mobile HDX Long Range PIT Tag Reader Kit; Oregon RFID) over the study area and in the stretches immediately upstream and downstream to it. A typical tracking session lasted approximately 4 -5 h. During manual tracking, the position of each fish was recorded in a coordinate system based on the study section. The substrate type, corresponding to the habitat use (macrophytes, gravel, sand, terrestrial vegetation, cement), was noted. Fish were manually tracked 6 times: every two weeks from 23 April to 5 June, and then again on 10 July. For fish tracked at least two times, the fish positions were converted to river meters and linear range was quantified as the distance from the most downstream to the most upstream tracked position (Schiavon *et al.*, 2024).

Transitions between antennas was used to quantify movement at a small scale (between single antennas, 6- 12 m) and at a large scale (between the two readers, 125 m). During the study period, fewer and fewer fish were detected by stationary antennas and during manual tracking. The last detection for each individual was used as proxy for departure date, and the departure for each species plotted over time.

Detection efficiency of the individual antennas was quantified using the formula $n_{detected}/n_{total}$, where $n_{detected}$ is the number of passages detected by the antenna and n_{total} is the total number of passages deduced from detected transitions from one antenna to another. Here, successful detections are quantified by detected transition to a specific antenna ($n_{detected}$). The total number of known passages (n_{total}) over the antenna is the sum of transitions to it and undetected crossings (detected movements between upstream and downstream antennas that were not detected by the focus antenna).

Macrophyte removal and recapture

On 6 July, removal of macrophytes and terrestrial riparian vegetation was carried out in the study area. In the study reach, two types of vegetation removal were applied alternately in the 12 sections: i) total removal of macrophytes and riparian vegetation; ii) partial removal of macrophytes without removal of riparian vegetation (Fig 3). For total removal, two cuts were made within the riverbed with the use of a boom mulcher, leaving about 0.5 m of macrophytes on the edges of the watercourse. For partial removal, only one cut with a boom mulcher was made within the riverbed, removing only about 0.5 m of macrophyte in the centre of the watercourse. This corresponds to approximately 50-71 % macrophyte removal area for the total removal reaches treatment, and 14-25 % for the partial removal reaches, depending on stream width. The riparian vegetation was removed to the edge of the bank for the total removal treatment, while it was left intact for about 0.5 m and 1.5 m from the edge of the two banks for the partial removal treatment. The total removal corresponds to normal maintenance practice, while the partial removal constituted a potentially fish friendly alternative.

On 23 July, by the end of the study period, the study reach as well as a buffer reach (25 m upstream and downstream of the study reach) was electrofished. Recaptured tagged individuals were measured for length and weight. Non-tagged individuals of the four benthic fish species were counted. All fish were assigned to the study section of capture, and hence also to a macrophyte removal treatment (i.e., total/partial) (Reyjol *et al.*, 2005).

Statistical analysis

Few individuals of the two spined loaches were detected during the study and were therefore excluded from quantitative comparisons. Differences in linear range, small and large scale movements, as well as detection probability, between *M. anguillicaudatus* and *P. bonelli* were compared using Wilcoxon Man Whitney tests. Habitat preference per species was tested by comparing the proportion of positions within macrophytes per individual with the expected number (macrophyte coverage in the stream at the time of mapping) using a Wilcoxon-Mann-Whitney test. Difference in habitat use between the two species was com-

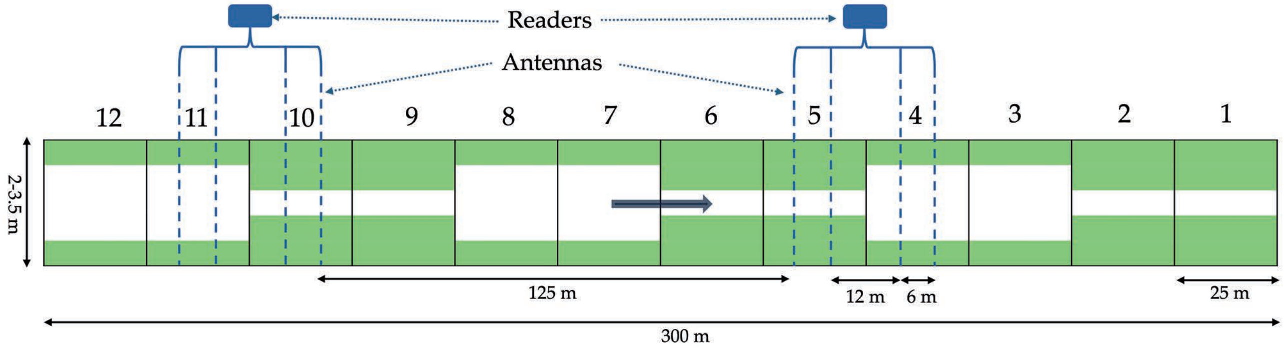

Fig. 3. Conceptual drawing of the study area including fish capture and release sectors (1-12) and the reaches subject to full (sections 3-4, 7-8 and 11-12) and partial (sections 1-2, 5-6 and 9-10) macrophyte removal. Macrophyte removal is displayed as white patches in the green stream. The two reader stations as well as the eight antennas are represented as boxes and dashed lines, respectively. Distances between antennas are averages. Flow direction is denoted with the thick arrow.

pared using a binary mixed model with tracked in macrophytes (yes/no) as response dependent variable, species as independent variable, and individual included as a random effect. The difference in departure proportion was compared using a Chi2-test on the fish remaining in July vs fish having disappeared. The effect of different types of vegetation removal on the benthic species community was tested using a Poisson mixed model, with the number of captured individuals as response variable, vegetation removal type (full/partial) and species as fixed effects, and section (1-12) as random effect. To test the effect of different types of vegetation removal on each species, four additional Poisson mixed models (one for each species) were employed, with the number of captured individuals used as response variable, the type of vegetation removal (full/partial) as fixed effect, and the section (1-12) as random effect. Overdispersion in the Poisson models was checked and not detected. Calculations and analyses were performed using R and Rstudio (R Core Team, 2024), and packages dplyr (Wickham and Francois, 2015), plyr (Wickham and Wickham, 2017), ggplot2 (Wickham, 2016), lme4 (Bates *et al.*, 2015), car (Fox *et al.*, 2007), and blmeco (Korner-Nievergelt *et al.*, 2015).

RESULTS

In total, 204 *M. anguillicaudatus*, 141 *P. bonelli*, 15 *C. bilineata*, 12 *C.* cf. *elongatoides* were tagged (Tab. 1). Macrophyte coverage was estimated to 67 % before removal.

Linear range

During the manual tracking, 21 *M. anguillicaudatus* (10 females, 11 males) and 33 *P. bonelli* (17 females, 10 males, 6 unsexed) were tracked more than once (2-4 times). The median linear range was 5 m (range = 0-417 m) for *M. anguillicaudatus* and 3 m (range 0-191 m) for *P. bonelli*. There was no difference between the two species (Wilcoxon Mann Whitney, *p*=0.20), or between males and females of the same species (*p*>0.42). Only 6 *C. bilineata* and 4 *C.* cf. *elongatoides* were successfully tracked more than two times, displaying median linear ranges of 24 m (0-198m) and 4.5 m (0-251 m) respectively.

Habitat use

All species were repeatedly detected among macrophytes. *M. anguillicaudatus*, C. *bilineata* and *C.* cf. *elongatoides* were primarily found among macrophytes while *P. bonelli* were also often found over gravel. Occasionally, fish were tracked over sand, mud, cement or in relation to terrestrial vegetation (Fig. 4). *M. anguillicaudatus* showed a preference for macrophytes (Wilcoxon-Mann-Whitney, *p*=0.04), while *P. bonelli* were tracked less in the macrophytes than expected by chance (Wilcoxon-Mann-Whitney, *p*=0.001). *M. anguillicaudatus* were significantly more likely to be found among macrophytes compared to *P. bonelli* (GLMM, Est =2.35, *p*=0.006). There was no difference in habitat use (likelihood to be tracked among macrophytes) between males and females in any of the two species (*p*>0.15).

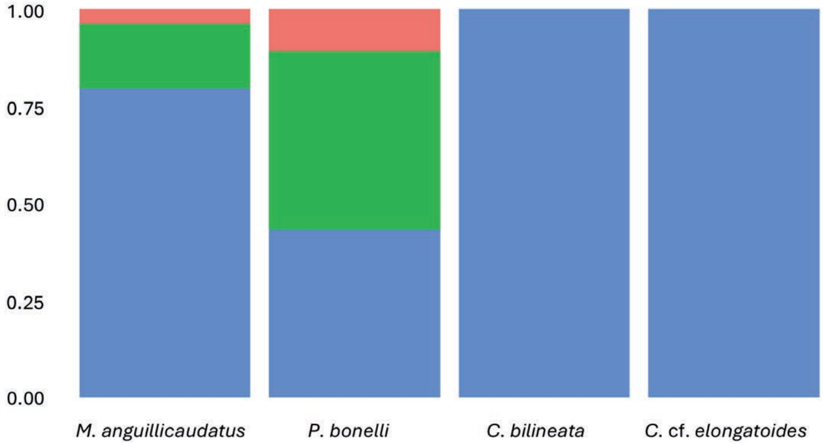

Fig. 4. Habitat use for *M. anguillicaudatus* (n=21), *P. bonelli* (n=33), *C. bilineata* (n=6), and *C.* cf. *elongatoides* (n=4) based on individual means: macrophytes (blue), gravel (green) and other (red; sand, terrestrial vegetation, cement).

Tab 1. Total number, mean and standard deviation (±sd) of length (cm) and weight (g), and number of males and females (where sex was attributed) of tagged fish of each species.

Species	N	Length	Weight	N males	N females
C. bilineata	15	71.6±4.8	1.8±0.4	1	13
C. cf. *elongatoides*	12	74.2±9.1	1.7±0.7	2	10
P. bonelli	141	65.4±9.6	3.9±1.9	58	56
M. anguillicaudatus	204	113.3±22.0	7.2±5.1	83	121

Movement rate

Overall, 75 *M. anguillicaudatus* (49 females, 26 males), 33 *P. bonelli* (15 females, 12 males, 6 unknown), 5 *C. bilineata*, and 3 *C.* cf. *elongatoides* were detected making from 1 to 26 transitions between antennas (6-12 m; Fig. 5). Time between the first and last arrival at an antenna after the presence at another was 11h (range: 1-87 h). There was no difference in number of transitions between *M. anguillicaudatus* and *P. bonelli*, nor between males and females in the respective species (Wilcoxon Mann Whitney; *p*>0.18).

In total, 48 *M. anguillicaudatus* (30 females, 18 males), 3 *P. bonelli* (2 females, 1 male), 4 *C. bilineata*, and 2 *C.* cf. *elongatoides* were detected making between 1 and 4 transitions between the two readers (125 m) (Fig. 6). *M. anguillicaudatus* performed substantially more movements between the upstream and downstream reader than *P. bonelli* (*p*<0.001). There was no difference between sexes (Wilcoxon Mann Whitney, *p*=1).

Departure

The majority of tagged fish from all species disappeared from the study area. The proportion of fish remaining in July (the final 10 days of the study) was higher in *P. bonelli* than in *M. anguillicaudatus* (Chi2, *p*<0.001). For *P. bonelli*, out of 113 fish detected by stationary antennas or manual tracking during the study period, 40 were found in July. This corresponds to 35%. Corresponding numbers for *M. anguillicaudatus* were 4 out of 149, or 3%. No tagged *Cobitis* was detected in July (Fig. 7). Among fish disappearing (no detections in July), the last detections were registered both on the upstream and downstream reader. Last detection on the upstream reader was more common both for *P. bonelli* (73%, n=23) and *M. anguillicaudatus* (63%, n=04) but not for *C. bilineata* (29%, n=7) or *C.* cf. *elongatoides* (33%, n=3).

Detection efficiencies

Stationary antennas were in continuous use during the study period. Detection efficiency on the stationary antennas was relatively low and varied by antenna (22-89%) and species. *P. bonelli* showed an overall detection efficiency of 89% (71-96%), while *M. anguillicaudatus* displayed a detection efficiency of 42% (10-81%). The two *Cobitis* species had too few antenna passages to make detailed efficiency estimates meaningful but displayed overall detection efficiencies of 38-42%.

Electrofishing post-study

The electrofishing following the study period resulted in 13 recaptured tagged fish, 12 *P. bonelli* and one *M. anguillicaudatus*. Of these, eight fish had been detected by stationary antennas or during the manual tracking in July, while four *P. bonelli* had not been observed since April-June.

In total, 140 *C. bilineata*, 1107 *P. bonelli*, 1419 *M. anguillicaudatus*, and 34 *C.* cf. *elongatoides* were caught during the electrofishing campaign after the removal of vegetation (Fig. 8). The probability of locating benthic fish was significantly higher in sections where partial removal was applied compared to those where total removal was carried out (GLMM, Est = 0.53, 95% CI [0.27, 0.80], *p*=0.00002). Looking at the four species separately, this was true for *P. bonelli* (GLMM, Est = 0.49, 95% CI [0.14, 0.84], *p*=0.003) and *M. anguillicaudatus* (GLMM, Est = 0.60, 95% CI [0.26, 0.95], *p*=0.0002).

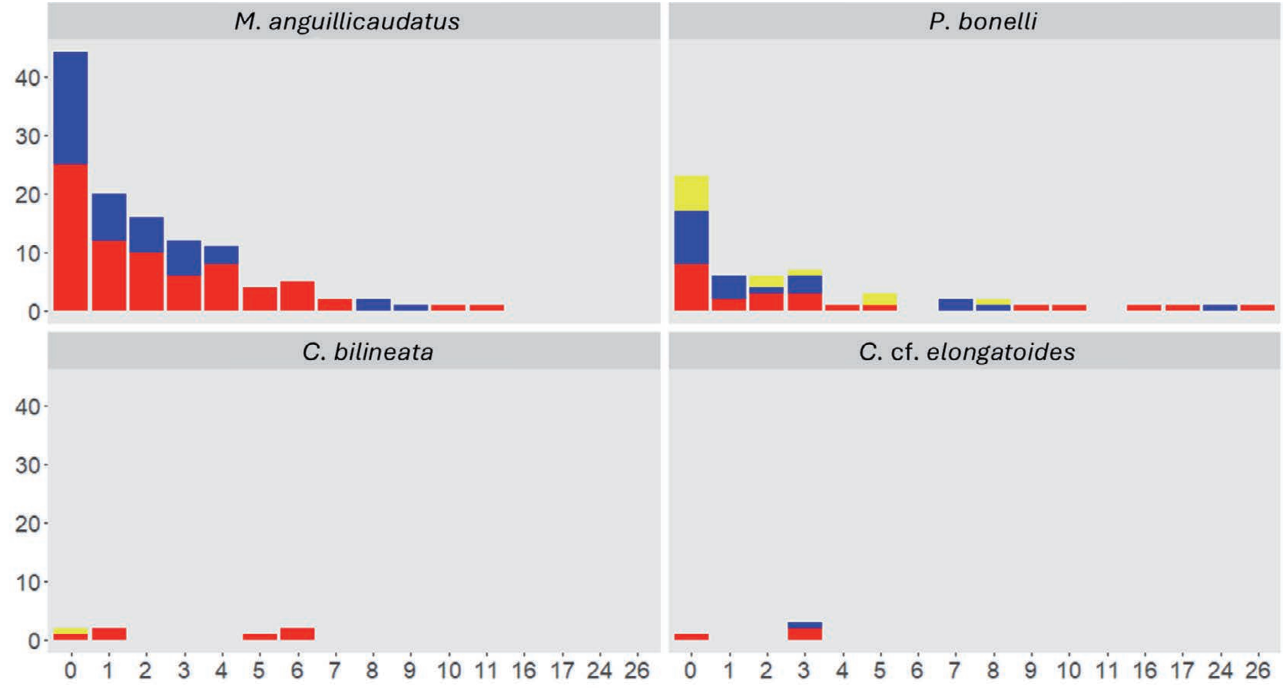

Fig. 5. Number of transitions detected between antennas for females (red), males (blue) and unsexed (yellow) detected at least once of the four species.

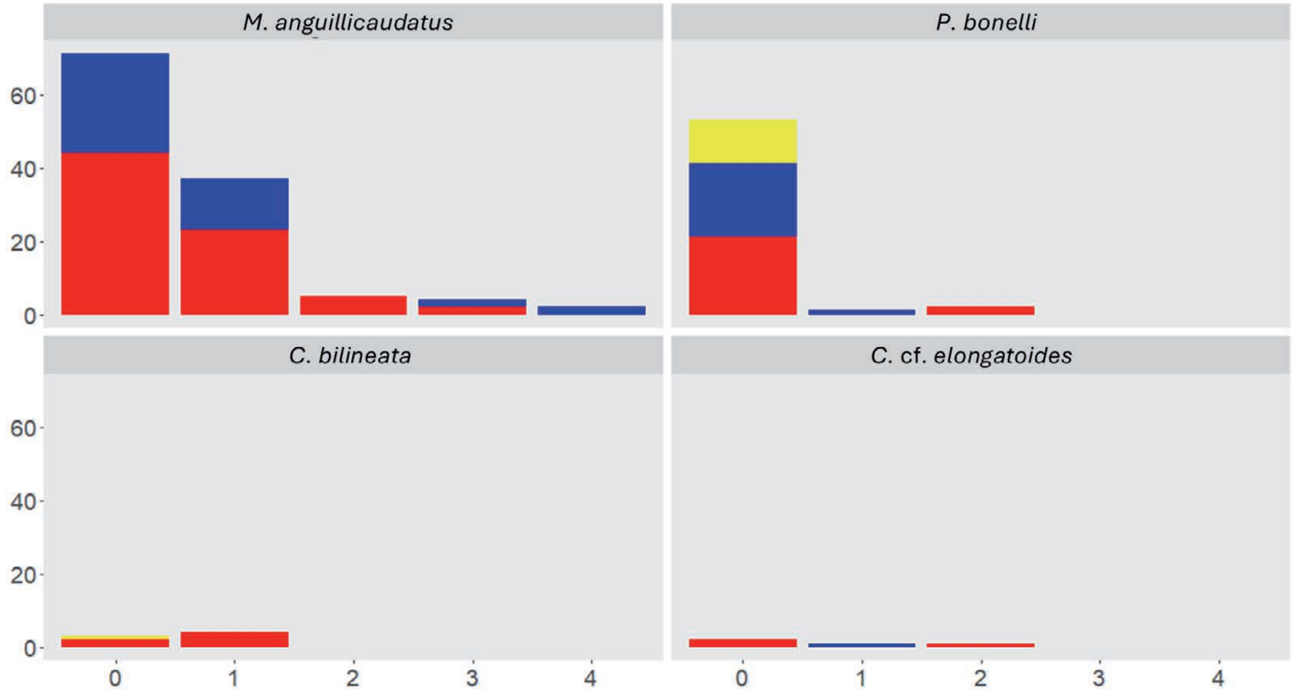

Fig. 6. Number of transitions detected between readers for females (red), males (blue) and unsexed (yellow) detected at least one antenna for the four species.

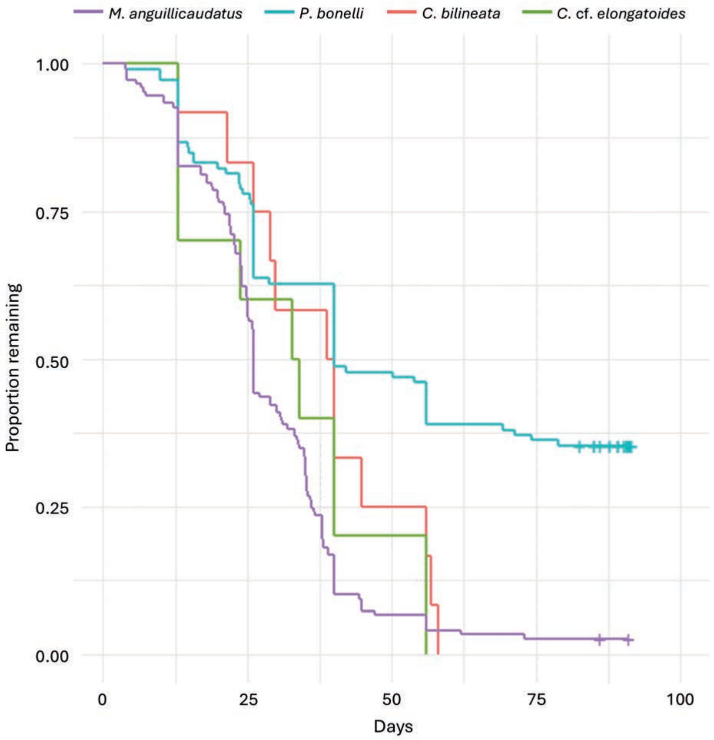

Fig. 7. Proportion of fish remaining in the study area over time for fish detected at least once by the stationary antennas or during the manual tracking. Departure is defined as the last detection either by stationary antennas or manual tracking. Fish detected in July (crosses) are included as censored observations, assuming that they remained in the system.

C. bilineata showed a non-significant tendency of preferentially inhabiting the sections where not all macrophytes were removed (GLMM, Est = 0.49, 95% CI [-0.09, 1.06], p=0.072). *C.* cf. *elongatoides* did not show any difference in capture probability between the two habitat types (GLMM, Est = -1.02, 95% CI [-3.20, 0.78], p=0.21) and was also captured at lower numbers than the other species.

DISCUSSION

This study was the first, to our knowledge, to use PIT-tag technology to monitor the movement and habitat preferences of native and non-native small benthic fish species within a spring-fed stream, focusing on an invasive (*M. anguillicaudatus*) and a native (*P. bonelli*) species. While still in the study reach, the majority of the fish of both species displayed a very limited movement range with a few individuals making longer distance movements. *M. anguillicaudatus* transitioned significantly more than *P. bonelli* within the study area but no difference in linear range was observed. While many *P. bonelli* and most *M. anguillicaudatus* disappeared from the study area, no direct migratory movement was detected. *M. anguillicaudatus* were mainly tracked in the macrophytes whereas *P. bonelli* were commonly found also over gravel substrate. After the removal of macrophytes, the benthic fish were more likely to be found in the reaches partly spared from removal, underlining the importance of macrophytes as a habitat.

The relatively stationary behaviour of the majority of tagged fish during the beginning of the study, with only a minority displaying more long distance movements, is in line with what has

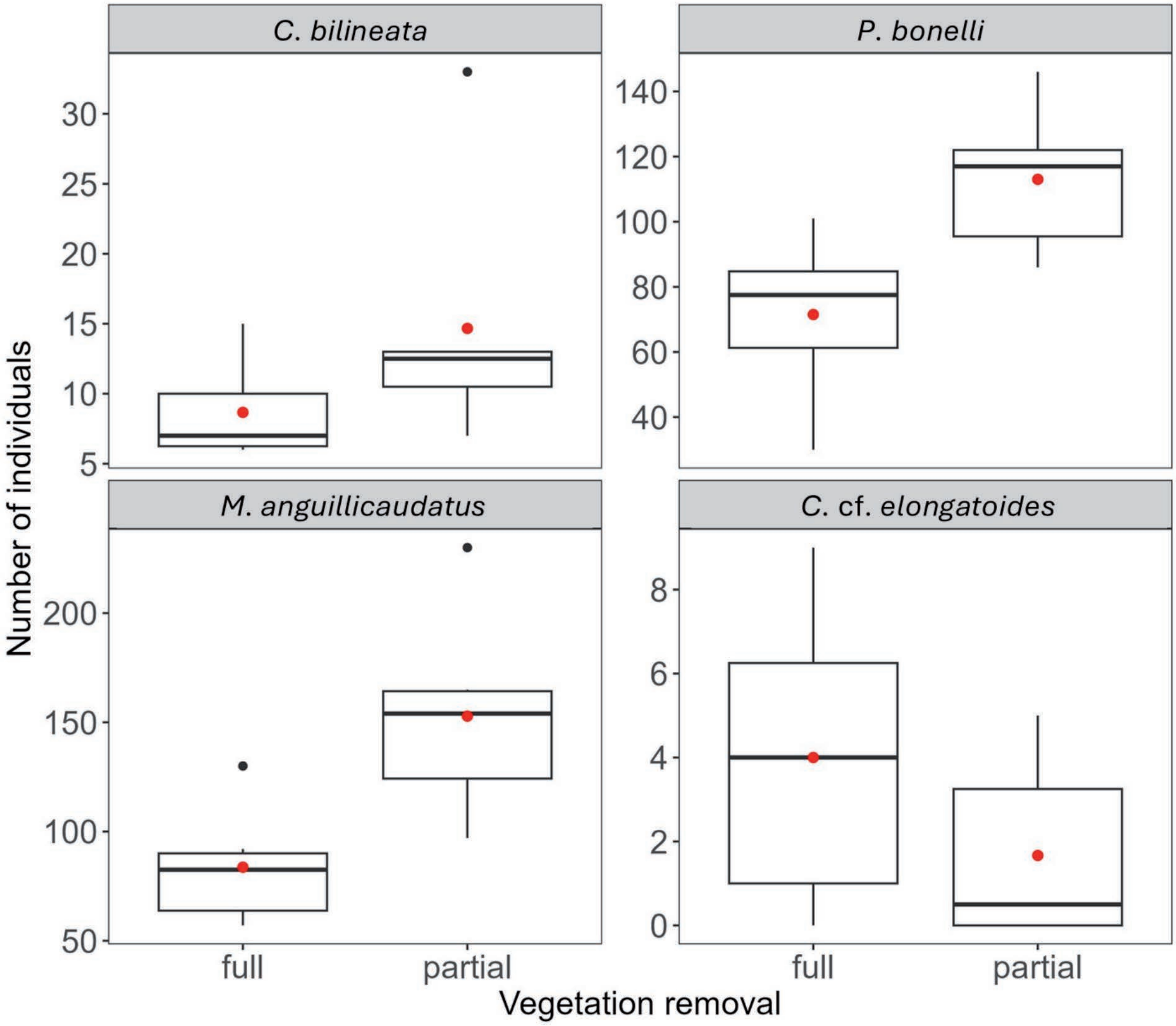

Fig. 8. Number of individuals of each species captured in sections where standard (full) and partial (partial) vegetation removal was applied. The red dot indicates the sample mean.

been reported for other fish species in both small (Stickler *et al.*, 2008; Schiavon *et al.*, 2024) and large (De Leeuw and Winter, 2008) rivers. Among benthic fish, a norm of high residency with a few more mobile individuals has been reported for both sculpins (Breen *et al.*, 2009) and gudgeons (Stott, 1967), as well as for a Japanese loach (*Lefua echigonia*) (Mitsuo *et al.*, 2013). The individual difference could correspond to different dispersal strategies, and be of relevance for connectivity between populations (Gowan, 2007) and the colonization of new areas (Radinger and Wolter, 2014). The difference in movement behaviour might also reflect different behavioural types (Fraser *et al.*, 2001) and have relevance for invasion success of non-native species (Rehage and Sih, 2004; Hirsch *et al.*, 2017). From this perspective, it is interesting, although maybe not surprising, to note that the invasive *M. anguillicaudatus* displayed higher movement activity in the study area compared to the native and territorial P. *bonelli* (Lugli *et al.*, 1992).

A relatively low proportion of tagged fish were subsequently detected. Detection efficiencies are known to vary with species and environments (Cucherousset *et al.*, 2010; Kelly *et al.*, 2017; Saboret *et al.*, 2021), and the thick macrophyte beds in our study likely made manual tracking relatively inefficient. Although this is the first time these taxa have been tracked in nature, the suitability of PIT-tagging has been evaluated for three of the four species in the laboratory environment. The effects of PIT-tagging on growth, survival and tag retention have been evaluated on *M. anguillicaudatus* (Kano *et al.*, 2013). The same effects, as well as those on activity and maximum swimming speed, were evaluated on *C. bilineata* and *P. bonelli* (Nyqvist *et al.*, 2023, 2024a). All three studies conclude that PIT tagging is a suitable method to track individuals of these species. *C. elongatoides* and *C. bilineata* have a very similar morphology and ecology (Delmastro *et al.*, 2021; Bovero *et al.*, 2022) and very likely respond similarly to tagging. Although tagging effects and tag retention may differ between the laboratory and the natural environment (Jepsen *et al.*, 2015; Šmejkal *et al.*, 2019), it is deemed unlikely that tag loss or tagging mortality have contributed substantially to the low detection proportion. That a substantial part of tagged fish were not detected again is not uncommon in PIT-tagging studies, particularly for small sized fish (Cookingham and Ruetz Iii, 2008; Nzau Matondo *et al.*, 2019; Saboret *et al.*, 2021), and is typically handled by focusing the study on the fish successfully tracked.

The manual tracking, antenna detection data, and the electrofishing data all showed that, with time, the tagged fish disappeared from the study area. The mechanisms behind the mass departure of fish are unknown and no directed movement was detected. The disappearance may hence be due to movement out of the study area without systematic detections by the stationary antennas or predation or exit from within the study area. Avian predators are known to be able to remove tagged fish from study areas (Cucherousset *et al.*, 2007; Jepsen *et al.*, 2018). Bird predators such as Grey Heron (*Ardea cinerea* (Linnaeus, 1758)), the Great Cormorant (*Phalacrocorax carbo* (Linnaeus, 1758)), and Sacred Ibis (*Threskiornis aethiopicus* (Latham, 1790)) are present and increasing in the area (Delmastro *et al.*, 2015). Nevertheless, an extremely high predation removal of tagged fish is not likely, particularly in light of the high number of untagged fish present in the study reach at the end of the study. Detection efficiencies were relatively low and variable, making missed detection quite frequent. Previous studies conducted in streams show varying detection rates depending on factors like water depth and substrate composition (Zentner *et al.*, 2021). Rising levels during operations to distribute water to surrounding rice fields may have favored fish passage over the antennas, this allowing fish to leave stream reaches without detection as well as being present without being detected (Kelly *et al.*, 2017). Increased water levels could also connect the stream with lateral channels, allowing lateral fish movements (Fujimoto *et al.*, 2008), and the combination of temporary low or high flows in the stream might also have caused a flushing of fish from the system (Schmutz *et al.*, 2015). For fish still present, electrofishing can compensate for low detection efficiencies (Sloat *et al.*, 2011) but in our study it did not change the general pattern of very few tagged fish remaining in the study area. All in all, lateral or longitudinal emigration seems the most likely reason for the exodus of the tagged fish, indicating relatively high mobility in the studied species in this system over time. Interestingly, during an independent tracking session conducted in April 2025, ten months after the study ended, 22 *P. bonelli* and 5 *M. anguillicaudatus* - previously thought to have left the study area - were again tracked within it. This suggests a potential return movement into the stream, possibly accompanied with improved manual tracking efficiencies due to the less dense macrophyte beds in spring compared to the summer 2024 campaign (*Supplementary Material, Section S1*).

The array of stationary antennas constitutes an innovative way to study small and medium scale movements in small streams. It is well known that fish behaviour, habitat, and environmental conditions influence detection efficiencies (Cucherousset *et al.*, 2010; Weber *et al.*, 2016; Kelly *et al.*, 2017; Saboret *et al.*, 2021). In our study, detection efficiency varied substantially between both species and antennas. The antennas were designed to cover fish passing within a few decimetres from the riverbed or within the sediment. Fish passing higher up the water column were, however, likely to be missed by the antennas. The much higher detection efficiencies in *P. bonelli* compared to the other species could indicate differences in swimming behaviour. While *P. bonelli* likely move on the bottom, the others could, to a higher extent, have utilized the water column (Shi *et al.*, 2017), or been moving within the mud substrate (Park *et al.*, 2018), and therefore less often detected by the antennas.

While *P. bonelli* were tracked both over gravel and among macrophytes, the loaches were tracked predominantly in macrophyte habitat. The importance of macrophytes for the studied fish is further evident by the preference for the macrophyte reaches among the fish capture after the macrophyte removal operation. This is in line with result for another species of weather loach (*Misgurnus fossilis* (Linneus, 1758)) and spined loach (*Cobitis paludica (*De Buen, 1930)), for which a substantial use of macrophyte habitat has been reported (Meyer and Hinrichs, 2000; Elvira *et al.*, 2022). Macrophytes are important habitat components for many different fish species, offering shelter from both predation and the water current as well as substrate for food resources (Savino and Stein, 1982; Sand-Jensen and Mebus, 1996; Dibble *et al.*, 1997; Miranda *et al.*, 2000). Indeed, macrophytes have been reported to be associated with higher abundance and diversity of fish compared to more barren habitat (Ritterbusch *et al.*, 2022), something supported also by the present study. Our study also indicates that limiting macrophyte removal to just part of stream can maintain necessary water flow for agricultural purposes while also leave important fish habitat. While based on a rather limited dataset, this encourages further work on fish friendly management of spring fed-streams in the agricultural landscape.

CONCLUSIONS

Our study provides the first data about movement behaviour of the studied fish species, showing limited movements in the short term, and potentially important large-scale displacements over time. Future studies need to account for the larger scale movements in the system, shedding light on the unexpected disappearance of the bulk of the species observed in our study. Further in-depth analysis is required to understand how different factors - such as habitat type, stream characteristics, food availability, or interspecific competition - drive the movement of small benthic fish species. This is particularly interesting regarding the potential ecological effects and dispersal ability of highly invasive species such as *M. anguillicaudatus*, and the native and non-native sister species (*C. bilineata* and *C.* cf. *elongatoides*). Spring-fed agricultural streams are emerging as a biodiversity hotspot in a heavily impacted area. Our study shows encouraging early results regarding the partial preservation of macrophytes as a fish friendly management method.

REFERENCES

Abbà M, Ruffino C, Bo T, Bonetto D, Bovero S, Candiotto A, et al., 2024. Distribution of fish species in the upper Po River Basin (NW Italy): a synthesis of 30 years of data. J Limnol 83:2194.

Bajer PG, Chizinski CJ, Sorensen PW, 2011. Using the Judas technique to locate and remove wintertime aggregations of invasive common carp. Fish Manag Ecol 18:497-505.

Baruch EM, Yarnell SM, Grantham TE, Ayers JR, Rypel AL, Lusardi RA, 2024. Mimicking functional elements of the natural flow regime promotes native fish recovery in a regulated river. Ecol Appl 34:3013.

Bates D, Maechler M, Bolker B, Walker S, Christensen RHB, Singmann H, et al., 2015. Package 'lme4.' convergence 12:2. https://cran.r-project.org/web/packages/lme4/lme4.pdf

Bovero S, Abbà M, Segreto C, Scoditti G, Favelli M, 2022. Biological traits of *Cobitis* cf. *elongatoides* (Actinopterygii: Cobitidae) in the Malone Stream drainage (Piedmont, NW Italy). It J Freshw Ichtyol 8:2-8.

Breen MJ, Ruetz CR, Thompson KJ, Kohler SL, 2009. Movements of mottled sculpins (*Cottus bairdii*) in a Michigan stream: how restricted are they? Can J Fish Aquat Scie 66:31-41.

Carosi A, Ghetti L, La Porta G, Lorenzoni M, 2017. Ecological effects of the European barbel *Barbus barbus* (L., 1758) (Cyprinidae) invasion on native barbel populations in the Tiber River basin (Italy). Eur Zool J 84:420-435.

Castro-Santos T, Haro A, Walk S, 1996. A passive integrated transponder (PIT) tag system for monitoring fishways. Fish Res 28:253-261.

Cooke SJ, Bergman JN, Twardek WM, Piczak ML, Casselberry GA, Lutek K, et al., 2022. The movement ecology of fishes. J Fish Biol101:756-779.

Cooke SJ, Midwood JD, Thiem JD, Klimley P, Lucas MC, Thorstad EB, et al., 2013. Tracking animals in freshwater with electronic tags: past, present and future. Anim Biotelemetry 1:5.

Cookingham MN, Ruetz III CR, 2008. Evaluating passive integrated transponder tags for tracking movements of round gobies. Ecol Freshw Fish 17:303-311.

Cucherousset J, Britton JR, Beaumont WRC, Nyqvist M, Sievers K, Gozlan RE, 2010. Determining the effects of species, environmental conditions and tracking method on the detection efficiency of portable PIT telemetry. J Fish Biol 76:1039–1045.

Cucherousset J, Olden JD, 2011. Ecological impacts of nonnative freshwater fishes. Fisheries 36:215–230.

Cucherousset J, Paillisson J-M, Roussel J-M, 2007. Using PIT technology to study the fate of hatchery-reared YOY northern pike released into shallow vegetated areas. Fish Res 85:159-164.

De Leeuw J, Winter H, 2008. Migration of rheophilic fish in the large lowland rivers Meuse and Rhine, the Netherlands. Fish Manage Ecol 15:409–415.

Delmastro G, Balma G, Bovero S, Candiotto A, 2021. [Massiccia presenza di un nuovo cobite esotico in Piemonte (Actinopterygii: Cobitidae)].[Article in Italian]. Riv Piemon Storia Nat 42:161–171.

Delmastro GB, Boano G, Conte PL, Fenoglio S, 2015. Great cormorant predation on Cisalpine pike: a conservation conflict. Eur J Wildl Res 61:743–748.

Dibble ED, Killgore KJ, Harrel SL, 1997. Assessment of fish-plant interactions. Available from: https://apps.dtic.mil/sti/citations/ADA330052

Dudgeon D, Arthington AH, Gessner MO, Kawabata Z-I, Knowler DJ, Lévêque C, et al., 2006. Freshwater biodiversity: importance, threats, status and conservation challenges. Biol Rev 81:163–182.

Egger B, Wiegleb J, Seidel F, Burkhardt□Holm P, Emanuel Hirsch P, 2021. Comparative swimming performance and behaviour of three benthic fish species: The invasive round goby (*Neogobius melanostomus*), the native bullhead (*Cottus gobio*), and the native gudgeon (*Gobio gobio*). Ecol Freshw Fish 30:391-405.

Elvira B, Nicola GG, Ayllón D, Almodóvar A, 2022. Seasonal patterns of microhabitat selection in the Southern Iberian spined-loach *Cobitis paludica*. Aquat Sci 84:34.

European Commission, 2024. LIFE public database. Available from: https://webgate.ec.europa.eu/life/publicWebsite/project/LIFE21-NAT-IT-LIFE-Minnow-101074559/small-fish-small-streams-big-challenges-conservation-of-endangered-species-in-tributaries-of-the-upper-po-river%20

Fortini N, 2016. [Nuovo atlante dei pesci delle acque interne italiane: guida completa ai pesci, ciclostomi e crostacei decapodi di acque dolci e salmastre].[Book in Italian]. Aracne Ed., Ariccia: 696 pp.

Fox J, Friendly GG, Graves S, Heiberger R, Monette G, Nilsson H, et al., 2007. The car package. R Foundation for Statistical computing.

Frank BM, Gimenez O, Baret PV, 2012. Assessing brown trout (*Salmo trutta*) spawning movements with multistate capture–recapture models: a case study in a fully controlled Belgian brook. Can J Fish Aquat. Sci 69:1091-1104.

Fraser DF, Gilliam JF, Daley MJ, Le AN, Skalski GT, 2001.

Explaining leptokurtic movement distributions: intrapopulation variation in boldness and exploration. Am Nat 158:124-135.

Freyhof J, Kottelat M, 2007. Handbook of European freshwater fishes. M. Kottelat: 646 pp.

Fujimoto Y, Ouchi Y, Hakuba T, Chiba H, Iwata M, 2008. Influence of modern irrigation, drainage system and water management on spawning migration of mud loach, *Misgurnus anguillicaudatus* C. Environ Biol Fish 81:185-194.

Gatz Jr. AJ, Adams SM, 1994. Patterns of movement of centrarchids in two warmwater streams in eastern Tennessee. Ecol Freshw Fish 3:35-8.

Gerking SD, 1953. Evidence for the concepts of home range and territory in stream fishes. Ecology 34:347–365.

Gomarasca S, 2002. [Indagine conoscitiva sui fontanili del Parco Agricolo Sud Milano].[Report in Italian]. Provincia di Milano. Available from: https://www.cittametropolitana.mi.it/export/sites/default/parco_agricolo_sud_milano/pubblicazioni/.content/allegati/volumi/Indagine_conoscitiva_fontanili.pdf

Gowan C, 2007. Short-term cues used by foraging trout in a California stream. Environ Biol Fish 78:317–331.

Gowan C, Young MK, Fausch KD, Riley SC, 1994. Restricted movement in resident stream salmonids: a paradigm lost? Can J Fish Aquat Sci 51:2626-2637.

Hirsch PE, Thorlacius M, Brodin T, Burkhardt-Holm P, 2017. An approach to incorporate individual personality in modeling fish dispersal across in-stream barriers. Ecol Evol 7:720–732.

Höjesjö J, ØKland F, Sundström LF, Pettersson J, Johnsson JI, 2007. Movement and home range in relation to dominance; a telemetry study on brown trout Salmo trutta. J Fish Biol 70:257-268.

Jepsen N, Ravn HD, Pedersen S, 2018. Change of foraging behavior of cormorants and the effect on river fish. Hydrobiologia 820:189-199.

Jepsen N, Thorstad EB, Havn T, Lucas MC, 2015. The use of external electronic tags on fish: an evaluation of tag retention and tagging effects. Anim Biotelemetry 3:49.

Kano Y, Kawaguchi Y, Yamashita T, Sekijima T, Shimatani Y, Taniguchi Y, 2013. A passive integrated transponder tag implanted by a new alternative surgical method: effects on the oriental weather loach (*Misgurnus anguillicaudatus)* and application in a small irrigation system. Landscape Ecol Eng 9:281-287.

Keeler RA, Breton A, Peterson DP, Cunjak RA, 2007. Apparent survival and detection estimates for PIT-tagged slimy sculpin in five small New Brunswick streams. T Am Fish Soc 136:281–292.

Kelly BB, Cary JB, Smith AD, Pregler KC, Kim S, Kanno Y, 2017. Detection efficiency of a portable PIT antenna for two small-bodied fishes in a piedmont stream. N Am J Fish Manage 37:1362-1369.

Klinard NV, Fisk AT, Kessel ST, Halfyard EA, Colborne SF, 2018. Habitat use and small-scale residence patterns of sympatric sunfish species in a large temperate river. Can J Fish Aquat Sci 75:1059–1069.

Korner-Nievergelt F, Roth T, Felten SV, Guelat J, Almasi B, Korner-Nievergelt P, 2015. blmeco: data files and functions accompanying the book "Bayesian Data Analysis in Ecology using R, BUGS and Stan." R package version 1:.

Langerhans RB, Reznick DN, 2010. Ecology and evolution of swimming performance in fishes: predicting evolution with biomechanics, p. 200-248 In: P. Domenici and B.G. Kapoor (eds.), Fish locomotion. CRC Press.

Lugli M, Bobbio L, Torricelli P, Gandolfi G, 1992. Breeding ecology and male spawning success in two hill-stream populations of the freshwater goby, *Padogobius martensi*. Environ Biol Fish 35:37-48.

Meyer L, Hinrichs D, 2000. Microhabitat preferences and movements of the weatherfish, *Misgurnus fossilis*, in a drainage channel. Environ Biol Fish 58:297–306.

Miranda LE, Driscoll MP, Allen MS, 2000. Transient physicochemical microhabitats facilitate fish survival in inhospitable aquatic plant stands. Freshwater Biol 44:617–628.

Mitsuo Y, Ohira M, Tsunoda H, Yuma M, 2013. Movement patterns of small benthic fish in lowland headwater streams. Freshwater Biol 58:2345–2354.

Nyqvist D, Calles O, Forneris G, Comoglio C, 2022. Movement and activity patterns of non-native wels catfish (*Silurus glanis* Linnaeus, 1758) at the confluence of a large river and its colder tributary. Fishes 7:325.

Nyqvist D, Schiavon A, Ashraf M, Candiotto A, Palazzi A, Parolini M, Comoglio C, 2024a. Survival and Swimming performance of small-sized gobiidae implanted with mini passive integrated transponders (PIT-Tags). Water 16:2745.

Nyqvist D, Schiavon A, Candiotto A, Comoglio C, 2024b. Interspecific differences in swimming performance, behavior and survival between native Italian gudgeon (*Gobio benacensis* Pollini, 1816) and non-native European gudgeon (*Gobio gobio* Linnaeus, 1758). Eur Zool J 91:906-914.

Nyqvist D, Schiavon A, Candiotto A, Mozzi G, Eggers F, Comoglio C, 2023. PIT-tagging Italian spined loach (Cobitis bilineata): Methodology, survival and behavioural effects. J Fish Biol 102:575–580.

Nzau Matondo B, Séleck E, Dierckx A, Benitez J, Rollin X, Ovidio M, 2019. What happens to glass eels after restocking in upland rivers? A long-term study on their dispersal and behavioural traits. Aquat Conserv 29:374-388.

Ovidio M, Detaille A, Bontinck C, Philippart J-C, 2009. Movement behaviour of the small benthic Rhine sculpin Cottus rhenanus (Freyhof, Kottelat & Nolte, 2005) as revealed by radio-telemetry and pit-tagging. Hydrobiologia 636:119–128.

Park C-W, Kim J-G, Yun S-W, Kim H-T, Park J-S, Choi W-S, et al., 2018. Habitat, diet, feeding and resting behaviour of the Korean endemic cobitid *Iksookimia hugowolfeldi* (Cobitidae, Pisces) in the wild. Folia Zool67:1–8.

Petty JT, Grossman GD, 2004. Restricted movement by mottled sculpin (pisces: cottidae) in a southern Appalachian stream. Freshwater Biol 49:631-645.

R Core Team, 2024. R Foundation for Statistical Computing. Vienna.

Radinger J, Wolter C, 2014. Patterns and predictors of fish dispersal in rivers. Fish Fish 15:456-473.

Rehage JS, Sih A, 2004. Dispersal behavior, boldness, and the link to invasiveness: a comparison of four Gambusia species. Biol Invasions 6:379–391.

Reyjol Y, Loot G, Lek S, 2005. Estimating sampling bias when using electrofishing to catch stone loach. J Fish Biol 66:589-591.

Ritterbusch D, Blabolil P, Breine J, Erős T, Mehner T, Olin M, Pet al., 2022. European fish-based assessment reveals high diversity of systems for determining ecological status of lakes. Sci Total Environ802:149620.

Rodríguez MA, 2002. Restricted movement in stream fish: the paradigm is incomplete, not lost. Ecology 83:1-13.

Rondinini C, Battistoni A, Teofili C, 2022. [Lista rossa IUCN dei vertebrati Italiani 2022].[Report in Italian]. Available from: https://www.iucn.it/pdf/Lista-Rossa-vertebratiitaliani-2022.pdf

Saboret G, Dermond P, Brodersen J, 2021. Using PIT-tags and portable antennas for quantification of fish movement and survival in streams under different environmental conditions. J Fish Biol 99:581-595.

Sand-Jensen K, Mebus JR, 1996. Fine-Scale patterns of water velocity within macrophyte patches in streams. Oikos 76:169-180.

Savino JF, Stein RA, 1982. Predator-prey interaction between largemouth bass and bluegills as influenced by simulated, submersed vegetation. T Am Fish Soc 111:255-266.

Schiavon A, Comoglio C, Candiotto A, Spairani M, Hölker F, Tarena F, et al., 2024. Navigating the drought: upstream migration of a small-sized Cypriniformes (*Telestes muticellus*) in response to drying in a partially intermittent mountain stream. Knowl Manag Aquat Ecosyst 425:6.

Schmutz S, Bakken TH, Friedrich T, Greimel F, Harby A, Jungwirth M, et al., 2015. Response of fish communities to hydrological and morphological alterations in hydropeaking rivers of Austria. River Res Appl 31:919–930.

Schwinn M, Baktoft H, Aarestrup K, Koed A, 2017. A comparison of the survival and migration of wild and F1-hatchery-reared brown trout (*Salmo trutta*) smolts traversing an artificial lake. Fish Res 196:47–55.

Shi X, Zhao S, Ding C, Jiang W, Kynard B, Liu L, et al., 2017. Comparison of vertical and horizontal swimming behaviour of the weather loach *Misgurnus anguillicaudatus*. J Fish Biol91:368–374.

Skov C, Jepsen N, Baktoft H, Jansen T, Pedersen S, Koed A, 2014. Cormorant predation on PIT-tagged lake fish. J Limnol 73:715.

Sloat MR, Baker PF, Ligon FK, 2011. Estimating habitat-specific abundances of PIT-tagged juvenile salmonids using mobile antennas: a comparison with standard electrofishing techniques in a small stream. N Am J Fish Manag 31:986–993.

Šmejkal M, Blabolil P, Bartoň D, Duras J, Vejřík L, Sajdlova Z, et al., 2019. Sex-specific probability of PIT tag retention in a cyprinid fish. Fish Res 219:105325.

Stickler M, Enders EC, Pennell CJ, Cote D, Alfredsen K, Scruton DA, 2008. Stream gradient-related movement and growth of Atlantic salmon parr during winter. T Am Fish Soc 137:371–385.

Stott B, 1967. The movements and population densities of roach (*Rutilus rutilus* (L.)) and gudgeon (*Gobio gobio* (L.)) in the River Mole. J Anim Ecol 36:407-423.

Thorlacius M, Hellström G, Brodin T, 2015. Behavioral dependent dispersal in the invasive round goby Neogobius melanostomus depends on population age. Curr Zool 61:529-542.

Thorstad EB, Rikardsen AH, Alp A, Okland F, 2013. The use of electronic tags in fish research: an overview of fish telemetry methods. Turk J Fish Aquat Sci 13:881–896.

Watz J, Calles O, Carlsson N, Collin T, Huusko A, Johnsson J, Nilsson PA, Norrgård J, Nyqvist D, 2019. Wood addition in the hatchery and river environments affects post□release performance of overwintering brown trout. Freshwater Biol 64:71-80.

Weber C, Scheuber H, Nilsson C, Alfredsen KT, 2016. Detection and apparent survival of PIT-tagged stream fish in winter. Ecol Evoln 6:2536–2547.

Wickham H, 2016. Ggplot2: Elegant graphics for data analysis. Springer: 213 pp.

Wickham H, Francois R, 2015. dplyr: A grammar of data manipulation. R package version 0.4 1:20. Available from: http://CRAN.R-project.org/package=dplyr

Wickham H, Wickham MH, 2017. Package ‘plyr.’ Available from: https://cran.r-project.org/web/packages/plyr/index.html

Zaccara S, Quadroni S, De Santis V, Vanetti I, Carosi A, Crosa G, et al., 2020. Genetic and phenotypic displacement of an endemic *Barbus complex* by invasive European barbel Barbus barbus in central Italy. Biolo Invasions 23:521-535.

Závorka L, Aldvén D, Näslund J, Höjesjö J, Johnsson JI, 2016. Inactive trout come out at night: behavioral variation, circadian activity, and fitness in the wild. Ecology 97:2223–2231.

Zentner DL, Wolf SL, Brewer SK, Shoup DE, 2021. A review of factors affecting PIT tag detection using mobile arrays of mobile antennas to detect PIT□tagged suckers in a wadeable Ozark stream. N Am J Fish Manag 41:697–710.

Online supplementary material:

Supplementary Tracking 2025.