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Individual movement behaviour and habitat use of a small-sized cypriniform (*Telestes muticellus*) in a mountain stream

Alfredo Schiavon · Claudio Comoglio · Alessandro Candiotto · Michele Spairani · Franz Hölker · Johan Watz · Daniel Nyqvist

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Abstract Knowledge about the biology and ecology of species is fundamental for their management and conservation. Despite this, many fish species and life stages are understudied, and there is a great need for research efforts to understand their ecology. Italian riffle dace (*Telestes muticellus*; order Cypriniformes) is a small-sized (< 15 cm) stream fish native to the Italian peninsula. There is a scarcity of research on its ecology and behaviour. In this study, we explored the movement ecology of *Telestes muticellus* in a Mediterranean mountain stream in Northern Italy using passive integrated transponder (PIT) telemetry. Over 15 months, 267 fish were located 2–27 times. Most fish remained stationary, while a few roamed over several hundreds of meters. Fish covered a larger linear range during spring and autumn than during other seasons. *T. muticellus* showed a strong preference for pools, and this preference was strongest during summer. We observed no differences in habitat use and movements between day and night, and fish size had no major effect. Within pools, many *T. muticellus* displayed remarkably small home ranges (median 8 m^2). Fish increased their linear ranges over a period of flood events, indicating that high-flow events may be

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A. Schiavon (✉) · F. Hölker
Leibniz Institute of Freshwater Ecology and Inland Fisheries (IGB), Berlin, Germany
e-mail: alfredo.schiavon@polito.it

F. Hölker
e-mail: franz.hoelker@igb-berlin.de

A. Schiavon · F. Hölker
Department of Biology, Chemistry, and Pharmacy, Freie Universität Berlin, Berlin, Germany
e-mail: franz.hoelker@igb-berlin.de

A. Schiavon · C. Comoglio · D. Nyqvist
Department of Environment, Land and Infrastructure Engineering, Politecnico Di Torino, Turin, Italy
e-mail: claudio.comoglio@polito.it

D. Nyqvist
e-mail: daniel.nyqvist@slu.se

A. Candiotto
Ittiologo Libero Professionista, Predosa, Italy
e-mail: ale.candiotto@libero.it

M. Spairani
FLUME S.R.L, Loc. Alpe Ronc 1, Gignod, 11010 Aosta, Italy
e-mail: michele.spairani@flumesrl.it

J. Watz
Department of Environmental and Life Sciences, RivEM, Karlstad University, Karlstad, Sweden
e-mail: johan.watz@kau.se

D. Nyqvist
Department of Aquatic Resources, Institute of Freshwater Research, Swedish University of Agricultural Sciences, Drottningholm, Sweden

important for the downstream and upstream dispersal of *T. muticellus* in small mountain streams.

Keywords Passive Integrated Transponders · Home range · Linear range · Movement ecology · Flood · Telemetry

Introduction

Freshwater ecosystems are home to approximately half of the world's fish species (Hughes 2021). This biodiversity is declining at unprecedented rates (IPBES 2019). Knowledge about the biology and ecology of species is fundamental for their management and conservation (Closs et al. 2016). Despite this, many fish species are understudied and there is a great need for research efforts to understand their ecology, especially in relation to anthropogenic stressors (Smialek et al. 2019; Maasri et al. 2022; Vøllestad 2023). Understanding how fish species respond to these stressors entails detailed insights into their spatial behaviour and habitat use as these are often key to their survival and adaptation. Here, movement ecology and telemetry techniques can play an important role, in informing evidence-based river management and conservation (Allen and Singh 2016; Crossin et al. 2017). Animal movement patterns are adapted to enhance fitness through increased survival, growth, or reproductive efficacy (Milner-Gulland et al. 2011). These patterns involve trade-offs, which balance benefits such as access to quality food and optimal reproductive conditions against costs, including net energy intake and predation risks, in a context of ontogenetic and seasonal change (Lucas et al. 2001). As a result, fish species have evolved diverse life history strategies, reflecting the ecological challenges that they face (Gross 1991; Lucas et al. 2001). A broad spectrum of spatial movement patterns has evolved, including residency, dispersal, nomadism, and migration, at scales from metres to hundreds of kilometres (Gerking 1959; Brodersen et al. 2019; Herrera-R et al. 2024). While some species demonstrate movements within small spatial scales, maintaining limited home ranges and high site fidelity (Hicks and Servos 2017; Marnane 2000), others exhibit extensive movement ranges (Herrera-R et al. 2024; Waldman and Quinn 2022). Additionally, movement patterns may vary within a single species or population and are influenced both by prevailing environmental conditions and individual responses to these (Elliott 1994; Verhelst et al. 2022). Even in relatively resident fish populations where most fish tend to remain within a restricted area, some individuals may engage in relatively large-scale movements (Brodersen et al. 2019; Okland et al. 2005).

In a given fish population, movement and habitat use are not uniform but shaped by life history, individual differences, environmental conditions, and their interactions (Riley et al. 1992; Cooke et al. 2022). Individual stream fish typically display variable movement patterns, sometimes related to fish size (Nakano et al. 1990), life stage (Morrissey and Ferguson 2011), or behavioural type (Watz 2019; Fraser et al. 2001). Further, correlations between the characteristics of habitat used and movement range have been reported for both cyprinids and salmonids (Heggenes 1988a, b; Aparicio and De Sostoa 1999; Harvey et al. 1999).

Movement patterns may also differ by season, often with reduced activity during winter (Hilderbrand and Kershner 2000; Mellina et al. 2005; Shuter et al. 2012). Even for stream-dwelling fish, partial reproductive, refuge, or feeding migration may cause peaks in movement during particular seasons or for specific phenotypes (De Leeuw and Winter 2008; Nunn et al. 2010). Many fish species also display diel changes in behaviour (Helfman 1986) that are reflected in their movements (Hilderbrand and Kershner 2000; Muhlfeld et al. 2003; Nyqvist et al. 2022). Both behaviour and habitat use are thus structured by seasonal and diurnal dynamics, which are reflected in movement patterns with often profound effects on fitness (Morantz et al. 1987; Heggenes and Saltveit 1990; Hölker et al. 2007; Nyqvist et al. 2022). Spatio-temporal variability in movement ecology is, therefore, of high importance for understanding the ecology of many species.

While movement behaviours have been extensively researched for some fish species, especially salmonids (e.g. Rikardsen et al. 2004; Schindler et al. 2010; Jonsson and Jonsson 2011), many other species remain largely unexplored (Booth et al. 2013; Vøllestad 2023). The lack of ecological knowledge, including movement behaviour, is particularly notable for small-sized fish species and species with little direct economic value (Smialek et al. 2019; Negro et al. 2021). For example, Mediterranean Europe is considered a 'biodiversity hotspot' for riverine fish (Reyjol et al. 2007), hosting numerous endangered (Rondinini et al. 2022) and endemic species (Tierno De Figueroa et al. 2013) that also face substantial environmental pressures, including those driven by climate change and alterations in hydrological regimes (Skoulikidis et al. 2017). While some studies on riverine fish movement in Mediterranean contexts exist (e.g. Aparicio and De Sostoa 1999; Pires et al. 2014; Aparicio et al. 2018), they remain scarce and insufficient.

Native to the Italian peninsula, Italian riffle dace (*Telestes muticellus*, Bonaparte 1837) is a small-sized (< 15 cm) cypriniform fish belonging to the Leuciscidae family. *Telestes muticellus* inhabits rivers and streams characterised by relatively cold and clear water (Fortini 2016). It is an omnivore fish, feeding primarily on aquatic invertebrates and epilithic algae. It spawns in spring in areas with gravel substrates and swift and shallow water flow and reaches sexual maturity at the age of 2 or 3 years (Fortini 2016). Despite various studies on the genetics and biogeography of *T. muticellus* (Stefani et al. 2004; Marchetto et al. 2010; Dubut et al. 2012; Buj et al. 2017), there is a scarcity of research on its behavioural ecology. Recent studies, however, have identified refuge migrations of this species in response to stream bed drying (Schiavon et al. 2024) while overwintering and anecdotal spawning migrations have been observed in other species of the same genus (Wocher and Rösch 2006; Barbieri et al. 2020).

In this study, we explore the movement ecology of *T. muticellus* in a mountainous Mediterranean stream in northern Italy. Using passive integrated transponder (PIT) telemetry, we tracked individual *T. muticellus* across diverse stream habitats. We describe individual home range and habitat use of *T. muticellus* Specifically, we quantify linear range and habitat use over annual, seasonal, and diurnal time scales. We expected that environmental factors, as well as intrinsic factors (fish size), would influence behaviour and habitat use. Therefore, we also tested for the effect of fish size, season, and day-night patterns on both movement and habitat use. In addition, and to our knowledge, for the first time for a cypriniform fish, we quantify the 2D-home range of individual *T. muticellus* within pools.

Methods

Study system

Rio Morsone (UTM 485693E, 4939751N, zone 32 T) is an Apennine stream in the Piedmont region, Italy, with a length of approximately 5 km and a drainage area of approximately 8.8 km^2. The river is a tributary of the Lemme River, belonging to the Po drainage basin (Fig. 1a). The stream has a pluvial discharge regime characteristic of Apennine streams, with low discharges in the summer and high discharges in the autumn and spring (Forneris et al. 2007). In the upper part of the catchment, crystalline siliceous rocks dominate, while sandstone, limestone, and conglomerate rocks characterise the lower part (Piana et al. 2017). The fish assemblage is typical of a small northern Apennine stream, with *T. muticellus* representing 73% of the relative abundance, followed by brook barbel (*Barbus caninus*, Bonaparte 1839) with 26%. There is a relative abundance of less than 1% of Italian chub (*Squalius squalus*, Bonaparte 1837) and brown trout (*Salmo trutta* L.). Brown trout is the only non-native species present, introduced for recreational fishing purposes in recent years (A. Candiotto *pers. obs.*).

Study reach

This study was conducted in an 850 m-long reach of the stream (Fig. 1b), 3.5 km upstream from the confluence with Lemme River. Fish movements from the Lemme River to Rio Morsone are prevented by a series of unpassable weirs located downstream of the study reach. On average, the stream width is 3.5 m, but it varies substantially, ranging from a few decimetres in the narrowest sections to as much as 9 m in the widest (Fig. 1c). The study reach has a slope of 4% (elevation of 395 to 421 m a.s.l). Habitat mapping, including discharge estimates in accordance with the ISO 748 (2021) standards, was performed utilising the MesoHABSIM protocol (Parasiewicz 2007, 2011; Vezza et al. 2014) on three occasions: March 3, 2022, with a discharge of 17 Ls^{-1} representing average flow conditions; July 14, 2022, at 5 Ls^{-1} indicative of low-water conditions; and January 31, 2023, with a discharge of 54 Ls^{-1} corresponding to high-water flow conditions. The most prevalent habitat types were riffles and pools, which comprised

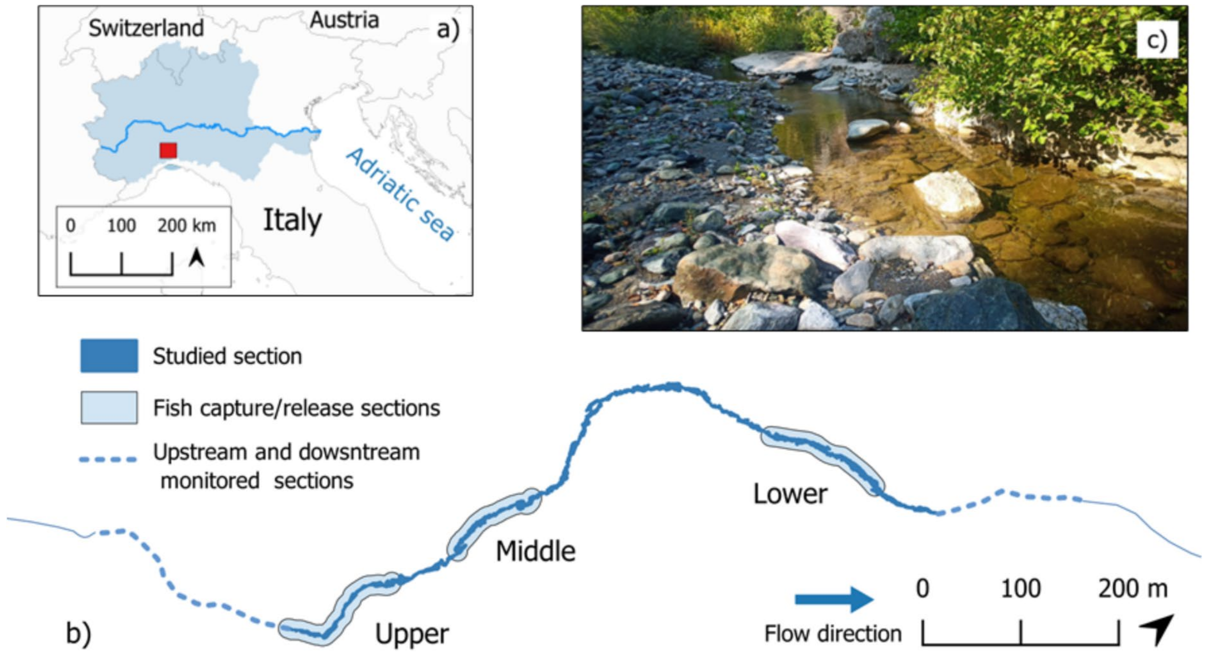

Fig. 1 **a** Study area (red rectangle) within the Po Drainage Basin (blue) in north Italy. **b** The study reaches fish capture/release sections. Dotted reaches upstream and downstream of the study reach were occasionally monitored during the study period. **c** A photo representative of the monitored section of Rio Morsone (summer 2022)

38% and 32% of the area, respectively, followed by glides (19%) and rapid (11%) during average flow conditions. Flow intermittence was observed in the downstream 80 m section of the study reach during low flow conditions, with the drying process occurring in both spring and summer of 2022 and 2023 (Schiavon et al. 2024). Throughout the study period, water temperature and water level were monitored at 20 min intervals using a temperature and water level sensor (HOBO MX2001; Fig. 2). The water level-temperature sensor was positioned 140m upstream of the intermittent reach.

PIT tagging

In March and October 2022, a total of 360 *T. muticellus* were caught with electrofishing and tagged (Table 1) with passive integrated transponders (PIT tags; Oregon, USA; 12 × 2.1 mm; 0.10 g) in the upper, middle, and lower section of the study reach (Fig. 1b). These sections, spanning a length ranging from 102 to 132 m, were characterized by diverse and comparable hydromorphological unit patterns and physical characteristics. Healthy fish exceeding 6 cm in length were selected for tagging. This threshold value corresponds to the length of Italian riffle dace successfully tagged previously (Schiavon et al. 2023) and is the approximate minimum length for sexual maturity in the species (gravid females of this size were observed in the study stream). Fish were anaesthetised (Aroma Labs, Kalamazoo, MI, USA; approximately 0.2 mL clove oil/L water) before 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, and the tag was inserted and pushed forward into the body cavity of the fish (see Nyqvist et al. 2024; Schiavon et al. 2023). Following tagging, each fish was measured for fork length and body mass before being placed in tanks filled with river water for recovery. After a brief recovery (≈ 30 min), fish were released back into the river at the same location where they were captured.

Fish tracking

The tagged fish were tracked using mobile backpack antennas (Mobile HDX Long Range PIT Tag Reader Kit; Oregon RFID). During the tracking,

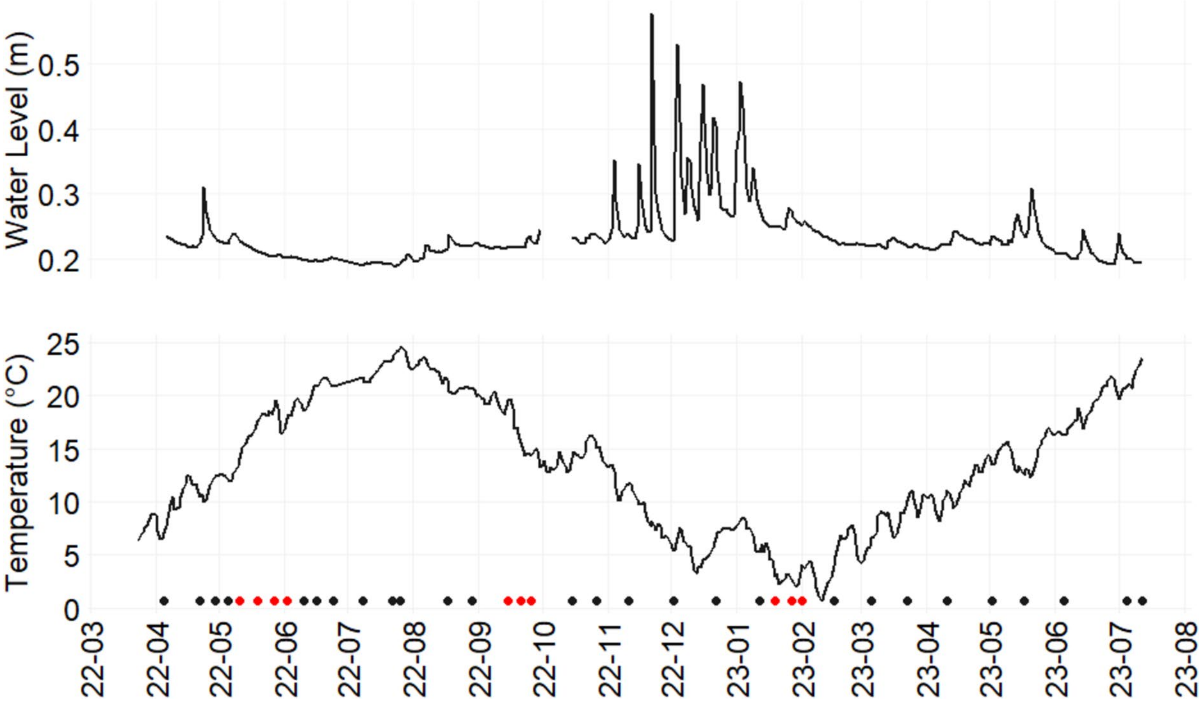

Fig. 2 Water level (m) and temperature (°C) patterns throughout the study period. Tracking events are indicated by black dots on the x-axis, whereas red dots denote coupled day-night tracking events. A water level-temperature sensor was deployed in the lower section (Fig. 1b), located 140 m upstream of the intermittent reach. Water level data is not available from 1 to 14 October 2022 due to technical problems

Table 1 The number of individuals tagged in March and October 2022 in each study section with fork length and weight data. In October, one fish was caught slightly upstream of the lower section, released at the captured location but assigned to the lower section

		Length (mm)				Weight (g)				
		Median	IQR	Min	Max	Median	IQR	Min	Max	*n*
March	**Lower**	76	19	60	140	5.7	5	2.6	36.7	201
	Middle	90	20	68	132	10.3	7.9	4.1	36.5	
	Upper	88	14	65	133	9.1	5.3	2.5	34.6	
October	**Lower**	78	20	61	145	5.3	4.6	2.6	34.9	159
	Middle	77	17	61	97	5.4	3.5	2.6	11.1	
	Upper	82	22	63	151	6.5	5.3	2.3	42.1	

the entire study reach was thoroughly scanned by wading upstream. Serial Bluetooth and Terminal, version 1.42, was used to display individual fish identification codes on an Android device. In a hydromorphological unit-based coordinate system, each fish was recorded with the date, time, depth, and position (±0.75 m), aided by a handheld rangefinder (Trupulse 360R Laser Technology). A visual observation of the fish or any movement that indicates a live fish was noted (Schiavon et al. 2024). A total of 37 tracking events were carried out between April 2022 and July 2023. In addition, 10 paired day-night tracking sessions were conducted to assess differences in diel behaviour in two subsections (lower section and upper section; Fig. 1b) of the study area: in spring 2022 (4 events), in late summer to early autumn 2022 (3 events), and in winter 2023 (3 events; Fig. 2). To assess the potential dispersal from the study reach, the reaches (≈ 150 m) upstream and downstream of the study reach were occasionally tracked (Fig. 1b).

Data analysis

Only fish assessed as alive at the time of detection were used in the analysis. This was deduced based on visual observations of the fish or movements against the current direction indicative of an alive specimen: small upstream distance movements (> 1 m) observed within a tracking session or larger (> 2 m) upstream movements between tracking occasions were considered as proof of a living fish. The alive status was then applied retrospectively, that is, if a fish is alive today it means it was alive since its tagging. Only fish with > 2 alive positions were included in the analysis. Fish from the three tagging sections were analysed together. Fish positions collected in the field were transformed into a linear reference system using the QGIS LRS plugin (LRS, version 1.2.3, retrieved from: http://blazek.github.io/lrs/). Two fish lacking length data from tagging were excluded from all analyses on the effects of length. Data on the sex of individuals were not collected, and therefore, potential sex-based differences could not be assessed.

Overall seasonal movement and habitat use

Linear range represents the distance between the most upstream and downstream positions observed for each fish during the tracking sessions and this metric is commonly used to describe home ranges in stream environments (Capra et al. 2018; Schiavon et al. 2024), Fish showed a widespread preference for pools that, therefore, became the focus of the habitat analysis. Pool use was quantified using a pool-score, the proportion of positions in pool habitat among all positions for the individual fish. Effects of fish length, pool score, and season (spring, 21 Mar–20 Jun; summer, 21 Jun–22 Sep; autumn, 23 Sep–20 Dec; winter, 21 Dec–20 Mar) on linear range were tested using linear mixed models with identification code (ID) as a random effect to account for repeated measures on the same fish. The number of detections (in respective seasons) was included in the model to consider potential effects on tracking time. Linear range and fish length were log-transformed to achieve a distribution suitable for the test. In the analysis, linear ranges calculated for the summer of 2023 were omitted due to the low number (2) of tracking sessions.

A preference for pools was tested by comparing pool scores (observed proportion) for each fish with the proportional area coverage of pools compared to the total area of the study reach (expected proportion if habitat distribution would be random). The habitat mapping in March 2022, representing an average flow condition, was used to estimate average habitat availability. To control for the effect of variable habitat availability under different flow conditions, the same test was performed per flow condition (as per the three habitat mappings) and period-specific habitat use and is presented in the Supplementary Material (Fig. S1). A Wilcoxon signed-rank test was used due to violations of the assumptions of normality and homogeneity of variance in the data. The effect of season and fish length on the habitat selection (pool yes/no) was tested using a generalised linear mixed model (GLMM) with ID as a random effect to account for repeated measures on the same fish.

Diurnal and nocturnal movement patterns, habitat use, and seasonal variability

Linear distance between day and night positions for the coupled tracking sessions was used to quantify the day-night range. We employed linear mixed models to analyse the influence of season and size on the day-night range, incorporating ID as a random effect to accommodate multiple measurements on individual fish. Paired day-night tracking session data was also used to test for diel patterns in habitat use. The effect of day/night on the habitat selection (pool yes/no) was tested using a generalised linear mixed model (GLMM) with ID as a random effect. Season (spring, late summer, and winter) and the interaction between the day-night and season were included in the model to test for seasonal differences in diel habitat use patterns.

Within pool movements

To evaluate within pool movements, minimum convex polygons (MCP) were estimated for fish with a minimum of ten valid detections within the same pool, excluding positions outside the residency pool. MCP is a common and straightforward method for estimating an organism's home range (Mohr 1947) and was calculated using adehabitatHR package in R (Calenge 2006) for each fish based on its positional coordinates. Extreme positions were excluded from the home range estimation by removing the 10% of relocations farthest away from the centroid to calculate 90% MCP (Calenge 2006). Our spatial estimates were refined by clipping the polygons derived from the MCP analysis to the contours of the known habitat pool, providing an actual spatial extent considering physical borders and barriers. We tested the effect of fish length and the number of detections on estimated home ranges using a linear mixed-effects model. The model included ‘length’ and ‘number of detections’ as fixed effects, with ‘pool ID’ as a random effect to account for repeated measures in the same pools. Models including pool area did not fulfil the model assumptions; instead, the relationship between pool area and home range was tested separately using Kendall’s tau-b correlation analysis.

Growth and apparent survival

In July 2023, fish were recaptured using electrofishing and measured for fork length. Growth was quantified for the fish tagged in spring and autumn 2022 separately. Similarly, recapture in July 2023 was taken as a proxy for apparent survival and quantified for the two groups separately. Effects of fish length, linear range, and pool score on growth and apparent survival were tested using linear and logistic regression, respectively.

Fish movement patterns in response to flood events

The study period lacked significant high-flow events. However, a significant flood occurred in the study area on 2–3 November, 2023, 4 months after the conclusion of the last tracking event conducted in July 2023. To take advantage of this event and to evaluate the potential movement response of *T. muticellus* to high-flow events, two additional not previously planned manual tracking sessions were carried out after the flooding across the entire study section and up to ≈ 150 m upstream and downstream of the study reach. Linear ranges for fish between June and November 2023, which included the period of the flood event, were then quantified and subsequently compared with the linear ranges of the same fish IDs throughout the entire study period from spring/autumn 2022 to summer 2023. Since the normality assumption was violated, we applied a non-parametric Wilcoxon signed-rank test for paired samples with a continuity correction to evaluate potential differences in the linear range.

Software

Statistical analyses were performed in RStudio (version 2022.02.2 ‘Prairie Trillium’ Release), and geospatial data processing was done in QGIS (version 3.24.3-Tisler). Data analysis was performed using the packages lme4 (Bates et al. 2015) and lmerTest (Kuznetsova et al. 2017), while model validations were carried out using the DHARMa package (Hartig and Hartig 2017).

Results

Overall and seasonal movement and habitat use

In total, 267 fish were tracked alive between 2 and 27 times (median = 7, IQR = 4–11) during the study period. The time interval between the first and last detections typically spanned over six months, with a median of 185 days (min–max = 7–462 days; IQR, 104–265 days). *T. muticellus* displayed a median linear home range of 16.4 m (min–max = 0.5–431.7 m; IQR, 6.6–49.8 m; Fig. 3a). Most of the fish (60%) remained within a localised area (± 10 m), whereas 27% of them moved upstream and 12% moved downstream (Fig. 3b). The distribution of linear ranges showed leptokurtosis (kurtosis = 10.4) and positive skewness (skewness = 3.0). For fish observed for over a year (*n* = 48), similar distribution patterns with positive kurtosis (kurtosis = 1.5) and skewness (skewness = 1.6) were found, indicating consistent distribution trends in linear home ranges across extended monitoring periods. Linear range was slightly but significantly higher in spring and autumn compared to summer and winter (Fig. 4; Table 2). Linear range tended to increase slightly with a decrease in pool preference but with a very small effect size (Table 2). The number of detections also influenced the estimated linear range; more detections were associated with a larger linear range. Fish length did not influence the linear range (Table 2).

Fish were tracked in pools, rapids, riffles, and glides but showed a strong preference for pool habitat (Fig. 5). Observed pool scores (median = 82.6%, IQR = 33–100%; mean = 65.8%, SE = 2.3%; Fig. 5) were much higher than the proportion of average pool habitat availability in the study system under average flow condition as determined by habitat mapping conducted in March 2022 (Wilcoxon, V = 32,992,

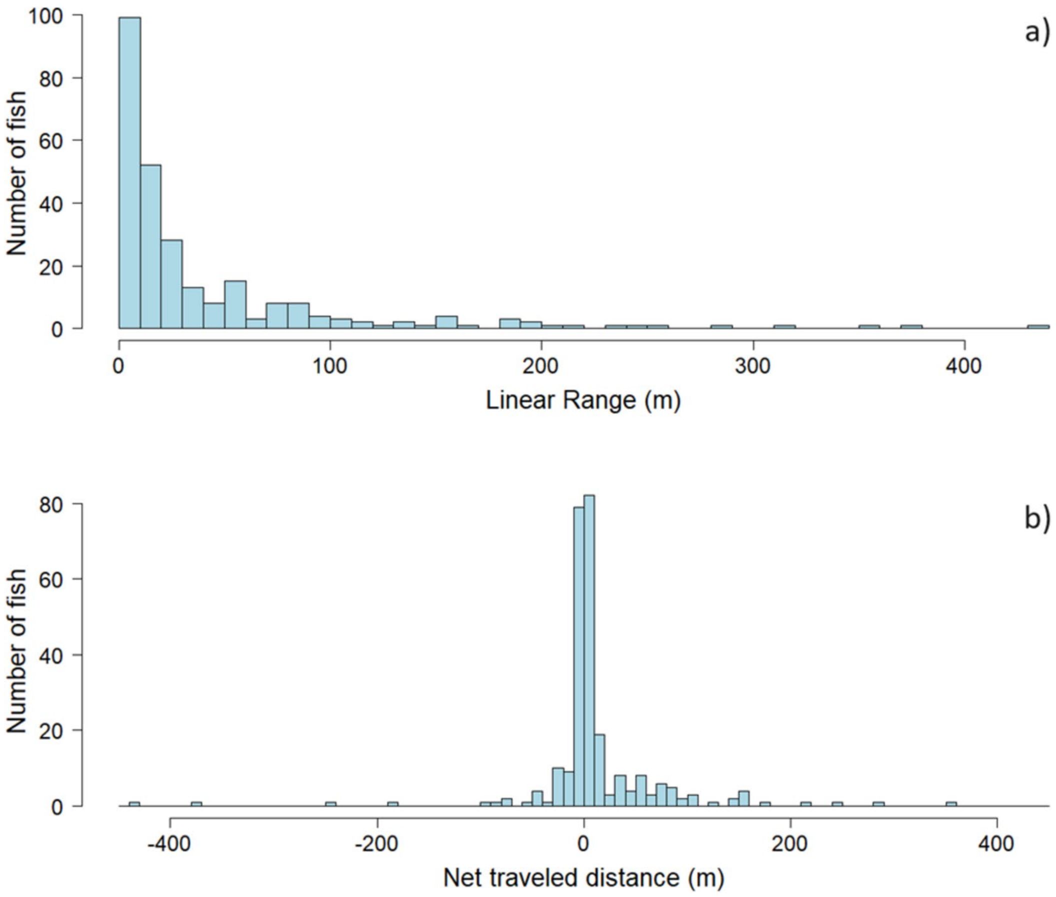

Fig. 3 Frequency distributions of movement metrics for 267 *T. muticellus* individuals in the Rio Morsone. **a** Linear range distribution demonstrates the limited movement of the sampled population, showcasing a leptokurtic distribution with the x-axis representing the linear range in m, and the y-axis indicating the count of fish. **b** Net travelled distance distribution, with positive values denoting upstream movement and negative values representing downstream movement

$p < 0.001$, $n = 238$). Although fish were mostly tracked in pools throughout the year, the pool preference was stronger in summer compared to autumn (GLMM; estimate $= -1.06489$, $p < 0.001$, $n = 265$), spring (GLMM; estimate $= -1.23439$, $p < 0.001$), and winter (GLMM; estimate $= -1.58916$, $p < 0.001$). No effect of fish length on pool use was detected (GLMM; $p = 0.230$).

Diurnal and nocturnal movement patterns, habitat use, and seasonal variability

Fish displayed small linear positional change between the paired day-night tracking sessions with a median day-night range of 1.5 m (min–max = 0–25.0 m; IQR, 0.5–3.9 m; $n = 132$). There was no effect of fish size on the extent of day-night movements (LMM; coefficient estimate $= 0.03$, $p > 0.15$, $n = 130$), but the day-night range was higher in spring than in late summer (LMM; coefficient estimate $= -0.2072$, $p = 0.005$). There was no difference between spring and winter (LMM; coefficient estimate $= -0.11$, $p = 0.11$). No effect of time of day (day-night; GLMM; $p = 0.36$, $n = 175$) or the interaction between time of day and season (GLMM, $p = 0.19$) on habitat choice (pool use) was detected. As for the general tracking data, the paired night-day data showed a stronger preference for pools in summer compared to spring (GLMM; coefficient estimate $= -2.9685$, $p = 0.01$) and winter (GLMM; coefficient estimate $= -4.4339$, $p < 0.01$).

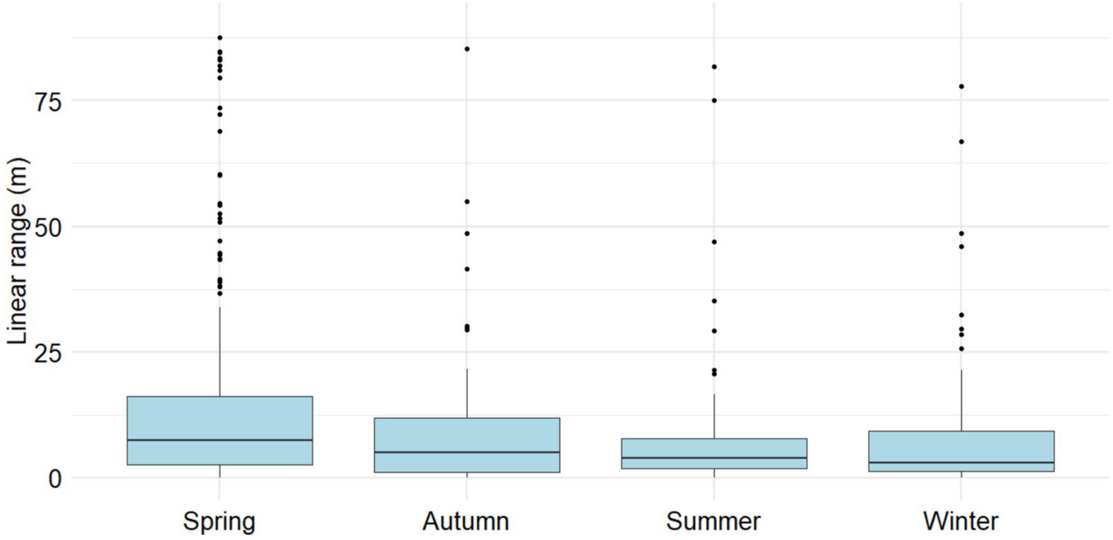

Fig. 4 Box plots of seasonal variation in the linear range (m) of *T. muticellus*. The box shows the interquartile ranges of detections for each season, and the whiskers indicate the 1.5 IQR range, with medians indicated by the horizontal line

Table 2 Summary of linear mixed model testing for effects on the linear range (logged transformed) of season, length (log-transformed), pool score, and the total number of detections. For the season, spring is the baseline category

Variable	Estimate	SD	*t*-value	*p*
Intercept	− 1.436	1.926	− 0.750	0.460
Autumn	− 0.145	0.210	− 0.690	0.490
Summer	− 0.722	0.188	− 3.840	< 0.001
Winter	− 0.671	0.181	− 3.700	< 0.001
Length	0.727	0.432	1.680	0.090
Number of detections	0.261	0.043	6.010	< 0.001
Pool score	− 0.011	0.002	− 4.970	< 0.001

Within pool movements

The minimum convex polygon (MCP) was calculated for 54 fish in 11 different pools. The median number of detections per fish in the respective pool was 15 (IQR = 13–20, min–max = 10–27), and the median monitoring period was 413 days (IQR = 225–439, min–max = 84–462). On average, these fish were detected 1.3 times outside their focal pool (median = 0, IQR = 0–1). The estimated 90% MCP home range was small, with a median value of 8.1 m^2 (IQR = 2.9–13.1, min–max = 0.1–29.8 m^2; see Fig. 6 and Supplementary Material Fig. S2). No effect of length or number of detections was detected (LMM; $p = 0.31$). The average pool area was 27.8 m^2 (range = 5.2–83.4 m^2), and the individual home ranges covered 1.2–58.0% (median = 17.6%) of the pool area. There was a statistically significant positive correlation (Kendall's tau = 0.381, $p < 0.001$) between pool area and home range. For fish with at least one other tagged fish present in a pool, individual home ranges overlapped with a median of 8 other tagged fish home ranges (range 1–16). The proportion of the home range that overlapped with one or more fish was on average 65.7% (median, range 16–100%). In all pools, non-tagged fish were also present, likely increasing both the number and the proportion of home-range overlap.

Growth and apparent survival

Forty-four fish tagged in spring 2022 were recaptured 478 days later, in July 2023. These fish had grown 11.6 ± 7.8% in length during this period. For fish tagged in autumn 2022, the length increases until July 2023 (258 days) was 7.9 ± 5.0% ($n = 69$). These length increases correspond to average daily growth rates of (mean ± SD) 0.03 ± 0.01% and 0.03 ± 0.02% for the two periods respectively. Smaller fish grew relatively faster than larger fish in both groups (Table 3). No effect on growth of linear range or pool score was detected (Table 3a) for the

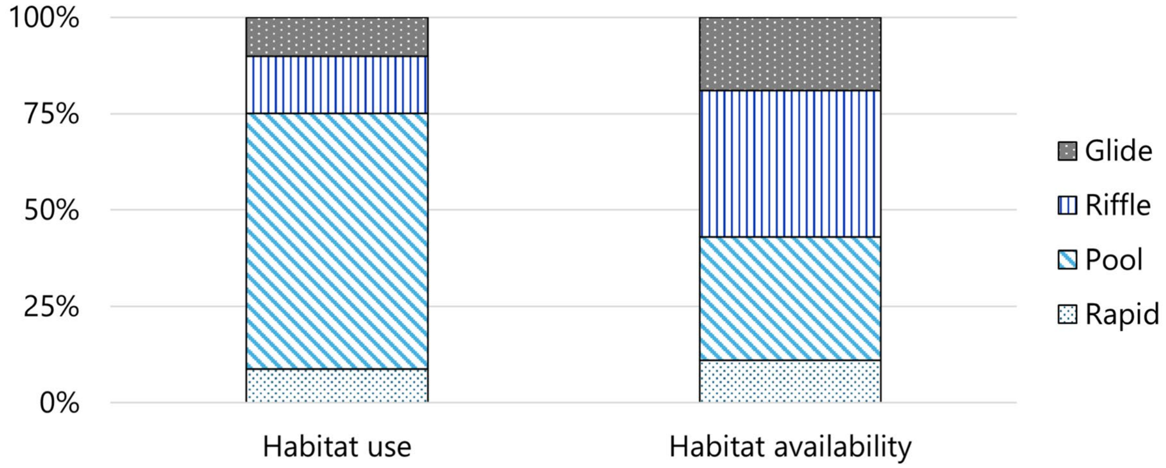

Fig. 5 Habitat use and availability. The left bar (habitat use) shows the percentage of positions within rapids, riffles, glides, and pools based on individual means. The right bar (habitat availability) shows the percentage of available habitat area for the same habitat types according to the habitat mapping under average flow conditions in March 2022

spring-tagged fish. However, a very small but statistically significant effect of pool score was detected for autumn-tagged fish (Table 3b).

Recapture in July 2023 was taken as a proxy for apparent survival. From the fish with at least two detections, 30% (45 of 148) tagged in spring 2022 (478 days) and 58% (69 of 119) tagged in fall 2023 (258 days) were recaptured. This corresponds to an apparent survival rate of 99.8% per day for both groups of fish. There was no effect of pool score, linear range, or fish length on recapture probability for any of the two tagging groups (logistic regression, $p > 0.08$; $n = 147$ and $n = 119$).

Fish movement patterns in response to flood events

A total of 36 alive fish were detected during the two tracking sessions after the flood events in November 2023. For these fish, the median linear range was 36.4 m during the summer-autumn period (overlapping with the high flow event) compared to 17.6 m during the whole study period. This difference was statistically significant (Wilcoxon, $V = 510$, $p < 0.01$, Fig. 7). From July to November, 33% of fish exhibited downstream movement, 22% displayed minimal mobility (less than 10 m displacement), and 44% of the observed fish showcased upstream movements.

Discussion

In this study, *T. muticellus* was tracked for over 15 months in a small mountain stream. Most fish remained relatively stationary, while a few roamed over several hundreds of metres. *T. muticellus*, although relatively resident the whole year, covered a larger linear range during spring and autumn compared to the other seasons. The fish showed a strong preference for pools, and this preference was more pronounced in summer compared to spring, autumn, and winter. They remained stationary with no difference in habitat use between day and night. Fish size did not influence movement range or habitat use. Within pools, many *T. muticellus* displayed remarkably small home ranges.

Half of the tracked fish displayed a linear range of less than 17 m, while a minority embarked on movements of up to 400 m. Similar studies have been carried out on, for example, Brown trout (*Salmo trutta*) (Watz et al. 2016), Atlantic salmon (*Salmo salar*) (Stickler et al. 2008), European eel (*Anguilla anguilla)* (Nzau Matondo et al. 2019), and mottled sculpins (*Cottus bairdii*) (Breen et al. 2009). In these studies, as in ours, the tracked fish can be categorised into stationary (the majority) and more mobile (the minority) fish. Similar patterns

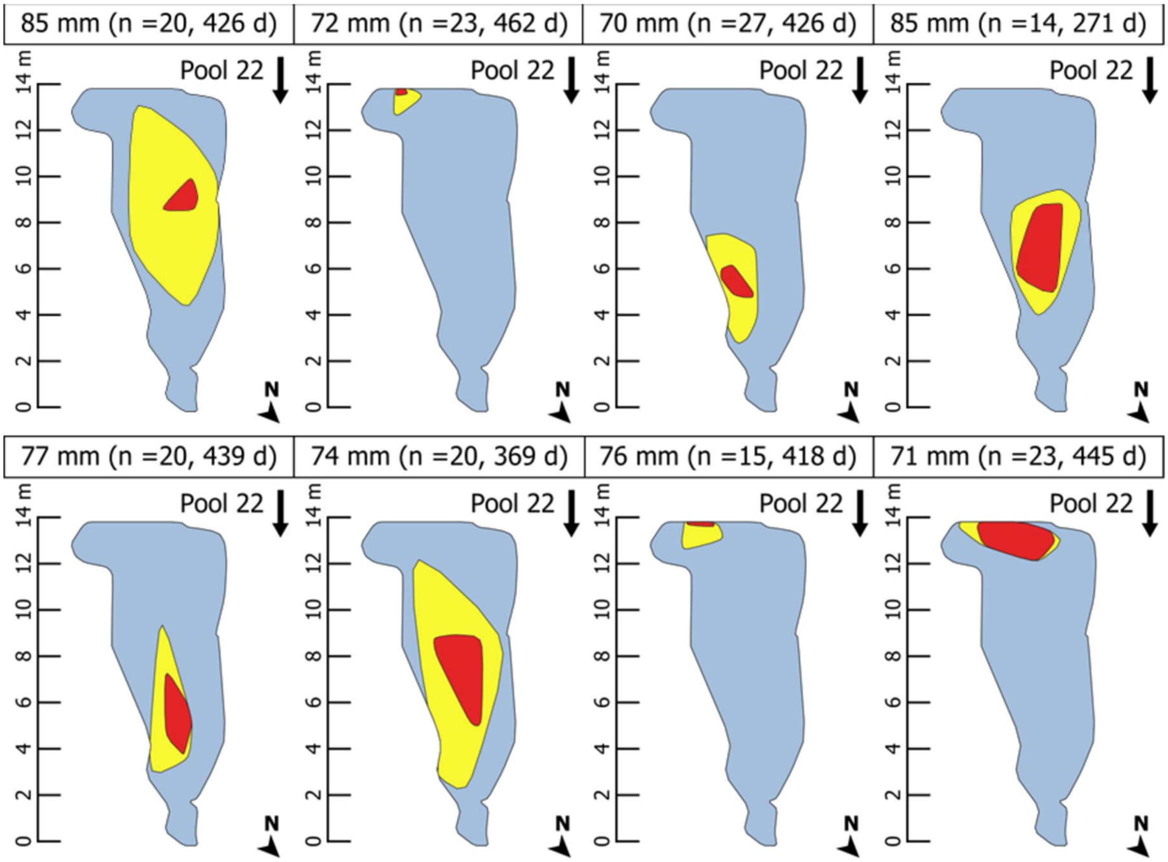

Fig. 6 Estimated 90% (yellow) and 50% (red) minimum convex polygon home ranges, based on the cumulative observations of 8 *T. muticellus* individuals within a single pool (Pool 22; blue) in the Rio Morsone. Fork length (mm), number of detections, and the duration (days) from the first to last detection are given for each fish within the plot. The black arrow indicates the direction of stream flow, and the compass arrow is the direction of the geographical north. The corresponding figure for all 54 fish, spread over 11 pools, is available in Supplementary Material (Fig. S2)

Table 3 Effect of linear range, pool score, and fish length (mm) on growth until July 2023 for fish tagged in a) spring 2022 (478 days, $n=45$) and b) autumn 2022 (258 days, $n=69$)

Variable	Estimate	SD	*t*-value	*p*
a) Growth from spring 2022 to summer 2023				
Intercept	0.598	0.554	1.081	0.286
Linear range	− 0.001	0.001	− 1.231	0.226
Pool score	− 0.002	0.003	− 0.824	0.415
Length	− 0.030	0.006	− 5.251	< 0.001
b) Growth from autumn 2022 to summer 2023				
Variable	**Estimate**	**SD**	***t*-value**	***p***
Intercept	− 0.605	0.13	− 4.78	< 0.001
Linear range	0.000	0.004	0.010	0.990
Pool score	− 0.002	0.001	− 2.570	0.010
Length	− 0.013	0.002	− 8.390	< 0.001

are also reported for cyprinids in larger river systems (De Leeuw and Winter 2008) and from mark-recapture studies on gudgeon (*Gobio gobio*) (Stott 1967) and bullhead (*Cottus gobio*) (Knaepkens et al. 2004), as well as several salmonid species (Heggenes 1988a, b; Nakano et al. 1990; Heggenes et al. 1991). Although close access to suitable habitat through the stream likely reduces the need to move long distances for our tagged fish, the pattern of movers and stayers is, in fact, present in a wide range of fish. At the population level, the minority of movers can be crucial for inter-population connectivity (Gowan et al. 1994) and play a decisive role in dispersal, colonisation, and recolonisation processes (Radinger and Wolter 2014). At the individual level, mobility may be a way to avoid (or a

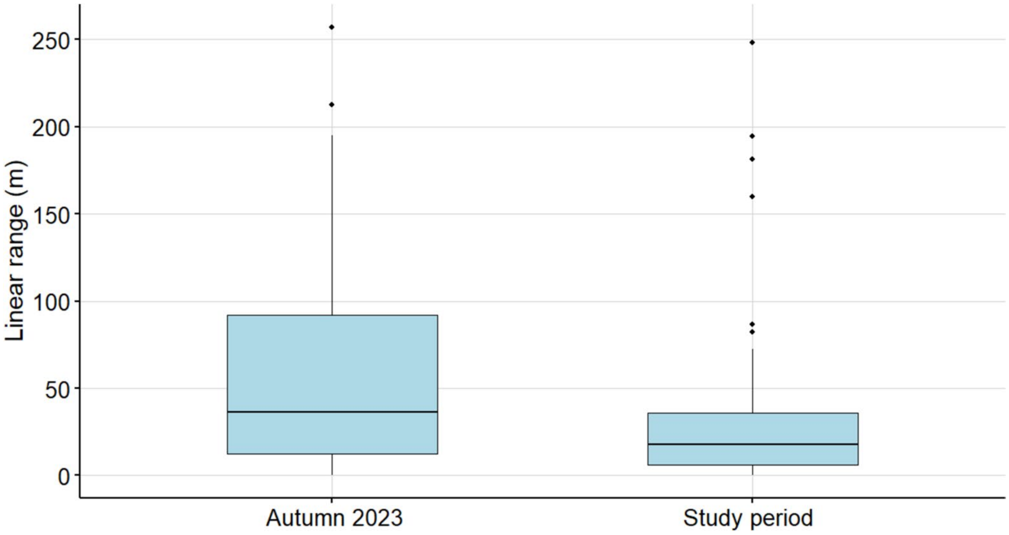

Fig. 7 Boxplot comparisons of the overall study period linear ranges versus the linear ranges from June 2023 to November 2023, for individual *T. muticellus* ($n = 36$). The plots highlight interquartile ranges (IQR) with boxes, whiskers with 1.5 IQR, and median values with horizontal lines; the points represent outliers

consequence of) competition (Hesthagen 1988) or to search for resources (Gowan 2007). What makes a fish stationary or resident has been attributed to personality, with stream movements correlating with other behavioural characteristics (Fraser et al. 2001). Sometimes, distance moved has been reported to correlate with size (Woolnough et al. 2009; Burbank et al. 2023), potentially related to aggressive interactions (Hilderbrand and Kershner 2004). We did not find any effect of fish size on the interindividual difference in movement, and future studies may further explore personality differences in these stream fish.

Albeit most *T. muticellus* were relatively stationary throughout the year, somewhat larger movement ranges were revealed during spring and autumn compared to the other seasons. In addition to lower activity in the cold winter water, accompanied by low prey densities (Shuter et al. 2012; Speers-Roesch et al. 2018) and restricted movement due to lower water levels in the summer (Pires et al. 2014), several factors may contribute to this result. Following the winter season, fish may become more active in anticipation of and during the spawning season. As this season approaches, the need to find appropriate spawning sites for reproduction may drive their movements. There is anecdotal evidence of other *Telestes* species partaking in spawning migrations to gravel substrate spawning sites (Barbieri et al. 2020). Although we did not observe any directed spawning migration, perhaps due to the high occurrence of spatially dispersed suitable spawning habitats in the stream, longitudinally undirected small-scale movements to find suitable spawning habitats are likely to occur. In addition, a subsection of the stream was also drying out during both spring seasons, causing fish present to migrate upstream to permanently wet areas resulting in higher movement ranges for these individual fish compared to neighbouring fish from perennially wetted reaches (Schiavon et al. 2024). Importantly, however, excluding these fish from our analysis does not change the results indicating that any movement triggered by lower water levels is a stream-wide phenomenon and not driven by the fish that were inhabiting the intermittent reach. In autumn, on the other hand, fish might move more to adjust to higher water levels after a dry summer, or in anticipation of overwintering (Heggenes and Saltveit 1990).

Fish habitat choice is typically the result of a trade-off between food availability, energetics, and predation risk and can be modulated by intraspecific interactions (Allouche and Gaudin 2001; Hölker et al. 2007; Piccolo et al. 2008; Naman et al. 2019). The tagged *T. muticellus*, despite its common name (Italian riffle dace), showed a strong preference for pools compared to other hydro-morphological habitat types. *T. muticellus* is considered an omnivore (Fortini 2016). During the study, fish were observed to feed from the bottom and along the water column, as well as swiftly striking at falling invertebrates at the surface and even jumping to feed on insects outside of the water. Consequently, food availability in pools can be assumed to be sufficient (Gustafsson et al. 2013), and prey is easier to catch than in more fast-flowing water (Piccolo et al. 2008). In addition, the low water velocity in the pools should reduce the cost of swimming for the fish, further adding to the benefits of pool residency (Videler 1993). Finally, fish may be less susceptible to predation in pools, especially in the deeper parts with access to refuges, compared to other shallower and more fast-flowing waters (Harvey and Stewart 1991). Juvenile coho salmon, for example, have been seen retreating to pools when predators are detected (Mason and Chapman 1965). Also, except for a few brown trout individuals, the stream was deprived of piscivorous predators, likely contributing to low predation risk in pools (Schlosser 1987). The even stronger preference for pools in summer is likely due to slight reductions in water levels, making other habitats even less suitable.

Interestingly, we observed an inverse correlation between pool preference and linear range; fish that displayed large moving ranges were also found in non-pool habitats such as riffle and glides to a relatively higher degree. The pattern that pool dwellers move less than fish that prefer shallow habitats has also been found for stream Catalonian barbel (Aparicio and De Sostoa 1999), cutthroat trout, and brown trout (Heggenes 1988a, b; Heggenes et al. 1991). In salmonids, however, these dynamics have been related to aggressive interactions and dominance hierarchies, with weaker competitors moving more (Nakano et al. 1990) and often residing in suboptimal habitats (Heggenes 1988a, b). Aggressive interactions, however, are not considered to play a major role in *T. muticellus* repertoire (not observed nor in this study or in laboratory studies; Schiavon et al. 2023; Tarena et al. 2023). Instead, the correlation between pool use and movement could be part of alternative strategies for finding and exploiting resources (Logan and Brooker 1983). Future studies are needed to explore these dynamics.

Within pools, numerous *T. muticellus* exhibited remarkable residency, with half of the home ranges being less than 8 m^2. Although home range correlated with pool area, most of the fish occupied only a small portion (median 18% of the total available pool space). To the best of our knowledge, this is the first time that such a restricted range has been recorded for a cypriniform fish. In salmonids, small home ranges are often related to territoriality and aggressive interactions (Watz et al. 2015), leading to dominance-related access to preferable feeding habitats (Nakano et al. 1990). Many other fish species defend territories during spawning (Tinbergen 1952; Bisazza and Marconato 1988). For *T. muticellus*, however, as mentioned above, no aggressive interactions have been observed, and the pattern is consistent for extended periods of time. The limited home range is even more surprising given that this species often displays an apparent roaming behaviour, intuitively conductive for movements over the whole pool. Even in environments with relatively uniform habitat quality, there can, however, be advantages of a restricted home range. By being in a familiar environment, fish are able to find shelters faster or more efficiently (Aronson 1971; Markel 1994). Learning about their immediate surroundings could also help fish exploit the hydrodynamic environment or food resources more efficiently (Brown and Schluessel 2023; Tarena et al. 2023). There is also the possibility that the limited home range within the pool has been partially caused by the tracking methodology, as fish return to shelters in response to the tracking disturbance. In any case, this behaviour indicates an affinity with specific subsections of the pool. Future studies, perhaps utilising an array of fixed stationary PIT-antennas (Whoriskey et al. 2019) or advanced video tracking (Zhang et al. 2022), should further explore the site fidelity of *T. muticellus* within pools.

Although we tracked a large subset of the population of *T. muticellus* in the study section of the Rio Morsone, our results say nothing about the movement of fish smaller than 6 cm. As for many species, the movement and displacement dynamics of fry and young fish remain unexplored (Lechner et al. 2016). Also, our tracking interval could have potentially missed movements of short intervals. For example, we observed only a modest increase in linear range during spring, the spawning season, and no clear directed movement. This, however, does not exclude limited return movements at a time scale shorter than our tracking interval, for example, a few days, as observed in other cypriniforms (Fredrich et al. 2003).

Additionally, the *T. muticellus* also inhabits larger rivers and streams, with stronger currents, deeper water, and less structure (Fortini 2016), and studying their movement behaviour in this different type of habitat is necessary for a more complete description of the species movement ecology.

The study period was characterized by the absence of significant high-flow events during the main study period. Interestingly, heavy rains in the autumn following the end of the study allowed us to track, during two extra surveys, tagged fish remaining in the system. This tracking revealed larger linear ranges during the 3–4 months from the end of the study to the post-flood tracking than during the full study period. By chance, 20 fish from our study were positioned in a separate pool study (unpublished) a few days before the high flow events on 25 October, showing that fish remained relatively close to their summer positions (range ± 12 m). This observation supports the idea that the fish were largely stationary during months without monitoring and that the autumn floods subsequently triggered longer movements in both directions within the system. Dispersal during high-flow events has been seen in a range of species (Schlosser 1987) and suggested to be a mechanism to access spawning or feeding habitat or to locate refuge from the flood itself (Albanese et al. 2004). Our results suggest that high-flow events are of high importance for the dispersal of *T. muticellus*, and may contribute to both up- and downstream movements in small mountain streams.

To our knowledge, together with a complementary study (Schiavon et al. 2024), this is the first time individual fish have been tracked over a prolonged period in a small Mediterranean stream. *T. muticellus* showed a strong preference for pools, and while most fish remained relatively stationary, a minority displayed linear ranges of several hundreds of meters. Our study provides valuable first insights into the movement ecology of an understudied endemic species. For practical purposes, despite the relatively high residency displayed by the studied fish, river management efforts need to ensure longitudinal connectivity for dispersal movements, refuge migration in relation to low water levels (Schiavon et al. 2024), and for the fish to cope with high flow events. In general, expanding the knowledge of understudied freshwater fish species, such as *T. muticellus*, is a critical priority for promoting coordinated efforts in the sustainable management and conservation of freshwater ecosystems (Negro et al. 2021; Maasri et al. 2022; Vøllestad 2023).

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Author contribution Conceptualisation, developing methods, and data interpretation: A.S., D.N., C.C., F.H., J.W., M.S., and A.C.; conducting the research: A.S., D.N., M.S., C.C., and A.C.; data analysis and writing: A.S., D.N., C.C., F.H. and J.W.; preparation figures and tables: A.S., and D.N.; funding: C.C., and F.H.

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Data availability The dataset is generated for this study. The data that support the findings of this study are available from the corresponding author.

Declarations

Ethics approval We conducted this study in accordance with the Ufficio Tecnico Faunistico e Ittiofauna of the Provincia di Alessandria (authorization numbers 65493 and DDAP2-939, dated November 11, 2021), as defined in Article 2 of Decree No.26/2014 (implementation of Directive 2010/63/EU), and with Aree Protette Appennino Piemontese's agreement (authorisation number: 1072, dated 15 February 2022).

Conflict of interest The authors declare no competing interests.

References

Albanese B, Angermeier PL, Dorai-Raj S (2004) Ecological correlates of fish movement in a network of Virginia streams. Can J Fish Aquat Sci 61(6):857–869. https://doi.org/10.1139/f04-096

Allen AM, Singh NJ (2016) Linking movement ecology with wildlife management and conservation. Front Ecol Evol 3:155. https://doi.org/10.3389/fevo.2015.00155

Allouche S, Gaudin P (2001) Effects of avian predation threat, water flow and cover on growth and habitat use by chub, *Leuciscus cephalus*, in an experimental stream. Oikos 94:481–492. https://doi.org/10.1034/j.1600-0706.2001.940310.x

Aparicio E, De Sostoa A (1999) Pattern of movements of adult *Barbus haasi* in a small Mediterranean stream. J Fish Biol 55:1086–1095. https://doi.org/10.1111/j.1095-8649.1999.tb00743.x

Aparicio E, Rocaspana R, De Sostoa A, Palau-Ibars A, Alcaraz C (2018) Movements and dispersal of brown trout (*Salmo trutta* Linnaeus 1758) in Mediterranean streams: influence of habitat and biotic factors PeerJ 6:e5730. https://doi.org/10.7717/peerj.5730

Aronson LR (1971) Further studies on orientation and jumping behavior in the gobiid fish, *Bathygobius soporator*. Ann N Y Acad Sci 188:378–392. https://doi.org/10.1080/24705357.2021.1892547

Barbieri R, Stoumboudi M, Kalogianni E, Leonardos I (2020) Spawning migration and early life development of a cyprinid species of the genus *Telestes*. J Appl Ichthyol 36(5):817–824. https://doi.org/10.1111/jai.14094

Bates D, Mächler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models using lme4. J Stat Softw 67(1):1–48. https://doi.org/10.18637/jss.v067.i01

Bisazza A, Marconato A (1988) Female mate choice, male-male competition and parental care in the river bullhead, *Cottus Gobio* L. (Pisces, Cottidae). Anim Behav 36(5):1352–1360. https://doi.org/10.1016/S0003-3472(88)80204-5

Booth MT, Hairston NG, Flecker AS (2013) How mobile are fish populations? Diel movement, population turnover, and site fidelity in suckers. Can J Fish Aquat Sci 70(5):666–677. https://doi.org/10.1139/cjfas-2012-0334

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 Sci 66:31–41. https://doi.org/10.1139/F08-189

Brodersen J, Hansen JH, Skov C (2019) Partial nomadism in large-bodied bream (*Abramis brama*). Ecol Freshw Fish 28(4):650–660. https://doi.org/10.1111/eff.12483

Brown C, Schluessel V (2023) Smart sharks: a review of chondrichthyan cognition. Anim Cogn 26(1):175–188. https://doi.org/10.1007/s10071-022-01708-3

Buj I, Marčić Z, Ćaleta M, Šanda R, Geiger MF, Freyhof J, Machordom A, Vukić J (2017) Ancient connections among the European rivers and watersheds revealed from the evolutionary history of the genus *Telestes* (Actinopterygii; Cyprinidae). PLoS ONE 12(12):e0187366. https://doi.org/10.1371/journal.pone.0187366

Burbank J, Gao K, Power M (2023) Factors influencing the home range of freshwater fishes. Ecol Freshw Fish 32:916–925. https://doi.org/10.1111/eff.12732

Calenge C (2006) The package "adehabitat" for the R software: a tool for the analysis of space and habitat use by animals. Ecol Model 197(3–4):516–519. https://doi.org/10.1016/j.ecolmodel.2006.03.017

Capra H, Pella H, Ovidio M (2018) Individual movements, home ranges and habitat use by native rheophilic cyprinids and non-native catfish in a large regulated river. Fish Manag Ecol 25(2):136–149. https://doi.org/10.1111/fme.12272

Closs G, Krkosek M, Olden JD (Eds) (2016) Conservation of freshwater fishes. Cambridge University Press, Cambridge

Cooke SJ, Bergman JN, Twardek WM et al (2022) The movement ecology of fishes. J Fish Biol 101(4):756–779. https://doi.org/10.1111/jfb.15153

Crossin GT, Heupel MR, Holbrook CM, Hussey NE, Lowerre-Barbieri SK, Nguyen VM, Raby GD, Cooke SJ (2017) Acoustic telemetry and fisheries management. Ecol Appl 27(4):1031–1049. https://doi.org/10.1002/eap.1533

De Leeuw JJ, Winter HV (2008) Migration of rheophilic fish in the large lowland rivers Meuse and Rhine, the Netherlands. Fish Manag Ecol 15(5–6):409–415. https://doi.org/10.1111/j.1365-2400.2008.00626.x

Dubut V, Fouquet A, Voisin A, Costedoat C, Chappaz R, Gilles A (2012) From late Miocene to Holocene: processes of differentiation within the *Telestes* genus (Actinopterygii: Cyprinidae). PLoS ONE 7(3):e34423. https://doi.org/10.1371/journal.pone.0034423

Elliott JM (1994) Quantitative ecology and the brown trout. Oxford University Press, Oxford

Englund G, Krupa JJ (2000) Habitat use by crayfish in stream pools: influence of predators, depth and body size. Freshw Biol 43:75–83. https://doi.org/10.1046/j.1365-2427.2000.00524.x

Fortini N (2016) Nuovo atlante dei pesci delle acque interne italiane: Guida completa ai pesci, ciclostomi e crostacei decapodi di acque dolci e salmastre. Aracne editrice, Canterano

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. https://doi.org/10.1086/321307

Fredrich F, Ohmann S, Curio B, Kirschbaum F (2003) Spawning migrations of the chub in the River Spree, Germany. J Fish Biol 63:710–723. https://doi.org/10.1046/j.1095-8649.2003.00184.x

Gerking SD (1959) The restricted movement of fish. Biol Rev 34(2):221–242. https://doi.org/10.1111/j.1469-185X.1959.tb01289.x

Gowan C (2007) Short-term cues used by foraging trout in a California stream. Environ Biol Fishes 78:317–331. https://doi.org/10.1007/s10641-006-9099-z

Gowan C, Young MK, Fausch KD, Riley SC (1994) Restricted movement in resident stream salmonids: a paradigm lost? Can J Fish Aquat Sci 51(11):2626–2637. https://doi.org/10.1139/f94-262

Gross MR (1991) Salmon breeding behavior and life history evolution in changing environments. Ecology 72(4):1180–1186. https://doi.org/10.2307/1941091

Gustafsson S, Österling M, Skurdal J, Schneider LD, Calles O (2013) Macroinvertebrate colonization of a nature-like fishway: the effects of adding habitat heterogeneity. Ecol Eng 61:345–353. https://doi.org/10.1016/j.ecoleng.2013.09.023

Hartig F, Hartig MF (2017) Package "DHARMa." R Development Core Team, Vienna, Austria

Harvey BC, Stewart AJ (1991) Fish size and habitat depth relationships in headwater streams. Oecologia 87:336–342. https://doi.org/10.1007/BF00634588

Harvey BC, Nakamoto RJ, White JL (1999) Influence of large woody debris and a bankfull flood on movement of adult resident coastal cutthroat trout (*Oncorhynchus clarki*) during fall and winter. Can J Fish Aquat Sci 56(11):2161–2166. https://doi.org/10.1139/f99-154

Heggenes J (1988) Effect of experimentally increased intraspecific competition on sedentary adult brown trout (*Salmo trutta*) movement and stream habitat choice. Can J Fish Aquat Sci 45:1163–1172. https://doi.org/10.1139/f88-139

Heggenes J (1988) Effects of short-term flow fluctuations on displacement of, and habitat use by, brown trout in a small stream. Trans Am Fish Soc 117(4):336–344. https://doi.org/10.1577/1548-8659(1988)117%3c0336:EOSFFO%3e2.3.CO;2

Heggenes J, Saltveit SJ (1990) Seasonal and spatial microhabitat selection and segregation in young Atlantic salmon (*Salmo salar* L.) and brown trout (*Salmo trutta* L.) in a Norwegian river. J Fish Biol 36(5):707–720. https://doi.org/10.1111/j.1095-8649.1990.tb04325.x

Heggenes J, Northcote TG, Peter A (1991) Spatial stability of cutthroat trout (*Oncorhynchus clarki*) in a small, coastal stream. Can J Fish Aquat Sci 48:757–762. https://doi.org/10.1139/f91-090

Helfman GS (1986) Fish behaviour by day, night and twilight. In: Pitcher TJ (ed) The Behaviour of Teleost Fishes. Springer, Boston, MA, pp 366-387

Herrera-R GA, Heilpern SA, Couto TB, Victoria-Lacy L, Duponchelle F, Correa SB, Anderson EP (2024) A synthesis of the diversity of freshwater fish migrations in the Amazon basin. Fish Fish 25(1):114–133. https://doi.org/10.1111/faf.12795

Hesthagen T (1988) Movements of brown trout (Salmo trutta) and juvenile Atlantic salmon (*Salmo salar*) in a coastal stream in northern Norway. J Fish Biol 32:639–653. https://doi.org/10.1111/j.1095-8649.1988.tb05404.x

Hicks KA, Servos MR (2017) Site fidelity and movement of a small-bodied fish species, the rainbow darter (*Etheostoma caeruleum*): Implications for environmental effects assessment. River Res Appl 33(7):1016–1025. https://doi.org/10.1002/rra.3161

Hilderbrand RH, Kershner JL (2000) Movement patterns of stream-resident cutthroat trout in Beaver Creek. Idaho-Utah Trans Am Fish Soc 129(5):1160–1170. https://doi.org/10.1577/1548-8659(2000)129%3c1160:MPOSRC%3e2.0.CO;2

Hilderbrand RH, Kershner JL (2004) Are there differences in growth and condition between mobile and resident cutthroat trout? Trans Am Fish Soc 133:1042–1046. https://doi.org/10.1577/T03-015.1

Hölker F, Dörner H, Schulze T, Haertel-Borer SS, Peacor SD, Mehner T (2007) Species-specific responses of planktivorous fish to the introduction of a new piscivore: implications for prey fitness. Freshw Biol 52(9):1793–1806. https://doi.org/10.1111/j.1365-2427.2007.01810.x

Hughes K, Harrison I, Darwall W (2021) The world's forgotten fishes. World Wide Fund for Nature (WWF)

IPBES (2019) Global assessment report on biodiversity and ecosystem services of the intergovernmental science-policy platform on biodiversity and ecosystem services. In: Brondizio ES, Settele J, Díaz S, Ngo HT (eds) IPBES Secretariat, Bonn, Germany. https://doi.org/10.5281/zenodo.3831673

ISO 748: 2021 Hydrometry. Measurement of liquid flow in open channels. Velocity area methods using point velocity measurements. https://www.iso.org/obp/ui/en/#iso:std:72754:en

Jonsson B, Jonsson N (2011) Ecology of atlantic salmon and brown trout: habitat as a template for life histories. Fish & Fisheries Series, vol. 33. Springer, Dordrecht

Knaepkens G, Bruyndoncx L, Eens M (2004) Assessment of residency and movement of the endangered bullhead (*Cottus gobio*) in two Flemish rivers. Ecol Freshw Fish 13:317–322. https://doi.org/10.1111/j.1600-0633.2004.00065.x

Kuznetsova A, Brockhoff PB, Christensen RHB (2017) lmerTest package: tests in linear mixed effects models. J Stat Softw 82(13). https://doi.org/10.18637/jss.v082.i13

Lechner A, Keckeis H, Humphries P (2016) Patterns and processes in the drift of early developmental stages of fish in rivers: a review. Rev Fish Biol Fisheries 26:471–489. https://doi.org/10.1007/s11160-016-9437-y

Logan P, Brooker MP (1983) The macroinvertebrate faunas of riffles and pools. Water Res 17(3):263–270. https://doi.org/10.1016/0043-1354(83)90088-6

Lucas MC, Baras E, Thom TJ, Duncan A, Slavík O (2001) Migration of freshwater fishes. Blackwell Science Ltd, Oxford

Maasri A, Jähnig SC, Adamescu MC et al (2022) A global agenda for advancing freshwater biodiversity research. Ecol Lett 25(2):255–263. https://doi.org/10.1111/ele.13931

Marchetto F, Zaccara S, Muenzel FM et al (2010) Phylogeography of the Italian vairone (*Telestes muticellus*, Bonaparte 1837) inferred by microsatellite markers: evolutionary history of a freshwater fish species with a restricted and fragmented distribution. BMC Evol Biol 10:111. https://doi.org/10.1186/1471-2148-10-111

Markel RW (1994) An adaptive value of spatial learning and memory in the blackeye goby (*Coryphopterus nicholsi*). Anim Behav 47(6):1462–1464. https://doi.org/10.1006/anbe.1994.1194

Marnane MJ (2000) Site fidelity and homing behaviour in coral reef cardinalfishes. J Fish Biol 57(6):1590–1600. https://doi.org/10.1111/j.1095-8649.2000.tb02234.x

Mason JC, Chapman DW (1965) Significance of early emergence, environmental rearing capacity, and behavioral ecology of juvenile coho salmon in stream channels. J Fish Res Board Can 22(1):173–190. https://doi.org/10.1139/f65-015

Mellina E, Hinch SG, MacKenzie KD, Pearson G (2005) Seasonal movement patterns of stream-dwelling rainbow trout in north-central British Columbia. Canada Trans Am Fish Soc 134(4):1021–1037. https://doi.org/10.1577/T03-188.1

Milner-Gulland EJ, Fryxell JM, Sinclair ARE (2011) Animal migration: a synthesis. Oxford Academic, Oxford

Mohr CO (1947) Table of equivalent populations of North American small mammals. Am Midl Nat 37:223–249. https://doi.org/10.2307/2421652

Morantz DL, Sweeney RK, Shirvell CS, Longard DA (1987) Selection of microhabitat in summer by juvenile Atlantic salmon (*Salmo salar*). Can J Fish Aquat Sci 44(1):120–129. https://doi.org/10.1139/f87-015

Morrissey MB, Ferguson MM (2011) Individual variation in movement throughout the life cycle of a stream-dwelling salmonid fish. Mol Ecol 20(2):235–248. https://doi.org/10.1111/j.1365-294X.2010.04921.x

Muhlfeld CC, Glutting S, Hunt R, Daniels D, Marotz B (2003) Winter diel habitat use and movement by subadult bull trout in the Upper Flathead River. Montana N Am J Fish Manag 23(1):163–171. https://doi.org/10.1577/1548-8675(2003)023%3c0163:WDHUAM%3e2.0.CO;2

Nakano S, Kachi T, Nagoshi M (1990) Restricted movement of the fluvial form of red-spotted masu salmon (*Oncorhynchus masou rhodurus*) in a mountain stream, central Japan. Jpn J Ichthyol 37(2):158–163. https://doi.org/10.11369/jji1950.37.158

Naman SM, Rosenfeld JS, Neuswanger JR, Enders EC, Eaton BC (2019) Comparing correlative and bioenergetics-based habitat suitability models for drift-feeding fishes. Freshw Biol 64:1613–1626. https://doi.org/10.1111/fwb.13358

Negro G, Fenoglio S, Quaranta E, Comoglio C, Garzia I, Vezza P (2021) Habitat preferences of Italian freshwater fish: a systematic review of data availability for applications of the MesoHABSIM model. Front Environ Sci 9:634737. https://doi.org/10.3389/fenvs.2021.634737

Nunn AD, Copp GH, Vilizzi L, Carter MG (2010) Seasonal and diel patterns in the migrations of fishes between a river and a floodplain tributary. Ecol Freshw Fish 19(1):153–162. https://doi.org/10.1111/j.1600-0633.2009.00399.x

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(6):325. https://doi.org/10.3390/fishes7060325

Nyqvist D, Schiavon A, Candiotto A, Tarena F, Comoglio C (2024) Survival and swimming performance in small-sized South European Cypriniformes tagged with passive integrated transponders. J Ecohydraul 9(2):248–258. https://doi.org/10.1080/24705357.2024.2306419

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: Mar Freshw 29:374–388. https://doi.org/10.1002/aqc.3062

Okland F, Thorstad EB, Hay CJ, Naesje TF, Chanda B (2005) Patterns of movement and habitat use by tigerfish (*Hydrocynus vittatus*) in the Upper Zambezi River (Namibia). Ecol Freshw Fish 14(1):79–86. https://doi.org/10.1111/j.1600-0633.2004.00080.x

Parasiewicz P (2007) The MesoHABSIM model revisited. River Res Appl 23:893–903. https://doi.org/10.1002/rra.1045

Parasiewicz P (2011) MesoHABSIM—a concept for application of instream flow models in river restoration planning. Fisheries 29(9):6–13. https://doi.org/10.1577/1548-8446(2001)026%3c0006:M%3e2.0.CO;2

Piana F, Fioraso G, Irace A, Mosca P, d'Atri A, Barale L, Falletti P, Monegato G, Morelli M, Tallone S, Vigna GB (2017) Geology of Piemonte region (NW Italy, Alps-Apennines interference zone). J Maps 13(2):395–405. https://doi.org/10.1080/17445647.2017.1316218

Piccolo JJ, Hughes NF, Bryant MD (2008) Development of net energy intake models for drift-feeding juvenile coho salmon and steelhead. Environ Biol Fishes 83:259–267. https://doi.org/10.1007/s10641-008-9330-1

Pires DF, Beja P, Magalhães MF (2014) Out of pools: Movement patterns of Mediterranean stream fish in relation to dry season refugia. River Res Appl 30:1269–1280. https://doi.org/10.1002/rra.2776

Radinger J, Wolter C (2014) Patterns and predictors of fish dispersal in rivers. Fish Fish 15:456–473. https://doi.org/10.1111/faf.12028

Reyjol Y, Hugueny B, Pont D, Bianco PG, Beier U, Caiola N, Casals F, Cowx I, Economou A, Ferreira T, Haidvogl G, Noble R, De Sostoa A, Vigneron T, Virbickas T (2007) Patterns in species richness and endemism of European freshwater fish. Glob Ecol Biogeogr 16:65–75. https://doi.org/10.1111/j.1466-8238.2006.00264.x

Rikardsen A, Thorpe J, Dempson J (2004) Modelling the life-history variation of Arctic charr. Ecol Freshw Fish 13(4):305–311. https://doi.org/10.1111/j.1600-0633.2004.00070.x

Riley SC, Fausch KD, Gowan C (1992) Movement of brook trout (*Salvelinus fontinalis*) in four small subalpine streams in northern Colorado. Ecol Freshw Fish 1(2):112–122. https://doi.org/10.1111/j.1600-0633.1992.tb00080.x

Rondinini C, Battistoni A, Teofili C (2022) Lista Rossa IUCN dei vertebrati italiani 2022. Comitato Italiano IUCN e Ministero dell'Ambiente e della Sicurezza Energetica, Roma.

Schiavon A, Comoglio C, Candiotto A, Spairani M, Hölker F, Tarena F, Watz J, Nyqvist D (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. https://doi.org/10.1051/kmae/2024003

Schiavon A, Comoglio C, Candiotto A, Hölker F, Ashraf MU, Nyqvist D (2023) Survival and swimming performance of a small-sized Cypriniformes (*Telestes muticellus*) tagged with passive integrated transponders. J Limnol 82(1). https://doi.org/10.4081/jlimnol.2023.2129

Schindler DE, Hilborn R, Chasco B, Boatright CP, Quinn TP, Rogers LA, Webster MS (2010) Population diversity and the portfolio effect in an exploited species. Nature 465(7298):609–612. https://doi.org/10.1038/nature09060

Schlosser IJ (1987) The role of predation in age- and size-related habitat use by stream fishes. Ecology 68:651–659. https://doi.org/10.2307/1938470

Shuter BJ, Finstad AG, Helland IP, Zweimüller I, Hölker F (2012) The role of winter phenology in shaping the ecology of freshwater fish and their sensitivities to climate change. Aquat Sci 74:637–657. https://doi.org/10.1007/s00027-012-0274-3

Smialek N, Pander J, Mueller M, van Treeck R, Wolter C, Geist J (2019) Do we know enough to save European riverine fish? A systematic review on autecological requirements during critical life stages of 10 rheophilic species at risk. Sustainability 11(18):5011. https://doi.org/10.3390/su11185011

Speers-Roesch B, Norin T, Driedzic WR (2018) The benefit of being still: energy savings during winter dormancy in fish come from inactivity and the cold, not from metabolic rate depression. Proc R Soc B 285:20181593. https://doi.org/10.1098/rspb.2018.1593

Stefani F, Galli P, Zaccara S, Crosa G (2004) Genetic variability and phylogeography of the cyprinid *Telestes muticellus* within the Italian peninsula as revealed by mitochondrial DNA. J Zool Syst Evol Res 42(4):323–331. https://doi.org/10.1111/j.1439-0469.2004.00272.x

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. Trans Am Fish Soc 137(2):371–385. https://doi.org/10.1577/T06-265.1

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(2):407–423. https://doi.org/10.2307/2922

Tarena F, Comoglio C, Candiotto A, Nyqvist D (2023) Artificial light at night affects fish passage rates in two small-sized Cypriniformes fish. Ecol Freshw Fish. https://doi.org/10.1111/eff.12766

Tierno De Figueroa JM, López-Rodríguez MJ, Fenoglio S, Sánchez-Castillo P, Fochetti R (2013) Freshwater biodiversity in the rivers of the Mediterranean Basin. Hydrobiologia 719(1):137–186. https://doi.org/10.1007/s10750-012-1281-z

Tinbergen N (1952) The curious behavior of the stickleback. Sci Am 187(6):22–27. http://www.jstor.org/stable/24944080

Verhelst P, Brys R, Cooke SJ, Pauwels I, Rohtla M, Reubens J (2022) Enhancing our understanding of fish movement ecology through interdisciplinary and cross-boundary research. Rev Fish Biol Fish. https://doi.org/10.1007/s11160-022-09741-8

Vezza P, Parasiewicz P, Spairani M, Comoglio C (2014) Habitat modeling in high-gradient streams: the mesoscale approach and application. Ecol Appl 24(4):844–861. https://doi.org/10.1890/11-2066.1

Videler JJ (1993) Fish swimming. Springer, Netherlands

Vøllestad LA (2023) A paradoxical bias in knowledge about Norwegian freshwater fishes: research efforts during 1980–2020. Fauna nor 42:6–30. https://doi.org/10.5324/fn.v42i0.4965

Waldman JR, Quinn TP (2022) North American diadromous fishes: drivers of decline and potential for recovery in the Anthropocene. Sci Adv 8(4):eabl5486. https://doi.org/10.1126/sciadv.abl5486

Watz J (2019) Structural complexity in the hatchery rearing environment affects activity, resting metabolic rate and post-release behaviour in brown trout (*Salmo trutta*). J Fish Biol 95(2):638–641. https://doi.org/10.1111/jfb.14049

Watz J, Bergman E, Calles O, Enefalk Å, Gustafsson S, Hagelin A, Nilsson PA, Norrgård JR, Nyqvist D, Österling EM, Piccolo JJ, Schneider LD, Greenberg L, Jonsson B (2015) Ice cover alters the behavior and stress level of brown trout (*Salmo trutta*). Behav Ecol 26(3):820–827. https://doi.org/10.1093/beheco/arv019

Watz J, Bergman E, Piccolo JJ et al (2016) Ice cover affects the growth of a stream-dwelling fish. Oecologia 181:299–311. https://doi.org/10.1007/s00442-016-3555-z

Whoriskey K, Martins EG, Auger-Méthé M, Gutowsky LFG, Lennox RJ, Cooke SJ, Power M, Mills Flemming J (2019) Current and emerging statistical techniques for aquatic telemetry data: a guide to analysing spatially discrete animal detections. Methods Ecol Evol 10:935–948. https://doi.org/10.1111/2041-210X.13188

Wocher S, Rösch R (2006) Migrations of soufie (*Leuciscus souffia agassizii*, VAL. 1844) in a natural river and a tributary determined by mark-recapture. Arch Hydrobiol 165(1):77–87. https://doi.org/10.1127/0003-9136/2006/0165-0077

Woolnough DA, Downing JA, Newton TJ (2009) Fish movement and habitat use depends on water body size and shape. Ecol Freshw Fish 18:83–91. https://doi.org/10.1111/j.1600-0633.2008.00326.x

Zhang C, Xu M, Lei F, Zhang J, Kattel GR, Duan Y (2022) Spatio-temporal distribution of *Gymnocypris przewalskii* during migration with UAV-based photogrammetry and deep neural network. J Ecohydraul 7(1):42–57. https://doi.org/10.1080/24705357.2021.1892547