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RESEARCH PAPER OPEN ACCESS

Navigating the drought: upstream migration of a small-sized Cypriniformes (*Telestes muticellus*) in response to drying in a partially intermittent mountain stream

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Abstract – River flow intermittence is a natural phenomenon intensified by human activities, such as water abstraction and the effects of climate change. A growing number of rivers are predicted to experience intermittent flows, which may impact the diversity and abundance of freshwater species. Dry riverbeds directly diminish the availability of habitats for freshwater organisms, and suitable environments can turn into ecological traps with reduced survival rates, posing a significant threat to population persistence. Even though fish movements can enable drought-affected populations to persist, little is known about individual fish movement between intermittent and perennial reaches. Here, we study the movement of individual PIT-tagged Italian riffle dace (*Telestes muticellus*) in an intermittent and perennial river reach before, during and after two severe drying events. A high proportion of fish from the intermittent reach survived the drying riverbed through directed upstream migration. This was manifested in fish living in the intermittent reach of the river displaying significantly higher linear ranges, and net travelled distances during the monitoring period than fish in the perennial reach, which remained resident with limited linear range and net distances travelled. This finding underscores the importance of conserving longitudinal river connectivity in the face of increased water scarcity and intermittent flow patterns.

Keywords: Climate change / fluvial connectivity / ires / pit telemetry / vairone

1 Introduction

The intermittent flow of rivers is a natural phenomenon, but human activities, including water diversions for domestic, industrial, and agricultural purposes, along with the impacts of climate change, have intensified its severity and frequency (Trenberth *et al.*, 2014; Sarremejane *et al.*, 2022; Datry *et al.*, 2023). Consequently, an increasing number of rivers are expected to experience intermittent flows (Datry *et al.*, 2014), which can lead to significant changes in species abundance and diversity within river communities (Bogan and Lytle, 2011). Drying of riverbeds directly reduces the availability of habitats for freshwater organisms (Cucherousset *et al.*, 2007; Marshall *et al.*, 2016; Parasiewicz *et al.*, 2019), and previously suitable environments can transform into ecological traps with reduced survival rates, posing a risk to population persistence (Vander Vorste *et al.*, 2020). The ability of aquatic organisms to cope with intermittent flows is a crucial factor for their persistence in periodically drying environments (Datry *et al.*, 2014; Labbe and Fausch, 2000). Despite the challenges faced by local fish populations in intermittent river systems (Skoulikidis *et al.*, 2017), these watercourses can play a significant role in providing spawning (Hooley-Underwood *et al.*, 2019), foraging and refuge habitats (Wigington *et al.*, 2006). Intermittence can occur in various forms, affecting the entire river or isolated reaches (Pires *et al.*, 1999; Pinna *et al.*, 2016; Di Sabatino *et al.*, 2023). The survival of fish in residual pools

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during flow cessation has been investigated in several studies (Gagen *et al.,* 1998; Wigington *et al.,* 2006; Marshall *et al.,* 2016) along with the recolonisation ability of re-wetted reaches (Gagen *et al.,* 1998; Adams and Warren, 2005; Albanese *et al*., 2009). Catastrophic mortality does occur (Tramer, 1977), but fish behaviour and hydro-morphological factors play a role in both dispersal and recolonisation; the understanding of fish movement during drought events is crucial for assessing population persistence (Lonzarich *et al*., 2000; Pires *et al*., 2014). Previous studies on fish have predominantly investigated the use of and movement between intermittent river reaches, using point sampling or mark-recapture techniques. These studies have observed fish movement from drying reaches to adjacent wetted reaches (Davey and Kelly, 2007; Hedden and Gido, 2020), as well as from perennial rivers to intermittent tributaries (Hooley-Underwood *et al*., 2019) and from remaining pools or waterholes to wetted intermittent rivers (Gagen *et al*., 1998; Labbe and Fausch, 2000; Marshall *et al*., 2016). The Mediterranean ecoregion is characterised by many rivers that exhibit predictable seasonal patterns of intermittent flow (Gasith and Resh, 1999). In addition, the region also faces an increase in irregular and unpredictable drought events (Skoulikidis *et al*., 2017). Numerous freshwater species, including several endemic ones, can be found in the region (Tierno De Figueroa *et al*., 2013). Many of these species are listed as threatened on the IUCN Red List (IUCN, 2022), and ecological knowledge and research about them are scarce (Smialek *et al.,* 2019; Negro *et al*., 2021). Given the significant hydrological seasonal variation, high river intermittency and the presence of numerous understudied species, it is crucial to investigate the dynamics of fish movement in the Mediterranean region. Italian riffle dace (*Telestes muticellus*, Bonaparte 1837) is a small-sized (<15 cm) Cypriniformes fish belonging to the *Leuciscidae* family. It is native to the Italian peninsula and is distributed across the Adriatic and Tyrrhenian basins. This species primarily inhabits piedmont rivers and creeks characterised by clear, cold water, although it can also be found in lowland springs (Fortini, 2016). *It* is a rheophilic omnivore, mainly consuming aquatic invertebrates and epilithic algae. It spawns in spring on gravel substrates with swift and shallow water flow (Fortini, 2016). While *Telestes muticellus* has been studied in terms of its genetics and biogeography (Stefani *et al*., 2004; Marchetto *et al*., 2010; Buj *et al.,* 2017), there remains a significant knowledge gap concerning its habitat use and individual patterns. Here, we use PIT telemetry to track individual movements of *Telestes muticellus* in a small mountain stream in Northern Italy. The study area experienced severe drought during the summer and spring of 2022 (Bonaldo *et al*., 2023), followed by a subsequent period of water scarcity in the winter and early spring of 2023 (ARPA Piemonte, 2023). We tracked tagged fish before, during and after these two separate drying events. The study aimed to evaluate the movement patterns and survival capabilities of *Telestes muticellus* in intermittent river conditions. Estimates of apparent survival, as well as linear range and net travelled distance were compared between an intermittent river reach and a neighbouring perennial reach.

2 Material and methods

2.1 General setting

The study was conducted in a section of the Morsone River (UTM 485693E, 4939751N, zone 32T) located in Piedmont region (NW Italy, Fig. 1). The river' has a catchment area of 8.78 km^2 an approximate length of 5 km, is a tributary of the Lemme River and forms part of the Po drainage basin. Considering the low altitude of the catchment area (between 309 and 1092 m a.s.l.) and the limited snowfall, the river is characterised by pluvial discharge regimes typical of Apennines streams, with a low summer discharge and high autumn and spring discharges (Forneris *et al*., 2007). In recent years, short reaches of the stream, close to and overlapping with part of the study area, have dried out completely during drought events. The geology of the catchment is composed of a complex of sandstone, limestone, conglomerate and crystalline siliceous rocks (Piana *et al*., 2017). The fish community in the study area was assessed through quantitative electrofishing sampling conducted in March 2022. The fish assemblage comprises a limited number of species, with *Telestes muticellus* being the most abundant, accounting for 73% of the relative abundance. Brook barbel (*Barbus caninus,* Bonaparte 1839) follows, comprising 26% of the relative abundance. Italian chub (*Squalius squalus,* Bonaparte 1837) and brown trout (*Salmo trutta* L.) have a relative abundance of less than 1%. It is worth noting that brown trout is the only non-native species present, introduced for recreational fishing purposes in recent years (A. Candiotto; pers. obs.).

2.2 Study reach

The study area consists of two distinct but adjacent river sections: one intermittent (80 m) and one perennial reach (122 m). The downstream limit of the study section was set based on the trackability of the stream and estimated passability for fish. The areas downstream of the study reach were characterized by debris and steep terrain, posing tracking challenges. Flow was also often reduced (because of hyporheic flow) in this reach, creating natural barriers to fish movements. The extent of the perennial upstream area was set to achieve similar hydrodynamic variability as in the intermittent reach. No artificial barriers obstruct the natural flow within the studied area. In 2022, the drying process in the intermittent reach commenced on May 11th and culminated on May 19th, resulting in a fully dry section in under nine days. This event was characterised by a rapid drop in water levels. In contrast, the drying in 2023 initiated on March 6th and the reach was fully dry by April 11th, spanning over a month. This latter event was characterised by a more gradual but steady decrease in the water-covered area. During the drying, water persisted in temporary pools and small disconnected sections, which eventually became completely dry. Habitat mapping, including discharge estimates (ISO, 2021), was conducted following the mesoHABSIM protocol (Parasiewicz, 2001; Parasiewicz, 2007; Vezza *et al*., 2014), in March 2022 prior to the drying event and again in July 2022 following the event, aimed to

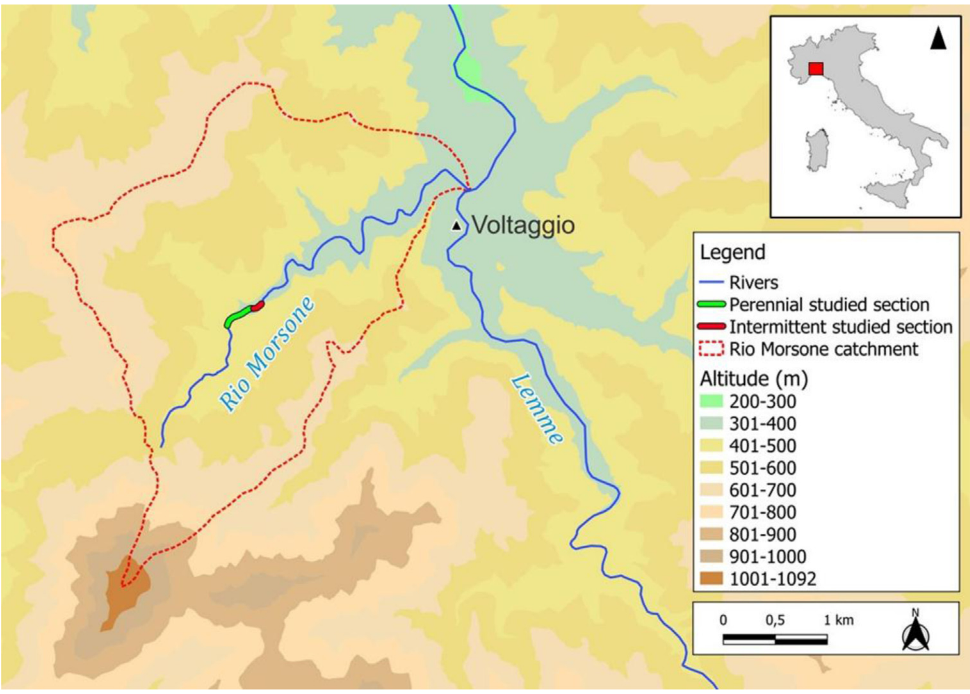

Fig. 1. The study site is situated in the Rio Morsone River in Piedmont region (NW Italy). The catchment area is represented by a dotted red line superimposed on a map displaying the altimetric contour lines. The red and green river reaches represent the perennial and intermittent reach, respectively.

detail the habitat types and their associated physical features. The study area showcased a series of hydromorphological units: riffles, rapids, glides, pools and backwaters. Both river sections displayed a similar pattern of hydromorphological units, and variability of depth, water velocity, shelter availability and substrate granulometry. Prior to the drying event in March 2022, the perennial reach had a mean depth of 17.4 cm (SD = 8.4 cm) with a discharge of 17 litres per second, whereas the intermittent reach registered a mean depth of 13.9 cm (SD = 6.1 cm). Following the drying phase, the perennial reach reported a mean depth of 12.1 cm (SD = 8.1 cm) with a discharge of 5 litres per second. Habitat mappings were not conducted for 2023 owing to the marked resemblance in hydromorphological conditions and drying patterns between 2 yr. Throughout the study period, water temperature and water level were monitored at 20 min intervals using a temperature and water level sensor (HOBO MX2001). The logger was situated in the perennial section, 140 m upstream from the uppermost location of the intermittent reach.

2.3 PIT tagging

Two electrofishing and PIT tagging campaigns were carried out within the study reach in March and October 2022. A subsample of the *Telestes muticellus* greater than 6.0 cm, corresponding to a size range of fish older than 1 yr, was tagged with Passive Integrated Transponders (PIT tags; Oregon, USA; 12 × 2.1 mm; 0.10 g). High survival and tag retention rates were reported for this species (Schiavon *et al.*, 2023). Before tagging, fish were anaesthetised with clove oil (Aromlabs, USA; approximately 0.2 mL clove oil per litre of water). An incision of 2-4 mm was made on the ventral side of the fish, slightly offset from the centre and frontal to the pelvic fins, before the tag was inserted and pushed forward in the abdomen (Nyqvist *et al.*, 2022; Schiavon *et al.*, 2023). Once the fish had been tagged, they were measured for fork length and weight and allowed to recover in tanks filled with river water. The fish were released after a few minutes of recuperation at the same site as captured.

2.4 Fish tracking

We used a mobile backpack antenna (Mobile HDX Long Range PIT Tag Reader Kit; Oregon RFID) to track the tagged fish in the study reach. The tracking system comprised an electronic reader backpack connected with a portable pole antenna. The process of fish tracking involved scanning the entire study area by walking or wading upstream (Nzau Matondo *et al.*, 2019; Watz *et al.*, 2019). For real-time visualization of individual fish identification codes, the mobile reader was connected to an Android smartphone device via Bluetooth using a terminal for serial devices (Serial Bluetooth Terminal, version 1.42). Datetime and position in a hydromorphological unit-based coordinate system (supported by a handheld rangefinder: Trupulse 360R Laser Technology) were noted for every detected fish. We noted any visual observations of the fish or if they exhibited movement indicative of a live fish (in contrast to a dead fish or lost tags). A 650 m upstream reach was monitored for potential movements upstream. Additionally, we periodically tracked a 150 m section just downstream of the intermittent reach. To visualize the individual positions and track fish movements over time, the precise fish locations (± 0.75 m) were imported into a Geographic Information System (GIS) environment. From

Table 1. Summary of the sample sizes, individual fork lengths and weights (median, interquartile range (IQR), and range) for the 98 *Telestes muticellus* individuals studied, categorised into years and intermittent and perennial groups.

Fish groups	Years	*n*	Fork length (mm)			Weight (g)		
			Median	IQR	Range	Median	IQR	Range
Intermittent	2022	9	76	70–87	60–99	5.6	4.1–8.7	2.6 –13.0
	2023	15	78	74–87	61–135	5.6	4.7–8.0	2.7–32.6
	2022 + 2023	24	77	72–87	60–135	5.6	4.4–8.5	2.6–32.6
Perennial	2022	32	74	70–85	61–104	5.2	4.1–7.8	2.8–14.0
	2023	42	74	70–86	61–128	4.9	4.1–8.3	2.6–30.8
	2022 + 2023	74	74	70–85	61–128	5.1	4.1–8.1	2.6–30.8

April 4th to August 16th, 2022, we conducted sixteen tracking events at an average interval of 10 days. In 2023, we carried out eleven tracking events between January 12th and June 5th, with an average interval of 14 days.

2.5 Data analysis

Fish were categorised into an intermittent or perennial group based on their positions prior to the initiation of drying, specifically on May 11th, 2022, and March 6th, 2023. The statistical analyses were conducted separately for 2 yr to account for inter-annual differences and repeated measures on a subset of fish. We analysed apparent survival to investigate potential differences in survival proportions among fish groups. The analysis of apparent survival included all the tracked fish that were confirmed to be alive before the start of the drying and/or after the peak riverbed drying. Mortalities included tags never tracked again in the river after the drying – presumably cases of predation or natural death followed by scavenger removal. We analysed the association between survival rates in the perennial and intermittent groups with Fisher exact tests. Individual linear range and net travelled distance were measured to assess differences in space use and movement patterns between the two groups throughout the study period. Additionally, the linear range was quantified also for the period after the drying events to detect any inherent behavioural variations among the groups. This movement analysis included fish that survived the drying events and were detected at least twice. Fish positions were transformed into a linear reference system using the QGIS LRS plugin (LRS, version 1.2.3, retrieved from: http://blazek.github.io/lrs/) for linearisation. The linear range represents the distance between the most upstream and downstream positions observed for each fish during the study period (Capra *et al.*, 2018). Net distance travelled was calculated as the linear distance between each fish's first and last detected position, also giving directionality of movement (negative values indicate downstream movements). Due to the violation of the normality assumption, we used a Mann-Whitney U test to assess potential differences in linear range, and net travelled distance between the perennial and intermittent groups. All the statistical analyses were performed using RStudio (Version 2022.02.2 "Prairie Trillium" Release) and IBM SPSS Statistic (version 25), while QGIS (Version 3.24.3-Tisler) was used for the handling of geospatial data.

3 Results

A total of 98 tagged fish were monitored and studied for their apparent survival and movements; 24 in the intermittent reach and 74 in the perennial reach (Tab. 1). There were no differences in lengths between fish from the intermittent and perennial reach groups for 2022 (Mann-Whitney U = 135, W = 631, p-value = 0.90) and 2023 (Mann-Whitney U = 261, W = 1164, p-value = 0.33). Over 2 yr, 21 from 24 fish present in the intermittent reach, successfully migrated upstream and were tracked in the perennial reach during the dry periods (Fig. 2). Two fish were not detected following the dry-up process, and one pit tag was found in the dry riverbed of the intermittent section. These three fish, one in the year 2022 and two in the year 2023, were considered mortalities. In the perennial group, before the onset of the dry periods, 74 fish, comprising 32 in the year 2022 and 34 in the year 2023, were tracked and confirmed to be alive. However, after drying, ten tags that disappeared were likely associated with mortality events, with one mortality in 2022 and nine in 2023. Differences in apparent survival were not observed between the intermittent and perennial fish groups in both 2022 (Fisher exact test, p-value = 0.40) or 2023 (Fisher exact test, p-value = 0.71). The apparent survival rates for fish in the intermittent group were 88.9% in 2022 and 86.7% in 2023. Fish from the intermittent reach responded to the riverbed drying with upstream movements. The observed linear ranges exhibited significant differences between intermittent and perennial groups (Fig. 3) during the years 2022 (Mann-Whitney U = 9, W = 505, p-value < 0.001) and 2023 (Mann-Whitney U = 31, W = 592, p-value < 0.001), with higher linear range values for the intermittent-reach group (mean detection counts$_{2022}$ = 7.9, mean detection counts$_{2023}$ = 3.5, n_{2022} = 8, n_{2023} = 13) compared to the perennial groups (mean detection counts$_{2022}$ = 7.5, mean detection counts$_{2023}$ = 4.3, n_{2022} = 31, n_{2023} = 33). A comparable trend emerged when examining the net travelled distance (Fig. 4), where fish from the intermittent group consistently exhibited higher values than the perennial group for both 2022 (Mann-Whitney U = 8, W = 504, p-value < 0.001) and 2023 (Mann-Whitney U = 9, W = 570, p-value $<$ 0.001). The analysis of the linear ranges during dry conditions, following the upstream migration of the intermittent group of fish showed no differences between the perennial and intermittent reach groups for 2022 (Mann-Whitney U = 89.5, W = 554.5, p-value = 0.556) and 2023 (Mann-Whitney

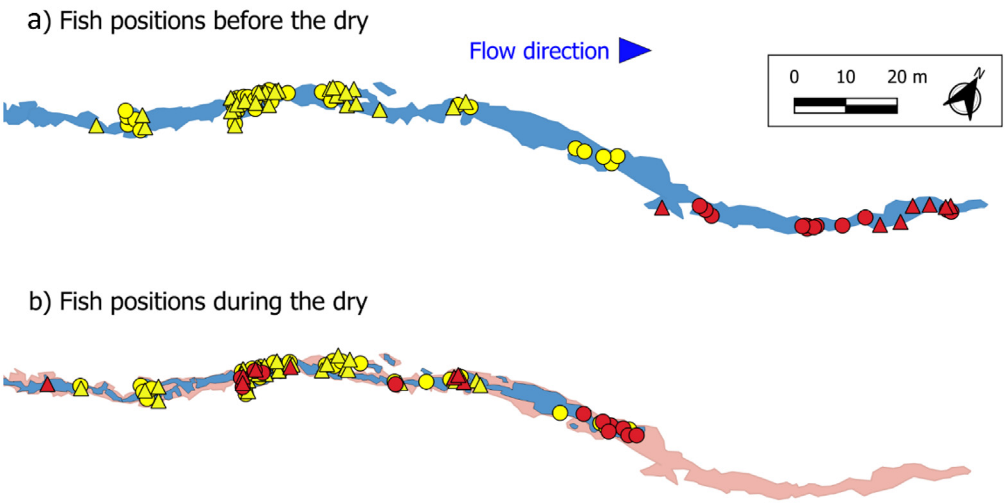

Fig. 2. The map shows *T. muticellus* net travelled distance positions before (a) and during (b) river dry conditions in 2022 (triangles) and 2023 (circles). Red markers represent the intermittent groups ($n = 21$), while yellow markers represent the perennial groups ($n = 64$). Blue indicates riverbed areas with flow, while light red represents the dried area during the dry periods; the contouring is based on habitat mapping performed in March (a) and July (b) 2022. Note that one fish from the perennial group moved 200 m upstream during the drying process and is not shown on panel b.

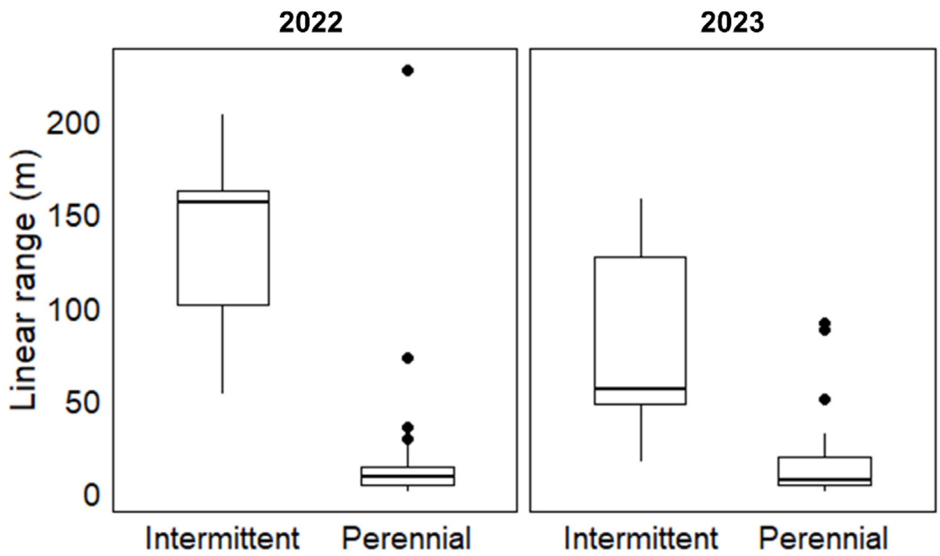

Fig. 3. Boxplot comparisons of the linear ranges for Intermittent ($n_{2022} = 8$; $n_{2023} = 13$) and Perennial ($n_{2022} = 31$; $n_{2023} = 33$) *T. muticellus* in 2022 and 2023, with the boxes representing the interquartile ranges (IQR), whiskers indicating the data ranges, and horizontal lines denoting the median values.

U = 97.5, W = 142,5, p-value = 0.469). In the intermittent reach group for the years 2022 and 2023, the medians of the linear ranges were 6.5 and 4.0 m (IQR_{2022} = 2.3 − 17.4 m, IQR_{2023} = 1.0–17.4, min − max_{2022} = 0.9–45.4 m, min − max_{2023} = 0.4–46.6 m, mean detection $counts_{2022}$ = 6.1, mean detection $counts_{2023}$ = 2.8, $n_{2022} = 7$, $n_{2023} = 9$) compared to 3.8 and 5.1 m (IQR_{2022} = 1.2–9.8 m, IQR_{2023} = 4.0–14.0 m, min − max_{2022} = 0.0–226.8 m, min − max_{2023} = 0.0–53.6 m, $n_{2022} = 30$, $n_{2023} = 26$) for the perennial one. Between the study periods in 2022 and 2023, two fish returned to he intermittent reach. The average water temperature during the drying-up process was 15.6 °C (min − max = 13.2–17.7 °C) in 2022 and 9.1 °C (min − max = 5.3–13.0 °C) in 2023, while temperatures throughout the study periods ranged between −0.1 °C and 25.5 °C.

4 Discussion

Almost 90% of the tagged *Telestes muticellus* in the intermittent reach exhibited a response to flow intermittence by migrating to upstream perennial reaches. In contrast, fish residing in perennial reaches did not show a similar upstream

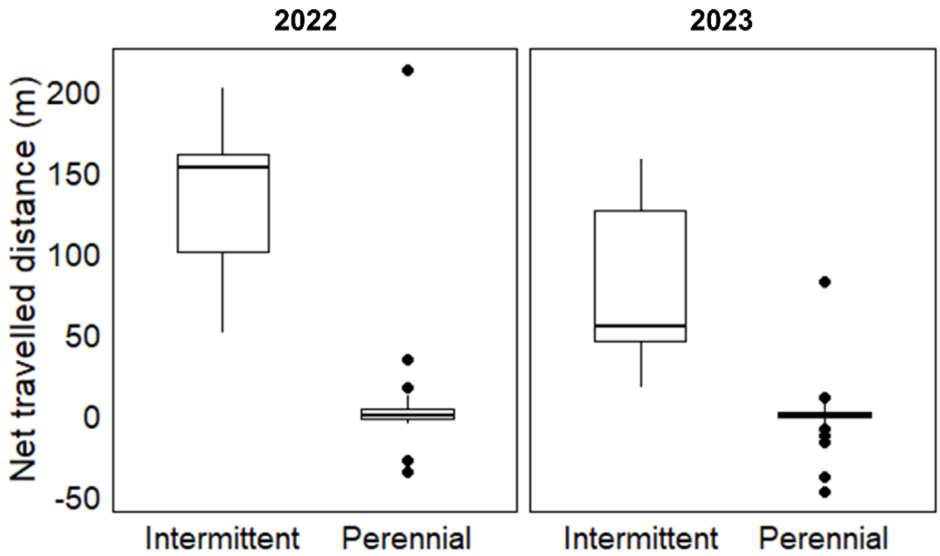

Fig. 4. Boxplot comparisons of the net travelled distance for Intermittent ($n_{2022} = 8$; $n_{2023} = 13$) and Perennial ($n_{2022} = 31$; $n_{2023} = 33$) *T. muticellus* in 2022 and 2023, with the box representing the interquartile ranges (IQR), whiskers indicating the data ranges, and horizontal lines denoting the median values.

movement and remained relatively stationary throughout the study period. This study provides evidence of drying inducing refuge migration of *Telestes muticellus* in a small mountain stream. The apparent survival for fish from both the perennial and the intermittent reaches was relatively high, contrasting with the severe adverse effects of drying events on fish populations reported elsewhere (Tramer, 1977; Archdeacon and Reale, 2020). The observed low mortality means that fish migrated upstream prior to becoming trapped in disconnected sections, such as pools. This anticipatory behaviour may have been triggered by specific environmental cues. The absence of similar movement patterns among the fish in the perennial reach suggests that these environmental cues likely operate at a localised spatial scale. Remarkably, the results were similar between the two tested years, despite drying events occurring two months earlier and at substantially lower water temperatures in 2023 than in 2022. This indicates that *Telestes muticellus* can cope with drying rivers by seeking refuge in neighbouring wetted areas, at least at the scale investigated and in the absence of barriers between intermittent and perennial sections (Pires *et al*., 2014). The disappearance of tags, likely linked to mortality events, may be attributed to a range of factors. Predation events or natural death followed by scavenger removal is likely to remove the tag from the study area (Cucherousset *et al*., 2008; Skov *et al*., 2014), a dead fish (or its remaining tag) may also drift out of detection range within the substrate (Cucherousset *et al*., 2008). In addition, some alive fish, despite repeated tracking efforts, may have remained undetected throughout the study. If this occurred, it could have resulted in a slight overestimation of the mortality rate.

Fish from the intermittent reach displayed a significantly larger linear range as well as net distance travelled than fish from the perennial reach, with the former exhibiting an average linear range that was twelve times greater. In contrast, most fish from the perennial reach exhibited linear ranges of less than 20 m, indicating strong site fidelity. Interestingly, fish from the intermittent reach demonstrated a similar behaviour once arriving to the perennial reaches. This shows that *Telestes muticellus*, under stable wetted conditions, displays limited home ranges. Their upstream movement was therefore not a result of innate tendencies in a biased subset of fish that were more prone to moving, but rather triggered by environmental cues. The limited home range also contrasts with several other rheophilic Cypriniformes, with linear ranges spanning km, albeit in larger river systems (Wocher, 2006; Capra *et al*., 2018; Panchan *et al*., 2022). The analysis of net distance travelled exhibited a similar pattern as the analysis of linear range and provided information about the direction of displacement. Fish from the intermittent reach groups covered a significantly greater distance, consistently moving upstream. Fish from the perennial groups, in contrast, showed limited and bidirectional net displacement, and only a single individual from the perennial groups embarked on a more significant upstream movement (>200 m). Previous studies on other fish species have reported bidirectional movements and as well as a higher likelihood of upstream than downstream movements in response to droughts (Davey and Kelly, 2007; Pires *et al*., 2014). In our study system, the upstream migrations observed did not necessarily occur due to a behavioural preference for upstream movement but rather because the downstream direction was blocked and completely dry throughout the study period. As all our fish were older than 1 yr at the time of tagging, we do not know what role experience or previous selection (Podgorniak *et al*., 2016; Tarena *et al*., 2024) may play in the observed drought induced migration, nor the fate young-of-the-year fish present in the intermittent reach. Only two of the tagged fish, however, experienced the drying of the intermittent section twice, indicating that prior experience is likely limited. Also, our study period overlapped with the reproductive period of the *Telestes muticellus*. Despite this, we did not observe any significant coordinated movement among the perennial or intermittent reach fish related to the spawning period, as reported for the genus elsewhere (Barbieri *et al.*, 2020). This does not exclude limited return movements at a time scale shorter than our tracking interval, for example, a few days (Fredrich *et al.*, 2003), but makes them relatively unlikely. Future studies are needed to fully understand the movement dynamics in *Telestes muticellus*.

Our results demonstrate the ability of a small-sized rheophilic species to cope with flow intermittence and provide new understandings about the movement ecology of this species. Previous research of fish in the Mediterranean region have focused on species inhabiting warmer water than that of our study (Pires *et al.*, 1999; Magalhães *et al*., 2007; Pires *et al*., 2014), and these species evolved in dynamic environments that are more commonly characterised by seasonal flow intermittence (Tierno De Figueroa *et al*., 2013). The widespread increase of flow intermittence in river systems (Datry *et al*., 2014; Skoulikidis *et al.*, 2017; Sarremejane *et al*., 2022) due to climate change and water diversion for human activities (Larned *et al.*, 2010; De Graaf *et al*., 2019) poses a new threat to rheophilic and cold water species. Comprehending the movement and behaviour of fish thus becomes crucial for mitigating local losses and ensuring the long-term persistence of populations in the face of disturbances. Further studies with larger sample sizes and in different systems encompassing different species will be necessary to enhance our understanding of this phenomenon and implement effective river management and restoration strategies that enhance population resilience (Magoulick and Kobza, 2003). It is crucial for river management efforts to consider longitudinal connectivity not only to facilitate spawning migrations and maintain population genetics but also to address emerging threats such as more frequent and severe droughts.

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Conflict of Interest

The authors declare no conflict of interest.

Data availability

Dataset generated for this study. The data that support the findings of this study are available from the corresponding author upon reasonable request.

Author contribution

Conception and design of the investigation: A.S., D.N., C.C., F.H. and J.W. Data generation: A.S., D.N., A.C, M.S. and F.T. Data analysis: A.S. and D.N. Manuscript preparation: A.S., D.N., C.C., F.H. and J.W. Funding: C.C. and F.H.

Ethical approval

The study was performed in accordance with the Ufficio Tecnico Faunistico e Ittiofauna of the Provincia di Alessandria (authorisation numbers: 65493 and DDAP2-939, dated November 11th, 2021) under the provisions of art.2 of the national Decree n.26/2014 (implementation of Dir. 2010/63/EU), and Aree Protette Appennino Piemontese (authorisation number: 1072, dated February 15th, 2022).

Supplementary material

Figure S1. Temporal variations in water level (m) and temperature (°C) throughout the study periods. The water levels are illustrated by a blue dashed line, while the temperature data, are represented by a red solid line. Triangles indicate tracking events: black for observations taken before the onset of dry conditions, and red for tracking events after the onset of dry conditions. The water level-temperature sensor was positioned 140 meters upstream of the intermittent reach. Note: Water level data is unavailable from June 25 to July 6, 2022.

Figure S2. Longitudinal position of individual *T. muticellus* over time in the study reach for 2022 (a) and 2023 (b). The horizontal dashed line demarcates the boundary between the intermittent and perennial reaches. Blue circles for fish in the perennial reach prior to drying red points for fish that were in the intermittent reach prior to drying.

The Supplementary Material is available at https://www.kmae-journal.org/10.1051/kmae/2024003/olm.

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