Nature Conservation

Nature Conservation 65: 197–226 (2026)
DOI: 10.3897/natureconservation.65.193904

Monograph

Biology and conservation of the European mudminnow (*Umbra krameri* Walbaum, 1792): an update of the monograph 30 years after the first international workshop

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Abstract

During the three decades following the publication of the first comprehensive monograph on the European mudminnow (*Umbra krameri* Walbaum, 1792), knowledge of the species' biology, distribution, genetics, ecology, and conservation has expanded substantially. In several countries, a dynamic distribution pattern has become apparent, with many local populations seemingly disappearing while new populations continue to be documented. However, many of these newly recorded occurrences likely represent previously overlooked remnant populations rather than genuine range expansions. Despite the uncertainty associated with detectability, the overall distribution pattern of *U. krameri* clearly reflects a large-scale process of range contraction and habitat fragmentation across most of its native range. Recent phylogeographic and population genetic studies have fundamentally improved understanding of the species by revealing pronounced drainage-based structuring, limited contemporary gene flow, and the existence of distinct evolutionarily significant units (ESUs). At the same time, the development of genomic resources, complete mitogenome assemblies, and environmental DNA (eDNA) approaches has created entirely new opportunities for monitoring and conservation. Numerous studies have also advanced knowledge of habitat use, trophic ecology, population dynamics, and conservation management, while conservation breeding and translocation programs have been initiated in several countries across the species' range. Considering the threats affecting the species,

OPEN ACCESS

Academic editor: Lukáš Kalous
Received: 1 April 2026
Accepted: 15 July 2026
Published: 9 October 2026

ZooBank: https://zoobank.org/B07FC81E-E264-4B60-A690-BFFCFC81B895

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Citation: Wanzenböck J, Rund H, Jung M, Ratschan C, Nagy AA, Trombitsky I, Moshu A, Gubanov V, Marić S, Stanković D, Sekulić N, Donabaum R, Koblmüller S, Pekárik L, Tatár S, Müller T, Takács P (2026) Biology and conservation of the European mudminnow (*Umbra krameri* Walbaum, 1792): an update of the monograph 30 years after the first international workshop. In: Wanzenböck J, Šmejkal M, Kalous L, Klefoth T, Geist J, Takacs P (Eds) Biology and conservation of wetland fishes in Europe. Nature Conservation 65: 197–226. https://doi.org/10.3897/natureconservation.65.193904

together with the documented population declines and numerous local extinctions, its current IUCN Red List status should be reassessed and upgraded from Vulnerable to Endangered, or possibly even Critically Endangered.

Key words: Distribution, genomics, population decline, vulnerability, wetland fishes

Introduction

The European mudminnow (*Umbra krameri* Walbaum, 1792) is among the rarest and most threatened freshwater fish species in Central Europe. It is endemic to the lowland regions of the Danube catchment and the lower Dniester basin. Following the first international workshop on the European mudminnow in 1995, a comprehensive monograph on the species was published (Wanzenböck 1995). Since then, substantial advances have been made in understanding the species, warranting a comprehensive update of that work.

The present review has two primary objectives:

- To synthesize the scientific literature published during the past 30 years on various aspects of the biology of the species, and
- To incorporate findings presented at the second international workshop on the species in 2025, particularly those not published as dedicated articles within this special issue (i.e., Sallai et al. 2026; Bajomi et al. 2026; Donabaum et al. 2026).

Many conservation programs targeting *U. krameri* have been implemented at local, regional, or national scales, often with only limited exchange of information among countries. A further objective of this review is therefore to provide an international overview of conservation activities and applied management projects, incorporating not only peer-reviewed publications but also relevant gray literature wherever possible.

To avoid unnecessary repetition, the present review deliberately refrains from repeating information already presented in the 1995 monograph and refers to earlier literature only where information in the original publication was incomplete or required clarification. Instead, the focus is on summarizing newer studies from the past 30 years.

The structure of this monographic update follows that of previous monographs on European freshwater fishes (e.g., the series of Aula-Verlag) and, in particular, the original monograph published in 1995.

Monographic update

1.0 Names and taxonomy

The valid scientific name remains *Umbra krameri* Walbaum, 1792. The species is commonly referred to as the European mudminnow in English; for common names in other languages and comments on nomenclature, see Wanzenböck (1995).

2.0 Systematics

The systematics of Umbridae within Esociformes has changed as a result of molecular genetic studies conducted in recent decades and new fossil discoveries (summarized in Kuehne and Olden 2014). López et al. (2004) and Campbell et al. (2013) provided genetic evidence that the genera *Dallia* and *Novumbra* should be placed in the family Esocidae rather than Umbridae. Campbell et al. (2013) argued that the family Umbridae should be abandoned and the genus *Umbra* placed in Esocidae. Nevertheless, the family name Umbridae continued to be used in subsequent studies (e.g., Marić et al. 2017; Jelić et al. 2025), referring exclusively to species of the genus *Umbra*, as recommended by Kuehne and Olden (2014).

3.0 Morphology

Following earlier discussions regarding the validity of a proposed subspecies (Wanzenböck 1995), the prevailing view was that intraspecific morphological variation was relatively limited. This assumption was later reassessed by Marić et al. (2015), who analyzed the morphology and genetic variability of two Serbian populations – one from the Danube drainage and one from the Sava drainage—together with a population from Bosnia and Herzegovina in the Sava drainage, using geometric morphometrics combined with mitochondrial DNA and microsatellite analyses. Both types of analyses clearly separated the Danube population from the two Sava populations. Moreover, the analysis of body shape variation indicated a smaller but significant difference between the two genetically indistinguishable Sava populations.

A geometric morphometric image analysis (Takács et al. 2025) demonstrated that *U. krameri* can be reliably distinguished from its two New World congeners, i.e., *Umbra limi* (central mudminnow) and *Umbra pygmaea* (eastern mudminnow). *U. krameri* is characterized by a deeper body, a more anteriorly positioned dorsal fin, a forward-shifted anal fin, a relatively larger head, and eyes positioned more dorsally on the head. In contrast, *U. limi* and *U. pygmaea* showed substantial morphological overlap with each other. These results are in strong agreement with classical morphological examinations conducted on museum specimens (Mohr 1940). Furthermore, morphometric analyses of recent samples revealed that, among the three evolutionarily significant units (ESUs; Danubian, Tisza, and Sava), the Sava ESU, including all populations, is clearly separated from the other two. Individuals belonging to the Sava ESU exhibit a more elongated body shape, a more anteriorly positioned dorsal fin, and a posteriorly shifted origin of the pectoral fin compared with the Danubian ESU (Takács et al., unpublished data), confirming the findings of Marić et al. (2015).

For genetic variability, see the section on population genetics below.

4.0. Fossil records

The study by Gaudant (2012) sheds new light on the paleontological history of *U. krameri* and its systematics (see section 2.0). Gaudant (2012) found that two umbrid genera, one relatively primitive and the other more advanced and including the extant species, coexisted in Europe over a period of 10 Ma.

5.0 Distribution

5.1. General

With regard to the general distribution of the species, no changes have been reported since 1995. The species is endemic to the lowland regions of the Danube catchment and the lower Dniester basin. The list of European countries mentioned in 1995—Austria, Slovakia, Hungary, Slovenia, Croatia, Serbia, Romania, Moldova, and Ukraine—must be amended: the species has also been found in Bulgaria (Velkov et al. 2004; Pehlivanov et al. 2011) and Bosnia and Herzegovina (Marić et al. 2015). Some reports mention introductions into Germany, Czechia, and Poland; however, at least in Poland, it remains unclear whether these stockings involved *U. krameri* or the North American *U. pygmaea*, which was introduced into other parts of Europe, such as Denmark, northwestern Germany, the Netherlands, and Belgium (Takács et al. 2025). At present, there is no confirmed overlap between the distributions of *U. krameri* and *U. pygmaea* in Europe (see the map in Kuehne and Olden 2014).

5.2. Distribution in different countries

5.2.1. Austria

No significant changes have been reported from Austria since 1995. Today, only two native populations are known from Austria: one from the Danube floodplain between Vienna and Bratislava, known as the Fadenbach population, and one situated southeast of Vienna in the Jesuitenbach, near the village of Moosbrunn (Wanzenböck and Spindler 1995; Bănăduc et al. 2022). A third population was established at the Austrian-Hungarian border east of Lake Neusiedl during a conservation project and persisted for approximately 15 years but was no longer detectable during recent monitoring in 2023 (Jung et al. 2025). *U. krameri* is still absent from the Austrian part of Lake Neusiedl (Jung et al. 2025), which had historically supported an important population until 1958 (Wanzenböck and Spindler 1995). Similarly, other small wetland species, such as weatherfish (*Misgurnus fossilis*), crucian carp (*Carassius carassius*), and tubenose goby (*Proterorhinus semilunaris*), were also absent for decades but naturally reappeared in small numbers after the stocking of eel (*Anguilla anguilla*) was banned in 1998 (Wolfram et al. 2022). However, *U. krameri* was rediscovered by Sallai (2019) in the southern, Hungarian part of the lake in 2017–2018, following a 50-year period during which the species was not recorded there.

5.2.2. Slovakia

At the beginning of the 21st century, the few populations in Slovakia were considered relatively stable, leading to the listing of the species as "Endangered" in the 2008 Red List (Koščo and Holčík 2008). This situation was confirmed by Pekárik et al. (2014), who provided a detailed overview of the historical and recent distribution of the species in the Danube Lowland area. However, the populations declined drastically during the second decade of the 21st century. The species disappeared from eastern Slovakia (Východolovenská nížína) because of droughts and the invasion of the Amur sleeper (*Perccottus glenii*), with the last record

reported in 2010 (Fedorčák and Koščo 2025). The population in western Slovakia (Záhorská nížína) was rediscovered at the original site, Bezedné, but the habitats supporting the population relocated from the Danube Lowland dried out. However, the population was preserved through further relocations, at least one of which was successful at Zelienka. The population in the Danube Lowland (Podunajská nížina) declined drastically because of droughts, and only the core population in Čiližský potok and the adjacent area, Čiližské močiare, survived.

5.2.3. Hungary

Over the past five decades, *U. krameri* has undergone a marked decline in Hungary and now persists at only approximately one-third of its historically recorded localities (Sallai et al. 2026, this issue). Habitat desiccation and the progressive fragmentation of wetland systems appear to be the dominant drivers of this contraction, frequently interacting with the expansion of *P. glenii*. Today, most remaining populations survive in artificial canal networks and small, isolated wetland fragments, reflecting a pronounced shift away from former floodplain habitats. The Fertő-Hanság-Szigetköz region and parts of the Bihari floodplain currently harbor the most stable populations, whereas several other regions have no recent confirmed occurrences. Without coordinated hydrological restoration and effective invasive species control, additional regional extinctions are expected.

5.2.4. Slovenia

Since 1995, knowledge of the species' distribution in Slovenia has improved substantially. *U. krameri* is a qualifying species for both the Mura and Drava Natura 2000 sites (SI3000215 and SI3000253, respectively), and most recent records have resulted from monitoring undertaken in accordance with the EU Habitats Directive. In 2006, a single specimen was recorded in the Drava, in a river branch south of Središče ob Dravi (Govedič and Šalamun 2006). To date, this remains the only confirmed contemporary record of the species in the Drava upstream of its confluence with the Mura. Several additional populations have since been discovered in the Mura, all but one in oxbows downstream of the confluence with the Ščavnica (Semrajc 2015, 2022; Marić et al. 2017). The exception is the Kapusnjek stream population near Veržej, which is isolated from the nearest known downstream populations by approximately 13 km. Despite these findings, some historically known populations are in marked decline or may already be locally extinct, as indicated by the Szent Kiraly/Muriša oxbow, where the species was last recorded in 2015 despite systematic monitoring in 2022 (Semrajc 2015, 2022).

5.2.5. Croatia

Soon after the distribution in Croatia was reported by Leiner (1995), new findings of the species emerged from the Drava River drainage (Delić et al. 1997). Another finding from this river system was published by Jelkić et al. (2019). The finding of *U. krameri* in the unusual habitat of the flowing Odra River (Marić et al. 2019), accompanied by bullhead (*Cottus gobio*) and stone loach (*Barbatula barbatula*), was rather surprising (Petravić et al. 2024). The newest data on

distribution and habitat characteristics in Croatia were provided by Jelić et al. (2024), showing more abundant populations in the Drava River system than in the Mura and Sava systems.

5.2.6. Serbia

Significant changes have been reported in Serbia since 1995. Three new native populations have been recorded, two from the Danube River system—the Lugomir channel system in 2008 and the Kraljevac channel system in 2014 (Sekulić et al. 2013; Miljanović et al. 2016, respectively)—and one from the Sava River system—the Zasavica pond in 1998 (Sekulić et al. 1998). Historically, 10 populations have been documented in Serbia since 1860 (Sekulić et al. 2013), but the three recently recorded populations are currently the only confirmed populations (Bănăduc et al. 2022).

5.2.7. Bosnia and Herzegovina

Significant changes have been reported in Bosnia and Herzegovina since 1995. Two new native populations have been recorded in the Sava River system: the Gromiželj marsh, identified in 2008 (Petronić et al. 2010), and the Matura River system, identified in 2016 (Marić et al. 2019; Bănăduc et al. 2022). Before these two populations were recorded, no explicit data on localities inhabited by *U. krameri* were available.

5.2.8. Romania

Over the last 30 years, the distribution and population status of *U. krameri* in Romania have changed substantially. In the northwestern part of the country, most previously known populations have disappeared (Wilhelm 2008; Telcean et al. 2014; Iftime and Otel 2025), primarily because of drainage activities and, more recently, severe droughts during the last 5 years, which in several cases led to the complete desiccation of suitable habitats. A similar decline has occurred in southern Romania, while populations in the Danube Delta also show decreasing trends. In eastern Romania, in the Siret and Prut River basins, the species has not been recorded during the past three decades. The largest remaining population is most likely still located in the Danube Delta (Bănăduc 2008). In addition, the second most important population in the country probably occurs in marshy habitats along the Jieț River. During the last 30 years, several previously unknown populations have been identified, including populations in the Timiș and Jieț River basins (Covaciu-Marcov et al. 2018; Cupșa et al. 2021; Lațiu et al. 2023), as well as in the Érmellék (Ér Valley) region and along the Régi Homoród (Old Homorod) River (Nagy et al. 2023). These records do not indicate a recent range expansion of the species but instead reflect the lack of detailed surveys in Romania during recent decades. At present, *P. glenii* is still absent from most known Romanian habitats of *U. krameri*; however, established populations already occur in adjacent areas. Its imminent spread into the majority of *U. krameri* habitats is therefore likely and may impose additional pressure on populations that are already declining. Several currently known populations occur outside protected areas, highlighting the need to designate

these sites for conservation. Moreover, in many cases, protected areas exist only nominally: species within them face threats similar to those outside protected areas. Although protected areas in Romania are formally managed by the National Agency for Environment and Protected Areas (ANMAP), management in practice is largely limited to administrative permitting. This is further evidenced by the fact that no active conservation measures specifically targeting the persistence of *U. krameri* populations have been implemented in Romania during the last century.

5.2.9. Bulgaria

The unclear situation in 1995 regarding the occurrence of the species in Bulgaria was resolved by Velkov et al. (2004), who rediscovered *U. krameri* in northeastern Bulgaria in a Danube backwater, Srebarna Lake, representing the first record since 1923. This was confirmed by Pehlivanov et al. (2011) in a survey of six wetlands along the Bulgarian Danube. However, Srebarna Lake remained the only location where *U. krameri* was found.

5.2.10. Moldova

The mudminnow was rediscovered in 2000 in the channel of the Turunchuk branch of the Dniester River near Kuchurgan Lake (Trombitsky et al. 2001). Currently, small populations have been recorded in irrigation channels and small water bodies in the village of Palanca along the Moldovan-Ukrainian border in the lower Dniester area. Efforts to reproduce *U. krameri* in aquaria were successful, but efforts to populate the old riverbed near the village of Talmaza were unsuccessful (Trombitsky et al. 2003). According to the Red Data Book of the Republic of Moldova (2015), the species is listed as “Endangered” (Crepis 2015).

5.2.11. Ukraine

According to Movchan (1995), the species was found in the upper Tisza and Prut rivers, as well as in the lower Danube and Dniester areas. Its occurrence in the lower Danube and Dniester was confirmed in the following decades (Voloshkevich 1999; Snigirov 2014; Snigirov et al. 2019, 2022; Afanasyev and Manturova 2021). Gubanov and Stepanok (2021) reported dramatic declines in the Dniester populations by 1990. Currently, *U. krameri* is found in low numbers in isolated ponds in the floodplains adjacent to the northern part of the Dniester Estuary, i.e., in the Lower Dniester National Park, and in the channels connecting the Dniester with Lake Bile. Single specimens of *U. krameri* have also been found in the coastal zone of the Dniester near the village of Mayaki (Gubanov and Stepanok 2021). Movchan (1995) and the Red Book of Ukraine (Akimov 2009) listed *U. krameri* in Transcarpathia, but there is no recent confirmation of its occurrence there.

5.3. Summary of distribution records

Within several countries, a dynamic distribution pattern has become evident, with many local populations apparently disappearing while new populations continue to be recorded. However, many of these recently documented oc-

currences likely represent previously overlooked remnant populations rather than genuine range expansions. This situation is partly related to the lack of extensive, dedicated surveys targeting noncommercial wetland-specialist fishes, particularly in regions where fish monitoring has historically focused on economically relevant species or large river systems. In addition, *U. krameri* is an elusive species with generally low catchability during conventional fish surveys, such as electrofishing campaigns designed to assess entire river fish communities. Typical habitats of *U. krameri* often comprise paleopotamon water bodies (Ward and Stanford 1995) located at the margins of floodplains and characterized by dense vegetation, thick mud layers, shallow water depths, and difficult accessibility. These conditions make standardized fish sampling particularly challenging, especially during low-water periods. Nonspecialists, therefore, often avoid sampling such habitats or do not expect fish to occur there. Consequently, *U. krameri* is sometimes detected incidentally during surveys targeting other organism groups, such as amphibians, using specialized trapping methods (Telcean et al. 2014; Covaciu-Marcov et al. 2018). Unless targeted surveys are conducted by experienced personnel, remaining populations are extremely difficult to detect, while local extinction is often equally difficult to confirm.

At the same time, despite the uncertainty associated with detectability, the overall distribution pattern of *U. krameri* clearly reflects a large-scale process of contraction and fragmentation across most of its native range. The persistence of the species increasingly depends on isolated wetland fragments, drainage canals, small marshes, and artificial refuge habitats, whereas formerly connected floodplain systems have undergone extensive hydromorphological degradation. Across the species' range, hydrological alteration, desiccation, and habitat fragmentation emerge as the most consistent drivers of decline, frequently acting together with pressures from invasive species (Bănăduc et al. 2022; Sallai et al. 2026, this issue). Although temporary habitat desiccation does not necessarily result in immediate extinction—as habitats may occasionally be recolonized from nearby source populations during periods of elevated water levels—large-scale and repeated drought events can lead to the permanent disappearance of suitable habitats and ultimately to regional extinctions. These processes complicate studies of population dynamics and hinder robust assessments of the species' actual distribution range and occupancy patterns across spatial scales.

Because of the uncertainties in detectability described above, the present review deliberately refrains from providing a detailed distribution map for the entire range, which is broadly described at the beginning of this section (5.1 General). Detailed distribution maps covering the entire range, such as the IUCN map, quickly become outdated and provide inaccurate or sometimes incorrect information for extended periods because of long update intervals. Consulting detailed national maps is therefore recommended where they are available (see Sallai et al. 2026, this issue, for Hungary). Otherwise, parts of the entire range should be regarded as "data deficient," with no reliable information available on the exact distribution (see the section on Romania).

Recent molecular approaches, particularly environmental DNA (eDNA) analysis, hold considerable promise for improving the detection and monitoring of *U. krameri* populations (Griffiths et al. 2025). The collection of

DNA fragments from water samples, followed by quantitative PCR or digital droplet PCR analysis, enables highly sensitive detection of rare and elusive species that are difficult to sample using conventional approaches, such as electrofishing. Similar workflows have already proven effective for other cryptic wetland fishes, including *M. fossilis* (Brys et al. 2021). The rapidly expanding genomic resources available for *U. krameri*, including complete mitogenome data (Wanzenböck et al., submitted), now provide an important basis for the development of species-specific eDNA assays (Rund et al. 2025). Collectively, these developments suggest that future conservation efforts will increasingly depend on integrating sensitive molecular monitoring with landscape-scale restoration of hydrological connectivity and the long-term maintenance of stable wetland refugia.

6.0 Ecology

6.1. Habitat

The basic information provided in 1995 still applies: the typical habitats of mudminnows are ponds and lakes at the outer margins of floodplains that are isolated from larger backwaters inhabited by many other fish species. These habitats are typical paleopotamon water bodies (Ward and Stanford 1995) and are located in inundation areas with associated marshes and drainage channels. More detailed studies of habitat characteristics were published by Pekárik et al. (2014), Sehr and Keckeis (2017), and Jelić et al. (2024), who found densely overgrown water bodies with muddy bottoms that experience oxygen shortages in summer and under ice cover. In addition, the unusual use of groundwater springs and cool rivulets as habitats was described by Petravić et al. (2024), confirming reports from Austria (Jesuitenbach; see the section on population dynamics), Hungary (Bíró and Paulovits 1995; Balatonedericsi Rivulet and Jamai Rivulet), and Romania (Cupșa et al. 2020; Jieț Rivulet).

6.2. Migration

Bayesian clustering of microsatellite data from 33 Hungarian stocks revealed a clear separation of populations and minimal recent admixture, supporting long-term isolation. An estimate of effective migration suggested very low contemporary gene flow ($Nm < 1$ in most comparisons), indicating that populations function largely as independent demographic units. These results demonstrate that natural migration is severely constrained by habitat fragmentation and hydrological disconnection and that recolonization potential is extremely limited without the restoration of connectivity (Takács et al. 2015). Marić et al. (2017), using an isolation-with-migration model applied to mitochondrial and microsatellite data collected throughout the species' entire range, confirmed generally low gene flow throughout the species' range, with somewhat higher levels between the Drava and Mura populations and between the lower Sava and Danube populations downstream of the Sava confluence. Later, Marić et al. (2019) demonstrated that *U. krameri* is considerably more widespread in the Sava than previously known. Consequently, this study also showed intermediate gene flow between the upper and lower Sava populations.

6.3. Food and feeding

In addition to the information available in 1995, newer studies on the food use of mudminnows were published by Sallai (2005) and Wilhelm (2007), confirming previous qualitative results. Quantitative examinations indicate that benthic prey items dominate both in frequency and biomass, reflecting bottom-oriented foraging. Seasonal variation in diet composition follows prey availability and water-level dynamics, with increased consumption of planktonic microcrustaceans during periods of higher water levels and expanded littoral zones (Sallai 2005). The species exhibits trophic plasticity within the invertebrate prey spectrum but remains strongly associated with structurally complex, vegetated microhabitats. Habitat modification, dredging, and reduction of macrophyte cover may indirectly influence growth and condition through altered prey communities (Guti 1993; Sallai 2005). Feeding ecology studies therefore link directly to population performance, suggesting that trophic resource stability and habitat structure are key determinants of local population persistence in wetlands. Experimental work was conducted specifically on larvae by Demény et al. (2014), who found faster growth when larvae were fed brine shrimp nauplii six times per day than when they were fed only four times per day. Food use in relation to *P. glenii* was studied by Grabowska et al. (2019) and Somogyi et al. (2023), who demonstrated strong competitive effects.

6.4. Growth

The growth of *U. krameri* in Hungary has been described mainly through detailed age and scale analyses conducted in wetland populations. In Kolon-tó (Kiskunság), age determination based on winter annuli and back-calculated length-at-age data showed relatively slow somatic growth and a small maximum size. The fitted von Bertalanffy growth model estimated an asymptotic length ($L\infty$) of approximately 86 mm and a theoretical maximum body mass ($W\infty$) of approximately 17 g, with close agreement between the observed and modelled values (Sallai 2005). Comparable growth parameters were reported from the Kis-Balaton region, confirming the species' small-bodied growth pattern under Hungarian environmental conditions (Mayer and Keresztessy 1994). Length-weight analyses demonstrated a strong positive relationship between body length and mass, allowing the evaluation of individual condition and population-level growth performance (Sallai 2005). Growth variability appears to be influenced by habitat stability and trophic conditions, with more consistent growth observed in vegetated, hydrologically stable wetlands. Overall, Hungarian studies characterize *U. krameri* as a slow-growing, small-bodied species with a limited maximum size and modest growth potential, consistent with its persistence in shallow, structurally complex wetland habitats (Mayer and Keresztessy 1994; Sallai 2005).

6.5. Population dynamics-examples from different countries

6.5.1. Austria

Since the rediscovery of the mudminnow in Austria in the Fadenbach in 1992 and the Jesuitenbach in 1995 (Wanzenböck and Spindler 1995), both populations have been repeatedly studied using electrofishing, allowing the

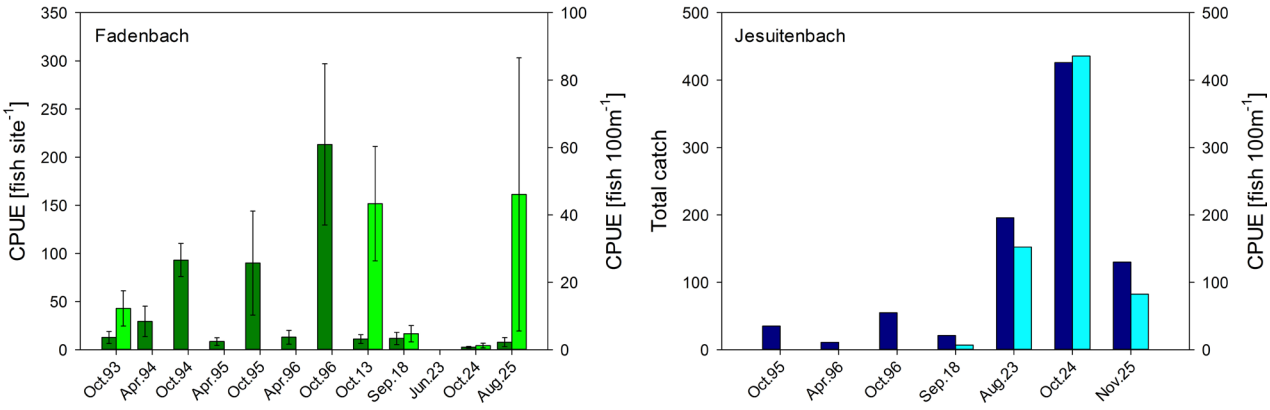

Figure 1. Population dynamics of *U. krameri* in the two native Austrian populations since their discovery in 1992 and 1995, respectively, shown as catch per unit effort (CPUE) during electrofishing campaigns. For most fishing campaigns conducted in the 1990s, no information on the lengths of the fished stretches was available. Therefore, the number of individuals caught per site is given for the Fadenbach, whereas the total catch is given for the Jesuitenbach, where the species occurs only within a very restricted area. Error bars indicate the standard error (no standard error was calculated for the Jesuitenbach because only two stretches were fished in some years).

analysis of population dynamics over the last three decades (Fig. 1). However, these studies were conducted by different teams using different methodological approaches, which has prevented the calculation of uniform abundance values.

In the 1990s, the Fadenbach supported a large metapopulation of mudminnows, and an approximately 9 km section was inhabited (Wanzenböck and Spindler 1995). Pronounced seasonal differences were observed (Fig. 1, left), with low densities in spring and much higher densities in autumn, indicating high winter mortality. However, the low catches in spring might also be attributable to the much higher water levels, resulting in a lower fish density per unit area and generally lower capture probability. In autumn 2013, high densities were observed, and the population had spread almost 3 km upstream (Sehr and Keckeis 2017), indicating the success of habitat improvement measures (Spindler 2006). In autumn 2018, catches were lower, most likely because of the high water levels at that time (Jung et al. 2018). Between 2018 and 2023, there were several periods of drought, and in 2023, the species could no longer be detected (Jung et al. 2024). This was followed by an extensive search in 2024, which confirmed the presence of a very small remaining population (Jung et al. 2025). In the summer of 2025, a slight population recovery and a high proportion of young fish were documented. However, the high abundance value was primarily attributable to the very low water level at that time and a limited sampling effort focused on the best mesohabitats of the Fadenbach.

Based on demographic parameters obtained through monitoring during the 1990s, a quantitative population model was developed using RAMAS GIS software to assess the metapopulation viability of the Fadenbach site (Wanzenböck 2004; Bănăduc et al. 2022). The time to extinction was estimated to be 24 years, with a probability of 50%, if the trends in habitat reduction observed at the time persisted. The habitat enhancements suggested by Spindler (2006) improved the situation by 2013; however, the population decline observed from 2018 to 2024 prompted new conservation measures, which were recently initiated (see the section on conservation projects).

In the Jesuitenbach system, mudminnows were restricted to a single spring pond and immediately adjacent areas along approximately 700 m of the rivulet and have never been detected farther upstream, downstream, or in the nearby moorland ditches. In the 1990s, this population was much smaller than that in the Fadenbach (Wanzenböck and Spindler 1995). Here, too, a spring survey yielded lower catch numbers than an autumn survey (Fig. 1, right). In 2018—similar to the 1990s—only approximately two dozen fish were recorded. Between 2018 and 2024, however, strong population growth occurred, peaking in 2024. In 2023, a very high proportion of young-of-the-year mudminnows was observed (Jung et al. 2024). By autumn 2025, the population had declined significantly again, possibly because of intraspecific competition, and the proportion of young fish was low (Jung et al. 2025). In contrast to the Fadenbach population, the Jesuitenbach population may have benefited from recent dry phases, which possibly reduced competition with other fish species, especially the abundant roach (*Rutilus rutilus*). Recently, beaver-induced impoundments may have further enhanced habitat suitability for *U. krameri* in the Jesuitenbach, although causal relationships remain unclear.

6.5.2. Slovenia

With few exceptions, *U. krameri* is confined to the oxbows and side channels of the Mura, which rank among the most threatened habitats in Slovenia. Estimated abundances in most oxbows are relatively low, amounting to several tens of individuals per 1,000 m² (Semrajc 2015, 2022). Monitoring data indicate that populations are declining in most oxbows along the Mura, with Nagy Parlag and Csiko Legelo representing the only known sites with stable abundances (Semrajc 2022). Although the Mura and Drava floodplains have been designated as Special Areas of Conservation (SACs) within the Natura 2000 network and are also part of the five-country Biosphere Reserve "Mura-Drava-Danube," their oxbows and river branches remain highly threatened, particularly by habitat destruction, pollution, invasive species, and inappropriate management (Povž 1995; Semrajc 2022; Govedič 2024; Semrajc et al. 2024). In view of the species' range contraction, declining population sizes, and loss of suitable habitat, its conservation status was evaluated as unfavorable in 2022 (Semrajc 2022).

6.5.3. Serbia

The magnitude of the species' areal reduction is critical in Serbia, where all 10 historically known populations recorded since 1860 had disappeared by 1995 (Sekulić et al. 2013; Marić et al. 2019). Since 1995, three new native populations have been reported from Serbia. In the Red Book of Fishes of Serbia, the species is classified as Vulnerable (VU) at the national level (Sekulić and Galamboš 2024). The estimated extent of occurrence is 12,376 km², and the area of occupancy is 52 km². Moreover, the existing populations are small, as the number of mature individuals in each was estimated to be ≤ 1,000, and a continued decline is predicted. Finally, a quantitative analysis showed that the probability of extinction in the wild is ≥ 10% within the next 100 years.

6.5.4. Romania

Considering the disappearance of the species from many of its former habitats, together with the consistently declining trends of the remaining populations across its entire distribution range, a reassessment of *U. krameri* under the IUCN Red List criteria, potentially leading to its classification as Endangered or Critically Endangered, appears warranted. Furthermore, the implementation of active conservation measures is urgently needed to prevent the complete collapse of its remaining populations.

6.6. Summary on ecology

Overall, population dynamics studies conducted during the last three decades across several parts of the species' range highlight the pronounced temporal instability of many *U. krameri* populations. Considerable fluctuations in abundance, recruitment success, and spatial distribution have been documented even within relatively small habitat systems, often in close association with hydrological conditions, drought periods, and habitat management interventions. While some populations showed temporary recovery following habitat restoration or favorable water conditions, others declined rapidly or nearly disappeared during prolonged dry periods. These observations suggest that many extant populations persist near their ecological tolerance limits and are highly sensitive to even short-term environmental changes. At the same time, the long-term persistence of certain populations, including those inhabiting highly modified or isolated habitats, demonstrates that *U. krameri* can survive under suboptimal conditions when minimal hydrological stability and suitable refuge habitats remain available. Collectively, these findings emphasize that the conservation of viable populations depends not only on local protection measures but also on maintaining long-term hydrological stability, habitat connectivity, and sufficient habitat heterogeneity at the landscape scale.

Ecological studies conducted during the last three decades consistently indicate that *U. krameri* is strongly associated with shallow, densely vegetated, hydrologically stable wetland habitats characterized by low competition pressure and structurally complex littoral zones. The species exhibits limited dispersal capacity, low contemporary gene flow (see the following section), and a strong dependence on habitat connectivity, making populations highly vulnerable to fragmentation and drought. At the same time, recent studies demonstrate that *U. krameri* retains a certain degree of ecological flexibility, occasionally persisting in atypical habitats such as springs, rivulets, drainage canals, or artificial refuge systems. This combination of strong habitat specialization and limited but detectable ecological plasticity may partly explain both the species' long-term persistence in fragmented landscapes and its continuing vulnerability under accelerating hydrological and climatic change.

7.0 Phylogeography, population genetics, and genomics

The intraspecific phylogeography and population genetics of *U. krameri* have been investigated in relatively few studies, and the available data are largely restricted to mitochondrial DNA sequences (cytochrome *b*) and a set of microsatellite markers (Winkler and Weiss 2009).

Mitochondrial analyses identified three major evolutionary lineages corresponding to the Danube, Sava, and Tisza drainages (Marić et al. 2015, 2017, 2019). Their divergence was likely driven by Pleistocene glacial cycles and tectonic processes that reshaped central and southeastern European river systems (Marić et al. 2017), as was the case for many European freshwater fishes (Bernatchez and Wilson 1998; Zangl et al. 2020; Cortéz-Guzmán et al. 2024). Within the Danube drainage, mitochondrial diversity is geographically structured but shallow. Upstream sections are largely dominated by a single widespread haplotype, whereas downstream areas, particularly the Danube Delta, harbor several additional haplotypes and overall higher diversity. A haplotype typical of the lower Danube also occurs in the Drava system and extends eastward into the Dniester Delta, where it coexists with a private local haplotype (Marić et al. 2017). In contrast, the Sava lineage consists of a single dominant haplotype, which was also detected in one middle Danube population near the Sava confluence, while the Tisza lineage comprises two haplotypes restricted to the investigated Tisza populations (Marić et al. 2017, 2019). The strict geographic segregation of these mitochondrial lineages mirrors present-day drainage boundaries and supports their recognition as ESUs.

Microsatellite analyses further corroborate strong population genetic structuring. Populations are often highly differentiated even across short geographic distances (Takács et al. 2015; Marić et al. 2017, 2019; Donabaum et al. 2026, this issue), reflecting limited dispersal capacity, strict habitat specialization in shallow, vegetated, often low-oxygen lentic and semi-lentic habitats, and the naturally patchy distribution of suitable environments. Historically, lateral connectivity within extensive Danube floodplains likely enabled intermittent gene flow, but such connectivity was probably episodic and hydromorphologically constrained; contemporary patterns therefore reflect both historical isolation by distance and more recent anthropogenic fragmentation.

Microsatellite-based analyses consistently report moderate to high levels of expected heterozygosity and allelic richness (Takács et al. 2015; Marić et al. 2017, 2019; Donabaum et al. 2026, this issue). Thus, despite severe habitat loss over the past century, many populations still retain appreciable neutral genetic diversity. Levels of nuclear genetic diversity show a clear spatial trend. The highest allelic richness and heterozygosity are found in the Danube and Dniester deltas, whereas upstream sections tend to harbor reduced diversity (Takács et al. 2015; Marić et al. 2017, 2019). This gradient likely reflects differences in population size and habitat stability, as deltaic systems provide extensive and continuous wetlands that support larger effective population sizes with reduced genetic drift, while upstream populations are often confined to small, isolated water bodies, where stochastic processes can rapidly erode genetic variation.

Comparisons among regions further suggest that historical hydrological connectivity has shaped present-day patterns of variation. In the Carpathian Basin, for example, populations situated within the former floodplain of the Tisza tended to exhibit weaker differentiation from one another than populations located outside this historically connected area (Takács et al. 2015). This finding supports the interpretation that past floodplain dynamics facilitated gene flow, whereas subsequent river regulation and habitat alteration intensified isolation. How recent desiccation and associated population declines have affected current differentiation and genetic diversity remains unclear (Sallai et

al. 2026, this issue), but evidence from *ex situ* breeding stocks indicates that measurable genetic divergence due to founder effects and genetic drift can arise rapidly once populations become separated (Donabaum et al. 2026, this issue), highlighting the species' sensitivity to population fragmentation.

Together, mitochondrial and nuclear data highlight deep drainage-based phylogeographic structuring and pronounced fine-scale population subdivision in *U. krameri*, underscoring the necessity of managing the species at the level of distinct ESUs and local populations. Conservation strategies should therefore prioritize the maintenance of genetic integrity within drainages and, where possible, the restoration of habitat connectivity to counteract ongoing genetic erosion in this highly fragmented species.

The increase in genome size in mudminnows was analyzed by Lehmann et al. (2021), who reported that the genome of *U. krameri* has expanded similarly to those of the two other *Umbra* species and that this expansion is driven by transposons. In 2025, a high-quality reference genome for *U. krameri* was made publicly available. The chromosome-level assembly was generated through the European Reference Genome Atlas (ERGA) within the Biodiversity Genomics Europe (BGE) project. Sample, sequence, and assembly metadata are available under the umbrella BioProject PRJEB85943, while the genome assembly itself can be accessed through the European Nucleotide Archive (ENA) under accession PRJEB85937. However, the annotation is not yet available. The complete mitogenome was assembled and annotated by Wanzenböck et al. (2026, submitted), forming the basis for eDNA primer development (Rund et al. 2025).

Together, recent phylogeographic, population genetic, and genomic studies have fundamentally changed the understanding of *U. krameri* population structure and evolutionary history by demonstrating pronounced drainage-based subdivision, limited contemporary connectivity, and substantial fine-scale differentiation across much of the species' range. These findings strongly support conservation planning at the level of distinct ESUs and local population units rather than treating the species as a genetically homogeneous taxon. At the same time, emerging genomic resources, including complete mitogenome and reference genome assemblies, provide an important foundation for future applications such as eDNA monitoring, conservation genomics, and the adaptive management of fragmented populations.

8.0. Parasites

Research on the parasites of the mudminnow expanded considerably during recent decades, particularly at the eastern edge of its distribution in Moldova and Ukraine (Gerasev et al. 2005; Moshu and Trombitsky 2007, 2016, 2025, 2026; Snigirov et al. 2019). Thirteen parasite species new to science were described: 12 protozoans and one monogenean worm (Gerasev et al. 2005; Moshu and Trombitsky 2007, 2016). In total, 176 species of eukaryotic commensal or parasitic symbionts were identified. The parasite diversity of the lower Dniester populations is much richer and differs from that of populations in the Danube basin. Although the Dniester populations have a rich parasite community, some typical "Dniester species" are absent or very rare. Almost all identified species are new records for this fish host and include 18 host-specific species; one species is shared with *U. limi*, and 12 species are shared with

Esox lucius. The overall parasite prevalence among mudminnows was 100%, meaning that every individual investigated harbored at least one parasite species. The maximum number of parasite species per fish was 18, and the usual number was 4–8. Males were slightly more heavily infested than females. Under certain circumstances, the burden of such a high number of pathogenic parasites may pose a potential threat to the survival of the unique populations in the Dniester River basin. Although there is currently no overlap between the distribution ranges of *U. krameri* and *U. pygmaea*, potential future introductions raise concerns regarding the spillover of co-introduced parasites that could be hazardous to *U. krameri*, e.g., *Gyrodactylus umbrae*.

9.0. Conservation of the European mudminnow

In recent decades, numerous projects have been launched across Europe to halt the decline of *U. krameri* populations (Bănăduc et al. 2022).

9.1. Austria

Several conservation measures have been implemented in the Danube National Park, specifically at the Fadenbach site. These efforts began with habitat restoration (Spindler 2006) and captive breeding in private ponds. Later, monitoring in accordance with the EU Habitats Directive was implemented (Jung et al. 2018, 2024). A reintroduction attempt was conducted in the Hanság wetland, a drainage-ditch system along the Austrian-Hungarian border. Offspring from the Fadenbach population were stocked there (Benesch 2004, 2008); however, the population persisted for approximately 15 years before it was found to be extinct during subsequent monitoring (Jung et al. 2025). Low population densities in the Fadenbach area in 2018 (see the section on population dynamics) led to a new conservation initiative by the Danube Floodplain National Park, the PonDiversity project, involving further habitat improvements and a captive breeding program accompanied by conservation genetic studies (Donabaum et al. 2026, this issue).

9.2. Slovakia

In the 1990s, mudminnows bred *ex situ* were released on several occasions in the Záhorská nížína, in wetlands and drainage canals along the lower reaches of the Morava River in Slovakia (Valachovič and Kováč 1998; Májsky and Hajdú 2004). The State Nature Conservancy of Slovakia (ŠOP SR) developed a detailed species conservation program, which was implemented between 2006 and 2008 in the Podunajská nížina (Great Rye Island), the Záhorská nížina (along the Morava River), and the Východoslovenská nížina (Eastern Slovak Lowland). During the program's implementation, comprehensive habitat surveys were conducted, covering water quality, aquatic vegetation, and fish assemblages. Silted-up and trash-filled melioration channels were intended to be cleaned and dredged; however, these activities were only partially implemented (Májsky and Hajdú 2004; Hajdú and Saxa 2008; Májsky and Hajdú 2008). Selected drainage canals were deepened in 50 m stretches, with excavations repeated at intervals of 50–100 m along the canals. Despite these efforts, some canal sections, including the deepened sections, dried out in subsequent years,

especially in the Záhorská nížina. Fish were rescued from a drying mudminnow drainage canal in the Záhorská nížina, as mentioned in the distribution section. Rescued juveniles of *U. krameri* were stocked at several sites where the species had not previously been recorded, and a highly successful population was established at the Zelienka site. Within the LIFE+ project focusing on the restoration of wetlands for the endemic rodent *Microtus oeconomus mehelyi*, the dry bed of the middle and lower thirds of Čiližský potok, a former small side arm of the Danube, was restored beginning in 2016. The upper third had previously been supplied with water and supported a large population of *U. krameri*. The middle third of Čiližský potok was supplied with water, and the mudminnow population became re-established there. In recent years, the lower third has also been restored, providing potential new habitats for *U. krameri*.

9.3. Hungary

Fen biotopes have formed in the habitat restoration area of the Southern Hanság, which was flooded in 2001 at the site of the former branches of the Rábca Stream. In 2005, *U. krameri* was introduced into these waters from the drying Kolon Lake, located in the Danube-Tisza Interfluve. These populations have persisted to the present and have even colonized new habitats (Ambrus and Sallai 2014). In recent years, there have been several instances in Hungary in which mudminnows required rescue because of drought and unsustainable water management (Nyeste et al. 2022a, 2022b). In 2024, the University of Debrecen and the Hungarian Society for Environmental Management and Rural Development (Magyar Környezetgazdálkodási és Vidékfejlesztési Társaság) released *U. krameri* into rehabilitated fens with a permanent supply of well water in the protected Navat and Nyíres lakes in Hungary. The selection of suitable habitats and identification of potential risks were made possible by the Tavirózsa Association's new "PRO UMBRA" habitat qualification system (Tatár et al. 2025). Based on monitoring results, the released fish successfully spawned during the spring of 2025. In 2008, the Tavirózsa Association launched a long-term project in Hungary. The main aim of the "European Mudminnow Conservation Pilot Program" is to preserve and increase the Hungarian population of *U. krameri* through captive breeding, *in situ* and *ex situ* conservation, wetland rehabilitation, and the creation of new habitats in the Szada Pilot Area (Bajomi et al. 2013, 2026; Tatár et al. 2017, 2026; Tóth et al. 2026). In 2009, members of the Szent István Campus of the Hungarian University of Agricultural and Life Sciences (MATE SZIC—formerly Szent István University) and the Danube-Ipoly National Park Directorate joined the program. The pilot program covered research on existing and newly created habitats, including water quality, aquatic vegetation, macroinvertebrates, and fish fauna; stock and population conservation; *in situ* and *ex situ* conservation biology; and breeding, rearing, and research related to resettlement. Since 2011, captive breeding, egg incubation, and larval and juvenile rearing under both laboratory and field conditions have been conducted (Müller et al. 2011; Demény et al. 2014; Tatár et al. 2017; Müller et al. 2025). These activities showed that hormone-induced spawning in closed systems failed, whereas controlled natural spawning, aided by an innovative spawning cage, produced viable offspring. This work was complemented by studies on sperm cryopreservation, spawning substrates, and feeding (Demény et al. 2014; Kucska et al. 2016). To date, more

than 8,700 individuals from five mudminnow populations have been produced at various life stages and reintroduced into original and surrogate habitats in the Szada Pilot Area. Part of the broodstock is currently maintained in the Botanical Garden ponds at MATE, and this novel habitat management approach is being adapted to address climate-change impacts (Müller et al. 2025). Parent fish were rescued from seven endangered habitats or populations and introduced into the ponds of the Szada Pilot Area. Two of the six stocked ponds have established self-sustaining populations (Bajomi et al. 2026).

9.4. Slovenia

The action plan for habitat restoration at the Natura 2000 Mura site has been adopted (Koren et al. 2019). This action plan is currently being implemented through the four-year conservation project "Restoration of River and Riparian Habitats of the Mura and Drava" (Natura Mura-Drava; 2025–2029), coordinated by the Institute of the Republic of Slovenia for Nature Conservation. Although this ambitious conservation project does not specifically target the conservation of *U. krameri*, it includes measures aimed at improving hydromorphological conditions through the restoration of oxbow lakes, widening of selected river sections, and re-establishment of natural fluvial processes on acquired land.

9.5. Croatia

A 10-year management action plan (2019–2029) covering the Virovitica subpopulation is underway. Planned measures include removing non-native species, improving connectivity among the seven identified locations, enhancing water quality by reducing fertilizer runoff, and improving canal maintenance techniques (Jelić et al. 2019).

9.6. Serbia

In 2021, *U. krameri* from the Special Nature Reserve Kraljevac were bred *ex situ*, and the parent stock and offspring were released into their original habitat. During Božanić's (2022) survey, physical, chemical, and biological data were collected from known Serbian mudminnow habitats, but no new populations were found. Breeding also took place as part of the project, and the offspring were used to reinforce populations in natural habitats. In 2025, the project "*Umbra krameri* Habitat Revitalization in the Special Nature Reserve Kraljevac" was implemented at Ćinkina Ćuprija. Approximately 1.3 km of canal was mechanically dredged to prolong water retention during the summer and autumn. The removal of thick silt deposits led to groundwater penetration and refilling of the habitat, resulting in considerably more favorable hydrological conditions (Marić et al. 2025).

9.7. Bosnia and Herzegovina

During 2016–2017, a comprehensive study of an older and a newly discovered mudminnow habitat was conducted, covering water quality, vegetation, invertebrate macrofauna, and fish fauna, and genetic samples were also collected from the species. In addition, students were involved in the fieldwork (Čolić 2017).

9.8. Romania

Between 2005 and 2007, as part of the Ecological Society AquaTerra's "Living Water II" project in Iași County, Romania, the water supply to the protected Teiva-Vișina oxbow and its surroundings in the Prut (Jijia) River valley was improved. One of the planned outcomes was to strengthen and increase the population; however, fish monitoring ultimately did not take place (G. Davideanu, personal communication, 2017). The society also organized an environmental competition involving local students (Teodosiu et al. 2005; Living Water 2007). In 2009, the National Agricultural Research and Development Institute prepared a project report that, in addition to other fish species, discussed breeding and rearing technologies for *U. krameri*, the risks associated with reintroductions, and habitat requirements (NARDI 2009).

9.9. Moldova

Between 2000 and 2003, the Moldovan BIOTICA Ecological Society reintroduced *U. krameri* propagated *ex situ* into small water bodies in the lower Dniester River basin. It should be emphasized that, before this project, the European mudminnow had not been detected in waters along the Dniester for 28 years (World Bank Group 2001; Aps et al. 2004). Later, Moshu and Trombitsky (2025) stated that attempts to populate new suitable habitats with fry were unsuccessful.

9.10. Summary of conservation efforts

The conservation efforts implemented during the last three decades (Table 1) demonstrate both the possibilities and limitations of *U. krameri* conservation in highly fragmented wetland systems. Numerous projects involving habitat restoration, hydrological rehabilitation, captive breeding, population reinforcement, and the establishment of surrogate habitats were launched across the species' range, in several cases successfully supporting local population persistence and recolonization of restored wetlands. Particularly promising results were achieved in habitats where long-term water supplies and habitat stability could be maintained, often combined with continuous monitoring and adaptive management. At the same time, many projects also highlighted the vulnerability of small, isolated populations and the limited effectiveness of short-term interventions lacking sustained hydrological management or long-term follow-up monitoring (Bajomi et al. 2026). In several cases, restored or newly established populations declined again following periods of drought, habitat desiccation, or renewed hydromorphological degradation. Across much of the species' range, climate-driven water shortages, habitat fragmentation, decreasing genetic diversity caused by isolation, and the spread of *P. glenii* increasingly interact as synergistic threats (Bănăduc et al. 2022; Tatár et al. 2026; Tóth et al. 2026). Consequently, the long-term conservation of *U. krameri* cannot rely solely on local translocations or isolated habitat restoration actions but requires landscape-scale hydrological management, maintenance of wetland connectivity, suppression of invasive species, comprehensive habitat assessment, and coordinated long-term conservation strategies integrating both *in situ* and *ex situ* approaches.

Table 1. Activities of conservation projects involving *U. krameri* in European countries during the last three decades. [1] Self-sustaining populations supported by long-term monitoring data. [2] Population extinct after 15 years (Jung et al. 2025). [3] Habitat rehabilitation is underway. [4] Populations persisting for 7 and 10 years in two created habitats (Bajomi et al. 2026). [5] Population at Zelienka persisting for approximately 15 years and population in the wetlands and drainage canals along the lower reaches of the Morava River becoming extinct after approximately 15 years. [6] No stocking or fish transfer was undertaken after the unsuccessful transfer of mudminnows from the Beloviči oxbow to a small gravel pit in 1991 (Povž 1995).

Country	Fish fauna survey	*Ex situ* breeding	*In situ* breeding	Habitat research	Habitat rehabilitation	Stocking	Long-term habitat monitoring	Long-term population monitoring	Self-sustaining populations in newly stocked habitats[1]
Austria	+	+	-	+	+	+	+	+	+[2]
Bosnia and Herzegovina	+	-	-	+	-	-	-	-	-
Bulgaria	+	-	-	-	-	-	-	-	-
Croatia	+	-	-	+	+[3]	-	-	+	-
Hungary	+	+	+	+	+	+	+	+	+[4]
Moldova	+	+	-	-	-	+	-	-	-
Romania	+	+	-	+	+	-	-	-	-
Serbia	+	+	-	+	+	+	+	+	-
Slovakia	+	+	-	+	+	+	+	+	+[5]
Slovenia	+	-	-	+	+	-[6]	+	+	-
Ukraine	+	-	-	+	-	-	-	-	-

10. Conclusion and future perspectives

During the three decades following the publication of the first comprehensive monograph on the European mudminnow, knowledge of the biology, distribution, genetics, ecology, and conservation of *U. krameri* has expanded substantially. New phylogeographic and population genetic studies have fundamentally changed the understanding of the species by revealing pronounced drainage-based structuring, limited contemporary gene flow, and the existence of distinct evolutionarily significant units (ESUs). At the same time, the emergence of genomic resources, complete mitogenome assemblies, and environmental DNA (eDNA) approaches has opened entirely new perspectives for monitoring and conservation. Numerous studies have also improved the understanding of habitat use, trophic ecology, population dynamics, and conservation management, while conservation breeding and translocation programs have been initiated in several countries across the species' range.

Despite these advances, the overall conservation picture of *U. krameri* has become considerably more alarming than it appeared in 1995. Although several previously undocumented populations have been discovered during recent decades, the general distribution pattern across much of the native range clearly reflects progressive fragmentation, hydrological degradation, and local population loss. Many surviving populations persist only in small, isolated wetland remnants, drainage canals, artificial refuge systems, or heavily modified floodplain habitats. Across countries and habitat types, similar large-scale processes repeatedly emerge: floodplain disconnection, wetland drainage, canalization, increasing drought frequency, and the loss of shallow paleopotamon habitats. Therefore, in combination with threats from invasive species, particularly *P. glenii*, the outlook for the long-term survival of the species appears very pessimistic. This pessimistic outlook is not adequately reflected in the current IUCN assessment of Vulnerable (Ford 2024), and a reassessment potentially leading to its classification as Endangered or Critically Endangered is warranted. *U. krameri* increasingly appears to function as an indicator spe-

cies of collapsing lowland wetland networks and declining floodplain connectivity in central and southeastern Europe. Many ecological and conservation patterns observed in *U. krameri* resemble those of other specialized wetland fishes, such as *Carassius carassius*, *Misgurnus fossilis*, and *Leucaspius delineatus*, which likewise depend on shallow, structurally complex wetlands and often persist in isolated refuge habitats, including oxbows, marshes, drainage canals, and small ponds.

The review also highlights several important knowledge gaps that remain unresolved despite recent progress. Long-term standardized monitoring data are still scarce across most of the species' range, limiting the understanding of population viability, metapopulation dynamics, and extinction risk. The effects of ongoing climate change, particularly the increasing frequency of droughts and hydrological instability, remain insufficiently quantified. Similarly, the ecological and genetic consequences of increasing habitat fragmentation, including the thresholds of functional connectivity required for population persistence, are poorly understood. Emerging threats such as parasite spillover, interactions with invasive fishes, and the potential role of non-native congeners, including *U. pygmaea*, also require further investigation. In parallel, many conservation interventions have lacked long-term post-restoration evaluation, making it difficult to assess their effectiveness under changing environmental conditions.

Future conservation of *U. krameri* will therefore require an integrated landscape-scale approach combining hydrological restoration, wetland reconnection, climate adaptation, invasive species management, and long-term ecological and genetic monitoring. Maintaining a stable water supply and restoring lateral floodplain connectivity will likely become increasingly important under projected climate scenarios. At the same time, newly available molecular and genomic tools, particularly eDNA-based monitoring and conservation genomics, provide promising opportunities for improving population detection, monitoring cryptic populations, and guiding adaptive conservation management. In highly fragmented regions where natural hydrological reconnection is no longer feasible, carefully documented conservation breeding and translocation programs may also contribute to maintaining genetic diversity and functional connectivity among isolated populations. However, such interventions should be guided by phylogeographic structure and ESU-level conservation principles to avoid unintended genetic homogenization or disruption of locally adapted population lineages. Given the highly fragmented distribution of the species and the transboundary nature of many floodplain systems, effective long-term conservation will also depend on coordinated international cooperation across the entire native range of *U. krameri*.

Acknowledgments

The authors thank Urban Hammerschied for improving the English. The authors are indebted to an anonymous reviewer, Jeroen VanWichelen, Lukáš Kalous, and Sabine Wanzenböck for their help in improving previous versions of the manuscript.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

Artificial Intelligence (AI) use

The authors accept full responsibility for the content of the manuscript, including the disclosure of any use of AI.
No AI tools were used in the preparation of this manuscript.

Funding

SM was funded by the Ministry of Education of the Republic of Serbia (Grant No. 451-03-34/2026-03/200178). In alignment with the United Nations 2030 Agenda for Sustainable Development, this study directly contributes to SDG 14 (Life Below Water) and SDG 15 (Life on Land). DS was funded by the Slovenian Research Agency (Research Program No. P1-0255). TM was funded by the Mohamed bin Zayed Species Conservation Fund (Grant No. 242533675).

Author contributions

Conceptualization: JW. Data curation: MJ. Supervision: JW. Validation: PT. Visualization: MJ. Writing - original draft: HR, ST, SM, RD, DS, AAN, NS, PT, JW, TM, SK, LP, IT, MJ. Writing - review and editing: NS, LP, AAN, SM, JW, HR, DS, PT, TM, SK, IT, MJ, ST, RD, AM, CR.

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Data availability

All of the data that support the findings of this study are available in the main text.