Nature Conservation

Nature Conservation 65: 85–97 (2026)
DOI: 10.3897/natureconservation.65.186939

Research Article

Temporal changes in the distribution of *Carassius carassius* and the invasive *Carassius gibelio* in Croatian freshwaters

David Dianežević[1], Zoran Marčić[1], Marko Ćaleta[2], Sven Horvatić[1], Monika Puhalović[1], Roman Karlović[1], Goran Tvrdinić[1], Perica Mustafić[1], Dinko Jelkić[3], Davor Zanella[1]

1 *Department of Biology, Faculty of Science, University of Zagreb, Rooseveltov trg 6, 10000 Zagreb, Croatia*
2 *Faculty of Teacher Education, University of Zagreb, Savska cesta 77, 10000 Zagreb, Croatia*
3 *Faculty of Agrobiotechnical Sciences, Josip Juraj Strossmayer University of Osijek, Vladimira Preloga 1, 31000 Osijek, Croatia*
Corresponding author: David Dianežević (david.dianezevic@biol.pmf.hr)

Abstract

Anthropogenic modification of freshwater ecosystems has drastically transformed freshwater habitats across Europe, contributing to the decline of limnophilic fish species and promoting the spread of invasive taxa. This study examines the long-term spatial and temporal changes in the distribution of the native crucian carp (*Carassius carassius*) and the invasive gibel carp (*C. gibelio*) in Croatian freshwater ecosystems. We compiled validated presence/absence data covering the period 1883–2025 from historical literature, national monitoring programmes, citizen science platforms, and verified angler records. The results reveal a pronounced shift in *Carassius* assemblages over time. Historically, *C. carassius* was widespread in the lowland waters of the Pannonian Ecoregion, showing preserved river–floodplain connectivity and presence in numerous shallow lentic habitats. Since the mid-20th century, extensive river regulation, floodplain disconnection, and land reclamation have facilitated the rapid expansion of *C. gibelio*, which now dominates freshwater systems across Croatia. Currently, *C. carassius* persists only in a small number of isolated localities, primarily oxbows, regulated channels, and slow-flowing lowland river sections with dense macrophyte vegetation. These populations are highly fragmented, occurring mainly at low densities, and are frequently overlooked by standard monitoring, indicating probable local extinctions. These findings highlight the urgent need for targeted conservation measures and improved management to safeguard persisting *C. carassius* populations in Croatia.

Key words: Croatia, crucian carp, fragmented habitat, freshwater, gibel carp, invasive species

OPEN ACCESS

Academic editor: Lukáš Kalous
Received: 29 January 2026
Accepted: 19 March 2026
Published: 9 October 2026

ZooBank: https://zoobank.org/A16AD90A-8580-4B10-B98D-201A4A3AEFE4

Citation: Dianežević D, Marčić Z, Ćaleta M, Horvatić S, Puhalović M, Karlović R, Tvrdinić G, Mustafić P, Jelkić D, Zanella D (2026) Temporal changes in the distribution of *Carassius carassius* and the invasive *Carassius gibelio* in Croatian freshwaters. 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: 85–97. https://doi.org/10.3897/natureconservation.65.186939

Copyright: © David Dianežević et al.
This is an open access article distributed under terms of the Creative Commons Attribution License (Attribution 4.0 International – CC BY 4.0).

Introduction

Anthropogenic modifications of freshwater ecosystems, including river regulation, dam construction, and changes in land use, have led to extensive fragmentation of wetland habitats and disruption of natural hydrological regimes across Europe (Reid et al. 2019; Keck et al. 2025; Šmejkal et al. 2025). These processes have reduced the longitudinal and lateral connectivity between rivers and their floodplains, leading to the loss of oxbows, backwaters, and wetlands

(Grizzetti et al. 2017; Hayes et al. 2018; Šmejkal et al. 2023, 2025). These alterations today pose major threats to freshwater biodiversity, particularly affecting species closely associated with lentic habitats.

Limnophilic fish species (e.g., *Carassius carassius* Linnaeus, 1758; *Umbra krameri* Walbaum, 1792; *Leucaspius delineatus* (Heckel, 1843); *Misgurnus fossilis* (Linnaeus, 1758)) that depend on preserved oxbows, ponds, and slow-flowing or stagnant waters, have experienced long-term population declines and increasing fragmentation of populations across Europe (Šmejkal et al. 2025). These negative trends are further intensified by the spread of invasive non-native species, such as *C. gibelio* (Bloch, 1782), *Pseudorasbora parva* (Temminck & Schlegel, 1846), *Perccottus glenii* Dybowski, 1877, *Ameiurus melas* (Rafinesque, 1820). They most often have a competitive advantage in degraded habitats due to broader ecological tolerance, higher reproductive success, and stronger competitive ability for resources (Blackburn et al. 2011; Šmejkal et al. 2024, 2025). One of the most illustrative cases of these combined anthropogenic and biological pressures is observed within the genus *Carassius* Jarocki, 1822, particularly *C. carassius* and the invasive *C. gibelio*.

The crucian carp (*C. carassius*) was formerly a widespread and abundant native species inhabiting small lentic and floodplain water bodies throughout Central and Eastern Europe, including Croatia (Kottelat and Freyhof 2007; Freyhof 2024). The species plays an important ecological role in periodically flooded, often hypoxic ponds, where it contributes to energy transfer as prey for predatory fishes. However, since the second half of the 20th century, *C. carassius* populations have declined sharply and disappeared from many localities (Fedorčák et al. 2023). The prominent drivers for the decline are habitat loss and degradation, limited food supply, competition with the non-native complex *Carassius* sp. *sensu* (*C. auratus*, *C. gibelio*, *C. langsdorfii*), and hybridisation with non-native *Carassius* taxa (Papoušek et al. 2008; Knytl et al. 2018, 2022; Lehoczky et al. 2025; Šmejkal et al. 2025).

The invasive gibel carp (*C. gibelio*) was massively introduced into European freshwater ecosystems in the mid-20th century, primarily as an unintentional associate of Asian cyprinids imported from the Amur Basin for aquaculture purposes (Drensky 1948; Bănărescu 1964; Plančić 1967; Szczerbowski 2002). The invasiveness of *C. gibelio* is linked to several biological traits, including gynogenetic reproduction, high ecological plasticity, strong competitive ability for resources, and negative impacts on the reproduction of native species (Šmejkal et al. 2025). Due to its high morphological similarity to other species of the genus *Carassius*, the early stages of its invasion often went unnoticed or undocumented, further complicating the reconstruction of the spatial and temporal dynamics of its spread. According to available literature, the first confirmed records of *C. gibelio* in the Drava and Danube Rivers within the territory of the former Yugoslavia date back to the 1960s (Plančić 1967). In addition, non-native *Carassius auratus* (Linnaeus, 1758) are occasionally recorded in Croatian freshwater ecosystems; however, these records are rare and spatially limited (personal observations).

In Croatia, *C. carassius* has traditionally been known under several vernacular names, such as *karas* or *karaš*, while older literature also refers to the species as *blatar*, *blatarka*, *karas žuti*, *karasac*, *koravac*, *koroselj*, and *plosnačica* (Hirtz 1956). Under current national legislation (Official Gazette 80/13, 15/18, 14/19, 127/19, 155/23), strict protection of the species applies only within designated protected areas, such as Lonjsko Polje Nature Park, Kopački Rit Nature Park,

and the Mura–Drava Regional Park. The IUCN Red List categorises *C. carassius* as Least Concern (LC) at both the global and European levels, although with a decreasing population trend (Freyhof 2024). Its conservation status in Croatia was previously assessed as Vulnerable (VU) (Mrakovčić et al. 2006). In contrast, *Carassius gibelio* is classified as an invasive alien species and has been assessed as high risk to Croatian freshwater ecosystems according to FISK and AS-ISK evaluations (Piria et al. 2018; Radočaj et al. 2021).

Despite these contrasting conservation statuses, long-term trends in the distribution and relative abundance of native and invasive *Carassius* species in Croatia have not been systematically analysed. Recent fish fauna surveys indicate that populations of *C. carassius* have become rare and disappeared from many localities, and the species is currently considered uncatchable by anglers. In contrast, *C. gibelio* is widespread and abundant across nearly all freshwater systems in Croatia.

Therefore, the main objective of this study was to analyse long-term spatial and temporal changes in the distribution of the native *C. carassius* and the invasive *C. gibelio* in Croatian freshwater ecosystems using historical and recent presence/absence data. Specifically, we aimed to: (i) reconstruct historical and current distribution patterns of both species across the major freshwater ecoregions of Croatia, (ii) quantify temporal shifts in their relative occurrence and dominance over distinct periods characterised by intensive hydromorphological alterations and the expansion of invasive species, and (iii) discuss the implications of these patterns for conservation and management of *C. carassius* in modified river–floodplain systems.

Methods

Study area

The territory of Croatia (area: 56,594 km^2) is divided into two major freshwater ecoregions according to the European Union Water Framework Directive (WFD, 2000/60/EC): the Pannonian Ecoregion (Hungarian Lowlands; ER11) and the Dinaric Ecoregion (Dinaric Western Balkan; ER5). The Dinaric Ecoregion is further subdivided into the Continental and Mediterranean Subecoregions.

The Pannonian Ecoregion encompasses the continental lowland part of the country and is drained mainly by the Sava, Drava, and Danube Rivers, all belonging to the Danube Basin. The Dinaric Ecoregion is predominantly karstic and includes both continental and Mediterranean hydrological systems. Watercourses of the Dinaric-Continental Subecoregion mostly drain into the Danube River Basin, whereas those of the Dinaric-Mediterranean Subecoregion belong to the Adriatic Sea Basin.

Data compilation and sources

Presence/absence data for *C. carassius* and *C. gibelio* were compiled from Croatian freshwater systems for the period 1883–2025, beginning with the earliest precisely georeferenced record of *C. carassius* documented by Mojsisovics (1883). A comprehensive database was created from multiple sources, including peer-reviewed literature, books, and field survey reports. Additional

information was obtained from online databases (the iNaturalist citizen science platform [accessed 5 Jan 2026], Biosweb platform of the Fisheries Research Institute of Slovenia [accessed 8 Jan 2026], and the Bioatlas database of the State Institute for Nature Protection of Croatia [accessed 20 Dec 2025]), and from the authors' published and unpublished observations collected over the past 20 years. Only records available up to the end of 2025 were considered, regardless of the access date. Recent records of *C. carassius* were also obtained from recreational anglers.

Data validation

Only records with clearly defined localities and years of observation were included. Records from the iNaturalist platform were accepted only after species identity was verified using photographic evidence and confirmation of locality and date. Angler records were considered only if accompanied by photographs allowing reliable species identification. Only images clearly showing diagnostic morphological characters (e.g., dorsal fin margin shape, caudal fin shape, presence of a caudal peduncle spot in individuals up to ~10 cm total length, and head shape) were accepted.

An additional source of potential error arises from the local use of vernacular names. For example, in parts of the Sava River basin the name *"karas"*, which formally refers to *C. carassius*, is often colloquially used for the invasive pumpkinseed (*Lepomis gibbosus* (Linnaeus, 1758)) (personal observation). To minimise misidentifications, all submitted photographs were therefore subjected to additional verification, substantially increasing the reliability of the database used in the analyses.

Older literature records referring only to vague geographic entities (e.g., entire rivers) without precise localities, as well as records with uncertain species identification or unknown years, were excluded. Duplicate records were removed, retaining only unique locality–year combinations. For historical records cited in multiple sources, only the original reference was retained.

Data analyses

To examine temporal changes in the representation of *Carassius* species in Croatia, the number of records reporting each species was summarised per year. Values were converted into proportional presence by dividing the number of records for each species by the total number of records in that year. Temporal trends were visualised using a five-year moving average calculated with a rolling mean. All data processing and statistical analyses were performed in R (version 4.5.2; R Core Team 2025) using the *tidyr*, *dplyr*, *ggplot2*, and *zoo* packages.

Occurrence data were analysed within the framework of the two freshwater ecoregions. Distribution maps were generated for three temporal periods: (A) prior to 1967, before the major expansion/intensification of river regulation and introduction of the invasive *Carassius* species; (B) 1967–2013, a period characterised by intensive river regulation, land reclamation, and increased introductions of Asian cyprinids; (C) 2014–2025, the most recent and data-rich period, including systematic data collection linked to Natura 2000 implementation and national surface water monitoring under the Water Framework Directive

(European Parliament & Council 2000). Distribution maps were produced using QGIS (version 3.40.4: QGIS Development Team 2024).

Abundance-based graphical analysis

Only localities with multi-year data and confirmed records of *C. carassius* were included in the abundance-based analysis. This selection was made to illustrate temporal detection patterns, including sites with recent non-detections and those with persistent presence over the study period.

For these localities, the relationship between the abundances of *C. carassius* and *C. gibelio* was analysed. Annual counts of sampled individuals were summarised for each locality and used for graphical presentation. To allow the use of a logarithmic scale while retaining zero values, a constant of one was added to all abundance values prior to plotting. Data visualisation was performed in Python version 3.10 (Python Software Foundation 2024), with data processing using the *pandas* library and figures generated with *matplotlib*.

Although *C. auratus* occurs sporadically in Croatian freshwater ecosystems, this species was not included in the analyses due to the very low number of reliable records and the lack of sufficient temporal continuity for assessment. Consequently, the analyses focused exclusively on the native *C. carassius* and the invasive *C. gibelio*.

Results

Analysis of presence/absence data collected between 1883 and 2025 revealed temporal changes in the proportions of native and non-native *Carassius* species in Croatian freshwater systems, based on multiple literature and online sources (Fig. 1). A notable increase in observations of *C. gibelio* was recorded following its introduction in the 1970s, with a particularly high number of records over the past 30 years. In the same period, the number of observations of the native species *C. carassius* declined.

The spatio-temporal distribution of validated *Carassius* observations in Croatia between 1883 and 2025 is summarised in three distribution maps (Fig. 2A–C).

In the period 1883–1966 (Fig. 2A), *C. carassius* was the only recorded species in Croatian freshwater systems. It was widely distributed across water bodies of the Pannonian Ecoregion, as reported in the literature, and confirmed with precise locality data for 23 observations. Additionally, two records represent translocations of the species, one in the Lika River (Continental–Dinaric Subecoregion) and one in Lake Vrana near Biograd na Moru (Mediterranean–Dinaric Subecoregion).

Between 1967 and 2013 (Fig. 2B), *C. gibelio* expanded across the Pannonian Ecoregion. At the same time both species were stocked for recreational fishing in water bodies of the Dinaric Ecoregion. During this period, many observations of *C. carassius* were recorded in gravel pits, fish ponds, and numerous oxbows, with a particularly high number of records in Lonjsko Polje, the largest wetland area in this part of Europe, protected as a nature park. Numerous observations were also reported in oxbows along the Mura River. In total, 87 observations of *C. carassius* occurred within the native range and 18 in the translocated range (seven in the Mediterranean-Dinaric and 11 in the Continental-Dinaric

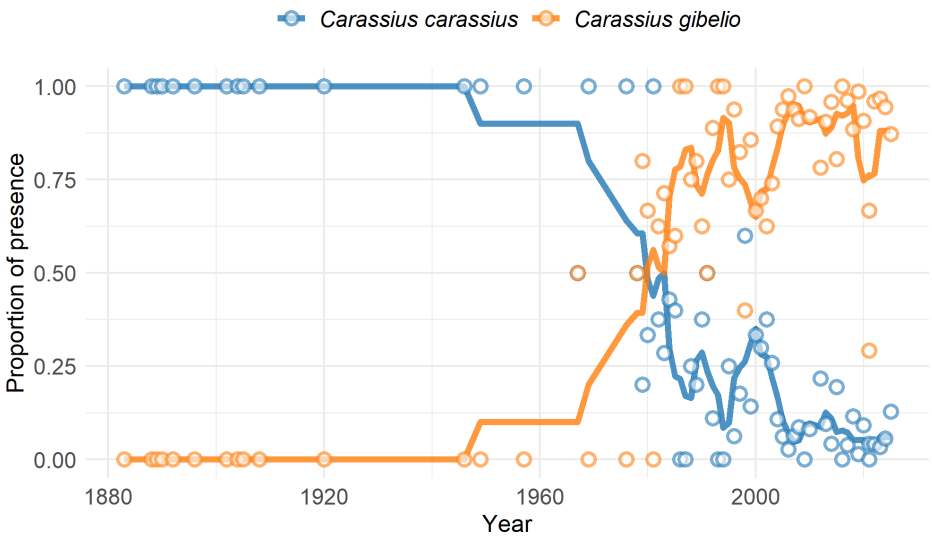

Figure 1. Temporal representation of the proportional presence of two *Carassius* species, native *C. carassius* (blue) and invasive *C. gibelio* (orange), based on revised occurrence records compiled from multiple data sources between 1883 and 2025. Lines represent the 5-year moving average of proportional presence, while points indicate individual annual records.

Subecoregion). During the same period, more than 1600 observations of *C. gibelio* were reported based on literature and monitoring data, and the species was recorded in nearly all water bodies throughout the country.

From 2014 to the present (Fig. 2C), *C. gibelio* dominates nearly all water bodies in both ecoregions. *C. carassius* is now mainly observed in low numbers and in coexistence with *C. gibelio*. During this recent period, 49 observations of *C. carassius* were recorded in Pannonian water bodies and 15 in the Dinaric Ecoregion, where it is considered a translocated species. The species was recorded exclusively in oxbows, regulated channels rich in submerged and floating vegetation, or in sections of lowland rivers with dense macrophyte vegetation and slow-flowing water. Several additional records were noted in ponds, reservoirs, and intermittent rivers in the Continental–Dinaric Subecoregion, where the species was translocated. Furthermore, *C. carassius* was confirmed at 21 sites in the Drava and Danube catchments and at 10 sites in the Sava catchment.

Discussion

Analysis of historical and recent distribution data of *Carassius* species in Croatia revealed pronounced long-term changes in freshwater fish communities, driven by changes in hydromorphology and water management practices, and expansion of the invasive *C. gibelio*. These changes reflect a broader degradation of limnophilic habitats and a shift towards homogenised fish assemblages.

During the earliest analysed period (1883–1966; Fig. 2A), *C. carassius* was widely distributed across the lowland waters of the Pannonian Ecoregion, indicating well-connected river–floodplain systems and a high availability of shallow lentic habitats suitable for this limnophilic species. In addition to its natural range, early records also point to initial, unintentional translocations, likely associated with stocking activities involving common carp (*Cyprinus carpio* Linnaeus, 1758), particularly in the Lika River and Lake Vrana (Plančić 1946; Pofuk et al. 2017).

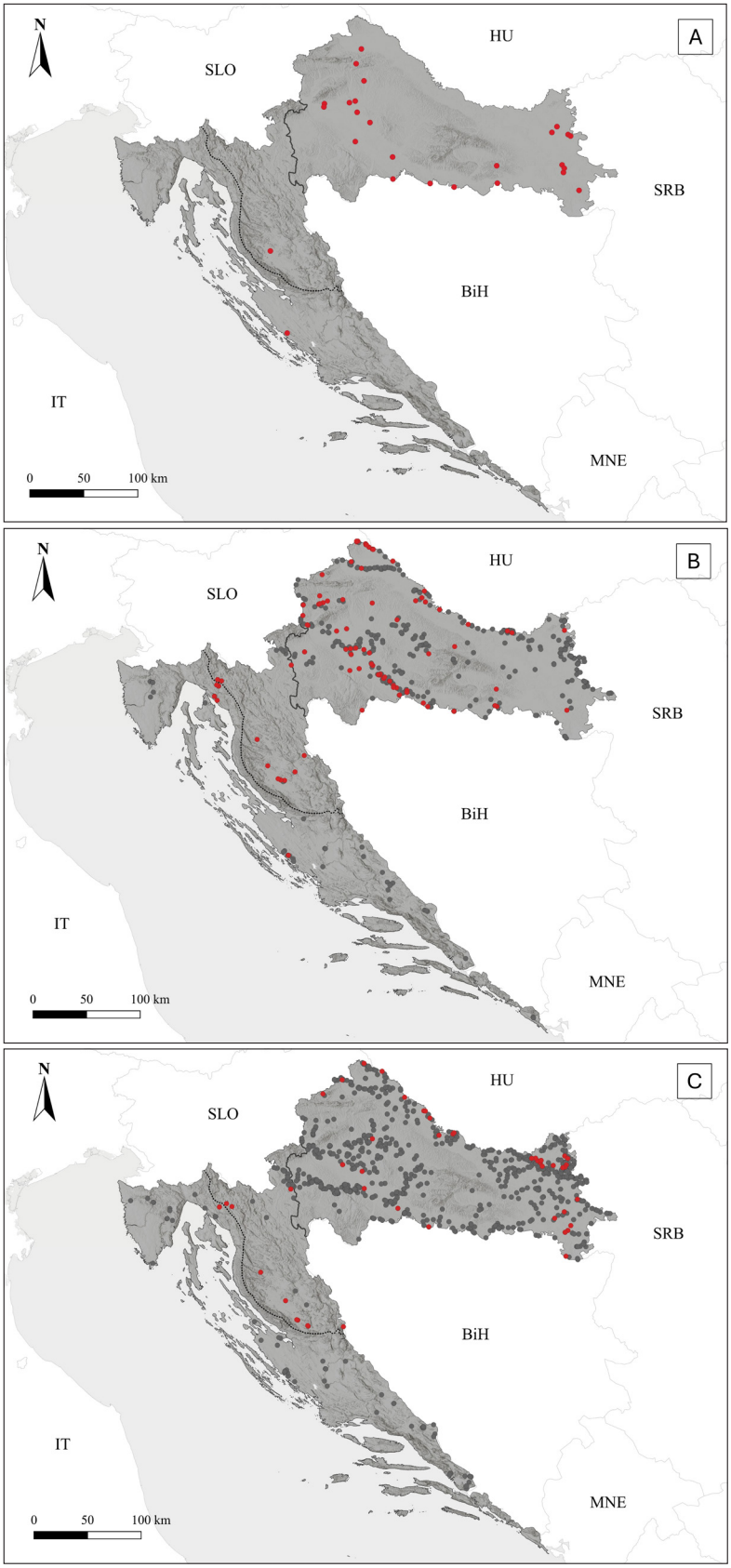

Figure 2. Distribution of the native *C. carassius* (red dots) and the non-native *C. gibelio* (grey dots) in the freshwaters of Croatia across three observation periods. **A**. 1883–1966; **B**. 1967–2013, and **C**. 2014–2025. Abbreviations refer to neighbouring countries. Black lines indicate ecoregion boundaries (solid: Pannonian–Dinaric; dashed: Mediterranean–continental Dinaric).

In the second period (1967–2013; Fig. 2B), the increase in precisely georeferenced records of *C. carassius* primarily reflects intensified research efforts rather than population recovery or growth. At the same time, the first clear signs of *C. gibelio* expansion become evident, coinciding with intensified river regulation, land reclamation, and the loss of natural floodplain habitats. Spatial clustering of records suggests that remaining *C. carassius* populations were already fragmented and restricted to a limited number of suitable refugial habitats.

Large-scale hydromorphological modifications of Croatian rivers represent a key driver of the long-term decline of limnophilic species. River regulation along the Sava and Drava Rivers began as early as the 18th century through the disconnection of side arms and meanders (Slukan-Antić 2002) and intensified significantly after major flood events in the second half of 20th century (Marušić 2022).

The interpretation of temporal trends should be considered with caution, as the dataset is derived from heterogeneous sources collected over a long period. Trends may be influenced by uneven sampling effort, changing observer intensity, the unequal composition of data sources through time, and improved monitoring in recent years. Consequently, apparent increases in records may reflect enhanced reporting rather than true changes in species occurrence, and the presented trends primarily represent relative proportions of recorded occurrences rather than actual population sizes.

The third period (2014–2025; Fig. 2C) illustrates the scope of these changes. Comprehensive monitoring reveals the near-complete dominance of *C. gibelio* across most water bodies, while *C. carassius* remains confined to a small number of isolated localities. This pattern strongly indicates a combined effect of habitat loss and competitive pressure with *C. gibelio*.

The collected data suggest that *C. gibelio* initially mostly spread naturally through the Sava and Drava River systems, with flood events facilitating its expansion into side channels, oxbows, gravel pits, and ponds. These habitats currently represent key zones of co-occurrence between native and non-native *Carassius* species in Croatia, as confirmed elsewhere in Europe (Fedorčák et al. 2023). Additional dispersal vectors are linked to aquaculture, where *C. gibelio* may have been unintentionally released during fish pond management. Recreational angling, particularly the use of live bait, appears to be a major mechanism of spread into the Dinaric Ecoregion. The same cause of spread has been observed in other countries (Elgin et al. 2014; Lyach 2022; Fedorčák et al. 2023; Šmejkal et al. 2024). Although the use of invasive species (live or dead) as bait is prohibited under the current legislation (Official Gazette 63/19), *C. gibelio* is frequently used for this purpose (personal observation). Lastly, recent findings suggest that eggs or embryos of *C. gibelio* can be dispersed without human intervention in the gut of waterbirds (e.g., mallards), proving bird-mediated dispersal ability of soft-membraned eggs undergoing active development (Lovas-Kiss et al. 2020).

Our analyses indicate that *C. carassius* has become a rare species in Croatia, particularly within its native range, and its detectability is strongly dependent on local conditions and sampling intensity. Three main scenarios of occurrence can be identified: (1) habitats where *C. carassius* co-occurs with *C. gibelio* at extremely low densities and is often missed during standard monitoring (Fig. 3A); (2) habitats where both species are present but *C. carassius* occurs in moderately higher numbers (Fig. 3B); and (3) historical habitats, especially rivers, side arms, and gravel pits, where the species has disappeared entirely, suggesting local extinctions (Fig. 3C).

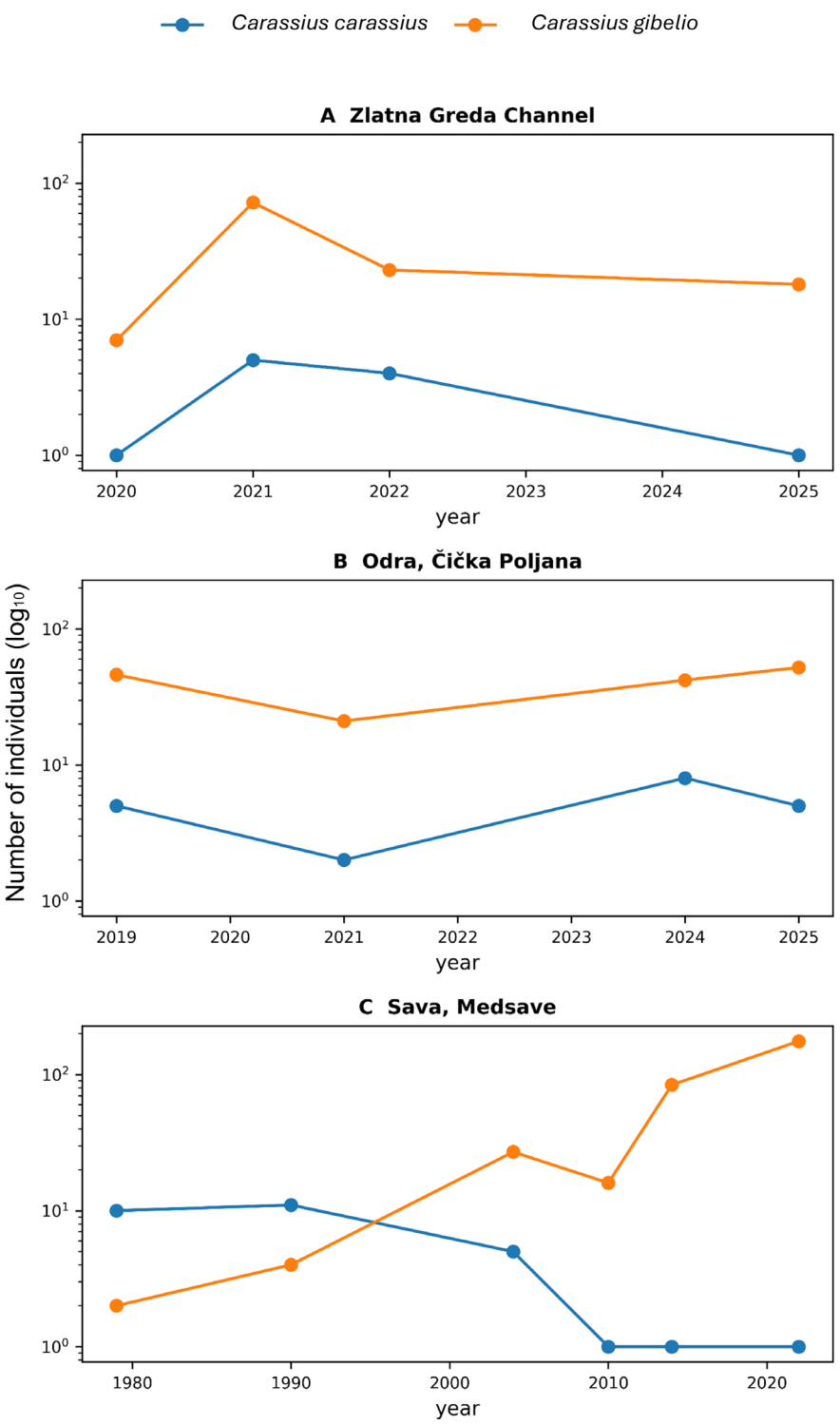

Figure 3. Temporal changes in the abundance of *Carassius carassius* and *C. gibelio* at three localities. **A**. Zlatna Greda Channel; **B**. Odra, Čička Poljana, and **C**. Sava, Medsave. The y-axis is presented on a logarithmic scale ($\log_{10}$), with a value of one added to all observations to allow inclusion of zero counts. Lines represent species-specific trends over time; points indicate individual sampling years.

Experience from successful conservation projects, such as those from England or Czech Republic (Sayer et al. 2011, 2020; Lyach 2022), demonstrate that *C. carassius* can persist and thrive in small, shallow ponds lacking

predatory fish, otters and invasive *C. gibelio* (Lyach 2022). We believe that similar initiatives could appear realistic and positive in Croatia, particularly through cooperation with recreational anglers, who have shown considerable interest in conserving *C. carassius*. Local examples, such as isolated ponds (managed by the Trakošćan sports fishing society) that support stable populations of *C. carassius* and *Tinca tinca* (Linnaeus, 1758), illustrate the potential of targeted, small-scale conservation actions (personal observation). However, the first step must be to assess the true genetic status of *C. carassius* and the extent of hybridisation with non-native *Carassius* species in Croatia. This is necessary to clearly determine where conservation efforts should be concentrated and targeted. Additionally, a comprehensive assessment of all non-native *Carassius* taxa present in Croatia is required. This is particularly important given the presence of *C. langsdorfii* Temminck & Schlegel, 1846 in the Neretva River basin in Bosnia and Herzegovina (Kalous et al. 2013; Rylková et al. 2013), which likely extends into Croatian waters. Genetic screening is therefore essential to detect cryptic lineages and assess the true extent of non-native *Carassius* taxa within Croatian freshwater ecosystems.

Conclusion

This study provides the first long-term synthesis of distributional changes in native and invasive *Carassius* species in Croatia. Our results reveal a clear shift from historically widespread populations of *C. carassius* to near-dominance of the invasive *C. gibelio*. Decline of *C. carassius* is closely linked to extensive hydromorphological alterations and the loss of river-wetlands connectivity, which has reduced suitable limnophilic habitats. Additionally, competitive pressure from *C. gibelio* further limits persistence. Today, *C. carassius* survives only in isolated habitats, mostly at low abundance. Effective conservation will require targeted habitat protection and restoration, stricter control of invasive species pathways, and genetic assessments of populations to support *ex situ* conservation measures. This study highlights the value of long-term, spatially explicit data in understanding biodiversity change and provides a scientific basis for future conservation and restoration of limnophilic fish in modified river–floodplain systems.

References

Bănărescu P (1964) Fauna Republicii Populare Romîne, Pisces – Osteichthyes (Peşti Ganoizi şi Osoşi). Editura Academiei Republicii Populare Romîne, Bucuresti.

Blackburn TM, Pyšek P, Bacher S, Carlton JT, Duncan RP, Jarošík V, Wilson JRU, Richardson DM (2011) A proposed unified framework for biological invasions. Trends in Ecology and Evolution 26: 333–339. https://doi.org/10.1016/j.tree.2011.03.023

Drensky P (1948) Synopsis and distribution of fishes in Bulgaria. Annulaire de l'Universite de Sofia, Faculte de Sciences 44(3): 11–71. [In Bulgarian]

Elgin EL, Tunna HR, Jackson LJ (2014) First confirmed records of Prussian carp, Carassius gibelio (Bloch, 1782) in open waters of North America. BioInvasions Records 3: 275–282. https://doi.org/10.3391/bir.2014.3.4.09

European Parliament & Council (2000) Directive 2000/60/EC of the European Parliament and of the Council establishing a framework for Community action in the field of water policy. Official Journal of the European Communities, L327, 1–72.

Fedorčák J, Križek P, Koščo J (2023) Which factors influence spatio–temporal changes in the distribution of invasive and native species of genus *Carassius*? Aquatic Invasions 18(2): 219–230. https://doi.org/10.3391/ai.2023.18.2.105240

Freyhof J (2024) *Carassius carassius*. The IUCN Red List of Threatened Species 2024: e. T3849A58294635. https://doi.org/10.2305/IUCN.UK.2024-1.RLTS.T3849A58294635.en

Grizzetti B, Pistocchi A, Liquete C, Udias A, Bouraoui F, Van De Bund W (2017) Human pressures and ecological status of European rivers. Scientific Reports 7: 1–11. https://doi.org/10.1038/s41598-017-00324-3

Hayes DS, Brändle JM, Seliger C, Zeiringer B, Ferreira T, Schmutz S (2018) Advancing towards functional environmental flows for temperate floodplain rivers. Science of the Total Environment 633: 1089–1104. https://doi.org/10.1016/j.scitotenv.2018.03.221

Hirtz M (1956) Rječnik narodnih zoologičnih naziva, Ribe (Pisces). Jugoslavenska akademija znanosti i umjetnosti, Zagreb, 478 pp. [In Croatian]

Kalous L, Rylková K, Bohlen J, Šanda R, Petrtýl M (2013) New mtDNA data reveal a wide distribution of the Japanese ginbuna *Carassius langsdorfii* in Europe. Journal of Fish Biology 82(2): 703–707. https://doi.org/10.1111/j.1095-8649.2012.03492.x

Keck F, Peller T, Alther R, Barouillet C, Blackman R, Capo E, Chonova T, Couton M, Fehlinger L, Kirschner D, Knüsel M, Muneret L, Oester R, Tapolczai K, Zhang H, Altermatt F (2025) The global human impact on biodiversity. Nature 641: 395–400. https://doi.org/10.1038/s41586-025-08752-2

Knytl M, Forsythe A, Kalous L (2022) A fish of multiple faces, which show us enigmatic and incredible phenomena in nature: biology and cytogenetics of the genus *Carassius*. International Journal of Molecular Sciences 23: 8095. https://doi.org/10.3390/IJMS23158095

Knytl M, Kalous L, Rylková K, Choleva L, Merila J, Ráb P (2018) Morphologically indistinguishable hybrid *Carassius* female with 156 chromosomes: a threat for the threatened crucian carp, *C. Carassius*, L. PLoS ONE 13: e0190924. https://doi.org/10.1371/journal.pone.0190924

Kottelat M, Freyhof J (2007) Handbook of European freshwater fishes. Kottelat, Cornol, Switzerland and Freyhof, Berlin, Germany.

Lehoczky I, Al Fatle FA, Nguyen Thi Q, Edviné Meleg E, Sallai Z, Szabó G, Fekete G, Kópor I, Várkonyi E, Péter D, Beliczky G, Kovács B, Urbányi B, Molnár T (2025) Genetic survey of crucian carp *Carassius carassius* populations in Hungary for a conservation project to establish live gene bank. Scientific Report 15: 8835. https://doi.org/10.1038/s41598-025-93468-6

Lovas-Kiss A, Vincze O, Löki V, Pallér-Kapusi F, Halasi-Kovács B, Kovács G, Green AJ, Lukács BA (2020) Experimental evidence of dispersal of invasive cyprinid eggs inside migratory waterfowl. Proceedings of the National Academy of Sciences of the United States of America 117(27): 15397–15399. https://doi.org/10.1073/pnas.2004805117

Lyach R (2022) In situ management options to improve crucian carp (*Carassius carassius*, L.) and brown trout (*Salmo trutta*, L.) population status in Central Europe: A case study from the Czech Republic. Ecology and Evolution 12(7): e9107. https://doi.org/10.1002/ece3.9107

Marušić J (2022) Iz povijesti vodnog gospodarstva: Studija regulacije i uređenja rijeke Save. Hrvatske vode 30(121): 255–259. https://hrcak.srce.hr/294521 [In Croatian]

Mojsisovics AE (1883) Zur Fauna von Bellye und Darda. Mitteilungen des naturwissenschaftlichen Vereines für Steiermark, 19, 103–194. [In German]

Mrakovčić M, Brigić A, Buj I, Ćaleta M, Mustafić P, Zanella D (2006) Red Book of Freshwater Fishes of Croatia. Ministarstvo kulture, Državni zavod za zaštitu prirode, Zagreb, 253 pp. [In Croatian with English abstract]

Papoušek I, Vetešník L, Halačka K, Lusková V, Humpl M, Mendel J (2008) Identification of natural hybrids of gibel carp *Carassius auratus gibelio* (Bloch) and crucian carp *Carassius carassius* (L.) from lower Dyje River floodplain (Czech Republic). Journal of Fish Biology 72: 1230–1235. https://doi.org/10.1111/j.1095-8649.2007.01783.x

Piria M, Simonović P, Kalogianni E, Vardakas L, Koutsikos N, Zanella D, Ristovska M, Apostolou A, Adrović A, Mrdak D, Tarkan AS, Miloševič D, Zanella LN, Bakiu R, Ekmekçi FG, Povž M, Korro K, Nikolić V, Škrijelj R, Kostov V, Gregori A, Joy MK (2018) Alien freshwater fish species in the Balkans-Vectors and pathways of introduction. Fish and Fisheries 19(1): 138–169. https://doi.org/10.1111/faf.12242

Plančić J (1946) Novonaseljene ribe u rijeci Lici. Croatian Journal of Fisheries 1(3): 31. [In Croatian]

Plančić J (1967) Prussian carp *Carassius auratus gibelio* a new member of our ichthyofauna. Ribarstvo Jugoslavije 22: 155–156. [In Yugoslavian]

Pofuk M, Zanella D, Piria M (2017) An overview of the translocated native and non-native fish species in Croatia: pathways, impacts and management. Management of Biological Invasions 8(3): 425–435. https://doi.org/10.3391/mbi.2017.8.3.16

Python Software Foundation (2024) Python Language Reference, version 3.10. https://www.python.org

QGIS Development Team (2024) QGIS Geographic Information System. Open Source Geospatial Foundation Project. http://qgis.osgeo.org

R Core Team (2025) R: A Language and Environmental for Statistical Computing R Development Core Team, R: a language and environment for statistical computing. https://doi.org/10.32614/r.manuals

Radočaj T, Špelić I, Vilizzi L, Povž M, Piria M (2021) Identifying threats from introduced and translocated non-native freshwater fishes in Croatia and Slovenia under current and future climatic conditions. Global Ecology and Conservation 27: e01520. https://doi.org/10.1016/j.gecco.2021.e01520

Reid AJ, Carlson AK, Creed IF, Eliason EJ, Gell PA, Johnson PT, Kidd KA, MacCormack TJ, Olden JD, Ormerod SJ, Smol JP, Taylor WW, Tockner W, Vermaire JC, Dudgeon D, Cooke SJ (2019) Emerging threats and persistent conservation challenges for freshwater biodiversity. Biological Reviews 94(3): 849–873. https://doi.org/10.1111/brv.12480

Rylková K, Kalous L, Bohlen J, Lamatsch DK, Petrtýl M (2013) Phylogeny and biogeographic history of the cyprinid fish genus *Carassius* (Teleostei: Cyprinidae) with focus on natural and anthropogenic arrivals in Europe. Aquaculture 380–383: 13–20. https://doi.org/10.1016/j.aquaculture.2012.11.027

Sayer CD, Copp GH, Emson D, Godard MJ, Zięba G, Wesley KJ (2011) Towards the conservation of crucian carp *Carassius carassius*: Understanding the extent and causes of decline within part of its native English range. Journal of Fish Biology 79(6): 1608–1624. https://doi.org/10.1111/j.1095-8649.2011.03059.x

Sayer CD, Emson D, Patmore IR, Greaves HM, West WP, Payne J, Davies GD, Tarkan AS, Wiseman G, Cooper B, Grapes T, Cooper G, Copp GH (2020) Recovery of the crucian carp *Carassius carassius* (L.): Approach and early results of an English conservation project. Aquatic Conservation 30(12): 2240–2253. https://doi.org/10.1002/aqc.3422

Slukan-Antić M (2002) Hidroregulacije Drave i njezini utjecaju na transformaciju prirodnog i kulturnog pejsaža Podravine. Podravina 1(2): 128–152. [In Croatian]

Szczerbowski JA (2002) Cyprinidae 2, part III: Carassius to Cyprinus. In: Banarescu PM, Päpke HJ (Eds.) The Freshwater Fishes of Europe. Aula, Wiesbaden, 305 pp.

Šmejkal M, Bartoň D, Duras J, Horký P, Muška M, Kubečka J, Pfauserová N, Tesfaye M, Slavík O (2023) Living on the edge: Reservoirs facilitate enhanced interactions among generalist and rheophilic fish species in tributaries. Frontiers in Environmental Science 11: 1099030. https://doi.org/10.3389/fenvs.2023.1099030

Šmejkal M, Thomas K, Kořen V, Kubečka J (2024) The 50-year history of anglers' record catches of genus *Carassius*: Circumstantial evidence of wiping out the native species by invasive conspecific. NeoBiota 92: 111–128. https://doi.org/10.3897/neobiota.92.121288

Šmejkal M, Kalous L, Auwerx J, Gorule PA, Jarić I, Dočkal O, Fedorčák J, Muška M, Thomas K, Takács P, Ferincz Á, Choleva L, Lamatsch DK, Wanzenböck J, Van Wichelen J (2025) Wetland fish in peril: A synergy between habitat loss and biological invasions drives the extinction of neglected native fauna. Biological Conservation 302: 110948. https://doi.org/10.1016/j.biocon.2024.110948

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

No funding was reported.

Author contributions

Conceptualization: DD. Data curation: PM, MĆ, SH, ZM, MP, DZ, DJ, DD. Formal analysis: DD. Investigation: DJ, ZM, MĆ, DZ, PM, SH, DD, RK, GT. Methodology: DD. Resources: DZ, PM. Supervision: DZ. Validation: DD. Visualization: DD. Writing - original draft: DD. Writing - review and editing: MP, SH, DZ, PM, DD, DJ, RK, MĆ, GT, ZM.

Author ORCIDs

D. Dianežević https://orcid.org/0009-0006-1094-6627
Z. Marčić https://orcid.org/0000-0002-4984-4453
M. Ćaleta https://orcid.org/0000-0002-4675-556X
S. Horvatić https://orcid.org/0000-0003-2944-9568
R. Karlović https://orcid.org/0009-0008-0258-9759
P. Mustafić https://orcid.org/0000-0002-9329-4241
D. Jelkić https://orcid.org/0000-0001-6415-3362
D. Zanella https://orcid.org/0000-0001-9984-5393

Data availability

The data presented in this study are available on request from the corresponding author.