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Damming and river flow intermittency shape the distribution of non-native fish in the Republic of Cyprus

Alessandro Balestrieri,[1*] Athina Papatheodoulou,[2] Richard W. Spare,[1,3] Bruno Boz,[4] Michele Spairani,[4] Ayis Iacovides,[2] Iakovos Tziortzis,[5] Gerald Dörflinger,[5] Paolo Tremolada[1]

[1]Department of Environmental Sciences and Policy, University of Milan, Italy; [2]I.A.CO Environmental and Water Consultant Ltd., Strovolos, Cyprus; [3]Biology Education Centre, Uppsala University, Uppsala, Sweden; [4]Flume – Fluvial Management and Ecology SC, Gignod (AO), Italy; [5]Water Development Department, Ministry of Agriculture, Rural Development and Environment, Pallouriotissa, Cyprus

Abstract

Fish introductions represent a major pressure on freshwater ecosystems, particularly in Mediterranean islands where hydrological stress and habitat fragmentation are pronounced. Water scarcity prompts provisioning, with artificial reservoirs often becoming recipients for introduced fish species. We provide the most comprehensive assessment to date of the distribution of non-native freshwater fish in the Republic of Cyprus, based on electrofishing surveys conducted between 2020 and 2025 at 136 sites across 31 river catchments. Eleven non-native species were detected at 54.4% of sampling sites. Salmonids were largely confined to high-altitude, perennial streams, whereas cyprinids and centrarchids were mainly associated with dammed watercourses and non-perennial stretches. Mosquitofish (*Gambusia holbrooki*) and common roach (*Rutilus rutilus*) were the most widespread and abundant species, reflecting their high ecological tolerance and invasive potential. Distance from the sea affected the distribution of both salmonids, which were recorded in the central part of the island, and mosquitofish, which occurred along the southern coast. Our results demonstrate that damming and flow intermittency shape the spread of non-native fish in Cypriot rivers. Given the limited feasibility of eradication and the vulnerability of Mediterranean freshwater ecosystems, prevention and long-term monitoring should be prioritized to prevent future introductions and ecological impacts.

Key words: introductions; barriers; Mediterranean rivers; freshwater ecosystems.

**Correspondence to: alebls@libero.it*

INTRODUCTION

The high dispersal ability of fish as well as the intensity with which humans spread them beyond their native range for economic and recreational activities make fish communities and freshwater ecosystems amongst the most invaded throughout the world (Gherardi, 2007; Gallardo *et al*., 2016; McFadden *et al*., 2023). Cyprinids, including grass carp *Ctenopharyngodon idellus* and silver carp *Hypophthalmichthys molitrix,* and salmonids, such as rainbow trout *Oncorhynchus mykiss,* brown trout *Salmo trutta* and brook charr *Salvelinus fontinalis,* stand amongst the most widely introduced species, followed by Ictaluridae and Centrarchidae (Lehtonen, 2002).

Introduced species inevitably affect native species and ecosystems through competition for resources, predation, pathogen transmission, and alteration of environmental conditions (Moyle and Barton, 1987), their impact being often amplified by other man-driven factors, such as pollution and habitat degradation (Marvier *et al.,* 2004; Milardi *et al*., 2022). Notwithstanding, fish introductions continue, mainly driven by aquaculture, ornamental trade and angling (Gozlan, 2008).

Islands, which often face disproportionate levels of anthropogenic disturbance due to higher-than-average population densities, are more vulnerable to introductions than continental areas (Jeschke and Genovesi, 2010). Although the negative effects of fish introductions on islands have been widely reported (Xiong *et al*., 2018; Rodríguez-Barreras *et al.,* 2020; MacNeil *et al*., 2024), most studies have focused on their management and socio-economic impacts (Russel *et al*., 2017), while knowledge on the diversity and spatial distribution of non-native species still remains limited (Gherardi *et al.,* 2009). In the Mediterranean basin, islands often suffer heavy variation in river flow, with intermittent and ephemeral streams being the dominant watercourses (Bonada and Resh, 2013) and global warming is expected to further increase the frequency of extreme hydrological events and duration of river drying (Xiong and Yang, 2025). Water scarcity, especially in the hot season, prompts management measures aiming at maximizing provisioning (Moyle, 2014; Borg Galea *et al*., 2019), which, in the past, mostly consisted of groundwater extraction and damming. While allowing water storage, artificial reservoirs alter the geophysical and ecological conditions of rivers (Chen *et al*., 2023) and often become recipients for introduced fish species (Fox *et al*., 2007). Reservoirs have been shown to be more

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prone to the establishment of non-native fish with respect to both natural lakes (Johnson *et al*., 2008) and undammed rivers (Liew *et al.*, 2016).

Cyprus, one of the smallest countries in the European Union, stands first in the list of EU Member States facing the most significant water scarcity conditions on the seasonal scale (European Environment Agency, 2025), ranks eighth in the absolute number of introduced species (23, of which 11 originating from other continents; Holčik, 1991) and second for introduced species density (0.24 non-natives per 100 km²), preceded only by Malta (Holčik, 1991). Introductions peaked during the late 1960s, primarily for recreational angling in reservoirs (Dill, 1990; Papatheodoulou *et al*., 2025). Most of these reservoirs are artificial, resulting from a total of 108 dams constructed for storing water for irrigation and accommodating the water needs of urban areas (Sofroniou and Bishop, 2014; Water Development Department, 2023); currently, about 30% is still managed for angling (Department of Fisheries and Marine Research, 2025).

In 2002, Lehtonen, when reviewing available sources about the introduction of non-European fish species, followed Holčik in listing for Cyprus 11 species and added mosquitofish (*Gambusia* sp.).

More recently, a document by the Standing Committee of the Bern Convention on the Conservation of European Wildlife and Natural Habitats reported 20 introduced species of which 15 successfully established (Elvira, 2011). Field surveys conducted by Zogaris *et al*. (2012) across 53 sites in 18 catchments downsized the number of confirmed non-native species hosted by Cyprus, confirming the presence of 12, seven of which occurring in lotic systems. The latter study also concluded that only a limited number of river stretches supported self-reproducing populations, with unpredictable chances of enduring increasing anthropogenic pressures (Zogaris *et al.*, 2012).

To improve available knowledge on fish distribution in the Republic's river network and assess the role played by reservoirs in driving the colonization of watercourses by introduced fish, we reviewed and analysed the data collected between 2020 and 2025 within the framework of biological quality element assessments mandated by Article 8 of the European Union Water Framework Directive (2000/60/EC). Overall, 136 river stretches were sampled across most island's major catchments. Based on their ecological requirements, we expected salmonids to be primarily associated with high-altitude perennial streams, where in winter water temperature is suitable for reproduction (Spairani *et al*., 2025). Reservoirs being known to host several non-native fish, the distribution of cyprinids and centrarchids was expected to be shaped by damming, with most species occurring in lowland river stretches, downstream of reservoirs.

Study area

The area under the effective control of the Republic of Cyprus covers 5759 km² and includes the western and central parts of the island (35° N, 33° E). The climate is Mediterranean, with hot dry summers (from mid-May to mid-September) and mild winters. The average annual rainfall for the period 1971-2022, was 471 mm (Department of Meteorology, 2024), making Cyprus the most water-stressed country of the European Union (Bixio, 2008; European Environment Agency, 2025). The hydrographic network extends for approximately 2000 km, with a total catchment area of 6000 km². Perennial flow occurs along 20% of the total riverine network length, mainly in the western and central parts of the Troodos massif and at elevations above 300 m. In contrast, around 58% of river stretches have intermittent flows and 22% are ephemeral or episodic (Papatheodoulou *et al.*, 2017; Water Development Department, 2023).

The European eel (*Anguilla anguilla*) is the only native fish occurring in Cyprus' watercourses (Zogaris *et al*., 2012; Balestrieri *et al*., 2026).

METHODS

Between September 2020 and September 2025, ichthyofaunal surveys were conducted at 136 river stretches (sampling stations) distributed across 31 major river catchments (Agios Ioannis, Atsas, Avdimou, Avgas, Chapotami, Chrysochou, Dhiarizos, Elias, Ezousa, Germasogeia, Geroskipou, Kampos, Kargotis, Kouris, Limnitis, Makounta, Marathasa, Maroni, Mavrokolympos, Oroklini, Pediaios, Pentaschoinos, Pouzis, Pyrgos, Serrachis, Sotira, Vasilikos, Xeros Pafos, Xeros Ayia Marina Chrysochou, Xeros Tyllirias,), of which only seven (22.5%; Agios Ioannis, Avgas, Geroskipou, Kargotis, Oroklini, Pyrgos, Yialia) did not include any reservoir (Fig. 1). Sampling stations were surveyed up to nine times (on average 2.7 per station, 63 sampled only once), for a total of 368 sampling events. From 2021-2025 two surveys were conducted annually, in spring and summer, for a total of 50-60 surveys per year. Fish were sampled by electrofishing (Auth. N. 22775955, 03/08/2020 by the Department of Fisheries and Marine Research), using a motor-driven backpack device (ELT60 II GI; power: 1300 W; max. 32 KW pulse). Surveys were conducted by wading, as mean water depth at all sites was always less than 0.8 m. Either direct or pulse direct current was used, depending on water conductivity, using a single anode. Water conductivity, as measured by a portable meter, was within the effective operating range for electrofishing at all sampling stations; therefore, alternative sampling methods (e.g., seine nets or fry nets) were not required.

To cover the whole diversity of habitats within sampling sites, electrofishing was conducted along a river stretch measuring 10-20 times the mean channel width, except where dense reed beds made portions of the stretch inaccessible. Captured fish were temporarily held in aerated 60 L containers filled with water, identified to species level and released at the site of capture. For each species captured at each station, a sample of caudal fin tissue was preserved in 98% ethanol for DNA extraction and barcoding purposes. Water temperature (°C) and per cent oxygen saturation were measured using a portable oxygen meter (Oxyguard Handy Polaris C; accuracy: ±0.1°C, ± .1%, respectively).

Observed frequencies of non-native fish in different flow regimes (permanent, intermittent, or ephemeral stretches) were compared to expected distributions using the chi-squared test (χ^2). Where appropriate, mean distances from the nearest reservoir were compared between positive and negative sampling stations by Mann-Whitney (U) test. The same test was used to compare mean water temperature and percent oxygen saturation between positive and fishless sampling stations.

Fish species presence was considered as the response variable in generalized linear mixed models (GLMMs) including flow type (perennial vs. non-perennial stretches), distance from the sea of the sampling station (positively correlated to altitude asl) or barrier occurrence (with four levels: no barrier, barrier upstream, barrier downstream, both barriers) as fixed effects and catchment as a random effect.

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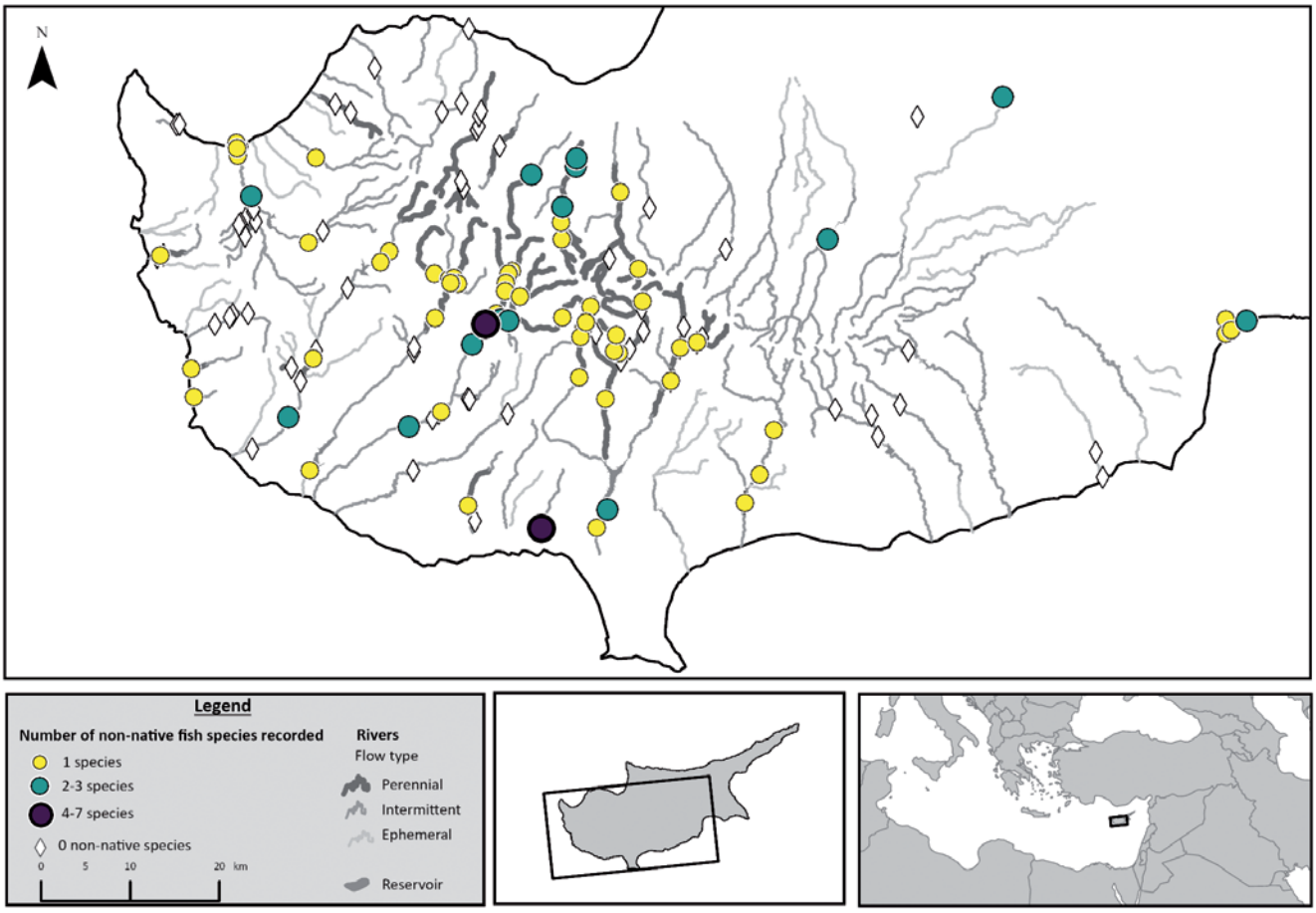

Fig. 1. Sampling stations surveyed in 2020-2025, showing the number of non-native fish species recorded at each station.

RESULTS

Across the 31 catchments surveyed, (mean area: 175 km^2, min-max: 51.3-867.8 Km^2) a total of eleven non-native species were recorded: brown trout (*Salmo trutta*), rainbow trout *(Oncorhynchus mykiss*), Eastern mosquitofish (*Gambusia holbrooki*), common roach (*Rutilus rutilus*), largemouth bass (*Micropterus salmoides*), goldfish (*Carassius auratus*), blue tilapia (*Oreochromis aureus*), channel catfish (*Ictalurus punctatus*), European perch (*Perca fluviatilis*), common carp (*Cyprinus carpio*) and pumpkinseed (*Lepomis gibbosus*). Native eel (*Anguilla anguilla*) occurred in 32% of sampling sites, mostly permanent river stretches below 600 m a.s.l. (see also Balestrieri *et al*., 2026), half of which (52%) hosted non-native species as well (mostly mosquitofish and common roach). In addition, four coastal species - flathead grey mullet (*Mugil cephalus),* thicklip grey mullet (*Chelon labrosus),* thinlip mullet (*Liza ramada)* and European seabass (*Dicentrarchus labrax*) -, were recorded in river estuaries and brackish lagoons.

Non-native fish were sampled in 74 out of 136 sampling sites (54.4%), distributed across 18 of the 31 monitored watersheds (58%); no non-native fish were recorded in the catchments of the rivers Agios Ioannis, Chapotami, Elias, Kampos, Limnitis, Maroni, Mavrokolympos, Pentaschoinos, Pouzis, Pyrgos, Vasilikos and Yialia. Three (Avgas, Geroskipou and Oroklini) out of the seven barrier-free catchments hosted mosquitofish and one (Kargotis) rainbow trout, while up to three non-native species (goldfish, mosquitofish and blue tilapia) were recorded in an interdunal pond at the mouth of the River Verki (Oroklini). Overall, 63.5% of dammed rivers hosted non-native fish, while in barrier-free watercourses the occurrence of introduced species was null or they did not include fish targeted by anglers. Most sampled river stretches (58, 78.4% of positive sites) hosted only one non-native species (mean ± SE: 0.76±0.1; min-max: 0-7), with 2-3 species co-occurring in 19% of positive sites; the richest community was recorded in the catchment of the River Dhiarizos (seven non-native species).

Brown trout, rainbow trout, and mosquitofish were the most frequently recorded non-native species, occurring at 14.5-16% of sampling stations. Brown trout were confined to three catchments (Dhiarizos, Xeros and Kouris) (Fig. 2), occurring in nine watercourses draining the southern slopes of Troodos mountains. Rainbow trout were recorded in eight catchments on both slopes of the ridge (Fig. 3). Both salmonids were recorded more frequently than expected in perennial river stretches (rainbow trout: $\chi^2 = 6.5$, p=0.039; brown trout: $\chi^2 = 10.1$, p=0.006), where mean water temperature was lower than in negative sites (18.4 *vs* 22.4 °C, U = 4.87, p<0.001). Both brown and rainbow trout usually formed monospecific assemblages, respectively in 84% and 65% of sampling sites, co-occurring in only three.

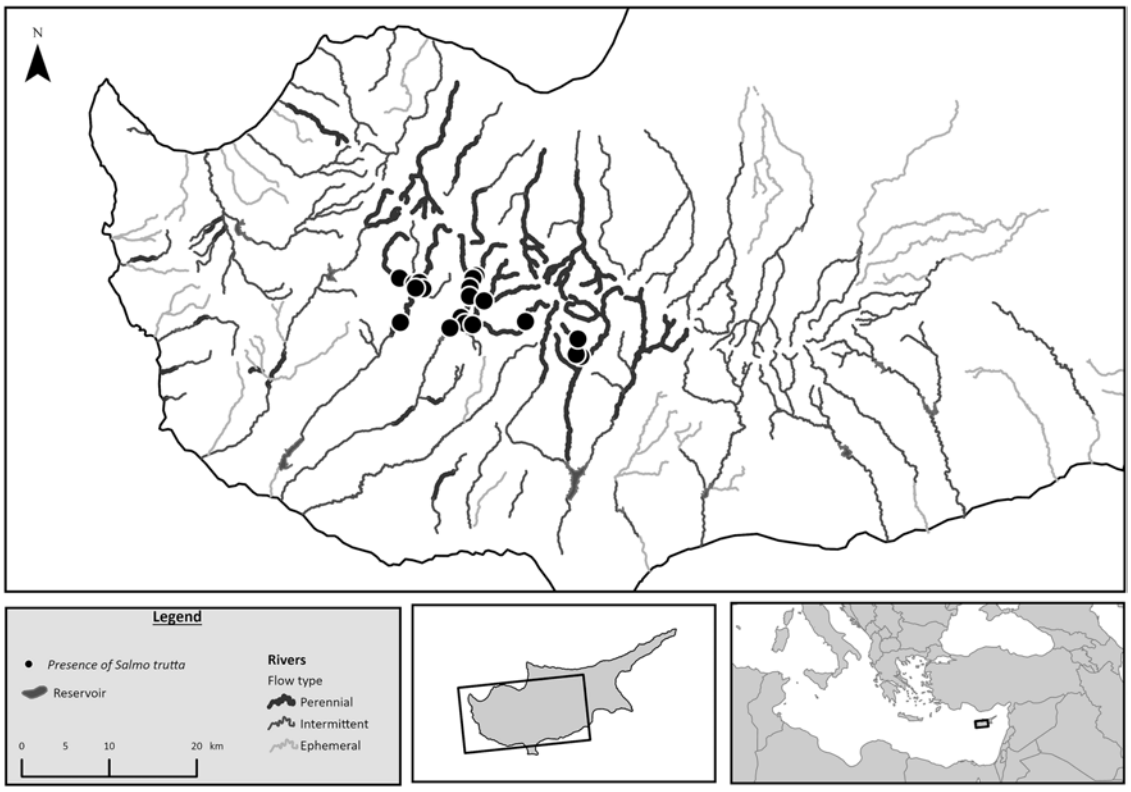

Fig. 2. Distribution of *Salmo trutta*.

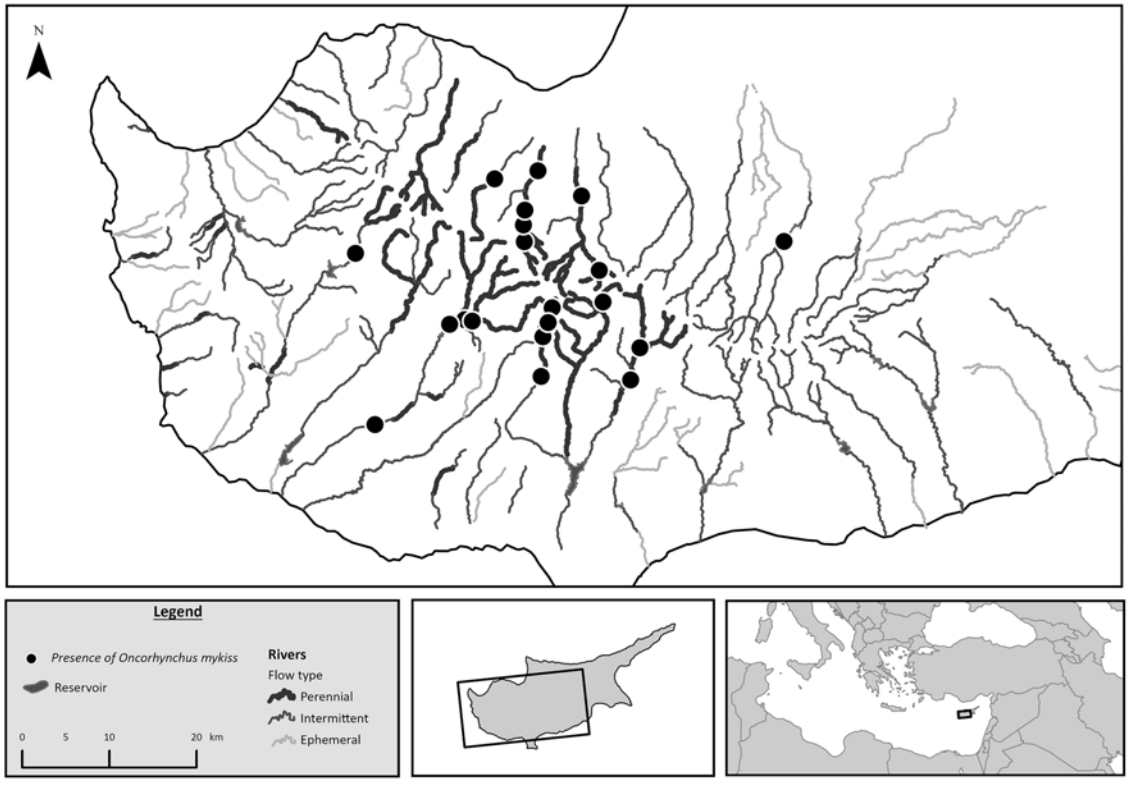

Fig. 3. Distribution of *Oncorhynchus mykiss*.

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Mosquitofish were widespread in lowland and coastal areas throughout the island (Fig. 4), primarily occurring in relatively hot (23.2 *vs* 19.4°C, U = 992.5, $p<0.001$), slow flowing, intermittent stretches ($\chi^2 = 12.17$, $p=0.002$). In 30% of sampling sites mosquitofish were recorded together with either common roach or goldfish.

Among cyprinids, the common roach was the most widespread species, occurring in eight catchments and 10.7% of sampling stations (Fig. 5), followed by goldfish (Fig. 6), while the common carp was only occasionally recorded (Fig. 7). The distance of the sampling stretch from the nearest dam was significantly lower for positive sites for both common roach (mean ± ES = 7.9±0.7 km *vs* 4.9±1.39 km; U = 859.0, $p=0.05$) and goldfish (mean ± ES = 7.9±0.65 km *vs* 2.5±0.9 km; U = 543.0, $p=0.015$). The common roach was often associated to 1-2 fish species (71% of sampling sites), mainly centrarchids and salmonids.

Centrarchids included largemouth bass and pumpkinseed, the latter being the most widespread (two *vs* four river catchments; Fig. 8). Pumpkinseed occurred more frequently than expected in non-perennial river stretches ($\chi^2 = 8.0$, $p=0.018$).

Blue tilapias were sampled in a pond downstream of Symvoulas dam, within the British Sovereign Base Area, and in Verki pond (Fig. 6). Channel catfish were recorded in only two sampling stations, in as many catchments (rivers Xeros Pafos and Pediaios), while the European perch was recorded only once in an intermittent river stretch immediately downstream of a large reservoir (Fig. 7).

GLMMs were run for the four most widespread species (Tab. 1).

Tab. 1. Distribution of non-native fish species in Cyprus' watercourses and number of tissue samples collected for genetic analyses.

Species	N of catchments	N of water courses	N (%) of sampling sites	Mean N ind/site (min-max)	N of tissue samples
Salmo trutta	3	9	19 (14.0)	20.5 (1-249)	48
Oncorhynchus mykiss	8	12	21 (15.4)	57.2 (1-428)	71
Rutilus rutilus	8	10	14 (10.3)	183.2 (1-1665)	23
Carassius sp.	6	6	8 (5.9)	11.5 (1-54)	16
Cyprinus carpio	2	2	3 (2.2)	13 (1-25)	5
Micropterus salmoides	2	2	5 (3.7)	25.8 (1-56)	6
Lepomis gibbosus	4	4	4 (2.9)	5.7 (1-6)	1
Gambusia holbrooki	10	11	20 (14.7)	125.6 (1-100s)	34
Ictalurus punctatus	2	2	2 (1.5)	2 (1-2)	1
Perca fluviatilis	1	1	1 (0.7)	4	3
Oreochromis aureus	2	2	2 (1.5)	7.5 (3-12)	2

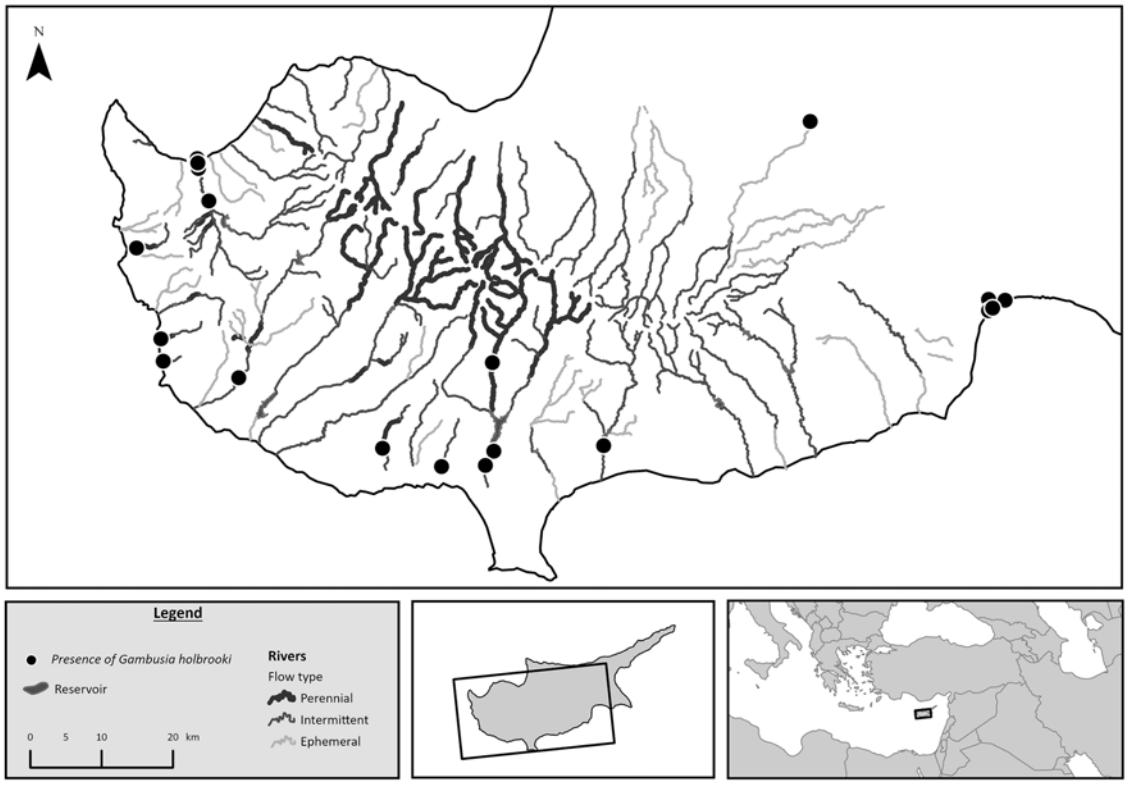

Fig. 4. Distribution of *Gambusia holbrooki*.

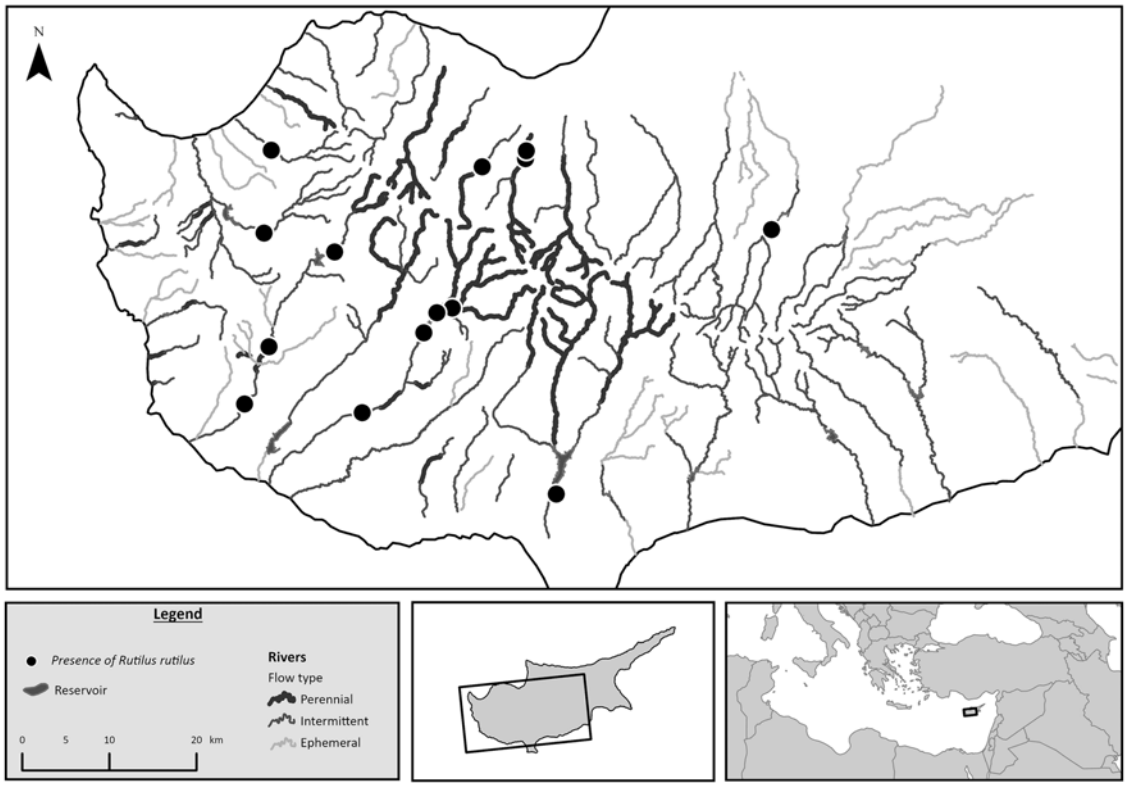

Fig. 5. Distribution of *Rutilus rutilus*.

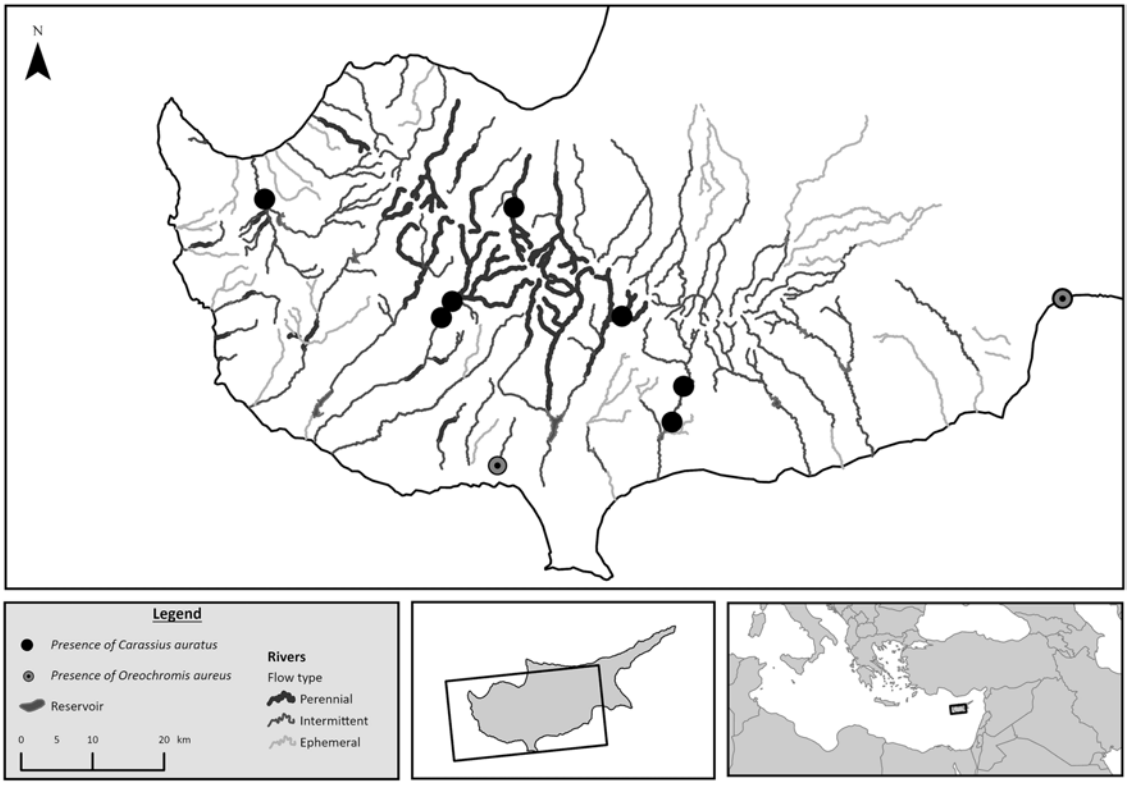

Fig. 6. Distribution of *Carassius auratus* and *Oreochromis aureu*s.

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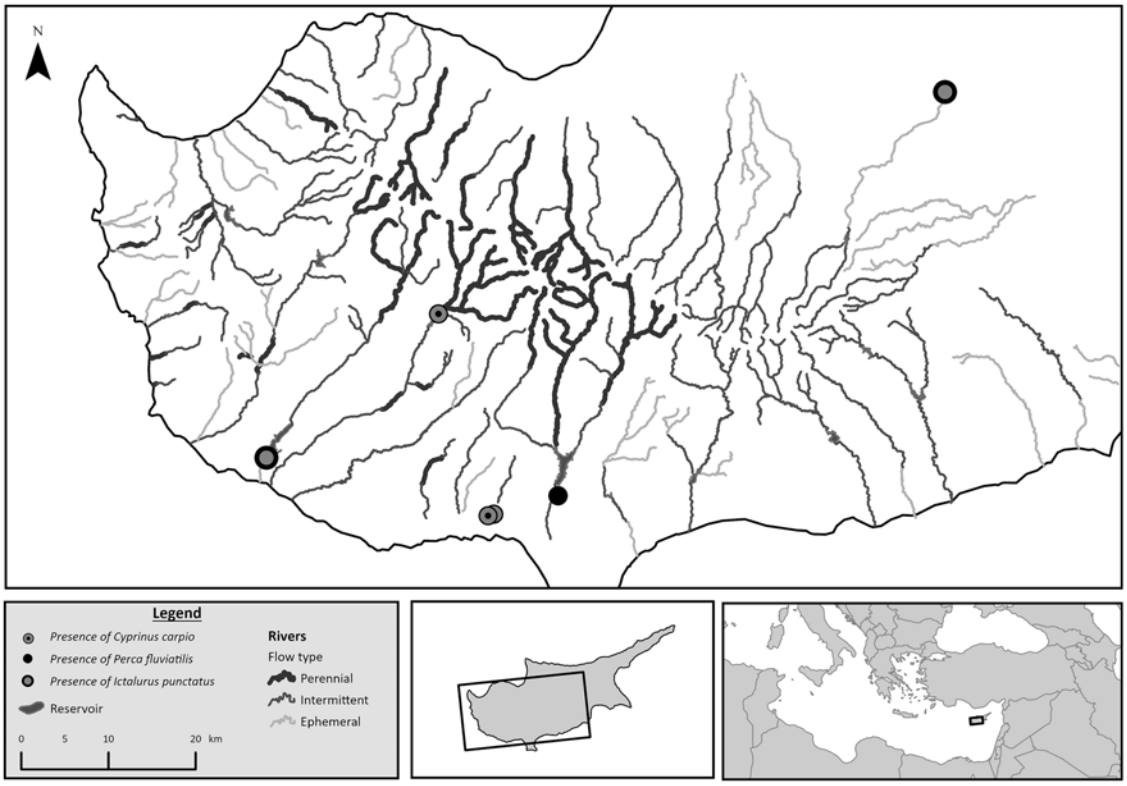

Fig. 7. Distribution of *Ictalurus punctatus*, *Perca fluviatilis* and *Cyprinus carpio*.

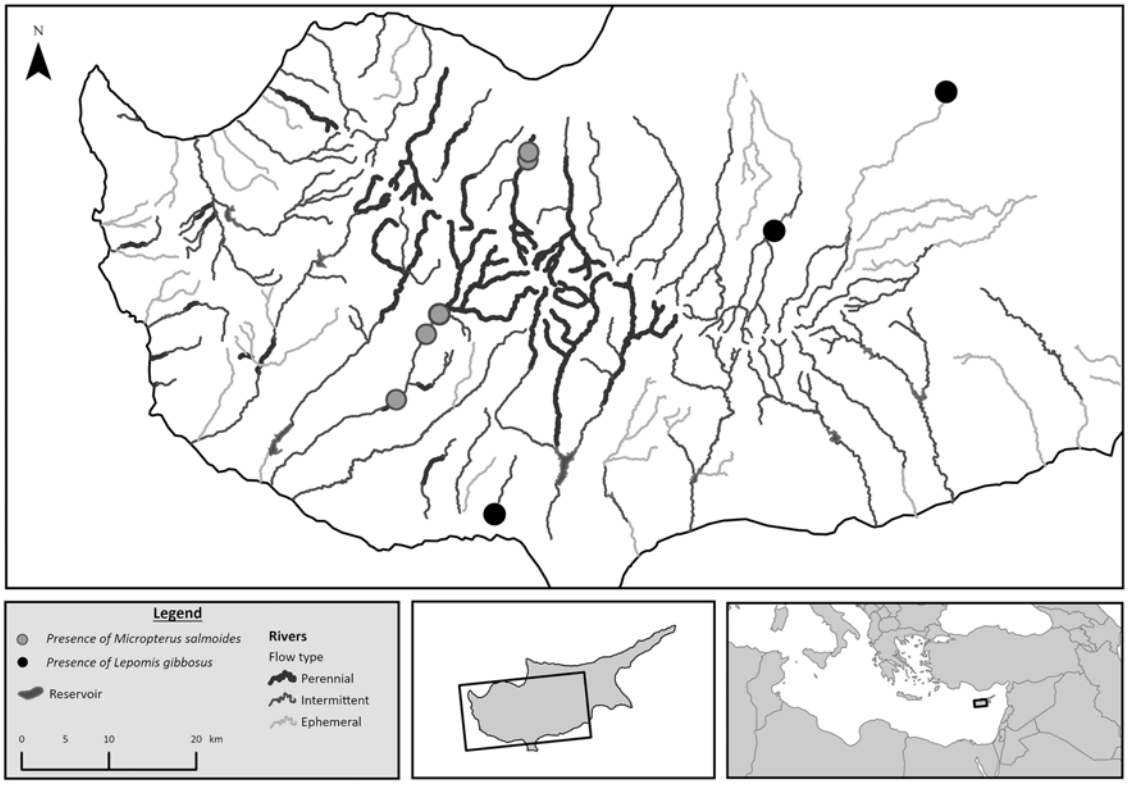

Fig. 8. Distribution of Centrarchidae.

Distance from (mean: 13.2 km; min-max: 0.1-29.5 km) the sea affected the distribution of both salmonids (rainbow trout: $\chi^2 = 6.2$, p=0.013; brown trout: $\chi^2 = 6.6$, p=0.01), which were recorded in the central part of the island, and mosquitofish ($\chi^2 = 3.89$, p=0.049), which occurred along the southern coast. Neither flow regime (number of permanent river stretches: 69; intermittent: 57), nor barrier occurrence affected significantly the distribution of the common roach, unless it was not recorded in any of the barrier-free catchments.

At sites where they occurred, common roach and mosquitofish formed the most abundant populations (Tab. 1). In total, 210 fin tissue samples were collected and preserved for genetic analyses (Tab. 1).

DISCUSSION

By integrating extensive field sampling over five years, we provided a comprehensive assessment of the distribution of non-native freshwater fish in the Republic of Cyprus, documenting the presence in the river network of 11 non-native species. When including three additional species confined to reservoirs (*Blicca bjoerkna, Alburnus alburnus, Sander lucioperca*; Papatheodoulou *et al*., 2025), the total number of non-native fishes presently recorded on the island rises to 14. This figure represents more than half of the 23 species previously reported as introduced (Holčik, 1991; Lehtonen, 2002), underscoring the lasting legacy of historical stocking and translocation practices. Salmonids (rainbow and brown trout) were primarily concentrated in the mountainous core of the island along the slopes of the Troodos mountains, where low water temperatures, high dissolved oxygen concentrations, and perennial flow provide suitable conditions (Bjornn and Reiser, 1991). While sporadic introduction attempts may date back to the early twentieth century (Welcomme, 1988; Crawford and Muir, 2008), following Dill (1990), three *Oncorhynchus* species were introduced in Cyprus in the 1980s, namely coho salmon *O. kisutch*, cutthroat trout *O. clarkii* and rainbow trout *O. mykiss*. Currently, the rainbow trout seems to be the only species occurring in the river network, although viable hybrids *mykiss x clarkii* may still occur in a few river stretches (Spairani *et al*., 2025). Brown trout were likely introduced in the mid-1940s under British administration (Thirgood, 1987, cited in Zogaris *et al*., 2012), and the high haplotype diversity observed in recent genetic analyses suggests multiple introduction sources and events. The possibility that native Mediterranean brown trout lineages were extirpated during the Middle Ages cannot be excluded (Schöffmann, 2021). Both salmonid species currently reproduce successfully in Cypriot rivers (Schöffmann, 2021; Spairani *et al.,* 2025). In contrast, Atlantic salmon (*Salmo salar*), brook trout (*Salvelinus fontinalis*), and Arctic charr (*Salvelinus alpinus*), although previously reported (Holčik, 1991), were not detected.

Mosquitofish have been introduced throughout Europe since the beginning of the 20th century (Di Tizio and Mojetta, 2020) and have been established in 13 countries (Savini, 2010). Currently, based on genetic analyses, *Gambusia holbrooki* is considered the only species widespread throughout Europe (Vidal *et al*., 2010; Vecchioni *et al*., 2025). The earliest record of this species in Cyprus dates back to 1926, while other bibliographic sources report its introduction in the 1940s (Arthington and Lloyd, 2008; Francis, 2012). Until recent years they have been spread throughout the island for the biological control of mosquito larvae (*Culex pipiens, Aedes* spp., *Culiseta* spp.) populations (Drakou *et al.,* 2020).

While recreational fishing is prohibited in natural watercourses, which should discourage fish introductions, angling remains a popular activity in reservoirs, where several non-native species are well established. Accordingly, except for salmonids, all the non-native species recorded in the river network had been previously reported in several reservoirs and fish of angling interest were not recorded in undammed rivers (Papatheodoulou *et al*., 2025).

The most widespread cyprinids - common roach and goldfish - were primarily associated with river stretches next to reservoirs; the latter was also introduced in small recreational ponds. The common roach was introduced in 1972 from the UK (Rocabayera Cano and Veiga Maceda, 2012). The goldfish is the most widespread species in Europe, where it was introduced in the 1600s as an ornamental species, with established wild populations in 29 countries (Smartt, 2001). Following Elvira (2011) the crucian carp *Carassius carassius* should also occur in Cyprus; genetic analysis of fin samples may allow to detect the occurrence of this species or hybrids. The occurrence of Centrarchidae (largemouth bass and pumpkinseed) and channel catfish was negligible. Pumpkinseed were recorded also in stretches many kilometers downstream of the barrier, such as in the centre of Nicosia (River Pediaios), where they were probably introduced as ornamental species. No other catfish was recorded, despite two *Clarias* species (walking catfish *C. batrachus* and African sharptooth catfish *C. gariepinus*) and the wels catfish *Silurus glanis* had been previously reported for Cyprus (Holčik, 1991; Lehtonen, 2002). Both carp (introduced from Palestine in 1945; Dill, 1990) and blue tilapia are mostly restricted to a few artificial ponds or small reservoirs, where they usually coexist with several other non-natives (*Carassius* spp., Centrarchidae and common roach). Carp included the variety "mirror carp", with large and sporadic scales. Grass carp *Ctenopharyngodon idella* and silver carp *Hypophthalmichthys molitrix* were not recorded, despite previous introduction attempts (Holčik, 1991; Elvira, 2011).

Considering both the number of positive sites and mean number of individuals per site, mosquitofish and common roach were the most successful non-natives in the riverine network of the study area.

The first is included in the top 10 species with the highest environmental and economic impact, mainly because of its impact on native species (van der Veer, 2015). High reproductive performances, rapid growth, as well as the ability to thrive in scarcely oxygenated waters, allow them to spread in introduction areas (Gandolfi *et al*., 1991). The common roach is a gregarious fish, which can live in a wide variety of lowland freshwater habitats and takes advantage of damming and slight organic pollution (Kottelat and Freyhof, 2007).

Except for these two species and salmonids, which were deliberately introduced in mountain creeks for angling, the distribution of most non-native fish was narrower than expected based on their widespread occurrence in reservoirs, particularly downstream of dams.

Streamflow intermittency, with most lowland river stretches being dry during summer and most of autumn, may explain the lower-than-expected dispersal of non-native fish. In intermittent and ephemeral streams hydrological connectivity change markedly over time, exacerbating the seasonal cycles of expansion and contraction of watercourses in response to flow variation (Boulton *et al*., 2017). Drought hinders longitudinal fish movements while

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habitat fragmentation generates isolated habitat patches hosting biota adapted to stressing environmental conditions (Datry *et al*., 2014). While native species might be resilient to intermittent flow conditions, only a few, habitat-generalist, introduced fish may be able to colonize such hydrologically unstable environments (Milardi *et al*., 2022). Among them, pumpkinseed and mosquitofish, which in Cyprus occurred more frequently than expected in non-perennial stretches, have been reported as successful invaders of intermittent rivers in both the Mediterranean basin and North America (Kerezsy *et al*., 2017). Common roach, as suggested by the mean distance of records from the nearest barrier, may move back to reservoirs in periods of drought. Upstream of reservoirs, where most rivers have permanent stretches, or flow for longer periods, fish spread may be hindered by natural morphological barriers, as the leaping abilities of the recorded species do not allow the surpassing of obstacles higher than a few dozen centimeters (Morán-López and Uceda Tolosa, 2017).

CONCLUSIONS

Our results agree with increasing evidence suggesting that habitat modifications may facilitate biological invasions (Grez *et al*., 2013; Liew *et al*., 2016). The ecological consequences of these introductions remain poorly quantified. Except for the pumpkinseed (Papatheodoulou *et al*., 2025), virtually no empirical data exist for the impacts of widespread non-native predators such as salmonids and mosquitofish on native fauna, including the European eel, amphibians, and protected semi-aquatic reptiles (Georghiou *et al*., 2024). Given the severe limitations on eradication imposed by social, economic, and logistical constraints, prevention remains the most effective management strategy. Targeted education and awareness campaigns involving local communities and secondary schools could play a crucial role in preventing future introductions and limiting the spread of non-native species (Wittenberg and Cock, 2001).

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