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Characterisation of the nuptial colouration pattern of *Phoxinus lumaireul* Schinz, 1840 (Teleostei, Leuciscidae) and first record in France

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Abstract – Recent molecular studies have highlighted the taxonomical complexity of the Eurasian minnows *Phoxinus* spp, pointing out their multiple endemic species to their respective catchments, and also the multiple translocations between drainages. Here, we report the first record of the Italian minnow *Phoxinus lumaireul* in France: a male specimen was caught in the Lake Geneva at Publier (Haute-Savoie department) the 31st May 2010 during an elecrofishing survey monitored by the ONEMA. The identification was done from a picture, according to morphological observations and the nuptial colouration pattern, in comparison with *P. lumaireul* from the Po catchment. We then attest the presence of a third minnow species in the Lake Geneva basin, in addition to *P. csikii* and *P. septimaniae*. The nuptial colouration pattern of *P. lumaireul* is diagnosable by very little developed nuptial tubercles on the head, pectoral fins yellowish hyaline, a green bluish stripe on Z3 until the caudal peduncle origin and black beyond, Z4 green yellowish and a belly shiny red from the throat to the caudal fin base for males, and pectoral, pelvic and anal fin bases pinkish, yellow spot on the operculum, Z4 slightly golden and Z5 white for female. Our morphological identification corroborates a molecular study from the Swiss part of the Lake Geneva basin. *Phoxinus lumaireul* is then the seventh and the first non-native minnow species occurring in France. Its introduction through human translocations seems to be ancient. We also discussed about ecological impacts for French and Swiss managers.

Keywords: Cryptic invasion / Italian minnow / Lake Geneva / Morphology / Nuptial colouration

1 Introduction

Eurasian minnows *Phoxinus* spp are small, gregarious, rheophilic and cryophilic leuciscids inhabitants of streams and clear lakes from Ireland and the Iberian Peninsula to Korea (Bănărescu & Coad, 1991; Esposito *et al.*, 2024a). They are generally described as having an olive-green colouration, a lighter longitudinal line above dark blotches on the flanks and a white-grey belly (*e.g.*, Kottelat, 2007). But during the reproductive season, nuptial tubercles on the head and throat appear (Witkowski & Rogowska, 1992; Chen & Arratia, 1996), as well as nuptial colourations with shiny colours on the body (*e.g.*, Denys *et al.*, 2020).

The taxonomic knowledge about this genus has considerably changed during the last two decades, with numerous species descriptions and revalidations of species names (see Esposito *et al.*, 2024a). However, the species delineations are also supported by molecular data and also morphological characters such as the snout and anal fin shapes, the presence of scales between the pectoral fins, the number of scales in the lateral series as well as different morphometrics data (Kottelat, 2007; Palandačić *et al.*, 2017, 2024a; Bogutskaya *et al.*, 2020, 2023; Denys *et al.*, 2020; Turan *et al.*, 2023; Artaev *et al.*, 2024a,b, 2025; Bayçelebi *et al.*, 2024; Bayçelebi, 2025).

However, not only these morphological characters are difficult (even impossible) to observe in the field on alive fish. But also, minnow species present some phenotypic plasticities (Bianco & De Bonis, 2015; Collin & Fumagalli, 2011, 2015;

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Palandačić *et al.*, 2017; Ramler *et al.*, 2017; Bogutskaya *et al.*, 2020; Scharnweber, 2020). All this means that riverine managers have the feeling of not having reliable diagnostic criteria to identify the different species of minnows, with as consequence the absence of the minnow species diversity into their management plans. Denys *et al.* (2020) then proposed an alternative to morphological criteria: the use of nuptial colouration patterns. They characterised the nuptial colouration pattern of both male and female of each evolutionary lineage in France from molecular data, allowing the delineation of six minnow species: *Phoxinus phoxinus* (Linnaeus, 1758) *sensu stricto* in the Rhine, Meuse and Seine drainages, *Phoxinus bigerri* Kottelat, 2007 in the Adour drainage, *Phoxinus septimaniae* Kottelat, 2007 in the Mediterranean basin, *Phoxinus csikii* Hankó, 1922 in the Rhine drainage, as well as *Phoxinus fayollarum* Denys, Dettai, Persat, Daszkiewicz, Hautecœur & Keith, 2020 and *Phoxinus dragarum* Denys, Dettai, Persat, Daszkiewicz, Hautecœur & Keith, 2020 which are respectively endemic to the Loire and the Garonne drainages. Further taxonomic revisions on other minnow species also demonstrated other nuptial colouration patterns which could be diagnostic (Bogutskaya *et al.*, 2023; Turan *et al.*, 2023; Artaev *et al.*, 2024a; Bayçelebi, 2025).

In the Lake Geneva basin, located in the Rhône River at the French-Swiss border, minnows are considered as rare (Jurine, 1825; Raymond, pers. com.). Nevertheless, the presence of two *Phoxinus* species is attested: *P. csikii* and *P. septimaniae* (Palandačić *et al.*, 2017; Denys *et al.*, 2020). Alexander & Seehausen (2021), during their DNA Barcoding of the whole of fish species in Swiss lakes program (*Projet Lac*), also detected a third minnow species in the Stockalper Canal using molecular data: the Italian minnow *P. lumaireul* (Schinz, 1840). This species is endemic to the Adriatic basin, including the Po River – its type locality (Palandačić *et al.*, 2017, 2020). In May 2010, the *Office National de l'Eau et des Milieux Aquatiques* (ONEMA; now called French Office of Biodiversity, OFB) conducted an electrofishing campaign in the Lake Geneva, catching a minnow on the 31st May 2010. Because of its rarity and its shiny breeding colourations, the fish was photographed before release. Several years later, the picture was sent to the Muséum national d'Histoire naturelle (MNHN, Paris) for identification.

The aim of this study is to identify this minnow with morphological criteria but also according to its nuptial colouration pattern. In order to do this, we will characterise the nuptial colouration pattern of *P. lumaireul* and we will compare it to those of *P. csikii* and *P. septimaniae* (Denys *et al.*, 2020). This study will then report the first record of *P. lumaireul* in France, being then the seventh minnow species and the first allochtonous one. We will also discuss about the consequence of its introduction on native minnow species and on the management.

2 Material and methods

2.1 Sampling

The French part of the Lake Geneva has been monitored for the first time by the ONEMA in 2010. The location at Publier (46°23'46" N, 6°32'22" E) is one of the three sites surveyed (Raymond *et al.*, 2010). The inventory consisted to catch fishes using multi-mesh gill nets according to the protocol DCE EN14757, as well as a prospecting of the riparian zone with depth inferior of 2 meters, by electrofishing following the punctual abundance sampling method, after mapping the aquatic habitats beforehand allowing the number of sampling points to be distributed per habitat (Degiorigi *et al.*, 2001). The water temperature was 14.8°C, whereas the substrate was composed in decreasing order by blocks, sand-silt, pebbles, gravels, afference zones, scattered helophytes and woody supports. Fish caught were conserved in a white bucket in order to limit the water warming by the sun, before being measured, photographed and released.

Concerning the Italian minnows from the Po catchment, fish were caught by electrofishing or hand net from June 2011 to June 2016 from four locations: Varaita Torrent at Costigliole Saluzzo (44°33'49''N – 7°28'29''E), Sangone Torrent at Trana (45°01'43''N – 7°23'42''E), Chisone Torrent at Pinerolo (45°51'42''N – 7°20'41''E) and Lago Laus at Roreto Chisone (45°03'00''N – 7°08'08''E). Alive and euthanised fish were then photographed after capture. Fish samples were genotyped in previous studies attesting their affiliation to *P. lumaireul* (Geiger *et al.*, 2014; Ramler *et al.*, 2017; Palandačić *et al.*, 2017; De Santis *et al.*, 2021) (Tab. 1; Fig. 1). Twelve photos including 27 specimens (22 males and 7 females) composed our material to characterise the nuptial colouration pattern of *P. lumaireul* (Fig. 2; Supplementary data 1).

2.2 Sexual determination

The sex of photographed specimens was identified on the pictures using external anatomy *i.e.* length and shape of the pectoral fin. A male minnow has a long, wide, thick and rounded pectoral fin, whereas the female's one is short and less rounded (Frost, 1943). Moreover, during the breeding period, female specimens are also identifiable by their gravid belly. These characteristics are only applicable for adult fish.

2.3 Morphological identification

The three species are *P. csikii*, *P. lumaireul* and *P. septimaniae* discriminated by about 15 morphological characters (Kottelat and Freyhof, 2007; Palandačić *et al.*, 2017; Denys *et al.*, 2020) (see Supplementary data 2). However, only five characters (the snout shape, the snout length (% head length HL), the position of the mouth, the anal fin margin and the ratio length/depth of the caudal peduncle) were visible and used for the morphological identification. Approximate lengths ratios (snout length and caudal peduncule depth) were done using pixels numbers counted on the photographs of the single Lake Geneva specimen (Supplementary data 3) using the GIMP software (https://www.gimp.org/).

2.4 Characterisation of the nuptial colouration pattern of *P. lumaireul*

We characterised separately the nuptial colouration pattern of both males and females *P. lumaireul* observing living animals in aquariums and also after electrofishing and handling (Tab. 1). We follow the terminology of Denys *et al.* (2020) (Fig. 3a) with five coloured zones Z1 to Z5 from the back to the

Table 1. Origin of Italian minnows genotyped as *P. lumaireul* according to previous studies, and used for the characterisation of the nuptial colouration pattern. Museums abbrevations: Museo Civico di Storia Naturale di Carmagnola, Carmagnola, Italy (MCCI); Muséum national d'Histoire naturelle, Paris, France (MNHN); Naturhistorisches Museum, Zoologische Abteilung, Fische, Vienna, Austria (NMW); Zoologisches Forschungsmuseum Alexander König, Bonn, Germany (ZFMK).

Figure	Site	Date of sampling	Number of pictures used	Sex of fish on pictures with number of fish per sex	Circumstances of picture taken	Molecular studies confirming a *P. lumaireul* affiliation	Preserved specimens
2a	Varaita Torrent at Costigliole Saluzzo 44°33'49''N – 7°28'29''E	8th June 2016	5	14 males and 6 females	Aquarium	De Santis *et al.* (2021)	No
2b	Chisone Torrent at Pinerolo 45°51'42''N – 7°20'41''E	13th June 2014	3	5 males	After electrofishing and euthanisation	Ramler *et al.* (2017)	MNHN (12 samples), NMW (60 samples), MCCI (30 samples)
2c	Lago Laus, Roreto Chisone 45°03'00'' N – 7°08'08''E	17th July 2014	2	2 males	After hand net capture	Ramler *et al.* (2017); Palandačić *et al.* (2017)	NMW (44 samples), MCCI (64 samples)
2d	Sangone Torrent at Trana 45°01'43'' N – 7°23'42''E	15th June 2011	1	1 male and 1 female	After electrofishing and euthanisation	Geiger *et al.* (2014); Ramler *et al.* (2017); Palandačić *et al.* (2017)	ZFMK (85 samples)
2e		24th May 2014	1	1 female	Aquarium		NMW (54 samples), MCCI (31 samples)

belly, for the description of the nuptial coat for male and female. The observed and characterized patterns were after compared to those of *P. csikii* and *P. septimaniae* for which the discriminations for both males and females between the two species are truly reliable (Denys *et al.*, 2020) (Fig. 3b,c).

3 Results and discussion

3.1 Nuptial colouration pattern of *Phoxinus lumaireul*

Phoxinus lumaireul is characterised by the following nuptial colouration pattern (Fig. 2):

Male (Fig. 2a,b,c,f): Lips and pectoral, pelvic and anal fin bases red, these fins yellowish hyaline. Nuptial tubercles on the head very weakly expressed. Red dot on the dorsal fin base. Snout and top of head dark greyish with red dots above the eyes. Cheeks white greyish. Operculum with a white spot at the uppermost corner followed by a yellow spot on the supraoperculum. Z1 and Z2 brownish overlayed with blackish bars. Green blueish stripe until the caudal-peduncle origin and black beyond along Z3. Z4 green yellowish. Z5 black between pectoral fin and anal fin base. Belly shiny red from the throat to the caudal fin base.

Female (Fig. 2d,e,g): Nuptial tubercles on the head quasi absent. Less brightly coloured, pectoral, pelvic and anal fin bases pinkish, these fins yellow. Z1 and Z2 brownish with black vermiculations, rather than stripes. Black stripe along Z3. Z4 slightly golden. Z5 white or silvery. Belly white.

Phoxinus lumaireul is native to the North Adriatic Sea basin, from the Esino and Potenza catchments (central Apennines) to the Western Balkans (Kottelat & Freyhof, 2007; Palandačić *et al.*, 2015, 2017; Vucić *et al.*, 2018; Caputo Barucchi *et al.*, 2022). Molecular data highlight at least six evolutionary lineages within this species (Palandačić *et al.*, 2015, 2017; Vucić *et al.*, 2018, 2022). Moreover, some morphological variabilities were observed among populations living in Western Balkans (Bianco & De Bonis, 2015; Palandačić *et al.*, 2017; Bogutskaya *et al.*, 2020). Our samples came from the Po catchment, the type locality, and are affiliated to the clade 1a *sensu* Palandačić *et al.* (2017). Thus, our diagnosis might be applicable only for this lineage, as we have no data about the nuptial colouration pattern from populations affiliated to the other lineages.

Comparing it to the two other minnow species of the perialpine lakes, *Phoxinus lumaireul* is then distinguishable from *P. csikii* by very little developed nuptial tubercles on the head (*vs.* well developed), a green bluish stripe on Z3 until the caudal peduncle origin (*vs.* green or blackish stripe fractioned in blotches) and a Z4 green yellowish (*vs.* green) for males (Fig. 3b), and a Z4 slightly golden (*vs.* golden) for females (Fig. 3b) (Denys *et al.*, 2020). It is also distinguishable from *P. septimaniae* by very little developed nuptial tubercles on the head (*vs.* well developed), the absence of a yellow spot between the eye and the mouth (*vs.* presence of a yellow spot), pectoral fins yellowish hyaline (*vs.* yellowish-orange with a red disc at inners side), a green bluish stripe on Z3 until the caudal peduncle origin and black beyond (*vs.* blackish stripe until the caudal fin origin), Z4 green yellowish (*vs.* greyish, without green colouration, except rarely around pectoral fin), and a belly shiny red from the throat to the caudal fin base (*vs.* white) for males (Fig. 3c), pectoral, pelvic and anal fin bases pinkish

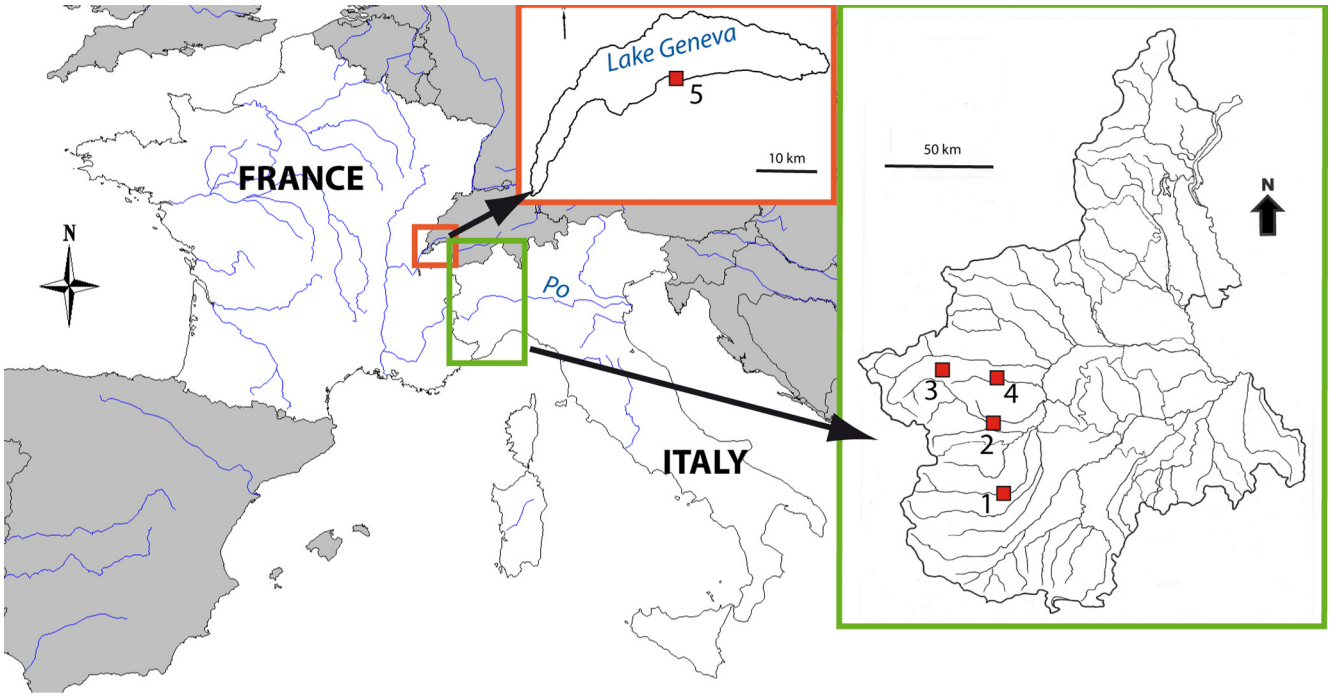

Fig. 1. Sampling locations (red squares) of minnows in the Po catchment in the Italian Piedmont (green box) where specimens of *P. lumaireul* were caught and used for the nuptial colouration characterisation (see Tab. 1, Figs. 2, 4b, and 5c), as well as in the French part of the Lake Geneva (red box) where the minnow specimen of unknown species was photographed and presented in Fig. 4a. Locations: 1) Varaita Torrent at Costigliole Saluzzo 44°33'49''N – 7°28'29''E, 2) Chisone Torrent at Pinerolo 45°51'42''N – 7°20'41''E, 3) Lago Laus, Roreto Chisone 45°03'00''N – 7°08'08''E, 4) Sangone Torrent at Trana 45°01'43''N – 7°23'42''E, 5) Lake Geneva at Publier 46°23'46"N – 6°32'22"E.

(*vs*. no pigmentation), presence of a yellow spot on the operculum (*vs*. no or an indistinct yellow spot on the operculum), Z4 slightly golden (vs. silvery white) and Z5 white (vs. black) for females (Fig. 3c) (Denys *et al.*, 2020).

Our observations in aquariums allowed the characterisation of the colouration patterns of the dorsal fin with a red spot on its basis. Denys *et al.* (2020) described nuptial colourations patterns on euthanised fish fitted on a shelf, which did not allow to see well the dorsal fin. So, this last character was not used to describe the nuptial colouration patterns of the six French minnow species. An observation in aquariums would be helpful to complete gap as well as to find other characters, and better resolve the taxonomy of this genus (Denys *et al.*, 2025).

3.2 The minnow from the Lake Geneva

One male minnow (65 mm total length (TL); Fig. 4a) was caught at Publier (Haute-Savoie department, France) along seven other fish species (*Perca fluviatilis* Linnaeus, 1758, *Rutilus rutilus* (Linnaeus, 1758), *Salariopis fluviatilis* (Asso, 1801), *Gobio gobio* (Linnaeux, 1758), *Salmo trutta* Linnaeus, 1758, *Cottus gobio* Linnaeus, 1758, *Squalius cephalus* (Linnaeus, 1758)) and the signal crayfish *Pacifastacus leniusculus* (Dana, 1852) (Raymond *et al.*, 2010). It was caught in bank rip-rap at 0.9 m of depth, not far from a tributary of Lake Geneva.

We attempted to identify the sample using morphological characters on photos provided by the ONEMA (Fig. 4a, Supplementary data 3). The following morphological data allows to identify the minnow from the Lake Geneva as *P. lumaireul*: combination of the very stout snout shape, the snout length 26% HL and the ratio length/depth of the caudal peduncle equal to 2.48 (Tab. 2). It therefore differs from *P. septimaniae* by its very stout snout shape and a shorter snout length. Similarly, it differs from *P. csikii* by a slightly smaller ratio length/depth of the caudal peduncle. Nevertheless, the different way of measurement (pixel *vs*. calliper) can induce a bias in the results (*e.g.*, Takács *et al.*, 2016) and then a misinterpretation risk. However, this approach was already helpful for taxonomic expertise on photos (*e.g.*, Cuinet *et al.*, 2024). Finally, our results are congruent with those of Ramler *et al.* (2017) who already highlighted that Italian minnows (namely *P. lumaireul*) could be discriminated from the Danubian populations (namely *P. csikii*) by the caudal peduncule depth.

The colouration pattern of the minnow photographed in Lake Geneva (Fig. 4a) is less shiny than those observed in other pictures of *P. lumaireul* (Fig. 2). Nonetheless its general nuptial colouration pattern is consistent with that of *P. lumaireul* as it was detailed above and in Figure 2. The remarkable character is the shiny red belly which is persistant, whereas colours in Z1-Z5 are generally less strongly expressed. The fish was caught by electrofishing and handled. These events are sources of stress wich disrupts the neuro-hormonal functioning of the skin pigmentation (*e.g.*, Bernier *et al.*, 2009; Vissio *et al.*, 2021). Our minnow was indeed conserved in a white bucket, inducing then melanosomes aggregation due to a diminution of the cells size within minnows (Abbott, 1973; Amiri, 1991). This new white environment induced a mechanism of background adaptation,

Fig. 2. *Phoxinus lumaireul* in the Po catchment with alive nuptial colourations: male (68 mm TL) from the Varaita Torrent at Costigliole Saluzzo (a), five males (57 to 64 mm TL) from the Chisone Torrent at Pinerolo (b), male (not measured) from the Lago del Lau at Roreto Chisone (c), two females (75 mm TL (d) and 81 mm TL (e)) from the Sangone Torrent at Trana, nuptial colouration pattern for male (f) and female (g); photo credits: G. Delmastro.

thus affecting the melanogenesis (see Fujii, 2000; Leclercq *et al.*, 2010), hence the absence of shiny colour pattern. However, the red belly is still well marked and seems to still be diagnostic. This colouration is similar to a *P. lumaireul* minnow caught in the Sangone Torrent at Trana (Fig. 4b).

3.3 First photographic evidence of *P. lumaireul* in France

The morphological observation and the nuptial colouration pattern corroborate the identification of the minnow caught in the Lake Geneva the 31st May 2010 as *Phoxinus lumaireul*. According to morphological data, this study confirms the molecular detection in the Stockalper Canal, a Swiss tributary of the Lake Geneva, and the presence of three minnow species in the Lake Geneva basin with *P. csikii* and *P. septimaniae*, as in other Swiss and Italian perialpine lakes (Alexander & Seehausen, 2021; De Santis *et al.*, 2021). However, minnows should be considered as occurring in the tributaries of Lake Geneva, as they are only rare in the Lake (Jurine, 1825). Nevertheless, hybridisation with *P. csikii* and *P. septimaniae* is known (Palandačić *et al.*, 2017; De Santis *et al.*, 2021). So, it

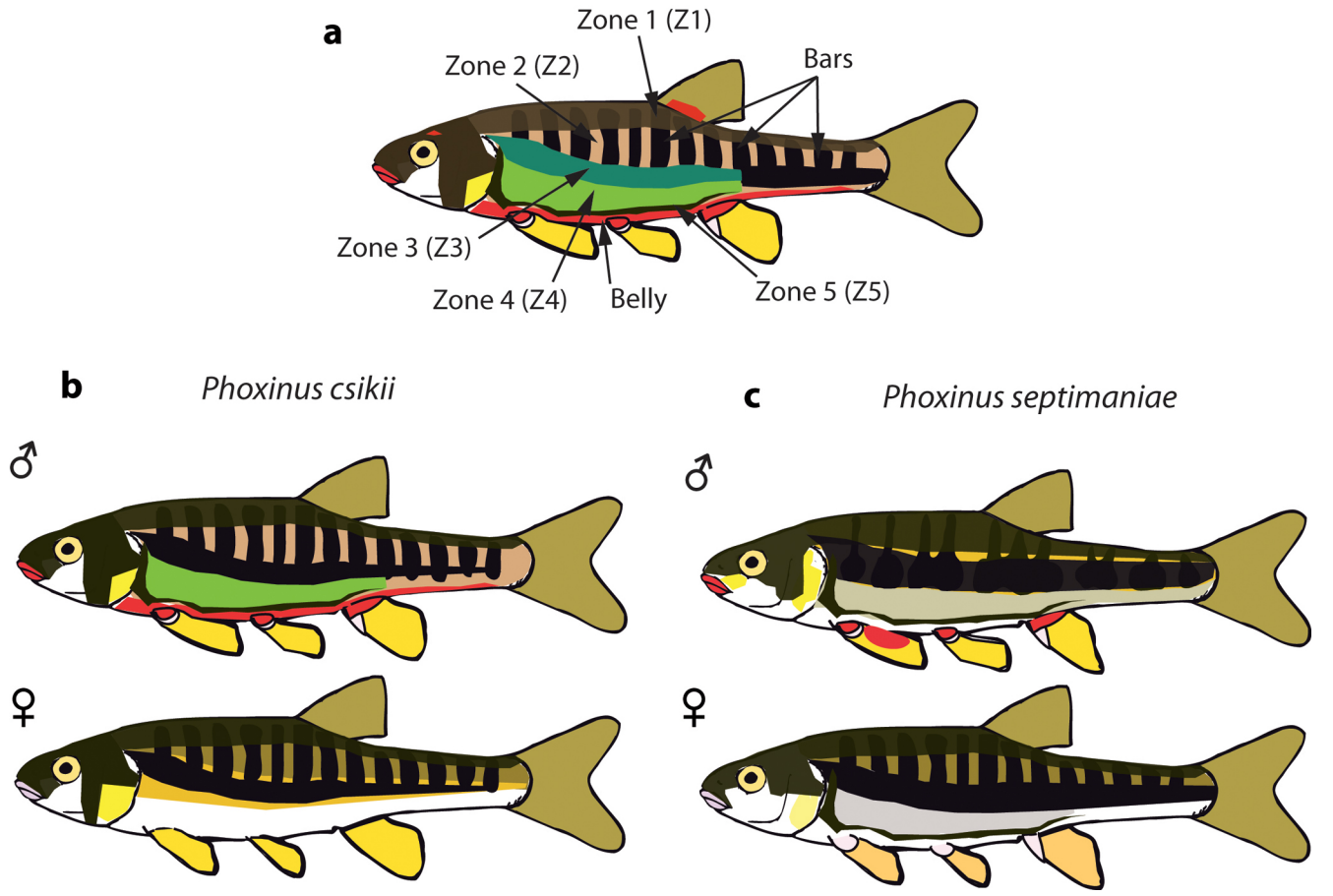

Fig. 3. The five zones on the minnow's flank characterising the nuptial colouration pattern (a) following Denys *et al.* (2020), and both male and female nuptial colouration patterns for respectively *Phoxinus csikii* (b) and *Phoxinus septimaniae* (c) according to Denys *et al.* (2020); drawings adapted and modified from Denys *et al.* (2020).

might be possible that this specimen could be in fact a hybrid, but that it is unlikely as the recorded morphological characteristics clearly match *P. lumaireul* from other populations.

Forel (1904) hypothetised that minnows, like most other fish species, were introduced in the Lake Geneva. However, considering the biogeographical context of the Lake Geneva, with the current and ancient connections with basin shifts between the Rhône and the Rhine catchments since the last Ice age (see Persat *et al.*, 2020), *P. csikii* and *P. septimaniae* seem to be native. At our knowledges, the only connection between the Rhône and the Po catchment occurred though the Durance river (southeastern France) during the late Pleistocene (Splendiani *et al.*, 2020). So the presence of *P. lumaireul* in the Lake Geneva must have an anthropogenic origin. Two other Italian fish species introduced in the Lake Geneva are known: the southern pike *Esox cisalpinus* Bianco & Delmastro, 2011 and the southern rudd *Scardinius hesperidicus* Bonaparte, 1845 (Denys *et al.*, 2014; Keith *et al.*, 2020; Alexander & Seehausen, 2021). All three species are native from the Padano Veneto region including the Po drainage (Lorenzoni *et al.*, 2019). Thus, *P. lumaireul* is then the seventh

Fig. 4. Male minnow (65 mm TL, a) in nuptial colouration with an unknown species origin caught in the Lake Geneva at Publier the 31st May 2010 and one male *Phoxinus lumaireul* (83 mm TL, b; identified by Geiger *et al.* (2014)) from the Sangone Torrent at Trana the 15th June 2011; photo credits: respectively J.-C. Raymond / OFB and G. Delmastro.

Table 2. Morphological observations and approximated lengths ratios taken on photograph (Fig. 4; in pixel numbers) of the male minnow caught in the Lake Geneva the 31st May 2010 compared to data from Kottelat and Freyhof (2007) (*), Palandačić *et al.* (2017) ($) and Denys *et al.* (2020) (£) on *P. csikii*, *P. lumaireul* and *P. septimaniae* from morphomeristic analyses with measurements issued from digital calliper; diagnostic characters are in bold; for the snout shape see the Supplementary data 2; HL means head length.

	Specimen from the Lake Geneva	*Phoxinus csikii*	*Phoxinus lumaireul*	*Phoxinus septimaniae*
Snout shape	**Very stout**	**Very stout, blunt** [$]	**Very stout** [$]	Slighty pointed [$£]
Snout length	**26% HL**	**24–33% HL** [$]	**26–29% HL** *	28–33% HL *
Position of the mouth	Subterminal	Subterminal [$£]	Terminal or subterminal [$]	Subterminal [$£]
Anal fin margin	Straight	Straight to slightly convex [$]	Straight to slightly concave [$]	Straight to slightly concave [$£]
Ratio length / depth of the caudal peduncle	**2.48**	2.5–4.0 [£]	**2.2–2.6** *	**2.1–2.9** *

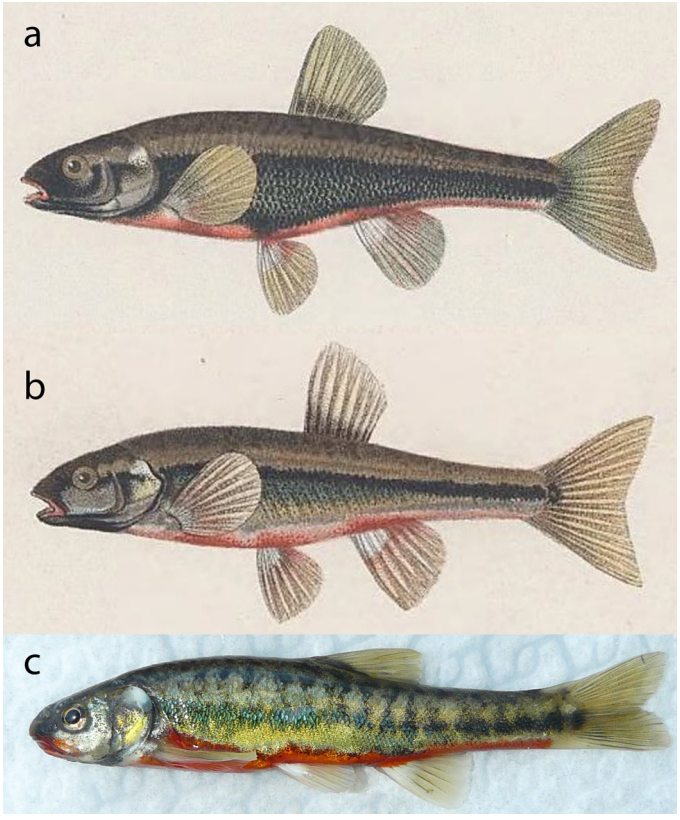

Fig. 5. Minnows drawings (a,b; modified symmetrically to the left side) from Lunel and Lunel (1874): a male identified as *Phoxinus csikii* by Denys *et al.* (2020) (a), another male having the nuptial coulouration pattern of *Phoxinus lumaireul* (b) like the male (57 mm TL) from the Chisone Torrent at Pinerolo (c; photo credits: G. Delmastro).

one, and the first allochtonous minnow species occurring in France, whereas this species is native in Switzerland but only in the Po drainage where minnows occure in few localities according to Pedroli *et al.* (1991). This species will then be listed in the French taxonomic register TAXREF (TAXREF, 2025) of the National Inventory of Natural Heritage (*Inventaire du Patrimoine Naturel* – INPN).

Minnows introductions are essentially due to their use as live bait for the angling of brown trout *Salmo trutta* Linnaeus, 1758 (Banha *et al.*, 2016), as it was already documented through Europe (Museth *et al.*, 2007; Miró & Ventura, 2015; Palandačić *et al.*, 2015, 2017, 2020, 2022; Corral-Lou *et al.*, 2019; Denys *et al.*, 2020; Garcia-Raventós *et al.*, 2020; Alexander & Seehausen, 2021; De Santis *et al.*, 2021; Esposito *et al.*, 2024b; Sternberg *et al.*, 2025), as well in Switzerland (Pedroli *et al.*, 1991). So, a recent introduction is plausible. However, an ancient introduction cannot be excluded. Palandačić *et al.* (2020) already highlighted minnow translocations during the 19th century. According to Denys *et al.* (2014), the introduction of the southern pike in the Lake Geneva might be due to a trade between the Geneva monastery and the Aosta church during the 12th century. Lunel & Lunel

(1874) described several nuptial colouration patterns of minnows from the Lake Geneva basin. Denys *et al.* (2020) identified one as *P. csikii* (Fig. 5a). However, the drawning presented in the Figure 5b seems to have the nuptial colouration pattern of *P. lumaireul* and looks like a male minnow from the Chisone Torrent in the Po catchment (Fig. 5c). So, the introduction of *P. lumaireul* in the Lake Geneva would be ancient.

3.4 Consequence for the management of the Lake Geneva

Introduction of a new allochtonous fish species in any environment always induces threats for native fauna such as competition, hybridisation and diseases transmissions (*e.g.*, Gozlan *et al.*, 2010; Cucherousset & Olden, 2011; Ribeiro & Leunda, 2012). Allochtonous minnow's introduction in one hand have never had a positive impact on brown trout population (Tiberti *et al.*, 2022), and in another hand, have had a negative impact on native species (Museth *et al.*, 2007; Miró *et al.*, 2018; Osorio *et al.*, 2022), as well as on native minnows' species. Some of these threats are already documented such as hybridisation (Palandačić *et al.*, 2017, 2020, 2024a; Corral-Lou *et al.*, 2019; De Santis *et al.*, 2021, Vucić *et al.*, 2022) and pathogen transmissions (*e.g.*, Esposito *et al.*, 2024a,b). Moreover, the mechanisms of establishement and invasiveness of an allochtonous minnow species is driven by a large trophic niche, a wide physiological tolerance, better immune response as well as a resistance to parasites and a genetic diversity (Thaulow *et al.*, 2013; Scharnweber, 2020; Cruz *et al.*, 2022). Even if the parasitofauna of *P. lumaireul* has been very little studied (see Esposito *et al.*, 2024a) and no knowledges are known about the trophism, it has therefore a phenotypic plasticity allowing it to adapt to its environment (Bianco & De Bonis, 2015; Ramler *et al.*, 2017; Palandačić *et al.*, 2017), and above all a high genetic variability (Geiger *et al.*, 2014; Palandačić *et al.*, 2015, 2017, 2020; Vucić *et al.*, 2018; De Santis *et al.*, 2021; Caputo Barucchi *et al.*, 2022; Reier *et al.*, 2022, 2025). So, some studies already pointed out its ability to migrate and to colonise new environments including karstic caves (Palandačić *et al.*, 2015, 2020; Reier *et al.*, 2022, 2025), which suggests that *P. lumaireul* appears to be a good candidate to be an invader minnow species. Fortunately, minnows are rare on the Lake Geneva coast, which requires some prospecting effort using for example environmental DNA (Blackman *et al.*, 2022) or citizen sciences (Palandačić *et al.*, 2024b) in order to get occurrences and knowledges about the three minnows'species from the Lake Geneva.

4 Conclusion

As time passes and the taxonomic knowledge increases, minnows start to become a baffling problem for riverine managers. They previously managed only had to consider a single species in their management efforts, but are now facing the problem of having to manage more species, which are often restricted and endemic to only a few drainages (see Esposito *et al.*, 2024a). Moreover, past introductions mean that today they have to consider allochtonous and potentially invasive species, and then with cryptic characters making them difficult to distinguish. However, our results confirms the observation of Denys *et al.* (2020) on French populations, that nuptial colouration patterns are diagnostic to distinguish minnow species and a precious character to allow managers to identify the minnows in the field during the breeding period.

We also confirm the presence of three minnow species in the Lake Geneva basin. The list of freshwater fish species occurring in this lake must be updated as well as both French and Swiss legislation. Further investigations are needed to understand the interactions between the three minnow species occurring in the lake, as well as the potential risks on the native fauna.

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Supplementary material

Supplementary data 1. Photos used to characterize the nuptial colouration pattern of *Phoxinus lumaireul*: Varaita Torrent at Costigliole Saluzzo (photo 1 – 5), Sangone Torrent at Trana (6 – 7), Chisone Torrent at Pinerolo (9 – 11) and Lago Laus at Roreto Chisone (12 – 13); photo credits: G.B. Delmastro.

Supplementary data 2. Characters used in the literature for distinguishing *P. csikii*, *P. lumaireul* and *P. septimaniae* according to Kottelat and Freyhof (2007), Palandačić *et al.* (2017), Denys *et al.* (2020) and this study; credits photos: Denys & Delmatro.

Supplementary data 3. Pictures of the male minnow caught in the Geneva Lake at Publier the 31st May 2010, focusing on the head and the caudal peduncle on which the head length (HL), the snout length (SnL) as well as the caudal peduncle length (CPL) and depth (CPD) were measured (grey lines); photo credits: J.-C. Raymond / OFB.

The Supplementary Material is available at https://www.limnology-journal.org/10.1051/limn/2025012/olm.

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