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INVASIVE FRESHWATER MOLLUSCS

How was France invaded? 170 years of colonisation of metropolitan France by freshwater mussels

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Abstract The introduction of freshwater mussels in France was unintentional and relatively recent. Two species were introduced in the second half of the nineteenth century, and a further eight after World War II. This note summarises the available information on introduced freshwater bivalves in France, focusing on the main pathways and vectors of dispersal, based on the data provided by the French National Database (INPN) and environmental DNA data. The introductions were either by sea (mainly for brackish water species, but also for Asiatic Clams), or by the European river system and its canals connecting the Danube to the Rhine (Dreissenidae, Sphaeriidae). A third mean of introduction was the transport of fish, for the Chinese pound mussel, which first established in southern France. Canals connect the major French basins (Rhine, Rhône, Seine, Loire and Garonne) and the route of dispersal of introduced species through natural hydrosystems and canals can be traced by looking at their progression, decade by decade. Fish transport within France is probably an important dispersal vector for the Chinese pound mussel, as occasional introductions appear to have contributed to its spread in the north-east and west of France. The use of the eDNA was an effective tool in completing the species distribution maps.

Keywords Colonisation routes · Invasive species · Dreissena · Sinanodonta · Rangia · Corbicula

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Introduction

Freshwater ecosystems are the most threatened globally (Carpenter et al., 2011; Albert et al., 2021) and are therefore highly sensitive to the introduction of exotic species. Ecosystems that are already impoverished and less stable would be more likely to favour the invasion and establishment of introduced exotic species (den Hartog et al., 1992). Introduced molluscs have a long history in Western Europe. In France, many of the edible snails are thought to have been introduced by the Romans. The nationally

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well-known "Escargot de Bourgogne" *Helix pomatias* Linnaeus, 1758, top seller at Christmas, is actually from Turkey. The "petit gris" *Cornu aspersum* (O.F. Müller, 1774) is one of the most consumed snail species in France and originates from North Africa (Guiller et al., 1994). Less conspicuous in contemporary French gastronomy are the Mediterranean species *Rumina decollata* (Linnaeus, 1758), *Zonites algirus* (Linnaeus, 1758) and *Otala punctata* (O.F. Müller, 1774), also introduced for human consumption by the Romans. Unintentional introductions are also recorded for many small-sized snails and slugs, mainly due to exchange of materials and plants (Hausdorf, 2023). Very little information is available on the consumption of freshwater molluscs in Europe. Their introduction was probably unintentional. Among the gastropods, *Potamopyrgus antipodarum* (Gray, 1843), *Galba truncatula* (O.F. Müller, 1774) and *Gyraulus chinensis* (Dunker, 1848), among others, are all very small species, probably introduced into France by the transport of materials or by dispersal via rivers and canals. Some of the freshwater mussels are large species, but none of them has been deliberately introduced for human consumption. However, their introduction is due to the human activities, mainly maritime and inland waterway transport, which is considered to be the main vector for the introduction of many species during the twentieth century (Mackie, 1999; Ricciardi, 2001; Grigorovich et al., 2003; Holeck et al., 2004; Duggan et al., 2005; Drake & Lodge, 2007). The impact of shipping has been exacerbated by the construction of canals, which act as corridors and link previously isolated catchments (Bij de Vaate et al., 2002). In European aquatic ecosystems, extensive farming, intensive aquaculture, ballast water and canals are the main sources of deliberate or accidental species introductions (Gherardi et al., 2009). One explanation for the success of alien species introductions is that most European aquatic ecosystems are already highly modified and disturbed by human activities: pollution, habitat alteration, interconnection of different basins through canals, overfishing, etc.

France is the European country with the richest biodiversity of freshwater bivalves (Lopes-Lima et al., 2016). Mainland France has recently been colonised by several introduced bivalve species. It currently hosts 10 species of exotic freshwater mussels: the Asiatic clams *Corbicula* cf. *leana* Prime, 1867, *Corbicula* cf. *fluminea* (Müller, 1774), *Corbicula fluminalis* (Müller, 1774), the Zebra Mussel *Dreissena polymorpha* (Pallas, 1771), the Quagga Mussel *Dreissena rostriformis bugensis* (Andrusov, 1897), the Dark False Mussel *Mytilopsis leucophaetea* (Conrad, 1831), the Gulf Wedge Clam *Rangia cuneata* (G. B. Sowerby I, 1832), the Oblong Orb Mussel *Sphaerium transversum* (Say, 1829), the Ridgebeak Peaclam *Euglesa compressa* (Prime, 1852) and the Chinese Pond Mussel *Sinanodonta woodiana* (I. Lea, 1834). Some have been introduced for a long time and seem to have stabilised their colonisation (e.g. *D. polymorpha*, introduced since the nineteenth century, Table 1), while others are in the process of colonising the national hydrological area (e.g. *R. cuneata*, first record in 2017).

Here, I summarise the current knowledge of introduced freshwater bivalve species in France, based on the French national citizen-based database, the recent detections by environmental DNA (eDNA) analyses and unpublished data.

Material and methods

The French national database was used to compile available data on invasive freshwater bivalves (OpenObs, MNHN & OFB, 2022, https://openobs.mnhn.fr). Additional data from the literature were also compiled, together with unpublished personal data. eDNA data were added to the final dataset. eDNA was collected by various actors (NGOs, private consultancies, managers, researchers… see Acknowledgements for main contributors) and all analysed by SPYGEN (Le-Bourget-du-Lac), following the methods described by Prié et al. (2021). Key points of this protocol are the sampling large amounts of water (twice 30 l at each site), the use of the 16S primers described by Prié et al. (2021) for Unionida and Venerida, twelve PCR replicates and a sequencing depth of 300 000 sequences for each primer pair.

Results

CORBICULA *CF.* *LEANA* PRIME, 1867/*CORBICULA CF. FLUMINEA* (MÜLLER, 1774)

Basionyms: *Corbicula leana* Prime, 1867; *Tellina fluminea* Müller, 1774.

Table 1 Introduced freshwater bivalve species in France, invasives and current dynamic

French introduced bivalve species		Invasiveness	Current dynamic in France
Unionida Gray, 1854	*Sinanodonta woodiana*	+ + +	↗
Sphaeriida Lemer, Bieler & Giribet, 2019	*Euglesa compressa*	+ +	?
	Sphaerium transversum	0	→
Venerida Gray, 1854	*Rangia cuneata*	+ +	↗
	Mytilopsis leucophaeata	0	→
	Dreissena r. bugensis	+ + +	↗
	Dreissena polymorpha	+ + +	→
	Corbicula fluminalis	0	→
	Corbicula cf. *leana* / *Corbicula* cf. *fluminea*	+ + +	→

Type localities: *C. leana*: Japan (without a precise location); *C. fluminea*: "in arena fluviali Chinae".

The Dordogne is often cited as the site of introduction of *Corbicula fluminea/leana* in France in 1980 (Mouthon, 1981). However, the first introduced Asiatic Clam in France was found in 1976 in the collections of the regional environment department in Val-de-Loire (Hesse et al., 2015), suggesting an even earlier introduction. The species spread very quickly. (Brancotte & Vincent, 2002). A decade after its first observation by Mouthon in the Garonne basin, it had already spread via the Canal du Midi to the Rhône estuary. At the beginning of the 2000s, it was already present in most of the major basins in France (Garonne, Loire, Rhône, Seine…), with the exception of the Adour in south-west France and the north-west (Brittany and Normandy). By 2010, all the major basins in France had been colonised (Fig. 1; Online Resource 1A), but only this year were the first *Corbicula* shells observed in Corsica Island (X. Cucherat, com. pers.)

Corbicula cf. *leana* and *C.* cf. *fluminea* are difficult to differentiate by morphology. Moreover, hybridisation has been documented in places where they have been introduced and become invasive, and the distinction of these two nominal taxa is now doubtful. Consequently, the available records in the French database have been grouped under the name *Corbicula fluminea*. Theoretically, the 'true' *Corbicula fluminea* would be restricted to the Rhône drainage, while the *Corbicula* populations in the rest of France would belong to *C. leana* (Pigneur et al., 2011, 2014), suggesting two different introduction events. However, things may have changed since these studies and one can hardly pretend to make a difference between these two nominal taxa in areas of introduction. The short fragment amplified by the eDNA bivalve primers (Prié et al., 2021) is not informative enough to distinguish these two taxa. Therefore, the available records have been combined under the name *Corbicula fluminea*.

The impact of the invasion of Asiatic Clams is still poorly understood and probably underestimated. Pigneur et al. (2013) showed that high densities of Asiatic Clams resulted in a significant decrease in chlorophyll a, a 70% loss in phytoplankton biomass and a 61% decrease in annual primary production. Asiatic Clams also had significant effects on the oxygen budget of the river and on nutrient cycling. Soussa et al. (2008) showed that the introduction of Asiatic Clams in the Mihno River had led to the extirpation of *Pisidium amnicum* (O. F. Müller,

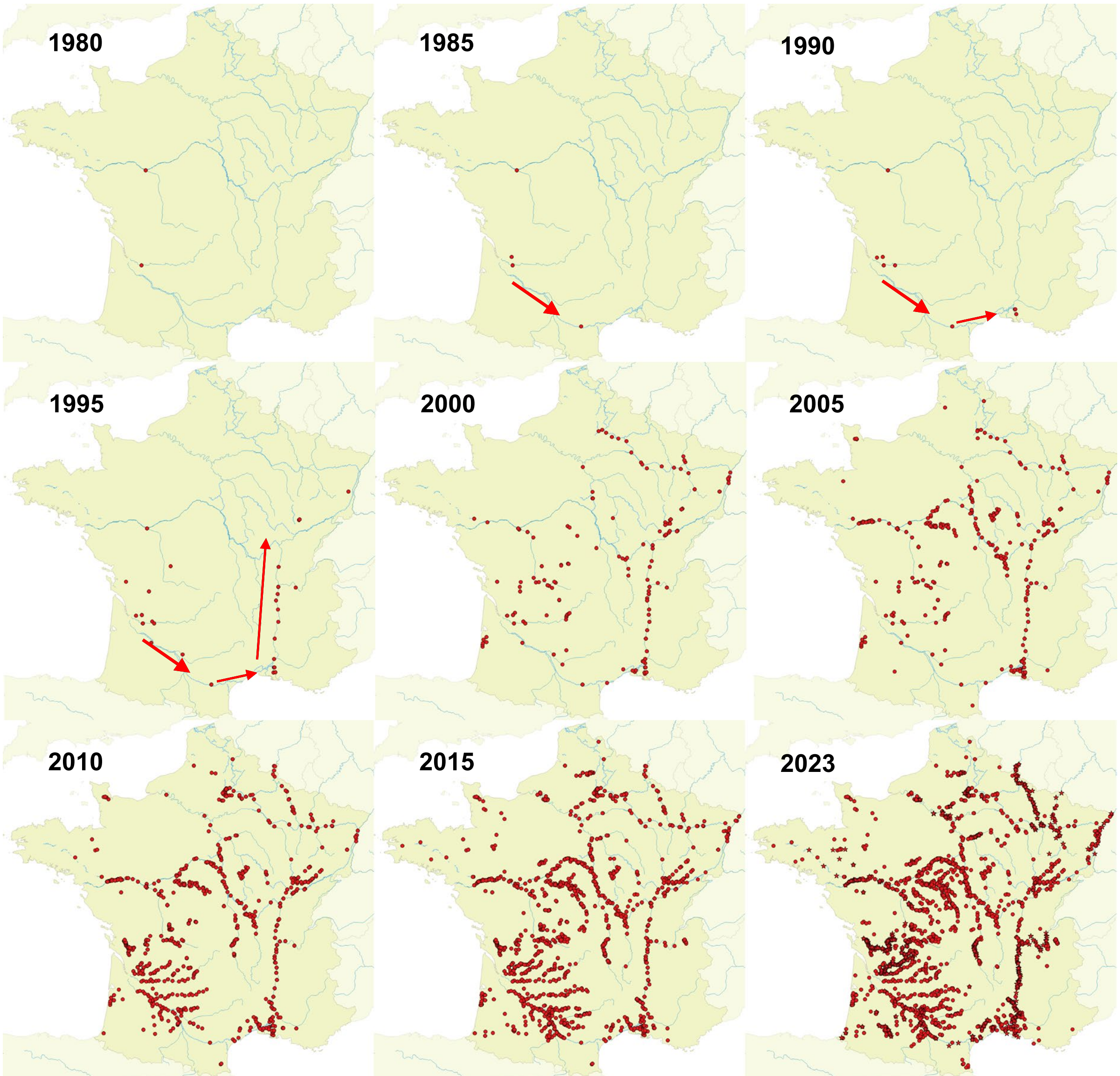


Fig. 1 *Corbicula* cf. *fluminea* spreading in France. Red dots: available data based on traditional methods/direct observations; red stars: species detected by eDNA analysis. Rivers are shown with blue lines, canals with dashed blue lines

1774). High densities of Asiatic Clams have a negative impact on Unionids, resulting in a lower growth and poorer physiological condition (studied on *U. delphinus* by Ferreira-Rodrigues et al., 2018) -which could be due to competition for food- and on the survival of glochidia (studied on *A. anatina* by Modesto et al., 2019).

In France, the invasion of large rivers by Asiatic Clams may explain the drastic decline of *Sphaerium solidum*. Apart from the headwater and upstream ecosystems, which are not suitable for Asiatic Clams, very few lowland rivers are spared. Two of these spared rivers were surveyed by eDNA, the Nizonne, a tributary of the Dronne River, and the Venelle, a tributary of the Saône River that flows underground before reaching the Saône. In both rivers, the diversity of Sphaerid was very high.

***CORBICULA FLUMINALIS* (MÜLLER, 1774)**

Basionym: *Tellina fluminalis* Müler, 1774.

Type locality: "In fluvio Afiae Euphrat".

In Europe, *C. fluminalis* was first recorded in 1984 in Germany, in the Weser estuary (Haesloop, 1992). In France, the date of the first record is uncertain to the possible confusion with *C.* cf. *fluminea*. The older reliable record is from 1995 in the Moselle River (Bachmann et al., 1995 in Mouthon, 2000). Mouthon (2000) illustrates specimens collected in the *Canal de Roanne*, along the Loire River and in the Saône River (Rhône tributary) between the confluence of the Doubs and Châlon-sur-Saône. *C. fluminalis* has not colonised France like *C. fluminea/leana* did. It does not seem to be invasive; the records are scarce and mostly consist in a few specimens. Most of the records come from north-eastern France (Online Resource 1B). Remarkably, a large population has recently been discovered in south-eastern France at Lake Broc (D. Beautheac com. pers.). This population is isolated, suggesting that *C. fluminalis* is capable of long-distance dispersal, either by zoochory or, more likely, by human transport. The short fragment amplified by the eDNA "bivalve" primers of Prié et al. (2021) allows recognition of at least one haplotype of *C. fluminalis*, but little is known about the genetic variability of this species and eDNA results may underestimate the distribution of the species if some of the haplotypes are shared with *C.* cf. *fluminea*. Although hybridisation has been mentioned elsewhere in Europe, this taxon appears to be morphologically distinct in France (Prié, 2017). The impact of *C. fluminalis* on autochthonous faunas is not known.

***DREISSENA POLYMORPHA* (PALLAS, 1771)**

Basionym: *Mytulus polymorphus* Pallas, 1771.

Type locality: The Volga and Yaik [nowadays Ural] rivers, the Caspian Sea.

Dreissena polymorpha was first recorded in Great Britain in 1824 and then in the Netherlands in 1826 (Bij de Vaate et al. 2002). It has been recorded in the Maestrich Canal in Belgium since 1834. The first records in northern France date from 1852, but the species was recorded in Lyon (Rhône drainage) in the same year. It was then recorded in the Seine River (1855), Loire River (1863) and at Agen (Garonne drainage) in 1866 (Kinzelbach, 1992). According to Locard (1893), the species was very common throughout France at the end of the nineteenth century. Some authors (Kinzelbach, 1992; Bij de Vaate, 2002) believe that the transport of wood (trunks) by flotation is the main way in which *D. polymorpha* spreads. *D. polymorpha* is widespread and abundant in northern and eastern France, but for some reason is not as common in the Atlantic and Mediterranean rivers. There are very few records from Britany and Normandy (Online Resource 1C). *D. polymorpha* is currently being replaced by *D. r. bugensis* in some of the lakes in the Rhône basin (e.g. in Lake Serre-Ponçon, Combrisson, 2023, and in Lake Bourget, pers. obs.), and perhaps also in north-eastern France. *D. polymorpha* can have a negative impact on native unionids by attaching itself to their shells, usually around the inhalation aperture, which impacts their filtration capacity.

***DREISSENA ROSTRIFORMIS BUGENSIS* (ANDRUSOV, 1897)**

Basionym: *Dreissena bugensis* Andrusov, 1897.

Type locality: The Bug River, Lyman near Mykolaïv, Ukraine.

The colonisation of Western Europe began in 2004 with the first records in the Danube River in Romania. The following year, the species was recorded in the River Main in Germany. In 2006, it was discovered in the Netherlands, where the original introduction may have occurred in 2004 or earlier (Molloy et al., 2007; Imo et al., 2010). The first records in France date back to 2010 in the Meuse (Bij de Vaate & Beisel, 2011) and in 2011 in the Moselle River (Marescaux et al., 2012). It was recorded in the French part of the Rhine in 2014 and in the Escaut in 2015. In 2016, it entered the Rhône basin via the Saône River (Prié & Fruget, 2017). Environmental DNA sampling was carried out in the Rhône in 2016, but was not analysed for bivalves until 2018. While Prié & Fruget (2017) give only a few records in the Rhône, we now know that the species was already widespread in the entire French section of the Rhône River at that time (Fig. 2; Online Resource 1D). The species was detected by eDNA analysis in 2018 in a pond in Montpellier and in the Lez River, upstream of Montpellier. This pond and the Lez River are connected to the *Canal Philippe Lamour*, which is not navigable but is used for irrigation and brings water from the Rhône. It is very likely that *D. r. bugensis* will follow the same route as *S. woodiana* and soon colonise the Garonne drainage. Ballast water is considered to be the most important mode of spreading for long-distance dispersal (Bij de Vaate & Beisel, 2011). Recreational

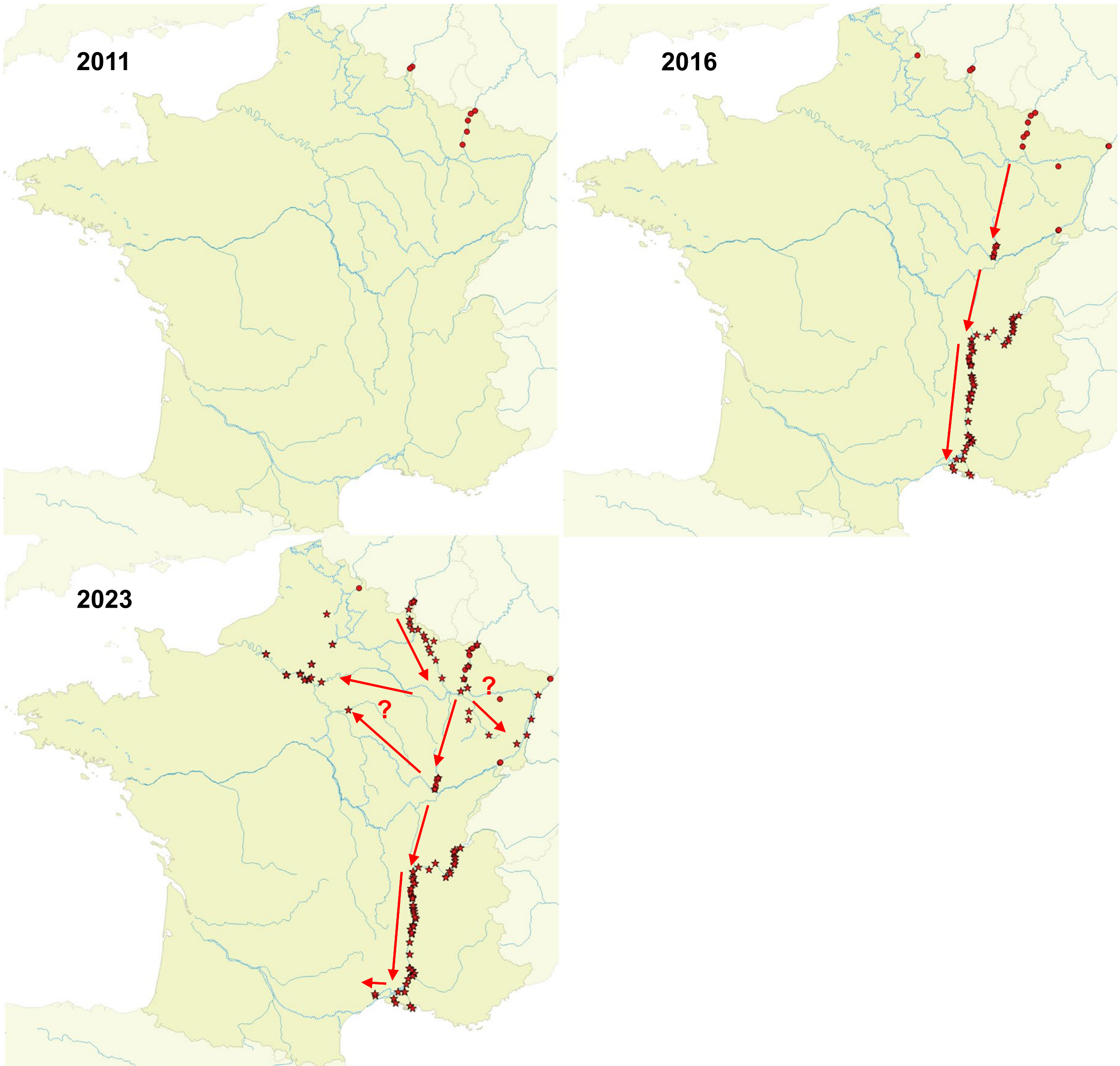


Fig. 2 *Dreissena r. bugensis* spreading in France. Red dots: available data based on traditional methods/direct observations; red stars: species detected by eDNA analysis. Rivers are shown with blue lines, canals with dashed blue lines

boats are another source of long-distance dispersal between lakes (shells attached to the hull). Large peri-alpine lakes such as Lake Geneva are thought to have been colonised by pleasure boats. However, the evolution of the distribution of the species in France shows that natural routes and canals are efficient corridors. Downstream transport in the Rhône and Seine drainages is probably favoured by the drifting stage of the veliger larvae. As these rivers were colonised from upstream, colonisation was very rapid. If the Garonne basin is colonised from upstream via the Canal du Midi, it is likely that the species will also spread rapidly downstream.

***MYTILOPSIS LEUCOPHAEATA* (CONRAD, 1831)**

Basionym: *Mytilus leucophaeatus* Conrad, 1831.

Type locality: "Inhabits in the southern coast of the U S".

The first European record dates from 1835, when it was found in the Scheldt estuary near Antwerp, Belgium and described as a new species, *Mytilus cochleatus* Nyst, 1835. This nominal species was first mentioned in France for the first time in 1872, in the Canal de Bergues, near Dunkerque, in the north of France (Locard, 1893). This first mention by Locard was then taken up by Germain (1931) and then by Boettger (1933), but these authors do not give any further records. It is known from the *Canal de Caen à la mer* since 1898 (Baffreau et al., 2018). The species is mentioned for the first time in the Atlantic side of France in Brittany by Maillard & Gruet (1972), in the marshes of Brière. These authors consider that the introduction dates back to 1933. The species has been recorded in the Ter estuary (town of Ploemer) by Gruet and Baudet (1997) and in the Rance estuary since 1992 (Le Mao, 2003). To the south, it has been recorded at the mouth of the Sèvre Niortaise and at Sainte-Radegonde-les-Noyers since 1980 (Bertrand ined. *in* Girardi, 2003) and at the Marais Poitevin on its Charente side (Jourde, 1997). It is now also known from Normandy (Lecaplain, pers. com.), the Rance River in Brittany and in the *Canal maritime du Môle d'Aigues-Mortes* (Gard, Girardi, 2003) and more recently was detected with eDNA in Port Saint-Louis, on the eastern side of the Camargue (Online Resource 1E). Shipping is the main mode of dispersal. According to Wolff (2005), hull fouling would be the most likely vector, while Laine et al. (2006) state that ballast water is the main vector. This species does not appear to be invasive in France. Although it has been introduced to France for a long time, it is only known from a few locations.

***RANGIA CUNEATA* (G.B. SOWERBY I, 1832)**

Basionym: *Gnathodon cuneatus* G. B. Sowerby I, 1832.

Type locality: Unkwnown ("… received from New Orleans; (…) sent unaccompanied with any particular information…").

Rangia cuneata was first recorded in Europe in 2005, in the port of Antwerp, Belgium (Verween et al., 2006). In France, the species was first recorded along the banks of the Caen Canal at Benouville—Ranville in August 2017 (Kerckhof et al., 2017). Since this first record in France, its presence and establishment have been confirmed by observations in Ouistreham (Faillettaz et al., 2020) and a small population was observed in the marshes of Brière in 2020 (M. Marquet & A. Petit, pers. com.), suggesting that the species is probably already more widespread in mainland France than previously thought (Online Resource 1F). It may be expanding in Brière as it is now recorded from 29 sites in the districts of Crossac, Donges, Montoir-de-Bretagne, Saint-Joachim, Saint-Malo-de-Guersac and Trignac (Mary Youen and Morzandec Manon, unpublished data). The main vectors of introduction would be transport via ballast water in the larval stage and transport of oysters and oyster farming equipment in the adult stage (Carlton, 1992; Pfitzenmeyer & Drobeck, 1964). The impact of the introduction of *R. cuneata* in France is not yet known.

***SPHAERIUM TRANSVERSUM* (SAY, 1829)**

Basionym: *Cyclas transversa* Say, 1829.

Type locality: North America.

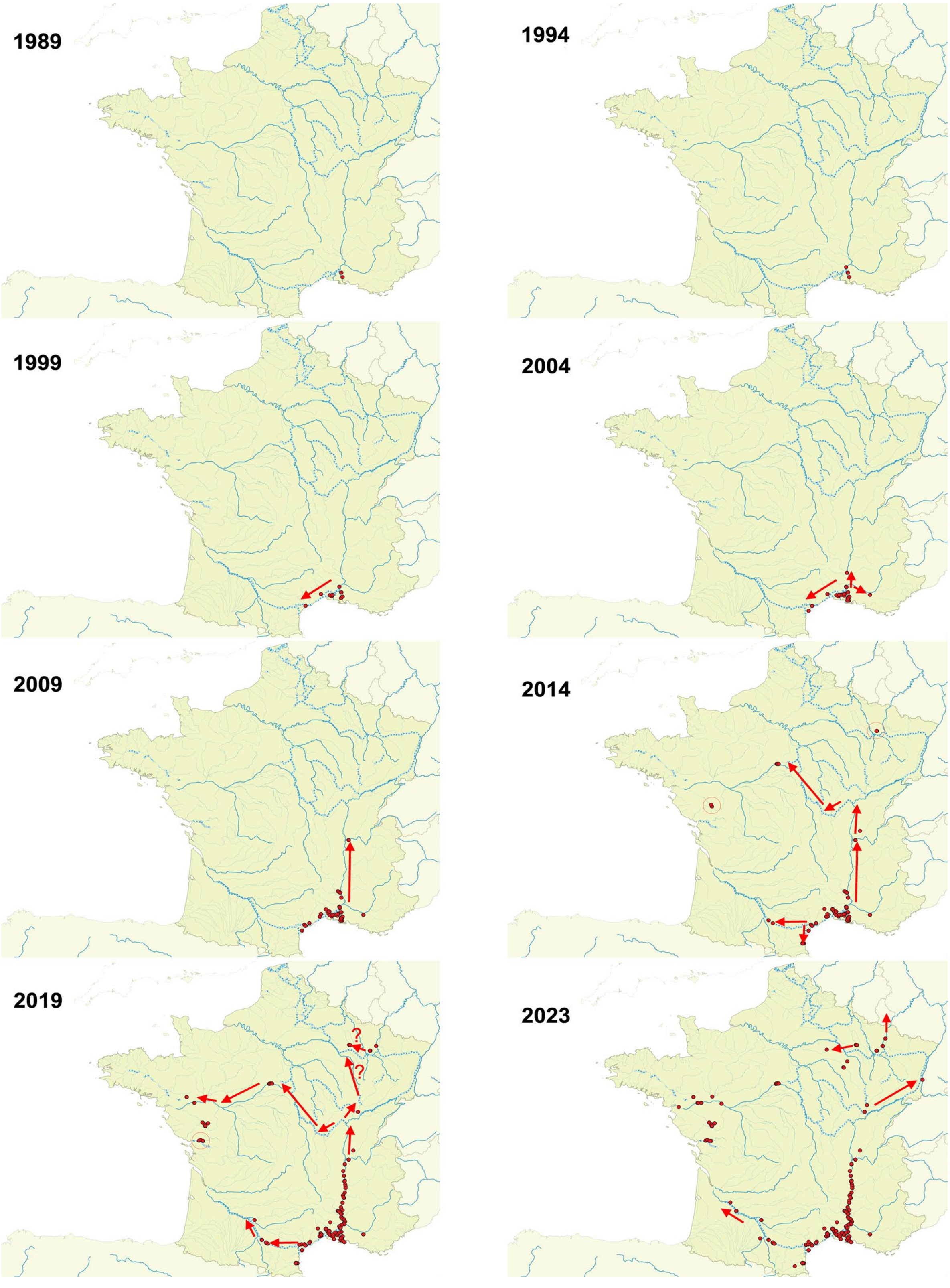
The first European record dates from 1856 in England. The species was first collected in France in 1980 in the Canal de Marck in northern France (X. Cucherat, com. pers., coll. Verdevoye), then recorded in the Oise canal by Mouthon & Loiseau (2000), and more recently in 2020 in the lower Seine (town of Poses) by eDNA analysis (Online Resource 1G). There is no further records in France. This species is conspicuous and easy to identify. Given the very few records, this species does not appear to be invasive. *S. transversum* has been found in France either near the coast or in canals used for commercial shipping. It is probably spread by boats, possibly in ballast waters. No impacts are known.

***EUGLESA COMPRESSA* (PRIME, 1852)**

Basionym: *Pisidium compressum* Prime, 1852.

Type locality: USA, Massachusetts, without a precise locality.

This species was first observed in France in 1989 in the Saône River (Rhône drainage) at Ouroux (Mouthon et al., 2018), then in the Rhône, the Seine, Rhine and Loire basins, as well as in various canals in eastern France (Mouthon & Taïr-Abbaci, 2012), but the collected specimens were not identified at this stage. It was only in 2017 that molecular studies allowed the identification of this sphaeriid as *E. compressa* (Mouthon & Forcellini, 2017). Subsequently, Mouthon et al. (2018) identified specimens from the Netherlands and Germany as belonging to this species and were able to show that its introduction into Europe occurred before the 1940s, probably via the Elbe estuary and the port of Hamburg. Given the apparent spread of the species across Western Europe since the 1990s, these


1989
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◀**Fig. 3** *Sinanodonta woodiana* spreading in France. Red dots: available data based on traditional methods / direct observations; red stars: species detected by eDNA analysis. Rivers are shown with blue lines, canals with dashed blue lines. In 2014, introductions within France are suspected to have occurred via fish transport in north-eastern and western France (circled)

authors suggest a second phase of introduction, about 50 years later, via the Rhine-Meuse delta.

The eDNA analysis allowed the detection of *E. compressa* at various sites in the lower Rhône River, in the Meuse and Moselle Rivers in north-eastern France, and at several sites in the Seine basin (Online Resource 1H), confirming the distribution of the species in France given by Mouthon et al. (2018). It was also detected in the upper Loire, and as an isolated record in the lower Loire, suggesting that it has already colonised most of the Loire basin. However, it has not yet been detected in the south-western part of France (from the Charente to the Garonne and Adour basins). According to Mouthon et al. (2018), the arrival of *E. compressa* in Europe was probably made possible by shipping activities. Since then, the interconnection of large rivers by artificial canals has probably facilitated the spread of the species in the Netherlands and France (Bij de Vaate et al., 2002).

The impact of this species is unknown, but probably not very important given its small size and apparently relatively low abundance.

***SINANODONTA WOODIANA* (I. LEA, 1834)**

Basionym: *Symphynota woodiana* I. Lea, 1834.

Type locality: "China, Canton". The type locality and the taxonomy are not clear (Lopes-Lima et al., 2020).

In Europe, the first records come from Hungary and Romania (Petro, 1984; Sarkany-Kiss, 1986) where *S. woodiana* was introduced in the early 1960s (Kiss & Petro, 1992; Kiss, 1995; Kiss & Pekli, 1988). The origin of the introduction is thought to be the import of glochidia-infested fish from the Amur and Yangtze basins for fish farming (Girardi & Ledoux, 1989). The species was introduced into France in 1982, when common carp *Cyprinus carpio* Linnaeus, 1758, and grass carp *Ctenopharyngodon idella* (Cuvier & Valenciennes, 1844) were imported from a fish farm in Hungary (Girardi & Ledoux, 1989). The species was introduced into the fish farm of the *Etang des Gravières* (commune of Fontvieille, Bouches-du-Rhône, near Arles), where its proliferation was noticed by the owner in 1985. In 1986, when Girardi & Ledoux (1989) made their first observations, the population was already very large with many individuals of all sizes. The first record in flowing water dates from 1989 (Girardi, 1989). Two adults were found in a canal south of Arles. Girardi (2000) observed the species in the Gardon River at its confluence with the Rhône and then in several localities in the Camargue (Girardi, 2002). In 2002, it was recorded further north at the mouth of the Ardèche River. In 2007, the species was discovered in a eutrophic reservoir upstream of Lyon (Mouthon, 2008). Adam (2010) documents the spread of the species along the Mediterranean coast. In 2016, it was detected in the Saône River by eDNA analysis. *S. woodiana* then spread over northwards to the Seine and Loire basins and westwards to the Garonne basin via the *Canal du Rhône à Sète* and the *Canal du Midi* (Fig. 3, Online Resource 1I). Occasional introductions by fish transport within France may also have occurred in ponds and reservoirs.

As has been observed elsewhere in Europe, native *Anodonta* species disappear a few years after the introduction of *S. woodiana*, probably due to the competition for host-fish (Donrovich et al., 2017). This phenomenon was observed downstream of the Hérault River, where *Anodonta anatina* was very abundant in 2007 (pers. obs.). *S. woodiana* was first recorded there in 2009. A few years later, *A. anatina* was no longer observed, even by scuba-diving. In 2017, eDNA analyses were carried out to check the persistence of *A. anatina*: it was not detected.

Discussion

The history of invasions begins in the late nineteenth century. *M. leucophaeata* was introduced from North America and *D. polymorpha* from Eastern Europe, both probably introduced by sea. Then, for about a century, no exotic bivalve species were introduced into France (Fig. 4). It was not until the second half of the twentieth century that the introduction process started again, with sea and inland waterway transport, colonisation via canals and fish transport. The increase in trade, particularly with the invention of the container, is probably the cause of this second wave of introductions.

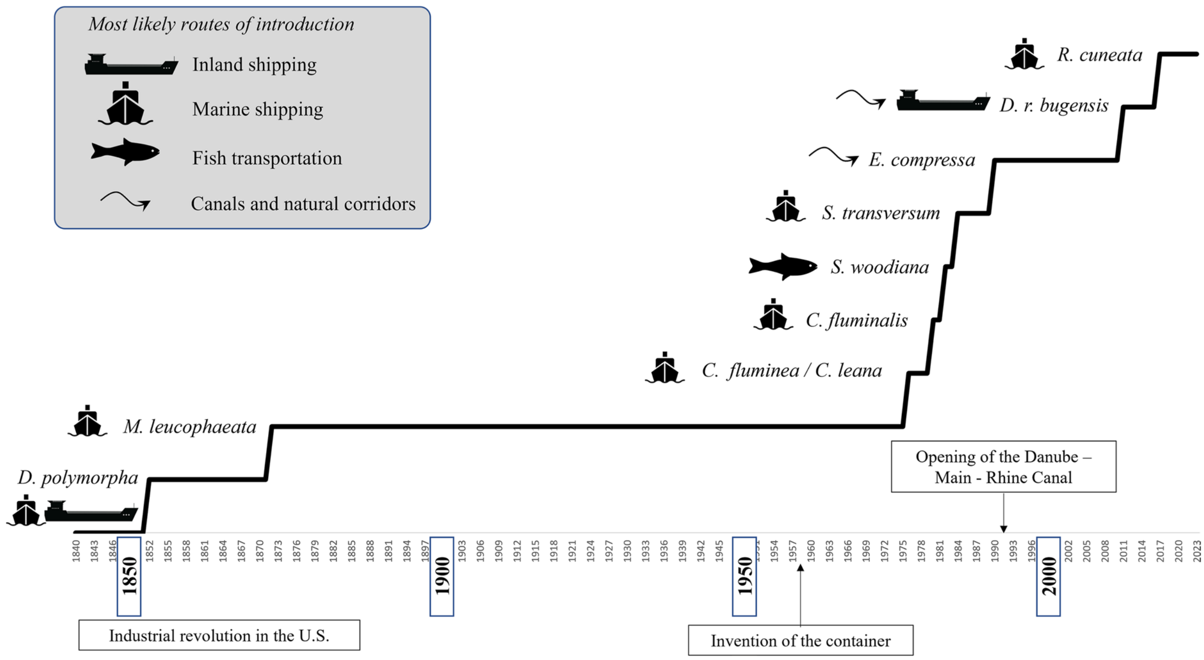

Fig. 4 History of freshwater mussel invasions in France

Despite being at the crossroads of the Mediterranean, Atlantic and Continental biomes of Western Europe, France is isolated for freshwater bivalves by major geographical barriers such as (i) the Pyrenees and the Alps, (ii) the sea and (iii) a highly industrialised area in the north-east (Prié et al., 2014). These biogeographical barriers are important for native species, but two of them, (ii) the sea and (iii) the industrialised area in the north-east, are potential corridors for invasive species. A third pathway is the transport of materials and fish.

With the globalisation of the economy and the increase in international trade, shipping has become a major route for invasive species. In the early nineteenth century, *M. leucophaeata* colonised Europe from North America, probably taking advantage of maritime trade. A century later, Asiatic Clams, originally from Asia but established in North America, followed the same route. The sphaerids *S. transversum* and *E. compressa* also took the same route to Europe in the second half of the twentieth century and *Rangia cuneata* also arrived in Europe (in Belgium) by boat (Verween et al., 2006). The sea, which was a major biogeographical barrier for freshwater species, has become a corridor.

Inland waterways also play an important role in the dispersal of freshwater invertebrates. Bij de Vaate et al. (2002) identified three main east–west corridors in Europe: a northern corridor linking the Volga to the Baltic Sea, a central corridor linking the Dnieper to the Rhine, and a southern corridor linking the Danube to the Rhine (Fig. 5A). Whatever the route from Eastern Europe to the Rhine, once in the Rhine, invasive species can colonise the Rhône via the *Canal du Rhône au Rhin* (Fig. 5B). From the lower Rhône, the *Canal du Rhône à Sète* (Fig. 5C) provides a link to the small coastal rivers east of the Rhône. The *Canal du Rhône à Sète* opens into the lagoon of the *Etang de Thau*, which is saline and about 17 km wide. It is unlikely that an amphidromous fish such as *Mugilus* sp. could make the connection between the *Canal du Rhône à Sète* to the east of the lagoon and the *Canal du Midi* to the west of the lagoon. However, many commercial boats use this route. Fish species may occasionally be transported in ballast water (e.g. Wonham et al., 2000). This is more likely to be the case for small juveniles fishes, which are most susceptible to glochidial infection. Infected fish may therefore be sucked in when the boats fill their ballast water and

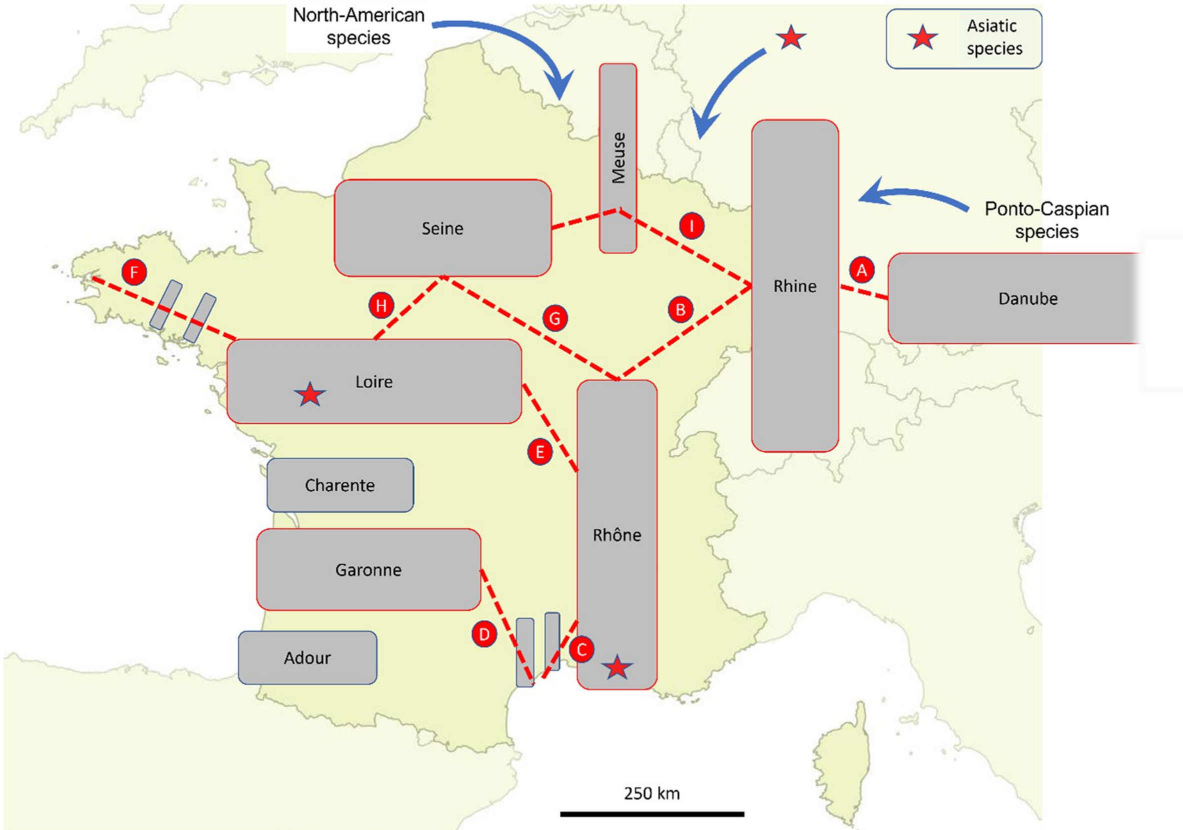

Fig. 5 Diagram of interconnections between the main river basins in France. A: Danube-Main-Rhine canal, B: Rhine-Rhône canal, C: Canal du Rhône à Sète, D: Canal du Midi, E: Canal du centre, F: Canal de Nantes à Brest, G: Canal de Bourgogne, H: Canal de Briare-canal du Loing, I: Canal de la Marne au Rhin. The Adour and Charente basins remain isolated and could be future refuges for native species, if the introduction of the Chinese Pond Mussel through the transport of fish can be avoided

released on the other side of the lagoon when the boats discharge their ballast water. On the other side of the *Etang de Thau*, the *Canal du Midi* (Fig. 5D) is an open door to the great Garonne basin on the Atlantic side of France.

The Rhône is connected to the Loire by the *Canal du Centre* (Fig. 5E). The Loire flows into the Atlantic, and at its mouth is the Canal de Nantes à Brest (Fig. 5F), which links many of the coastal rivers of Britany. The Rhône is also connected to the Seine by the *Canal de Bourgogne* (Fig. 5G), and the Loire to the Seine by the *Canal de Briare / Canal du Loing* (Fig. 5H). The Rhine is also connected to the Seine basin by the *Canal de la Marne au Rhin* (Fig. 5I), which also connects the Meuse to the Rhine and the Seine. Thus, since the (re)opening of the Danube-Main-Rhine Canal in 1992, species from Eastern Europe such as *D. r. bugensis* or species introduced in the Netherland/Belgium/Germany by shipping activities, such as *E. compressa* or *C. fluminalis*, have been able to colonise most of France. Of the major rivers, only the Charente and Adour basins are isolated from the network of interconnected rivers. Although they have already been colonised by Asiatic Clams and Zebra mussel, they offer a unique opportunity to preserve autochthonous unionids from the Chinese Pond Mussel.

Unfortunately, some introductions can come “out of the blue”. The Chinese Pond Mussel was introduced by fish transport to Romania, then to Hungary, and from there to France. It then spread via natural routes and canals, but it has probably also been transported at least twice within France, to the ponds of north-eastern and western France

(Fig. 3). Individual human introductions are difficult to document and may be more important than thought, especially when it comes to fish translocation, an activity that is (unfortunately) legal and common in France.

The Sphaeriidae, which have a very efficient dispersal capacity, are not the family with the highest number of introduced species. This is probably due to their efficient natural dispersal: geographical barriers do not play a major role in the distribution of these species, and colonisation of suitable landscapes has occurred long time ago. Only the Atlantic Ocean may have played a role in isolating the European and American faunas. As a result, only a few North American species have been introduced into Europe.

Our records provide a blurred picture of the reality of introduction and spread of invasive alien species. *D. polymorpha* was recorded in northern France and in the middle Rhône in the same year, and about 15 years later in the Garonne basin, suggesting an earlier overlooked colonisation of French rivers. The same is true for *D. r. bugensis* on a the European scale: This species was observed in the lower Danube in 2004, and the same year it was found in the Netherlands. We lack effective monitoring methods for freshwater invasive species. Although eDNA analysis has only been used in France for about 6 years, it undoubtedly gives an accurate picture of the distribution of invasive species. It has shown that some of the alien species are more widespread than what traditional data would suggest. *D. r. bugensis* has been detected 10 times in the Seine drainage by eDNA analysis, but there are still no data available from traditional surveys. *E. compressa* was also missed in the Rhine, Meuse, and Loire basins, but was detected by eDNA analysis. The implementation of large-scale monitoring of freshwater mussels using eDNA is likely to be the future of river monitoring, provided that optimised methods are implemented.

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Data availability Most of the data used for this paper are already in the French National Database (INPN, Inventaire National du Patrimoine Naturel, https://inpn.mnhn.fr/). The eDNA data which may not yet be in the French National Database is public and is intended to be transferred to the French National Database in the near future by the operators who ordered the analyses.

Declarations

Conflict of interest The author declares no conflict of interest.

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