

Conservation status of freshwater mussels in Europe: state of the art and future challenges

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ABSTRACT

Freshwater mussels of the Order Unionida provide important ecosystem functions and services, yet many of their populations are in decline. We comprehensively review the status of the 16 currently recognized species in Europe, collating for the first time their life-history traits, distribution, conservation status, habitat preferences, and main threats in order to suggest future management actions. In northern, central, and eastern Europe, a relatively homogeneous species composition is found in most basins. In southern Europe, despite the lower species richness, spatially restricted species make these basins a high conservation priority. Information on freshwater mussels in Europe is unevenly distributed with considerable differences in data quality and quantity among countries and species. To make conservation more effective in the future, we suggest greater international cooperation using standardized protocols and methods to monitor and manage European freshwater mussel diversity. Such an approach will not only help conserve this vulnerable group but also, through the protection of these important organisms, will offer wider benefits to freshwater ecosystems.

Key words: biology, ecology, Europe, freshwater bivalves, naiads, Margaritiferidae, Unionidae.

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I. INTRODUCTION

Freshwater bivalves of the Order Unionida Gray 1854, also known as freshwater mussels, freshwater clams or naiads, are remarkable organisms. They may live for over a century and their unique life history includes parental care (i.e. brooding) and larval parasitism on freshwater fishes (and occasionally other vertebrates) (Lopes-Lima *et al.*, 2014c). Freshwater mussels are also important components of aquatic ecosystems (Vaughn & Hakenkamp, 2001), sometimes constituting >90% of the benthic biomass of rivers (Negus, 1966). An individual mussel is capable of filtering around 40 l of water each day (Tankersley & Dimock, 1993) and the combined filtration of a mussel population can account for approximately 50% of the observed seston retention in a river during the summer (Pusch, Siefert & Walz, 2001). Their transfer of matter and energy from the water column to the benthos may have strong effects on primary and secondary production, biogeochemical cycles, sedimentation rates, and water clarity (Strayer *et al.*, 1999). In addition, their shells function as an important substrate for many other organisms (Vaughn & Hakenkamp, 2001; Spooner *et al.*, 2013). Because of their direct and indirect effects on fresh waters, mussels are often described as ecosystem engineers (Gutiérrez *et al.*, 2003). Their key role in ecosystems is exemplified by the higher diversity of associated macroinvertebrates at sites which carry higher densities of mussels (Aldridge, Fayle & Jackson, 2007). Freshwater mussels also provide important direct services to humans, such as water purification, serving

as important prey for several commercial fishes, providing a direct source of protein, and providing valuable materials such as shells and pearls (Haag, 2012).

Mussels are declining precipitously worldwide (Strayer *et al.*, 2004). For example, 224 (44%) of the 511 freshwater mussel species are classified as Near Threatened or Threatened in the 2015 *IUCN Red List of Threatened Species*. Much of the global awareness of freshwater mussel declines stems from North American Unionida, which constitute the continent's most imperilled fauna (Williams *et al.*, 1993; Strayer *et al.*, 2004). Over 70% of North American species are considered imperilled at some level (Williams *et al.*, 1993) and 37 species are presumed extinct (Lydeard *et al.*, 2004).

In recent years, Europe's freshwater mussels have also received increasing attention. More rivers and lakes are being surveyed and molecular techniques are helping to discern phylogenies and resolve synonymies. Increased international collaboration is revealing widespread and rapid declines at the regional level (Sousa *et al.*, 2008; Geist, 2010; Prić, Molina & Gamboa, 2014). Despite this increasing awareness, conservation has focused on a handful of species, such as *Unio crassus* Philipsson 1788, and the pearl mussels *Margaritifera margaritifera* (Linnaeus 1758) and *Margaritifera auricularia* (Spengler 1793). Some populations of these species have disappeared within living memory or have been reduced to small, localized, non-recruiting populations (e.g. Araujo & Ramos, 2001). Considerably less attention has been paid to the other European Unionida mussels, and this probably reflects the assumption that they are widespread,

abundant and recruiting. The absence of baseline data makes the quantification of population change challenging, and the recent discoveries of new populations of some species can even give the impression of population increase (Aldridge, 2004).

To date, no publication has attempted to synthesize our collective understanding of the ecology, distribution, and conservation status of the European freshwater mussel species. To address this, we have assembled the knowledge and expertise of malacologists from across Europe to (i) list the presently accepted European Unionida species and discuss their taxonomy; (ii) characterize their distribution; (iii) describe their basic biological characteristics and habitat preferences highlighting research gaps on life history and their functional role; (iv) assess their conservation status; (v) summarize the major threats to these species and highlight the critical knowledge gaps that impair conservation efforts; and (vi) suggest a logical path for future work.

II. LIST OF SPECIES, TAXONOMY AND DISTRIBUTION

(1) List of European freshwater mussel species

In the early 1900s, European mussel diversity was grossly overestimated (about 1500 species) due to numerous synonyms applied to variable shell forms, particularly by the French *École Nouvelle* (Graf, 2010). By the end of the 20th century many synonymies had been resolved, merging the previous descriptions into 12 recognized species with several subspecies (e.g. Germain, 1931; Haas, 1969; Araujo & de Jong, 2015). In recent years, this number has increased reflecting molecular advances in taxonomy (Araujo, Toledo & Machordom, 2009b; Reis & Araujo, 2009; Prié, Puillandre & Bouchet, 2012) and will likely continue to increase as more research efforts are made in this field (Graf, 2010). Currently, 16 species of European Unionida are recognized (Figs 1 and 2). Based on this recent work, we present a revised checklist of the European Unionida species (Table 1, see also online supporting information, Appendix S1).

(2) Taxonomy and systematics (Unionida Gray 1854)

The order Unionida is represented in Europe by two families: (i) the Margaritiferidae Henderson 1929 (1910), which comprises only two species: *M. auricularia* and *M. margaritifera* and; (ii) the Unionidae, represented by 14 species in five genera (*Anodonta* Lamarck 1799; *Microcondylaea* Vest 1866; *Potomida* Swainson 1840; *Pseudanodonta* Bourguignat 1877; and *Unio* Philipsson 1788).

(a) Family Margaritiferidae Henderson 1929 (1910)

In Unionida phylogeny, the Margaritiferidae was regarded until recently as the most basal family due to the lack of more specialized anatomical features (Bogan & Roe, 2008). However, molecular studies place margaritiferids

as sister to (or nested within) the Unionidae (Hoeh *et al.*, 2002; Graf & Cummings, 2006). The interspecific relationships within the Margaritiferidae have also remained contentious. Using mainly conchological and anatomical characters, Smith (2001) divided the family into three genera: *Margaritifera* Schumacher 1816, *Margaritanopsis* Haas 1912, and *Pseudunio* Haas, 1910. However, a study using molecular techniques indicated polyphyly in these genera, and instead suggested that the genus *Margaritifera* should encompass all margaritiferid species (Huff *et al.*, 2004).

Although distinct evolutionary lineages or subspecies of *M. margaritifera* have been described [e.g. *M. m. durrovensis* Philips 1928 and *M. m. brunnea* (Bonhomme 1840)], these are not supported by molecular data (Fig. 1; Chesney, Oliver & Davis, 1993; Machordom *et al.*, 2003). Within the species, a gradient in genetic diversity is evident, with higher variation observed in northern than in south-western Europe (Geist & Kuehn, 2005; Geist *et al.*, 2010b). The pronounced genetic structure across *M. margaritifera* populations may reflect reproductive isolation (Geist & Kuehn, 2005) and/or differentiation according to use of different host fishes (*Salmo trutta* or *Salmo salar*) (Karlsson, Larsen & Hindar, 2014).

The generic affiliation of *M. auricularia* has been controversial. This species was allocated to the genus *Pseudunio* to distinguish it from *M. margaritifera* (Haas, 1910) and 1 year later re-synonymized with *Margaritifera* (Ortmann, 1911). *Pseudunio* was subsequently resurrected as a subgenus to distinguish *M. auricularia* and its subspecies *M. a. marocana* Pallary 1918 from the remaining *Margaritifera* species (Haas, 1969). Since then, *Pseudunio* was used again as a genus based on morphological characters (Smith, 2001; Nienhuis, 2003). The first comprehensive phylogenetic study on margaritiferids, using nuclear and mitochondrial molecular data, associated *M. auricularia* with the North American *Margaritifera monodonta* (Huff *et al.*, 2004). However, this association was not well supported and the mitochondrial data alone presented an alternative pattern dividing both species into separate lineages. More recent molecular studies showed that although both *M. auricularia* and the re-described North African *M. marocana* form a monophyletic clade (Araujo *et al.*, 2009c), the use of *Pseudunio* as either a genus or subgenus is not supported (Araujo *et al.*, 2009a).

(b) Family Unionidae Rafinesque 1820

The family Unionidae is represented in Europe by two subfamilies: Unioninae and Gonideinae (Graf & Cummings, 2015). Within the Unioninae, the European species are divided into two tribes: (i) the Anodontini, including two *Anodonta* species and *Pseudanodonta complanata* (Rossmässler 1835) and (ii) the Unionini, which comprises all *Unio* species. In the Gonideinae, two species are recognized: *Potomida littoralis* (Cuvier 1798) and *Microcondylaea bonellii* (A. Ferussac 1827), both restricted to southern Europe. Although preliminary molecular data support their presence in Gonideinae (E. Froufe & M. Lopes-Lima, unpublished data), the monophyly of this subfamily remains

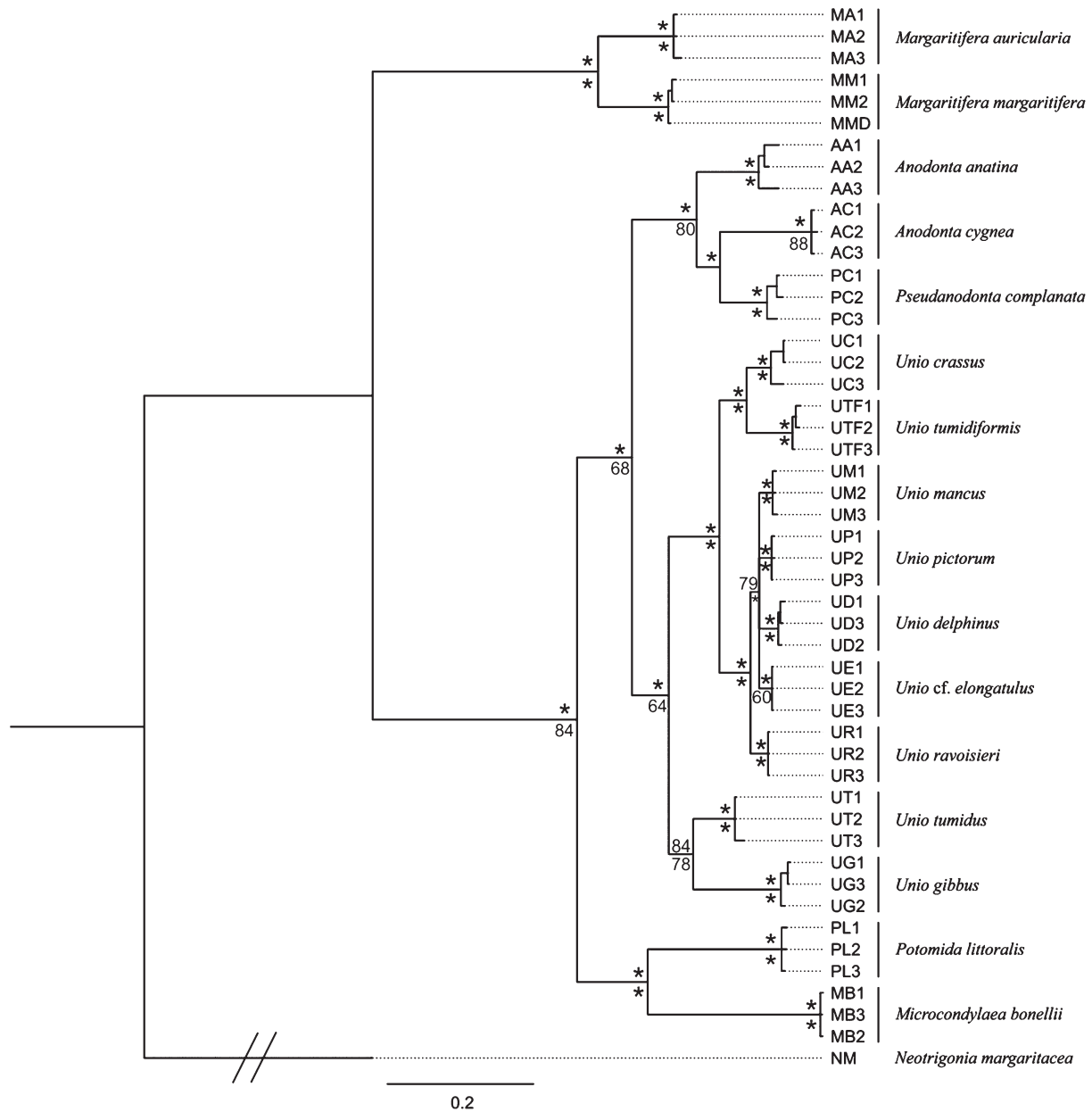


Fig. 1. Phylogenetic tree obtained by Bayesian inference analysis using the GTR + I + G model and maximum likelihood (ML) using the TPM2uf + I + G model of the combined mtDNA fragments [cytochrome oxidase subunit I (COI) and 16S]. Support values are given as Bayesian posterior probability above nodes and as bootstrap support below nodes, except for those with values below 50 and within the species level, which have been omitted for clarity. Values above 90 are represented by *. The tree topologies resulting from ML and BI approaches were congruent. The tree was rooted with *Neotrigonia margaritacea*. See Appendix S1 and Table S1 for available sequences downloaded from GenBank and new sequence codes.

uncertain and further studies are needed to clarify their status.

(i) *Sub-family Unioninae Rafinesque 1820. Tribe Anodontini Rafinesque 1820.* The number of *Anodonta* species in Europe was unclear and their taxonomy in disarray until the middle of the 20th century when all species were merged into the single taxon *Anodonta cygnea* (Linnaeus 1758) (Haas, 1969). Since then, an additional species, *Anodonta anatina* (Linnaeus 1758), is recognized (Fig. 1; Nagel, Badino & Celebrano,

1998; Araujo *et al.*, 2009a). The high plasticity (Zieritz & Aldridge, 2011) and similarity of some morphotypes can make visual distinction between *Anodonta* species extremely difficult, with molecular identification keys producing more reliable results (Källersjö *et al.*, 2005; Zieritz *et al.*, 2012). A study of the cytochrome oxidase I (COI) mitochondrial gene of Anodontini from across Europe identified three clades of *A. anatina*, but recognised only two species (*A. anatina* and *A. cygnea*; Froufe *et al.*, 2014). Nagel, Badino

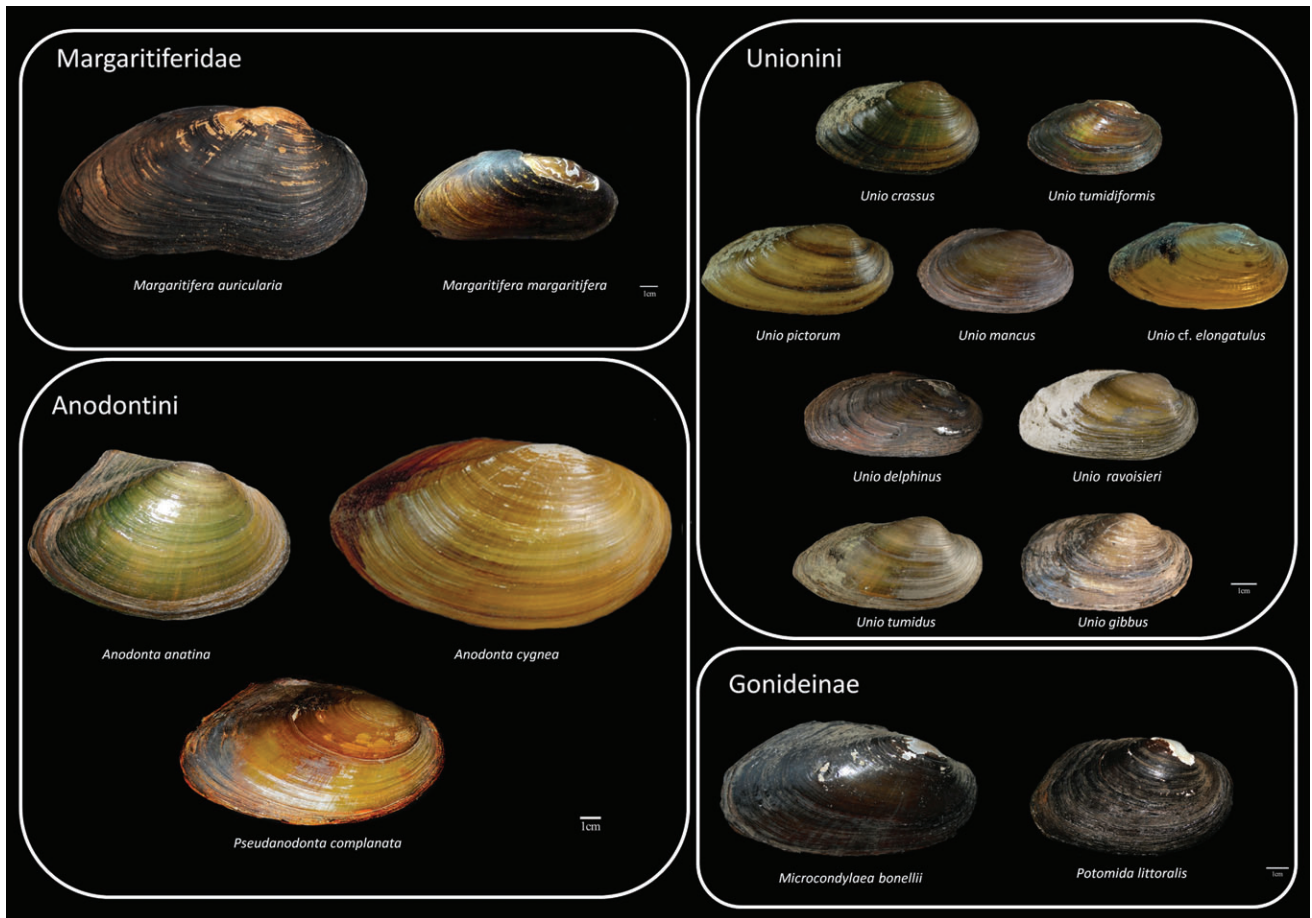


Fig. 2. Shells of representative freshwater mussel taxa in Europe.

& Alessandria (1996) suggested that some populations of *Anodonta* in Italy and Switzerland belong to one or two additional lineages and this warrants further investigation; however, no *Anodonta* subspecies are currently accepted.

The phylogeny and taxonomy of *P. complanata* remains unresolved. Some studies recognize three geographically separated species in Europe: *P. complanata*; *P. elongata* Holandre 1836 and *P. middendorffi* (Siemaschko 1849), the latter comprising two subspecies (Haas, 1969; Araujo & de Jong, 2015). Additional *Pseudanodonta* taxa are also included in other regional checklists (e.g. Kantor *et al.*, 2010). However, *Pseudanodonta* has not been subject to rigorous genetic studies across its distribution, and its taxonomic status is unclear. Because these issues are unresolved we follow traditional usage and recognize *Pseudanodonta* as containing a single species, *P. complanata* (e.g. Graf, 2007; Skidmore *et al.*, 2010).

Tribe Unionini Rafinesque 1820. The genus *Unio* in Europe is divided into four main lineages: *crassus*, *pictorum*, *tumidus* and *gibbus* (Table 1; Fig. 1). This division is based on the most recent molecular data (Araujo *et al.*, 2009a; Reis & Araujo, 2009; Khalloufi *et al.*, 2011; Prié *et al.*, 2012; Prié & Puillandre, 2014) although further research is needed to enlighten inter- and intraspecific relationships.

U. crassus lineage – the *crassus* lineage was recently divided into two species, *U. crassus* and *Unio tumidiformis* Castro 1885 (Reis & Araujo, 2009). Within *U. crassus sensu stricto*, several subspecies have been recognized (e.g. Haas, 1969; Kantor *et al.*, 2010; Araujo & de Jong, 2015), but the validity of most is unknown (see Table 1). *Unio c. courtillieri* was recently confirmed as a distinct lineage based on 16S and COI gene fragments (Prié & Puillandre, 2014). In this study, we recognize only *U. tumidiformis* and two subspecies within *U. crassus*, *U. c. crassus* and *U. c. courtillieri*, but other previously described subspecies deserve further attention (see Table 1).

U. pictorum lineage – over the last decade, the *pictorum* lineage has been divided into *Unio pictorum* (Linnaeus 1758), *Unio mancus* Lamarck 1819, *Unio delphinus* Spengler 1793, and *Unio ravoisieri* Deshayes 1848 (Araujo, Gómez & Machordom, 2005; Araujo *et al.*, 2009b; Khalloufi *et al.*, 2011; Reis, Machordom & Araujo, 2013). In addition, a number of subspecies have been described (Haas, 1969; Araujo & de Jong, 2015), but the validity of most remains uncertain (e.g. Prié & Puillandre, 2014). Despite the nomenclatural priority of *mancus* over *elongatulus*, some authors have not considered *U. mancus* as a valid species (e.g. Haas, 1969). Instead, they have placed *U. mancus* under the name *U. elongatulus*

Table 1. Checklist of European freshwater mussel species (Unionida Grey 1854)

	Falkner, Bank & Von Proschwitz (2001)	Araujo & de Jong (2015)	This study
Genus <i>Margaritifera</i> Schumacher 1816			
Haas (1969)			
<i>M. margaritifera</i> Linnaeus 1758	<i>M. margaritifera</i>	<i>M. margaritifera</i>	<i>M. margaritifera</i>
<i>M. margaritifera margaritifera</i> (Linnaeus 1758)	<i>M. m. brunnea</i> (Bonhomme 1840) <i>M. m. durrovensis</i> Phillips 1928 <i>M. m. parvula</i> (F. Haas 1908)		
<i>M. auricularia auricularia</i> (Spengler 1793)	<i>Pseudunio auricularius auricularius</i>	<i>M. auricularia</i>	<i>M. auricularia</i>
Genus <i>Anodonta</i> Lamarck 1799			
Haas (1969)			
<i>A. cygnea</i> Linnaeus 1758	Falkner <i>et al.</i> (2001)	Araujo & de Jong (2015)	This study
	<i>A. a. anatina</i> <i>A. a. attenuata</i> Held 1836 <i>A. a. radiata</i> (O. F. Müller 1774) <i>A. a. rostrata</i> Rossmässler 1836	<i>A. anatina</i>	<i>A. anatina</i>
	<i>A. c. cygnea</i> <i>A. c. deplanata</i> M. von Gallenstein 1852 <i>A. c. sokaris</i> Held 1839	<i>A. cygnea</i>	<i>A. cygnea</i>
Genus <i>Pseudanodonta</i> Bourguignat 1877			
Haas (1969)			
<i>P. complanata</i> (Rossmässler 1835)	Falkner <i>et al.</i> (2001)	Araujo & de Jong (2015)	This study
	<i>P. c. complanata</i> <i>P. c. dorsuosa</i> (Drouët 1881) <i>P. c. graptopæana</i> (Gassies 1849) <i>P. c. kletti</i> (Rossmässler 1835) <i>P. c. kuesteri</i> F. Haas 1913 <i>P. c. ligurica</i> Bourguignat 1880 <i>P. c. elongata</i>	<i>P. complanata</i>	<i>P. complanata</i>
<i>P. elongata</i> (Holandre 1836)		<i>P. elongata</i>	<i>P. elongata</i> ?
<i>P. middendorffi middendorffi</i> (Siemaszko 1849)		<i>P. m. middendorffi</i>	<i>P. m. middendorffi</i> ?
<i>P. middendorffi compacta</i> (Zelebor 1851)		<i>P. m. compacta</i>	<i>P. m. compacta</i> ?
Genus <i>Unio</i> Philipsson 1788			
Haas (1969)			
<i>U. crassus crassus</i> Philipsson 1788	Falkner <i>et al.</i> (2001)	Araujo & de Jong (2015)	This study
	<i>U. c. crassus</i> <i>U. c. riparius</i> C. Pfeiffer 1821	<i>U. c. crassus</i>	<i>U. c. crassus</i>
<i>U. c. bruguierianus</i> Bourguignat 1853		<i>U. c. bruguierianus</i>	<i>U. c. bruguierianus</i> ?
<i>U. c. carneus</i> Kuster 1854		<i>U. c. carneus</i>	<i>U. c. carneus</i> ?
<i>U. c. cytherea</i> Kuster 1833	<i>U. c. cytherea</i> <i>U. c. decuratus</i> Rossmässler 1835 <i>U. c. ondovensis</i> Hazay 1885	<i>U. c. cytherea</i>	<i>U. c. cytherea</i> ?
<i>U. c. gontieri</i> Bourguignat 1856		<i>U. c. jonicas</i>	<i>U. c. gontieri</i> ?
<i>U. c. jonicas</i> Drouët 1879		<i>U. c. batavus</i>	<i>U. c. jonicas</i> ?
<i>U. c. batavus</i> (Maton & Rackett 1807)	<i>U. c. albensis</i> Hazay 1885 <i>U. c. courtillieri</i> Hattemann 1859	<i>U. c. batavus</i>	<i>U. c. batavus</i> ?
<i>U. pictorum pictorum</i> (Linnaeus 1758)	<i>U. p. pictorum</i> <i>U. p. deshayesi</i> Michaud 1831 <i>U. p. tistanus</i> Nescmann 1993	<i>U. tumidiformis</i> Castro 1885 <i>U. p. pictorum</i>	<i>U. c. courtillieri</i> <i>U. tumidiformis</i>
			<i>U. p. pictorum</i>

crassus
lineage

Table 1. Continued

<i>U. p. gaudioni</i> Drouet 1881	<i>U. p. latirostris</i>	<i>U. p. gaudioni</i>	<i>U. p. gaudioni</i> ?
<i>U. p. latirostris</i> Kuster 1854		<i>U. p. latirostris</i>	<i>U. p. latirostris</i> ?
<i>U. p. platyrhynchoideus</i> Dupuy 1849	<i>U. p. platyrhynchus</i>	<i>U. p. platyrhynchoideus</i>	<i>U. p. platyrhynchoideus</i> ?
<i>U. p. platyrhynchus</i> Rossmässler 1835		<i>U. p. platyrhynchus</i>	<i>U. p. platyrhynchus</i> ?
<i>U. p. praeposterus</i> Kuster 1854		<i>U. p. praeposterus</i>	<i>U. p. praeposterus</i> ?
<i>U. p. proechistus</i> Bourguignat 1870		<i>U. p. proechistus</i>	<i>U. p. proechistus</i> ?
<i>U. p. rostratus</i> Lamarck 1819	<i>U. p. rostratus</i>	<i>U. p. rostratus</i>	<i>U. p. rostratus</i> ?
<i>U. p. schrenkianus</i> Clessin 1880		<i>U. p. schrenkianus</i>	<i>U. p. schrenkianus</i> ?
<i>U. p. delphinus</i> Spengler 1793		<i>U. delphinus</i>	<i>U. delphinus</i>
<i>U. p. mucidus</i> Morelet 1845			
<i>U. e. penchinatianus</i> Bourguignat 1865		<i>U. e. penchinatianus</i>	<i>U. ravoisieri</i>
<i>Unio elongatulus elongatulus</i> C. Piciffier 1825		<i>U. e. elongatulus</i>	<i>U. cf. elongatulus</i>
<i>U. e. glaucinus</i> Porro 1838	<i>U. m. glaucinus</i>	<i>U. e. glaucinus</i>	
<i>U. e. laevyanus</i> Gentiluomo 1868		<i>U. e. laevyanus</i>	
<i>U. e. mancus</i> Lamarck 1819	<i>Unio mancus mancus</i>	<i>U. mancus</i>	
<i>U. e. aleronii</i> Companyo & Massot 1845	<i>U. m. aleronii</i>		
<i>U. e. valentinus</i> Rossmässler 1854			
<i>U. e. bourgeticus</i> Bourguignat 1882	<i>U. m. bourgeticus</i>	<i>U. e. bourgeticus</i>	<i>U. m. mancus</i>
<i>U. e. moquintanus</i> Dupuy 1843	<i>U. m. moquintanus</i>	<i>U. e. moquintanus</i>	
<i>U. e. rousii</i> Dupuy 1849	<i>U. m. rousii</i>	<i>U. e. rousii</i>	
<i>U. e. gargottae</i> Philippi 1836	<i>U. m. brindosianus</i> De Folin & Bérillon 1874		
<i>U. e. pallens</i> Rossmässler 1842		<i>U. e. gargottae</i>	<i>U. e. gargottae</i> ?
<i>U. e. requienii</i> Michaud 1831		<i>U. e. pallens</i>	<i>U. e. pallens</i> ?
<i>U. e. turtonii</i> Payraudeau 1826		<i>U. e. requienii</i>	<i>U. m. requienii</i>
		<i>U. e. turtonii</i>	<i>U. m. turtonii</i>
<i>Unio tumidus tumidus</i> (Philipsson 1788)	<i>Unio t. tumidus</i>	<i>U. t. tumidus</i>	<i>U. t. tumidus</i>
	<i>U. t. depressus</i> (Donovan 1802)		
	<i>U. t. vincelus</i> De Joannis 1859		
	<i>U. t. godetianus</i> Clessin 1890		<i>U. t. godetianus</i> ?
	<i>U. t. zelebori</i> Zelebor 1851		<i>U. t. zelebori</i> ?
<i>U. t. borysthensis</i> Kobelt 1879		<i>U. t. borysthensis</i>	<i>U. t. borysthensis</i> ?
		<i>Unio gibbus</i> Spengler 1793	<i>Unio gibbus</i>
Genus <i>Potomida</i> Swainson 1840			
Haas (1969)	Falkner et al. (2001)	Araujo & de Jong (2015)	This study
<i>Potomida littoralis littoralis</i> (Cuvier 1798)	<i>Potomida l. littoralis</i>	<i>P. littoralis</i>	<i>P. l. littoralis</i>
	<i>Potomida l. cuneata</i> (Jacquemin 1835)		
	<i>Potomida l. pianensis</i> (Boubee 1833)		
<i>Potomida l. umbonata</i> (Rossmässler 1844)			<i>P. l. acarnanica</i> ?
<i>Potomida l. acarnanica</i> (Kobelt 1879)			
Genus <i>Microcondylaea</i> Vest 1866			
Haas (1969)	Falkner et al. (2001)	Araujo & de Jong (2015)	This study
<i>Microcondylaea compressa</i> (Menke 1828)	<i>M. bonellii</i> (A. Ferrussac 1827)	<i>M. compressa</i>	<i>M. bonellii</i>

(Haas, 1969). However, in recent years these lineages have been consensually reassigned to *U. mancus* (Araujo *et al.*, 2005; Prié *et al.*, 2012). Recent molecular studies revealed three genetically distinct subspecies within *U. mancus* in Spain and France: *U. m. mancus*, *U. m. requienii*, and *U. m. turtonii* (Araujo *et al.*, 2005; Prié *et al.*, 2012). Additionally, a population from northern Italy is genetically divergent from French and Spanish *U. mancus* and is referred to as *Unio* cf. *elongatulus* following Prié & Puillandre (2014). The status of two previously described subspecies of the *elongatulus/mancus* complex, *U. e. gargottae* and *U. e. pallens*, still need validation.

The species *U. ravoisieri* and *U. delphinus* were once included within *U. elongatulus* and *U. pictorum*, respectively (Haas, 1969). Both species were recently shown to be distinct, based on molecular, reproductive and morphological characters (Araujo *et al.*, 2009a; Khalloufi *et al.*, 2011). Within the *U. pictorum* lineage we recognise five species: *U. pictorum*, *U. delphinus*, *U. ravoisieri*, *U. cf. elongatulus* and *U. mancus* with three subspecies: *U. m. mancus*, *U. m. requienii*, and *U. m. turtonii* (Table 1).

U. tumidus lineage – relatively little attention has been paid to *U. tumidus* Philipsson 1788. Although subspecies have been described, recent molecular assessment of material from France did not support the assignment of any subspecies (Prié & Puillandre, 2014; Table 1).

U. gibbus lineage – in Europe, this lineage includes only *U. gibbus* Spengler 1793, based on morphological, reproductive, and molecular characters (Araujo *et al.*, 2009b).

(ii) *Sub-family Gonideinae* Ortmann 1916. *Microcondylaea bonellii* (A. Ferussac 1827) and *Potomida littoralis* (Cuvier 1798) were previously assigned to the North American subfamilies Amblesinae (Nagel *et al.*, 1998) and Quadrulinae (Haas, 1940, 1969), respectively. Both species were later considered as *incertae sedis* (Graf & Cummings, 2007). Subsequent studies placed them in the Gonideinae (Whelan, Geneva & Graf, 2011), despite a lack of unequivocal support for the monophyly of the subfamily. In this study, both species are provisionally considered as part of the Gonideinae. In the present study, newly sequenced individuals associate *M. bonellii* with *P. littoralis* within the European Unionida (Fig. 1; see online Appendix S1).

P. littoralis was formerly divided into several subspecies, but molecular studies covering the Iberian Peninsula and France have detected no valid subspecies within this region (Araujo *et al.*, 2009a). Populations of *P. littoralis* in Greece and Turkey show considerable isolation and are worthy of further taxonomic evaluation (Reis *et al.*, 2013). However, based on the current evidence we recognize no subspecies under *P. littoralis*.

Very low genetic diversity was detected for *M. bonellii* populations from Italy using allozymes (Nagel & Badino, 2001), but more research is needed from across its distribution to understand better the phylogeography of this species.

(3) Distribution

Data on the distribution of European freshwater mussels were derived from published distribution data, supplemented with information from the most recent surveys performed by the authors of this review (Figs 3–6; see online Appendix S2). For many European regions, there is a paucity of detailed surveys, and even scarcer are studies addressing possible changes in density, biomass or spatial distributions over time. There are also considerable differences in data quality and quantity across regions, with much more information available for France, Germany, Great Britain, Iberia and Scandinavia than for the Balkans and Eastern Europe. There is also an imbalance in data available for different species, with considerable detail on *M. margaritifera*, *M. auricularia* and *U. crassus*, but relatively little information for *P. complanata*, *M. bonellii* and *U. cf. elongatulus*.

Highest species richness *per* basin is found in central, northern, and eastern Europe (Fig. 7), but the freshwater mussel fauna of these regions is relatively homogeneous. By contrast, southern Europe is characterized by lower species richness *per* basin but a higher number of distribution-restricted species (e.g. *M. bonellii* and *U. tumidiformis*).

(a) Family Margaritiferidae

The genus *Margaritifera* is distributed discontinuously across Europe. The holarctic *M. margaritifera* has a wide distribution (Araujo & Ramos, 2001; Young, Cosgrove & Hastie, 2001; Geist, 2010) occurring in oligotrophic streams in northern and central Europe from the British Isles in the west to Norway in the north and northern Russia in the east. The species extends southwest to the northern Iberian Peninsula where it is found in the north-western Atlantic rivers (Fig. 3). While *M. margaritifera* is still found in most of its historical distribution, the species has disappeared from many streams and is now probably extinct in Belarus, Denmark, Lithuania, and Poland (Cuttelod, Seddon & Neubert, 2011). *M. auricularia* was once widespread in western Europe. Ninetieth century historical records exist from the Iberian Peninsula to France, and the Po basin in Italy, but since the 20th century its distribution has been restricted to south-western France and the Ebro basin in Spain (Smith, 2001) (Fig. 3).

(b) Family Unionidae

The family Unionidae is present in all European countries including UK and Ireland (Haas, 1969).

(i) *Anodontini*. The two *Anodonta* species are distributed widely from the UK in the west to Russia in the east (Fig. 4A, B) and occur in all southern European countries. However, *A. anatina* has a much wider distribution than *A. cygnea* and can occupy a wider variety of habitats. *P. complanata* is present in most of northern and central Europe from the UK in the west to Russia in the east, but is not known from southern Europe (Fig. 4C).

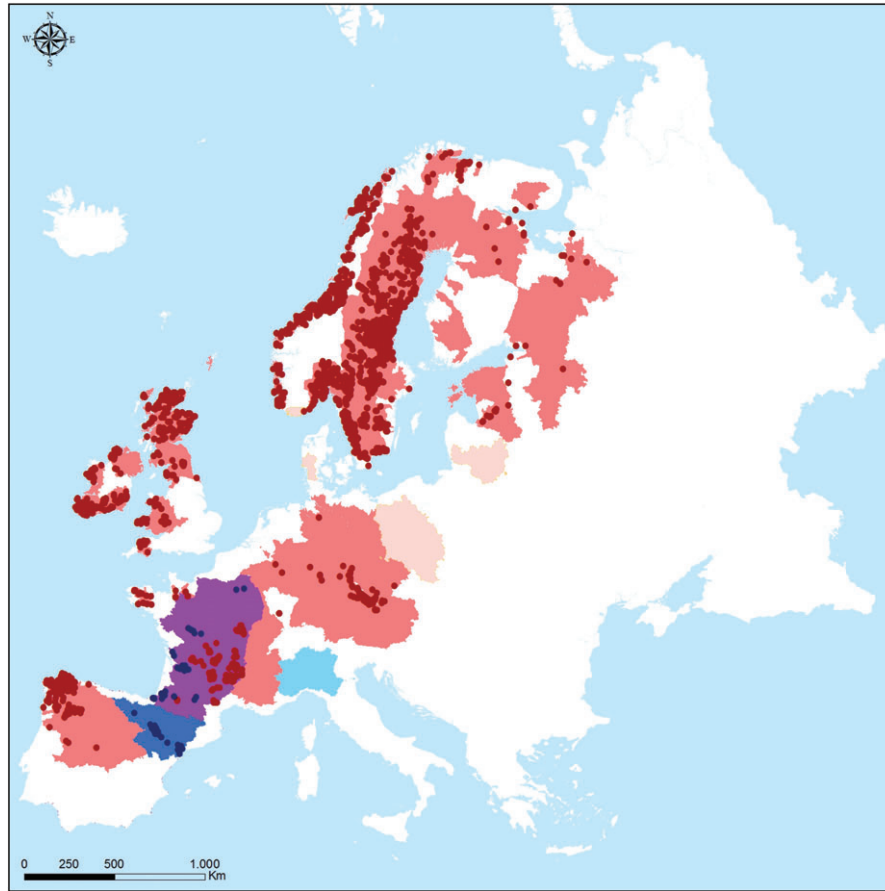


Fig. 3. Distribution of Margaritiferidae in Europe. Light shades correspond to historical distribution in hydrographical basins (prior to 1992), dark shades correspond to present distribution in hydrographical basins (after 1992) and dots represent present known populations (after 1992). Known distribution of *Margaritifera auricularia* (blue), *M. margaritifera* (red), and both (purple). Distribution data are based on recent surveys performed by the authors of this review and published distributions (see online Appendix S2).

(ii) *Unionini*. The genus *Unio* is present in all European countries. *U. crassus* is widely distributed in central, south-eastern and northern Europe from France in the west to Russia in the east (Fig. 5A). *U. tumidiformis* is present only in the south-west of the Iberian Peninsula (Fig. 5A). In the *pictorum* lineage, *U. pictorum* is the most widespread, being distributed in central, south-eastern and northern Europe from the British Isles in the west to Russia in the east (Fig. 5B). *U. delphinus* and *U. ravoisieri* are restricted to different regions of the Iberian Peninsula, with *U. delphinus* present in western Iberia and *U. ravoisieri* known from just two locations (River Ser and Lake Banyolas) in Catalonia (Araujo *et al.*, 2009a) (Fig. 5C). *U. mancus* is present in Mediterranean Iberia, France (where it is possibly sympatric with *U. pictorum*), Italy and Croatia, where in the last two countries it may co-occur with *U. cf. elongatulus* (Fig. 5C). *U. tumidus* is also widespread with a distribution similar to *U. pictorum*, although *U. tumidus* has not been recorded from Ireland (Fig. 5D). *U. gibbus*, which is distributed through north-west Africa, was once widely present in southern Iberia but it is now restricted to the River Barbate near Cadiz in the south of Spain (Fig. 5D).

(iii) *Gonideinae*. The two Gonideinae, *M. bonellii* and *P. littoralis*, have an interesting and non-overlapping distribution in southern Europe (Fig. 6). *M. bonellii* is present from the Italian Peninsula to the Adriatic drainages of the Balkans. By contrast, *P. littoralis* has a disjunct distribution in south-western Europe including Iberia and France to Greece and Turkey in the south-east, but eastern populations potentially represent a separate species (see Section II.2b.ii).

III. GENERAL BIOLOGY AND ECOLOGY

(1) Biology and life history

Freshwater mussels can be very long lived and possess a remarkable life history where the female mussel broods her eggs in a modified gill (the marsupium). Fertilization takes place across the gill surface with sperm entering the mantle cavity *via* the inhalant current. Fertilized eggs develop into a specialized larva (the glochidium), which must parasitize a host fish (or in rare cases other vertebrates) upon which it encysts and metamorphoses. This parasitic

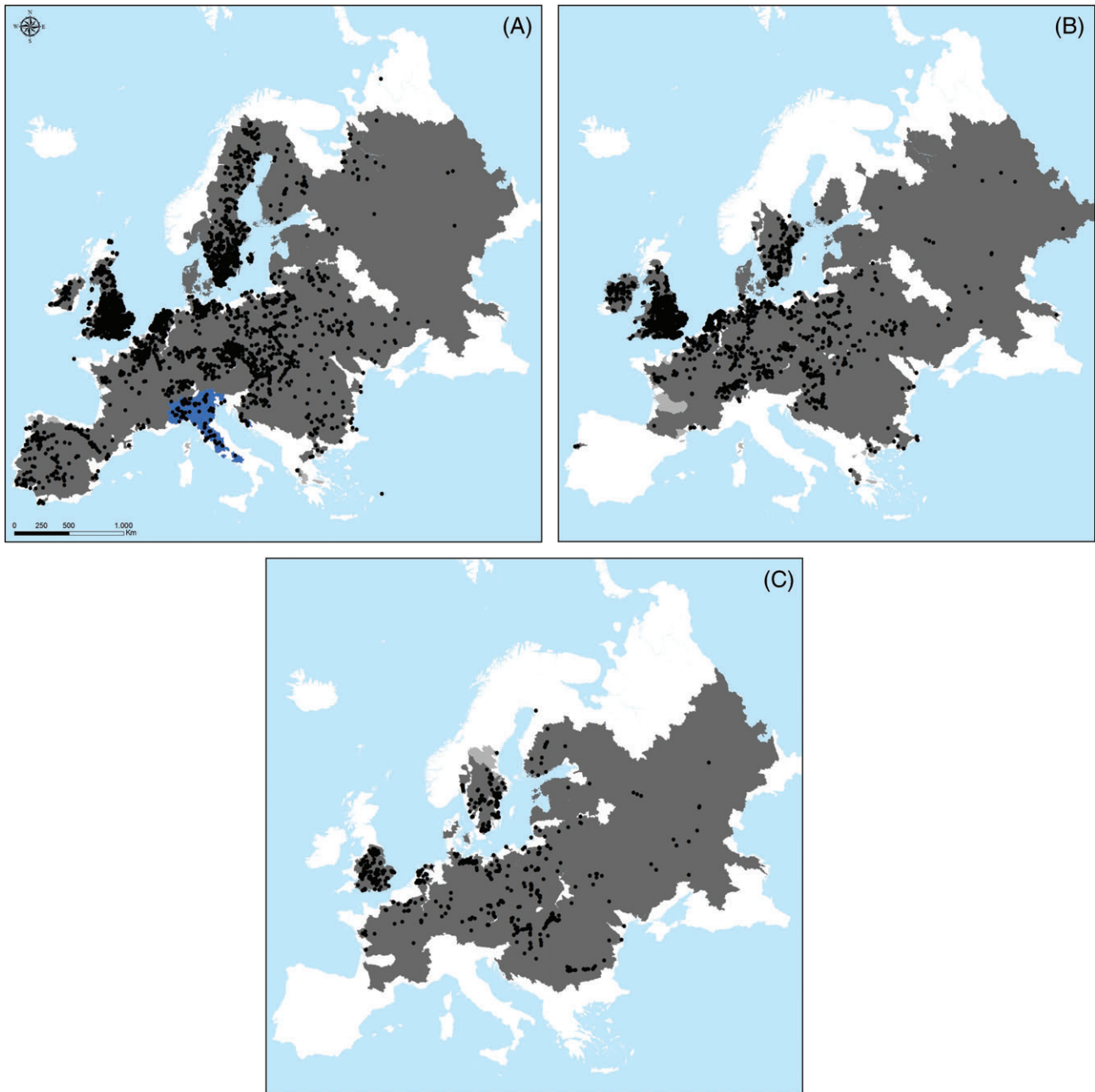


Fig. 4. Distribution of Anodontini in Europe. Light shades correspond to historical distribution in hydrographical river basins (prior to 1992), dark shades correspond to present distribution in hydrographical river basins (after 1992) and dots represent present known populations (after 1992). (A) Distribution of *Anodonta anatina* (grey) and *Anodonta* sp. (blue); (B) distribution of *A. cygnea*; (C) distribution of *Pseudanodonta complanata*. Distribution data are based on recent surveys performed by the authors of this review and published distributions (see online Appendix S2).

life stage may benefit the mussel through dispersal and provides a source of nutrients (Denic, Tæubert & Geist, 2015). The brooding behaviour and selectivity of hosts varies among mussel species. A summary of life-history traits is given in Table 2 (see also online Appendix S3). Information on host fishes is poorly known for most mussel species and local adaptations to specific host populations can occur (e.g. Tæubert *et al.*, 2010, 2012b; Karlsson *et al.*, 2014).

(a) Margaritiferidae

Margaritiferids typically live for more than 80 years, reaching reproductive maturity at approximately 10 years of age (Table 2). Both European margaritiferids are short-term brooders (tachytictic), incubating the brood for 5–7 weeks in the four gill demibranchs (tetrabranchy). *M. margaritifera* is generally considered to be dioecious (Ziuganov *et al.*, 1994)

Table 2. Summary of main biological traits of European freshwater mussels

	Max length (mm)	Lifespan (years)	Maturity (years)	Brooding period	Glochidia discharge	Host fish	References
<i>M. auricularia</i>							
West	N	N	N	N	N	N	Araujo & Ramos (2000), Araujo <i>et al.</i> (2000), Araujo, Bragado & Ramos (2001), Araujo, Cámara & Ramos (2002), Araujo, Quirós & Ramos (2003), Araujo <i>et al.</i> , 2009, R. Araujo ^U ; Grande <i>et al.</i> (2001) and Lopez <i>et al.</i> (2007)
South-west	170	80 ^U	>5 ^U	Feb–Mar	Feb–Mar	<i>Acipenser baerii</i> ; <i>Acipenser naccarii</i> ; <i>Acipenser sturio</i> ; <i>Gambusia holbrooki</i> ; <i>Salapia fluviatilis</i>	
<i>M. margaritifera</i>							
North	120–169 ^U	280	10–15	Jun–Oct	Aug–Oct	<i>Salmo salar</i> ; <i>Salmo trutta</i>	Dunca, Söderberg & Norrgrann (2011), Geist <i>et al.</i> (2006), B. Larsen ^U , Oulasvirta (2011) and Von Proschwitz, Lundberg & Bergengren (2006)
British Isles	110–160	100–120	12–15	Jul–Sep	Aug–Sep	<i>Salmo salar</i> ; <i>Salmo trutta</i>	Moorkens & Killen (2009)
West	91–120 ^U	50–80 ^U	N	Jun–Sep ^U	Jul–Aug ^U	<i>Salmo trutta fario</i> ^U	K. Groh ^U ; J. Jungbluth ^U ; G. Motte ^U ; F. Thielen ^U
Central	113–144	100	15–20	Jun–Aug	Aug–Sep	<i>Hucho hucho</i> [*] ; <i>Salmo trutta fario</i>	Bauer (1987, 1988, 1991), Beran (1998), Geist <i>et al.</i> (2006), Jung <i>et al.</i> (2013), Scheder, Gumpinger & Csar (2011) and Taubert <i>et al.</i> (2010)
East	110–149	70–130	12–20	Jun–Aug	Aug–Sep	<i>Salmo salar</i> ; <i>Salmo trutta</i>	Bespalya <i>et al.</i> (2007, 2012), Bolotov <i>et al.</i> (2012, 2013), Makhrov <i>et al.</i> (2014), Ostrovsky & Popov (2011) and Zauganov <i>et al.</i> (1994)
South-west	123	65	6–12	Jul–Oct	Sep–Oct	<i>Salmo salar</i> ; <i>Salmo trutta fario</i> ; <i>Salmo trutta trutta</i>	Araujo <i>et al.</i> (2009a), Lois <i>et al.</i> (2014), San Miguel <i>et al.</i> (2004) and Varandas <i>et al.</i> (2013)
<i>A. anatina</i>							
North	140–199 ^U	13–21 ^U	1–4	Jul–May	Mar–Jun	<i>Abramis brama</i> ; <i>Acerina cernua</i> ; <i>Blicca bjoerknae</i> ; <i>Cottus poeciliopus</i> ; <i>Esox lucius</i> ; <i>Gymnocephalus cernuus</i> ; <i>Lota lota</i> ; <i>Perca fluviatilis</i> ; <i>Phoxinus phoxinus</i> ; <i>Rutilus rutilus</i> ; <i>Salmo trutta</i> ^U	Haukioja & Hakala (1978), Jokela, Valtonen & Lappalainen (1991), B. Larsen ^U , Pekkarinen (1993), Rudzite <i>et al.</i> (2010), Taskinen, Mäkelä & Valtonen (1997), Taskinen & Valtonen (1995) and von Proschwitz <i>et al.</i> (2006)
British Isles	75–120	20–28	>2	Dec–Mar	N	N	Aldridge (1999) and Moorkens & Killen (2009)
West	96–113 ^U	8–13 ^U	N	N	N	<i>Gobio gobio</i> ^U	K. Groh & G. Weitmann ^U ; G. Motte ^U ; F. Thielen ^U
Central	80–163	10–15	>3	Jul–Apr ^U	Jan–Apr	<i>Abramis brama</i> ; <i>Abramis bjoerknae</i> ; <i>Anguilla anguilla</i> ; <i>Barbus barbus</i> ; <i>Cottus gobio</i> ; <i>Esox lucius</i> ; <i>Gasterosteus aculeatus</i> ; <i>Gobio gobio</i> ; <i>Leucaspis delinaeatus</i> ; <i>Leuciscus idus</i> ; <i>Leuciscus leuciscus</i> ; <i>Oncorhynchus mykiss</i> ; <i>Perca fluviatilis</i> ; <i>Phoxinus phoxinus</i> ; <i>Rhodeus amarus</i> ; <i>Rutilus rutilus</i> ; <i>Salmo trutta fario</i> ; <i>Sander lucioperca</i> ; <i>Scardinius erythrophthalmus</i> ; <i>Squalius cephalus</i> ; <i>Squalius leuciscus</i> ; <i>Tmea tinca</i> ; <i>Vimba vimba</i>	Abraszewska-Kowalczyk (2002), Beran (1998), Domagala (1998), Douda <i>et al.</i> (2013), K. Douda ^U , Niemeyer (1993), Ožgo & Abraszewska (2009) and Weber (2005)
East	99–150 ^U	17 ^U	2–3	Sep–Apr	May	<i>Gobio gobio</i> ; <i>Gymnocephalus cernua</i> ; <i>Leuciscus idus</i> ; <i>Perca fluviatilis</i>	Y. Beshpalaja ^U , Laenko (2012), T. Trichkova ^U and Zhadin (1952)

Table 2. Continued

	Max length (mm)	Life span (years)	Maturity (years)	Brooding period	Glochidia discharge	Host fish	References
South-west	180 ^U	15 ^U	> 4 ^U	Oct–Mar	March	<i>Achondrostoma oligolepis</i> ; <i>Luciobarbus bocagei</i> ; <i>Pseudochondrostoma duranense</i> ; <i>Squalius caroliterti</i> ; <i>Squalius alburnoides</i> ; <i>Salmo trutta fario</i>	R. Araujo ^U , Douđa et al. (2013), Hinzmann et al. (2013) and M. Lopes-Lima ^U
A. cygnea							
North	90–220	> 18	N	N	N	<i>Perca fluviatilis</i>	Rudzić et al. (2010) and von Proschwitz et al. (2006)
British Isles	140–200	20–37	> 2	Dec–Apr	N		Aldridge (1999) and Moorjens & Killen (2009)
West	138 ^U	9 ^U	N	N	N	<i>Gobio gobio</i> ^U	K. Groh & G. Weitmann ^U ; F. Thielen ^U
Central	120–260	15	> 2	Jul–Apr	Feb–Apr	<i>Abramis lyeorba</i> ; <i>Abramis brama</i> ; <i>Alburnus alburnus</i> ; <i>Barbus barbus</i> ; <i>Colinus gobio</i> ; <i>Esox lucius</i> ; <i>Gasterosteus aculeatus</i> ; <i>Gobio gobio</i> ; <i>Gymnocephalus cernuus</i> ; <i>Leuciscus idus</i> ; <i>Leuciscus leuciscus</i> ; <i>Oncorhynchus mykiss</i> ; <i>Perca fluviatilis</i> ; <i>Phoxinus phoxinus</i> ; <i>Rhodeus amarus</i> ; <i>Rutilus rutilus</i> ; <i>Salmo trutta fario</i> ; <i>Sander lucioperca</i> ; <i>Scardinius erythrophthalmus</i> ; <i>Squalius cephalus</i> ; <i>Squalius leuciscus</i> ; <i>Tinea tinca</i> ; <i>Vimba vimba</i>	Beran (1998), Claes (1987), Niemeyer (1993) and Weber (2005)
East	200–260 ^U	20	2–3	Sep–Apr	May	<i>Alburnus alburnus</i> ; <i>Leuciscus idus</i> ; <i>Perca fluviatilis</i>	Laenko (2012), T. Trichkova ^U and Zhadin (1952)
South-west	180	N	N	Oct–Mar	March ^U	<i>Achondrostoma oligolepis</i> ; <i>Alburnus alburnus</i> ; <i>Anguilla anguilla</i> ; <i>Cobitis calderoni</i> ; <i>Cobitis paludica</i> ; <i>Cyprinus carpio</i> ; <i>Esox lucius</i> ; <i>Gambusia holbrooki</i> ; <i>Lepomis gibbosus</i> ; <i>Luciobarbus bocagei</i> ; <i>Micropterus salmoides</i> ; <i>Pseudochondrostoma duranense</i> ; <i>Salmo trutta fario</i> ; <i>Squalius alburnoides</i> ; <i>Squalius caroliterti</i>	Lima et al. (2012) and M. Lopes-Lima ^U
South-east	15 ^U	> 3 ^U	N	N	N	<i>Abramis brama</i> ^U ; <i>Barbus barbus</i> ^U ; <i>Cyprinus carpio</i> ^U ; <i>Carassius gibelio</i> ^U ; <i>Leuciscus cephalus</i> ^U ; <i>Salmo trutta</i> ^U	M. Paunovic ^U
P. complanata							
North	80–111	10–32	2–3	Jul–May	May–Jun		Pekkarinen (1993), Rudzić et al. (2010) and Saarinen & Taskinen (2003)
British Isles	85–100	15	4	Sep–Apr	April		Aldridge (1999) and McKvor & Aldridge (2007)
West	N	N	N	N	N		Beran (1998) and Hüby (1988)
Central	77–98	8–15	N	N	N	<i>Gasterosteus aculeatus</i> ; <i>Perca fluviatilis</i> ; <i>Pungitius pungitius</i> ; <i>Salmo trutta fario</i> ; <i>Sander lucioperca</i>	Drensky (1947), Melnychenko, Janovich & Kornushin (2001) and Zhadin (1952)
East	70–100	N	2–3	Aug–May	Jun	<i>Leuciscus idus</i> ; <i>Perca fluviatilis</i>	M. Paunovic ^U
South-east	N	15 ^U	> 3 ^U	N	N	<i>Abramis brama</i> ^U ; <i>Barbus barbus</i> ^U ; <i>Carassius gibelio</i> ^U ; <i>Cyprinus carpio</i> ^U ; <i>Leuciscus cephalus</i> ^U ; <i>Salmo trutta</i> ^U	E. Dunca ^U , Pekkarinen (1993), Rudzić et al. (2010) and von Proschwitz et al. (2006)
U. crassus							
North	50–110	50–90 ^U	N	Apr–Jul	Jun–Jul	<i>Alburnus alburnus</i> ; <i>Lota lota</i> ; <i>Rutilus rutilus</i>	K. Groh & G. Weitmann ^U ; G. Motte ^U ; F. Thielen ^U
West	48–99 ^U	9–27 ^U	> 4 ^U	Apr–Jul ^U	Apr–Jul ^U	<i>Cottus gobio</i> ^U ; <i>Phoxinus phoxinus</i> ^U ; <i>Squalius cephalus</i> ^U	Abraszewska-Kowalczyk (2002), Beran (1998), Douđa et al. (2012) and Tautbert et al. (2012a,b)
Central	79–95	8–50	> 2	Apr–Jul	Apr–Jul	<i>Alburnus alburnus</i> ; <i>Chondrostoma nasus</i> ; <i>Cottus gobio</i> ; <i>Gasterosteus aculeatus</i> ; <i>Gymnocephalus cernuus</i> ; <i>Leuciscus idus</i> ; <i>Leuciscus leuciscus</i> ; <i>Perca fluviatilis</i> ; <i>Phoxinus phoxinus</i> ; <i>Pseudorasbora parva</i> ; <i>Squalius cephalus</i> ; <i>Scardinius erythrophthalmus</i>	

Table 2. Continued

	Max length (mm)	Lifespan (years)	Maturity (years)	Brooding period	Glochidia discharge	Host fish	References
East	58–93	8–30	3–4	Apr–May	May–Jun	<i>Alburnus alburnus</i> ; <i>Gymnocephalus cernuus</i> ; <i>Perca fluviatilis</i> ; <i>Phoxinus phoxinus</i> ; <i>Rutilus rutilus</i> ; <i>Scardinius erythrophthalmus</i>	Laenko (2012)
South-east	N	N	N	N	N	N	
<i>U. delphinus</i>							
South-west	93	13 ^U	N	May–Jul	May–Jul ^U	<i>Achondrostoma oligolepis</i> ^U ; <i>Luciobarbus bocagei</i> ^U ; <i>Pseudochondrostoma durense</i> ^U ; <i>Sabno trutta fario</i> ^U ; <i>Squalius alburnoides</i> ^U ; <i>Squalius caroliterii</i> ^U	Araujo <i>et al.</i> (2009a) and M. Lopes-Lima ^U
<i>U. gibbus</i>							
South-west	N	N	N	Feb–Mar	Spring	N	Araujo <i>et al.</i> (2009b)
<i>U. mancus</i> /cf. <i>elongatulus</i>							
West	N	N	N	N	N	N	
South-west	N	N	>2 ^U	Spring	Apr–Aug	<i>Barbus haasi</i> ; <i>Luciobarbus gaelesi</i> ; <i>Parachondrostoma niégisi</i> ; <i>Phoxinus phoxinus</i> ; <i>Salaria fluviatilis</i> ; <i>Squalius cephalus</i> ; <i>Squalius pyrenaicus</i>	Araujo <i>et al.</i> (2005, 2009a) and R. Araujo ^U
South-central	114–117	20		Feb–Jul	Apr–Jul	<i>Ameiurus melas</i> ; <i>Barbus meridionalis</i> ; <i>Barbus plebejus</i> ; <i>Lepomis gibbosus</i> ; <i>Padogobius bonelli</i> ; <i>Squalius cephalus</i> ; <i>Scardinius erythrophthalmus</i> ; <i>Telestes souffia</i>	Castagnolo (1977) and Nagel & Castagnolo (1991)
South-east	N	N	N	N	N	N	
<i>U. pictorum</i>							
Northern	90–140	15–20	N	Apr–Jul	Jul–Aug	<i>Esox lucius</i> ; <i>Gymnocephalus cernuus</i> ; <i>Lota lota</i> ; <i>Perca fluviatilis</i> ; <i>Rutilus rutilus</i>	Pekkarinen (1993), Rudzite <i>et al.</i> (2010) and von Proschwitz <i>et al.</i> (2006)
British Isles	108–130	22	N	Apr–May	June	N	Aldridge (1999) and Aldridge & McIvor (2003)
West	100 ^U	N	N	N	N	N	K. Groh & G. Weitmann ^U
Central	76–130	5–15	N	Apr–Jul	Apr–Jul	<i>Carassius carassius</i> ; <i>Gasterosteus aculeatus</i> ; <i>Gobio gobio</i> ; <i>Perca fluviatilis</i> ; <i>Rutilus rutilus</i> ; <i>Scardinius erythrophthalmus</i> ; <i>Squalius cephalus</i> ; <i>Tinca tinca</i>	Abraszewska-Kowalczyk (2002), Beran (1998), Fleischauer-Rössing (1990), Ózgo & Abraszewska (2009) and Piechocki (1999)
East	90–137	7–15	2–3	Mar–Apr	May–Jul	<i>Abramis brama</i> ; <i>Esox lucius</i> ; <i>Gymnocephalus cernuus</i> ; <i>Perca fluviatilis</i> ; <i>Rutilus rutilus</i>	Drensky (1947); Rizhinashvili (2009); Zhadin (1952)
South-central	100 ^U	N	N	N	N	N	K. Nagel ^U
South-east	N	15 ^U	>3 ^U	N	N	<i>Abramis brama</i> ^U ; <i>Barbus barbus</i> ^U ; <i>Carassius gibelio</i> ^U ; <i>Chondrostoma nasus</i> ^U ; <i>Cyprinus carpio</i> ^U ; <i>Leuciscus cephalus</i> ^U ; <i>Rhodeus amarus</i> ^U ; <i>Sabno trutta</i> ^U ; <i>Vimba vimba</i> ^U	M. Paunovic ^U
<i>U. ravoisieri</i>							
South-west	N	N	N	Apr–Jul	May–Jul	<i>Barbus meridionalis</i> ^U ; <i>Squalius laietanus</i>	Araujo <i>et al.</i> (2009a) and R. Araujo ^U
<i>U. tumidiformis</i>							
South-west	57	7	>2	Mar–Aug	N	<i>Squalius alburnoides</i> ; <i>Squalius aradensis</i> ; <i>Squalius caroliterii</i> ; <i>Squalius pyrenaicus</i> ; <i>Squalius togalensis</i>	Araujo <i>et al.</i> (2009a), Reis & Araujo (2009) and Reis <i>et al.</i> (2014)
<i>U. tumidus</i>							
North	60–120	15–20	N	Apr–Jul	Jul–Aug	<i>Esox lucius</i> ; <i>Gymnocephalus cernuus</i> ; <i>Lota lota</i> ; <i>Perca fluviatilis</i> ; <i>Rutilus rutilus</i>	Pekkarinen (1993), Rudzite <i>et al.</i> (2010) and von Proschwitz <i>et al.</i> (2006)
British Isles	120	21	N	June	N	N	Aldridge (1999); Aldridge & McIvor (2003)

Table 2. Continued

	Max length (mm)	Lifespan (years)	Maturity (years)	Brooding period	Glochidia discharge	Host fish	References
West Central	75 ^U 90–120	N 5–15	N N	N Apr–Jul	N Apr–Jul	N <i>Gasterosteus aculeatus</i> ; <i>Gymnocephalus cernua</i> ; <i>Perca fluviatilis</i> ; <i>Rutilus rutilus</i> *; <i>Scardinius erythrophthalmus</i> *; <i>Tinca tinca</i>	K. Groh & G. Weitmann ^U Abraszewska-Kowalczyk (2002), Beran (1998), Flieschauer-Rössing (1990), Prechocki (1999) and Weber (2005)
East	80–104	9–16	2–3	Mar–Apr	May–Jul	<i>Abramis brama</i> ; <i>Esox lucius</i> ; <i>Gymnocephalus cernua</i> ; <i>Perca fluviatilis</i> ; <i>Rutilus rutilus</i>	Drensky (1947), Rizhinashvili (2009) and Zhadin (1952)
South-east	N	15 ^U	>3 ^U	N	N	<i>Abramis brama</i> ^U ; <i>Barbus barbus</i> ^U ; <i>Carassius gibelio</i> ^U ; <i>Chondrostoma nasus</i> ^U ; <i>Cyprinus carpio</i> ^U ; <i>Leuciscus cephalus</i> ^U ; <i>Rhodeus amarus</i> ^U ; <i>Salmo trutta</i> ^U ; <i>Vimba vimba</i> ^U	M. Paunovic ^U
M. bonellii							
South-central	100	> 10	N	Mar–Jun	Apr–Jun	N	Nagel <i>et al.</i> (2007)
South-east	N	N	N	N	N	N	
P. littoralis							
West	N	N	N	N	N	N	
South-west	90 ^U	15 ^U	>4 ^U	Mar–Oct	N	<i>Achondrostoma oligolepis</i> ^U ; <i>Luciobarbus bocagei</i> ^U ; <i>Pseudochondrostoma duriense</i> ^U ; <i>Salmo trutta fario</i> ^U ; <i>Squalius alburnoides</i> ^U ; <i>Squalius caroliteiri</i> ^U	R. Araujo ^U , Nagel (2004) and M. Lopes-Lima ^U
South-east	N	N	N	N	N	N	

N, no data; U, unpublished data; *, probable hosts. Biological data are based on unpublished studies by the authors of this review and on published information (see online Appendix S3). Host information is not comprehensive for each region and likely underestimates host breadth.

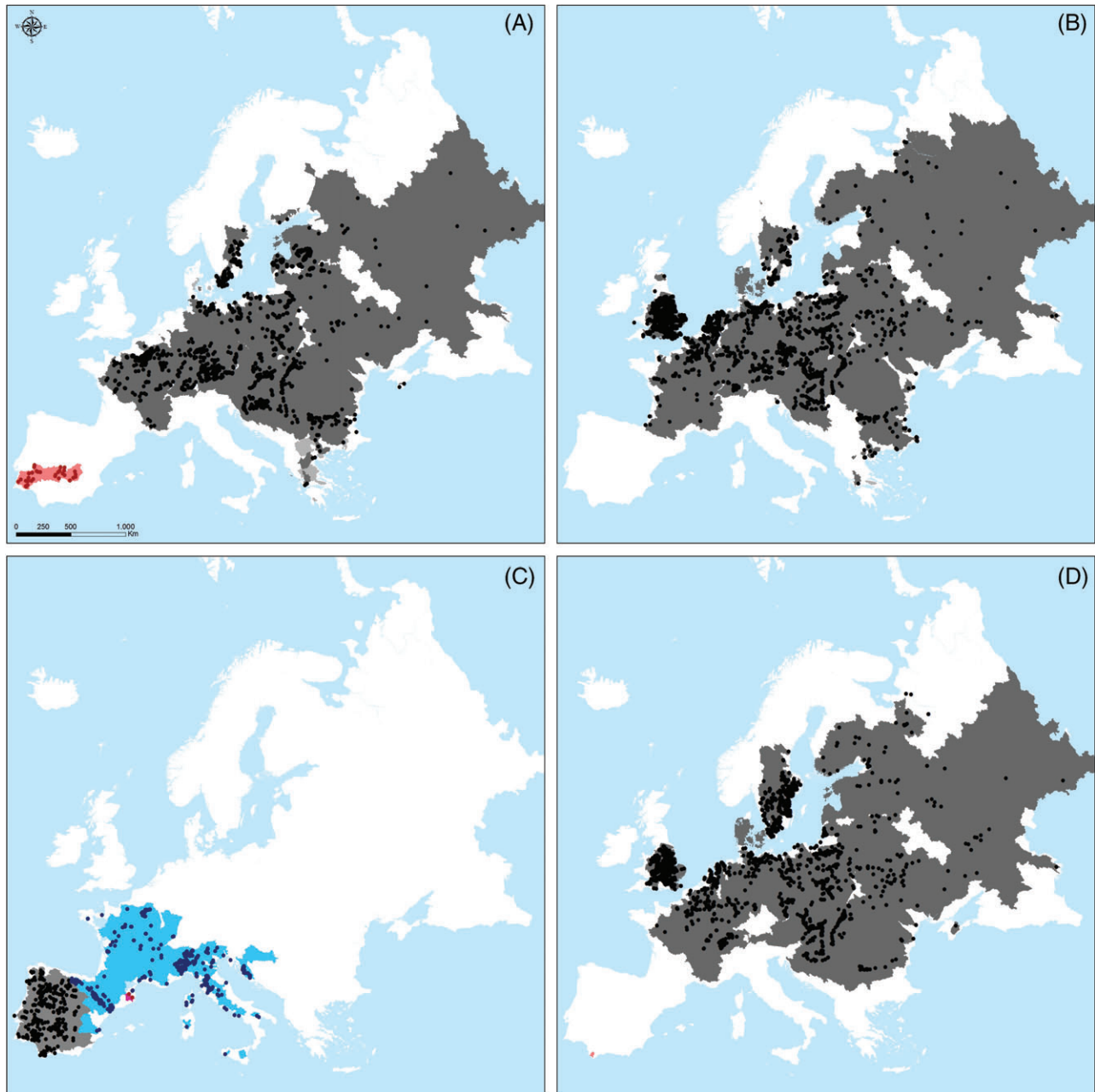


Fig. 5. Distribution of Unionini in Europe. Light shades correspond to historical distribution in hydrographical river basins (prior to 1992), dark shades correspond to present distribution in hydrographical river basins (after 1992) and dots represent present known populations (after 1992). (A) Distribution of *Unio crassus* (grey) and *U. tumidiformis* (red); (B) distribution of *U. pictorum*; (C) distribution of *U. manicus* + *U. cf. elongatulus* (blue), of *U. delphinus* (grey) and *U. ravoisieri* (red); (D) distribution of *U. tumidus* (grey) and *U. gibbus* (red). Distribution data are based on recent surveys performed by the authors of this review and published distributions (see online Appendix S2).

but females may switch to hermaphroditism at low population densities (Bauer, 1987). However, some high-density populations can comprise 100% hermaphrodites (Grande, Araujo & Ramos, 2001). Seventy per cent of the *M. auricularia* in the Canal Imperial, Ebro River basin, Spain, were hermaphroditic and 30% were females (Grande, Araujo & Ramos, 2001). The D-shaped, unhooked glochidia are

small (maximum lengths 45–70 μm for *M. margaritifera* and 127–144 μm for *M. auricularia*) (Araujo & Ramos, 1998) and are broadcast into the water column. Margaritiferid larvae grow on the host fish to an up to 10-fold size increase until metamorphosis is complete. *M. margaritifera* uses exclusively salmonid hosts (mainly *S. salar* and *S. trutta*) in Europe (Young, 1991; Geist, Porkka & Kuehn, 2006; Österling & Larsen,

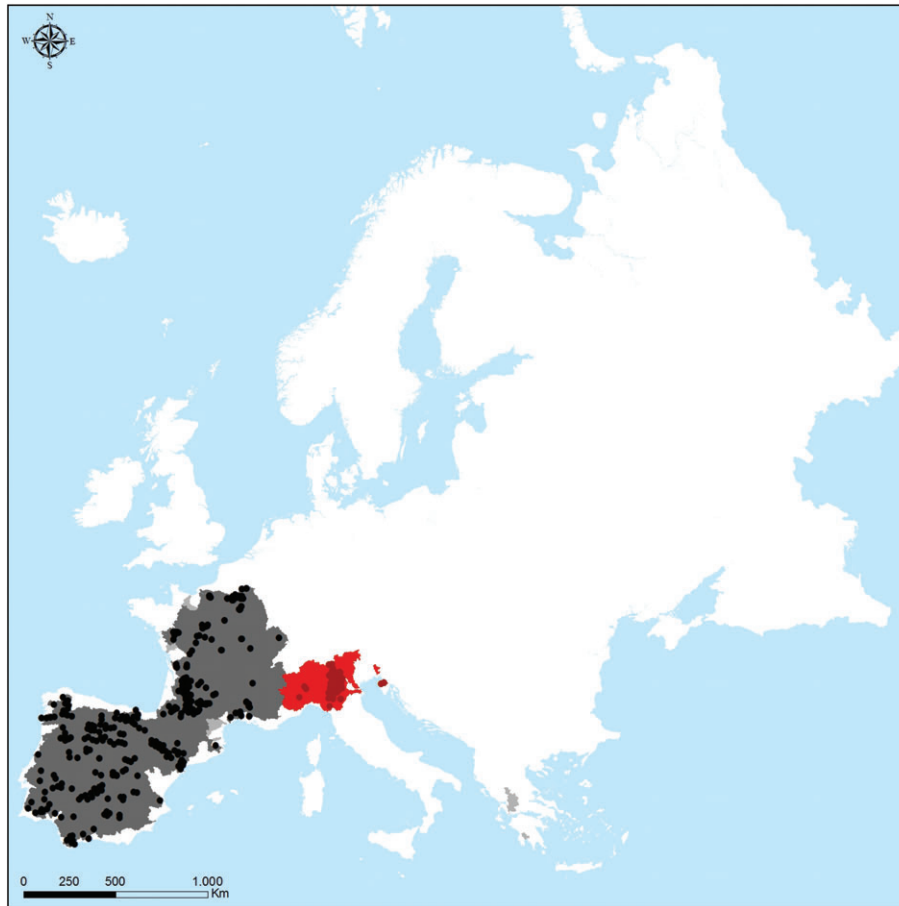


Fig. 6. Distribution of Gonideinae in Europe. Light shades correspond to historical distribution in hydrographical river basins (prior to 1992), dark shades correspond to present distribution in hydrographical river basins (after 1992) and dots represent present known populations (after 1992). Distribution of *P. littoralis* (grey), *M. bonellii* (red). Distribution data are based on recent surveys performed by the authors of this review and published distributions (see online Appendix S2).

2013), while *M. auricularia* uses European sturgeon (*Acipenser sturio*) and other Acipenseridae, Eastern mosquitofish (*Gambusia holbrooki*), and freshwater blenny (*Salaria fluviatilis*) (Table 2).

(b) Unionidae

(i) *Anodontini*. European Anodontini typically live for less than 30 years and are sexually mature at 1–4 years (Table 2). Both *Anodonta* species favour hermaphroditism in lentic habitats and gonochorism in lotic habitats (Hinzmann *et al.*, 2013). *P. complanata* is either completely or predominantly dioecious (McIvor & Aldridge, 2007). Both *Anodonta* species and *P. complanata* are long-term brooders (bradytictic), keeping the larvae over winter and releasing them from late winter/early spring through the summer. The marsupium is located solely in the outer gill demibranchs (ectobranchy) (Graf & Cummings, 2007; Hinzmann *et al.*, 2013). The glochidia of Anodontini are triangular, hooked and large (335–409 μm ; Aldridge & Horne, 1998; Wächter, Dreher-Mansur & Richter, 2001). Both *Anodonta* species and *P. complanata* are host generalists, metamorphosing on fish from a wide range of families (Table 2). Anodontines

release glochidia in mucous webs (Wood, 1974; Haag & Warren, 1997) and the release of glochidia by *A. anatina* can be stimulated by the presence of the fish host (Jokela & Palokangas, 1993).

(ii) *Unionini*. European unionines generally mature between 2 and 4 years of age and live less than 30 years, but longer lifespans have been recorded for countries at higher latitudes (Table 2). With the exception of some populations of *U. gibbus*, which brood glochidia in four gill demibranchs (Araujo *et al.*, 2009b), the *Unio* species are generally dioecious, ectobranchs, and short-term brooders, having the capacity to generate multiple broods each year generally in the spring and summer months (Aldridge, 1999; Bauer, 2001; Araujo *et al.*, 2009a). However, the reproductive cycles of many *Unio* species are poorly known. The larvae of *Unio* species are triangular, hooked (with the exception of *U. gibbus* which are unhooked) and intermediate in size (200–232 μm ; Wächter *et al.*, 2001). *U. crassus* exhibits an unusual host-infestation strategy in which females move to the shoreline and spurt water containing glochidia a short distance into the air; the resulting surface disturbance attracts host fishes (Vicentini, 2005). Glochidia are released in mucous webs by *U. pictorum*

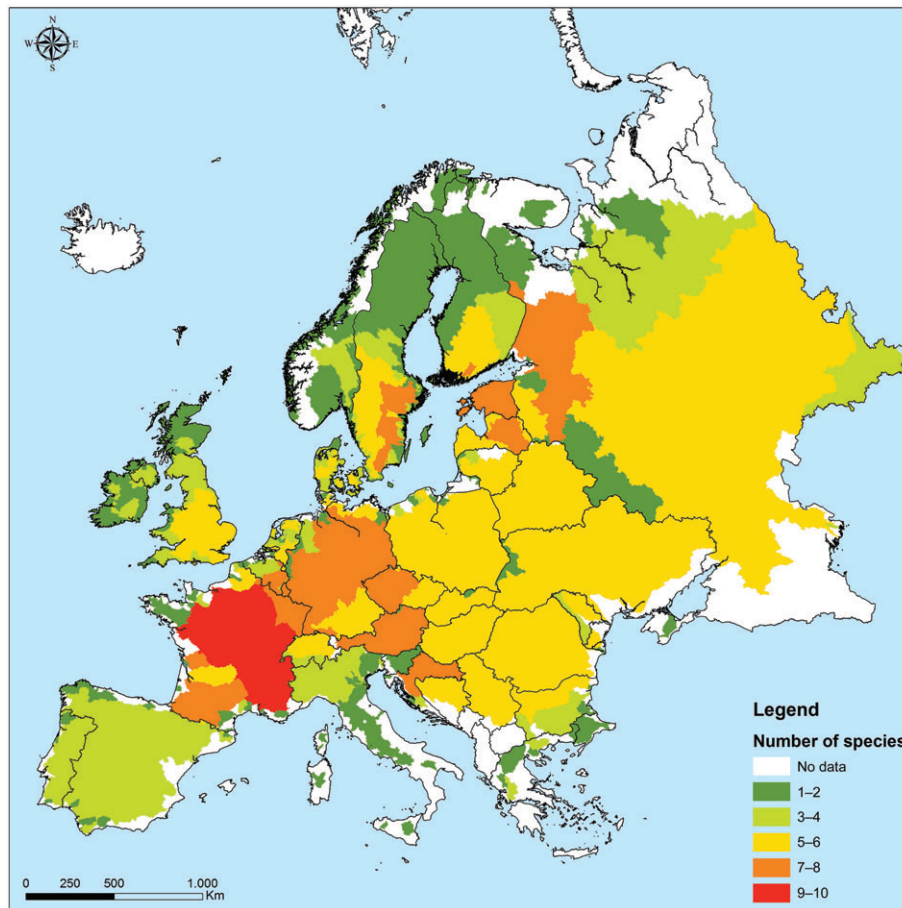


Fig. 7. Species richness of European freshwater mussel species in hydrographical river basins.

(Aldridge & McIvor, 2003). Many *Unio* species (including *U. crassus*, *U. pictorum* and *U. tumidus*) release conglomerates (packets of larvae). In North America, such conglomerates may mimic food items that serve to attract host fishes (Haag & Warren, 2003), but conglomerate release by European mussels likely reflects a response to stress (e.g. hypoxia) because conglomerates are always composed of immature larvae or eggs (e.g. Aldridge & McIvor, 2003; Gascho Landis *et al.*, 2012). *U. pictorum* and *U. tumidus* are able to use a wide range of host fishes (Table 2), while *U. tumidiformis* is a host specialist using only Iberian *Squalius* species (Reis & Araujo, 2009; Reis, Collares-Pereira & Araujo, 2014).

(iii) *Gonideinae*. The two *Gonideinae* genera are relatively poorly studied, but have been observed to live for >10 years. They brood larvae in both inner and outer demibranchs (tetrabranchy), are dioecious and probably short-term brooders (Nagel, 2004; Nagel *et al.*, 2007). The glochidia of both genera are elliptical and unhooked but larger in *P. littoralis* (~200 µm) than in *M. bonellii* (132–154 µm) (Araujo, Bragado & Ramos, 2000; Nagel *et al.*, 2007). The infestation strategy is unknown for *P. littoralis*. *M. bonellii* releases glochidia in worm-like conglomerates, unlike the conglomerates of *Unio*, those of *M. bonellii* are composed mostly of mature glochidia and appear to attract

fish hosts (Nagel *et al.*, 2007). *P. littoralis* uses a wide range of native fishes, while the hosts for *M. bonellii* remain unknown (Table 2).

(2) Ecology and habitat requirements

The forces that determine distributions of Unionida species can be best described by: (i) biogeographic history; (ii) host fish distribution; and (iii) local environment including biotic and abiotic factors (Vaughn & Taylor, 2000). First, in Europe, several biogeographic barriers exist which may explain the distribution of freshwater mussels. For example, the presence of the Alps and the Pyrenees can explain the isolation of several freshwater mussel species in the Italian and Iberian Peninsulas. Large-scale range expansions of freshwater mussels may be also the result of glacial and interglacial periods and river captures (Froufe *et al.*, 2014). Second, mussel distributions are determined to a large extent by the distribution of their host fishes. Species such as *M. auricularia*, that specialize on host fishes with constrained habitat requirements, typically have more restricted distributions than generalist mussel species such as many of the unionines and anodontines (Table 2). Third, at the local scale, habitat characteristics such as current velocity or water and sediment quality and biotic interactions

such as competition, predation, parasitism and facilitation are usually considered key aspects determining Unionida species composition, density and distribution (for a review, see Strayer, 2008).

Habitat preferences are quite distinct in both European Margaritiferidae species (Table 3; see online Appendix S4). *M. margaritifera* is a habitat specialist found mostly in cool upland streams with bedrock, cobble, and gravel substratum, moderate flow velocities, low nutrient concentrations and low carbonate content, with salmonid hosts being present (Geist, 2010). By contrast, the few remaining *M. auricularia* populations all occur in large rivers, and even in a canal, with warm temperatures, high conductivity and carbonate content, and outside typical habitat for salmonids (Araujo *et al.*, 2009a).

Similar diversity in habitat use is also seen in the Unionidae. While *P. complanata* generally prefers flowing rivers and streams, *A. cygnea* is typically associated with canals, eutrophic lakes and ponds where its thin shell allows it to float at the sediment–water interface (Killeen, Aldridge & Oliver, 2004). *A. anatina* has a relatively high plasticity and tolerance to different abiotic conditions and can thus be found from fast-flowing streams to lentic habitats (Zieritz & Aldridge, 2011). Such diversity of habitat requirements is also observed in *Unio*. For example, *U. crassus* is typically found in streams with low shear stress (Zajac & Zajac, 2011) often with high amounts of fine sediments and organic matter (Denic *et al.*, 2014). *U. tumidiformis*, is able to survive and aggregate in pools subject to high summer temperatures (up to 35°C), in temporary Mediterranean rivers (Reis & Araujo, 2009). All of the species from the *pictorum* lineage and *U. tumidus* have similar habitat requirements and generally occur in slow-flowing large rivers or lentic habitats with dominance of fine substrate. Ecophenotypes of *U. pictorum* have been described, with distinctly different growth forms occurring in lentic and lotic sections of the same river system (Zieritz *et al.*, 2010). The two Gonideinae species are generally present in lotic habitats but can be occasionally found in spring-fed lakes (Araujo *et al.*, 2009a; Albrecht *et al.*, 2011).

IV. CONSERVATION

(1) Conservation status

Using the last IUCN Red List assessment, of the 16 European species recognized in the present work, 12 are on the Threatened or Near Threatened categories where three are Critically Endangered, two are Endangered, two are Vulnerable, and five are Near Threatened (synonymising *U. mancus* with *U. cf. elongatulus*). One species (*U. ravoisieri*) was still not assessed and the remaining three species are assessed as Least Concern (Table 4 and also see online Appendix S5).

(a) Margaritiferidae

Both margaritiferids were classified as Critically Endangered in the 2011 IUCN European assessment on non-marine molluscs (Cuttelod *et al.*, 2011).

M. margaritifera has been exploited in Europe since pre-Roman times for its pearls and for this reason many populations have been managed and protected by local authorities. Therefore, with the exception of the Iberian populations, where most populations have been located only recently (Reis, 2003; Morales *et al.*, 2004; Varandas *et al.*, 2013; Lois *et al.*, 2014), in most countries the historical distribution and extent of recent decline are well known (Young *et al.*, 2001; Geist, 2010). European *M. margaritifera* populations have decreased dramatically since the beginning of the 20th century (up to 90%) and this trend is ongoing (Geist, 2010). The species is most likely extinct in Belarus, Denmark, Lithuania, and Poland, and more than 95% of the remaining populations in southern and central Europe are highly fragmented and functionally extinct due to the lack of recent recruitment (Young *et al.*, 2001; Geist, 2010). Many *M. margaritifera* populations have also disappeared in northern latitudes (e.g. Finland and Russia; Oulasvirta, 2011; Makhrov *et al.*, 2014). The largest European populations with recent recruitment are found in the least densely populated areas of northern Europe (e.g. Kola peninsula, Scotland; Geist, 2010). Poor recruitment in *M. margaritifera* has been attributed to the long juvenile phase (>5 years) where animals bury within coarse, well-oxygenated substrates; such habitat has been lost as a result of anthropogenic eutrophication and siltation (Geist & Auerswald, 2007). Since 1992 this species has been listed in annexes II and V of the European Commission (EC) Habitats Directive and has attracted the main portion of European Community funds devoted to freshwater bivalve conservation (Gum, Lange & Geist, 2011). The decline of *M. auricularia* in both abundance and extent of occurrence is estimated to be over 90% (Prié, 2010), and it is now almost extinct, surviving only in Spain and France. The few remaining populations are aging with only the Charente, Vienne (Loire), Luy (Adour) and Dronne (Garonne) Rivers still showing signs of recruitment within the past 15 years. The probable primary host (*A. sturio*) is extinct in the Ebro basin and has almost disappeared from France (Gessner *et al.*, 2010).

(b) Unionidae

(i) *Anodontini*. Neither *Anodonta* species is considered to be threatened in Europe because population numbers and distribution are large (Hinzmann *et al.*, 2013). Like many anodontines in other parts of the world (Strayer, 2008; Haag, 2012), European *Anodonta* seem to be rather adaptable and have persisted in or colonized many highly altered or degraded habitats. However, while *A. anatina* is currently listed by the IUCN as Least Concern (Lopes-Lima, 2014), some populations of *A. cygnea* are declining and the species was assessed as Near Threatened in 2011 (Killeen & Aldridge, 2011). Recent studies have identified regional genetic differences for both *A. anatina* (Froufe *et al.*, 2014) and *A. cygnea* (Geist, Geismar & Kuehn, 2010a), and such studies are helping to identify important conservation or management units. For example, one of the *A. anatina* lineages, which includes individuals from Italy and the Ebro

Table 3. Principal habitats occupied by European freshwater mussels

Species	Lentic				Lotic				Other habitats		
	Upland lakes and tarns	Lowland lakes and reservoirs	Ponds	Swamps	Marsh drains	Trickles and ditches	Large, slow-flowing lowland rivers	Streams and small flowing rivers	Upland rivers and streams	Mediterranean temporary rivers	Canals
<i>Margaritifera auricularia</i>											
<i>Margaritifera margaritifera</i>											
<i>Anodonta anatina</i>											
<i>Anodonta cygnea</i>											
<i>Pseudanodonta complanata</i>											
<i>Unio crassus</i>											
<i>Unio delphinus</i>											
<i>Unio gibbus</i>											
<i>Unio mancus</i>											
<i>Unio cf. elongatulus</i>											
<i>Unio pictorum</i>											
<i>Unio ravoisieri</i>											
<i>Unio tumidiformis</i>											
<i>Unio tumidus</i>											
<i>Microconchylaea bonellii</i>											
<i>Potomida littoralis</i>											

Dark grey, often present; light grey, occasionally present; white, no data. Ecological data are based on unpublished studies by the authors of this review and on published information (see online Appendix S4).
Table structure adapted from Killeen *et al.* (2004).

Table 4. Conservation status and current legal protection of freshwater mussels in Europe (see online Appendix S5)

Region	Status/protection	Source/authority	References
<i>M. auricularia</i>			
Europe	Critically Endangered	IUCN European Red List of non-marine molluscs	Cuttelod <i>et al.</i> (2011)
European Union	Strictly protected	Bern convention	EC (1979)
Spain	Requiring strict protection	Habitats and species directive	EC (1992)
	Protected	National legislation	—
	Endangered	Spanish catalogue of threatened Species	—
France	Protected	French list of protected species	—
Italy	Requiring strict protection	Directory of Italian protected fauna	—
Europe	Critically Endangered	IUCN European Red List of non-marine molluscs	Cuttelod <i>et al.</i> (2011)
European Union	Protected	Bern convention	EC (1979)
	Requiring SACs	Habitats and species directive	EC (1992)
	Community Interest	Habitats and species directive	EC (1992)
Austria	Critically Endangered	Austria Red List of molluscs	Reischütz & Reischütz (2007)
Belarus	Extinct	Red Book of the Republic of Belarus	Laenko (2006)
Belgium	Critically Endangered	Project report	Motte (2012)
	Strictly protected	National legislation	—
Czech Republic	Critically Endangered	Czech Republic Red List (invertebrates)	Farkač, Král & Škorpík (2005)
	Strictly protected	National legislation	—
Finland	Endangered	Red List of Finnish species	Rassi <i>et al.</i> (2010)
France	Protected	French list of protected species	—
Germany	Critically Endangered	Red List of German species	Binot-Hafke <i>et al.</i> (2011)
	Strictly protected	National legislation	—
Great Britain	Critically Endangered	Great Britain Red List	Seddon, Killeen & Fowles (2014)
	Protected	National legislation	—
Ireland	Critically Endangered	Irish Red List	Byrne <i>et al.</i> (2009)
	Protected	National legislation	—
Latvia	Endangered	Red Book of Latvia	Spuris (1998)
	Protected	National legislation	—
Lithuania	Extinct	Red Book of Lithuania	Balevičius (1992)
Norway	Vulnerable	Norwegian Red List	Kålås <i>et al.</i> (2010)
	Protected	National legislation	—
Northern Ireland	Critically Endangered	Irish Red List	Byrne <i>et al.</i> (2009)
	Protected	National legislation	—
Portugal	Requiring SACs	National legislation	—
	Requiring strict protection	National legislation	—
	Strictly protected	National legislation	—
Poland	Extinct	Polish Red Book (invertebrates)	Głowaciński & Nowacki (2004)
	Strictly protected	National legislation	—
Russia	Vulnerable	Red Book of Russia	Damitov-Damilian (2001)
Spain	Requiring special protection	National legislation	—
	Endangered	Invertebrates Red Book of Spain	Verdú & Galante (2006)
	Endangered	Red List of Swedish species	Gärdenfors (2010)
Sweden	Protected	National legislation	Gärdenfors (2010)

Table 4. Continued

	Region	Status/protection	Source/authority	References
<i>A. anatina</i>	Europe	Least Concern	IUCN Europe Red List of non-marine molluscs	Cuttelod <i>et al.</i> (2011)
	Austria	Near Threatened	Austria Red List of molluscs	Reischütz & Reischütz (2007)
	Ireland	Vulnerable	Irish Red List	Byrne <i>et al.</i> (2009)
	Germany	Near Threatened	Red List of German species	Binot-Hafke <i>et al.</i> (2011)
		Protected	National legislation	—
	Great Britain	Near Threatened	Great Britain Red List	Seddon <i>et al.</i> (2014)
	Northern Ireland	Vulnerable	Irish Red List	Byrne <i>et al.</i> (2009)
	Romania	Vulnerable	Journal article	Sárkány-Kiss (2003)
	Switzerland	Vulnerable	Switzerland Red Book of molluscs	Rüetschi <i>et al.</i> (2011)
	Europe	Near Threatened	IUCN European Red List of non-marine molluscs	Cuttelod <i>et al.</i> (2011)
	Austria	Near Threatened	Austria Red List of molluscs	Reischütz & Reischütz (2007)
	Czech Republic	Vulnerable	Czech Republic Red List (invertebrates)	Farkač <i>et al.</i> (2005)
<i>A. cygnea</i>	Germany	Protected	National legislation	—
		Vulnerable	Red List of German species	Binot-Hafke <i>et al.</i> (2011)
		Protected	National legislation	—
	Great Britain	Near Threatened	Great Britain Red List	Seddon <i>et al.</i> (2014)
	Ireland	Vulnerable	Irish Red List	Byrne <i>et al.</i> (2009)
	Norway	Endangered	Norwegian Red List	Kålås <i>et al.</i> (2010)
	Northern Ireland	Vulnerable	Irish Red List	Byrne <i>et al.</i> (2009)
	Poland	Endangered	Polish Red Book (invertebrates)	Głowaciński & Nowacki (2004)
		Strictly protected	National legislation	—
	Ukraine	Rare	Journal article	Korniushin (2002)
	Switzerland	Endangered	Switzerland Red Book of molluscs	Rüetschi <i>et al.</i> (2011)
	Europe	Near Threatened	IUCN European Red List of non-marine molluscs	Cuttelod <i>et al.</i> (2011)
Austria	Critically Endangered	Austria Red List of molluscs	Reischütz & Reischütz (2007)	
Belarus	Endangered	Red Book of the Republic of Belarus	Laenko (2006)	
Czech Republic	Endangered	Czech Republic Red List (invertebrates)	Farkač <i>et al.</i> (2005)	
Germany	Critically Endangered	Red List of German species	Binot-Hafke <i>et al.</i> (2011)	
	Strictly protected	National legislation	—	
Great Britain	Near Threatened	Great Britain Red List	Seddon <i>et al.</i> (2014)	
Hungary	Endangered	Journal article	Fehér, Majoros & Varga (2004)	
	Protected	National legislation	—	
Poland	Endangered	Polish Red Book (invertebrates)	Głowaciński & Nowacki (2004)	
	Endangered	National legislation	—	
Romania	Strictly protected	Journal article	Sárkány-Kiss (2003)	
Russia	Rare	Journal article	Korniushin (2002)	
Slovakia	Endangered	Red List of molluscs of Slovakia	Šteftek (1994)	
Sweden	Near Threatened	Red List of Swedish Species	Gärdenfors (2010)	
Ukraine	Rare	Journal article	Korniushin (2002)	
Europe	Endangered	IUCN Red List of Threatened Species	Lopes-Lima <i>et al.</i> (2014a)	
European Union	Requiring SACs	Habitats and species directive	EC (1992)	
	Requiring strict protection	Habitats and species directive	EC (1992)	
Austria	Critically Endangered	Austria Red List of molluscs	Reischütz & Reischütz (2007)	

Table 4. Continued

Region	Status/protection	Source/authority	References
Belarus	Vulnerable	Red Book of the Republic of Belarus	Laenko (2006)
Belgium	Strictly protected	National legislation	—
Bulgaria	Protected	National legislation	—
Croatia	Strictly protected	National legislation	—
Czech Republic	Endangered	Czech Republic Red List (Invertebrates)	Farkač <i>et al.</i> (2005)
	Protected	National legislation	—
Finland	Vulnerable	Red list of Finnish species	Rassi <i>et al.</i> (2010)
France	Protected	French list of protected species	—
Germany	Critically Endangered	Red List of German species	Binot-Hafke <i>et al.</i> (2011)
	Strictly protected	National legislation	—
Hungary	Rare	Journal article	Fehér <i>et al.</i> (2004)
	Protected	National legislation	—
Latvia	Vulnerable	Red Book of Latvia	Spuris (1998)
	Protected	National legislation	—
Lithuania	Extinct	Red Book of Lithuania	Balevičius (1992)
Poland	Endangered	Polish Red Book (invertebrates)	Głowaciński & Nowacki (2004)
	Strictly protected	National legislation	—
Romania	Endangered	Journal article	Sárkány-Kiss (2003)
Slovakia	Vulnerable	Red List of molluscs of Slovakia	Šteffek (1994)
	Protected	National legislation	—
Sweden	Endangered	Red List of Swedish Species	Gärdenfors (2010)
	Protected	National legislation	Gärdenfors (2010)
Switzerland	Critically Endangered	Switzerland Red Book of molluscs	Rüetschi <i>et al.</i> (2011)
Europe	Near Threatened	IUCN European Red List of non-marine molluscs	Cuttelod <i>et al.</i> (2011)
Spain	Near Threatened	Invertebrates Red Book of Spain	Verdú & Galante (2006)
Europe	Critically Endangered	IUCN European Red List of non-marine molluscs	Cuttelod <i>et al.</i> (2011)
Europe ^a	Near Threatened	IUCN European Red List of non-marine molluscs	Cuttelod <i>et al.</i> (2011)
European Union ^a	Protected	Bern convention	EC (1979)
	Community Interest	Habitats and species directive	EC (1992)
Italy	Community Interest	National legislation	—
Spain	Near Threatened	Invertebrates Red Book of Spain	Verdú & Galante (2006)
Switzerland	Endangered	Switzerland Red Book of molluscs	Rüetschi <i>et al.</i> (2011)
Europe	Least Concern	IUCN European Red List of non-marine molluscs	Cuttelod <i>et al.</i> (2011)
Austria	Near Threatened	Austria Red List of molluscs	Reischütz & Reischütz (2007)
Czech Republic	Strictly protected	National legislation	—
Germany	Near Threatened	Red List of German species	Binot-Hafke <i>et al.</i> (2011)
	Protected	National legislation	—
Great Britain	Near Threatened	Great Britain Red List	Seddon <i>et al.</i> (2014)
Romania	Vulnerable	Journal article	Sárkány-Kiss (2003)
Sweden	Near Threatened	Red List of Swedish species	Gärdenfors (2010)
Switzerland	Endangered	Switzerland Red Book of molluscs	Rüetschi <i>et al.</i> (2011)
Europe ^a	Near Threatened	IUCN European Red List of non-marine molluscs	Cuttelod <i>et al.</i> (2011)
European Union ^a	Protected	Bern convention	EC (1979)
	Community Interest	Habitats and species directive	EC (1992)

U. delphinus***U. gibbus******U. mancus/U. cf. elongatulus******U. pictorum******U. ravoisieri***

Table 4. Continued

	Region	Status/protection	Source/authority	References
<i>U. tumidiformis</i>	Spain	Near Threatened	Invertebrates Red Book of Spain	Verdú & Galante (2006)
	Europe ^b	Vulnerable	IUCN European Red List of non-marine molluscs	Cuttelod <i>et al.</i> (2011)
	European Union ^b	Requiring SACs	Habitats and species directive	EC (1992)
		Requiring strict protection	Habitats and species directive	EC (1992)
	Portugal ^b	Requiring SACs	National legislation	—
		Requiring strict protection	National legislation	—
	Spain	Vulnerable	Invertebrates Red Book of Spain	Verdú & Galante (2006)
	Europe	Least Concern	IUCN European Red List of non-marine molluscs	Cuttelod <i>et al.</i> (2011)
	Austria	Vulnerable	Austria Red List of molluscs	Reischütz & Reischütz (2007)
	Czech Republic	Vulnerable	Czech Republic Red List (invertebrate)	Farkač <i>et al.</i> (2005)
<i>U. tumidus</i>	Germany	Endangered	Red List of German species	Binot-Hafke <i>et al.</i> (2011)
		Protected	National legislation	—
	Great Britain	Near Threatened	Great Britain Red List	Seddon <i>et al.</i> (2014)
	Romania	Vulnerable	Journal article	Sarkány-Kiss (2003)
	Slovakia	Vulnerable	Red List of molluscs of Slovakia	Šteffek (1994)
	Switzerland	Endangered	Switzerland Red Book of molluscs	Rüetschi <i>et al.</i> (2011)
	Europe	Vulnerable	IUCN European Red List of non-marine molluscs	Cuttelod <i>et al.</i> (2011)
	European Union	Protected	Bern convention	EC (1979)
	Italy	Community Interest	Habitats and species directive	EC (1992)
	Switzerland	Community Interest	National legislation	—
<i>P. littoralis</i>	Europe	Extinct	Switzerland Red Book of molluscs	Rüetschi <i>et al.</i> (2011)
	Spain	Endangered	IUCN Red List of Threatened Species	Lopes-Lima <i>et al.</i> (2014b)
		Vulnerable	Invertebrates Red Book of Spain	Verdú & Galante (2006)

SACs, special areas of conservation.

^aAs *Unio elongatulus*.

^bAs *Unio crassus*.

basin, in Spain (Froufe *et al.*, 2014), is especially restricted in distribution and is decreasing rapidly (Araujo *et al.*, 2009a). *P. complanata* is rare across its entire distribution and there is evidence for widespread declines (>50% over the last few decades) in populations from the UK, central Europe, and Ukraine (Tudoranca, 1972; Aldridge, 2004; McIvor & Aldridge, 2007). This species is listed by the IUCN as Near Threatened (Van Damme, 2011a) and is already protected in several countries (Table 4).

(ii) *Unionini*. *U. crassus*, once considered the most abundant unionid in Europe, declined dramatically (up to 50% both in the number of individuals and populations) in western and central Europe during the second half of the 20th century (Bauer, Hochwald & Silkenat, 1991; Lopes-Lima, Kebapçı & Van Damme, 2014a). This species is protected and considered critically endangered in several European countries (Table 4). In 2014 it was assessed as Endangered by the IUCN (Lopes-Lima *et al.*, 2014a) and is listed in annexes II and IV of the EC Habitats Directive. Populations seem to be stable only in the Baltic and eastern European countries (Lopes-Lima *et al.*, 2014a). However, in recent surveys several recruiting populations were newly discovered in Germany (Stoeckl, Taubert & Geist, 2015), indicating that gaps in known distribution are even present in the most intensely monitored species. In contrast to *M. margaritifera*, where increased loads of fine sediment appear to be problematic, this factor is unlikely to be responsible for the observed declines in *U. crassus* (Denic *et al.*, 2014). Instead, direct threats such as predation by invasive muskrat (*Ondatra zibethicus*) (Zahner-Meike & Hanson, 2001), dredging and insufficient host fish populations appear to be the main causes of decline, at least in central Europe (Taubert, Gum & Geist, 2012a; Taubert *et al.*, 2012b; Stoeckl *et al.*, 2015).

U. tumidiformis has a restricted distribution in small rivers of southern Iberia, a region severely affected by water extraction (Benejam *et al.*, 2010). The populations are very scattered and sparse, with recent declines in number of populations of 30–35% (Araujo, 2011e). The species is considered Vulnerable by the IUCN over its entire distribution (Araujo, 2011e), and is protected (as *U. crassus*) in Portugal and Spain under annexes II and IV of the EC Habitats Directive.

U. pictorum is one of the most widespread unionid species in Europe where it has been assessed as Least Concern by the IUCN (Van Damme, 2011b). Although no comprehensive surveys and monitoring programmes have been carried out across its entire distribution, due to recent declines it is of emerging concern in some countries (e.g. Austria, Germany, Great Britain, and Sweden) where it is listed as Near Threatened.

U. mancus has undergone a strong decline in both number of populations and individuals in its western distribution (Araujo *et al.*, 2009a; Prié *et al.*, 2012). It was listed as Near Threatened in Europe in 2011 by the IUCN (Araujo, 2011d), although more recent data suggest each of three French subspecies could be considered as Endangered (Prié *et al.*, 2012). There are no data regarding the conservation status of *U. mancus* in south-eastern Europe. *U. mancus* is protected

in Spain under the Habitats and Species Directive Annex V under the name *U. elongatulus*.

Unio cf. *elongatulus* can be locally abundant, but the number of populations is declining. Surveys from 2012 to 2014 (N. Riccardi, unpublished data) confirmed only 59 of the 97 populations reported by Bodon *et al.* (2005). It has not been assessed by the IUCN since it has only recently been recognized.

The status of *U. delphimus* has not been determined rigorously, but a recent assessment estimated a 20–30% population loss over the last 50 years (Araujo, 2011b). The species was considered as Near Threatened by the IUCN (Araujo, 2011b).

U. ravoisieri has never been evaluated formally but the species should be considered as Endangered or even Critically Endangered in Europe, due to a very low abundance and a European distribution restricted to a single small Mediterranean basin (River Ser) and a single small lake (Lake Banyolas) in Catalonia, Spain. Additionally, the Lake Banyolas fish fauna has changed dramatically in recent years with the introduction of 12 non-native species (including largemouth bass, *Micropterus salmoides*, pumpkinseed sunfish, *Lepomis gibbosus* and roach, *Rutilus rutilus*), which may reduce the availability of suitable hosts (García-Berthou & Moreno-Amich, 2008). *Unio ravoisieri* is protected in Spain under the Habitats and Species Directive Annex V under the name *U. elongatulus*.

U. tumidus is considered to be abundant and widespread in its entire distribution, having been assessed as Least Concern in Europe by the IUCN (Van Damme, 2011c). However, should be considered Vulnerable in France where >70% reduction in its historical distribution has been estimated (Prié *et al.*, 2014).

U. gibbus is probably the most endangered freshwater mussel species in Europe. It is found only in the Barbate basin in southern Spain (Araujo *et al.*, 2009b) and only two live individuals have been found since 2007. It is listed as Critically Endangered by the IUCN (Araujo, 2011c).

(iii) *Gonideinae*. The conservation status of *P. littoralis* was recently assessed by the IUCN as Endangered (Lopes-Lima, Prié & Seddon, 2014b). *P. littoralis* has suffered a strong decline in both the number of populations and individuals and almost 75% of its recorded populations in the Iberian Peninsula have disappeared or are likely to disappear within the next 10 years (Araujo, 2011a). In France, although historically known from all main drainages, where empty shells can still be found, living individuals are becoming rare and many populations are declining with a suggested distribution contraction of around 75% (Prié *et al.*, 2014). It is probably extirpated from the Seine River basin and from several small Mediterranean basins.

M. bonellii is listed on Annex V of the EC Habitats and Species Directive as a protected species. It has been assessed as Vulnerable in Europe by the IUCN (Albrecht *et al.*, 2011). In Italy the number of populations is very small and it is presumed extinct in Switzerland (Rüetschi *et al.*, 2011). The best-known recruiting populations occur in the Po

River tributaries Marcova, Rotaldo, Stura (N. Riccardi, unpublished data) and one Isonzo tributary Versa (Nagel *et al.*, 2007).

(2) Major threats

Globally, known major threats to freshwater biodiversity include loss, fragmentation and degradation of habitat, overexploitation, pollution, introduction of non-native invasive species, and climate change (Dudgeon *et al.*, 2006; Geist, 2011). European freshwater mussels are vulnerable to all these threats. Other currently unknown factors may also play a role.

(a) Habitat loss, fragmentation and degradation

Most streams and rivers in Europe are highly altered physically and damage to mussel habitats continues to be a concern (Geist, 2014). Dams and channelization alter the physical characteristics of aquatic ecosystems and can disrupt natural meta-population structure by preventing gene flow (e.g. Geist & Kuehn, 2005). The resulting fragmentation is also a threat to long-term population persistence because it eliminates the possibility of recolonization after a severe disturbance (e.g. drought, toxic spill) due to the interruption of fish host migration from adjacent non-disturbed areas (Haag, 2012). Even small dams can be a major barrier to the dispersal of fish carrying glochidia (Watters, 1996). This situation may be more acute in freshwater mussels such as *M. margaritifera* that are dependent on mobile or migratory host fishes, but less important in mussel species such as *A. anatina* that use less-mobile hosts (Douda *et al.*, 2013). In Europe, about 7000 large (> 15 m high) dams exist (Limburg & Waldman, 2009). There is a high pressure for establishing new dams for hydropower in central Europe (e.g. Germany and Poland) and for irrigation in the Iberian Peninsula and the Balkans. Dams typically favour lentic or generalist taxa such as *A. anatina* and reduce or eliminate lotic species such as *M. margaritifera* (Burlakova *et al.*, 2011; Mueller, Pander & Geist, 2011).

Dams also negatively affect mussel habitat through changes in sediments, river flow, and temperature (Mueller *et al.*, 2011). Increased sedimentation upstream of dams and decreases in sediment porosity are particularly harmful to rheophilic mussel species such as *M. margaritifera*, directly by increasing juvenile mortality (Geist & Auerswald, 2007; Österling, Arvidsson & Greenberg, 2010), and indirectly by reducing hatching rates of salmonid hosts (Sternecker & Geist, 2010; Sternecker, Cowley & Geist, 2013). Other riverine freshwater mussel species such as *U. crassus* appear to be much more tolerant of fine sediments (Zajac & Zajac, 2011; Denic *et al.*, 2014). Water releases from dams often result in both abnormally high and low flows (Vaughn & Taylor, 1999). High water velocities can displace adults and juveniles and may impair recruitment. By contrast, extended periods of low flow below impoundments can result in mussel mortality due to stranding and low dissolved oxygen levels. Changes to thermal regimes as a result of dams can

have strong effects on fish communities, on the reproductive ability of freshwater mussels (Heinricher & Layzer, 1999), as well as the timing and successful development of mussel larvae on their fish hosts (Taeubert, El-Nobi & Geist, 2014). Dredging of river beds and weed removal using mechanical excavators can directly remove large numbers of mussels and may increase the risk of smothering through the temporary suspension of fine sediments (Aldridge, 2000; Cosgrove & Hastie, 2001). Interestingly, old and stable side channels and ditches often offer refuge to mussels from highly managed main channels. For example, in Spain *P. littoralis* predominates in rice ditches and side channels in the Valencia region, and *M. auricularia* persists in the Channel of Tauste in the Ebro River basin (Gómez & Araujo, 2008).

(b) Overexploitation

In Europe, pearl fishing has historically been a major threat to many central and northern European populations of *M. margaritifera* (Young *et al.*, 2001; Makhrov *et al.*, 2014). Strict laws now prohibit these activities but poaching continues in some countries (e.g. Scotland and Russia) (Hastie, 2006; Bolotov *et al.*, 2012). Until the 1990s, a craft industry existed in the Region of Aragon, Spain, for the use of *M. auricularia* nae to make buttons and decorate jack-knife hilts (Álvarez, 1998). Occasional reports also describe the direct consumption of some mussel species by humans and domestic animals in Europe (e.g. Tudorancea, 1972). Although overexploitation of freshwater mussels may be responsible for local declines, it cannot account for declines at the European scale.

(c) Pollution and eutrophication

There is a wide variety of contaminants that can potentially affect freshwater mussels, despite the small number of studies that explicitly address this issue in European species. In general, free glochidia larvae are more vulnerable to pollutants than glochidia attached to fish, or juvenile mussels and adults (Bringolf *et al.*, 2007; Taskinen *et al.*, 2011). The effects of point-source contamination can be highly detrimental to freshwater mussels, as was the case with a heavy metal spill in River Tisza in 2000, which probably affected freshwater mussel populations (Fleit & Lakatos, 2003). However, diffuse sources appear much more important than point sources of pollution in Europe. For example, increased loads of road de-icing salt, which can flush into watercourses along large parts of their length, have been shown to alter filtration behaviour in adult *A. anatina* (Hartmann *et al.*, in press), and to reduce the attachment success of *A. anatina* glochidia to their host fishes, with peak concentrations of salt application typically coinciding with the timing of glochidial release (Beggel & Geist, 2015). Diffuse pollutants such as road salt are difficult to manage and no legally prescribed environmental quality standards for salt have been established in Europe (Cañedo-Argüelles *et al.*, 2013). Both point-source and diffuse pollution typically differ in terms of scale with the latter being a greater and region-wide problem.

Heavy metals such as copper and cadmium (typically from industrial pollution) can affect the calcification and formation of mussel shells, with toxicity increasing at low pH values (e.g. Pynnönen, 1995). Environmental pollutants such as the organochlorine insecticide DDT, its metabolite DDE, and cadmium have been linked to mussel specimens with thinner and less calcified shells from declining *M. margaritifera* populations (Frank & Gerstmann, 2007). The direct and indirect effects of acidification from airborne pollution have been particularly problematic in poorly buffered areas of Fennoscandia, Sweden, with liming activities used to mitigate the effects of poor shell deposition in *M. margaritifera* populations (Degerman *et al.*, 2009).

The introduction of nutrients and fine sediment from agricultural run-off is considered a major threat for European freshwater mussels. Nitrogen and phosphorous concentrations are elevated and increasing in most European regions (Galloway *et al.*, 2008; Douda, 2010; Grizzetti *et al.*, 2011). Eutrophication and fine-sediment deposition are particularly detrimental to highly specialized species such as *M. margaritifera* (Bauer, 1988; Geist & Auerswald, 2007; Denic & Geist, 2015), whereas habitat generalist species such as *Anodonta* sp. can, to a certain degree, tolerate or even benefit from eutrophication (Patzner & Müller, 2001). For rheophilic species, buried juvenile mussels are especially affected by eutrophication and siltation because they require well oxygenated substrates. In *M. margaritifera*, juveniles depend on a well-sorted stream bed with high exchange rates with the water column for the first 5 years of life. Eutrophication-driven siltation and colmation of stream beds has been linked with recruitment failure in this species (Geist & Auerswald, 2007). Low redox potential in the stream bed can trigger the reduction of nitrate to toxic nitrite and ultimately ammonium, which is in a pH-dependent equilibrium with toxic forms of ammonia. Eutrophication-associated reduction in dissolved oxygen can also induce hypoxic stress in Unionida mussels, promoting the release of eggs and immature glochidia, which in turn can lead to reduced reproductive success (Aldridge & McIvor, 2003).

Pharmaceutical compounds, dioxins and brominated flame retardants can have acute and chronic effects on the reproduction and survival of freshwater mussels (Augspurger *et al.*, 2007; Connon, Geist & Werner, 2012). The number of studies specifically addressing the effects of these compounds on European freshwater mussels is currently too small for a sound assessment of their importance (Strayer & Malcom, 2012).

(d) Loss of fish hosts

In recent decades European ecosystems have been subject to the disappearance of native freshwater fish species, especially in areas with high freshwater fish endemism (e.g., Iberian Peninsula; Hermoso *et al.*, 2011). Host limitation is most likely to occur for mussel species with restricted host fish spectra, such as *M. margaritifera* and *M. auricularia*. Observed declines in salmonids and sturgeon (e.g. Gessner *et al.*,

2010; Geist, 2015) have put those mussel species high on the agenda for conservation. On the other hand, in *M. margaritifera* habitats, a high richness, density and biomass of fish can also be indicative of eutrophication and habitat degradation (Geist *et al.*, 2006). Since its fish host has a much shorter substrate-dependent phase it can benefit from slight eutrophication in the form of an increased population density and biomass. In that study, non-recruiting populations of *M. margaritifera* had significantly higher density and biomass of brown trout (*S. trutta*) compared to recruiting ones, which indicates that even slight eutrophication can result in adverse effects on pearl mussel recruitment. Furthermore, declines in host-generalist European Unionida mussels, such as *U. crassus*, can be linked to declines of their host fish species in certain areas (Douda, Horký & Bílý, 2012; Taubert *et al.*, 2012a,b; Stoeckl *et al.*, 2015).

(e) Invasive species

Hundreds of non-native species are now established in European freshwater ecosystems (DAISIE, 2009). The invasive bivalve species in European freshwater ecosystems include *Corbicula fluminea* (Müller 1774), *Corbicula fluminalis* (Müller 1774), *Dreissena rostriformis bugensis* (Andrusov 1897), *Dreissena polymorpha* (Pallas 1771) and *Sinanodonta woodiana* (Lea 1834), and all these bivalves may be especially detrimental to native Unionida freshwater mussels.

Corbicula is native to Asia and was first found in Europe in the early 1980s. The species is now present from Portugal in the west to Romania in the east, and the UK and Ireland in the north (Crespo *et al.*, 2015). *C. fluminea* has been shown to reduce the growth and survival of sympatric *P. complanata* in UK rivers, and this may be attributable to the organic enrichment of sediments through biodeposition of faeces and pseudofaeces.

D. r. bugensis and *D. polymorpha* are native to the Ponto-Caspian region. *D. polymorpha* established broadly through Europe in the 18th and 19th centuries and is now present in north-west Russia, much of central and western Europe, and Scandinavia (reviewed in Aldridge, Elliott & Moggridge, 2004). *D. r. bugensis* is a more recent invader into western Europe and is spreading rapidly (e.g. Aldridge, Ho & Froufe, 2014). Direct competition for food is thought to be one of the major mechanisms for the decline of Unionida mussels in North America (Strayer & Malcom, 2007). In addition, dreissenid bivalves possess byssus threads which allow them to attach to the valves of native mussels. Fouling from *D. polymorpha* can make it more difficult for Unionida mussels to burrow and move through sediments, the increased weight can result in the underlying Unionida mussel becoming buried in soft sediments, while higher drag can increase the likelihood of dislodgment by water motion. In some cases, *D. polymorpha* can prevent valve movement of the underlying Unionida mussel, thus hampering filter feeding, respiration, and reproduction. Dreissenid fouling of Unionida mussels can lead to a depletion of biomass and total energy stores, and can result in localized extirpations of European Unionida mussels

(Sousa, Pilotto & Aldridge, 2011; Bódis, Tóth & Sousa, 2014a).

S. woodiana is a unionid native to south-eastern Asia and has colonized several European countries (from Spain in the south-west to Ukraine in the east and Sweden in the north; reviewed in Lajtner & Crnčan, 2011). Dense populations of *S. woodiana* may compete with native Unionida mussels for food, increase resistance to glochidia in potential host fish, and serve as vectors of introduction of new parasites and diseases (see Sousa *et al.*, 2014). However, many of these impacts remain speculative.

The introduction of non-native macrophytes can also impair the survival of freshwater bivalves. In the Iberian Peninsula, *A. cygnea* populations are located in three small lakes in the north of Portugal, all of which are heavily invaded by the water hyacinth (*Eichhornia crassipes*). When this invasive plant undergoes mass mortality at the end of the summer, this results in the accumulation of dead organic matter and consequent reduction in redox potential and decrease in oxygen leading to high mortalities in *A. cygnea* (M. Lopes-Lima & R. Sousa, unpublished data). Other invasive plants such as *Myriophyllum aquaticum*, *Elodea canadensis*, *Elodea nuttallii* and *Egeria densa* may have similar effects on European freshwater mussels.

Recent studies showed that invasive fish species have a lower suitability as a host of *A. anatina* than native fish species (Douda *et al.*, 2013). Reproductive success of freshwater mussels could be reduced if there is an increased likelihood of glochidia attaching to a less-suitable host. Introduction of bivalve predators such as crayfish, fishes, and mammals may also be responsible for declines in native freshwater mussels (Zahner-Meike & Hanson, 2001; Aldridge, 2004). In the case of *U. crassus*, the presence of the muskrat was responsible for significant local density declines (up to 80% in 1 year for a Swiss population) in a very short period of time in Luxembourg, Germany and Switzerland (Vicentini & Pfändler, 2001).

(f) Water abstraction and climate change

Growing demands for water by agricultural, industrial and recreational activities, especially in southern European countries (e.g. Portugal, Spain, Italy and Greece), has caused significant negative impacts on Mediterranean freshwater ecosystems including decline and loss of endemic freshwater biodiversity (Benejam *et al.*, 2010). These impacts may be exacerbated by predicted climatic change towards an increased inter-annual variability in precipitation and consequent effects in river flows (Millán, Estrela & Miró, 2005). In addition, extreme climatic events are predicted to become more frequent and intense in the future (Diez *et al.*, 2012). Droughts and floods have already contributed to massive die-offs of European freshwater mussels (e.g. Hastie *et al.*, 2001; Mouthon & Daufresne, 2006; Sousa *et al.*, 2012; Bódis, Tóth & Sousa, 2014b). Even small temperature changes can strongly affect metamorphosis success and larval development in freshwater mussels (Taeubert, Gum & Geist, 2013; Taeubert *et al.*, 2014), with knock-on consequences to

recruitment success (Sousa *et al.*, 2013, 2015). Particularly affected may be freshwater mussel populations at the edges of their distribution, such as those in the south of Europe, where intolerance to increased temperatures combined with low dispersal capacity may impair their survival in these regions (Santos *et al.*, 2015).

In many instances freshwater mussels are likely to be exposed to multiple stressors, such as pollution, invasive species and climate change at the same time, which can place species at even greater risk. For example, a recent study modelled the projected distribution across Europe of the Near Threatened unionid *P. complanata* and the invasive, *D. polymorpha* under 2050 future climatic scenarios (Gallardo & Aldridge, 2013). These authors found that while *D. polymorpha* may benefit strongly from climate changes (increase of 15–20% in distribution), *P. complanata* would experience considerable loss (14–36% shrinkage in distribution). Furthermore, the overlap of the two species was predicted to increase by up to 24%, meaning that *P. complanata* would be subject to increased risk of fouling with fewer refugia.

(g) Other threats

In addition to the above identified threats, many aquatic ecosystems have experienced massive mussel declines in the last decades, even though the habitat appears intact with healthy populations of fish, insects, gastropods, and other biota. Similar observations were also made in North America (e.g. Haag, 2012; Haag & Williams, 2014). Consequently, further research into currently unknown stressors, and the interaction of multiple stressors warrants further attention.

(3) Conservation and management measures

Conservation of European freshwater mussels is essential to maintain the ecosystem functions and services they provide. Unfortunately, the European Natura 2000 network has a primary focus on terrestrial biodiversity, failing sufficiently to cover freshwater species in general (Hermoso *et al.*, 2015), and Unionida mussels in particular.

Effective conservation plans should be aimed at multiple scales, striving to identify distinct populations or evolutionarily significant units (ESUs), populations threatened at the local scale, biodiversity hotspots and to promote river management in response to species' needs. An evidence-based structured conservation approach that includes defining conservation objectives, as well as an evaluation of conservation action and adaptive management, could greatly improve conservation success, but is still rarely applied in Europe (Geist, 2015). As a second step after the definition of objectives, information on current distribution and population size of each species is required to define conservation priorities. These conservation priorities must be assessed species-specifically and at the regional population level because even in co-occurring mussel species different factors may limit their recruitment. For example, whereas deficiencies in central European *M. margaritifera* recruitment

can mostly be explained by excess amounts of fine sediment (Geist & Auerswald, 2007), *U. crassus* populations seem to be more tolerant to these conditions (Denic *et al.*, 2014) but host fishes are often limiting (Douda *et al.*, 2012; Tæubert *et al.*, 2012a,b; Stoeckl *et al.*, 2015). Ideally, sound conservation projects should incorporate ecological and genetic information (Geist & Kuehn, 2005; Geist, 2010). The genetically most valuable populations can be identified based on their respective contribution to the variation in the gene pool across its entire species distribution (Geist & Kuehn, 2008). Isolated lineages representing unique or rare genotypes should be afforded due importance.

Based on ecological criteria, prioritization should include protection of the healthiest populations in the most intact habitats. Identifying sites which harbour multiple mussel species may often serve as a focus for conservation efforts at the national or regional scale. For example, the River Mustionjoki (Svartå) in southern Finland harbours all of the seven mussel species that occur in that country and the River Wye hosts all six of the UK's mussel species. Conservation priority should be also given to regions that harbour species with a very restricted distribution (e.g. *U. gibbus* in the River Barbate basin) that, due to their localized distribution, are especially vulnerable to extinction. In some cases, willingness of local communities and stakeholders to support restoration should also be taken into account when prioritizing sites for conservation (Geist, 2015).

Where populations are facing extinction, conservation can take two principal directions: the restoration of aquatic habitats including their catchments, or artificial culture and propagation. Ideally, the two approaches should be combined. Restoration of aquatic habitats, especially of substratum properties, can be extremely time-consuming, expensive, and conflicting management goals may arise (Geist, 2011; Pander & Geist, 2013). Artificial propagation is likely to produce a much quicker output, particularly in species where the methodology is established. In Europe, most propagation has focussed on *M. margaritifera* (Gum *et al.*, 2011). However, cultured mussels need to be released in suitable habitats and therefore this method can only be effective if there are suitable candidate areas for release or if it is realistic that habitats can be restored.

To date, there have been 28 projects within the LIFE program (the European Union's funding instrument for the environment) devoted to the restoration of freshwater mussel habitats, with a total funding of 64 million Euros. However, the funding distribution has been uneven with the majority being directed to the conservation of *M. margaritifera* (18) and *U. crassus* (5), with three additional projects targeting both species. Such Europe-wide and national-scale conservation projects have had different levels of success. Whilst the production of juvenile mussels in larger quantities has become feasible (reviewed in Gum *et al.*, 2011), the number of successful habitat restorations remains extremely limited. One project on the Lutter River in northern Germany restored recruitment of *M. margaritifera* after reduction of fine-sediment inputs and restoration of the entire catchment

area (Geist, 2010). Another project at the Biała River (Poland) removed four dams, which increased fish migration and allowed for successful recolonization of *U. crassus* (Zajac *et al.*, 2013). These two examples illustrate that restoration of freshwater mussel habitats is possible, but it also shows that substantial effort and time are needed to achieve success. While successful examples of freshwater mussel conservation schemes are likely to be recorded in peer-review journals and reports, unsuccessful examples also carry important information and convey important lessons. Resources such as www.conservationevidence.com provide an effective portal for capture of such information.

Since the successful recruitment of freshwater mussels is highly dependent on the availability of suitable host fish, the integration of fisheries management in rivers with known mussel populations should also be part of conservation plans. For freshwater mussel populations that are known or suspected to be limited by host availability, e.g. *U. crassus* (Douda *et al.*, 2012; Tæubert *et al.*, 2012a; Stoeckl *et al.*, 2015), the abundance of key host fish species should be actively supported, even if they are considered to be of low economic value (Tæubert *et al.*, 2012a,b).

Despite ongoing international discussions on freshwater mussel research, current conservation approaches are typically directed towards solving local problems. Whilst conservation actions necessarily need to work at the regional scale, it would be highly beneficial if strategic planning for conservation followed a more standardized approach. This requires better international collaboration in the development of tools for the mapping of mussel distributions, and quantifying density and recruitment status. Conservation prioritization should include socio-economic arguments concerning the value of aquatic biodiversity (see also Geist, 2010, 2011). By way of example, experts from across Europe have recently collaborated on the development of a European CEN (*Comité Européen de Normalisation*) standard that can serve as a guideline and aid the conservation management of *M. margaritifera*. Similar actions for all other 15 species could be very helpful. The declining rates of European freshwater mussels and the increasing threats to them, along with the targets of NATURA 2000 and the European Water Framework Directive, provide strong arguments for immediate action. This multi-author review by freshwater mussel specialists from all over Europe indicates that there is a critical mass of experts that needs to be more strongly engaged in future conservation planning.

V. CONCLUSIONS

(1) Currently, 16 species are recognized in European Unionida: two species of Margaritiferidae and 14 species of Unionidae. Most basins in northern, central, and eastern Europe have a relatively homogeneous species composition containing mostly up to six different species. Southern Europe has an overall lower species richness, but several

species with spatially restricted geographical distributions are found in this area. Information on freshwater mussels in Europe is unevenly distributed with considerable differences in data quality and quantity among countries and species.

(2) Freshwater mussels are an important component of aquatic ecosystems. Changes in their diversity and population structure are being driven by habitat loss and fragmentation, overexploitation, pollution, loss of host fishes, introduction of non-native species, water abstraction and climate change. Resultant declines may have important repercussions in ecosystem functions and services. While we have considerable understanding of the fundamental ecological requirements of some species, such as *M. margaritifera*, we know very little about most recognized European species especially *U. gibbus* and *M. bonellii*. In addition, great variability in knowledge exists across different European regions; some central European countries have been well studied but almost no data are available for south-eastern European countries such as Albania, Macedonia, and Greece. Therefore, more studies should be conducted in order to fill these gaps, which may enhance our ability to apply effective management measures.

(3) As a first step, a systematic understanding of the limiting factors in the life cycle of every species is crucial, since even closely related species may have different ecological requirements. For species for which suitability of host fishes is unclear or unknown (e.g. *U. gibbus* and *M. bonellii*) or for which detailed information concerning habitat preferences is scarce (e.g. *U. tumidus* and *P. complanata*), these factors must be investigated. In addition to the required knowledge of life history and habitat requirements of mussels and their fish hosts, a continuous update on taxonomy (including genetics) and distribution data considering ESUs and conservation units is required. Ideally, such data should be generated in a harmonized, cross-European approach instead of the focus on national conservation management that is currently practiced. This could ultimately lead to priority setting among and within species on a European scale, which would make conservation more effective.

(4) Despite dramatic declines and extinction risk existing for several European freshwater mussel species, there are reasons to be optimistic. For example, water quality has improved greatly in recent decades, allowing mussels to return to several rivers, ponds and lakes. Media coverage has brought attention to the conservation status of this faunal group and so more people recognize these animals as an important conservation target. Finally, the number of European scientists studying freshwater mussels has increased greatly in recent decades. As a result, more information about ecological aspects and new ways to conserve these species are emerging. Efforts to conserve native freshwater mussel diversity on a larger scale would benefit from the formulation of a European action plan, or strategy, to consolidate the energies of academics, natural resource agencies, and the general public.

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VIII. SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article.

Appendix S1. Genetic sequences table and methodology.

Appendix S2. Distribution data bibliography.

Appendix S3. Biological traits bibliography.

Appendix S4. Principal habitats bibliography.

Appendix S5. Conservation and protection status bibliography.

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