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REVIEW ARTICLE

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Captive breeding of European freshwater mussels as a conservation tool: A review

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Abstract

1. Freshwater mussels are declining throughout their range. Their important ecological functions along with insufficient levels of natural recruitment have prompted captive breeding for population augmentation and questions about the usefulness and applicability of such measures.
2. This article reviews the current state of captive breeding and rearing programmes for freshwater mussels in Europe. It considers the various species, strategies, and techniques of propagation, as well as the different levels of effort required according to rearing method, highlighting the key factors of success.
3. Within the last 30 years, 46 breeding activities in 16 European countries have been reported, mainly of *Margaritifera margaritifera* and *Unio crassus*. Some facilities propagate species that are in a very critical situation, such as *Pseudunio auricularius*, *Unio mancus*, and *Unio ravoisieri*, or multiple species concurrently. In some streams, the number of released captive-bred mussels already exceeds the size of the remaining natural population.

Juergen Geist, Frankie Thielen and Louise Lavictoire are the Principal authors.

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4. Rearing efforts range from highly intensive laboratory incubation to lower intensity methods using in-river mussel cages or silos. Most breeding efforts are funded by national and EU LIFE(+) grants, are well documented, and consider the genetic integrity of the propagated mussels. Limited long-term funding perspectives, the availability of experienced staff, water quality, and feeding/survival during early life stages are seen as the most important challenges.
5. Successful captive breeding programmes need to be combined with restoration of the habitats into which the mussels are released. This work will benefit from an evidence-based approach, knowledge exchange among facilities, and an overall breeding strategy comprising multiple countries and conservation units.

KEYWORDS
aquaculture, captive breeding, conservation translocation, freshwater mussel culturing, *Margaritifera margaritifera*, propagation, reintroduction, *Unio crassus*

1 | INTRODUCTION

The global decline of freshwater biodiversity has prompted many efforts addressing its conservation (Geist, 2011). This holds particularly true for freshwater mussels, which are among the most threatened taxa throughout Europe (Lopes-Lima et al., 2017). From a conservation perspective, endangered freshwater mussels, particularly the freshwater pearl mussel (*Margaritifera margaritifera* L.), are considered target species for the conservation of aquatic ecosystems, as they simultaneously fulfil the criteria of flagship, indicator, keystone, and umbrella species (Geist, 2010). The continuing declines and lack of natural recruitment of freshwater mussels in Europe has led to an increasing number of rearing approaches for population augmentation. It has also led to controversies about the usefulness of captive breeding in the context of mussel conservation, particularly if such activities are not properly monitored or are conducted without considering habitat restoration (Preston, Keys & Roberts, 2007; Schmidt & Vandré, 2010; Gum, Lange & Geist, 2011; Patterson et al., 2018).

Rearing methods developed for North American mussel species and conditions (Gatenby, Neves & Parker, 1996; Beaty & Neves, 2004; Neves, 2004; Jones, Mair & Neves, 2005; Barnhart, 2006; Hua & Neves, 2007; Patterson et al., 2018) have often been transferred to European mussel species, but without systematic evaluation of the success of such actions. Recent studies reveal that some captive breeding practices, such as the use of a low number of parents, can result in erosion of the genetic constitution of offspring compared with the original populations, both in freshwater mussels (Geist et al., 2021) as well as fishes (Stoeckle et al., 2022). Co-adaptation or co-evolution of mussels to certain fish hosts (Geist & Kuehn, 2008; Taeubert et al., 2010; Taeubert, Gum & Geist, 2012; Salonen et al., 2017; Taskinen & Salonen, 2022), the effects of host fish age (Marwaha et al., 2019), duration of the parasitic phase (Marwaha et al., 2017), water temperature (Taeubert, El-Nobi & Geist, 2014), and rearing conditions (Eybe et al., 2013; Eybe et al., 2015; Lavictoire et al., 2016; Lavictoire et al., 2020) all have an impact on the performance of captive-bred mussels, with potential consequences if such interactions are not taken into account. Cross-exposure experiments indicate that stock origin and environmental conditions affect both the survival and the growth of juvenile freshwater mussels after their release (Denic et al., 2015). Based on an earlier review of European and North American captive breeding programmes, Gum, Lange & Geist (2011) suggested that captive breeding should only be a rescue tool to retain the evolutionary potential of priority populations that would not persist long enough to benefit from habitat restoration practices. This is in line with Rytwinski et al. (2021), who identified a need for evidence to evaluate the effectiveness of conservation-oriented captive breeding and release programmes for imperilled freshwater mussels. This is particularly important given the worldwide increase in captive breeding programmes for highly threatened freshwater mussels (Strayer et al., 2004; Barnhart, 2006; Thomas, Taylor & Garcia de Leaniz, 2010; Gum, Lange & Geist, 2011; Patterson et al., 2018).

The aim of this article is to review the current state of freshwater mussel captive breeding programmes in Europe. The critical challenges associated with these activities were identified from personal interviews with key groups involved in the captive breeding of freshwater mussels throughout Europe, including information on the context of these programmes, the coverage of species, the intensity and type of rearing practices, and their timelines. This information was then used to make recommendations for effective conservation of freshwater mussels through captive breeding, and to identify priorities for its future use.

2 | METHODS

All the institutions and organizations listed in Table 1 were contacted by one of the three main authors and interviewed using the same questions, to gather standardized information. The interviews took

TABLE 1 Captive breeding methods of freshwater mussels utilized by different projects in Europe. See table legend for explanation of abbreviations.

Country	Region/institution	Species	Years/since (ending date)	Level of intensity and method	Rearing success, release, and ratio to wild population age or size	Funding source	GM	Main challenges	References
Austria	Upper Austria/ blattfisch e.U. Consultancy Company	*M.m.*	2011–present	LI: medium–high HF: *Salmo trutta* (hatchery) MB: kept permanently at the breeding facility IC: incubator boxes OC: sediment boxes, Buddensiek cages, and mussel silos in the stream	In total: 2,100 reared ind. still in caging systems. 30 mussels (11 years old) released (compared with 19 remaining adult mussels in this population) Survival of mussels >1 mm in the first winter is about 50%	National & EU	PM and JM	High mortality among juveniles shortly after harvesting High mortality among parent mussels, with low fitness presumed Long-term funding unsure	Gumpinger C., Daill D. (pers. comm., 2022) Pichler-Scheder C. (pers. comm., 2011) Geist et al. (2021)
Belgium	Ardennes Region/ Service Public de Wallonie (SPW) Since 2017 cooperation with Luxembourg (see Luxembourg in this Table)	*M.m.*	2005–present	LI: medium HF: *Salmo trutta* (hatchery) MB: glochidia collected in the field; mussels stay in the river IC: none OC: side channel in catchment of rivers Arlune and Rulles	Between 2007 and 2014, 95% of freshly metamorphosed mussels released in two outdoor rearing channels. No survival or no mussels found during follow-up monitoring in the years 2007, 2014, and 2018 5% of juveniles released directly in River Anlier (2% of this population come from cultured ind.)Rulles River: 99% of this population come from cultured ind.	National & EU LIFE-project	PM	Limited budget and staff Cleaning of channels difficult because of changing staff Emerging beaver populations make it difficult to find good release sites	Geist et al. (2021); Motte G. (pers. comm., 2022)
Czech Republic	South Bohemia/ Nature Conservation Agency of the	*M.m.*	1990–present	LI: high HF: *Salmo trutta* (wild and hatchery)	Approx. 1,000 released into Zlatý potok and approx. 50,000 released	National & EU	PM	Collection of natural food (detritus) in winter difficult	Spisar O., Zelenková E., Švaříčková J. & Dort B. (pers. comm., 2022)

(Continues)

TABLE 1 (Continued)

Country	Region/institution	Species	Years/since (ending date)	Level of intensity and method	Rearing success, release, and ratio to wild population age or size	Funding source	GM	Main challenges	References
	Czech Republic, Šumava National Park Administration; practical work Gammarus cz, s.r.o., Bohumil Dort West Bohemia BIVALVIA s.r.o.: Ondřej Spisar			MB: glochidia collected in the field IC: incubator boxes OC: sediment boxes in side channels	into Blanice in 1995–; in 2019, 72 ind. 6+; in 2022, 322 ind. 6+ Blanice: released juveniles make up 10% of the total population Vltava River: May/June 2021, release of 1,000 8–10 year olds; May/June 2022, release of >1,000 6–7 year olds, ~1,000 5-year-old ind. are planned to be released 2023/2027 Malse River: approx. 300 small juveniles have already been released; approx. 1,000 ind. are planned to be released in 2022/24 Lužní Potok: 810 juveniles aged 3+ to 5+ years released in 2016–2019			Difficulties in monitoring released juveniles Vltava River: carp-like fish (cyprinids) spread upstream from Lipno dam, with impacts on trout, which are being displaced from mussel localities Long-term funding is unsure Ensure the quality and quantity of breeding station staff	Hruska (1999); Hruska (2000); Švanyga et al. (2013); Simon et al. (2015); Simon et al. (2017); Bílý et al. (2018); Černá et al. (2018); Bílý et al. (2021); Miloš Holub (pers. Comm., 2022)
Estonia	North of Estonia/ State Forest Management Centre	*M.m.*	2020–present	LI: medium–high HF: *Salmo trutta* (wild) MB: mussels stay in the river and are not disturbed. Host fish are	In total 10,000 0+ mussels in incubator boxes and approx. 440 1+ and 150 2+ mussels in the	National & EU-LIFE projects	No – plan to do in near future	Mussel growth in incubator boxes is low (less than 1 mm on average) by the end of the first autumn; as a result, mortality in	Klaas K. & Kaldma K. (pers. comm., 2023)

TABLE 1 (Continued)

Country	Region/institution	Species	Years/since (ending date)	Level of intensity and method	Rearing success, release, and ratio to wild population age or size	Funding source	GM	Main challenges	References
				caught by electrofishing and detached juveniles are collected with nets. Approx. 100 infested trout are caught from between three and seven river sections and transported to a quarantine centre. If possible, host fish are released after the collection of *M.m.* juveniles IC: incubator boxes OC: Buddensiek cages	native river in Buddensiek cages Incubator boxes: during the first summer juvenile survival was 70%. During the first year, mussel survival was approx. 60% Buddensiek cages in river: in the first summer juvenile survival was 25%. In the first winter 0+ mussel survival was 17%. In the second summer 1-year-old mussel survival was 65%. In the second winter 1+ mussel survival was 82%			the cages was high in the first winter Silt and fine sediments in the river Active beaver population, despite constant hunting	
Finland	University of Jyväskylä/ Konnevesi Research Station	*M.m.*	2016–present	LI: high HF: *Salmo trutta* (hatchery), *Salmo salar* (hatchery). Local fish used, if available in hatcheries. If local fish not available, at least the preferred host (salmon or trout) used, if the most suitable host fish species is known. If it is not known whether the *M.m.*	River Mustionjoki/ Svartå: 200 1-year-old juveniles introduced in gravel boxes in 2019; 93% alive after 3 years. 14,000 0+ juveniles introduced in gravel boxes in 2022. Current population size in river is 1,200. Adult mussels have lost their	National, EU & EU LIFE projects	PM	Problem with copper in pipes when new facility established Only two suitable detritus sources. Collection of detritus difficult in winter Problems with clogging of culture installations Detachment of high numbers of juveniles within a short period of time—high	Hyvärinen et al. (2021) Taskinen J. (pers. comm., 2022).

(Continues)

TABLE 1 (Continued)

Country	Region/institution	Species	Years/since (ending date)	Level of intensity and method	Rearing success, release, and ratio to wild population age or size	Funding source	GM	Main challenges	References
				population is adapted to salmon or trout, then both species are used at the beginning MB: glochidia collected in the field and glochidia collected from adult mussels kept in the facility. In two cases, mussels in poor condition were rehabilitated in the facility for 2 years and they started releasing glochidia. Adult mussels fed with shellfish diet, Nanno, and detritus IC: incubator boxes and trough/flume. Pulsed flow-through system tested but not in regular use now. Fed with shellfish diet, Nanno, and detritus OC: in-river cages, sediment boxes, and Buddensiek cages	reproductive capacity, but recovered with 2-year rehabilitation in captivity River Ähtävänjoki/Esseå: 1,200 2-year-old juveniles introduced in gravel boxes in 2021; 94% survival over 1 year. Current size of the natural population is 800. Adult mussels have lost their reproductive capacity, but recovered with 2-year rehabilitation in captivity River Lutto: 2,000 0+ juveniles introduced in gravel boxes in 2021; 60% survival over 1 year. 4,000 0+-year-old juveniles introduced in gravel boxes in 2022. Current size of the natural population is ~30,000, but the required salmon host cannot ascend to the river			seasonal variation in laboratory Continuation and sustainability of funding	

TABLE 1 (Continued)

Country	Region/institution	Species	Years/since (ending date)	Level of intensity and method	Rearing success, release, and ratio to wild population age or size	Funding source	GM	Main challenges	References
					River Isojoki: 125,000 0+ juveniles introduced in gravel boxes and Buddensiek cages in 2022. Current size of the natural population is 150				
France	Brittany & Normandy/ Fédération de Pêche du Finistère Bretagne Vivante, CPIE des Collines Normandes	*M.m.*	2011–present	LI: high HF: *Salmo trutta* (hatchery) MB: glochidia collected in the field IC: trough/flume fed with commercial algae OC: side channel, sediment boxes, mussel silos, in-river cages	Production: since 2012, several million 0+ *M.m.* harvested and cultured in the trough/flume (in six rivers) Release: several millions, but 96% were 0+, with little indication of survival. Older mussels released at 3–4 cm in size (kept inside facility for 3 years and further kept in outdoor systems until they reach 3–4 cm) Release of approx. 200,000 ind. ranging in age between 1+ and 4+ years Natural population consists of approx. 14,000 adults	National & EU LIFE-project	PM & JM	Cessation of growth in indoor systems after about 3–4 years Funding difficulties after 10 years of operation	Geist et al. (2021); Blaize C. (pers. comm. 2022)
France	Département Dordogne – Région Nouvelle Aquitaine/	*M.m.*	2016–2020	LI: high HF: *Salmo trutta* (hatchery)	During the LIFE programme a total of approx. 30,000 juveniles >8	EU LIFE-project	PM	No continuation of rearing activities at the end of the LIFE project	Legeay A. & Baudrimont M. (pers. comm., 2022)

(Continues)

TABLE 1 (Continued)

Country	Region/institution	Species	Years/since (ending date)	Level of intensity and method	Rearing success, release, and ratio to wild population age or size	Funding source	GM	Main challenges	References
	Université de Bordeaux - Parc Naturel Régional Périgord Limousin			MB: glochidia collected in the field IC: trough/flume fed with commercial and freshly cultured algae OC: in-river cages (cylinder cages)	months (3,300 aged 3 years and between 5–9 mm + 4,300 2 years + 14,800 1 year + 8,000 8 months) and 115,000 post-parasitic ind. have been reintroduced directly in the river 50% of this population come from culture No monitoring of released mussels as the LIFE project ended			Culture of fresh algae as food difficult From time to time water quality issues (pollution) from river used for culture Predation of juvenile mussels in sand trough systems	Belamy et al. (2020)
France	Region Centre-Val de Loire/ Département Indre-et-Loire/ Université de Tours	*P.a.*	2014–2018	LI: high HF: *Acipenser baerii* (hatchery) MB: new mussels collected in the wild every year and kept at breeding facility until release of glochidia IC: incubator boxes and trough/flume fed with commercial algae diet, self-prepared detritus with leaves. Use of egg white as protein source OC: none	Juveniles collected/ year: >10,000 Not able to produce animals older than 4 months No survival in artificial channel No release of older juveniles Freshly metamorphosed juveniles released (2,000) No monitoring of released juveniles	EU LIFE-project	PM & JM	Water quality used in culture. Silt? Pollution? Survival low during first few months Project duration was short. Not enough staff for rearing activity	Soler J. (pers. comm., 2022). Soler et al. (2018a); Soler et al. (2018b); Soler et al. (2019); Wantzen et al. (2019)
Germany	Lower Saxony/ University of Hannover, Lower Saxony State	*M.m.*	1986–2002; 2009–present (Gerdau)	LI: Low – medium HF: *Salmo trutta* (wild)	Survival rate 5%–20% after 1–2 years and <5% after 52 months	National and private	None	N/A	Buddensiek (1995) Altmüller & Dettmer (2006); Altmüller (2023)

TABLE 1 (Continued)

Country	Region/institution	Species	Years/since (ending date)	Level of intensity and method	Rearing success, release, and ratio to wild population age or size	Funding source	GM	Main challenges	References
	Agency for Ecology (FjN) since 2009 FfN and as a retired volunteer		2019–present (Bornbach)	MB: Glochidia collected in the field or mussels kept shortly in aquaria until release of glochidia IC: No OC: In-river cages (Buddensiek/ invented here). Release of wild-caught trout immediately after being infested with glochidia Reintroduction effort River Gerdau: since 2009, release of wild-caught trout immediately after being infested with glochidia from the River Lutter *M.m.* population Reintroduction effort in River Bornbach: since 2019, release of wild-caught trout immediately after being infested with glochidia from the River Lutter *M.m.* population	Release of infested autochthonous *Salmo trutta* and restoration work over decades helped to re-establish a viable population in the River Lutter (increase from 2,500 ind. in 1984 to 16,500 ind. in 2016) No control of success until now in Gerda and Bornbach				Altmüller & Dettmer (pers. comm., 2023) Altmüller & Dettmer (pers. comm., 2023)
Germany	Saxony/Vogtland mussel hatchery	*M.m.*	2001–2007	LI: high HF: *Salmo trutta* (hatchery) MB: glochidia collected in the field or mussels	Two populations from four streams: >9,000 produced; reach 6 mm in three growth seasons; reach	EU Interreg project	JM	Short project duration	Lange (2005), Lange (2009); Lange & Selheim (2011); Geist et al. (2021)

(Continues)

TABLE 1 (Continued)

Country	Region/institution	Species	Years/since (ending date)	Level of intensity and method	Rearing success, release, and ratio to wild population age or size	Funding source	GM	Main challenges	References
				kept briefly in aquaria until release of glochidia IC: incubator boxes, fed detritus from wetland ditches and animal protein OC: in-river cages (Hruška and Buddensiek)	~20 mm after 5 years 4,000 released up to 2010				
Germany	Bavaria/Oberpfalz, fish hatchery Kleeberg	*M.m.*	1997–2007	LI: medium HF: *Salmo trutta* (hatchery) MB: glochidia collected in the field IC: none OC: in-river cages (Buddensiek and other), sediment boxes, and mesh baskets using spring and river water	<100; survival rate <1% in OC	National & EU	None	Low survival	Schmidt & Vandré (2010)
Germany	Saxony/Sächsische Landesstiftung Natur und Umwelt (LaNU) & Vogtlandkreis	*M.m.*	2012–present	LI: high HF: *Salmo trutta* (hatchery) MB: glochidia collected in the field IC: incubator boxes, fed a mixture of detritus (from riparian areas), stream water, and Nanno3600® (*Nannochloropsis* sp.) OC: in-river cages (Buddensiek and	10,000–15,000 0+ juveniles harvested each year. Survival during first summer season, 60%–70%. Survival during first year, up to 30%. Survival during the first 2 years, up to 5%–10% Since 2020, around 1,400 semi-adult mussels have been released in five streams (2020,	National	PM & JM	Variable detritus quality in the field cages during different years Strong annual differences of juvenile performance within the different streams used for release	Jecke et al. (2022); Grunicke et al. (2023); Geist et al. (2021); Grunicke F. (pers. comm., 2022)

TABLE 1 (Continued)

Country	Region/institution	Species	Years/since (ending date)	Level of intensity and method	Rearing success, release, and ratio to wild population age or size	Funding source	GM	Main challenges	References
				other) and sediment boxes	release of 144 subadults (5–7 cm); 2021, release of >1,200 subadults up to 20 years old) Mussel populations in the streams consist mainly of reintroduced mussels from the rearing station and only a few old ind. (around 150 mussels) from the natural populations Released mussels are tagged with shellfish tags; subsample tagged with PIT tags. Release monitoring funded until 2027				
Germany	Bavaria/ Landschaftsp flegeverband Passau	*M.m.*	2007–present	LI: medium–high HF: *Salmo trutta* (hatchery) MB: glochidia collected in the field. Small number of mussels kept at facility for short time together with the host fish for more natural but uncontrolled infestation IC: incubator boxes (since 2019) OC: sediment boxes (wooden boxes,	Survival in the first year about 60% So far, >3,000 juveniles (5+) have been released to support wild populations of about 10,000–13,000 Released ind. have been tagged (Hallprint, subsample PIT tagged). Release monitoring funded until 2027 Releases to wild when juveniles	National	PM & JM	Long development time of species leads to problems in standardizing the procedure, and requires constant adaptation of the processes to variable environmental conditions every year Long-term success in stabilizing the population highly dependent on current stream conditions	Elender F. & Mayr R. (pers. comm., 2011); Denic M. (pers comm., 2022); Geist et al. (2021)

(Continues)

TABLE 1 (Continued)

Country	Region/institution	Species	Years/since (ending date)	Level of intensity and method	Rearing success, release, and ratio to wild population age or size	Funding source	GM	Main challenges	References
				invented here) and Buddensiek cages	measure >15 mm. May take 5–6 years to reach releasable size			Ensure continuity concerning financing and experienced staff	
Germany	Bavaria/Bund Naturschutz Hof	*M.m.*	2018–present	LI: High HF: *Salmo trutta* (different hatcheries and self-bred) and wild. MB: Glochidia collected in the field IC: Incubator boxes OC: In-river cages (Buddensiek) & sediment boxes	Juvenile survival from first cycle 2018–2019 from 3 populations: several hundreds Cycle 2020–2021: >1,000 Cycle 2021–2022: >20,000 Survival rate is growing by better management 3+/4+ old ind.: several hundred from one population Use of PIT tags is planned	EU Interreg & National	PM & JM	Ensure sufficient and consistent funding after initial phase Sufficient water quality and quantity in natural streams Variable detritus quality, in particular during winter cycle Delivery issues with commercial algae	Geist et al. (2021); Degelmann W. (pers. comm., 2022); Höllering D. (pers. comm., 2022)
Germany	North Rhine–Westphalia/ Biological Station StädteRegion Aachen	*M.m.*	2006–present	LI: high HF: *Salmo trutta* (hatchery) MB: mussels kept briefly in aquaria until release of glochidia or glochidia collected in the field Since 2020 collection of glochidia from already cultured animals in the field IC: incubator boxes OC: in-river cages (Buddensiek) and sediment boxes (wood)	River Perlenbach strain, between 2006–2010: 1,000–2,000 juveniles of >1 mm produced per year; 190 juveniles of >30 mm produced using in-river cages Still alive in 2021: 170 animals of >40–70 mm in length In 2020, the first cultured animals started to produce glochidia River Nister strain: 100 animals >20	EU Interreg & National	PM & JM	Sequence of short funding periods by various public donors to start initial phase and afterwards ensure continuity concerning financing staff Difficulties concerning run-off regime, which results in lack of river structure Difficulties maintaining infested fish in public fish hatchery	Selheim H. (pers. comm., 2022)

TABLE 1 (Continued)

Country	Region/institution	Species	Years/since (ending date)	Level of intensity and method	Rearing success, release, and ratio to wild population age or size	Funding source	GM	Main challenges	References
					mm (Rhineland–Palatinate) No animals released free in the river so far				
Germany	Bavaria/Landschafts-architektur Niederlöhner	*U.c.*	2019–2023	LI: medium HF: *Squalius cephalus*, *Chondrostoma nasus*, *Phoxinus phoxinus*, either from local hatchery or caught in the wild MB: new mussels collected in the wild every year and kept in aquaria until release of glochidia. Broodstock then returned to river IC: large sand aquaria OC: trough/flumes	Juveniles >3 mm produced: 200 Released at length of 3–5 mm: 200 Control in the river 1 year later showed 100% survival and good growth About 5% of animals in this population are from cultured ind. Aquaria culture in 2021 was not successful	National	PM	High floods Colmation of substrate in rearing tanks Limited budget for rearing activities (staff and equipment) Loss of host fish in aquaria trial	Pagel M. (pers. comm., 2022)
Germany	North Rhine–Westphalia and Rhineland–Palatinate/Arge Nister/Obere Wied e.V.	*U.c.*	2020–2022	LI: high HF: *Phoxinus phoxinus* (wild), plan to use *Leuciscus leuciscus* and *Squalius cephalus* (wild) as well as *Chondrostoma nasus* (hatchery) MB: new mussels collected in the wild every year and kept in aquaria until release of glochidia. Mussels returned to river	2020: approx. 28,500 juveniles harvested; survival rate during the first phase (0+), depending on breeding location, between 28% and 72%; survival rate after 1 year (1+), 32% Release of approx. 6,500 1+ juveniles by October 2021 into several stream sections 2021: approx. 16,600 juveniles	National	PM & JM	Ensure funding over a period longer than 2 years to ensure long-term investments in mussel monitoring, conservation, and breeding Finding enough adult mussels burrowed deeply into the highly colmated substrate at River Nister	Hugo R. (pers. comm., 2020 & 2021); Koester M. (pers. comm., 2022)

(Continues)

TABLE 1 (Continued)

Country	Region/institution	Species	Years/since (ending date)	Level of intensity and method	Rearing success, release, and ratio to wild population age or size	Funding source	GM	Main challenges	References
				IC: incubator boxes, sand aquaria, and trough/flumes OC: outdoor trough/flumes, sediment boxes	harvested; survival during the first phase (0+), 64% (>10,500 juveniles); release of approx. 2,500 0+ juveniles; around 8,000 kept in flow channels at the breeding station Stein-Wingert				
Germany	North Rhine–Westphalia/Kreis Paderborn and Münster Biologische Station Kreis Paderborn-Senne NABU-Biostation Münster	*U.c.*	2003–present	LI: low HF: *Phoxinus phoxinus*, *Gasterosteus aculeatus* (wild) MB: new mussels collected in the wild every year and kept at fish hatchery until release of glochidia. Mussels retuned to River Paderborn area and Münster area IC: none OC: infested fish released in the respective river	Paderborn area release, of approx. 1,000 infested fish/year Follow up monitoring in 2014 in River Tallebach showed some survival. Most animals lost as a result of muskrat predation in later years	National	None	Coordination between different administrations difficult Project not actively followed and supported by relevant administrations	Dettmer R. (pers. comm., 2022)
Ireland	County Tipperary-South Riding/Aherlow fish farm	*M.d.*	2005–2014	LI: Medium HF: *Salmo trutta* (hatchery & wild) MB: Broodstock on site for encystment of fish. IC: No OC: Juveniles drop-off of hosts into gravel on the tank	Nore population was approx. 300 at the time. Carried out release of approx. 30,000 newly excysted juveniles using the short-term breeding method (Moorkens, 2018).	National	PM	Having dedicated staff who are trained and appropriate facilities that are in the right place In 2013, major silt input from clear-fell forestry upstream killed all	Geist et al. (2018); Moorkens (2018)

TABLE 1 (Continued)

Country	Region/institution	Species	Years/since (ending date)	Level of intensity and method	Rearing success, release, and ratio to wild population age or size	Funding source	GM	Main challenges	References
				bottom (straight and circular tanks used). Different tank for each year class.	Half were buried in best habitat patches and other half released into open water. Survival confirmed 1 year later; more comprehensive checks to take place in 2024 Total was approx. 15,000 juveniles across all cohorts (up to 28 months old and approx. 2.5 mm shell length)			juveniles and many of adult broodstock Danger of another high-silt event possible	
Ireland	County Mayo/ Marine Institute	*M.m.*	2020–present	LI: medium HF: *Salmo salar* (hatchery), *Salmo trutta* in future MB: adult mussels kept at facility to collect glochidia IC: no OC: juveniles drop off hosts into gravel on the tank bottom (straight and circular tanks used). Different tank for each year class	Checked juveniles in gravel at bottom of tank for survival and growth in October and December 2021. Some found and they had grown Wild population consists of approx. 50,000. Plan to put some back into Newport River and perhaps use these juveniles for putting into other rivers, too. Plan to be confirmed	National	None	Still in licensing and learning process Limited experience Very steep learning curve	De Eyto E. (pers. comm., 2022)
Ireland	County Waterford/ Kilmeaden Water Treatment Plant	*M.m.*	2019–present	LI: high HF: *Salmo trutta* (wild and hatchery in season 4)	Good encystment on fish but juvenile capture level was low (none in years	National	None	Capture of juveniles post excystment	Carroll P. (pers. comm., 2022)

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TABLE 1 (Continued)

Country	Region/institution	Species	Years/since (ending date)	Level of intensity and method	Rearing success, release, and ratio to wild population age or size	Funding source	GM	Main challenges	References
				MB: adult mussels kept at facility to collect glochidia IC: limited success in capturing juveniles to date OC: none	1 and 2; 50 juveniles in year 3)			Poor survival rates of host fish from the wild	
Luxembourg	Ardennes Eifel Region/Fondation Hëllef fir d'Natur by natur & ëmwelt	*M.m.*	2008–present	LI: high HF: *Salmo trutta* (hatchery) MB: glochidia collected in the field. IC: incubator boxes, sand aquaria, and trough/flumes OC: sediment boxes, silos, and floating cages on a pond	Juveniles >3 mm produced/year: 3,000–4,000 Released at length of 10 mm/year: 1,000–1,500 River Our strain released in cages: 1,300 3–4 years old River Our strain released in cages alive in 2021: 570 7–9 years old. 100% of this population from cultured ind. Belgium strains released: 8,000 3–4 years old 94% of this population come from cultured ind. German strains released: 800 3–4 years old 100% of this population from cultured ind. Survival at facility until release approx. 3%	EU LIFE project and national funding from LU, BE & DE	PM & JM	Keep survival high during the first year Adequate feeding of 0+, 1+, and 2+ animals at facility Water quality issues in the streams in the area	Eybe et al. (2013); Eybe et al. (2015)

TABLE 1 (Continued)

Country	Region/institution	Species	Years/since (ending date)	Level of intensity and method	Rearing success, release, and ratio to wild population age or size	Funding source	GM	Main challenges	References
Luxembourg	Ardennes Eifel Region/Fondation Hëllef fir d'Natur by natur & ëmwelt	*U.c.*	2012–present	LI: high HF: *Phoxinus phoxinus* (minnow) caught in the wild MB: new mussels collected in the wild every year and kept at breeding facility until release of glochidia. Mussels returned to river IC: incubator boxes, sand aquaria, and trough/flumes OC: sediment boxes, silos, and floating cages on a pond	Juveniles >5 mm produced/year: 2,500–3,000 Released at length of 10 mm/year: 1,000–1,500 River Our strain 2,200 > 2 years old released 13% of this population come from cultured ind. River Sauer strain 3,400 > 2 years old released 22% of this population come from cultured ind. Survival at facility until release approx. 5%	EU LIFE project & national funding from LU & BE	PM	Keep survival high during the first year Adequate feeding of 0+ and 1+ animals at facility Water quality issues in the streams in the area	Eybe et al. (2013); Eybe et al. (2015)
Luxembourg	Ardennes Eifel Region/Fondation Hëllef fir d'Natur by natur & ëmwelt	*U.p.*	2020 single try	LI: medium HF: *Squalius cephalus* caught in the wild MB: mussels collected in the wild and kept at breeding facility until release of glochidia. Mussels returned to lake IC: not used OC: not used	No success in 2020 Almost complete loss of infested host fish Not able to collect juvenile mussels during single try in 2020	National	None	Find adequate host fish strain for this species	Thielen F. (pers. comm., 2022)

(Continues)

TABLE 1 (Continued)

Country	Region/institution	Species	Years/since (ending date)	Level of intensity and method	Rearing success, release, and ratio to wild population age or size	Funding source	GM	Main challenges	References
Norway	Austevoll in Vestland County/University of Bergen	*M.m.*	2012–present	LI: high HF: *Salmo salar* and *Salmo trutta* (2+) bred from wild strains MB: adult mussels collected in the field and kept at the facility to collect glochidia. Mussels returned to the wild after 1 year in quarantine IC: incubator boxes and trough/flume with live algae and detritus OC: sediment boxes	In 2022, 5,400 2+ mussels released directly into three rivers. In 2021, 14,000 mussels released directly into one river. In addition, 50,000 recently dropped mussels were released directly into another river (excess production). Previous releases total 6,400 1- to 7-year-old juveniles into 22 rivers. Releases into boxes for the first years; now (since 2021) only releases into river gravel Releasing ind. at 4 mm length in boxes is acceptable, but free release at larger sizes is better Rivers that have no recruitment are priorities. Many populations have very few mussels left. In most populations, propagated juveniles account for at least 10–100	National	PM & JM	Initially getting systems in place for high survival was a challenge, but systems now refined and no longer a problem Releasing juveniles into rivers with poor water quality limits survival in the wild Evaluating success	Jakobsen P. & Mageroy J.H. (pers. comm., 2022)

TABLE 1 (Continued)

Country	Region/institution	Species	Years/since (ending date)	Level of intensity and method	Rearing success, release, and ratio to wild population age or size	Funding source	GM	Main challenges	References
					times the number of wild adults				
Norway	Storelva River, Tingvoll Municipality, Møre og Romsdal County/ Naturfaglige Konsulent-tjenester and Fisk og miljø-undersøkelse	*M.m.*	2017–2020	LI: high HF: *Salmo salar* (2+) bred from wild strains MB: adult mussels collected in the field and kept at the facility to collect glochidia. Mussels returned to the wild after 1 year in quarantine IC: incubator boxes and trough/flume with live algae and detritus OC: sediment boxes	This was done as a precautionary measure, together with other measures, associated with road construction. The number of mussels released (28) was low compared with the population estimate of at least 3,000 mussels	Regional	None	Difficulties with water quality at the cultivation facility led to very few mussels being produced	Mageroy J.H. (pers. comm., 2022)
Poland	South–Central Poland/The Institute of Nature Conservation of the Polish Academy of Sciences in Krakow	*U.c.*	2020–present	LI: high HF: *Cottus gobio* and trials with *Phoxinus phoxinus* and *Gobio gobio* (wild) MB: new mussels collected in the wild every year and kept at breeding facility until release of glochidia. Mussels returned to river IC: incubator boxes, sand aquaria, and trough/flumes OC: none	In the first year, 30 fish infested with larvae from 30 adult mussels Juveniles collected approx. 100 ind. Approx. 35 10 months old ind. in early 2022 left No release of mussels yet 50–60 adult mussels left in River Nida	EU LIFE+ Project	PM	Lack of mussel culture experience at the beginning of project Breeding facility long distance from project river Not possible to use river water for rearing systems Cages used to keep infested fish in the River Nida were removed and destroyed	Zajac T. (pers. comm., 2022)
Portugal	District Vila Real/ Boticas Parque – Boticas municipality –	*M.m.*	2019–present	LI: high HF: *Salmo trutta* (hatchery)	About 35,000 juveniles from the target populations (rivers Beça and Rabaçal) produced	National/private	PM	Time consuming to train technicians as no previous experience with freshwater mussels	Reis J. (pers. comm., 2022)

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TABLE 1 (Continued)

Country	Region/institution	Species	Years/since (ending date)	Level of intensity and method	Rearing success, release, and ratio to wild population age or size	Funding source	GM	Main challenges	References
	MARE (University of Lisbon)			MB: glochidia collected in the field IC: incubator boxes and trough/flume OC: in-river cages and encysted trout in rivers	so far. To date, no juveniles released to river. Very good survival and growth in raceways. 2020, first drop off, 1,500; 2021, second drop off, 5,000. Trying to grow to taggable size				
Portugal	Northern Portugal/ Castrelos aquatic rearing facility	*M.m.*	2019–2021	LI: high HF: *Salmo trutta* (hatchery) MB: glochidia collected in the field IC: incubator boxes and trough/flume OC: release of encysted trout in rivers	About 6,500 juveniles from the target populations (rivers Paiva, Neiva, and Rabaçal) produced intensively. Estimated 60,000 dropped off from trout in raceways. Encysted trout also released in rivers	EU & National	PM	Time consuming to train technicians as no previous experience with freshwater mussels High fine sediment content of water leading to high fish mortality	Reis J. (pers. comm., 2022)
Portugal	District Viseu/ Campelo aquatic rearing facility managed by Quercus	*M.m.*	2013–2016	LI: high HF: *Salmo trutta* (hatchery) MB: glochidia collected in the field IC: incubator boxes and trough/flume OC: in-river cages and sediment boxes	Over 225,000 juveniles from the target population (River Paiva) produced in 3 years (2013–2015). High mortality caused by lack of detritus in closed systems. Good survival and growth in flow-through systems Some mussels released after 1 year in captivity (2–4 mm in length)	EU LIFE	None	No source for detritus collection to feed the mussels in closed systems Administrative constraints in organization meant follow-up project not possible	Reis J. (pers. comm., 2022)

TABLE 1 (Continued)

Country	Region/institution	Species	Years/since (ending date)	Level of intensity and method	Rearing success, release, and ratio to wild population age or size	Funding source	GM	Main challenges	References
Portugal	District Viseu/ Campelo aquatic rearing facility managed by Quercus	*U.t.*	2013–2016	LI: high HF: *Squalius alburnoides* and *Squalius aradensis* (hatchery) MB: collection of glochidia in the wild IC: trough/flume OC: in-river cages	About 25,000 juveniles from the target population (River Torgal) produced in 2013 and 5,000 in 2015. High mortality owing to inadequate water quality (calcium deficiency) and need to optimize diet. Juveniles could survive up to 10 weeks and grow up to 1 mm	EU LIFE project	None	No source for detritus collection to feed the mussels in closed systems. Administrative constraints in organization meant follow-up project not possible	Reis J (pers. comm., 2022)
Spain	Galicia – Lugo/ University of Santiago de Compostela	*M.m.*	2012–present	LI: high HF: *Salmo trutta* (hatchery and wild) and *Salmo salar* (hatchery) MB: adult mussels kept at facility to collect glochidia. Mussels returned to rivers IC: incubator boxes and suspended sieves on open-circuit aquaria supplied by river water and fed with algae OC: in-river cages (Buddensiek) and sediment boxes	Box culture: achieved a survival rate close to 90% during the first 100 days. Survival after 6 months dropped to approx. 50%. Aquaria: currently, survival to 6 months is around 90% Buddensiek cages: survival results highly variable, survival rate of 50% in the first 6 months Production: incubator boxes, 20,000 (0+ years); aquaria, 30,000 (from 0–2 years); Buddensiek cages,	EU LIFE & National	PM	Perform genotyping of successive cohorts prior to release Conservation status of the species in the Ulla basin not clear. Impact of LIFE project actions not clear Find suitable release sites. Improve breeding protocol for *M.m.* that improves survival and growth while being more efficient Get long-lasting funding from relevant administration	Ondina P. & Varela C. (pers. comm., 2022) Araujo et al. (2018); Castrillo et al. (2020); Castrillo et al. (2021); Castrillo et al. (2022)

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TABLE 1 (Continued)

Country	Region/institution	Species	Years/since (ending date)	Level of intensity and method	Rearing success, release, and ratio to wild population age or size	Funding source	GM	Main challenges	References
					25,000 (0–8 years); in-river cages (sediment boxes), 300 (7, 8 and 9 years old). Total of 75,000 juveniles from different cohorts, 0–9 years old In 2017, 25,400 juveniles at size of 1 mm released in two stretches of the Ulla River Populations in the wild: Eo River, 45,500, hope to release 200 within next 5 years; Arnego River, 20,500, hope to release 1,000 within next 5 years; Ulla basin, 11,500, hope to release 20,000 within next 5 years				
Spain	Aragón/Government of Aragón	*P.a.*	2001–present	LI: high HF: *Acipenser baerii* (hatchery) and *Salaria fluviatilis* (wild) MB: new mussels collected in the wild every year and kept at breeding facilities until release of glochidia.	Juveniles (0+) collected/year: 2,000,000–3,000,000 (99% goes to the Ebro River and canals; 1% is used for breeding in captivity and to perform ecotoxicological tests)	EU (Feader/Leader) & National	PM one river basin More planned	Question on how and where to release the cultured >50 mm animals needs to be solved Issues with adult fertility in the wild Mortality is still high during the first year. Space issues for larger animals at the OC facility	Nakamura K. (pers. comm., 2022) Nakamura et al. (2019)

TABLE 1 (Continued)

Country	Region/institution	Species	Years/since (ending date)	Level of intensity and method	Rearing success, release, and ratio to wild population age or size	Funding source	GM	Main challenges	References
				Broodstock returned to rivers IC: incubator boxes and sand aquaria OC: outdoor trough/ flume supplied with river water; sediment boxes at the bottom of the Ebro River	Juveniles >1 mm produced/year: 500–2,000. Juveniles 20–50 mm > 1,200 in 2022 Release: trials in sediment boxes in Ebro River with few ind. (>40 mm) in summer 2021. Good results (100% survival). Subsequently more than 300 juveniles >40 mm were incorporated in sediment boxes in summer 2022. Once all animals are released, 20%–30% in this population from cultured ind.				
Spain	Girona/Laboratory for breeding naiads at l'Estany de Banyoles, managed by the Consorci de l'Estany	*U.m.*	2010–present	LI: high HF: *Barbus meridionalis* (main use), *Luciobarbus graellsii*, *Squalius laietanus*, and *Salaria fluviatilis* (wild) MB: new mussels collected in the wild every year and kept at breeding facility until release of glochidia. Mussels returned to rivers	Ter and Fluvià river basins (in the river and tributaries) Released infested fish: 4,475 ind. Stocking of released newly excysted juveniles: 87,724 ind. Stocking of juveniles >2 years: 3,596 ind. Banyoles Lake, water intake streams and their drainage channels: estimated	EU LIFE projects & National	None	Adequate feeding and automation of dosage during the first year of life Technical improvements in the feeding and maintenance of juveniles during the fattening phase (from the second year of life) Implementation of the in vitro culture technique Genetic study of parents and	Araujo et al. (2015) Compos M. (pers. comm., 2022)

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TABLE 1 (Continued)

Country	Region/institution	Species	Years/since (ending date)	Level of intensity and method	Rearing success, release, and ratio to wild population age or size	Funding source	GM	Main challenges	References
				IC: trough/flume with cages and sand OC: pools and trough/flume with natural sand at the bottom. Continuous water recirculation and renewal with natural water from Lake Banyoles. Cages placed at the bottom of the lake and floating cages	population of 1,000–2,000 ind. Released infested fish: 3,100 ind. Stocking of released newly excysted juveniles: 71,651 ind. Stocking of juveniles >2 years: 1,267 ind. An overall survival at facility of 5% is estimated			captive bred juveniles	
Spain	Girona/Laboratory for breeding naiads at l'Estany de Banyoles, managed by the Consorci de l'Estany	*U.r.*	2010–present	LI: high HF: *Barbus meridionalis* (main use), *Luciobarbus graellsii*, *Squalius laietanus*, and *Salaria fluviatilis* (wild) MB: new mussels collected in the wild every year and kept at breeding facility until release of glochidia. Mussels returned to rivers IC: trough/flume with cages and sand OC: pools and trough/flume with natural sand at the bottom, and continuous water recirculation and	Banyoles Lake, water intake streams and drainage channels: Between 2010–2013, a population of between 100–200 ind. Was estimated. Released infested fish: 1,910 ind. Stocking of juveniles >2 years: 741 ind. An overall survival of 5% is estimated for this facility	EU LIFE projects & National	None	See Spain *U.m.*	See Spain *U.m.*

TABLE 1 (Continued)

Country	Region/institution	Species	Years/since (ending date)	Level of intensity and method	Rearing success, release, and ratio to wild population age or size	Funding source	GM	Main challenges	References
				renewal with natural water from Lake Banyoles. Cages placed at the bottom of the lake					
Spain	Girona/Laboratory for breeding naiads at l'Estany de Banyoles, managed by the Consorci de l'Estany	*P.l.*	2019–2022 several successful attempts	LI: high HF: *Barbus meridionalis* and *Squalius laietanus* (wild) MB: new mussels collected in the wild every year and kept at breeding facility until release of glochidia. Mussels returned to rivers IC: trough/flume with cages and sand OC: pools and trough/flume with natural sand at the bottom, and continuous water recirculation and renewal with natural water from Lake Banyoles	Between 2010 and 2013, a population of 10–25 ind. was estimated (six ind. were located) in Lake Banyoles, inlet streams, and drainage canals To date, no ind. have been released into the wild	National	None	Technical improvements in the survival of juveniles during the first year of life: feeding and maintenance Technical improvements in the feeding and maintenance of juveniles during the fattening phase (from the second year of life)	Campos M. (pers. comm., 2022)
Spain	Girona/Laboratory for breeding naiads at l'Estany de Banyoles, managed by the Consorci de l'Estany	*A.a.*	2019–2022 several successful attempts	LI: high HF: *Barbus meridionalis* and *Squalius laietanus* (wild) MB: new mussels collected in the wild every year and kept at breeding facility	Between 2010 and 2013, a population of between 50 and 75 ind. was estimated (20 ind. were located) in Lake Banyoles and drainage canals In 2019, 10 ind. of 5–7 cm were	National	None	Improved knowledge of the biological cycle to enhance the capture of glochidia (in local water bodies) Technical improvements in the survival of juveniles during	Campos M. (pers. comm., 2022)

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TABLE 1 (Continued)

Country	Region/institution	Species	Years/since (ending date)	Level of intensity and method	Rearing success, release, and ratio to wild population age or size	Funding source	GM	Main challenges	References
				until release of glochidia. Mussels returned to rivers IC: trough/flume with cages and sand OC: pools and trough/flume with natural sand at the bottom, and continuous water recirculation and renewal with natural water from Lake Banyoles	released in a ditch in Lake Banyoles. In 2021, 100% survival was observed			the first year of life: feeding and maintenance	
Sweden	Gothenburg/Swedish Anglers Association	*M.m.*	2021–2026	LI: medium HF: *Salmo trutta* (hatchery) MB: adult mussels kept at facility to collect glochidia IC: incubator boxes OC: installation of plastic boxes with holes drilled into sides and gravel on bottom holding two to four mussels and host fish to become naturally infested. Fish and mussels released after infestation has occurred	Population sizes vary, but approx. 200–2,000 adults. Hope that the number of mussels reared will exceed number of adults in the wild	EU LIFE	PM	Flatworms eating juveniles	Wengström, N. (pers. comm., 2022)
Sweden	Southern Sweden/ Karlstad University and Hemmestorps mölla	*U.c.*	2012–2018	LI: medium HF: *Phoxinus phoxinus*, *Cottus gobio*, and *Alburnus alburnus* (wild). Some other fish	Released several thousand at size of 0.4–0.6 mm In 2017 as part of AfterLIFE programme	EU LIFE & National	PM	Getting the breeding station right – filtering the water, ensuring the pump worked, and	Österling M. & Schneider L. D. (pers. comm., 2022) Schneider et al. (2017)

TABLE 1 (Continued)

Country	Region/institution	Species	Years/since (ending date)	Level of intensity and method	Rearing success, release, and ratio to wild population age or size	Funding source	GM	Main challenges	References
				species were tested MB: adult mussels kept at facility to collect glochidia IC: incubator boxes and sand aquaria OC: infestations of wild fish in the field and direct release upon infestation. Use of fish cages installed in the rivers for several weeks. Use of Buddensiek cages, cylinder cages, adjusted Withlock–Vibert boxes, and release of juveniles free to the rivers	released 1,200 ind. into two rivers Prolonged breeding between 2017 and 2018 with release of 1,400 1-year-old juveniles to the habitat restored rivers in 2018. No wild ind. in these rivers Translocation of adult mussels to habitat restored rivers and monitoring on an annual basis between 2015 and 2017, and in 2021 Monitoring done in 2021 – no juveniles recorded but some of the translocated adult mussels were found to be gravid			maintenance of the system Resource-intensive and time-consuming Difficulties in evaluating reintroduction success as no juvenile mussels were found post reintroduction	
Sweden	County Sormlrand/ Swedish Anglers Association	*U.c.*	2018–present	LI: high HF: *Phoxinus phoxinus*, *Cottus gobio*, and *Rutilus rutilus* (wild) MB: adult mussels kept at facility to collect glochidia IC: sediment boxes in a flow-through system OC: none	Number of adults: Forsaån, <500; Vedaån, >500 No release yet	National	None	Flatworms eating juveniles Longer-term funding challenge Keeping juveniles alive is a problem	Wengström, N. (pers. comm., 2022)
Switzerland	Canton of Aargau/ Canton of Solothurn/	*U.c.*	2012–present	LI: high HF: *Phoxinus phoxinus* and	Juveniles collected/ year: 1,000–2,000.	National, Cantonal & by	PM	Find suitable rivers for release	Schwarzer A. (pers. comm., 2022)

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TABLE 1 (Continued)

Country	Region/institution	Species	Years/since (ending date)	Level of intensity and method	Rearing success, release, and ratio to wild population age or size	Funding source	GM	Main challenges	References
	Independent consultant			*Squalius cephalus* (wild) MB: new mussels collected in the wild every year and kept at breeding facility until release of glochidia. Mussels returned to river IC: incubator boxes and sand aquaria OC: sediment boxes for 4–5 years	Juvenile growth/ year: 20–30 mm Release in cages: 75 ind. in selected streams Release completely free into river: eight 5-year-old ind. in selected streams	independent foundations		Difficulties achieving stable survival and growing conditions during the first months Vandalism on outdoor rearing cages	
UK, Northern Ireland	County Tyrone/ Ballinderry Rivers Trust	*M.m.*	2009, 2014–2017	LI: medium HF: *Salmo trutta* (hatchery) MB: mussels kept at hatchery to infest fish IC: Trough/flume. Juvenile mussels fall naturally into gravel-filled flume OC: Mussel silos for bioindication	2,819 released to date: 150 released across three sites in 2009; 328 at one site in 2014; 118 at one site in 2015; 88 at one site in 2016; 2,135 across three sites in 2017 PIT and Bee tags used Straight to river substrate and Barnhart silos 20,000 fish encysted each year between 1999 and present	National & EU LIFE	None	Some release patches have been scoured out completely, whereas others show good persistence	Preston, Keys & Roberts (2007); Wilson, Roberts & Reid (2011)
UK, Scotland	County Aberdeenshire/ University of Aberdeen – Culterty Field Station	*M.m.*	2001–2003	LI: medium HF: *Salmo salar* (hatchery) MB: mussels kept for some time at hatchery to infest fish IC: no	<100 several-year-old juveniles produced; 1%–11% survival rate <10 months, later 80% loss of cage systems	EU LIFE	None	N/A	Hastie & Young (2003)

TABLE 1 (Continued)

Country	Region/institution	Species	Years/since (ending date)	Level of intensity and method	Rearing success, release, and ratio to wild population age or size	Funding source	GM	Main challenges	References
				OC: sediment baskets supplied with flowing river water. In-river cages (Buddensiek). Release of artificially infested fish					
UK, England	Cumbria/Freshwater Biological Association (FBA)	*M.m.*	2007–present	LI: high HF: *Salmo salar* and *Salmo trutta* (wild and hatchery, respectively) MB: new broodstock collected every 1–3 years. Adult mussels kept at facility to collect glochidia IC: downwelling aquarium and flumes OC: trough/flume and FLUPSYS supplied with filtered lake water	Approx. 30,000 juveniles (>3 mm length) from six different English and one Welsh populations. High survival observed for >3–5 mm. Released >1,300 juveniles/subadults (>15 mm) into Irt in 2021 (wild population remaining was 300 adults) Other river releases planned for next 5 years are:Brathay, 80, current population, 9;Clun, 1,500, current population, approx. 1,500;Ehen, 3,000, current population, approx. 300,000; Esk, 200, current population, approx. 1,500;Kent, 4,000, current population, 4. Releases to wild when juveniles	National & EU LIFE.	PM & JM	Long term (>3 years) commitment to funding Staffing too low to cover both breeding and release activities Number of juveniles in each cohort now large so space issues within current set-up	Lavictoire et al. (2016); Lavictoire et al. (2020); Geist et al. (2021)

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TABLE 1 (Continued)

Country	Region/institution	Species	Years/since (ending date)	Level of intensity and method	Rearing success, release, and ratio to wild population age or size	Funding source	GM	Main challenges	References
					measure >15 mm. Takes 5–8 years to reach release size. To date, released ind. have been tagged (PIT tags and Hallprint tag; Hindmarsh Valley, Australia)				
UK, Wales	County Powys Cynrig Hatchery (Brecon), Clywedog Hatchery, Llanidloes	*M.m.*	2005–present	LI: high HF: *Salmo trutta* (wild/local and farmed), *Salmo salar* (northern rivers), and *Salvelinus alpinus* – research MB: mussels kept long term in living gene bank IC: initial rearing in incubator boxes and recirculating troughs and aquaria; transfer at 2 mm to reservoir-fed site; flow-through troughs up to 7 mm OC: transfer to tanks of 2 m in diameter in baskets of gravel up to 6+ years	Early attempts: survival in flow-through river water systems poor Now: 50%–70% survival in plastic boxes; 70% survival in re-circulating troughs; 90%+ survival from 1+ to 6+ in semi-natural flow-through reservoir-fed system Current stock for release: 1,200 4–6 year olds, 2,000 2+, 10,000 1+, 30,000 0+ in early culture. At present there are five wild populations with approximately 300, 300, 150, 50, and <10 adults remaining	National & EU	None	Initially: low resource provision; difficulty in securing a representative founder population, with adults generally sparsely spread out; most donor populations are low in numbers and very old; quality of juveniles unpredictable Box rearing requires high resources. Occasional problems with excessive flatworm predation. Growth of older juveniles (4+) is slow	McIvor & Aldridge (2008); Thomas, Taylor & Garcia de Leaniz (2010); Scriven et al. (2011); Thomas, Taylor & Garcia de Leaniz (2013); Taylor J. (pers. comm., 2022)
UK, England	Northumberland/ Kielder Salmon Centre,	*M.m.*	2010–present	LI: high HF: *Salmo trutta* (hatchery successful) and	Fish with glochidia released 2011–2018. Approximate estimate of	National	PM & JM	Low encystment rate (low in % of fish encysted and in	Gosselin (2015)

TABLE 1 (Continued)

Country	Region/institution	Species	Years/since (ending date)	Level of intensity and method	Rearing success, release, and ratio to wild population age or size	Funding source	GM	Main challenges	References
	Environment Agency			*Salmo salar* (hatchery unsuccessful) MB: mussels kept at hatchery to infest fish IC: incubator boxes OC: juveniles moved to flow-through trough/flume supplied with river water. Release of artificially infested fish	glochidia released: 825,000. Current living juveniles from 2017/2018 spring/summer collection approx. 20 > 1.5 cm, 2019 spring/summer collection approx. 200 > 5 mm, 2021 spring/summer collection approx. 80 > 1 mm, 2022 winter collection approx. 200 < 1 mm. High mortality in each year group, especially in first few months, common obvious cause of mortality *Saprolegnia* infection Plan to release mussels when >15 mm			encystment density) High mortality in each year group especially in first few months, common obvious cause of mortality: *Saprolegnia* infection (mortality rates >60%)	

Note: Method level of intensity (LI) is provided together with details about host fish used (HF), mussel broodstock situation (MB), indoor culture (IC), and outdoor culture (OC) systems used. GM, genetic monitoring (PM, parent mussels; JM, juvenile mussels).
Abbreviations: *A.a.*, *Anodonta anatina*; ind., individuals; *M.d.*, *Margaritifera durrovensis*; *M.m.*, *Margaritifera margaritifera*; *P.a.*, *Pseudunio auricularius*; *P.l.*, *Potomida littoralis*; *U.c.*, *Unio crassus*; *U.m.*, *Unio mancus*; *U.p.*, *Unio pictorum*; *U.r.*, *Unio ravoisieri*; *U.t.*, *Unio tumidiformis*.

place primarily via video-conferencing, by phone, or, to a lesser degree, by email. The answers given were formatted in a standardized way, to enable comparison, and are presented in Table 1.

3 | RESULTS AND DISCUSSION

3.1 | Existing rearing and culturing programmes for freshwater mussels in Europe

In this review, 46 captive rearing and culturing initiatives dating back to 1989 were identified (Table 1). These initiatives cover 16 countries and 10 species of freshwater mussels. This includes the endangered freshwater pearl mussel *M. margaritifera* and the Irish *Margaritifera durrovensis*, as well as the giant freshwater pearl mussel *Pseudunio auricularius*, occurring only in Spain and France. Five *Unio* species (the thick-shelled river mussel *Unio crassus*, the painter's mussel *Unio pictorum*, as well as *Unio mancus*, *Unio ravoisieri*, and *Unio tumidiformis*) and *Potomida littoralis* have also been propagated. Among the pond mussels (Anodontinae), only *Anodonta anatina* has been propagated.

The efforts for captive breeding are very unevenly distributed among these 10 species, with the vast majority of activities being exclusively focused on *M. margaritifera*, and, to a lesser but increasing extent, on *U. crassus*. Some activities focus on propagating species in a very critical situation, such as *P. auricularius*, *U. mancus*, and *U. ravoisieri*, or multiple species concurrently. In proportion with the efforts put into captive breeding, most is known about glochidial release times as well as culturing and rearing practices for the freshwater pearl mussel, followed by the thick-shelled river mussel and the giant freshwater pearl mussel, whereas far less is known about these aspects for all other species.

In most cases, existing breeding programmes cover the core areas of species distribution, with some exceptions. For instance, it is alarming that currently only the Spanish captive breeding programme is in place for the highly endangered *P. auricularius*, as previous programmes covering the remaining core distribution area of this species in France have come to an end. Several countries operate multiple breeding stations for the same species to address geographical coverage and risk mitigation, whereas some programmes serve populations in several countries. Most breeding programmes have received funding through either national or EU LIFE(+) projects of limited duration (typically a maximum of 5–8 years; Table 1).

In *M. margaritifera*, the species upon which the majority of captive breeding efforts have been focused, there is already evidence that some of the released captive-bred mussels have started to reproduce, e.g. in the River Lutter (Germany). In some streams, the number of released captive-bred mussels already exceeds the size of the remaining natural population.

3.2 | Different intensities of rearing techniques

Most rearing techniques try to bridge the critical juvenile stages in the life cycle of mussels (i.e. the parasitic and early post-parasitic phases) by providing optimal conditions during this time. Breeding approaches vary greatly in the intensity, size, species, numbers of juveniles produced, and the age/size at which they are released into the wild (Figure 1; Table 1,). They also differ in monitoring intensity with regards to the genetic monitoring of the offspring, which is in place in about half of the programmes. At the highest intensity level, parent mussels are collected in the wild and transferred into a hatchery where they remain either permanently (ark-type system) or for extended periods of time. Examples are the Windermere station in the UK, where freshwater pearl mussels from five rivers are kept, typically for between 2 and 36 months, before being returned to the wild, although one broodstock population has been present at the Ark for 13 years. Upon glochidial release, host fish, also maintained at the facility, are infested, and after drop-off juvenile mussels are maintained in a variety of recirculating and flow-through systems until they reach a size of about 15–20 mm. Sizes can vary depending on species and location. Such highly intensive systems are usually free from many of the adverse conditions in mussel rivers, but also bear a greater risk of a total loss of multiple populations owing to the aggregation of mussels in one place (e.g. when systems fail and suitable emergency systems are absent). These high-intensity programmes tend to be looked upon less favourably by conservationists, unless habitat and catchment restoration is being carried out concurrently with the captive breeding activities. The feeding of juveniles is considered a major challenge as maintaining mussels in the hatchery often requires the labour-intensive collection of detritus from natural sources. In addition, commercially available algal food is often used (Gatenby, Neves & Parker, 1996), which together with water and detritus from the same habitat as the parent mussels, have yielded successful results for juvenile survival and growth.

At the other extreme, some programmes, such as the freshwater pearl mussel conservation programme in the River Lutter, are largely field based and independent of technical facilities. Each year a small number of ripe mussels are collected from the river and used to infest wild electrofished or hatchery-reared host fish with those glochidia, before releasing the infested fish into the river. This system has a low risk of affecting the genetic constitution of the offspring, especially if different parent mussels are used each year, but it bears the risk of being largely unsuccessful if stages other than the parasitic phase of the life cycle are the main bottleneck. This is often the case with the freshwater pearl mussel, where colmated and oxygen-deficient stream beds are considered the main bottleneck for recruitment in Europe (Geist & Auerswald, 2007; Denic & Geist, 2015; Simon et al., 2015), as low oxygen levels evidently compromise the survival of juveniles (Hyvärinen et al., 2022).

The methods used in any particular facility depend upon factors such as the infrastructure available, the water source, and the amount of staff time and funding available. Where specialist facilities are available and there are staff to monitor broodstock, fish, and juveniles, high and medium intensity methods, as described in Figure 1, can be used. Pulsed flow-through systems (Patterson et al., 2018; Hyvärinen et al., 2021), incubator/detritus boxes (Eybe et al., 2013; Scheder et al., 2014; Nakamura et al., 2018; Grunicke et al., 2023), flumes, aquaria systems (Lavictoire et al., 2016; Lavictoire et al., 2020), and the

FIGURE 1 Captive breeding methods used for freshwater mussels throughout Europe. Coloured dots on the map refer to the different techniques described in the note boxes. Boxes 1 and 2 describe high-intensity methods, requiring maintenance at least once per week; boxes 3–5 describe medium-intensity methods, requiring maintenance at least once per fortnight; and boxes 6–10 describe low-intensity methods, requiring maintenance approximately monthly, or as needed

Floating Upweller System (FLUPSYS) (Patterson et al., 2018) all require medium to high levels of attention. The most resource-intensive systems per juvenile reared are the incubator/box and the pulsed flow-through systems (Kunz et al., 2020; Hyvärinen et al., 2021). In the incubator system, juveniles are kept in static water in boxes (with usually 200–500 individuals per box) and are cleaned and supplied with fresh water, food, and detritus one or two times per week. The pulsed flow-through system provides water (and food) changes at regular intervals (as much as once per hour), but there are usually no more than 50–100 juveniles per beaker. The lower resource-intensive systems are the downwelling aquarium system (with 1000 juveniles per sieve, and containing 12–15 sieves, cleaned every 2 weeks), the sand aquaria (with 150–500 juveniles per system, and a weekly water exchange), FLUPSYS (with several hundred to 1000 juveniles per bucket, and cleaned when necessary), and flumes (with several thousand individuals per flume, and cleaned when necessary).

The lower intensity and more field-based systems (boxes 6-10, Figure 1) can be used when space in specialist facilities is limited or absent. The smallest juveniles (freshly excysted from fish) can be placed into in-river cage systems. These systems, placed in mussel rivers, still need regular cleaning and maintenance, but are relatively low effort in relation to facility-based systems. Juveniles of >4 mm can be placed into mussel silos, again with regular cleaning (monthly), whereas slightly larger juveniles (>10 mm) can be placed in sediment boxes (Bílý et al., 2018) or into side channels (often referred to as Hruška channels; Hruska, 1999; Hruska, 2001; Gum, Lange & Geist, 2011), as a soft-release method before being stocked into final release sites. Sediment boxes need some cleaning and maintenance, but the side-channel method requires almost no maintenance.

3.3 | Challenges associated with mussel captive breeding programmes

The primary challenges identified in the majority of captive breeding programmes are related to limitations in budget or staffing, and to rearing conditions such as water quality, feeding, and the survival of juveniles during early life stages (Table 1). Concerning budget limitations, the short duration of funding schemes over only a few years, especially for long-lived species such as *M. margaritifera*, is a more serious constraint than the funding level when starting new programmes. As *M. margaritifera* only become mature at an age of 10–15 years (Young & Williams, 1984), the typical funding schemes, with a maximum duration of 3–6 years in this species, only cover the rearing of a few cohorts of sexually immature juveniles. Furthermore, uncertainty in the continuation of funding decreases the retention of experienced staff and is out of step with the biological pace of some freshwater mussel species. Frequently, setting up and maintaining breeding programmes can also be complicated by water quality issues, the provision of natural or purchased feed for early life stages, and high mortality rates, sometimes culminating in the loss of an entire year cohort. Rearing systems dependent on an external water supply especially face a greater risk of unforeseen water quality issues, such as cyanobacteria blooms (Norwegian breeding station Austevoll), excess turbidity, and fine sediment loading (Austrian breeding station), as well as water quantity issues (as observed in dry summers in the German breeding station near Hof). At later stages of the mussel life cycle, the identification and limited availability of habitat of sufficient quality into which the juveniles can be released are reported as additional challenges (Table 1). In addition to the challenges directly associated with the captive breeding of mussels, monitoring them after their release is another key issue. Such monitoring is essential for assessing the suitability of recipient water bodies for captive-bred juveniles, identifying the ideal release sites, and determining the ideal captive breeding procedures that result in the greatest survival in the wild.

3.4 | Recommendations for the future

Despite progress in the captive breeding of freshwater mussels, their sustainable conservation will always depend on the conservation or restoration of habitats and catchments. While conservation and restoration projects continue, captive breeding programmes can help to save small populations from extinction and boost the number of individuals for eventual release back into the wild once the habitats are capable of supporting early-stage juvenile mussels. Based on information from current freshwater mussel breeding stations in Europe, the following measures are suggested for improvement.

3.4.1 | Provision of species- and basin-wide European conservation strategies for freshwater mussel species with long-term funding commitments

The provision of long-term funding options to secure acquired specific knowledge and continuous action for long-lived mussel species is crucial and key to success. The fauna discussed here are long-lived, slow-growing species, and mussel catchments are so significantly degraded that in most cases habitat restoration may take more than a decade. Also, from a genetic point of view, continued captive breeding over multiple generations can help to prevent the erosion of genetic diversity (Geist et al., 2021). Owing to the dominance of funding for captive breeding provided by the European Union LIFE/LIFE+ programmes and national funds with limited running times of 5 years or less, easy options for project extensions following an objective and independent review at intermediate stages would be most welcome and useful. Species- and basin-wide European conservation strategies for freshwater mussels will ensure that programmes have the best chance of success.

3.4.2 | Science- and evidence-based support in the development and evaluation of breeding programmes

A significant volume of work has been carried out by breeding programmes to improve efficiencies and increase the number of juveniles surviving in captivity. However, much of this valuable work does not get published in the primary literature, limiting its impact. Although there is a strong and collaborative European network of mussel breeding programmes, more science- and evidence-based support (with the subsequent publication and dissemination of results) is needed to drive faster paced positive outcomes. The development of breeding programmes requires the integration of genetic information, as demonstrated for the freshwater pearl mussel (Geist et al., 2021), as well as a critical evaluation of the impacts of captive breeding procedures on the progeny, and ultimately on the long-term success of different rearing methods in aiding the re-establishment of functional populations in the wild.

3.4.3 | Increased knowledge exchange and training opportunities

Although the diversity of different approaches to mussel breeding is generally useful, by increasing the overall system resilience and minimizing the high losses of juvenile mussels, e.g. related to feeding, these issues could be reduced by an increased level of information exchange and training. There are often very limited or no funds for exchange and training opportunities. Therefore, there is a need to provide trans-European funding, which allows scientific and practical exchange among existing and newly planned breeding programmes. In the past, most of the exchange among breeding stations has happened through local conferences held, for example, within existing LIFE(+) projects, thus being sporadic in time and place. Within the European COST project CONFREMUS (2023), an intensified exchange among mussel experts and mussel breeders has been initiated for the first time, albeit time-limited to when this project ends in 2024. Continuation and expansion (where appropriate) of such successful initiatives is important for ensuring a well-connected network of experts who communicate new findings in a timely manner and who are available for training those new to mussel conservation.

3.4.4 | Coordinated action related to species and geographical representation as well as genetic aspects

Despite the success stories of many captive breeding efforts at the European scale, there is still no coordinated approach among them in terms of species, geographical, and genetic representation. The development of a coordinated European strategy for captive mussel breeding, ideally integrated into habitat and catchment restoration plans – all of which should be evidence-based and supported by scientific research – would be needed to increase the effectiveness of such programmes. This should ideally be integrated into the development of minimal standards for captive mussel breeding, concerning animal welfare aspects of host fish use, disease prevention, maintaining genetic integrity of captive-bred mussels, and minimizing extinction risk, as well as requirements of tracking and assessing the success of mussel releases. It may also be necessary to prioritize conservation actions (Geist, 2015) to ensure the best remaining occupied sites within each catchment are secured, rather than spreading conservation action too thinly to attempt to conserve marginal populations and risk failure owing to a lack of resources.

3.4.5 | Guidelines for assessment of success of the breeding action and risk mitigation

Together with the production of country-wide/European conservation strategies, the production of guidelines to assess breeding programme success and how to mitigate risks would be valuable for new programmes. Guidelines would also help to standardize the way in which current breeding programmes communicate their outputs, driving an increased awareness of factors affecting success and how risks can be minimized. In future, information on which species, numbers, and sizes/ages of mussels are being stocked at which locations needs to be collected more systematically and beyond the level of individual stations. The successful development and implementation of a standard approach for monitoring freshwater pearl mussel (*M. margaritifera*) populations in European rivers (Boon et al., 2019) and the continuing development of a new European Committee for Standardization (CEN) standard on mussel monitoring for a wider range of species illustrate that such action is possible, even with limited levels of funding. This parallels strategic conservation approaches in North America, where a national strategy for the conservation of native freshwater molluscs has been developed (FMCS, 2016).

CONFLICT OF INTEREST

The authors have no conflicts of interest associated with this work.

AUTHOR CONTRIBUTIONS

JG, LL, and FT jointly led the study, conducted and analysed the interviews, and are the principal authors. *Conceptualization*: JG, LL, and FT. *Methodology*: JG, LL, and FT. *Data curation*: all authors. *Visualization*: LL, FT, and RH. *Investigation*: JG, LL, and FT. *Writing—original draft*: JG. *Writing—review and editing*: all authors. All authors have read and agreed to the published version of the article.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author, upon reasonable request.

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