ADDRESSING THE CONSERVATION AND REHABILITATION OF *MARGARITIFERA MARGARITIFERA* (L.) POPULATIONS IN THE REPUBLIC OF IRELAND WITHIN THE FRAMEWORK OF THE HABITATS AND SPECIES DIRECTIVE

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Abstract *The freshwater pearl mussel* Margaritifera margaritifera *is in serious decline in Europe and is protected under the EU Habitats and Species Directive (92/43/EEC). In the Republic of Ireland, most populations require habitat rehabilitation through catchment management in order to secure their future. A series of six filters have been developed to aid prioritisation of measures to be undertaken in order to provide the best return for effort in terms of attaining sustainable populations in favourable conservation status. The results show that prioritisation of the largest populations in the closest to sustainable conditions is of key importance, and that appropriate catchment management measures need to be urgently implemented as there can be a long time delay in the recovery of suitable habitat conditions. The methodology may serve as an example and could be adapted by other countries to produce a scientific rationale for their own prioritisation strategies.*

Key words Margaritifera margaritifera, *freshwater bivalves, catchment management, conservation strategy.*

INTRODUCTION

Unionoid freshwater mussels are among the most endangered group of species in the world (Bogan, 1993; Neves, 1993). In Europe, the decline of the freshwater pearl mussel *Margaritifera margaritifera* (L.) has been highlighted regularly over the last thirty years (Bauer, 1986; Araujo & Ramos, 2001; Young *et al*., 2001) and work has been carried out on populations across the EU, including many EU-funded projects under the LIFE programme (e.g. Vandré, 2006; Henrikson, 2006).

The Republic of Ireland has approximately 12 million adult individuals of freshwater pearl mussel in 139 rivers, and has designated 19 Special Areas of Conservation for the species under the EU Habitats and Species Directive (92/43/EEC) that includes 27 populations in 37 rivers, one population of which is the Nore pearl mussel *Margaritifera durrovensis*, which is listed as a separate taxon under the directive and is highly endangered (Moorkens & Costello, 1994; Moorkens, 2006). Under the direction of the Minister for the Environment, 27 catchment management plans are being finalised with the objective of the rehabilitation of favourable habitat conditions for this declining species (NS2, 2010). The conclusions from the catchment plans are that a very large effort of necessary conservation management is needed and highlighted that these efforts must be strategically prioritised.

Conservation of the freshwater pearl mussel is complicated by the species' unusual longevity and life history (Moorkens, 1999; Skinner *et al*., 2003). *Margaritifera* is highly demanding of very clean river habitats in order to be self-sustaining, but it lives for over 100 years, and thus non-sustainable populations of adult mussels can persist for many years after negative changes in the habitat have occurred (Araujo & Ramos, 2000; Hastie *et al*., 2000; Geist, 2010).

While a range of possible causes of decline can exist (e.g. direct habitat damage, acidification of rivers, depletion of mussels from pearl fishing activities), the overwhelming majority of population declines in Europe have been due to poor conditions in juvenile habitats, which cause juvenile mortality (Buddensiek *et al*., 1993). Specifically, most population problems can be linked to sediment accumulation in the river bed gravels, often exacerbated by elevated nutrients, cutting off the supply of oxygen to juvenile mussels, which live entirely within the river bed sediment. Under these conditions, new generations of mussels cannot be recruited, while older adults that were born before the habitat deterioration remain alive as they are filtering open rather than interstitial water.

The source of pressures that lead to this decline come from the catchment into the river, thus protection and rehabilitation of mussel populations

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is impossible without effective catchment management that is protective to the juvenile mussel habitat. The work carried out in Ireland to date has demonstrated strong correlations between the largest and most successfully recruiting populations and low-intensity land management (Moorkens, in press). However, some famous historical populations persist in low numbers in large, lowland rivers, where adults may be living in habitats that could not possibly sustain juveniles. This is because the shallower areas they were born in have become degraded and remaining adults are often those that are washed into pools downstream, particularly at silted bank edges. Thus the genuine mussel habitat to be rehabilitated may not even be in the vicinity of the current adults.

Margaritifera requires the presence of a temporary host salmonid fish to complete its life cycle, and in different rivers this host may be either trout or salmon, and the interaction of native strains of mussels and fish may be important to the success of the mussel population. Mussel genetics also vary across Europe, and thus conservation of genetic units are considered to be important in conserving enough variation to allow for adaptive change into the future (Geist & Kuehn, 2008; Geist, 2010).

The freshwater pearl mussel is unique in the combination of factors that need to be addressed in order to direct conservation management that will lead to positive and sustainable results. Thus it is vital across the EU range to identify the populations and efforts that need to be prioritised to allow the recovery of these populations. The Natura 2000 sites for the freshwater pearl mussel were largely chosen during the 1990s, before detailed information could be collected and a comprehensive strategy for conservation developed. Therefore, the conservation priorities implicit in some Natura 2000 site designations may not have been well founded. Scientifically, it is useful to look more critically on what level of rehabilitation is achievable, both inside and outside the Natura 2000 network, in order to focus conservation work on that which is most likely to produce sustainable *Margaritifera* populations.

This paper presents a possible strategy based on a scientific approach and outlines the likely consequences of that strategy. The technique could have application in other regions trying to conserve *Margaritifera*.

Methods

The catchment plans for the 27 pearl mussel populations have been written following a large body of work undertaken during 2008 and 2009 (NS2, 2010). The results of this work have been used in the interpretation of the issues in each catchment and in the development of this strategy. Of the 27 populations, 12 have had full baseline monitoring throughout their catchments, and the rest have had at least some survey work carried out in the past. The methodologies and information accumulated in the present project are described below.

Margaritifera *density and habitat survey* The river and tributaries were either waded upstream and examined using a bathyscope or snorkelled downstream according to standard Irish survey methods (Anonymous 2004). Densities of mussels were evaluated according to an abundance scale as follows:

1. Abundant / at capacity in places (> 1,500 / 100 m length river, if at capacity > 250 / m^2 in appropriate habitat)
2. Common to good numbers, not at capacity (301–1,500 / 100 m length river)
3. Frequent (41–300 / 100 m length river)
4. Occasional / Rare (1 to 40 / 100 m length river)
5. Absent

Where mussels were absent but potential habitat was present, this was noted in the survey.

Population demographics and juvenile searches As lack of recruitment of young mussels is the main way in which mussel populations decline, it is important to establish whether effective recruitment is taking place. This was done by measuring individual mussels to establish the population profile (ideally at least 250 mussels). As exact aging of mussels cannot be carried out on live individuals, mussel lengths are measured and ages are estimated by fitting size profiles to age profiles established in previous studies.

The size structure of a population is determined by removing all of the mussels from a fixed area of substrate and measuring them. This was done in a stable area of mussel bed such that it did not destabilise the disturbed area or the area surrounding it. The method consisted of laying a 0.5 m×0.5 m metal quadrat on the river bed and counting the number of mussels visible from the surface. The visible mussels were then carefully removed from the quadrat with as little disturbance to the substrate as possible. The substrate was then disturbed with the fingertips and any additional mussels counted and removed. Finally, an aluminium framed sampling net equipped with a 0.5 mm nylon mesh bag was placed vertically on the downstream side of the quadrat and the substrate was gently agitated with the fingertips to allow any remaining mussels to come to the surface and any very young (<15 mm) individuals to be swept by the water current into the net. All mussel lengths were measured and the population demographic profile established. The measured mussels were then carefully reburied in the substrate they were taken from. In addition, all dead shells found in the surveys were collected and measured. Sufficient quadrats were sampled to provide at least 250 mussels from the river.

Habitat condition and pressures The habitat condition and the extent of pressures potentially affecting the population were assessed in each catchment from the uppermost part of the catchment downstream to the last record of freshwater pearl mussels. An assessment of the hydro-morphological conditions was made using the River Hydromorphology Assessment Technique (RHAT), developed to classify rivers in terms of their morphology (Northern Ireland Environment Agency, 2009). RHAT surveys were used as a method to aid identification of high risk areas which were then correlated with ecological factors from other surveys. RHAT classifies river hydromorphology based on a departure from naturalness, and assigns a morphological classification directly related to that of the Water Framework Directive: high, good, moderate, poor, and bad, based on semi-quantitative criteria. The eight criteria that are scored are:

1. Channel morphology and flow types
2. Channel vegetation
3. Substrate diversity and embeddedness
4. Channel flow status
5. Bank and bank top stability
6. Bank and bank top vegetation
7. Riparian land use
8. Floodplain connectivity

Where nutrient enrichment and siltation have been identified as likely causes of the decline and recruitment failure of the pearl mussel population, investigations were undertaken to identify the significant sources of these pollutants within the catchment. Firstly, a desktop study was used to identify pressures and their sources from national datasets and detailed aerial imagery. This was followed by extensive catchment walk-over surveys to investigate the actual sources on the ground. The main sources investigated were: drains (erosion of, enrichment of, siltation in/at mouth); areas of exposed bare soil in the catchment; overly-enriched land; river bank erosion/collapse; patterns of sediment deposition in the river.

The level and type of siltation was investigated at sites throughout the catchment by kicking of sediment and assessment of silt plume extent, and by using redox potential measurements within the pearl mussel habitat. The decline in interstitial water quality in silted gravels has been detailed by Buddensiek (1989), and Buddensiek *et al*. (1993). Fine sediments in gravels were shown to increase mortality in juvenile mussels to 100% (Buddensiek, 2001). The differences in the redox potential between the water column and substrate were measured using the equipment and methodology of Geist & Auerswald (2007).

Further information on the sources of pressures came from sampling of macroinvertebrates, diatoms, macrophytes and macroalgae throughout the catchment. The details of all survey methods and individual catchment results can be found at the Water Framework Directive website (NS2, 2010).

Extinction curves Extinction curves were calculated for each population, and are presented within each catchment plan (NS2, 2010).

The process for determination of the extinction curve was carried out as follows:

Each population was divided into 5 mm size classes (percentages) based on the quadrat investigations described above. These were converted into ten year age classes by using von Bertalanffy (1938) growth curve data where they have been previously produced for that population (Ross, 1988; Beasley, 1996). Where no von Bertalanffy curves were available, growth lines of living younger mussels were used to find the best fit curve as a proxy. Prediction of future population numbers followed the assumption that the mussels would live for an average of 100 years, and

Table 1 The population size estimates and recruitment status of the 27 populations of *Margaritifera* within SACs designated for the species in the Republic of Ireland.

River	Total number of adult individuals	Recruitment of juveniles
North West 1	250,000	inadequate
North West 2	200,000	inadequate
North West 3	50,000–100,000	inadequate
North West 4	10,000	inadequate
North West 5	< 10,000	almost absent
North West 6	< 10,000	absent
West 1	2,000,000	good
West 2	1,000,000	inadequate
West 3	1,000,000	inadequate
West 4	150,000	inadequate
South West 1	2,800,000	inadequate
South West 2	2,800,000	inadequate
South West 3	200,000	inadequate
South West 4	100,000	inadequate
South West 5	100,000	inadequate
South West 6	50,000	inadequate
South West 7	10,000–20,000	almost absent
South West 8	<10,000	almost absent
South West 9	<10,000	absent
South West 10	5,000	almost absent
South East 1	<10,000	absent
South East 2	<10,000	absent
South East 3	<10,000	absent
South East 4	<1,000	absent
South East 5	400	absent
South East 6	300	absent
South East 7	0	absent

that the last ten year age class would die and be replaced by the current level of recruitment in the population. Maximum age has been shown to vary considerably, from a low of 35 years in Spain to over 200 years in arctic areas (San Miguel *et al*., 2004; Ziuganov *et al*., 2000), so 100 years is taken as likely average for Irish conditions. In addition, where rivers were exhibiting an increased level of adult mortality based on repeat survey results over time, the measured level of mortality was also included in the calculation process.

Results

The 27 populations within SACs are presented in Table 1 according to their location within the Republic of Ireland. The estimate of numbers of adult individuals and level of recruitment are presented for comparison.

The strategy for prioritisation of effort arises out of the need to carry out expensive programmes of measures in a manner that chooses the correct sequence of effort that results in the most return in terms of sustainable populations of mussels.

Based on the field surveys and other available datasets, a series of filters was used to separate the populations. Each filter was applied independently. The prioritisation process is summarised in Table 2 followed by a description of each filter.

Table 2 Filters used in prioritisation process.

Filter Number	Filter Name	Justification
Filter 1	Population size	Very large populations should be prioritised as protecting them can secure most of the national resource.
Filter 2	Demography	Populations with a more intact age structure are more likely to have time to recover.
Filter 3	Population distribution	Populations that are widely distributed within a river system are likely to recover better than very fragmented or restricted distributions.
Filter 4	Habitat rehabilitation versus time to extinction	Provides a level of confidence in the ability to rehabilitate the river in a timely manner.
Filter 5	Extent of pressures	This separates the pressure sources from the habitat effects and prioritises catchments whose problems arise from fewer pressures, as better results are expected at a population level from less effort at a catchment level where pressures are less.
Filter 6	Range	This filter prioritises catchments that have had a low prioritisation from the filters above but have a high importance due to genetic differences or potential range loss.

Table 3 Filter 1. Population Size.

Passed	**Failed**
West 1 South West 1 South West 2	All others

Table 4 Filter 2. Demography.

Prioritise Populations with greatest numbers of age classes
Proxy: use size classes:
0–30 mm
31–65 mm
66–75 mm
76–85 mm
86–95 mm
96–105 mm
106+
Prioritise populations with 6 or 7 size classes represented

Passed		**Failed**
West 1	South West 3	All others
West 2	South West 5	
West 3	South West 6	
South West 1	South West 7	
South West 2	North West 4	

Filter 1. Population Size This first filter prioritises populations with 15% or more of the national adult population of mussels. This is the percentage used in the Habitats and Species Directive EU Standard Data Form to distinguish A rated populations. In the case of the Republic of Ireland this equates to populations with greater than 1.8 million individuals. Three populations pass this category, and the result is shown in Table 3.

Filter 2. Demography This second filter prioritises populations with the greatest numbers of size classes, as a proxy for the greatest range of ages. Populations with a greater range of age are likely to have time to recover. The filter prioritises populations that have 6 or 7 of the 7 size classes represented (Table 4).

Filter 3. Population Distribution This filter prioritises populations with the broadest distribution of mussels within the potential habitat in the river system. This filter requires extensive survey work to have been completed. It is based on the premise that where mussels are restricted to a small area of occupancy within their former habitat, there is probably less chance for their recovery than in populations where mussels are still well distributed within their habitat. The cut off point chosen was 60% occupancy of potential habitat, as it was considered that the population could spread naturally from this level of occupancy if habitat became suitable. A total of 12 of the 27 populations passed this criterion (Table 5).

Table 5 Filter 3. Population Distribution.

Prioritise populations with > 60% potential habitat occupied

Passed		**Unknown**	**Failed**
West 1	South West 3	South West 6	All others
West 2	South West 5		
West 3	South West 7		
West 4	North West 1		
South West 1	North West 2		
South West 2	North West 4		

Filter 4. Habitat rehabilitation timescale v time to extinction This filter prioritises populations with longest time left before extinction compared with the time it would take to rehabilitate their habitat. This assumes catchment management measures are undertaken immediately. The timescale to extinction was estimated using the extinction curves as shown in the methodology. Examples of extinction curves are presented in Figs 1–6.

Six categories were used as estimates for the likely timescale for rehabilitation. The likely time for recovery is based on how long it would take for nutrients to be removed from the system once their supply to the river has been cut off, or loss of fine sediment from the river by movement through normal flows and floods once the supply from the catchment has been cut off:

(i) Nutrient source present, but no silt problem = 3 years
(ii) Fine sediment present but not compacted = 5 years
(iii) Mobile coarse sediment moving into and through river = 10–20 years
(iv) Compacted fine sediment = 10–25 years

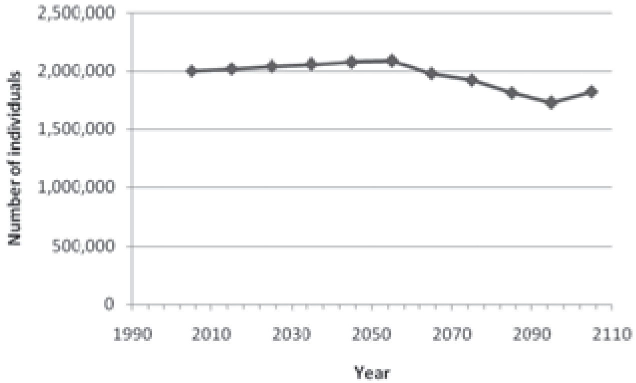

Figure 1 Extinction curve for Population West 1.

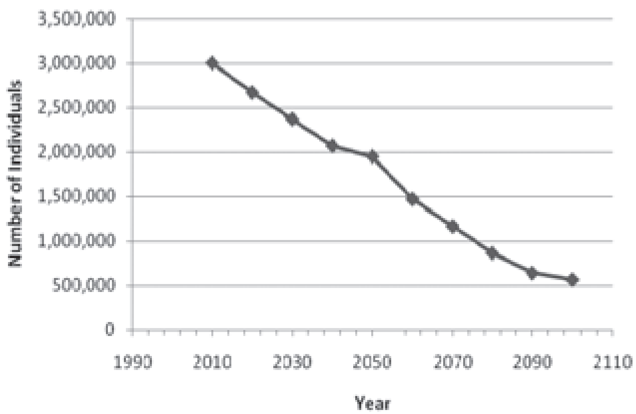

Figure 2 Extinction curve for Population South West 1.

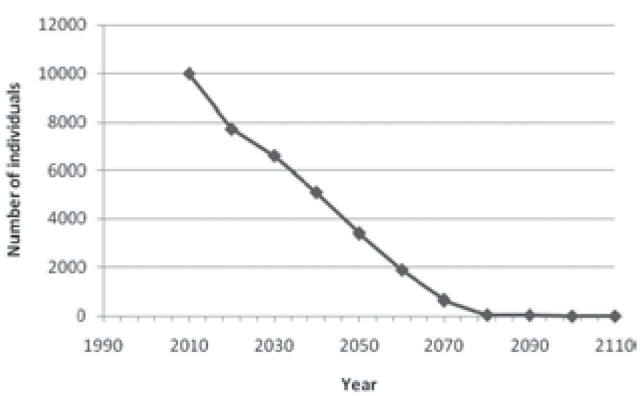

Figure 3 Extinction curve for Population North West 4.

(v) Catchments where intensive agriculture has over-fertilised soil, where Phosphorus release will continue after removal of source nutrient= 20 years

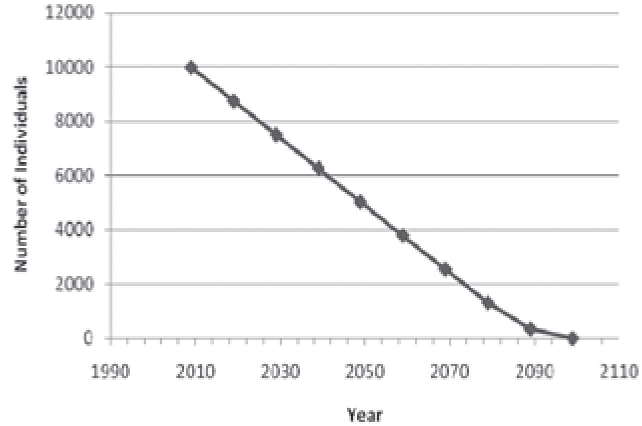

Figure 4 Extinction curve for Population South West 7.

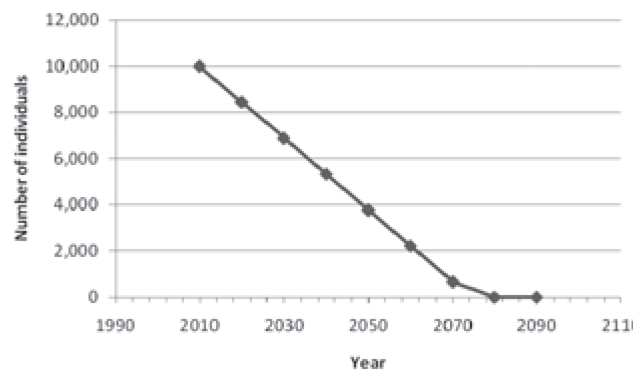

Figure 5 Extinction curve for Population South East 1.

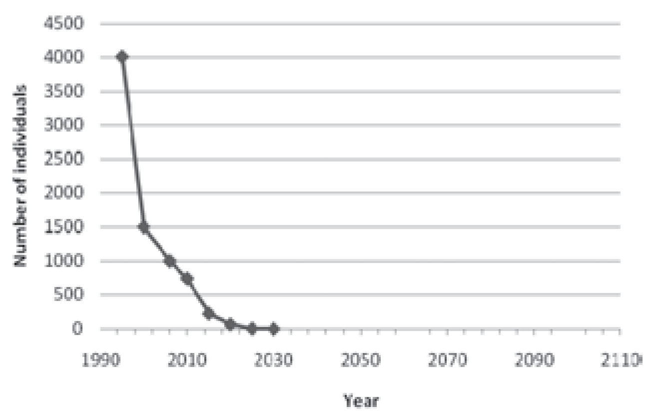

Figure 6 Extinction curve for Population South East 4.

(vi) Fine compacted sediment with long term excessive nutrient history manifesting in rooted macrophytes = 15–25 years

Table 6 Filter 4. Habitat rehabilitation timescale v time to extinction.

Prioritise populations with timescale to extinction > timescale to rehabilitate				
Passed			**Unknown**	**Failed**
West 1	South West 3	North West 1	North West 5	All others
West 2	South West 4	North West 2	North West 6	
West 3	South West 5	North West 3		
West 4	South West 6	North West 4		
South West 1	South West 7			
South West 2	South West 8			

Table 7 Filter 5. Extent of intensification of pressures.

Passed		**Failed**	
West 1	South West 4	North West 3	South East 3
West 2	South West 5	South West 6	South East 4
West 3	South West 10	South West 7	South East 5
South West 1	North West 4	South West 9	South East 6
South West 2	North West 5	South East 1	South East 7
South West 3		South East 2	

A total of 17 of the 27 populations were considered to have a longer likely lifespan than rehabilitation time. These are shown inTable 6.

Filter 5. Extent of intensification of pressures This filter prioritises populations with the most managable pressures in the catchment. The data used for this filter were from mapped datasets already available through river basin district management under the Water Framework Directive (2000/60/EEC). Although the cut-off points could be considered arbitrary, the basis of this filter is that it is likely that rehabilitation of a non-intensively managed catchment would be more successful than that of a highly intensively managed catchment, and as the cut off point cannot be currently identified, a level of middle intensity was neither prioritised nor failed.

Catchments were prioritised where a combination of factors prevailed. The first factor was the combination of coniferous plantation forestry and intensive agriculture (defined as greater than 1.5 livestock units per hectare). Catchments passed where this was less than 20% of the catchment area, and failed where it was greater than 40% of the catchment area.

The second factor was numbers of licensed point sources. Catchments passed where these were less than 5 in the catchment, and failed where they were greater than 10 in the catchment.

The third factor was numbers of on-site waste water treatment systems. Catchments passed where these were less than 4.2 per km^2, and failed where they were greater than 6.8 per km^2 in the catchment.

Populations were prioritised where they passed on all three factors, and were rejected where they failed in all three factors.

The information was taken from Central Statistics Office, Forest Service, and An Post (postal service) data, and statistics from local authority datasets. Use could also be made of CORINE landuse data where available. Using CORINE data, where 80% or more of a catchment area with low intensity landuse was used as a pass and less than 40% low intensity landuse as a failure gave equivalent results. With this filter 11 catchments were prioritised, 11 failed and the remaining 5 catchments were considered to be in an intermediate state of intensification (Table 7).

Following the assessment of each catchment through all five filters, the number of prioritisations and the number of rejections was compared (Table 8) and the prioritisation of the populations ordered into nine categories, based on

Table 8 Summary of results of 5 filter assessments.

	Number of Prioritisations					Number of Rejections				
Filter:	1	2	3	4	5	1	2	3	4	5
North West 1		1	1	1		1				
North West 2		1	1	1		1				
North West 3				1		1	1	1		1
North West 4		1	1	1	1	1				
North West 5					1	1	1	1		
North West 6						1	1	1		
West 1	1	1	1	1	1					
West 2		1	1	1	1	1				
West 3		1	1	1	1	1				
West 4		1	1	1		1				
South West 1	1	1	1	1	1					
South West 2	1	1	1	1	1					
South West 3		1	1	1	1	1				
South West 4		1		1	1	1		1		
South West 5		1	1	1	1	1				
South West 6				1		1	1	1		1
South West 7		1	1	1		1				1
South West 8		1		1		1		1		
South West 9						1	1	1	1	1
South West 10				1	1	1	1	1		
South East 1						1	1	1	1	1
South East 2						1	1	1	1	1
South East 3						1	1	1	1	1
South East 4						1	1	1	1	1
South East 5						1	1	1	1	1
South East 6						1	1	1	1	1
South East 7						1	1	1	1	1

Table 9 Order of prioritisation of rivers based on the results of 5 filter assessments.

	Number of Prioritisations	Number of Rejections	Priority Class
West 1	5	0	1
South West 1	5	0	1
South West 2	5	0	1
West 2	4	1	2
West 3	4	1	2
North West 4	4	1	2
South West 3	4	1	2
South West 5	4	1	2
West 4	3	1	3
North West 1	3	1	3
North West 2	3	1	3
South West 4	3	2	4
South West 7	3	2	4
South West 8	2	2	5
South West 10	2	3	6
North West 5	1	3	7
South West 6	1	4	7
North West 3	1	4	7
North West 6	0	3	8
South West 9	0	5	9
South East 1	0	5	9
South East 2	0	5	9
South East 3	0	5	9
South East 4	0	5	9
South East 5	0	5	9
South East 6	0	5	9
South East 7	0	5	9

the number of prioritisations and rejections determined by the filters (Table 9).

The prioritisation order from 1 to 9 establishes, on a scientific basis only, which populations are the most likely to respond to catchment management efforts. Categories 7 and 8 have been assigned to rivers that require more survey work to be carried out, but the other assignments are based on a wide body of data. With categories 3 to 6 there is chance of recovery before extinction, but not as good a chance as with those populations in categories 1 and 2, where every effort needs to be made to bring the catchments into sustainable conditions. If habitat conditions remain in their current state, the extinction curves estimate that, over the next ten years, over 2 million individuals will be lost from priority classes 1 and 2, almost 67,000 from classes 3–6, and over 20,000 from classes 9–10, emphasising the need to prioritise effort where manpower and funding are limited, and programmes need to be rolled out over time.

Filter 6. Range and representation of genetic variation
This filter is applied after the populations have been prioritised using filters 1–5 to check whether there is enough range and genetic representation within the region (in this case the Republic of Ireland). From a range perspective, there should be prioritisation from each of the regions as well as from the Nore Catchment (listed above as South East 5), as *Margaritifera durrovensis* is protected as a separate taxon under the Habitats and Species Directive. This filter is summarised in Table 10. In countries where genetic studies from individual populations have been undertaken, the results of such studies can be used for this filter. However, very little genetic studies have been carried out on Republic of Ireland populations. Therefore, as

Table 10 Regional and taxonomic prioritisation.

Region/taxon	Number of Priority 1 and 2 populations	Additional prioritisation needed
North West	2	No
West	4	No
South West	4	No
South East	0	Yes, need to prioritise at least one of the SACs or a population that is outside the SAC network but may have better chance of recovery
Nore	0	Yes, need to prioritise this population

a precaution, at least one population from each region should be protected.

DISCUSSION

The freshwater pearl mussel is endangered worldwide, and thus it is important that meaningful, objective-based conservation effort is employed with urgency. In situations of serious endangerment, it is a natural response to protect all populations with equal vigour, or to carry out emergency responses on the most depleted populations, such as taking wild mussels into captivity for a breeding programme. However, following assessment with the six filters, it is clear that if resources are concentrated on a laboratory based approach to maintain very poor populations without catchment management of the best populations, much more will be lost from the wild than will be gained in captivity.

Many measures have been proposed with the aim of reducing catchment pressures, but they largely fall into two categories, either reducing the source of the problem, or intercepting the problem (i.e. sediment or nutrient) along the pathway between its source and the river so that it does not damage the habitat. If pearl mussel conservation is to be considered with conservation of other species and habitats, reduction of the source of problems clearly has wider nature conservation benefits than reduction along pathways. Rehabilitating a catchment to less intensive management would result in benefits to both terrestrial and aquatic habitats and species, whereas reduction along pathways would mainly benefit the aquatic habitats and species only. However, source reductions have a greater impact on current users of the catchment.

The pearl mussel is a protected species under Irish law, and direct damage (including pearl fishing) is outlawed, with large fines and prison sentences acting as deterrents. While it is possible to implement legal protection across all populations, once-off projects such as programmes of work to upgrade sewage treatment plants, inspect and remediate septic tanks, fence and construct sediment traps cannot all be done simultaneously, and could therefore be phased on the above prioritised basis. Costs of ongoing repairs to fences, future inspections and maintenance of sediment traps will need to be planned for into the future, but these will be less than the initial programme and can also be carried out on a phased basis.

Damage to mussel populations and their habitat by indirect pollution and habitat deterioration are very difficult to prevent, due to lack of effective legal controls acting on the river at catchment level. This is true particularly outside Natura 2000 sites and also within catchments where the river is within an SAC, but in Ireland the boundary of the SAC is just 2.5 m from the bank where no other qualifying interest occurs. Intensification of land use through removal of hedges, and land reclamation through drainage need to be appropriately assessed rather than being exempt from development control in catchments prioritised for the protection of this species.

The argument for prioritising the largest mussel populations is underlined by the speed with which negative influences have caused declines. At least eight of the Irish SAC populations changed in characteristic in the ten years from 1996 to 2006. The changes manifested in distribution patterns, from densely packed mussels across the width of the river in unshaded habitat with high numbers of juveniles, to populations with very poor conditions in the open central channel (through siltation and macrophyte and filamentous algal growth), and adults becoming concentrated close to the river banks under the shade of overhanging trees, with little or no effective recruitment. It is imperative that populations that remain high in number and densely distributed are given full protection. Protection of these populations requires the maintenance of or the return to low intensity land usage, and should be most effective through farming agreements and strict planning control. These small catchments should be prioritised for terrestrial conservation management if it is compatible with protection of the river. For example, the recovery of one SAC population of *Margaritifera* in Ireland was associated with the de-stocking of sheep in a project designed to improve habitat for the red grouse *Lagopus lagopus*. Co-prioritisation of habitat and species protection is a more sensible approach than a fragmented approach that spreads resources thinly over a wide area.

Prioritisation of populations from the best to the worst is likely to result in the extinction of populations, particularly of those that fail at Filter 4. Where there are limited resources and 139 rivers with *Margaritifera*, this is inevitable, but underlines the importance of gathering and interpreting enough data to understand which populations are possible to bring to sustainability in the wild. A scientific approach can then be used to determine if some rivers outside the SAC system may be better suited to rehabilitation measures than others within the system. It is reasonable to have a stopgap policy of captive breeding while such data are accumulated as a very short term response, but using limited resources on captive breeding rather than ecological improvements on an ongoing basis is unwise as it could delay catchment improvement to beyond the likely time of extinction without captive breeding success. Relatively high rates of loss of adult mussels kept in captivity (up to 50% in a year) and the low success rates of juvenile survival in attempts at captive breeding in the Republic of Ireland demonstrate that such ex-situ captive breeding attempts are unlikely to be useful for long term projects where parallel river habitat rehabilitation would be slow to achieve its aims.

Recovery of populations with depleted adults and no effective recruitment is possible, as demonstrated by the successful rehabilitation project in the Lutter River, Germany (Altmüller & Dettmer, 2006). The time, effort and expense involved in this recovery are well documented, and involved buying considerable areas of catchment for conservation purposes. It is unlikely that such resources will be forthcoming for many more depleted populations. However, the Lutter project has shown that electrofishing salmonids and placing them with *Margaritifera* in simple buckets at the river bank to enhance in-situ encystment of glochidia can help to repopulate a mussel river after catchment management improvements have been carried out.

Seriously depleted populations provide the greatest challenge in terms of strategy choice, but in gathering enough catchment and population information, the resources available can be most wisely employed. Resources that may seem excessive in regions with many mussel rivers remaining may have to be employed in very poor rivers if their loss would result in severe range reduction. Thus countries with very few mussels may need to spend more money per individual mussel than would be needed in a catchment with abundant mussels elsewhere, in order to protect the range. In Ireland, the above results suggest that it may be more beneficial to try to rehabilitate one south east population well, rather than to divide resources equally among seven different populations with little chance of success. The inevitable result of this strategy would be to lose six populations to extinction for the prize of achieving one sustainable population.

Populations of freshwater pearl mussels will take time to recover, they will continue to decline as adults die and are not sufficiently replaced until the year that the habitat becomes clean enough to support large numbers of juvenile mussels, thus conservation effort is finally and dramatically rewarded rather than in small increments. In contrast, other elements of the habitat will slowly improve, and can be measured using redox potential meters (Geist & Auerswald, 2007), measuring reductions in macrophyte and filamentous algal growth and using open water turbidity loggers. In order to achieve habitat improvement to the level of sustainable juvenile recruitment, all pressures need to be addressed and removed, therefore all land users need to be part of conservation efforts. This is likely to be difficult at times, but the rewards could not be greater.

The government agencies responsible for the protection of *Margaritifera* at favourable conservation status are in a difficult position. It would be easier to carry out small projects on each population in order to show that some effort has been made on each. However, if such efforts will not save populations from extinction then this approach is not in the best interest of the species. In order to provide the best chance of sustainable populations in the future, it is most important that work is prioritised, fully documented (including costs) and monitored, with regular reviews of policy. Thus there can be genuine accountability to show that the best possible strategy is being followed. Much more research has been recommended to fill the current gaps in our knowledge of *Margaritifera* (Araujo & Ramos, 2001; Geist, 2010). While continuing research is essential and will aid the conservation effort, remaining gaps cannot be allowed to delay catchment improvements any longer. Enough is known about the causes of the demise of *Margaritifera* to provide confidence that conservation management work is the best chance for this complex animal.

The work carried out on the Irish *Margaritifera* populations and their catchments has facilitated the development of a prioritisation strategy. While some countries have dispersed funding arrangements and often tend to spend money on various catchments as it becomes available, the results of this study suggest that this is not a good strategy for safeguarding catchments and sustainable *Margaritifera* populations into the future. The above methodology may serve as an example and could be adapted by other countries to facilitate a more scientific rationale for their own prioritisation strategies. This is important in order to make best use of resources in countries with large numbers of mussels as well as those where populations are severely depleted and catchment rehabilitation will be most difficult.

Acknowledgements

The Irish sub-basin catchment management plan project is a North-South share project under the Water Framework Directive. Funding is from Donegal County Council and the Department of the Environment, Heritage and Local Government. The project team is managed by RPS consulting. All members of the project team are gratefully acknowledged. Pearl mussel data is derived from survey work carried out by Eugene Ross and Ian Killeen as well as myself, and their expertise is gratefully acknowledged. My thanks to all the dedicated *Margaritifera* scientists across Europe for many hours of discussion and visits to the populations in their countries.

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