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The freshwater pearl mussel
(Margaritifera margaritifera)

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Introduction

The freshwater pearl mussel, *Margaritifera margaritifera*, has been exploited in Britain since pre-Roman times. Indeed, its occurrence here may have been an important factor in inducing the first Roman invasion of Britain in 55BC (Cosgrove *et al.* 2000a). Scottish pearls were traded in Europe during the 12th Century, and commercial exploitation on a much larger scale developed during the 16th Century across Britain and Ireland, when river bailiffs were employed to ensure that all valuable pearls were kept for the King.

Many people worked in the industry during the 19th Century, but this level of exploitation was apparently unsustainable and the fishery declined sharply. Since then, there has been a constant but small-scale pearl fishery, traditionally plied by travelling people, until the mussel was afforded complete legal protection in 1998. The pearl mussel is now highly threatened and seriously endangered in every part of its range.

Status and distribution

Protected under Schedule 5 of the Wildlife and Countryside Act (1981) and the Wildlife (Northern Ireland) Order 1985, the freshwater pearl mussel is also listed on Annexes II and V of the EC Habitats and Species Directive and Appendix III of the Bern Convention. It is included on the IUCN Invertebrate Red List, where its status is described as Vulnerable (IUCN 1990). Classified as a priority species by the UK Biodiversity Steering Group, a national Species Action Plan has been prepared to encourage measures for its survival.

The freshwater pearl mussel is distributed from the arctic and temperate regions of western Russia through Europe to the north eastern seaboard of North America. Recent studies have revealed that there have been dramatic declines throughout its Holarctic range: for example, Bauer estimates a 95-100% decline in known populations in Central and Southern Europe (Bauer 1986, 1988). Substantial populations with active recruitment are now found on fewer than 50 rivers in Canada, north west Russia and north east Scandinavia, with a handful of sites in Bavaria, the Czech Republic and Austria (Young *et al.* 2000).

Formerly widespread and abundant in areas of England (such as the South West and north west Midlands) and Wales, recent surveys revealed most former populations to be virtually extinct, with very little active recruitment (Chesney & Oliver, 1998). There have been major declines in Northern Ireland, with recent survey work again showing population declines and scant recruitment (Kerney 1975, Beasley and Roberts 1996), including the rare hard-water form, *Margaritifera margaritifera durrovensis* (Phillips) which is unique to Ireland (Moorkens & Costello, 1994).

Originally widely distributed throughout Scotland, a comprehensive survey from 1996 to 1999 revealed that the freshwater pearl mussel is now extinct in most of the lowlands, and scarce everywhere except for a handful of Highland rivers (Cosgrove *et al.* 2000b). If the present rates of extinction continue, it has been estimated that surviving Scottish populations may only persist for a further 25 years. Public disclosure of precise locations is therefore considered unwise due to continued illegal pearl fishing (Cosgrove & Young, 1998).

The early causes of decline were undoubtedly pearl fishing (Young *et al.* 2000) and industrial pollution. The current lack of recruitment may be due to a number of factors, including increasing siltation and eutrophication of rivers (Bauer 1983, 1988). The recent declines in stocks of migratory salmonid fish upon which the larvae are dependent are also giving cause for concern. River engineering for hydro-schemes, flood defence purposes and fishery improvements continues to pose a serious localised threat. Forestry operations, acidification, effluent from fish farms and chemical sheep dip are further threats to the declining populations (Young *et al.* 2000).

Up to half the worlds' known remaining populations with active recruitment now occur in Scotland (Young *et al.* 2000). Actions taken within the UK will therefore have a direct consequence for the global survival of this species.

Life history

The freshwater pearl mussel is one of the longest-lived invertebrates known, and individuals can survive for over 100 years (Bauer 1992). The mussels live buried or partly buried in coarse sand and fine gravel in clean, oligotrophic, fast-flowing and unpolluted rivers and streams. The mussels subsist by inhaling and filtering water through their exposed siphons for the minute organic particles on which they feed. Where the species was formerly abundant, it is possible that this filtration acted to clarify river water to the benefit of other species, including juvenile Atlantic salmon, *Salmo salar*, and brown or sea trout, *Salmon trutta* (Zuiganov *et al.* 1994).

The freshwater pearl mussel is typically dioecious, in common with other freshwater bivalves. It matures at 10-15 years, when the length generally exceeds 65 mm. In early summer (June to July), the males shed sperm into the water, and it is inhaled by the females. The fertilised eggs develop in a pouch on the gills for several weeks, and are released from July to September as tiny larvae, measuring 60-70µm, known as glochidia. Each female ejects between 1 and 4 million glochidia in a sudden, highly synchronised event, usually over one to two days (Hastie 2001b). It is likely that a threshold temperature, or other environmental cue, may trigger glochidial release. The proportion of adults producing glochidia is relatively high, varying from 30-60%, even in sparse populations (Young & Williams 1983). The glochidia resemble tiny mussels, but their shells are held apart until they encounter a suitable host, when they snap shut onto the gill filaments of juvenile fish (Young & Williams 1984). Infective glochidia can remain viable for up to 6 days (Zuiganov *et al.* 1994), but most attachments probably occur within a few hours (Young & Williams 1984).

Almost all the glochidia are swept away and die, but a small number are inhaled by juvenile Atlantic salmon and brown or sea trout. Landing on the gills, the glochidia encyst, live and grow as parasites in the hyper-oxygenated environment until the following spring. They drop off in May and early June, and must land in clean, sandy or gravelly substrates to settle and start to grow. This parasitism does not appear to harm the fish, and enables young mussels to colonise new areas upstream. Young mussels are typically yellowish-brown, becoming darker with maturity.

Freshwater pearl mussels develop very slowly and can live for more than 100 years, when they may reach 12-15 cms in length. The life span and maximum size reached are highly variable between populations, depending on environmental conditions, particularly hydrochemistry and water temperature (Zuiganov *et al.* 1994). Freshwater pearl mussel populations tend to be faster growing and shorter lived in the southern part of their range, with a lower reproductive output (Hastie 2001b) than those in the upper (cooler) reaches of catchments and more northerly latitudes (Bauer 1992, Hruska 1992). The mussels can re-bury themselves if dislodged, and can also move slowly across sandy sediments. Most have about a third of their shells exposed, but some adults and virtually all juveniles burrow completely into the substrate and under loose stones (Hastie *et al.* 2000a).

The huge losses involved in this unusual life cycle make the freshwater pearl mussel particularly vulnerable to adverse conditions.

Population dynamics

Low adult mussel mortality and great longevity historically compensated for the characteristic life cycle of very poor glochidial success and low juvenile recruitment. There is no current scientific agreement about what constitutes a functional mussel population in terms of a viable size/age profile or proportion of juveniles. Intuitively, age structures in a viable population should reflect both active recruitment and longevity. Adequate recruitment may be indicated by some 20% of the population being less than 20 years old (Young *et al.* 2001, Hastie *et al.* 2001b). Very few rivers now show this level of recruitment (Cosgrove *et al.* 2000a, Young *et al.* 2000). Adult mortality of 10% per decade has been suggested as sustainable if recruitment is normal (Bauer 1983, 1986 and 1992). There remains some debate as to the natural rate of recruitment and adult mortality in established populations, and this area requires further research.

According to most workers, sex ratios are typically 1:1 (Bauer 1979). Fertility (the total number of glochidia produced during a lifetime) increases with longevity, so populations with older age classes should be more viable unless juvenile mortality is high. Reduction in aged mussel numbers can be a result of pearl fishing, but higher temperatures, eutrophication and increases in nitrate levels may also reduce longevity. This effect is exacerbated at low latitudes by naturally reduced life spans (Bauer 1986,1992). The age maximum is therefore different for each population and the target should be as high as is naturally possible. In Britain, age maxima of less than 40 years impose severe stress on successful recruitment and indicate possible extinction (Hastie *et al.* 2000b). In some rivers, longevity may also be reduced where surrounding limestone strata increases calcium input (Bauer 1992). However, this is a natural phenomenon and should not require remedial action.

Genetic diversity is regarded as low, and most researchers regard the eastern North American populations as the same species as those in Europe. However, virtually nothing is known about the genetic basis of observed population differences in the Margaritiferidae, and this area needs urgent investigation (Chesney & Oliver 1998). Transplantation of mussels from river to river is relatively unsuccessful, with mortalities of over 50% in the first three years, compared to short-term survival rates of 90% from a translocation exercise within the same river system (Valovirta 1998). There may be either physiological accommodation or a genetic adaptation to particular rivers. The implication is that species recovery plans that are dependent on introducing new stock may not be successful in the long term. Translocation exercises should therefore be limited to those situations where the threat is particularly severe, and action should be concentrated on maintaining and enhancing all current populations. The longevity of the species means that, given the correct conditions for recruitment, small populations can be sustainable over the long term. The Life in the UK Rivers project and Aberdeen University are currently investigating techniques for captive breeding of the species as a means of reinforcing recruitment within catchments.

Current research on population genetics using DNA analyses is underway, and an initial study using RAPD techniques has indicated differences in variability within populations. The results suggest that there are differing factors acting on genetic variation as, for example, mussels from larger rivers showed greater variation than those from small streams. The study also showed that Irish populations were more variable than those from the Lake District. This work is continuing (Oliver, pers. comm.).

Glochidium and host attributes

Only sea trout, brown trout and Atlantic salmon are known to host complete metamorphosis in Europe, where they are the only native host species (Young & Williams 1984). Brown trout are the main host species in Ireland (Beasley 1996) and in Germany, where salmon are now thought to be extinct. American brook charr, *Salvelinus fontinalis*, acts as a host in North America and has been introduced into Europe. However, the rainbow trout, *Oncorhynchus mykiss*, is completely unsuitable (Young & Williams 1984).

Salmo trutta exists in two forms: the resident brown trout and the migratory sea trout. Rivers carry varying population ratios, but their relative importance for freshwater pearl mussel has not been studied. The differing reproductive behaviour of these forms most probably affects mussel recruitment. The conservation of both brown and sea trout involves different parameters, and it is therefore necessary to determine the relative importance of the hosts in any one river through appropriate research. 0^+ salmon are often more abundant than 0^+ trout, and are therefore likely to be the most important hosts of the freshwater pearl mussel in most rivers. However, there is a number of mussel populations in small streams in Scotland that have no (or very few) salmon, and these must be considered to be largely trout-dependent.

Host fish become progressively resistant to glochidial infection (Bauer & Vogel 1987, Zuiganov *et al.* 1994). Those in the first three year classes (but mostly 0+ and 1+ years) form the majority of the host population (Young & Williams, 1984). Older fish may be less susceptible to infection for a number of reasons, including reduced exposure (older fish prefer deeper water away from mussel beds), and acquired immunity due to previous infections (Bauer & Vogel 1987, Zuiganov *et al.* 1994).

The minimum density of fish required to maintain mussel population densities in the long term can theoretically be calculated from a variety of factors, including the fecundity of female mussels; the probability of a glochidium finding a host, of a glochidium reaching metamorphosis, and of young mussels reaching sexual maturity; and the number of generations. However, the huge mortalities make any such calculations (which are based mainly on laboratory studies and not field data) extremely difficult, and results need to be treated with caution. The figure of 0.2 fish m^{-2} given by Bauer (1991) is based on observations of host density and presence of viable mussel populations, and was not calculated. The figure for salmon of 0.05 fish m^{-2} from Zuiganov *et al.* (1994) is calculated, but a real figure from the Varzuga River is 0.29 fish m^{-2}. An acceptable level of brown trout has been suggested to be in the order of 0.3 fish m^{-2} (Zuiganov 1994), but this has not been adequately researched.

Increased glochidial infection can theoretically be achieved by increasing host numbers or through the artificial infection of host fish. This strategy should result in more post-glochidial juveniles being introduced into the community, providing mussel numbers are limited by low fish populations rather than lack of suitable habitat. Such measures will only be effective in rivers with appropriate water quality and substrate conditions, such as those where populations have been depleted by over-fishing (Young 1991). Even mild eutrophication can be detrimental to successful reproduction and therefore hamper recovery programmes.

Habitat requirements

The freshwater pearl mussel life cycle involves an adult stage, living as a filter feeder, a juvenile stage living interstitially in sediment, and a larval (glochidial) stage living attached to the gills of trout or salmon. All life stages therefore need consideration, as does the viability of the host species of fish. Adults are more tolerant of a wider range of in-river conditions than juveniles (Hastie *et al.* 2000a).

Water quality

Water chemistry has received much attention and is widely quoted in the literature when environmental parameters for optimum mussel survival are under discussion. Bauer (1988) is most often quoted, and there is a general acceptance that the pearl mussel prefers oligotrophic conditions – poor in nutrients, slightly less than neutral pH (7.5 or less) and with low overall conductivity. The actual figures cited by Bauer were based on the correlation of field conditions to mussel presence or absence in central European rivers.

Similar correlations have been noted in the UK but exceptions do exist. The target levels given here reflect the current situation in the Scottish rivers where the populations are large and recruitment is present. The situation in English rivers with large adult populations and scant recruitment is currently unfavourable, and no conclusions can therefore be drawn from the present water quality. A few atypical populations in England and Ireland appear to be adapted to tolerate more calcareous water chemistry, where the surrounding geology increases calcium content beyond the levels suggested by Bauer.

Pearl mussels are most vulnerable to human influences at the stage where they leave the host fish and establish in the sediment. This stage will die out completely if even a slight degree of pollution is present. The juveniles are also far less tolerant than the adults, and persistent intermediate levels of eutrophication could prevent long term recruitment, resulting in aged stocks (Bauer 1988).

The critical parameters affecting recruitment are BOD, calcium and phosphate levels in the water. Bauer (1988) observed that adult mortality was correlated with nitrate concentration, and that increased levels of phosphate, calcium and BOD were correlated with decreasing survival and establishment of juveniles.

Research has indicated that nitrate levels must not exceed 1.0 mg l^{-1}, although higher values of 1.5 mg l^{-1} may be encountered in some rivers in Britain. Phosphates should be <0.03 mg l^{-1}, and conductivity must not exceed 100 μs cm^{-1}, although higher values of 120 μs cm^{-1} may be natural on limestone influenced stretches (EN Research contract; Oliver 2000).

BOD and dissolved oxygen are therefore undoubtedly of importance to pearl mussel survival. These parameters are currently measured by sampling of the water column, and are therefore relevant only to the adult phase. Juvenile mussels live interstitially, but no monitoring of substrate oxygen levels is currently undertaken. The levels tolerated by juveniles have only been measured by Buddensiek *et al* (1993) for four rivers in Germany. Monitoring and research on the interstitial environment is therefore an urgent priority.

Water quantity

The influence of stream hydrological processes on microhabitat, particularly hydrodynamic effects on juvenile recruitment, is poorly understood. Most workers report minimum/maximum depths and velocities for *M. margaritifera, M. laevis* and *M. falcata* within the ranges of 0.1–2 m and 0.1–2 m s^{-1}. (Vannore & Minshall, 1982). Optimum depth and velocity in Scottish rivers were found by Hastie *et al.* (2000a) to be 0.3–0.4 m deep and 0.25– 0.75 m s^{-1}. Work on complex characteristics of flow has shown shear stress over existing mussel beds to be a major factor in determining recruitment in some mussel species in the USA, but this work did not include the freshwater pearl mussel (Layzer & Madison 1995).

No absolute figures are available for a minimum suitable flow velocity. Until such factors have been quantified by further research, a precautionary approach should be followed. Low summer flow velocities can allow the formation of algal mats and reduce interstitial - water column mixing. The uncovering of shallow riffle areas and the aggregation of detrital silt are indicators of poor conditions for both adult and juvenile mussels. Water flow in summer should therefore be sufficient so as not to induce low oxygen levels or heat stress, and sufficient to reduce the sedimentation of fine particles and detritus, especially in areas where juveniles aggregate. Research into the effects of flow velocities (including summer spates) on pearl mussel habitat is urgently required.

Moderate flooding may have a positive effect in cleaning silts from gravel beds and riffles. Autumn flows can wash out algal mats and sediments accumulated over the summer, but severe floods can remove large numbers of mussels from their beds and are potentially disastrous for populations where recruitment is not taking place (Hastie *et al.* 2001b). This study showed that an estimated 1:100 year return period flood directly killed between 4–8% of the population due to significant channel reformation and large scale movements of substrata. Climate change appears to be resulting in increased frequency of high flow occurrence and greater annual run-off events (Black 1996), which may be a cause for future concern.

Even slight hydrological changes may result in serious degradation of habitat due to the very specific sediment requirements of juveniles (Bauer 1988, Buddensiek *et al.* 1993). Catchments should therefore be monitored for alterations to land drainage, and all work that has the potential to increase siltation or the speed of run-off should be subject to rigorous examination and environmental impact assessment. Regulated rivers with alternating high and low flows (or those where regulation is proposed) should give particular cause for concern if they support thriving populations with active recruitment.

Substrate

The characteristics of riverbed substrata are of critical importance for freshwater pearl mussel populations. The typical substrate preference is small sand patches stabilised amongst large stones or boulders in fast flowing streams and rivers. Such boulder-sheltered mussel beds may be critical for recruitment after heavy floods (Vannote & Minshall, 1982). Riffle areas with mixtures of rocks, cobbles and sand are important habitats in low-gradient sections, providing a well-oxygenated and silt-free environment. Juveniles are mostly associated with such riffles, and require fine sediment within which to shelter.

There is consensus among workers that the early post-settlement period, when juveniles establish themselves in sediment, is the most sensitive and critical phase in the pearl mussel life cycle (Hastie 2001b). Juveniles are thought to require sediment of low organic content for their further development (Bauer *et al.* 1980), with a structure that allows a high rate of exchange between the free water body and the interstitial water. Oxygen, pH and ammonia appear to be important chemical parameters in this respect (Buddensiek *et al.* 1993).

Gradient could affect mussel distribution indirectly by determining the stability of the substrata. Purser (1985) demonstrated that an intermediate gradient range of 0.8–3 m km^{-1} was preferred. The majority of adult mussels live in dense beds in substrates of mixed cobble, stone and sand at the tail end of pools or in the moderate flow channels of river bends. In these sites, stability of the bed is important. By contrast, loose sands and gravels on the inner curves of river channels are rarely inhabited by mussels because of their instability (Hastie *et al.* 2000a). Densely vegetated areas are unlikely to be suitable, since these tend to trap silt and organic debris.

Siltation of suitable substrates is therefore a severe problem that can be caused by increased sediment load and detrital production due to eutrophication. While bank erosion, flooding and land drainage can all affect sediment load and threaten adult mussel beds, even small amounts of sediment can alter the interstitial environment of the juveniles. If the interstitial spaces are clogged, the young mussels suffocate (Hastie *et al.* 2000a). The level of 30 mg l^{-1} of suspended solids has been noted by Valovirta (1998) as the limit of tolerance by adult mussels. This level may not be critical if it occurs for a short time during floods. However, long-term levels of suspended solids should be much less. Levels consistently above 10 mg l^{-1} should give cause for concern.

Stable gravel/cobble and riffle sites should therefore have very low levels of silt in the interstitial spaces of the substrate, but this has not been quantified by field research. Research is urgently needed into the effects of and tolerance to interstitial siltation.

Channel structure and management

Mussel aggregations in many of the rivers surveyed in England and Wales are associated with areas of shade, normally created by overhanging herbaceous vegetation, scrub and bank-side trees, with little or no bank erosion. Shade keeps water temperatures down during the summer months and inhibits the growth of filamentous algae. Algal mats overgrowing mussel beds can impair respiration, feeding, fertilisation and the release of glochidia (Hastie 2001b). In Scotland many populations occur in areas not currently forested. It is therefore suggested that tree cover in itself is not necessary where nutrient levels are low enough to prohibit algal blooms and flows are sufficient to prevent high summer temperatures. Stable channels with little bed transport except in floods are important features, and channel structure should not be altered in any way that will impede water flow, increase flooding, or alter the distribution of substrates.

It is widely accepted that eutrophication is a major cause of mussel decline and that agricultural practices, particularly efficient field drainage and the use of fertilisers, are major contributors to this process. To reduce this effect, a buffer of natural vegetation may promote the removal of nutrients. Costello *et al.* (1998) suggested a buffer zone of 10 m with intercepted field drains, but effective size will depend on soil type and slope (and therefore vulnerability to erosion), river width and catchment land use. Cattle drinks and poached banks are undesirable features as they cause additional siltation.

The importance of surrounding vegetation has been stressed by Hruska (1996), not only in ameliorating nutrient run-off but also as a supplier of food for the juvenile stage. Hruska suggests that surrounding areas of wet grass meadows are most beneficial to juvenile growth. Whilst of relevance to some rivers in the UK, the situation is different in Scotland, and this study needs careful consideration if its findings are to be applied in the UK.

River engineering for hydro-electric schemes, flood protection or fisheries reasons may cause local extinctions (Young 1995). Activities such as dredging, canalisation, scouring and weir construction cause alteration or loss of suitable river bed substrata (Young & Williams 1983). Any such activities or proposals should therefore be subject to rigorous environmental assessment.

Other factors

Host fish stocks

The long-term survival of the freshwater pearl mussel depends ultimately upon host availability. There is concern that significant changes in salmon and sea trout stocks may threaten populations (Cosgrove *et al.* 2000a, Chesney & Oliver, 1998). Salmon catches in northwest Scotland, where the majority of the pearl mussel populations are concentrated, exhibited a marked decline during the 1990s and are now at historically low levels. Several migratory trout stocks have collapsed, and sea trout catches are now at the lowest levels ever recorded (Hastie & Cosgrove 2001). The cause has been attributed to many factors including climate change, over-fishing and predation, infestation by sea lice (now unequivocally linked to the decline in sea trout stocks), acidification and degradation of habitat (Marshall 1998).

It is not known whether brown trout produce enough fry to sustain Scottish mussel populations over the long term, and there is an urgent need to know more about the relationship between host stock sizes and the reproductive success of mussels (Chesney & Oliver 1998). It is possible that there is a mutually beneficial relationship between the freshwater pearl mussel and host fish. Adult mussels can filter up to 50 litres of water per day (Zuiganov *et al.* 1994), and mussel beds may provide a micro-habitat for invertebrates on which juvenile salmon feed (L. Hastie pers.obs.).

Research is urgently needed to investigate the coincidental decline in salmonid fish stocks and the freshwater pearl mussel. Life in UK Rivers and Aberdeen University are currently undertaking work that will enable models to be developed relating mussel recruitment to the age and species of salmonid fish. This should assist in the production of guidance for appropriate fish management. It is also important to ensure that there are no barriers to fish migration and no acidification of tributaries, as these factors could have an adverse effect on salmonid fry availability.

Disturbance while electrofishing to assess salmonid stocks appears to have no short-term adverse effect on pearl mussel populations (Hastie & Boon 2001). However, regular trampling should be kept to a minimum.

Eutrophication

Filamentous algal mats, high phytoplankton production and the detritus formed by their decay indicate undesirable levels of eutrophication, with the resultant inhibition of both juvenile success and adult well being. A build-up in summer can also indicate inadequate flow rates. The appearance of obvious algal production is therefore an indicator of poor river condition and should warn of environmental conditions that are deleterious to freshwater pearl mussel populations.

Inorganic pollutants

Pyrethroid sheep dip is known be highly toxic to freshwater arthropods, but the direct effect on freshwater pearl mussels is not known. Indirect effects could occur through a reduction in salmonid fish numbers.

Acidification

Acidification is known to have deleterious effects on juvenile trout and salmon, and could therefore have an indirect effect on freshwater pearl mussels. Acidification may also alter juvenile habitat. According to Meyer & Klupp (1980) the decline in pearl mussels in some German rivers may be due to lowered pH values, exacerbated by spruce monocultures. The practice of catchment liming as a counter measure to restore salmonid habitat may also have an adverse effect, given the sensitivity of pearl mussels to high calcium levels.

Introduced species

Mussel viability is dependent on host salmonid viability, so any threats to native trout and salmon stocks should be avoided. There has been a tendency for angling societies and individuals to release non-native salmonids such as rainbow and brook trout. These species are a potential threat to the long-term survival of the freshwater pearl mussel as they may out-compete the native species and do not act as glochidial hosts.

Priorities for research

- The effects of flow rate on habitat, particularly substrate.
- The effects of eutrophication (and water quality requirements, especially in England.
- The effects of siltation.
- Genetic variation.
- The importance of different host species and appropriate densities.
- Key aspects of the interstitial environment for juveniles.
- Techniques for artificially rearing juveniles.
- Tolerance to acidity and sheep dip.
- Recruitment processes and rates, related to growth and water temperature (and therefore climate change).

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