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The Threat of Climate Change to Freshwater Pearl Mussel Populations

Changes in climate are occurring around the world and the effects on ecosystems will vary, depending on the extent and nature of these changes. In northern Europe, experts predict that annual rainfall will increase significantly, along with dramatic storm events and flooding in the next 50–100 years. Scotland is a stronghold of the endangered freshwater pearl mussel, *Margaritifera margaritifera* (L.), and a number of populations may be threatened. For example, large floods have been shown to adversely affect mussels, and although these stochastic events were historically rare, they may now be occurring more often as a result of climate change. Populations may also be affected by a number of other factors, including predicted changes in temperature, sea level, habitat availability, host fish stocks and human activity. In this paper, we explain how climate change may impact *M. margaritifera* and discuss the general implications for the conservation management of this species.

INTRODUCTION

During the past 100 years, the freshwater pearl mussel, *Margaritifera margaritifera* (L.), has declined throughout its holarctic range to the extent that it is now listed by IUCN as an endangered species (1). The main causes are considered to be gross industrial and agricultural (organic) pollution, over-exploitation by pearl fishermen, decline of salmonid host stocks and physical riverbed habitat degradation due to hydroelectric operations and river management schemes (2). *Margaritifera margaritifera* is now protected in Britain under the UK Wildlife and Countryside Act 1981. It is also listed on Appendix III of the Bern Convention and Annexes II and V of the EC Habitats Directive. Annex II lists species of community interest whose conservation requires the designation of Special Areas of Conservation (SACs), and Annex V lists species whose exploitation must be subject to management (although pearl fishing is now banned completely in most countries). In the UK, it is also listed under the Biodiversity Action Plan as a 'Priority Species' requiring the development and implementation of a Species Action Plan dedicated to its survival.

There is no doubt that remaining populations are now better protected by widespread bans on pearl fishing, stronger pollution control measures and restrictions on river engineering activity (3). However, in addition to potential problems with salmonid host stocks (4), it is likely that climate change will pose a serious new threat to the survival of a number of *M. margaritifera* populations over a large part of its range.

It is now widely accepted that changes in climate are occurring around the world (5) and that the effects on different ecosystems will vary (e.g. 6–8). In northern Europe, the most recent and conservative estimates predict that annual rainfall will increase significantly, along with storm events and large-scale flooding in the next 50–100 years (5). In northwestern Scotland, there is evidence that significant changes in the hydrological behavior of rivers occurred during the late 1980s (9). The rivers in this area are a global stronghold of *M. margaritifera* (2), and a number of important populations may be threatened by these changes. For example, large floods have been shown to adversely affect mussels (10), and although these stochastic events were historically rare, there is evidence to suggest that they may now be occurring more often as a result of climate change (9). Populations may also be detrimentally affected by a number of other climatic factors, including changes in temperature, sea level, habitat availability, host fish stocks and human activity.

In this paper, we investigate the direct and indirect threats posed by suggested climate scenarios for the present century, and discuss the general implications for the conservation management of threatened *M. margaritifera* populations and their habitats.

THE FRESHWATER PEARL MUSSEL LIFE CYCLE

Margaritifera margaritifera is one of the longest-lived invertebrates known, capable of reaching ages > 100 yrs (11). In common with other freshwater bivalves, it is typically dioecious, with both sexes maturing at age 12–20 yrs (12). An annual cycle of gametogenesis is apparent (4). Fertilization is external and occurs in early summer; the female mussels inhale sperm by normal filtering action. In mid-late summer, following an incubation period of several weeks, the females discharge their larvae (*glochidia*) into the river. *Glochidia*, which resemble miniature mussels (measuring 0.06–0.08 mm across: 13), are obligate parasites of fish, usually found encysted on the gills and/or fins of their hosts. Margaritiferid *glochidia* are associated with salmonids; those of *M. margaritifera* can only complete their development on the gills of Atlantic salmon, *Salmo salar* (L.) or brown trout, *Salmo trutta* (L.). A few *glochidia* are ingested or inhaled by host fish and manage to attach to and encyst on their gills. In *M. margaritifera*, the parasitic phase lasts for several months before the *glochidia* metamorphose into tiny mussels (by then ~ 0.4 mm across), excyst from the host gills and drop off and settle onto the riverbed (12). Those that settle in clean, stable sand (recruits) may survive to adulthood. A diagram of the complete *M. margaritifera* life cycle is provided in Figure 1.

CLIMATIC FACTORS LIKELY TO AFFECT MUSSEL POPULATIONS

Temperature

Changes in temperature may influence a number of factors that are important to survival, including individual growth, longevity and reproductive success (11, 14). *Margaritifera margaritifera* is a holarctic species that is patchily distributed in northwestern Europe and northeastern North America, between 40°N and 70°N (1). In Scotland, which is situated well within this latitudinal range (55–60°N), the temperatures of small streams supporting mussel populations can vary from 0–25°C in some years (unpubl. data), so this species exhibits a considerable degree of thermal tolerance.

During the 20th century, the global mean air surface temperature warmed by 0.3–0.6°C with Europe experiencing warming above the global average at 0.8°C (15). Sometime around the

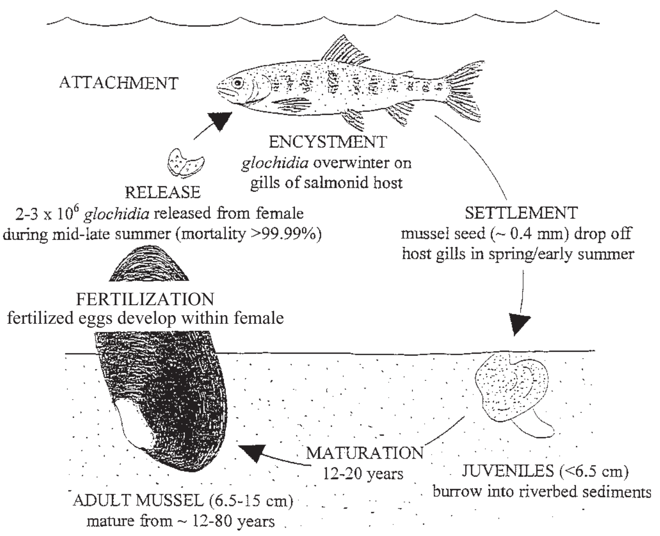


Figure 1. The freshwater pearl mussel life cycle. (Quantitative data from ref. 12).

Table 1. Climate change scenarios for Scotland for the 30-yr periods centered on the 2020s and 2050s with respect to the 1961–1990 average (16), and sea level rise projections for Scotland (17).

Year	Temperature (°C)	Precipitation (%)	CO_2 (ppmv)	Sea level (m)
1990	——	——	353	——
2020s	+0.5 → +1.2	+3 → +6	415 → 434	——
2050s	+0.8 → +2.0	+3 → +5	467 → 528	+0.08 → +0.72

2020s (i.e. 2010–2039) it is possible that Scotland will witness a 1°C increase in mean air surface temperature and a 2°C rise sometime around the 2050s (i.e. 2040–2069) (Table 1). These figures are based on global circulation models published in 1996 (5) that have since been revised upward to predict a global warming of between 1.4°C and 5.8°C (18). How this will affect the hydrothermal regimes of rivers is not known as there is a dearth of long-term freshwater temperature monitoring. There is typically a strong relationship between air and surface water temperature across a range of catchment types and sizes (19). Daily maximum water temperatures in the Girnock Burn, an upland stream in northeastern Scotland, increased by ~ 2°C over a 30-yr period, due to the effect of increased air temperatures (1968–1997) (20).

There is some historical evidence that elevated water temperatures may enhance recruitment (post-settlement survival) in *M. margaritifera* populations. For example, the best recruiting years (as indicated by peaks in age-frequency profiles) of a population in the River Foyle catchment, Northern Ireland, appeared to coincide with warmer-than-average summers (21). In the Czech Republic, Hruska (14) has associated large year classes with elevated monthly temperatures during the period of *glochidial* development. This may be explained by the observations that *i*) *glochidia* appear to grow faster (and larger) in warm conditions (14); and *ii*) there is a strong positive relationship between initial size and survival of newly-settled mussels (13). Therefore, it is possible that a slight elevation of mean temperature will actually benefit some *M. margaritifera* populations.

However, the most significant ecological temperatures are the minimum and maximum values. Although individual mussels may acclimatize to a gradual warming of rivers, they are more likely to be affected by changes in extreme thermal events. For example, the expected increases in maximum temperatures and the frequency and duration of exceptionally warm periods in summer may be detrimental, particularly to mussels in small streams (which tend to heat up rapidly). At present, the critical upper thermal limits for survival and normal functioning in this species are unknown.

A number of studies have indicated that the timing of reproduction in *M. margaritifera* is influenced by temperature—mussels tend to spawn earlier in warm conditions (22). This has also been reported for the closely-related *M. falcata* in North America (23). According to Ross (24), annual spawnings of *M. margaritifera* may vary by several months, due to thermal effects. The timing of mussel and host fish reproductive cycles may be linked—in Scottish rivers, for example, mussels spawn when salmon and trout fry are abundant (12). Differential effects of temperature change may cause problems by uncoupling the timing of mussel and salmonid reproduction. Changes in host fish availability and other possible indirect effects of climate change are discussed later.

Precipitation

The consequent increase in evaporation and alterations in air mass circulation also increases cloud cover. This was most marked across the west coast of Scotland where the average mean daily hours of bright sunshine decreased between 1941–1971 and 1964–1993 by around 16% (25). Although the Northern Hemisphere only saw an increase in precipitation levels of around 1% (26), Scotland experienced much higher increases. The most extreme cases of increasing precipitation levels were in the west during the winter months, increasing by up to 15–20% between 1941–1971 and 1964–1993 (27). The Loch Rannoch area experienced an increase of 57–58% more rain during March between 1916–1950 and 1961–1990 (27). Some of this rain has been experienced as greater storm events (9), which also alter the habitat structure of mussel beds (10).

A close match between historical precipitation (rainfall) and *M. margaritifera* recruitment patterns (1957–1991) was observed in the River Kerry, northwestern Scotland (Fig. 2). In general, the mussels appeared to recruit well during wet years and *vice versa*. With annual average increases in precipitation expected to be about 3–6% over the next five decades (Table 1), there is no evidence to suggest that recruitment in the Kerry population is threatened by an overall increase in rainfall in this time. On the contrary, recruitment levels may even rise as a result of more wet years. Juvenile *M. margaritifera* have specific microhabitat

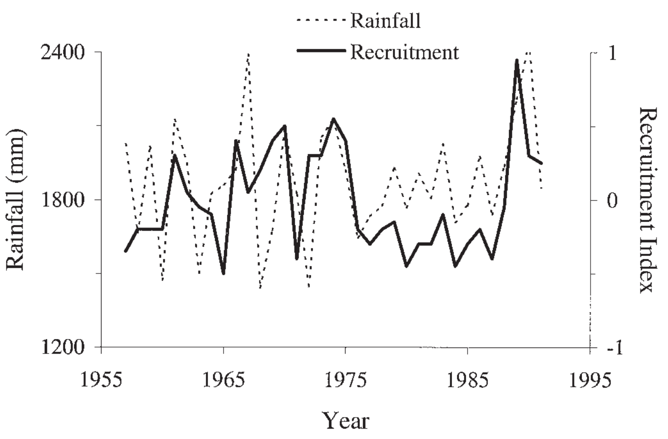


Figure 2. Annual precipitation levels (UK Met. Office data, broken line) and mussel recruitment index values (main stem site, solid line) recorded for the River Kerry, northwest Scotland during 1957–1991. The latter, based on a sample of mussel ages (n > 1000), are residuals above and below an expected decline of numbers-at-age (year of settlement).

requirements and tend to recruit only in stable riverbeds that contain very clean, well aerated sand (28). Thus, the higher flows associated with wet years may help to cleanse the riverbed sediments and make more suitable microhabitat available for recruitment.

It should be noted that the Kerry is a small, partly regulated river (overall length < 20 km). In the much larger Foyle system in Northern Ireland (> 200 km), mussels appear to have recruited more successfully in drier conditions over the period 1920–1980 (21). Thus, the effects of increased precipitation on the recruitment success of different populations may vary according to the size and hydraulic characteristics of each parent river.

However, changes in the seasonal pattern may threaten the mussels in many rivers if springs and summers continue to become drier. By 1961–1990, summers were drier by up to 20% in some areas (27). During prolonged dry periods, some mussel beds are at risk of drying out (pers. obs.). Furthermore, the amount of silt deposits, algal growth, and organic debris on the riverbed may increase considerably as a result of reduced flows. This process is detrimental to newly-settled mussels living in the riverbed sediments (13).

Periodic floods are thought to have some beneficial effects. For example, a mussel bed may be 'improved' as potentially harmful materials, built up during low flow conditions, are flushed out of the sediments (29). Although some mortality occurs when mussels are dislodged and washed downstream (30), in most cases this is probably compensated for by the increased (post-flood) survival of juvenile mussels in the clean sediments. However, over a number of years, the size and frequency of floods are likely to be important factors in determining the net effect on local mussel populations. When exceptionally large floods occur, the ecological effects can be catastrophic (31).

In Scotland, there is anecdotal and quantitative evidence that a number of populations have been adversely affected by these events. For example, 'great numbers' of mussels in the River Avon were apparently destroyed by a huge flood in 1829 (unpubl. letter, Grant 1852). In 1970, a record flood of the River Spey destroyed several large mussel beds (Suttie, pers. comm.). In 1998, a 100-yr return flood of the River Kerry killed > 50 000 mussels (≈ 5–10% of the total population) (10). Figure 3 shows how badly the mussel beds in the lower reaches of the river were affected. At this particular site, 40% of the visible mussels disappeared from the riverbed. There were major floods throughout northwestern Scotland in 1998, and other *M. margaritifera*

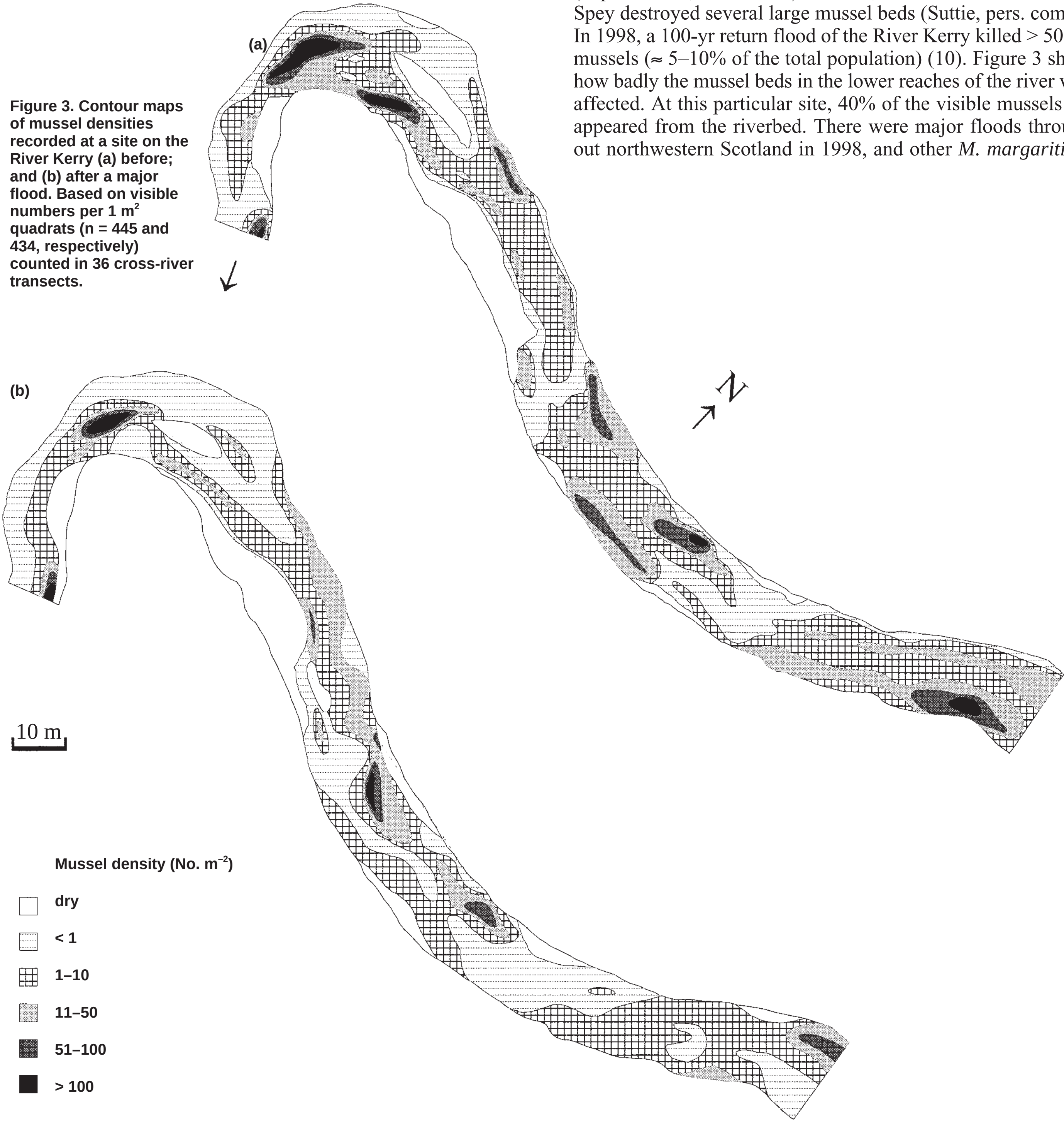


Figure 3. Contour maps of mussel densities recorded at a site on the River Kerry (a) before; and (b) after a major flood. Based on visible numbers per 1 m^2 quadrats (n = 445 and 434, respectively) counted in 36 cross-river transects.

populations were also affected (10), but the effects were not quantified.

Significant changes in the hydrological behavior of Scottish rivers occurred in the late 1980s. These included new maximum flood records, increases in frequencies of high flow occurrence and greater annual runoffs (9). Record floods occurred in 8 of the 16 largest rivers in Scotland during the 1990s. Climate change is thought to be responsible (32), although in some areas, upland drainage schemes have probably contributed (10). Since it is predicted that Scotland may continue to experience heavy rain events more frequently with greater winter and annual precipitation levels, and a higher frequency of storms during the next 50–100 years (16), these trends will probably continue. Thus, it seems that Scottish *M. margaritifera* populations are now more at risk from catastrophic floods than they were before.

Similar changes have also been observed in Texas, where the impact of large-scale flooding on unionid mussel populations (as a result of overgrazing and land clearance) has been exacerbated by increased precipitation during the last 20 years (33).

INDIRECT EFFECTS OF CLIMATE CHANGE

Sea Level Rise

Scotland is re-bounding geologically from the loss of ice 10 000 years ago. Despite this, sea level rise is expected to occur around the Scottish coast within the next 50 years. Estimates vary from 0.12-0.38 m in a UK model (16) to 0.08–0.71 m in a more detailed assessment of the Scottish coast (17). The extreme northwest and Northern Isles, where > 90% of surviving *M. margaritifera* populations in Scotland occur (2), are expected to experience the greatest rise (17). Those populations that are distributed in the lower reaches of rivers are at greatest risk of immersion in seawater.

Margaritifera margaritifera cannot tolerate saline conditions. However, in some rivers, live mussels occur in freshwater below the official high watermark but above the usual upstream limit of salt/brackish water (34). Although only a few individuals would typically be killed by permanent immersion in seawater, there are some low-lying rivers where the numbers may be more significant. Furthermore, greater numbers would also be affected by sporadic incursions of salt/brackish water that occurred as a result of extreme conditions (e.g. spring tides, storm events, onshore winds). It is worth mentioning that storm surges, which can greatly magnify the maximum tidal level (and therefore are far more detrimental than the insidious creep of sea level rise), are expected to have the greatest impact on coastal habitats, and therefore, by implication, the lowest reaches of rivers (17). If the adjacent reach, 0.5–1.0 m above present sea level, is considered to be a real 'danger zone' in this respect, i.e. where mussels are at considerable risk, then several populations may be affected (Table 2). Based on our knowledge of current mussel distributions (34), 16 populations in northwestern Scotland may suffer significant losses (i.e. > 1% population and/or > 5% suitable riverbed habitat) as a result of the predicted rise in sea level during the next 100 years.

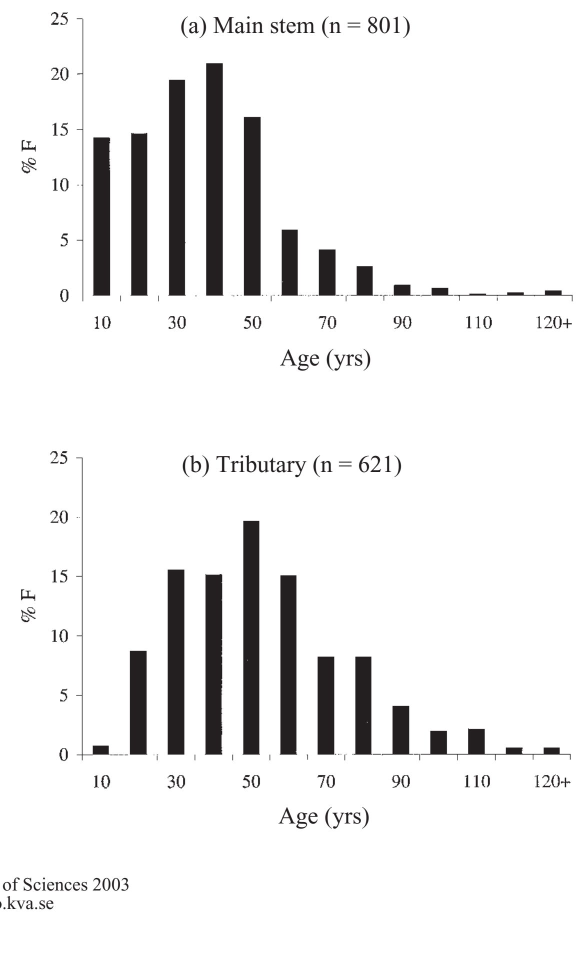
Table 2. Numbers of known Scottish *M. margaritifera* populations expected to be adversely affected by a 0.5–1.0 m rise in sea level. Not considered significant unless > 1% of mussel population and/or > 5% of suitable riverbed habitat destroyed by saltwater incursion. Based on knowledge of current mussel distributions (34).

Impact	No. populations (%)
No significant effect	33 (57)
Mussels directly affected	16 (27.5)
Unknown	9 (15.5)

Habitat Reduction

At present, a number of Scottish populations are showing signs of reduced recruitment (35). Small streams in particular have very few juvenile mussels. This is demonstrated by comparing the age-frequency profiles of mussels in the main stem and a small tributary of the River Kerry (Fig. 4). These rivers are in the same catchment, have identical water quality and similar densities of host fish; so what has affected the mussels in the tributary? We observed that streams that lacked juveniles appeared to have very little suitable substrata (stable, clean sand) and suggested that recruitment in these populations may be limited by habitat availability (35). Based on the large numbers of adult mussels still found in some streams, there must have been substantial amounts of suitable habitat (for recruitment) in these previously. Some populations in Scotland may be threatened by the progressive reduction of suitable habitat, a phenomenon that has not yet been quantified (3). Rainfall may influence habitat availability. High flows and increased runoff can lead to significant changes in patterns of erosion and deposition that degrade the riverbed habitat (36). Small streams generally respond faster to hydrological events than large rivers and are, therefore, relatively less stable (37). As a result, streambeds are often severely scoured during floods, leaving very little suitable substrata for juvenile *M. margaritifera*. Therefore, the apparent loss of suitable habitat in many streambeds may be associated with the increased runoff that has occurred in northwest Scotland. As the fine sediments are effectively shifted downstream, some populations may eventually be restricted to low reaches that are at

Figure 4. Age-frequency profiles of *M. margaritifera* observed in samples from (a) a main stem site; and (b) a small tributary stream of the River Kerry. Samples were taken in 1997 and 1998, respectively.



risk from sea level rise. The mussel populations in small streams certainly seem to be more vulnerable to the effects of climate change.

Decline in Host Fish Stocks

The larvae (*glochidia*) of *M. margaritifera* are very host specific and can only complete their development on either *S. salar* or *S. trutta* (usually 0+ fish) (12). Although very little is known about the mussel:host relationship, long-term survival clearly depends on host availability, and there is concern that significant changes in wild salmonid stocks now threaten mussel populations (4). Low host densities may be limiting recruitment in some mussel populations (11, 38). In northwestern Scotland, several migratory trout stocks have collapsed recently and some salmon stocks are declining (39). Catches of both species are now at historical low levels (Fig. 5). The causes for this general decline have been attributed to a number of factors, including climate change, overfishing, increased predation, sea lice infestations, pollution (acidification) and physical habitat degradation (40). Whatever the reasons, the survival of all remaining *M. margaritifera* populations in northwestern Scotland is threatened unless wild salmonid stocks recover (4).

Depleted salmonid stocks may be affected by climate change. Salmonids are sensitive to temperature rise. Thermal stress resulting from elevated temperatures may exceed critical levels in some small streams. The critical upper limits for survival of *S. salar* and *S. trutta* are 28–33°C and 25–30°C, respectively, depending on acclimation (41). The upper limits for successful growth and egg development in these species are much lower (< 20°C) (41). Dissolved oxygen content is inversely related to water temperature, and the lowered levels associated with temperature rise may also be an important factor. The oxygen requirements of salmonids are considerably higher than those of most other fish species (41). Therefore, the host fish populations may be adversely affected by the expected increase in temperature over the next 50–100 years.

The increased precipitation and associated hydrological changes may also have serious consequences for host fish. For example, during the winter, the gravel spawning beds (redds) of salmon and trout are sometimes completely destroyed by large floods—a process known as 'redd washout' (42). Increased riverbank and riverbed erosion may also adversely affect salmonids by siltation of redds further downstream (36). Since large floods are becoming more common in northwestern Scotland (9), it is likely that more 'washouts' will occur in future. As a result, egg survival will be lowered, which in turn may lead to declines in the numbers of juvenile fish produced in some rivers. Butler (42) observed a negative correlation between total winter runoff and the densities of salmon fry the following summer in a river in northwestern Scotland. In other words, fewer young salmon hatched successfully after wet winters and *vice versa*.

Those that do hatch successfully are also vulnerable to subsequent floods. In 1997, for example, a 100-yr return flood 'washed out' large numbers of 0+ fish in the River Oder in Central Europe (43). These observations suggest that, as a result of the predicted increases in precipitation and associated hydrological changes in Scottish rivers, depleted stocks of host fish may be further reduced in the next 50–100 years.

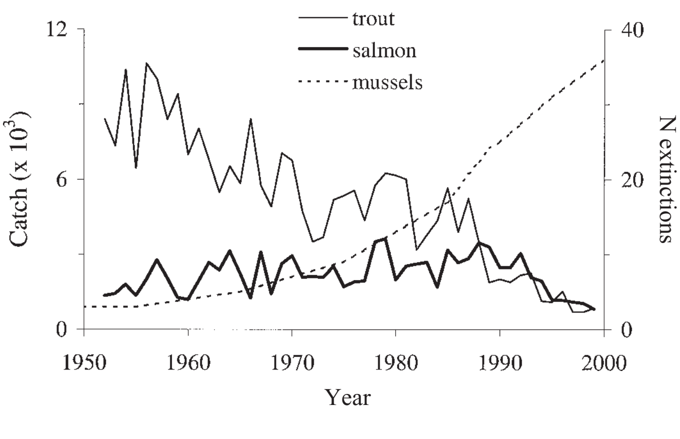


Figure 5. The coincidental declines of migratory salmonids and freshwater pearl mussels in northwest Scotland during 1952–2000. Presented as annual rod and line catches recorded (Scottish Fisheries Research Services) and estimated (cumulative) number of mussel population extinctions (Cosgrove: unpubl. data).

Changes in Human Activity

Finally, it is important to consider how the human response to climate change will impact mussel populations. Two main themes are dealt with here, *i*) schemes designed to deal with the consequences of climate change (remedial schemes); and *ii*) schemes designed to reduce further climate change (preventative schemes).

Remedial schemes

In the UK, as a result of recent increases in precipitation and large-scale flooding, there is political pressure to build extensive flood prevention schemes in a number of catchments. Several studies have identified that physical habitat disturbance by river engineering can seriously impact *M. margaritifera* populations (see ref. 3 for review). Engineering works associated with flood prevention and post-flood (infrastructural) repairs have caused considerable habitat degradation and high mussel mortality; up to 50% of suitable riverbed habitat damaged and 10 000 mussels killed in the worst known cases (3). Since river engineering could become more common as a result of large floods, some populations may be seriously threatened by this potentially destructive activity in future.

Preventative schemes

Another effect is that people around the world are becoming increasingly alarmed about the perceived global warming process. Developed countries are now under international pressure to reduce the high levels of greenhouse gas emissions that are thought to be responsible for this phenomenon. As a result of commitments made at the intergovernmental summits in Rio (1992) and Kyoto (1997), the UK government has promised to deliver a 20% cut in CO_2 emission by 2010. Greenhouse gases continue to build up steadily in the atmosphere (CO_2 concentrations may double in this century (18)), and it is vital that governments succeed in their efforts to reduce emissions. However, this will be extremely difficult to achieve in the short term and there are likely to be other environmental costs incurred along the way.

In Europe, various measures have been taken in order to reduce emissions by restricting fossil-fuel burning. For example, proposed renewable energy generation schemes (e.g. hydroelectric stations) have been actively encouraged. The climate and much of the topography of Scotland are suitable for hydroelectric generation and many schemes were built in the last century. During the past 10–20 years, under the Scottish Renewable Obligation (SRO), a large number of hydroelectric schemes were carried out and some *M. margaritifera* populations were adversely affected (3). In addition to the disturbance during dam construction, certain operations such as the increased production of electricity during periods of high demand (known as 'peaking operations') cause rapid alterations of high and low flows. These often produce short-term near-flood and near-drought conditions which are clearly incompatible with maintaining mussel populations (44). According to Ziuganov et al. (38), a number of mussel populations in northwestern Russia disappeared following large-scale hydroelectric schemes.

IMPLICATIONS FOR CONSERVATION

Global Issues

There is a general awareness that a number of endangered species and ecosystems are threatened by climate change (e.g. 7, 8), but little attention has been paid to the freshwater mussels (Unionacea) in this respect. On a global scale, they are a highly threatened group (45). During the past 50–100 years, many species around the world have either become extinct or have declined considerably. The present conservation status, complex life histories and specific habitat requirements of unionaceans suggest that they may be quite sensitive to climate change, and appropriate research in this area is urgently required.

At present, it is impossible to predict what exactly the overall impact of climate change on *M. margaritifera* conservation will be. If present climatic trends continue, how relevant will the present list of EU (pearl mussel) candidate SACs be in 50-yrs time? Will other undesignated rivers with marginal populations gradually become more important? Only time will answer these questions. What does seem likely is that the effects of climate change will be largely detrimental. Thus, climate change must be considered to be a real threat to extant populations. It is, therefore, important that effective conservation management strategies are drawn up to deal with this problem.

The endangered *M. margaritifera* is likely to be yet another victim of climate change unless effective action is taken soon. In the first instance, the issues of tackling climate change and conserving species that are likely to be threatened must be dealt with at the international level. The main solution for all species may ultimately be to encourage governments to drastically reduce greenhouse gas emissions in the hope that current climatic trends be halted. Unfortunately, owing to economic and political pressure, this is probably the most difficult one to achieve.

Local Issues

The remaining *M. margaritifera* populations in Scotland appear to be at considerable risk and it is important that these are monitored. Baseline studies have been carried out recently (2, 35), thus providing valuable information for future comparisons. However, in addition to mussel population characteristics such as adult mortality rates and recruitment success, host fish stocks and local environmental conditions should also be monitored.

Conservation managers will also have to deal with the expected increase in proposed river engineering projects that are likely to impact some populations. In Scotland, a number of river engineering projects (including hydroelectric schemes) have been carried out on mussel rivers, recently (3). This practice is likely to continue in the foreseeable future. In theory, *M. margaritifera* and its habitat are protected under domestic and European law, especially those populations in SACs. Therefore, it must be ensured that any proposed work affecting mussels is allowed to proceed only if it is unavoidable, and that it is carried out in a sympathetic manner. A number of Scottish populations reside in regulated rivers (3). How these rivers are managed may be critical—although *M. margaritifera* is legally protected, certain hydrological regimes can threaten its long-term survival (10). However, there are no clear guidelines because the effects of extreme flows are poorly understood at present. It is clear that further investigations on this subject are worthwhile.

In certain situations, the artificial translocation of threatened adult mussels may be considered as a conservation tool. However, translocation has not yet been shown to be effective in the long term, and therefore should be considered experimental and last resort (3). Valovirta (46) has reported short-term survival rates of 90% for within-river transfers of *M. margaritifera*, but only 50% for between-river transfers. The most sensible approach would therefore be to limit transfers to those situations where the threat is unavoidable and particularly severe. For example, in Finland, ~ 600 mussels were transferred from one river to another prior to large-scale engineering works (46).

It may be necessary to establish new mussel beds in other areas in order to ensure that overall populations persist. For example, hydrological changes may cause different rivers (or reaches of riverbeds) to become either more or less suitable as mussel habitats. In some rivers it may be possible to transfer upstream small numbers of mussels that are threatened by sea level rise. It is worth considering that significant climatic changes are expected to occur within 50–100 years, whilst natural colonization of new sites by *M. margaritifera* may take far longer, thus requiring a 'helping hand' *via* translocation and/or captive breeding.

The culture of endangered freshwater mussels has recently been attempted, with some success (47, 48). At present, there is an EU-funded *M. margaritifera* cultivation project underway in Scotland. The objective there will be to restore populations depleted by pearl fishing in many rivers where the habitat is still considered to be suitable. By the end of the century, however, it is possible that climate change will result in a further reduction of habitat. It may be that future conservation strategies will only be effective at the international level. For example, it may eventually become necessary to find more suitable *M. margaritifera* sites in Scandinavia and northern Russia.

One of the key opportunities available to offset the effects of climate change on *M. margaritifera* lies in the restoration of suitable riparian habitat, especially native woodland. The roots of riparian tree species such as alder, *Alnus glutinosa* (Gaertn.), help reduce erosion by stabilizing river banks (36). In Ireland and Central Europe, mussel beds are often found in association with tree cover (49, 50). It is thought that deciduous trees lining the river bank may benefit mussels by shading the watercourse and thus reducing hydrothermal fluctuations and preventing excessive algal growth on the riverbed (49). The removal of bankside trees and subsequent erosion of riverbanks have been implicated in the decline of some German *M. margaritifera* populations (1). Therefore, riparian woodland may act as a countermeasure to the potential effects of climate change (i.e. by thermoregulation and erosion/deposition control). In prehistoric times (> 2000-yrs ago), most of Scotland was covered in forest. Today, only a fraction of this cover remains (36) and most of the surviving Scottish *M. margaritifera* populations are found in catchments denuded of native riparian and floodplain woodland. This provides conservation bodies and river managers an opportunity to target woodland restoration towards key populations in denuded catchments. In the UK, public funding of woodland restoration projects is possible through the Woodland Grant Scheme and a number of agri-environment schemes. Any action taken to increase riparian woodland cover for *M. margaritifera* is also likely to benefit other species.

CONCLUSIONS

During this century, many of the remaining pearl mussel populations in Scotland and elsewhere may be seriously threatened by climate change. Although a considerable amount of work has been carried out on *M. margaritifera* conservation and ecology, significant gaps in our knowledge remain that need to be addressed. Recent developments in statutory protection, habitat restoration, captive breeding, and other areas allow a degree of optimism. However, it is clear that more research is required in order to assess the extent to which populations will be affected and what conservation measures will be appropriate in future. Whether or not endangered freshwater mussel populations survive the challenge of climate change may depend greatly on how effectively we can manage and protect them.

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