

Ecology of the River, Brook and Sea Lamprey

Lampetra fluviatilis, *Lampetra planeri* and
Petromyzon marinus



Conserving Natura 2000 Rivers
Ecology Series No. 5



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Conserving Natura 2000 Rivers

This account of the ecology of the river, brook and sea lamprey (*Lampetra fluviatilis*, *L. planeri* and *Petromyzon marinus*) has been produced as part of **Life in UK Rivers** – a project to develop methods for conserving the wildlife and habitats of rivers within the Natura 2000 network of protected European sites. The project's focus has been the conservation of rivers identified as Special Areas of Conservation (SACs) and of relevant habitats and species listed in annexes I and II of the European Union Directive on the Conservation of Natural Habitats and of Wild Fauna and Flora (92/43/EEC) (the Habitats Directive).

One of the main products is a set of reports collating the best available information on the ecological requirements of each species and habitat, while a complementary series contains advice on monitoring and assessment techniques. Each report has been compiled by ecologists who are studying these species and habitats in the UK, and has been subject to peer review, including scrutiny by a Technical Advisory Group established by the project partners. In the case of the monitoring techniques, further refinement has been accomplished by field-testing and by workshops involving experts and conservation practitioners.

Life in UK Rivers is very much a demonstration project, and although the reports have no official status in the implementation of the directive, they are intended as a helpful source of information for organisations trying to set 'conservation objectives' and to monitor for 'favourable conservation status' for these habitats and species. They can also be used to help assess plans and projects affecting Natura 2000 sites, as required by Article 6.3 of the directive.

As part of the project, conservation strategies have been produced for seven different SAC rivers in the UK. In these, you can see how the statutory conservation and environment agencies have developed objectives for the conservation of the habitats and species, and drawn up action plans with their local partners for achieving favourable conservation status.

Understanding the ecological requirements of river plants and animals is a prerequisite for setting conservation objectives, and for generating conservation strategies for SAC rivers under Article 6.1 of the Habitats Directive. Thus, the questions these ecology reports try to answer include:

- What water quality does the species need to survive and reproduce successfully?
- Are there other physical conditions, such as substrate or flow, that favour these species or cause them to decline?
- What is the extent of interdependence with other species for food or breeding success?

For each of the 13 riverine species and for the *Ranunculus* habitat, the project has also published tables setting out what can be considered as 'favourable condition' for attributes such as water quality and nutrient levels, flow conditions, river channel and riparian habitat, substrate, access for migratory fish, and level of disturbance. 'Favourable condition' is taken to be the status required of Annex I habitats and Annex II species on each Natura 2000 site to contribute adequately to 'favourable conservation status' across their natural range.

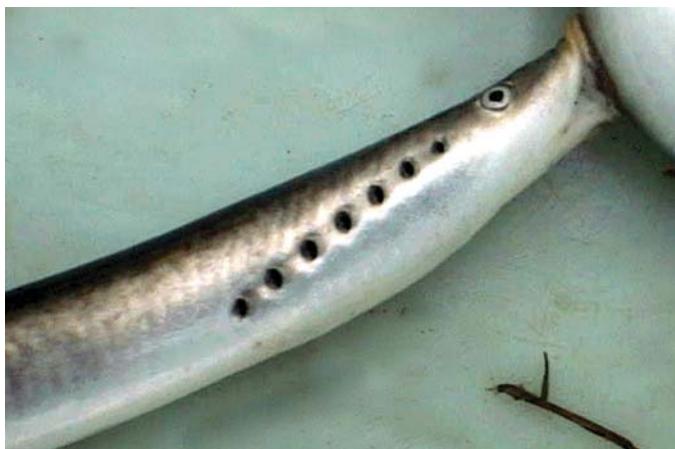
Titles in the Conserving Natura 2000 Rivers ecology and monitoring series are listed inside the back cover of this report, and copies of these, together with other project publications, are available on the project website: www.riverlife.org.uk.

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General Introduction

The lampreys (family Petromyzonidae, stone suckers) belong to a small but important group known as Agnatha – literally, jawless – the most primitive of all living vertebrates. They are not true fish, though it is normally convenient to refer to them as such. They are quite distinct from other fish in the British Isles, which have upper jaws fixed closely to the skull, and hinged lower jaws. The lampreys, in contrast, have no lower jaws, and the mouth is surrounded by a round, sucker-like disc within which, in the adults, are strong, horny, rasping teeth. These vary in shape, size, position and number among the species, and are an important aid to identification.



Environment Agency

Adult lampreys are eel-like in shape and have seven gill pores behind each eye that open directly to the gills.

Lampreys have several other very characteristic features. They are always eel-like in shape, but have neither paired fins nor scales. They have no bones, all the skeletal structures being made up of strong, flexible, cartilage. There is only one nostril, situated on top of the head, just in front of the eyes, the latter rarely being functional or even visible in the young. The gills open directly on each side of the head (there is no gill cover or operculum) forming a row of seven gill pores behind each eye. Adult lampreys have two dorsal fins, which are often continuous with the elongate tail fins.

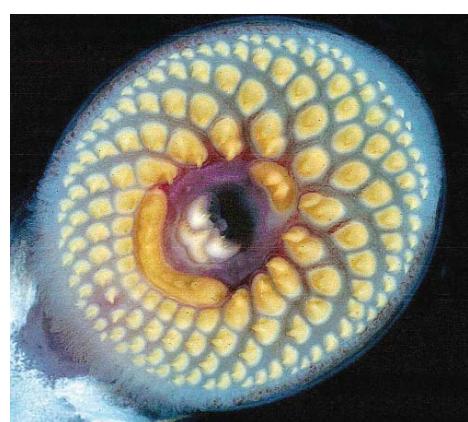
Lampreys occur in the temperate zones of both the northern and southern hemispheres. Fossils are available from the late Silurian and Devonian periods, 450 million years ago.

Life cycle

Most species of lamprey have a similar life cycle (Maitland & Campbell 1992), which involves the migration of adults upstream into rivers to reach the spawning areas, normally stony or gravelly stretches of running water. There they spawn in pairs or groups, laying eggs in crude nests – shallow depressions previously created by lifting away small stones with their suckers. These stones surround and sometimes cover and protect the eggs, while the nest itself may often be under a large stone, log or clump of vegetation. Frequently, however, the nest is in the open in shallow water, and the spawning adults are very vulnerable to predators.



Both photos by Ross Gardiner



Ammocoetes, like this sea lamprey larva (left), have undeveloped suckers and teeth. Adults, however (right), have rasping teeth inside a fully developed sucker. The tooth pattern is different in each species.

After hatching, the young elongate larvae, known as ammocoetes, swim or are washed downstream by the current to areas of sandy silt in still water where they burrow and spend the next few years in tunnels. They are blind, the sucker is incomplete and the teeth are undeveloped. These ammocoetes feed by creating a current that draws organic particles (coated with bacteria) and minute plants (and algae such as diatoms) into the pharynx. There they become entwined in a slimy mucus string, which is constantly swallowed by the larvae.

The metamorphosis from larva to adult is a dramatic change, which takes place in a relatively short time – usually a few weeks – after several years of larval development. The rim of the mouth (previously in the form of an oral hood) develops into a full sucker inside which are the rasping teeth; and the skin becomes much more silvery and opaque except over the eyes, where it clears to give the lamprey proper vision for the first time. The lampreys then migrate, usually downstream, away from the nursery areas.

Some species, such as the brook lamprey, never feed as adults. After metamorphosing they spawn and then die. Most, however, prey on various other fish, either in large freshwater lakes and rivers or in the sea, where most of the adult life is spent. They attach themselves to the sides of fish and rasp away the skin, eating it and the body fluids and muscle underneath. The prey may never recover from such an attack (especially if the body cavity is penetrated), and in some waters lampreys are serious pests of commercial fish stocks. The most famous example of this is in the Great Lakes of North America, where canalisation gave the sea lamprey access, for the first time, to the upper lakes. Various commercial fish stocks there became seriously depleted, particularly the American lake charr (*Salvelinus namaycush*), whose populations collapsed.

On reaching sexual maturity, the adult lamprey stop feeding and migrate back to their spawning streams. All species die after spawning.

British lamprey

There are three species of lamprey in Britain: river lamprey (*Lampetra fluviatilis*); brook lamprey (*Lampetra planeri*), and sea lamprey, (*Petromyzon marinus*). Although they have much in common, there are significant ecological differences among the three species, so they are dealt with separately in this report. However, since for many of the attributes there is very little information available, where targets are given and the ecology is believed to be similar, values may have had to be transposed from one species to another. Inevitably, this means some repetition in the text.

It should be noted that almost all authors regard the river and brook lamprey as being very closely related, and some (Eneqvist 1937, Privolnyev 1964) consider them effectively the same species. The term 'paired species' was used for the first time by Zanandrea (1959) for these two lampreys – the description being applied to pairs of morphologically similar lampreys, one a non-parasitic species probably derived from the other, a parasitic species (Potter 1980). A new term for this relationship, 'satellite species', was coined by Vladkov and Kott (1979), and both terms are now in common usage.

River Lamprey

Introduction

The river lamprey (*Lampetra fluviatilis*) is known in various parts of the British Isles as the juneba, lamper eel, lampern, nine-eyed eel, nine eyes, seven eyes, and stone gris. Of the three British lampreys, the river lamprey is intermediate in size between the large sea lamprey and the small brook lamprey. The average adult length is around 30 cm with a corresponding weight of about 60 g, but specimens over 40 cm can be found, and the unusual race in Loch Lomond is often less than 20 cm. It is a migratory species, which grows to maturity in estuaries around Britain and then moves into fresh water to spawn in clean rivers and streams. The larvae spend several years in silt beds before metamorphosing and migrating downstream to estuaries.



Brian Morland

The river lamprey spawns in fresh water, and the larvae live in silt beds before migrating to estuaries.

The river lamprey has declined in Britain over the last hundred years and, though not yet distinctly threatened, is in need of general conservation measures to restore populations to their former status (Maitland & Campbell 1992).

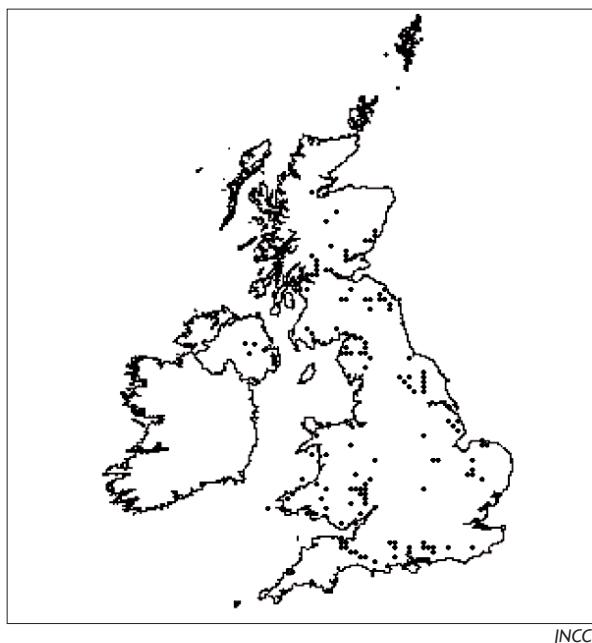
Young river lampreys (ammocoetes) before metamorphosis are usually a dull grey-brown in colour and indistinguishable from the ammocoetes of brook lampreys. However, they metamorphose at a smaller size (9–12 cm on average, compared with the 12–15 cm brook lamprey), when they become silvery along the sides and belly, darkening to grey on the back. During their feeding stage in the sea they retain this silvery colour, but as the time to return to fresh water to spawn draws near, they lose the silvery sheen and become darker all over. The back (which is not mottled like the sea lamprey) is a uniform dark olive to dark grey, and this changes to a brownish yellow on the sides, gradually lightening ventrally. The fins are mainly dark brown. The large eye has a golden iris, flecked with brown.

The river lamprey is easily distinguished from the sea lamprey on the basis of size and colouration, and the patterning of the teeth is also quite different. However, the general body shape of the two species is similar. Thus the river lamprey has a long, streamlined, eel-like body with two dorsal fins that are separate from each other until near spawning time; the second is continuous with the tail fin. There are



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The river lamprey is found mainly in western Europe in coastal waters, estuaries and rivers.



JNCC

The river lamprey has disappeared from many UK rivers due to obstructions preventing passage to spawning grounds.

conservation requires the designation of Special Areas of Conservation (SAC); in Appendix III of the Bern Convention, which permits some exploitation of its population; and as a Long List Species in the UK Biodiversity Action Plan. There is no Red Data Book for fish in Britain, nor is this species listed in the 1981 Wildlife and Countryside Act, but Maitland (2000a) considers this species to be Vulnerable. The Red Data Book for Ireland (Whilde 1993), published before the IUCN (1994) revision of categories, lists the river lamprey as Indeterminate.

no paired fins. The seven gill openings on each side of the head are obvious, and easily distinguish this fish from the eel (*Anguilla anguilla*), which has only one small opening on each side, just in front of the paired pectoral fins. The body is slimy and extremely difficult to hold when it is alive.

River lamprey are of considerable commercial value in parts of Europe, and in both Sweden and Finland there are major fisheries for them, using mainly basket traps, during the upstream spawning migration (Tunnainen et al. 1980). Substantial fisheries did once exist for this species on some large British rivers (for example, the Severn). However, it is no longer of any commercial importance in Britain.

Status and distribution

The river lamprey is found from southern Norway to the western Mediterranean, in coastal waters, estuaries and accessible rivers. The species is mainly anadromous but there are a few land-locked, non-migratory populations isolated from the sea in Finland, Russia and Scotland. The species has disappeared from many rivers due to pollution, river engineering and various impassable barriers (weirs, dams, etc.).

In Britain, the ammocoetes of river lamprey occur in silt beds in many rivers from the Great Glen in northern Scotland southwards. Occasionally, they are found in suitable silts in large lakes. They are absent from a number of rivers because of pollution or obstacles that the adults cannot surmount during the spawning migration, such as natural waterfalls or artificial dams. River lamprey often occur in association with the other two British lamprey species, but occasionally – for example, in the River Teme (Hardisty & Huggins 1970) – they may, for unknown reasons, occur as pure populations.

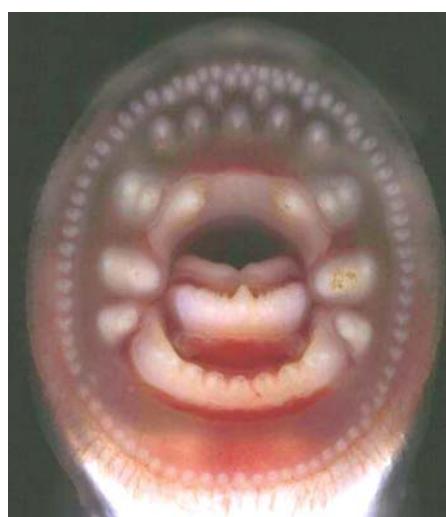
Because of its decline, the river lamprey is now given some protection. It is listed in annexes IIa and Va of the European Union Habitats Directive as a species of community interest, whose

Life history

After metamorphosis, young river lampreys can still burrow, but their main aim is to descend downstream to the sea. In the estuaries of major rivers they can be found in some numbers, feeding on a variety of estuarine fish, but particularly herring (*Clupea harengus*), sprat (*Sprattus sprattus*) and flounder (*Platichthys flesus*). They often inflict extensive damage on these fish by rasping away large amounts of flesh from the back. The lampreys themselves have a very bloated appearance at this time due to the entire gut being full of blood and fish flesh (Maitland et al. 1984, Stephenson et al. 1995). The dwarf race of river lamprey in Loch Lomond feeds there mainly on powan (*Coregonus lavaretus*) (Slack, 1955, Maitland 1980).



Brian Morland



David Bird



Peter Maitland

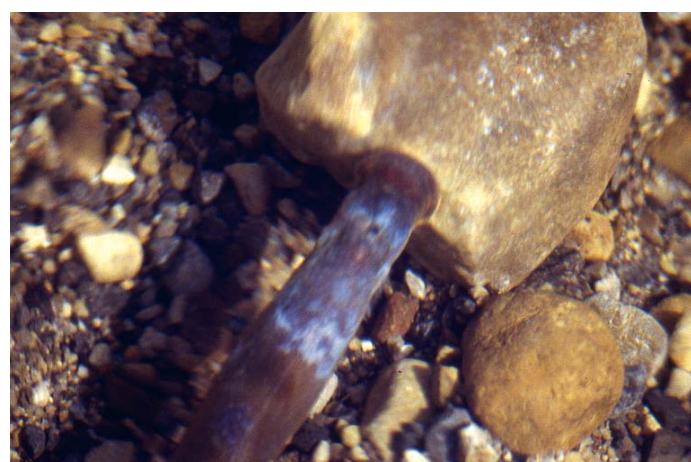
River lampreys inflict extensive damage on fish with their teeth-filled discs, rasping away flesh from their backs. Above left is a transformer disc in winter, when the discs of river and brook lamprey are similar. These powan have sustained wounds from river lampreys.



Having spent up to two years in estuaries, river lamprey migrate up rivers to spawning grounds during winter and spring. They mate in March and April, when water temperatures are at least 10°C.



Male river lamprey urogenital papilla.



River lamprey moving stones to clear an area for spawning. Eggs will then be laid in a depression in the substrate.



Female river lamprey laying eggs. The eggs adhere to sand particles and hatch after 15–30 days. Adult river lamprey die after spawning.

Mature river lamprey, having spent one to two years mainly in estuaries, stop feeding in the autumn and move upstream into medium to large rivers, usually migrating into fresh water from October to December. These mature adults require a migration route free of obstacles – natural, such as waterfalls, or man-made (for example, dams, weirs or pollution barriers) – in order to reach their spawning grounds with minimum effort and delay. During winter and early spring they continue to migrate upstream at night when conditions are suitable, hiding under stones and vegetation during the day.

Spawning in British rivers starts when the water temperature reaches 10–11°C, usually in March and April (Morris & Maitland 1987). The spawning grounds are areas of small stones and gravel in flowing water. The nest, which may be constructed by up to a dozen or more adults, is an oval depression, 30–70 cm across and 2–10 cm deep. Spawning of each female may take place over several days. The whitish eggs (Hardisty 1964) immediately adhere to sand particles when they are laid, and mostly become embedded in the nest substrate (Hagelin and Steffner 1958; Hagelin 1959). There is a high mortality at this time from various piscivorous birds and mammals, and all lampreys die after spawning (Larsen 1980).

After an incubation period of some 15–30 days, depending on prevailing water temperatures, the larvae hatch and immediately start to drift downstream and burrow in suitable silt beds. The ammocoete larvae are about 7 mm on hatching and grow to about 50 mm after one year (Hardisty 1961). The eventual weight and length after just over four years in a river is 1.5 g and 100–120 mm, compared to 70 g and 200–240 mm after 2.5 years feeding in estuaries. The main food of the larvae is fine particulate matter, mainly micro-organisms such as desmids and diatoms. After metamorphosis (July–September) at three to five years of age, the young adults migrate during darkness to estuaries.

Habitat requirements and associations

Considerable information is now available about the biology of the river lamprey in fresh water, though much less is known about its habits in estuaries and the sea. During its life cycle, the critical habitat requirements relate to:

- Suitable estuarine conditions, free from pollution, with suitable prey fish species.
- A clear migration route from estuary to the spawning grounds, with suitable river flows and no barriers.
- At the spawning areas, suitable hiding places and clean spawning gravels.
- After hatching, slower flowing nursery areas of sandy silt in fresh water, above the estuary.

Population parameters

Where spawning sites are scarce, egg densities can be high – Tuikkala (1971) has estimated many thousands per square metre at some sites in Finland. Small larvae (8–36 mm) may also be abundant near the spawning areas, and estimates of 40–2,000 individuals m⁻² have been recorded (Tuikkala 1971).

Larval densities have been determined by a number of researchers and found to be very variable, both from place to place and from year to year in the same place (Ojutkangas *et al.* 1985, Potter *et al.* 1986). In three rivers in Finland studied by Kainua & Valtonen (1980), the densities of larvae older than 0+ found in the main stem reaches occupied by lampreys were 5.7 (Kalajoki River), 11.8 in 1977, 15.3 in 1978 (Pyhajoki River) and 21.3 (Siikajoki River) larvae m⁻². In the Pyhajoki River densities were much lower above large rapids: 3.2 in 1977 and 1.7 in 1978.

There have been few quantitative studies of adult numbers. Tuunainen *et al.* (1980) reported that, during the late 1970s, commercial fisheries existed on 28 Finnish rivers, and that the total catch was 2–2.5 million lampreys weighing approximately 100 tonnes. The retail value of this catch was US\$1.7 million. Quantitative data (minimal estimates) on two of these rivers (Kalajoki and Pyhajoki), based on tagging

and returns from the commercial catch, have been provided by Valtonen (1980), as follows:

Kalajoki	35.6	40	202,029 (1977) 228,410 (1978)
Pyhajoki	30.8	20	498,026 (1977) 169,696 (1978)
Ricklea	13.2	15	Ca. 210,000
Lestijoki	11.4	30	Ca. 500,000

Data on smaller rivers, the Ricklea in Sweden (Asplund and Sodergren 1974) and the Lestijoki in Finland (Valtonen and Niemi 1979) are also included above.

Various subspecific forms of the river lamprey have been recognised by different authors, and three of them are relevant to the British Isles.

- 1 The 'normal' form, which has a length of 260–385 mm (Berg 1948) and has an average post-larval life of 2.5–2.75 years (Hardisty & Potter 1971). Most populations in Britain are of this type.
- 2 The 'praecox' form, which has a length of 180–245 mm (Berg 1948) and an average post-larval life of 1.5–1.75 years (Hardisty & Potter 1971). This form occurs in some British rivers, for example, the River Teme (Huggins & Thompson 1970) and the River North Esk (Maitland, unpubl.).
- 3 The dwarf, purely freshwater, form, which has a length of 170–243 mm and an average post-larval life of perhaps one year. In Britain this form is known only from the Loch Lomond system where, unlike either of the other forms, its life cycle is entirely restricted to fresh water (Robertson 1875; Lamond 1922; Maitland 1980a, 1980b; Morris 1989; Maitland et al. 1983, 1994).

Hardisty and Potter (1971) have suggested that this variability in body size may be attributable to differences in the duration of the feeding stage. 'Because of the restricted and seasonal nature of metamorphosis, downstream migration and spawning, such differences must be discontinuous, and the overall duration of adult life (between transformation and breeding) will vary in multiples of one year.'

Several authors have recorded sex ratios in adult populations of river lamprey, and males almost always predominate (Eglite 1958, Lohnisky 1966). Hardisty & Potter (1971) have pointed out that sex ratios in *Lampetra* vary from near-equality to as much as five males to one female, and suggest that the annual fluctuations are due to environmental factors such as temperature or water levels, and that these factors vary from one river system (and one year) to another.

Hardisty & Huggins (1970) found that the duration of larval life in *Lampetra fluviatilis* was four years, though others have suggested three years (Hubbs 1925, PrivoInyev 1964). In three British rivers the variation in length at metamorphosing was 83–119 mm, with a mean length of 99.3 mm.

River lamprey and brook lamprey have been observed spawning in the same areas (Huggins & Thompson 1970), but Hardisty & Potter (1971) note that no examples of interspecific pairing have been reported. However, hybridisation has frequently been achieved by artificial fertilisation (Weissenberg 1925; Eneqvist 1938; Cotronei 1942).

Valtonen (1980) noted that: 'Areas of good larval production may occur even 40–50 km from the river mouth... and the proportional larger production area seems to allow a genuine increase in numbers.'

Water quantity requirements

Few data are available concerning actual water quantity requirements for river lamprey, and most published data concern flow velocity (Entec 2000a, 2000b).

Baxter (1954a, b) analysed the distribution of lamprey in Britain in a variety of running waters with varying profiles, and found that the existence of local populations coincided generally with average stream gradients of $1.9\text{--}5.7 \text{ m km}^{-1}$, and that they rarely occurred where the gradients were greater than 7.6 m km^{-1} . However, Hardisty & Potter (1971) emphasised that, although they were a useful general guide, these gradients do not define the precise location of larval habitats, which 'may be regarded as micro-environments protected from all but the most catastrophic changes in water level and current flow'.

Larvae

Water velocities measured by Kainua and Valtonen (1980) in midstream in the areas occupied by larvae ranged from $1\text{--}5 \text{ cm s}^{-1}$ to about 50 cm s^{-1} , with smaller larvae being proportionately more numerous in habitats where the flow was rapid. Where larvae were found in shallow water, the rate of flow was almost constantly below 10 cm s^{-1} . These speeds were all measured under summer conditions. In winter, with low water levels, the speeds may be less, and during spates they may be much higher.

However, it is a common observation (Maitland, unpubl.) that larval nursery beds are at the edges of streams and rivers, well away from the main current, and that the current over them is often not only very slow, but is actually a backwater in reverse of the main current. Relatively slow speeds ($8\text{--}10 \text{ cm s}^{-1}$) have been recorded over *Lampetra* burrows by Hardisty (1986), which agrees with Hjulstrom (1935), who found that the deposition of sand and silt occurs only at velocities less than 7 cm s^{-1} .

Ammocoete larvae can swim quite fast for short distances, but are unable to maintain themselves in open water for long periods against strong currents. Data for other species suggest that maximum swimming speeds are always less than 0.45 m s^{-1} and more normally between 0.1 and 0.3 m s^{-1} . Thus, although larvae can swim short distances when disturbed or when seeking out better food resources (Eneqvist 1938), most of their distribution results from passive downstream migration.

Adults

Eglite (1958) noted flows of $1\text{--}2 \text{ m s}^{-1}$ in rivers where adult river lampreys spawned. Ryapolova (1962) found that adult lampreys running from estuaries into rivers in Latvia were influenced by a number of factors. The runs were characteristically in short, sharp bursts, and there was a close correlation between the size of the runs and the freshwater flow into the estuary, which could be influenced by the wind regime.

The general conclusion, as appears to be the case with other migratory species, is that high flows during spates are likely to be detrimental to populations of river lamprey, not only by making it difficult for them to access spawning grounds, but also by lowering recruitment after spawning, probably due to



Ross Gardiner

In common with other lamprey species, river lamprey ammocoetes are blind and do not have a fully developed sucker or teeth. After hatching they swim or drift downstream to beds of sandy silt where they burrow, feeding on algae such as diatoms.

eggs and larvae being swept downstream into the sea. However, as with many migratory fish species, very low flows may also be detrimental, both in preventing the passage of upstream migrants over very shallow areas, and in exacerbating the impact of poor water quality in those rivers affected by pollution.

Water quality requirements

There are relatively few data available concerning the water quality requirements of river lamprey (Alabaster & Lloyd 1982). Occasional mortalities have been reported that have been ascribed to pollution, but few details are available. Two of these were in Scotland some years ago, when numbers of dead adult river lamprey were reported, on one occasion near the mouth of the River Annan, and on another occasion near the mouth of the River Devon at Cambus.

Larvae

Potter *et al.* (1970) have shown that oxygen tension is a major factor in the maintenance of the burrowing habit. Larvae can survive almost anoxic conditions in their burrows for only a few hours, after which they must come out of their burrows or die. However, they can tolerate low oxygen tension, and may remain in their burrows for some time under these conditions (Hill & Potter 1970, Schoonoord & Maitland 1983).

Laboratory studies on the effect of temperature on the development of embryos have shown that successful hatching of free-swimming ammocoetes is only possible within a relatively restricted range of water temperatures (Damas 1950). Hardisty & Potter (1971) note that 'the kind of fluctuations that sometimes occur in the spring (particularly in small streams) might adversely affect the production of hatched larvae'. Thomas (1962) has shown that in *Lampetra lamottenii* (and *Petromyzon marinus*), ammocoetes are most active at water temperatures between 10 and 14°C.

The onset of larval transformation usually occurs in a short period (three to four weeks), and temperature may be the operative factor (Potter 1970, Hardisty & Potter 1971). There are also indications that in successive years, the time of onset of metamorphosis in *Lampetra fluviatilis* in the field has varied according to the prevailing spring temperatures (Hardisty & Potter 1971).



Both photos by Ross Gardiner

River lamprey transformer in April. The onset of ammocoete hatching and metamorphosis of larvae may be dependent on water temperature.

Adults

There is no doubt that significant pollution can eliminate whole populations of river lamprey from rivers, and there are several examples where this has happened in the past (for example, the River Thames and the River Clyde). In such cases, it is usually severe pollution in the lower reaches that prevents upstream migration and kills downstream migrants – in spite of the fact that there may be hundreds of kilometres of river upstream where the water quality is good and there is plenty of good spawning and larval habitat. In the case of the River Clyde, it is of interest to note that, following significant improvements in water quality, Atlantic salmon (*Salmo salar*) started to return 20 years before river lampreys appeared again.

Spawning in British rivers starts when the water temperature reaches 10–11°C, usually in March or April (Hardisty & Potter 1971), and may continue at higher temperatures (Hardisty 1986). Further north it may not proceed until later. In Sweden, for example, Sjoberg (1980) found that river temperatures did not reach 10°C until May or June, when spawning began, and that having been strictly nocturnal previously, the lampreys were active both day and night. However, the critical spawning period for river lampreys normally lies between 8.5°C and 12.0°C (Hardisty & Potter 1971).

Some pollution in the lower reaches appears to be tolerated, and in the absence of specific tolerance data for river lamprey it must be assumed that conditions in all parts of any river where lamprey occur, or pass through on migration, are at least UK Water Quality Class A2 in Scotland or B in England, Wales and Northern Ireland.

Substrate requirements

Unless otherwise indicated, particle size descriptions (sand, silt, clay, etc.) are based on the scales first described by Wentworth (1922).

Larvae

Typically, the substrate varies in depth from a few centimetres to 30 cm or more; it often contains a relatively high organic content and has been variously described as composed of mud, silt, or silt and sand (Hardisty & Potter 1971). Especially in slow-flowing stretches, the more favourable habitats include, in addition to sand and silt, a clay fraction forming an open-structured sediment (Potter 1970).

However, Kainua & Valtonen (1980) showed that, in Finland, most ammocoetes were found in substrates with a mean particle size of 0.05–0.20 mm. They did not occur in finer material (clay). 0+ larvae were most common in sandy biotopes. Ryapolova (1972) suggested that, although ammocoetes could be found among plant debris and macrophytes, in general they preferred a plant-free substrate.

Adults

Most spawning of river lampreys occurs where there is some water flow through the substrate. This is usually found at the tails of pools where the gravels have been deposited from upstream and the scouring of pools but the current is still reasonably fast. This is broadly similar to the situation favoured by stream salmonids (Stuart 1953) and is the area where there is maximum penetration of gravels by water currents. The particle size is variable but is usually described as gravel with some sand (Chapman 1988, Crisp & Carling 1989).

Many traditional spawning grounds for lamprey have probably been damaged by the removal of gravel, a common practice in some areas (McEwan & Lewis 1999).

Channel structure and management

Clearly, there must be no significant obstacles (chemical or physical) on their migration routes if river lamprey are to travel from the estuaries and reach their spawning grounds successfully. Hydroelectric dams and weirs presently deny lamprey access to many valuable spawning grounds. Apart from actual barriers, any significant alteration or management of channels that removes resting cover or creates stretches of fast flow ($>2 \text{ m s}^{-1}$) must be avoided all along the migration route. In particular, the habitat in those stretches used for spawning should retain areas of suitable gravel with interstitial currents that attract nest building.

Average stream gradients in stretches of river where *Lampetra* larvae have been found were estimated by Hardisty (1986) to be 0.2–0.6 m km⁻¹. Water depth in nursery areas is 'typically 0.1 to 0.5 m' (Entec 2000a, 2000b), but can range from 0–100 cm, and possible deeper in some cases (Maitland, unpubl.). The water depth where adults spawn is usually some 20–150 cm (Eglite 1958, Ryapolova 1972).

Impacts, threats and exploitation

Impacts

Because most polluting effluents are directed into running waters (and so to the sea), many rivers became grossly polluted in the past and lost their populations of lamprey, which are almost entirely riverine animals. In addition to direct toxic effects, pollution can have a major impact on lamprey by smothering both spawning gravels and nursery silts.

The migrations of anadromous species such as river lamprey are especially affected by pollution barriers because considerable journeys are often necessary from the estuary to the spawning grounds. One extreme belt of pollution between these two habitats can have a major effect on lamprey populations in a river.

Similarly, engineering works of various kinds (dams, weirs, etc.) can be obstacles to upstream migration and the success of local populations of lamprey. Such works include some aspects of fishery management, such as dredging to create fishing pools and the construction of croys, groynes, weirs, etc., to aid angling.

Channelisation can also be damaging to lampreys, mainly through destruction of their habitat. The removal of areas of riffle and associated spawning gravels, and the dredging of essential nursery silt beds, may entirely eliminate lampreys and other fish from a river (Côté *et al.* 1999).



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Silt beds, such as these in the River Endrick, Scotland, are essential nursery habitat for lamprey ammocoetes, so populations can be damaged or eliminated by dredging.

Threats

Both water abstraction and land drainage are likely to have similar negative effects on lamprey populations. They may lead to unstable habitats with variable water levels that flood and disturb both spawning gravels and nursery silts at some times, but leave them high and dry at others (Maitland *et al.* 1988).

Eutrophication acts in a similar way to some other forms of pollution: the abundant algae and bacteria

resulting from increased nutrients smother both the spawning gravels (preventing spawning or killing eggs) and the nursery silts, creating anoxic conditions there.

Given that a large proportion of the life cycle of lampreys is spent in burrows in silt beds, special attention must be paid to these (not normally considered as important fish habitat), and to spawning gravels, in any consideration of the impact of a development proposal affecting a river. Fishery management for one particular group may adversely affect other fish and wildlife and their habitat. For example, action aimed at improving conditions for salmonids (e.g. dredging of ammocoete silts or the provision of fish passes only surmountable by salmonids) may be detrimental to lampreys.

Some river lampreys are taken by power station intake pipes, but there is no evidence in the UK that the numbers concerned are detrimental to stocks, and such catches can be a valuable tool in monitoring (Maitland 1997b, 1998b).

It is uncertain how climate change may affect the river lamprey (Maitland 1991), but one scenario is that the species may be able to inhabit rivers further north.

Exploitation

Although the species was formerly fished extensively in the River Severn and several other rivers in Britain, it is now exploited in only a few rivers in Europe, in Russia, Finland and Sweden. It is unlikely that a commercial fishery will ever start again in Britain, but if it were ever proposed it must be managed under strict guidelines to ensure sustainability.

However, there has always been an interest in them (both ammocoetes and adults) by anglers as bait, and this seems to have increased in recent years (*Angler's Mail*, 30 January, 1999) and to favour adult river lamprey especially. Indiscriminate trapping of adults could damage populations, and the search for larvae (by digging out substrate) not only affects the population directly but also causes significant damage to their habitat.

Recommendations for research

The main recommendations for research are:

- 1 To provide better data on the distribution of the river lamprey in Great Britain, especially in the north of Scotland where its status is uncertain (Maitland 1985, 1993).
- 2 To consider and carry out research relevant to the reintroduction of the river lamprey to some of its historic sites, from which it has been excluded by dams and weirs, assuming that these can be removed or fish passes provided.
- 3 To carry out further research on the biology and conservation requirements of the notable population of dwarf river lamprey, found only in Loch Lomond and the River Endrick.
- 4 To further international collaboration to investigate the genetic diversity and relationships among the various populations of river lamprey in Europe.
- 5 To measure sex ratios of spawning populations regularly and relate these to population density and environmental factors.

Current monitoring

There is little current monitoring specifically for river lampreys anywhere in Britain. However, the Habitats Directive has stimulated both conservation reviews (Maitland 1997a, 1998a, 2000b) and considerable survey work (Gardiner et al. 1995; Gardiner & Stewart 1997; APEM 1996, 1997; Maitland & Lyle 2000) in several parts of the country. The recent creation of several rivers as SACs (Special Areas of Conservation) places an obligation to monitor populations there. Following a review of available techniques, **Life in UK Rivers** has produced a best-practice monitoring protocol for lamprey.

Some incidental, but valuable, monitoring of lampreys is carried out at a number of sites. For example, the Scottish Environment Protection Agency (SEPA) carries out regular monitoring by trawl in the estuaries of the rivers Clyde, Forth and Tay (lampreys are taken regularly in the Forth). There has also been regular sampling in recent years at Longannet Power Station on the Forth estuary, where there is a large intake of river lamprey each year (Maitland 1998b). Similar sampling has been carried out at power stations in England, for example on the River Severn (Claridge *et al.* 1973, Abou-Seedo & Potter 1979).

References

- Abou-Seedo FS & Potter IC (1979). The estuarine phase in the spawning run of the river lamprey *Lampetra fluviatilis*. *Journal of Zoology* 188, 5–25.
- Alabaster JS & Lloyd R (1982). *Water quality criteria for freshwater fish*. Butterworths, London.
- APEM (1996). *A survey of six English rivers for lamprey*. English Nature, Peterborough.
- APEM (1997). *Monitoring guidelines for lampreys*. English Nature, Peterborough.
- Asplund C & Sodergren S (1974). Flodnejonogats (*Lampetra fluviatilis* L.) lekvandering I Ricklean. Zool. Revy. 36, 11–119.
- Baxter EW (1954a). *Studies on the biology of lampreys*. Unpublished PhD Thesis, University of London.
- Baxter EW (1954b). Lamprey distribution in streams and rivers. *Nature* 180, 1145.
- Berg LS (1948). *Freshwater fish of the USSR and adjacent countries*. Israel Program of Scientific Translation, Jerusalem.
- Chapman DW (1988). Critical review of variables used to define effects of fines in redds of large salmonids. *Transactions of the American Fish Society* 117, 1–21.
- Claridge PN, Potter IC & Hughes GM (1973). Circadian rhythms of activity, ventilatory frequency and heart rate in the adult river lamprey, *Lampetra fluviatilis*. *Journal of Zoology* 191, 230–250.
- Cote IM, Vinyoles D, Reynolds J, Doadrio I and Perdices A (1999). Potential impacts of gravel extraction on Spanish populations of river blennies *Salaria Fluviatilis* (Pisces, Blenniidae). *Biological Conservation* 87, 359–367.
- Crisp DT and Carling P (1989). Observations on siting, dimensions and structure of salmonid redds. *Journal of Fish Biology* 34, 119–134.
- Damas H (1950). La ponte en aquarium des lamproies fluviatiles et de planer. *Ann. Soc. R. Zool. Belg.* 81, 151–162.
- Eglite R (1958). Feeding habits of river lamprey in the Latvian SSR. *Gidrol. Issled., Tallinn*. 1, 234–269.
- Eneqvist P (1938). The brook lamprey as an ecological modification of the river lamprey. On the river and brook lampreys of Sweden. *Arkiv for Zoologi*. 29A, 1–22.
- Entec (2000a). *River Eamont acceptable Drought Order flow regime recommendation: suitability for British lamprey*. Environment Agency, Penrith.
- Entec (2000b). *Generically acceptable flows for British lamprey*. Environment Agency, Penrith.
- Gardiner R, Taylor R and Armstrong J (1995). *Habitat assessment and survey of lamprey populations occurring in areas of conservation interest*. Scottish Natural Heritage, Edinburgh.
- Gardiner R and Stewart D (1997). *Spawning habitat assessment and survey of lamprey populations occurring in areas of conservation interest*. Scottish Natural Heritage, Edinburgh.
- Hagelin LO (1959). Further aquarium observations on the spawning habits of the river lamprey (*Petromyzon fluviatilis*). *Oikos* 10, 50–64.
- Hagelin LO & Steffner N (1958). Notes on the spawning habits of the river lamprey (*Petromyzon fluviatilis*). *Oikos* 9, 221–238.
- Hardisty MW (1961). The growth of larval lampreys. *Journal of Animal Ecology* 30, 357–371.
- Hardisty MW (1964). The fecundity of lampreys. *Archiv fur Hydrobiologie* 60, 340–357.
- Hardisty MW (1986). Petromyzontiforma. In: Holcik J (ed) *The freshwater fishes of Europe*. Aula-Verlag, Wiesbaden.
- Hardisty MW & Huggins RL (1970). Larval growth in the river lamprey, *Lampetra fluviatilis*. *Journal of Zoology* 161, 549–559.

- Hardisty MW & Potter IC (eds) (1971). *The biology of lampreys*. Academic Press, London.
- Hill BJ & Potter IC (1970). Oxygen consumption in the ammocoetes of the lamprey *Ichthyomyzon hubbsi*. *Journal of Experimental Biology* 53, 47–57.
- Hjulstrom F (1935). Studies in the morphological activity of rivers as illustrated by the River Fyris. *Geological Institute of the University of Uppsala Bulletin* 25, 221–528.
- Hubbs CL (1925). The life cycle and growth of lampreys. *Papers of the Michigan Academy of Science* 4, 587–603.
- Huggins RJ & Thompson A (1970). Communal spawning of brook and river lampreys, *Lampetra planeri* Bloch and *Lampetra fluviatilis* L. *Journal of Fish Biology* 2, 53–54.
- IUCN (1994). *IUCN Red List categories*. International Union for the Conservation of Nature and Natural Resources, Gland.
- Kainua K & Valtonen T (1980). Distribution and abundance of European river lamprey (*Lampetra fluviatilis*) larvae in three rivers running into Bothnian Bay, Finland. *Canadian Journal of Fisheries and Aquatic Sciences* 37, 1960–1966.
- Lamond H (1922). Some notes on two of the fishes of Loch Lomond: the Powan and the lamprey. *Fish. Scotl. Salmon Fish.* 1923, 3–10.
- Larsen LO (1980). Physiology of adult lampreys, with special regard to natural starvation, reproduction and death after spawning. *Canadian Journal of Fisheries and Aquatic Sciences* 37, 1762–1769.
- Lohnisky K (1966). The spawning behaviour of the brook lamprey, *Lampetra planeri* (Bloch, 1784). *Vest. Cesk. Spol. Zool.* 30, 289–307.
- Maitland PS (1980a). Review of the ecology of lampreys in northern Europe. *Canadian Journal of Fisheries and Aquatic Sciences* 37, 1944–1952.
- Maitland PS (1980b). Scarring of whitefish (*Coregonus lavaretus*) by European river lamprey (*Lampetra fluviatilis*) in Loch Lomond, Scotland. *Canadian Journal of Fisheries and Aquatic Sciences* 37, 1981–1988.
- Maitland PS (1985). Criteria for the selection of important sites for freshwater fish in the British Isles. *Biological Conservation* 31, 335–353.
- Maitland PS (1991). Climate change and fish in northern Europe: some possible scenarios. *Proceedings of the Institute of Fishery Management Annual Study Course* 22, 97–110.
- Maitland PS (1993). *Sites in Great Britain for freshwater and estuarine fish on the EC Habitats and Species Directive*. Fish Conservation Centre Report to JNCC, Peterborough.
- Maitland PS (1997a). *Species Action Plans for lampreys in England*. Fish Conservation Centre Report to English Nature, Peterborough.
- Maitland PS (1997b). *Fish entrainment in the Firth of Forth at Longannet and Cockenzie Power Stations*. Fish Conservation Centre Report to Scottish Power, Kincardine-on-Forth.
- Maitland PS (1998a). *Species Action Plan: River lamprey (Lampetra fluviatilis)*. Fish Conservation Centre Report to Edinburgh District Council, Edinburgh.
- Maitland PS (1998b). *Fish entrainment at power stations on the Firth of Forth*. Fish Conservation Centre Report to Scottish Power, Kincardine-on-Forth.
- Maitland PS (2000a). *Guide to freshwater fish of Britain and Europe*. Hamlyn, London.
- Maitland PS (2000b). *Fish*. In: Ward SD (ed) *Local Biodiversity Action Plans – technical information on species: IV. Vertebrate animals*. Scottish Natural Heritage Review No 10, 81–91.
- Maitland PS & Campbell RN (1992). *Freshwater fishes of the British Isles*. HarperCollins, London.
- Maitland PS, East K & Morris KH (1983). *Lamprey populations in the catchments of the Forth and Clyde estuaries*. Annual Report, Institute of Terrestrial Ecology, 17–18.

- Maitland PS & Lyle AA (2000). *Distribution of lampreys in the River Teith*. Report to Scottish Natural Heritage, Stirling.
- Maitland PS, Morris KH & East K (1994). The ecology of lampreys (Petromyzonidae) in the Loch Lomond area. *Hydrobiologia* 290, 105–120.
- Maitland PS, Morris KH, East K, Schoonoord MP, van der Wal B & Potter IC (1984). *Journal of Zoology*. 203, 211–225.
- Maitland PS, Newson M & Best G (1988). *The impact of afforestation and forestry practice on fresh waters*. Report to the Nature Conservancy Council, Peterborough.
- McEwan LJ and Lewis SG (1999). *Sediment budget of the Endrick Water catchment*. Scottish Natural Heritage, Edinburgh.
- Morris KH (1989). A multivariate morphometric and meristic description of a population of freshwater-feeding river lampreys, *Lampetra fluviatilis* (L.), from Loch Lomond, Scotland. *Zoological Journal of the Linnaean Society* 96, 357–371.
- Morris KH & PS Maitland (1987). A trap for catching adult lampreys (Petromyzonidae) in running water. *Journal of Fish Biology* 31, 513–516.
- Ojutkangas E, Aronen K and Laukkonen E (1985). Distribution and abundance of river lamprey (*Lampetra fluviatilis*) ammocoetes in the regulated River Perhonjoki. *Regulated Rivers: Research and Management* 10, 239–245.
- Potter IC (1970). The life cycles and ecology of Australian lampreys of the genus *Mordacia*. *Journal of Zoology* 161, 487–511.
- Potter IC, Hilliard RW, Bradley JS & McKay RJ (1986). The influence of environmental variables on the density of larval lampreys in different seasons. *Oecologia* 70, 433–440.
- Potter IC, Hill BJ & Gentleman S (1970). Survival and behaviour of ammocoetes at low oxygen tensions. *Journal of Experimental Biology* 53, 59–73.
- Privolnyev TI (1964). Ecological and physiological features of the larval river lamprey, *Lampetra fluviatilis* (L.). *Izv. uses. nauchno-issled Inst. ozern. rechn. ryb. Khoz.* 58, 180–185.
- Robertson D (1875). On *Petromyzon fluviatilis* and its mode of preying on *Coregonus clupeoides*. *Proceedings of the Natural History Society of Glasgow* 2, 61–62.
- Ryapolova NI (1972). Some regularities of migrations of river lamprey (*Lampetra fluviatilis*) into the Latvian rivers. *ICES Baltic-Belt Seas Committee* 18, 1–3.
- Schoonoord MP & Maitland PS (1983). Some methods of marking larval lampreys (Petromyzonidae). *Fisheries Management* 14, 33–38.
- Sjoberg K (1980). Ecology of the European river lamprey (*Lampetra fluviatilis*) in northern Sweden. *Journal of the Fisheries Research Board of Canada* 37, 1974–1980.
- Slack HD (1955). Factors affecting the productivity of *Coregonus clupeoides* Lacepede in Loch Lomond. *Ver. Int. Verh. Limnol.* 12, 183–186.
- Stephenson A, Crompton DWT, Stoddart RC & Maitland PS (1995). Endoparasitic helminths from Scottish lampreys. *Transactions of the Royal Society of Tropical Medicine and Hygiene* 89, 588–595.
- Stuart TA (1953). Spawning migration, reproduction and young stages of loch trout (*Salmo trutta* L.). HMSO, Edinburgh.
- Thomas MLH (1962). *Observations on the ecology of ammocoetes of Petromyzon marinus L. and Entosphenus lamottenii (Le Sueur) in the Great Lakes watershed*. MSc Thesis, University of Toronto.
- Tuikkala A (1971). Nahkiaisen elintavoista ja sen pyynnista Pyhajoella. *Kalatalous-saat. Monist. Julk.* 40, 1–59.
- Tuunainen P, Ikonen E & Auvinen H (1980). Lamprey and lamprey fisheries in Finland. *Canadian Journal of Fisheries and Aquatic Sciences* 37, 1953–1959.

Valtonen T (1980). European river lamprey (*Lampetra fluviatilis*) fishing and lamprey populations in some rivers running into Bothnian Bay, Finland. *Canadian Journal of Fisheries and Aquatic Sciences* 37, 1967–1973.

Valtonen T & Niemi A (1979). The present state of fishing in Lestijoki, a small river in Finland. *Ver int ver limnol.* 20, 2085–2089.

Weissenberg R (1925). Fluss- und Bachneunauge (*Lampetra fluviatilis* L. und *Lampetra planeri* Bloch), ein morphologisch-biologischer Vergleich. *Zool. Anz.* 63, 293–306.

Wentworth CK (1922). A scale of grade and class terms for clastic sediments. *Journal of Geology* 30, 377–392.

Whilde A (1993). *Threatened mammals, birds, amphibians and fish in Ireland: Irish Red Data Book 2: vertebrates*. HMSO, Belfast.

Brook Lamprey

Introduction

The brook lamprey (*Lampetra planeri*) is the smallest of the British lampreys, and is known colloquially as the mud lamprey or the pride. It matures at a length of 13–15 cm. Some populations are known where the adults may be much smaller than this – for example, adults spawning in the small lakes on the Isle of Skye may be less than 10 cm – and at some sites they may be larger. In the River Endrick, which flows into Loch Lomond, adults may reach 16 cm and occasionally 17 cm (Maitland et al. 1983, 1994).



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The brook lamprey is the smallest of its kind, with adults generally reaching a length of between 10 and 17 cm. The brook lamprey is the most abundant and widespread lamprey in British rivers.

The larvae of this species are virtually indistinguishable from those of the river lamprey except when nearing metamorphosis (Eneqvist 1938). The adults are small, eel-like fish with two dorsal fins, usually touching both each other and the tail fin. There are no paired fins. The eyes, which are covered by opaque skin in the larvae, are large and bright in the adults. The teeth are blunt and much less developed than those of the two predaceous species. The maxillary plate is wide but there are no lower labial teeth; the mandibular plate has 5–9 blunt teeth.

The ammocoetes are semi-translucent and mainly dull grey-brown in colour, though a 'golden' form does appear from time to time, with very much reduced pigment. After metamorphosis the transformers (macrophthalmia) are much more silvery, especially along the sides and belly. The back remains dark grey-brown.

The ammocoete larvae, like those of other lampreys, occur in suitable silt beds, mainly in running water but sometimes in large numbers in silt banks in lakes. Large larvae have been found in considerable numbers in several Scottish lochs.

The brook lamprey is the most abundant and widespread of the British lampreys and is often found in the absence of the other two species, for example above a pollution or physical barrier that prevents the anadromous species reaching that part of the river.

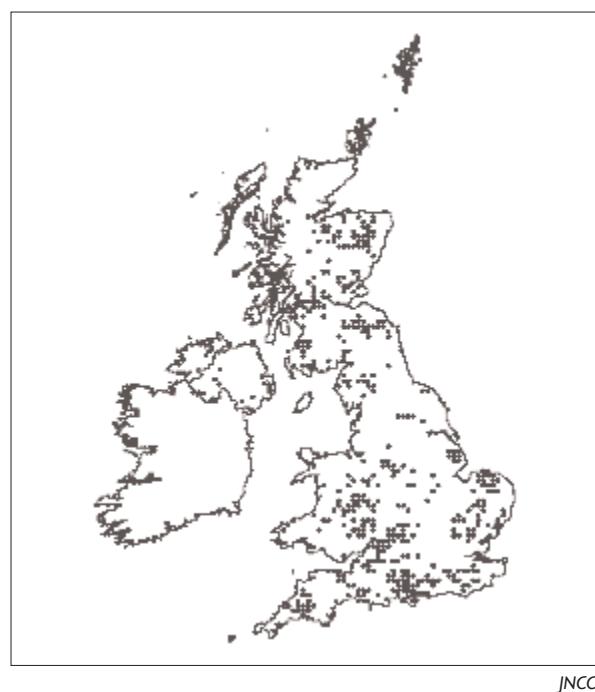
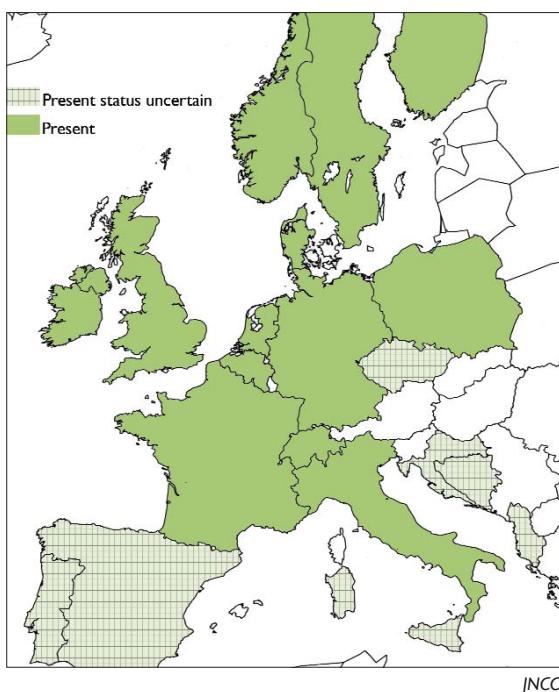
Lampreys are rarely seen by the general public except at spawning time, when they become very

obvious. Then the otherwise cryptic and nocturnal creatures move into shallow, clear water in broad daylight to start their complex and fascinating communal nest-building activities. The brook lamprey is the species most often seen, and in April and May it can be readily observed in thousands of streams in different parts of Great Britain. At this time the lampreys are extremely vulnerable and are eaten in considerable numbers by herons, gulls and sawbill ducks.

Status and distribution

Lampetra planeri is a purely freshwater species occurring in streams and occasionally in lakes in northwest Europe, particularly in basins associated with the North and Baltic seas. Although it is the most common of the British lampreys and occurs over much of the British Isles, it is apparently absent from much of Scotland north of the Great Glen, including the Northern Isles and all but a few of the Western Isles.

Because of a decline in several parts of Europe (Kappus et al. 1995), the brook lamprey is now given some legal protection. It is listed in annexes IIa and Va of the Habitats Directive, Appendix III of the Bern Convention, and as a Long List Species in the UK Biodiversity Action Plan. There is no Red Data Book for fish in Britain, but Maitland (2000) considers this species to be Vulnerable. The Red Data Book for Ireland (Whilde (1993), published before the IUCN (1994) revision of categories, lists the brook lamprey as Indeterminate.



The brook lamprey has been steadily declining across Europe, so is now given legal protection. In the UK, it is the most common species of lamprey, and can be found over most of England, Wales and Scotland, except for northern Scotland and the Northern Isles.

Life history

This species does not feed as an adult, so other fish provoke no response from it. The larvae have light-sensitive cells in the skin and are negatively phototactic, for the most part remaining sedentary within their burrows. However, if disturbed, they will swim around rapidly until they find suitable silt into which to burrow. They are capable of completely disappearing into sand in just a few seconds.

As spawning time approaches the metamorphosed adults move out from the silts and start to migrate upstream, often in large numbers, until they reach suitable spawning grounds. These are areas of small

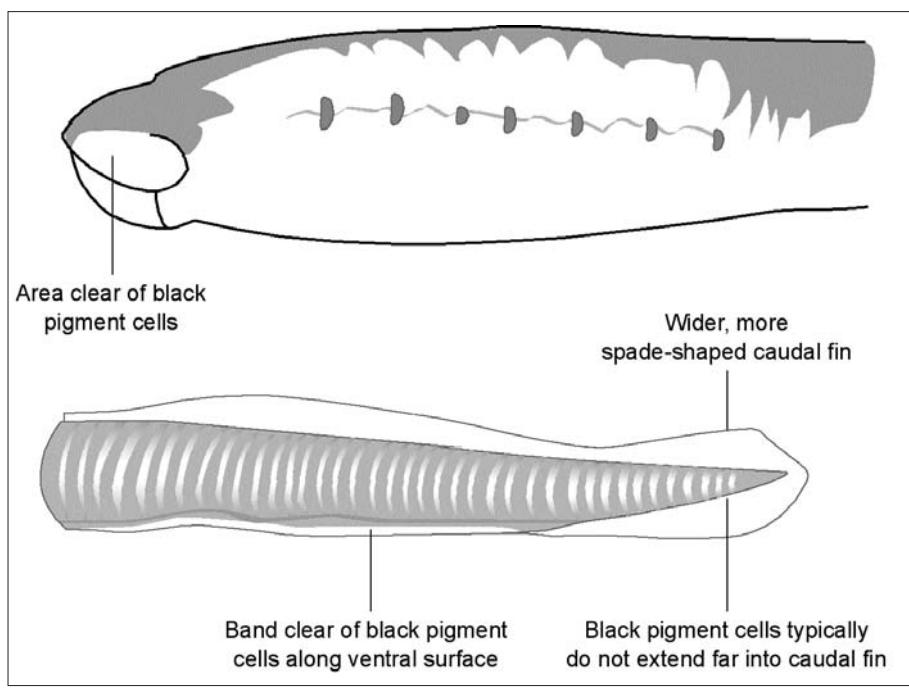
stones and gravel in flowing water where the current is present but not too strong. Characteristically, they spawn at the lower ends of pools, just where the water is starting to break up into a riffle (Maitland 1980, Maitland & Campbell 1992).

The spawning season of this species in British rivers starts when the water temperatures reach 10–11°C. There is a clear relationship between water temperature and the number of fish at spawning sites, numbers declining as the temperature drops (Hardisty 1970). The nest, which may be constructed by up to a dozen or more adults, is normally an oval depression about 20–40 cm across and 2–10 cm deep.

The actual spawning act is similar to that of other lampreys (Lohniský 1966) though the brook lamprey, on account of its small size, is less fecund, producing only about 1,500 eggs per female (Hardisty 1964). After hatching the young larvae leave the nest and distribute themselves by drifting downstream and burrowing in suitable areas of silty sand.

By this time all the adults are dead, for none survives long after spawning.

Larval life seems to vary considerably in different parts of Europe, but in the British Isles is about 6.5 years (Hardisty 1961a, 1961b). The larvae are 3–5 mm on hatching and about 12–15 cm at metamorphosis. This takes place between July and September, usually simultaneously (within three to four weeks) in any one population (Bird & Potter 1979a, 1979b). The adults usually migrate upstream after metamorphosis but continue to burrow like ammocoetes or hide under stones during the day. Since they no longer feed, they lose weight (and length) up to spawning time, when the females



Diagrams of head and tail of brook or river lamprey ammocoete, showing important recognition features. Brook lamprey ammocoetes live on micro-organisms as they gradually drift downstream from hatching areas.



Two age 0+ river or brook lamprey ammocoetes showing that the distinctive pigmentation patterns of the head and tail are already visible.

Ross Gardiner

suddenly become heavier as the eggs take up water prior to spawning.

The larvae feed by filtering fine organic particles, especially diatoms and other algae, as well as protozoans and detritus, from the surface of the silt around the mouths of the burrows in which they spend virtually all their larval years. The ciliary mechanism and the mucus threads involved in the collection of this food form a complex, but very efficient, feeding mechanism. The adults do not feed after metamorphosis.

Habitat requirements and associations

Although the brook lamprey is closely related to the river lamprey (Potter & Osborne 1975, Potter 1980), it does not need to undertake the long migrations of river and sea lamprey from estuaries and the sea. Nevertheless, after metamorphosis, most adults migrate upstream, sometimes for considerable distances, to find suitable spawning substrates. These may well be the same areas used by their parents, though there is little evidence of actual homing to a precise natal area. The behaviour is obviously adaptive for, while the strong tendency of the larval population is to drift downstream after hatching and during the larval phase, this positive movement of the adult population upstream compensates and allows the general position of the population to be reasonably stable.

Thus, from the autumn onwards, the adults migrate upstream at night, providing that there are no obstacles – natural (for example, waterfalls) or man-made (such as dams, weirs or pollution barriers). Once in the vicinity of their spawning gravels, they hide under stones or among vegetation until March or April when water temperatures reach 10–11°C (Hardisty & Potter 1971). In some parts of Scotland, particularly in the north and in waters at higher altitude, spawning may be as late as May or even June.

Apart from clear migration routes, the critical habitat requirements of adults relate to the spawning areas and nursery habitat (see below).

Population parameters

Following the implementation of the Habitats Directive, there have been several studies of lampreys in Britain (Duncan 1996; Gardiner *et al.* 1995; APEM 1996, 1997; Gardiner & Stewart 1997; Maitland & Lyle 2000).

There is considerable variation in the final size reached by adult brook lamprey at metamorphosis. In Scotland, adults in small streams in Skye may only be 100 mm, whereas in the River Endrick, many adults are over 150 mm and some as large as 170 mm. One notable feature found in most populations is a reduction in length of individuals between metamorphosis and spawning (Hardisty & Potter 1971). In addition, smaller animals appear to spawn slightly later (Maitland *et al.* 1994). Huggins & Thompson (1970) found brook and river lamprey spawning communally.

Hardisty & Huggins (1970) found six age classes in the populations of *Lampetra planeri* they studied, metamorphosis taking place when the fish were 120–175 mm, with a modal length of 150 mm.

Growth is more rapid in the spring than in the autumn at comparable water temperatures (Hardisty 1961a, 1961b; Potter 1970; Malmqvist 1978). The rate of growth decreases during the winter and in some cases there may actually be a reduction in the length of larvae at this time. Maximum growth in length tends to occur in the first year, decreasing in subsequent years, with retardation or complete arrest in the final year (Hardisty & Potter 1971).

Malmqvist (1980) found densities of 10–113 larvae m⁻² in some Swedish rivers. Other authors found similar densities (Waterstraat and Krappe 1998, Maitland & Lyle 2000).

Several authors have recorded sex ratios in adult populations of brook lamprey, and males almost always predominate (Zanandrea 1951, Abakumov 1964). Hardisty & Potter (1971) have pointed out that in *Lampetra*, sex ratios vary from near equality to as much as five males to one female, and suggest that the annual fluctuations are due to environmental factors, such as temperature or water level, and that



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There is great variation in body size in brook lamprey at metamorphosis. The rate of growth increases during the spring, with maximum growth in the first year.

these factors vary from one river system (and one year) to another. However, as in the sea lamprey (Smith 1971), there is an apparent correlation between the sex ratios in different years and the relative abundance of the spawning population (Hardisty 1944, 1961b, 1965), the numbers of males being high when the population is large, and vice versa.

Water quantity requirements

As in the case of water quality, there are few reliable data available on the specific water quantity requirements of brook lamprey, and most available data concern stream gradients (Baxter 1954a, 1954b) and flow velocities (Entec 2000a, 2000b).

Larvae

Schroll (1959) found that the flow rate over ammocoete beds of *Lampetra planeri* was remarkably constant, with average values of 0.5 m s^{-1} at the water surface and 0.4 m s^{-1} at a depth of 25 cm. However, it is a common observation that larval nursery beds are at the edges of streams and rivers, well away from the main current, and that the current over them is often not only very slow, but is actually a backwater in reverse of the main current. Relatively slow speeds ($8\text{--}10 \text{ cm s}^{-1}$) have been recorded over *Lampetra* burrows by Hardisty (1986), which agrees with Hjulstrom (1935), who found that the deposition of sand and silt occurs only at velocities less than 7 cm s^{-1} .

Adults

At two spawning sites in Czechoslovakia, Lohnisky (1966) found that current speeds were $1.0\text{--}1.4$ and 4.0 m s^{-1} respectively. These speeds seem very fast and presumably represent surface velocities. Hardisty & Potter (1971) note velocities of $30\text{--}50 \text{ cm s}^{-1}$.

Water quality requirements

As with other lamprey species, there are relatively few data available concerning the water quality requirements of the brook lamprey (Alabaster & Lloyd 1982). Occasional mortalities have been reported that have been ascribed to pollution, but few details are available.

Larvae

Potter *et al.* (1970, 1986) have shown that oxygen tension is a major factor in the maintenance of the burrowing habit of larvae. They can survive almost anoxic conditions in their burrows for only a few hours, after which they must come out or die. However, they can tolerate low oxygen tension, and may remain in their burrows for some time under these conditions (Hill & Potter 1970).

Laboratory studies on the effect of temperature on the development of embryos have shown that successful hatching of free-swimming ammocoetes is only possible within a relatively restricted range of water temperatures (Damas 1950). Hardisty & Potter (1971) note that 'the kind of fluctuations that sometimes occur in the spring (particularly in small streams) might adversely affect the production of hatched larvae'. Thomas (1962) has shown that, in *Lampetra lamottenii* (and *Petromyzon marinus*), ammocoetes are most active at water temperatures between 10°C and 14°C. The preferred temperature for *Lampetra planeri* was identified by Schroll (1959) as 12°C.

The onset of transformation of larvae usually occurs in a short period (three to four weeks) and it may be that temperature is the operative factor (Potter 1970, Hardisty & Potter 1971). There are also indications that, in successive years, the time of onset of metamorphosis in *Lampetra planeri* in the field has varied according to the prevailing spring temperatures (Hardisty & Potter 1971).

Adults

The brook lamprey is regarded as being sensitive to pollution, but few data appear to be available. Some pollution in the lower reaches of quite a number of rivers in Britain appears to be tolerated. In the absence of specific tolerance data for this species it must be assumed that conditions in all parts of any river where brook lampreys occur, or pass through on migration, are at least UK Water Quality Class B (in England, Wales and Northern Ireland) or A2 (in Scotland).

Substrate requirements

Unless otherwise indicated, particle size descriptions (sand, silt, clay, etc.) are based on the scales first described by Wentworth (1922).

Larvae

Typically, the preferred substrate varies in depth from a few cm to 30 cm or more. It often contains a relatively high organic content, and has been variously described as composed of mud, silt, or silt and sand (Hardisty & Potter 1971). Especially in slow flowing stretches, the more favourable habitats include, in addition to sand and silt, a clay fraction forming an open-structured sediment (Potter 1970). Schroll (1959) has put the optimum particle size at 180–380 µm.

A discriminant analysis of substrates used by the larvae of brook lampreys in a stream in Sweden showed that, although a few larvae occurred in far-from optimal habitats, most larvae selected those with a low current velocity, low water depth, a low number of particles in the 0.5–1 mm range and with a low chlorophyll a content. Other factors normally considered important, such as organic content, shade and the presence of algae (Hardisty & Potter 1971) did not improve the discriminant model. Streambed stability was considered to be of great importance but was not possible to estimate quantitatively. Larvae were absent from beds characterised by frequent sand drift.

Some authors have considered the presence of at least some rooted macrophytes to be a positive part of the larval habitat of the brook lamprey (Hardisty 1944, Schroll 1959).

Adults

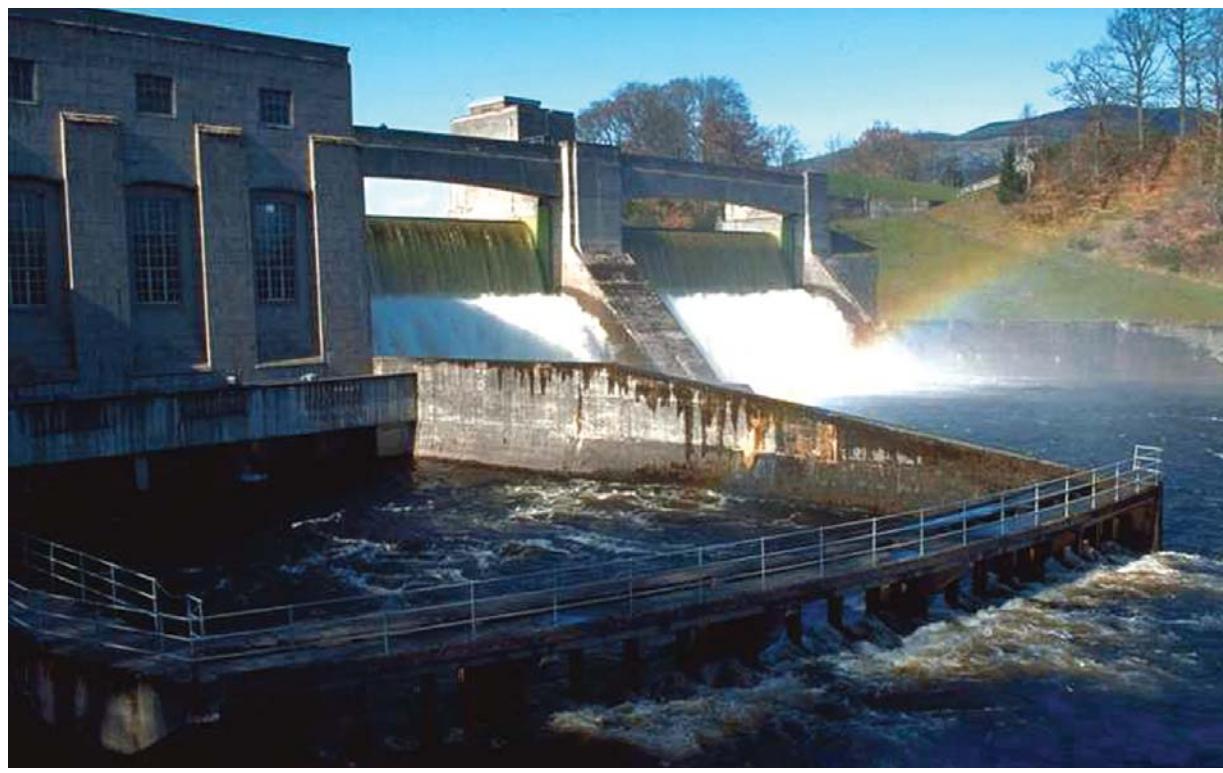
Most of the substrates at the spawning sites identified in British rivers are described as 'gravel'. The size of the gravel beds involved varies, but can range from $<1\text{ m}^2$ (for example, many burns in the west of Scotland), to $>10\text{ m}^2$ in larger rivers. Little is known about the precise nature of the gravel beds used for spawning.

However, it seems likely, from the position of brook lamprey spawning beds at the tails of pools, and the requirement of eggs for shelter and oxygen, that the preferences are likely to be similar to those of salmonids (Chapman 1988, Crisp & Carling 1989), such as brown trout, which have been well described by Stuart (1953) and others. Here, the spawning gravels 'are composed of stones up to 3 in. in diameter with a large proportion of smaller materials, the effect of which is to consolidate the mass while leaving it permeable to the water. Stones embedded in fine sands or silts which form a hard bed are avoided, as are also uniform gravels and shingles of small size which move easily in a flood. ... The location of the redds in an ideal pool is towards the tail, where the gravel slopes gently upward, spreading more or less evenly from bank to bank by the slackening of the current. The depth of water here is at a minimum'.

The presence of currents through the gravels actually chosen by brown trout was demonstrated by the passage of dyes through them (Stuart 1953).

Channel structure and management

There must be no significant obstacles (chemical or physical) in the river channel on their migration routes if brook lamprey are to successfully travel upstream from their nursery beds to their spawning grounds. Apart from actual barriers, any significant alteration or management of channels that removes too much cover or creates long stretches of very fast flow ($> 2\text{ m s}^{-1}$) must be avoided all along the migration route.



Lorne Gill/SNH

Dams and weirs can be obstacles to all lamprey, preventing them from migrating upstream to spawning areas. Although brook lamprey are weaker swimmers than other species, they do not generally undertake long migrations, so are less likely to be affected by river structures.

However, though they are of smaller size and are weaker swimmers than the other two lampreys, brook lampreys are less likely to be affected by obstacles than the others. Although some populations have been affected by barriers (both chemical and physical), overall, the brook lamprey is believed to be relatively less affected by river barriers than either the river or sea lamprey. This is because it does not have to undertake such long migrations, and its complete life cycle requirements can often be found in quite short stretches of river.

Average stream gradients in stretches of river where *Lampetra* larvae have been found were estimated by Hardisty (1986) to be 0.2–0.6 m km⁻¹.

Water depth in nursery areas is 'typically 0.1 to 0.5 m' (Entec 2000b), but can range from 0–100 cm, and possibly deeper in some cases (Maitland, unpubl.). The water depth where adults spawn is stated to be 3–30 cm (Hardisty 1986) or less than 40 cm (Hardisty & Potter 1971).

Impacts, threats and exploitation

Impacts

Because most polluting effluents are directed into running waters (and so to the sea), many rivers became grossly polluted in the past and lost their populations of lampreys, which are almost entirely riverine fish. In addition to direct toxic effects, pollution can have a major impact on lampreys by smothering both spawning gravels and nursery silts.

The migrations of brook lamprey are much less extensive than those of anadromous species such as the river lamprey. The latter have to undertake considerable migrations from the estuary to the spawning grounds and from the nursery areas to the estuary. However, even brook lamprey may undertake significant migrations upstream from nursery areas to spawning grounds, and vice versa for the next generation. One belt of pollution between these two habitats can have a major effect on lamprey populations in a river.

Similarly, engineering works such as dams and weirs can be obstacles to upstream migration and the success of local populations of lampreys. These include some aspects of fishery management, such as dredging to create fishing pools and the construction of croys, groynes, weirs, etc., to aid angling.

Channelisation can also be damaging to lampreys, mainly through destruction of their habitat. The removal of areas of riffle and associated spawning gravels, and the dredging of essential nursery silt beds, may entirely eliminate lampreys from a river.

Threats

Both water abstraction and land drainage have negative effects on lamprey populations. They often lead to unstable habitats with variable water levels, which flood and disturb spawning gravels and nursery silts at some times but leave them high and dry at others. The increasing threat of climate change is likely to produce similar problems, with periods of heavy rain in the autumn and winter, and drought in the summer (Maitland 1991).

Eutrophication acts in a similar way to some other forms of pollution: the abundant algae and bacteria resulting from increased nutrients smother both the spawning gravels (preventing spawning or killing eggs) and the nursery silts, creating anoxic conditions there.

Given that a large proportion of the life cycle of lampreys is spent in burrows in silt beds, special attention must be paid to these (not normally considered as important fish habitat), and to spawning gravels, in any consideration of the impact of a development proposal on a river. Fishery management for one particular group may adversely affect other fish and wildlife and their habitat. For example, action aimed at improving conditions for salmonids (for example, dredging of ammocoete silts or the provision of fish passes only surmountable by salmonids) may be detrimental to lampreys.

Although brook lampreys have never been important commercially, there has always been an interest in them (both ammocoetes and adults) from anglers as bait, and this seems to have increased in recent



Brian Morland

Brook lamprey are often collected in large numbers to be used as live bait. The trapping of adults can damage lamprey populations, while the digging out of ammocoetes also damages spawning habitat.

years (*Angler's Mail*, 30 January, 1999). Indiscriminate trapping of adults could damage populations, and the search for larvae (by digging out substrate) not only affects the population directly but also causes significant damage to their habitat.

There is no information on the impact of introduced species on the brook lamprey. However, various species of non-native fish, such as rainbow trout, are present in many lamprey rivers, and it would seem reasonable that the Precautionary Principle should apply until adequate data are available – that there are no introductions to lamprey rivers, and fish farm escapes should be minimised.

Recommendations for research

Although the brook lamprey is quite a common species, several aspects of its ecology still need to be researched in Britain. These should also address the needs of the less common river and sea lamprey, which have many of the same habitat requirements and may even be collected in the same samples.

The main recommendations for research are:

- 1 To provide better data on the distribution of the brook lamprey in Great Britain, especially in the north of Scotland and the Inner Hebrides, where its present status is uncertain.
- 2 To consider and carry out research relevant to the reintroduction of the brook lamprey to some of its historic sites, from which it has been excluded by pollution, dams and weirs.
- 3 To carry out further research on the population of brook lamprey in the River Endrick, where there are a number of features of interest, notably their large size, the occurrence of a 'golden' form and their relationship with the dwarf river lamprey (Morris 1989), found in Britain only in Loch Lomond and the River Endrick.

- 4 To investigate the importance of lake sediments as nursery areas for larval brook lamprey.
- 5 To measure sex ratios of spawning populations regularly and relate to population density and environmental factors.

Current monitoring

There is little current monitoring specifically for brook lamprey anywhere in Britain. However, the recent creation of several rivers as SACs for this species places an obligation to monitor populations there. Following a review of available techniques, **Life in UK Rivers** has produced a best-practice monitoring protocol for lamprey.

References

- Abakumov VA (1964). On the systematics and ecology of the brook lamprey. *Vop. Ikhtiol* 34, 423–430.
- Alabaster JS & Lloyd R (1982). Water quality criteria for freshwater fish. Butterworths, London.
- APEM (1996). A survey of six English rivers for lamprey. English Nature, Peterborough.
- APEM (1997). Monitoring guidelines for lampreys. English Nature, Peterborough.
- Baxter EW (1954a). Studies on the biology of lampreys. Unpublished PhD Thesis, University of London.
- Baxter EW (1954b). Lamprey distribution in streams and rivers. *Nature* 180, 1145.
- Bird DJ & Potter IC (1979a). Metamorphosis in the paired species of lamprey, *Lampetra fluviatilis* (L.) and *Lampetra planeri* (Bloch). I. A description of the timing and stages. *Zoological Journal of the Linnaean Society of London* 65, 127–143.
- Bird DJ & Potter IC (1979b). Metamorphosis in the paired species of lamprey, *Lampetra fluviatilis* (L.) and *Lampetra planeri* (Bloch). 2. Quantitative data for body proportions, weights, lengths and sex ratios. *Zoological Journal of the Linnaean Society of London* 65, 127–143.
- Chapman DW (1988). Critical review of variables used to define effects of fines in redds of large salmonids. *Transactions of the American Fish Society* 117, 1–21.
- Crisp DT & Carling P (1989). Observations on siting, dimensions and structure of salmonid redds. *Journal of Fish Biology* 34, 119–134.
- Damas H (1950). La ponte en aquarium des lamproies fluviatiles et de planer. *Ann. Soc. R. Zool. Belg.* 81, 151–162.
- Duncan W (1996). Brook lamprey survey on the upper River Endrick. Scottish Natural Heritage, Edinburgh.
- Eneqvist P (1938). The brook lamprey as an ecological modification of the river lamprey. On the river and brook lampreys of Sweden. *Arkiv for Zoologi*. 29A, 1–22.
- Entec (2000a). River Eamont Acceptable Drought Order Flow Regime Recommendation: Suitability for British Lamprey. Environment Agency, Penrith.
- Entec (2000b). Generically acceptable flows for British lamprey. Environment Agency, Penrith.
- Gardiner R, Taylor R & Armstrong J (1995). Habitat assessment and survey of lamprey populations occurring in areas of conservation interest. Scottish Natural Heritage, Edinburgh.
- Gardiner R & Stewart D (1997). Spawning habitat assessment and survey of lamprey populations occurring in areas of conservation interest. Scottish Natural Heritage, Edinburgh.
- Hardisty MW (1944). The life history and growth of the brook lamprey (*Lampetra planeri*). *Journal of Animal Ecology* 13, 110–122.
- Hardisty MW (1961a). The growth of larval lampreys. *Journal of Animal Ecology* 30, 357–371.
- Hardisty MW (1961b). Studies on an isolated spawning population of the brook lamprey (*Lampetra planeri*). *Journal of Animal Ecology* 30, 339–335.
- Hardisty MW (1964). The fecundity of lampreys. *Archiv fur Hydrobiologie* 60, 340–357.
- Hardisty MW (1965). Sex differentiation and gonadogenesis in lampreys. Part I. The ammocoete gonads of the brook lamprey (*Lampetra planeri*). *Journal of Zoology* 146, 305–345.
- Hardisty MW (1970). The relationship of gonadal development to the life cycles of the paired species of lamprey, *Lampetra fluviatilis* (L.) and *Lampetra planeri* (Bloch). *Journal of Fish Biology* 2, 173–181.
- Hardisty MW (1986). Petromyzontiforma. In: Holcik J (ed). *The freshwater fishes of Europe*. Aula-Verlag, Wiesbaden.
- Hardisty MW & Huggins RL (1970). Larval growth in the river lamprey, *Lampetra fluviatilis*. *Journal of Zoology* 161, 549–559.

- Hardisty MW & Potter IC (eds) (1971). *The biology of lampreys*. Academic Press, London.
- Hill BJ & Potter IC (1970). Oxygen consumption in the ammocoetes of the lamprey *Icthyomyzon hubbsi*. *Journal of Experimental Biology* 53, 47–57.
- Hjulstrom F (1935). Studies in the morphological activity of rivers as illustrated by the River Fyris. *Geological Institute of the University of Uppsala Bulletin* 25, 221–528.
- Huggins RJ & Thompson A (1970). Communal spawning of brook and river lampreys, *Lampetra planeri* Bloch and *Lampetra fluviatilis* L. *Journal of Fish Biology* 2, 53–54.
- IUCN (1994). *IUCN Red List categories*. International Union for the Conservation of Nature and Natural Resources, Gland.
- Kappus B, Janse W, Fok P & Rahman H (1995). Threatened lamprey (*Lampetra planeri*) populations of the Danube Basin within Baden-Wuerttemberg, Germany. *Micellanea Zoologica Hungarica* 10.
- Lohnsky K (1966). The spawning behaviour of the brook lamprey, *Lampetra planeri* (Bloch, 1784). *Vestnik Ceskoslovenske Spolecnosti Zoologicke* 4, 289–307.
- Lyle AA & Maitland PS (1992). Conservation of freshwater fish in the British Isles: the status of fish in National Nature Reserves. *Aquatic Conservation* 2, 19–34.
- Maitland PS (1980). Review of the ecology of lampreys in northern Europe. *Canadian Journal of Fisheries and Aquatic Sciences* 37, 1944–1952.
- Maitland PS (1985). Criteria for the selection of important sites for freshwater fish in the British Isles. *Biological Conservation* 31, 335–353.
- Maitland PS (1991). Climate change and fish in northern Europe: some possible scenarios. *Proceedings of the Institute of Fishery Management, Annual Study Course* 22, 97–110.
- Maitland PS (1993). *Sites in Great Britain for freshwater and estuarine fish on the EC Habitats and Species Directive*. Fish Conservation Centre Report to JNCC, Peterborough.
- Maitland PS (1997). *Species Action Plans for lampreys in England*. Fish Conservation Centre Report to English Nature, Peterborough.
- Maitland PS (2000a). *Guide to freshwater fish of Britain and Europe*. Hamlyn, London.
- Maitland PS (2000b). Fish. In: Ward SD (ed). Local Biodiversity Action Plans – technical information on species: IV. Vertebrate animals. *Scottish Natural Heritage Review* 10, 81–91.
- Maitland PS & Campbell RN (1992). *Freshwater fishes of the British Isles*. HarperCollins, London.
- Maitland PS, East K & Morris KH (1983). *Lamprey populations in the catchments of the Forth and Clyde estuaries*. Annual Report, Institute of Terrestrial Ecology, 17–18.
- Maitland PS & Lyle AA (2000). *Distribution of lampreys in the River Teith*. Report to Scottish Natural Heritage, Stirling.
- Maitland PS, Morris KH & East K (1994). The ecology of lampreys (Petromyzonidae) in the Loch Lomond area. *Hydrobiologia* 290, 105–120.
- Malmqvist B (1978). Population structure and biometry of *Lampetra planeri* (Bloch) from three different watersheds in south Sweden. *Arch Hydrobiol.* 84, 65–86.
- Malmqvist B (1980). The spawning migration of the brook lamprey, *Lampetra planeri* Bloch, in a south Swedish stream. *Journal of Fish Biology* 16, 105–114.
- Morris KH (1989). A multivariate morphometric and meristic description of a population of freshwater-feeding river lampreys, *Lampetra fluviatilis* (L.), from Loch Lomond, Scotland. *Zoological Journal of the Linnaean Society of London* 96, 357–371.
- Potter IC (1970). The life cycles and ecology of Australian lampreys of the genus *Mordacia*. *Journal of Zoology* 161, 487–511.

- Potter IC (1980). The Petromyzoniformes with particular reference to paired species. *Canadian Journal of Fisheries and Aquatic Sciences* 37, 1595–1615.
- Potter IC & Osborne TS (1975). The systematics of British larval lampreys. *Journal of Zoology* 176, 311–329.
- Potter IC, Hill BJ & Gentleman S (1970). Survival and behaviour of ammocoetes at low oxygen tensions. *Journal of Experimental Biology* 53, 59–73.
- Potter IC, Hilliard RW, Bradley JS & McKay RJ (1986). The influence of environmental variables on the density of larval lampreys in different seasons. *Oecologia* 70, 433–440.
- Schroll F (1959). Zur Ernährungsbiologie der steirischen Ammocoten *Lampetra planeri* (Bloch) und *Eudontomyzon danfordi* (Regan). *Int. Rev. ges. Hydrobiol. Hydrogr.* 44, 395–429.
- Smith BR (1971). Sea lampreys in the Great Lakes of North America. In: Hardisty MW & Potter IC (eds). *The biology of lampreys*. Academic Press, London, 207–247
- Stuart TA (1953). *Spawning migration, reproduction and young stages of loch trout (Salmo trutta L.)*. HMSO, Edinburgh.
- Thomas MLH (1962). *Observations on the ecology of ammocoetes of Petromyzon marinus L. and Entosphenus lamottenii (Le Sueur)*. in the Great Lakes watershed. Unpublished MSc Thesis, University of Toronto.
- Waterstraat A & Krappe M (1998) Distribution and abundance of *Lampetra planeri* populations in the Peene drainage (NE Germany) in relation to isolation and habitat conditions. *Italian Journal of Zoology* 65, 137–143.
- Wentworth CK (1922). A scale of grade and class terms for clastic sediments. *Journal of Geology* 30, 377–392.
- Whilde A (1993). *Threatened mammals, birds, amphibians and fish in Ireland: Irish Red Data Book 2: Vertebrates*. HMSO, Belfast.
- Zanandrea G (1951). Rilievi confronti e biologici sul *Petromyzon (Lampetra) planeri* Bloch, nelle acque della Marca Trevigiana. *Boll. Pesca Piscic. Idrobiol* 6, 53–78.

Sea Lamprey

Introduction

The sea lamprey (*Petromyzon marinus* L) is by far the largest of the British lampreys and may reach a length of 100 cm and a weight of 2.5 kg. It is known colloquially as the marine lamprey or lamprey eel. The normal adult length is around 50 cm. There are no angling records.

The body is very long and cylindrical, except at the tail, which is laterally compressed. The overhung (inferior) mouth has the form of a large circular sucker frilled with extensions of the skin known as fimbriae. When closed, the mouth has the form of a slit, but when open for attachment it forms an oval sucking disc whose diameter is greater than that of the head or pharynx behind. Inside the mouth are numerous hard, sharp teeth arranged in concentric rows. Above and around the tongue, the teeth are especially large and bicuspid; below the tongue is a huge multiple transverse tooth with up to 10 cusps. The tongue itself has several large complex teeth.



Andy Strevens/Environment Agency

The sea lamprey is the largest lamprey and weighs up to 2.5 kg. Although the sea lamprey is protected across Europe, it is regarded as a pest in North America, particularly in the Great Lakes.

The eyes are of moderate size and positioned on each side of the head just behind the single nostril and in front of the seven pairs of gill openings. The two dorsal fins are distinctly separate in the young, but much closer in the adults. The first of these (the lower) originates just behind the middle of the body; the second (which is slightly higher) terminates just in front of the small tail fin. There are no paired fins. The skin is smooth and scaleless. There are 67–74 distinct muscle blocks (myotomes) along the body, but there is no lateral line and no vertebrae, the entire skeleton being cartilaginous.

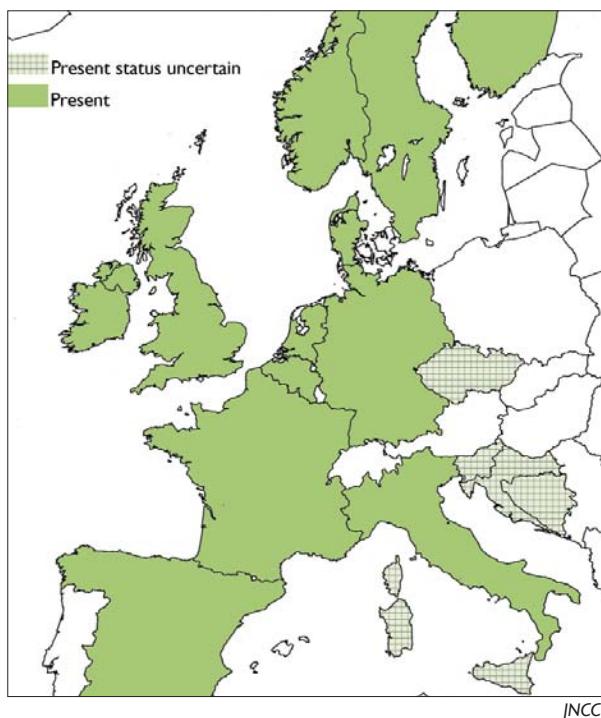
At spawning time, the males develop a distinct ridge along the back, while the females have a pronounced fold of skin behind the vent.

Colour varies greatly with age. The ammocoete larvae are dark greyish brown above and a light grey below. Occasionally, specimens are found that are lacking in pigment and these have a yellowish gold appearance. Newly metamorphosed animals are a slaty grey-blue above changing gradually to a metallic bluish on the sides to a pale white on the belly.

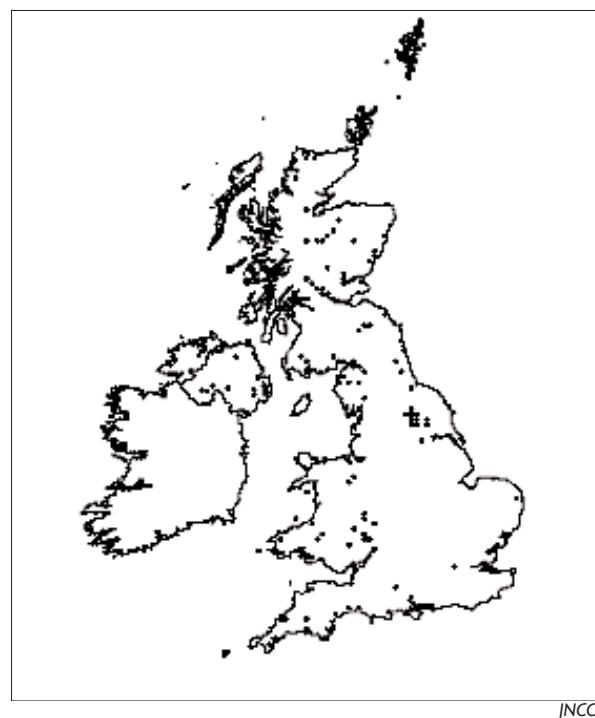
In adults, the main body colour is brownish grey (paler ventrally) with extensive black mottling. The body colour lightens to a golden brown (almost orange sometimes) at spawning time.

Status and distribution

The anadromous sea lamprey occurs over much of the Atlantic coastal area of western and northern Europe, from northern Norway to the western Mediterranean, and eastern North America. It is also found in estuaries and easily accessible rivers in these regions. Occasional specimens are taken in midwater in the Atlantic Ocean (Lelek 1973).



Although common in North America, the sea lamprey is declining across Europe and is now protected.



The sea lamprey can be found in some British rivers, but has become extinct in many areas.

In the British Isles it is absent from many northern rivers, and has become extinct in a number of southern ones due to pollution and engineering barriers (Maitland 1980a). There are several landlocked populations in North America, but in Britain the only site where the species is known to feed in fresh water is Loch Lomond (Maitland et al. 1994).

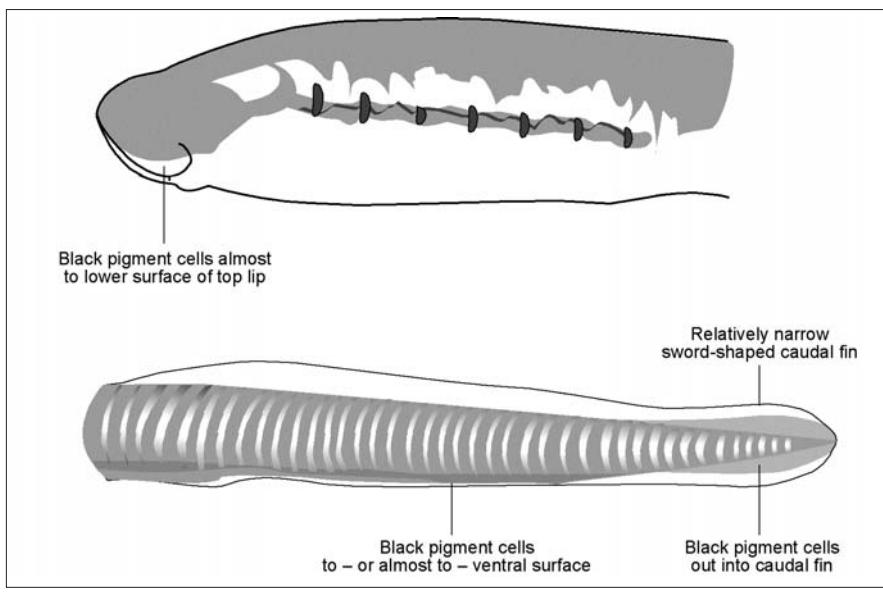
Because of its decline across Europe, the sea lamprey is now given some legal protection. It is listed in annexes IIa and Va of the Habitats Directive, Appendix III of the Bern Convention, and as a Long List Species in the UK Biodiversity Action Plan. There is no Red Data Book for fish in Great Britain, but Maitland (2000a) considers this species to be Vulnerable. The Red Data Book for Ireland (Whilde 1993), published before the IUCN (1994) revision of categories, lists the sea lamprey as Indeterminate.

In contrast, it is regarded as a pest in parts of North America, and the Great Lakes Fishery Commission spends several million dollars each year trying to control it (Maitland 1980b).

Life history

The sea lamprey usually spawns in late May or June in British rivers, when the water temperature reaches at least 15°C. Normally, males appear on the nesting sites first and are apparently highly attractive to females, possibly by the secretion of an olfactory sex attractant. The numbers of eggs produced by the females in some populations have been estimated by research workers and average about 172,000 per female. The eggs are small (0.80–1.25 mm in diameter) and are an opaque white colour when laid.

After hatching, larvae leave the nest and drift downstream, distributing themselves among suitable silt beds. The duration of larval life varies, but averages about five years. The age of larvae has mainly been calculated from length frequency analyses, for there is no known method of ageing them.

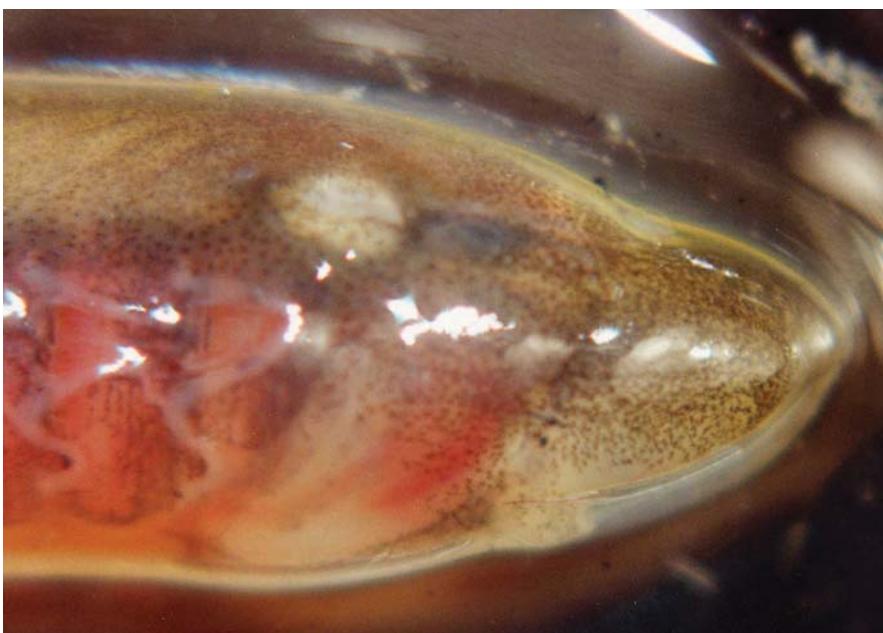


Head and tail of sea lamprey ammocoete, showing features important for distinguishing it from a river or brook lamprey.

Metamorphosis to the adult form takes place between July and September and the process usually takes a few weeks (Potter 1980). The time of the main migration downstream seems to vary from river to river (Applegate & Brynildson 1952) and relatively little is known about them after they reach the sea, where they have been found in both shallow coastal and deep offshore waters.

The spawning migration in Europe usually takes place in April and May when the adults start to migrate back into fresh water (Hardisty 1969).

There is little evidence for any differences in the food or feeding habits of the ammocoete stage of the three British species of lamprey (Newth 1930). All appear to feed from within their burrows on fine particulate matter, mainly micro-organisms, desmids and diatoms in particular. In addition, various unicellular animals, including ciliates, euglenoids and rhizopods, have been



Head of a small sea lamprey ammocoete.



Brian Morland

Adult sea lamprey have a series of sharp teeth within their oral discs. They prey on a variety of fish, including cod, sturgeon, haddock, sea trout and salmon. They have even been seen attached to basking sharks (right).

found in ammocoete guts in some numbers. The role of detritus as food is uncertain, but large amounts appear to be eaten during the summer months. Most of the food taken in by the larvae comes from the superficial sediments in the vicinity of the larval burrows. The system of ciliated tracts in the pharynx, used as a means of transporting food on strands of mucus towards the intestine, is complex (Sutton & Bowen 1994).

After metamorphosis and the downstream migration to the sea, the adults feed on fish there, but detailed evidence on their feeding habits is fragmentary (except in the specialised case of the purely freshwater populations in North America that have been intensively studied) (Lennon 1954). They seem to feed on a wide variety of marine and anadromous fishes, including sturgeon (*Acipenser sturio*), herring (*Clupea harengus*), salmon (*Salmo salar*), cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*). Salmon and sea trout (*Salmo trutta*) entering rivers often bear fresh scars attributable to attacks by this species.



Bill Sanderson/Aquatic Us

Habitat requirements and associations

Mature adults enter the estuaries of many North Atlantic rivers from April onwards, and migrate some distance upstream, providing that there are no obstacles; either natural, such as waterfalls, or man-made, such as dams, weirs or pollution barriers. The upstream migration from the estuary appears to be triggered by temperature.

Apart from clear migration routes, the critical habitat requirements of adults (Young *et al.* 1990; Maitland 1993, 1995, 1997, 2000b) relate to the spawning areas and nursery habitat (see below). The Habitats and Species Directive has lead to a considerable amount of recent work on lampreys in the British Isles (Gardiner *et al.* 1995; Gardiner & Stewart 1997; Maitland & Lyle 2000; APEM 2001a, 2001b), much of which is ongoing.

The ammocoetes are usually found in silty sands in running water, though in some places they may occur in silt and gravel beds in large lakes, such as Loch Lomond. Where suitable substrates are present they occur in streams and rivers upstream as far as the adults are able to migrate; they are stopped by high waterfalls or weirs, dams and severe pollution. The habitat occupied by the larvae of all species seems to be very similar: indeed, in the British Isles, sea, river and brook lamprey may often be found together at the same site, such as in eddies, backwaters, behind obstructions or at the edges of streams.

Relatively little is known about the precise habitats occupied by adult sea lampreys. Although adults are sometimes caught at sea, the precise conditions in which they occur have not been described, nor is it certain which fish are the main prey species. Most adults found in fresh water are either migrating upstream to spawn or dying after spawning. Habitat seems only to be important in relation to their ability to get to the spawning beds. Just before spawning they may be found in calmer water above the spawning areas or below protecting obstructions, etc. The nests are normally built in areas of flowing shallow water amid gravel.

Population parameters

Applegate (1950) studied three areas where larvae apparently prospered and found densities of 150, 108 and 86 m⁻². He noted, however, that 'within that portion of the river where ammocoetes occur most abundantly, a few larvae could be found in almost every location where the bottom permitted burrowing.' Smith & McLain (1962) estimated the ammocoete populations of entire streams in Michigan and found numbers as follows:

	(km)		
Furnace Creek	0.762	3,984	329
Snyder Creek	4.023	30,317	269
Ogonz River	14.481	166,154	170,570

McCauley (1963) studied the temperature requirements of the sea lamprey and found that, of all stages, the eggs have the most exacting temperature requirements necessary for successful hatching, being 15–25°C.

In Britain, Hardisty (1969) found five well-defined modes in populations of larval sea lampreys. In North America, Applegate (1950) found only four year-classes, while others found as many as seven (Wigley 1959, Stauffer 1962). Studies in the Big Garlic River indicated that, in special circumstances, many more year-classes could be found (Manion & Smith 1978).

Applegate & Thomas (1965) and Smith (1971) have shown that, in the Great Lakes area, there is a shift in sex composition towards males as the population increases (a maximum of 72% males was recorded in 1952), and then to females as the population declines (a minimum of 46% males was recorded in 1969). They suggest that this may be a natural population control.

Attempts to model larval habitat selection (Lee 1989) have emphasised the importance of substrate lattice to properties such as permeability. There was no evidence from the laboratory of density-dependent interactions among ammocoetes, which supports the earlier conclusions of Malatt (1983) and Morman (1987).

Water quantity requirements

Morman et al. (1980) noted that, in general, sea lamprey favour larger streams and rivers, though overall, a wide range of stream size is occupied, ranging from small coastal tributaries with flows less than $0.03 \text{ m}^3 \text{ s}^{-1}$ to large intake channels such as the St Clair River with low flows of $4,400 \text{ m}^3 \text{ s}^{-1}$. Stauffer & Hansen (1958) reported that larval abundance was greatest in Lake Superior tributaries with flows larger than $0.8 \text{ m}^3 \text{ s}^{-1}$. The median low flow of 74 streams that contained populations of larvae in the Lower Peninsula of Michigan was $0.4 \text{ m}^3 \text{ s}^{-1}$ (Morman 1979). In contrast, of 380 streams that did not contain larvae 296 (78%) were intermittent or extremely low in flow during late summer. Some data are available on flow velocities (Entec 2000a, 2000b) and stream gradients (Baxter 1954a, b).



Brian Morland

Rivers in spate are detrimental to sea lamprey. High flows may prevent them from reaching spawning areas, or sweep eggs and larvae downstream after spawning, thereby affecting recruitment.

Larvae

Thomas (1962) concluded that for *Petromyzon marinus*, flow rates of $0.6\text{--}0.8 \text{ m s}^{-1}$ represented an upper limit, beyond which burrowing would not occur. However, the mean water velocity over areas of high ammocoete density was often no more than about 0.03 m s^{-1} . Thomas (1962) reported that ammocoetes were concentrated in the low-velocity parts of a stream's high-velocity sections (mean velocity $0.2\text{--}0.3 \text{ m s}^{-1}$), but were evenly distributed throughout the entire streambed in a low-velocity section (mean velocity $<0.2 \text{ m s}^{-1}$).

However, it is a common observation that larval nursery beds are at the edges of streams and rivers, well away from the main current, and that the current over them is often not only very slow, but is actually a backwater in reverse of the main current.

Adults

Applegate (1950) concluded that at least some current passing consistently in one direction over the nest is essential to successful spawning. Very swift currents hinder or preclude successful mating and eggs may be swept beyond the nest and lost. In his study of hundreds of nesting sites he found that current velocities over the nests ranged from 39.6–158.5 cm s⁻¹. Beamish (1974) recorded 30 cm s⁻¹, whereas Hardisty (1986) noted 100–200 cm s⁻¹.

As with shad and other migratory species, the spawning migration of sea lampreys is likely to be influenced by tides and river flows. The larger size of sea lampreys compared to the other two species means that they are probably better able to swim against fast currents. Thomas recorded swimming speeds of 11–26 cm s⁻¹. However, there is no evidence that they swim further upstream than river lampreys, even though suitable spawning gravels may be available in these upstream stretches.

The general conclusion is that high flows during spates are likely to be detrimental to populations of sea lamprey, not only in making it difficult for them to access spawning grounds, but also by lowering recruitment after spawning, probably due to eggs and larvae being swept downstream. However, as with many migratory salmonids, very low flows may also be detrimental, both in preventing the passage of upstream migrants over very shallow areas, and in exacerbating the impact of poor water quality in those rivers affected by pollution.

The best conditions for high recruitment might be relatively high water from April to June to aid upstream migration and increase the areas of spawning gravel available, followed by lower flows from June onwards, which would help larvae to disperse across suitable habitat downstream, but not wash them away.

Water quality requirements

There are relatively few data available concerning the water quality requirements of sea lampreys (Alabaster & Lloyd 1982). Occasional mortalities have been reported that have been ascribed to pollution but few details are available.

Larvae

Potter *et al.* (1970, 1986) have shown that oxygen tension is a major factor in the maintenance of the burrowing habit. They can survive almost anoxic conditions in their burrows for only a few hours, after which they must come out of their burrows or die. However, they can tolerate low oxygen tensions and may remain in their burrows for some time under these conditions (Hill & Potter 1970).

Laboratory studies on the effect of temperature on the development of embryos have shown that successful hatching of free-swimming ammocoetes is only possible within a relatively restricted range of water temperatures (Damas 1950). Hardisty & Potter (1971) note that 'the kind of fluctuations that sometimes occur in the spring (particularly in small streams) might adversely affect the production of hatched larvae'. Thomas (1962) has shown that, in *Lampetra lamottenii* (and *Petromyzon marinus*) ammocoetes are most active at water temperatures between 10 and 14°C.

The onset of transformation of larvae usually occurs in a short period (three to four weeks) and it may be that temperature is the operative factor (Potter 1970, Hardisty & Potter 1971). There are also indications that in successive years, the time of onset of metamorphosis in *Lampetra fluviatilis* in the field has varied according to the prevailing spring temperatures (Hardisty & Potter 1971).

Applegate (1950) reported a mean daily temperature range of 18.6–24.2°C with daily extremes of 16.1–26.1°C in the Ocqueoc River during development and hatching of sea lamprey embryos. Meyer & Howell (1973) found in experimental studies that growth and survival of larvae increased as temperature increased and that optimum temperatures were from 15.6–21.1°C. Reynolds & Casterlin (1978) produced similar results, with experimental temperature preferenda ranging from 10–19°C (mean 13.6°C). However, embryos will develop at much lower temperatures (10.0–11.7°C), although development is slow (Manion & Hanson 1980). It has been suggested by Morman (1979) that habitat

partition may occur among lamprey species along temperature gradients, with each species electing a different temperature regime. The thermal niche proposed for sea lamprey by Holmes & Lin (1994) is 17.8–21.8°C.

Low oxygen is rarely a factor limiting the distribution of larvae for two reasons. First, ammocoetes can tolerate low oxygen levels because of low metabolic activity, their blood characteristics and branchial pumping ability (Mormann *et al.* 1980). Second, more harmful conditions such as pollution and high temperatures usually occur with low oxygen levels and are usually the lethal factors.

Adults

There is no doubt that significant pollution can eliminate whole populations of sea lamprey from rivers and there are several examples where this has happened in the past (including the River Thames and River Clyde). In such cases, it is usually severe pollution in the lower reaches that prevents upstream migration and kills downstream migrants – in spite of the fact that there may be hundreds of kilometres upstream where the water quality is good and there is plenty of good spawning and larval habitat.

Farmer *et al.* (1977) demonstrated that adult sea lamprey survived and grew in a wide range of water temperatures (4–20°C) and temperatures of 17–19°C have been reported by Hardisty (1986) for British rivers. The timing, duration and consistency of spawning runs is closely related to temperature (Applegate 1950). Peak migration usually coincide with temperatures that remain above 10°C and continues until temperatures reach 18°C. Runs are erratic and of shorter duration in small runoff streams where water temperatures may be quite unstable. Water temperatures of 11–25°C appear essential for successful spawning.

The sea lamprey is known to be sensitive to pollution, and although few data are available, it has certainly disappeared from rivers that have become polluted. However, some pollution in the lower reaches of rivers appears to be tolerated, and migrating adults can pass through such waters to reach their spawning grounds in cleaner water upstream.

In the absence of specific tolerance data for sea lampreys it must be assumed that conditions in all parts of any river where they occur, or pass through on migration, are at least UK Water Quality Class B in England, Wales and Northern Ireland or A2 in Scotland.

Beamish (1974) reported that the oxygen consumption of adult sea lamprey at various temperatures is comparable to salmonids of similar weight.

Substrate requirements

Unless otherwise indicated, particle size descriptions (sand, silt, clay, etc.) are based on the scales first described by Wentworth (1922).

Larvae

Several research workers have measured the conditions at places occupied by the ammocoetes in an attempt to define their habitat precisely. The optimum particle size of the beds of sediment in which they occur is said to be 0.18–0.38 mm, and to include clay, silt and sand fractions. Shade (which appears to be related to the types of micro-organisms on the surface) and water velocity are important factors connected to the suitability of sites.

Normally, suitable sites are found only in some parts of each river system, and in some rivers there may be none at all. In British streams, most populations occur where the average stream gradients are 1.9–5.7 m km⁻¹. Lampreys are rarely found where gradients exceed 7.8 m km⁻¹. Within the stretches of suitable gradient, adequate sites are often found in conditions of slowing current, where deposition of sand and silt occurs.

Typically, the substrate in which larvae live varies in depth to more 30 cm. It often contains a relatively high organic content and has been variously described as composed of mud, silt, or silt and sand

(Hardisty & Potter 1971). In slow-flowing stretches in particular, the more favourable habitats include, in addition to sand and silt, a clay fraction, forming an open-structured sediment (Potter 1970). Thomas (1962) has defined the characteristics of a suitable substrate in terms of densitometer readings as one in which a force of less than 2,200–2,700 g is required to press a cone-shaped penetrometer into the bottom.

Manion & McLain (1971) found larvae to be most abundant where the substrate consisted of about 90% sand particles finer than 0.5 mm. Applegate (1950) observed that the largest concentrations of ammocoetes in a given bed were among small patches of aquatic plants (*Najas*, *Potamogeton*, *Sagittaria*). Other authors have also considered the presence of at least some rooted macrophytes to be a positive part of the larval habitat of sea lampreys (Thomas 1962).

Applegate (1950) noted that the depth to which larvae burrow generally relate to their size, as follows:

<20	12.7
31-41	19.1 - 25.4
50-90	50.8 - 76.2
100-160	127.0 - 152.4

Adults

Applegate (1950) concluded that two essential physical conditions, other than suitable water temperatures, must be fulfilled before sea lampreys may spawn 'with any degree of success'. First, gravel 9.5–50.8 mm in diameter must be present for nest construction. Secondly, small amounts of sand must be available to which the eggs will adhere and which will imbed them in the interstices of the gravel in the nest rim. Morman et al. (1980) note that sea lampreys require mostly gravel (15–115 mm diameter) for constructing nests, although they use other materials (rubble, clam shells and lumps of clay) when gravel is scarce or absent.

In streams devoid of gravel, the incidental introduction of gravel at highway and railroad crossings provides lampreys with spawning sites (Morman et al. 1980).

Larvae

The distribution of larvae is closely associated with spawning sites and, generally, larval density is inversely related to the distance downstream from spawning areas (Morman et al. 1980). In Michigan, the absence of suitable spawning habitat was a limiting factor in 118 of 380 streams that did not support populations of sea lamprey larvae.

Spawning-run sea lampreys are known to be attracted to streams containing ammocoete populations (Moore & Schleen 1980). This has been proved experimentally with chemical attractants, showing that sexually immature sea lamprey migrants select water containing rinses from ammocoetes over other water (Teeter 1980).

Most of the substrate at the spawning sites is described as 'gravel'. The size of the gravel beds involved varies from a few square metres to hundreds of square metres in some large rivers.

Little is known about the precise nature of the gravel beds used for spawning, but it seems likely, from the position of lamprey spawning beds at the tails of pools and the obvious requirement of lamprey eggs for shelter and oxygen, that the requirements are similar to those of brown trout (*Salmo trutta*), which have been well described by Stuart (1953) and others. Here, the spawning gravels 'are composed of stones up to 3 in. in diameter with a large proportion of smaller materials, the effect of which is to consolidate the mass while leaving it permeable to the water. Stones embedded in fine sands or silts which form a hard bed are avoided, as are also uniform gravels and shingles of small size which move



Erling Svenson

Adult sea lamprey begin spawning in British rivers when the water temperature reaches 15°C. Sand and gravel must be present for successful nest digging and egg laying.

easily in a flood. The location of the redds in an ideal pool is towards the tail, where the gravel slopes gently upward, spreading more or less evenly from bank to bank by the slackening of the current. The depth of water here is at a minimum...'.

The presence of currents through the gravels actually chosen by brown trout was demonstrated by the passage of dyes through them (Stuart 1953).

Channel structure and management

Applegate (1950) studied hundreds of nesting sites and found that there was no evident relationship between the degree of cover/shade and the incidence of spawning activity. In the same river system, nests were found in shallow riffles with no cover and completely exposed to the sun, and elsewhere in dense shade where the sun seldom struck the water.

Water depth at spawning sites seems to be relatively unimportant, and depths of 5–152 cm have been recorded, with an extreme instance of 370 cm. Applegate (1950) found that the average depth over a nest in the Ocqueoc River was 23–51 cm, with extremes of 15–81 cm. Elsewhere, he recorded depths of 13–170 cm. The water depth where adults spawn is usually 40–60 cm (Hardisty 1986).

Water depth in nursery areas is 'typically 0.1 to 0.5 m' (Entec 2000a, 2000b), but can range from 0–100 cm, and deeper in some cases (Maitland unpubl.). Thomas (1962) was unable to correlate ammocoete abundance with water depth. Ammocoetes have been known to inhabit substrates at a depth of up to 2.2 m in some rivers and 16 m in lakes. Larger larvae are more common in deep water than smaller ones (Manion & Smith 1978).

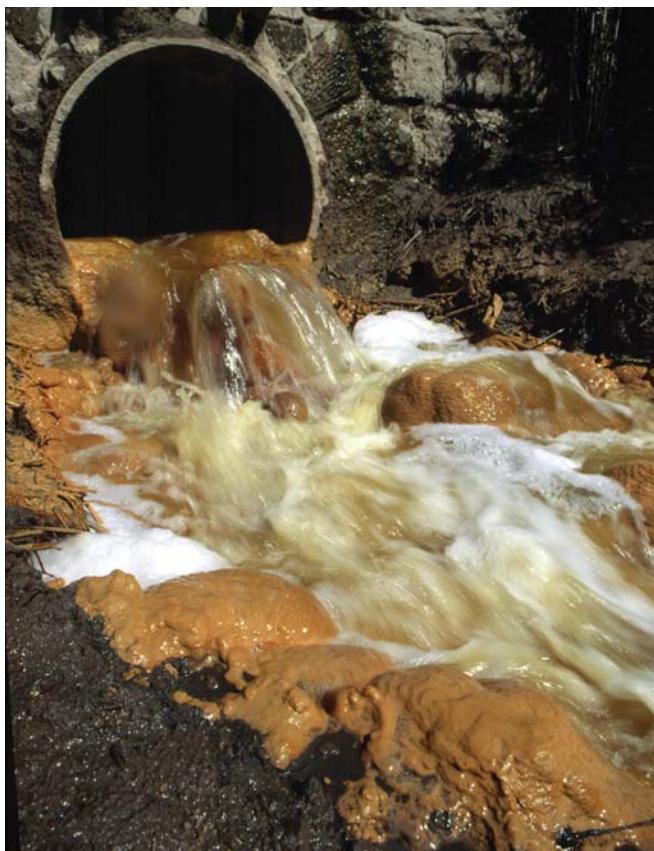
There must be no significant obstacles (chemical or physical) in the river channel on their migration

routes if sea lampreys are to reach their spawning grounds. Apart from actual barriers, any significant alteration or management of channels that removes resting cover or creates stretches of fast flow ($> 2\text{m s}^{-1}$) must be avoided all along the migration route.

Impacts, threats and exploitation

Impacts

Because most polluting effluents are directed into running waters (and so to the sea), many rivers became grossly polluted in the past and lost their populations of lampreys. In addition to direct toxic effects, pollution can have a major impact on lampreys by smothering both spawning gravels and nursery silts.



Roger Covey/English Nature

Adult sea lamprey are very sensitive to pollution, and have disappeared from rivers where this has been a problem.

lampreys is spent in burrows in silt beds, special attention must be paid to these (not normally considered as important fish habitat), and to spawning gravels, in considering the impact of a proposed development on a river. Fishery management for one group may adversely affect other wildlife and its habitat. For example, action to improve conditions for salmonids (for example, dredging or the provision of fish passes only surmountable by salmonids) may be detrimental to lamprey.

In rivers with intermittent flow (for example due to hydro schemes, etc.) lamprey larvae can live for some time in exposed beds but are often found dead. In general, flow intermittency is considered limiting to ammocoete populations (Morman *et al.* 1980). Low and unstable flows were considered by Morman (1979) to be two of the major limiting factors for the absence or scarcity of larvae in many streams, other factors of importance being pollution, sedimentation and hard or unstable bottoms.

The migrations of anadromous species such as the river lamprey are particularly affected by pollution barriers because considerable migrations are often necessary from the estuary to the spawning grounds. One extreme belt of pollution between these two habitats can have a major effect on lamprey populations in a river.

In a similar way, engineering works of various kinds (dams, weirs, etc.) can be obstacles to upstream migration and the success of local populations of lampreys.

Channelisation can also be damaging to lampreys, mainly through destruction of their habitat. The removal of areas of riffle and associated spawning gravels, and the dredging of essential nursery silt beds, may entirely eliminate lampreys from a river.

Threats

River management and development

Both water abstraction and land drainage can have negative effects on lamprey populations, leading to unstable habitats with variable levels of water. Consequently, spawning gravels and nursery silts may be flooded and disturbed at some times but left high and dry at others.

Since a large proportion of the life cycle of lampreys is spent in burrows in silt beds, special attention must be paid to these (not normally considered as important fish habitat), and to spawning gravels, in considering the impact of a proposed development on a river. Fishery management for one group may adversely affect other wildlife and its habitat. For example, action to improve conditions for salmonids (for example, dredging or the provision of fish passes only surmountable by salmonids) may be detrimental to lamprey.

Some sea lampreys are caught in power stations intakes, but there is no evidence in the UK that the numbers concerned are detrimental to stocks, and such catches can be a valuable tool in monitoring.

Pollution

Various types of pollution, either alone or in combination with other factors, limit the distribution of sea lampreys (Morman et al. 1980). Streams affected by domestic or industrial pollution or agriculture usually have no larvae or only small, discrete populations. Formation of methane in bottom habitats was considered to be one reason for the mortality and disappearance of sea lamprey larvae from some areas where they were formerly abundant (Wilson 1955).

Eutrophication acts in a similar way to other forms of pollution. Lush growths of algae and bacteria associated with increased nutrients smother both the spawning gravels (preventing spawning or killing eggs) and nursery silts, creating anoxic conditions there.

Barriers

Physical barriers on streams, stream flow, water temperature and streambed composition can have a major effect on the distribution of spawning sea lamprey (Haro & Kynar 1997). The distribution of larvae is affected most by the location of spawning sites, stream flow, water temperature, streambed pollution and downstream migrations.

Predators

Mortality rates in ammocoete populations are probably rather low and consistent throughout the larval period. Apart from the effect of fluctuating physical factors, especially during the embryonic period, it is known that the larvae are eaten by eels, sticklebacks and other fish, as well as several different birds (such as herons). Losses may be particularly high during dispersal from the nest to the ammocoete silt beds, and a high mortality probably occurs at metamorphosis. There are a number of records of birds and mammals attacking adult sea lampreys, especially at spawning time.

Only a few parasites have been recorded from lampreys and nothing is known about their effect on the host.

Introduced species

There is no information on the impact of introduced species on sea lamprey. However, some species of alien fish (for example, rainbow trout, *Oncorhynchus mykiss*) are present in some rivers. It would therefore seem reasonable that the Precautionary Principle should apply until adequate data are



Erling Svenson

Sea lamprey larvae are preyed upon by a range of species, including the eel.

available (there should be no introductions to lamprey rivers, and fish farm escapes should be minimised).

Exploitation

Although the sea lamprey is considered a pest in North America, it is commercially important in a number of countries in Europe, including Spain and Poland. Humans must be considered as the most serious threat to the species in view of these fisheries, the extensive use of lampricides in North America, and the serious effects of pollution and barriers to upstream migration in many rivers.

Although the sea lamprey was formerly fished extensively in the River Severn, among several other British rivers, it is now exploited in only a few rivers in Europe – notably in Portugal, where it is regarded as a delicacy and fetches a high price. The siting of a fishery (including a cannery) for sea lampreys on the River Severn was proposed in 1998, the products to be exported to France where stocks have declined. If a commercial fishery is ever to start again in Britain it should be managed under strict guidelines to ensure sustainability.

There has always been an interest in lampreys (both ammocoetes and adults) from anglers as bait, and this seems to have increased in recent years (*Angler's Mail*, 30 January, 1999) and to favour adult river lampreys in particular. Indiscriminate trapping of adults could damage populations, and the search for larvae (by digging out substrate) not only affects the population directly but also causes significant damage to their habitat.

Recommendations for research

Although there has been extensive research on this species in North America, this is the least common of the three British lampreys and further research needs to be carried out here.

In order to restore this species to sites where it previously occurred but is now extinct, large numbers of larvae could be reared. Hanson *et al.* (1974) have shown that it is possible to culture sea lamprey from eggs obtained by stripping adults. Densities of up to 600 m⁻² can be reared in this way.

The main recommendations for research are:

- 1 To provide better data on the distribution of sea lampreys in Britain, especially in northern Scotland where its status is uncertain.
- 2 To consider and carry out research relevant to the reintroduction of the sea lamprey to sites from which it has been excluded by pollution, dams and weirs.
- 3 To carry out further research on the population of sea lampreys in the River Leven and Loch Lomond, the only location in Britain where this species is known to feed on fish in fresh water.
- 4 To further international collaboration to investigate the genetic diversity and relationships among the various populations of sea lamprey in Europe.
- 5 To measure sex ratios of spawning populations regularly and relate them to population density and environmental factors.

Current monitoring

There is little current monitoring specifically for the sea lamprey anywhere in Britain. However, the designation of several rivers as Special Areas of Conservation places an obligation to monitor populations there. Following a review of available techniques, **Life in UK Rivers** has produced a best-practice monitoring protocol for lamprey.

References

- Alabaster JS & Lloyd R (1982). *Water quality criteria for freshwater fish*. Butterworths, London.
- APEM. (2001a). *Assessing sea lamprey distribution and abundance in the River Spey: Phase 1. Electric fishing techniques: desk review and field trial report*. Scottish Natural Heritage, Edinburgh.
- APEM (2001b). *Assessing sea lamprey distribution and abundance in the River Spey: Phase 1. An assessment of gradient as a tool for lamprey habitat identification*. Scottish Natural Heritage, Edinburgh.
- Applegate VA (1950). *Natural history of the sea lamprey, Petromyzon marinus, in Michigan*. US Fish and Wildlife Service Special Scientific Report 55, 1–237.
- Applegate VA & Brynildson CL (1952). Downstream movement of recently transformed sea lampreys in the Carp Lake River, Michigan. *Transactions of the American Fisheries Society* 81, 275–290.
- Applegate VA & Thomas MLH (1965). Sex ratios and sexual dimorphism among recently transformed sea lampreys. *Journal of the Fisheries Research Board of Canada* 22, 695–711.
- Baxter EW (1954a). *Studies on the biology of lampreys*. Unpublished PhD Thesis, University of London.
- Baxter EW (1954b). Lamprey distribution in streams and rivers. *Nature* 180, 1145.
- Beamish FWH (1974). Swimming performance of adult seal lampreys in relation to weight and temperature. *Journal of the Fisheries Research Board of Canada* 30, 1376–1380.
- Damas H (1950). La ponte en aquarium des lamproies fluviatiles et de planer. *Ann. Soc. R. Zool. Belg.* 81, 151–162.
- Entec (2000a). *River Eamont acceptable drought order flow regime recommendation: suitability for British lamprey*. Environment Agency, Penrith.
- Entec (2000b). *Generically acceptable flows for British lamprey*. Environment Agency, Penrith.
- Farmer GF, Beamish FWH & Lett PF (1977). Influence of water temperature on the growth rate of the landlocked sea lamprey (*Petromyzon marinus*) and the associated rate of host mortality. *Journal of the Fisheries Research Board of Canada* 34, 1373–1378.
- Gardiner R, Taylor R & Armstrong J (1995). *Habitat assessment and survey of lamprey populations occurring in areas of conservation interest*. Scottish Natural Heritage, Edinburgh.
- Gardiner R and Stewart D (1997). Spawning habitat assessment and survey of lamprey populations occurring in areas of conservation interest. Scottish Natural Heritage, Edinburgh.
- Hanson LY, King EL, Howell JH & Smith AJ (1974). A culture method for sea lamprey larvae. *The Progressive Fish-Culturist* 36, 122–128.
- Hardisty MW (1969). Information on the growth of the ammocoete larvae of the anadromous sea lamprey, *Petromyzon marinus*, in British rivers. *Journal of Zoology* 159, 139–144.
- Hardisty MW (1969). A comparison of gonadal development in the development of the landlocked and anadromous forms of the sea lamprey, *Petromyzon marinus*. *Journal of Fish Biology* 1, 153–166.
- Hardisty MW (1986). Petromyzontiforma. In: Holcik J (ed). *The freshwater fishes of Europe*. Aula-Verlag, Wiesbaden.
- Hardisty MW & Potter IC (1971). *The biology of lampreys*. Academic Press, London.
- Haro A & Kynar B (1997). Video evaluation of passage efficiency of American shad and sea lamprey in a modified ice harbour fishway. *North American Journal of Fisheries Management* 17.
- Hill BJ & Potter IC (1970). Oxygen consumption in the ammocoetes of the lamprey *Icthyomyzon hubbsi*. *Journal of Experimental Biology* 53, 47–57.
- Holmes JA & Lin P (1994). Thermal niche of larval sea lamprey, *Petromyzon marinus*. *Canadian Journal of Fisheries and Aquatic Sciences* 51, 253–262.

- IUCN (1994). *IUCN Red List Categories*. International Union for the Conservation of Nature and Natural Resources, Gland, Switzerland.
- Lee DS (1989). Quantified laboratory assessment of larval substrate habitat selection. Great Lakes Fishery Commission Research Report, Ann Arbor.
- Lelek A (1973). Occurrence of the sea lamprey in midwater off Europe. *Copeia* 1, 136–137.
- Lennon RE (1954). Feeding mechanism of the sea lamprey and its effect on host fishes. *US Fish and Wildlife Service Fisheries Bulletin* 56, 247–293.
- Maitland PS (1980a). Review of the ecology of lampreys in northern Europe. *Canadian Journal of Fisheries and Aquatic Sciences* 37, 1944–1952.
- Maitland PS (1980b). Assessment of lamprey and fish stocks in the Great Lakes in relation to control of the sea lamprey, *Petromyzon marinus*: report from the SLIS Assessment Measurements Task Force. *Canadian Journal of Fisheries and Aquatic Sciences* 37, 2197–2201.
- Maitland PS (1993). *Sites in Great Britain for freshwater and estuarine fish on the EC Habitats and Species Directive*. Fish Conservation Centre Report to JNCC, Peterborough.
- Maitland PS (1995). *The ecological requirements of threatened and declining freshwater fish species in the United Kingdom*. Fish Conservation Centre Report to JNCC, Peterborough.
- Maitland PS (1997). *Species Action Plans for lampreys in England*. Fish Conservation Centre Report to English Nature, Peterborough.
- Maitland PS (2000a). *Guide to freshwater fish of Britain and Europe*. Hamlyn, London.
- Maitland PS (2000b). Fish. In: Ward SD (ed). Local Biodiversity Action Plans – technical information on species: IV. Vertebrate animals. *Scottish Natural Heritage Review* 10, 89–91.
- Maitland PS & Campbell RN (1992). *Freshwater fishes of the British Isles*. HarperCollins, London.
- Maitland PS & Lyle AA (2000). *Distribution of lampreys in the River Teith*. Report to Scottish Natural Heritage, Stirling.
- Maitland PS, Morris .H & East K (1994). The ecology of lampreys (*Petromyzonidae*) in the Loch Lomond area. *Hydrobiologia* 290, 105–120.
- Mallat J (1983). Laboratory growth of larval lampreys (*Lampetra (Entosphenus) tridentata* Richardson) at different food concentrations and animal densities. *Journal of Fish Biology* 22, 293–301.
- Manion PJ & Hanson LH (1980). Spawning behaviour and fecundity of lampreys from the upper three Great Lakes. *Canadian Journal of Fisheries and Aquatic Sciences* 37, 1635–1640.
- Manion PJ & McLain AL (1971). Biology of larval sea lampreys (*Petromyzon marinus*) of the 1960 year class, isolated in the Big Garlic River, Michigan, 1960–65. *Great Lakes Fishery Commission Technical Report* 16, 1–35.
- Manion PJ & Smith BR (1978). Biology of larval and metamorphosing sea lampreys, *Petromyzon marinus*, of the 1960 year class in the Big Garlic River, Michigan. Part II, 1966–72. *Great Lakes Fishery Commission Technical Report* 30, 1–35.
- McCauley RW (1963). Lethal temperatures of the developmental stages of the sea lamprey, *Petromyzon marinus* L. *Journal of the Fisheries Research Board of Canada* 20, 483–490.
- Meyer FP & Howell JH (1973). Biological studies on the sea lamprey, 1973. *Annual Report, Great Lakes Fisheries Commission* 1975, 61–75.
- Moore HH & Schleen LP (1980). Changes in spawning runs of sea lamprey (*Petromyzon marinus*) in selected streams of Lake Superior after chemical control. *Canadian Journal of Fisheries and Aquatic Sciences* 37, 1851–1860.
- Morman RH (1979). Distribution and ecology of lampreys in the Lower Peninsula of Michigan, 1957–75. *Great Lakes Fishery Commission Technical Report* 33, 1–59.

- Morman RH (1987). Relationship of density to growth and metamorphosis of caged larval sea lampreys, *Petromyzon marinus* Linnaeus, in Michigan streams. *Journal of Fish Biology* 30, 173–181.
- Morman RH, Cuddy DW & Rugen PC (1980). Factors influencing the distribution of sea lamprey (*Petromyzon marinus*) in the Great Lakes. *Canadian Journal of Fisheries and Aquatic Sciences* 37, 1811–1826.
- Newth HG (1930). The feeding of ammocoetes. *Nature* 126, 94–95.
- Potter IC (1970). The life cycles and ecology of Australian lampreys of the genus *Mordacia*. *Journal of Zoology* 161, 487–511.
- Potter IC (1980). Ecology of larval and metamorphosing lampreys. *Canadian Journal of Fisheries and Aquatic Sciences* 37, 1641–1657.
- Potter IC, Hill BJ & Gentleman S (1970). Survival and behaviour of ammocoetes at low oxygen tensions. *Journal of Experimental Biology* 53, 59–73.
- Potter IC, Hilliard RW, Bradley JS & McKay RJ (1986). The influence of environmental variables on the density of larval lampreys in different seasons. *Oecologia* 70, 433–440.
- Reynolds WW & Casterlin ME (1978). Behavioural thermoregulation by ammocoete larvae of the sea lamprey (*Petromyzon marinus*) in an electronic shuttlebox. *Hydrobiologia* 61, 145–147.
- Schoonoord MP & Maitland PS (1983). Some methods of marking larval lampreys (Petromyzonidae). *Fisheries Management* 14, 33–38.
- Smith BR (1971). Sea lampreys in the Great Lakes of North America. In: Hardisty MW & Potter IC (eds) *The biology of lampreys*. Academic Press, London, 207–247.
- Smith BR & McLain AL (1962). Estimation of the brook and sea lamprey ammocete populations of three streams. *Great Lakes Fishery Commission Technical Report* 4, 1–26.
- Stauffer TM (1962). Duration of larval life of sea lampreys in Carp Lake River, Michigan. *Transactions of the American Fisheries Society* 91, 422–423.
- Stauffer TM & Hansen MJ (1958). Distribution of sea lamprey ammocoetes in Michigan tributaries of Lake Superior. 1954–57. *Michigan Department of Conservation, Institute of Fisheries Research Miscellaneous Publication*, 11, 1–25.
- Stuart TA (1953). Spawning migration, reproduction and young stages of loch trout (*Salmo trutta* L.). HMSO, Edinburgh.
- Sutton TM & Bowen SH (1994). Significance of organic detritus in the diet of larval lamprey in the Great Lakes basin. *Canadian Journal of Fisheries and Aquatic Sciences* 51, 2380–2387.
- Teeter J (1980). Pheromone communication in sea lampreys (*Petromyzon marinus*): implications for population management. *Canadian Journal of Fisheries and Aquatic Sciences* 37, 2123–2132.
- Thomas MLH (1962). *Observations on the ecology of ammocoetes of Petromyzon marinus L. and Entosphenus lamottenii (Le Sueur), in the Great Lakes watershed*. Unpublished MSc Thesis, University of Toronto.
- Whilde A (1993). *Threatened mammals, birds, amphibians and fish in Ireland: Irish Red Data Book 2: Vertebrates*. HMSO, Belfast.
- Wigley RL (1959). Life history of the sea lamprey of Cayuga Lake, New York. *US Fish and Wildlife Service Fisheries Bulletin* 59, 559–617.
- Wilson FH (1955). Lampreys in the Lake Champlain basin. *American Midland Naturalist* 54, 163–172.
- Young RJ, Houston KA, Weisse JG & Kelso JRM (1990). The effect of environmental variables on the population dynamics of sea lamprey (*P. marinus*). *Canadian Technical Report, Fisheries and Aquatic Sciences* 1736, I–VI.

General References

- Eneqvist P (1937). Das bachneunauge als okologische modification des Flussneunauges. Über die Flussneunaugen und Bachneunaugen Schwedens. *Arkiv for Zoologi*. 20, 1–22.
- Maitland PS & Campbell RN (1992). *Freshwater fishes of the British Isles*. Harper Collins, London.
- Potter IC (1980). The Petromyzoniformes, with particular reference to paired species. *Canadian Journal of Fisheries and Aquatic Sciences* 37, 1595–1615.
- Privolnyev TI (1964). Ecological and physiological features of the larval river lamprey, *Lampetra fluviatilis* (L.). *Izv. uses. nauchno-issled Inst. ozern. rechn. ryb. Khoz.* 58, 180–185.
- Vladkov VD & Kott E (1979). Satellite species among the holarctic lampreys (Petromyzonidae). *Canadian Journal of Zoology* 57, 860–867.
- Zanandrea G (1959). Speciation among lampreys. *Nature* 184, 380.

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