A REVIEW OF THE ECOLOGY AND DISTRIBUTION OF THREE LAMPREY SPECIES, *LAMPETRA FLUVIATILIS* (*L.*), *LAMPETRA PLANERI* (BLOCH) AND *PETROMYZON MARINUS* (*L.*): A CONTEXT FOR CONSERVATION AND BIODIVERSITY CONSIDERATIONS IN IRELAND

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ABSTRACT

Lampreys are distinguished from other fish by their eel-like bodies, round sucker-like mouths, poorly developed fins and by a row of seven breathing holes instead of gills. Most species have a life cycle of several years' duration, involving an adult parasitic feeding phase, an upstream spawning migration of adults and a gradual downstream movement of juvenile stages to silt beds, where they burrow. Following metamorphosis, the young adult lampreys migrate downstream.

The three species of lamprey recorded in Ireland are designated in the European Union (EU) Habitats Directive as species requiring conservation within member states. However, the scientific database available to assess the distribution, status, habitat use and conservation requirements of these species in Ireland is very limited and is largely composed of records of known spawning locations, with little by way of a literature on aspects of ecology.

This paper provides a context for conservation management and biodiversity considerations with regard to these species in Ireland. It reviews an extensive European and North American literature to provide a detailed and comparative account of lamprey ecology, particularly those riverine stages most likely to be affected by human activity, and points to those areas in which more information is required to form a basis for decision-making with regard to conservation requirements for these species in Ireland.

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INTRODUCTION

Lampreys (Family: Petromyzonidae, 'stone suckers') belong to a group of primitive vertebrates, the Agnatha or 'jawless fish' (Maitland and Campbell 1992). This group is characterised by the absence of both jaws and pelvic fins, while the pectoral fins, if present, lack dermal rays (Hubbs and Potter 1971). Lampreys are distinguished from other fish by their eel-like bodies, round sucker-like mouths and very poorly developed fins, by the absence of scales and by a row of seven breathing holes instead of gills (Phillips and Rix 1985). They have no bones, all the skeletal structures being made of strong, flexible cartilage. There is only one nostril, situated on top of the head, anterior to the eyes. A round sucker-like disc surrounds the mouth, within which, in the adults, are strong rasping teeth. These vary in shape, size, position and number among the species.

The majority of lamprey species have a similar life cycle (Fig. 1), which involves the migration of adults upstream into rivers to reach the spawning areas, where they spawn in pairs or groups, laying eggs in crude nests or shallow depressions in alluvial material. After hatching, the young larvae swim or are carried downstream by the current to areas of fine sediment in still water, where they burrow. Metamorphosis from larva to adult takes place over several months, after some years of larval development. The young adult lampreys then migrate downstream away from the larval habitats. Most species of lamprey are parasitic as adults on various species of marine and anadromous fish. On completion of the feeding phase, the adult lampreys migrate upstream to spawning

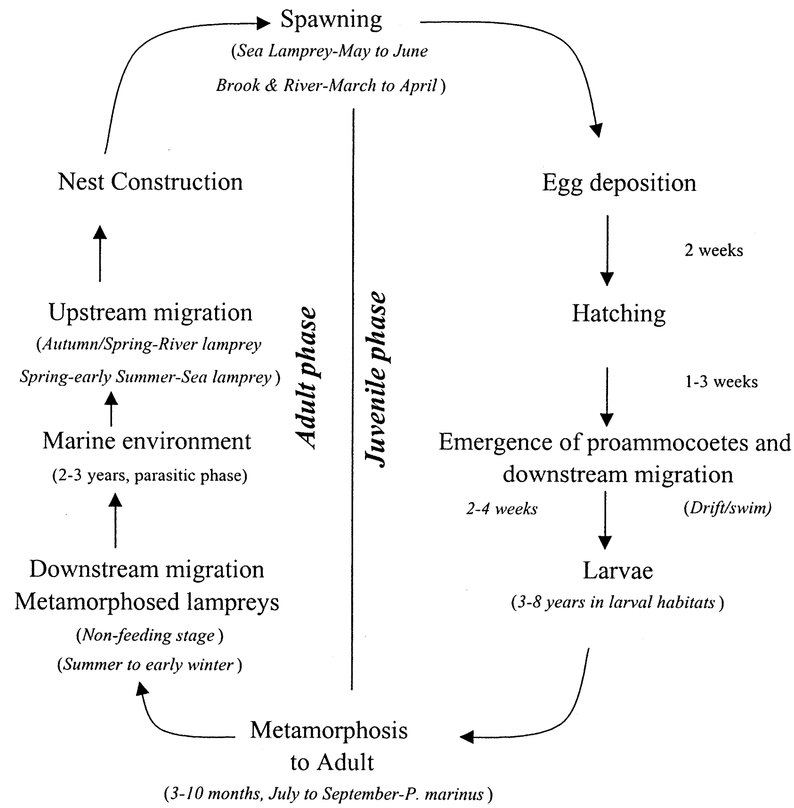

Fig. 1—General life cycle of anadromous lampreys.

streams. All lampreys show considerable development of secondary sexual features: the females have a crescent-shaped extra 'anal fin', the males have a penis, and both sexes show a definite thickening of the anterior edge of the second dorsal fin at spawning time. However, the thickening in females is less distinct than in males (Gibson 1953). The spent adults of the species recorded in Europe die after spawning (Maitland and Campbell 1992).

Lampreys occur in the temperate zones of both the northern and southern hemispheres (Maitland 1992). Their success as a group is attributed to the protracted freshwater stage, during which the larval form lies concealed in the silt deposits of rivers and streams for several years (Hardisty and Potter 1971b). There are 39 recognised lamprey species (Potter 1980a), of which three are present in Ireland: brook lamprey (*Lampetra planeri* (Bloch)), river lamprey (*Lampetra fluviatilis* (L.)) and sea lamprey (*Petromyzon marinus* L.) (Maitland 1980a).

The brook lamprey (*L. planeri*) is the smallest of the three lampreys native to Ireland, and the adults range in size from 150mm to 200mm. It is the only one of the three species that is non-parasitic and spends all its life in freshwater (Maitland and Campbell 1992). Its two dorsal fins are continuous, whereas in the sea lamprey and the river lamprey the two fins are distinctly separated (Phillips and Rix 1985). There are also small differences in the mouth structure of the three species (Potter 1980a; Maitland and Campbell 1992). The river lamprey (*L. fluviatilis*) is larger than the brook lamprey, the adults being 200–500mm long. Uncertainty about the relationship between the brook and river lamprey has led to the term 'paired' or 'satellite' species (Johns and Gibson 1998; Potter 1980a; Zanandrea 1959). It is generally assumed that *L. planeri* evolved from an ancestral parasitic form (*L. fluviatilis*) and became non-parasitic (Hubbs and Potter 1971; Malmqvist 1978). Glaciation may have promoted evolution of non-parasitic species by blocking migratory routes and preventing anadromy (Bell and Andrews 1997). Although the two forms have been seen at the same spawning sites, they have not been observed breeding together in such situations (Potter 1980a). This may be due to the rapid post-metamorphic growth of the river anadromous lamprey, which results in a large difference in size between the adults of the two forms (Bell and Andrews 1997). The brook and river lamprey do not differ notably in chromosome number or in nuclear DNA contents (Schreiber and Engelhorn 1998). For the purposes of this review, the two forms are treated separately because their management requirements differ greatly.

The sea lamprey (*P. marinus*) is the largest of the three species in Irish waters, with adults ranging from 600mm to 900mm in length. It is yellowish green, mottled with black or brown on the back. There are about 100 teeth, arranged in radiating rows all round the disk—those on the upper side being large and often paired (Maitland and Campbell 1992).

A literature search by the present authors yielded almost 600 published responses between 1980 and 2000. Of this total, more than 60 per cent dealt with biochemical, physiological and neurological aspects of the lamprey, particularly of the nervous system. There was a marked difference in emphasis between North American and European work dealing with aspects of distribution and ecology. The American material focused strongly on management aspects of the landlocked species in the North American Great Lakes, including field and laboratory studies of aspects of the life cycle of *P. marinus* and strategies to control this species. The European references dealt primarily with aspects of distribution, factors affecting the European species and conservation requirements to augment the status of the species.

The review by Maitland (1980a) was important in compiling a baseline reference source on the ecology of four lamprey species found in Europe. The Habitats Directive of the European Union (CEC 1992) lists five species of lamprey (Petromyzoniformes) and identifies the need for special conservation measures to be taken in member states of the union to protect these species. The present paper builds on and updates the review by Maitland (1980a) and reviews an extensive literature on three of the lamprey species listed in the EU Habitats Directive and recorded in the Republic of Ireland. The intention is to provide a detailed and comparative account of the ecology of these species, particularly of those riverine stages most likely to be adversely affected by anthropogenic factors, and of the various environmental requirements of different life-cycle stages, placed in the broad context of European and North American research carried out on these species. As such, this paper provides a context for biodiversity considerations with regard to these species and outlines requirements for their conservation in Ireland.

DISTRIBUTION

Lampreys have an antitropical distribution, restricting them to cooler regions of the world (Hubbs and Potter 1971; Potter 1980a). They are found to the north and south of the 20°C annual ocean isotherm in the Northern and Southern hemispheres, respectively. In general, the species that attain the largest body size have the widest distribution (Potter 1980a). The distribution of lampreys within river systems is a result of two behavioural characteristics (Hardisty and Potter 1971b): the upstream spawning movement of the adult, dependent on its rheotactic response and the passive downstream migration of the larvae throughout the larval period, determined by the burrowing habit of the larvae and by local hydrographical conditions (Hardisty and Potter 1971b). The upstream migration into the higher reaches of a catchment allows the adults to find suitable conditions for spawning, and enables the subsequent slow but continuous downstream drift of the larvae into the slower currents and more silted bottoms of the middle and lower reaches, where conditions are conducive to the feeding and burrowing activities of the larvae.

In the British Isles, all three species may sometimes be found at the same sites (Hardisty and Potter 1971a). The Loch Lomond area is of particular significance in this regard because it also has a landlocked population of the river lamprey, *L. fluviatilis* (Maitland *et al.* 1994). Samples from British rivers in which all three species occur generally show a far higher proportion of the larvae of brook lamprey compared with those of the anadromous *P. marinus* and *L. fluviatilis*. However, there is usually some degree of ecological separation, as the brook lamprey tends to occur alone in the higher reaches, although 'flushing' downstream ensures that it will also be distributed into the lower reaches of the river where the parasitic species are likely to predominate (Maitland and Campbell 1992).

IRISH RECORDS

While all three species co-occur and spawn in a number of Irish waters (Table 1) (Kurz and Costello 1999), the status of the three species in Ireland as a whole has been recorded as indeterminate (Whilde 1993), largely due to the very limited records in the scientific literature. The desk study by Kurz and Costello (1999) is valuable in gathering information on locations where lamprey species have recently (1960–95) been encountered on the basis of river catchments and hydrometric regions, and in identifying shortfalls in our current knowledge base. The 40 hydrometric areas in the island of Ireland (Fig. 2), lampreys are listed as unspecified or to species level in 27, and no records are provided for the hydrometric areas within Northern Ireland. The 9 hydrometric areas in the Republic with no records listed by Kurz and Costello (1999) are all coastal areas with short rivers that discharge to the sea without large estuarine areas. These channels would have higher channel gradients relative to many of the country's longer rivers or to rivers discharging to the river Shannon in the centre of the country. However, it is possible that lampreys occur in these areas and have simply not been reported. Much of the material reported comes from fisheries management studies or from water-quality assessment using benthic kick sampling methods, the latter yielding abundant larval material. Many of the observations compiled by Kurz and Costello (1999) refer to 'unspecified lampreys' or to larvae that could not be identified to species level. Although many such records are likely to refer to the small brook lamprey, it is certain that the genuine difficulty of correctly allocating material (particularly the larval material) to particular species in the field does not encourage an increased interest among those encountering these species.

The National Museum of Ireland, Natural History Division, is also a source of material for Ireland, housing preserved specimens of all three species, many dating from the nineteenth century. Despite the limited extent of the material (14 of *L. fluviatilis*, 4 of *L. planeri* and 26 of *P. marinus*), some of the records are of interest in the context of subsequent erection of barriers to river migration, pollution of rivers and parasitic feeding in both fresh- and seawater. Thus, whereas Kurz and Costello (1999) report *L. planeri* as the only recent lamprey record from both the river Liffey and its tributary the river Dodder in the environs of Dublin city, the National Museum records *L. fluviatilis* from both channels (in 1899 and 1889, respectively) and has two records of similar vintage for *P. marinus* in the river Liffey in Dublin (M. Holmes, pers. comm.).

A limited number of non-migratory sea lampreys were positively identified from Irish freshwaters in the late 1950s and early 1960s by Dr Michael Kennedy, at that time Director of the Inland Fisheries Trust (now the Central Fisheries Board).

The samples were provided by anglers concerned about any potential threat to wild trout and salmon angling. The number of confirmed samples was small, and no evidence exists that lamprey parasitism or competition poses a significant problem in the conservation of Irish salmonid fisheries (Kennedy 1960). The lampreys were reported in Lough Conn, Lough Corrib and two large reservoirs on the river Lee between 1959 and 1965. However, the specimens from the river Lee reservoirs may have represented a temporary phase following the construction of the reservoirs in 1957 (Inland Fisheries Trust unpublished data 1952–68). Anglers regularly report scarring of trout and other fish such as pike by lampreys on Lough Derg, but few specimens have been presented for confirmation (ESB 1998).

DISTRIBUTION OF THE RIVER LAMPREY (*L. FLUVIATILIS*)

L. fluviatilis is restricted to European watersheds (Hubbs and Potter 1971), where its range extends from southern Norway to the western Mediterranean. It has also been reported from Turkey (Erguven 1989). The species is mainly anadromous, but landlocked populations have been reported from Finland (Tuunainen *et al.* 1980), Lake Ladoga in the Baltic drainage (Hubbs and Potter 1971) and Loch Lomond (Maitland 1980a). The Loch Lomond population feeds in freshwater on the endemic powan and brown trout (Giles 1994). In Sweden the river lamprey occurs along the entire coast, although it is common only in the northern coastal regions (Sjöberg 1980). *L. fluviatilis* is also common along the coast of Finland but landlocked populations have also been reported (Tuunainen *et al.* 1980). Comparison of *L. fluviatilis* populations in the eastern Baltic Sea indicated a gradient of increasing size and weight moving southward from Finland through Latvia and Lithuania, with the largest specimens being found in Poland (Bartel *et al.* 1993). The distribution of river lampreys is sparse in Germany, and the species is threatened with extinction in Bavaria (Bohl 1995a; 1995b). In Estonia river lampreys are widespread and are exploited commercially (Saat *et al.* 2000). Little is known about the distribution of lampreys in Slovenia, as most information is anecdotal (Povz and Šumer 2000). The river lamprey is distinctly rare but scattered in the United Kingdom (Maitland 1980a). Its numbers have been reduced by pollution of estuaries and by weirs. It is still common on the rivers Dee and Clwyd in north Wales. In Northern Ireland it has been recorded in Lough Neagh (Winfield *et al.* 1989). The river

Table 1—List of Irish locations for the three species of lamprey (*Lampetra planeri*, *Lampetra fluviatilis* and *Petromyzon marinus*) after Kurz and Costello (1999) and Byrne *et al.* (2001). Unspecified lamprey records are not included. See Fig. 2 for location of hydrometric regions.

Hydrometric region	*River/catchment*	*Lampetra planeri (brook lamprey)*	*Lampetra fluviatilis (river lamprey)*	*Petromyzon marinus (sea lamprey)*
7	R. Boyne (Lough Bane)	⋆		
9	R. Liffey (incl. R. Dodder)	⋆		
10	R. Aughrim		⋆	
12	R. Slaney	⋆	⋆	⋆
14	R. Barrow	⋆	⋆	⋆
15	Nore catchment	⋆	⋆	
16	R. Suir	⋆	⋆	⋆
17	R. Foyle			⋆
18	Munster Blackwater	⋆	⋆	⋆
19	R. Lee	⋆		⋆
22	Killarney National Park	⋆	⋆	⋆
25	R. Shannon (lower)	⋆	⋆	⋆
26	R. Shannon (upper)	⋆		⋆
27	R. Fergus			⋆
29/30	Lough Corrib catchment	⋆		⋆
34	Moy catchment			⋆
35	Lough Arrow catchment	⋆		
35	Lough Gill catchment	⋆	⋆	⋆
36	Erne catchment			⋆

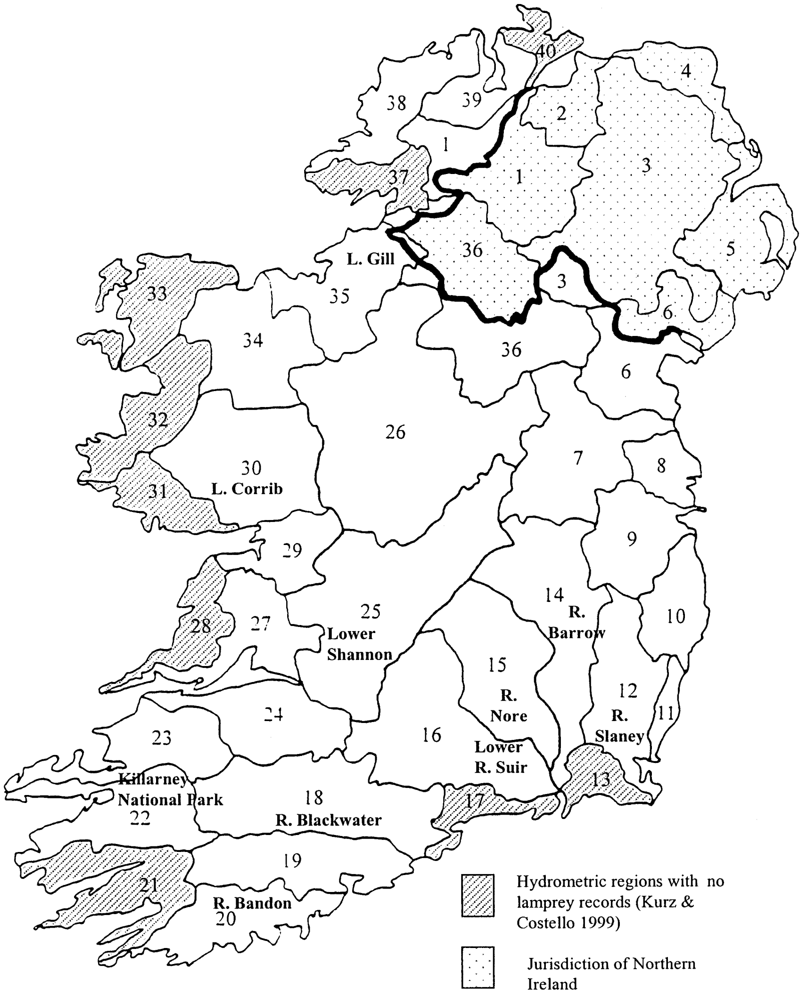

Fig. 2—Hydrometric regions of Ireland. Shaded areas indicate absence of lamprey records. No records in Kurz and Costello (1999) for Northern Ireland. Locations named are proposed candidate Special Areas of Conservation (SACs).

lamprey has been less widely reported from Irish rivers (Table 1) than either the sea or brook lamprey (Kurz and Costello 1999).

DISTRIBUTION OF THE BROOK LAMPREY (*L. PLANERI*)

Lampetra planeri is a non-parasitic derivative of *L. fluviatilis* and occupies the same geographical range (Hubbs and Potter 1971). It is a purely freshwater form occurring in streams and occasionally in lakes in north-west Europe, especially in basins associated with the North and Baltic Seas (Maitland 1980a). It has also been recorded from Western tributaries of the river Danube (Kappus and Rahmann 1995a; 1995b), where its presence may be explained by the ancient interconnections between river basins in Central Europe (Holcik 1995). The brook lamprey is widely distributed in freshwater in Finland (Tuunainen *et al.* 1980) and in Estonia (Saat *et al.* 2000). In coastal rivers of Brittany, it has been reported as occupying areas of cover provided by in-stream aquatic plants close to the bank in the presence of fine sediments (Haury and Baglinière 1996). It is the most abundant and widespread of the three species present in Britain and is often found in the absence of the other two species (Hardisty and Potter 1971b). It is common in many river catchments in Ireland (Table 1), as summarised by Kurz and Costello (1999), and its distribution has recently been examined in the Lough Corrib catchment (Byrne *et al.* 2001).

DISTRIBUTION OF THE SEA LAMPREY (*P. MARINUS*)

Petromyzon marinus is anadromous and occurs in estuaries and easily accessible rivers in Atlantic drainages of North America from a northern latitude of 53° off the coast of Labrador to as far south as Florida, at a latitude of 30°. In Europe it is distributed as far north as Varanger Fjord in Norway (70°N) and as far south as the western Mediterranean (Hubbs and Potter 1971; Beamish 1980). It has recently been documented from the Aegean Sea by Economidis *et al.* (1999), which represents the first report from the eastern Mediterranean. Sea lampreys occur in highest densities at latitudes between 35° and 45°. The vertical depth range inhabited by sea lampreys is among the greatest exhibited by marine animals, with reports of findings down to 985m (Beamish 1980) and 4099m (Haedrich 1977). There are several landlocked populations in North America, but none are reported for Europe. Reports of sea lampreys off the Finnish coast are rare, most of the captures being on the southern coast and only a few in rivers (Tuunainen *et al.* 1980). They are a commercially important species in Spain and Portugal (Maitland and Campbell 1992). Sea lampreys are reasonably widespread in UK rivers (Brown *et al.* 1997) and in Ireland (Kurz and Costello 1999), where they ascend many of the larger rivers on the south coast.

BIOLOGY OF LARVAE

In general appearance, lampreys are worm-like when they hatch and are so different from the parents that they were formerly called *Ammocoetes branchialis* (Hardisty and Potter 1971b). The eyes lie below the skin surface and are barely visible externally. On the dorsal surface of the head is a transparent patch of skin, the pineal spot, below which is the pineal organ, a structure concerned with a daily rhythm of colour change. The fins are not well developed, consisting of a low, continuous and partially notched dorsal fold that begins in the trunk region and extends around the tail as a caudal fin. An oral hood overhanging the mouth forms the blunt anterior end (Hardisty and Potter 1971b).

Larvae of different species have overlapping size ranges. The taxonomic discrimination of species is therefore more problematic in the larval stages than in the adult stages (Hardisty and Potter 1971b). The larvae of sea lamprey differ from those of brook lamprey in myotome numbers, pigment distribution and fin structure. The most obvious diagnostic feature is the shape of the tail. The sea lamprey has a blunter and more rounded extremity and has pigment extending from the tip of the body axis to the fin margin (Vladykov 1960).

DOWNSTREAM MIGRATION

Hatching occurs two weeks after egg deposition. Within a further one to three weeks, the larvae emerge from the spawning substrate and pass downstream, where they burrow into silt beds in sheltered areas. They take on the definitive larval form approximately five weeks after hatching, at which time they occupy habitats where the substrate is composed of fine particles. Later in larval life (macrophthalmia stage), they migrate further downstream to areas where the average particle size is greater (Potter 1980b).

The initial migration from the spawning site appears to be a result of a mass emergence from the nest substrate caused by sudden changes in the larvae at the critical stage of yolk absorption (Applegate 1950). The subsequent distribution of the larvae within the channel depends on the gradient and flow characteristics of the river (Potter 1980b). The downstream movement of larvae is seasonal, temperature-dependent and mainly nocturnal. In rivers with a shallow longitudinal profile, where the flow is more limited, comparatively little further downstream movement may occur, beyond the initial annual redistribution of the young. On the other hand, where the stream has a high or logarithmic profile and average gradients tend to be greater, there is often a marked gradation in the proportions of larvae of different size groups according to the distance below the spawning areas, with the older larvae becoming increasingly predominant in the downstream regions (Hardisty and Potter 1980). Passive migration during flooding is also a major factor in the redistribution of larvae. Conversely, the movement of larvae can also be produced by a reduction in water levels during periods of low rainfall (Hardisty and Potter 1971b). The various patterns of movement are believed to enable the animals to disperse within a river system and colonise favourable new habitats (Potter 1980b).

THE BURROWING HABIT

The burrowing process is initiated by whip-like contractions of the tail, forcing the head vertically downwards into the substrate until the branchial region is covered, after which the tail is laid horizontally over the bed surface. The body is pulled into the substrate by muscular contraction, with the flared-out oral hood acting as an anchor. Once buried, the body is arched in order to bring the snout towards the bed surface (Hardisty and Potter 1971b).

In shallow, clear and slow-flowing water, the location of larval burrows may be detected by funnel-shaped depressions on the mud surface. The mouth is normally directed towards the current. Although they seldom leave the burrows, the larvae have been seen to change position frequently. Mechanical disturbance or changes in light intensity normally cause them to move deeper into their burrows. Depth of the burrow is related to the size of the larva, varying from less than 12mm for 20mm-long larvae to 150mm for larvae more than 100mm long (Hardisty and Potter 1971b).

LARVAL HABITATS

Larval burrows are characteristically found at eddies or backwaters, on the inside of bends or behind obstructions, where current velocity is below that of the main stream and where organic material tends to accumulate (Hardisty and Potter 1971b). These areas, which are often partially shaded, are favourable for the growth of diatoms. Studies on larvae of the Australian species *Geotria australis* showed that larval density increased with shade and with increases in organic material and unicellular algae in the sediments (Potter *et al.* 1986). Applegate (1950) observed that the largest concentrations of larvae in a given bed were among small patches of aquatic plants. Larvae are rarely found in stagnant or highly eutrophic waters. It has been suggested that heavy siltation and slow currents are unfavourable for larval lampreys (Morman *et al.* 1980). According to Morman *et al.* (1980), larvae inhabit water depths up to 2.2m in streams and 16m in lakes for landlocked species. Larger larvae are more commonly found in deep water.

Physical variables recorded in a range of studies at larval sites are summarised in Table 2. Malmqvist (1978) emphasised the importance of particle size, low current velocities and water depth for *L. planeri* larvae in a Swedish stream. There is general agreement on the role of particle diameter and the importance of fine sediments, including sand, silt and clay (Hardisty 1944; Manion and McLain 1971; Kainua and Valtonen 1980; Maitland 1980a; Potter 1980b; Almeida and

Quintella 2000). All of these authors refer to the importance of an organic component in the bed material. Stream gradient determines the overall velocity of the current, the type of substrate particles that are deposited and the accumulation of organic debris (Hardisty and Potter 1971a). In British streams, brook lamprey larvae occurred where the average stream gradients were 0.19–0.57% but were rarely found where gradients exceeded 0.78% (Maitland 1980a). Kainua and Valtonen (1980) found that the gradient in areas (Bothnian Bay, Finland) mainly occupied by lamprey larvae was 1–2%. However, these specifications do not define the precise location of ammocoete habitats, which may be regarded as microenvironments protected from all but the most catastrophic changes in water levels and current flow (Hardisty and Potter 1971b).

Schroll (1959) has stated that the flow rate over larval burrows of *L. planeri* is remarkably constant, with average values of 0.5m s^{-1} at the water surface and 0.4m s^{-1} at a depth of 0.25m. Thomas (1962) concluded that flow rates of 0.6–0.8m s^{-1} represented an upper limit for larvae of *P. marinus*. On the other hand, the mean water velocity over areas of high larval concentration was considerably lower, no more than 0.03m s^{-1}. In Finland, water velocities ranged from 0.01–0.05m s^{-1} to about 0.5m s^{-1}, with small larvae being proportionally more numerous in habitats where the flow was rapid. Where larvae were found in shallow water, the rate of flow was almost constantly below 0.1m s^{-1} (Kainua and Valtonen 1980).

FEEDING OF LARVAL LAMPREYS

Larval lampreys are filter feeders, creating a current that draws organic particles into the pharynx, where they are trapped in mucus (Mallatt 1981). Although most of their food is suspended material, the constant shifting of sediments and movement of larvae indicate that benthic organisms may also be consumed (Moore and Mallatt 1980). Evidence suggests that larvae are not selective feeders (Beamish 1980). Algae such as diatoms and desmids, as well as detritus, are frequently eaten by larvae, whereas protozoans, nematodes and rotifers are occasionally found among the gut contents. Algae, primarily diatoms, were the organisms most frequently found in the intestinal tract of larval anadromous sea lampreys by Moore and Beamish (1973), whereas Sutton and Bowen (1994) found that organic detritus made up 97% of the diet in larval sea lamprey in the Great Lakes basin, the remainder being composed of algae and bacteria.

DURATION OF LARVAL LIFE AND GROWTH RATES

L. fluviatilis has a relatively short larval life of 4.5 years in comparison to *L. planeri*, which has an estimated larval life of 6.5 years in the United Kingdom (Hardisty 1961b) and 5–9 years in Sweden (Malmqvist 1978). However, there are large differences in growth rate because of local variation, nutritional factors, stability of larval beds and the degree to which the population is subjected to washing-out during periods of heavy rainfall (Hardisty 1944). The duration of larval life in sea lampreys has been estimated to be at least 5–6 years in English streams (Hardisty 1961b; Potter 1980b), 5 years in Scotland (MacDonald 1959) and 6–8 years in North America (Beamish 1980). Malmqvist (1978) also found that the duration of larval life varies within populations. Metamorpho-

Table 2—Physical features recorded in locations of juveniles of *L. fluviatilis*, *L. planeri* and *P. marinus*.

Species	*Substrate size (mm)*	*Velocity on ammocoete beds (m s^{-1})*	*Gradient (%)*	*Source*	*Location*
L. fluviatilis	1.8–3.8	0.01–0.5	0.3–0.9	Potter 1980a; 1980b	UK
	0.5–2.0	0.01–0.05 to 0.5	1.0–2.0	Kainua and Valtonen 1980	Finland
L. planeri	1.8–3.8	—	0.19–0.57	Hardisty 1961b	UK
	—	0.3–0.5 (surface)	0.3–0.9	Maitland 1980a	UK
	—	0.5 (surface) 0.4 (depth = 0.25m)	—	Schroll 1959	Germany
P. marinus	1.8–3.8	—	—	Maitland 1980a	UK
	90% <5.0	—	—	Manion and McLain 1971	USA
	—	0.6–0.8 (upper limit) 0.3 (mean)	—	Thomas 1962	USA

sis has been shown to take place in larvae as young as 2 years in one highly productive channel in Michigan (Morkert *et al.* 1998).

LARVAL MORTALITY

Assessments of mortality rates for larvae suggest that these are probably uniform and comparatively low throughout the greater part of larval life (Okkelberg 1922; Hardisty 1961a). However, mortality at the beginning of larval life may be high owing to predation by various teleosts, including *Phoxinus* spp (minnow), *Anguilla* spp (eels), *Artediellus* spp (sculpins), *Perca* spp (perch) and *Cottus* spp (bullheads) (Hardisty 1961a; 1961b; Heard 1966; Manion 1968; Tuunainen *et al.* 1980). A diving beetle (*Dysticus* sp.) was found to be the only predator of sea lamprey larvae detected in a study in the Big Garlic River, United States of America (Potter 1980a). Mortality may also be high in the period immediately after the larvae leave their nests (Potter 1980b). Hardisty (1961b) has suggested that mortality is relatively low and uniform during the rest of larval life. A significant factor in reducing the effects of predation is the fact that the larvae spend most of their time burrowed. Larval density on the stream bed may be an important factor in determining survival to metamorphosis (Manion and Smith 1978; Malmqvist 1983b). Using experimental cages in a natural stream, Morman (1987) found that 92–6% of larval sea lampreys from low-density groups survived to age 5, as opposed to 52–68% of larvae from high-density groups. Another vulnerable stage in the life cycle may be the period of metamorphosis, when locomotory ability is low (Hardisty and Potter 1971a).

It has been suggested by McLain (1952) that parasites do not play an important role in the mortality of *P. marinus* larvae, although nematodes do occur in a small proportion of ammocoetes. Larvae of *L. planeri* were found to serve as natural obligate intermediate hosts to the nematode *Cucullanus truttae* in a trout stream in Czechoslovakia (Moravec 1980). Malmqvist and Moravec (1978) recorded an infestation level of 89% by larvae of the nematomorph *Gordius aquaticus* L. in larvae of *L. planeri* and *L. fluviatilis* in a Swedish river.

ADULT PHASE

METAMORPHOSIS

After a period of 3–8 years in freshwater, depending on species and location, the larva undergoes a metamorphosis into a sexually mature non-feeding stage known as the macrophthalmia. In contrast to the larva, this is an active, large-eyed, silvery form, which moves to stonier areas of the channel to avoid silt damage to the gills. At this stage, the macrophthalmia has the ability to osmoregulate (Pickering 1993).

Lamprey metamorphosis is a highly programmed and synchronised event (Bird and Potter 1979a; 1979b; Youson 1980), and its duration is extremely variable, extending from 3 to 10 months (Hardisty and Potter 1971a). The age at which metamorphosis is initiated is related to both the size and growth rate of the animal. Metamorphosis can be divided into seven stages in *P. marinus* (Potter *et al.* 1978; Youson and Potter 1979—see Table 3), whereas nine stages have been described for *L. planeri* and *L. fluviatilis* (Bird and Potter 1979a; 1979b). In most species, transformation generally begins during the summer months (Hubbs 1925; Applegate 1950; Hardisty 1961a; Youson 1980). In Ireland, Byrne *et al.* (2001) reported capturing transforming ammocoetes only during the August–September period in a survey of channels in the Lough Corrib catchment (Fig. 2: hydrometric region 30), whereas the present authors captured fully developed macrophthalmia of *L. fluviatilis* in mid-September in the lower river Suir (Fig. 2: hydrometric region 16). The main external changes associated with metamorphosis are initiated from mid-July to September (Hardisty *et al.* 1970; Hardisty and Potter 1971a), and onset may be associated with a change in water temperature and a marked change in day length found in the spring/summer months immediately prior to transformation (Potter 1980b). Youson (1997) reported that sea lamprey metamorphosis was initiated when body size, condition factor and lipid stores reached appropriate levels and that it coincided with a post-winter rise in water temperature. Youson also considered that metamorphosis in the sea lamprey was facultative, in that it was initiated or inhibited by a combination of environmental, metabolic and hormonal cues, a view shared by Purvis (1980), who found that metamorphosis may begin at age III in fast-growing populations and not until age VII in slow-growing populations. Manion and Smith (1978) found that metamorphosis of a single year class in *P. marinus* occurred over a considerable number of years. The development of sexual maturity is accompanied by a decrease in weight and length (Hardisty 1961b). Initial external alterations include small changes in the appearance of the eye and a slight enlargement of the 'lips' of the oral hood (Youson and Potter 1979).

DOWNSTREAM (FEEDING) MIGRATION

The downstream migration of metamorphosed animals is nocturnal and is influenced by a marked increase in freshwater discharge (Potter 1980b). According to Hardisty and Potter (1971a), the downstream movement of landlocked sea lampreys begins in late October or early November and continues throughout the winter until the following April. Downstream migration in the anadromous form occurs earlier. In France it was reported that the downstream movement to the sea was restricted to December and early January (Léger 1920). Observations on the Atlantic coastal rivers of North America have shown that downstream movement of sea lampreys in this region takes place in late autumn and early winter (Davis 1967). In at least some rivers, a portion of the young adults of *P. marinus* overwinter in the natal stream without feeding. Whether they migrate in the autumn or wait until the following spring appears to depend on whether the environmental stimuli, such as increased discharge, are strong enough in October/November, before the water temperature decreases. It also depends on the completion of metamorphosis, which renders the animal susceptible to the influence of the environmental stimulus for downstream migration (Youson and Potter 1979).

Spring flooding may also be responsible for a high degree of synchrony. In Siberian rivers, the downstream movement is restricted to the period from late May to July, reaching a peak in the first half of June (Hardisty and Potter 1971a). The downstream movement of *L. fluviatilis* takes place between late winter and early summer (Hardisty *et al.* 1970).

During daylight the macrophthalmia either burrow or move into protected areas that provide cover. Hardisty and Potter (1971a) considered that feeding does not appear to take place in rivers during downstream migration. However, Bird *et al.* (1994) reported capturing a large sample of recently metamorphosed sea lampreys in the river Severn in late November during heavy freshwater discharges. Given the size and morphology of the fish, and the time of capture, Bird *et al.* (1994) concluded that these fish had been feeding for several weeks. Feeding during the downstream descent may explain the reports of small *P. marinus* attaching themselves to trout in Lough Conn and Lough Corrib in the west of Ireland (Hardisty and Potter 1971a).

FEEDING ECOLOGY OF ANADROMOUS LAMPREYS

The marine interval (parasitic phase) of sea lampreys is reported to last from 18 to 28 months (Farmer 1980). They are known to attack a variety of marine fish (Table 4). Salmon are prone to attack, particularly when congregating in inshore

Table 3—Metamorphosis in the anadromous sea lamprey *Petromyzon marinus* L.: Timing of the different stages and description of the main external changes (after Youson and Potter 1979).

Date	*Stage*	*Description*
Mid-July	1	Appearance of the eyes as small grey, irregular patches
Mid- to late July	2	Eye is round. Prominent papilla-like projections on the inner surface of the oral hood. Lips of oral hood are thickened.
Mid-July to mid-August	3	First differentiation of eye into a dark inner pupil and a lighter outer iris. Lips of oral hood form a rectangular entrance into the oral cavity.
Late July to late August	4	Oral hood becomes modified into a small disc. Two dorsal fins develop.
Mid-August to early September	5	Raised points (precursors of teeth) are visible on oral disc. The piston is visible.
Mid-August to mid-September	6	Teeth are blunt projections. Bottom half of body has a silvery sheen. Can use disc for attachment for the first time.
September, October, early November	7	Teeth are whitish yellow. Lingual laminae have fine serrated edges.
December to June	Newly metamorphosed	Teeth bear sharp tips. Prominent rasp-like appearance of lingual laminae.

waters prior to the upstream migration. Cannibalism among small adult lampreys has also been reported (Davis 1967). River lampreys also attack a wide range of species (Table 4). A limited record of 80 sea lampreys captured in the north-west Atlantic indicated that those less than 390mm long were almost all taken in bottom trawls on the continental shelf or in coastal trap nets, whereas most animals more than 560mm long were captured in mid-water trawls along the shelf edge or over the continental slope (Halliday and Mott 1991). The same authors considered that, following the first winter after metamorphosis, sea lampreys may be pelagic, and the wide range in distribution may be associated with large pelagic hosts. The Irish National Museum's collection of lamprey material includes a specimen of *P. marinus* taken on the Porcupine Bank in the Atlantic Ocean 400km off the Irish coast in 1988, as well as inshore samples of *P. marinus* from the south-west coast (M. Holmes and D. Quigley, pers. comm.). The latter material included specimens attached to fish such as herring, trout and coalfish. Exactly when adult lampreys cease feeding before their upstream movement is not known (Beamish 1980).

FEEDING ECOLOGY OF LANDLOCKED SPECIES

Studies from the upper Great Lakes in North America have shown that in spite of marked preferences for certain host species, the sea lamprey will turn readily to alternative hosts. In the early stages of the invasion in the Great Lakes, the lake trout (*Salvelinus namaycush*) suffered most severely, after which other fish were affected, including rainbow trout, whitefish, burbot and yellow perch (Hardisty and Potter 1971a). It has been reported that of the 74 species of freshwater fish inhabiting Lake Cayuga, none was immune to lamprey predation (Hardisty and Potter 1971a). Applegate (1950) has estimated the average duration of the parasitic phase for landlocked sea lampreys in Lake Huron as 14–15 months, with a range of 12–20 months. More recent studies by Bergstedt and Swink (1995) indicated a growth to adult size and maturity of landlocked sea lampreys in one growing season, with a sharp increase in growth in autumn. On the basis of laboratory studies, Parker and Lennon (1956) estimated that the average fish kill by a wild lamprey exceeds 8.5kg. Results of a study on the landlocked river lamprey in Loch Lomond indicated that three species of fish—

Table 4—List of prey species of sea lamprey (*Petromyzon marinus*) and river lamprey (*Lampetra fluviatilis*) (Beamish 1980; Farmer 1980; Pickering 1993).

Lamprey species	*Prey species*	
	Common name	*Species*
Petromyzon marinus	Basking shark	*Cetorhinus maximus* Gunnerus
	Sturgeon	*Acipenser* spp
	Shad	*Alosa* spp
	Herring	*Clupea* spp
	Atlantic salmon	*Salmo salar* L.
	Atlantic cod	*Gadus morhua* L.
	Haddock	*Melanogrammus aegelefinus* L.
	Atlantic mackerel	*Scomber scombus* L.
	Pollock	*Pollachius virens* (L.)
	Hake	*Urophycis* spp
	Swordfish	*Xiphias gladius* L.
	Striped bass	*Roccus saxatilis*
Lampetra fluviatilis	Bluefish	*Potamomus salatrix*
	Smelt	*Osmerus eperlanus* L.
	Sprat	*Sprattus sprattus* L.
	Baltic herring	*Clupea* spp
	Powan	*Coregonus clupeoides clupeoides* Lacépède
	Sea trout	*Salmo trutta trutta* L.
	Shad	*Alosa* spp
	Flounder	*Platichthys flesus* L.

trout, powan and roach—were being parasitised. Powan were the most heavily parasitised, with 26–50% of those caught over a 28-year period having scar marks where attacks had been made. Small whitefish less than 250mm long were rarely scarred (Maitland 1980b). In Lake Ladoga, the landlocked river lamprey is reported to feed on smelt and salmon (Abakumov 1960).

FEEDING MECHANISMS AND STRATEGIES

The food of the sea lamprey generally consists of blood, other body fluids and products of tissue cytolysis (Farmer *et al.* 1975). The initial wound is made by the tongue-like piston, which has two sets of plates at the oral end that bear denticles, which form cutting edges. The sucker remains in one place while the teeth revolve and rasp into the flesh of the victim (Dawson 1905). The oval disc provides a powerful sucking apparatus, and the host's blood is largely drained out of its tissues. In addition, glands in the lamprey's mouth secrete a substance that both inhibits clotting of the blood and breaks down the muscle tissue of the prey's body. Fish eggs and a 150mm fish have also been reported in the gut contents of feeding adult lampreys (Farmer 1980). Among the gut contents of *L. fluviatilis*, various fish tissues, organs and blood have been reported.

Evidence suggests that when sea lampreys are presented with a choice of hosts of different sizes but of the same species, they most frequently select the largest individuals (Swink 1991). The ventral surface of the host appears to be the preferred area of attachment. Scarring on Atlantic salmon was most prevalent on the ventral area between the operculum and the caudal peduncle (Beamish 1980; Farmer 1980). Lamprey scars have been observed below the lateral line of brown trout in Lough Derg (ESB 1998), pointing to the possible presence of a landlocked population in this Irish lake. Farmer and Beamish (1973) found that 69% of the scars on various teleosts were below the lateral line between the head and tail. However, *L. fluviatilis* has been reported to show a preference for the area above the lateral line (Beamish 1980; Maitland 1980a), and Maitland (1980b) observed lamprey marks most frequently on the backs of whitefish from Loch Lomond, Scotland, where a landlocked population of *L. fluviatilis* is present. The selection of specific areas on larger hosts serves to maximise food intake and duration of feeding, while ensuring food material with a more constant energy content (Farmer 1980). The duration of attachment of lampreys that killed their hosts was a function of the host's survival time, with the longest period being 14 days (Beamish 1980). The duration of host survival is dependent on blood loss in relation to blood volume. Lampreys cease active feeding for some time before spawning (Gibson 1953).

SPAWNING

UPSTREAM (SPAWNING) MIGRATION

The timing of the upstream migration of both the river and sea lamprey varies with latitude, temperature and discharge (Hardisty and Potter 1971a). Migration takes place almost exclusively at night and is influenced by high water levels in the rivers and low light intensity. One factor that determines the time of migration of the landlocked sea lamprey from the lakes into the river mouths appears to be the relative temperatures in these areas (Applegate 1950), with movement commencing when the temperature of the river rises above that of the lake. In northern and western Europe, the run time of spawning *L. fluviatilis* varies enormously, but generally begins in the late summer and autumn of the year before spawning (Pickering 1993). In Ireland, the authors captured adult *L. fluviatilis* in mid-September in the lower river Suir (Fig. 2: hydrometric region 16) in a survey that also yielded mature macrophthalmia of the same species.

Males outnumbered females in autumn runs of *L. fluviatilis* in Polish rivers (Witkowski and Koszewski 1995). Autumn-run animals were found to be larger than the spring-run animals, but gonad mass and gonadosomatic index were higher in spring-run specimens (Witkowski and Koszewski 1995). Sexual dimorphism was also more evident in spring-run *L. fluviatilis* in Polish rivers (Kuszewski and Witkowski 1995). Size of river lampreys at the time of upstream migration in the river Severn varied from 32g to 116g in females and 32g to 104g in males (Abou-Seedo and Potter 1979).

The upstream migration of the anadromous sea lamprey occurs between spring and early summer, one or two months before spawning, and is more synchronous than the spawning run of the river lamprey (Hardisty and Potter 1971a). Male and female landlocked *P. marinus* that have reached a specific stage of sexual maturity have been shown to release pheromones that attract conspecifics of the opposite sex (Teeter 1980). Tagging experiments with metamorphosed sea lampreys from one tributary in the Lake Huron catchment showed that marked fish moving to spawn were taken in a number of tributary channels other than the source of the marked fish, indicating that there did not appear to be a homing response but that selection of spawning channels was a response to 'innate attraction to some other sensory cues' (Bergstedt and Seelye 1995). Such cues may include chemicals released by populations of larvae in a channel: sexually immature males of *P. marinus* have been shown to exhibit a preference for waters in which sea lamprey larvae have been held (Teeter 1980). Migration in *P.*

marinus is correlated with lack of food intake, loss of marine osmoregulatory capacity and atrophy of the intestine. This period of natural starvation, from upstream migration until death after spawning, is characterised by a dramatic remodelling of the body and involves atrophy of most organs and tissues at the same time as the gonads are developing (Larsen 1980). These findings are mirrored in work on migrating *L. fluviatilis* in Poland (Witkowski and Koszewski 1995). The development of secondary sexual characters and gonad maturation is hormone-mediated, and environmental cues such as increasing temperature or increase in daylight do not appear to be important factors (Larsen 1980). When sea lampreys enter the river to spawn, they are 600–900mm in length and weigh approximately 2–2.5kg.

The migration of non-parasitic species to upstream spawning grounds takes place over short distances. In *L. planeri*, movement appears to begin only a short time before the onset of spawning, and the distances travelled are often less than 1km, although this varies with the character of the stream and its gradient (Hardisty and Potter 1971a). In a Swedish study on *L. planeri*, the critical temperature for onset of migration was 7.5°C and migration was essentially nocturnal, although daytime migration was also observed late in the season (Malmqvist 1980b). Sokolov *et al.* (1992) reported on spawning activity and ecology of spawning habitats of *L. planeri* in a channel in the upper Volga basin near Moscow.

Where the current is strong, migrating animals generally move along the edges of the main stream in comparatively shallow water. Weirs and pollution both render rivers unsuitable for the lampreys' migratory ascent (Applegate 1950). When faced by barriers, they exhibit sustained exploratory movements, passing backwards and forwards along the surface in search of a passage (Hardisty and Potter 1971a). According to Applegate (1950), they are able to pass quite high weirs or falls by a series of intermittent and violent wriggling movements, although they seldom 'jump' more than 600mm vertically. The number of upstream migrants is subject to natural fluctuations. Periodic climatic fluctuations are likely to be responsible for this (Hardisty and Potter 1971a). Above impassable barriers, only the non-migratory *L. planeri* occurs (Maitland 1980a). Migrating adults may be susceptible to predation. Sjöberg (1989) found that the seasonal and diel activities of goosanders and gulls were closely related to that of migrating *L. fluviatilis*, with birds showing a nocturnal peak in fishing activity during the peak of the lamprey spawning.

SPAWNING

According to Hardisty and Potter (1971a), water temperature is the decisive factor in determining the onset of spawning. However, the influence of temperature is a general effect of metabolism and motor activity rather than a specific influence on sexual maturity mediated through the pituitary (Hardisty 1961b). Timing of the spawning season for a particular species will therefore be dependent on latitude and climatic factors, as the literature indicates. In Finland, spawning of the river lamprey is generally delayed until June (Abakumov 1956). Even when spawning activity is well under way, a sudden but slight drop in temperature has often resulted in the almost complete disappearance of the animals from the nests. Spawning of *L. planeri* began in the German Odenwald in May, following a rise in air and water temperatures (Salewski 1991). In British rivers, the spawning season for both *L. planeri* and *L. fluviatilis* generally extends from March to April and begins when water temperatures reach 10–11°C. The anadromous *P. marinus* does not usually breed until late May or June at a water temperature of at least 15°C. The authors observed adult *P. marinus* at known spawning areas in the river Suir (see Fig. 2) in late May 2000 and observed spawning in this channel from early June to late July 2000.

Important physical features of the channel that affect spawning success include bed gradient, bed type, water velocity, depth and the presence of impassable barriers (Table 5). It has been suggested that an average river-bed gradient of 0.3–0.9% is the optimum for the existence of conditions suitable for spawning. The lamprey spawning habitat requires a gravel bottom with swift-running water and nearby backwaters with muddy bottoms for the larvae (Wheeler 1969). According to Morman *et al.* (1980), sea lampreys primarily require gravel 15–115mm in diameter, but other materials such as rubble and lumps of clay may be used if gravel is scarce or absent. In typical brook lamprey streams, the water over the spawning area is moderately swift (0.3–0.5m s^{-1}), bed material is gravel and sand, and water depth to the base of the nest rarely exceeds 400mm, although in large rivers it is possible that the species spawns in deeper water (Hardisty 1944). Water depth does not appear to be a critical factor in the distribution of lamprey spawning. Water depth at spawning grounds in 32 streams in northern Michigan (USA) ranged from 50 to 1520mm, and the average depth range was 230–510mm (Morman *et al.* 1980). Nesting sites are commonly located immediately below obstructions such as weirs or falls, which halt upstream movement. Hardisty (1944) observed that brook lamprey nests were frequently situated either directly under a bridge or only a short distance below, suggesting a role for shade in site selection. Where the spawning grounds were not under a bridge, the position was usually partly shaded by trees or buildings. In every case nests were found in either a depression or in front of some obstruction such as stones or driftwood. At the approach of spawning, the negative response to light characteristic of the sexually immature animal may change quite sharply to an apparent tolerance or even preference for lighted areas during the spawning act (Hardisty and Potter 1971a). This negative response is reported by Tuunainen *et al.* (1980) in *L. fluviatilis*, which has a more extended migration season than *P. marinus*. The positive response to light exhibited by migrating *P. marinus* (Purvis *et al.* 1985) may be due to the more sexually mature state of these animals compared to *L. fluviatilis*, which migrates several months before spawning.

The eggs are laid in a nest excavated by both males and females. The earliest stages of nest-building are carried out by the male. In most species, females join in later in the construction work (Malmqvist 1983b). Early stages in nest-building are characterised by stone-lifting using the oral disc, which eventually leads to the development of a depression in the bed of the stream. Large stones are pushed or dragged along for a short distance, usually in a downstream direction, but where the current over the nest is weak, they may be moved to the side or even upstream of the nest (Hardisty and Potter 1971a). The lampreys also vibrate vigorously in order to move loose stones, pebbles and fine material, which are carried down and across the stream. The structure of the lamprey nest varies with the body size of the species and with the nature of the bed material but shows essentially similar features in all forms that have been described. On a normal bed of sand and gravel of varying particle size, the nest of the brook lampreys is normally an oval depression. The size of the *L. planeri* nest varies considerably according to the number of animals it contains, ranging from 150mm to 450mm along the greater diameter and from 25mm to 100mm in depth. In places where the bed material consists mainly of larger pebbles, there may be little or no depression, but merely a small area where stones have been dislodged. Sand and gravel tend to be heaped up on the downstream side, creating a vortex in the opposite direction to the main current. Thus, the animals are able to move freely within the nest without being swept downstream, and the deposited eggs remain within the heaped-up gravel on the downstream side. In *P. marinus* the nests may reach 1.5m or more in diameter (Hardisty and Potter 1971a).

Before egg release, the female attaches herself to a stone. The male then uses his disc to fasten himself to the female, usually to one side of her head and twisting his body round hers. At this moment the female starts to vibrate rapidly, and eggs and milt are extruded in a backward stream. The vibration whirls up sand, and the externally fertilised eggs become embedded in the downstream end of the nest (Malmqvist 1986). The eggs, which may number up to 300,000 in the sea lamprey, are deposited in the depression (Beamish 1980). The sea lamprey normally spawns in small groups. In observations on a large number of nest sites during spawning on the river Mulkear in 1999, the authors noted 2–4 sea lamprey adults per nest. Brook lampreys, in contrast, often spawn in large groups of 10–30 in a nest. Malmqvist (1983a) noted a significant positive correlation in size between partners, suggesting an assortative mating; large differences in partner size reduced the efficiency of fertilisation. The same author also noted that males competed for mating opportunities, with additional males frequently coiled around the same female and 'satellite' males circling round the tails of copulating pairs, possibly fertilising eggs (Malmqvist 1983a). In a study on fecundity of the river lamprey on the Trent and Severn rivers, Hardisty (1944) found that egg numbers ranged from 7500 to 40,000 per female, and diameter ranged from 180mm to 350mm. The eggs in the brook lamprey are a little larger than in the river lamprey and number approximately 1500 (Hardisty 1964). Byrne *et al.* (2001) reported a mean egg count of 358 eggs g^{-1} body weight in a small sample of *L. planeri* examined, corresponding to approximately 900 eggs per female. Similar egg numbers, 873–1356 eggs per female, were reported in Swedish populations (Malmqvist 1978),

Table 5—Physical features recorded in spawning locations of *L. fluviatilis*, *L. planeri* and *P. marinus*.

Species	*Substrate size (mm)*	*Spawning nest dimensions (mm)*	*Water depth on spawning nests (mm)*	*Velocity on spawning nests ($m\ s^{-1}$)*	*Gradient (%)*	*Author*	*Locality*
L. fluviatilis (river lamprey)	—	230 (diameter) 50–80 (depth)		—	—	Huggins and Thompson 1969	UK
L. planeri (brook lamprey)	—	150–450 (diameter) 25–100 (depth)	<450	0.3–0.5	0.3–0.9	Hardisty and Potter 1971	UK
						Hardisty 1961b	UK
						Hardisty 1944	UK
P. marinus (sea lamprey)	15–115	<1500	150–1520 (mean 230–510)	—	—	Morman *et al.* 1980	USA

whereas Hardisty (1944) reported a much lower mean egg count of 440 eggs per female in *L. planeri*. The adults of all three species die shortly after spawning (Wheeler 1969; Maitland 1980a).

THE DECLINE OF LAMPREYS IN EUROPE

ECONOMIC IMPORTANCE AND RECENT ECOLOGICAL STUDIES

Lampreys have long been considered a gastronomic delicacy in Europe, encouraging the development of commercial fisheries for these species. The river lamprey is an important source of income for many fishermen in Sweden and Finland (Maitland and Campbell 1992; Ojutkangas *et al.* 1995). In the 1980s, the stock of salmon and sea trout and of anadromous white fish fell dramatically in many Finnish rivers, and the river lamprey became the most important catch (Ojutkangas *et al.* 1995). The total yearly catch of lampreys in Finland in the 1980s was 2 million–2.5 million fish (Eklund *et al.* 1984). In France, Ducasse and Leprince (1982) reported that commercial fisheries for *P. marinus* continued to be important in the river Dordogne but were declining due to water pollution, erection of dams and dredging of channels. The sea lamprey is a commercially important species in Spain and Portugal (Maitland and Campbell 1992), where live lamprey can have a market value of \$25 lb^{-1} (Gunderson 1998). There is also an important inland fishery for *P. marinus* in the Guadiana basin in Portugal (Collares-Pereira *et al.* 2000). Historically, commercial river lamprey fisheries were present on British rivers (Giles 1994). King Henry I of England is reputed to have died from eating an excess of lampreys.

However, throughout Europe populations of anadromous lampreys have declined dramatically over the last 30 years, mainly due to pollution, to the construction of dams associated with hydroelectric power stations, weirs and other manmade barriers in rivers and channelisation and land-management practices that lead to increased siltation on spawning gravels (Hunn and Youngs 1980; Kainua and Valtonen 1980; Valtonen 1980; Eklund *et al.* 1984; Witkowski 1992; Meyer and Brunken 1997; Ojutkangas *et al.* 1995). Channelisation is thought to have destroyed 40% of the most productive area in the river Perhonjoki in Finland through destruction of suitable habitats, including areas of silt deposition that are essential for larval survival (Ojutkangas *et al.* 1995). Fishermen in Finland observed that the building of a new bridge with bright streetlights prevented lampreys migrating upstream of the bridge, inducing a negative phototaxis in the autumn–winter migrating river lamprey (Tuunainen *et al.* 1980). Comparing the historical record with the present status, Lusk (1989) reported that two species of lamprey were extinct in the then Czechoslovakia. In Bavaria, Bohl (1995a) was unable to confirm the presence of *L. fluviatilis*, and the status of the other species encountered, *L. planeri* and *Eudontomyzon* sp., is classified as 'threatened by extinction' because of toxic run-offs and eutrophication (Bohl 1995b). Waterstraat and Krappe (1998) found that populations of *L. planeri* were confined to 15 tributaries in the Peene drainage in north-east Germany, although suitable habitat conditions existed in 36 channels. The same authors estimated that construction of up to 70 weirs with fish passes would be required to reduce population isolation and to enable resettlement in currently unoccupied channels (Waterstraat and Krappe 1998). Threats to *L. planeri* and conservation requirements for lampreys in Switzerland have also recently been compiled (Kirchhofer 1995; OFEFP 1996). Access to the full main channel of the river Tagus, which flows through Portugal and into Spain, was formerly possible for the sea lamprey (Assis 1990). While *P. marinus* remains common in the Portuguese portion of this river, it is prevented from ascending to the Spanish jurisdiction because of two dams lacking appropriate fish-passage mechanisms (Assis 1990). According to Kurz and Costello (1999), lamprey numbers have declined in Ireland in recent years. However, there is no substantive baseline of information for this to be quantified.

In order to promote the conservation of freshwater fish in Europe, proposals for the conservation of lampreys, including *P. marinus*, were put forward: these proposals include the maintenance of free access and special pollution control measures in some of the rivers in which populations are still present (Maitland 1980a). Tuunainen *et al.* (1980) proposed that lamprey stocks in affected rivers could be strengthened by transporting migrating spawners over dams, building lampreyways into power stations and dams, improving the quality of sewage treatment and reducing regulation of water levels in spawning rivers. Artificial rearing in hatchery facilities may also have a role in conservation of the species. Renaud (1997) cited similar causes of decline and called for similar conservation requirements when discussing the status of lamprey species in the northern hemisphere, including *L. fluviatilis* and *P. marinus*.

The compilation of Red Data Books by individual nations in Europe has been important in documenting the status of a range of plant and animal species considered to be in decline within their natural ranges and in highlighting shortcomings in distributional information necessary for framing conservation management decisions. The Red Data Books for fish and lampreys for Slovenia (Povz 1996), the Wadden Sea (Berg *et al.* 1996) and Sweden (Gärdenfors 2000) list *Eudontomyzon marinus* and *L. planeri* (Slovenia), *L. fluviatilis* and *P. marinus* (Wadden Sea), and *L. planeri* and *P. marinus* (Sweden) as endangered. All three lamprey species discussed in this review are listed in *The Irish Red Data Book. Volume 2: Vertebrates* as being of indeterminate status (Whilde 1993). This term means that the status of the three species is 'endangered', 'vulnerable' or 'rare', but allocation to a particular category is not possible because of an inadequate database.

THE AMERICAN EXPERIENCE—A CONTRAST

This European perspective is in marked contrast to the experience in North America, where the opening of navigation between the Atlantic Ocean and the Great Lakes from the 1820s onwards enabled sea lampreys from Atlantic drainages to colonise progressively each of the catchments of the Great Lakes (Morman *et al*. 1980; Smith and Tibbles 1980; Great Lakes Fishery Commission 1999). Once established, this species contributed to the decline of major fish stocks in lakes Huron, Michigan and Superior, and many commercial fisheries had collapsed by the late 1950s (Maitland 1980b). The Great Lakes Fishery Commission was established between the United States of America and Canada in 1955 to formulate and implement a programme to eradicate or minimise sea lamprey populations in the Great Lakes (Great Lakes Fishery Commission 1999). Early efforts at control were concentrated on prevention of spawning by adult sea lampreys by means of mechanical and electrical weirs (Smith and Tibbles 1980). However, sea lampreys have the ability to withstand a relatively severe electric shock without apparent physical harm (Hunn and Youngs 1980). In the late 1950s, a selective toxicant, TFM (3-trifluoromethyl-4-nitrophenol), which could be applied to streams to kill larval sea lampreys, was developed (Smith and Tibbles 1980). This has remained the main method of control and has helped to reduce sea lamprey populations in the Great Lakes by 90%. Since the 1970s, state, federal, provincial and tribal agencies in both the United States and Canada have participated in the Integrated Management of Sea Lamprey Programme (Klar *et al*. 1996). Although the American and European studies generally have quite different aims, there is no doubt that the American investigations have been very important in carrying out fundamental research into aspects of lamprey biology and ecology and in advancing our knowledge of these species.

THE EU HABITATS DIRECTIVE

In 1992 the European Union (EU) adopted Council Directive 92/43/EEC on the conservation of natural habitats and of wild fauna and flora, also known as the Habitats Directive. The main goal of the Directive is:

> ... to contribute towards ensuring biodiversity through conservation of natural habitats and of wild fauna and flora in the European territory of the member states to which the Treaty applies.

The Directive requires the establishment of a European network of important, high-quality conservation sites that will contribute significantly to the conservation of the 169 habitat types and 623 species identified in Annexes I and II of the Directive. The three lamprey species discussed in this review are listed in Annex II, which lists

Table 6—List of proposed special areas of conservation (SACs) for the three species of lamprey (*Lampetra planeri*, *Lampetra fluviatilis* and *Petromyzon marinus*) in the Republic of Ireland.

Hydrometric region	*River/catchment*	*L. planeri*	*L. fluviatilis*	*P. marinus*
12	Slaney River valley	*	*	*
14	River Barrow	*	*	*
15	River Nore	*	*	*
16	Lower River Suir	*	*	*
18	R. Blackwater (Cork, Waterford)	*	*	*
22	Killarney National Park, Macgillicuddy Reeks and Caragh River	*	*	*
25	Lower River Shannon	*	*	*
35	Lough Gill	*	*	*
30	Lough Corrib			*
20	Bandon river	*		

animal and plant species of interest to the European Community whose conservation requires the designation of special areas of conservation (SACs). The river lamprey is also listed in Annex V of the Directive, which lists those animal and plant species of European Community interest whose exploitation and taking in the wild may be subject to management measures.

Integrated policies for the protection of inland waters are in place in many areas of Europe, for example the North Sea, the Baltic Sea, the Rhine, the Elbe and the Danube (European Environment Agency 1999). In the United Kingdom a site list of SACs for the river, brook and sea lamprey has been compiled (Brown *et al.* 1997), representing a range of high-quality river types in which the species occur. The selected sites are generally extensive river systems, including important tributaries, to provide conservation of habitat features required by the various life stages of lampreys (Brown *et al.* 1997). SACs for lampreys must be characterised by good water quality, clean substrate at spawning grounds and the presence of silt beds downstream of spawning areas. For *P. marinus* and *L. fluviatilis*, access to spawning areas from the sea must also be ensured (Kurz and Costello 1999).

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A list of SACs for lampreys has recently been compiled for Ireland (Table 6). The listing, which is based on the desk study of distribution by Kurz and Costello (1999), gives particular emphasis to channels in which the three species are known to co-occur. The upstream extent of any SAC for the anadromous species was delineated by identifying the most-upstream known extent of migration and extending the conservation area to the next road bridge upstream of this point. Where species were known to inhabit a tributary of a designated channel, the SAC was extended to embrace both tributary and main channel.

More information on the distribution of lampreys in Ireland is essential both to confirm the representativeness of the SAC list already compiled and to form a valid baseline against which the future status of populations can be measured. Whilde (1993) pointed to the lack of such information when assessing Red Data Book status for the species in Ireland, and he called for effective recording of each of the species wherever they were encountered, in addition to ecological studies of known major haunts. Kurz and Costello (1999) have suggested carrying out specific lamprey surveys and establishing a central collection/database of information found during such specific surveys or as a by-product of other studies or surveys. Specific lamprey surveys would provide a focus for research efforts and would permit the collection of data on species distribution and important habitat factors that affect the various life stages. Such an approach could provide a baseline for lamprey status in already-designated SACs and, in the longer term, would be a valuable means of assessing the effectiveness of conservation measures or the requirement for additional measures within any SAC. In addition, such surveys could indicate those catchments where the anadromous species may be absent or of low status. This information might lead in turn to the initiation of necessary fishery or catchment management measures to enhance the status of the species in such waters. Several of the large catchments on the island, such as the Foyle, Erne and Blackwater–Bann systems (Fig. 2), have a large component of river corridor in both the Republic and Northern Ireland. It is imperative that liaison between fisheries and conservation agencies on both sides of the border takes place to ensure that major surveys on these systems are as comprehensive as possible and to permit co-operation in implementing lamprey conservation measures in any of the cross-border channels.

In Kurz and Costello's 1999 survey, many adult and juvenile lampreys were not identified to species level. This is an important fact to consider when compiling information on the location of spawning and nursery areas for the three species. It would be extremely beneficial if a reliable, non-destructive field method were available to permit rapid identification of juveniles to species level by competent individuals. An awareness campaign among those institutions and organisations that carry out routine river survey work would also be helpful in familiarising staff with the lamprey life forms. Such a campaign should enable feedback to a central collation point of information on distribution and conservation status of the three lamprey species.

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those of the authors and should not be seen as expressing the views of the Central Fisheries Board or of any other agency.

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