Ecology of the Allis and Twaite Shad

Alosa alosa and *Alosa fallax*

Conserving Natura 2000 Rivers

Ecology Series No. 3

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This document was produced with the support of the European Commission's LIFE Nature Programme. It was published by **Life in UK Rivers**, a joint venture involving English Nature (EN), the Countryside Council for Wales (CCW), the Environment Agency (EA), the Scottish Environment Protection Agency (SEPA), Scottish Natural Heritage (SNH), and the Scotland and Northern Ireland Forum for Environmental Research (SNIFFER).

ISBN 1 85716 705 8

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This document should be cited as: Maitland PS & Hatton-Ellis TW (2003). *Ecology of the Allis and Twaite Shad.* Conserving Natura 2000 Rivers Ecology Series No. 3. English Nature, Peterborough.

Technical Editor: Lynn Parr
Series Ecological Coordinator: Ann Skinner

Cover design: Coral Design Management, Peterborough.
Printed by Astron Document Services, Norwich, on Revive, 75% recycled post-consumer waste paper, Elemental Chlorine Free. 1M.

Cover photo: Environment Agency

Conserving Natura 2000 Rivers

This account of the ecological requirements of the allis and twaite shad (*Alosa alosa and A. fallax*) 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 European 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 via the project website: www.riverlife.org.uk.

Contents

Introduction

The allis shad (*Alosa alosa* L), and the twaite shad (*Alosa fallax* Lacépède) are both members of the herring family, Clupeidae. The shads form a large group of pelagic fishes found in seas all over the world except the Antarctic. Many species have a high economic value. Most are marine, but some enter fresh water to spawn, their young subsequently coming back to the sea to grow, and a few live permanently in fresh waters. There are several genera with a total of about 200 species.

Allis and twaite shad are the only two members of the herring family found in fresh water in the UK. Both resemble large herring (adult allis shad can be over 2 kg in weight). Shad have a generally westerly distribution in Europe, with the largest populations being in major rivers flowing into the Atlantic.

Rob Hillman/Environment Agency

The simplest way to distinguish the allis and twaite shad is by size, number of lateral line scales and number of gill rakers on the first gill arch. The last of these is the most important and critical point of distinction. Allis shad (below) are usually 30–50 cm, with more than 70 scales along the lateral line and more than 90 fine gill rakers on the first gill arch. Twaite shad are usually 25–40 cm, with less than 70 scales along the lateral line and less than 60 coarse gill rakers on the first gill arch. Any shad that has more than 60 but less than 90 gill rakers is likely to be a hybrid between the two species. Spot pattern is not a reliable indicator of species.

Medium-energy systems with erosive channels seem to be favoured, and shad do not generally utilise rivers that are heavily modified or less than 10 m wide.

Twaite and allis shad were once widely fished in Europe, and were formerly eaten in Britain. In the Severn Estuary during the middle of the 19th Century, shad made up about one-third of all catches, with their value rivalling that of salmon (Salmon Fisheries Commission 1861). Both allis and twaite shad have declined across Europe and are now absent from many rivers where they once flourished and supported thriving fisheries. Allis shad are still caught and eaten in parts of France and some other European countries. Twaite shad are not usually eaten, as they are considered too bony (hence the alternative name of 'Bony Horseman'). Most fisheries have now collapsed due to construction of barriers to migration.

Detailed and up-to-date reviews of most aspects of European shad biology can be found in Aprahamian *et al*. (2002), Aprahamian & Aprahamian (2001), and Baglinière & Elie (2000).

Allis shad

Status and distribution

Adult allis shad can be found along the coasts of western Europe from southern Iceland and Norway to Spain. They occur mainly in shallow coastal waters and estuaries, but during the spawning migration adults penetrate well upstream in some of the larger European rivers, mainly in France, Spain and Portugal (Table 1).

Table 1. Principal rivers utilised by allis shad for spawning (after Aprahamian *et al*. 1998 and Baglinière 2000).

Adour	France	Present
Aulne	France	Recolonising
Charente	France	Abundant
Dordogne	France	Very Abundant
Douro	Portugal	Virtually Extinct
Elbe	Germany	Extinct
Garonne	France	Very Abundant
Guadiana	Spain / Portugal	Rare
Lima	Spain / Portugal	Abundant
Loire	France	Recovering
Meuse	Netherlands / Belgium / France	Extinct
Minho	Spain / Portugal	Much Reduced
Mondego	Portugal	Much Reduced
Nivelle	France	Present
Orne	France	Recolonising
Rhine	Netherlands / Germany / France	Extinct
Sebou	Morocco	Extinct
Seine	France	Extinct
Severn	UK	Very rare
Tagus (Tejo)	Spain / Portugal	Rare
Thames	UK	Extinct
Vilaine	France	Recolonising

In northern Europe, populations formerly existed in the Rhine and Elbe, but these are thought to be extinct due to pollution and obstructions to migration, while the Moroccan populations are also thought to have been eradicated by dam construction. A few landlocked populations have been recorded, at least some of which are of recent origin, due to the stocks being trapped in reservoirs above impassable dams. The allis shad has suffered considerably from pollution, over-fishing and river obstructions, and is now a rare fish over most of its range. Recently, there has been some evidence of recovery/recolonisation, mainly on rivers in north-west France.

Although previously believed to spawn in some British rivers, such as the River Severn, and recorded by Ellison (1935) as breeding in the River Wye, allis shad have been caught only rarely in recent years (Aprahamian & Aprahamian 1990). There are now no known spawning sites for this species in Britain, though both sub-adults and sexually mature adults are still regularly found around the British coast, including the Solway Firth (Maitland & Lyle 1991, 1995), and in the English and Bristol channels (Hillman 2002). A similar position exists in Ireland, where there have been no recent records verifying the existence of any spawning populations (Whilde 1993), but occasional specimens are taken around the coasts and in some of the larger rivers.

Because of this decline, the allis shad is now given considerable legal protection. It is listed in annexes II and V of the EU Habitats and Species Directive, Appendix III of the Bern Convention, Schedule V of the Wildlife and Countryside Act (1981) and as a Priority 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 Critically Endangered. The Red Data Book for Ireland (Whilde 1993), published before the IUCN (1994) revision of categories, lists the allis shad as Endangered.

Life history

Mature fish that have spent most of their lives in the sea stop feeding and move into the estuaries of large rivers, migrating into fresh water during late spring (April to June), thus giving the shad the name of 'May Fish' in some areas. Males migrate upstream first, followed by females one or two weeks later. In some of the larger European rivers, allis shad have been known to ascend upstream for several hundred kilometres – for example, more than 500 km in the River Loire (Boisneau *et al.* 1985). They used to migrate upstream as far as Shrewsbury and Welshpool in the River Severn (Salmon Fisheries Commission 1861).

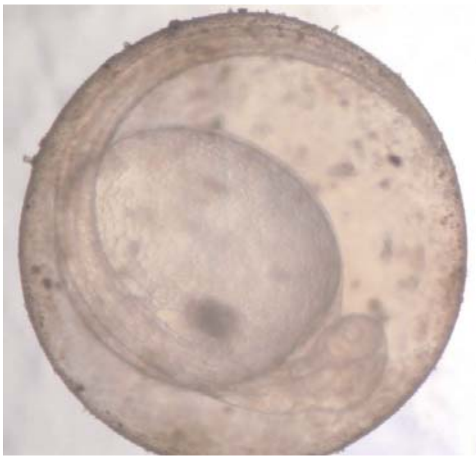
In the breeding areas, shoals of fish accumulate in suitable pools. Spawning, which involves much noisy splashing at the surface as males chase females, takes place at night in flowing water over clean gravel beds. Almost all allis shad die after spawning. Surviving adults drop downstream to the sea.

According to Douchement (1981), in the rivers Adour, Garonne and Loire, allis shad spawn only once in their lives. Sabatié (1990) reported similar findings from the River Sebou in Morocco. In contrast, Taverny (1991) found repeat spawning (17.9% for females and 9.1% for males) in the Gironde system, as did Mennesson-Boisneau & Boisneau (1990) in the River Loire (1.8% of females and 0.8% of males). A proportion (20%) of female repeat spawners was also reported from the River Aude in France, though the sample size on which it is based (five fish) was small (Douchement 1981).

The clear eggs are non-adhesive, semi-buoyant and 2.5–4.5 mm in diameter. They are laid above gravelly shallows, in water currents between 1 and 1.5 m s^{-1}, and tend to drift downstream, most falling to the bottom and remaining there in crevices until they hatch four to eight days later. Some eggs drift for long distances below the spawning areas, sometimes several tens of kilometres (Hass 1965).

Tristan Hatton-Ellis/CCW

Shad migrate upstream for several hundred kilometres, where they accumulate in suitable pools to spawn.



Alan Henshaw/Environment Agency

Ben Wilson/Environment Agency

Shad eggs are clear and measure 2.5–4.5 mm. They are laid over gravel and hatch after 4–8 days.

Females may lay 50,000–636,000 eggs each (Vincent 1894; Hoek 1888; Fatio 1890; Roule 1925; Dottrens 1953; Hoestlandt 1958; Rameye *et al*. 1976; Cassou-Leins & Cassou-Leins 1981; Eiras 1981; Phillippart & Vranken 1982; Dautrey & Lartigue 1983; Sabatié 1990). The relative fecundity, defined as the number of eggs per kilogram of total body weight, has ranged from 60,000 eggs per kg in the Sebou in Morocco (Sabatié 1990) to 236,000 eggs per kg in the River Garonne in France (Cassou-Leins & Cassou-Leins 1981). There is an indication of an increase in relative fecundity with increasing latitude, from approximately 60,000 in Morocco to 200,000 in the River Loire.

After hatching, the young remain in the slow-flowing reaches of the lower parts of rivers, then move into the estuary and eventually into coastal waters and the open sea, occasionally occurring in water up to 300 m deep. The fry are about 10 mm on hatching but rapidly grow to between 80 and 140 mm after one year. By this time many of them have descended to the sea and the remainder follow during their second year.

Anadromous populations of the allis shad mature at between three and eight years, with the majority of females maturing at five and six years, and males at four and five years (Douchement 1981; Sabatié 1990; Taverny 1991; Lambert *et al*. 2000; Veron *et al*. 2000). Most studies have estimated the age at first spawning from catch data that consisted of a number of cohorts with no correction for gear selectivity. The exception is the study by Lambert *et al*. (2000) who estimated the age at maturity from three year-classes from the Gironde system.

As they move slowly to the sea, young allis shad usually occupy open habitat at the edges of pools where the current is less strong, and these lowland stretches can be particularly important (Bervoets *et al*. 1990). The food of these young fish is mainly benthic river invertebrates, especially midge larvae and crustaceans. The adults feeding in salt water also rely largely on invertebrates, especially planktonic crustaceans such as calanoids, mysids and euphausids, but also to some extent on small fish (Maitland & Lyle 1995).

Population structure and demography

No subspecies of allis shad are recognised, but there is some evidence that they return to the natal river (Quignard & Douchement 1991a), suggesting that there may be some genetic integrity within populations. Alexandrino & Boisneau (2000) reviewed the genetic diversity of both allis and twaite shad. They concluded that allis shad show both low genetic diversity and little genetic differentiation among populations. The genetic data also suggest that allis shad may have originated from twaite shad and that hybridisation is common, especially where obstacles prevent the upstream migration of allis shad.

Hybrids between allis and twaite shad occur in a number of rivers, such as the River Loire, and in some estuaries (for example, the Solway Firth). In a few systems, such as the rivers Loire and Lima, these hybrids may form a significant proportion of the population (Quignard & Douchement 1991a). Since hybrids are probably fertile (Alexandrino *et al.* 1992, 1996), this is bound to have an impact on the genetic integrity of the stocks of both species. In these populations, introgression may occur, where hybrids backcross with the most abundant species (usually twaite shad). If this process is repeated regularly, the two shad species could merge into one; largely resembling twaite shad, but with some of the characteristics of allis shad.

It has been suggested that extensive hybridisation is a result of man-made obstacles to migration, which force both species to use the same spawning grounds. Boisneau *et al.* (1992) found that the highest percentages of hybrids in the River Loire were collected at shared spawning grounds that had converged after habitat disturbance upstream. Similarly, in the River Lima, major dams have denied shads access to traditional spawning sites upstream (Alexandrino *et al.* 1996).

Rob Hillman/Environment Agency

The spots along the flanks of allis shad are often obscured by scales, and may not be visible in juveniles. Allis and twaite shad sometimes hybridise if they are unable to reach traditional spawning grounds.

The maximum age reached by allis shad is about 10 years. Females grow faster than males and may reach about 600 mm and 3000 g in seven years. Equivalent males would be about 550 mm and 2500 g. Maturity is reached at three to four years (300–400 mm in length), and most spawning adults are between three and six years old. Specimens of around 700 mm have been recorded, but most adults are 300–500 mm.

Marcy (1976) believed that, for the American shad (*Alosa sapidissima*), the number of adults available for spawning had some influence on subsequent year-class strengths. Crecco & Savoy (1987) concluded that density-dependent factors accounted for 10–25% of the variability of recruitment, and models incorporating flow and rainfall accounted for 80–90% of the variability in stock recruitment (Crecco *et al.* 1986; Crecco & Savoy 1984, 1987).

Recruitment in the River Loire (Mennesson-Boisneau & Boisneau 1990) was significantly correlated with flow during the period of upstream migration (March 15 to June 15), though the relationship was heavily influenced by the flow in any one year. The relationship between year-class strength and flow can be described by the equation:

YCS = 0.068e(0.0016F)

where YCS = year-class strength, and F = mean flow (m^3 s^{-1}) for the period March 15 to June 15.

The implication is that, in the River Loire, the population is regulated by the amount of spawning and/or nursery area available. High flows allow the fish to penetrate further up the river system and thus increase the potential rearing area, reducing the level of density-dependent mortality.

Twaite shad

Status and distribution

The twaite shad (*Alosa fallax*) occurs along most of the west coast of Europe, from southern Norway to the eastern Mediterranean Sea, and in the lower reaches of large accessible rivers along these coasts. Spawning populations have been recorded from Estonia, Germany (especially the Elbe), Britain, Ireland, western France, Spain, Portugal, Morocco, Belgium and the Netherlands (ssp. *Alosa f. fallax*), southern France and Italy (ssp. *Alosa fallax rhodanensis*) and much of the eastern Mediterranean (ssp. *Alosa fallax nilotica*). There are several non-migratory populations of this fish in a few of the larger European lakes, including Como, Garda, Iseo, Lugano, Maggiore and Lough Leane (O'Maoileidigh *et al.* 1988); these are often given subspecific or even specific status (see Kottelat 1997 for a discussion).

With the exception of these isolated populations, the normal habitat of this species is the sea, and the lower reaches of large unpolluted rivers where there is easy access to spawning grounds. In general, populations of twaite shad have declined across Europe (Koehler 1981, Groot 1990), though not as severely as the allis shad, perhaps due to an ability to use spawning sites close to the sea, often in smaller rivers.

In Britain, spawning populations of twaite shad are still found in the rivers Severn, Wye, Usk and Tywi and appear to be reasonably stable (Aprahamian *et al.* 1998). Remnant populations may still be present in other rivers (Maitland 1993, 1995), especially where spawning takes place in estuaries, as appears to be the case in the River Cree (Maitland & Lyle 1995). In Ireland, although there has been a decline (Went 1953), spawning populations still occur in the rivers Suir, Nore and Barrow, and the Cork Blackwater (Whilde 1993).

Because of this decline, the twaite shad is now given legal protection. It is listed in annexes II and V of the EU Habitats and Species Directive, Appendix III of the Bern Convention, and as a Priority 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 Endangered. The Red Data Book for Ireland (Whilde 1993), published before the IUCN (1994) revision of categories, lists the twaite shad as Vulnerable.

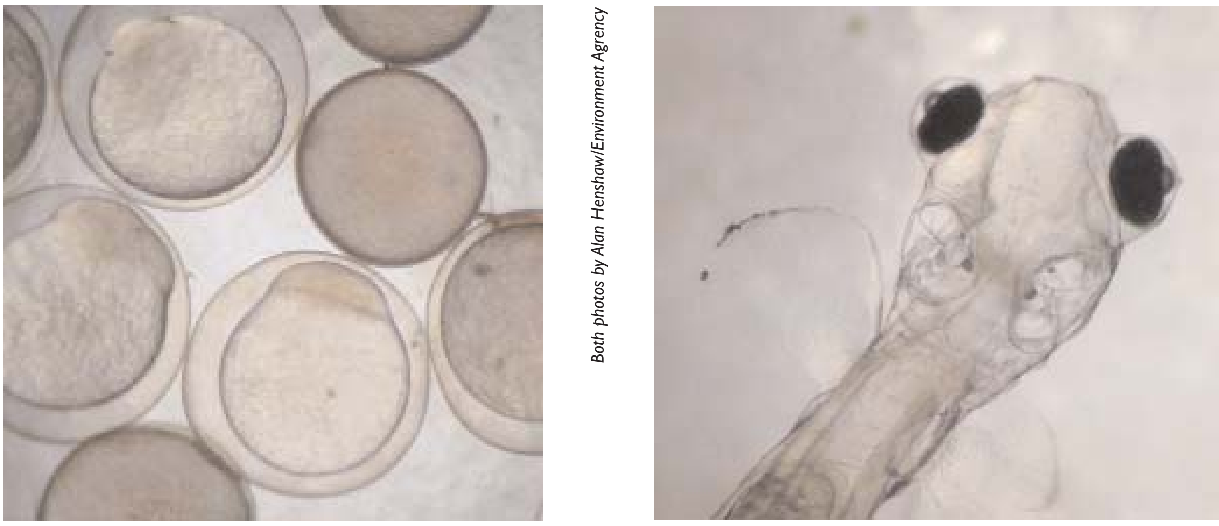
Rob Hillman/Environment Agency

Unlike allis shad, twaite shad still spawn in British rivers, and populations appear to be stable.

Life history

At maturity, adult twaite shad stop feeding and gather in the estuaries of suitable rivers in early summer (April and May), moving upstream to spawn from mid-May to mid-July. The males usually move upstream first, but they are soon joined by the females. As with allis shad, spawning is a noisy affair, with much splashing and chasing near the surface above appropriate areas of clean gravel.

Spawning takes place in flowing water over stones and gravel, among which the eggs sink. The eggs, which measure 1.5–3.5 mm in diameter, take about four to six days to hatch. The young fish then drop quickly downstream in the current to the quieter waters of the upper estuary where they start to feed and grow.



Both photos by Alan Henshaw/Environment Agency

Twaite shad eggs and larvae are transparent. After hatching, the young fish gradually move into estuaries until the end of their second summer, when they move into coastal waters.

The absolute fecundity of the subspecies *Alosa fallax fallax*, which occurs in Britain, has been reported to range from 25,942 to 675,000 eggs (Vincent 1894; Jenkins 1902; Bounhiol 1917; Hass 1965; Aprahamian 1982; Dautrey & Lartigue 1983; Taverny 1991; Sabatié 1990). The relative fecundity has been reported to range from 42,540 to 302,358 eggs per kg: 139,479 in the River Severn (Aprahamian unpublished), 147,378 in the Gironde system (Taverny 1991), and 103,270 in the Sebou (Sabatié 1990). Highest fecundities were found in the Guadiana River (250,000-675,000), followed by the River Mira (82,000-580,000) (Pina *et al.* 1999), and the Nyamunas River (83,900-362,700).

Growth in the first year is fairly rapid; juveniles can reach 50 mm in six months and 100–150 mm after one year (Aprahamian 1988). Thereafter, growth is steady and most fish reach 200–250 mm after two years and 250–300 mm after three years. The males start to mature after three years and are therefore spawning with older and larger females at first. The females themselves do not start to mature until they are about five years old.

The young fish feed mainly on invertebrates, especially estuarine zooplankton, but as they grow they take larger crustaceans of various types (for example, shrimps and mysids) and also small fish (Aprahamian 1989; Assis *et al.* 1992; Taverny 1991). Adults feed to an appreciable extent on other fish, especially the young of other members of the Clupeidae, such as sprat and herring (Maitland & Lyle 1995).

Unlike allis shad, which normally spawn only once, twaite shad may spawn several times in their lives (Aprahamian 1982). Evidence for partial spawning has been observed in populations of twaite shad and allis shad in Portugal, and in the American shad in the USA (Olney *et al.* 2001), but has not been demonstrated in the UK.

Population structure and demography

Several subspecies of twaite shad have been recognised by various authors, and the review by Quignard & Douchement (1991b) recognises six. Only one of these, *Alosa fallax fallax*, occurs in Britain, but the Killarney shad (*Alosa fallax killarnensis*) is found in Ireland (Lough Leane), where it is considered by Whilde (1993) to be Endangered. Within *Alosa f. fallax* there is some variation: 'Each population is characterised by mean averages for meristic features that are statistically distinctive' (Eiras 1980, 1981, 1983; Douchement 1981; Quignard & Douchement 1991b). This provides strong circumstantial evidence for some degree of homing in the species.

Variation in recruitment, as measured by the coefficient of variation, was estimated for twaite shad in the 0+ age class from the Severn Estuary to be 110.34% (n = 18, 1981–1998). This compares well with the estimate of 124.45% (n = 20, 1972-1991) for female twaite shad aged six years (Aprahamian & Aprahamian 2001). Recruitment in shads has been shown to be strongly linked to abiotic factors, notably summer temperature (see habitat requirements, below).

Hybrids between twaite and allis shad have been found in a number of rivers (such as the River Loire) and in some estuaries (including the Solway Firth). In some systems, such as the rivers Loire and Lima, these hybrids may form a significant proportion of the population (Quignard & Douchement 1991a). Since hybrids are probably fertile (Alexandrino *et al*. 1996), this is bound to have an impact on the genetic integrity of the stocks of both species. It has been suggested that extensive hybridisation is a result of man-made obstacles to migration, which force both species to use the same spawning grounds. Boisneau *et al*. (1992) found that the highest percentages of hybrids in the River Loire were collected at shared spawning grounds which had converged after habitat disturbance upstream.

Habitat requirements and associations of allis and twaite shad

Relatively little is known about the ecology of European shads in fresh water, and even less about their habits at sea. However, in general, they appear to be rather similar, and so are treated together in the following sections. Known differences among species are highlighted in the text.

Marine habitat

The requirements of shads at sea are very poorly understood, but they appear to be mainly coastal and pelagic in habit. Allis shad have been reported from depths of 10–150 m, and twaite from depths of 10–110 m, with a preference for water 10–20 m deep (Taverny 1991) although Roule (1925) recorded them at depths of 200–300 m. As noted above, allis shad are almost exclusively planktivorous, whereas twaite shad also feed on small fish such as sprats, and this is likely to be reflected in their habitat selection.

A suitable estuarine habitat is likely to be very important for shad, both for passage of adults and as a nursery ground for juveniles.

Freshwater habitat

After returning from the sea, the critical habitat requirements are:

- March–June: A clear migration route to the spawning grounds, with suitable river flows and no barriers.

Peter Wakely/English Nature

Estuaries are important for both allis and twaite shad, as a nursery for juveniles, and to provide a clear route to spawning grounds for adults.

- Late May–late June: suitable resting pools and clean gravels at the spawning areas.
- Mid June–late September: Slow-flowing nursery areas for juveniles in fresh water above the estuary after hatching (Menneson-Boisneau *et al.* 1986; Belaud *et al.* 1991; Prouzet *et al.* 1994).

Adult migration behaviour and requirements

Mature adults enter the estuaries of many European rivers from April onwards and migrate some distance upstream, though the exact distance is variable. In France, allis shad typically migrate further upstream in rivers where both occur, and in the Elbe twaite shad spawn in tidal waters (Hass 1965, Thiel *et al.* 1996). Twaite shad may spawn in, or just above, the tidal reaches of rivers, but many stocks spawn in freshwater well upstream of this (Ehrenbaum 1894; Meek 1916; Hoestlandt 1958; Maitland 1972; Aprahamian 1982). In the River Wye, some fish travel over 190 km to reach their spawning grounds at Builth Wells. Recently, a population of what appears to be allis shad has been found spawning in a tidal riffle in the Tamar, below an impassable weir (Hillman 2002). Unlike salmonids, however, shads do not enter narrow streams even when these are accessible.

In practice, the location of spawning grounds is often limited by obstacles to migration. Such obstacles include natural barriers such as waterfalls, or man-made dams and weirs. Pollution can also create a barrier to movement.

The upstream migration from the estuary appears to be triggered by temperature. Claridge & Gardner (1978) found that twaite shad migration started when the water reached 12°C, and Aprahamian (1982) confirmed that peak migratory activity occurred at temperatures of 10–14°C. The temperature at which the upstream migration of allis shad commences seems to be similar; Boisneau *et al.* (1985) suggest 11°C and Belaud *et al.* (1985)16°C.

Spawning runs are also influenced by other factors, notably estuarine tides and river flows. Twaite shad appear to move up estuaries on spring tides (Bracken & Kennedy 1967, Aprahamian 1982) and although migration has been recorded at its peak during relatively high discharge levels, if flows are too high then numbers drop (Aprahamian 1982, Steinbach *et al*. 1986).

In the River Severn, it was noted by Yarrell (1859) that allis shad preferred to move upstream when the water was clear, but 'if there happen to be a flood, they wait till the waters are restored to their former purity, and if they meet with a flood in their progress upward, they immediately return and keep below Gloucester.'

Channel structure and management

Sexually mature adults require a migration route free of obstacles, both natural (such as waterfalls) and man-made dams, weirs or pollution barriers, in order to reach their spawning grounds with minimum effort and delay. Suitable fish passes can be provided around dams if necessary (Belaud & Labat 1985, Environment Agency 1998) although these are not often effective, because shad avoid confined spaces and areas of turbulent flow.

Navigation weirs, hydropower barrages and other in-stream barriers are a major cause of population decline or loss, having affected the populations of both allis and twaite shad in the Rhine, Rhône, Minha, Mira, Sebou, Severn and Thames by denying access to many valuable spawning grounds. Apart from actual barriers, any significant alteration or management of channels which removes resting pools or creates stretches of fast flow (> 2m s^{-1}) or very shallow water (< 10 cm) must be avoided all along the migration route.

Allis shad have difficulty swimming upstream if the current exceeds 2 m s^{-1} (Cassou-Leins & Cassou-Leins 1981). Where man-made obstacles to upstream migration are present, or new structures planned that are potential obstacles, then modification of these to allow the passage of shad should be considered. The main features to avoid are flows of less than 2 m s^{-1} and any significant vertical falls.

There is considerable experience in France, both in modifying existing structures previously impassable to shad and in building suitable fish passes within new structures. An example of the latter is in the

Catherine Duigan/CCW

An obstruction such as a weir can prevent shad from migrating upstream to preferred spawning grounds.

Tristan Hatton-Ellis/CCW

Man-made obstacles to allis shad migration can be overcome by the use of a vertical fish lift, like this one on the River Garonne in France. Up to 90,000 shad successfully pass through this lift each year.

River Garonne at Golfech, where a successful fish pass involving a vertical lift was incorporated in a dam for a nearby nuclear power station. Around 40,000–90,000 shad pass through this successfully each year (Ghaappe *et al.* 2000). Any barriers, especially those near the mouth of a river, pose a threat to the genetic integrity of shad stocks by increasing the likelihood of hybridisation.

The general conclusion is that high flows during spates are likely to be detrimental to populations of allis shad, not only in making it difficult for them to access spawning grounds, but also by lowering recruitment after spawning, probably due to eggs and fry being swept downstream into the sea. 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.

Spawning requirements in fresh water

Throughout the range of the allis shad, reproduction occurs from April to July, but in Britain, May to July seems to have been the main period when allis shad spawned. The actual temperature at which spawning begins seems to vary regionally across Europe but is mostly above 15°C (Quignard & Douchement 1991a). The eggs are sensitive to water temperatures below 16–18°C (Hoestlandt 1958; Cassou-Leins & Cassou-Leins 1981), so temperatures above 18°C in June and July should be most favourable for incubation. Climate change may make some British rivers more favourable for allis shad than in the past (Maitland 1991).

In the Wye and Teme, twaite shad accumulate in pools during the day, moving out onto the shallow, sandy-gravel riffle areas of 30 cm or so in depth to spawn during the night (Aprahamian 1982). The current is generally described as 'fast flowing', occasionally as 'riffle' and at one site (River Severn at Haw Bridge) as 'smooth'. Commonly, however, there is an area of deep water or a deep pool close by (a juxtaposition of pools and riffles) (Aprahamian *et al.* 1998). In contrast, at the spawning reserve for

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Rivers in spate are detrimental to shad, by making it difficult to reach spawning grounds and reducing recruitment after spawning.

allis shad on the River Garonne at Agen, the river is mostly 1–1.5 m in depth (Maitland *et al.* 1995) with a current of about 1 m s^{-1}.

In France, twaite shad have been recorded as spawning in relatively slow-flowing deep water, and in the River Severn some may spawn at depths of up to 3 m. The fact that egg density was found to decline with depth suggests that, in these particular rivers, twaite shad prefer to deposit their eggs in shallow areas where the water depth is around 45 cm. Cassou-Leins & Cassou-Leins (1981) and Dautrey & Lartigue (1983) suggest that, in most cases, the depth of water over spawning beds is not over 1.5 m. Similar findings were reported by Bracken & Kennedy (1967) and Phillippart & Vranken (1982), though in the River Garonne, eggs have been reported as deposited over mud where aggregate extraction has removed much of the gravel from a traditional spawning site. The spawning success at this site is unknown.

Although spawning sites are not necessarily very deep, they are always in places where the river is still tens of metres wide. In Britain, the narrowest site in which spawning has been recorded (on the River Teme) is around 20 m wide (M Aprahamian pers. com.) but spawning sites are typically 30–60m wide (Caswell & Aprahamian 2001). On larger rivers in France some spawning sites are considerably wider than this, with sites on the Garonne and its tributaries often being in the order of 150 m or more, and one site on the Rhône estimated at 250 m wide (Cassou-Leins *et al.* 2000). This preference for wider rivers is probably due to the aversion shown by shad to narrow channels and turbulent flow. It should be noted, however, that both the Garonne and Rhône have significant obstacles to migration that restrict upstream penetration.

Habitat in those stretches used for spawning should remain diverse, with deep pools and overhanging banks for rest and shelter before and after spawning, and adjacent areas of suitable gravel over which to spawn. At the spawning reserve for allis shad at Agen on the River Garonne, there has been some channel straightening and bank alteration, but this has now been stopped in the hope that the river will return to a more natural condition (Maitland *et al.* 1995).

After spawning, the eggs lodge among the interstices of the gravel or are washed a short distance downstream. After hatching, the young inhabit the slow-flowing reaches of the lower parts of rivers until they move into the estuary, where they remain until the end of their second summer (Bracken & Kennedy 1967, Thiel *et al*. 1996). Apart from clear migration routes, the critical habitat requirements of adults relate to the spawning areas and nursery habitat (see below).

Substrate requirements of spawning grounds

Allis shad may spawn anywhere along the river in fresh water where the current is swift and the substrate is clean. They deposit their eggs over a substrate that can vary from sand (0.02–2 mm) to pebbles (2–20 cm), in water depths of 0.5–1.5 m, and where the current ranges from 0.5–1.5 m s^{-1} (Roule 1923; Ellison 1935; LeClerc 1941; Dottrens 1952; Hoestlandt 1958; Cassou-Leins & Cassou-Leins 1981; Dautrey & Lartigue 1983; Boisneau *et al*. 1990). They show a preference for spawning in swift currents at the end of pools where gravelly shallows begin (Le Clerk 1941; Hoestland 1958; Boisneau *et al*. 1990).

Most of the substrates at the twaite shad spawning sites identified in rivers in England and Wales (Aprahamian *et al.* 1998) are described as 'gravel'. The size of the gravel beds involved varies, but one (on the River Wye at Hampton Bishop) is described as 75 x 10 m; another (on the River Wye at Wilton Island) as 90 x 20 m; and a third (on the River Wye at Foy) as 170 x 27 m. In the River Teme at Powic Weir there is a spawning bed of 50 x 10 m. In the River Usk, downstream of the Usk Town bridge, the habitat (mainly cobble with some gravel and coarse sand) is similar upstream and downstream for approximately 2.5 km. It is possible that shad may use the whole of this area to spawn (Aprahamian *et al*. 1998).

The spawning habitat of twaite shad in the rivers Wye, Usk, Tywi and Teme comprises a fast-flowing, shallow area of unconsolidated gravel/pebble and/or cobble substrate. The River Habitat Survey flow

Tristan Hatton-Ellis/CCW

Twaite shad prefer to spawn in shallow, fast-flowing water with an unconsolidated gravel or cobble bed, such as the River Usk in Wales. Shad spawning requirements may be similar to those of brown trout.

types 'smooth flow', 'rippled flow' and 'unbroken standing waves' were significantly ($P < 0.05$) associated with the presence or absence of shad eggs, and the absence of eggs was significantly associated with the lower energy flow type 'smooth flow' (Caswell & Aprahamian 2001). The channel structure described for identified spawning sites in England and Wales varies. At one (River Wye at Builth Wells), there are 'shallow shelving banks with a few trees', whereas at others, undercut banks with overhanging trees are present. In-stream vegetation (commonly water crowfoot, *Ranunculus* spp.) may provide cover at some sites, and at many the surrounding land is pasture.

At the spawning reserve for allis shad on the River Garonne at Agen, the substrate is mainly gravel and pebble, with little sand or silt (Maitland *et al.* 1995). Cassou-Leins & Cassou-Leins (1981) define the substrate there as pebbles of mean size 7–8 cm, with a range of 3–16 cm. On the River Dordogne, the majority of spawning took place over a substrate dominated by pebbles ranging from 2–20 cm, whereas in contrast, the spawning site on the River Loire (Boisneau *et al.* 1990) was dominated by sand followed by gravel (2–20 mm).

Little is known about the precise nature of the gravel beds used for spawning by shads. It seems likely, from the position of shad spawning beds at the tails of pools, and the obvious needs of shad 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 inches (7.5 cm) 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). However, such comparisons should be made with caution, as shad do not cut redds, and may therefore require both cleaner and coarser gravels into which the eggs can settle. Hillman (2002) has also found evidence that allis shad may spawn in tidal river sections and work is in progress to substantiate this.

Although there is some evidence of homing in shads (Quignard & Douchement, 1991a,b), it is not known if adults return to their natal gravels or the same gravels over which they may have previously spawned. Many traditional spawning grounds for shad have probably been damaged by the removal of gravel, a common practice in some areas (Aprahamian *et al.* 1998).

Hass (1965) and Thiel *et al.* (1996) reported twaite shad spawning in the upper reaches of the Elbe estuary where the salinity was in the region of 0.3 parts per thousand. The current stirs up the eggs and there is a general increase in egg density with water depth. Larvae here showed a preference for the mid-channel and areas of greatest depth, where the current is maximal, and a preference for temperatures in the range 17–21°C for larvae 7.7–15.2 mm in length, and from 17–21.5°C for larvae 18.4–23.8 mm in length (Gerkens & Thiel 2001).

In general, the habitat in those stretches used for spawning should remain diverse, with deep pools and overhanging banks for rest and shelter before and after spawning, and adjacent areas of suitable gravel over which to spawn.

Juvenile requirements in fresh water and estuaries

In the River Wye, most young twaite shad were found by Aprahamian (1981, 1982) to occur in deep pools close to the bank where they could avoid the faster river currents. Larvae feed primarily on insect larvae, especially chironomids and simuliids (Aprahamian 1989), while somewhat larger juveniles take an increased proportion of mayfly larvae (Ephemeroptera) (Cassou-Leins & Cassou-Leins 1981).

Temperature seems to be an important influence in determining year-class strength. Crecco *et al.* (1986) and Crecco & Savoy (1987) came to the conclusion that climatic factors – notably river flow

David Withrington/English Nature

In the River Wye (above), young twaite shad tend to remain in deep pools near the banks, avoiding fast currents. They remain in the Wye until the first flood after spawning. Populations in other rivers migrate to estuaries as soon as the temperature drops to a certain level, which may be immediately after spawning.

and rainfall in May and June – are a major regulatory factor for shad populations, and models incorporating these factors were found to explain 80–90% of the variability in stock recruitment.

Aprahamian *et al*. (1998) found that mean July temperature explained the greatest proportion (67.1%) of the variance in 0+ twaite shad year-class strength from the Severn Estuary, followed by August (50.9%) and June (30.9%). Claridge & Gardner (1978) attributed the highly successful spawning of twaite shad in 1975 and 1976 to exceptionally high temperatures, which may have encouraged spawning activity and enhanced subsequent larval survival and growth. Part of this variation can be associated with variation in temperature – for example, Holmes & Henderson (1990) reported that good recruitment was associated with warm years.

Taking the mean temperature for the three-month period improved the proportion of variability explained to 77.1% (Aprahamian & Aprahamian 2001). Crecco & Savoy (1984) found that, for the American shad, year-class strength was positively related to river temperature in June. Marcy (1976) also believed that temperature was important in juvenile production of this species.

There are few reliable data available on the specific requirements of shad relating to water quantity. However, Aprahamian & Aprahamian (2001) found a strong positive correlation between year-class strength and water temperature in the Severn, where water temperature is strongly correlated with discharge.

Crecco & Savoy (1984) found that for the American shad, year-class strength was inversely related to rainfall and river flow, the latter explaining 46.2% of the year-class strength. Marcy (1976) reported that 46% of the variation in the production of this species could be explained by river discharge during June, though this was not significant at the 5% level of probability. The results were disputed by others, who felt that Marcy had miscalculated his data (Aprahamian *et al*. 1998), and that river discharge was much less important, explaining only 0.7–3.0% of the variation in the abundance of juveniles.

In the Wye, young twaite shad remained in the river until the first flood after spawning. In contrast, it was found in the River Severn that most juveniles migrated towards the estuary when the water temperature drops below 19°C, often soon after hatching. Channelisation, which reduces habitat for young shad, has been more severe in the River Severn than in the Wye, and this may be the reason for the early departure of young fish from the former.

Once in brackish water, the young remain in the estuary for the remainder of the summer. Although a wide range of foods are taken, the primary item is nearly always mysids and copepods (Aprahamian 1989; Taverny 199). An abundant supply of these crustaceans is probably essential for good recruitment. In the Severn Estuary, juvenile twaite shad gorge themselves on the mysids feeding at the salt wedge near the head of the tide (M Aprahamian, pers. comm.).

General water quality requirements

Although Quignard & Douchement (1991a) state that 'Nothing is known about its resistance to chemical pollution', in the Rivers Loire and Garonne in France (two of the present strongholds of shad) some pollution in the lower reaches appears to be tolerated (Labat *et al.* 1984). Some chemical data for these rivers (and for the rivers Thames and Severn in Great Britain in which allis shad used to occur) are available (Table 2). In the River Thames, pollution, which is thought to have wiped out the population of shad, is much less than formerly. Although some fish species have returned, water quality may still not be good enough for shad, which may be more sensitive to pollution than other estuarine species (Alabaster & Lloyd 1982).

Twaite shad is reported as being sensitive to pollution, but few data appear to be available. Whelan (1989) suggests that it is highly sensitive to pollution and that around Ireland this species has suffered from river, estuarine and coastal pollution, as well as the blocking of rivers by weirs, dams and locks (Whilde 1993). Some chemical data for these rivers are available and given in Table 2. Bird (2002) reviewed the likely impacts of pollutants in the Severn Estuary and noted that (i) pollutants increase in bioavailability with decreasing conductivity and (ii) as well as causing mortality, metals may affect migration behaviour by sublethal effects on locomotion and olfaction. In estuarine waters, Bird (2002) considered that the synergistic effects of different metals were more important than the concentration of any single pollutant, with cadmium and copper being the most significant risk factors in terms of their relative toxicity to clupeids and respective concentrations in the estuary.

These data give a very general indication only of the chemical quality of these rivers. In the absence of specific tolerance data for shad it must be assumed that conditions in all parts of any river where shad occur, or pass through on migration, are at least UK Environment Agency Water Quality Class B for England and Wales, and A2 in Scotland.

Table 2. Physical and annual mean chemical data from the rivers Loire (at La Poissonière) and Garonne (at Couthures), sampled in 1988–89, and available data for the rivers Thames and Severn (Eurostat 1995).

Catchment (km^2)	118,000	85,000	15,000	11,600
Length (km)	1,010	575	340	–
Annual discharge (m^3 s^{-1})	1,015	666	–	–
pH	8.3	7.8	–	–
Conductivity (µS cm^{-1})	328	268	–	–
Chloride (mg l^{-1})	25	14	–	–
Oxygen (mg l^{-1})	10.9	9.9	8.0	10.6
BOD5 (mg l^{-1})	5.5	1.3	2.4	2.4
COD (mg l^{-1})	29.5	8.5	–	–
Ammonium nitrogen (mg l^{-1})	0.2	0.2	0.4	0.2
Nitrate/nitrite (mg l^{-1})	3.4	2.3	7.0	6.0
Total phosphorus (mg l^{-1})	0.1	0.1	–	1.0

Exploitation, disturbance and the impact of introduced species

Although the allis shad was formerly fished in the River Severn and is still exploited in a few rivers in Europe (for example, the River Garonne), it is rare in the UK. The only fish taken are individual specimens accidentally caught in rivers by anglers or at sea by commercial fishermen (Lyle & Maitland 1995). The present British rod-caught record weighed 2.166 kg and was caught off Chesil Beach in Dorset in 1977. It is now illegal to fish for allis shad in Britain, given its protection under the Wildlife and Countryside Act (1981). Evidence from the River Garonne indicates that healthy stocks are able to survive some types of disturbance (such as gravel extraction near spawning beds, which was eventually stopped) and the presence of some species of alien fish (rainbow trout). However, little is known about the impact of such factors and the precautionary principle should apply until adequate data are available.

Twaite shad are exploited in Britain much less than formerly. Most fish are taken as by-catches of netting or trapping for Atlantic salmon, by anglers fishing for other species, or by commercial fishermen who take a few each year at sea. Although several hundred are usually taken each year by anglers in the River Wye and other rivers in which twaite shad run, there is no evidence that this has had a detrimental effect on stocks. The British rod-caught record stands at 1.417 kg for two fish – one caught in 1949 near Deal in Kent, and the other in 1954 near Torbay in Devon. Elsewhere in Europe the species is still taken commercially in a number of European rivers.

Some shad are taken in at the water intakes of power stations. Henderson (2003) estimated that as many as 50,000 juvenile twaite shad may be entrained annually on the screens of the power stations in the Bristol Channel. Paradoxically, such catches have proved a valuable tool in monitoring and understanding the relationships between adult run size, recruitment and temperature. Similar problems have been experienced elsewhere, especially in France (Taverny & Elie 1988; Elie & Taverny 1989; Taverny 1990) and any new proposals for power stations should be subject to rigorous environmental assessment.

There is no information on the impact of introduced species on twaite shad. However, some species of alien fish, such as rainbow trout, are present in shad rivers, and it would seem reasonable that the precautionary principle should apply until adequate data are available (i.e. that there are no introductions to shad rivers and fish farm escapes should be minimised). The education of local fishery managers (Maitland 1999a, 1999b) is an important aspect of this.

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Twaite and allis shad are not caught commercially in the UK as much as in previous years, although they are still fished in parts of Europe.

Recommendations for research

The main recommendations for research are to:

- Collect further data on the occurrence of shad in British waters, in both time and space, especially the verification of any further spawning populations. Ensure that any shad collected are identified correctly, so that the true status of allis shad (in relation to the generally commoner twaite shad) is clear. Gill raker counts should be made of every individual identified as allis shad or whose length exceeds 40 cm.
- Determine which barriers to migration are the most significant in preventing the re-establishment of allis shad.
- Carry out further research on shad in areas where adults are regularly found but spawning sites are unknown (for example, the Solway Firth).
- Further international collaboration to investigate the genetic diversity and relationships among the various populations of allis shad in Europe.
- Consider, and carry out research relevant to, the reintroduction of allis shad to one or more of its historic sites if natural recolonisation cannot be achieved.
- Monitor important populations. Following a review of available techniques, **Life in UK Rivers** has produced a best-practice monitoring protocol for shad.

Conclusions

As understood at present, the general habitat requirements of shad can be summarised as:

- Larger rivers with a slow to moderate current speed and without significant natural or artificial obstructions in the lower reaches.
- Accessible shallow gravel beds for spawning, adjacent to slow flowing pools or glides that are not susceptible to strong flushing flows.
- A relatively unpolluted estuary with a good supply of small crustaceans, especially mysids.
- Moderate flows in spring to allow good penetration into the catchment, followed by low flows and/or warm summer temperatures to stimulate growth.

The following can be considered significant risk factors:

- Dams, barrages, weirs, sluices, etc., even if passable by salmonids.
- Water intakes, especially from power stations or other industrial processes.
- Habitat modification resulting in uniform channel structure.
- Poor water quality, especially in summer.
- Overfishing.

Relatively little is known about the detailed ecological and habitat requirements of shads, and for this reason it is difficult to define and set absolute targets for favourable condition based on science (Maitland 1989). The generic conservation objectives are regarded as feasible and, if achieved, of significant benefit to shad populations, but these may require adjustment in the light of future knowledge.

In view of the lack of detailed information on the ecological requirements of the species, it is clear that initiatives to restore chemical and physical conditions in the river(s) concerned to those pertaining when shad were more widespread would be sensible (Maitland 1992).

It seems possible that, since there are no known spawning populations of allis shad left in the UK, reintroduction programmes may be needed. However, given the widespread evidence of the re-colonisation of rivers by shad in France and the Baltic, and the regular detection of individual allis shad ascending UK rivers, a preferred strategy would be to encourage natural recolonisation through the removal or alteration of barriers to migration.

Much more research is needed on the biology and ecology of this species.

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Life in UK Rivers was established to develop methods for conserving the wildlife and habitats of rivers within the Natura 2000 network of protected European sites.

Set up by the UK statutory conservation bodies and the European Commission's LIFE Nature programme, the project has sought to identify the ecological requirements of key plants and animals supported by river Special Areas of Conservation.

In addition, monitoring techniques and conservation strategies have been developed as practical tools for assessing and maintaining these internationally important species and habitats.

The allis and twaite shad are the only members of the herring family in Britain. Once widely fished across Europe, they are now declining across their range, and there are no known breeding sites for allis shad in Britain. Most shad fisheries have collapsed due to the construction of river barriers that prevent them from reaching upstream spawning grounds, and the two species are often forced to interbreed because they cannot reach spawning areas.

Vulnerable to a wide range of threats, allis and tawite shad are now at the heart of a major European effort to conserve key freshwater animals and plants and the river habitats that sustain them.

This report describes the ecological requirements of the allis and twaite shad in a bid to assist the development of monitoring programmes and conservation strategies that are vital for their future.

Information on Conserving Natura 2000 Rivers and Life in UK Rivers can be found at
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This document was produced with the support of the European Commission's LIFE Nature programme and published by Life in UK Rivers – a joint venture involving English Nature, the Countryside Council for Wales, the Environment Agency, the Scottish Environment Protection Agency, Scottish Natural Heritage and the Scotland and Northern Ireland Forum for Environmental Research.