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► **To cite this version:**

Miran Aprahamian, Paulo Alexandrino, Carlos Henggeler Antunes, F. Cobo, Jimmy King, et al.. Shads state of the art: 3. Report of the ICES Workshop on Lampreys and Shads (WKLS), 2015, pp.46-105. <hal-02602614>

HAL Id: hal-02602614

<https://hal.inrae.fr/hal-02602614v1>

Submitted on 16 May 2020

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3 SHADS STATE OF THE ART

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3.1 LIFE CYCLE

3.1.1 Life History

Allis shad, *Alosa alosa* (Linnaeus, 1758) belong to the herring family living most of their life in seawater but migrating to freshwater to spawn. They mature at 3-6 years of age and migrate many hundreds of kilometres upstream into their natal river to spawn. Spawning occurs during spring months in the main River and major tributaries, in shallow waters over gravel substrate. The adults usually die after spawning. Allis shad larvae hatch within 4-5 days after spawning, spend the summer in freshwater, and migrate into the river estuaries during autumn. Before they complete their first year of life they migrate back into the ocean.

Twaiite shad, *Alosa fallax* (Lacépède, 1803), is an anadromous species, the adults living in seawater, and migrating to fresh water to spawn. Anadromous populations of *Alosa fallax* mature from 2 to 9 years old, with the majority of females maturing at age 4 and 5 years and the males one year earlier. Nearly all anadromous populations of *A. fallax* have an iteroparous life history with the populations having a high proportion of repeat spawners, the exception being the Moroccan populations in the Sebou and Loukos which are semelparous (Sabatié 1993). Spawning occurs in the spring / summer with the juveniles migrating seaward in the autumn. A portion of the one-year-old fish re-enter the estuary in the spring before again migrating seaward in the autumn (Aprahamian 1988).

3.1.2 Species distribution

Allis shad historically occurred along the Atlantic coast from Norway to Morocco, extending to the British Isles, the coasts of Germany, Holland, Belgium, and France, and then down to Spain and Portugal (Blanc *et al.* 1971; Lelek 1980). Although less abundant than in the Atlantic, allis shad also occurred in the Western Mediterranean along the coast of Spain, especially in the Ebro River (Lozano-Cabo 1964). Its presence along the Mediterranean coast of France was rare and uncertain (Roule 1925; Hoestlandt 1958).

Alosa fallax has been reported from as far North as Iceland (Saemundsson 1949), to Morocco in the south (Sabatié 1993) and as far east as Scandinavia (Pethon 1979) and the Baltic Sea (Manyukas 1989). A spawning population of *A. fallax* has been reported from the Nemunas (Neman / Nyamunas) River, Lithuania (Manyukas 1989). In the past they were able to ascend 400 km up river to spawn, however,

since the construction of the Kaunas hydroelectric dam in 1959 they were confined to the lower 224 km upstream of the mouth. Arising from the construction of the Kaunas hydroelectric dam and elevated pollution from poorly treated wastewater from paper mills in the lower river the population declined (Maksimov and Toliušis 1999; Repečka 1999, 2003a and b; Žiliukas and Žiliukienė 2002). However, since the late 1990s they have become increasingly more abundant (Maksimov 2004; Repečka 2003a, 2012).

On the south shore of the Baltic Sea *A. fallax* has been found in the lower reaches of the River Vistula, Poland (Chmielewski 1965) and has been reported sporadically in the River Oder (Waterstraat 1986). In the first half of the twentieth century the Elbe, Weser, and Ems rivers all supported commercial fisheries for *A. fallax* (Drimmelen 1951; Nolte 1976). A spawning population exists in the River Elbe (Hass 1965, 1968; Möller and Dieckwisch 1991; Thiel *et al.* 1996) and the River Weser (Scheffel and Schirmer 1991). *Alosa fallax* has been reported from the River Ems in the past (Lohmeyer 1909; Svetovidov 1963), and the recent report that juveniles have been caught in the Ems Estuary during the 1990s (Haddingh and Jager 2002), suggests that a spawning population may still exist. There are indications of increasing numbers of twaite shad in coastal and offshore areas of the southern North Sea for the period during the late 1990s-early 2000s (Stelzenmüller *et al.* 2004, Neudecker and Damm 2005, Thiel and Backhausen 2006), though no significant increase has yet been observed in the Wadden Sea (Jager *et al.* 2009). There are indications of an increase in the stock of *A. fallax* in the Weser estuary (Scholle and Schuchardt 2012).

Ripe and running adult *A. fallax* are regularly recorded from five estuaries around Denmark; Randers Fjord, Limfjord, Nissum Fjord, Ringkøbing Fjord and the Wadden Sea though the actual spawning sites are not known (<http://europa.eu.int/comm/environment/nature/>; Volk *et al.* 2007).

A spawning population of *A. fallax* existed in the Rhein (Rhine) (Hoek 1899; Redeke 1938) until the middle of the twentieth century (de Groot 1989). The most significant factor in its decline was the damming of the river (de Groot 1989) and resulting increase in sedimentation (De Nie 1996), and today the species is only rarely encountered (de Groot 1989; Bartl and Troschel 1995).

In Belgium, at the turn of the nineteenth century, Cunningham (1891-92), citing a work by Metger and Hoek, reported the presence of a spawning population of *A. fallax* in the River Meuse. However, by 1950 *A. fallax* were no longer found in the Walloon part of the rivers Escaut and Meuse (Philippart and Vranken 1981, 1982) as a result of over-exploitation, pollution, habitat destruction and the building of weirs (Philippart *et al.* 1988). Maes *et al.* (1998) and Vrielynck *et al.* (2003) reported that historically *Alosa fallax* used to spawn just above the tidal limit in the River Scheldt on sandy beaches near Schelle. The decline was associated with environmental degradation. However, recently twaite shad have been recorded from the Lower River (Maes *et al.* 2005; 2008). Historically, there were well-established populations of *Alosa alosa* on the Scheldt (De Selys-Llongchamps 1842), however by the end of the 1930s they had become extinct (Poll 1945).

Alosa fallax has been reported from most areas around the British Isles (O'Maoileidigh *et al.* 1988; Potts and Swaby 1993; Aprahamian *et al.* 1998). Spawning populations of *A. fallax* exist in the rivers Severn, Wye, Usk, and Tywi (UK) and in the Barrow, Nore, and Munster Blackwater in Ireland (Aprahamian and Aprahamian 1990; King and Roche 2008). In Ireland twaite shad numbers have decreased substantially in the Suir and Slaney (King and Roche 2008). Fahy (1982) reported shads in the Slaney as a by-catch of

mullet and other species. Isolated occasional samples now occur on the Slaney. A small number of Twaité shad were taken by angling in the Suir in 2011 (Inland Fisheries Ireland, unpublished data: <http://www.fisheriesireland.ie/fisheries-research-1/279-national-programme-habitats-directive-and-red-data-book-fish-species-executive-report-2011-1/file>). The River Thames supported a spawning population up until the middle of the nineteenth century. Its decline has been attributed to deterioration in water quality (Aprahamian and Aprahamian 1990). A spawning population of *Alosa fallax* may currently exist in the Solway Firth area (Scotland) [Maitland and Lyle 2005] and there is some evidence to suggest that *Alosa alosa* are spawning in the River Tamar (England) [Hillman 2003].

Along the North French coast a spawning population of both species previously existed in the Seine (Vincent 1889; Roule 1920a), but the extension of the dam at Poses in 1886 (LeClerc 1941) dramatically affected these species. The number of allis shad caught in the lower River Seine in 1897 dramatically decreased, with 'no more than 20 fish caught during the entire season' (Gadeau de Kerville 1897). Twaité shad maintained their abundance up to 1950, after which the population declined rapidly because of a deterioration in water quality (Belliard 1994). In recent years a few allis shad have been reported from the Seine (Belliard *et al.* 2009), their re-occurrence being associated with an improvement in water quality and the construction of fish passes (Rochard *et al.* 2007; Belliard *et al.* 2009). Spawning populations of *A. fallax* have been reported in the rivers Orne and Vire (lower Normandy) (Baglinière *et al.* 2003; Rochard, *et al.* 2007) and the Brittany rivers Aulne and Blavet (Véron 1999).

Of the rivers entering the Atlantic, spawning populations of *A. alosa* and *A. fallax* are present in the Vilaine, Loire, Charente, Garonne and Dordogne, Adour and Nivelle (Mennesson-Boisneau and Boisneau 1990; Taverny 1991a; Prouzet *et al.* 1994a; Véron 1999; Baglinière 2000). On the Vilaine access to the river was blocked in 1970 by the construction of Arzal Dam, in 1996 a fish pass was installed and the number of *Alosa* spp. has increased steadily. In the Garonne and Dordogne the original distribution of *A. alosa* had become restricted because of dams at Bazacle (1774), Mauzac (1843) and Golfech (1971). However, the construction of fish pass facilities at these obstructions since 1987 have been successful in extending access for *A. alosa* to the upper river.

Along the Atlantic coast of the Iberian Peninsula spawning populations of both shad species have been reported in the rivers Bidasoa, Asón, Deva, Sella, Nalón, Narcea, Eo, Ulla, Umia, Lérez, Verdugo, Louro, Tea, Tamuxe, Minho, Douro, Lima, Mondego, Tagus, Erjas, Guadalquivir, Ardilla, Guadiana, Guadiaro, Hozgarganta (Nobre, 1932; Ribeiro, 1971; Eiras, 1980; Assis, 1990; Alexandrino, 1996a; Collares-Pereira *et al.* 2000; Doadrio *et al.* 2011; Nachón *et al.*, 2013; Nachón *et al. in press*). The Douro and Tagus river basins are two good examples of the reduction of the suitable habitat for the shads caused by the construction of dams and weirs. For the River Tagus the main habitat loss occurred in the 1950's with the building of two large dams, Castelo de Bode and Belver. In the Douro, after the construction of the Crestuma dam in 1985 (21 km from the river mouth), the situation became worse almost leading to the disappearance of the shad populations from this river. Spawning populations of *A. fallax* exist in the rivers Mira, Cávado, and Sado (Alexandrino 1996a) and in the River Guadalquivir (Doadrio *et al.* 1991). There are three landlocked populations of allis shad in Portugal, one in the Aguieira dam reservoir (Mondego river basin) another in the Castelo de Bode dam reservoir (Tagus river basin) (Collares-Pereira

et al. 1999), and the most recent in the Alqueva reservoir (Guadiana river basin), that were prevented from returning to the sea after the construction of the dams.

In the Moroccan Oueds draining into the Atlantic Ocean, spawning populations of *A. fallax* are now only present in the Loukos and Sebou (Sabatié 1993). However, the construction of barrages and degradation of the habitat has resulted in a number of populations becoming extinct. The most important population was in the Oued Sebou however, the construction of the barrage at Idriss ler in the early 1970s drowned out a number of spawning areas in the Oued Inaouen with the resulting decline in the population with the catch declining to ~10t yr⁻¹ from 700-800 t yr⁻¹. Though a fish pass was incorporated into the barrage it was ineffective. In the 1980s the situation for the shad in the Oued Sebou was further compounded by pollution from sugar factories, paper mills, yeast factories and from urban and agricultural sources. Together with high fishing pressure and, in the 1990s, a new dam being built at Lalla Aïcha, 40 km from the mouth of the estuary, these various pressures resulted in the species becoming extinct in the Oued Sebou (Sabatié 1993). Other Oueds which used to support spawning populations of *Alosa alosa* were the Bou Regreg, Oum er Rbia and the Massa (south of Oued Oum er Rbia). The populations have become extinct following the construction of weirs in 1968-69, 1929 and 1973 respectively. Historically, the most southern population of *Alosa* was in the Oued Massa.

In the Mediterranean, Lozano Rey (1935, 1950) mentions the occurrence of *A. alosa* in the Ebro (Spain) and Doadrio *et al.* (2011) reported the occurrence of *A. fallax* in the rivers Ebro and Fluviá. However, the construction of the Ribarroja (1967) and Mequinenza (1964) reservoirs in the lower reaches has meant that allis shad are now confined to the river's delta (Sostoa and Sostoa 1979; Sostoa and Lobon-Cervia 1989). Recent studies (López *et al.* 2007, 2011) pointed to an ongoing recuperation of twaite shad population in the River Ebro (Spain). Of the French rivers draining into the Mediterranean, Douchement (1981) mentions the presence of a spawning population of *A. alosa* in the rivers Aude and Rhône, though the number of gill rakers suggests that they might be hybrids. The presence of *A. alosa* in the Rhône was also reported by Le Roux (1928) and Rameye *et al.* (1976). Rameye *et al.* (1976) considered them to be rare. In a recent intensive study on the Rhône by Le Corre *et al.* (1997) none were recorded, suggesting that the population may now be extinct. A population of *A. alosa* may also exist in the River Argens (Didry 1953; Changeux and Pont 1995).

Of the Moroccan rivers draining into the Mediterranean a spawning population of *A. alosa* used to exist in the Oued Moulouya, but became extinct in 1953 following the construction of the Mechra-Hommadi dam (Sabatié 1993).

3.1.3 Freshwater Phase: habitat preferences, ecology, behavior

Allis shad spawn between April and mid-August at sites typically located in the middle or upstream reaches of the river (as far as 650 km from the sea in the Loire; Mennesson-Boisneau and Boisneau 1990). Spawning habitat is characterized by an area of coarse substrate limited upstream by a pool and downstream by shallow water with fast-moving currents. Spawning takes place at night in a succession of characteristic behavioural sequences (rapid circular swimming near the surface) with the emission of

a splashing known as the “bull phenomenon”. Spawning is highly dependent on water temperature (generally between 16°C and 18°C) and ceases during strong spates.

After spawning, the eggs (1–2 mm in diameter) drift in the current before hitting the bottom where they become embedded in small crevices in the substrate. The incubation period is short (4–8 d), but the temperature must be over 17°C (Taverny *et al.* 2000b). Larvae are 7–12 mm TL (total length) at hatch, when they move to open water and exhibit a positive phototropism. They adopt a nektonic behaviour that persists until they are 36 d old. Larvae prefer low current (Véron *et al.* 2003). This habitat preference and distribution of prey could explain movements from mid-channel spawning grounds to shallow banks observed in rivers at early stages (Taverny *et al.* 2000b). Downstream migration toward the sea begins with these local movements. Seaward emigration occurs in schools, taking place in the summer and fall of their first year of life, and lasts from 3 to 6 months. This occurs earlier in southern rivers. As with the adults, juvenile migration is modulated by water temperature, river discharge, and biological factors (size and level of adaptability to marine conditions). Most young of the year reach the sea at the beginning of winter at lengths ranging from 50 to over 130 mm TL and weighing 2–20 g. Their growth is variable according to year, geographical location, and the position of the spawning site within the watercourse. Juvenile allis shad are generalist feeders, using a wide range of trophic resources available in the continental and estuarine environments, including aquatic insect larvae, mollusks and zooplankton.

Alosa fallax eggs successfully develop between 15°C and 25°C (Vincent 1894a) with incubation taking 72 to 120 h at 16.4°C (Ehrenbaum 1894) and 96 to 120 h at 19°C (Pouchet and Biéatrix 1889a; Vincent 1894a; Wheeler 1969). The spawning habitat of twaite shad in the UK and Ireland comprises a fast-flowing shallow area of unconsolidated gravel/pebble and/or cobble substrate (Caswell and Aprahamian 2001; J.J. King personal communication). The depth of water at spawning can range from 0.15 to 1.20 m (Aprahamian 1981; Caswell and Aprahamian 2001; J.J. King personal communication), suggesting that, in these particular rivers, *A. fallax* prefer to deposit their eggs in the shallow areas where the water depth is less than 0.45 m (Aprahamian 1981). In France, the substrate has ranged from mud to cobble (mean size = 70 mm) (Anon. 1979; Cassou-Leins and Cassou-Leins 1981; Taverny 1991). On the River Elbe, Hass (1968) and Thiel *et al.* (1996) reported *Alosa fallax* spawning in the upper reaches of the estuary in tidal fresh water, in depths of up to 8.0 to 9.5 m. The eggs are maintained in the water column, by the current and also possibly by the buoyancy derived from the large peri-vitelline space, peak density occurring at depths more than 4 m below the surface (Hass 1968; Thiel *et al.* 1996).

The larvae and juveniles are usually found in backwaters, areas of low current velocity (Aprahamian 1982). In the Elbe estuary, where fish spawn in tidal fresh water, larvae (total length (TL) = 7.7–23.8 mm) were more abundant in the side-channels, which because of their slower currents provides better nursery and feeding areas (Gerken and Thiel 2001). It appeared that the larvae actively avoided shallow areas, close inshore. Temperature preferences for larvae between 7.7 and 15.2 mm were in the range of 17.0 to 20.0°C and for larvae from 18.4 to 23.8 mm were between 17.0 and 21.5°C. Juveniles (age 0+) avoided areas of low dissolved oxygen (<4 mg/L), the majority being caught in water of between 4 and 5 mg O₂/L (Möller and Scholz 1991).

Age 0+ fish migrate seaward during the autumn in the surface layers of the water column (Taverny 1991). In the rivers Severn and Elbe, a proportion of juvenile *A. fallax* (Age 1) reappear in the estuary in the spring (April to May) and remain until the following autumn (October) (Claridge and Gardner 1978; Aprahamian 1988; Taverny 1991; Thiel *et al.* 1996). It has been concluded that this represents a migration from the sea into the estuary as opposed to a seaward migration by fish over-wintering in the river or estuary (Hass 1965; Aprahamian 1988; Thiel *et al.* 1996). In the Gironde, however, it would appear that a portion of the juvenile population do reside overwinter in the estuary and/or in fresh water, and migrate seaward during the following October to March (Taverny 1991).

In the freshwater reaches of the River Wye and Sebou the diet of the larvae and juveniles was dominated by Uniramia, particularly the orders Ephemeroptera and Diptera, Chironomidae (pupae and larvae), and Simuliidae (larvae) (Aprahamian 1989; Sabatié 1993).

In the Severn estuary, the diet of the 0+ age group consisted mainly of Crustacea Harpacticoidea and Mysidacea, followed by Gammaridae and Calanoidea (Aprahamian 1989). The smaller members of the zooplankton (Copepoda and Cladocera) were more prominent in the diet during summer than in autumn. In the autumn, the larger crustacean members of the zooplankton (Mysidacea, Amphipoda) and Isopoda predominated, together with fish. This may be a function of gape size or it may reflect variation in the abundance of prey organisms. Similar findings were reported from the Sebou (Sabatié 1993) and Gironde (Anon. 1979 in Taverny 1991) with the exception that in the Sebou, Decapoda, and in the Gironde, Uniramia, were more important, particularly for the larger juveniles.

In the Elbe, larval *A. fallax* measure 4.25 to 6.0 mm (Ehrenbaum 1894) at hatching whereas in the Wye, larvae measure 6.2 to 9.2 mm (Aprahamian 1982). At the time the fish migrate seaward in the autumn they have reached a mean TL of between 60 and 80 mm. Little growth occurs over winter (Claridge and Gardner 1978; Anon. 1979; Aprahamian 1988; Taverny 1991; Thiel *et al.* 1996).

3.1.4 Marine phase: habitat use

Alosa alosa has been reported from depths ranging from 10 to 150m (Laroche 1985; Taverny 1991a) up to c. 300m (Roule 1933; Dottrens 1952; Lithogoe and Lithogoe 1971) and *A. fallax* from 10 to 110m with a preference for water of 10 to 20m deep (Taverny 1991a). A recently study (Bao *et al.* 2015) reported the depth distribution of both shad species in NW Iberian Peninsula waters, where *A. alosa* occurs between 9 and 311 m (mean depth 174 m) and *A. fallax* occurring between 18 and 390 m (mean depth 148 m). Taverny and Elie (2001a) showed that the depth at which both species were caught was significantly positively correlated with their age and size. Similarly, Trancart *et al.* (2014) found that for both species depth explained the greatest deviance in the data, with a preference for shallow areas (< 100 m), followed by salinity with a preference for low salinity areas. There was some suggestion that allis shad preferred mud while twaite shad preferred a gravel substrate. In relation to water temperature, Laroche (1985) observed that *A. alosa* in Moroccan coastal waters was closely associated with water in the temperature range of 14 to 18°C.

In the Adriatic, Morović (1959) found that *A. fallax nilotica* could be caught at depths ranging from the surface to 160m, with the fish preferring to be close to the bottom during the winter months.

3.1.5 Migrations

3.1.5.1 *Juvenile seaward migration*

Alosa alosa

Seaward emigration occurs in schools, taking place in the summer and fall of their first year of life, and lasts from three to six months (Baglinière *et al.* 2003). In the Loire juvenile *Alosa alosa* start the freshwater phase of their downstream migration during late June and the migration period extends until the middle of October (Boisneau *et al.* 2008).

Lochet *et al.* (2008) showed, using variation in the Sr:Ca ratio in the otoliths, that allis shad enter the estuary between 58 and 123 days after hatching with a median duration of 88 days. By the end of summer or early autumn, most 0+ juveniles are in the estuary (Poll 1947; Hoestlandt 1958; Anon. 1979a), the largest arriving at the river mouth around August and the smallest remaining in fresh water until September or October (Quignard and Douchement 1991a). In the Sebou (Morocco) it was relatively rare to find juvenile *A. alosa* in the estuary during July to September, though numbers increased by December (Sabatié 1993).

During their period in the estuary juveniles tend to be found at the surface and close inshore (Taverny 1991a). Castelnaud *et al.* (2001) reported juveniles to be ~ 10 times more abundant in the surface layers compared with samples taken 0.2 m above the bottom.

In the Gironde estuary, the juveniles first arrive in the estuary in August with the migration from the estuary to the sea commencing in October, reaching a peak in December and ceasing by the end of February (Albiges *et al.* 1985a; Elie *et al.* 1988a; Sertier *et al.* 1990; Taverny 1991a). Lochet *et al.* (2008) showed that the estuarine phase lasted from 4 to 36 days, with a median value of 11 days. Seaward exit occurred in fish aged from 63 to 150 days, with a median age of 99 days.

The temporal increasing trend in juveniles' size in the tidal freshwater area of the River Minho suggests a size-dependent seaward migration and, thus, the existence of an estuarine time window (Mota *et al.* 2015).

The downstream migration of the juveniles did not appear to be initiated either by a change in temperature or flow (Taverny 1991). However in the Sebou (Morocco), the downstream migration of both juvenile *A. alosa* and *A. fallax* was found to be closely associated with the autumn floods (Sabatié 1993). During the summer months the fall in water level results in the juvenile populations becoming isolated by the development of impassable fords, which only become passable with increasing discharge during the autumn.

The 1+ age group showed a similar pattern with December being the main month for migration seaward. This suggests that a portion of the juvenile population may remain in the river or estuary for a second year. A similar conclusion was reached by Hoek (1888), Meek (1916), Roule (1925), Lithogoe and Lithogoe (1971) and Wheeler (1969a).

Alosa fallax

The seaward migration of juvenile *Alosa fallax* has been studied on the River Severn, England (Claridge and Gardner 1978; Aprahamian 1988), the River Elbe, Germany (Thiel *et al.* 1996) the Gironde, France (Boigontier and Mounié 1984; Taverny 1991a; Castelnaud and Rochard 1993, 1994) and the Oued Sebou, Morocco (Sabatié 1993).

The juveniles can be found throughout the water column but have a preference for the surface layers where the fish were ~ 9 times more abundant when compared with samples taken 0.2 m above the bottom (Castelnaud *et al.* 2001). In the Gironde-Garonne-Dordogne system, Locht *et al.* (2009) showed, using variation in the Sr:Ca ratio in the otoliths, that twaite shad enter the estuary between 7 and 84 days after hatching and remain in the estuary for between 7 and 57 days with a median of 21 days. The 0+ fish migrate seaward during the autumn in the surface layers of the water column (Taverny 1991a). In the majority of cases the juveniles make a single migration (Locht *et al.* 2009; Magath *et al.* 2013) leaving by the end of October (Claridge and Gardner 1978; Thiel *et al.* 1996a), while in the Garonne it is not until the end of February that the majority have migrated seaward (Taverny 1991a). Magath *et al.* (2013), however, has shown that a proportion of the juvenile population undertake a two phase migration during their first year of life with juveniles making a migration into sea water, then subsequently returning to fresh water before migrating again into marine waters.

Claridge and Gardner (1978) considered the main environmental factor involved with the initiation of the seaward migration to be declining temperature. In the Severn estuary the authors found the peak migration of juvenile *Alosa fallax* to be associated with a decline in temperature below 19°C, with virtually none being caught once temperatures had fallen to less than 9°C. The effect of discharge alone did not appear to affect the timing of the juveniles' seaward movement (Aprahamian 1982).

In the rivers Severn and Elbe, juvenile *A. fallax* (Age 1) reappear in the estuary in the spring (April to May) and remain until the autumn (October) (Claridge and Gardner 1978; Aprahamian 1988; Taverny 1991a; Thiel *et al.* 1996a). It has been suggested that a small portion of the population overwinters in the estuary and emigrates seaward once the temperature reaches 7°C (Claridge and Gardner 1978). However, studies carried out over a wider spatial scale suggest that the juveniles may, in fact, be making an onshore migration into the estuary at this time (Aprahamian 1988; Thiel *et al.* 1996a), and similar conclusions were also reached by Hass (1965).

In the Gironde, however, it would appear that a portion of the juvenile population do in fact reside overwinter in the estuary and/or in fresh water, and migrate seaward during the following October to March (Taverny 1991a).

3.1.5.2 **At Sea**

Except for the study by Sabatié (1993) little information exists on shad movements at sea. Sabatié (1993) reported that juvenile *A. alosa* from the River Sebou in Morocco migrate south to an area of upwelling between Essaouira and Agadir (Latitude 31°N) a distance of approximately 600 km. The fish remain in this rich feeding area until they mature when they return to the Sebou to spawn.

At sea *Alosa alosa* and *Alosa fallax* are coastal in their habit and clumped in aggregations around the major catchments for reproduction (Quero *et al.* 1989; Taverny 1991a). The study of Martin *et al.* (2015) showed that some fish could migrate considerable distances, with some travelling more than 700 km from their natal river to their river of capture. Though the species is capable and does make extensive migrations, the existence of genetically (Alexandrino 1996a) and morphologically (Sabatié *et al.* 2000) distinct populations of *A. fallax*, despite their geographical proximity, seems to suggest an instinct to return to the river of origin or "homing" (Douchement 1981; Alexandrino and Boisneau 2000; Aprahamian *et al.* 2003). The existence of homing is very important because a population that has disappeared from a basin will not be renewed for a fraction of any of all stocks of the Atlantic continental shelf (Taverny 1991). However, more information and new data to evaluate and quantify the phenomenon of homing are needed. The work of Tomas *et al.* (2005) shows that discrimination of the natal stream of *A. alosa* is possible from the study of the chemical composition of otoliths, providing a promising way to clarify this question.

Martin *et al.* (2015) used both otolith microchemistry and genetic markers to determine river fidelity. Otolith fingerprints were used to define a new population baseline by grouping individuals from the same natal river, and then used this new baseline to assign all fish for which genetic data was available to potential groups, using GeneClass (Piry *et al.* 2004). These results were then compared to those obtained previously. The new baseline as defined by otolith natal origins was composed of eight groups representing the major French drainages. These new groups displayed similar level of genetic diversity when compared to populations defined according to their sampling site. Levels of Fis were also reduced. When using the new baseline 17 other individuals were assigned to a potential group at a 90% probability (Table 3.1). According to the new baseline, a greater number of individuals were mis-assigned to other rivers than their sampling river except for the Aulne, Nivelle and Vire rivers, where high rate of self-assignment were observed using the genetic baseline.

Table 3.1. Number of individuals from each river assigned to the otolith baseline. Only known origin individuals inferred from otolith chemistry ($n = 275$) were used in the baseline. All individuals ($n = 287$) were used in assignment tests. Only individuals with $P > 90\%$ were reported here.

River	Reference populations based on otolith natal origin							
	Adour R.	Oloron	Aulne	Dordogne	Blavet	Loire	Nivelle	Vilaine
Adour (46)	6 (13%)	9 (20%)	1				1	
Aulne (14)		1	9 (64%)		1			
Dordogne (69)	1	4 (6%)		3 (4%)		2		1
Blavet (17)					7 (41%)			
Loire (24)						11 (46%)		
Nivelle 2009 (17)							16 (64%)	
Scorff (10)					2			1
Vire (29)								18 (62%)
Garonne 2012 (25)								
Garonne 2013 (36)		1		5 (14%)				

Trancart *et al.* (2014) described the change in distribution of twaite and allis shad from the middle of the Bay of Biscay to the English Channel (ranging from 51.08 to 45.22° N and -6.09 to 1.45°E) using a presence/absence model based on bycatch data from commercial fishery surveys. The model predicted that during January and February, allis shad would be minimally present in the sea and primarily located near estuaries or in coastal areas, from March to August their presence was predicted in coastal areas and from September to December, the models predicted the presence of shad in oceanic waters (Figure 3.1). For twaite shad the distribution was similar; from January to February, twaite shad were predicted to occur primarily in the English Channel; from March to August, a high concentration of twaite shad was predicted in coastal waters, and more often than the allis shad; and from September to December, they were predicted to move to oceanic waters (Figure 3.2).

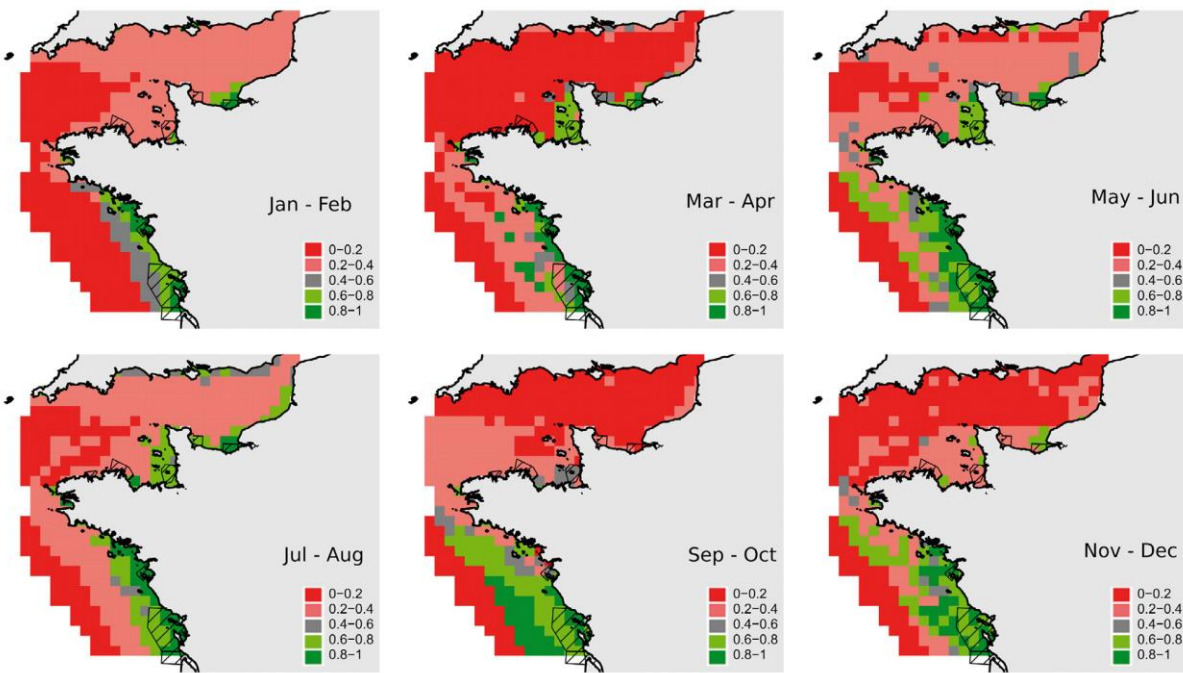


Figure 3.1. *Alosa alosa*. Prediction maps for allis shad (20 × 20 km cells) in the 2-mo-period approach. Colours show probabilities. Probabilities <0.4 may indicate the absence of shad (Trancart *et al.* 2014).

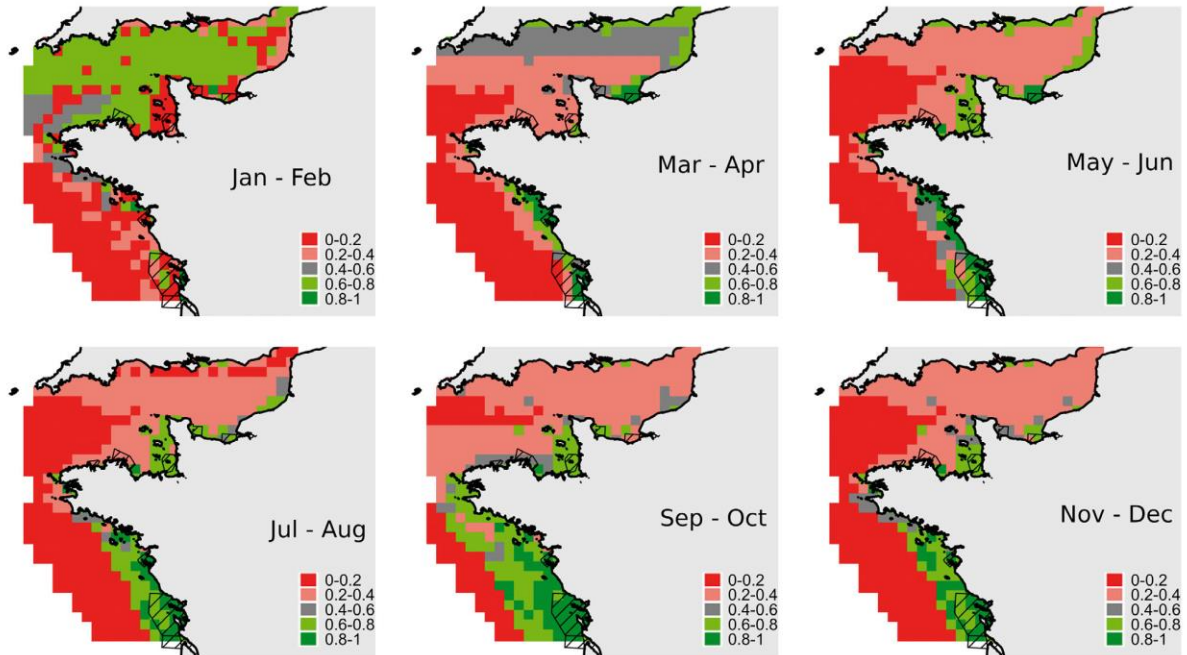
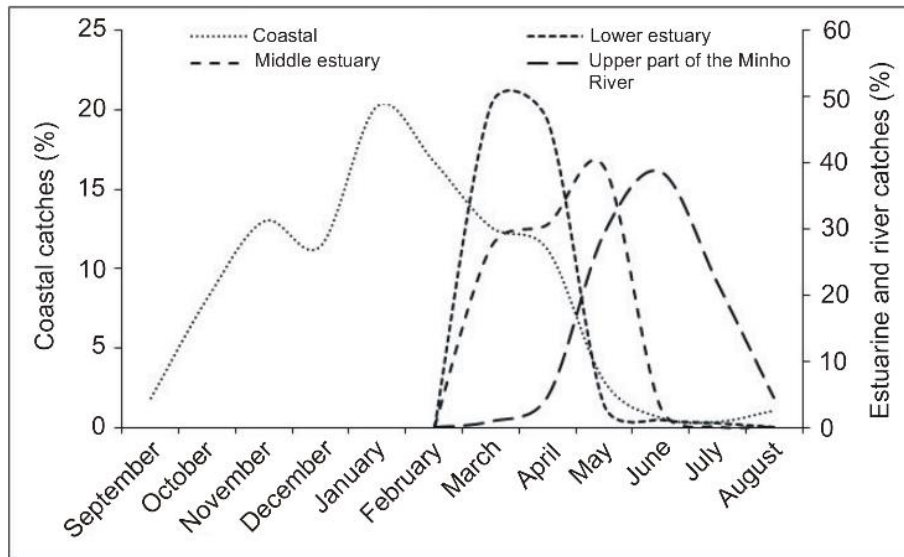


Figure 3.2. *Alosa fallax*. Prediction maps for twaite shad (20 × 20 km cells) in the 2-mo-period approach. Colours show probabilities. Probabilities <0.4 may indicate the absence of shad (Trancart *et al.* 2014).

A recent study (Nachón *et al. in press*) reported seasonal movements in coastal waters based on both bycatch data from commercial fishery surveys and freshwater field sampling campaigns. The authors observed, by coupling information obtained both for marine and river environments, that catches at sea declined since January, most probably due to the onset of the migration to the rivers (Figure 3.3).

a)



b)

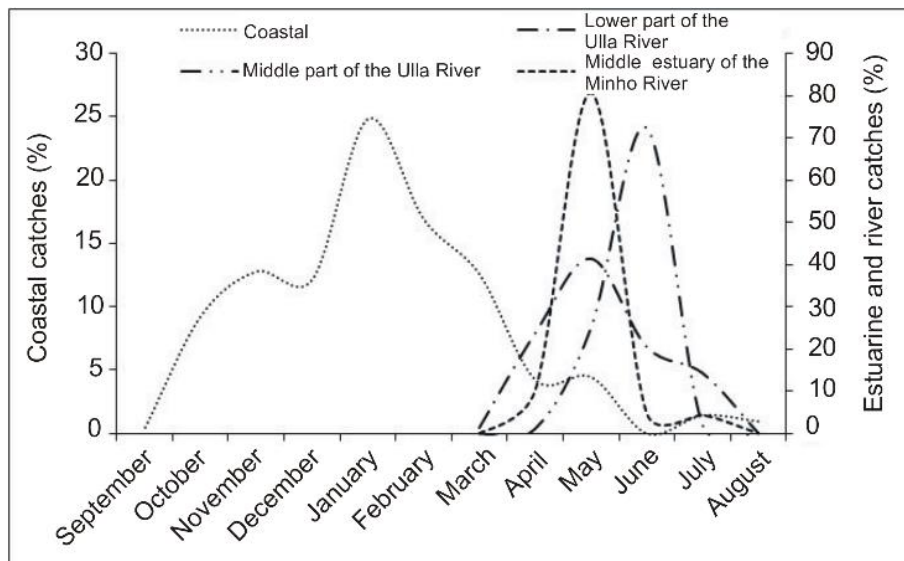


Figure 3.3. Monthly catches of a) *A. alosa* and b) *A. fallax* in each of the studied zones (Nachón *et al.* in press).

3.1.5.3 Adult spawning migration

The first information on migration of shads is from the early twentieth century but the information was fragmentary and the first works on migration only appeared in the 80s, both in Europe and in North Africa. However, there are certain difficulties in interpreting the data, due on one hand to methodological factors and on the other hand to factors of biological type (Mennesson-Boisneau *et al.*

2000). Regarding the methodological factors there is great variability of techniques used for sampling specimens that made it difficult to compare the information on migration between populations. In addition most of the data come from commercial fisheries, so data collection is subject to regulatory conditions of fisheries. Finally, the information typically comes only from a single point along the river axis: in the estuary (most cases) or at a point of the river. Related to the biological factors there are few data on the populations of the Mediterranean coast compared to the Atlantic coast, where moreover, most studies were focused on populations of *A. alosa*. Regarding *A. fallax* studies were practically restricted to estuarine areas. Despite these difficulties, there is a good overview on migration of shads along the east coast of the Atlantic Ocean. Both shad species have many similarities in the migration-spawning behaviour; however they differ in time and location. *A. fallax* penetrates about a month later in rivers, its activity comprises less months (three to three and a half against four or four and a half for *A. alosa*) and shows less variability in the starting and ending dates of spawning migration (Mennesson-Boisneau *et al.* 2000). Furthermore *A. fallax* travels shorter distances upstream to reach spawning areas (Mennesson-Boisneau *et al.* 2000).

Alosa alosa

The timing of the freshwater phase of their spawning migration is dependent on latitude. Populations towards the south of the range migrate earlier in the year than those further north (Table 3.2).

Tidal state explained the greatest proportion of variation in catch of *A. alosa* in the Loire (Mennesson-Boisneau *et al.* 1999) with catches increasing towards spring tides and decreasing as tidal height declined. Tidal state accounted for between 23.2 and 53.1% of the overall variability followed by flow (1.0 to 16.1%) and temperature (0.1 to 15.8%). However, in the Gironde, Rochard (2001) found that peak catches were correlated with neap tides, and the relationship between catch and tidal state was not consistent between years, with catch significantly correlated with tidal state 0 to 6 days prior to capture.

3.2 Temperature has long been considered one of the main factors affecting the timing of the freshwater phase of their spawning migration with migration starting once temperatures have reached 10 to 12°C (Roule 1925). In the case of the Sebou, temperature at the start of migration was 16°C, but decreased to 12°C at the peak (Sabatié 1993). This accounts for the negative correlation between the number of fish caught in the estuary per unit of effort and water temperature 14 days prior to capture ($r^2 \approx 0.2$). Sabatié (1993) reported a significant correlation between fish abundance and the flow 5 days prior to capture, and between abundance and flow in combination with temperature between 5 and 12 days prior to entry into the Sebou estuary ($r^2 \approx 0.2$). On the Adour, flow was of secondary importance to the strength of the tidal current in explaining variation in the catch of *A. alosa* (Prouzet *et al.* 1994a). In the Gironde estuary the temperature at the start of the migration varied between years, ranging from 7.5 to 10.0°C (N = 4). In any one year 50% of the migration occurred at temperatures either <15.0 or <16.0°C and 90% from temperatures ranging from <17.5 to <20.0°C (Rochard 2001).

Tidal state explained the greatest proportion of variation in catch of *A. alosa* in the Loire (Mennesson-Boisneau *et al.* 1999) with catches increasing towards spring tides and decreasing as tidal height declined. Tidal state accounted for between 23.2 and 53.1% of the overall variability followed by flow

(1.0 to 16.1%) and temperature (0.1 to 15.8%). However, in the Gironde, Rochard (2001) found that peak catches were correlated with neap tides, and the relationship between catch and tidal state was not consistent between years, with catch significantly correlated with tidal state 0 to 6 days prior to capture.

3.2. Timing of the freshwater phase of the spawning migration of *Alosa alosa*.

Table River, Country	Start	Peak	End	Reference
Sebou, Morocco	XII (XI)	II-III	IV (V)	Sabatié (1993)
Lima, Portugal	II-III	III-IV	V	Alexandrino (1996b)
Miño, Portugal	(III) II (I)	IV-V	VI	Lozano Rey (1935); Mota and Antunes (2011)
Douro, Portugal	III	V	VI	Eiras (1981b)
Adour, France	III (II)	IV-V	VI (VII)	Prouzet <i>et al.</i> (1994a)
Gironde, France	III (II)	V	VI (VII)	Anon. (1979a); Cassou-Leins and Cassou-Leins (1981); Rochard (2001)
Loire, France	III	IV-V	VI	Menesson-Boisneau and Boisneau (1990)
Seine, France	III	IV		Vincent (1894b); Roule (1920, 1925)
Rhine, Germany	III (IV)	IV-V	VI	Hoek (1888,1899); Fatio (1890); Mohr (1941)
Severn, England		IV-V		Salmon Fisheries Commission (1861)

In fresh water, Mennesson-Boisneau and Boisneau (1990), Dartiguelongue (1996a, 1996b) and Travade *et al.* (1998) have shown that *Alosa alosa* migrate upriver in several waves. On the Loire, Boisneau *et al.* (1985) reported a positive correlation between the daily change in water temperature and the number of *A. alosa* caught per hour ($r^2 = 0.18$), numbers declining with a fall in temperature and increasing with increasing temperature. No relationship between abundance and flow or the daily change in flow was apparent (Boisneau *et al.* 1985).

The speed of migration in the Loire has been estimated at 20 km day⁻¹ for the fluvial part (Steinbach *et al.* 1986) and 21 km day⁻¹ for migration through the estuary and river (Menesson-Boisneau and Boisneau 1990; Mennesson-Boisneau *et al.* 1999). Through the Gironde estuary, Rochard (2001) estimated the speed of migration to vary between 17 and 23 km day⁻¹.

The timing of the migration has varied between years. Travade *et al.* (1998) observed that the date at which 50% of the *Alosa alosa* population had been recorded migrating past a particular point, varied by up to a month between years. Part of this variation may be related to temperature, little up-river movement being reported at temperatures less than 11°C (Boisneau *et al.* 1985) or below 15 to 16°C (Vincent 1894a; Belaud *et al.* 1985). Certainly, Dautrey and Lartigue (1983) and Bellariva and Belaud (1998) reported a significant positive correlation between the abundance of *A. alosa* and temperature ($r^2 = 0.26-0.50$ and 0.56 respectively). The association with temperature may relate to the swimming capabilities of *A. alosa*, as their swimming speed is inhibited when water temperatures fall below 12°C (Steinbach *et al.* 1986).

In relation to discharge, Dautrey and Lartigue (1983) observed a negative correlation with flow ($r^2 = 0.28-0.29$) though Bellariva and Belaud (1998) found the relationship with discharge was inconclusive, except that at high discharges (mean = $721 \text{ m}^3\text{s}^{-1}$) migration ceased.

Migration upstream occurs mainly during the day; it increased gradually from 08:00h, reaching a peak at 19:00h after which it declined steadily until 23:00h. There was little upstream movement between 00:00 and 07:00h (Travade *et al.* 1998).

Alosa fallax

Migration into the estuary begins between February (for populations at the southern limit of their range) and May (for those at the northern limit), and usually extends for three to four months for southern populations, and two to three months for northern stocks (Table 3.3). The timing of the onset of migration has been associated with temperatures reaching 10 to 12°C (Roule 1922a, 1925). Similar findings have been observed on the Severn (Claridge and Gardner 1978; Aprahamian 1982, 1988), the Sebou (Sabatié 1993) and the Loire (Mennesson-Boisneau and Boisneau 1990). In warmer years, migration can initiate approximately a month earlier than normal (Mennesson-Boisneau and Boisneau 1990).

In the river, twaite shad migrate mainly during the day between 05:00 and 20:00, in the lower half of the water column close to the river bed, where water velocity is lowest (Clabburn 2002). A diel pattern was also noted by Švagždys (1999) who reported that catches of twaite shad were higher during the day than night. The fish enter the river in a series of waves (Aprahamian 1981).

Once it penetrates in the river, *A. fallax* usually migrates short distances, since spawning is typically in areas influenced by tides (Spillman 1961; Hass 1968; Taverny 1991; Thiel *et al.* 1996; Maitland and Hatton-Ellis 2003). However, some stocks can travel long distances to reach their spawning grounds, as in the case of the Loire River where *A. fallax* can spawn at more than 250 km far from the sea (Mennesson-Boisneau and Boisneau 1990) or in Lithuania where they reach 400 km (Manyukas 1989). In practice, the location of the spawning grounds is often limited by barriers to migration, which include natural barriers, such as waterfalls, and man-made barriers, such as dams, weirs, dikes, etc. (Assis 1990; Mennesson- Boisneau and Boisneau 1990; Maitland and Hatton-Ellis 2003). Water contamination can also create a barrier to the movement (Maitland and Hatton-Ellis 2003).

After spawning, the spent fish migrate downstream in the middle to upper part of the water column where water velocities are greatest (Clabburn 2002).

Table 3.3. Timing of the freshwater phase of the spawning migration of *Alosa fallax*.

River, Country	Start	Peak	End	Reference
Sebou, Morocco	II (XII-I)	IV	V	Sabatié (1993)
Guadiana, Portugal	I	V	VI	Esteves (personal communication)
Mira, Portugal	II	IV	VI	Esteves (personal communication)
Tejo, Portugal	II		VI	Baglinière <i>et al.</i> (2001)
Lima, Portugal	III (II)	IV-V	VI	Alexandrino (1996b)
Minho, Spain-Portugal	IV	V	VII	Nachón <i>et al.</i> (<i>in press</i>)
Ulla, Spain	III	V	VII	Nachón <i>et al.</i> (<i>in press</i>)
Adour, France		V-VI		Douchement (1981)
Gironde, France	IV (III)	V	VI	Anon. (1979a)
Loire, France	V (IV)	V	VII	Mennesson-Boisneau and Boisneau (1990)
Seine, France	IV	V	VI	Roule (1922a)
Rhine, Germany	IV	V	VI	Böcking (1982)
Elbe, Germany	IV	V	VI (VII)	Hass (1965); Thiel <i>et al.</i> (1996a)
Nyamunas, Lithuania	V	VI	VII	Manyukas (1989); Švagždys, (1999)
Barrow-Nore-Suir, Ireland	IV	V	VI	Bracken and Kennedy (1967)
Wye, Wales	IV	V	VI	Aprahamian (1982); Gregory (personal communication)
Severn, England	IV	V	VI	Aprahamian (1981,1982)

3.1.6 Genetics

Morel (1974) found significant differences in muscle proteins between *Alosa alosa* and *Alosa fallax*. However, Boisneau *et al.* (1992) reported a lack of genetic variation between anadromous *A. alosa* and *A. fallax* in the River Loire (France) at the 22 loci investigated. A high degree of genetic similarity was also revealed for anadromous and landlocked populations of *Alosa fallax* in Ireland (O'Maoileidigh *et al.* 1988) and Italy (Rizzotti and Gioppato 1997). Though Rizzotti and Gioppato (1997) reported no evidence of polymorphism, nor any difference according to sex or season, they did report an ontogenetic change in the acidic and basic components of haemoglobin.

Analysis of mitochondrial DNA by Bentzen *et al.* (1993) did indicate a low level of differentiation between *Alosa alosa* and *Alosa fallax*. Alexandrino (1996a) found that 4 out of the 15 protein loci examined in *Alosa* populations from Portugal were polymorphic; haemoglobin (HBA), adenosine deaminase (ADA), mannose phosphate isomerase (MPI) and alcohol dehydrogenase (ADH), (Table 3.4). Significant differences in allele frequency exist between *Alosa alosa* and *Alosa fallax*, with 57% of the total genetic variability being explained by between-species differences. Similar findings were reported by Véron *et al.* (2001) for *A. alosa* and *A. fallax* from the Charente and by Le Corre *et al.* (1998a) for *A. fallax rhodanensis*. Significant differences in allele frequency existed between the various populations of *Alosa fallax*, though this was not the case for *Alosa alosa* who exhibited low levels of polymorphism (Alexandrino 1996a).

Table 3.4. Allele frequency for four polymorphic loci; hemaglobin (HBA), adenosine deaminase (ADA), mannosephosphate isomerase (MPI) and alcohol dehydrogenase (ADH) in populations of *Alosa alosa* from the rivers Aulne (A), Charente (C), Mondego (M) and Lima (L) and the landlocked population of Castelo de Bode (CB) and *A. fallax* from the rivers Charente, Lima, Mondego, Tego (T), Guadiana (G), Rhône (R) and Aude (Ad) (Alexandrino 1996a; Le Corre *et al.* 1998a and b; Véron *et al.* 2001).

Allele	<i>Alosa alosa</i>					<i>Alosa fallax</i>						
	A	C	L	M	CB	C	L	M	T	G	R	Ad
HBA*F	0.85	0.77	1.00	0.97	1.00	0.00	0.12	0.15	0.02	0.00	0.01	0.00
HBA*S	0.15	0.23	0.00	0.03	0.00	1.00	0.88	0.85	0.98	1.00	0.99	1.00
ADA*1F	0.08	0.03	0.00	0.04	0.00	0.15	0.43	0.63	0.32	0.52	0.96	1.00
ADA*1S	0.79	0.95	0.99	0.92	1.00	0.35	0.23	0.06	0.10	0.00	0.01	0.00
ADA*2	0.13	0.02	0.01	0.04	0.00	0.50	0.33	0.31	0.58	0.48	0.00	
ADA*3											0.03	
MPI*1	0.11	0.05	0.10	0.00	0.00	0.97	0.64	0.74	0.75	0.91	1.00	1.00
MPI*2	0.89	0.95	0.90	1.00	1.00	0.03	0.36	0.26	0.25	0.09	0.00	0.00
ADH*1	1.00	0.96	1.00	1.00	1.00	0.71	1.00	0.71	0.18	0.50	1.00	0.86
ADH*2	0.00	0.01	0.00	0.00	0.00	0.29	0.00	0.29	0.82	0.50	0.00	0.14
ADH*3		0.03				0.00						

Based on a previous screening of 31 protein loci (Alexandrino 1996a,b; Castro *et al.* 1999; Alexandrino and Boisneau 2000), eight of the 10 loci known to be polymorphic in European shad species were used to analyze 19 populations of both species and their hybrids (Alexandrino *et al.* 2006). Results clearly showed that *A. alosa* and *A. fallax* populations are genetically distinct, forming two different groups with the hybrids having an intermediate position in relation to parental populations (Figure 3.4).

Bentzen *et al.* 1993 described for the first time the existence of polymorphism at the mitochondrial DNA (mtDNA) level between *Alosa alosa* and *A. fallax* with the two species showing a high degree of similarity (98.8%) (Figure 3.4). Alexandrino *et al.* (1996), combining the data from their study with that of Boisneau *et al.* (1992), concluded that *Alosa alosa* and *Alosa fallax* are still at an early stage of divergence. The findings are consistent with those of Bentzen *et al.* (1993), who found an absence of major difference in mtDNA (1.2%) between the two species, based on restriction site mtDNA data. Bentzen *et al.* (1993) estimated that the two genotypes may have diverged approximately 600,000 years ago. These findings are in concordance with more recent molecular data (Alexandrino *et al.* 2006), based on direct sequencing of 515 bp of cytochrome b mtDNA gene, that reveals two distinct haplotype clades separated by 6 base substitutions (1.3% mean divergence) (Figure 3.5). Similarly, the study of Coscia *et al.* (2013) estimated a major split (4.3% divergence) between the two clades at 580,000 (BP).

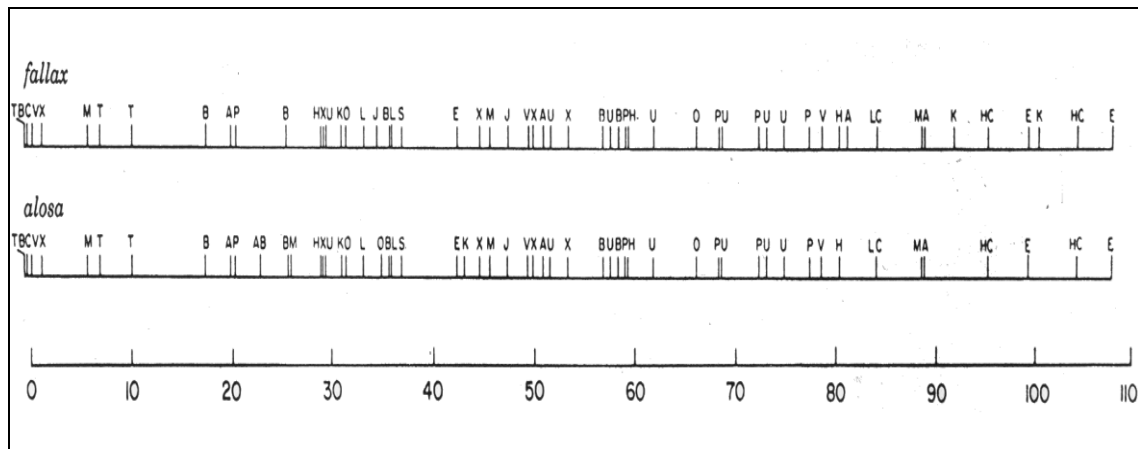


Figure 3.4. Restriction site maps of the mtDNAs of *Alosa alosa* and *Alosa fallax*. The map for each species corresponds to the most common genotype observed for that species. Abbreviated names of restriction sites are as follows: T, *SstII*; P, *PstI*; E, *EcoRI*; L, *Sall*; S, *SstI*; J, *Clal*; C, *EcoRV*; X, *XbaI*; H, *HpaI*; M, *BstEII*; K, *KpnI*; V, *PvuII*; B, *BglI*; A, *Scal*; U, *StuI*; O, *BclI*. One map unit corresponds to approximately 168 base pairs (Bentzen *et al.* 1993).

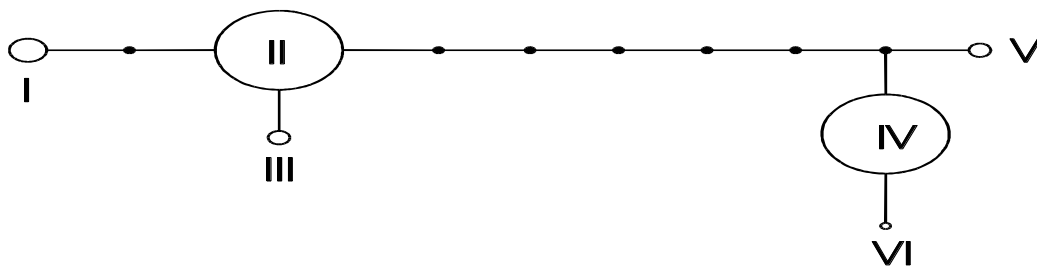


Figure 3.5. Network representing 6 mtDNA haplotypes (515 bp of the 5' -end mtDNA cytochrome b gene) found in 70 *Alosa spp* individuals (25 *A. alosa* and 45 *A. fallax*). Each branch represents a single nucleotide change, solid circles represent missing haplotypes, and size of empty circles reflects the frequency of each haplotype. I, II and III: *Alosa fallax* haplotypes; IV, V and VI: *Alosa alosa* haplotypes (from Alexandrino *et al.* 2006).

In a broader phylogeographic analysis Faria *et al.* 2012 used two concatenated mtDNA genes (448 bp fragment of the cyt b and 975 bp of the ND1 genes) to analyze genetic diversity and differentiation in nine *A. alosa* populations, 29 *A. fallax* populations and the Black Sea species complex. Results confirm that despite introgressive hybridization occurring in some populations, *A. alosa* and *A. fallax* are genetically divergent. Three similarly divergent mtDNA clades were recognized within both *A. fallax* and *A. alosa*, most likely originated during common periods of isolation during the Pleistocene among the studied oceanographic regions (Figure 3.6).

The present day geographic distribution of mtDNA genetic diversity within European *Alosa* sp. (Figures 3.6 and 3.7) suggests the existence of a strong but permeable barrier between the Atlantic Ocean and the Mediterranean Sea, as shown for a number of other aquatic species. Overall mtDNA diversity is considerably lower for *A. alosa* compared to *A. fallax*, suggesting that the former species is more sensitive to climatic as well as anthropogenic changes. For *A. fallax*, migration from the Mediterranean to the Atlantic was detected but not in the opposite direction, with (re)colonization of the North Atlantic probably occurring after last glacial maximum (Faria *et al.* 2012).

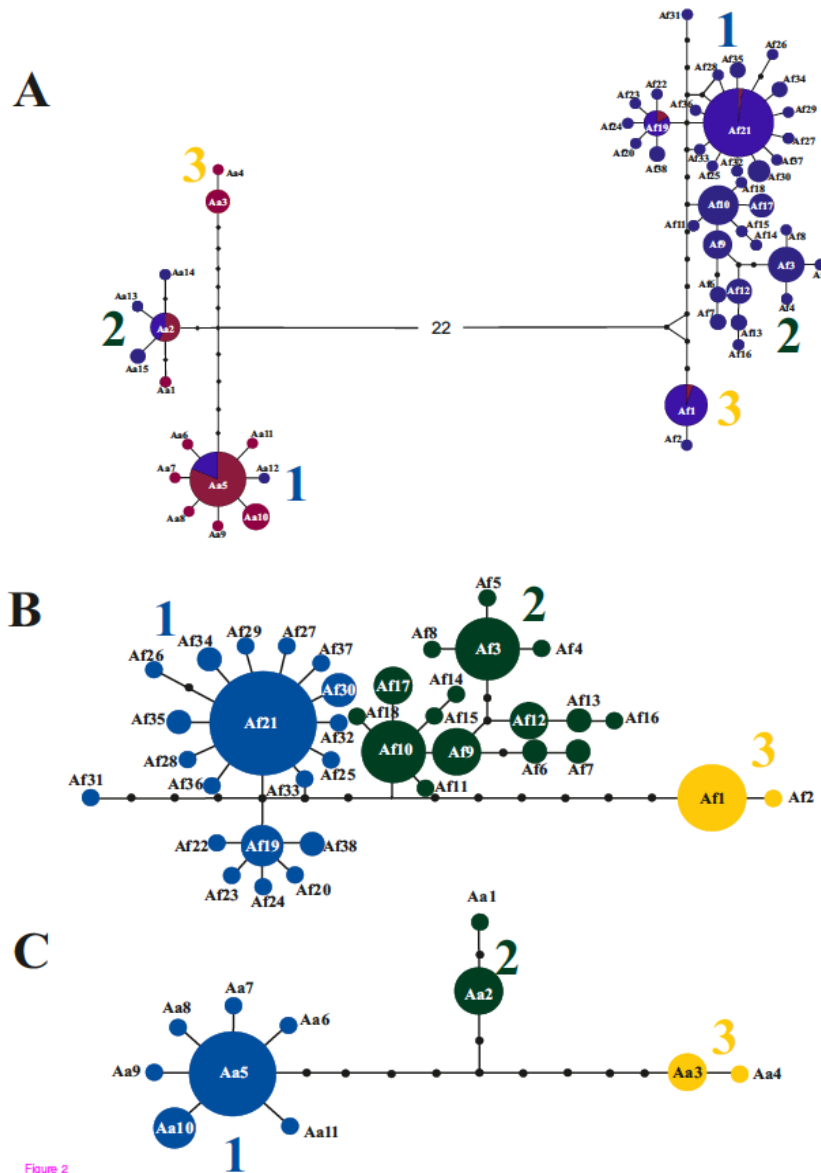


Figure 2

Figure 3.6. Haplotype networks for two concatenated mtDNA genes (ND1 and cyt b) analysed in nine *A. alosa* and 29 *A. fallax* populations by Faria *et al.* (2012). A) Including all individuals analyzed in the study. Haplotypes found in individuals classified morphologically as *A. fallax* are represented in purple, while haplotypes found in individuals classified morphologically as *A. alosa* are colored in dark red. Shared haplotypes are represented by pie charts with the proportions reflecting the relative frequency of those haplotypes in *A. alosa* (dark red) and *A. fallax* (purple). B) Haplotypes found in the 29 populations of *A. fallax* analyzed, excluding putative introgressed individuals; C) Haplotypes found in the nine populations of *A. alosa* analyzed, excluding putative introgressed individuals. In figures B and C, each clade is represented by different colors to facilitate the comparison with Figure 3.7 (from Faria *et al.* 2012).

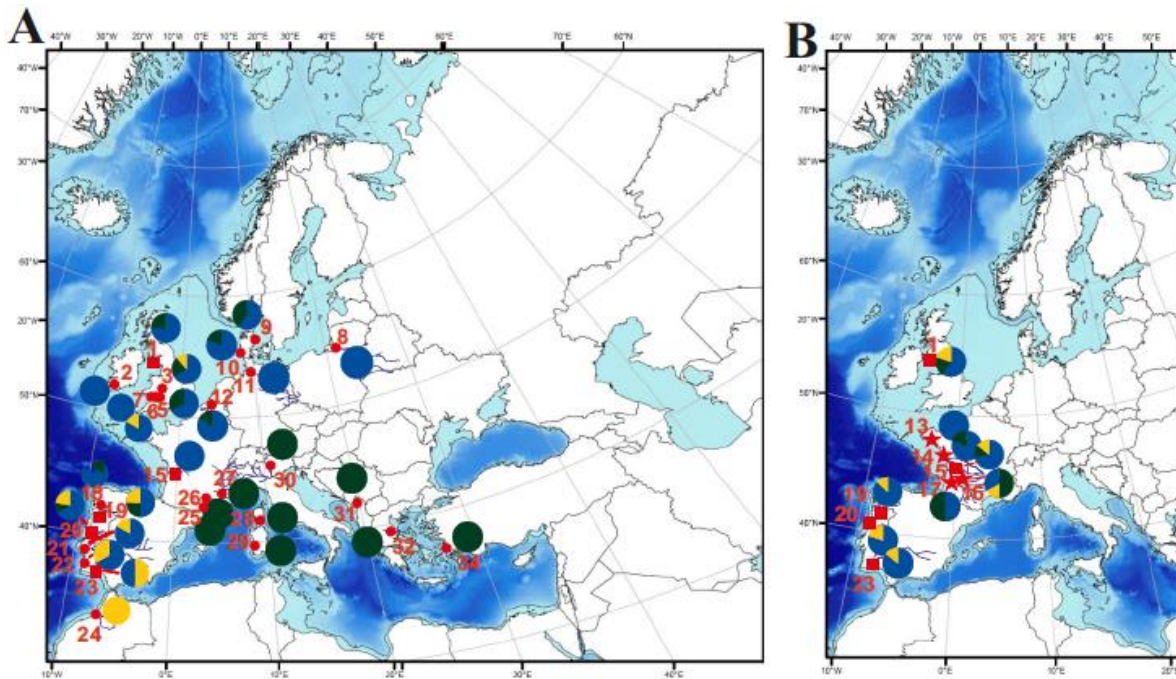


Figure 3.7. Geographic distribution of the main mtDNA haplogroups shown in Figure 3.6. A) frequency of the *A. fallax* haplogroups found in 29 populations of twaite shad; and B) frequency of the *A. alosa* haplogroups found in 9 populations of allis shad (from Faria *et al.* 2012).

For *Alosa fallax* in Ireland, Coscia *et al.* (2013) using the mtDNA control region, found that the species divided into two major clades approximately 400,000 years ago (Figure 3.8). The first of these (Twaite 1) included only two individuals, while the second clade included all the remaining twaite and the landlocked Killarney shad, *A. f. killarneyensis* (from Lough Leane). This clade could be further divided into three well-supported, shallow lineages, with the Killarney shad being divided amongst two of these lineages (Killarney1 and Killarney2, Figure 3.8), and shared haplotypes with twaite shad. The times to most recent common ancestor (tMRCA) of these two lineages containing the Killarney shad are respectively 12,348 and 14,596 years ago. These estimates coincide with the period between the retreat of the ice sheet covering the whole of the island of Ireland (which began approximately 19,000 years BP; Clark *et al.* 2012) and the onset of the Younger Dryas glaciation (12,900–11,700 years BP). Further analysis suggests that Lough Leane was invaded in two separate events by two twaite clades that were present along the coast: the first entrance occurred during a time that coincides with the retreat of the ice sheet from the South West of Ireland 16,380 years BP (Killarney1) whilst the second event occurred 7,710 years BP (Killarney2) (with the Killarney1 lineage splitting from an unsampled population).

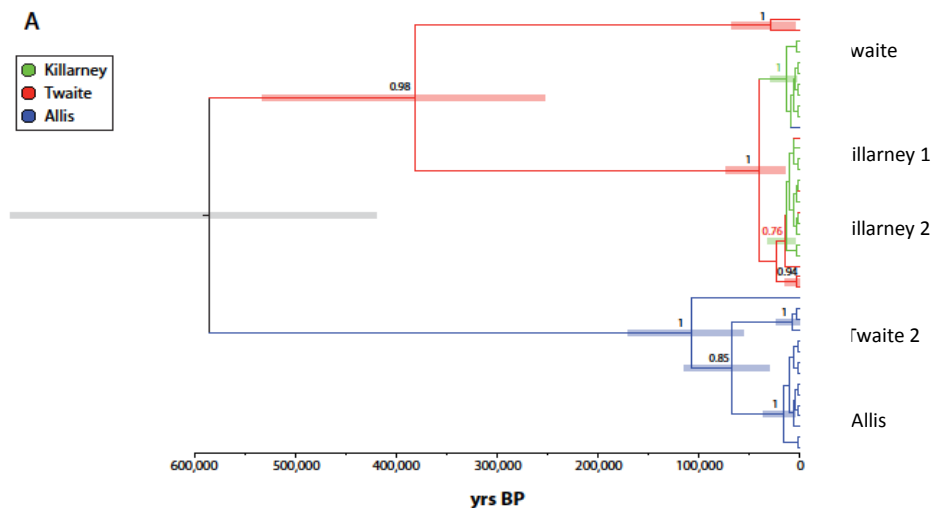


Figure 3.8. Coalescent tree based on the mtDNA control region. The bar represents the years Before Present (BP) (From Coscia *et al.* 2013).

The observation of typical *A. alosa* haplotypes in several *A. fallax* populations, and vice versa, suggests that hybridization and introgression are widespread geographically (Faria *et al.* 2011). Ancestral polymorphism could, in theory, be responsible for shared alleles between these two species, the correlation of genotype and gill raker counts (Alexandrino *et al.* 2006) clearly supports the inference of hybridization and introgression. Likewise, the coincident occurrence of shared nuclear and mtDNA haplotypes where the two species co-occur, and the virtual absence of this signal in locations where a single species is found, supports introgression rather than ancestral polymorphism (Faria *et al.* 2011). An exception to this pattern was observed in the United Kingdom (rivers Severn and Usk), where, although *A. alosa* is absent or rare, Faria *et al.* (2011) found the highest levels of mtDNA introgression among all *A. fallax* populations. Also in the Mediterranean rivers, despite nowadays *A. alosa* being practically absent, mtDNA haplotypes of this species were found to be present in *A. fallax* populations from the Hérault and Rhône rivers, although in low frequencies (Faria *et al.* 2011). This probably results from ancient introgression with the now extinct Mediterranean populations of *A. alosa*, or is a consequence of a documented translocation of *A. alosa* from the Dordogne River to the Rhône in 1953 (Hoestlandt 1958).

Andree *et al.* (2011) used microsatellite markers together with the mtDNA genes NADH dehydrogenase (ND1) and cytochrome-B (Cyt-B) to investigate the genetic background of the twaite shad from the Ebro River (Spain) as compared to other populations of this species from the Mediterranean basin. Morphometric data obtained from fish caught in the Ebro (number of gill rakers and body biometric indices) indicated they were all *A. fallax*. However, analysis of the ND1 sequences showed two distinct clades with several *A. fallax* haplotypes clustering within the *A. alosa* clade. As the alleles of mitochondrial genes are not freely exchanged, but inherited only along maternal lines, this result showed clear indications of inter-specific hybridization as observed by Alexandrino *et al.* (2006). In the

ND1 gene 21 haplotypes comprised of 47 polymorphic sites were identified, with seven of those haplotypes being unique to the Ebro population. This strongly suggests that the return of *A. fallax* to the Ebro River is the recovery of a population in its natal drainage and is not primarily due to contribution of individuals from nearby drainages. Two of the ND1 haplotypes were shared between *A. fallax* from the Ebro and *A. alosa* indicating inter-specific hybridization with *Alosa alosa* and one haplotype was uniquely shared between the Ebro and Rhone populations indicating intra-specific hybridization between the Ebro and the Rhone population. This suggests a common genetic background, or possibly some admixing between the Ebro and Rhone populations. The total absence of *A. alosa* captures in the Ebro suggests that the interspecies hybridization that is evident in mtDNA sequences is from past interbreeding and begun when access to upstream habitat was blocked by the Xerta weir.

Protein, meristic and morphometric differences seem to indicate that there are distinct populations of *Alosa*, most likely promoted by homing to their natal river (Alexandrino and Boisneau 2000; Sabatié *et al.* 2000).

Allozyme data indicated that of the eleven populations of *Alosa fallax* studied (Alexandrino 1996a; Le Corre *et al.* 1998a; Véron *et al.* 2001; Alexandrino *et al.* 2006; Sabatié unpublished data) three groups are apparent (Figure 3.9). There is one group comprising *Alosa fallax rhodanensis* from the rivers Rhône, Hérault and Aude draining into the Mediterranean and *Alosa fallax fallax* from the Sebou (Morocco) which drains into the Atlantic. The other two groups consist of *Alosa fallax fallax*; the first comprising the rivers Tejo, Mira and Guadiana in Southern Portugal and the second consisting of the Northern Portuguese rivers Mondego, Lima and Minho and the French river, Charente, all of which drain into the Atlantic Ocean. Within this group, the relative divergence of *Alosa fallax* from Mondego and Lima results from introgression with *Alosa alosa* due to the high level of hybridisation observed in those basins (Alexandrino 1996a; Alexandrino *et al.* 1996; Alexandrino *et al.* 2006).

Alexandrino (1996a) concluded that the genetic dissimilarity between geographically close populations of *Alosa fallax fallax* could only be explained if fish were homing to their natal river. Similar conclusions were reached using meristic data (Sabatié *et al.* 2000). The characters having the greatest ability to discriminate between populations were the total number of branchial gill rakers on the first gill arch, the total number of scales on the lateral median axis, the number of anal fin rays, and the number of pre-pelvic scutes. However, the same conclusion could not be reached for *Alosa alosa* because of the low level of polymorphism and population differentiation (Alexandrino *et al.* 2006; Faria *et al.* 2012). From the six anadromous populations analyzed only a slight divergence is observed in *Alosa alosa* from the southern and northernmost populations of Guadiana and Charente, respectively. Martin *et al.* (2015) observed for *A. alosa* that a significant proportion of individuals hatched and grown in a different watershed than the one in which they were collected. They concluded that while *A. alosa* exhibited a high fidelity to the natal site on an ecological timescale, as inferred from otolith microchemistry, they showed weak genetic differentiation between collection sites, suggesting that the amount of straying is sufficient to explain the lack of a genetic structure for the Atlantic coast *A. alosa* populations.

Martin *et al.* (2015) reported that most individuals returned to their natal watersheds, some fish did stray and this occurred most frequently between neighboring river basins. Long distance straying was evident but not frequent, for example where fish were born in France but caught on their spawning

(Barrow, Tywi, Usk, Wye and Severn) and marine environments (Solway Firth, Looe bay, Hastings and Sizewell) (Jolly *et al.* 2012). Non-significant differences were observed only between the populations from the Solway Firth and River Tywi, between the River Wye and River Tywi, between the River Usk and River Wye, between the River Wye and River Severn, and between the sea-caught samples of Hastings and Sizewell. The most genetically distinct *A. fallax* population was the landlocked subspecies *A. fallax killarnensis*. Analysis of population structure identified four most likely genetic clusters among the 9 sampled populations of *A. f. fallax* (Figure 3.10); (1) Looe bay, (2) River Barrow, Solway Firth and River Tywi, (3) Rivers Usk, Wye and Severn, and (4) coastal catches from Hastings and Sizewell.

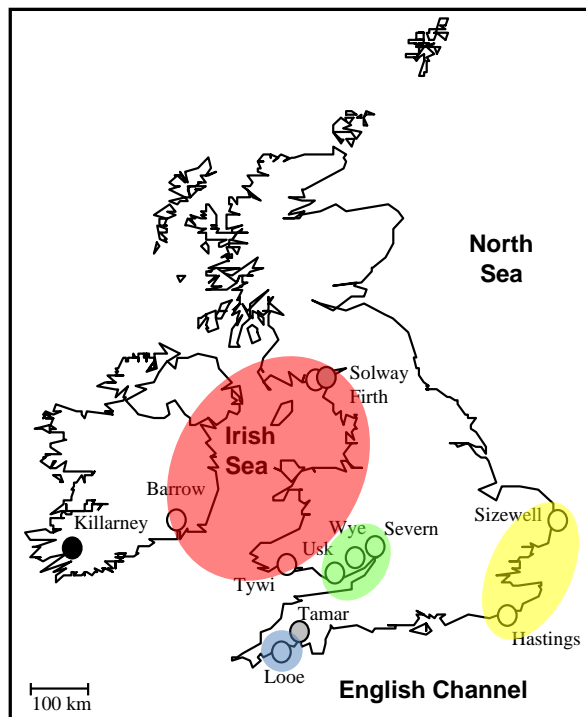


Figure 3.10. Population structure of *Alosa fallax fallax* in the British Isles as identified by Jolly *et al.* (2012). Colours represent distinct genetic clusters.

Samples from Looe bay and Hastings-Sizewell exhibited the strongest genetic divergence, suggesting that movement within the marine environment is limited. The lack of significant genetic differences between the *A. f. fallax* populations of the Solway Firth and River Tywi also suggests that some migration could occur over spatial scales as great as 300 km. Importantly, a pattern of isolation-by-distance was observed in *A. f. fallax*, indicating that spatial genetic population structure is governed to a large extent by gene flow with neighboring populations at the regional scale (Figure 3.11).

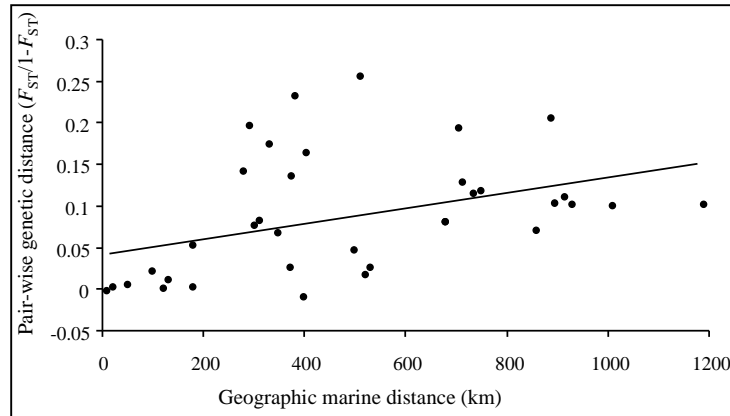


Figure 3.11. Association between genetic distance and marine geographic distance (km) for *Alosa fallax fallax* (Jolly et al. 2012).

In France, Rougemont (2012) similarly showed that for both *A. fallax* and *A. alosa* there was a significant relationship between the degree of isolation and geographic distance (Figure 3.12). For both *A. alosa* and *A. fallax*, Rougemont (2012) suggested there were four groups (Figure 3.13). For *A. alosa* the populations could be grouped as follows 1) rivers draining into the Atlantic (Charente, Dordogne, Garonne, Loire and Vilaine), 2) rivers draining into the Bristol Channel (Orne and Vire), 3) rivers of North West France (Aulne, Trieux and Scorff) and 4) the River Nivelle, which, though draining into the Atlantic, was quite distinct from the others. For *A. fallax* the groupings were similar 1) rivers draining into the Atlantic (Dordogne and Loire), 2) rivers draining into the Bristol Channel (Orne), 3) rivers of southern France which flow into the Mediterranean (Aude, Rhone and Vidourle), 4) the rivers of Corsica (Tavignano), and the river Ulla (Spain), which is quite distinct from the others.

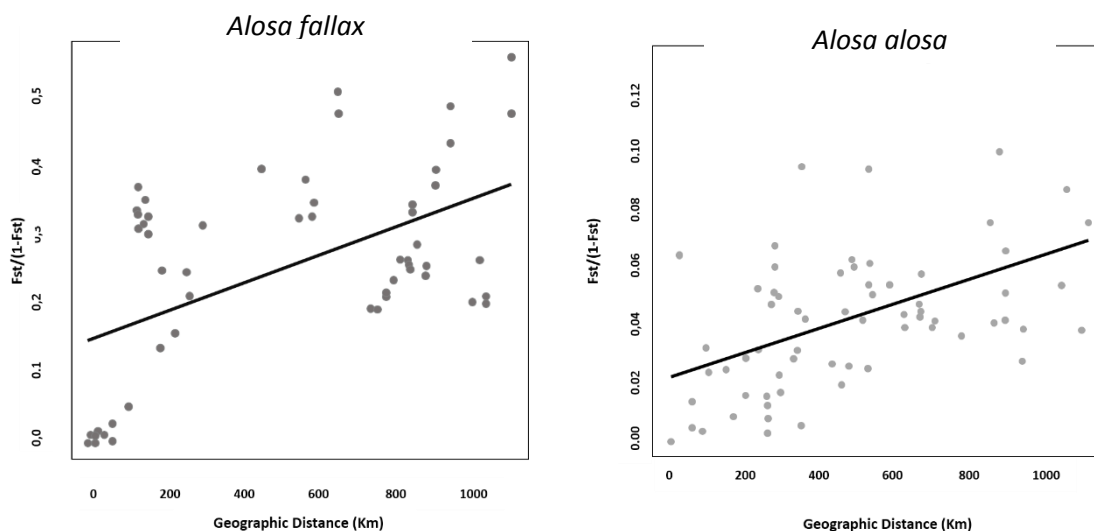


Figure 3.12. Association between genetic distance and marine geographic distance (km) for *Alosa fallax fallax* and *Alosa alosa* from France (from Rougemont 2012).

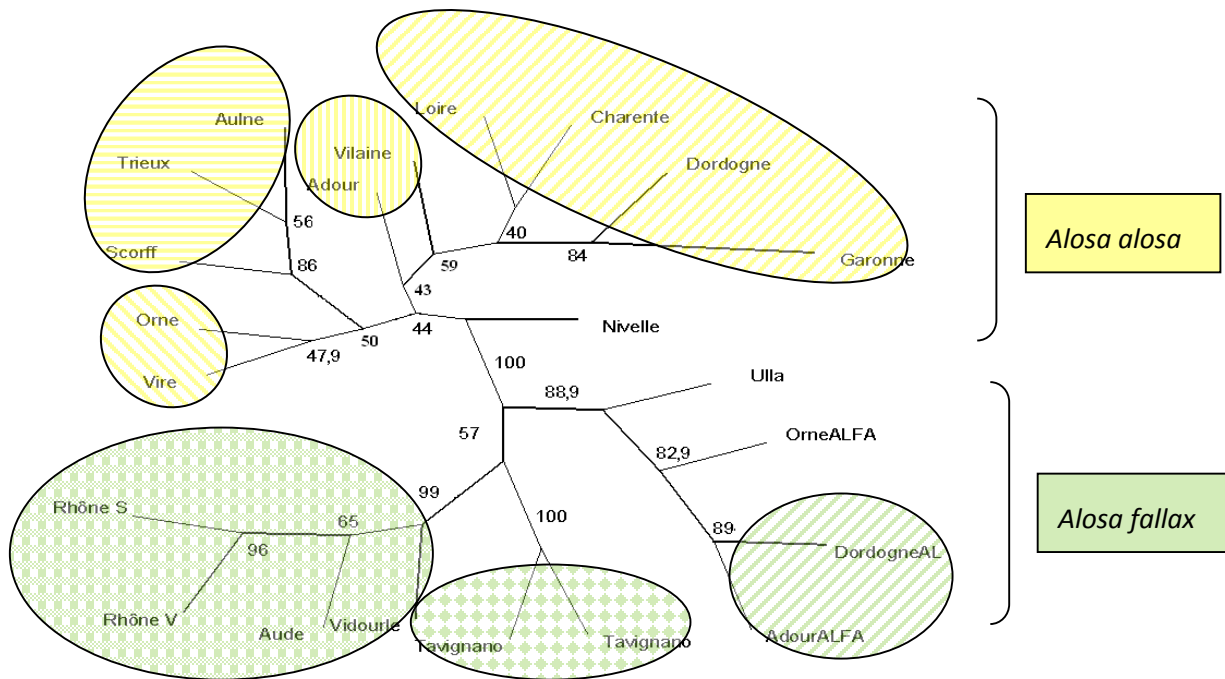


Figure 3.13. Phylogenetic analyses using the Neighbour-Joining method (from Rougemont 2012), Rhône S=Rhône Sauveterre and Rhône V=Rhône Vallabrègues.

These results are in accordance with those recently found by Sabatino *et al.* (unpublished data) based on the analysis of 21 microsatellite loci in 14 *A. alosa* and 23 *A. fallax* putative populations distributed across the present geographic area of distribution of both species. Bayesian Analysis of Population Structure (BAPS) identified 4 groups for anadromous *A. alosa* populations (1- the French populations from Charente, Garonne, Vienne and the Solway in UK; 2- the Aulne, in France; 3 – the Portuguese west populations from Minho, Lima, Mondego and Tejo and, 4 – the southern Portuguese population from Guadiana), arising the landlocked population from Castelo de Bode already as an additional genetic distinct group (Sabatino *et al.* unpublished data, Figure 3.13). These results, taking together with Rougemont, 2012, Jolly *et al.* 2012 and Martin *et al.* (2015), appear to define at least 5-6 distinct genetic groups in *A. alosa*: southern Portugal (Guadiana), west Portuguese populations (Minho, Lima, Mondego, Tejo), west French populations (Garonne, Dordogne, Charente, Loire), Brittany and south UK populations (Aulne, Scorff, Tamar) and, eventually, a Normandie group (Vire, Orne) and a Biscay group (Nivelle) (Figure 3.14).

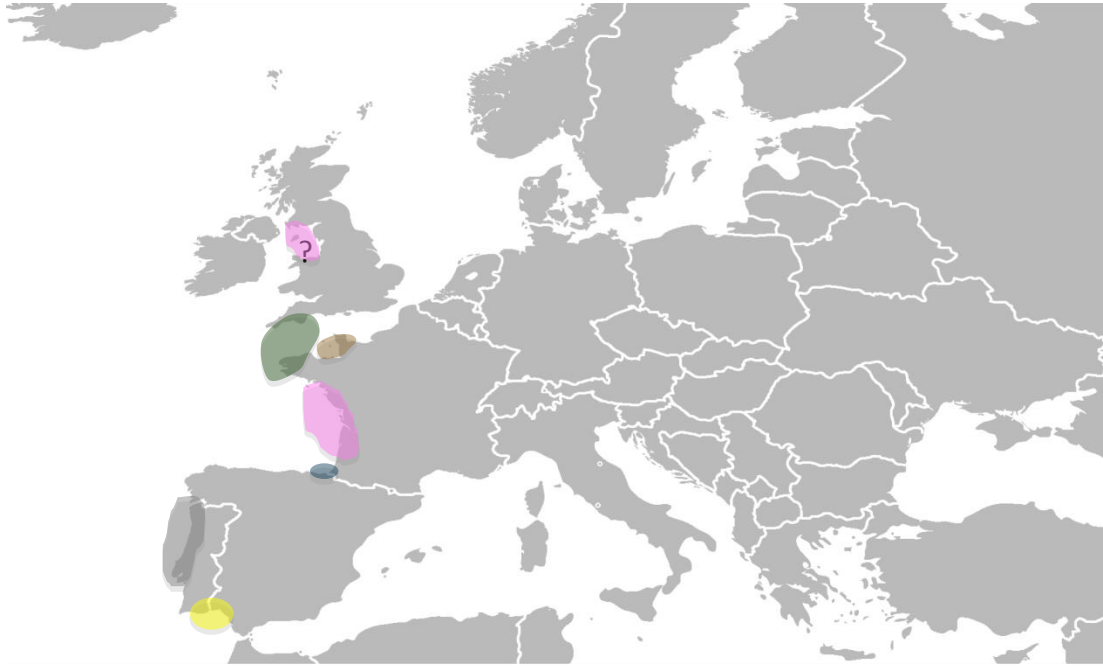


Figure 3.14. Genetic distinct anadromous population groups/stocks (landlocked populations excluded) defined in *A. alosa* based on microsatellite loci data and clustering analysis (data from Sabatino *et al.* unpublished data; Jolly *et al.* 2012; Rougemont 2012).

For *A. fallax* around 17 distinct groups (13 corresponding to anadromous populations, Figure 3.15) were identified, and genetic differentiation among anadromous populations of *A. fallax* was consistently found throughout much of its range (Sabatino *et al.* unpublished data). The following distinct genetic groups were defined: **Atlantic:** 1- Baltic sea (Curonian lagoon); 2- north Sea (Nissum and Ringkobing Fjords, Denmark, Scheldt estuary, Belgium, Solway, UK); 3- Severn group, UK (Severn, Wye, Usk); 4- Towy, UK; 5 - west France (Charente); 6 – northwest Portugal (Minho, Lima, Mondego); 7- southwest Portugal (Tejo, Mira); 8 - south Portugal (Guadiana); 9 - Morocco (Sebou); **Mediterranean:** 10 – Southern France (Rhone, Herault, Aude); 11 – Corsega/Sardinia (Tavignano, Tirso); 12 – Adriatic (Po, lake Skadar); 13 – Aegean Sea (Pinios, Izmir bay); **Landlocked populations:** 14- Killarney, Ireland; 15 – lake Maggiore, Italy; 16 – lake Como, Italy; 17 – lake Garda, Italy (Sabatino *et al.* unpublished data).

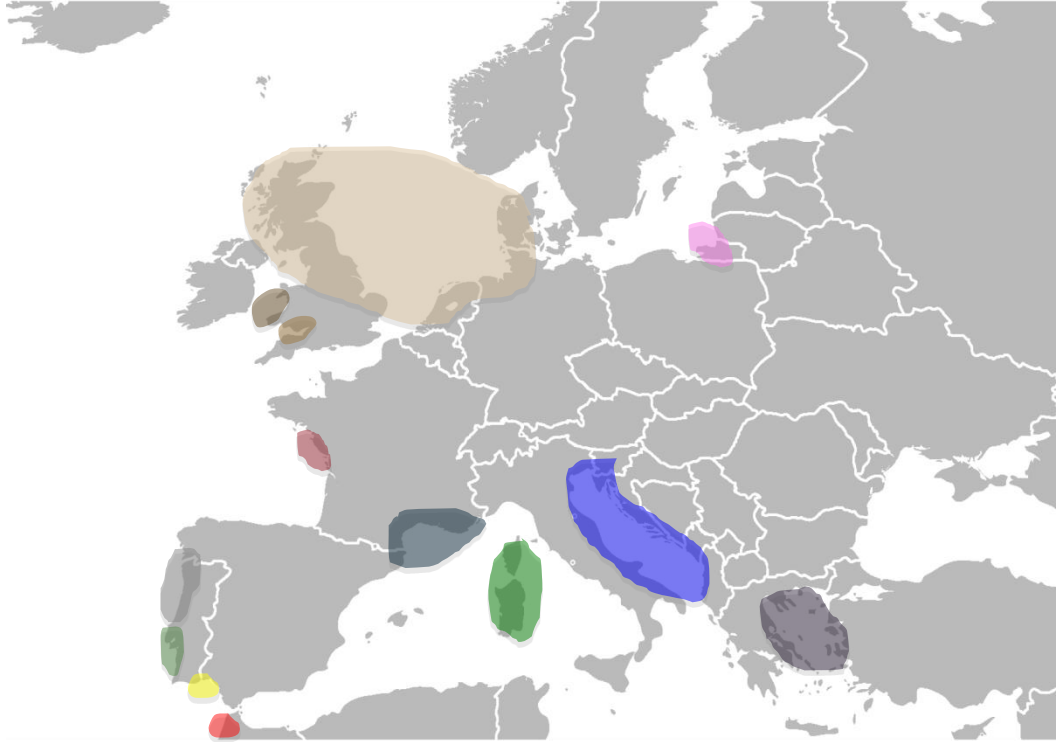


Figure 3.15. Genetic distinct anadromous population groups/stocks (landlocked populations excluded) defined in *A. fallax* based on microsatellite loci data and clustering analysis (data from Sabatino *et al.* unpublished data; Jolly *et al.* 2012; Rougemont 2012).

Populations in almost all drainages were observed to be genetically isolated, including some less than a few hundred kilometers apart. The pattern of isolation by distance observed in *A. fallax* found in this study indicates that, as previously noted (Alexandrino *et al.* 1996; Alexandrino *et al.* 2006; Jolly *et al.* 2012), this species appears to exhibit, in general, a natal homing.

3.2 COMMERCIAL EXPLOITATION

3.2.1 History of exploitation

Shad are essentially harvested by commercial fisheries over their current distribution area. They can be fished in an estuary or in the mid sections of rivers for anadromous form, or in lakes for resident form. The fish are generally caught when they migrate from their feeding areas towards their spawning grounds. A few catches are recorded at sea or along the coast (Baglinière *et al.* 2003). Also, sport fishing for *Alosa alosa* has recently developed in France, mainly in the Charente River and the Gironde-Garonne-Dordogne System, and in England and Wales for *Alosa fallax*. Sport fishing is also popular in

some rivers of the NW of the Iberian Peninsula, such as the River Ulla (Spain) for *A. fallax* and River Minho (Spain-Portugal) for both species.

Shads are marketed for human consumption, either fresh, frozen or smoked and are a traditional dish in Portugal and Morocco (Baglinière and Elie 2000). In France, this tradition has always been very localized in the past (Lacépède 1803) and is even more localized today, mainly in the south-west of France, and their quality has been praised for a long time (Rondelet 1558; Quatrefages 1849).

3.2.2 Directed fisheries

3.2.2.1 *Alosa alosa*

The FAO reports on fishing statistics present nominal catches of shad. Indeed, these data either underestimate or overestimate the catch and do not make the distinction between the two species of eastern Atlantic shad. It is therefore more reliable to present data derived from local fishery surveys. However, data are only available for a few river systems and no angling catch data are recorded.

From 1978 to 1999, approximate total landings ranged from 357 to 1,198 tonnes in their current distribution area (Figure 3.16). On average 72.5 % and 98.7 % of the total landings, come from France and the Gironde-Garonne-Dordogne system, respectively. In this watershed catches range from 338 to 1007 tonnes and are much higher than in other rivers. In the Gironde-Garonne-Dordogne system part of the decline in catch may relate to the decline in effort which has decreased steadily since 1984 (Castlenaud *et al.* 2001). However, though the decline in catch may reflect a decline in effort, CPUE increased from the late 1970s to the early part of 2000 before decreasing markedly (Figure 3.17) (Beaulaton 2008). Fishing mortality (F) for *Alosa alosa*, in the same system, ranged from 1.86 – 3.32 with a mean (\pm c.i.) of 2.42 (\pm 0.24) for the 1991 – 2002 cohorts (Rougier *et al.* 2012). Levels of exploitation for *A. alosa* on the Gironde-Garonne-Dordogne (France) over the period 1987 to 1998 (excluding 1988) ranged from 47.5% to 87.5% with a mean (\pm 95% CI) of 67.8% (\pm 8.2%) (Martin-Vandembulcke, 1999), and is similar to that reported by Chanseau *et al.* (2005) (61% between 1987 and 2001) and by Rougier *et al.* (2012) (58% between 1994 and 2007). The fishery closed in 2008.

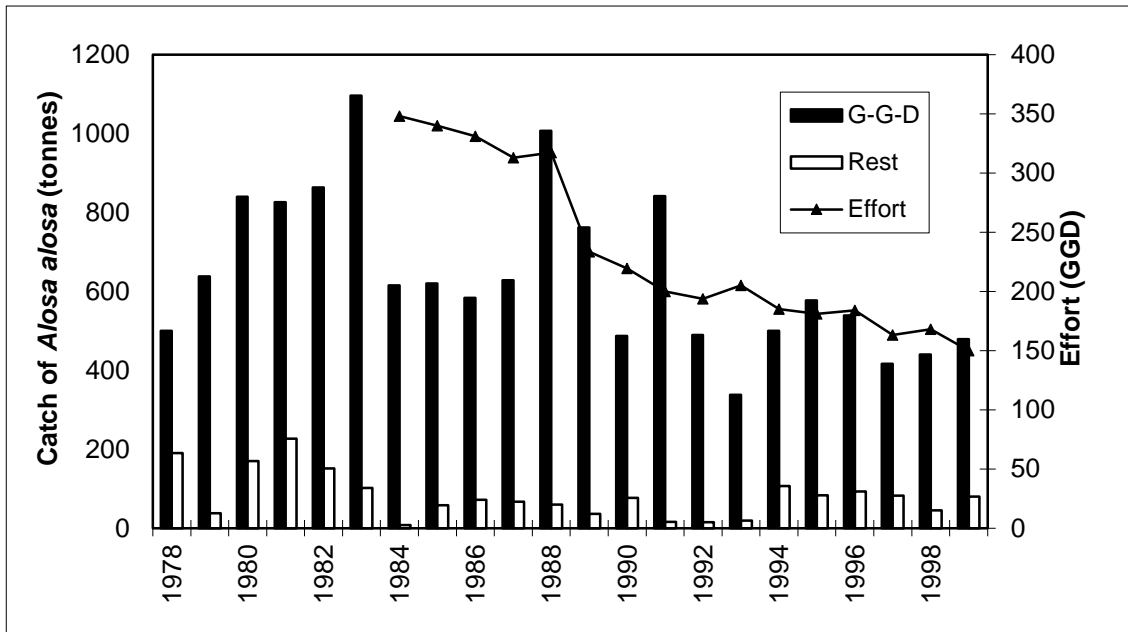


Figure 3.16. Total landings of *Alosa alosa* from 1978 – 1999 and effort data from the Gironde-Garonne-Dordogne system (France). Solid area indicates catches from the Gironde-Garonne-Dordogne system and clear area represents the combined catches from other river systems and at sea, data from Baglinière *et al.* (2003) and Castelnaud *et al.* (2001).

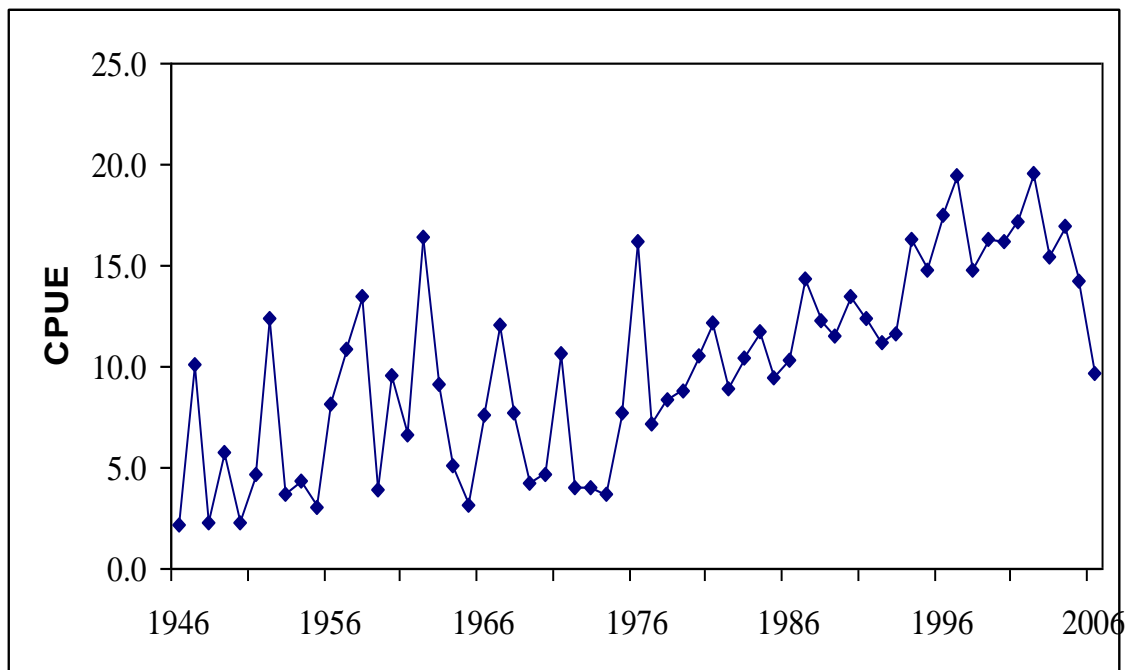


Figure 3.17. Number of *Alosa alosa* catch per day (CPUE) in the Gironde-Garonne-Dordogne system (France) from 1946 – 2006 (Beaulaton 2008).

In France, catches in the River Loire are low, do not often exceed 10 t and had decreased to about 1t in 1995 and 1996. Average annual catches in the River Adour were approximately 19 tonnes between 1985 and 1999. Catches at sea have been recorded off the Aquitaine coasts and exceed the total catch from all French rivers, except from the Gironde system, between 1994 and 1999.

In France, during the 1989-1997 period, shad landings, of which 98% were of *A. alosa*, represented the highest production of anadromous fish and agnathans (33.1 % of the total production) with a turn-over of 1.3 million euros (Baglinière *et al.* 2003). In 1997, 280 commercial fishermen were recorded fishing for allis shad; equivalent to 19.8 % of the total number of fishermen (Castelnaud 2000).

In Portugal, the catch comes mainly from the River Minho, where historically the catch was about 300t but declined dramatically (about 90%) after the construction of the first dams in the 1950s (Figure 3.18). In the last 20 years mean annual catches reached about four tonnes. Recently, catches from coastal areas have also become important, especially from the central region of the country, landing an average of 30 tonnes per year in the last 20 years (10-70 tonnes).

In the River Lima the catch was abundant at the beginning of the 1990's, 2 to 10 tonnes annually, but has decreased markedly by 1998, and no catches were registered after 1999.

After the collapse of the Gironde allis shad population at the beginning of the 2000s (Rougier *et al.* 2012), the Minho river population seems to be one of the largest populations in the southern part of the species' distribution. Allis shad still has important commercial and heritage values in the Minho river (Mota and Antunes 2011; Figure 3.18).

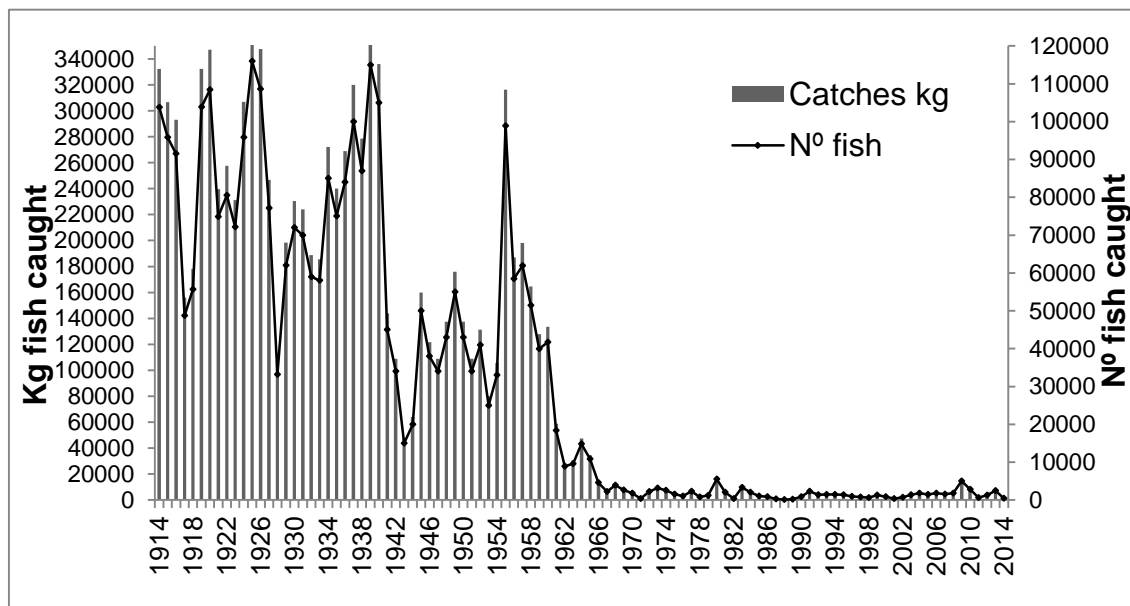


Figure 3.18. Total weight and number of *Alosa alosa* caught in the River Minho (Portugal) in the period 1914-2014 (Mota 2014).

In the Sebou Wadi (Morocco) which was the main and last river to support important allis shad fishery in Africa, the total catch has fallen over a 25 year period from 846 t in 1968 to 2 t in 1993.

3.2.2.2 *Alosa fallax fallax*.

Assessing the economic importance of *A. fallax fallax* is complicated by the fact that the *Alosa* catch is not separated by species and the majority of the catch is of *A. alosa* (Aprahamian *et al.* 2003). In some countries, like Germany, *A. fallax fallax* has been of considerable economic importance with catches in the Lower Rhine in the late 1930s exceeding a million fish per year (de Groot 1989). Their importance increased with the decline in the population of *Alosa alosa*. Similarly, in the North Sea catches between 1910 – 1914 and 1915 – 1919 averaged 900 and 200 tonne per year, respectively and that in the Baltic Sea were 2,100 and 1,700 tons per year, respectively (Svetovidov 1952). In the Nyamunas River the average catch for the periods 1930-4; 1935-47; 1948-52 and 1953-57 were 16,100 kg, 28,500 kg, 29,800 kg and 2,200 kg, respectively (Manyukas 1989). After 1960 the fishery ceased. In the Seine the annual catch at the end of the nineteenth century ranged from 7,490 to 32,869 kg y⁻¹ (Vincent 1894b). In the River Elbe the reported catch (five year mean) between 1886 and 1919 ranged from 11 to 83 t y⁻¹, mostly sold in the Rhine area following the collapse of its *A. alosa* fishery at the start of the 19th century (Möller 1989). Today *A. fallax* is no longer acceptable to consumers. In the River Weser shads represented between 10 and 15% of the catch during the period between 1891 and 1930, after which their contribution was negligible (Busch *et al.* 1988).

In the Sebou, prior to the construction of the barrage at Idress ler, annual landings of *Alosa fallax* ranged from 15 to 79 tons, after which the catches declined markedly and showed a similar trend to that of *Alosa alosa* (Sabatié 1993).

The major fishery is on the Gironde-Garonne-Dordogne system (France) with an estimated annual catch of between 13 and 15 tons per year. Prior to 1989 the annual catch was higher at between 60 and 192 tons with a value ranging from 46,000 to 229,000 euros (Castelnaud *et al.* 2001). The fishery on the Severn was very much a by-catch to the salmon (*Salmo salar*) fishery and in most cases the fish are discarded. The catch after 1999 is insignificant as the start of the fishing season changed from April 15th to June 1st, by which time the majority of the fish had migrated from the estuary into the river. In France, a small marine fishery exists for *A. fallax fallax* with the declared annual catch from 1994 to 1999 of between 1.2 to 3.6 tons per year.

3.2.3 Bycatch

The ICES Working Group on Bycatch of Protected Species (WGBYC) continues to compile and assess data from Member State reports under Regulation 812/2004 and/or from the DCF (ICES 2014). Clupeids are most commonly caught in bottom otter trawls (Table 3.5). There appear to be some differentiation between the two species, with a higher preponderance of *Alosa alosa* being reported from set gill nets while *Alosa fallax* appears to be more commonly caught in beam trawls and midwater pair trawls.

Table 3.5. Total number of bycaught *Alosa* spp. in all observed sampled hauls in the DCF programme per species and per gear type (level 4) from 1995 to 2013. It is worth noting that sampling effort across gear types was not the same and was not reported back by all countries; in consequence, results are only comparable on a more general, descriptive level.

Gear Type	<i>Alosa alosa</i>	<i>Alosa fallax</i>	<i>Alosa</i> spp.
Dredges	0	0	17
Beam trawl	12	340	21
Bottom otter trawl	433	448	386
Midwater otter trawl	2	0	0
Otter trawl multirigg	2	17	0
Bottom pair trawl	8	30	6
Midwater pair trawl	0	188	111
Purse-seine	0	0	0
Anchored seine	0	0	0
Fly shooting-seine	0	0	0
Drift net	1	11	3
Set gill net	622	77	434
Trammel net	67	45	174
Pots and trap	0	0	0
Set long lines	0	0	1
Pot and pool lines	0	0	0

Over the period 2009-2012 an average of approximately 4 t of *Alosa* sp. were reported as bycatch, with 3777 kg being declared from the North Sea and English Channel, Sweden, the Netherlands and the United Kingdom (Figure 3.19), and 258 kg (*Alosa fallax*) from Italian fisheries (ICES 2014).

A recent study (Nachón *et al. in press*) revised the official statistical data of marine landings (in kg) produced in all fish markets of Galicia (NW of Iberian Peninsula) (Figure 3.20 and 3.21) over the 17 year period 1997-2013. Up to 97.5% of *A. alosa* catches were landed at zone A (Rías Baixas) (Figure 3.21), being A Guarda (7475 kg; 70.3% of the total catches) the most important landing port. Cambados and Vigo accumulated 14.9% (1583 kg) and 6.4% (684 kg) of the total catches respectively. The following markets in number of catches were Malpica (493 kg; 4.6%) and Corunha (259 kg; 2.4%), both located in zone B (Costa da Morte). All landings of *A. fallax* were made in Zone A (Rías Baixas), being Baiona (215 kg; 96.4% of total catches) the most important landing port (Figure 3.21).

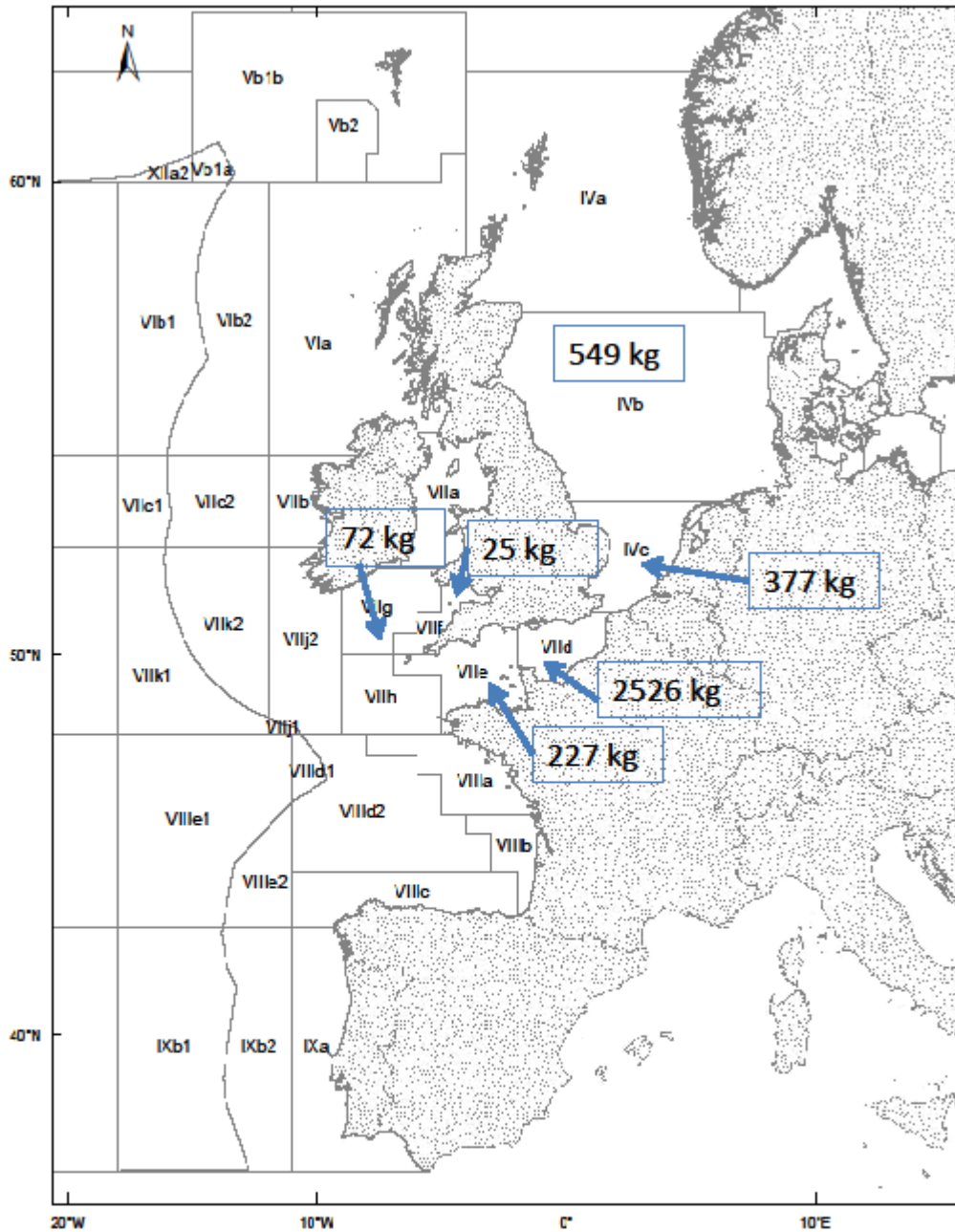


Figure 3.19. Mean weight (kg) of *Alosa* spp. declared as bycatch by Sweden, the Netherlands and the United Kingdom between 2009-2012 by ICES subdivision (ICES 2014).

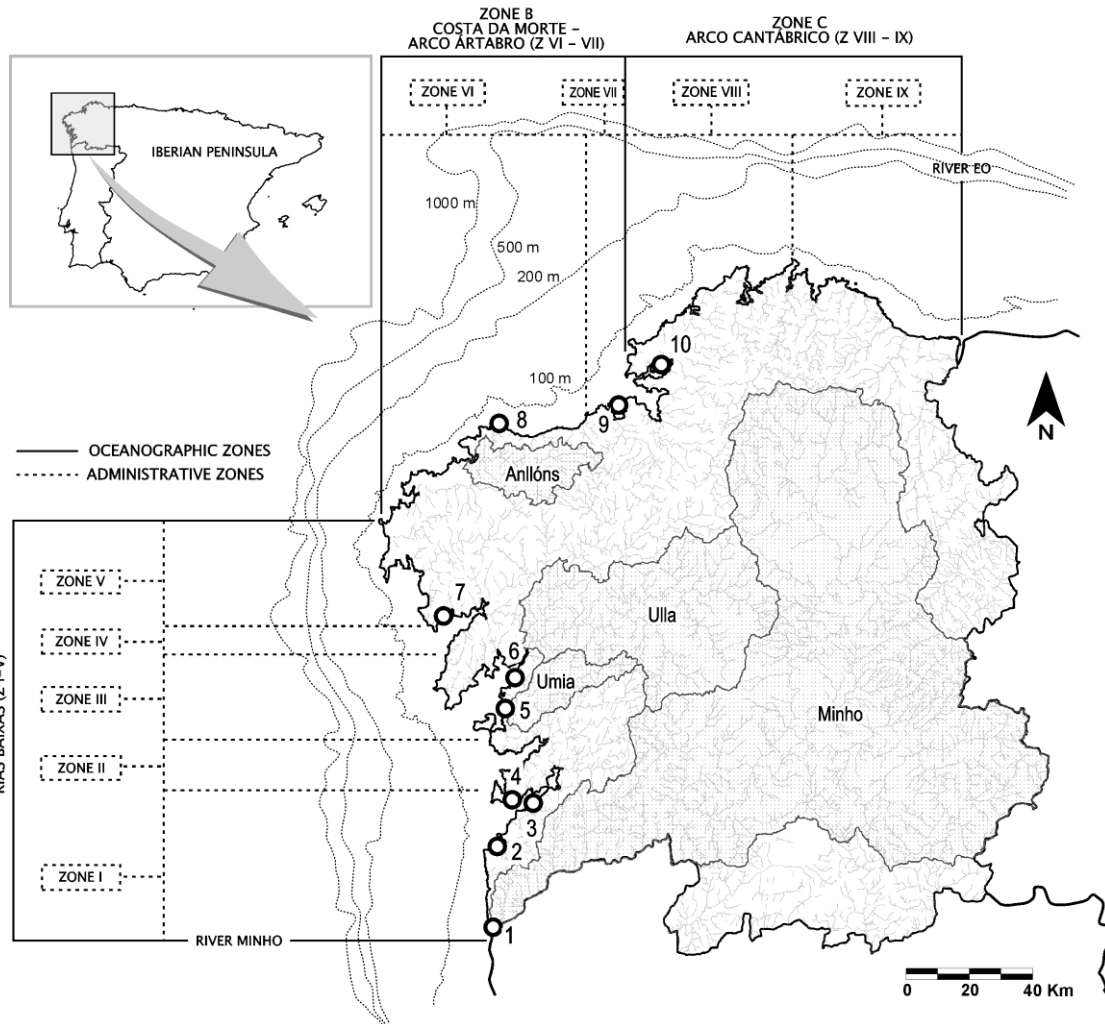


Figure 3.20. Location of Galician fish markets where shads were landed (white dots); administrative and ecogeographical zones for artisanal fishing: 1.- A Guarda, 2.- Baiona, 3.- Vigo, 4.- Cangas, 5.- Cambados, 6.- Carril, 7.- Muros, 8.- Malpica, 9.- Corunha, 10.- Ferrol, Nachón *et al.* (*in press*).

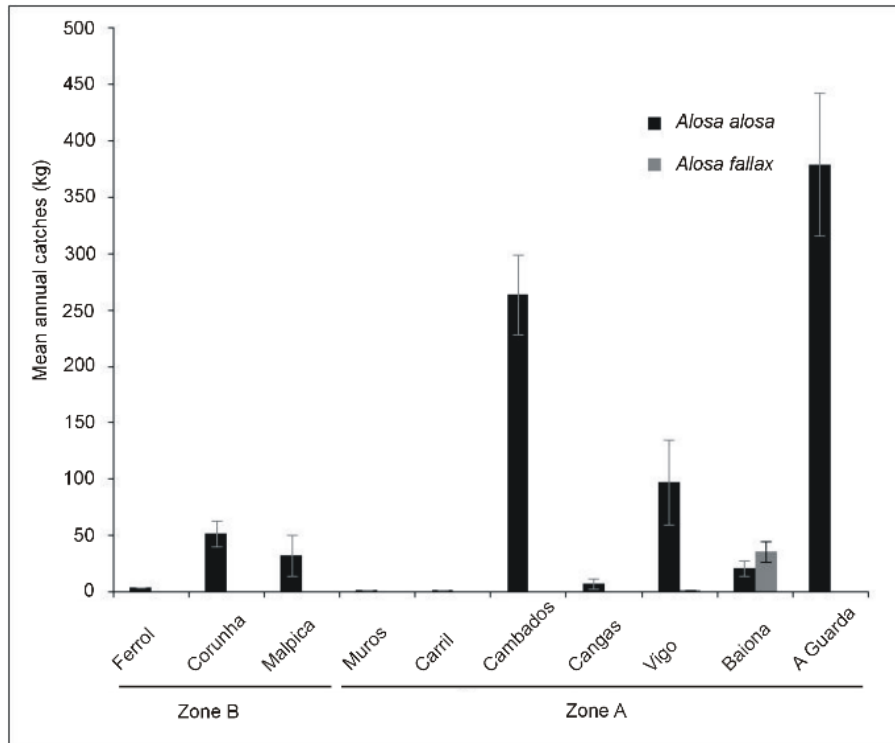


Figure 3.21. Distribution of mean annual (\pm SE) catches (kg) of *A. alosa* and *A. fallax* in the Galician markets between 1997-2013, Nachón *et al.* (in press).

3.3 RECREATIONAL FISHERIES

Recreational fishing for shad, using a rod, used to be practiced in Great Britain, mainly in the rivers Severn and Wye, but since 1998 this activity became illegal. In Ireland there is a small recreational fishery on the River Barrow for *Alosa fallax*. In the River Ulla (NW of Spain) sport fishing is very popular with undulated fishing spoons for *A. fallax*. In the River Minho (boundary between Spain and Portugal, NW of Iberian Peninsula) undulated fishing spoons and fly fishing flies are used to capture both shad species.

In France, particularly in the rivers Charente, Garonne and Rhône, as well as in a number of small rivers, recreational fisheries have become increasingly popular. Fishermen either use a light fishing rod and small rubber sand eels, or small white or golden colored fly spoons fitted with a single hook (mepps), or lures or spinners that are retrieved slowly using jerky movements in fast currents. It is also possible to catch them using a taut line with two or three leaders, each one equipped with a spinner. Shad can also be caught with a fly rod for which it is necessary to use a sinking line and a large nymph covered with bright colours so that it sparkles. The hooks need to be needle sharp to prevent hooked fish being lost, as shad have a hard and bony mouth.

3.4 STOCKING

There were a number of studies carried out, during the second half of the eighteenth and first half of the nineteenth century, which were concerned with the artificial propagation of *A. fallax* (Pouchet and Biéatrix 1889b; Vincent 1894b; Hoek 1899; Pirola 1930; Chiappi 1933). In recent years, there have been great advances in the techniques used in the artificial culture of *Alosa* (see Hendricks 2003 and Clave 2010).

Two LIFE projects have been held to recover the populations of allis shad in the Rhine, one in the period 2008-2010 (LIFE06 NAT/D/000005) and the other from 2011 until 2015 (LIFE09 NAT/DE/000008). In the first project, some 4.8 million larvae were released in the Rhine river system, and in the on-going project an estimated 1.5-2 million larvae per year are being released (Silva *et al.* 2015; see “Chapter 3. Habitat recovery and related conservation efforts” for further details).

3.5 MAIN CONSERVATION CONCERNS

3.5.1 Habitat loss and fragmentation

Other than maintaining access to their spawning grounds and safe passage for the juveniles on their out-migration (Travade and Larinier 1992a), the other main habitat features that need to be maintained are:

Deep pools where the adults can congregate prior to spawning. These need to be:

- Silt free spawning gravels to ensure that the eggs do not suffocate. Twaite shad have shown some flexibility in habitat type. In the Nyamunas (Neman) River (Lithuania) twaite shad had historically migrated 400 km to spawn however in 1959 a dam was built preventing access to the spawning grounds. Recently Švagždys (2000) reported that the fish were now spawning near the mouth of the river and in the shallow water (1.5 – 2m) of the Curionian Lagoon.
- Areas of reduced current / backwaters, as these are the preferred habitat of the juveniles in fresh and estuarine waters.

Sites with particular importance for the persistence of the population must be given special protection. For example on the River Garonne at Agen (France) a sanctuary for *Alosa alosa* was created by Ministry decree on May 15th 1981. The site measures 4.78 km² and is one of the main spawning areas on the river. Prior to 1981 the size of the spawning ground was decreasing because of gravel extraction. The effect of the decree is to ban exploitation of the species, any flood defence works and gravel extraction in the area.

For *Alosa fallax fallax* a sanctuary area exists on the River Garonne at Tartifume (France).

In Ireland, a series of Special Areas of Conservation (SACs) has been designated for Twaite shad (*Alosa fallax*) (see “Chapter 3. Habitat recovery and related conservation efforts” for further details). No SACs have been designated for Allis shad as spawning populations of this species have not been confirmed in Ireland.

In the UK, under the Wildlife and Countryside Act (1981) it is an offence to obstruct access to spawning areas or to destroy gravels used for spawning. There have been significant improvements in shad access in the lower-middle Usk, resulting in an increase in the habitat area having good accessibility (see “Chapter 3. Habitat recovery and related conservation efforts” for further details).

In France, the construction of Arzal Dam in 1970 blocked the access to River Vilaine, but in 1996 a fish pass was installed and the number of *Alosa* spp. has increased steadily (Figure 3.22). Similarly, in the Garonne and Dordogne the original distribution of *A. alosa* had become restricted because of dams at Bazacle (1774), Mauzac (1843) and Golfech (1971). However, the construction of fish pass facilities at these obstructions since 1987 has been successful in extending access for *A. alosa* to the upper river.

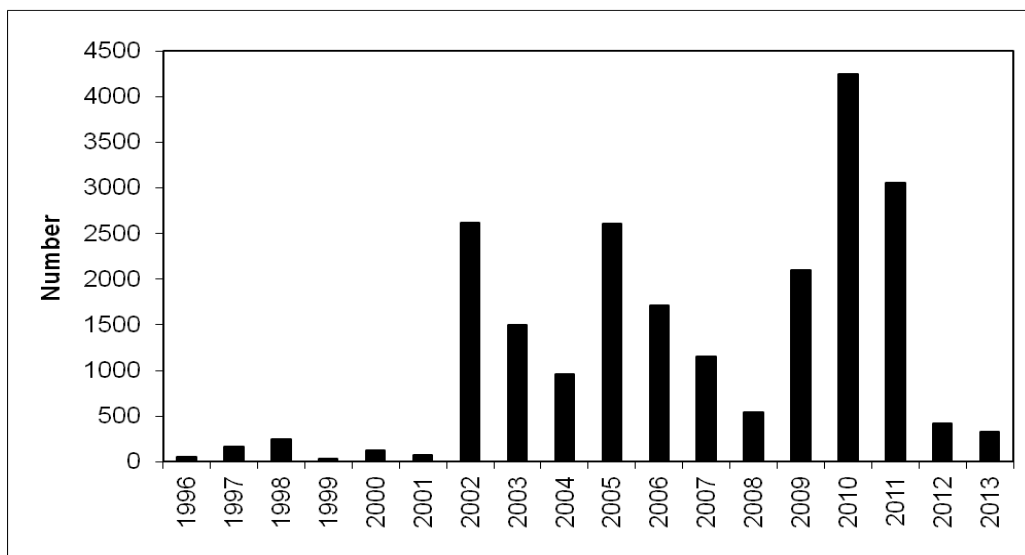


Figure 3.22. Number of *Alosa* spp. migrating upstream through the Arzal Dam fish pass (River Vilaine, France) between 1996-2013. (http://www.eptb-vilaine.fr/site/telechargement/migrateurs/Suivi_passe_bassins_2013.pdf).

3.5.2 Fishing mortality (target and bycatch)

Fishing mortality (F) for *Alosa alosa* in the Gironde-Garonne-Dordogne (France), ranged from 1.86 – 3.32 with a mean (\pm c.i.) of 2.42 (\pm 0.24) for the 1991 – 2002 cohorts (Rougier *et al.* 2012). Levels of exploitation calculated for *A. alosa* on the Gironde-Garonne-Dordogne over the period 1987 to 1998 (excluding 1988) ranged from 47.5% to 87.5%, with a mean (\pm 95% CI) of 67.8% (\pm 8.2%) (Martin-Vandembulcke 1999), and is similar to that reported by Chanseau *et al.* (2005) (61% between 1987 and 2001) and by Rougier *et al.* (2012) (58% between 1994 and 2007).

3.5.3 Other anthropogenic impacts (industrial pumping)

Fish entrainment has been an issue in power station cooling water take-off situations (Claridge and Gardner 1978, Arahamian 1988, Maes *et al.* 2005). Taverny (1991) investigated the potential impacts of the power station the shrimp and glass eel fishery on the abundance of the 0+ population of shad in the Gironde estuary. The power station was estimated to take between 2.5-5.8% of the *A. fallax* 0+ population and between 9.6-11% of the *A. alosa* 0+. The glass eel fishery took less than 1% of both species. The impact of the shrimp fishery was only evaluated for *A. fallax* of which between 11-26% was estimated to be killed in the fishery.

3.5.4 Pollution

Barriers to migration can be created as a result of poor water quality, in particular low levels of dissolved oxygen. In estuaries this can arise naturally in the upper estuary, where re-suspension of the sediment is maximized causing a sag in dissolved oxygen. This condition can be exacerbated by input of organic matter from domestic sewage and industry, causing a water quality barrier (Pomfret *et al.* 1991). Such a barrier was perceived to exist in the Elbe estuary (Germany). The improvement in water quality after 1991 (Gerkens and Thiel 2001) was considered to be the main reason why *Alosa fallax* currently migrate a further 20 km upstream to spawn (Costa *et al.* 2002) compared to the situation in the 1960s (Hass 1968) and 1980s (Möller and Dieckwisch 1991).

At present there is little information that can be used to derive a water quality standard which will safeguard shad in estuaries. However, the study by Möller and Scholz (1991) on juvenile *Alosa fallax* suggests that a dissolved oxygen level of $>4 \text{ mgL}^{-1}$ (section 3.2.2) would protect shad. For adults, Maes *et al.* (2008) inferred from their study on the Scheldt estuary that the level of dissolved oxygen required to ensure passage upstream through the estuary needed be $> 5 \text{ mg l}^{-1}$.

The decline of the population of *A. fallax fallax* has been reported from the Nemunas (Neman / Nyamunas) River (Lithuania) as a result of the construction of the Kaunas hydroelectric dam and elevated pollution from poorly treated wastewater from paper mills in the lower river (Maksimov and Toliušis 1999; Repečka 1999, 2003a and b; Žiliukas and Žiliukienė 2002). During the 1970s and early 1990s, *A. fallax fallax* were only occasionally caught in the Curonian Lagoon (Mileriene 1997; Repečka 1999, 2012) as well as over the Baltic Sea region (Thiel *et al.* 2008; Wiktor 1989; Winkler 1991), and were considered very rare.

However, since the late 1990s, they have become increasingly more abundant (Maksimov 2004; Repečka 2003a, 2012), with large abundance of juveniles in the Baltic Sea and the northern part of the lagoon (Repečka 2012). This may be the result of 1) a 2-3 fold reduction in phosphates, nitrates and BOD_7 in the River Nemunas and Curonian Lagoon, 2) the deepening of the Klaipeda Strait (1984-6) improving access to the Nyamunas (Repečka 2003a and b, 2005, 2012) and 3) the ban on catching and landing twaite shad (Maksimov 2004).

Maes *et al.* (1998) and Vrielynck *et al.* (2003) reported that historically *Alosa fallax* used to spawn just above the tidal limit in the River Scheldt on sandy beaches near Schelle. The decline was associated with

environmental degradation. However, recently twaite shad have been recorded from the lower river (Maes *et al.* 2005; 2007.), associated with an improvement in water quality.

The River Thames supported a spawning population up until the middle of the nineteenth century. Its decline has been attributed to deterioration in water quality (Aprahamian and Aprahamian 1990).

3.5.5 Reduction of genetic diversity

The occurrence of hybrids may be indicative of a pressure, either in the form of low population levels or of restrictions, natural or man-made, preventing access to spawning (Rameye *et al.* 1976; Manyukas 1989; Menesson-Boisneau *et al.* 1993). The occurrence of hybrids of *A. alosa* x *A. fallax fallax* have been reported from Ireland (King and Roche 2008; Coscia *et al.* 2010), from the Solway Firth, U.K. (Maitland and Lyle 2005; Jolly *et al.* 2011), the Rhine, Germany (Hoek 1899; Redeke 1938), the French rivers Loire, Charente, Adour (Douchement 1981; Boisneau *et al.* 1992; Rougemont 2012) and Aude (Douchement 1981), from the Mondego and Lima, Portugal (Alexandrino *et al.* 1996; 2006) and from the Sebou, Morocco (Sabatié 1993).

It has been suggested that the prevalence of hybridization is related to the presence of obstructions to the free passage of migrants upstream, resulting in the use of communal areas for spawning (Boisneau *et al.* 1992) and there is some evidence of their temporal stability (Jolly *et al.* 2011).

Faria *et al.* (2011) found higher levels of nuclear-mtDNA introgression in *A. fallax* (up to 52% with *A. alosa* haplotypes) compared to *A. alosa* (up to 15% with *A. fallax* haplotypes). As hypothesized by Alexandrino *et al.* (2006), the overall introgression patterns suggest that hybridization occurred more frequently between *A. alosa* females and *A. fallax* males, than in the opposite direction. On a European scale, Faria *et al.* (2012) observed that three out of the nine *A. alosa* populations analyzed had *A. fallax* haplotypes, and in 12 of the 29 populations of *A. fallax* varying percentages of *A. alosa* haplotypes were detected. Relatively high levels (25-63%) were reported from populations in the United Kingdom (Usk and Tywi), similar to those of Jolly *et al.* (2011), and from Portugal (Lima and Tejo).

The complexity of the hybridisation was examined by Coscia *et al.* (2010) for 46 *Alosa* spp, caught in the rivers and around the coast of southern Ireland (Table 3.6). The study compared the identification of *Alosa* spp using three techniques, mitochondrial DNA, morphology (gill- raker count) and microsatellite genotyping, and found that 28 (20 *A. alosa* and 8 *A. fallax*) were pure bred (60.9%). It is also evident that morphological – meristic methods cannot be relied upon to classify the species as a pure bred or hybrid, with between 13.0 - 15.2 % misclassified, depending on the programme (Structure / NewHybrids) used to assign individuals to their respective group.

Table 3.6. Comparative identification of *Alosa* spp caught in the rivers and around the coast of southern Ireland, based on mitochondrial DNA, morphology and microsatellite genotyping, using Structure and NewHybrids software.

mtDNA	Visual identification (gill raker count)	Microsatellites		Sample size
		Structure	NewHybrids	
<i>A. alosa</i>	<i>A. alosa</i>	<i>A. alosa</i>	<i>A. alosa</i>	20
<i>A. alosa</i>	Hybrid	<i>A. alosa</i>	<i>A. alosa</i>	1
<i>A. alosa</i>	<i>A. fallax</i>	<i>A. alosa</i>	<i>A. alosa</i>	1
<i>A. alosa</i>	Hybrid	<i>A. fallax</i>	Hybrid	1
<i>A. alosa</i>	<i>A. alosa</i>	<i>A. fallax</i>	Hybrid	1
<i>A. alosa</i>	Hybrid	Hybrid	Hybrid	3
<i>A. alosa</i>	<i>A. alosa</i>	Hybrid	Hybrid	1
<i>A. fallax</i>	<i>A. fallax</i>	<i>A. fallax</i>	<i>A. fallax</i>	8
<i>A. fallax</i>	<i>A. fallax</i>	<i>A. fallax</i>	Hybrid	1
<i>A. fallax</i>	<i>A. alosa</i>	<i>A. alosa</i>	<i>A. alosa</i>	7
<i>A. fallax</i>	Hybrid	<i>A. fallax</i>	Hybrid	1
<i>A. fallax</i>	Hybrid	<i>A. fallax</i>	<i>A. fallax</i>	1

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