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The Allis Shad *Alosa alosa*: Biology, Ecology, Range, and Status of Populations

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Abstract.—For the allis shad *Alosa alosa* (also known as allice shad), no subspecies have been identified. The species is morphologically distinct from the twaite shad *A. fallax fallax* with which it coexists, but hybridization between the two species does occur. Allis shad populations are mainly anadromous, but some landlocked populations have arisen as a result of dam construction. All anadromous populations have common biological characteristics. Migration (December–June) and reproduction (April–July) occur only when the water temperature exceeds 11°C and 15°C, respectively. Age of adults ranges from 3 to 8 years old, and females grow faster and mature later than males. Populations are semelparous, and their spawning behavior is similar. A latitudinal gradient in ecological features exists with southern populations migrating upstream earlier and growing faster. Allis shad is commercially fished with traditional fishing methods. Catches range from 360 to 1,200 metric tons/year, mostly from the Gironde–Garonne–Dordogne basin, France. Historically, allis shad populations extended along the eastern Atlantic coasts from Norway southward to Morocco and into the western Mediterranean Sea. Today, the range is restricted to the Atlantic coasts of France and Portugal. Recently, restoration and conservation programs have been initiated. These include the installation of fish passes and the protection of spawning areas. Currently, no stocking program exists since artificial culture has not proved reliable. At present there are only five large rivers with functional nonresidual stocks, as compared to the 29 rivers that were colonized at the beginning of the 20th century. To conserve and enhance the allis shad, priority areas for further research include ecology of the juvenile stage in freshwater, the degree of homing, the marine phase, and detailed population dynamics.

Introduction

The allis shad *Alosa alosa* (also known as allice shad) is one of the seven species of the alosine Clupeidae (Pisces, Clupeiformes). The genus *Alosa* includes nearly half of the species in the subfamily (Nelson 1994). Currently, the allis shad occurs along the northeastern Atlantic coasts and is sympatric with the twaite shad *A. fallax*.

Although some biological aspects of the allis shad have long been known (Lacépède 1803), the

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most important studies were carried out at the beginning of the 20th century by Roule (1925). Additional published studies included those of Lahaye (1962) on ovogenesis, artificial propagation (Leclerc 1941; Hoestlandt 1958), and problems of taxonomic identity (Svetovidov 1973). New research has been undertaken since the 1980s on the biology and ecology of this species in the eastern Atlantic. These studies are mainly focused on the adult and migrating juvenile stages in some large rivers of France (Loire, Gironde–Garonne–Dordogne, Adour), Portugal (Lima, Mondego), and Morocco (Oued Sebou) (Figure 1). This research includes the influence of human activities on population status and is synthesized in a recent book (Baglinière and Elie 2000).

This paper provides an overview of the current biological knowledge, including the native and current distributions of the allis shad, in order to highlight prognoses for the conservation of stocks and to direct future research.

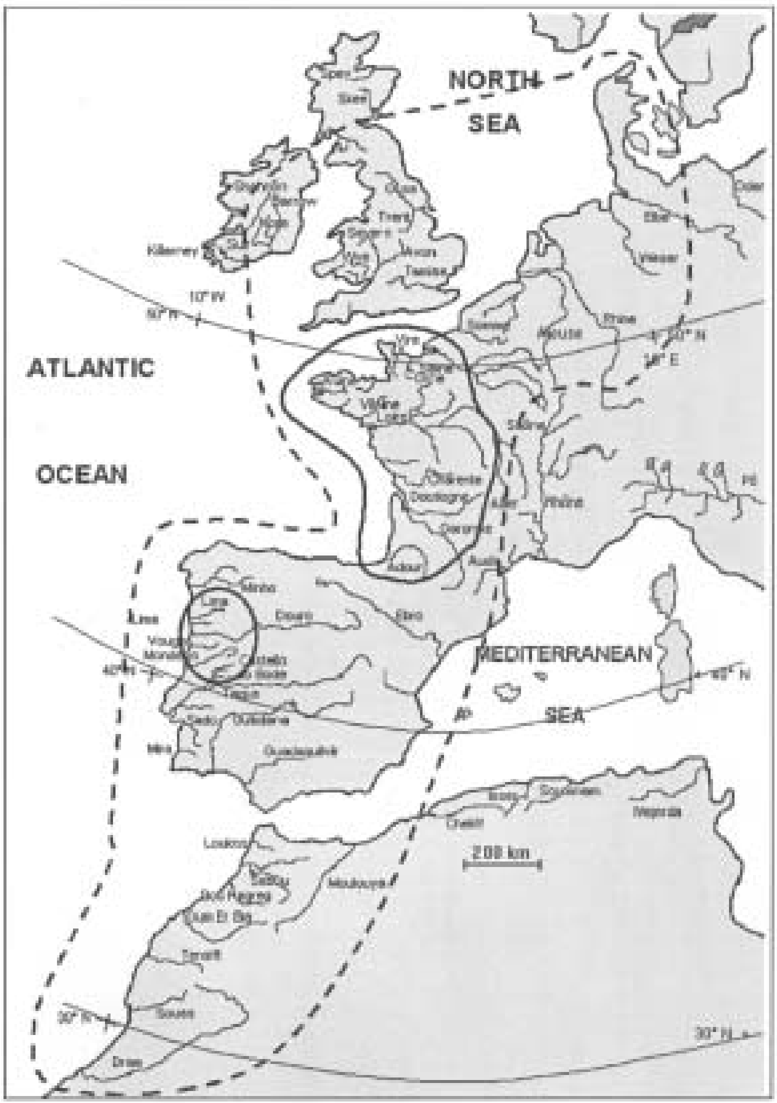


Figure 1.—Historic (dashed line) and current (solid line) distribution areas of allis shad in the eastern Atlantic. Shown are the main rivers colonized at the end of the 19th, beginning of the 20th, and beginning of the 21st centuries and where the most extensive studies have been carried out.

Taxonomy and General Characteristics

Taxonomy and Validity of Subspecies

The systematics and the taxonomy of these alosine clupeids is confusing (see Baglinière 2000). The study of fossil clupeid fishes reveals phylogenetic complexity in the group and has led Legall (2000) and Zaragüeta (2001) to question the validity of the genus *Alosa*, even if Eschmeyer (1990) and Kottelat (1997) consider this genus and the species *A. alosa* to be valid. Taxonomic difficulties arise from the extensive polymorphism in *Alosa* (Fredj and Maurin 1987) and the resulting instabilities in nomenclature, both at the level of the genus and the subspecies (see details in Baglinière 2000).

No subspecies has been recognized in allis shad, but two morphological types which have been wrongly attributed to the allis shad (i.e. *A. alosa bulgarica* and *A. a. macedonica*; Blanc et al. 1971; Lelek 1980) have been put back in the subspecies of *A. caspia* (known as Caspian shad) (Whitehead 1985).

General Characteristics

The body of the allis shad is fusiform and laterally compressed. The head is large, high, and laterally compressed. There is a median notch on the upper jaw, characteristic of the genus *Alosa*, and a ventral keel of scutes is present as for the other members of Clupeidae (Whitehead 1985). The gill arches are equipped with a thick comb of fine gill rakers. The back is dark blue or blue-green and the sides are silvery. The caudal fin is distinctly forked and homocercal (Figure 2), and the lateral line is absent. There are from 60 to 90 well-developed, deciduous cycloid scales on the longitudinal line. No apparent sexual dimorphism exists in the adult stage. Some meristic (number of gill rakers) and morphological (size and relative length of head) characteristics can differ between sexes, but the overlapping of these characteristics prevents reliable discrimination. In other aspects, males are always spermating during upstream migration and can be distinguished from females. At the adult stage, allis shad, along with American shad *A. sapidissima*, attain the largest size of all the *Alosa* species (Baglinière 2000).

The allis shad can be distinguished from the twaite shad by its larger size and by its high head and curved forehead, compressed at the sides. The number of gill rakers is greater in allis shad (>90 as opposed to <60; Figure 3), and scaling is irregular on the longitudinal line (as opposed to regular scaling in twaite shad).

The distinction is made more complicated by the hybridization between the two eastern Atlantic shads. This phenomenon, observed since the beginning of the century (Roule 1925), is now seen throughout the range of allis shad (Alexandrino and Boisneau 2000). The genetically confirmed hybrid individuals have morphometric, meristic, and biometric characteristics that are intermediate between the two species, and, moreover, they appear to be fertile (Alexandrino and Boisneau 2000). Parent species and hybrids can be distinguished by means of gill raker counts (Figure 3).

Allis shad is basically an anadromous species. However, it has developed very localized geographic forms that live in freshwater (see *Impact of Human Activities*). Irrespective of where it lives, allis shad is a species that migrates from growing areas (sea or lake) to spawning areas (river; Figure 4).

Native Distribution, Biology, and Ecology

Native Distribution

Allis shad historically occurred along the Atlantic coast from Norway to Morocco, extending along the British Isles, the coasts of Germany, Holland,

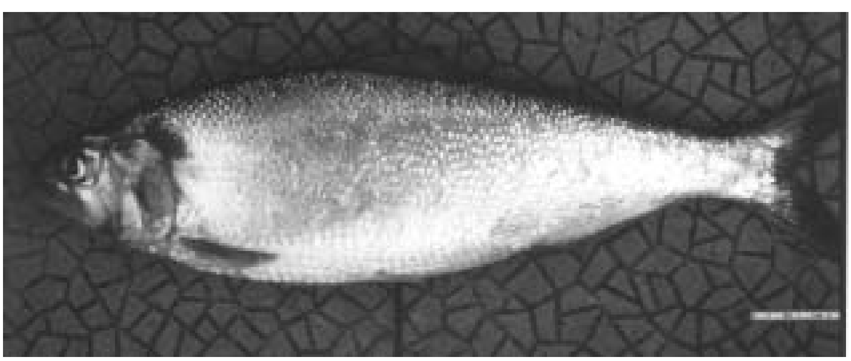


Figure 2.—Photograph of allis shad. Photo by M.R. Sabatié.

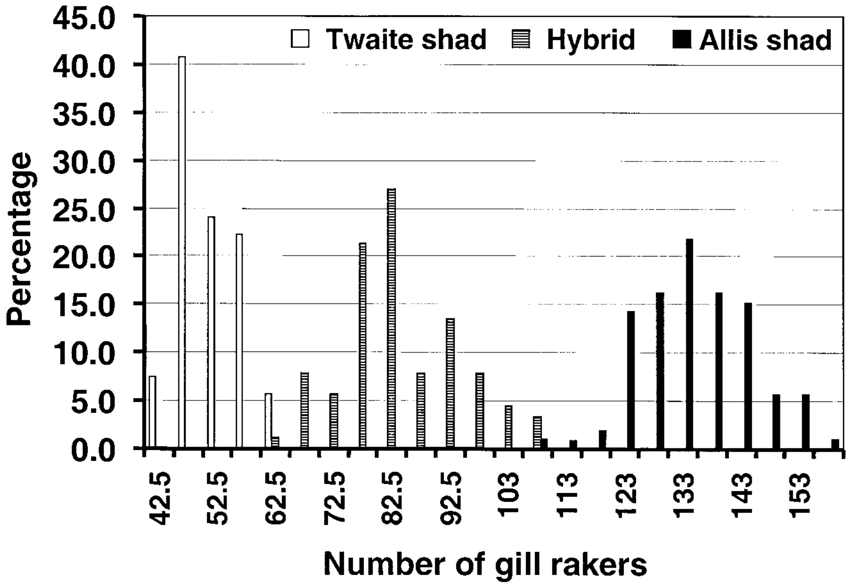


Figure 3.—Frequency distribution of gill raker number in allis shad, twaite shad, and allis–twaite hybrid shad in the Lima River, Portugal.

Belgium, and France, and then down to Spain and Portugal (Blanc et al. 1971; Lelek 1980; Figure 1). Although less abundant than in the Atlantic, allis shad also occurred in the western Mediterranean along the coast of Spain, and especially in the Ebro River (Lozano Cabo 1964). Its presence along the Mediterranean coast of France was rare and even doubtful (Roule 1925; Hoestlandt 1958).

The original latitudinal distribution of allis shad in the eastern Atlantic (between 28°N and 60°N latitude) was larger than that of the American shad (between 25°N and 50°N latitude). This may be due to varying positions of the 0°C and 20°C isotherms linked to the presence of cold currents on both Atlantic seaboards. Temperature plays an important role in the distribution of shad (Cassou-Leins and Cassou-Leins 1981).

Biology and Ecology

Adult Phase.—The spawning migration of adults occurs along a latitudinal gradient from south to north and takes place from December to August,

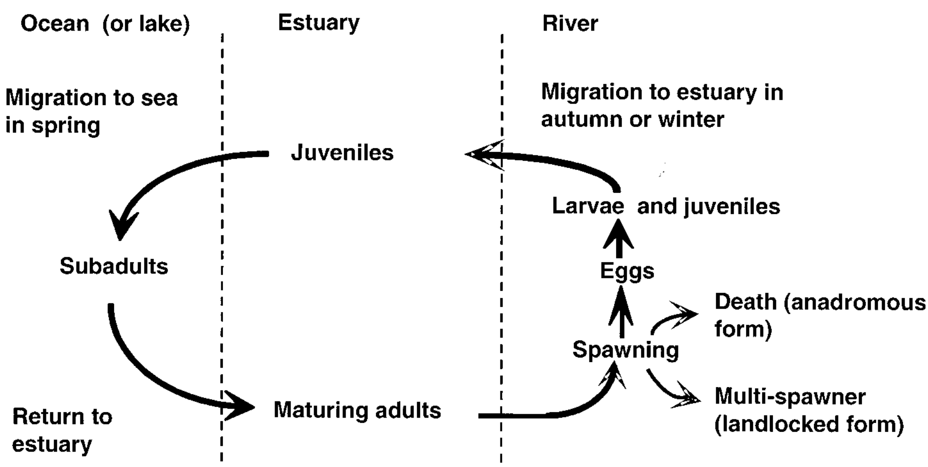


Figure 4.—Biological cycle of allis shad.

mainly during the day. The pattern of migratory dynamics corresponds to a dense influx of fish with one or two peaks of migration (Mennesson-Boisneau et al. 2000a; Rochard 2001). This influx has an internal rhythm modulated by environmental and biological factors (Mennesson-Boisneau et al. 2000a; Rochard 2001; Figure 5).

Water temperature, which has a strong influence both in estuaries and freshwater, is the most important environmental factor moderating migratory behavior. Spawning migrations generally take place when temperature ranges from 12–20°C. When temperatures are 10–11°C, migration behavior is weak. The tidal cycle also plays a role in migration, mainly in estuaries, but it can act in freshwater bodies up to 150 km from the sea (Figure 5). River discharge also has an influence, notably by halting the migration during strong spates.

The most important biological factors are sex (males seem to migrate earlier than females) and sexual maturity. The influence of these factors increases as migration proceeds usptream (Figure 5), and they can act on the pattern of fish influx in relation to the halts and mortality of spawners on the spawning grounds distributed along the river (Mennesson-Boisneau et al. 2000a).

Adult shad do not feed during their upstream migration. Weight loss after spawning is high. Allis shad can lose 59% of their prespawning weight, depending on the length of spawning migration and the location of the spawning grounds (Mennesson-Boisneau et al. 2000a).

Age can generally be determined from scales, but it may be appropriate to use otoliths in some cases (eroded scales, older fish with confused growth marks, age validation; Mennesson-Boisneau and Baglinière 1992). Adult ages range from 3 to 8 years, with dominant age-classes from 4 to 6 years (Figure 6). Generally, anadromous allis shad are considered semelparous since no more than 5–6% of the Atlantic stock spawn more than once (Mennesson-Boisneau et al. 2000b). The mean size of adults in all colonized rivers is 550 mm total length (TL) with a mean weight of 1.8 kg, but they can attain up to 800 mm (5.0 kg) in Portugal and Morocco. Mean size and age-distribution change according to year, sex, and geographical position. Female spawners are older and larger than males and they attain sexual maturity later (at age 5, on average, versus age 4 in males) in all stocks. Females have a high specific fecundity (100–150 × 10^3 eggs/kg), and fecundity decreases in southern stocks (Cassou-Leins et al. 2000).

Unlike the anadromous stocks, landlocked adult allis shad are smaller (often about 400 mm TL), most likely because food resources are limited. Landlocked populations are iteroparous (Mennesson-Boisneau et al. 2000b).

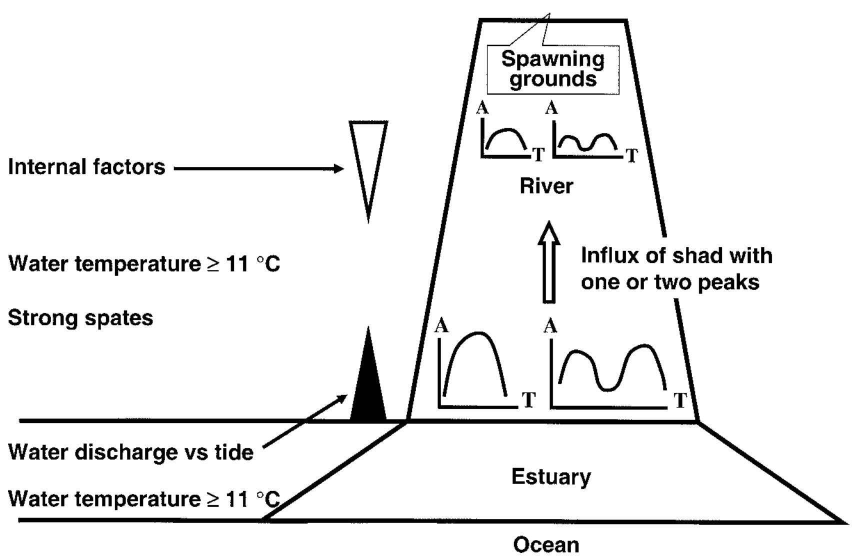
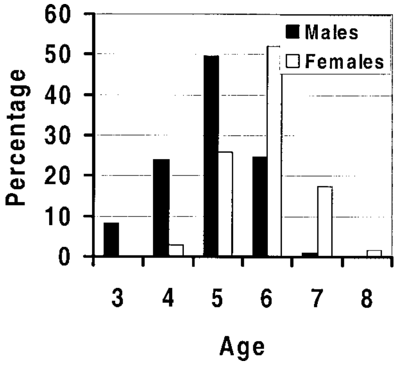


Figure 5.—Diagram showing migratory dynamics of allis shad and external and internal factors acting on the migration from the estuary to the spawning zones (modified from Mennesson-Boisneau et al. 2000a; A = abundance; T = time). Effects of tidal cycle on spawning migration decrease as shad enter freshwater (solid triangle); effects of internal factors increase as shad move upstream to the spawning grounds (open triangle).



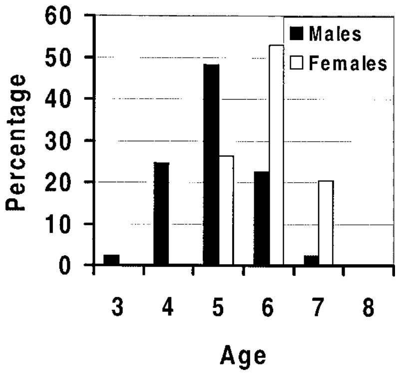


Figure 6.—Distribution frequency of age-classes according to sex in allis shad populations for the rivers Loire (top panel) and Lima (bottom panel; Mennesson-Boisneau et al. 2000b).

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 behavioral 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.

A method for estimating the numbers of spawners has been developed using the counting of "bull" splashing noises within a spawning zone. This provides an annual abundance index of allis shad spawning escapement (Cassou-Leins et al. 2000).

Larval and Juvenile Phase.—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 at hatch, when they move to open water and exhibit a positive phototropism. They adopt a nektonic behavior that persists until they are 36 d old. Larvae prefer low current (Véron et al. 2003, this volume). 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). The residence time in the estuary is not well known. 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 position, and the position of the spawning site within the water course. 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, zooplankton, and mysidacea (Taverny et al. 2000a).

Very few data are available for the marine phase. Nevertheless, some observations in the Bay of Biscay show that allis shad remain on the continental shelf in water depths of 70–300 m (Taverny and Elie 2001a). They form schools and feed mainly on zooplankton. The largest individuals may be piscivorous (Taverny and Elie 2001b). Observations along the Moroccan Atlantic coast (and possibly the coast of Portugal) show that allis shad remain in the productive upwelling zones (Sabatié 1993).

Discrimination of Populations.—There have been no tagging studies of juvenile allis shad and it is not known if adults home to their natal river. A genetic analysis based on protein loci shows that allis shad populations in Portugal form a distinct and less variable group than those in France. Population discrimination is difficult because of the low level of genetic variability in allis shad (Alexandrino and Boisneau 2000). Nevertheless, allis shad populations can be divided in two ways, ecologically and morphologically. Ecologically, we can consider two groups: a southern population including Portuguese and Moroccan populations and a northern one including French populations. Southern populations show a higher growth rate due to higher water temperatures in freshwater (Taverny et al. 2000b) and the proximity of upwelling zones that may increase the trophic resources (Mennesson-Boisneau et al. 2000b). Morphologically, using multivariate discriminant functions with some morphological criteria (number of gill rakers, dorsal and anal fin rays, and prepelvic and postpelvic scutes), we can identify several groups, but the morphological distance between them is low (Sabatié et al. 2000; Figure 7).

Impact of Human Activities and Status of Stocks

Due to their anadromous behavior, allis shad undergo considerable challenges during their life cycle from natural as well as anthropogenic causes. Impacts of human activities on allis shad populations started at the beginning of the 19th century and increased throughout the course of the 20th century. Human activities can act either directly by causing mortality of fish (e.g., fishing, hydraulic turbines, or pollution) or indirectly by changing or decreasing the available habitat or the migration conditions (e.g., dams). Direct or indirect causes can have cumulative effects in both space and time throughout the native range. These result first in reduced stock abundances, then in the formation of residual populations, and eventually in the extinction of populations.

Harvesting

General Characteristics.—Allis shad are harvested by commercial fisheries throughout their range in estuaries, the middle sections of rivers, or in their resident form in lakes. The fish are generally caught when they migrate from their feeding areas toward their spawning grounds. A few catches are recorded in the sea or along the coast. A sport fishery has recently been developed in France. The legal catch size limit imposed on both commercial and sport fishers is greater than or equal to 30 cm TL.

Despite being an important resource, the economic value of allis shad has been seriously reduced as a result of the elimination or decline of stocks.

Fishing Techniques.—Various stationary and mobile fishing gears are used in commercial fisheries along the migratory route and generally follow regional traditions. The two most commonly used techniques are stop net and drift trammel net (for descriptions see Elie et al. 2000 and Sabatié et al. 2001). Recreational anglers use either a light fishing rod with small spoon lures or spinners or a fly rod with white or gold flies (Sabatié et al. 2001).

Catches.—Nominal catches of shad reported by the Food and Agriculture Organization of the United Nations either underestimate or overestimate the catches or do not make a full distinction between the two species of eastern Atlantic shad. Thus, it is more reliable to obtain data from local fisheries surveys. However, these data are restricted to certain stocks and do not include recreational catches (Table 1).

From 1978–1998, approximate total landings ranged from 355 to 1,198 metric tons in the cur-

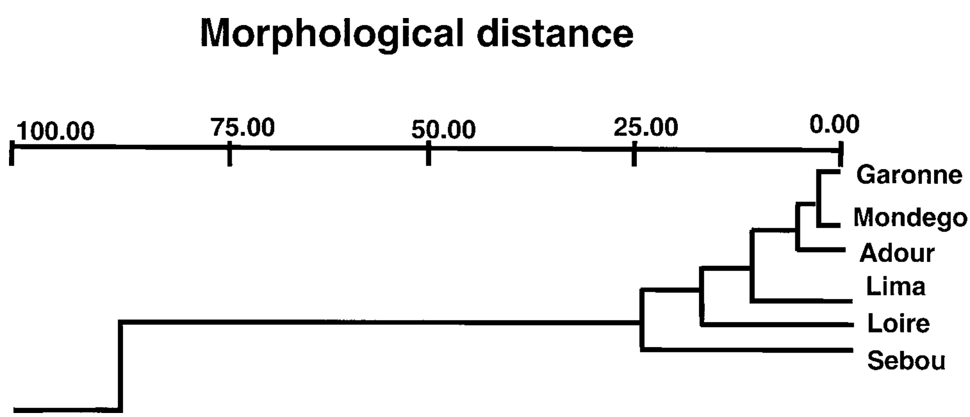


Figure 7.—Morphological comparison of allis shad populations analyzed by the Unweighted Pair-Groups Method Averaging aggregate–pooling method using five meristic criteria (see text; Sabatié et al. 2000).

Table 1.—Landings (in metric tons) of allis shad in the eastern Atlantic from 1978 to 1999. G–G–D = Gironde–Garonne–Dordogne system; an empty cell designates no data. Subtotals and totals are approximate. Data from Véron 1999; Elie et al. 2000; D. Baudry, P. Prouzet, and F. X. Cuende, Institution interdépartementale pour l'aménagement hydraulique du bassin de l'Adour and IFREMER, Laboratoire halieutique d'Aquitaine, unpublished data; and P. Boisneau, Association Nationale des Pêcheurs commerciaux fluviaux, and A. Grandpierre, Centre de traitement statistique des affaires maritimes, personal communication. The subtotals for Portugal include an unknown number of allis shad landings in rivers other than the Lima River.

	Year																					
River	1978	1979	1980	1981	1982	1983	1984	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999
France																						
Loire	3	5	6	5	12	8	5	23	5	21	19	16	4							9	9	9
Charente								0.5				2						5	5			
G–G–D	500	638	840	826	863	1,096	615	620	583	628	1,007	762	487	841	489	338	500	577	539	416	440	
Adour								9	38	26	22	14	8	13	9	11	27	21	32	22	12	27
Atlantic Ocean																	74	47	56	59	33	53
Subtotal	503	643	846	831	875	1,104	620	653	626	675	1,048	794	499	854	498	349	601	650	632	506	494	89
Portugal																						
Lima														2	5	6	6	10				0
Subtotal										43		38	23	>2	>5	>6	>6	>10				
Morocco																						
Sebou	186	32.6	163	222	137	93	3	25	29	20	18	4	65	3	1	2	0	0	0	0	0	0
Loukos	1	0.8	1	0.2	2	0.7	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Subtotal	187	33	164	222	139	94	3	25	29	20	19	4	65	3	1	2	0	0	0	0	0	0
Total	690	676	1,010	1,053	1,014	1,198	623	678	655	738	1,067	836	587	859	504	357	607	660	632	506	494	89

rent distribution area (Table 1). About 94% of the total landings are in France with 89% from the Gironde–Garonne–Dordogne system alone. Indeed, catches in this system range from 338 to 1,007 metric tons and are very high compared to catches in other rivers. Catches in the Loire River are low, often not exceeding 10 metric tons and declining sharply to about 1 metric ton in the years 1995 and 1996. Average catches in the Adour River were approximately 19 metric tons between 1985 and 1999. Sea catches recorded near the Aquitaine, France, coast exceeded catches in French rivers other than the Gironde system during the years 1994–1999. Thus, it appears that ocean landings are increasing. In Portugal, total catches are small and come mainly from small rivers such as the Lima. Here, the catches were abundant at the beginning of the 1990s but showed sharp declines in 1998. The total landings in Morocco decreased strongly during this period, as observed in Oued Sebou, the last main river to have an important allis shad fishery. In fact, the species seems to have disappeared in the Oued Sebou at the beginning of the 1990s after a drastic decrease in catches over a 25-year period (760 metric tons in 1968 as opposed to 2 metric tons in 1993).

In France, during 1989–1997, allis shad landings represented the highest proportion of anadromous fish (33.1% of total production). It was valued at 1.3 million euros, considerably lower than for the glass eel *Anguilla anguilla* (also known as European eel; Table 2), in great demand by Asian markets. In 1997, 280 commercial fishermen were recorded as fishing allis shad, about 19.8% of the total number of fishermen (Castelnaud 2001).

Table 2.—Mean total production and value of anadromous fish caught by commercial fisheries in France from 1989 to 1997 (Castelnaud et al. 2001).

Species	Production (metric tons)	Value (million euros)
Glass eel of *Anguilla anguilla*	410.5	62.6
Eel[a] *A. anguilla*	302	2.8
Shad *Alosa alosa* (98% allis shad)	581	1.3
Marine lamprey[b] *Petromyzon marinus*	140	2.3
Atlantic salmon *Salmo salar*	11.5	0.2
Sea trout[c] *Salmo trutta*	2.8	< 0.1
Mullet *Liza ramada*	246	0.3
Flounder[d] *Platichthys flesus*	57.5	0.9

[a] Also known as European eel.
[b] Also known as sea lamprey.
[c] Also known as brown trout.
[d] Also known as European flounder.

Habitat Degradation, Migration Conditions, and Fishing: Cumulative Effects.—The construction of dams has been the primary factor affecting the abundance of allis shad populations over its entire distribution area. At first, dams were often built without fish passes or with fish passes that were either ill adapted or did not accommodate the lack of jumping behavior in allis shad. The negative effects of dams are dependent on their number and position in the watercourse along the migratory route. These effects can be amplified by other factors such as the deterioration of water quality and changes in the direction and shape of waterways. Dams prevent adults from reaching certain river basins or spawning sites inside the catchment, thus leading to stock extinction or a strong decrease in abundance. One noteworthy example is the effect of multiple dams constructed on the River Rhine in The Netherlands, where catches decreased from 150,000–250,000 fish in the decade 1880–1890 to less than 1,000 at the end of the first World War and then fell to zero (de Groot 1989; Figure 8). Declines in the Douro and Minho rivers in Portugal serve as more recent examples. Up until 1970, the Douro was probably the river with the highest allis shad catches in the Iberian Peninsula, with an average annual catch of 616 metric tons (Eiras 1977). The building of nine dams, the last one in an estuarine zone, together with the degradation of water quality, resulted in the complete and rapid (<20 years) extinction of allis shad by the end of the 1980s (Alexandrino 1996). In the Minho River, the building of five dams resulted in a large decline in annual catches from 62,000 fish in the middle of the 20th century to less than 1,000 fish today (Figure 9).

The present lacustrine forms of allis shad derive from anadromous populations landlocked in large reservoirs created by the construction of dams in the middle of the 20th century, such as El Kansera on the Oued Sebou in Morocco (Sabatié 1993) and Castelo do Bode on the River Tagus in Portugal (Alexandrino 1996). Other landlocked populations have appeared much more recently (after 1980) in the River Mondego (Aguieira reservoir, Portugal) (Collares-Pereira et al. 1999) and in the River Guadiana (Spain).

The existence of dams (even of small size; fall height < 1 m) remains a problem today. Several dams are being built in estuarine zones (Lima) or are in the planning stages (Loire, Minho, and Tagus; Taverny et al. 2000a). Present dams influence behavior of allis shad by modifying the migratory pattern or slowing down or halting movements

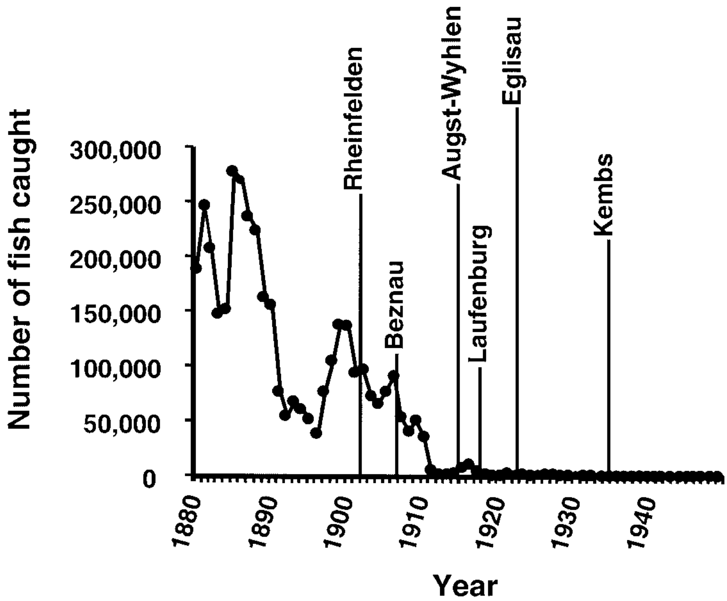


Figure 8.—Evolution of allis shad catches (metric tons) by Netherlands commercial fisheries in the Rhine from 1880 to 1950 (de Groot 1989). Dates of dam construction from Vibert (1950).

(Taverny et al. 2000a). When upstream migration is prevented, allis shad spawn in the lower part of the river on atypical sites or "forced sites" that may be different from the natural ones (Cassou-Leins et al. 2000). This situation has two outcomes: (1) egg survival could decrease strongly in relation to the amount of fine particles deposited on the bottom; and (2) allis shad spawn on the same zones as those colonized by twaite shad, resulting in the production of hybrids. The appearance of such individuals results from the genetic similarity of the two species (Alexandrino 1996) and from changes in the habitat and / or decreases in populations. Dams led to the disappearance of spatial and behavioral barriers against hybridization (Boisneau et al. 1992). The medium-term evolution of this hybridization

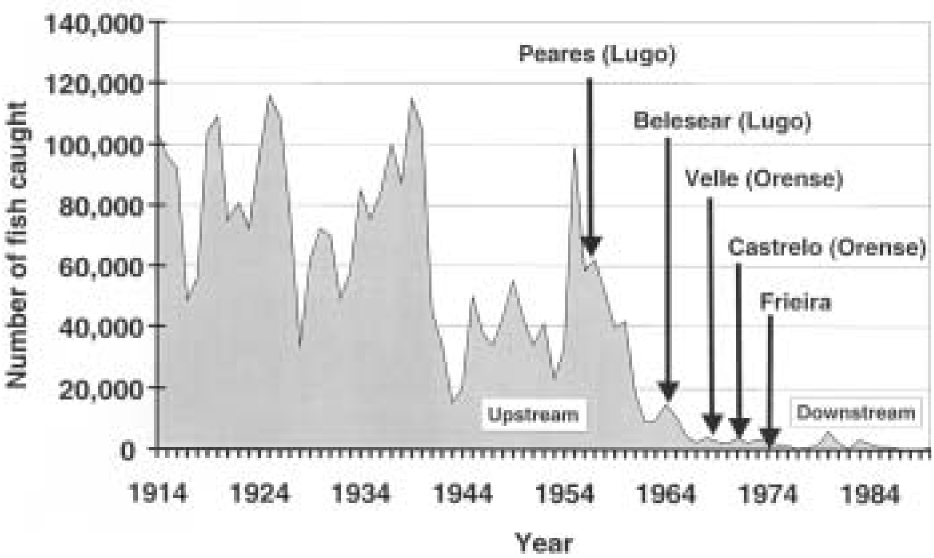


Figure 9.—Evolution of allis shad catches (number) by commercial fisheries in the Minho River, Portugal, from 1914 to 1989 (Alexandrino 1996).

process that could be detrimental either to allis or twaite shad is not known at the present time because the extent of the phenomenon within the range has been not quantified. The allis shad is less plastic (low polymorphic level; Alexandrino 1996) and would seem more sensitive to human activities than the twaite shad, due to the spawning requirements in the upper reaches of rivers.

Lastly, hydroelectric dams induce mortality in juvenile shads depending on turbine type and fall height (Larinier et al. 2000). Until recently, mortality rates for juvenile shad had been over-estimated because of the experimental protocols and techniques used. But recent experiments showed mortality rates were similar to those observed in salmonids (10–15%). The extraction of gravel has contributed to the decrease in stock abundance by damaging spawning sites and juvenile habitats. In the Adour River, the intensive extraction of beach gravel in a long stretch of spawning sites is linked to a decrease of commercial catches over 7 years from 36 metric tons (1986) to 11 metric tons (1993). This extraction has been recently reduced and even halted in some rivers by regulatory action in France (Taverny et al. 2000a).

Fishing is rarely the primary factor involved in the reduction of stock abundance in allis shad, although it has been invoked in the case of the Rhine population (de Groot 1989). However, we often lack sufficient data to analyze the impact of fishing, and formal stock assessments of allis shad have only just begun. Nevertheless, fishing pressure exerted on stocks that are challenged by other factors can enhance population decline. For example, the maintenance of high fishing pressure both over time (e.g., no weekend ban) and in space (sea, estuary, and spawning zones) seemed to have forced the allis shad stock in the Oued Sebou River, already threatened by industrial pollution and dam building, to a residual level in many tributaries. Subsequently, a new dam built in the early 1990s near the estuary brought the stock to extinction (Figure 10; Sabatié 1993).

Conservation Strategies

The specific biological requirements of allis shad and its severely limited distribution area make it useful as a bioindicator species for the middle sections of major river basins. The species is also a strong candidate for the development of restoration efforts carried out in anadromous fish river basins where allis shad is still present. Recently, two protective measures have been taken in Europe. Allis shad has been included in Appendix III of the Bern Convention (Baglinière et al. 2000) that requires member states to make provisions to ensure conservation of flora and fauna and their habitats, with particular attention to endangered and vulnerable species, including migratory species. The species has also been incorporated into Annexes II and V of the European Community Habitats Directive, a directive on the conservation of natural habitats and wild flora and fauna. This places an obligation on members of the European Union to assess numbers and exploitation of the populations and to designate "special areas for conservation"

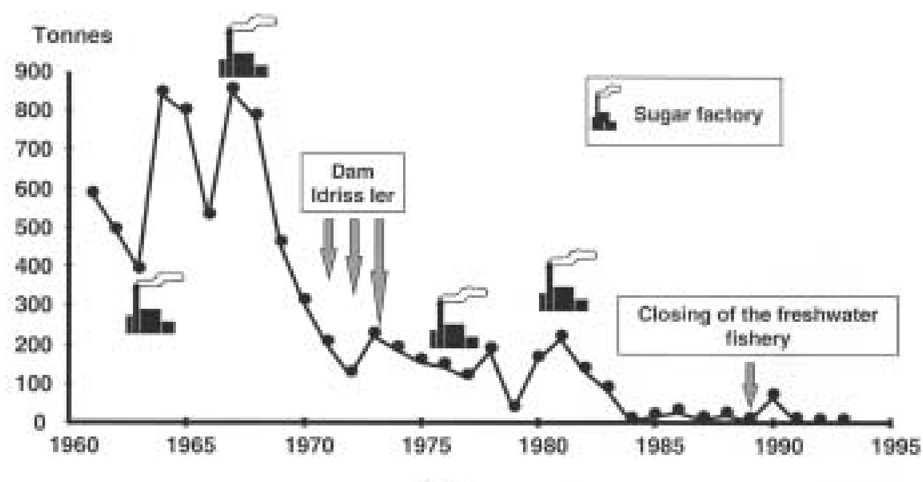


Figure 10.—Evolution of allis shad catches (metric tons) by commercial fisheries in the Oued Sebou estuary, Morocco, from 1960 to 1995 (Sabatié 1993).

or "sites of community interest" to safeguard populations. To uphold these obligations, the legal and regulatory structures necessary to apply adequate measures generally exist in all countries.

Sanctuary Areas and Habitat Protection

Special protection has been given to sites particularly important for the persistence of the population. For example, in 1981, the French Ministry of the Environment created a sanctuary on the Garonne River at Agen. The site was one of the most important spawning areas on the river before fish passages opened upstream spawning sites. Before 1981, the spawning ground was strongly disturbed due to gravel extraction. Commercial exploitation, flood control construction, and gravel extraction in the area are now prohibited.

As in the case of Agen, protection and conservation of habitat for allis shad throughout its range is required. Special attention should be paid to the protection of existing spawning grounds where habitat quality and location play an important role in the occurrence of introgressive hybridization between the two eastern Atlantic species of shad.

Introductions

There is only one reported introduction of allis shad, in contrast to the other *Alosa* species (Baglinière 2000; Aprahamian et al. 2003, this volume). Hoestlandt (1958) transferred approximately 500,000 allis shad eggs from the Dordogne to the Rhône in 1953. Up to that time, its presence in the Rhône was doubtful (see *Native Distribution*). It is difficult to determine whether the transfer was successful, although subsequently the presence of allis shad was recorded by Douchement (1981). In a recent study, Le Corre (1999) captured no allis shad, suggesting that the population may now be extinct. In the Hoestlandt (1958) case, allis shad were introduced into the native habitat of a different species, twaite shad *A. fallax rhodanensis* (Le Corre 1999). In the future, the technique of adult or juvenile introduction might be developed further in the framework of a recovery plan, although its success rate can be affected by numerous biological factors (Minckley 1995). Before using this technique, knowledge of genetic structure in the introduced and native populations is required.

Artificial Breeding

Like many other fish, and using techniques parallel to those developed for salmonids, shads have been artificially reproduced in order to reintroduce and increase stocks as well as extend the species distribution. In Europe, the first attempts with allis shad were made at the end of the 19th century and continued up to the middle of the 20th century (see Quignard and Douchement 1991; Baglinière 2000). All were short-term (<3 years) and used no marked larvae, preventing any evaluation of planting success. All the attempts to date are considered failed because the stocked populations went on to decrease. These failures must be attributed to the cessation of hatchery production, the progressive deterioration of environment, and technical problems encountered at all stages of shad culture. No attempt has been made to increase stocks since the middle of the 20th century.

Improvement of Migration Conditions

Shads are more sensitive than migratory salmonids to the presence of obstacles during their migration since they do not jump and cannot swim as long as salmonids. Shad passage efficiency is considered excellent when it reaches 50% through all fish passes on a given water course. Values between 10% and 20% are most frequent (Larinier and Travade 1992). Recent studies have described the behavior of allis shad below dams and have led to new approaches to ensure effective passage of shad (e.g., pool-type fish pass). Fish pass efficiency has recently been greatly improved (Larinier et al. 2000), leading to the restoration and increase of certain stocks in France. Until 1980, construction of fish passes never targeted shad. They concentrated on migrating salmonids, particularly Atlantic salmon. This situation is changing due to our recent growing awareness of the shad's importance as a natural resource, especially in the Gironde–Garonne–Dordogne system (Taverny et al. 2000a). Since 1985, a large number of ineffective fish passes have been improved and some dams (Golfech, 210 km from the Gironde mouth) have been equipped with a fish lift. An increase in the overall stock abundance is now confirmed by the increased number of fishes crossing over the Golfech Dam (Figure 11). Other recent examples are recolonization in the Vire in Lower Normandy and the Aulne and the Vilaine in Brittany, France. A turning point in the management of anadromous fish has taken place recently in France with the removal of the Maison Rouge Dam built in 1924 on the Vienne River, a tributary of the Loire River, which previously halted any migratory fish. Notably, this has resulted in the recolonization of a historical spawning site for allis shad in this system.

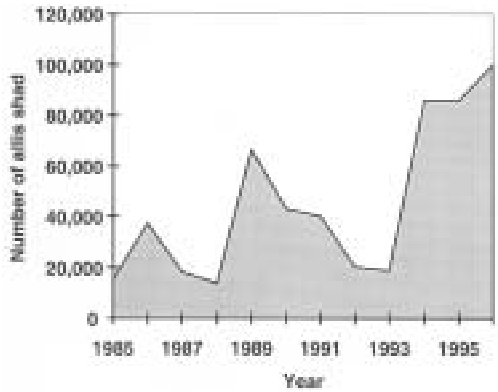


Figure 11.—Evolution of allis shad number crossing over the Golfech Dam on the Garonne River, France, from 1985 to 1996 (MIGADO, Association Migrateurs Garonne-Dordogne).

Fishing Regulations

At present, no stocks are protected by fishing moratorium. Furthermore, it is difficult to ascertain the true impact of fishing on stock levels for several reasons: (1) the available data are restricted to only a few stocks (Loire, Dordogne, Garonne, Adour, and Lima; Elie et al. 2000); (2) there are few studies on the population dynamics; (3) fluctuations in the abundance of these populations are large; and (4) recent works in population dynamics (Martin-Vandembulcke 1999) must be supplemented since they lack information on stock–recruitment relationships (if any exist), natural mortality, setting reference points (Potter 2001), and conservation thresholds above which fishing pressure should be reduced. For example, recent work resulted in the estimation of the exploitation rate (41% and 48%) of allis shad in the Gironde–Garonne–Dordogne populations (Lambert et al. 2001).

At present, commercial fishing, research surveys, and analyses of catches on each river allow the establishment of a presence–absence index and a health or abundance index using catch per unit effort (Mennesson-Boisneau and Boisneau 1990; Castelnaud et al. 2001).

Current Distribution and Status of Stocks

The impact of human activities has led to a drastic restriction and fragmentation of the distribution area of allis shad (Baglinière 2000; Baglinière et al. 2000; Sabatié et al. 2001) (Figure 1) and has contributed to the placement of allis shad on the red list of threatened species in Europe (Table 3).

Before describing the present distribution of allis shad and the current status of stocks, it should be noted that abundance of these populations may vary annually under the influence of ecological, physiological, and demographic factors. The presence of migrating allis shad along the coast in no way implies that they regularly spawn in the adjacent watercourses. Thus, the following assessment is based on the presence of regular and abundant stocks in each river system. The extent to which restoration programs and large-scale climate changes result in increased stock, recent colonization, or recolonization is unknown.

At present, allis shad have totally disappeared from northern Europe. The species is no longer found in the British Isles, although mature individuals can be found on the southern coast of Scotland. The northern limit of the species, excluding

Table 3.—Conservation status of allis shad by country in the eastern Atlantic Ocean and western Mediterranean Sea according to IUCN (1994) criteria.

Conservation status	Criteria	Countries
Extinct	There is no reasonable doubt that the last individual has died.	Belgium, Luxembourg, Sweden
Critically endangered	Species is facing an extremely high risk of extinction in the wild in the immediate future.	Denmark, Great Britain, Ireland, Spain (Mediterranean Sea)
Endangered	Species is not critically endangered but is facing an extreme risk of extinction in the wild in the near future.	Germany, The Netherlands, Portugal, Spain (Atlantic Ocean)
Vulnerable	Species is not critically endangered or endangered but is facing a high risk of extinction in the wild in the medium-term future.	France

relic or residual populations, is the River Loire, where abundance appears to be low due to the presence of a pollution plug in the estuary. Farther to the north, allis shad never completely disappeared from the Rhine River, and a small population might remain there today. Recent observations have shown that allis shad (identified by genetic analysis; Véron 1999) have not totally disappeared or perhaps have reappeared in certain small rivers in Lower Normandy and Brittany (the Rivers Vire, Aulne, and Vilaine). This colonization does not seem to be an isolated occurrence since spawning is observed annually. Farther south, allis shad is abundant in the River Charente (France) and very abundant in the Dordogne–Garonne river system where its numbers have increased, possibly as a result of a restoration program for Atlantic salmon. It is also found in the Adour and the Nivelle rivers, France. The species is still present along the coast of Portugal in the Minho, Lima, Vouga, and Mondego rivers. However, abundance has decreased sharply since the beginning of the 1960s in the Minho River and very recently in the Lima River. In contrast, abundance has recently increased in the Mondego River owing to improvement in habitat quality. Anadromous stocks are probably residual in the Tagus and Guadiana rivers, but land-locked forms occur in larger numbers. Finally, the southern limit of allis shad distribution was southern Morocco. It has now shifted considerably toward the north (Mondego and Vouga rivers) because the Moroccan land-locked and anadromous forms of the species now seem to be extinct. Allis shad have disappeared totally from the Mediterranean basin, both along the coast of Morocco and in the River Ebro.

Thus, the current status of allis shad stocks is the following (Table 4): 13 populations are extinct, five rivers have critically endangered populations, and only five large rivers support functional, nonresidual stocks (Charente, Dordogne, Garonne, Adour, and Mondego), as compared with the 29 rivers that were still colonized at the end of the 19th and beginning of the 20th centuries.

Conclusions

At present, most of our understanding of the biology and ecology of allis shad is based on the adult component of the population and much less on the juvenile stage. Studies have been carried out in most of the rivers still colonized by the species. Sampled fish come mainly from estuarine zones and the middle reaches of rivers or spawning sites, and only a few data have been recorded in the sea or along the coast. The larger proportion of allis shad in catches compared with twaite shad (Aprahamian et al. 2003) indicates that the sampling is commercial fisheries dependent.

Information on differences in morphological and ecological characteristics among populations exist, but genetic studies demonstrate that it is difficult to separate populations due to the low level of polymorphism in this species. The homing instinct needs to be confirmed, requiring the use of DNA techniques (Baglinière et al. 2000; J. L. Baglinière, P. Alexandrino, and M. Le Corre, unpublished data) and natural biogeochemical tracers such as elemental signatures measured in otoliths (e.g., Thorrold et al. 1998). The close relationship between spawning stock and river is important to consider since the conditions of the freshwater environment during the embryo–larval stage play an important role in development.

Demographic characteristics, migration behavior within the estuary and river, and spawning history of adult fish are sufficiently well known. In other respects, the role of the marine phase in controlling the abundance variability is not known. In comparison, very few studies have been carried out on the juvenile life phase in rivers before downstream migration. This phase seems to have an influence on the morphological and demographic characteristics of adults and the inter-year recruitment variability. Studies on juvenile ecology are just beginning under experimental as well as natural conditions. These will focus on habitat preferences, growth conditions in larvae and juveniles, and characteristics of the emigrating juveniles. Nevertheless, control of artificial breeding is still difficult. However, it remains a major objective to avoid extinction.

Allis shad present advantages from the scientific, ecological, and natural resource points of view (diversity of habitats, no impact from hatchery-reared fish). This species is an excellent indicator of connectivity and biological quality of the middle reaches of large European river basins.

Like the other diadromous fishes, the allis shad has suffered from the progressive impact of human activities in all the major river systems since the beginning of the 20th century. This human activity has resulted in a pronounced fragmentation of the allis shad's distribution area and a sharp decrease in abundance levels. Some recent restoration programs have started by taking into account the biological specificity of this species. Its populations seem genetically similar and particularly sensitive

Table 4.—Conservation status of allis shad stocks in eastern Atlantic and western Mediterranean seas according to IUCN (1994) criteria. CSP = Conseil Supérieur de la Pêche, France; FNRS = Fonds National de la Recherche Scientifique, Belgium.

	IUCN criteria											
River	Extinct	Extinct in the wild	Critically endangered	Endangered	Vulnerable	Lower risk	Data deficient	Not evaluated	Conservation dependent	Near threatened	Least concern	References
Severn		+										Aprahamian and Aprahamian (1990)
Wye		+										Aprahamian and Aprahamian (1990)
Elbe	+											Thiel et al. (1996)
Rhine							+					Roche (1997)
Meuse	+											J. C. Philippart, FNRS, unpublished data
Seine	+											Taverny et al. (2000a)
Orne							+					A. Richard, CSP, personal communication
Vire							+					Richard, personal communication
Aulne							+					Véron (1999)
Vilaine							+					Véron (1999)
Loire			+									Mennesson-Boisneau et al. (1999)
Charente							+					Véron et al. (2001)
Dordogne						+			+			Castelnaud et al. (2001)
Garonne						+			+			Castelnaud et al. (2001)
Adour						+			+			Prouzet et al. (2001)
Minho			+									Taverny et al. (2000a)
Lima			+									Taverny et al. (2000a)
Douro		+										Taverny et al. (2000a)
Vouga							+					This paper
Mondego							+					This paper
Tagus			+									Taverny et al. (2000a)
Guadiana			+									Taverny et al. (2000a)
Guadalquivir		+										Maitland and Crivelli (1996)
Loukos		+										Taverny et al. (2000a)
Sebou		+										Taverny et al. (2000a)
Bou regreg		+										Taverny et al. (2000a)
Oum Er Bia		+										Taverny et al. (2000a)
Souss		+										Taverny et al. (2000a)
Ebro	+											Taverny et al. (2000a)

to handling and the presence of dams. Allis shad is also a sustainable natural resource which can be harvested over its entire distribution area and represents an indisputable socio-economic asset. Special reference should be made to the stock of the Gironde–Garonne–Dordogne system, where the high abundance is far above levels in other eastern Atlantic populations.

Nevertheless, it is absolutely necessary to improve our knowledge of the eco-biological aspects regarding stock–recruitment relationships, population dynamics (through improved modeling), and the genetic discrimination of stocks. Furthermore, we need to maintain the recording of long-term data in some index rivers and populations (even those settling in newly colonized rivers) in order to separate natural variations (global changes) from anthropogenic variations. These data are crucial in enabling us to forecast fluctuations and in establishing an objective basis for allis shad stock management, as well as providing an integrated approach to natural resource management by catchment area.

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