

SHAD OF THE NORTHEASTERN ATLANTIC AND THE WESTERN MEDITERRANEAN: BIOLOGY, ECOLOGY, AND HARVESTING

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Summary

Shads (*Alosa* sp.) belong to one of the numerous genera of the *Clupeidae* family, which mainly consists of pelagic and coastal marine fishes. Currently two species occur along the coasts of the Eastern Atlantic and the Western Mediterranean Sea in the northern hemisphere, the Allis shad (*Alosa alosa*) and the Twaite shad (*Alosa fallax*). The *Alosinae* subfamily contains 16 species and a total of 27 morphological types

(subspecies), but the taxonomy of clupeids have not yet been clearly established. The *Alosa* genus is present in all types of water environment, from the coastal and pelagic marine areas to the river corridors and lakes via the estuary environments. Only a few species developed land-locked types in fresh water lakes. They migrate from growing to spawning areas (March-June) and anadromous migration is a characteristic of the *Alosa* genus. Shads return instinctively to their native river although they can colonize new environments. Three major groups can be distinguished according to the geographical distribution: Eastern Atlantic-Mediterranean group, a Pontocaspian group (Black, Caspian, and Azov Seas), and a Western Atlantic group. Factors of anthropic origin modified the original distribution of shads: (building of dams, water pollutions, gravel quarrying). In addition to these indirect effects, over fishing may also have a direct effect in some cases. The Allis shad is now absent from the Mediterranean Sea or along the Moroccan coasts. Shads, which constitute sustainable exploited natural resources, are mainly exploited by commercial fishery. Finally, the *Alosa* genus presents socio-economic (professional fishery), scientific, ecological, and patrimonial interests (diversity in the habitats, presence of numerous anadromous species, stock-river relationship, absence of jumping behavior, and very limited impact of the rearing species). This genus is thus a good indicator of the physical and biological quality of the middle courses of large river basins.

1. Introduction

Shad of the genus *Alosa* are fish whose fossils were discovered by paleontologists in sediments from the Tertiary (Oligocene and Miocene) and the Quaternary. Occurring along the present Eastern Atlantic coast and in the Mediterranean sea, they have survived the major tectonic phenomena which took place during their 37 million years of evolution and which progressively led to the drying up and enclosing of the Mediterranean at the end of the Miocene (± 5 MY), followed by the reopening of the Strait of Gibraltar during the same period. They also lived through the successions of glaciations and warming which affected the fauna and flora, in general, and through the last Ice Age of the Late Pleistocene (-20 000 years) which led to the lowering of the water level of the sea by several hundred meters, completely changing the coastline as we know it today.

The two species which presently occur along the Eastern Atlantic and Western Mediterranean coasts were known well before the Roman era, but were probably not identified as today. In the sixteenth century, the Portuguese fished for shad in the big rivers of Morocco, which were heavily fished locally and already divided into fishing allotments. The two species of the genus *Clupea*, abundant in France and prized for the quality of their meat had already been described at that time by Rondelet, then by Duhamel du Monceau, and Lacépède who finally identified the two shad species. It was Cuvier and Valenciennes who eventually defined the genus *Alosa*. In the 1950s, these species were finally given their present taxonomic name (*Alosa alosa*, Allis shad; *Alosa fallax*, and Twaite shad).

Shad are a sustainable natural resource and are harvested, in large part, by commercial fisheries over their general distribution area. In addition to their socio-economic value, they are also of interest to scientists. Shad appear to provide interesting material for the

study of evolutionary biology and especially that of speciation. In fact, these species combine both wide ecobiological plasticity as well as difficulties related to their taxonomic and genetic identification (genus, species). The complexity of this problem is made evident by their lacustrine adaptations, the hybridization between Allis shad and Twaite shad, and the phylogenetic relationship between the genus *Alosa* and the *Clupeidae* family.

2. Systematics and General Characteristics

Shad belong to the order of Clupeiforms (83 genera and 357 species), to the *Clupeidae* family, whose gregarious members, often-pelagic sea-dwelling plankton feeders (herring, sardine, and sardinella), are found throughout the world and have considerable commercial value.

The genus *Alosa*, which belongs to the subfamily of the *Alosinae*, includes 15 species to which the species *Alosa macedonica* can be added. Moreover, the existence of 27 morphs, leading to ambiguities (particularly in the case of the Twaite shad) in a taxonomic system which was developed without the use of genetic criteria, are recognized as a subspecies at this time. These different morphs belong to five species: *Alosa alabamae*, *kessleri*, *fallax*, *brashnikovi*, and *caspia*.

No other subspecies has been identified among the Allis shad. These taxa are identified by meristic characteristics (number of gill rakers, vertebrae, radius of dorsal and anal fins, and number of scales on the lateral line), morphological characteristics (body shape, presence of palatine, and vomerine teeth), as well as by their geographic distribution and behavioral and biometric characteristics. This genus occurs in the northern hemisphere and is divided into three distinct geographic areas: the Western Atlantic of North America; the Eastern Atlantic and Mediterranean (herring group); and the Ponto-Caspian (Caspian shad) (shad group).

The bodies of shad are generally fusiform and somewhat compressed. The back is dark blue or blue-green and the sides are silvery. The mouth is superior and the upper jaw has a distinct median notch; jaw teeth are small, often not discernible. The gill arches have a crowded comb of gill rakers, which act as an efficient gill filter. The relatively short dorsal fin is located in the middle of the back, the pectoral fins are low on the sides and the pelvic fins are on the abdomen.

The caudal fin is distinctly forked, homocercal and supported by a series of small bones. The lateral line is absent. The well-developed cycloid scales number from 40 to 50 on the longitudinal line and are deciduous. A ventral keel of scutes is generally present.

The Allis shad (*Alosa alosa*) can be distinguished from the Twaite shad by its larger size (an average length of 550 mm for an average weight of 1460 g; up to 800 mm in Morocco and Portugal) and by its high head and curved forehead, compressed on the sides (see Figure 1).

The number of gill rakers is greater (> 90 as opposed to <60). It may also have a large black spot posterior to the gill opening whereas the Twaite shad has a row of 4 to 8

distinct small black spots. Its scaling is irregular on the lateral line. These two taxa show no real sexual dimorphism except, perhaps, the larger size of the females compared to males of the same age. The diagnosis of the male is D IV–VI/13–18, A III–IV/18–24, Pt I/13–16, and Pv I/9; number of pre-pelvic scutes: 19–25, post-pelvic scutes: 13–17, number of transversal scales: 20–26, on the longitudinal line: 60–90, number of gill rakers on the first gill arc: 85–160; and vertebrae: 53–58.

Six sub-species have been identified among the Twaite shad (see Figure 2). Two of these, which are smaller, are endemic to lakes (*A. f. killarnensis* and *lacustris*) and present morphological characteristics different from the four other anadromous morphs (*A. f. fallax*, *nilotica*, *algeriensis*, and *rhodanensis*).

The diagnosis of the adult Atlantic Twaite shad is: D IV–VI/12–16, A III–IV/16–22, Pt I/13–16, and Pv I/8; number of pre-pelvic scutes: 18–23, post-pelvic scutes: 12–18, number of transversal scales: 16–20, on the longitudinal line: 54–71; number of gill rakers on the first gill arc: 35–60 (see Figure 3); and vertebrae: 49–59. Its average length is 420 mm for an average weight of 660 g.

Morphologically speaking, the Twaite shad of the Rhone (*A. f. rhodanensis*), is similar to the Atlantic taxa, but it is generally bigger (488 mm) and weights 1115 g. The number of gill rakers is smaller, very similar to the number found in *A. fallax nilotica*. The diagnosis for this subspecies is: D IV–VI/13–16, A III–IV/17–21, Pt I/13–15, and Pv I/8; number of pre-pelvic scutes: 18–23, post-pelvic scutes: 13–18, number of transversal scales: 16–20, on the longitudinal line: 54–64; number of gill rakers on the first gill arc: 30–49; and vertebrae: 54–59.



Figure 1. Allis Shad (*A. alosa*) female and male (below); Charente River (French Atlantic coast; picture: R. Sabatié).



Figure 2. Twaité Shad (*A. f. fallax*) females and males (below); Sebou River (Morocco Atlantic coast; picture: R. Sabatié).



Figure 3. Twaité Shad (*A. f. rhodanensis*) female and male (below); Rhone River (French Mediterranean coast; picture: R. Sabatié).

The presentation of this classification, which is based on rigorous morphological studies, cannot hide the fact that the taxonomy of these clupeids remains ambiguous. These difficulties arise from the large degree of phenotypic plasticity of the genus *Alosa* and the members of the *Clupeidae* family in general. This same phenomenon can be observed in the subfamily of the *Coregoninae*.

But these difficulties also arise from the methodological problems which occur when taxa are defined on approximate bases, small numbers of individuals, absence of a scale for morphometric and meristic criteria for certain biogeographic groups, and the use of a reduced number of these criteria. Indeed, certain of which may vary in space and in time in relation to age and size, in a geographic area with the hybridization phenomenon (see Figure 4), and with respect to the environment colonized during the cycle and the environmental conditions during the embryo-larval phase. To this must be added the great propensity of ichthyologists since the beginning of the nineteenth century, to use the term of sub-species to describe geographic breeds. The genus *Alosa*, which includes 27 morphs, is a good example of this.

These taxonomic difficulties have resulted in uncertainties and/or changes which lead to a lack of homogeneity at all levels of systematics but especially concerning species and sub-species. In his general presentation of the classification of shad for the FAO catalogues, Whitehead clearly states that the taxonomy of Ponto-Caspian and Eastern Atlantic and Mediterranean shad still requires extensive research. He considers that the best way to solve the taxonomic problems related to shad in the absence of a complete diagnosis of meristic and morphometric characteristics, particularly for the purpose of validating or invalidating the existence of sub-species, is to use molecular genetics and biochemical techniques.



Figure 4. First gill raker of the three taxons; left (*A. alosa*); middle (*A. hybrid*); right (*A. f. fallax*), picture: R. Sabatié.

3. Distribution and Biology

3.1 Distribution

The genus *Alosa* was originally found in the North Atlantic and in the Mediterranean, Black, and Caspian Seas as well as the Sea of Azov. Three major groups can be identified in relation to their geographic distribution (see Figure 5):

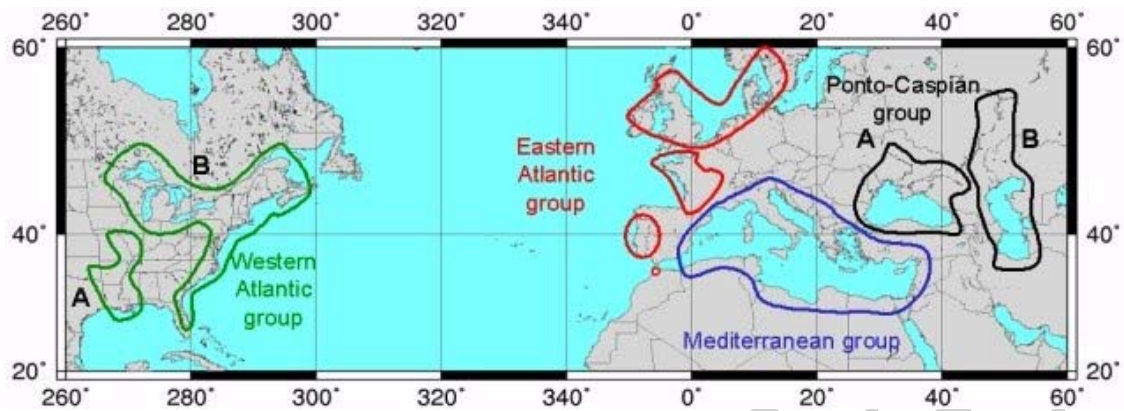


Figure 5. Map of Shad distribution: Western Atlantic group ((A) *Alosa alabamae*, *chrysochloris*; (B) *A. aestivalis*, *mediocris*, *sapidissima*, *pseudoharengus*): Atlantic and Mediterranean group (A. *alosa*; *A. fallax fallax*): Ponto Caspian group ((A) *A. caspia*, *pontica*, *maeotica*; (B) *A. caspia*, *kessleri*)

The North American group includes six species: *Alosa aestivalis*, *A. alabamae*, *A. chrysochloris*, *A. mediocris*, *A. pseudoharengus*, and *A. sapidissima*. It extends from the southern coast of Labrador to the center of Florida and to the north of the Gulf of Mexico. The American shad (*A. sapidissima*) and the alewife (*A. pseudoharengus*) are the most widely distributed and the most northern. All of the species are anadromous and only *A. pseudoharengus* has developed forms, which live in big lakes or in dam reservoirs.

The Ponto-Caspian group (Pontic shad) with 7 species. Four of them are specific to the Caspian Sea (*Alosa brashnikovi*, *A. kessleri*, *A. saposhnikovi*, *A. sphaerocephala*) and two others to the Black Sea and the Sea of Azov (*A. maeotica* and *A. pontica*). On the other hand, the Caspian shad (*Alosa caspia*) occurs in all three of these seas as a result of its many subspecies. A last one is endemic to the lakes of Northern Greece where *Alosa macedonica* is also found and can be considered to be part of this group. With the exception of these last two freshwater species and two others, which live uniquely in the sea, all of these fish are anadromous. The Eastern Atlantic and Mediterranean group (see Figure 6) includes one species and several subspecies: *Alosa alosa* and *A. fallax* sp. Their original longitudinal distribution in the Eastern Atlantic (between 28° and 60° Lat. N) is much larger than that of the American shad (between 25° and 50° Lat. N). This is due to the different position of the 0° and 20° isotherms related to the presence of cold currents on the two Atlantic seabords, playing an important role in the distribution of shad. The group seems to connect to the Caspian group uniquely through hydrographic networks in the Northern Aegean Sea where the species *Alosa fallax nilotica*, *A. macedonica* and *A. caspia vistonis* can be found.

Allis shad occurred along the Atlantic coast from Norway to Morocco, passing by the British Isles, the coasts of Germany, Holland, Belgium, and France and then down to

Spain and Portugal. Although less abundant than in the Atlantic, Allis shad also occurred along the coast of Spain and especially in the Ebro River. Its presence along the Mediterranean coast of France was always rare and even questionable. The Twaite shad in the form of the subspecies *Alosa fallax fallax* has an Atlantic distribution, which is extremely similar to that of the Allis shad, but its distribution is more Nordic since it may extend all the way to Iceland. Moreover, the populations of Twaite shad are more abundant along the Scandinavian coast (Baltic Sea) and the British Isles (including Scotland). This species, as opposed to the Allis shad, is present all around the Mediterranean basin with its three sub-species (*A. f. rhodanensis*, *algeriensis* and *nilotica*).

The Allis shad and the Twaite shad with its four morphs mentioned above are anadromous species. However, they have developed forms, which live in freshwater and are very localized geographically. This development came about naturally in the case of the Twaite shad with its two sub-species (or ecophenotypes), which are present, in the case of *A. f. lacustris*, in the lakes of Northern Italy, and the other, *A. f. killarnensis*, found only in the Killarney Lake (Southwest Ireland). But these resident forms also come from anadromous populations landlocked in big lakes by dams, such as those of El Kansera (Morocco) and of Castelo do Bode (Portugal) in the case of Allis shad; and like those of Omodeo, Medioflumendosa (Sardinia), and Sidi Mohamed Ben Abdallah (Morocco).

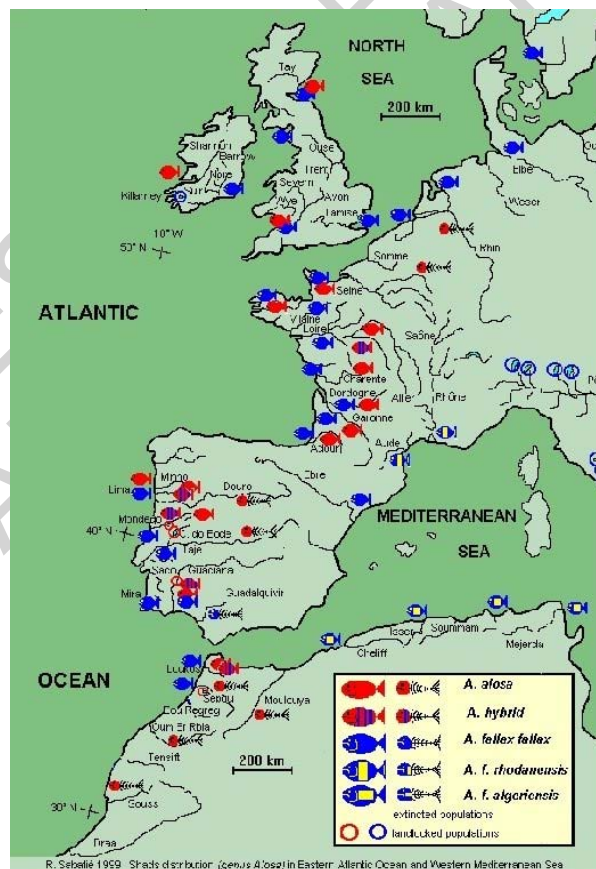


Figure 6. Map of Shad distribution (*genus Alosa*) in Eastern Atlantic Ocean and Western Mediterranean Sea.

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Biographical Sketches

Richard Sabatié earned a Ph. D. in Biological Oceanography in 1993 from Brest University (France) after 15 years in technical cooperation in Morocco, where he was working on biology and ecology of shads and on many local scientific projects (molluscs, fisheries and aquaculture). Currently, he is employed in a french National Agronomical High School *Agrocampus-Rennes* as a Fisheries Biologist in a *Fisheries and Aquatic Sciences Center*. He is working on many programs with the french *Institut National de la Recherche Agronomique* (INRA) which are dealing with biology, ecology and restoration of shads (*A. alosa* and *A. fallax*) and lampreys (*P. marinus*). He collaborated on the first Conference on European Shads (may 22-25, 2000 in Pessac, France) in the organising and scientific committee. He is involving in a new project with the french *Institut de Recherche pour le Développement* (IRD) on tunas predation (top-down control) and trophic cascades in african marine ecosystems.

Jean-Luc Baglinière graduated from Rennes University with his Ph. D. in Animal Biology in 1975. His first research works dealt with the biology and ecology in salmonids (brown trout (river and sea) and Atlantic salmon). Now, he is employed in the french *Institut National de la Recherche Agronomique* (INRA) in the *UMR Ecobiology and Quality of Continental Hydrosystems* set up in Rennes (Brittany, France) as senior scientist (research director). He is working on many programs concerning population dynamics in salmonids, impact of human activities on river environments and biology, ecology and restoration of shads (*A. alosa* and *A. fallax*). He collaborated on the trout Symposium (1988 Paraquet, France) and the first Conference on European Shads (2000 in Pessac France) in the organising and scientific committee. He published many scientific papers and some books dealing with the biology and ecology of the brown and sea trout, the hard structures and individual age in vertebrates and the ecobiology and populations variability of Shads.

Philippe Boisneau was a young passionate naturalist and angler. As a logical consequence, he was graduated from Paris XII University with a Ph. D. in Sciences and Environmental techniques in 1990 regarding shad from the Loire River. This work allowed him to gain high competences in ecology of diadromous fish and especially the shad. He teaches student of Tours University restoration of rivers, protection of fish and freshwater ecosystems. He is involved in many conservation organizations and governmental commissions such Aquatic Natural Ecosystem of Loire-Brittany Watershead or Management of diadromous fish in Loire River, and other private associations. In 1994, he became a professional fisherman in Loire River and was elected as President of the freshwater Fishermen Association in Loire watershed and then as president of freshwater Fishermen in France. Now, he is the official speaker in the face of Ministry of Agriculture and Fisheries or Ministry of Environment and National development.